Combined impacts of climate and land use change on future biodiversity at global and regional scales

Inaugural dissertation of the Faculty of Science,

University of Bern

presented by

Chantal Hari

from Adelboden (BE)

Supervisors of the doctoral thesis:

Prof. Dr. Edouard Davin

Wyss Academy for Nature at the University of Bern

Climate and Environmental Physics

Oeschger Centre for Climate Change Research

University of Bern

and

Prof. Dr. Markus Fischer

Institute of Plant Sciences

Botanical Garden

Oeschger Centre for Climate Change Research

University of Bern

Combined impacts of climate and land use change on future biodiversity at global and regional scales

Inaugural dissertation of the Faculty of Science,
University of Bern

presented by

Chantal Hari
from Adelboden (BE)

Supervisors of the doctoral thesis:
Prof. Dr. Edouard Davin
Wyss Academy for Nature at the University of Bern
Climate and Environmental Physics
Oeschger Centre for Climate Change Research
University of Bern
and
Prof. Dr. Markus Fischer
Institute of Plant Sciences
Botanical Garden
Oeschger Centre for Climate Change Research
University of Bern

Accepted by the Faculty of Science.

Bern, 16.04.2025

The Dean
Prof. Dr. Jean-Louis Reymond

Abstract

Biodiversity is declining at an unprecedented rate due to human activities, with climate and land use change being recognized as direct drivers. However, a lack of understanding remains regarding their combined impacts on future biodiversity. This thesis addresses research questions related to these knowledge gaps, focusing on the impacts of climate and land use change on future biodiversity from global to regional scales. It examines these drivers' separate and combined importance across different combinations of Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs) scenarios. Additionally, it assesses the effectiveness of protected area (PA) expansion strategies in mitigating biodiversity loss and explores how regional climate and land use change impact vegetation dynamics in arid and semi-arid lands (ASALs).

To investigate these questions, this thesis employs one modeling approach at a global scale and another at a regional scale. At the global scale, we combine climate-driven species distribution models (SDMs) with land use change projections to assess the impact of climate and land use change on terrestrial vertebrate diversity under two differing future scenarios. Additionally, we evaluate how different PA expansion strategies impact biodiversity outcomes under these projected changes. Global analyses highlight African ASALs as particularly vulnerable to biodiversity loss, motivating a regional study. At a regional scale, we analyze simulations of the adaptive dynamic global vegetation model (aDGVM) designed explicitly for African savanna ecosystems. We investigate how climate-driven vegetation changes in Kenya's ASALs, which are increasingly threatened by woody encroachment. We further compare the findings from the aDGVM simulations to land use change projections from integrated assessment models (IAMs). By integrating these two modeling approaches across scales, this thesis provides new insights into biodiversity impact assessments under future climate and land use change.

Our results indicate that climate and land use changes drive biodiversity loss equally, with climate-induced biodiversity loss scaling with the climate scenario. While land use change exacerbates these losses under an "inequality" (SSP2-RCP6.0) scenario, it can alleviate them under a "sustainability" (SSP1-RCP2.6) scenario. Low and mid-latitude regions were found to be particularly affected, with sub-Saharan Africa emerging as a high-risk area where land use change is the dominant driver of biodiversity loss. Building on this first global analysis, we further assess the effectiveness of PA expansion strategies under different PA and SSP-RCP scenarios. While PA expansion to 30% (in line with the Global Biodiversity Framework (GBF) target of reaching 30% of PAs globally by 2030) of land reduces species richness loss compared to the current 17% of PAs, its effectiveness in reducing biodiversity loss depends on adequate management and sustainable land use policies. Notably, we find

that climate mitigation and sustainable land use have a stronger leverage on reducing biodiversity loss than PA expansion alone.

After establishing the broader global patterns of biodiversity change and identifying high-risk regions for biodiversity loss, the thesis focuses on a particularly vulnerable biodiversity hotspot—sub-Saharan Africa—to investigate climate-driven vegetation shifts and land use change projections at a regional scale. Our results indicate a projected increase in woody encroachment, reducing savanna and grassland ecosystems, especially under a high-emission scenario. These vegetation changes have profound implications for biodiversity conservation, as many species depend on savanna ecosystems that are projected to decline. However, when comparing these climate-driven projections to land use change projections, we find that the projected rise in woody aboveground biomass (AGB) may be constrained by land use change, especially agricultural expansion under SSP2-RCP4.5.

Overall, this thesis provides key advancement in our understanding of future biodiversity change under climate and land use change at global and regional scales. It provides novel insights into the scenario- and region-dependent importance of these drivers and additionally provides necessary methodological advancements in developing a modeling framework that integrates land use change projections into climate-driven SDM projections. From the learnings at a global scale, the thesis zooms into a region identified where biodiversity is most at risk. With this, the thesis offers a second scale and employs a second modeling approach (DGVM) to provide a more holistic perspective on projections of future biodiversity change.

The findings highlight the urgent need for immediate action on both climate and land use change to curb biodiversity loss. While PA expansion offers some buffering capacity, following a more sustainable, low-emission development pathway remains the most effective strategy. Delayed action risks severe biodiversity loss, with cascading consequences for nature and people.

Acknowledgments

I would like to begin by expressing my gratitude to my supervisors. I am deeply thankful to **Prof. Dr. Edouard Davin** for his support throughout my PhD and for giving me the opportunity to pursue this degree. Special thanks go to my second supervisor, **Prof. Dr. Markus Fischer**, for taking on the role, co-supervising me along the journey, and especially for always finding the right words of encouragement when I needed them most.

I would also like to thank **Prof. Dr. Clara Zemp** for taking on the role of external referee for my dissertation and **Dr. Dirk Karger**, who ultimately set me on this path – or, as one might say, “got me into this mess.” Thank you for your guidance and for introducing me to the world of academia.

I would also like to extend my thanks to all my current and former colleagues in the **RT Climate team** at the Wyss Academy. I am grateful to **Marie-Estelle** for her invaluable support, for taking me along to Kenya, and for giving me the opportunity to engage in work beyond my PhD that enriched my experience with valuable non-scientific knowledge. Special thanks go to **Myke** for being a fantastic colleague and for always having an open ear for me. I am also grateful to **Jan** for contributing to memorable adventures in Kenya - and for the memorable warning about the dead snake in the shower. Special thanks also to **Qing** for being a wonderful office mate, for always sharing snacks, for letting me into the “jungle” without expecting me to contribute to keeping any of the plants alive, and for teaching me how to win over **Einstein**. I also thank **Merel** and **Inne** for being inspiring and supportive colleagues.

My PhD journey would not have been the same without the amazing people at **KUP**. I am extremely grateful to my various office mates for welcoming me, and to all the staff for taking me in and making me one of their own. Thank you for including me in your fun circle, coffee breaks, and after-work beers – your company and friendships made this experience infinitely more enjoyable.

I am also grateful to the **Wyss Academy** for giving me the opportunity to pursue a PhD and to all its members for the inspiring discussions, and unforgettable adventures I was fortunate to experience with some of you. Special thanks go to the **Hub EAF** for both the enriching collaboration and for generously accommodating me twice during my PhD, and to the members of the **ID Water Scarcity** team for their excellent collaboration.

I am deeply grateful to my family – **Claudia, Christoph, Cécile, Bruno, Mathias, Cleo, and Hermine** – for their unwavering support and love. Thank you for allowing me to pursue this path without ever questioning my decisions or my ability to succeed.

To my **friends**, I am deeply grateful for your presence throughout the years – for growing up together as we each pursue our individual yet parallel paths.

During my PhD, I was fortunate to have the support of the **Schaub family**. Your kindness, warmth, and support mean a lot to me.

Finally, words cannot adequately express my gratitude to **Andrea**. Your endless support, patience, and belief in me have meant more than I can put into words. Thank you for being by my side throughout the journey, I could not have asked for a better and more loving partner. My deepest appreciations go to you – no words of thanks could ever be enough.

Contents

Abstract I

Acknowledgments III

Chapter 1 9

Introduction 9

1.1 Climate and land use change as global drivers of biodiversity loss 9

1.1.1 Land use change impacts on biodiversity 9

1.1.2 Climate change impacts on biodiversity 9

1.1.3 Interactions between climate and land use change 10

1.1.4 Global biodiversity projections 10

1.2 Towards solutions of biodiversity conservation 12

1.2.1 Global conservation efforts 12

1.2.2 Regional conservations efforts 13

1.3 Modeling approaches for biodiversity projections under future change 14

1.3.1 Species distribution models 14

1.3.2 Dynamic global vegetation models 16

1.4 Aims and outline of the thesis 17

1.5 References 20

Chapter 2 33

Future climate and land use change will equally impact global terrestrial vertebrate diversity 33

Abstract 34

2.1 Introduction 35

2.2 Methods 36

2.2.1 Species distribution modeling 36

2.2.2 Land use filtering 36

2.2.3 Land use only calculation 38

2.2.4 Sensitivity analyses 39
2.2.5 Species richness aggregation 39
2.3 Results 40
2.3.1 Land use change trajectories and their impact on species habitats 40
2.3.2 Combined species richness changes under climate and land use 42
2.3.3 Species richness changes per region and land use category 42
2.3.4 Land area affected by species richness change 45
2.4 Discussion 46
2.5 Acknowledgments 50
2.6 References 51
2.7 Supplementary materials 58
Chapter 3 69
The roles of climate mitigation, sustainable land use and area-based conservation in curbing future biodiversity loss 69
Abstract 70
3.1 Introduction 71
3.2 Results 73
3.2.1 Spatial distribution of changes in future species richness 73
3.2.2 Contributions of climate mitigation, sustainable land use, and PAs to avoid species richness loss 74
3.2.3 Regional effects of PA effectiveness 75
3.2.4 Taxon specific global change in species richness per PA scenario 77
3.3 Discussion and conclusions 78
3.4 Methods 81
3.4.1 Species distribution model output and species richness aggregation 81
3.4.2 “No explicit PA” scenario 82
3.4.3 17%-PA scenario 83
3.4.4 30%-PA scenario 84
3.4.5 Land use filtering adjusted to PA scenarios 85

3.4.6 Separation of climate mitigation, sustainable land use, and area-based conservation 87
3.5 Acknowledgments 88
3.6 References 89
3.7 Supplementary materials 96
Chapter 4 107
Assessing the impacts of climate and land use change on vegetation dynamics in Kenya's arid and semi-arid lands 107
Abstract 108
4.1 Introduction 109
4.2 Methods 111
4.2.1 Adaptive dynamic global vegetation model simulations 111
4.2.2 Derivation of potential natural vegetation maps 112
4.2.3 Land use change projections 112
4.2.4 Comparison to other datasets 113
4.3 Results 114
4.3.1 Present-day biomes and comparison to observational data 114
4.3.2 Projected shifts in biomes and bioclimatic variables 115
4.3.3 Projected tree cover change 117
4.3.4 Woody encroachment and the trends of woody and grassy aboveground biomass 117
4.3.5 Comparison of aDGVM simulations to land use change projections 119
4.4 Discussion and conclusions 120
4.5 Acknowledgments 123
4.6 References 124
4.7 Supplementary materials 130
Chapter 5 139
Summary and conclusions 139
5.1 Climate and land use change impacts on future biodiversity under different scenarios 139
5.2 Ecological effectiveness of PA expansion 140
5.3 Climate-driven vegetation shifts and land use change impacts in Kenya 140

5.4 Bridging global and regional biodiversity assessments 140

5.5 Opportunities for future research 142

5.6 Implications for the scientific community and decision-makers 142

5.7 Final conclusions 143

5.8 References 144

Declaration of consent 145

Chapter 1

Introduction

1.1 Climate and land use change as global drivers of biodiversity loss

Biodiversity encompasses the variability among living organisms across ecosystems, including the diversity within and between species (IPBES, 2024). It is essential for our very existence as a support for water and food supplies, our health, as well as the stability of climate (IPBES, 2024; IPCC, 2022). Furthermore, biodiversity and provided ecosystem services are at the heart of our cultures, identities, and well-being (Díaz et al., 2019). Yet, biodiversity is undergoing a decline at unprecedented rates (Díaz et al., 2019; IPCC, 2023). In contrast to past observed global biodiversity declines, this ongoing crisis is directly driven by human activities through climate change, land and sea-use change, unsustainable exploitation, pollution, and invasive alien species (IPBES, 2024). Indirect drivers, including economic, demographic, cultural, and technological change (such as overconsumption and waste), are underlying causes of direct drivers and further exacerbate their impacts (IPBES, 2024).

1.1.1 Land use change impacts on biodiversity

The historically dominant driver of biodiversity loss through habitat loss, fragmentation, and degradation has been land use change (IPCC, 2023; Jaureguiberry et al., 2022; Sala et al., 2000) and will likely also remain a dominant driver in the future (Marques et al., 2019). Over 77% of terrestrial ecosystems have been modified by human activities, reducing wild mammal biomass by 83% and leading to the accelerated decline of biological diversity (Díaz et al., 2019). Habitat destruction, fragmentation, and degradation have occurred due to agricultural expansion, urbanization, and infrastructure development (Hof, 2021; Newbold et al., 2015). Additionally, land use change interacts synergistically with climate change, exacerbating the risk for biodiversity by reducing habitat connectivity and limiting species' ability to track suitable climatic conditions, which impedes species' ability to disperse and adapt to changing environmental conditions (Hof, 2021; Mantyka-pringle et al., 2012; Opdam & Wascher, 2004).

1.1.2 Climate change impacts on biodiversity

Climate change has emerged as a key driver over the past century and could even become the dominant driver in the future (Pereira et al., 2024). Anthropogenic greenhouse gas emissions, mainly driven by the burning of fossil fuels and extensive alterations to terrestrial land surfaces, have resulted in rapid shifts in the global climate system, including rising temperatures, altered precipitation regimes, increased frequency of extreme weather events, and changes in ocean dynamics (IPCC, 2023). These climatic shifts have been linked to changes in species distributions (e.g., Lenoir et al., 2020; Pacifici et al., 2015; Parmesan, 2006) and abundance (Bowler et al., 2017), population dynamics, and overall ecosystem functionality (Bellard et al., 2022; Chen et al., 2011; Parmesan, 2006). Species response to climate change occurs in three directions: through spatial range shifts, mostly to higher latitudes and elevations (Chen et al., 2011; Lenoir & Svenning, 2015; Ramalho et al., 2023); temporal adjustments (e.g., phenology) (Parmesan, 2007), and through physiological and genetic adaptations at the individual and population levels (Bellard et al., 2012). The latter includes phenotypic plasticity, allowing individuals to adjust physiologically, and genetic adaptation over generations or persistence through plasticity (Hof, 2021; Kissling, 2015; Methorst et al., 2017). However, not all species can adapt to changing environmental conditions due to limited dispersal abilities, physiological constraints, and altered biotic interactions, increasing extinction risk for many (Thomas et al., 2004; Urban, 2024).

1.1.3 Interactions between climate and land use change

Additionally, climate and land use change can have interacting effects that can have amplifying adverse effects on biodiversity (Brook et al., 2008; Hof et al., 2011; Mantyka-pringle et al., 2012). Climate change has direct effects on land cover and land use by altering vegetation dynamics and indirectly through policy responses and socioeconomic shifts aimed at mitigating or adapting to climate change impacts (IPCC, 2019). Additionally, extreme climate events, such as droughts, can exacerbate high-intensity land use practices, including shifts in cropping patterns and irrigation expansion (Oliver & Morecroft, 2014). Conversely, land use change also affects climate by influencing carbon fluxes, surface albedo, and energy balances, which can especially affect regional climate patterns (Davin et al., 2020; Dutta et al., 2022; Mahmood et al., 2014; Stocker et al., 2014; Zhao et al., 2021).

While the individual effects of climate and land use change on biodiversity are well understood, the interacting effects on biodiversity between these drivers are less frequently studied (Oliver & Morecroft, 2014). An extensive review by Oliver & Morecroft, (2014) highlight two key challenges in addressing this knowledge gap: first, the difficulty in attributing biodiversity changes to either driver due to their often nonlinear impacts, and second, the presence of threshold effects in population persistence and habitat fragmentation. These thresholds mean that even small changes in either climate or land use can disproportionately impact biodiversity and ecosystem stability. However, large uncertainties remain regarding the nature and magnitude of these thresholds (Oliver & Morecroft, 2014).

1.1.4 Global biodiversity projections

Given the synergistic and interacting effects of climate and land use change, projections that explicitly integrate both are essential for understanding future biodiversity patterns (Cabral et al., 2024; Newbold, 2018; Titeux et al., 2016). Studies on biodiversity projections have focused on either climate or land use change impacts, often comparing scenario-based frameworks. Earlier research relied on the Representative Concentration Pathways (RCPs) to assess climate change impacts, while more recent work combines Shared Socioeconomic Pathways (SSPs) with RCPs to get the full SSP-RCP scenario framework developed for the Intergovernmental Panel on Climate Change's (IPCC) Sixth Assessment Report (IPCC, 2023). This framework provides five main scenarios ranging from SSP1-1.9 to SSP5-8.5, representing diverse potential futures with varying levels of emissions and socioeconomic development (Riahi et al., 2017).

Research focusing on climate-driven biodiversity projections is mostly based on species distribution models (SDMs) to assess the effects of different warming levels. They found that warming scenarios above 2°C are projected to lead to significantly more potential loss of species than reaching a lower warming scenario (Smith et al., 2018; Warren et al., 2013). While earlier studies indicated a linear increase in biodiversity risk between 1.5°C to 4.5°C warming (Warren et al., 2018), a recent meta-analysis by Urban, (2024) has concluded that extinctions will accelerate rapidly if global temperatures exceed 1.5°C. Other studies focus on projections of land use change impacts on biodiversity. They project a continuous decline in biodiversity, with rates of loss from 2010 to 2050 potentially exceeding those from 1970 to 2010 (Leclère et al., 2020). Land use change alone could imperil around 1700 terrestrial vertebrates by 2070 (Powers & Jetz, 2019). Recent research by Cabernard et al. (2024) estimates that land use change has led to a cumulative global potential species loss of 1.4% since 1995, with nearly 80% of recent global land use change impacts associated with increased agri-food exports from Latin America, Africa, and Southeast Asia + Pacific (excluding China).

In recent years, an increasing number of studies have called for more integrated biodiversity impact research that takes into account both climate and land use changes (Cabral et al., 2024; Hof et al., 2018). Some research has made first advances in this direction, however, results have been focused on specific aspects such as habitat range sizes or particular species groups, limiting broader generalizations (Beyer & Manica, 2020; Carlson et al., 2022). Much of the existing research, especially on a global scale, focuses on terrestrial vertebrates due to the availability of species range and habitat data from sources such as the International Union for Conservation of Nature (IUCN). This data allows researchers to include a large number of species spanning diverse habitats. Furthermore, terrestrial vertebrates are well-studied, providing substantial information for analysis and comparison, and changes in vertebrate populations can also reflect broader ecosystem changes, which may impact other less-studied species groups (Newbold, 2018).

In response to the alarming projections of future biodiversity loss, there has been an increased focus on developing and implementing conservation strategies and the need for transformative changes across economic, social, political, and technological factors to halt the decline in biodiversity and ecosystem services (IPBES, 2019).

1.2 Towards solutions of biodiversity conservation

1.2.1 Global conservation efforts

Effective conservation methods are needed to reduce the impact of human activities on biodiversity. Protected areas (PAs) have become the cornerstone of modern conservation (Mi et al., 2023; Rodrigues & Cazalis, 2020; Schulze et al., 2018; Visconti et al., 2019; Watson et al., 2014). As of early 2025, around 17% of terrestrial and inland waters are protected (UNEP-WCMC and IUCN, 2025). With growing recognition of their importance, efforts through international agreements such as the Convention on Biological Diversity's (CBD) signed Kunming-Montreal Global Biodiversity Framework's (GBF) Target 3 are underway to further expand protection, aiming to cover 30% of the land by 2030 (CBD, 2022). Some proposed targets even go beyond that and propose halting and even reversing the currently declining global trends in biodiversity and conserving half of the Earth (Wilson, 2016).

PAs have been shown to effectively reduce human pressure and, consequently, reduce threats to biodiversity, such as mitigating habitat loss (Geldmann et al., 2013; Langhammer et al., 2024; Wauchope et al., 2022). However, their long-term ecological effectiveness is increasingly questioned amidst ongoing environmental changes and a continuous decline in biodiversity (Butchart et al., 2015; Dobrowski et al., 2021; Pörtner et al., 2021; Pulido Chadid et al., 2024). The ecological effectiveness of PAs depends on various interlinked factors, such as location, spatial design, management, governance, connectivity, and size (Durán et al., 2020; Graham et al., 2021; Rodrigues & Cazalis, 2020). With regards to management, a major shortfall of many PAs is inadequate funding to properly provide refuge for species and maintain ecosystem services (Geldmann, 2019; Geldmann et al., 2013; Negret et al., 2020). Consequently, many PAs are referred to as 'paper parks' (Dudley & Stolton, 1999). They fall short of their definition of long-term nature conservation by reducing or even eliminating human threats within their boundaries (Geldmann et al., 2013; Schulze et al., 2018; Visconti et al., 2019). Furthermore, many PAs have been established in remote areas of low human pressures and low agricultural potential, which has negated their conservation impact (Pulido Chadid et al., 2024). Moreover, PAs have faced criticism for their establishment process, which often disregards the presence and rights of local communities (Sarkki et al., 2015). This approach has led to social issues, including the displacement of Indigenous peoples and local communities, further reducing their effectiveness (Geldmann, 2019; Gulte et al., 2023).

Assessing the effectiveness of PAs mostly involves comparing biodiversity trends inside and outside of PAs. This approach has proven useful in evaluating conservation outcomes and establishing baseline biodiversity conditions (Regos et al., 2016). However, such assessments must account for long-term global changes, particularly climate change, which increasingly affects species distributions and ecosystem dynamics. Moreover, climate-driven habitat shifts can result in spatial mismatches between current PA locations and future species distributions, which reduces PA effectiveness under changing climatic conditions (Dobrowski et al., 2021). As species shift to track suitable climates, they may encounter fragmented or degraded habitats outside the static PA boundaries, which increases their risk of extinction (Hoffmann et al., 2019). Consequently, climate refugia and ecologically resilient landscapes have been identified as critical components for maintaining PA effectiveness in a changing environment (Dobrowski et al., 2021; Elsen et al., 2020).

Given these challenges, the ecological effectiveness of area-based conservation efforts as PA expansion must be assessed in the light of future environmental change driven by climate and land use change. An integrative approach that considers both climate and land use change can provide a comprehensive framework for evaluating PA expansion strategies to mitigate biodiversity loss by reducing land use pressures that negatively impact species habitats and accounting for projected changes in species distribution. Therefore, future conservation planning should incorporate projections of climate and land use change to optimize PA expansion and ensure long-term ecological effectiveness (Asamoah et al., 2021; Mi et al., 2023; Montesino Pouzols et al., 2014).

1.2.2 Regional conservations efforts

Importantly, the conservation challenges posed by climate and land use change and their potential benefits in limiting land use change to dampen biodiversity loss are not globally evenly distributed (Langhammer et al., 2024; Smith et al., 2022). Past research has shown that biodiversity-rich regions such as sub-Saharan Africa, alongside parts of South America, are likely to experience the highest biodiversity losses due to the intersection of pressures from climate and land use change (Hof et al., 2011; Leclère et al., 2020; Newbold, 2018; Trisos et al., 2022; Visconti et al., 2016). Moreover, Africa is particularly vulnerable to climate change, with continental warming projected to exceed the global average (Trisos et al., 2022). This climatic change interacts non-linearly with additional threats, including habitat destruction, fragmentation, and rapid population growth, exacerbating biodiversity loss beyond what would be expected from these stressors in isolation (Sintayehu, 2018). Given this projected change, region-specific conservation planning is essential to ensure the resilience of biodiversity under future global changes (Cayton, 2023). For example, Kenya, with its unique characteristic of being predominately composed of arid and semi-arid lands (ASALs), faces distinct conservation challenges and priorities. The Kenya Vision 2030, recognizes these challenges and the ecological and socio-economic importance of the country’s ecosystems and wildlife (Ojwang’ et al., 2017). Its flagship project focuses on securing wildlife corridors and dispersal areas to maintain landscape connectivity, mitigate habitat fragmentation, and support species survival. This objective has been driven by a growing sense of urgency, as Kenya’s wildlife populations have dramatically declined over the last few decades due to pressures from climate and land use change, combined with increasing population pressures and poverty. In response, wildlife corridors have emerged as a critical conservation approach (Ojwang' et al., 2017). However, region-specific knowledge of vegetation dynamics and biodiversity is required for adequate planning of the corridors. To the best of my knowledge, no study has investigated climate-driven vegetation changes in Kenya using a process-based model. In general, regional studies assessing future biodiversity outcomes under climate and land use change remain underdeveloped. While numerous studies have examined climate change impacts on vegetation dynamics at the continental scale in Africa (e.g., Higgins & Scheiter, 2012; Pinheiro et al., 2022; Stevens et al., 2017), regional-scale analyses that also incorporate land use change are lacking.

1.3 Modeling approaches for biodiversity projections under future change

Quantitatively assessing the future outcomes for biodiversity in the face of global change remains a pressing issue (Bellard et al., 2022). Two different modeling approaches are mostly used to project the impacts of climate change on biodiversity: SDMs and dynamic global vegetation models (DGVMs) (Moncrieff et al., 2016).

The key difference between the two approaches is that while SDMs are statistical models that correlate species distributions with environmental variables (Guisan et al., 2017), DGVMs are process-based models that simulate complex ecological processes and vegetation dynamics (Prentice et al., 2007).

1.3.1 Species distribution models

SDMs (also ecological niche models or habitat suitability models) are a widely used modeling framework to project changes to geographic distributions of species based on environmental variables (Guisan et al., 2017; Guisan & Zimmermann, 2000; Piirainen et al., 2023; Prentice et al., 2007). They were developed based on Hutchinson's ecological niche theory, which Booth et al. later refined (1988). SDMs typically fit a statistical relationship between georeferenced species occurrence data - such as presence, presence-absence, or abundance data – and environmental data that can be both biotic and abiotic conditions (Farashi & Alizadeh-Noughani, 2023; Guisan & Thuiller, 2005). Among these, bioclimatic variables are the most widely used predictors (Merkenschlager et al., 2023). This statistical relationship is used to project habitat suitability and potential species distributions across various spatial and temporal scales (Araújo et al., 2019; Guisan et al., 2017; Guisan & Zimmermann, 2000).

SDMs play a major role in quantitative ecology studies but also in climate impact research due to their ability to integrate future global climate model (GCM) projections and ecological information, making them the leading approach for projecting future species distributions under changing climate conditions (Araújo et al., 2019; Zurell, Franklin, et al., 2020). Moreover, they can inform conservation planning and guide species translocations (Piirainen et al., 2023; Rondinini et al., 2011). The application of SDMs has rapidly expanded in terrestrial ecosystems in past decades (Araújo et al., 2019).

From a methodological perspective, SDMs encompass a variety of statistical and machine-learning approaches, including generalized linear models (GLM), generalized additive models (GAM), generalized boosted regression models (GBM), maximum entropy models (MaxEnt), Bayesian models, neural networks, and classification methods (Elith et al., 2011; Elith & Leathwick, 2009; Guisan & Zimmermann, 2000).

Despite their widespread application, SDMs face challenges, including biases and lack of accuracy in species occurrence data, model uncertainty, and extrapolation limitations (Farashi & Alizadeh-Noughani, 2023). A fundamental limitation of SDMs is their reliance on purely statistical correlations without accounting for process-based mechanisms (Carneiro et al., 2016). While SDMs can effectively capture current distribution patterns, their inability to incorporate underlying biological processes restricts their capacity to project responses to novel environmental conditions or account for species interactions and adaptive potential (Zurell et al., 2020). This limitation is particularly evident when projecting future distributions under climate change scenarios, where species may encounter conditions outside their current environmental envelope (Wilson et al., 2016). To address these limitations, mechanistic SDMs are being developed to incorporate known physiological processes and biophysical principles. However, mechanistic SDMs require extensive physiological and trait data, which are unavailable for many species, limiting their widespread application (Kearney & Porter, 2009).

Another major limitation of traditional SDMs is their failure to explicitly incorporate land use change. Some studies have made first steps to address this gap by combining SDMs with statistically derived land use impacts (Newbold, 2018; Newbold et al., 2020; Pereira et al., 2024) while others have begun incorporating land use change projections (Beyer & Manica, 2020). Recent work by Carlson et al. (2022) has demonstrated the feasibility of integrating land use projections based on integrated assessment models (IAMs) with SDMs, but their study focused on zoonotic disease risk and was limited to a specific application of assessing cross-species viral transmission risk rather than explicitly quantifying global biodiversity outcomes. Thus, while research has advanced toward integrating land use change with climate-driven SDMs, a consistent framework is still lacking. This inconsistency in methodology and scenario analysis makes it difficult to directly compare studies that incorporate both drivers (Newbold, 2018).

Beyond these integration challenges, SDMs also suffer from the lack of standardization of the algorithms and validation protocols, which further complicates model comparison and interpretation. A multi-model ensemble approach has been proposed to account for uncertainty by comparing results from multiple algorithms recommended, as each algorithm has its strengths and weaknesses and can affect predictions differently (Araújo et al., 2019). Additionally, model precision should be evaluated using multiple validation metrics such as AUC-ROC curves and goodness-of-fit measures (Salamma & Boyina, 2014). Also, the difficulty of including rare and endemic species in SDMs presents a major challenge (Qazi et al., 2022). Beyond species-level projections, SDMs have also been used to model biome distributions (e.g., Conradi et al., 2020).

1.3.2 Dynamic global vegetation models

DGVMs are process-based ecosystem models that simulate vegetation dynamics, biogeophysical, and biogeochemical processes in response to climate, atmospheric CO_2, and other environmental variables and disturbances (e.g., fire; Prentice et al., 2007). They explicitly represent fundamental ecological processes such as establishment, tree growth, competition, death, and nutrient cycling (Prentice et al., 2007). Vegetation can be further differentiated by age and size classes per grid cell. Most models use plant functional type (PFT)-specific state variables, which dynamically evolve throughout the simulations (Prentice et al., 2007). PFTs group similar species together into a functional type (Fisher et al., 2018). Additionally, DGVMs dynamically adjust factors influencing resource acquisition, such as light, water, and nutrient availability. These adjustments include changes in leaf area index, root density, and population density, which reflect environmental conditions and competitive interactions (Prentice et al., 2007). The dynamic adaptation makes DGVMs essential tools for understanding the feedback between terrestrial ecosystems and the climate system through the carbon cycle (Zaehle & Friend, 2010).

DGVMs can be classified into different types of models; gap models, cohort-based models, and individual-based models. Gap models, represent forest dynamics through the concept of forest patch models and focus on fine-scale ecological processes; their global applicability is limited (Sitch et al., 2003). Alternatively, cohort-based models simulate plants grouped into PFTs to optimize computational efficiency compared to the individual-based models. However, this simplification has been criticized, leading to two major developments in vegetation modeling (Scheiter & Higgins, 2009). First, individual-based models represent vegetation at the individual plant level, allowing for finer-scale dynamics, for example, competition for light and resources (Smith et al., 2001). Second, second-generation DGVMs allow plant traits to vary dynamically in response to environmental conditions (Fisher et al., 2010). Examples include aDGVM (Scheiter & Higgins, 2009) and LPJmL-FIT (Sakschewski et al., 2015), which move away from fixed PFTs and instead use a trait-based approach, where plant traits emerge from ecological processes rather than being predefined (Scheiter et al., 2013). Beyond these advances, biomes remain widely used to map vegetation formations on large spatial scales and to study their distributional shifts under past, present, and future climate conditions (e.g., Conradi et al., 2020; Fischer et al., 2022; Martens et al., 2021; Scheiter et al., 2024).

The advancements in DGVMs, particularly the shift toward trait-based approaches, improve the ability to simulate vegetation responses to environmental change with greater ecological realism. To achieve this, DGVMs incorporate a series of nested time loops, allowing them to capture ecological processes operating on different timescales (Schulze et al., 2018). Fast processes, such as energy and gas exchange between the canopy, soil, and atmosphere, occur on a diurnal timescale. Daily and seasonal processes, including plant phenology, growth, and decomposition, are typically simulated on a monthly basis. Vegetation dynamics, such as recruitment and mortality, act on annual or longer timescales (Zaehle & Friend, 2010).

Given the complexity of these models, evaluation is conducted across spatial scales from individual sites to global ecosystems and over temporal scales from hours to decades. Observations for model validation come from multiple sources, including ground-based measurements (e.g., eddy covariance gas exchange, biomass inventories), satellite remote sensing, and atmospheric greenhouse gas monitoring (Prentice et al., 2007).

DGVMs are powerful tools for studying past, present, and future vegetation dynamics and have advanced our understanding of the global distribution of major vegetation types, and ecosystem functioning, which is linked to ecosystem services such as biomass production, biodiversity habitat, and water availability, and land-climate feedback (Prentice et al., 2007). Despite different types of DGVMs and advances in the diversity in DGVM structure and in how vegetation is represented (PFT-based vs. individual-based), the complexity of physiological and ecological processes included, and the spatial and temporal resolution at which they operate leads to vast differences in model predictions (Fisher et al., 2010; Fisher et al., 2018). Additionally, the integration of disturbance regimes, such as fire dynamics and nutrient cycling (e.g., nitrogen and phosphorus availability), has further contributed to divergent projections of CO_2 fertilization effects under different levels of elevated atmospheric CO_2 (Higgins & Scheiter, 2012; Martens et al., 2021).

1.4 Aims and outline of the thesis

In the preceding sections, the key knowledge gaps were identified in understanding the impacts of climate and land use change on biodiversity. Specifically, research integrating these two major drivers into biodiversity projections remains limited, particularly in terms of distinguishing their separate and combined effects. Furthermore, despite the well-recognized importance of PAs for biodiversity conservation, there is a lack of assessments about the ecological effectiveness of PA expansion under climate and land use change. Finally, we have established that future biodiversity assessments at the regional scale remain underdeveloped, particularly in ASALs, where climate-driven vegetation shifts combined with other pressures, including land use change, may lead to substantial ecosystem transformations with cascading effects on biodiversity.

This PhD thesis aims to address the two most commonly used models to estimate biodiversity change due to climate and land use change. First, we aim to build upon existing SDM simulations by integrating land use change to assess their separate and combined impact on global biodiversity, focusing on terrestrial vertebrates following previous studies conducted for the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP). Furthermore, we incorporate different scenarios of PA expansion into this framework, where unsustainable land use change is prohibited within PAs, while outside PA boundaries, land use changes follow projections based on the respective socioeconomic pathway and according to the specific PA expansion scenario. Additionally, we aim to address the lack of regional biodiversity assessment studies, especially in a region predominated by ASALs. For this purpose, we aim to make use of DGVM simulations instead and compare them to land use change projections. Understanding these vegetation shifts is crucial, as they directly shape ecosystem structures and species distributions, providing the foundation and first steps for integrating land use change and climate projections into biodiversity impact assessments. With this more holistic perspective, the main objective is to contribute to improving biodiversity impact assessments and make necessary methodological advancements.

The overarching research questions guiding this thesis are:

- *How do climate change and land use change impact future biodiversity and vegetation at global to regional scales under different scenarios?*
- *What is the relative importance of climate change versus land use change in driving future biodiversity impacts, and how does this vary across different socioeconomic (SSP-RCP) scenarios?*
- *How effective are different protected area expansion scenarios in mitigating future biodiversity loss from climate and land use change?*
- *How do regional climate and land use changes impact vegetation in arid and semi-arid lands?*

To address these questions, this thesis is structured in three main chapters (Chapters 2 to 4), followed by a conclusion chapter (Chapter 5).

- **Chapter 2** develops an integrated framework that quantifies the separate and combined impacts of climate and land use change on terrestrial vertebrate diversity at a global scale. By applying a land use filtering approach to climate-driven SDMs, this chapter disentangles the relative contributions of each driver and assesses their variation across different SSP-RCP scenarios and regions. With this, we provide a framework that can be applied to different taxa, scenarios, and spatial scales, and allows for greater comparability across studies focusing on biodiversity outcomes based on the drivers of climate and land use change.

- **Chapter 3** extends the framework developed in Chapter 2 by incorporating PAs into biodiversity projections of combined climate and land use change to evaluate the ecological effectiveness considering different SSP-RCP scenarios as well as different spatially explicit PA expansion scenarios. By preventing unsustainable land use change within PAs while allowing for changes outside, this chapter provides a quantitative assessment of how different PA expansion strategies affect biodiversity projections.
- **Chapter 4** puts the results of the previous chapters into a regional context where climate and land use changes are expected to have strong negative impacts on biodiversity. This chapter investigates climate-driven vegetation changes in Kenya using simulations from a second-generation DGVM, the adaptive DGVM (aDGVM). This chapter examines how climate-induced biome shifts and woody encroachment alter ecosystems that serve as habitats for biodiversity. Additionally, it incorporates an ad hoc comparison of land use change projections to assess the combined effects of climate and land use on future vegetation.
- Lastly, **Chapter 5** concludes the thesis by summarizing the key findings and providing an overall conclusion and remarks regarding potential future research.

1.5 References

Araújo, M. B., Anderson, R. P., Márcia Barbosa, A., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, *5*(1), eaat4858. https://doi.org/10.1126/sciadv.aat4858

Asamoah, E. F., Beaumont, L. J., & Maina, J. M. (2021). Climate and land-use changes reduce the benefits of terrestrial protected areas. *Nature Climate Change*, *11*(12), 1105–1110. https://doi.org/10.1038/s41558-021-01223-2

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bellard, C., Marino, C., & Courchamp, F. (2022). Ranking threats to biodiversity and why it doesn't matter. *Nature Communications*, *13*(1), 2616. https://doi.org/10.1038/s41467-022-30339-y

Beyer, R. M., & Manica, A. (2020). Historical and projected future range sizes of the world's mammals, birds, and amphibians. *Nature Communications*, *11*(1), Article 1. https://doi.org/10.1038/s41467-020-19455-9

Booth, T. H., Nix, H. A., Hutchinson, M. F., & Jovanic, T. (1988). Niche analysis and tree species introduction. *Forest Ecology and Management*, *23*(1), 47–59. https://doi.org/10.1016/0378-1127(88)90013-8

Bowler, D. E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R., Baert, L., Bauer, H.-G., Blick, T., Brooker, R. W., Dekoninck, W., Domisch, S., Eckmann, R., Hendrickx, F., Hickler, T., Klotz, S., Kraberg, A., Kühn, I., Matesanz, S., … Böhning-Gaese, K. (2017). Cross-realm assessment of climate change impacts on species' abundance trends. *Nature Ecology & Evolution*, *1*(3), 1–7. https://doi.org/10.1038/s41559-016-0067

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Butchart, S. H. M., Clarke, M., Smith, R. J., Sykes, R. E., Scharlemann, J. P. W., Harfoot, M., Buchanan, G. M., Angulo, A., Balmford, A., Bertzky, B., Brooks, T. M., Carpenter, K. E., Comeros-Raynal, M. T., Cornell, J., Ficetola, G. F., Fishpool, L. D. C., Fuller, R. A., Geldmann, J., Harwell, H., … Burgess, N. D. (2015). Shortfalls and Solutions for Meeting National and Global Conservation Area Targets. *Conservation Letters*, *8*(5), 329–337. https://doi.org/10.1111/conl.12158

Cabernard, L., Pfister, S., & Hellweg, S. (2024). Biodiversity impacts of recent land-use change driven by increases in agri-food imports. *Nature Sustainability*, *7*(11), 1512–1524. https://doi.org/10.1038/s41893-024-01433-4

Cabral, J. S., Mendoza-Ponce, A., da Silva, A. P., Oberpriller, J., Mimet, A., Kieslinger, J., Berger, T., Blechschmidt, J., Brönner, M., Classen, A., Fallert, S., Hartig, F., Hof, C., Hoffmann, M., Knoke, T., Krause, A., Lewerentz, A., Pohle, P., Raeder, U., … Zurell, D. (2024). The road to integrate climate change projections with regional land-use–biodiversity models. *People and Nature*, *6*(5), 1716–1741. https://doi.org/10.1002/pan3.10472

Carlson, C. J., Albery, G. F., Merow, C., Trisos, C. H., Zipfel, C. M., Eskew, E. A., Olival, K. J., Ross, N., & Bansal, S. (2022). Climate change increases cross-species viral transmission risk. *Nature 2022 607:7919*, *607*(7919), 555–562. https://doi.org/10.1038/s41586-022-04788-w

Carneiro, L. R. de A., Lima, A. P., Machado, R. B., & Magnusson, W. E. (2016). Limitations to the Use of Species-Distribution Models for Environmental-Impact Assessments in the Amazon. *PLoS ONE*, *11*(1), e0146543. https://doi.org/10.1371/journal.pone.0146543

Cayton, H. (2023, November 13). *Priorities for achieving 30x30 goals*. Conservation Corridor. https://conservationcorridor.org/digests/2023/11/priorities-for-achieving-30x30-goals/

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Conradi, T., Slingsby, J. A., Midgley, G. F., Nottebrock, H., Schweiger, A. H., & Higgins, S. I. (2020). An operational definition of the biome for global change research. *New Phytologist*, *227*(5), 1294–1306. https://doi.org/10.1111/nph.16580

Davin, E. L., Rechid, D., Breil, M., Cardoso, R. M., Coppola, E., Hoffmann, P., Jach, L. L., Katragkou, E., de Noblet-Ducoudré, N., Radtke, K., Raffa, M., Soares, P. M. M., Sofiadis, G., Strada, S., Strandberg, G., Tölle, M. H., Warrach-Sagi, K., & Wulfmeyer, V. (2020). Biogeophysical impacts of forestation in Europe: First results from the LUCAS (Land Use and Climate Across Scales) regional climate model intercomparison. *Earth System Dynamics*, *11*(1), 183–200. https://doi.org/10.5194/esd-11-183-2020

Díaz, S., Settele, J., Brondízio, E., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Watson, R. T., Baste, I. A., Larigauderie, A., Leadley, P., Pascual, U., Baptiste, B., Demissew, S., Dziba, L., Erpul, G., Fazel, A., … Vilá, B. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*.

Dobrowski, S. Z., Littlefield, C. E., Lyons, D. S., Hollenberg, C., Carroll, C., Parks, S. A., Abatzoglou, J. T., Hegewisch, K., & Gage, J. (2021). Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes. *Communications Earth & Environment*, *2*(1), Article 1. https://doi.org/10.1038/s43247-021-00270-z

Dudley, N., & Stolton, S. (1999). *Conversion of '"Paper Parks"' to Effective Management Developing a Target*. IUCN, WWF, WCPA.

Durán, A. P., Green, J. M. H., West, C. D., Visconti, P., Burgess, N. D., Virah-Sawmy, M., & Balmford, A. (2020). A practical approach to measuring the biodiversity impacts of land conversion. *Methods in Ecology and Evolution*, *11*(8), 910–921. https://doi.org/10.1111/2041-210X.13427

Dutta, D., Gupta, S., & Chakraborty, A. (2022). Effect of different land use land cover on surface heat budget – A case study from a tropical humid region of India. *Remote Sensing Applications: Society and Environment*, *25*, 100675. https://doi.org/10.1016/j.rsase.2021.100675

Elith, J., & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Elsen, P. R., Monahan, W. B., Dougherty, E. R., & Merenlender, A. M. (2020). Keeping pace with climate change in global terrestrial protected areas. *Science Advances*, *6*(25), eaay0814. https://doi.org/10.1126/sciadv.aay0814

Farashi, A., & Alizadeh-Noughani, M. (2023). Basic Introduction to Species Distribution Modelling. In S. Dhyani, D. Adhikari, R. Dasgupta, & R. Kadaverugu (Eds.), *Ecosystem and Species Habitat Modeling for Conservation and Restoration* (pp. 21–40). Springer Nature. https://doi.org/10.1007/978-981-99-0131-9_2

Fischer, J.-C., Walentowitz, A., & Beierkuhnlein, C. (2022). The biome inventory – Standardizing global biogeographical land units. *Global Ecology and Biogeography*, *31*(11), 2172–2183. https://doi.org/10.1111/geb.13574

Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H., Shuman, J. K., … Moorcroft, P. R. (2018). Vegetation demographics in Earth System Models: A review of progress and priorities. *Global Change Biology*, *24*(1), 35–54. https://doi.org/10.1111/gcb.13910

Geldmann, J. (2019). *A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures*. https://doi.org/10.1073/pnas.1908221116

Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M., & Burgess, N. D. (2013). Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation*, *161*, 230–238. https://doi.org/10.1016/j.biocon.2013.02.018

Graham, V., Geldmann, J., Adams, V. M., Grech, A., Deinet, S., & Chang, H.-C. (2021). Management resourcing and government transparency are key drivers of biodiversity outcomes in Southeast Asian protected areas. *Biological Conservation*, *253*, 108875. https://doi.org/10.1016/j.biocon.2020.108875

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). Habitat Suitability and Distribution Models: With Applications in R. *Habitat Suitability and Distribution Models*. https://doi.org/10.1017/9781139028271

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*, 147–186.

Gulte, E., Tadele, H., Haileslassie, A., & Mekuria, W. (2023). Perception of local communities on protected areas: Lessons drawn from the Bale Mountains National Park, Ethiopia. *Ecosystems and People*, *19*(1), 2227282. https://doi.org/10.1080/26395916.2023.2227282

Higgins, S. I., & Scheiter, S. (2012). Atmospheric CO2 forces abrupt vegetation shifts locally, but not globally. *Nature*, *488*(7410), 209–212. https://doi.org/10.1038/nature11238

Hof, C. (2021). Towards more integration of physiology, dispersal and land-use change to understand the responses of species to climate change. *Journal of Experimental Biology*, *224*. https://doi.org/10.1242/jeb.238352

Hof, C., Araújo, M. B., Jetz, W., & Rahbek, C. (2011). Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, *480*(7378), 516–519. https://doi.org/10.1038/nature10650

Hof, C., Voskamp, A., Biber, M. F., Böhning-Gaese, K., Engelhardt, E. K., Niamir, A., Willis, S. G., & Hickler, T. (2018). Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(52), 13294–13299. https://doi.org/10.1073/pnas.1807745115

Hoffmann, S., Irl, S. D. H., & Beierkuhnlein, C. (2019). Predicted climate shifts within terrestrial protected areas worldwide. *Nature Communications*, *10*(1), 4787. https://doi.org/10.1038/s41467-019-12603-w

IPCC. (2023). Future Global Climate: Scenario-based Projections and Near-term Information. In *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 553–672). Cambridge University Press. https://doi.org/10.1017/9781009157896.006

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services. . S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages.* Zenodo. https://doi.org/10.5281/zenodo.3553579

IPBES. (2024). *Summary for policymakers of the thematic assessment report on the interlinkages among biodiversity, water, food and health of the intergovernmental science-policy platform on biodiversity and ecosystem services* (P. D. McElwee, P. A. Harrison, T. L. van Huysen, V. Alonso Roldán, E. Barrios, P. Dasgupta, F. DeClerck, Z. V. Harmáčková, D. T. S. Hayman, M. Herrero, R. Kumar, D. Ley, D. Mangalagiu, R. A. McFarlane, C. Paukert, W. A. Pengue, P. R. Prist, T. H. Ricketts, M. D. A. Rounsevell, … D. Obura, Eds.). IPBES Secretariat. https://doi.org/10.5281/zenodo.13850290

IPCC. (2019). *Summary for Policymakers. In: Climate Change and Land: An IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. IPCC. https://doi.org/10.1017/9781009157988.001

IPCC. (2022). *Summary for Policymakers [H.-O. Pörtner, D.C. Roberts, E.S. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem (eds.)]. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]*. Cambridge University Press. https://doi.org/10.1017/9781009325844

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*(45), eabm9982. https://doi.org/10.1126/sciadv.abm9982

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Kissling, W. D. (2015). *Ecology of Climate Change: The Importance of Biotic Interactions* . Monographs in Population Biology, Volume 52. By Eric Post. Princeton (New Jersey): Princeton University Press. $59.50. xxv + 373 p.; ill.; index. ISBN: 978-0-691-14847-2. 2013. *The Quarterly Review of Biology*, *90*(2), 213–214. https://doi.org/10.1086/681462

Langhammer, P. F., Bull, J. W., Bicknell, J. E., Oakley, J. L., Brown, M. H., Bruford, M. W., Butchart, S. H. M., Carr, J. A., Church, D., Cooney, R., Cutajar, S., Foden, W., Foster, M. N., Gascon, C., Geldmann, J., Genovesi, P., Hoffmann, M., Howard-McCombe, J., Lewis, T., … Brooks, T. M. (2024). The positive impact of conservation action. *Science*, *384*(6694), 453–458. https://doi.org/10.1126/science.adj6598

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*(7826), 551–556. https://doi.org/10.1038/s41586-020-2705-y

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*(8), 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. https://doi.org/10.1111/ecog.00967

Mahmood, R., Pielke Sr., R. A., Hubbard, K. G., Niyogi, D., Dirmeyer, P. A., McAlpine, C., Carleton, A. M., Hale, R., Gameda, S., Beltrán-Przekurat, A., Baker, B., McNider, R., Legates, D. R., Shepherd, M., Du, J., Blanken, P. D., Frauenfeld, O. W., Nair, U. s., & Fall, S. (2014). Land cover changes and their biogeophysical effects on climate. *International Journal of Climatology*, *34*(4), 929–953. https://doi.org/10.1002/joc.3736

Mantyka-pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, *18*(4), 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x

Marques A, Martins Is, Kastner T, Plutzar C, Theurl Mc, Eisenmenger N, Huijbregts Maj, Wood R, Stadler K, Bruckner M, Canelas J, Hilbers Jp, Tukker A, Erb K, & Pereira Hm. (2019). Increasing impacts of land use on biodiversity and carbon sequestration driven by population and economic growth. *Nature Ecology & Evolution*, *3*(4). https://doi.org/10.1038/s41559-019-0824-3

Martens, C., Hickler, T., Davis-Reddy, C., Engelbrecht, F., Higgins, S. I., Maltitz, G. P., Midgley, G. F., Pfeiffer, M., & Scheiter, S. (2021). Large uncertainties in future biome changes in Africa call for flexible climate adaptation strategies. *Global Change Biology*, *27*(2), 340–358. https://doi.org/10.1111/gcb.15390

Merkenschlager, C., Bangelesa, F., Paeth, H., & Hertig, E. (2023). Blessing and curse of bioclimatic variables: A comparison of different calculation schemes and datasets for species distribution modeling within the extended Mediterranean area. *Ecology and Evolution*, *13*(10), e10553. https://doi.org/10.1002/ece3.10553

Methorst, J., Böhning-Gaese, K., Khaliq, I., & Hof, C. (2017). A framework integrating physiology, dispersal and land-use to project species ranges under climate change. *Journal of Avian Biology*, *48*(12), 1532–1548. https://doi.org/10.1111/jav.01299

Mi, C., Ma, L., Yang, M., Li, X., Meiri, S., Roll, U., Oskyrko, O., Pincheira-Donoso, D., Harvey, L. P., Jablonski, D., Safaei-Mahroo, B., Ghaffari, H., Smid, J., Jarvie, S., Kimani, R. M., Masroor, R., Kazemi, S. M., Nneji, L. M., Fokoua, A. M. T., … Du, W. (2023). Global Protected Areas as refuges for amphibians and reptiles under climate change. *Nature Communications*, *14*(1), 1389. https://doi.org/10.1038/s41467-023-36987-y

Moncrieff, G. R., Scheiter, S., Langan, L., Trabucco, A., & Higgins, S. I. (2016). The future distribution of the savannah biome: Model-based and biogeographic contingency. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1703), 20150311. https://doi.org/10.1098/rstb.2015.0311

Montesino Pouzols, F., Toivonen, T., Di Minin, E., Kukkala, A. S., Kullberg, P., Kuusterä, J., Lehtomäki, J., Tenkanen, H., Verburg, P. H., & Moilanen, A. (2014). Global protected area expansion is compromised by projected land-use and parochialism. *Nature*, *516*(7531), 383–386. https://doi.org/10.1038/nature14032

Negret, P. J., Marco, M. D., Sonter, L. J., Rhodes, J., Possingham, H. P., & Maron, M. (2020). Effects of spatial autocorrelation and sampling design on estimates of protected area effectiveness. *Conservation Biology*, *34*(6), 1452–1462.

Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881). https://doi.org/10.1098/rspb.2018.0792

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nature Ecology & Evolution*, *4*(12), Article 12. https://doi.org/10.1038/s41559-020-01303-0

Ojwang', G. O., Wargute, P. W., Said, M. Y., Worden, J. S., Davidson, Z., Muruthi, P., Kanga, E., Ihwagi, F., & Okita-Ouma, B. (2017). *Wildlife Migratory Corridors and Dispersal Areas: Kenya Rangelands and Coastal Terrestrial Ecosystems*. https://www.kws.go.ke/content/report-wildlife-corridors-and-dispersal-areas

Oliver, T. H., & Morecroft, M. D. (2014). Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change*, *5*(3), 317–335. https://doi.org/10.1002/wcc.271

Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, *117*(3), 285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., Corlett, R. T., Huntley, B., Bickford, D., Carr, J. A., Hoffmann, A. A., Midgley, G. F., Pearce-Kelly, P., Pearson, R. G., Williams, S. E., … Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, *5*(3), 215–225. https://doi.org/10.1038/nclimate2448

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, *13*(9), 1860–1872. https://doi.org/10.1111/j.1365-2486.2007.01404.x

Pereira, H. M., Martins, I. S., Rosa, I. M. D., Kim, H., Leadley, P., Popp, A., van Vuuren, D. P., Hurtt, G., Quoss, L., Arneth, A., Baisero, D., Bakkenes, M., Chaplin-Kramer, R., Chini, L., Di Marco, M., Ferrier, S., Fujimori, S., Guerra, C. A., Harfoot, M., … Alkemade, R. (2024). Global trends and scenarios for terrestrial biodiversity and ecosystem services from 1900 to 2050. *Science*, *384*(6694), 458–465. https://doi.org/10.1126/science.adn3441

Piirainen, S., Lehikoinen, A., Husby, M., Kålås, J. A., Lindström, Å., & Ovaskainen, O. (2023). Species distributions models may predict accurately future distributions but poorly how distributions change: A critical perspective on model validation. *Diversity and Distributions*, *29*(5), 654–665. https://doi.org/10.1111/ddi.13687

Pinheiro, L. F. S., Kansbock, L., Rossatto, D. R., & Kolb, R. M. (2022). Woody plant encroachment constrains regeneration of ground-layer species in a neotropical savanna from seeds. *Austral Ecology*, *47*(3), 674–684. https://doi.org/10.1111/aec.13156

Pörtner, H.-O., Scholes, R. J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W. L. (William), Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M. A., Handa, C., Hickler, T., Hoegh-Guldberg, O., … Ngo, H. (2021). *Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change*. https://doi.org/10.5281/ZENODO.5101125

Powers, R. P., & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change 2019 9:4*, *9*(4), 323–329. https://doi.org/10.1038/s41558-019-0406-z

Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., Sitch, S., Smith, B., & Sykes, M. T. (2007). Dynamic Global Vegetation Modeling: Quantifying Terrestrial Ecosystem Responses to Large-Scale Environmental Change. In J. G. Canadell, D. E. Pataki, & L. F. Pitelka (Eds.), *Terrestrial Ecosystems in a Changing World* (pp. 175–192). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-32730-1_15

Pulido Chadid, K., Rahbek, C., & Geldmann, J. (2024). *Are protected areas tracking threats to terrestrial biodiversity?* https://doi.org/10.1101/2024.10.15.618162

Qazi, A. W., Saqib, Z., & Zaman-ul-Haq, M. (2022). Trends in species distribution modelling in context of rare and endemic plants: A systematic review. *Ecological Processes*, *11*(1), 40. https://doi.org/10.1186/s13717-022-00384-y

Ramalho, Q., Vale, M. M., Manes, S., Diniz, P., Malecha, A., & Prevedello, J. A. (2023). Evidence of stronger range shift response to ongoing climate change by ectotherms and high-latitude species. *Biological Conservation*, *279*, 109911. https://doi.org/10.1016/j.biocon.2023.109911

Regos, A., D’Amen, M., Titeux, N., Herrando, S., Guisan, A., & Brotons, L. (2016). Predicting the future effectiveness of protected areas for bird conservation in Mediterranean ecosystems under climate change and novel fire regime scenarios. *Diversity and Distributions*, *22*(1), 83–96. https://doi.org/10.1111/ddi.12375

Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O’Neill, B. C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaresma, J. C., Kc, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., … Tavoni, M. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change*, *42*, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009

Rodrigues, A. S. L., & Cazalis, V. (2020). The multifaceted challenge of evaluating protected area effectiveness. *Nature Communications*, *11*(1), 5147. https://doi.org/10.1038/s41467-020-18989-2

Rondinini, C., di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., Hoffmann, M., Schipper, J., Stuart, S. N., Tognelli, M. F., Amori, G., Falcucci, A., Maiorano, L., & Boitani, L. (2011). Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1578), 2633–2641. https://doi.org/10.1098/rstb.2011.0113

Salamma, S., & Boyina, R. (2014). Distribution and conservation status of Croton scabies’s Bedd. (Euphorbiaceae), an endemic tree species of southern Eastern Ghats of Andhra Pradesh, India. *Journal of Threatened Taxa*, *6*, 6363–6370. https://doi.org/10.11609/JoTT.o4060.6363-70

Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peñuelas, J., & Thonicke, K. (2015). Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology*, *21*(7), 2711–2725. https://doi.org/10.1111/gcb.12870

Sala, O. E., Stuart, F., Iii, C., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, *287*, 1770–1774.

Sarkki, S., Rantala, L., & Karjalainen, T. (2015). Local people and protected areas: Identifying problems, potential solutions and further research questions. *International Journal of Environment and Sustainable Development*, *14*, 299–314. https://doi.org/10.1504/IJESD.2015.070137

Scheiter, S., & Higgins, S. I. (2009). Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. *Global Change Biology*, *15*(9), 2224–2246. https://doi.org/10.1111/j.1365-2486.2008.01838.x

Scheiter, S., Kumar, D., Pfeiffer, M., & Langan, L. (2024). Biome classification influences current and projected future biome distributions. *Global Ecology and Biogeography*, *33*(2), 259–271. https://doi.org/10.1111/geb.13784

Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: Learning from community ecology. *New Phytologist*, *198*(3), 957–969. https://doi.org/10.1111/nph.12210

Schulze, K., Knights, K., Coad, L., Geldmann, J., Leverington, F., Eassom, A., Marr, M., Butchart, S. H. M., Hockings, M., & Burgess, N. D. (2018). An assessment of threats to terrestrial protected areas. *Conservation Letters*, *11*(3), e12435. https://doi.org/10.1111/conl.12435

Sintayehu, D. W. (2018). Impact of climate change on biodiversity and associated key ecosystem services in Africa: A systematic review. *Ecosystem Health and Sustainability*, *4*(9), 225–239. https://doi.org/10.1080/20964129.2018.1530054

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., & Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*(2), 161–185. https://doi.org/10.1046/j.1365-2486.2003.00569.x

Smith, B., Prentice, I. C., & Sykes, M. T. (2001). Representation of vegetation dynamics in the modelling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography*, *10*(6), 621–637. https://doi.org/10.1046/j.1466-822X.2001.t01-1-00256.x

Smith, P., Arneth, A., Barnes, D. K. A., Ichii, K., Marquet, P. A., Popp, A., Pörtner, H. O., Rogers, A. D., Scholes, R. J., Strassburg, B., Wu, J., & Ngo, H. (2022). How do we best synergize climate mitigation actions to co-benefit biodiversity? *Global Change Biology*, *28*(8), 2555–2577. https://doi.org/10.1111/GCB.16056

Smith, P., Price, J., Molotoks, A., Warren, R., & Malhi, Y. (2018). Impacts on terrestrial biodiversity of moving from a 2°C to a 1.5°C target. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *376*(2119), 20160456. https://doi.org/10.1098/rsta.2016.0456

Stevens, N., Lehmann, C. E. R., Murphy, B. P., & Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global Change Biology*, *23*(1), 235–244. https://doi.org/10.1111/gcb.13409

Stocker, B. D., Feissli, F., Strassmann, K. M., Spahni, R., & Joos, F. (2014). Past and future carbon fluxes from land use change, shifting cultivation and wood harvest. *Tellus B: Chemical and Physical Meteorology*, *66*(1). https://doi.org/10.3402/tellusb.v66.23188

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Ferreira De Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*, 145–148.

Titeux, N., Henle, K., Mihoub, J.-B., & Regos, A. (2016). Biodiversity scenarios neglect future land-use changes. *Global Change Biology*, *22*, 2505–2515. https://doi.org/10.1111/gcb.13272

Trisos, C. H., I.O. Adelekan, E. Totin, A. Ayanlade, J. Efitre, A. Gemeda, K. Kalaba, C. Lennard, C. Masao, Y. Mgaya, G. Ngaruiya, D. Olago, N.P. Simpson, & S. Zakieldeen. (2022). Africa. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. In *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (1st ed., pp. 1285–1455). Cambridge University Press. https://doi.org/10.1017/9781009325844.011

UNEP-WCMC and IUCN. (2025). *Protected Planet: The World Database on Protected Areas (WDPA) [Online]* [Dataset]. UNEP-WCMC and IUCN. www.protectedplanet.net

United Nations Convention on Biological Diversity. (2022). *Kunming-Montreal Global Biodiversity Framework*.

Urban, M. C. (2024). Climate change extinctions. *Science*, *386*(6726), 1123–1128. https://doi.org/10.1126/science.adp4461

Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S. H. M., Joppa, L., Alkemade, R., Di Marco, M., Santini, L., Hoffmann, M., Maiorano, L., Pressey, R. L., Arponen, A., Boitani, L., Reside, A. E., van Vuuren, D. P., & Rondinini, C. (2016). Projecting Global Biodiversity Indicators under Future Development Scenarios. *Conservation Letters*, *9*(1), 5–13. https://doi.org/10.1111/conl.12159

Visconti, P., Butchart, S. H. M., Brooks, T. M., Langhammer, P. F., Marnewick, D., Vergara, S., Yanosky, A., & Watson, J. E. M. (2019). Protected area targets post-2020. *Science*, *364*(6437), 239–241. https://doi.org/10.1126/science.aav6886

Warren, R., Price, J., VanDerWal, J., Cornelius, S., & Sohl, H. (2018). The implications of the United Nations Paris Agreement on climate change for globally significant biodiversity areas. *Climatic Change*, *147*(3–4). https://doi.org/10.1007/s10584-018-2158-6

Warren, R., Vanderwal, J., Price, J., Welbergen, J. A., Atkinson, I., Ramirez-Villegas, J., Osborn, T. J., Jarvis, A., Shoo, L. P., Williams, S. E., & Lowe, J. (2013). Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, *3*(7), 678–682. https://doi.org/10.1038/nclimate1887

Watson, J. E. M., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, *515*(7525), 67–73. https://doi.org/10.1038/nature13947

Wauchope, H. S., Jones, J. P. G., Geldmann, J., Simmons, B. I., Amano, T., Blanco, D. E., Fuller, R. A., Johnston, A., Langendoen, T., Mundkur, T., Nagy, S., & Sutherland, W. J. (2022). Protected areas have a mixed impact on waterbirds, but management helps. *Nature*, *605*(7908), 103–107. https://doi.org/10.1038/s41586-022-04617-0

Wilson, E. O. (2016). *Half-earth: Our planet's fight for life*. W. W. Norton & Company.

Wilson, K. A., Auerbach, N. A., Sam, K., Magini, A. G., Moss, A. St. L., Langhans, S. D., Budiharta, S., Terzano, D., & Meijaard, E. (2016). Conservation Research Is Not Happening Where It Is Most Needed. *PLOS Biology*, *14*(3), e1002413. https://doi.org/10.1371/journal.pbio.1002413

Zaehle, S., & Friend, A. D. (2010). Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. *Global Biogeochemical Cycles*, *24*(1). https://doi.org/10.1029/2009GB003521

Zhao, F., Lan, X., Li, W., Zhu, W., & Li, T. (2021). Influence of Land Use Change on the Surface Albedo and Climate Change in the Qinling-Daba Mountains. *Sustainability*, *13*(18), Article 18. https://doi.org/10.3390/su131810153

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., … Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*(9), 1261–1277. https://doi.org/10.1111/ecog.04960

Zurell, D., Zimmermann, N. E., Gross, H., Baltensweiler, A., Sattler, T., & Wüest, R. O. (2020). Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography*, *47*(1), 101–113. https://doi.org/10.1111/jbi.13608

Chapter 2

Future climate and land use change will equally impact global terrestrial vertebrate diversity

Chantal Hari,[1,2,3] Thomas Hickler,[4,5] Christian Hof,[6] Christopher P.O. Reyer,[7] Inne Vanderkelen,[1,2,3,8,9] Alke Voskamp,[4] Matthias F. Biber,[10] Markus Fischer,[3,11] Édouard L. Davin,[1,2,3]

[1] Wyss Academy for Nature at the University of Bern, University of Bern, Bern, Switzerland
[2] Climate and Environmental Physics, Physics Institute, University of Bern, Bern, Switzerland
[3] Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland
[4] Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany
[5] Department of Physical Geography at Goethe University, Frankfurt/Main, Germany.
[6] Chair of Global Change Ecology, Biocenter, University of Würzburg, Germany
[7] Potsdam Institute for Climate Impact Research, Member of the Leibniz Association, Potsdam, Germany
[8] Department of Earth and Environmental Sciences, KU Leuven, Leuven, Belgium
[9] Royal Meteorological Institute Belgium (RMIB), Brussels, Belgium
[10] Senckenberg Research Institute and Nature Museum, Terrestrial Zoology, Frankfurt am Main, Germany
[11] Institute of Plant Sciences, Plant Ecology, University of Bern, Bern, Switzerland

This chapter is under revision in the peer-reviewed journal *Global Ecology and Biogeography*.

Abstract

Aim: Terrestrial biodiversity is impacted by both climate and land use change. Yet, future biodiversity projections have rarely considered these two drivers in combination. In this study, we aim to assess the individual and combined impact of future climate and land use change on global terrestrial vertebrate diversity under a "sustainability" (SSP1-RCP2.6) and an "inequality" (SSP4-RCP6.0) scenario.

Location: Global land, excluding Antarctica.

Time period: 1995, 2080

Major taxa studied: Amphibians, birds, and mammals.

Methods: We combined global climate-driven species distribution model (SDM) projections of 13903 vertebrates (amphibians, birds and mammals) with future and present land use projections from the Land Use Harmonization 2 (LUH2) project. We refined the SDM outputs by the habitat requirements of each species using a land use filtering approach. We then analyzed future species richness changes globally, per region and per land use category and also looked at taxon-specific effects.

Results: Under both scenarios, decreases in future species richness dominate at low and mid-latitudes with climate and land use change playing an equally important role. Land use change can be either an alleviating (SSP1-RCP2.6) or an exacerbating (SSP4-RCP6.0) factor of climate-induced biodiversity loss. Sub-Saharan Africa is projected to become a high-risk area for future land use-driven biodiversity loss under the "inequality" scenario. Under SSP1-RCP2.6, forested and non-forested land areas increase, while SSP4-RCP6.0 leads to higher rates of deforestation and pasture expansion. Mammals experience the largest climate-driven losses, affecting 56.4% of land area under SSP4-RCP6.0, while amphibians are particularly vulnerable to land use-driven losses, especially under SSP4-RCP6.0.

Main conclusions: Generally, our results suggest that both climate and land use pressures on biodiversity will be highest in lower latitudes which harbor the highest levels of biodiversity.

2.1 Introduction

Biodiversity loss, land degradation, and climate change are some of the key environmental challenges faced by humanity (IPBES, 2019; Rosenzweig et al., 2008). The current biodiversity crisis has been referred to as the "sixth mass extinction" in Earth's history (Bellard et al., 2012). An increasing amount of land has been converted from its natural state to agricultural land, affecting nearly a third (32%) of the global land area over the past six decades, a rate around four times greater than previously estimated from long-term land change assessments (Winkler et al., 2021).

This widespread conversion has led to fragmentation, degradation, and the destruction of species habitat (IPBES, 2019). While past biodiversity loss has mainly been driven by changes in habitat due to land use and land cover changes (Sala et al., 2000; Warren et al., 2018), climate change emerges as an additional risk for biodiversity at the global scale (IPBES, 2019; Pecl et al., 2017). Without stringent climate change mitigation, climate change can lead to potentially large contractions in species' ranges as they may no longer be able to adapt to the environmental conditions in a given region (Bellard et al., 2012; Jenkins et al., 2021; Warren et al., 2013). Moreover, climate and land use change can have interacting effects on species and ecosystems (Brook et al., 2008; Hof et al., 2011; Mantyka-pringle et al., 2012). For instance, land use change can limit species' abilities to respond to climate change through dispersal (Hof, 2021; Jenkins et al., 2021; Opdam & Wascher, 2004).

To comprehensively understand the intertwined impacts of climate and land use change and their relative importance, it is essential to consider both factors in future biodiversity projections. However, most global research focused solely on the impacts of climate (Biber et al., 2023; Warren et al., 2018) or land use change (Leclère et al., 2020; Newbold et al., 2015; Powers & Jetz, 2019), even though land use change will occur alongside a changing climate (Jenkins et al., 2021; Methorst et al., 2017), with potentially different outcomes. To date, few studies have made first steps to overcome these deficiencies, for example, by combining species distribution models (SDMs) with land use impacts from a statistical model (Newbold, 2018; Newbold et al., 2020; Pereira et al., 2024). Other global studies consider both drivers but do not assess their separate and combined effects (Beyer & Manica, 2020). Recent work by Hof et al., (2018), evaluated the potential future impacts of climate and land use changes on global species richness of terrestrial vertebrates under a low and high-emission scenario, with large-scale deployment of Bioenergy with Carbon Capture and Storage (BECCS) for climate mitigation (Hof et al., 2018). However, their analysis did not explicitly account for the habitat requirements of individual species, but rather only considered a spatial overlap of projected species distributions with future land use.

In this study, we quantify the intertwined impact of climate and land use change on biodiversity by combining climate-driven SDM projections with future land use projections from integrated assessment models (IAMs). To capture a wide range of possible futures, we consider two contrasted combinations of Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs). We assess changes on a global scale as well as regionally and across specific taxa.

2.2 Methods

2.2.1 Species distribution modeling

Future projections with SDMs for 15496 terrestrial vertebrate species (2964 amphibians, 8493 birds and 4039 mammals) were obtained from Hof et al. (2018). These projections were based on two types of SDMs, generalized additive models (GAM) and generalized boosted regression models (GBM). GAM is an additive model, whereas GBM is a classification and regression tree-based modeling approach. These two approaches were selected because they perform comparatively well to other modeling approaches (Araújo et al., 2005; Elith et al., 2010; Hof et al., 2018; Meynard & Quinn, 2007). The SDMs were calibrated using expert range maps from International Union for Conservation of Nature (IUCN) for amphibians and mammals and from Birdlife International and Nature Serve for birds (IUCN, 2023; Lenoir & Svenning, 2015) and present-day (centered around 1995) global climate information from EWEMBI (Lange, 2016). The SDMs were projected into the future (2080) using climate data from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) phase 2b (Frieler et al., 2017) based on four global climate models (GCMs; MIROC5, GFDL-ESM2M, HadGEM2-ES, and IPSL-CM5A-LR) from the Coupled Model Intercomparison Project Phase 5 (CMIP5) under a low (RCP2.6) and high warming scenario (RCP6.0). Note that the CMIP5-based climate scenarios do not explicitly consider a SSP, but for simplicity we refer to both the climate change and the land use change scenarios as “SSP1-RCP2.6” and “SSP4-RCP6.0” since they combine climate information from the RCPs and land use information from the SSPs (see next section). The results analyzed in this study were based on a 30-year mean centered around the year 2080. The same analysis was done for the year 2050, with the results provided in the supplementary material (Fig. S2.1). We included projections for 2050 to account for the increasing uncertainty in species range projections as the time horizon extends further into the future (Baker et al., 2015). The SDM output was given as probabilities of occurrence per individual species.

2.2.2 Land use filtering

To account for the impact of future land use change on biodiversity, we use historical and future data from the Land Use Harmonization 2 (LUH2) dataset (Hurtt et al., 2020). This data comes at a 0.25° resolution and was first aggregated to 0.5° resolution to match the spatial resolution of the SDM simulations and the resulting probability of occurrence per species. All LUH2 data before 2015 is based on historical reconstructions and remote sensing (Hurtt et al., 2020). After 2015, data are based on projections from IAMs under different SSPs and RCPs. SSP1-RCP2.6 is based on the IAM IMAGE 3.0 (Stehfest et al., 2014) and SSP4-RCP6.0 is based on the Global Change Assessment

Model (GCAM; Wise et al., 2014). SSP1 projects a future under a sustainable development paradigm. It emphasizes high economic growth with environmentally friendly technologies and population growth that decreases in the second half of the 21st century (van Vuuren et al., 2017). SSP4 describes a world with large inequalities in economic opportunity and political power both across and within countries. High-income countries strongly regulate land use change, but in contrast, in poor countries, tropical deforestation continues (Popp et al., 2017). Both scenarios are not directly linked to climate projections, however, assumptions about the climate mitigation policies consistent with the respective RCP are added to the SSP baseline scenarios (Hurtt et al., 2020). LUH2 entails 12 land use categories, namely, forested primary land, non-forested primary land, potentially forested secondary land, potentially non-forested secondary land, managed pasture, rangeland, urban land, and five types of croplands. Habitat preferences for each species were derived from the IUCN Habitat Classification Scheme (v.3.1). To match the 104 IUCN habitat classes with the 12 LUH2 land use categories, they were converted using the lookup table from Carlson et al. (2022; Fig. 2.1). The 12 LUH2 land use categories were then further grouped into 5 generalized land cover classes (forested land, non-forested land, pasture, cropland, and urban) according to Powers & Jetz (2019). We combined forested primary land and potentially forested secondary land into forested land, all non-forested primary land and potentially non-forested secondary land into non-forested land, managed pasture, and rangeland into pasture, and the five crop types into cropland. The final 12 land use categories were then linked to each species separately to account for their individual habitat classification. For 260 amphibians, 1233 birds, and 100 mammals we were not able to apply the land use filtering because there was no available information on their habitat preferences or because the land use filtering resulted in an empty array (this was the case for 16 (of the 260) amphibians, 2 (of the 1233) birds, and 84 (of the 100) mammals). This occurred where all grid cells had a land use fraction of zero in areas with non-zero probability of occurrence. As a result, these species were removed from the analysis resulting in 13903 species (2704 amphibians, 7260 birds, 3939 mammals) included in our analysis. If for a given species the habitat was labeled as “suitable” according to the IUCN habitat classification, the probability of occurrence projected by the SDM is multiplied by the grid cell fraction occupied by this habitat (Fig. 2.1). Since a given species can have multiple suitable habitats, the probability of occurrence was weighted by the grid cell fraction occupied by the sum of all suitable habitats (Fig. 2.1). This land use filtering step was done for both time periods 1995 and 2080. As the land use type “urban” is not considered a suitable habitat for any species according to the IUCN habitat classifications, it is not further included in the land use filtering and thus not affecting the probabilities of occurrence.

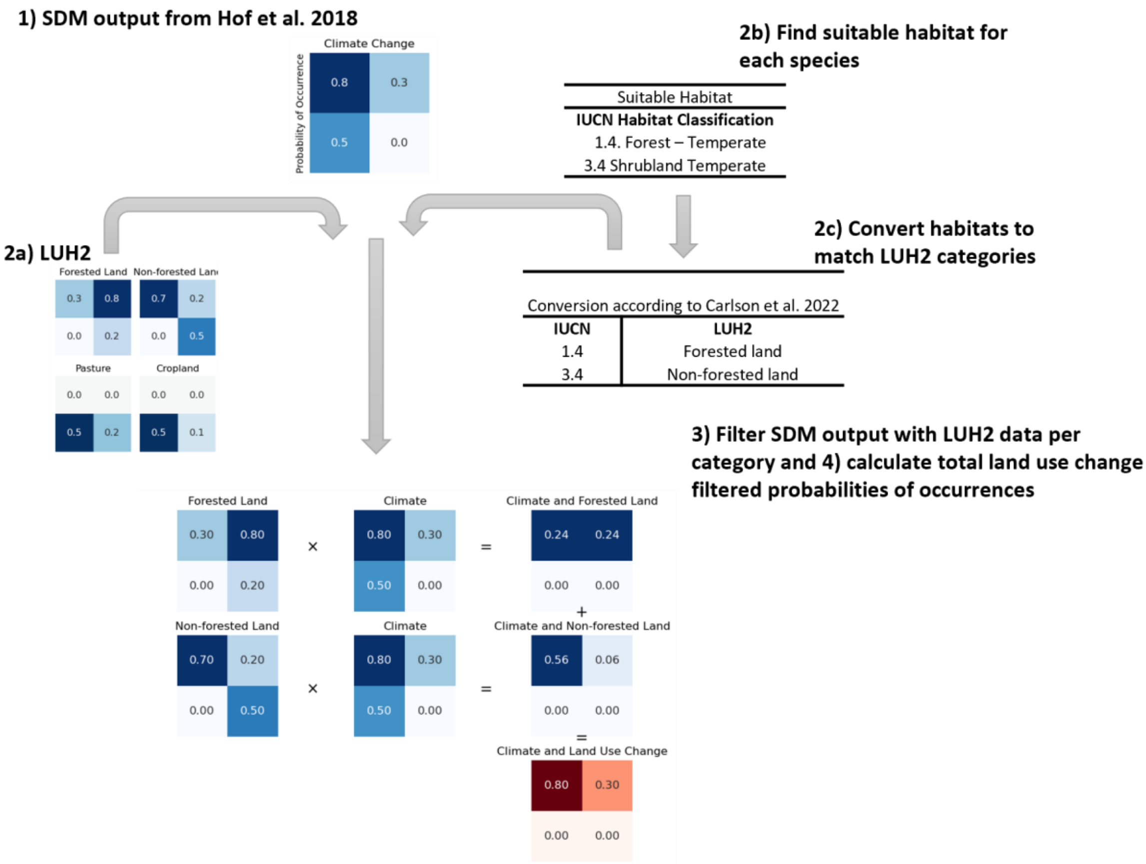

Fig. 2.1 Schematic overview of the different methodological steps of the land use filtering approach. *The process is illustrated over 4 grid cells for a single hypothetical species having forested and non-forested land as habitat preference. 1) We use SDM output from Hof et al., (2018) as probabilities of occurrences. 2) Using the LUH2 dataset (Hurtt et al., 2020), we classify land into five main categories: forested land, non-forested land, pasture, cropland, and urban areas. Each species' habitat preference is determined according to the IUCN Habitat Classification Scheme (IUCN, 2023) and matched to the LUH2 land use categories following the conversion table from Carlson et al. (2022). 3) We apply the land use filter by weighting the SDM-derived probabilities of occurrence by the fraction of grid cell occupied by suitable land use categories for each species. 4) These weighted probabilities are then summed to obtain the total land use-filtered probabilities of occurrences.*

2.2.3 Land use only calculation

For the analysis of climate-only versus land use-only change, we employed a stepwise approach. Initially, our intention was to calculate the combined effects of climate and land use change and subtract the climate change impact to isolate land use change. However, this method can produce misleading results when the land use fraction of a grid cell is zero, as the resulting change may incorrectly be attributed to land use change, when it is in fact driven solely by climate change (see Fig. S2.2A). To address this, we filtered both the 1995 and 2080 probabilities of occurrence from the SDMs using the 1995 land use data from the LUH2 dataset as a baseline (Fig. S2.2B). This allowed us to hold land use constant and isolate the effects of climate change. Climate change impact was then calculated as the difference between future and present conditions, keeping land use constant. Therefore, when referring to "climate change" in this analysis, the calculation was always based on the 1995 baseline. The land use change impact was computed by subtracting the climate change-only scenario from the combined climate and land use change projections for the future. This ensured that the land use change attribution stemmed solely from the land use change simulations.

2.2.4 Sensitivity analyses

We conducted two sensitivity analyses to test how certain methodological assumptions affect the results. First, because previous studies have shown that different dispersal assumptions represent a major uncertainty in SDM projections, we considered here two dispersal assumptions in order to test the robustness of our results, following the methods of Hof et al. (2018). The main results presented here were based on the assumption of limited dispersal in which a buffer of d/4 is applied to each range polygon, where *d* is the diameter of the largest range polygon of a species. In addition, we also presented in the Supplementary Materials a sensitivity analysis with a "No dispersal" assumption corresponding to a situation where species are not allowed to migrate beyond their current range (Fig. S2.3). More methodological details on the SDM approach used, including input data, pre-processing, model validation, bioclimatic variable and pseudo-absence selection, as well as spatial autocorrelation are provided by Hof et al., (2018). Secondly, we have tested the sensitivity of the results towards our habitat suitability assumptions. We have applied the land use filter on species with habitat suitability marked as "suitable" according to the IUCN Habitat Classifications Scheme, which is defined as "the species occurs in the habitat regularly or frequently" (IUCN, 2023). For the sensitivity analysis, we have also included species with habitat suitability marked as "marginal" (i.e., "the species occurs in the habitat only irregularly or infrequently" or "only a small proportion of individuals are found in the habitat" (IUCN, 2023).

2.2.5 Species richness aggregation

For our study, we worked with a large matrix of 13903 species over three taxa, two scenarios (SSP1-RCP2.6 and SSP4-RCP6.0), four GCMs (MIROC5, GFDL-ESM2M, HadGEM2-ES, and IPSL-CM5A-LR), and two SDMs (GAM and GBM). We estimated the global species richness for historical (1995) and future time (2080) slices for each combination of taxa, SDM, GCM and climate scenario. The probability of occurrence data per species were first summed across taxa for each scenario, GCM and SDM. The change in species richness was calculated as the summed probabilities of occurrence over all species for 2080 relative to 1995. We presented the relative difference in species richness, computed as the difference between future (2080) and present (1995) species richness standardized by the present baseline and the absolute difference in species richness for the supplementary materials. We applied a minimum threshold of 1e-6 on the stacked probabilities of occurrences to exclude near-zero values to avoid division by zero for the relative difference calculations. Non-zero changes were further constrained to within ±100% to avoid statistical anomalies. To compute regional means, we used region definitions based on the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) assessments (IPBES, 2019). From the 17 IPBES subregions, we derived 10 regions that were used for the analysis (Table S2.1). The proportion of global land area affected by species richness gain and loss was calculated by summing the area of individual grid cells affected by gain or loss and normalizing the result by the total land area (excluding Antarctica).

2.3 Results

2.3.1 Land use change trajectories and their impact on species habitats

The sustainability scenario (SSP1-RCP2.6, Fig. 2.2A) assumes strong environmental regulations that reduce tropical deforestation (Hurtt et al., 2020). Forested and non-forested land (e.g., grassland) is projected to increase by 0.5 million square kilometres (Mkm^2) and 2 Mkm^2 from 1995 to 2080, mainly at the expense of pasture (-5.4 Mkm^2; Fig. 2.2). The decrease in pasture reflects the decreasing consumption of animal products. Cropland is projected to increase by 2.3 Mkm^2 particularly in low- and medium-income regions. In contrast, land use is only regulated in high-income countries under the inequality scenario (SSP4-RCP6.0, Fig. 2.2B), resulting in higher deforestation rates in tropical regions. Forested land is projected to decrease by -1.8 Mkm^2 in 2080 relative to 1995 and non-forested land is projected to decrease by -4.8 Mkm^2. Cropland and pasture both increase by 3.3 Mkm^2 and 2.6 Mkm^2 respectively, as this scenario includes increased bioenergy use and considers that animal calorie shares converge to a stable level towards the end of the century (Hurtt et al., 2020).

The two contrasting land use trajectories directly affect species distribution since habitat preferences differ per species (Table 2.1). For instance, 78.5% of all species included in this study have forested land as a suitable habitat (i.e., suitable according to the IUCN Habitats Classification Scheme; see Materials and Methods) and will therefore be affected by the decrease in forested land in SSP4-RCP6.0. Conversely, 11.1% of species have pasture as a suitable habitat and thus will be directly affected by the decrease in pasture under SSP1-RCP2.6. Moreover, 56.1% of the species require non-forested land and 13.8% cropland as suitable habitats (Table 2.1). It is important to note that 59.3% of all included species occur in multiple habitats (Table 2.1), thus species having forest as a suitable habitat are not necessarily forest specialists and can also occur in other habitats.

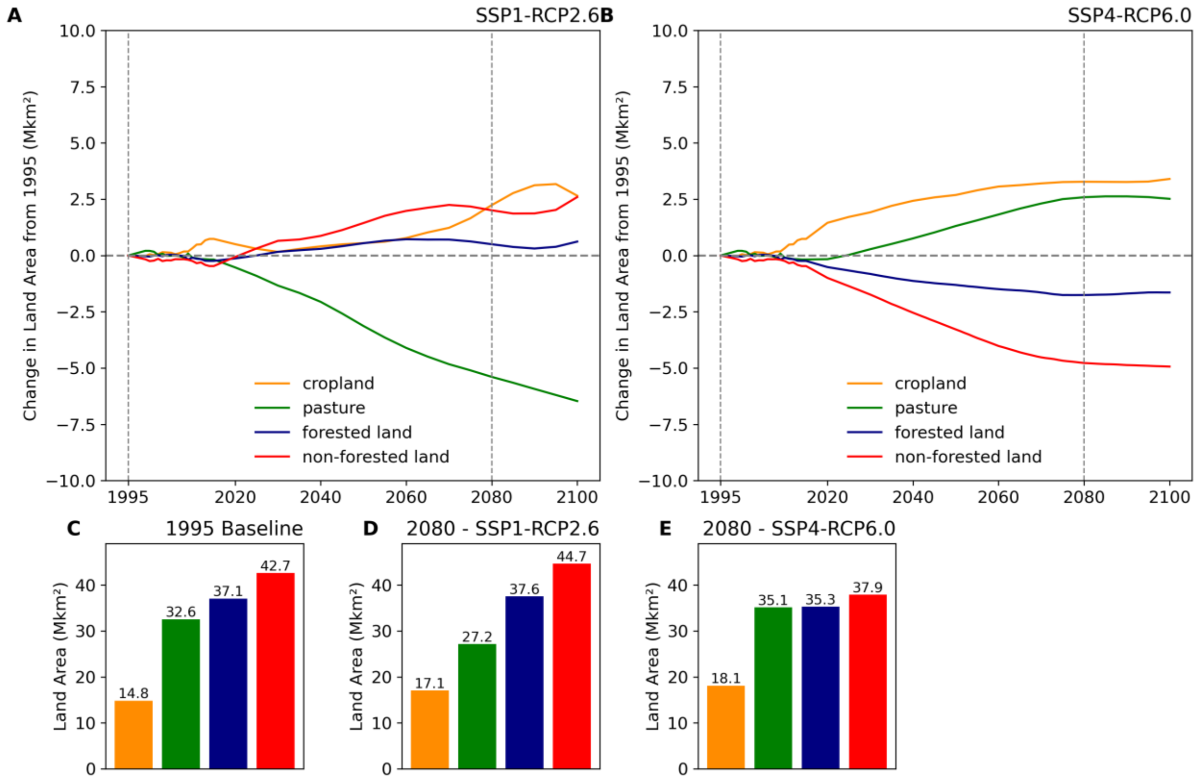

*Fig. 2.2 **Future land use scenarios.** Land use change in (**A**) the "sustainability" (SSP1-RCP2.6) from IMAGE (24; see Material and Methods) scenario and (**B**) the "inequality" (SSP4-RCP6.0) scenario from GCAM (25; see Material and Methods), in reference to the year 1995 based on the LUH2 dataset (22) as well as (**C**) the land area per land use category for 1995, (**D**) for 2080 under SSP1-RCP2-6) and (**E**) for 2080 under SSP4-RCP6.0).*

Table 2.1. Number of species per taxa and habitat. *Species were included if their habitat was categorized as 'suitable' according to the IUCN Habitats Classification Scheme. Species can occur in multiple habitats and may thus be listed in multiple categories. Numbers in brackets indicate the relative proportion in reference to the total number of species per taxa.*

	Total # of species	Forested land	Non-forested land	Pasture	Cropland	Single habitat	Multiple habitats
Amphibians	**2704 (19.5%)**	2235 (82.7%)	2211 (81.8%)	642 (23.7%)	615 (22.7%)	660 (24.4%)	2044 (75.6%)
Birds	**7260 (52.2%)**	5770 (79.5%)	4644 (64.0%)	2096 (28.9%)	1987 (27.4%)	2622 (36.1%)	4638 (63.9%)
Mammals	**3939 (28.3%)**	2907 (73.8%)	2210 (56.1%)	436 (11.1%)	542 (13.8%)	2372 (60.2%)	1567 (39.8%)
Total	**13903**	**10912 (78.5%)**	**9065 (65.2%)**	**3174 (22.8%)**	**3144 (22.6%)**	**5654 (40.7%)**	**8249 (59.3%)**

2.3.2 Combined species richness changes under climate and land use

For both, the sustainability, and the inequality scenario, we then assessed the global implications of climate and land use changes on species richness separately and in combination. Climate-driven species richness increases at higher latitudes for both scenarios and widely decreases at mid- to lower latitudes (Fig. 2.3A & C). Both scenarios show a similar spatial pattern, which is amplified in the inequality scenario. Accounting for future land use change leads to more spatial variability of future species richness (Fig. 2.3B & D). Overall land use change has a positive impact under SSP1-RCP2.6, while it mostly exacerbates species losses under SSP4-RCP6.0 (Fig. S2.4). Global patterns in the climate-driven impact and the combined impact under SSP1-RCP2.6 widely vary worldwide. Sub-Saharan Africa shows the most pronounced negative difference in species richness change between SSP1-RCP2.6 and SSP4-RCP6.0. Especially under SSP4-RCP6.0, species richness mainly increases in the higher latitudes and decreases in the mid- to lower latitudes, also when land use change impact is included (Fig. 2.3D).

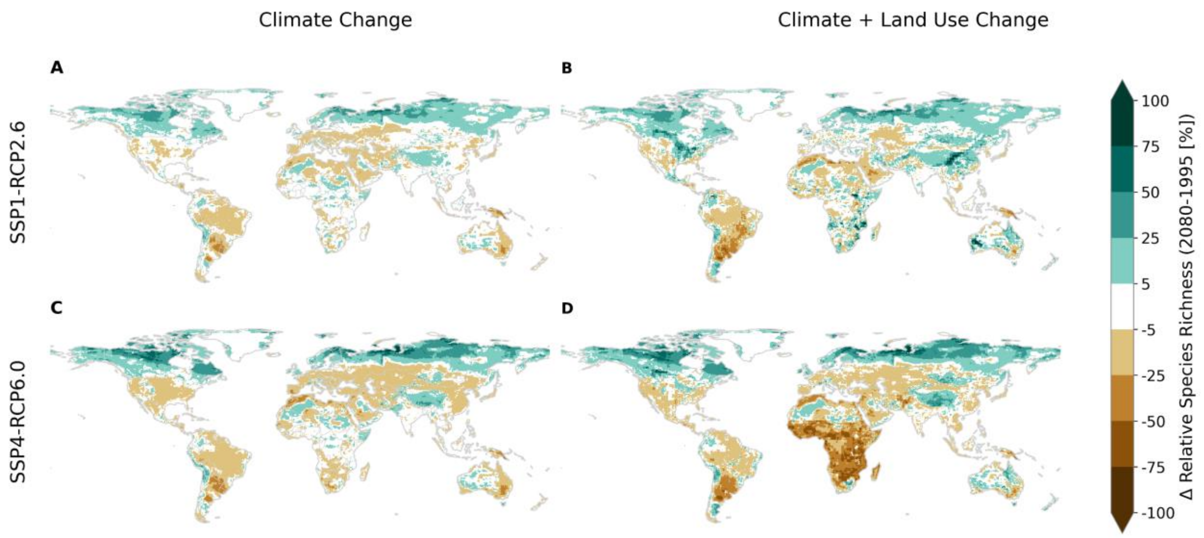

Fig. 2.3 Relative climate and land use impacts on future species richness. *Projected relative species richness change for the year 2080 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future (A and C) and combined climate and land use change with present and future land use data respectively (B and D). Results are shown for SSP1-RCP2.6 (climate, A and land use, B) and SSP4-RCP6.0 (climate, C and land use, D). Species richness is calculated as the summed probabilities of occurrence over all species of the taxa amphibians, birds, and mammals. The mean over all GCM and SDM combinations is shown here. A minimum threshold of 1e-6 is introduced on the stacked probabilities of occurrences to exclude near-zero values and thus, avoid division by zero for the relative difference calculations. The results for the year 2050 compared to 1995 can be found in the Supplementary Material (Fig. S2.1) as well as the results for 2080 compared to 1995 for individual taxa (Fig. S2.5-S2.7).*

2.3.3 Species richness changes per region and land use category

Assessing the relative changes in species richness in 2080 compared to 1995 over various world regions (Fig. 2.4; Fig. S2.8), showed that climate change alone leads to species richness losses in all world regions except for boreal regions (Eastern Europe and North America) and relative changes are also amplified under the inequality scenario. Climate-driven species richness loss is highest in South America with an overall relative decrease of -7.2% and -9.1% in SSP1-RCP2.6 and SSP4-RCP6.0 respectively. When combined with land use change, the losses are generally dampened, and gains are amplified in most regions in the sustainability scenario. In the inequality scenario, however, losses are aggravated and the differences between the two scenarios are exacerbated. In SSP1-RCP2.6, the inclusion of land use change leads to a relative increase in species richness from -1.2% to 2.2% in West, Central, East and South Africa and higher species richness in most regions except North Africa and Western Asia and South America. The contrary is the case for SSP4-RCP6.0, where the inclusion of land use change leads to a further decrease in species richness in all regions except Central and Western Europe, Eastern Europe, and North America (Fig. 2.4; Fig. 2.3). This is most pronounced in West, Central, East and South Africa, regardless of the land use category. Overall, the results vary substantially between the different regions and the underlying land use scenarios driven by the respective IAM.

To understand how the different land use narratives translate into biodiversity outcomes, we examine projected changes per land use category. For the three land use categories forested land, non-forested land, and cropland, most of the projected species richness loss is due to land use change for the inequality scenario. For forested land, -29.4% loss is due to land use change in this West, Central, East & South Africa, and only -0.7% loss due to climate change impact, with a standard deviation of 3.4% over all GCMs and SDMs. Similarly, non-forested land projections result in a -27.5% decline in projected species richness loss due to land use change and -3% +/- 2.1% SD from climate change in the same region and for the same scenario (Fig. 2.4). Both forested land and non-forested land are projected to decrease substantially over West, Central, East and South Africa under the SSP4-RCP6.0 scenario (Fig. S2.9). For SSP1-RCP2.6, the species richness in this region increases mostly due to increases in forested land, non-forested land, and cropland, while only pasture substantially decreases in this region (Fig. S2.9). This is directly reflected in the relative loss of species richness of -1.4% +/- 1.3% SD from climate change and -2% from land use change for pasture in West, Central, East and South Africa. While climate change and land use change generally have reinforcing negative or positive impacts, their impacts can also diverge, even compensating for each other (e.g., Oceania for forested land SSP1-RCP2.6 and SSP4-RCP6.0; Fig. 2.4).

Eastern Europe and North America show the most notable relative gains in projected species richness over all land use categories and scenarios (Fig. 2.4). The majority of gain is climate-driven with the most pronounced species richness increase for the land use category pasture, where under SSP4-RCP6.0 22.6% +/- 3.8% SD of the gain is due to climate change and 1.1% due to land use change (Fig. 2.4). This increase in the higher latitudes, however, is sensitive to the underlying dispersal assumption. Additional projections with a no-dispersal assumption, where the future ranges correspond to the present ranges of the species, indicate less gain in the higher latitudes and more loss of species richness in the mid-latitudes (Fig. S2.3). When also including species with habitat suitability marked as “marginal” as part of the sensitivity analysis, the geographical patterns are consistent and there are only minor differences in the relative species richness change (Fig. S2.10).

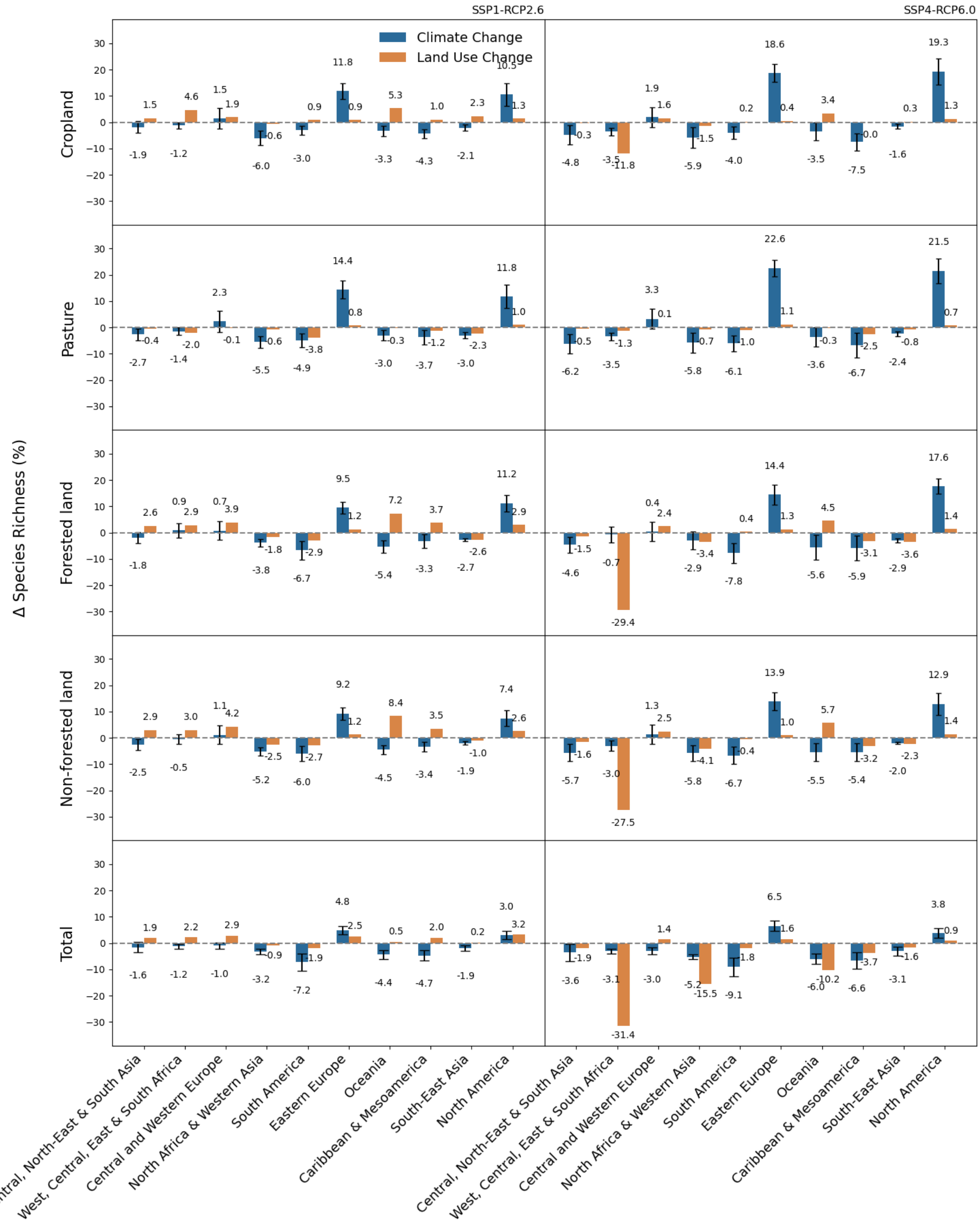

Fig. 2.4 Relative change in species richness from 1995 to 2080 per habitat separately and in total and region. *The climate and land use change impact for the two scenarios SSP1-RCP2.6 and SSP4-RCP6.0 per habitat forested land, non-forested land, cropland, pasture, and the total over all habitats. The total is based on the*

relative species richness change from above (Fig. 2.3). The weighted mean calculation was first done for each combination of GCM and SDM before it was aggregated per regions. The land use change-only impact is calculated as the residual between the overall impact and the climate-only impact. The error bars indicate the standard deviation over all GCMs and SDMs. The world regions are based on merged Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) regions (Table S2.1) and results are spatially aggregated using a latitude-weighted mean.

2.3.4 Land area affected by species richness change

To put biodiversity impacts into perspective, we calculate the proportion of global land area affected by species richness gains and losses. In both scenarios and across all taxa, losses dominate under climate change only, and land area with losses being more widespread under the inequality scenario (Fig. 2.5). For example, 54.2% of land area loses species richness for mammals due to climate change in SS1-RCP2.6, while 37.4% of land area gains species (Fig. 2.5C). For SSP4-RCP6.0, land area with species richness loss increases to 56.4%, and the proportion of area with gains also increases slightly to 37.6%, at the expense of the area with no change (Fig. 2.5I). The effect of land use change shows a more contrasted picture with a relatively equal proportion of losses and gains under SSP1-RCP2.6 (and even a predominance of gains for mammals with 48.5% of the land area) and a predominance of losses for the SSP4-RCP6.0 scenario (Fig. 2.5F & L). Also, for the other taxa the proportion of area leading to species richness loss from land use change is exacerbated for SSP4-RCP6.0 compared to SSP1-RCP2.6. The proportion of losses increases by 9.5% for birds (Fig. 2.5E & K) and by 6.5% for amphibians (Fig. 2.5D & J). It shows that land use change can be either a global alleviating (sustainability scenario) or exacerbating (inequality scenario) factor of climate-induced biodiversity loss, although it does contribute to both regional losses and gains in both scenarios.

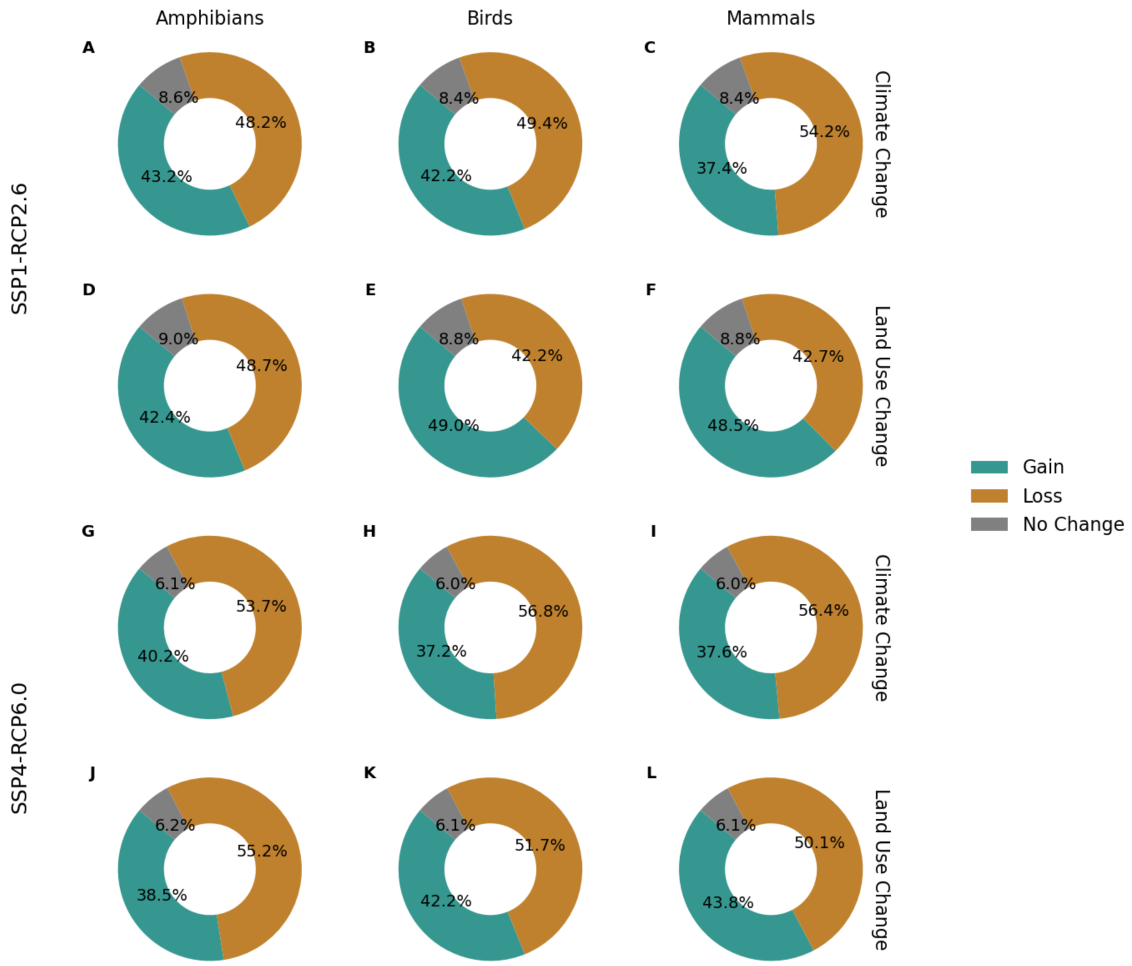

Fig. 2.5 Climate and land use-driven changes in land area. *Proportion of the total land area (excluding Antarctica) affected by species richness gain or loss for each taxon and scenario for climate and land use change. If the change equals 0, it was classified as no change. The species richness was first calculated as the summed probabilities of occurrence over all species for each taxon and scenario. For each combination of GCM and SDM, the probabilities are aggregated by calculating the latitudinal weighted mean. All future projections are then compared with the data of 1995. Based on this, the gains and losses are separated and based on the grid cell we calculate the proportion of global area affected.*

The proportion of losses is larger for all taxa under SSP4-RCP6.0 compared to SSP1-RCP2.6 for both climate and land use change. For mammals and birds, the proportion of global area with a climate-driven species richness loss is larger for SSP4-RCP6.0 with a loss of 56.4% and 56.8% respectively in comparison to the land use-driven species richness loss (51.7% and 55.2% respectively). For amphibians, however, the projected share of global area with a species richness loss due to land use change is 55.2% and 53.7% from climate change.

2.4 Discussion

Our analysis has demonstrated that including land use change in future biodiversity projections leads to different species richness impacts than if investigating climate change alone. While the climate change impact mostly scales with the climate scenario, the land use impact has a strong scenario dependency. Indeed, we find that land use change can be either a global alleviating (sustainability scenario) or an exacerbating (inequality scenario) factor of climate-induced biodiversity loss. Overall, our findings are in line with existing literature showing that climate change leads to a projected species shift towards higher latitudes, whereas land use change may limit this projected expansion (Methorst et al., 2017). A study by Newbold (2018) also showed that the impacts of climate change and land use change on biodiversity are expected to vary significantly across different regions. It highlights how these pressures are likely to combine and intensify in tropical grasslands, savannas, and the edges of tropical forests, leading to significant losses of species. In contrast, the heartlands of tropical forests and northern boreal regions might see less impact from land use changes but are still at risk of considerable biodiversity loss due to climate change. Meanwhile, temperate regions could experience relatively minor changes in species richness as a result of future climate change (Newbold, 2018).

The increase in forested and non-forested land over the course of the century projected for SSP1-RCP2.6 directly translates into species richness change by habitat and into overall species richness changes as most of the species included in our study have either forested (78.5%) or non-forested land (65.2%) or both categories as suitable habitats (Table 2.1, Fig. 2.4). Especially, West, Central, East and South Africa shows that under increasing forest and non-forested land, species richness in 2080 is projected to increase compared to 1995 levels and land use change will be the main driver of this change. However, this positive effect strongly depends on the quality of the land use change. For example, whether forest gains benefit biodiversity will depend on the type of reforestation. In the tropics, most reforestation currently occurs with non-native species and on natural land with high biodiversity, such as savannas, which can also be detrimental to biodiversity (Parr et al., 2014).

In our study, primary and secondary forest are combined into the category of forested land. To support the decision of combining primary and secondary forests into a single 'forested land' category in our study, we refer to findings by Rozendaal et al. which demonstrate that secondary forests can rapidly regain species richness, achieving 80% recovery within two decades, yet require centuries to fully match the species composition of old-growth forests. This suggests a differentiated value of secondary forests in biodiversity conservation, reinforcing our approach by highlighting the complementary roles of both forest types in maintaining biodiversity within human-modified tropical landscapes, thereby justifying their collective consideration (Rozendaal et al., 2019).

Furthermore, the land use scenarios used for this study, especially the SSP1-RCP2.6 scenario, assume a biodiversity-conscious world (Hurtt et al., 2020). Other IAM projections under the same scenario have been shown to result in more negative outcomes for biodiversity (Leclère et al., 2020). Many other IAM projections under this scenario assume a more bioenergy-extensive world (Hof et al., 2018), whereas our LUH2 projections assume reforestation and afforestation in high- and medium-income countries with an assumption of global forest cover increase (Hurtt et al., 2020). Thus, even resulting in an increase in forested land in South America under SSP4-RCP6.0 (Fig. S2.9).

Our results show that when forested and non-forested land are projected to decrease under SSP4-RCP6.0, the species richness loss amounts to more than 30% compared to 1995 values in West, Central, East and South Africa. Other studies have also shown similar projected declines in sub-Saharan African species richness (Visconti et al., 2016) because increases in human population led to a reduction in natural vegetation (PBL, 2012). Our results have shown that only regions in the higher latitudes show an increase in species richness in the future, even for the SSP4-RCP6.0 scenario (Fig. 2.4). Many studies have discussed species' range shifts towards higher latitudes as a response to climate change (Chen et al., 2011; Lenoir & Svenning, 2015; Parmesan & Yohe, 2003; Ramalho et al., 2023). Our results show a more complex pattern for land use change impacts on biodiversity but are in line with other studies that evaluate habitat suitability and risks, such as the study by Powers and Jetz, which underscores significant global habitat declines and the urgency of national stewardship in biodiversity-rich regions like South America, Southeast Asia, and Africa. Their work also highlights the critical need to identify and prioritize the most vulnerable species and locations, a point that aligns with our findings and reinforces the importance of proactive conservation planning in mitigating biodiversity threats (Powers & Jetz, 2019). The species richness increase in the higher latitudes can be attributed to climate change and highly depends on the underlying dispersal assumption. Interestingly, the mid-latitudes are projected to profit from land use change in the future. Our results suggest that countries known to create a large part of their biodiversity footprints outside their own country's borders by importing large amounts of agricultural products from regions with high biodiversity loss (Schwarzmueller & Kastner, 2022), namely, countries in Western Europe, North America, and the Middle East show a projected increase in future land use change-driven species richness. This has implications for conservation planning and global equity discussions regarding the externalization of biodiversity loss at the benefit of national biodiversity protection.

These results were computed under a limited-dispersal assumption. However, a sensitivity analysis using a no-dispersal scenario showed that they are still optimistic (Fig. S2.3). The underlying dispersal ability assumptions are important to consider when analyzing climate change impacts on species, as different assumptions can have substantial effects on the projected future ranges (Methorst et al., 2017; Newbold, 2018; Thuiller et al., 2019). In addition, we have tested the sensitivity of the results towards our habitat suitability assumptions. We performed an additional analysis including species with "marginal" suitability according to the IUCN classification alongside the "suitable" habitat. This inclusion resulted in minimal changes in the resulting patterns of projected species richness change (Fig. S2.10). But despite this little sensitivity of the results towards our habitat suitability assumptions, it is important to note that our analysis includes only four land use categories, which is a crude summary of 104 categories that are available in the IUCN Habitat Classification Scheme. The summary of primary forested and secondary forested land further misses reforestation and afforestation activities. This could potentially confound our results, as it assumes that a species that has lost its primary forest can simply find habitat in a secondary forest. Although evidence from the Amazon shows that at least some species groups are not faring well in secondary forests or plantations (Barlow et al., 2007). Furthermore, non-forested land including for example, both savannas and wetlands are harboring very specific species closely tied to their habitats, which in our study are not separated. The decision described above, to combine secondary and primary forest due to their potential complementarity might also present disadvantages, as it does not fully account for species that are closely tied to primary forest habitat. Also, we lack “urban” as a land use category, which is an important habitat for many bird species (Ortega-Álvarez & MacGregor-Fors, 2009). This is especially relevant to our study since more than half of the species considered in this study are birds. Going forward, it would thus be important to include the impacts of urban areas and urbanization in a combined climate and land use change study. However, integrating urban areas into such studies requires specific information about species for which “urban” areas serve as suitable habitats – information currently not part of the IUCN habitat classification scheme. But a study by Simkin et al. (2022) highlights the rapid urbanization expected in biodiversity-rich regions, including sub-Saharan Africa, South America, Mesoamerica, and Southeast Asia and underscores the urgent need to consider urban land in conservation strategies. Despite these simplifications we assume our categories to be constructive for a global analysis, which is key to understanding and identifying global biodiversity patterns. An important area for future discussion is the combined effects of climate and land use change on biodiversity. While this study investigates the separate and combined impacts of these two drivers, it is crucial to acknowledge that they often interact synergistically, potentially leading to even greater biodiversity loss than the sum of their individual effects. Additionally, this analysis focuses on just two of many anthropogenic drivers (Jaureguiberry et al., 2022). As Rillig et al., (2019) highlight, including more factors like pollution, invasive species, and habitat fragmentation can significantly alter the projected outcomes. A broader consideration of these combined and interacting pressures will provide a more realistic picture of future biodiversity change.

Besides the importance of climate and land use change impacts on species ranges as well as the significance of the choice of scenarios and their underlying narratives, we have also quantified the uncertainty from the set of two SDMs (GAM and GBM) and four GCMs (MIROC5, GFDL-ESM2M, HadGEM2-ES, and IPSL-CM5A-LR) used in this study. However, we could not assess the uncertainty from the land use change projections as each scenario is based on one IAM. Future studies should focus on including a wider range of IAMs especially since we have shown that the contribution from land use change is substantial and tied to climate change impacts. Additionally, opportunities for further improvement and refinement regarding the use of SDMs need to be recognized. First, the SDMs were run using expert range maps from IUCN (IUCN, 2023) and Birdlife International and Nature Serve (Birdlife International, 2015). The extent of occurrence expert range maps tend to overestimate the actual species distribution (Piirainen et al., 2023) and can be imprecise or incomplete (IUCN, 2023). Second, only species are included in the study that could properly be modeled by SDMs, species with a range smaller than ten grid cells were excluded from the SDM analysis as otherwise, the combination of few occurrences and many predictor variables can easily lead to model overfitting (Breiner et al., 2015; Hof et al., 2018; Platts et al., 2014). Consequently, many narrow-ranging species that are most threatened to go extinct are disregarded from our study. We recognize that this method may be unsuitable to draw conclusions about the impacts of climate and land use change on individual species. Still the method does allow inferring general patterns across a wide array of species.

Overall, we have shown that species richness losses predominate in terms of affected global land area for all scenarios and taxa under the combined effect of climate and land use change. This underlines the importance of climate mitigation efforts to curb the rise in global mean temperature. Furthermore, when we recalculate the loss in species richness to reflect land use change specifically, we found a greater projected loss under SSP4-RCP6.0 scenario compared to SSP1-RCP2.6 for all three taxonomic groups. Thus, land use policies will have a key role in fighting global biodiversity loss, especially in lower latitudes. Conservation efforts should therefore account for both drivers, climate and land use change, according to their respective impact. Finally, the regional differences shown in this study highlight the crucial need for region-specific conservation strategies.

2.5 Acknowledgments

Calculations were performed on UBELIX (https://www.id.unibe.ch/hpc), the HPC cluster at the University of Bern.

Competing interests: The authors declare that they have no competing interests.

Data and materials availability: The data generated and analyzed during the current study are available from the corresponding author. The data underlying the main analysis and figures are uploaded to Zenodo and are available from https://doi.org/10.5281/zenodo.11119306. All code used in this study is available from https://doi.org/10.5281/zenodo.14093900.

2.6 References

Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species-climate impact models under climate change. *Global Change Biology*, *11*(9), 1504–1513. https://doi.org/10.1111/J.1365-2486.2005.01000.X

Baker, D. J., Hartley, A. J., Burgess, N. D., Butchart, S. H. M., Carr, J. A., Smith, R. J., Belle, E., & Willis, S. G. (2015). Assessing climate change impacts for vertebrate fauna across the West African protected area network using regionally appropriate climate projections. *Diversity and Distributions*, *21*(9), 991–1003. https://doi.org/10.1111/ddi.12337

Barlow, J., Gardner, T. A., Araujo, I. S., Ávila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., … Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences*, *104*(47), 18555–18560. https://doi.org/10.1073/pnas.0703333104

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Beyer, R. M., & Manica, A. (2020). Historical and projected future range sizes of the world's mammals, birds, and amphibians. *Nature Communications*, *11*(1), Article 1. https://doi.org/10.1038/s41467-020-19455-9

Biber, M. F., Voskamp, A., & Hof, C. (2023). Potential effects of future climate change on global reptile distributions and diversity. *Global Ecology and Biogeography*, *32*(4), 519–534. https://doi.org/10.1111/geb.13646

Birdlife International. (2015). *Birdlife International and NatureServe* (Version Bird Species Distribution Maps of the World, Version 5.0) [Dataset].

Breiner, F. T., Guisan, A., Bergamini, A., & Nobis, M. P. (2015). Overcoming limitations of modelling rare species by using ensembles of small models. *Methods in Ecology and Evolution*, *6*(10), 1210–1218. https://doi.org/10.1111/2041-210X.12403

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Carlson, C. J., Albery, G. F., Merow, C., Trisos, C. H., Zipfel, C. M., Eskew, E. A., Olival, K. J., Ross, N., & Bansal, S. (2022). Climate change increases cross-species viral transmission risk. *Nature 2022 607:7919*, *607*(7919), 555–562. https://doi.org/10.1038/s41586-022-04788-w

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Frieler, K., Lange, S., Piontek, F., Reyer, C. P. O., Schewe, J., Warszawski, L., Zhao, F., Chini, L., Denvil, S., Emanuel, K., Geiger, T., Halladay, K., Hurtt, G., Mengel, M., Murakami, D., Ostberg, S., Popp, A., Riva, R., Stevanovic, M., … Yamagata, Y. (2017). Assessing the impacts of 1.5ĝ€°C global warming—Simulation protocol of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP2b). *Geoscientific Model Development*, *10*(12), 4321–4345. https://doi.org/10.5194/gmd-10-4321-2017

Hof, C. (2021). Towards more integration of physiology, dispersal and land-use change to understand the responses of species to climate change. *Journal of Experimental Biology*, *224*. https://doi.org/10.1242/jeb.238352

Hof, C., Araújo, M. B., Jetz, W., & Rahbek, C. (2011). Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, *480*(7378), 516–519. https://doi.org/10.1038/nature10650

Hof, C., Voskamp, A., Biber, M. F., Böhning-Gaese, K., Engelhardt, E. K., Niamir, A., Willis, S. G., & Hickler, T. (2018). Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(52), 13294–13299. https://doi.org/10.1073/pnas.1807745115

Hurtt, G. C., Chini, L., Sahajpal, R., Frolking, S., Bodirsky, B. L., Calvin, K., Doelman, J. C., Fisk, J., Fujimori, S., Klein Goldewijk, K., Hasegawa, T., Havlik, P., Heinimann, A., Humpenöder, F., Jungclaus, J., Kaplan, J. O., Kennedy, J., Krisztin, T., Lawrence, D., … Zhang, X. (2020). Harmonization of global land use change and management for the period 850-2100 (LUH2) for CMIP6. *Geosci. Model Dev*, *13*, 5425–5464. https://doi.org/10.5194/gmd-13-5425-2020

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services. . S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A.*

Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages. Zenodo. https://doi.org/10.5281/zenodo.3553579

IUCN. (2023). *The IUCN Red List of Threatened Species. Available at https://www. Iucnredlist.org/resources/spatial-data-download* [Dataset]. https://www.iucnredlist.org/resources/spatial-data-download

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*(45), eabm9982. https://doi.org/10.1126/sciadv.abm9982

Jenkins, R. L. M., Warren, R. F., & Price, J. T. (2021). Addressing risks to biodiversity arising from a changing climate: The need for ecosystem restoration in the Tana River Basin, Kenya. *PLoS ONE*, *16*(July). https://doi.org/10.1371/journal.pone.0254879

Lange, S. (2016). *EartH2Observe, WFDEI and ERA-Interim data Merged and Bias-corrected for ISIMIP (EWEMBI). GFZ Data Services.* [Dataset]. https://doi.org/10.5880/pik.2016.004

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*(7826), 551–556. https://doi.org/10.1038/s41586-020-2705-y

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. https://doi.org/10.1111/ecog.00967

Mantyka-pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, *18*(4), 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x

Methorst, J., Böhning-Gaese, K., Khaliq, I., & Hof, C. (2017). A framework integrating physiology, dispersal and land-use to project species ranges under climate change. *Journal of Avian Biology*, *48*(12), 1532–1548. https://doi.org/10.1111/jav.01299

Meynard, C. N., & Quinn, J. F. (2007). Predicting species distributions: A critical comparison of the most common statistical models using artificial species. *Journal of Biogeography*, *34*(8), 1455–1469. https://doi.org/10.1111/j.1365-2699.2007.01720.x

Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881). https://doi.org/10.1098/rspb.2018.0792

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. *Nature Ecology & Evolution*, *4*(12), Article 12. https://doi.org/10.1038/s41559-020-01303-0

Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, *117*(3), 285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Ortega-Álvarez, R., & MacGregor-Fors, I. (2009). Living in the big city: Effects of urban land-use on bird community structure, diversity, and composition. *Landscape and Urban Planning*, *90*(3), 189–195. https://doi.org/10.1016/j.landurbplan.2008.11.003

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature 2003 421:6918*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*, *29*(4), 205–213. https://doi.org/10.1016/j.tree.2014.02.004

PBL. (2012). *Roads from Rio+20 Pathways to achieve global sustainability goals by 2050* (p. The Hague, The Netherlands.).

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214. https://doi.org/10.1126/science.aai9214

Pereira, H. M., Martins, I. S., Rosa, I. M. D., Kim, H., Leadley, P., Popp, A., van Vuuren, D. P., Hurtt, G., Quoss, L., Arneth, A., Baisero, D., Bakkenes, M., Chaplin-Kramer, R., Chini, L., Di Marco, M., Ferrier, S., Fujimori, S., Guerra, C. A., Harfoot, M., … Alkemade, R. (2024). Global trends and scenarios for terrestrial biodiversity and ecosystem services from 1900 to 2050. *Science*, *384*(6694), 458–465. https://doi.org/10.1126/science.adn3441

Piirainen, S., Lehikoinen, A., Husby, M., Kålås, J. A., Lindström, Å., & Ovaskainen, O. (2023). Species distributions models may predict accurately future distributions but poorly how distributions change: A critical perspective on model validation. *Diversity and Distributions*, *29*(5), 654–665. https://doi.org/10.1111/ddi.13687

Platts, P. J., Garcia, R. A., Hof, C., Foden, W., Hansen, L. A., Rahbek, C., & Burgess, N. D. (2014). Conservation implications of omitting narrow-ranging taxa from species distribution models, now and in the future. *Diversity and Distributions*, *20*(11), 1307–1320. https://doi.org/10.1111/ddi.12244

Popp, A., Calvin, K., Fujimori, S., Havlik, P., Humpenöder, F., Stehfest, E., Bodirsky, B. L., Dietrich, J. P., Doelmann, J. C., Gusti, M., Hasegawa, T., Kyle, P., Obersteiner, M., Tabeau, A., Takahashi, K., Valin, H., Waldhoff, S., Weindl, I., Wise, M., … Vuuren, D. P. van. (2017). Land-use futures in the shared socio-economic pathways. *Global Environmental Change*, *42*, 331–345. https://doi.org/10.1016/j.gloenvcha.2016.10.002

Powers, R. P., & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change 2019 9:4*, *9*(4), 323–329. https://doi.org/10.1038/s41558-019-0406-z

Ramalho, Q., Vale, M. M., Manes, S., Diniz, P., Malecha, A., & Prevedello, J. A. (2023). Evidence of stronger range shift response to ongoing climate change by ectotherms and high-latitude species. *Biological Conservation*, *279*, 109911. https://doi.org/10.1016/j.biocon.2023.109911

Rillig, M. C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C. A., Buchert, S., Wulf, A., Iwasaki, A., Roy, J., & Yang, G. (2019). The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science*, *366*(6467), 886–890. https://doi.org/10.1126/science.aay2832

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., & Imeson, A. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, *453*(7193), 353–357. https://doi.org/10.1038/nature06937

Rozendaal, D. M. A., Bongers, F., Aide, T. M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J. M., Bentos, T. V., Brancalion, P. H. S., Cabral, G. A. L., Calvo-Rodriguez, S., Chave, J., César, R. G., Chazdon, R. L., Condit, R., Dallinga, J. S., de Almeida-Cortez, J. S., de Jong, B., de Oliveira, A., … Poorter, L. (2019). Biodiversity recovery of Neotropical secondary forests. *Science Advances*, *5*(3), eaau3114. https://doi.org/10.1126/sciadv.aau3114

Sala, O. E., Stuart, F., Iii, C., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, *287*, 1770–1774.

Schwarzmueller, F., & Kastner, T. (2022). Agricultural trade and its impacts on cropland use and the global loss of species habitat. *Sustainability Science*, *17*(6), 2363–2377. https://doi.org/10.1007/s11625-022-01138-7

Simkin, R. D., Seto, K. C., McDonald, R. I., & Jetz, W. (2022). Biodiversity impacts and conservation implications of urban land expansion projected to 2050. *Proceedings of the National Academy of Sciences*, *119*(12), e2117297119. https://doi.org/10.1073/pnas.2117297119

Stehfest, E., van Vuuren, D., Kram, T., Bouwman, L., Alkemade, Bakkenes, M., Bouwman, A., den Elzen, M., Janse, J., Lucas, P., van Minnen, J., & Gerdien Prins, A. (2014). *Integrated Assessment of Global Environmental Change with IMAGE 3.0—Model description and policy applications* (p. 370) [Text]. https://www.pbl.nl/en/publications/integrated-assessment-of-global-environmental-change-with-IMAGE-3.0

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, *10*(1). https://doi.org/10.1038/s41467-019-09519-w

van Vuuren, D. P., Stehfest, E., Gernaat, D. E. H. J., Doelman, J. C., van den Berg, M., Harmsen, M., de Boer, H. S., Bouwman, L. F., Daioglou, V., Edelenbosch, O. Y., Girod, B., Kram, T., Lassaletta, L., Lucas, P. L., van Meijl, H., Müller, C., van Ruijven, B. J., van der Sluis, S., & Tabeau, A. (2017). Energy, land-use and greenhouse gas emissions trajectories under a green growth paradigm. *Global Environmental Change*, *42*, 237–250. https://doi.org/10.1016/j.gloenvcha.2016.05.008

Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S. H. M., Joppa, L., Alkemade, R., Di Marco, M., Santini, L., Hoffmann, M., Maiorano, L., Pressey, R. L., Arponen, A., Boitani, L., Reside, A. E., van Vuuren, D. P., & Rondinini, C. (2016). Projecting Global Biodiversity Indicators under Future Development Scenarios. *Conservation Letters*, *9*(1), 5–13. https://doi.org/10.1111/conl.12159

Warren, R., Price, J., VanDerWal, J., Cornelius, S., & Sohl, H. (2018). The implications of the United Nations Paris Agreement on climate change for globally significant biodiversity areas. *Climatic Change*, *147*(3–4). https://doi.org/10.1007/s10584-018-2158-6

Warren, R., Vanderwal, J., Price, J., Welbergen, J. A., Atkinson, I., Ramirez-Villegas, J., Osborn, T. J., Jarvis, A., Shoo, L. P., Williams, S. E., & Lowe, J. (2013). Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, *3*(7), 678–682. https://doi.org/10.1038/nclimate1887

Winkler, K., Fuchs, R., Rounsevell, M., & Herold, M. (2021). Global land use changes are four times greater than previously estimated. *Nature Communications*, *12*(1), 2501. https://doi.org/10.1038/s41467-021-22702-2

Wise, M., Calvin, K., Kyle, P., Luckow, P., & Edmonds, J. (2014). Economic and physical modeling of land use in GCAM 3.0 and an application to agricultural productivity, land, and terrestrial carbon. *Climate Change Economics*, *05*, 1450003. https://doi.org/10.1142/S2010007814500031

2.7 Supplementary materials

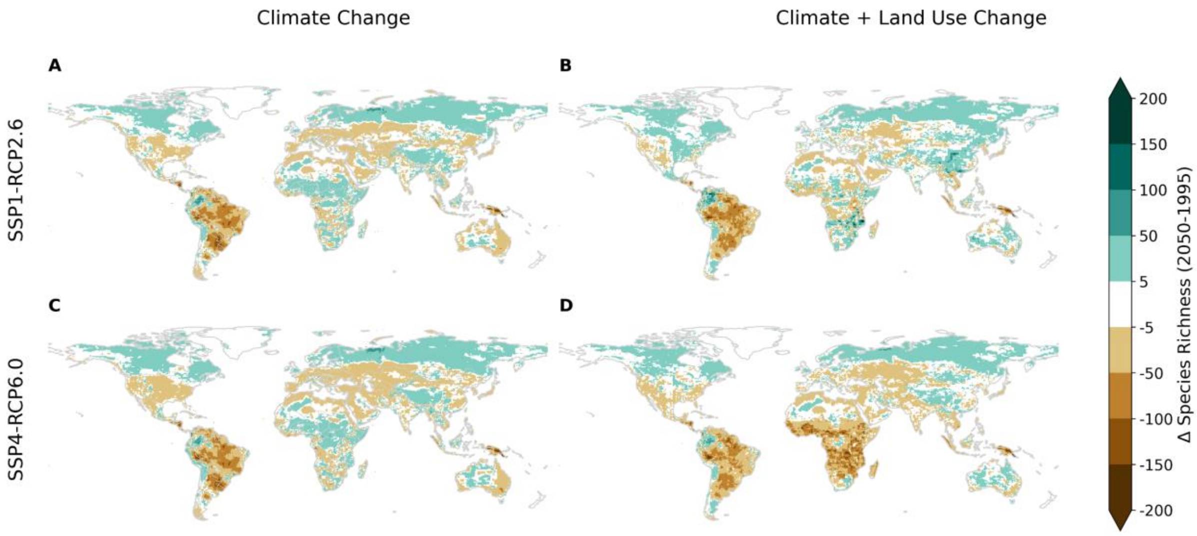

Fig. S2.1 Projected species richness for the year 2050 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future and climate and land use change with present and future land use data respectively. Results are shown for SSP1-RCP2.6 and SSP4-RCP6.0. Species richness is calculated as the summed probabilities of occurrence over all species of the taxa amphibians, birds, and mammals. The mean over all GCM and SDM combinations is shown here.

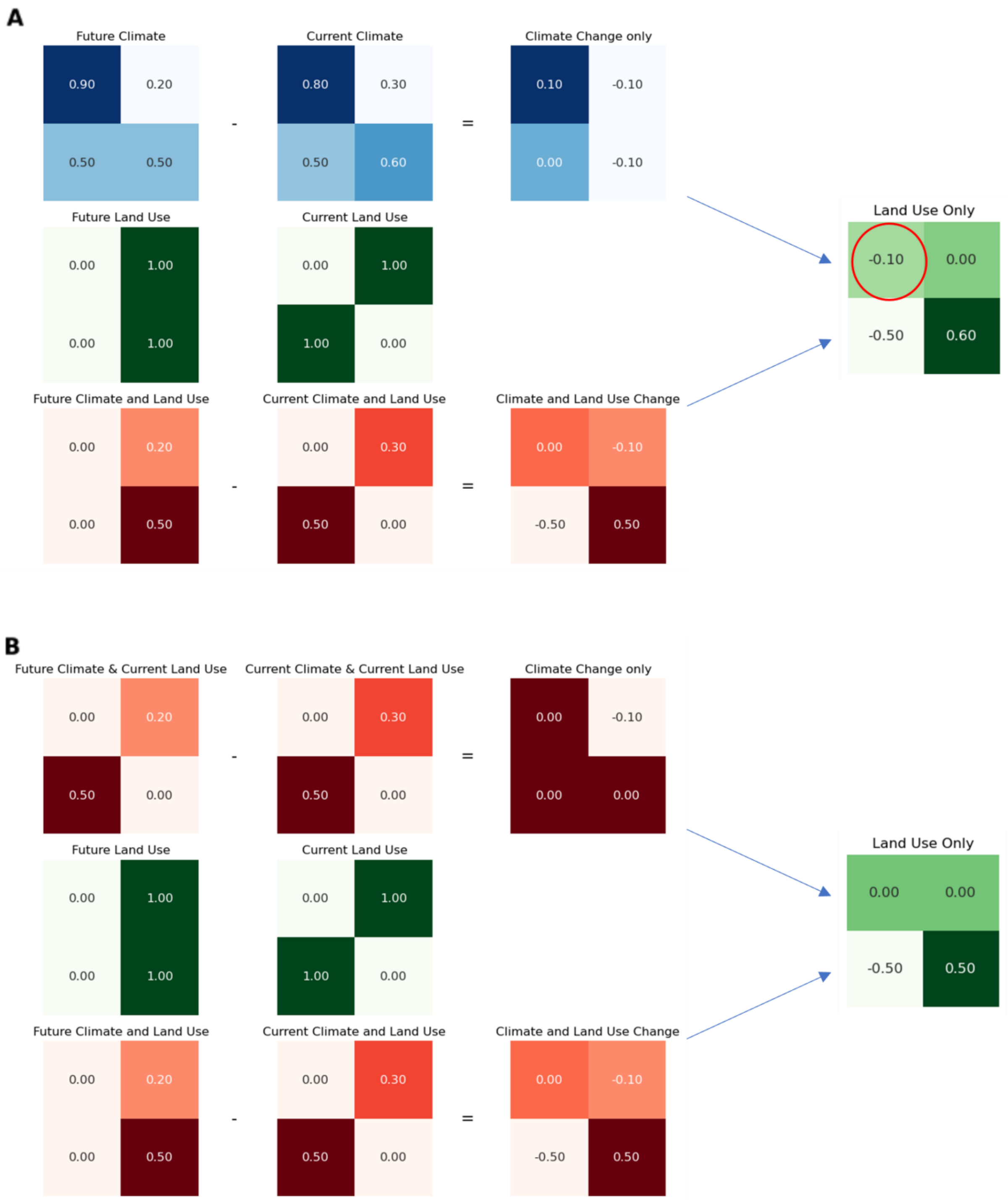

Fig. S2.2 Schematic overview of the different methodological steps for the calculation of the land use residual based on the initial method calculating the land use-only change as a residual directly from the probabilities of occurrences (i.e. the SDM output unfiltered) (A) and in this study used method, where climate change impact is filtered by the 1995 land use as a baseline and then climate- only is calculated as the residual of the future and present with constant land use change (B).

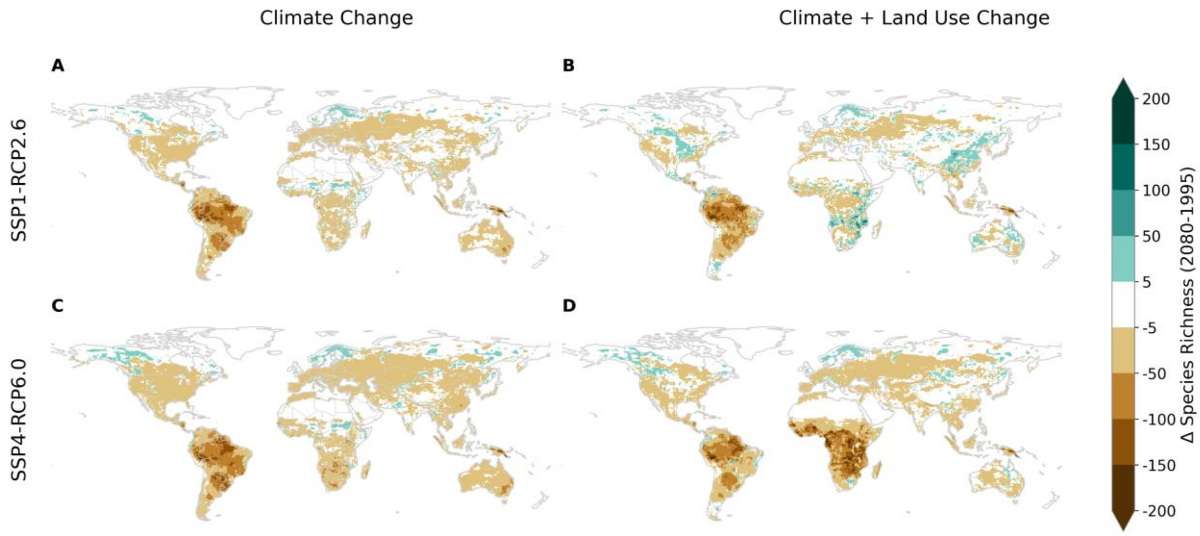

Fig. S2.3 Projected species richness for the year 2080 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future and climate and land use change with present and future land use data respectively for a no dispersal assumption. Results are shown for SSP1-RCP2.6 and SSP4-RCP6.0. Species richness is calculated as the summed probabilities of occurrence over all species of the taxa amphibians. The mean over all GCM and SDM combinations is shown here.

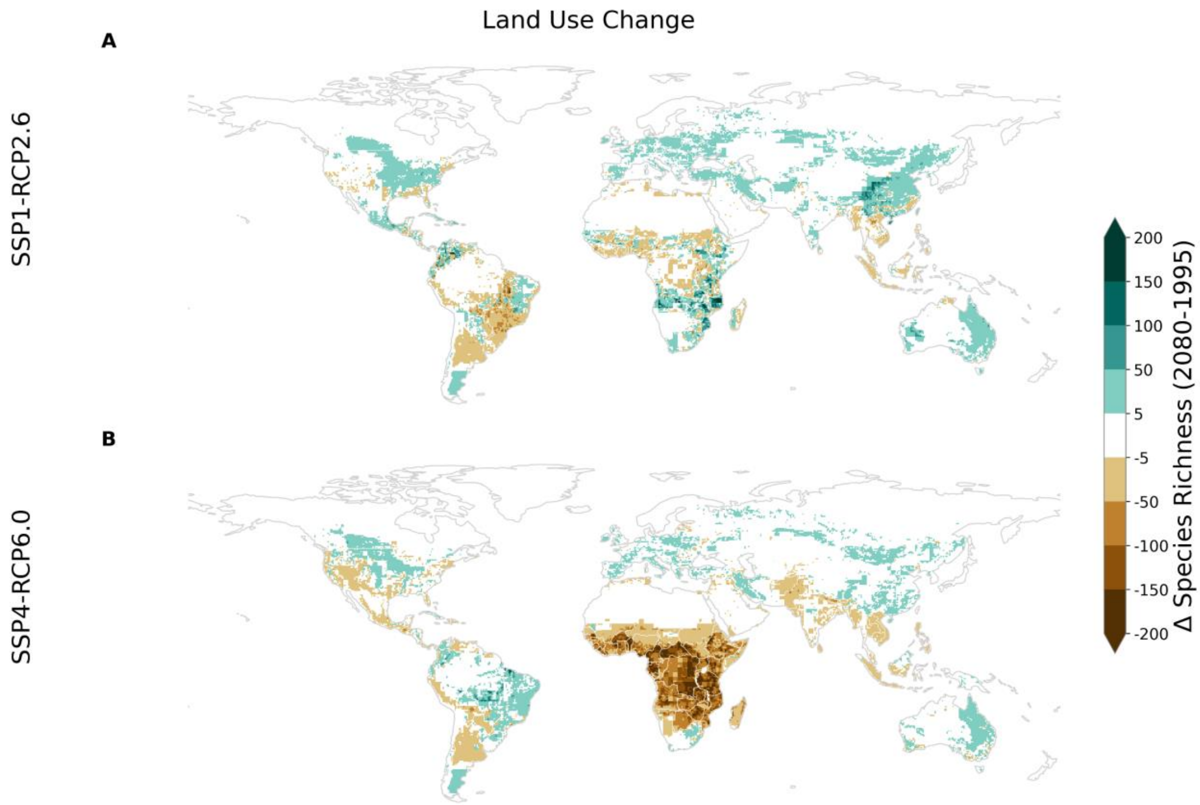

Fig. S2.4 Projected species richness for the year 2080 compared to 1995 for land use change only. Land use change is calculated as the residual from climate and land use change impact combined and climate change only.

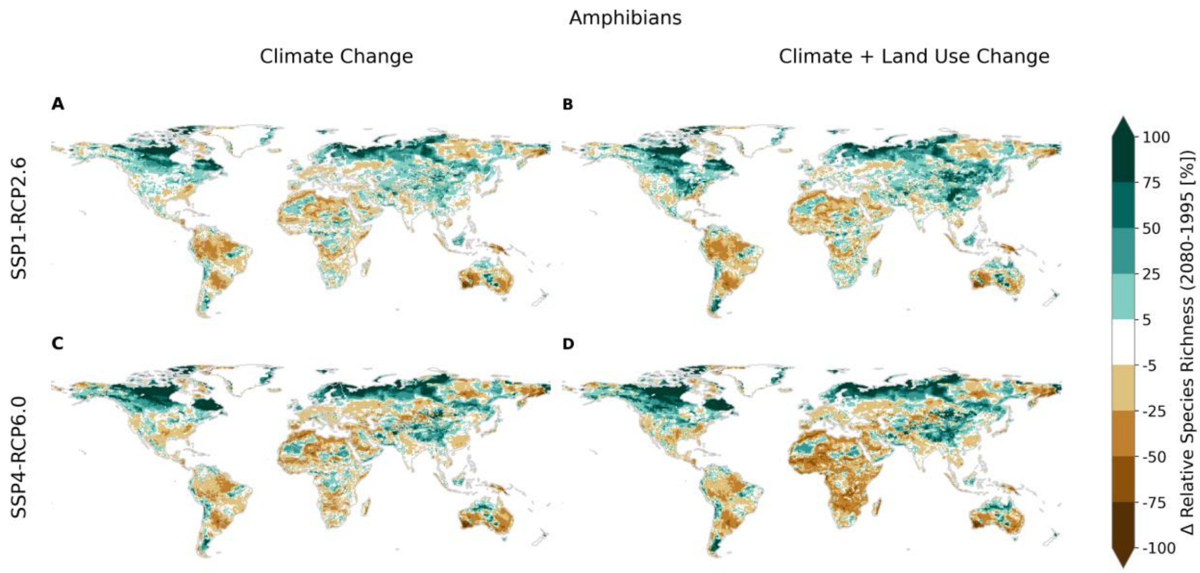

Fig. S2.5 Projected species richness for the year 2080 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future and climate and land use change with present and future land use data respectively. Results are shown for SSP1-RCP2.6 and SSP4-RCP6.0. Species richness is calculated as the summed probabilities of occurrence over all species of the taxa amphibians. The mean over all GCM and SDM combinations is shown here.

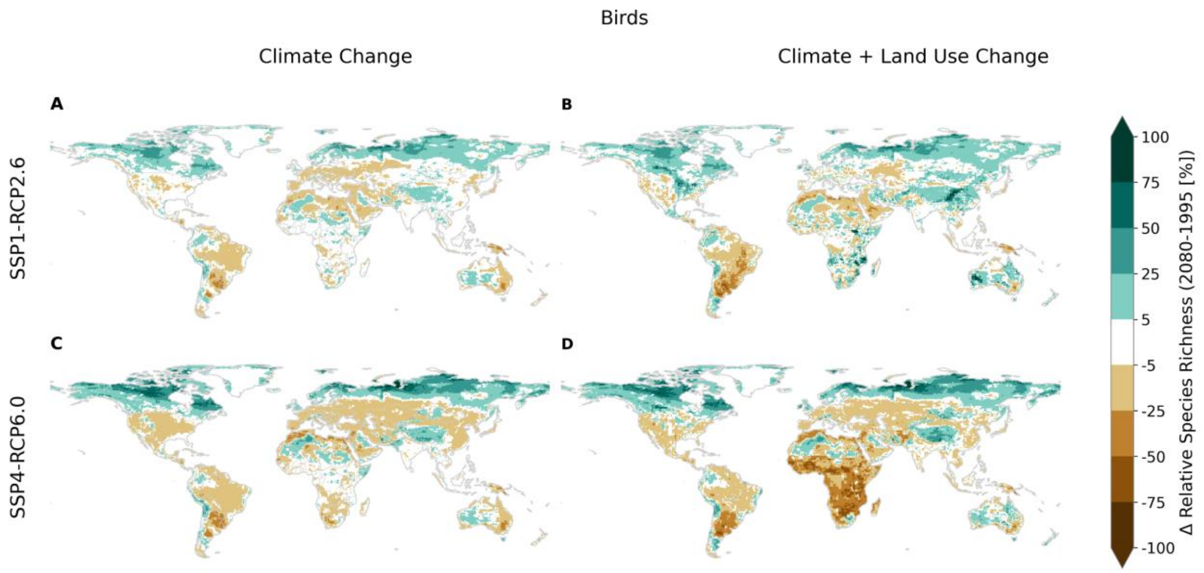

Fig. S2.6 Projected species richness for the year 2080 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future and climate and land use change with present and future land use data respectively. Results are shown for SSP1-RCP2.6 and SSP4-RCP6.0. Species richness is calculated as the summed probabilities of occurrence over all species of the taxa birds. The mean over all GCM and SDM combinations is shown here.

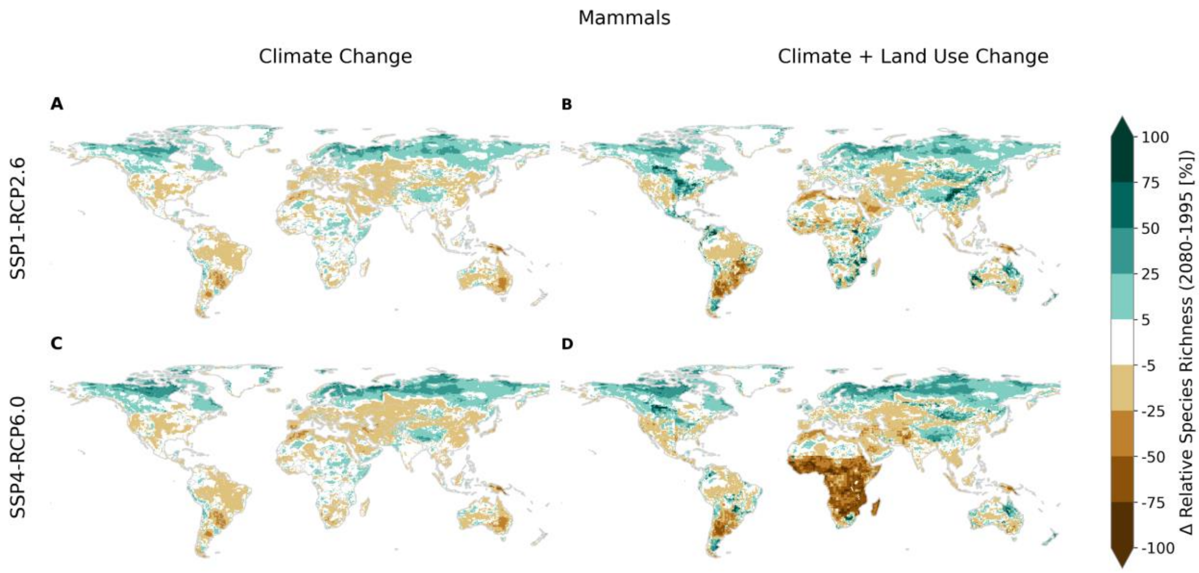

Fig. S2.7 Projected species richness for the year 2080 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future and climate and land use change with present and future land use data respectively. Results are shown for SSP1-RCP2.6 and SSP4-RCP6.0. Species richness is calculated as the summed probabilities of occurrence over all species of the taxa mammals. The mean over all GCM and SDM combinations is shown here.

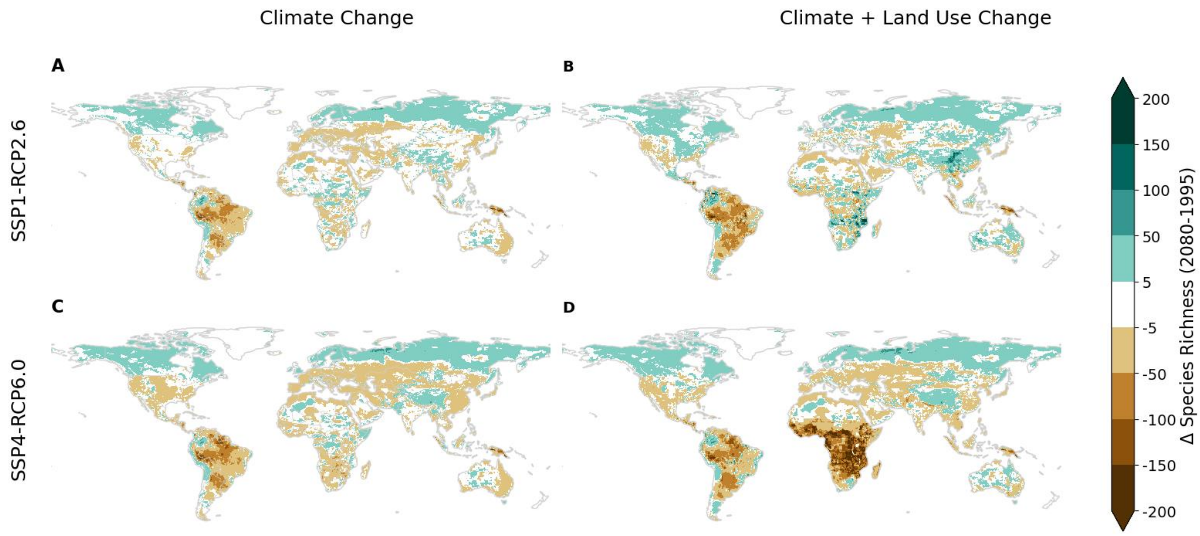

Fig. S2.8 Projected absolute species richness for the year 2080 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future and climate and land use change with present and future land use data respectively. Results are shown for SSP1-RCP2.6 and SSP4-RCP6.0. Species richness is calculated as the summed probabilities of occurrence over all species of the taxa amphibians, birds, and mammals. The mean over all GCM and SDM combinations is shown here.

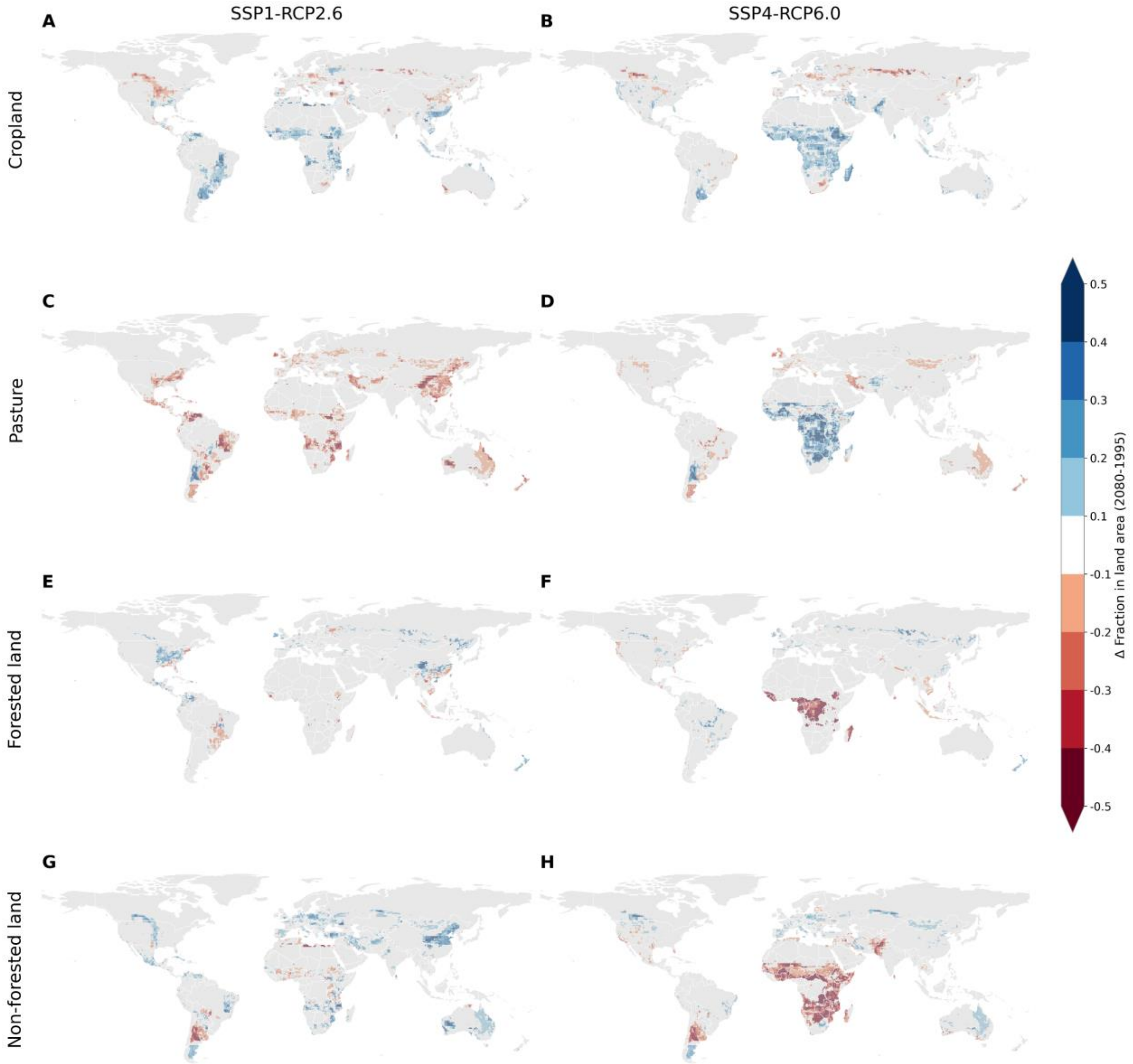

Fig. S2.9 Projected change in land use category as fraction per grid cell for 2080 compared to 1995 based on LUH2.

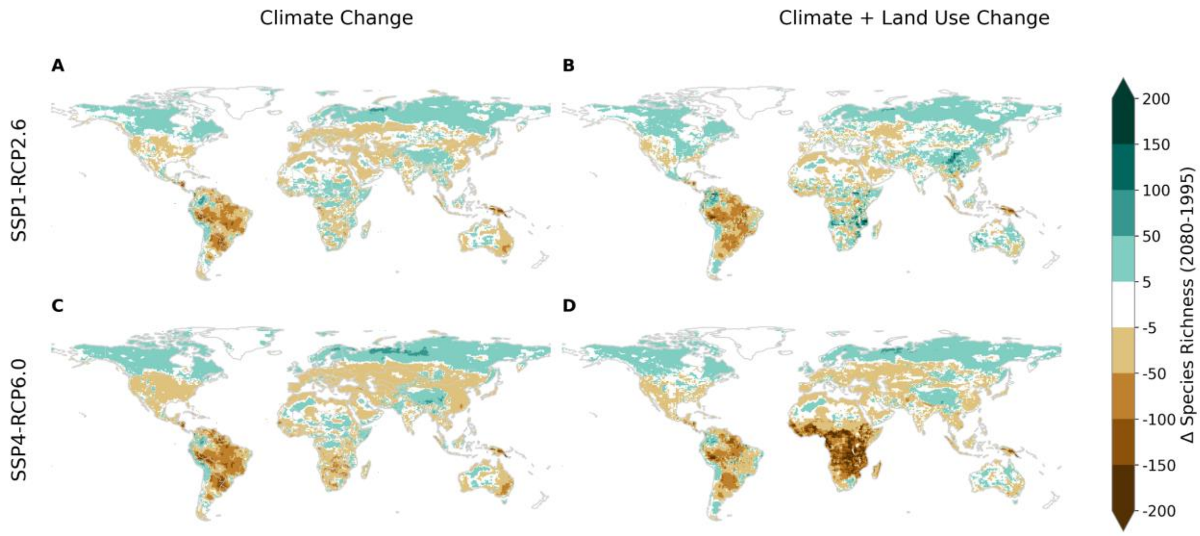

Fig. S2.10 Projected species richness for the year 2080 compared to 1995 under climate change only with the 1995 land use as a baseline for the present and future and climate and land use change with present and future land use data respectively. All habitats labeled as "suitable" and "marginal" by the IUCN Habitat Classification Scheme are included. Results are shown for SSP1-RCP2.6 and SSP4-RCP6.0. Species richness is calculated as the summed probabilities of occurrence over all species of the taxa amphibians. The mean over all GCM and SDM combinations is shown here.

Table S2.1 Regions used in this study and their connection to the IPBES subregions (IPBES, 2019).

Regions in this study	**IPBES subregions**
Caribbean & Mesoamerica	Caribbean
	Mesoamerica
West, Central, East & South Africa	Central Africa
	East Africa and adjacent islands
	Southern Africa
	West Africa
Central and Western Europe	Central and Western Europe
Central, North-East & South Asia	Central Asia
	Nort-East Asia
	South Asia
Eastern Europe	Eastern Europe
North Africa & Western Asia	North Africa
	Western Asia
North America	North America
Oceania	Oceania
South America	South America
South-East Asia	South-East Asia

Chapter 3

The roles of climate mitigation, sustainable land use and area-based conservation in curbing future biodiversity loss

Chantal Hari,[1,2,3] Matthias F. Biber,[4] Jonas Geldmann,[5] Thomas Hickler,[6,7] Pablo J. Negret,[1,8] Christopher P.O. Reyer,[9] Alke Voskamp,[6] Markus Fischer,[3,10] Édouard L. Davin,[1,2,3]

[1] Wyss Academy for Nature at the University of Bern, University of Bern, Bern, Switzerland
[2] Climate and Environmental Physics, Physics Institute, University of Bern, Bern, Switzerland
[3] Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland
[4] Terrestrial Zoology, Senckenberg Research Institute and Nature Museum, Frankfurt am Main, Germany
[5] Center for Macroecology, Evolution and Climate, Globe Institute, University of Copenhagen, Denmark
[6] Senckenberg Biodiversity and Climate Research Center (SBiK-F), Frankfurt am Main, Germany
[7] Department of Physical Geography at Goethe University, Altenhöferallee 1, 60438 Frankfurt/Main, Germany
[8] Hawkesbury Institute for the Environment, Western Sydney University, Australia
[9] Potsdam Institute for Climate Impact Research, Member of the Leibniz Association, Potsdam, Germany
[10] Institute of Plant Sciences, Plant Ecology, University of Bern, Bern, Switzerland

This chapter is in preparation for submission to a peer-reviewed journal.

Abstract

Biodiversity loss is a pressing global challenge. Protected Areas (PAs) are recognized as a crucial measure to curb species and ecosystem declines, yet their long-term ecological effectiveness amid future climate and land use changes remains uncertain. Here, we assess future biodiversity changes under different climate, land use, and PA expansion scenarios for ~14,000 terrestrial vertebrates. Three PA scenarios (no explicit PA, current 17% coverage, and a 30% target) are investigated alongside two Shared Socioeconomic Pathway (SSP) and Representative Concentration Pathway (RCP) combinations; the “sustainability” (SSP1-RCP2.6) and the “inequality” scenario (SSP4-RCP6.0).

The results show that sustainable land use is the biggest lever in preventing future biodiversity decline, with a projected avoided species richness loss of 7.9-8.6% by 2080, exceeding the contribution of PA expansion. PAs provide an additional but smaller contribution to avoided species richness loss, particularly under the “inequality” scenario, showing the need for PA expansion under unsustainable climate and land use policies. Birds and mammals benefit most from PA expansion. While expanding PAs supports biodiversity, integrating them with broader climate and land use policies is crucial.

3.1 Introduction

Biodiversity loss has been identified as a primary threat to economic prosperity and in many places human wellbeing (IPBES, 2019). Yet, ongoing climate and land use change profoundly affect the integrity of ecosystems worldwide (Leclère et al., 2020; McElwee et al., 2024; Newbold, 2018; Powers & Jetz, 2019; Xu et al., 2022). Conservation actions are urgently needed to halt the decline in biodiversity and safeguard essential ecosystem services. Protected areas (PAs) have been identified as a crucial measure to curb biodiversity loss and maintain ecosystem services (Butchart et al., 2012; Maxwell et al., 2020; Waldron et al., 2020; Watson et al., 2014). By 2025, around 17% of the global terrestrial area was protected (UNEP-WCMC and IUCN, 2025). However, there is a broad consensus that current land and sea protection levels fall short of meeting international targets aimed at reducing biodiversity decline (Butchart et al., 2015; Coad et al., 2019; Langhammer et al., 2024; Venter et al., 2014; Waldron et al., 2020). Area-based conservation targets, such as target 3 of the Kunming-Montreal Global Biodiversity Framework (GBF), which aims to protect 30% of terrestrial and marine ecosystems globally by 2030 (CBD, 2022), guide global and national conservation efforts.

Recent studies have proposed ways to prioritize PA expansion to reach the 30% GBF target by optimizing the achievement of several biodiversity and sustainability indicators (e.g., Allan et al., 2022; Eckert et al., 2023; Jung et al., 2021). For example, Jung et al. (2021) proposed a global prioritization framework that identifies areas critical for species conservation accounting for key ecosystem services, including carbon storage and water quality regulation. This species conservation criterion aims to conserve a minimum of species' habitat necessary to ensure species qualify for the 'Least Concern' conservation status following the International Union for Conservation of Nature (IUCN) Red List criteria. However, the combined roles of future climate and land use changes on biodiversity have not been covered by these studies.

Despite the importance of sustaining and expanding protection globally to safeguard biodiversity, the effectiveness of any PA expansion strategy should be assessed considering future environmental shifts, such as climate and land use change. For example, Asamoah et al. (2021) and Mi et al. (2023) emphasized the importance of incorporating climate and land use changes into global conservation priorities to address habitat shifts and biodiversity risks. Similarly, Montesino Pouzols et al. (2014) found that land use change threatens the potential effectiveness of PA expansion. Dobrowski et al. (2021) and Elsen et al. (2020) highlighted the value of climate refugia and resilient landscapes with enhanced connectivity to support species conservation under changing environmental conditions. On the other hand, there are studies that have assessed the combined impacts of future land use and climate change on global biodiversity (Hari et al., 2024; Hof et al., 2018; Newbold, 2018; Newbold et al., 2020; Pereira et al., 2024), but there is still a knowledge gap concerning how the combined effect of climate and land use changes will influence the outcomes of PA expansion strategies, such as the 30% target.

To address this gap, we generated global projections of terrestrial vertebrate diversity accounting for the impacts of future climate change and land use change, under different scenarios of PA expansion. For this analysis we used species distribution model (SDM) output for 15496 species of amphibians, birds, and mammals from Hof et al. (2018). Additionally, we used land use scenarios from the Land Use Harmonization Project 2 (LUH2; Hurtt et al., 2020), selected for its global coverage and availability of different scenarios, integrating them into the SDM projections using a filtering approach from Hari et al. (2024). We assessed the impacts on future species richness for the three taxa under two contrasting Shared Socioeconomic Pathways (SSPs) coupled with Representative Concentration Pathways (RCPs): The SSP-RCPs represent coupled climate and socio-economic changes according to different scenario storylines and assumption, namely, a "sustainability" scenario (SSP1-RCP2.6) and an "inequality" scenario (SSP4-RCP6.0). SSP1-RCP2.6 is characterized by a world focusing on sustainable development and green technologies and strong climate action which results in lower climate warming. SSP4-RCP6.0 is characterized by a world suffering from strong inequalities between countries and groups and stronger climate warming (van Vuuren et al., 2017). We then compared three PA scenarios, which were overlaid to the LUH2 scenarios: (1) a “No explicit PA” scenario, where PAs are not explicitly represented meaning that future land use follows the LUH2 scenarios; (2) a current PA scenario (hereafter 17%-PA), based on the existing PAs documented in the World Database on Protected Areas (WDPA; UNEP-WCMC and IUCN, 2023); and (3) a 30% global PA expansion scenario (30%-PA) based on Jung et al. (2021). For the latter two scenarios, land use change also follows LUH2 expect within the PAs, where adjustments are made to represent protection measures (see methods).

Additionally, we compared the ecological effectiveness of the PA scenarios with climate and land use mitigation strategies under different SSP-RCP scenarios, focusing on the projected loss of species richness. We also assessed how limited management effectiveness influences these outcomes. This integrative approach provides a comprehensive framework for evaluating the potential of PA expansion strategies to mitigate biodiversity loss by reducing land use change that negatively impacts species habitats under future global change.

3.2 Results

3.2.1 Spatial distribution of changes in future species richness

Without accounting for PA expansion ("No explicit PA" scenario), the combined effect of climate and land use change is projected to lead to a loss of species richness, particularly in tropical and equatorial regions, by 2080 compared to 1995 (Fig. 3.1A & B). Conversely, any level of area-based conservation, as represented by the PA expansion scenarios (17%-PA and 30%-PA scenarios, illustrated in Fig. S3.1), is projected to result in an overall reduction in species richness loss. The main differences are projected to occur in tropical and equatorial regions under both the "inequality" (SSP4-RCP6.0) and "sustainability" (SSP1-RCP2.6) scenarios.

The region projected to experience the highest biodiversity loss under the "inequality" scenario (SSP4-RCP6.0) and the "No Explicit PA" scenario is sub-Saharan Africa, with an estimated loss of 34.5% in species richness by 2080 compared to 1995 (see Fig. 3.1A & B). In comparison, the 17%-PA scenario under the "inequality" scenario (SSP4-RCP6.0) is projected to avoid a loss of 6.3% in species richness in the same region. Overall, the greatest avoided species richness losses are projected in tropical and equatorial regions compared to the "No explicit PA" scenario for both the "inequality" (SSP4-RCP6.0) and "sustainability" (SSP1-RCP2.6) scenarios when considering the 17%-PA scenario (Fig. 3.1C & D). These results are further amplified under the 30%-PA scenario (Fig. 3.1E & F), with several other regions in the lower latitudes also showing projected avoided species richness loss compared to the "No explicit PA" scenario.

In South America, we project avoided species richness loss of 2.1% and 1.5% for the "inequality" (SSP4-RCP6.0) and the "sustainability" (SSP1-RCP2.6) scenarios, respectively, under the 17%-PA scenario compared to the "No explicit PA" scenario. These projected avoided species richness losses for both the 17%-PA and the 30%-PA scenarios, especially in tropical South America, can be attributed to an increase in forested land (Fig. S3.5, Fig. S3.6). Whereas the greater projected loss in species richness under the "No explicit PA" and the "inequality" scenario (SSP4-RCP6.0) is primarily attributed to reductions in both forested and non-forested land (Fig. S3.5, Fig. S3.6).

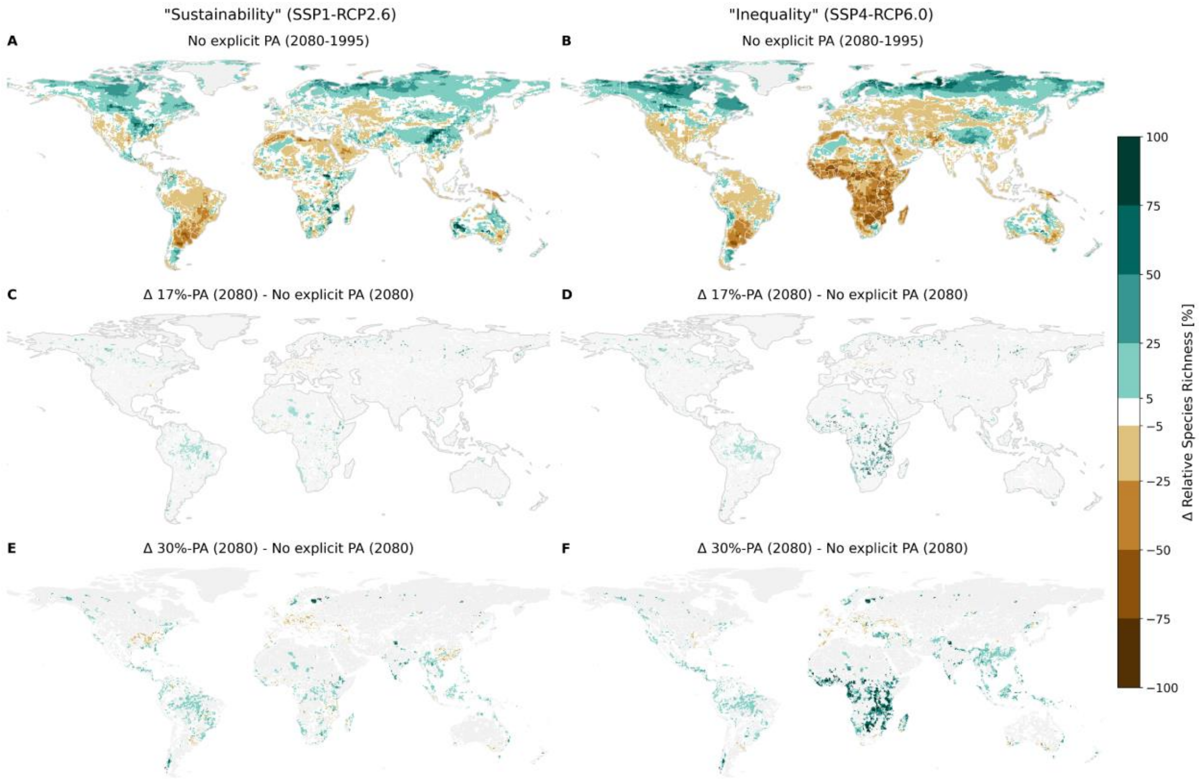

Fig. 3.1 Comparison of different PA scenarios for climate and land use change impact on future species richness under a limited dispersal assumption. *Projected species richness (probability of occurrence summed over all species and averaged over all four climate models and the two SDMs; see Methods) for 2080 relative to 1995 under climate and land use change for the "No explicit PA" scenario (A and B). Additionally, the results are shown for the relative difference between the future species richness with the scenario of the current PA network (17%-PA) compared with the "No explicit PA" scenario (C and D). The same is shown in the comparison between the 30%-PA scenario and "No explicit PA" scenario (E and F). The results are shown for the "sustainability" scenario (SSP1-RCP2.6; A, C, and E) and the "inequality" scenario (SSP4-RCP6.0; B, D, and F).*

3.2.2 Contributions of climate mitigation, sustainable land use, and PAs to avoid species richness loss

The role of climate mitigation, inferred by comparing RCP2.6 with RCP6.0 under present-day land use (see methods), is projected to prevent a global mean species richness loss of 0.85% by 2080, relative to 1995 (Fig. 3.2). Furthermore, adopting a sustainable land use pathway (SSP1 instead of SSP4) is projected to avoid 8.58% of global species richness loss over the same period (Fig. 3.2).

Under the "sustainability" scenario (SSP1-RCP2.6), the 17%-PA scenario is projected to avoid an additional 0.88% of species richness loss compared to the "No explicit PA" scenario, while the 30%-PA scenario results in 1.5% of additional avoided loss (Fig. 3.2). However, when accounting for PA management effectiveness, these values are reduced to 0.21% and 0.35%, respectively (Fig. S3.7). In contrast, under the "inequality" scenario (SSP4-RCP6.0), the avoided species richness loss is higher for both PA expansion scenarios, with 2.29% for 17%-PA and 4.45% for the 30%-PA. When considering limited management effectiveness, these reductions decrease to 1.05% and 0.54%, respectively (Fig. S3.7).

Notably, when climate change is not mitigated, and sustainable land use pathways are not followed (i.e., SSP4-RCP6.0 instead of SSP1-RCP2.6), the importance of conservation increases (Fig. 3.2). In that case, strong PA expansion (i.e. 30%-PA over 17%-PA) result in the greatest avoided species richness loss. Furthermore, the results highlight that a larger total area of global PA percentage enhances resilience to climate change and unsustainable land use change, as indicated by higher avoided species richness loss under the 30%-PA scenario compared to the 17%-PA scenario (Fig 3.2).

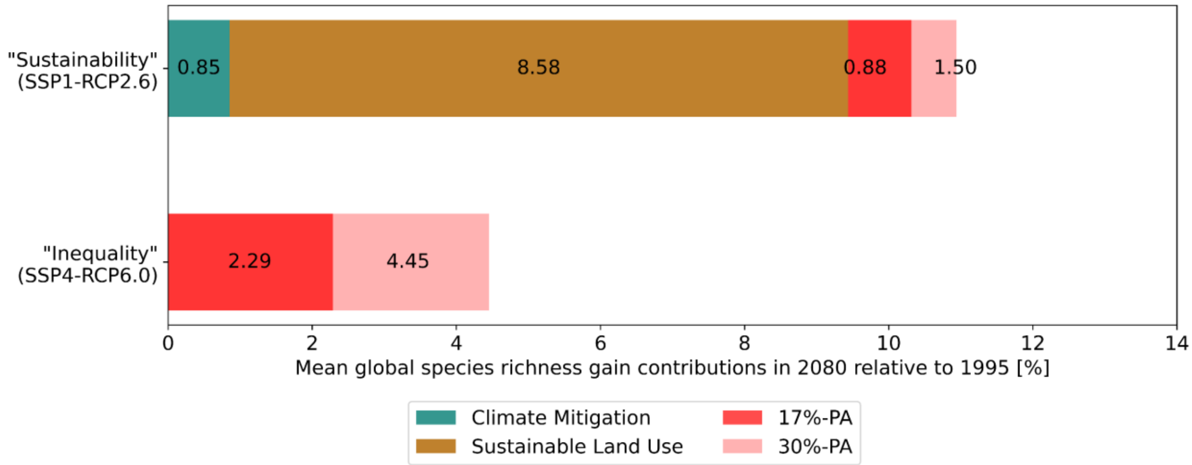

Fig. 3.2 Comparison of the global mean avoided species richness loss due to climate mitigation, sustainable land use, and area-based conservation efforts for the "sustainability" scenario (SSP1-RCP2.6) and the "inequality" scenario (SSP4-RCP6.0). The "sustainability" scenario (SSP1-RCP2.6) shows the cumulative effects of climate mitigation, land use pathways, and PA expansion on avoiding species richness loss compared to the "inequality" scenario (SSP4-RCP6.0). The bars represent the respective contributions of each factor in terms of global mean species richness in 2080 relative to 1995. The second row depicts the global mean avoided species richness loss solely through area-based conservation (17%-PA and 30%-PA scenario), as there are no climate mitigation or sustainable land use benefits under this scenario compared to the "sustainability" scenario (SSP1-RCP2.6).

3.2.3 Regional effects of PA effectiveness

Synergies and trade-offs in projected species richness depend on both the climate and land use (SSP-RCP) and the PA scenarios (Fig. 3.2). Under the "sustainability" scenario (SSP1-RCP2.6), the largest decrease in species richness loss relative to 1995 is projected to occur in South America ranging from -9.06% ± 0.65% (No explicit PA) to -6.89%±0.65% (30% PA; Fig. 3.3). Across all regions with projected losses compared to 1995 under the "No explicit PA" scenario, expanding the PAs consistently reduces species richness loss, and even leads to regional gains in species richness in South-East Asia, where a loss of -1.66%±0.23% under the "No explicit PA" scenarios converted to a gain of 1.68%±0.23% under the 30%-PA assumption (Fig. 3.3). However, there are exceptions, such as North Africa and Western Asia and Central and Western Europe, where the 17%-PA and the 30%-

PA scenario results minor changes only compared to the “No explicit PA” scenario. While the 30%-PA scenario generally outperforms the 17%-PA scenario in mitigating species richness loss, the 17%-PA scenario shows slightly higher species richness gains in specific regions, such as North America and Eastern Europe. However, these differences fall within the uncertainty range (Fig. 3.3).

Under the “inequality” scenario (SSP4-RCP6.0), 17%-PA consistently results in lower projected species richness loss or higher projected gains compared to the No explicit PA baseline. The 30%-PA scenario shows the same, yet even stronger, pattern, except for Eastern Europe where 17%-PA is projected to lead to a minor gain compared to 30%-PA. Notably, North America and Eastern Europe are the only regions projected to have a net gain in species richness under this SSP-RCP scenario (Fig. 3.3). The largest avoided losses are projected in West, Central, East and South Africa, where the 17%-PA scenario reduces species richness loss by up to 6.3%±0.7% compared to No explicit PA, and the 30%-PA scenario achieves an even greater reduction of up to 9.82%±0.23% (Fig. 3.3). These findings highlight the critical importance of PA expansion under the “inequality” scenario.

Insufficient financial investments in PA management undermine their ability to mitigate external pressures such as habitat loss, degradation, and other threats. When we incorporate this into our analysis, using data collated by Waldron et al. (2020; see methods), the benefits of PA expansion are reduced, particularly in West, Central, East & South Africa under the “inequality” scenario (SSP4-RCP6.0; Fig. 3.3). In this region under the “inequality” scenario (SSP4-RCP6.0), limited management effectiveness is projected to result in a decrease in species richness of 4.81%±0.7% under the 17%-PA scenario and 8.54%±0.7% under the 30%-PA scenario, compared to projections under full management effectiveness of the PAs, where no funding gap exists (Fig. 3.3). Similarly, in South-East Asia, the 30%-PA scenario under the “inequality” scenario (SSP4-RCP6.0) shifts from a projected gain in species richness to a loss of -2.64%±0.23% due to limited management effectiveness (Fig. 3.3).

While some regions like North America, South America, and Eastern Europe also show differences in species richness, the impact is relatively moderate compared to South-East Asia and sub-Saharan Africa (Fig. 3.3). For instance, North America shows a difference ranging from 0.4%±1.22% to 2.3%±1.22% across the scenarios, indicating less sensitivity to reduced management effectiveness in these regions (Fig. 3.3).

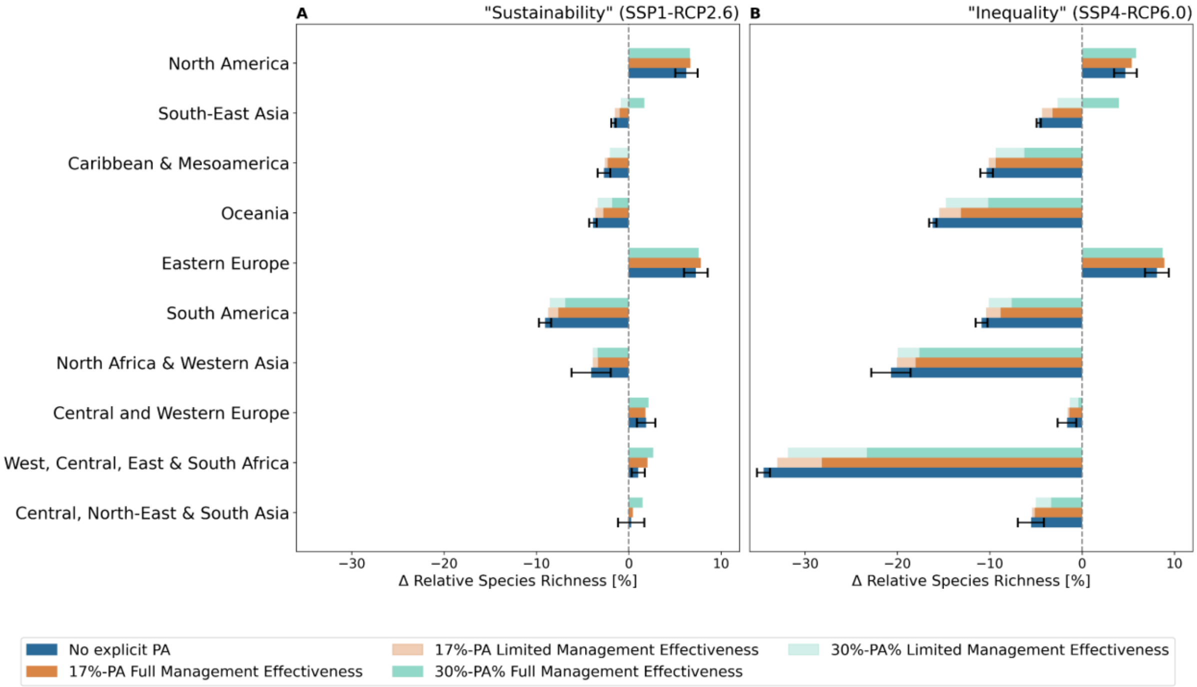

Fig. 3.3 Relative change in species richness from 1995 to 2080 per region. *Projected species richness for 2080 relative to 1995 per region (IPBES regions, see methods or supplementary) for No explicit PA,17%-PA, and 30%-PA scenario of PA expansion. The results are shown for the "sustainability" scenario (SSP1-RCP2.6) (A) and the "inequality" scenario (SSP4-RCP6.0) (B) for full effectiveness and limited effectiveness. The error bars indicate the standard deviation over all global climate models (GCMs) and SDMs.*

3.2.4 Taxon specific global change in species richness per PA scenario

On the taxonomic level, the overall change in global mean species richness highly varies and so do the effects of climate and land use change and PA expansion scenarios. For the "sustainability" scenario (SSP1-RCP2.6), birds and mammals showed relative gains in global species richness when PAs were included, with the magnitude of the gains increasing progressively from the 17%-PA scenario (1.65%±0.44% and 1.93%±0.23%, respectively) to the 30%-PA scenario (2.09%±0.44% and 2.67%±0.23%, respectively; Fig. 3.4A). For amphibians, however, there was no net gain in species richness even under this SSP-RCP scenario, but the magnitude of species richness loss decreased as the PA extent increased, from -6.26%±0.54% under the 17%-PA scenario to -5.76%±0.54% under the 30%-PA scenario (Fig. 3.4A).

Under the "inequality" scenario (SSP4-RCP6.0), species richness is projected to decline across all taxa, with PAs mitigating losses to varying extents. The No explicit PA scenario resulted in the most severe declines for all taxa, particularly amphibians, which experienced the largest losses. The 17%-PA scenario reduced losses moderately, while the 30% showed further reductions in species richness loss. For mammals, species richness losses were reduced by 2.6%, from −8.57%±0.27% under No explicit PA scenario to −5.95%±0.27% under the 17%-PA scenario, and by 5.1% to −3.53%±0.27% under the 30%-PA scenario (Fig. 3.4B). Similarly, for birds, losses were reduced by 1.9%, from

-6.82%±0.6% under No explicit PA to -4.87%±0.6% under the 17%-PA scenario, and by 3.6% to -3.2%±0.6% under the 30%-PA scenario (Fig. 3.4B). However, limited management effectiveness reduces the benefits of PAs in mitigating species richness losses under both climate and land use change scenarios (Fig. S3.8).

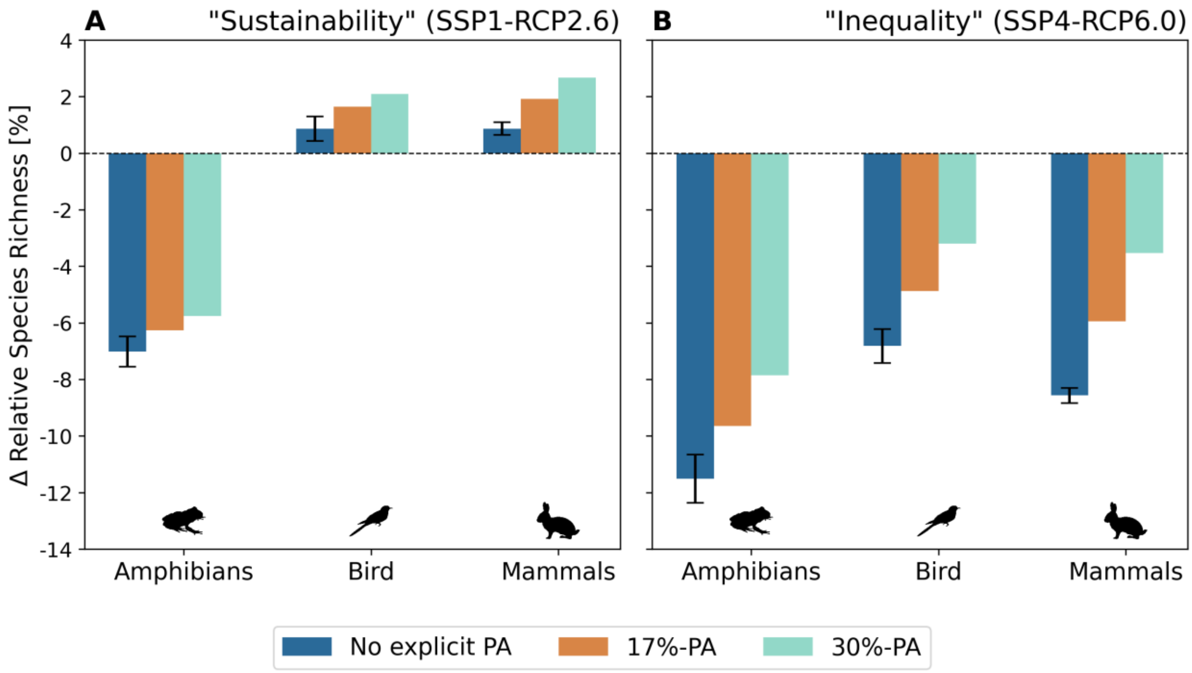

Fig. 3.4 Global species richness changes from 1995 to 2080 per taxon. *The results are shown for the three PA scenarios under full effectiveness SSP1-RCP2.6 (A) and SSP4-RCP6.0 (B). The error bars indicate the standard deviation over all GCMs and SDMs.*

3.3 Discussion and conclusions

Our findings highlight the importance of combining climate mitigation, sustainable land use, and PA expansion to maximize biodiversity conservation. The combination of a lower-emission scenario and a more sustainable land use pathway (SSP1-RCP2.6) results in higher avoided species richness loss than any of the PA scenarios alone due to avoided agricultural expansion. Under a “sustainability” scenario (SSP1-RCP2.6), climate mitigation prevents a global mean species richness loss of 0.85%, while sustainable land use avoids 8.58% of loss by 2080 compared to an “inequality” scenario (SSP4-RCP6.0), having a higher level of climate change and less sustainable land use practices. PA expansion to cover 30% of the global land area, provides additional benefits, reducing species richness losses, especially in tropical and equatorial regions. However, these benefits are diminished when accounting for limited management effectiveness. Taxonomic responses show that birds and mammals benefit most from PA expansion, while amphibians experience reduced losses but no net gains.

Our study introduces a novel framework that integrates multiple PA expansion scenarios with climate and land use pathways, offering new insights into the combined effects of these levers on biodiversity conservation. This approach demonstrates that under the “sustainability” scenario (SSP1-RCP2.6), species richness loss is notably lessened. Furthermore, under the “inequality” scenario (SSP4-RCP6.0), characterized by global inequality and higher emissions (Hurtt et al., 2020), the expansion of the PA network shows the highest avoided biodiversity loss, particularly in regions vulnerable to future species richness loss due to environmental changes. Our findings emphasize, that the strategic location of PAs is as important as the area covered (Visconti et al., 2019), particularly in equatorial and tropical regions where species richness is highest and projected losses are most severe (Asamoah et al., 2021; Geldmann, 2019; Gray et al., 2016). Moreover, we project that expanding PAs beyond their current extent (e.g., from the WDPA to the 30% PA scenario) will lead to reductions in species richness loss in the future, especially in biodiversity hotspots (Fig. 3.1, Fig. 3.3). This aligns with the findings of Leclère et al. (2020), who advocated an integrated strategy combining PA expansion, restoration, and sustainable management that could halt biodiversity decline by mid-century. Similarly, our results are in line with other studies that found that minimizing human-dominated land use leads to greater biodiversity protection (Asamoah et al., 2021; Gray et al., 2016) and supports the conclusion that limiting climate change is critical to conserving unique ecosystems (Martens et al., 2022).

Limited management effectiveness, as represented by the 23.6% funding availability (Waldron et al., 2020), substantially diminishes the benefits of PA expansion, as our results have shown, for example, under the “inequality” scenario (SSP4-RCP6.0) in West, Central, East, and South Africa, where projected species richness loss is much higher under a limited management effectiveness assumption. (Fig. 3.3). The management effectiveness of PAs is even more sobering when considering the findings of Coad et al., (2019). Their research revealed that only 22.4% of PAs report adequate resources in terms of staffing and budgets, covering a mere 25.4% of PA areas assessed. In contrast, nearly half (47.7%) of the total PA area reported inadequate resources. Coad et al. (2019) argue that assuming full management PA effectiveness, may overestimate effective coverage globally by up to 400% and vertebrate representation by up to 700%. This emphasizes the critical need for increased investment and improved management to realize the full potential of PAs in conserving biodiversity.

Our results highlight the importance of tailoring conservation strategies to regional contexts. While expanding PAs is crucial in biodiversity hotspots like the Amazon and South-East Asia, mid-latitude regions may benefit more from integrated cultural landscape management. Increased total area of PAs can buffer species against the adverse effects of climate change, particularly when expansion strategies prioritize connectivity and minimize fragmentation (Duncanson et al., 2023; Xu et al., 2022). However, expanding PAs without improving their management effectiveness will limit their impact, underscoring the need for adequate funding and governance interventions.

While our analysis provides valuable insights, it is influenced by some assumptions and limitations. First, our study is limited to two land use scenarios which are not representative of the full spectrum of possible land use futures. Additionally, each SSP scenario originates from a different Integrated Assessment Model (IAM), meaning that the scenario uncertainty that would result from using different IAMs for a given SSP cannot be assessed (Riahi et al., 2017). Future research should incorporate different IAMs to account for scenario uncertainty. The treatment of conservation measures within IAMs also presents challenges. Conservation efforts are implicitly included in the IAMs used to generate the land use scenarios, which makes it challenging to strictly disentangle land use change from PA expansion. Currently, IAMs do not explicitly and consistently account for PAs, treating them in a largely implicit or ad-hoc manner within broader land use assumptions. This lack of transparency makes it difficult to assess the direct contribution of PAs to biodiversity outcomes and necessitates external post-processing approaches like the one applied in this study. Future IAM developments should incorporate explicit, standardized representations of PAs and their management effectiveness to improve projections of biodiversity outcomes under different policy scenarios and should focus on either integrating area-based conservation directly into IAMs or separating its effect from other land use changes that are driven by economic and human pressures rather than conservation efforts, as has been explored in studies assessing land use and land use management projections under different SSP-RCP scenarios (Molina Bacca et al., 2024). Additionally, the definition of a PA does not always preclude land use change (UNEP-WCMC, 2016). For instance, the IUCN's categories V and VI allow for sustainable land use change, emphasizing that conservation efforts should incorporate sustainable land use while recognizing and respecting the rights of indigenous and local communities[1].

Our findings suggest that while PA expansion can contribute to biodiversity conservation, its role is ultimately limited compared to the greater influence of following a lower-emission pathway for climate mitigation efforts and broader land use policies. IAMs highlight the importance of valuing land through policy interventions, such as increasing land prices or shifting agricultural production to less biodiverse areas, to reduce land conversion pressures and enhance species persistence. Indeed, these strategies — including efforts to reduce greenhouse gas emissions, promote sustainable land management, and implement land valuation policies that discourage habitat conversion — address the systemic drivers of biodiversity loss and create a foundation for preserving ecosystems in the face of future environmental challenges. Moving forward, conservation policies must prioritize both immediate action through PA expansion and the broader, long-term transition to sustainable land use and climate pathways to maximize biodiversity outcomes in the face of global change.

[1] https://www.cbd.int/gbf/targets

3.4 Methods

This study assessed the impacts of climate change, land use change, and area-based conservation strategies on global terrestrial biodiversity, focusing on species richness across amphibians, mammals, and birds. Using SDMs and future projections of climate and land use, we evaluated future biodiversity changes under two scenarios: SSP1-RCP2.6 and SSP4-RCP6.0. In addition, we considered three different assumptions about the spatial extent of future PAs: (1) “No explicit PA” scenario, (2) current PA coverage (17%-PA), and (3) a 30% global PA expansion scenario (30%-PA). For each PA assumption, species occurrence probabilities were adjusted for habitat preferences, land use changes, and PA effectiveness to estimate species occurrence under all combinations of climate, land use and PA pathways for present-day (centered around 1995, hereafter referred to as 1995) and future (centered around 2080, hereafter referred to as 2080) timeframes. This allowed us to isolate the contribution of climate change, land use pathways, and PA assumptions to changes in future species richness. Our projections are based on two contrasting SSP-RCP scenarios representing a "sustainability" (SSP1-RCP2.6) and an "inequality" (SSP4-RCP6.0) scenario.

3.4.1 Species distribution model output and species richness aggregation

We used climate-driven SDM projections for around 15496 terrestrial species (amphibians, mammals, and birds) that were obtained from Hof et al. (2018). These projections are based on two SDM types (generalized additive models, GAM, and generalized boosted regression models, GBM). The SDMs were calibrated based on species range maps from the IUCN Red List of Threatened Species for amphibians and mammals and from Birdlife International and Nature Serve for birds (Birdlife International, 2015; IUCN, 2023) and present-day (centered around 1995) climate data from EWEMBI (Lange, 2016). The future projections were based on climate data from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) phase 2b (Frieler et al., 2017) using the ensemble mean over four GCMs (MIROC5, GFDL-ESM2M, HadGEM2-ES, and IPSL-CM5A-LR) from the Coupled Model Intercomparison Project Phase 5 (CMIP5) database under a low (RCP2.6) and high warming scenario (RCP6.0) centered around the year 2080. The SDM output was provided as probabilities of occurrence per individual species. We computed the results based on a limited dispersal assumption with a d/4 buffer applied to each range polygon (d; diameter of the largest range polygon of a species) (Hof et al., 2018).

Global species richness was calculated for present-day (1995) and future (2080) time slices, encompassing 13908 species across three taxa each based on the two SSP-RCP scenarios, the four GCMs, the two SDMs, and the three PA scenarios. The land use corrected probability of occurrence data per PA scenario (see sections below) per species were first summed across taxa for each SSP-RCP scenario, GCM, and SDM to get an overall mean to represent the species richness. Then we calculated the mean of the sums across all GCMs and SDMs to get an overall species richness for each scenario. Finally, we calculated the relative change in species richness by comparing the 2080 values to the baseline (1995).

Regional aggregation was based on the same species richness as computed for the global results. However, additionally a land mask is applied for each sub-region to summarize the results per region. We used region definitions based on the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) assessments (IPBES, 2019). From the 17 terrestrial IPBES subregions, we derived 10 summary-regions that were used for the analysis (Hari et al., 2024). The relative difference in species richness was computed as the ratio between future (2080) and past (1995) species richness. To avoid division by zero errors, in cases where the historical value was zero, the relative difference was set to 0%.

3.4.2 “No explicit PA” scenario

For the future terrestrial biodiversity projections without any explicit assumption about PAs, we used the combined climate and land use change projections developed in Hari et al. (2024). To account for the impact of future land use change on biodiversity, the SDM output in the form of probabilities of occurrence was combined with historical (based on reconstructions and remote sensing) and future land use data (based on two IAMs) from the LUH2 dataset (Hurtt et al., 2020). This dataset was aggregated to a resolution of 0.5° to match the species probability of occurrence. We used the future land use projections for the “sustainability” scenario (SSP1-RCP2.6) and an “inequality” scenario (SSP4-RCP6.0). SSP1-RCP2.6, based on the IAM IMAGE 3.0 model (Stehfest et al., 2014), envisioning a sustainable development future characterized by high economic growth, environmentally friendly technologies, and declining population growth in the latter half of the 21st century (van Vuuren et al., 2017). In contrast, SSP4-RCP6.0, was derived from the GCAM model (Wise et al., 2014) and depicts a world marked by significant economic and political inequality, where high-income countries impose strict regulations on land use, while tropical deforestation persists in poorer nations (Popp et al., 2017). Notably, the land use scenarios from LUH2 do not directly include outputs from climate models but are harmonized representations of land use change derived from IAMs, specifically associated with the SSP-RCP framework. Whilst the IAMs themselves do not simulate climate change impacts on land use, such as crop yield effect, they generate land use projections that are in line with the socioeconomic and policy assumptions of the respective SSPs (Hurtt et al., 2020).

We have named the first PA scenario “No explicit PA” scenario as the spatial representations and enforcements of the PAs within the IAMs are not clearly defined. In IMAGE 3.0 which is used for SSP1, the extension is assumed to be between 17% to 30%, based on the 2016 WDPA data, where the PA coverage was around 14% (Stehfest et al., 2014). Similar to our approach, agricultural expansion was not permitted within existing PAs. However, the exact spatial distribution and methodology for determining PAs in SSP1 remain internal to the model logic. Furthermore, the harmonization process within LUH2 further modifies or dilutes these representations without explicitly documenting how PAs are treated.

The treatment of PAs in GCAM 3.0 used for SSP4 is even more complex as PAs to our knowledge, are not explicitly accounted for, meaning that they must be defined separately within the scenario framework. This requires specifying proportions of certain land use categories that are effectively restricted from conversion (Wise et al., 2014). Additionally, since GCAM allocates land based on productivity and assigns a price per unit of land, it can be inferred that the least productive land is more likely to be designated as protected, while more productive areas are allocated for agricultural or other economic purposes (Wise et al., 2014). Furthermore, a downscaling process is applied to these scenarios, adding an additional layer of uncertainty and making spatial interpretations of PA distributions even more challenging (Le Page et al., 2016).

The 12 land use categories from LUH2 were then merged to five categories according to Powers & Jetz (2019): forested land, non-forested land, pasture, cropland, and urban (explained in detail in Hari et al. (2024) and matched with the habitat preferences for each species derived from the IUCN Habitat Classification Scheme (v3.1) (IUCN, 2023), based on a lookup table from Carlson et al., (2022), resulting in a land use-corrected probability of occurrence by multiplying the probabilities of occurrences per species by the respective LUH2 category (fraction of grid cell), based on the respective suitable habitat (Hari et al., 2024). For example, if 50% of a grid cell was covered by croplands and the species did not occur in croplands, the occurrence probability simulated by the climate-driven SDMs was multiplied by 0.5. If the species does occur in croplands, no land use correction was applied (see Fig. 3.5 below for more details). Throughout the whole study, we have excluded marine habitats and also marine PAs as we have focused on the climate and land use change impacts on the terrestrial realm. For species with multiple suitable habitats, the probability of occurrence was weighted by the grid cell fraction occupied by the sum of all suitable habitats (Hari et al., 2024; Fig. 3.1). This land use filtering step was done for both time periods 1995 and 2080. As the land use type “urban” was not considered a suitable habitat for any species according to the IUCN habitat classifications, it was not further included in the land use filtering and thus did not affect the probabilities of occurrence. Additionally, to this No explicit PA scenario, in which we did not directly consider any area-based conservation strategies, we compared two spatially explicit PA expansion scenarios. One scenario used the current extent of the PA network (WDPA; 17%-PA scenario) and one scenario worked with an assumed expansion of the PA network to a global coverage of 30%.

3.4.3 17%-PA scenario

In the second scenario we accounted for current protected areas. To do this, we, extracted data on PAs from the global World Database on Protected Areas (WDPA, September 2023 version), excluding all proposed PAs and those lacking "national" designation (Bingham et al., 2019; Jung et al., 2020; UNEP-WCMC and IUCN, 2023; Venter et al., 2014). We have included all PAs classified under any IUCN management category with information on size, shape, location, and date of establishment following Geldmann et al. (2014). In the version used here, the total number of PA records amounts to 285429, with 273219 polygons covering 244 countries and territories (Fig S1). To ensure spatial consistency and minimize potential inaccuracies in area calculations and spatial overlays, we excluded the 12210 point-represented PAs from our analysis. While this approach likely underestimates the total PA, incorporating these point-represented records would introduce uncertainty regarding the precise spatial locations of the PAs (UNEP-WCMC, 2016). We compile the polygon data using the merge tool in ArcGIS Pro 3.1.12, following the WDPA manual guidelines (UNEP-WCMC, 2016). Overlapping polygons were dissolved to create a "flat" layer that eliminates double counting, ensuring an accurate representation of the PAs. To further process the data, we generated in Python a binary mask from the WDPA polygon dataset. For the binary mask, we assigned a value of 1 to grid cells identified as PA representing full management effectiveness (Fig. 3.5) and a value of 0 to all other grid cells. The resulting raster was created at a spatial resolution of 0.5° based on center cell assignment raster transformation.

3.4.4 30%-PA scenario

In the third scenario, the assumed PA coverage was based on the "30 by 30" agenda. We used the resulting PA network defined by Jung et al. (2021), which aimed to identify areas of global conservation importance for terrestrial biodiversity, maximize carbon retention, and water quality regulation using a joint optimization approach, ranking terrestrial conservation priorities globally, minimizing the number of threatened species whilst also maximizing carbon retention and water quality regulation. They found that protecting the top-ranked 30% of terrestrial land area would protect 60.7% of the estimated total carbon stock, 66% of all clean water, and meet conservation targets for 57.9% of all species considered, including all extant terrestrial vertebrates (mammals, amphibians, birds, and reptiles) and a representative proportion (~41%) of all accepted species in the World Checklist of Vascular Plants (Jung et al., 2021). By giving priority to biodiversity alone, managing 30% of terrestrial land area may even be sufficient to meet conservation targets for 81.3% of terrestrial plant and vertebrate species considered (Jung et al., 2021). We use this data of the top-ranked 30% of PAs based on biodiversity alone for our "30% PAs" scenario. We downloaded the map from this study for the "biodiversity only" setting at 10km resolution in Mollweide projection. To match the other data, we reprojected it to a PlateCarree projection and aggregated the data to a 0.5° spatial resolution using the nearest-neighbor method. A binary mask was generated, where each grid cell within the selected PA was assigned a value of 1, and all other grid cells were assigned a value of 0.

3.4.5 Land use filtering adjusted to PA scenarios

For the "No explicit PA" scenario, the land use filter was applied to all grid cells globally, as described under the "No explicit PA" scenario. When adjusting for the different PA scenarios, ranging from the current PA network (WDPA), up to a scenario with 44% of the terrestrial land area being protected, we "froze" the grid cells from the respective binary masks in the LUH2 data for each scenario at the year 2023 respectively. This means that where the binary masks were located (i.e., the respective PAs were located), the land use change projections in the future did not change anymore (Fig. 3.5).

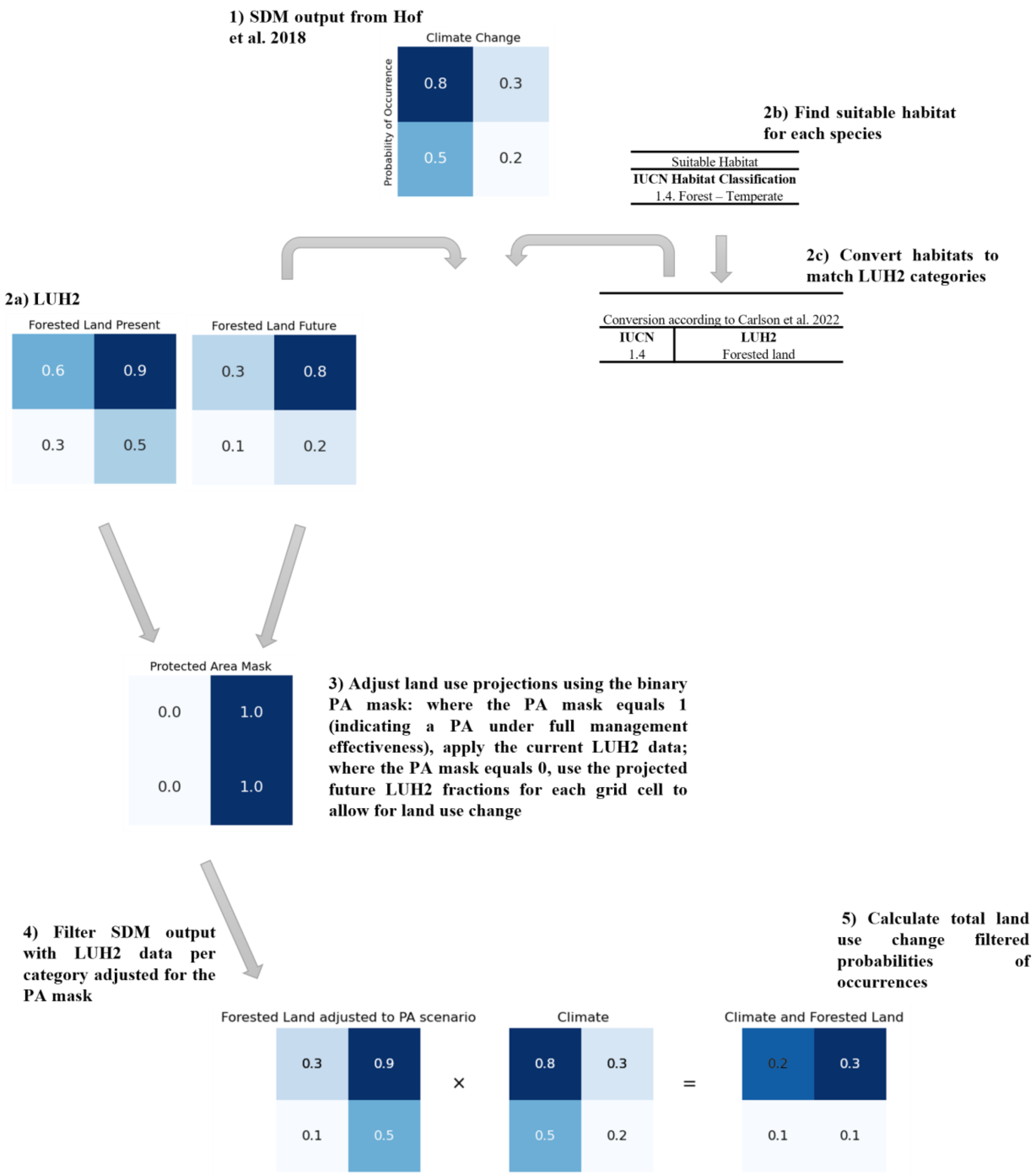

Fig. 3.5 Schematic overview of the different methodological steps of the land use filtering approach and the inclusion of PA scenarios. *The process is illustrated over 4 grid cells for a single hypothetical species having forested land as habitat preference. 1) We use SDM output from Hof et al., (2018) as probabilities of occurrences. 2) Using the LUH2 dataset (Hurtt et al., 2020), we classify land into five main categories: forested land, non-forested land, pasture, cropland, and urban areas. Each species' habitat preference is determined according to the IUCN Habitat Classification Scheme (IUCN, 2023) and matched to the LUH2 land use categories following the conversion table from Carlson et al. (2022). 3) We adjust the land use projection by the PA scenario by freezing the present-day land use in the grid cells where the PA mask equals 1 (PA present) and let land use change occur in the other grid cells where the PA mask equals 0. 4) We filter the SDM output with the PA-adjusted LUH2 data by weighting the SDM-derived probabilities of occurrence by the fraction of grid cell occupied by suitable land use categories for each species. 5) These weighted probabilities are then summed to obtain the total land use-filtered probabilities of occurrences. The same schematic but for limited management effectiveness can be found in the supplementary material (Fig. S3.9).*

However, as this approach also meant avoiding, for example, reforestation efforts and, depending on the SSP-RCP scenario, even expanding agricultural area within the PA in the future compared to the present state, which is an unrealistic assumption for the PA, we adjusted the approach as follows. We first identified natural areas (forested land and non-forested land) and agricultural areas (pasture and cropland). For natural areas, the respective fraction of grid cells matching with the respective PA scenario binary mask was kept constant in the future at the 2023 state. The fraction of grid cells that were identified as agricultural areas in 2023, on the other hand, were not kept constant but can change, however, only to either forested or non-forested land. Thus, agriculture could not expand within the PAs and reforestation efforts were still possible, depending on the SSP-RCP scenario. For all areas outside the PA (i.e., outside the binary masks), the land use change followed the LUH2 projections as for the No explicit PA scenario without any further constraints (see Fig. S3.10).

Management effectiveness within PAs can be compromised not only by external pressures such as climate and land use change but also by inadequate financial investments (Geldmann, 2019; Geldmann et al., 2013; Graham et al., 2021; Lessmann et al., 2024; Watson et al., 2014). The current global PA funding gap identified by (Waldron et al., 2020) includes $67.6 billion annually to manage existing PAs and an additional $35.5 billion to $110 billion per year for PA expansion, with 69% to 91% of these costs expected to be incurred in low- and middle-income countries. Insufficient funding for PA management undermines their ecological effectiveness, particularly in maintaining biodiversity and mitigating external pressures, and exaggerates problems of habitat loss and degradation (Jones et al., 2018; Waldron et al., 2020).

To account for the limited management effectiveness of PAs due to financial constraints, we additionally applied a limited effectiveness constraint to all PA scenarios based on the Waldron report's effectiveness rate of 23.6%. For all land use categories within PAs, the actual values were calculated as a weighted average: 23.6% of the 2023 (frozen) state plus 76.4% of the projected change according to the SSP-RCP scenario (Fig. S3.9). This meant that while agricultural expansion was still prevented in PAs, and conversion of agricultural land to natural land (including reforestation) was allowed, these changes are only 23.6% as effective as they would be without this constraint. Natural areas were partially protected from decrease, and potential increases (including reforestation) were partially realized, all at this 23.6% effectiveness rate.

3.4.6 Separation of climate mitigation, sustainable land use, and area-based conservation

To evaluate the impacts of climate change, land use change, and area-based conservation strategies on species richness, we first calculated the global mean species richness. This was determined as the stacked probability of occurrence under two separate scenarios: climate change alone and land use change alone. Climate change effects were calculated by holding land use change constant at 1995 levels, whereas the effects of land use change were derived by subtracting the impacts of climate change from the total climate and land use change (i.e., total minus climate change). These calculations were conducted as the difference between two scenarios, SSP1-RCP2.6 and SSP4-RCP6.0.

Next, we integrated the PA expansion scenarios into each SSP-RCP scenario. For SSP1-RCP2.6, the effects of area-based conservation were quantified by subtracting the combined impacts of climate and land use change without PA expansion from those with PA expansion, with results compared to the historical baseline. Similarly, for SSP4-RCP6.0, the impacts of conservation were calculated as the difference between scenarios with and without PA expansion, also relative to the historical baseline. Finally, the means were normalized against the historical values for climate and land use change from 1995. This normalization ensured consistent comparisons across scenarios and highlighted the relative contributions of area-based conservation strategies to mitigating the effects of climate and land use change.

3.5 Acknowledgments

Calculations were performed on UBELIX (https://www.id.unibe.ch/hpc), the HPC cluster at the University of Bern.

Competing interests: The authors declare that they have no competing interests.

Data and materials availability: The data generated and analyzed during the current study are available from the corresponding author.

3.6 References

Allan, J. R., Possingham, H. P., Atkinson, S. C., Waldron, A., Di Marco, M., Butchart, S. H. M., Adams, V. M., Kissling, W. D., Worsdell, T., Sandbrook, C., Gibbon, G., Kumar, K., Mehta, P., Maron, M., Williams, B. A., Jones, K. R., Wintle, B. A., Reside, A. E., & Watson, J. E. M. (2022). The minimum land area requiring conservation attention to safeguard biodiversity. Science, 376(6597), 1094–1101. https://doi.org/10.1126/science.abl9127

Asamoah, E. F., Beaumont, L. J., & Maina, J. M. (2021). Climate and land-use changes reduce the benefits of terrestrial protected areas. Nature Climate Change, 11(12), 1105–1110. https://doi.org/10.1038/s41558-021-01223-2

Bingham, H. C., Juffe Bignoli, D., Lewis, E., MacSharry, B., Burgess, N. D., Visconti, P., Deguignet, M., Misrachi, M., Walpole, M., Stewart, J. L., Brooks, T. M., & Kingston, N. (2019). Sixty years of tracking conservation progress using the World Database on Protected Areas. Nature Ecology & Evolution, 3(5), 737–743. https://doi.org/10.1038/s41559-019-0869-3

Birdlife International. (2015). Birdlife International and NatureServe (Version Bird Species Distribution Maps of the World, Version 5.0) [Dataset].

Butchart, S. H. M., Clarke, M., Smith, R. J., Sykes, R. E., Scharlemann, J. P. W., Harfoot, M., Buchanan, G. M., Angulo, A., Balmford, A., Bertzky, B., Brooks, T. M., Carpenter, K. E., Comeros-Raynal, M. T., Cornell, J., Ficetola, G. F., Fishpool, L. D. C., Fuller, R. A., Geldmann, J., Harwell, H., … Burgess, N. D. (2015). Shortfalls and Solutions for Meeting National and Global Conservation Area Targets. Conservation Letters, 8(5), 329–337. https://doi.org/10.1111/conl.12158

Butchart, S. H. M., Scharlemann, J. P. W., Evans, M. I., Quader, S., Aricò, S., Arinaitwe, J., Balman, M., Bennun, L. A., Bertzky, B., Besançon, C., Boucher, T. M., Brooks, T. M., Burfield, I. J., Burgess, N. D., Chan, S., Clay, R. P., Crosby, M. J., Davidson, N. C., Silva, N. D., … Woodley, S. (2012). Protecting Important Sites for Biodiversity Contributes to Meeting Global Conservation Targets. PLOS ONE, 7(3), e32529. https://doi.org/10.1371/journal.pone.0032529

Carlson, C. J., Albery, G. F., Merow, C., Trisos, C. H., Zipfel, C. M., Eskew, E. A., Olival, K. J., Ross, N., & Bansal, S. (2022). Climate change increases cross-species viral transmission risk. Nature 2022 607:7919, 607(7919), 555–562. https://doi.org/10.1038/s41586-022-04788-w

CBD. (2022). Kunming-Montreal Global Biodiversity Framework.

Coad, L., Watson, J. E., Geldmann, J., Burgess, N. D., Leverington, F., Hockings, M., Knights, K., & Di Marco, M. (2019). Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. Frontiers in Ecology and the Environment, 17(5), 259–264. https://doi.org/10.1002/fee.2042

Dobrowski, S. Z., Littlefield, C. E., Lyons, D. S., Hollenberg, C., Carroll, C., Parks, S. A., Abatzoglou, J. T., Hegewisch, K., & Gage, J. (2021). Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes. Communications Earth & Environment, 2(1), Article 1. https://doi.org/10.1038/s43247-021-00270-z

Duncanson, L., Liang, M., Leitold, V., Armston, J., Krishna Moorthy, S. M., Dubayah, R., Costedoat, S., Enquist, B. J., Fatoyinbo, L., Goetz, S. J., Gonzalez-Roglich, M., Merow, C., Roehrdanz, P. R., Tabor, K., & Zvoleff, A. (2023). The effectiveness of global protected areas for climate change mitigation. Nature Communications, 14(1), Article 1. https://doi.org/10.1038/s41467-023-38073-9

Eckert, I., Brown, A., Caron, D., Riva, F., & Pollock, L. J. (2023). 30×30 biodiversity gains rely on national coordination. Nature Communications, 14(1), Article 1. https://doi.org/10.1038/s41467-023-42737-x

Edo, M., Entling, M. H., & Rösch, V. (2023). Agroforestry supports high bird diversity in European farmland. Agronomy for Sustainable Development, 44(1), 1. https://doi.org/10.1007/s13593-023-00936-2

Elsen, P. R., Monahan, W. B., Dougherty, E. R., & Merenlender, A. M. (2020). Keeping pace with climate change in global terrestrial protected areas. Science Advances, 6(25), eaay0814. https://doi.org/10.1126/sciadv.aay0814

Frieler, K., Lange, S., Piontek, F., Reyer, C. P. O., Schewe, J., Warszawski, L., Zhao, F., Chini, L., Denvil, S., Emanuel, K., Geiger, T., Halladay, K., Hurtt, G., Mengel, M., Murakami, D., Ostberg, S., Popp, A., Riva, R., Stevanovic, M., … Yamagata, Y. (2017). Assessing the impacts of 1.5ĝ€°C global warming—Simulation protocol of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP2b). Geoscientific Model Development, 10(12), 4321–4345. https://doi.org/10.5194/gmd-10-4321-2017

Geldmann, J. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. https://doi.org/10.1073/pnas.1908221116

Geldmann, J., Barnes, M., Coad, L., Craigie, I. D., Hockings, M., & Burgess, N. D. (2013). Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biological Conservation, 161, 230–238. https://doi.org/10.1016/j.biocon.2013.02.018

Geldmann, J., Joppa, L. N., & Burgess, N. D. (2014). Mapping Change in Human Pressure Globally on Land and within Protected Areas. Conservation Biology, 28(6), 1604–1616. https://doi.org/10.1111/cobi.12332

Graham, V., Geldmann, J., Adams, V. M., Grech, A., Deinet, S., & Chang, H.-C. (2021). Management resourcing and government transparency are key drivers of biodiversity outcomes in

Southeast Asian protected areas. Biological Conservation, 253, 108875. https://doi.org/10.1016/j.biocon.2020.108875

Gray, C. L., Hill, S. L. L., Newbold, T., Hudson, L. N., Börger, L., Contu, S., Hoskins, A. J., Ferrier, S., Purvis, A., & Scharlemann, J. P. W. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nature Communications, 7, 12306. https://doi.org/10.1038/ncomms12306

Hari, C., Hickler, T., Hof, C., Reyer, C. P. O., Vanderkelen, I., Voskamp, A., Biber, M. F., Fischer, M., & Davin, É. L. (2024). Future climate and land use change will equally impact global terrestrial vertebrate diversity [preprint] (p. 2024.12.13.627895). bioRxiv. https://doi.org/10.1101/2024.12.13.627895

Hof, C., Voskamp, A., Biber, M. F., Böhning-Gaese, K., Engelhardt, E. K., Niamir, A., Willis, S. G., & Hickler, T. (2018). Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. Proceedings of the National Academy of Sciences of the United States of America, 115(52), 13294–13299. https://doi.org/10.1073/pnas.1807745115

Hurtt, G. C., Chini, L., Sahajpal, R., Frolking, S., Bodirsky, B. L., Calvin, K., Doelman, J. C., Fisk, J., Fujimori, S., Klein Goldewijk, K., Hasegawa, T., Havlik, P., Heinimann, A., Humpenöder, F., Jungclaus, J., Kaplan, J. O., Kennedy, J., Krisztin, T., Lawrence, D., … Zhang, X. (2020). Harmonization of global land use change and management for the period 850-2100 (LUH2) for CMIP6. Geosci. Model Dev, 13, 5425–5464. https://doi.org/10.5194/gmd-13-5425-2020

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services. . S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages. Zenodo. https://doi.org/10.5281/zenodo.3553579

IPCC. (2022). Summary for Policymakers [H.-O. Pörtner, D.C. Roberts, E.S. Poloczanska, K. Mintenbeck, M. Tignor, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem (eds.)]. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. https://doi.org/10.1017/9781009325844

IUCN. (2023). The IUCN Red List of Threatened Species. Available at https://www. Iucnredlist.org/resources/spatial-data-download [Dataset]. https://www.iucnredlist.org/resources/spatial-data-download

Jones, K. R., Venter, O., Fuller, R. A., Allan, J. R., Maxwell, S. L., Negret, P. J., & Watson, J. E. (2018). One-third of global protected land is under intense human pressure. Science, 360(6390), 788–791.

Jung, M., Arnell, A., de Lamo, X., García-Rangel, S., Lewis, M., Mark, J., Merow, C., Miles, L., Ondo, I., Pironon, S., Ravilious, C., Rivers, M., Schepaschenko, D., Tallowin, O., van Soesbergen, A., Govaerts, R., Boyle, B. L., Enquist, B. J., Feng, X., … Visconti, P. (2021). Areas of global importance for conserving terrestrial biodiversity, carbon and water. Nature Ecology & Evolution, 5(11), 1499–1509. https://doi.org/10.1038/s41559-021-01528-7

Jung, M., Dahal, P. R., Butchart, S. H. M., Donald, P. F., De Lamo, X., Lesiv, M., Kapos, V., Rondinini, C., & Visconti, P. (2020). A global map of terrestrial habitat types. Scientific Data 2020 7:1, 7(1), 1–8. https://doi.org/10.1038/s41597-020-00599-8

Lange, S. (2016). EartH2Observe, WFDEI and ERA-Interim data Merged and Bias-corrected for ISIMIP (EWEMBI). GFZ Data Services. [Dataset]. https://doi.org/10.5880/pik.2016.004

Langhammer, P. F., Bull, J. W., Bicknell, J. E., Oakley, J. L., Brown, M. H., Bruford, M. W., Butchart, S. H. M., Carr, J. A., Church, D., Cooney, R., Cutajar, S., Foden, W., Foster, M. N., Gascon, C., Geldmann, J., Genovesi, P., Hoffmann, M., Howard-McCombe, J., Lewis, T., … Brooks, T. M. (2024). The positive impact of conservation action. Science, 384(6694), 453–458. https://doi.org/10.1126/science.adj6598

Le Page, Y., West, T. O., Link, R., & Patel, P. (2016). Downscaling land use and land cover from the Global Change Assessment Model for coupling with Earth system models. Geoscientific Model Development, 9(9), 3055–3069. https://doi.org/10.5194/gmd-9-3055-2016

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. Nature, 585(7826), 551–556. https://doi.org/10.1038/s41586-020-2705-y

Lessmann, J., Geldmann, J., Fajardo, J., & Marquet, P. A. (2024). The role of funding in the performance of Latin America’s protected areas. Proceedings of the National Academy of Sciences, 121(36), e2307521121. https://doi.org/10.1073/pnas.2307521121

Martens, C., Scheiter, S., Midgley, G. F., & Hickler, T. (2022). Combined impacts of future climate-driven vegetation changes and socioeconomic pressures on protected areas in Africa. Conservation Biology, 36(6). https://doi.org/10.1111/cobi.13968

Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S. L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B. B. N., Wenger, A., Jonas, H. D., Venter, O., & Watson, J. E. M. (2020). Area-based conservation in the twenty-first century. Nature, 586(7828), 217–227. https://doi.org/10.1038/s41586-020-2773-z

McElwee, P., Harrison, P. A., van Huysen, T., Roldán, V. A., Barrios, E., Dasgupta, P., DeClerck, F., Harmáčková, Z. V., Hayman, D. T. S., Herrero, M., Kumar, R., Ley, D., Mangalagiu, D., McFarlane, R. A., Paukert, C., Pengue, W. A., Prist, P. R., Ricketts, T., Rounsevell, M., … Obura, D. (2024). Summary for policymakers of the thematic assessment of the interlinkages among biodiversity, water, food and health (nexus assessment). Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). https://www.ipbes.net

Mi, C., Ma, L., Yang, M., Li, X., Meiri, S., Roll, U., Oskyrko, O., Pincheira-Donoso, D., Harvey, L. P., Jablonski, D., Safaei-Mahroo, B., Ghaffari, H., Smid, J., Jarvie, S., Kimani, R. M., Masroor, R., Kazemi, S. M., Nneji, L. M., Fokoua, A. M. T., … Du, W. (2023). Global Protected Areas as refuges for amphibians and reptiles under climate change. Nature Communications, 14(1), 1389. https://doi.org/10.1038/s41467-023-36987-y

Montesino Pouzols, F., Toivonen, T., Di Minin, E., Kukkala, A. S., Kullberg, P., Kuusterä, J., Lehtomäki, J., Tenkanen, H., Verburg, P. H., & Moilanen, A. (2014). Global protected area expansion is compromised by projected land-use and parochialism. Nature, 516(7531), 383–386. https://doi.org/10.1038/nature14032

Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. Proceedings of the Royal Society B: Biological Sciences, 285(1881). https://doi.org/10.1098/rspb.2018.0792

Newbold, T., Oppenheimer, P., Etard, A., & Williams, J. J. (2020). Tropical and Mediterranean biodiversity is disproportionately sensitive to land-use and climate change. Nature Ecology & Evolution, 4(12), Article 12. https://doi.org/10.1038/s41559-020-01303-0

Pereira, H. M., Martins, I. S., Rosa, I. M. D., Kim, H., Leadley, P., Popp, A., van Vuuren, D. P., Hurtt, G., Quoss, L., Arneth, A., Baisero, D., Bakkenes, M., Chaplin-Kramer, R., Chini, L., Di Marco, M., Ferrier, S., Fujimori, S., Guerra, C. A., Harfoot, M., … Alkemade, R. (2024). Global trends and scenarios for terrestrial biodiversity and ecosystem services from 1900 to 2050. Science, 384(6694), 458–465. https://doi.org/10.1126/science.adn3441

Popp, A., Calvin, K., Fujimori, S., Havlik, P., Humpenöder, F., Stehfest, E., Bodirsky, B. L., Dietrich, J. P., Doelmann, J. C., Gusti, M., Hasegawa, T., Kyle, P., Obersteiner, M., Tabeau, A., Takahashi, K., Valin, H., Waldhoff, S., Weindl, I., Wise, M., … Vuuren, D. P. van. (2017). Land-use futures in the shared socio-economic pathways. Global Environmental Change, 42, 331–345. https://doi.org/10.1016/j.gloenvcha.2016.10.002

Powers, R. P., & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nature Climate Change 2019 9:4, 9(4), 323–329. https://doi.org/10.1038/s41558-019-0406-z

Rabbetts, M., Fahrig, L., Mitchell, G. W., Hannah, K. C., Collins, S. J., & Wilson, S. (2023). Direct and indirect effects of agricultural land cover on avian biodiversity in eastern Canada. Biodiversity and Conservation, 32(4), 1403–1421. https://doi.org/10.1007/s10531-023-02559-1

Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B. C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaresma, J. C., Kc, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., … Tavoni, M. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. Global Environmental Change, 42, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009

Stehfest, E., van Vuuren, D., Kram, T., Bouwman, L., Alkemade, Bakkenes, M., Bouwman, A., den Elzen, M., Janse, J., Lucas, P., van Minnen, J., & Gerdien Prins, A. (2014). Integrated Assessment of Global Environmental Change with IMAGE 3.0—Model description and policy applications (p. 370) [Text]. https://www.pbl.nl/en/publications/integrated-assessment-of-global-environmental-change-with-IMAGE-3.0

Stehfest, E., van Zeist, W. J., Valin, H., Havlik, P., Popp, A., Kyle, P., Tabeau, A., Mason-D'Croz, D., Hasegawa, T., Bodirsky, B. L., Calvin, K., Doelman, J. C., Fujimori, S., Humpenöder, F., Lotze-Campen, H., van Meijl, H., & Wiebe, K. (2019). Key determinants of global land-use projections. Nature Communications, 10(1). https://doi.org/10.1038/s41467-019-09945-w

UNEP-WCMC. (2016). World Database on Protected Areas User Manual 1.4 UNEP-WCMC. Available at: http://wcmc.io/WDPA_Manua

UNEP-WCMC and IUCN. (2023). Protected Planet: The World Database on Protected Areas (WDPA) [Online] [Dataset]. UNEP-WCMC and IUCN. www.protectedplanet.net

UNEP-WCMC and IUCN. (2025). Protected Planet: The World Database on Protected Areas (WDPA) [Online] [Dataset]. UNEP-WCMC and IUCN. www.protectedplanet.net van Vuuren, D. P., Stehfest, E., Gernaat, D. E. H. J., Doelman, J. C., van den Berg, M., Harmsen, M., de Boer, H. S., Bouwman, L. F., Daioglou, V., Edelenbosch, O. Y., Girod, B., Kram, T., Lassaletta, L., Lucas, P. L., van Meijl, H., Müller, C., van Ruijven, B. J., van der Sluis, S., & Tabeau, A. (2017). Energy, land-use and greenhouse gas emissions trajectories under a green growth paradigm. Global Environmental Change, 42, 237–250. https://doi.org/10.1016/j.gloenvcha.2016.05.008

Venter, O., Fuller, R. A., Segan, D. B., Carwardine, J., Brooks, T., Butchart, S. H. M., Marco, M. D., Iwamura, T., Joseph, L., O'Grady, D., Possingham, H. P., Rondinini, C., Smith, R. J., Venter, M., & Watson, J. E. M. (2014). Targeting Global Protected Area Expansion for Imperiled Biodiversity. PLOS Biology, 12(6), e1001891. https://doi.org/10.1371/journal.pbio.1001891

Visconti, P., Butchart, S. H. M., Brooks, T. M., Langhammer, P. F., Marnewick, D., Vergara, S., Yanosky, A., & Watson, J. E. M. (2019). Protected area targets post-2020. Science, 364(6437), 239–241. https://doi.org/10.1126/science.aav6886

Waldron, A., Adams, V., Allan, J., Arnell, A., Asner, G., Atkinson, S., Baccini, A., Baillie, E., Balmford, A., Beau, J. A., Brander, L., Brondizio, E., Bruner, A., Burgess, N., Burkart, K., Butchart, S., Button, R., Carrasco, R., Cheung, W., … Zhang, Y. (2020). Protecting 30% of the planet for nature: Costs, benefits and economic implications.

Watson, J. E. M., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. Nature, 515(7525), 67–73. https://doi.org/10.1038/nature13947

Wise, M., Calvin, K., Kyle, P., Luckow, P., & Edmonds, J. (2014). Economic and physical modeling of land use in GCAM 3.0 and an application to agricultural productivity, land, and terrestrial carbon. Climate Change Economics, 05, 1450003. https://doi.org/10.1142/S2010007814500031

Xu, X., Huang, A., Belle, E., De Frenne, P., & Jia, G. (2022). Protected areas provide thermal buffer against climate change. Science Advances, 8(44), eabo0119. https://doi.org/10.1126/sciadv.abo0119

3.7 Supplementary materials

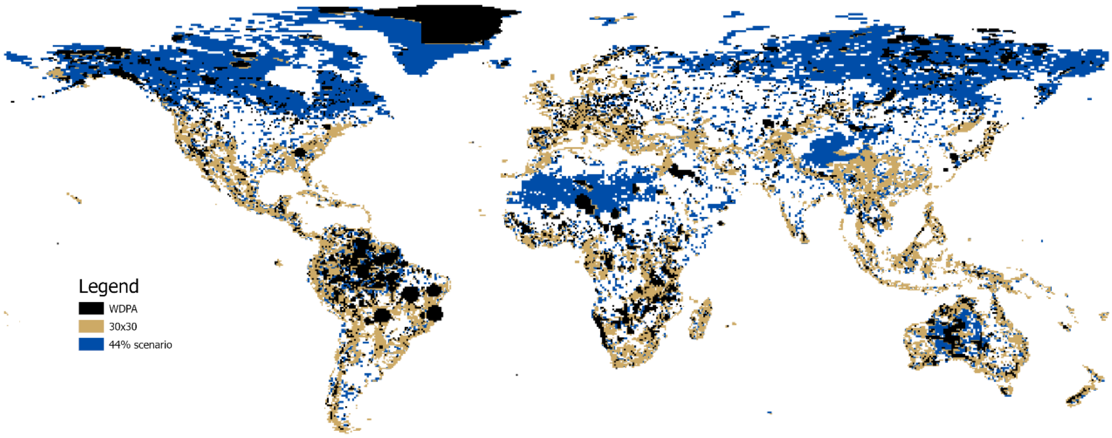

Fig. S3.1 Global map of the three PA expansion scenarios included in this study.

.

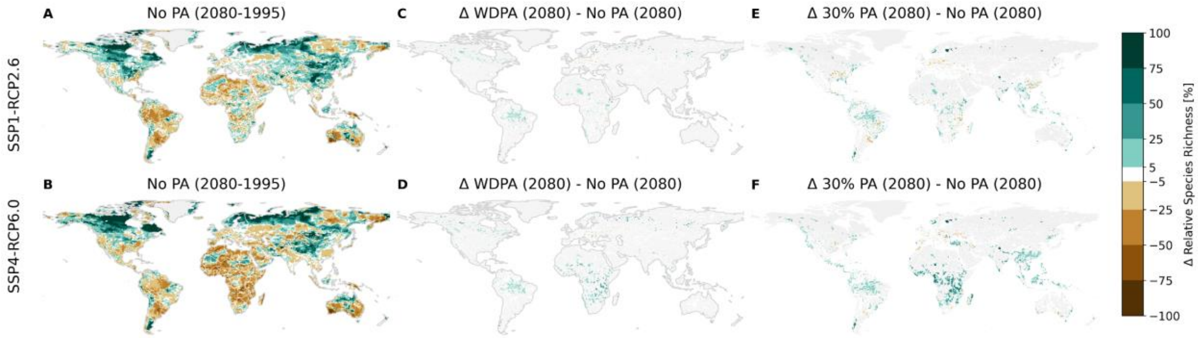

Fig. S3.2 Same as Fig. 3.1 in main text but for amphibians only.

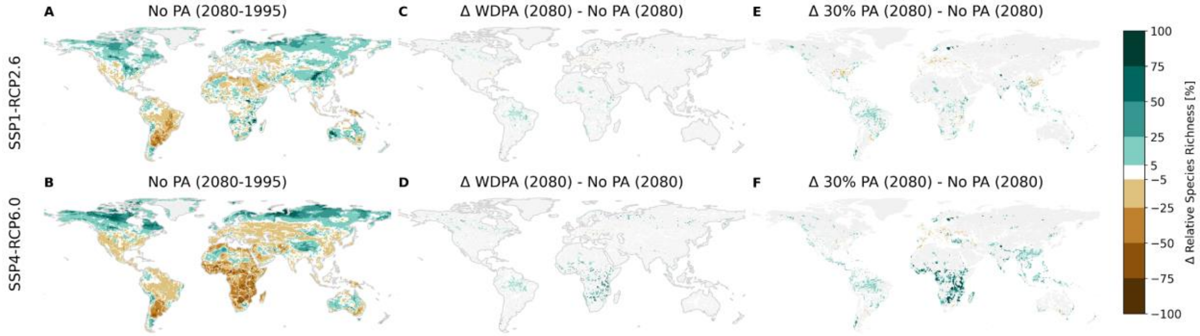

Fig. S3.3 Same as Fig. 3.1 in main text but for birds only.

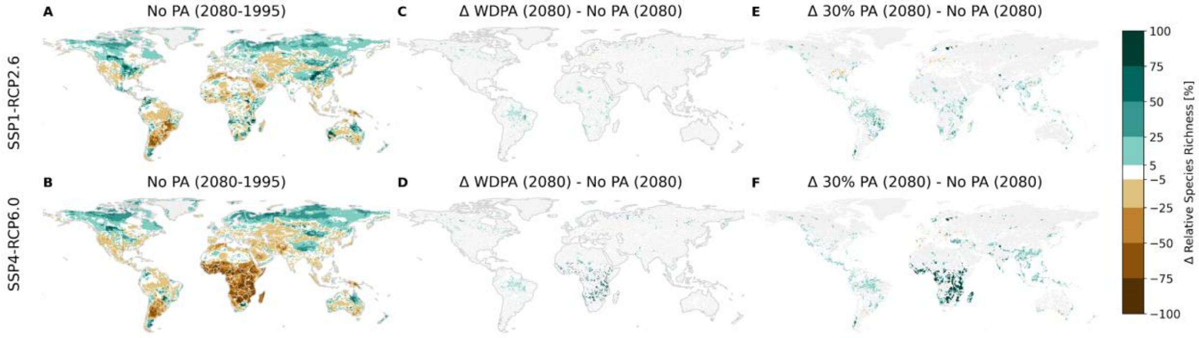

Fig. S3.4 Same as Fig. 3.1 in main text but for mammals only.

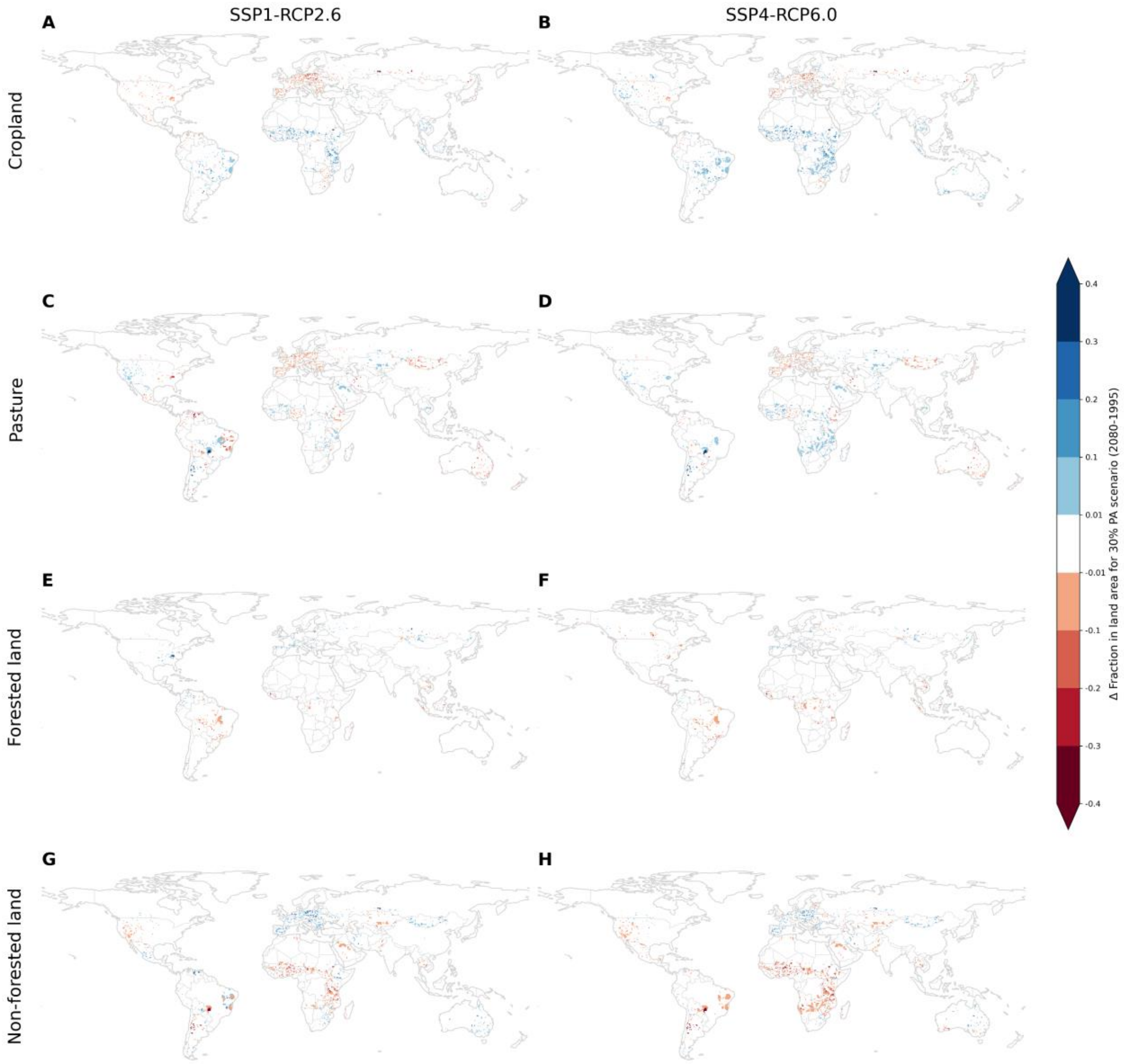

Fig. S3.5 Future (2080) LUH2 projections frozen at the year 2030 where they overlap with the current protected area network (WDPA) data compared to LUH2 in the year 1995.

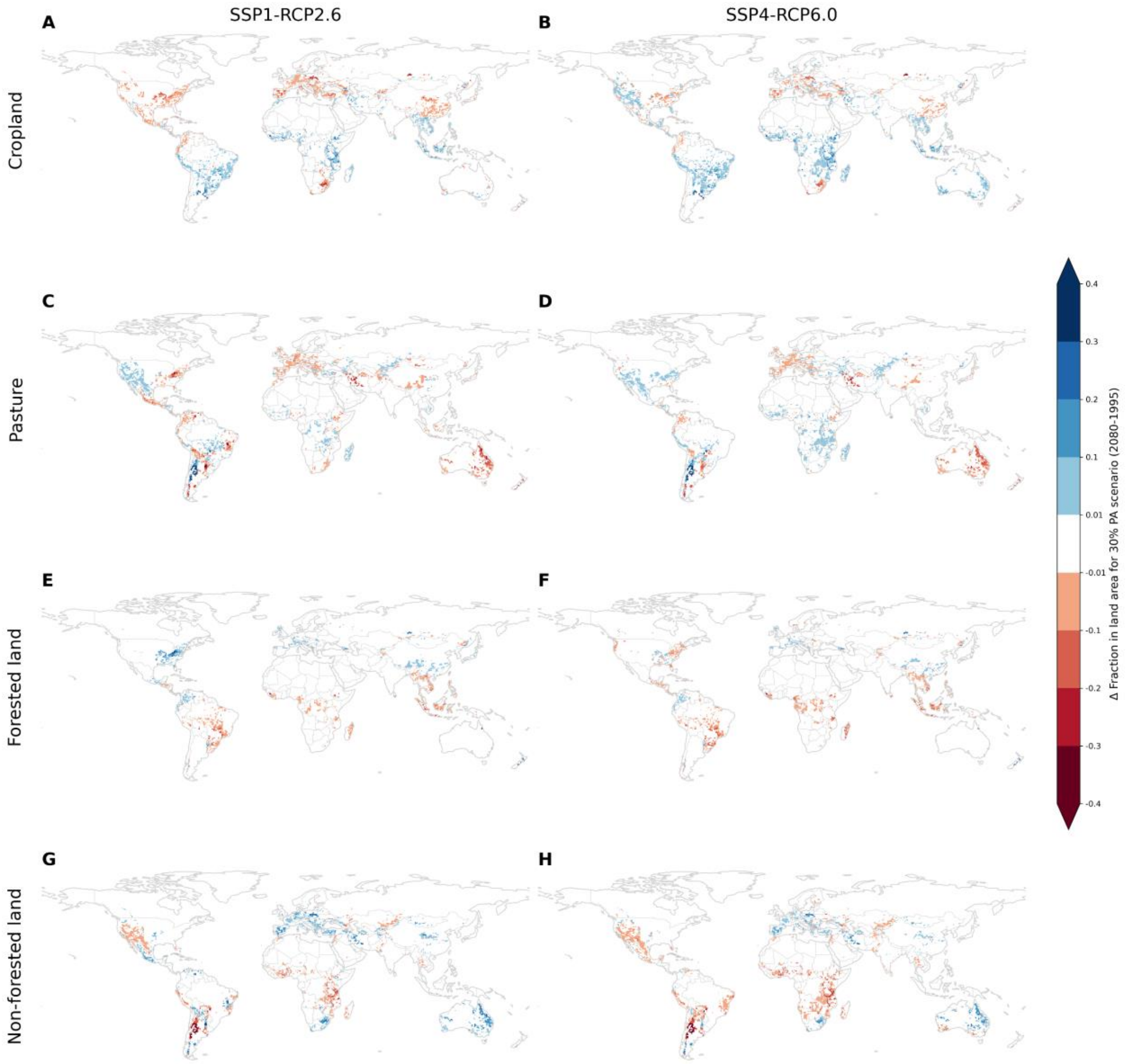

Fig. S3.6 Future (2080) LUH2 projections frozen at the year 2030 where they overlap with a 30% PA scenario data compared to LUH2 in the year 1995.

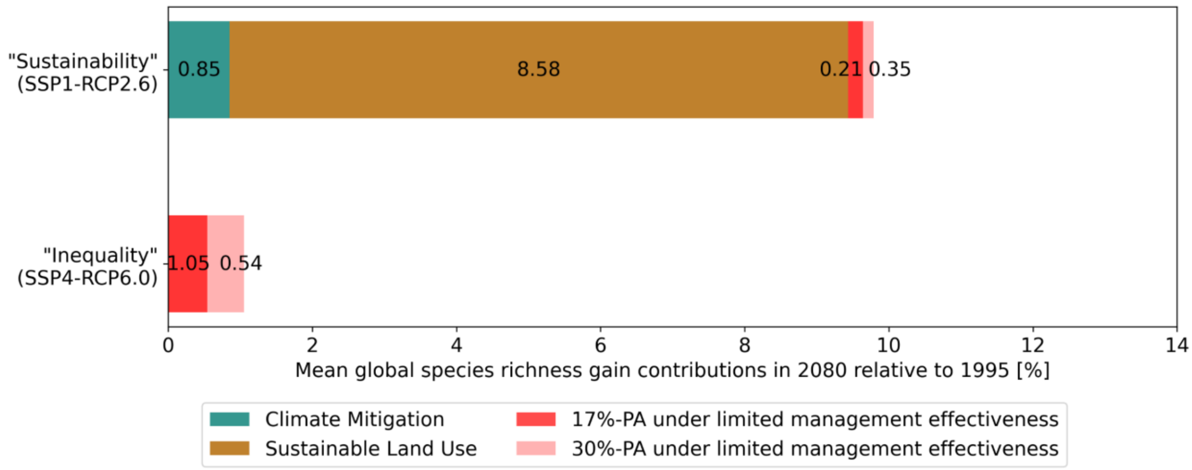

Fig. S3.7 Same as Fig. 3.2 but under a limited management effectiveness assumption of 23.6%.

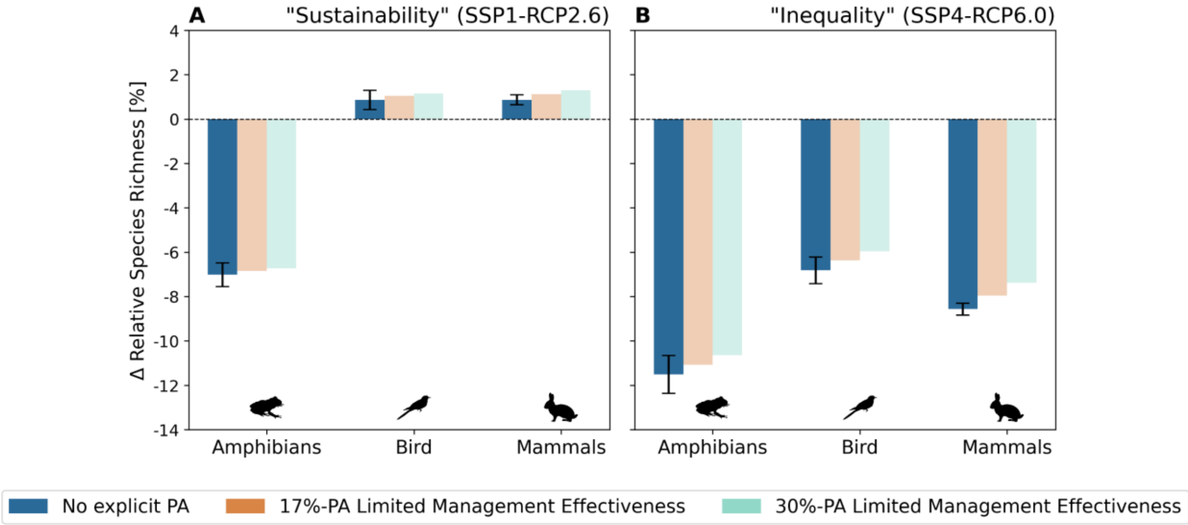

Fig. S3.8 Same as Fig. 3.4 but under a limited management effectiveness assumption of 23.6%.

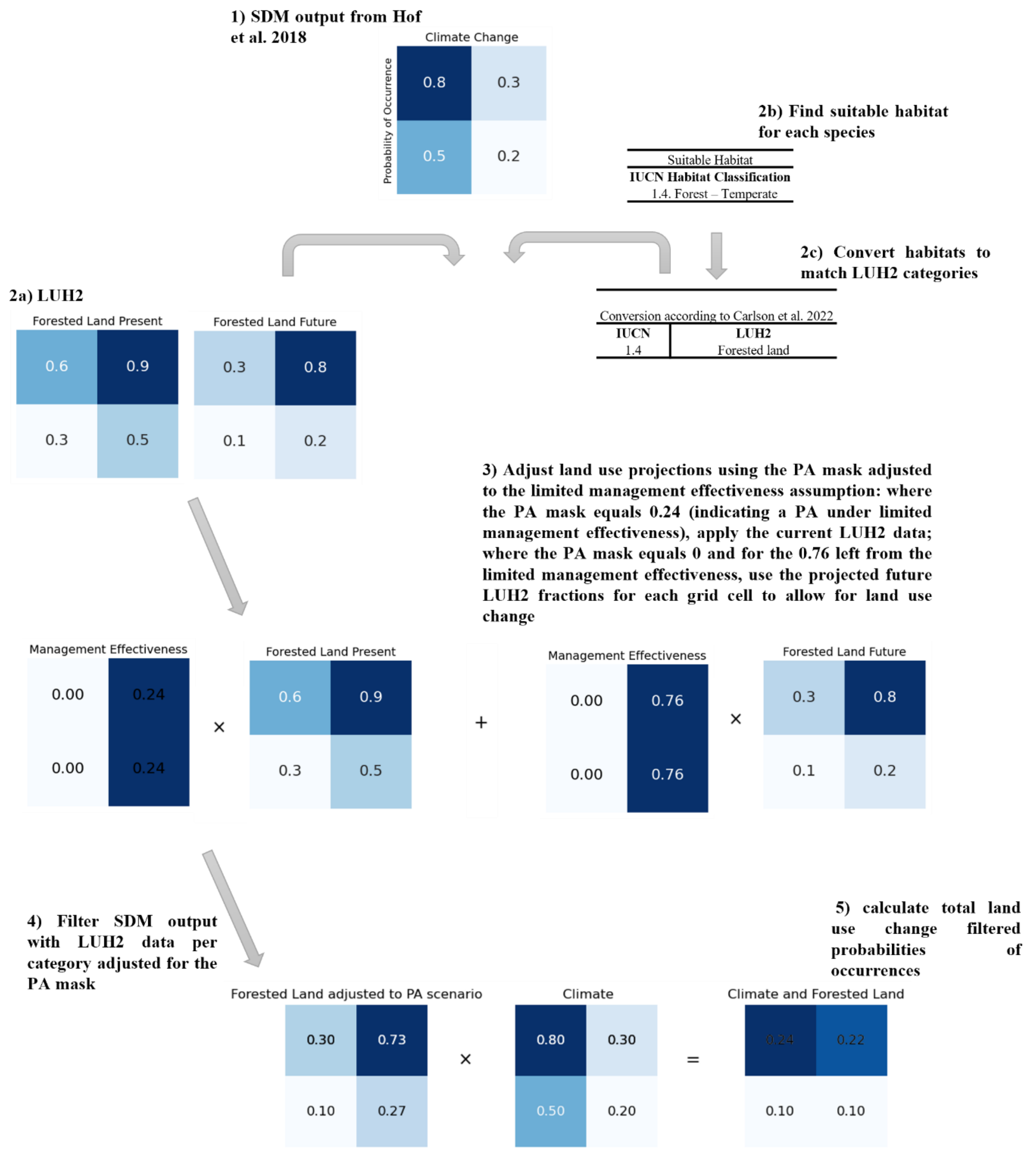

Fig. S3.9 Schematic overview of the methodological steps to apply a land use filtering approach and including PA masks under a limited effectiveness assumption of 23.6%.

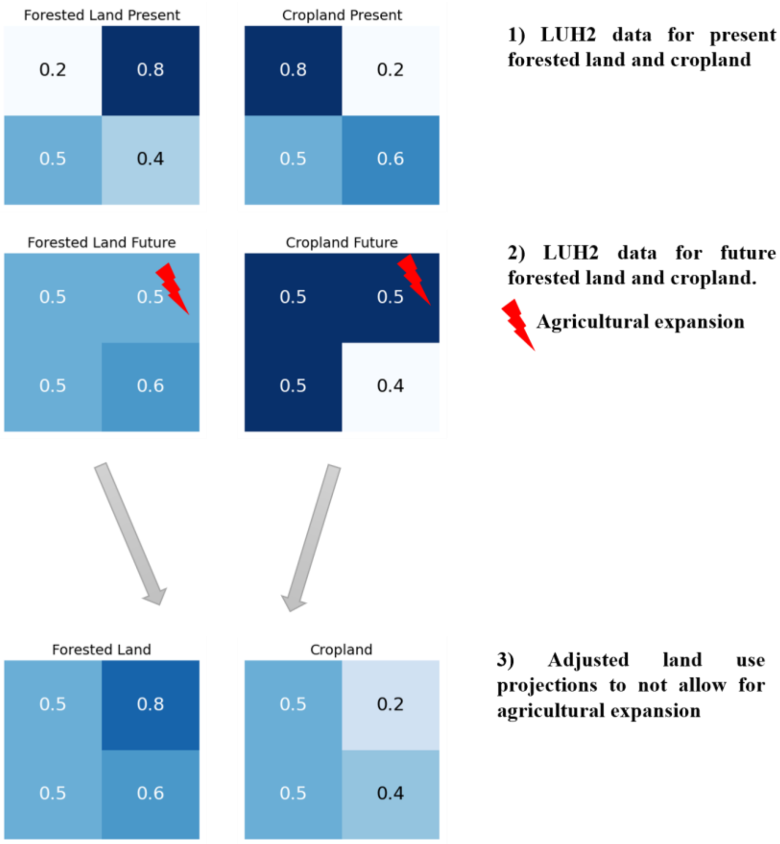

Fig. S3.10 Schematic overview of the methodological steps behind the agricultural expansion assumption.

Chapter 4

Assessing the impacts of climate and land use change on vegetation dynamics in Kenya's arid and semi-arid lands

Chantal Hari,[1,2,3] Simon Scheiter,[4,5] Thomas Hickler,[4,5] Marie-Estelle Demory,[1,2,3] Carola Martens,[6] Markus Fischer,[3,7] Édouard L. Davin,[1,2,3]

[1] Wyss Academy for Nature at the University of Bern, University of Bern, Bern, Switzerland
[2] Climate and Environmental Physics, Physics Institute, University of Bern, Bern, Switzerland
[3] Oeschger Centre for Climate Change Research, University of Bern, Bern, Switzerland
[4] Senckenberg Biodiversity and Climate Research Center (SBiK-F), Senckenberganlage 25, 60325 Frankfurt/Main, Germany
[5] Department of Physical Geography at Goethe University, Altenhöferallee 1, 60438 Frankfurt/Main, Germany.
[6] Independent Researcher
[7] Institute of Plant Sciences, Plant Ecology, University of Bern, Bern, Switzerland

This chapter is in preparation for submission to a peer-reviewed journal.

Abstract

Understanding the impacts of climate change on vegetation dynamics is critical for biodiversity conservation, especially in regions where ecosystems are highly sensitive to climatic variability, such as arid and semi-arid lands (ASALs). This study investigates future vegetation dynamics in Kenya under two climate change scenarios (RCP4.5 and RCP8.5) using simulations from the adaptive dynamic global vegetation model (aDGVM). The model, specifically designed for African ecosystems, captures key processes such as fire dynamics, carbon allocation, and the interactions between grasses and trees. We focus on woody encroachment—a key phenomenon associated with shifts in grass and tree aboveground biomass (AGB)—to detect patterns of change in the savanna biome, which supports biodiversity, carbon storage, and livelihoods.

Our analysis reveals that changes in biome composition are projected for Kenya by the end of the 21st century. Forested areas are expected to expand substantially under both RCP scenarios, particularly at the expense of savannas and grasslands. Under RCP8.5, the forest biome is projected to increase by up to 86.1% compared to present-day, while savanna cover is projected to decrease by up to 21.2%, indicating woody encroachment across large portions of the country. Grass AGB shows a more gradual increase, with notable interannual variability. The expansion of woody vegetation is exacerbated by elevated atmospheric CO_2 concentrations, as indicated by suppressed CO_2 fertilization simulations. However, our comparison of aDGVM outputs with land use projections from the Land Use Harmonization 2 (LUH2) dataset suggests that forest expansion driven by climate change alone may be overestimated when land use change is not considered, as cropland expansion into natural areas could mitigate or even reverse these trends. This study contributes to a deeper understanding of potential ecological outcomes under future climate scenarios by identifying regions susceptible to biome shifts and woody encroachment. The results provide valuable insights for biodiversity conservation, particularly in the context of Kenya's Vision 2030 development goals.

4.1 Introduction

Climate change drives shifts in ecosystems worldwide, affecting biodiversity, vegetation extent and distribution, and ecosystem services (IPBES, 2019). These changes are particularly pronounced in arid and semi-arid lands (ASALs), which cover vast areas of Africa and have been shown to be particularly vulnerable to hydrological shifts and climate variability (Martens et al., 2022; Trisos et al., 2022). Kenya, where ASALs make up over 80% of the land area and support over 90% of its wildlife, is especially vulnerable to climate-driven ecosystem transformations (Njoka et al., 2016). Kenya's wildlife is a critical economic and cultural asset, contributing substantially to national revenue through tourism and providing essential ecosystem services (Ojwang’ et al., 2017). These habitats also support renewable energy, water, agriculture, livestock, health, and fisheries sectors (Ojwang’ et al., 2017). Recognizing the importance of biodiversity and intact ecosystems, the Kenya Vision 2030 aims to conserve wildlife for future generations by protecting key wildlife habitats, corridors, and dispersal areas, vital for maintaining landscape connectivity and ecological resilience (Ojwang’ et al., 2017). This long-term development plan aims to transform Kenya into a newly industrializing, middle-income country with a high quality of life by 2030 in a clean and secure environment (Ojwang’ et al., 2017). The country's long-term plan envisions securing all wildlife ecosystems to ensure their protection in the face of increasing environmental pressures (Jenkins et al., 2021). A clear understanding of future vegetation dynamics is required to achieve such conservational and sustainable land management goals.

Savannas and tropical grasslands, key ecosystems in Kenyan ASALs, provide critical habitats for wildlife and contribute to overall ecosystem diversity (Njoka et al., 2016). Covering approximately 20% of the Earth’s land surface, savannas play a critical in the global carbon cycle (Grace et al., 2006), while on regional scale also supporting millions of people and their livelihoods by providing resources for livestock farming, agriculture, resource extraction, and tourism (Moncrieff et al., 2016; Stevens et al., 2017). Savannas are a very complex biome, varying widely in ecosystem structure and function (Moncrieff et al., 2016). This complexity, combined with their ecological and cultural relevance, makes it crucial to understand how different savanna ecosystems may respond to future climate change scenarios (Moncrieff et al., 2016; Stevens et al., 2017).

Despite their importance, savannas face severe threats from habitat degradation, climate change, and land use intensification (Kiteme et al., 2021). Among the key climate-driven threats to savannas is thus to the habitats of many species is woody encroachment—the increase in abundance of woody plants, such as shrubs and bushes, at the expense of herbaceous vegetation– into savannas (Martens et al., 2022). The drivers of woody encroachment are multifaceted, including rising atmospheric CO_2 levels, changes in fire regimes, herbivory movement patterns and precipitation patterns (Aleman et al., 2016; Martens et al., 2022; Venter et al., 2018). Although this process increases total vegetation biomass, it can have detrimental effects on terrestrial biodiversity, particularly on mammalian diversity, by altering habitat structure and reducing the availability of food, cover and space (Soto-Shoender et al., 2018).

Numerous studies have investigated past and future woody encroachment and broader vegetation changes in the savanna ecosystems, emphasizing the importance of modeling future vegetation dynamics to better understand climate change's impacts (Higgins & Scheiter, 2012; Pinheiro et al., 2022; Stevens et al., 2017). However, most of these studies have been conducted at continental scales (e.g., Ardö, 2015; D'Onofrio et al., 2020; Martens et al., 2021, 2022; Pfeiffer et al., 2020; Scheiter et al., 2012), leaving a critical gap in assessments on national scale, particularly for Kenya. Previous analyses focusing on future vegetation dynamics in Kenya, have relied on statistical models (Parracciani et al., 2023). Under high-emission scenarios, their projections indicated an expansion of savannas and a decline in forest. Their model was driven by temperature, soil moisture, livestock density, and topography but did not account for rising atmospheric CO_2 levels, a key factor influencing vegetation responses in process-based models (Parracciani et al., 2023).

The lack of studies assessing climate-driven vegetation shifts in Kenya using DGVMs – particularly in relation to woody encroachment represents a major knowledge gap, especially in light of Kenya Vision 2030's goal to protect key ecosystems and ensure sustainable land management. Furthermore, land use change must also be considered, as it plays a critical role in shaping future vegetation dynamics and ecosystem stability in Kenya (Njoka et al., 2016). This study aims to address these knowledge gaps by presenting and analyzing existing simulations of projections of future vegetation changes in Kenya due to climate change, with a specific focus on comparing future woody versus grassy aboveground biomass (AGB) to detect patterns of woody encroachment. By presenting biome-level distributions and investigating relative changes in grassy and woody AGB, we aim to understand shifts in ecosystem composition over time. Using the adaptive Dynamic Global Vegetation Model (aDGVM)- which, unlike other DGVMs, is specifically designed for African ecosystems and savanna dynamics- we analyze future biome distributions in Kenya under different climate change scenarios (Representative Concentration Pathways; RCPs). To take initial steps toward assessing the combined impacts of climate and land use change on a regional scale, we made an ad hoc comparison of future land use change projections from the Land Use Harmonization 2 dataset onto the aDGVM vegetation projections to understand potential compounded impacts on vegetation distribution and biodiversity.

4.2 Methods

4.2.1 Adaptive dynamic global vegetation model simulations

aDGVM is a process-based model specifically developed for tropical and subtropical grass-tree ecosystems (see Scheiter & Higgins, 2009 for more details). It is an individual-based model, incorporating adaptive modules for phenology, carbon allocation, and fire (Prentice et al., 2007; Scheiter & Higgins, 2009). In aDGVM, the leaf phenology and allocation are a function of resource availability. Carbon is preferentially allocated to roots when water is limited, allowing plants to improve water uptake. Similarly, carbon is allocated to stems when light is limited, or a fire removes AGB (Scheiter & Higgins, 2009). The daily carbon fixation rate for each individual is influenced by temperature, atmospheric CO_2, photosynthetically active radiation (PAR), stomatal conductance, and competition for light and water. Leaf phenology responds to photosynthetic rates, water availability, and temperature. Grasses are represented as "super-individuals" simulating grass underneath and between tree canopies, while individual trees are tracked for root, stem, leaf biomass, carbon status, phenology, and fire responses. The aDGVM includes both C3 and C4 grasses (Scheiter et al., 2012).

Fire shapes the tree population by reducing establishment rates and increasing the mortality of small trees (<2 m), which are often "topkilled" by fire, forcing them to resprout repeatedly. Repeated topkill compromises the carbon balance, increasing the likelihood of mortality unless several fire-free years allow trees to grow large enough to escape the "fire trap" (Bond & Midgley, 2000; Scheiter & Higgins, 2009). Savanna trees have higher resprouting rates than forest trees and can therefore persist in fire-driven ecosystems whereas forest trees are excluded (Scheiter et al., 2012).

For this study, we used the aDGVM simulations conducted by Martens et al. (2021). The simulation design is described in detail in Martens et al. (2021). The aDGVM was forced with daily climate data from six global climate models (GCMs; ACCESS, CCSM4, CNRM, GFDL, MPI, NorESM1M) which were part of the Coupled Model Intercomparison Project 5 (CMIP5). These climate inputs were downscaled for Africa to a 0.5° resolution with the conformal-cubic atmospheric model (CCAM) (McGregor & Dix, 2008), a mechanistic atmospheric model, forced with bias-corrected sea surface temperature and sea ice data derived from the GCMs (Engelbrecht et al., 2015) for both RCP4.5 and RCP8.5 scenarios. Soil parameters for the simulations were based on the Global Soil Data Task Group (2000). A spin-up period of 210 years was run first based on the ensemble of climate data from the six GCMs over Africa to allow vegetation to reach an equilibrium state, followed by a transient phase using CCAM-derived climate data covering 1971–2099. Vegetation dynamics in each 0.5° grid cell were modeled using a 1-hectare stand simulation, which was scaled to the full grid cell under the assumption of homogeneity. For each RCP scenario, the results were averaged across the ensemble of six aDGVM simulations for subsequent analyses (Martens et al., 2022).

The simulated vegetation was categorized into seven biome types: desert, C3 and C4 grasslands, C3 and C4 savannas, woodland, and forest. The classification is based on a thresholding of simulated tree cover, grass AGB, and the relative abundance of tree cover and grass types (Martens et al., 2021; Scheiter et al., 2012). Grasslands are defined by a minimum AGB threshold (Martens et al., 2021; Scheiter et al., 2018) and savannas are distinct from woodlands by the dominance of savanna or forest tree types, which is closely linked to fire dynamics. Fire plays a critical role in shaping biome composition by influencing tree establishment and mortality, particularly in fire-prone ecosystems where frequent fires maintain open-canopy savannas while limiting the expansion of woodlands and forests (Martens et al., 2021).

4.2.2 Derivation of potential natural vegetation maps

The aDGVM outputs were post-processed to generate present-day and future potential natural vegetation maps (PNVMs) and tree cover maps for Kenya. For this, we processed rasterized biome grids for three periods: 2000–2019 (present-day), 2080–2099 under RCP4.5, and 2080–2099 under RCP8.5. The biome projections with spatial resolutions aligned to 0.5° × 0.5° grid cells were provided for the whole continent of Africa. Thus, we masked the biome data to the extent of Kenya using the country's shapefile from the Natural Earth dataset (resolution: 1:110m). The biome data were then visualized on latitude-longitude axes with consistent boundaries (longitude: 33°–42°E; latitude: -5°–6°N) across all projections for the biome categories defined and used in previous studies (Martens et al., 2021). Additionally, we have added a mask to delineate counties classified as ASALs based on data from Chepkochei et al. (2024).

4.2.3 Land use change projections

We conducted an ad hoc comparison between the aDGVM simulation outputs to land use change projections. We used historical and future data from the Land Use Harmonization 2 (LUH2) dataset (Hurtt et al., 2020). The data comes at a 0.25° resolution and thus had first to be aggregated to the 0.5° resolution grid of the aDGVM output. All data before 2015 constitutes historical data and are based on historical reconstructions and remote sensing data (Hurtt et al., 2020). After 2015, data are based on projections from Integrated Assessment Models (IAMs) under different Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs). To match the climate scenarios run for aDGVM, we selected the IAM projections for SSP2-RCP4.5 and SSP5-RCP8.5. The IAM projection for SSP2-RCP4.5 is based on MESSGAE-GLOBIOM, an energy system model coupled with the Global Biosphere Management Model (GLOBIOM), a land use dynamics model (Havlik et al., 2011). SSP2-RCP4.5 is a low stabilization scenario that never exceeds 4.5 W m−2 (∼ 650 ppm CO_2 equivalent) before 2100. SSP5-RCP8.5 is a scenario based on rapid and resource-intensive development coupled with very high levels of fossil fuel use, tripling greenhouse gas emissions over the course of the century. The scenario is based on the REMIND-MAgPIE IAM framework consisting of the Regionalized Model of Investment and Development (REMIND) and the Model of Agriculture Production and its Impacts on the Environment (MAgPIE) (Hurtt et al., 2020; Kriegler et al., 2017).

The 12 LUH2 land use categories were aggregated into five generalized land cover classes: forested land, non-forested land, pasture, cropland, and urban, based on the classification framework of Powers & Jetz (2019). Specifically, primary and potentially forested secondary lands were grouped as "forested land", while primary and potentially non-forested secondary lands were categorized as "non-forested land". Managed pastures and rangelands were combined into the "pasture" class, and the five distinct crop types were consolidated under "cropland".

4.2.4 Comparison to other datasets

To assess projected climate changes, three bioclimatic variables were masked to the extent of Kenya, namely mean annual temperature, annual precipitation, and precipitation seasonality. The first two variables represent annual trends, whereas precipitation seasonality indicates the annual range in precipitation. For each GCM-driven and RCP scenario, we then computed the model ensemble mean by averaging the six GCM-derived bioclimatic variables. The present-day mean was calculated once and compared against the future means for RCP4.5 and RCP8.5 to produce spatial difference maps (future minus historical values).

To compare woody versus grassy AGB, we visualized the relative change in grass and tree AGB over time for the two scenarios, RCP4.5 and RCP8.5. Separate subplots were used for RCP4.5 and RCP8.5 to facilitate comparison.

We compared the same simulated AGB outputs from aDGVM to the Joint UK Land Environment Simulator (JULES-ES) AGB outputs. JULES-ES is driven by GCMs from the CMIP6 Inter-Sectoral Impact Model Intercomparison Project Phase 3b (ISIMIP3b) projections. The JULES-ES land surface model was run at a 0.5° spatial resolution and included key components such as TRIFFID for dynamic vegetation, TRIFFID-Crop for managed land, nitrogen limitation, river routing, land use change, and the INFERNO fire module (Mathison et al., 2023).

We compare the AGB outputs of aDGVM and JULES-ES for Kenya against observational estimates of total AGB. To assess the agreement between model outputs and observations, we use Taylor diagrams to visualize the standard deviation, correlation, and centered root mean square error (RMSE) of the AGB estimates. The observational datasets included ESA’s Biomass Climate Change Initiative global maps of AGB for 2010, derived from Earth observation data from Sentinel-1, Envisat’s ASAR, and ALOS-1 and 2 (Santoro & Cartus, 2021). Additionally, NASA’s Global Aboveground and Belowground Biomass Carbon Density maps for 2010, at a 300-m spatial resolution, provided harmonized estimates of biomass carbon density (Spawn & Gibbs, 2020). Both datasets were aggregated to the 0.5° spatial resolution of the model simulations with a nearest-neighboring technique to ensure consistency in the spatial comparison.

In addition to the above-described comparisons, we also compared two land cover products to the present-day aDGVM simulations by re-categorizing the land cover categories to match the aDGVM biome classifications. We used two land cover maps, the ESA WorldCover at a 10m resolution of the year 2021 (Zanaga et al., 2022) and the Kenya Sentinel-2 Land Use Land Cover (LULC) 2016 dataset (Regional Centre for Mapping of Resources for Development (RCMRD), European Space Agency (ESA), 2016). The ESA WorldCover product is based on Sentinel-1 and Sentinel-2 data and classifies land cover according to the UN-FAO's Land Cover Classification System. The ESA WorldCover 2021 v200 map is an updated version of the 2020 map and features improved algorithms for increased accuracy (Zanaga et al., 2022). The dataset was aggregated to match the 0.5° spatial resolution of the model simulations using a majority aggregation technique to align with the model's spatial framework. The Kenya Sentinel-2 Land Use Land Cover (LULC) 2016 dataset was used to provide region-specific land cover information for Kenya. This dataset represents a land cover map clipped from Sentinel-2 global data. The dataset includes classes such as forests, settlements, and other land use types for the year 2016 (RCMRD, ESA, 2016). The dataset was also aggregated to a 0.5° spatial resolution using a majority aggregation method. Land use categories were reclassified to match the seven biome classifications used in aDGVM to ensure compatibility with its vegetation framework (Table S4.1).

4.3 Results

4.3.1 Present-day biomes and comparison to observational data

The present-day biome distribution, according to the aDGVM generated PNVM, shows a dominance of C4 savanna (325.27 kkm², 51% of the area), forest (118.28 kkm², 19%), and woodland (105.14 kkm², 17%; Fig. 4.1A, Fig. S4.1). Savanna is mainly found in eastern Kenya. In central and western Kenya, forest is the most dominant biome. Grassland occupies a region in northwest Kenya with a total area of 10% (C4 grassland: 65.71 kkm²) and desert covers 9.86 kkm² (3%; Fig. 4.1A, Fig. S4.1). C3 grassland and C3 savanna are not simulated in the present-day PNVM (; Fig. 4.1A, Fig. S4.1).

The spatial comparison between the aDGVM present-day PNVM and land cover maps derived from Sentinel data and an ESA product reveals a mixed pattern of agreement and discrepancies (Fig. 4.1B). The aDGVM simulations consistently overestimate the extent of the forest biomes, particularly when compared to the Sentinel-derived land cover map. aDGVM also overestimates the presence of C4 savanna compared to Sentinel but is more realistic when compared to the ESA WorldCover product (Fig. 4.1B&C). The Sentinel land cover map indeed shows a broader distribution of the C4 grassland biome, spread across much of the country, which covers a large part of the C4 Savanna area compared to ESA WorldCover.

Despite these differences, all datasets agree that C4 savanna is the dominant biome, with minimal representation in southwestern Kenya. The ESA land cover map suggests an even greater extent of C4 savanna compared to the Sentinel map but also shows a higher number of grid cells classified as C4 grassland compared to the aDGVM output. Notably, the southwestern forested region identified in the aDGVM PNVM is also captured in the ESA land cover map, indicating some agreement in this area (Fig. 4.1C). For both the Sentinel and ESA land cover maps, the dominant biome categories include C4 savanna, C4 grassland, and forest. Additionally, the Sentinel map includes the "other" category, reflecting areas that could not be categorized within the aDGVM biomes used in this study.

Beyond biome classification, the comparison of total AGB simulations between aDGVM and JULES for Kenya shows that JULES achieves stronger agreement with observational data (Fig S4.2) The aDGVM simulations exhibit a correlation coefficient of 0.27 with ESA AGB observations and 0.27 with NASA AGB observations (Fig. S.4.1A). In contrast, JULES demonstrates higher correlations, with values of 0.47 and 0.51 for ESA and NASA observations, respectively (Fig. S.4.1B).

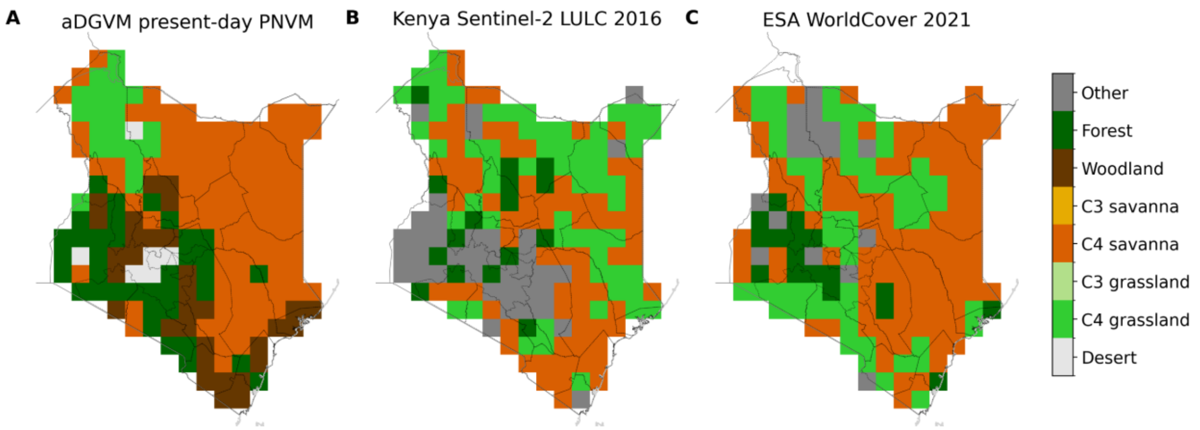

Fig. 4.1 Comparison of simulated aDGVM present-day PNVM (A) compared to two land cover maps (see Methods) from ESA WorldCover 2021 dataset (B) and Kenya Sentinel-2 LULC 2016 dataset (C).

4.3.2 Projected shifts in biomes and bioclimatic variables

The future projections of the PNVM for RCP4.5 show a noticeable increase in forest area with an increase of 86.11% compared to the present-day extent (Fig. 4.2A; Fig. S4.1). The expansion occurs mainly into C4 savanna (-2.02%) and woodland (-43.75%). Nevertheless, savanna is projected to remain the main biome as it also expands into grassland areas in western Kenya, reducing C4 grassland by 85% and desert by 17% compared to the present-day extent. C3 savanna (6.57 kkm²) and C3 grassland (3.29 kkm²) are projected to appear in western Kenya.

Under RCP8.5, the changes towards forested biomes are even more exacerbated with an additional expansion of 75.57 kkm² into savanna regions (-21.21% compared to present-day climate; Fig. 4.2B, Fig. S4.1). Forest is thus projected to become the dominant biome over the period 2080-2099 (Fig. S4.1). Also, woodland is projected to decrease drastically by 78.12% under RCP8.5 compared to present-day PNVM. C4 and C3 grasslands are projected to occupy a larger area under RCP8.5 (16.43 kkm2 and RCP8.5: 13.14 kkm²; respectively) than RCP4.5 (9.86 kkm2 and 3.29 kkm²; respectively) (Fig. S4.1).

These biome shifts are closely related to the spatial patterns of bioclimatic changes. The analysis of the bioclimatic variables shows that the areas with the highest temperature increase (leading to a shift in vegetation) are in Central to West Kenya (Fig. S4.3). This region currently experiences lower temperatures due to its topography, but under RCP8.5, warming is intensified, likely due to a change in albedo from snow melt (Fig. S4.3). Additionally, this region (Central-West Kenya) is where the uncertainties of the climate models are high (Fig. S4.4). For future precipitation changes, we find the strongest increase in annual precipitation in both scenarios in eastern and northern Kenya (Fig. S.4.5). Furthermore, the largest increase in annual precipitation is in line with projected biome shifts from forests into former savanna regions. The uncertainty from the climate models is especially large over the Mount Kenya region and is exacerbated in RCP8.5 (Fig. S4.6). The precipitation seasonality also differs greatly depending on the climate scenario. While under RCP4.5, it mainly decreases, with some exceptions in Southern Kenya, it increases under RCP8.5 everywhere, except on the southeastern coast (Fig. S4.7).

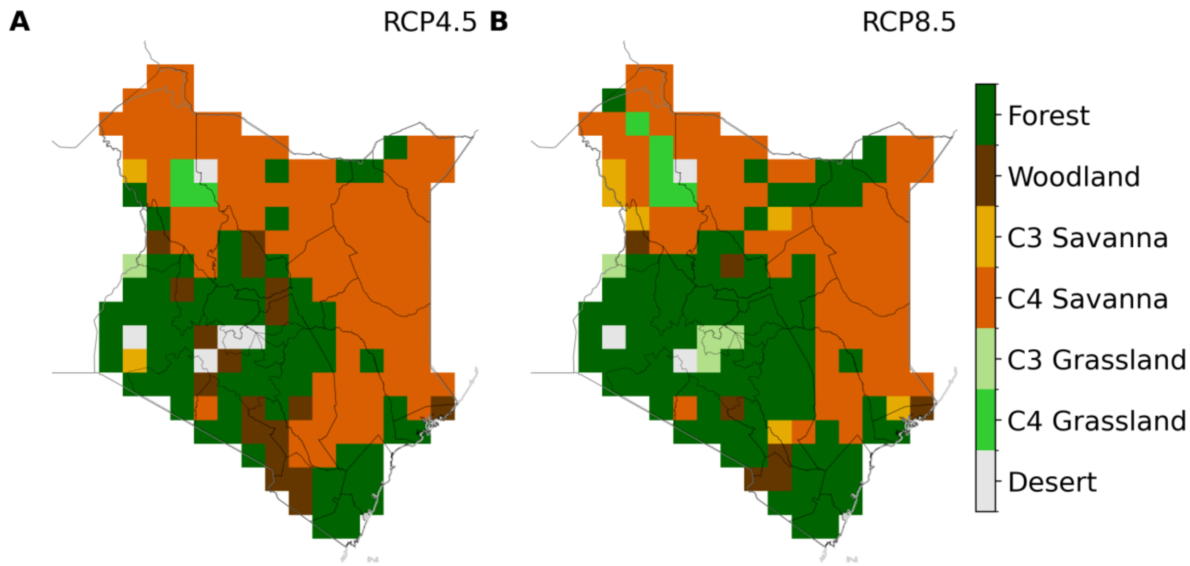

Fig. 4.2 PNVM of consensus biome type simulated by the aDGVM for (A) future RCP4.5 (2080 – 2099) and (B) RCP8.5 (2080-2099).

4.3.3 Projected tree cover change

Changes in tree cover, simulated as a state variable, drive biome shifts when certain thresholds are crossed. Substantial increases in tree cover can lead to shifts in biome classification, with woody encroachment potentially transitioning savannas toward more forested states, particularly under elevated CO_2 conditions (Bond & Midgley, 2012; Higgins & Scheiter, 2012; Martens et al., 2021) Interestingly, our projections indicate a general increase in tree cover across most regions of Kenya, with notable exceptions in southwestern Kenya (Fig. 4.3). In this region, decreases in tree cover coincide with a projected decline in precipitation, rising temperatures, and an expansion of grasslands, woodlands, and savanna areas into former forested regions (Figs. 4.2, S4.3 and S4.5).

This suggests that tree cover changes are not solely driven by forest encroachment into savannas but also occur extensively within regions projected to remain classified as savannas under both climate scenarios. This indicates woody encroachment into savannas (Fig. 4.3).

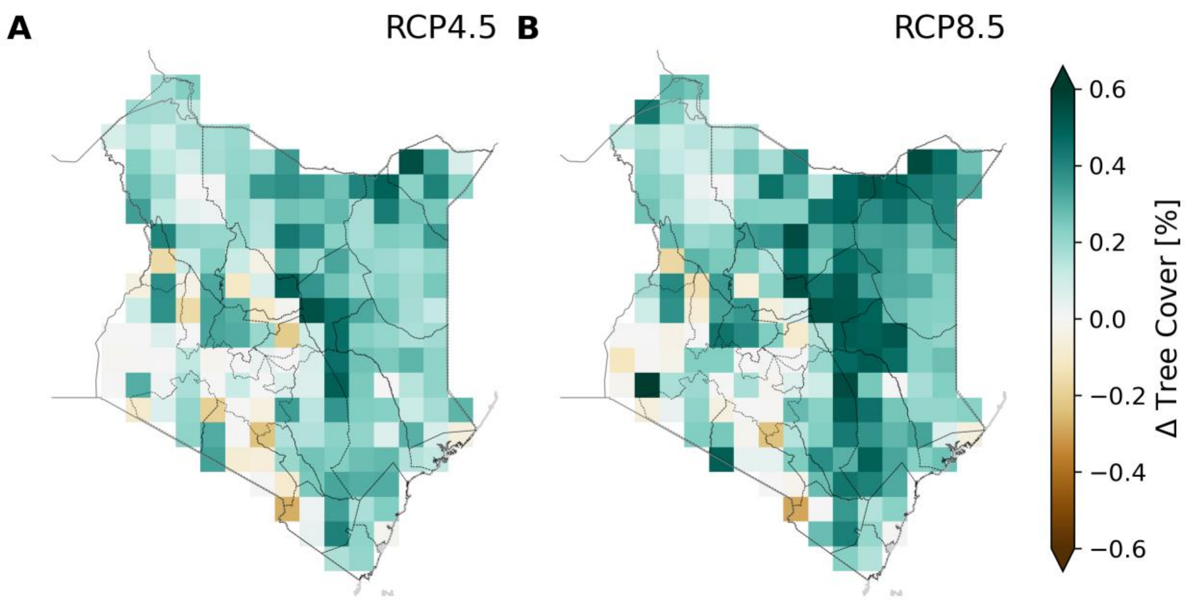

Fig. 4.3 Projected changes in tree cover across Kenya for the future (2080-2099) relative to present-day (2000-2019) for (A) RCP4.5 and (B) RCP8.5 respectively.

4.3.4 Woody encroachment and the trends of woody and grassy aboveground biomass

The relative change in grass AGB under RCP4.5 and RCP8.5 demonstrates a gradual increase over time, but with notable differences in magnitude and variability between the two scenarios. For RCP4.5, grassy AGB steadily increases, reaching 39.32% (± 19.18%) relative change in 2080-2099 compared to the historical baseline (20-year mean over 2000-2019; Fig. 4.4A). Nonetheless, the interannual variability is evident. Conversely, under the higher RCP8.5 emission scenario, grassy AGB exhibits a sharper increase, especially after 2020, reaching 84.35% (± 27.76%) relative change by the end of the century (Fig. 4.4A).

On the other hand, the relative change in tree AGB, closely tied to woody encroachment, shows a more pronounced and consistent increase compared to grass AGB under both scenarios. Under RCP4.5, tree AGB increases and then levels off towards the end of the century, reaching a relative change of 81.03% (± 17.41%) compared to the baseline (Fig. 4.4B). The uncertainty range mostly remains narrow throughout the century and notably increases towards the end of the century. Under RCP8.5, the relative change in tree AGB continues to increase without leveling off as in RCP4.5, reaching up to 137.43% (± 27.36) by 2100 (Fig. 4.4B). Notably, the uncertainty range broadens considerably after 2050.

The temporal evolution of total AGB projections under different RCPs and CO_2 assumptions (eCO_2: elevated CO_2, fCO_2: fixed CO_2) shows that the largest differences in AGB projections arise from differences in CO_2 fertilization (eCO_2 vs. fCO_2) rather than the RCPs (RCP4.5 vs. RCP8.5; Fig. S4.8).

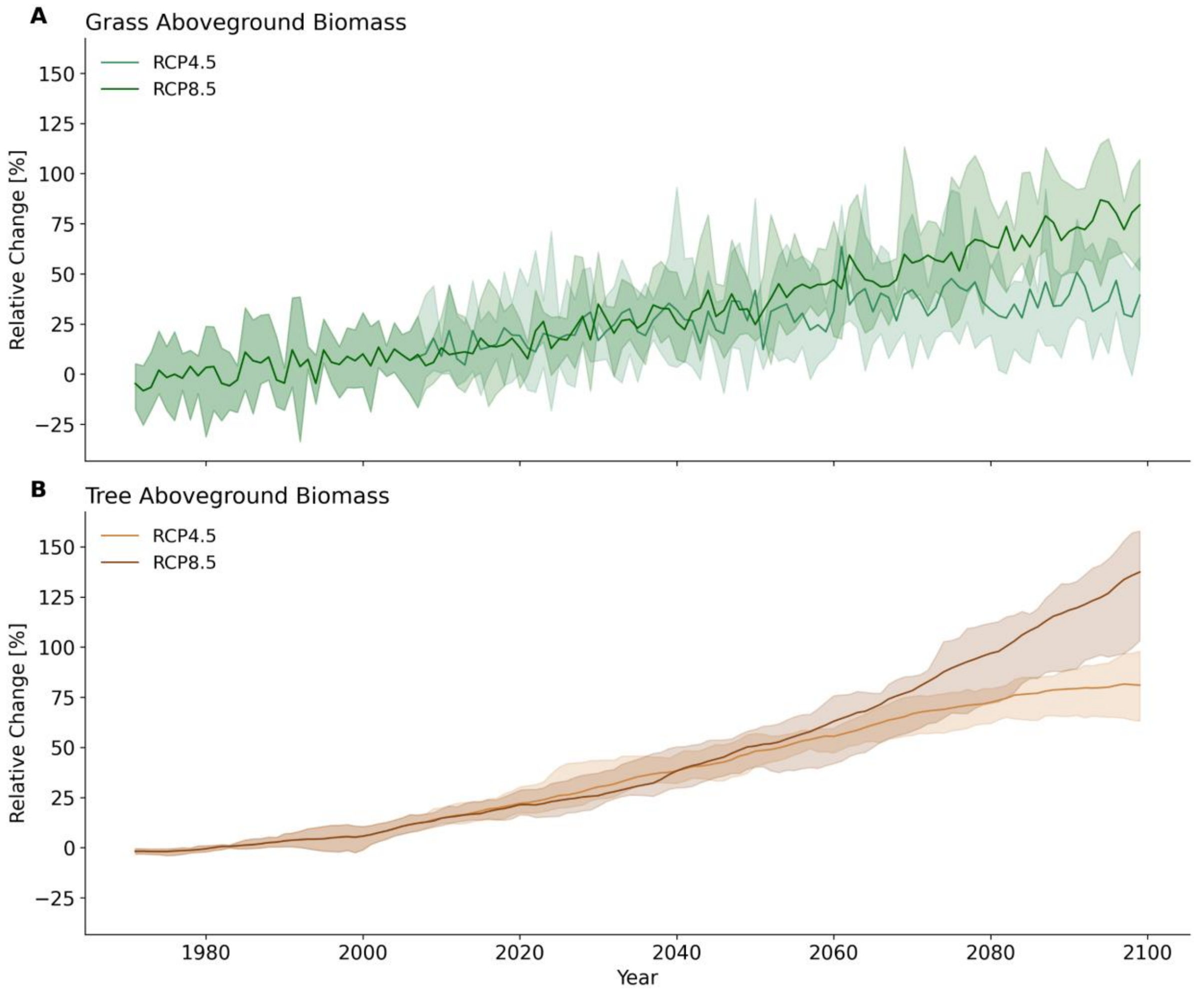

Fig. 4.4 Relative change for grassy (A) compared with tree (B) AGB. The solid line represents the mean relative change to the baseline period (first 20 years) for the scenarios RCP4.5 and RCP8.5 and displays the mean over the six GCM-driven aDGVM simulations. The shaded areas represent the uncertainty range, defined as the difference between the minimum and maximum relative changes at each timestep.

4.3.5 Comparison of aDGVM simulations to land use change projections

In this section, we analyze how projected land use changes, specifically cropland, and pasture expansion, compare to the projected biome shifts from aDGVM in Kenya. While previous sections have outlined the climate-driven changes in vegetation and tree cover, here we assess how land use may reinforce or counteract these trends.

In the present-day aDGVM biome distribution, the land use category non-forested land is simulated to be mainly found in C4 savannas (Fig. 4.5A). ‘Pasture, however, is distributed more broadly across all simulated biomes, with the largest fraction also in C4 savannas, followed by woodland, forest, and C4 grassland. Cropland is found also in all simulated biomes, however, makes up less total land use fraction than pasture. Forest is represented in the forest biome, but to a lesser extent than the other land use categories (Fig. 4.5A).

Keeping the biomes as present-day, the future projections for SSP2-RCP4.5 of land use indicate a decrease of non-forested land and cropland within the C4 savanna biome at the expense of an increase in pasture in the future. Also, in the forest biome, cropland is projected to be the dominant land use category, followed by non-forested land and cropland, with forest being the lowest represented land use category (Fig. 4.5B).

RCP8.5 is mainly projected to differ with regards to the land use category representation in the C4 savanna biome, where non-forested land is higher than under RCP4.5 and cropland makes out a much smaller part than pasture. In the forest biome, the forest land use category is also projected to represent the smallest part, with cropland projected to be the dominant land use category in this scenario, followed by natural land and pasture (Fig. 4.5C).

This is in line with our projections for tree cover and cropland expansion, which indicate a general increase in tree cover across most regions of Kenya (Fig. 4.3). Under RCP4.5, tree cover is projected to expand from 11.43% (2000–2019) to 15.86% (2080–2099), while under RCP8.5, it increases from 11.36% to 17.28%. This corresponds to a net increase of 4.44% and 5.92%, respectively. However, cropland expansion is projected to be significantly larger, particularly under SSP2-4.5, where cropland area is expected to increase from 8.85% to 31.27% (a 22.42% rise). Even under the more extreme SSP5-8.5 scenario, cropland expansion (from 8.85% to 20.33%) still outpaces tree cover gains.

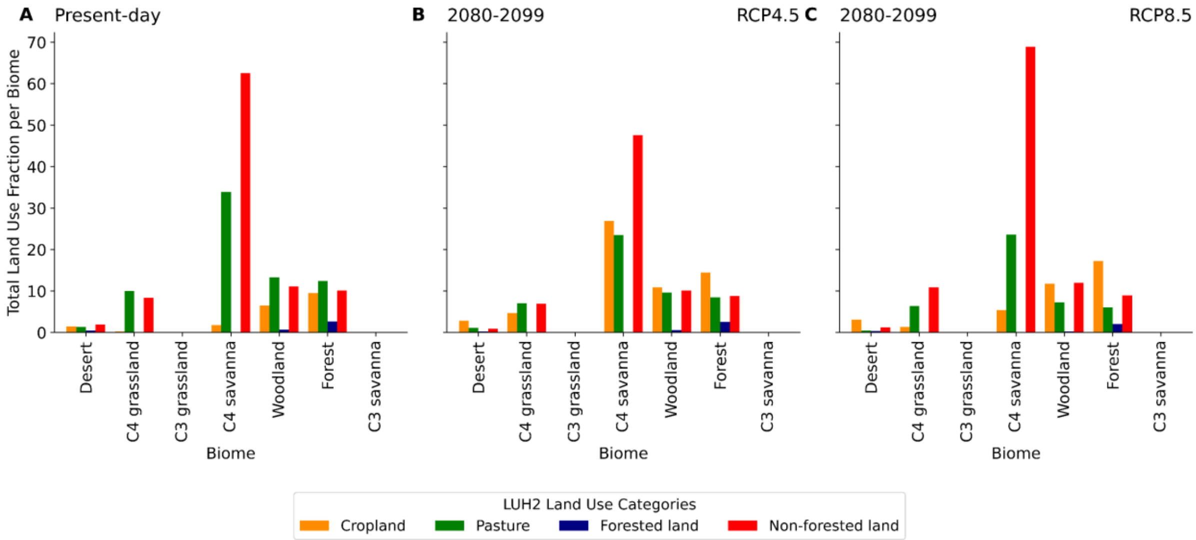

Fig. 4.5 Distribution of LUH2 land use categories per biome simulated by aDGVM in Kenya. (A) Shows the total land use fraction from LUH2 (Hurtt et al., 2020) per biome according to the present-day aDGVM PNVM (Fig. 4.1A) show the projected LUH2 land use fractions as total land use fraction per biome according to the present-day aDGVM PNVM for SSP2-RCP4.5 (B) and SSP5-RCP8.5 (C). For each grid cell of each biome class, the fraction of grid cells from the land use categories were counted and summed up to give a total land use fraction per land use category within each biome class.

4.4 Discussion and conclusions

This study aimed to assess climate-driven vegetation shifts in Kenya, with a particular focus on woody encroachment, by using the adaptive Dynamic Global Vegetation Model (aDGVM) to project future changes in biome composition and AGB under different climate scenarios. Our findings highlight the substantial biome shifts projected in Kenya under both RCP4.5 and RCP8.5, emphasizing the potential climate-driven transformation of the country's ecosystems. The PNVMs derived from the aDGVM suggest that forests will expand substantially at the expense of savannas and grasslands by the end of the century. Specifically, savanna, the current dominant biome, is projected to decrease by up to 21.2%, with forest area increasing by 86.1% and becoming the dominant biome under the RCP8.5 scenario. This projected reduction in savanna towards forest cover contrasts the finding of Parracciani et al. (2023), who found, based on standard national-scale remote sensing indices and statistical models, under the same high-emission scenario that savannas expand at the expense of forested areas using a statistical model approach driven by environmental variables, including temperature, soil moisture, livestock density, and topography. They noted a forest re-expansion in southwestern Kenya between 2050 and 2100 due to increased soil moisture and milder temperature increases in that region. This divergence underscores the influence of different modeling approaches on projected vegetation outcomes (Parracciani et al., 2023). Their projections did not detect woody encroachment. This may be due to differences in used models and data sources, as remote sensing indices reflect existing vegetation conditions that can already show signs of land degradation. In contrast, the aDGVM relies on GCM inputs and mechanistic processes, representing ecological interactions such as competition, fire dynamics, and CO_2 fertilization effects explicitly. However, differences in projections, as highlighted by Martens et al. (2021), can often be attributed to varying modeling methodologies and climate datasets.

Furthermore, as emphasized by Midgley & Bond (2015) and Moncrieff et al. (2016), projections of African terrestrial ecosystems can vary significantly due to differences in modeling approaches and contrasting precipitation scenarios. Given that African ecosystems are largely disturbance-driven, statistical modeling approaches such as Species Distribution Models (SDMs) may be unreliable in novel environmental conditions and often fail to incorporate competitive interactions (Zurell et al., 2020). Process-based models like the aDGVM, designed to represent physiological processes, offer an alternative approach that explicitly incorporates these dynamics. Our analysis, based on simulations from Martens et al. (2021), aligns with previous continental-scale studies using aDGVM, that projected AGB change was driven by CO_2 fertilization also in Kenya. Stevens et al. (2017) documented widespread woody encroachment across African savannas and noted that regions with low initial woody cover are more susceptible to rapid encroachment due to reduced competitive constraints. This pattern aligns with our findings that open savannas in Kenya are the most vulnerable to encroachment. Additionally, our study supports research projecting increased woody cover in response to elevated atmospheric CO_2 levels, as discussed by Higgins & Scheiter (2012) and Martens et al. (2021).

Precipitation trends introduce a major source of uncertainty in vegetation projections for East Africa, including Kenya (Jenkins et al., 2021). Our analysis indicates that eastern Kenya may experience increased annual precipitation, potentially supporting forest expansion, while western Kenya, currently a forested region, may face reduced rainfall and increased temperatures, leading to ecosystem stress. This aligns with studies such as those by Gebrechorkos et al. (2023) and Messmer et al. (2024), which indicate overall increases in projected precipitation based on different global or regional climate models. Precipitation has been identified as a key correlate of woody encroachment, with high-rainfall sites more prone to fluctuations in woody cover (Messmer et al., 2024; Stevens et al., 2017). Messmer et al. (2024) further demonstrated that regional precipitation patterns primarily shape grass species distributions, while temperature largely determines the maximum elevation that grass species can inhabit.

Woody encroachment has profound implications for biodiversity. Encroaching woody plants alter ecosystem characteristics by modifying vegetation structure and microclimates, impacting a wide range of species, including wildlife (Selemani et al., 2019). Soto-Shoender et al. (2018) projected reduced species richness in encroached savannas, highlighting that structural changes in vegetation can compromise ecosystem functioning and biodiversity. Additionally, tree cover change has been linked to habitat loss (Aleman et al., 2016), which in turn is an important driver for biodiversity loss

(Martens et al., 2022). Whilst Martens et al. (2022) showed increases in tree cover on the continental scale, indicating habitat loss in savanna and grassland, we have shown an increase in tree cover also for Kenya in savanna and grassland biome, reinforcing projected habitat loss. Aleman et al. (2016) have pointed out that even though tree cover is projected to increase, this is not automatically beneficial for biodiversity as they have also shown increased forest fragmentation, which further exacerbates biodiversity loss.

Human pressure, as land use change is another critical factor that influences biome distributions. Our comparison of aDGVM outputs with land use projections from the LUH2 dataset suggests that forest expansion driven by climate change alone may be overestimated when land use dynamics are excluded. LUH2 projections indicate cropland expansion into natural areas, which could mitigate or even reverse forest expansion trends. However, even with land use change considered, savannas remain vulnerable to habitat degradation and biodiversity loss.

Several limitations of our study should be acknowledged. The aDGVM does not include nutrient limitations, which may lead to an overestimation of the CO_2 fertilization effect (Hickler et al., 2015). Nutrient availability, for example, nitrogen and phosphorus, plays a crucial role in moderating plant responses to elevated CO_2. Previous studies (e.g., Martens et al., 2021) have explored the CO_2 fertilization effect and demonstrated the continued utility of aDGVM despite this limitation. Furthermore, we acknowledge that biome classifications vary across studies and influence the interpretation of vegetation distribution patterns (Fischer et al., 2022; Scheiter et al., 2024). This underscores the need for caution when comparing results across different models and classification schemes. Nonetheless, the here used classifications have been employed in previous studies, allowing for comparison of the results.

Another limitation is that our study does not simulate the influence of animals on vegetation dynamics. Both wild and domestic animals can significantly shape savanna ecosystems and contribute to potential biome shifts. Several DGVM studies have incorporated animal-vegetation interactions in a management context (e.g., Pachzelt et al., 2013; Pfeiffer et al., 2019; Scheiter et al., 2019). Including for example, African elephant impacts in future studies could enhance the realism of modeled savanna dynamics and improve our understanding of vegetation responses to climate and land use change (Scheiter & Higgins, 2012).

Comparing aDGVM outputs with observational datasets reveals notable discrepancies, particularly in biome classifications. While previous studies have demonstrated good agreement between aDGVM simulations and vegetation maps across Africa (Scheiter & Higgins, 2009), our comparisons indicate only fair agreement. However, variations even among the observational datasets and land cover maps derived from remote sensing data themselves show substantial variations and disagreement. Further, they include land use change, while this is not accounted for in aDGVM. Nevertheless, we do believe aDGVM to be the most suitable DGVM for such a study, due to the inability of many other DGVMs to simulate savanna distribution correctly (Scheiter & Higgins, 2009). Furthermore, this research is particularly valuable as there is little research on the future vegetation distribution for Kenya.

Future research should integrate dynamic land use change scenarios into DGVMs to enhance projections of biome distributions. Additionally, incorporating nutrient cycling processes and improving regional climate model outputs for East Africa could refine projections further. This knowledge is particularly crucial for informing biodiversity conservation strategies and wildlife corridor planning within Kenya's Vision 2030 framework. Understanding future vegetation dynamics is essential for developing adaptive management plans that support ecosystem resilience and biodiversity conservation in the face of climate change and land use pressures.

4.5 Acknowledgments

Calculations were performed on UBELIX (https://www.id.unibe.ch/hpc), the HPC cluster at the University of Bern. The authors would also like to thank Richard Pettifor for his feedback on this study.

Competing interests: The authors declare that they have no competing interests.

Data and materials availability: The data generated and analyzed during the current study are available from the corresponding author.

4.6 References

Aleman, J. C., Blarquez, O., & Staver, C. A. (2016). Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa. *Global Change Biology*, *22*(9), 3013–3025. https://doi.org/10.1111/GCB.13299

Ardö, J. (2015). Comparison between remote sensing and a dynamic vegetation model for estimating terrestrial primary production of Africa. *Carbon Balance and Management*, *10*(1), 8. https://doi.org/10.1186/s13021-015-0018-5

Bond, W. J., & Midgley, G. F. (2000). A proposed CO2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology*, *6*(8), 865–869. https://doi.org/10.1046/j.1365-2486.2000.00365.x

Bond, W. J., & Midgley, G. F. (2012). Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1588), 601–612. https://doi.org/10.1098/rstb.2011.0182

Chepkochei, L., Karanja, F., & Siriba, D. (2024). Historical Evolution of Access Regulations on Grasslands and Their Socio-Economic Impacts in Kenya: A Review. *Advances in Historical Studies*, *13*, 255–276. https://doi.org/10.4236/ahs.2024.134013

D'Onofrio, D., Baudena, M., Lasslop, G., Nieradzik, L. P., Wårlind, D., & von Hardenberg, J. (2020). Linking Vegetation-Climate-Fire Relationships in Sub-Saharan Africa to Key Ecological Processes in Two Dynamic Global Vegetation Models. *Frontiers in Environmental Science*, *8*. https://doi.org/10.3389/fenvs.2020.00136

Engelbrecht, F., Adegoke, J., Bopape, M.-J., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., Werner, M., Ichoku, C., & Gatebe, C. (2015). Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters*, *10*(8), 085004. https://doi.org/10.1088/1748-9326/10/8/085004

Fischer, J.-C., Walentowitz, A., & Beierkuhnlein, C. (2022). The biome inventory – Standardizing global biogeographical land units. *Global Ecology and Biogeography*, *31*(11), 2172–2183. https://doi.org/10.1111/geb.13574

Gebrechorkos, S. H., Taye, M. T., Birhanu, B., Solomon, D., & Demissie, T. (2023). Future Changes in Climate and Hydroclimate Extremes in East Africa. *Earth's Future*, *11*(2), e2022EF003011. https://doi.org/10.1029/2022EF003011

Global Soil Data Task Group. (2000). *Global gridded surfaces of selected soil characteristics (IGBP-DIS)*. ORNL Distributed Active Archive Center. https://doi.org/10.3334/ORNLDAAC/569

Grace, J., José, J. S., Meir, P., Miranda, H. S., & Montes, R. A. (2006). Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography*, *33*(3), 387–400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Havlik, P., Schneider, U. A., Schmid, E., Bottcher, H., Fritz, S., Skalsky, R., Aoki, K., De Cara, S., Kindermann, G., Kraxner, F., Leduc, S., McCallum, I., Mosnier, A., Sauer, T., & Obersteiner, M. (2011). Global land-use implications of first and second generation biofuel targets. *Energy Policy*, *39*(10), Article 10. https://doi.org/10.1016/j.enpol.2010.03.030

Hickler, T., Rammig, A., & Werner, C. (2015). Modelling CO2 Impacts on Forest Productivity. *Current Forestry Reports*, *1*(2), 69–80. https://doi.org/10.1007/s40725-015-0014-8

Higgins, S. I., & Scheiter, S. (2012). Atmospheric CO2 forces abrupt vegetation shifts locally, but not globally. *Nature*, *488*(7410), 209–212. https://doi.org/10.1038/nature11238

Hurtt, G. C., Chini, L., Sahajpal, R., Frolking, S., Bodirsky, B. L., Calvin, K., Doelman, J. C., Fisk, J., Fujimori, S., Klein Goldewijk, K., Hasegawa, T., Havlik, P., Heinimann, A., Humpenöder, F., Jungclaus, J., Kaplan, J. O., Kennedy, J., Krisztin, T., Lawrence, D., … Zhang, X. (2020). Harmonization of global land use change and management for the period 850-2100 (LUH2) for CMIP6. *Geosci. Model Dev*, *13*, 5425–5464. https://doi.org/10.5194/gmd-13-5425-2020

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services. . S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages.* Zenodo. https://doi.org/10.5281/zenodo.3553579

Jenkins, R. L. M., Warren, R. F., & Price, J. T. (2021). Addressing risks to biodiversity arising from a changing climate: The need for ecosystem restoration in the Tana River Basin, Kenya. *PLOS ONE*, *16*(7), e0254879. https://doi.org/10.1371/journal.pone.0254879

Kiteme, B., Breu, T. M., Bastide, J., Eckert, S., Fischer, M., Gonzalez Rojí, S. J., Hergarten, C., Hurni, K., Messmer, M. B., Raible, C., Snethlage, M. A., Stocker, T., Torre-Marin Rando, M. del A., & Wiesmann, U. M. (2021). *Towards sustainable futures for nature and people. An appraisal report for the Mt. Kenya– Ewaso Ng'iro North landscape, Kenya*. University of Bern. https://doi.org/10.48350/161382

Kriegler, E., Bauer, N., Popp, A., Humpenöder, F., Leimbach, M., Strefler, J., Baumstark, L., Bodirsky, B. L., Hilaire, J., Klein, D., Mouratiadou, I., Weindl, I., Bertram, C., Dietrich, J.-P., Luderer, G., Pehl, M., Pietzcker, R., Piontek, F., Lotze-Campen, H., … Edenhofer, O. (2017). Fossil-fueled development (SSP5): An energy and resource intensive scenario for the 21st century. *Global Environmental Change*, *42*, 297–315. https://doi.org/10.1016/j.gloenvcha.2016.05.015

Martens, C., Hickler, T., Davis-Reddy, C., Engelbrecht, F., Higgins, S. I., Maltitz, G. P., Midgley, G. F., Pfeiffer, M., & Scheiter, S. (2021). Large uncertainties in future biome changes in Africa call for flexible climate adaptation strategies. *Global Change Biology*, *27*(2), 340–358. https://doi.org/10.1111/gcb.15390

Martens, C., Scheiter, S., Midgley, G. F., & Hickler, T. (2022). Combined impacts of future climate-driven vegetation changes and socioeconomic pressures on protected areas in Africa. *Conservation Biology*, *36*(6). https://doi.org/10.1111/cobi.13968

Mathison, C., Burke, E., Hartley, A. J., Kelley, D. I., Burton, C., Robertson, E., Gedney, N., Williams, K., Wiltshire, A., Ellis, R. J., Sellar, A. A., & Jones, C. D. (2023). Description and evaluation of the JULES-ES set-up for ISIMIP2b. *Geoscientific Model Development*, *16*(14), 4249–4264. https://doi.org/10.5194/gmd-16-4249-2023

McGregor, J. L., & Dix, M. R. (2008). An updated description of the conformal-cubic atmospheric model. In K. Hamilton & W. Ohfuchi (Eds.), *High resolution numerical modelling of the atmosphere and ocean* (pp. 51–75). Springer New York. https://doi.org/10.1007/978-0-387-49791-4_4

Messmer, M., Eckert, S., Torre-Marin Rando, A., Snethlage, M., González-Rojí, S. J., Hurni, K., Beyerle, U., Hemp, A., Kibet, S., & Stocker, T. F. (2024). Major distribution shifts are projected for key rangeland grasses under a high-emission scenario in East Africa at the end of the 21st century. *Communications Earth & Environment*, *5*(1), 1–12. https://doi.org/10.1038/s43247-024-01731-x

Midgley, G. F., & Bond, W. J. (2015). Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change. *Nature Climate Change*, *5*(9), 823–829. https://doi.org/10.1038/nclimate2753

Moncrieff, G. R., Scheiter, S., Langan, L., Trabucco, A., & Higgins, S. I. (2016). The future distribution of the savannah biome: Model-based and biogeographic contingency. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1703), 20150311. https://doi.org/10.1098/rstb.2015.0311

Njoka JT, Yanda P, Maganga F, Liwenga E, Kateka A, & Henku A. (2016). *Kenya: Country situation assessment. Working paper.* https://idl-bnc-idrc.dspacedirect.org/server/api/core/bitstreams/9b334416-a601-4bb2-a93e-c74d776004c3/content

Ojwang', G. O., Wargute, P. W., Said, M. Y., Worden, J. S., Davidson, Z., Muruthi, P., Kanga, E., Ihwagi, F., & Okita-Ouma, B. (2017). *Wildlife Migratory Corridors and Dispersal Areas: Kenya*

Rangelands and Coastal Terrestrial Ecosystems. https://www.kws.go.ke/content/report-wildlife-corridors-and-dispersal-areas

Pachzelt, A., Rammig, A., Higgins, S., & Hickler, T. (2013). Coupling a physiological grazer population model with a generalized model for vegetation dynamics. *Ecological Modelling*, *263*, 92–102. https://doi.org/10.1016/j.ecolmodel.2013.04.025

Parracciani, C., Buitenwerf, R., & Svenning, J.-C. (2023). Impacts of Climate Change on Vegetation in Kenya: Future Projections and Implications for Protected Areas. *Land*, *12*(11), Article 11. https://doi.org/10.3390/land12112052

Pfeiffer, M., Kumar, D., Martens, C., & Scheiter, S. (2020). Climate change will cause non-analog vegetation states in Africa and commit vegetation to long-term change. *Biogeosciences*, *17*(22), 5829–5847. https://doi.org/10.5194/bg-17-5829-2020

Pfeiffer, M., Langan, L., Linstädter, A., Martens, C., Gaillard, C., Ruppert, J. C., Higgins, S. I., Mudongo, E. I., & Scheiter, S. (2019). Grazing and aridity reduce perennial grass abundance in semi-arid rangelands – Insights from a trait-based dynamic vegetation model. *Ecological Modelling*, *395*, 11–22. https://doi.org/10.1016/j.ecolmodel.2018.12.013

Pinheiro, L. F. S., Kansbock, L., Rossatto, D. R., & Kolb, R. M. (2022). Woody plant encroachment constrains regeneration of ground-layer species in a neotropical savanna from seeds. *Austral Ecology*, *47*(3), 674–684. https://doi.org/10.1111/aec.13156

Powers, R. P., & Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change 2019 9:4*, *9*(4), 323–329. https://doi.org/10.1038/s41558-019-0406-z

Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., Sitch, S., Smith, B., & Sykes, M. T. (2007). Dynamic Global Vegetation Modeling: Quantifying Terrestrial Ecosystem Responses to Large-Scale Environmental Change. In J. G. Canadell, D. E. Pataki, & L. F. Pitelka (Eds.), *Terrestrial Ecosystems in a Changing World* (pp. 175–192). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-32730-1_15

Regional Centre for Mapping of Resources for Development (RCMRD), European Space Agency (ESA). (2016). *Kenya Sentinel2 Land Use Land Cover 2016* [Dataset].

Santoro, M., & Cartus, O. (2021). *SA Biomass Climate Change Initiative (Biomass_cci): Global datasets of forest above-ground biomass for the years 2010, 2017 and 2018, v3. NERC EDS Centre for Environmental Data Analysis, 26 November 2021*. [Dataset].

Scheiter, S., Gaillard, C., Martens, C., Erasmus, B. F. N., & Pfeiffer, M. (2018). How vulnerable are ecosystems in the Limpopo province to climate change? *South African Journal of Botany*, *116*, 86–95. https://doi.org/10.1016/j.sajb.2018.02.394

Scheiter, S., & Higgins, S. I. (2009). Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. *Global Change Biology*, *15*(9), 2224–2246. https://doi.org/10.1111/j.1365-2486.2008.01838.x

Scheiter, S., & Higgins, S. I. (2012). How many elephants can you fit into a conservation area. *Conservation Letters*, *5*(3), 176–185. https://doi.org/10.1111/j.1755-263X.2012.00225.x

Scheiter, S., Higgins, S. I., Osborne, C. P., Bradshaw, C., Lunt, D., Ripley, B. S., Taylor, L. L., & Beerling, D. J. (2012). Fire and fire-adapted vegetation promoted C4 expansion in the late Miocene. *New Phytologist*, *195*(3), 653–666. https://doi.org/10.1111/j.1469-8137.2012.04202.x

Scheiter, S., Kumar, D., Pfeiffer, M., & Langan, L. (2024). Biome classification influences current and projected future biome distributions. *Global Ecology and Biogeography*, *33*(2), 259–271. https://doi.org/10.1111/geb.13784

Scheiter, S., Schulte, J., Pfeiffer, M., Martens, C., Erasmus, B. F. N., & Twine, W. C. (2019). How Does Climate Change Influence the Economic Value of Ecosystem Services in Savanna Rangelands? *Ecological Economics*, *157*, 342–356. https://doi.org/10.1016/j.ecolecon.2018.11.015

Selemani, I. S., Sangeda, A. Z., Selemani, I. S., & Sangeda, A. Z. (2019). Spatial and Temporal Vegetation Dynamics: Opportunities and Constraints behind Wildlife Migration in Eastern Africa Savanna Ecosystem. In *Wildlife Management—Failures, Successes and Prospects*. IntechOpen. https://doi.org/10.5772/intechopen.72617

Soto-Shoender, J. R., McCleery, R. A., Monadjem, A., & Gwinn, D. C. (2018). The importance of grass cover for mammalian diversity and habitat associations in a bush encroached savanna. *Biological Conservation*, *221*, 127–136. https://doi.org/10.1016/j.biocon.2018.02.028

Spawn, S. A., & Gibbs, H. K. (2020). *Global aboveground and belowground biomass carbon density maps for the year 2010*. ORNL Distributed Active Archive Center. https://doi.org/10.3334/ORNLDAAC/1763

Stevens, N., Lehmann, C. E. R., Murphy, B. P., & Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global Change Biology*, *23*(1), 235–244. https://doi.org/10.1111/gcb.13409

Trisos, C. H., I.O. Adelekan, E. Totin, A. Ayanlade, J. Efitre, A. Gemeda, K. Kalaba, C. Lennard, C. Masao, Y. Mgaya, G. Ngaruiya, D. Olago, N.P. Simpson, & S. Zakieldeen. (2022). Africa. In: Climate

Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. In *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (1st ed., pp. 1285–1455). Cambridge University Press. https://doi.org/10.1017/9781009325844.011

Venter, Z. S., Cramer, M. D., & Hawkins, H.-J. (2018). Drivers of woody plant encroachment over Africa. *Nature Communications*, *9*(1), 2272. https://doi.org/10.1038/s41467-018-04616-8

Zanaga, D., Van De Kerchove, R., Daems, D., De Keersmaecker, W., Brockmann, C., Kirches, G., Wevers, J., Cartus, O., Santoro, M., Fritz, S., Lesiv, M., Herold, M., Tsendbazar, N. E., Xu, P., Ramoino, F., & Arino. (2022). *ESA WorldCover 10 m 2021 v200 (Version v200) [Data set]. Zenodo.* [Dataset]. https://doi.org/10.5281/zenodo.7254221

Zurell, D., Zimmermann, N. E., Gross, H., Baltensweiler, A., Sattler, T., & Wüest, R. O. (2020). Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography*, *47*(1), 101–113. https://doi.org/10.1111/jbi.13608

4.7 Supplementary materials

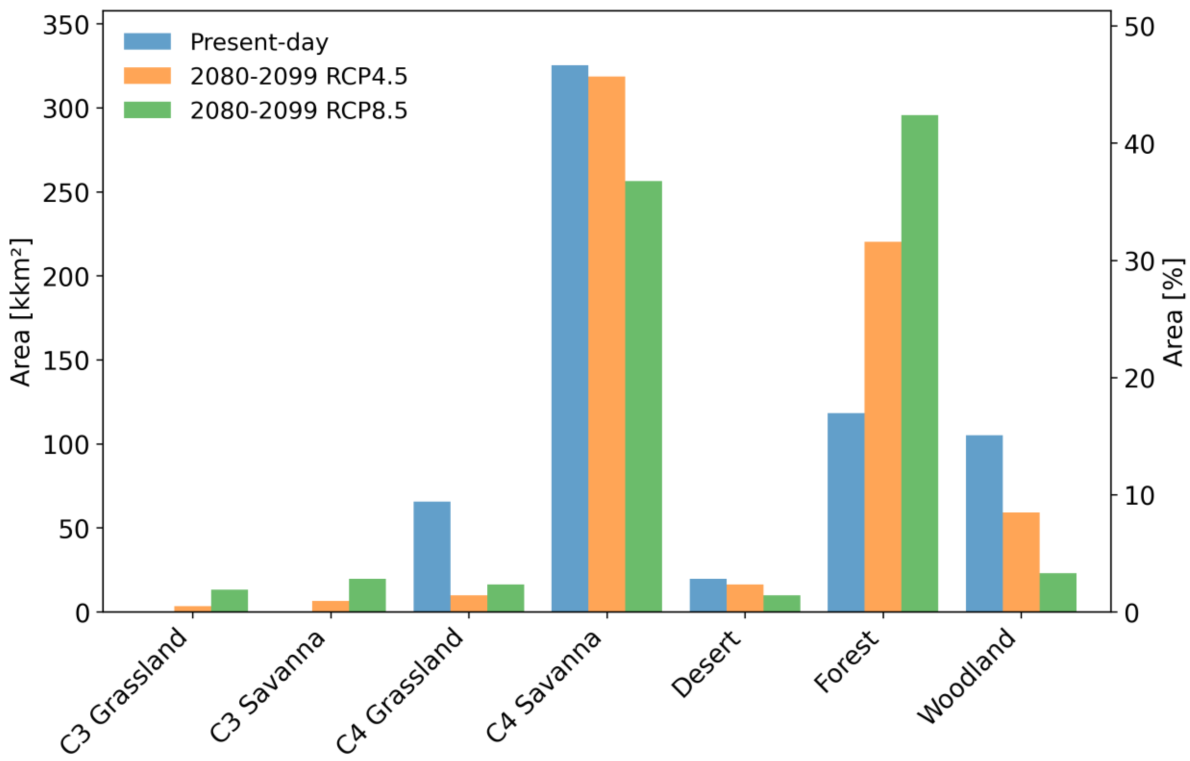

Fig. S4.1 Projected biome extent indicated in, given in thousand square kilometers [kkm2] and percentage [%] for present-day (2000-2019) and future simulations of aDGVM over Kenya.

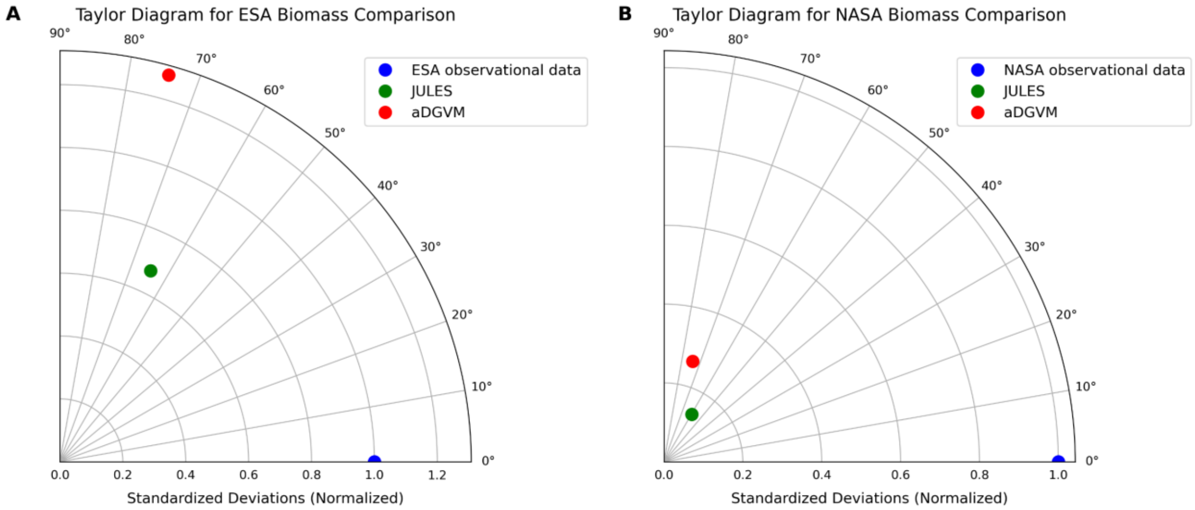

Fig. S4.2 Talyor diagrams for AGB comparing present-day (2000-2019) aDGVM and JULES simulations to observational data from ESA (A) and NASA (B; see Methods).

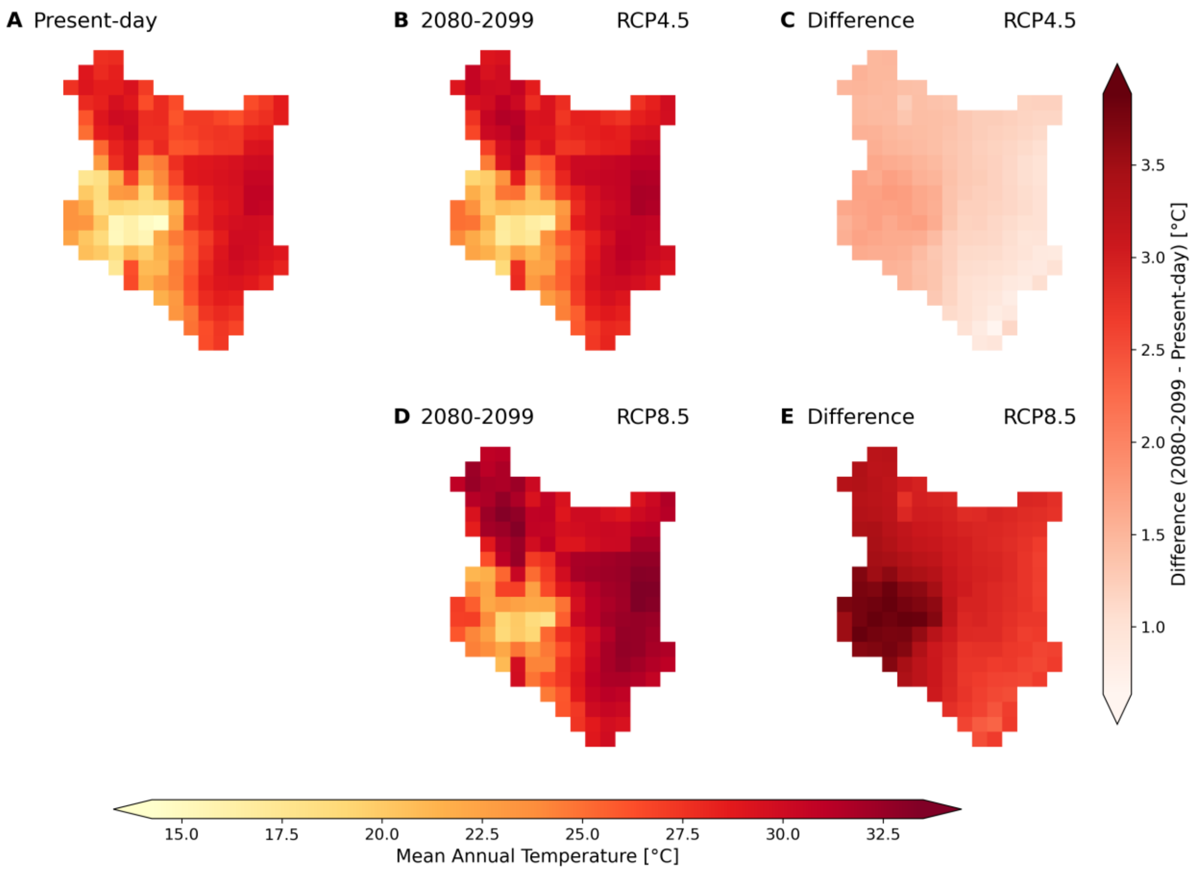

Fig. S4.3 CMIP5 GCM ensemble for mean annual temperature [°C] for present-day climate (A), future projections under RCP4.5 (B) and RCP8.5 (D), and the respective differences between future and present-day climates (C, E). The difference maps (C, E) illustrate projected temperature changes for the future compared to the present-day period for RCP4.5 and RCP8.5, respectively.

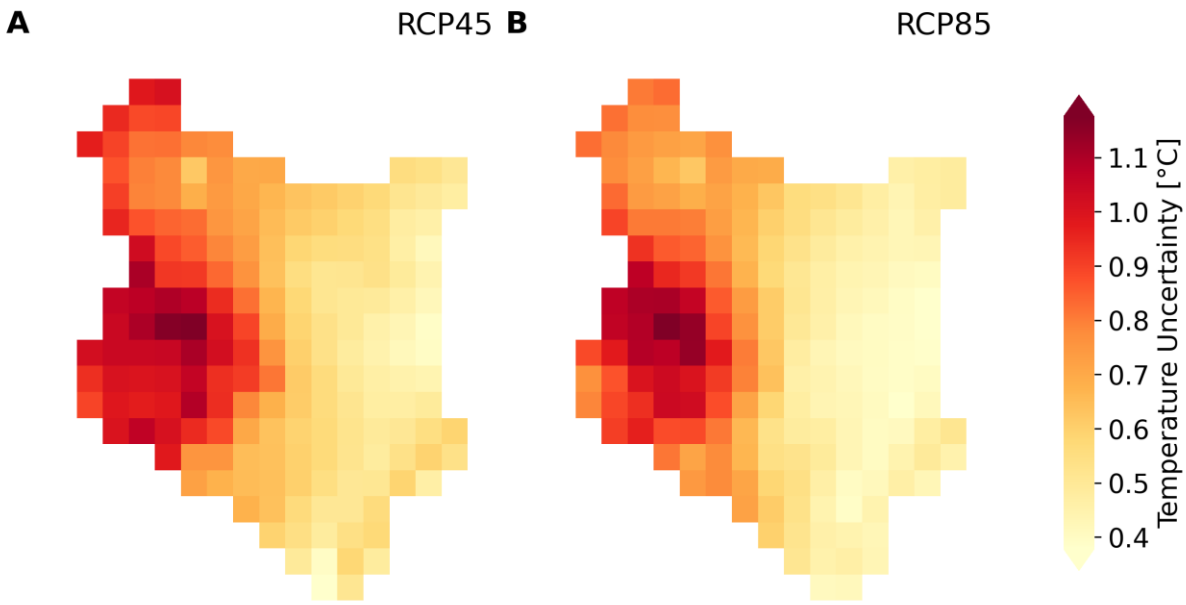

Fig. S4.4 Temperature uncertainty, given as the standard or mean annual temperature [°C] over all GCM for the future (2080-2099) under (A) RCP4.5 and (B) RCP8.5.

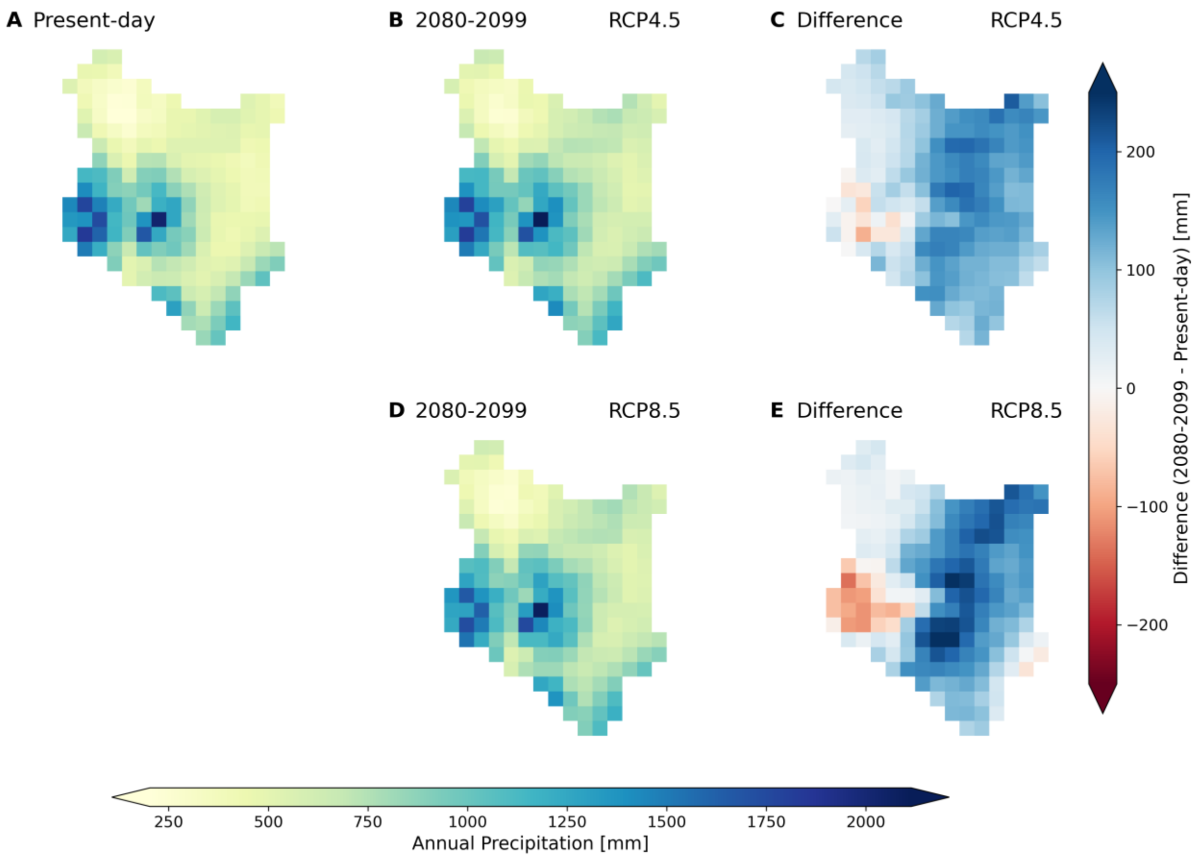

Fig. S4.5 CMIP5 GCM ensemble for mean annual precipitation [mm] for present-day climate (A), future projections under RCP4.5 (B) and RCP8.5 (D), and the respective differences between future and present-day climates (C, E). The difference maps (C, E) illustrate projected precipitation changes for the future compared to the present-day period for RCP4.5 and RCP8.5, respectively.

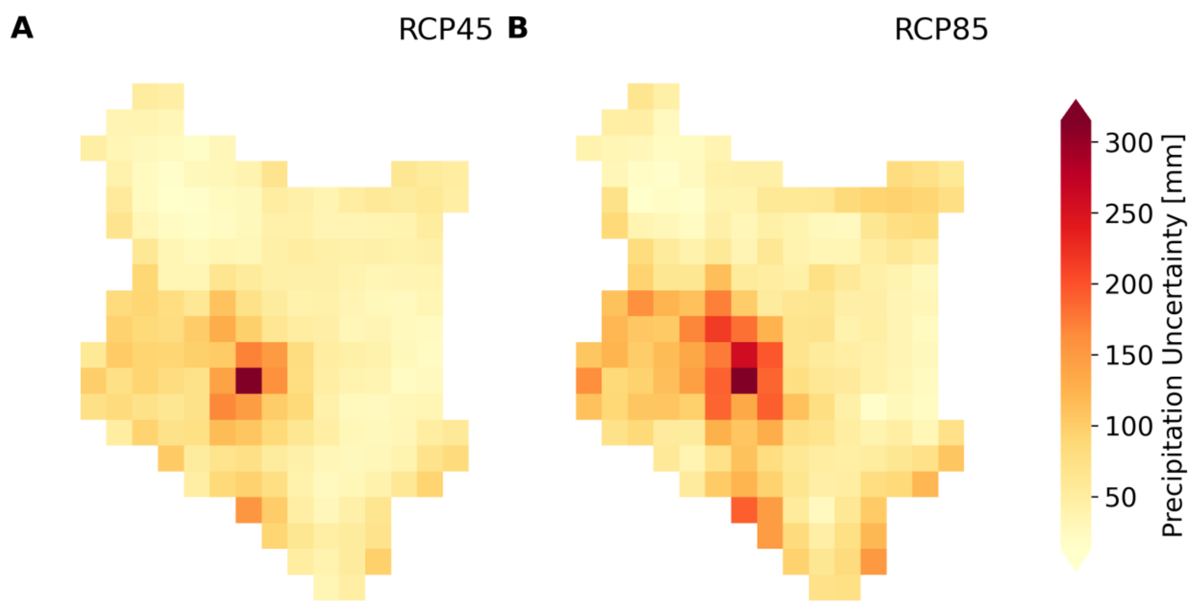

Fig. S4.6 Precipitation uncertainty, given as the standard deviation for mean annual precipitation [mm] over all GCM for the future (2080-2099) under (A) RCP4.5 and (B) RCP8.5.

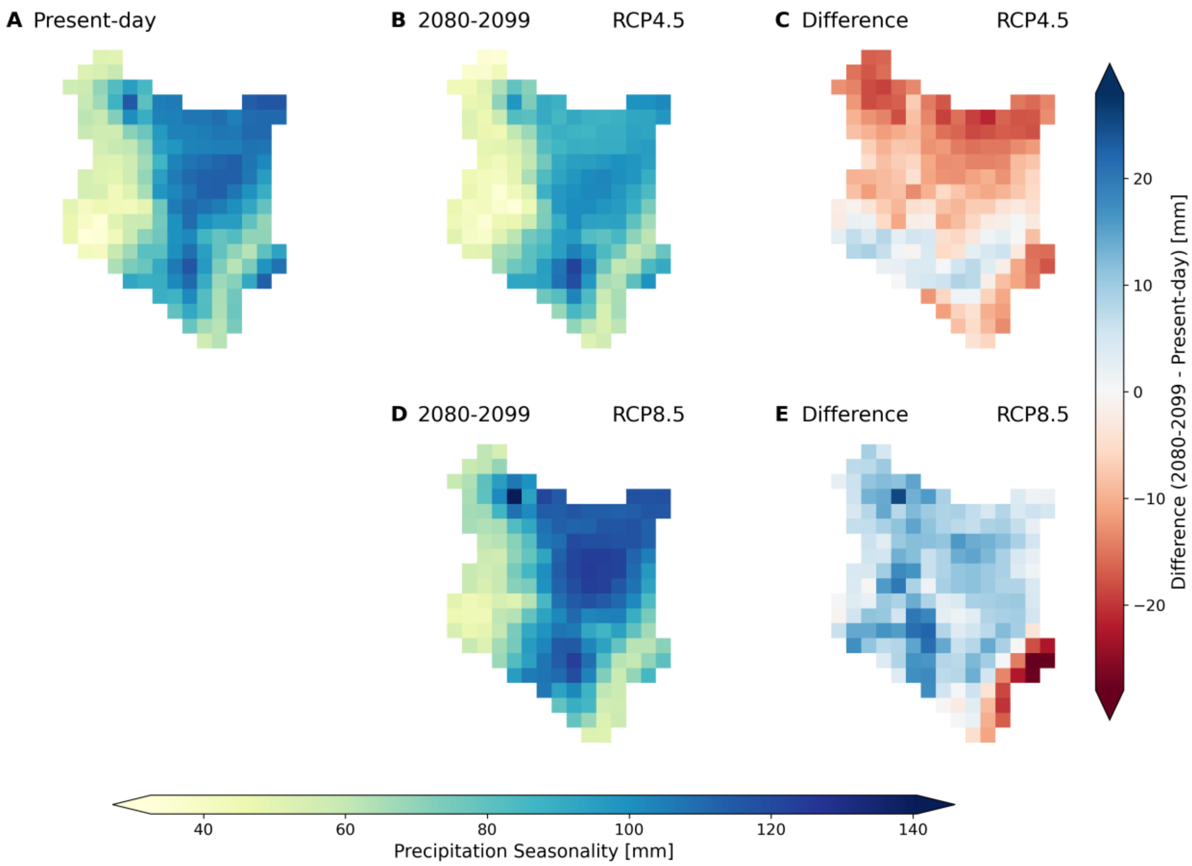

Fig. S4.7 CMIP5 GCM ensemble for precipitation seasonality (i.e. annual range in precipitation) [mm] for present-day climate (A), future projections under RCP4.5 (B) and RCP8.5 (D), and the respective differences between future and present-day climates (C, E). The difference maps (C, E) illustrate projected precipitation seasonality changes for the future compared to the present-day period for RCP4.5 and RCP8.5, respectively.

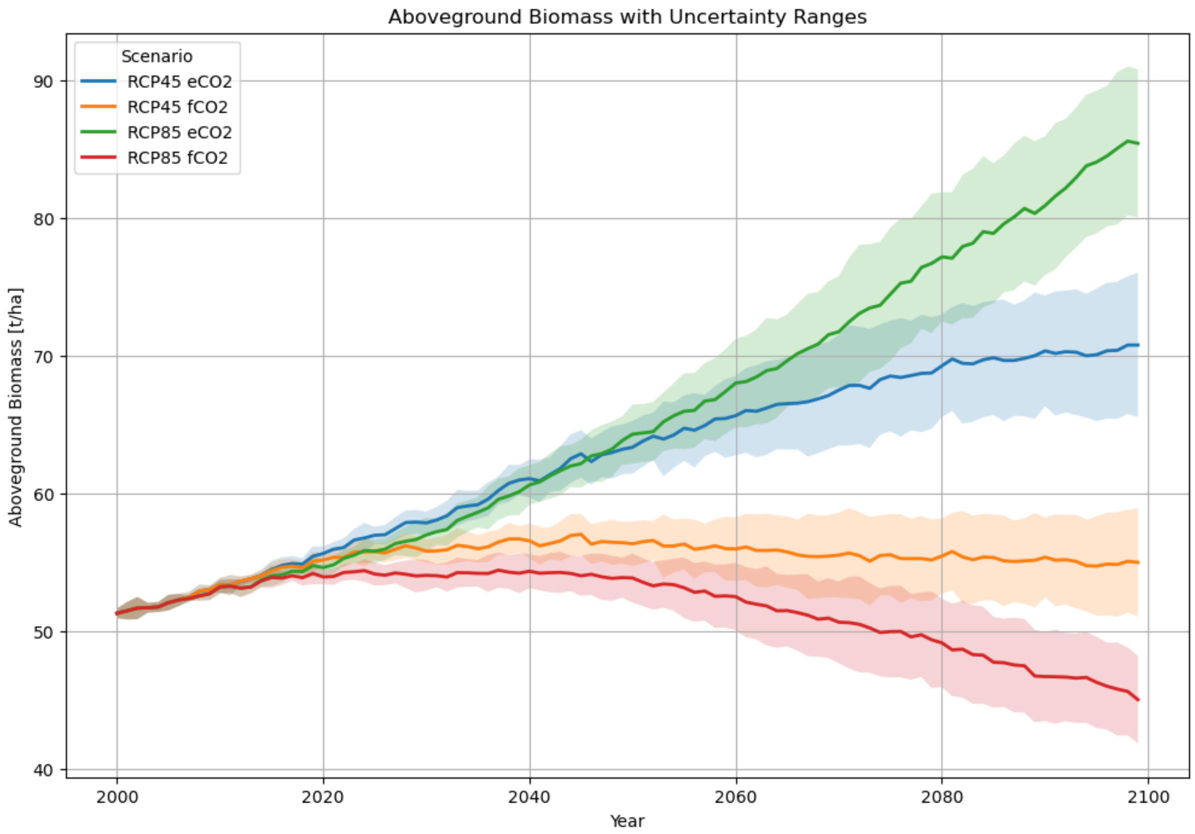

Fig. S4.8 Comparison of total AGB over Kenya for two RCP scenarios (RCP4.5 and RCP8.5) and two CO_2 assumptions (eCO_2: elevated CO2, fCO_2: fixed CO_2). For the eCO_2 simulation design, CO_2 increased according to the RCP2. For the fCO_2 set up the simulations were repeated with climate conditions following the two RCP scenarios but with CO_2 rising only to 400ppm and then keeping it fixed at that level (Martens et al., 2021).

Table S4.1 Reclassification of observed land cover categories into biome classifications used in the aDGVM simulations.

aDGVM	**Kenya Sentienl-2 LULC 2016**	**ESA WorldCover 2021**
Desert		
C4 grassland	3 Grassland	30 grassland, 90 herbaceous wetland
C3 grassland		
C3 savanna		
C4 savanna	2 Shrub cover, 6 lichen mosses/sparse vegetation, 7 bare areas	20 shrubland, bare/sparse vegetation, 100 moss and lichen
Woodland		95 mangroves
Forest	1 tree cover	10 tree cover

Chapter 5

Summary and conclusions

This thesis identifies and addresses key knowledge gaps in biodiversity research, specifically: (1) the lack of integrated climate and land use change projections in species distribution models (SDMs), (2) limited assessments of protected area (PA) effectiveness under future climate and land use change, and (3) the need for regional-scale biodiversity assessment studies in highly vulnerable arid and semi-arid lands (ASALs). To tackle these gaps, I investigated how climate change, land use change, and their combined effects impact future biodiversity at both global and regional scales. At the global scale, I integrated land use change projections into climate-driven SDMs. At the regional scale, I assessed climate-driven vegetation dynamics using a dynamic global vegetation model (DGVM) and compared these with land use change projections.

5.1 Climate and land use change impacts on future biodiversity under different scenarios

In addressing the first two posed research questions of how climate change and land use change impact biodiversity and their relative importance under different scenarios, the first global assessment (Chapter 2) demonstrates that climate change and land use change are both major drivers of biodiversity loss, with their relative importance varying by scenario and region. Climate-driven biodiversity loss is projected to scale with emissions, with higher projected losses under higher-emission scenarios. Land use change is highly scenario-dependent. Under SSP1-RCP2.6, land use change is projected to alleviate climate-driven biodiversity loss, whereas under SSP4-RCP6.0, land use change exacerbates biodiversity loss.

The findings further indicate that climate change is projected to drive species shifts toward higher latitudes, while land use change either facilitates or constrains these shifts, depending on the scenario. In the mid-to lower-latitude regions, both drivers contribute to projected biodiversity loss. Sub-Saharan Africa emerges as a high-risk region, where projected deforestation and pasture expansion under SSP4-RCP6.0 make land use change the dominant driver of biodiversity loss. Consequently, the regional analysis focuses on a sub-Saharan country characterized by distinct ecosystem challenges in its ASALs. At the regional scale (Chapter 4), climate-driven vegetation shifts in Kenya indicate increasing woody encroachment under the high-emission scenario, reducing savanna biomes critical for biodiversity. However, when land use change is incorporated, cropland expansion surpasses the projected tree cover increase under SSP2-RCP4.5.

5.2 Ecological effectiveness of PA expansion

We also assessed how effective different PA expansion strategies are in mitigating biodiversity loss under future climate and land use change (Chapter 3). Results show that climate mitigation and sustainable land use consistently provide stronger projected biodiversity benefits than PA expansion alone. Climate mitigation prevents a projected 0.85 percentage point loss in global mean species richness, while sustainable land use prevents an 8.58 percentage point loss by 2080 under SSP4-RCP6.0. We have shown that expanding PAs to 30% can reduce projected biodiversity loss, but benefits diminish when management effectiveness of the PAs is limited.

5.3 Climate-driven vegetation shifts and land use change impacts in Kenya

The regional case study of Kenya (Chapter 4) further highlights the complexity of biodiversity responses to climate and land use change. By the end of the 21st century, Kenya’s vegetation is projected to undergo substantial shifts, with forests expanding at the expense of savannas and grasslands under both RCP4.5 and RCP8.5. Under RCP8.5, forest biomes may increase by up to 86.1%, while savanna cover could decline by up to 21.2%, signifying woody encroachment. This encroachment is driven by elevated atmospheric CO_2 levels, altered precipitation patterns, and rising temperatures (Aleman et al., 2016; Martens et al., 2022; Venter et al., 2018). However, land use pressures, such as agricultural expansion, may counteract these trends, altering the extent of woody encroachment and emphasizing the need for an integrated assessment approach.

5.4 Bridging global and regional biodiversity assessments

This thesis provides key advancements in understanding future biodiversity change driven by climate and land use change at global and regional scales. The first global assessment offers novel insights into the scenario- and region-dependent combined and relative importance of these drivers, shining light on where climate or land use change is the dominant factor. To achieve this, a methodological advancement in biodiversity modeling was necessary. In this thesis, I developed and presented a modeling framework that enables the incorporation of land use change projections from integrated assessment models (IAMs) into climate-driven SDMs through a land use filtering approach. Furthermore, I highlight the need for regional-scale studies by demonstrating the uneven global impact patterns of climate and land use change. Thus, at the regional scale, this thesis addresses a critical knowledge gap by providing new insights into climate-driven vegetation changes in Kenya, a region characterized by its large ASAL extent. Using a DGVM, Chapter 4 of this thesis examines potential vegetation shifts under climate change and compares them with land use change projections from IAMs. By incorporating both global and regional perspectives, this thesis provides a more holistic view of climate and land use change impacts on biodiversity. The inclusion of two scales in one thesis strengthens our ability and underlines the need to evaluate biodiversity responses across different ecological complexities: from shifts in species distribution to vegetation. In the following, I will discuss key insights from the global assessments, their relevance for regional-scale biodiversity assessments, the added value of integrating both scales and how regional findings can refine global biodiversity models.

First, the two global assessments provide complementary insights. In Chapter 2, I present a framework and first results to assess the impacts of climate change, land use change, and their combined effects on biodiversity. However, an important dimension not directly accounted for in this first assessment of biodiversity change was the role of area-based conservation strategies in mitigating biodiversity loss. Chapter 3 expands on this by incorporating PAs into the modeling framework, revealing that while PAs can mitigate biodiversity loss, their effectiveness is constrained by overarching climate and land use trends. Thus, Chapter 3 builds upon and refines the findings of Chapter 2.

Both global studies highlight sub-Saharan Africa as a region particularly at risk for climate and land use change-driven biodiversity loss, the latter being the main driver under a scenario of inequality (SSP4-RCP6.0) with PA expansion to 30%, this region is still most vulnerable, and if the management effectiveness falls short, then there is still a lot of biodiversity loss in this region, motivating a regional analysis. SDMs are a state-of-the-art tool for projecting future species distributions; however, their reliance on correlations with environmental variables limits their ability to capture dynamic ecological processes, which are particularly important in savanna ecosystems. Recognizing this limitation, Chapter 4 makes use of DGVM simulations to more accurately investigate climate-driven vegetation dynamics in Kenya, a country predominated by ASALs. This approach is essential for capturing key processes such as woody encroachment, a climate-driven shift that alters ecosystem structure and biodiversity.

While the regional study provides crucial insights into Kenya’s ecosystem dynamics, it also offers valuable insights for global biodiversity assessments. First, it highlights the importance of process-based models for capturing ecosystem shifts that drive biodiversity change. Second, even though the regional study conducted an ad hoc comparison with land use change, the results suggest that integrating land use impacts into process-based models should be a priority for future biodiversity assessments.

By combining global and regional approaches, this thesis provides a more holistic perspective on biodiversity change. It confirms that climate and land use change are dominant drivers of biodiversity loss, with high-emission scenarios amplifying these impacts. While PAs offer some mitigation potential, their effectiveness remains limited without sustainable land management and effective climate policies.

The main methodological contribution of this thesis is the development of an integrated framework that combines land use change projections with climate-driven SDMs. Additionally, at the regional scale, the analysis of DGVM simulations provides insights into ecosystem dynamics, offering a complementary perspective. By integrating these two modeling approaches across scales, this work provides a more holistic assessment of biodiversity change and highlights the complexity of interactions between climate, land use, and ecological processes. This cross-scale approach strengthens biodiversity impact assessments, informing both global policy decisions and region-specific conservation strategies.

5.5 Opportunities for future research

While this study provides key methodological advancements, limitations remain. The coarse 0.5°×0.5° spatial resolution, dictated by global climate model (GCM) data, restricts finer-scale analyses, particularly for regional assessments like Kenya. Land use change occurs at much finer spatial scales than the provided spatial resolution of the Land Use Harmonization 2 (LUH2) dataset (0.25°x0.25°), meaning that future studies should use higher-resolution land use data to enable direct integration into DGVMs. Additionally, higher-resolution climate data is essential to achieve this integration and improve the accuracy of the projections.

A major constraint at the regional scale was the limited ability to assess land use change as a primary driver of biodiversity loss. While the global assessments identify land use change as a dominant driver in sub-Saharan Africa, the regional study relied on climate-driven DGVMs. The lack of region-specific high-resolution land use projections prevented a more detailed examination of land use effects. Future studies should include land use change already into the DGVM simulation runs, for which however, good quality land use data for the region are necessary.

Another key limitation is the reliance on a single IAM per SSP-RCP scenario. Recent advances in the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP; Molina Bacca et al., 2024) now enable the use of multiple IAMs per scenario, improving uncertainty quantification. Future research should also push for greater specificity in IAM land use projections, particularly regarding PA representation, which is currently insufficiently detailed for conservation applications.

Beyond refining IAM-driven analyses, future work should close a crucial gap: the feedback loop between biodiversity, land use, and climate change. While this study focuses on the unidirectional impacts of climate and land use change on biodiversity, these interactions are reciprocal. Biodiversity loss affects land use dynamics (e.g., ecosystem services, agricultural productivity) and influences climate processes (e.g., carbon sequestration, albedo effects). Future studies should integrate this feedback for a more holistic understanding of biodiversity-climate-land use interactions.

5.6 Implications for the scientific community and decision-makers

Improvements needed for DGVM modeling at the regional scale have been outlined above. Additionally, the land use filtering framework developed in this thesis for SDMs could be further integrated with DGVM-based assessments of vegetation shifts, improving SDM-based biodiversity projections. This would be an additional added value to the framework, to better account for species habitat changes. While habitat changes are currently accounted for through IAM-derived land use projections, incorporating DGVM outputs would allow the framework to capture additional ecological processes, such as climate-driven vegetation shifts, providing a more comprehensive representation of habitat dynamics. Conversely, DGVMs have started to incorporate animal-vegetation interactions (e.g., Pachzelt et al., 2013; Pfeiffer et al., 2019; Scheiter et al., 2019). In this context, SDMs can help refine DGVM simulations by improving species distribution inputs.

From the perspective of decision-makers, this thesis emphasized the need for a shift in conservation priorities. While expanding and improving PA management is important, it cannot substitute for the root causes of biodiversity loss—climate change and land use change. Resources should be directed toward climate mitigation and sustainable land use transformation rather than allocating inadequate funding to conservation efforts that only partially offset biodiversity declines. Lower-emission scenarios consistently yield better biodiversity outcomes, reinforcing the urgency of immediate action. To safeguard biodiversity effectively, it is imperative to follow the SSP1-RCP2.6 pathway and avoid exceeding this threshold, as higher-emission scenarios result in increasingly severe consequences for biodiversity. Preventing habitat destruction and reducing emissions at the source remain the most effective strategies for long-term biodiversity conservation.

5.7 Final conclusions

The overarching message from this thesis is clear: biodiversity loss is driven by both climate change and land use change, and addressing these threats requires immediate action. Our results confirm that biodiversity declines are consistently greater under higher-emission scenarios, with land use change exacerbating losses under an inequality (SSP2-RCP6.0) scenario. While PAs provide some buffering capacity, their effectiveness is ultimately constrained by broader climate and land use trends. These findings underscore the urgent need for global climate mitigation and sustainable land management. Lower-emission scenarios consistently lead to better biodiversity outcomes, reinforcing the necessity of coordinated international efforts to reduce greenhouse gas emissions. In sub-Saharan Africa, particularly in Kenya, where ecosystems are highly sensitive to both climate change and land use pressures, proactive conservation strategies are essential, as exemplified by the wildlife corridors outlined as the flagship project in the Kenya Vision 2030 (Ojwang’ et al., 2017). Measures such as improved land use planning, habitat connectivity, and adaptive conservation management must be prioritized to prevent ongoing biodiversity loss. By fostering more sustainable pathways for climate and land use, we can secure not only the future of biodiversity, but essential ecosystem services it provides—ensuring water and food security, human health, cultural integrity, and climate stability for future generations.

5.8 References

Aleman, J. C., Blarquez, O., & Staver, C. A. (2016). Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa. *Global Change Biology*, *22*(9), 3013–3025. https://doi.org/10.1111/GCB.13299

Martens, C., Hickler, T., Davis-Reddy, C., Engelbrecht, F., Higgins, S. I., Maltitz, G. P., Midgley, G. F., Pfeiffer, M., & Scheiter, S. (2021). Large uncertainties in future biome changes in Africa call for flexible climate adaptation strategies. *Global Change Biology*, *27*(2), 340–358. https://doi.org/10.1111/gcb.15390

Martens, C., Scheiter, S., Midgley, G. F., & Hickler, T. (2022). Combined impacts of future climate-driven vegetation changes and socioeconomic pressures on protected areas in Africa. *Conservation Biology*, *36*(6). https://doi.org/10.1111/cobi.13968

Molina Bacca, E. J., Stevanović, M., Bodirsky, B. L., Doelman, J. C., Parsons Chini, L., Volkholz, J., Frieler, K., Reyer, C., Hurtt, G., Humpenöder, F., Karstens, K., Heinke, J., Müller, C., Dietrich, J. P., Lotze-Campen, H., Stehfest, E., & Popp, A. (2024). Future land-use pattern projections and their differences within the ISIMIP3b framework. *EGUsphere*, 1–54. https://doi.org/10.5194/egusphere-2024-2441

Ojwang', G. O., Wargute, P. W., Said, M. Y., Worden, J. S., Davidson, Z., Muruthi, P., Kanga, E., Ihwagi, F., & Okita-Ouma, B. (2017). *Wildlife Migratory Corridors and Dispersal Areas: Kenya Rangelands and Coastal Terrestrial Ecosystems*. https://www.kws.go.ke/content/report-wildlife-corridors-and-dispersal-areas

Pachzelt, A., Rammig, A., Higgins, S., & Hickler, T. (2013). Coupling a physiological grazer population model with a generalized model for vegetation dynamics. *Ecological Modelling*, *263*, 92–102. https://doi.org/10.1016/j.ecolmodel.2013.04.025

Pfeiffer, M., Langan, L., Linstädter, A., Martens, C., Gaillard, C., Ruppert, J. C., Higgins, S. I., Mudongo, E. I., & Scheiter, S. (2019). Grazing and aridity reduce perennial grass abundance in semi-arid rangelands – Insights from a trait-based dynamic vegetation model. *Ecological Modelling*, *395*, 11–22. https://doi.org/10.1016/j.ecolmodel.2018.12.013

Scheiter, S., Schulte, J., Pfeiffer, M., Martens, C., Erasmus, B. F. N., & Twine, W. C. (2019). How Does Climate Change Influence the Economic Value of Ecosystem Services in Savanna Rangelands? *Ecological Economics*, *157*, 342–356. https://doi.org/10.1016/j.ecolecon.2018.11.015

Venter, Z. S., Cramer, M. D., & Hawkins, H.-J. (2018). Drivers of woody plant encroachment over Africa. *Nature Communications*, *9*(1), 2272. https://doi.org/10.1038/s41467-018-04616-8

Declaration of consent

on the basis of Article 18 of the PromR Phil.-nat. 19

Name/First Name: Hari Chantal

Registration Number: 14-117-287

Study program: Climate Sciences

Bachelor ☐ Master ☐ Dissertation ☑

Title of the thesis: Combined impacts of climate and land use change on future biodiversity at global and regional scales

Supervisor: Prof. Dr. Edoaurd Davin and Prof. Dr. Markus Fischer

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 paragraph 1 litera r of the University Act of September 5th, 1996 and Article 69 of the University Statute of June 7th, 2011 is authorized to revoke the doctoral degree awarded on the basis of this thesis.
For the purposes of evaluation and verification of compliance with the declaration of originality and the regulations governing plagiarism, I hereby grant the University of Bern the right to process my personal data and to perform the acts of use this requires, in particular, to reproduce the written thesis and to store it permanently in a database, and to use said database, or to make said database available, to enable comparison with theses submitted by others.

Bern, 26.02.2025

Place/Date

C. Hari

Signature