Drivers of biodiversity change in the Anthropocene

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Declaration

I declare that this thesis has been composed by myself and that the work has not been submitted for any other degree or professional qualification. I confirm that the work submitted is my own, except where work which has formed part of jointly- authored publications has been included. My contribution and those of the other authors to this work have been explicitly indicated below. I confirm that appropriate credit has been given within this thesis where reference has been made to the work of others.

The following work has been previously published or submitted for publication:

Chapter 2

The chapter "Representation of global change drivers across biodiversity datasets" is in revision at Nature Ecology and Evolution (ID: NATECOLEVOL-210613960A, decision letter 8th Sept 2021) and is available as a preprint on EcoEvoArxiv:

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Any additional author contributions are acknowledged in the relevant chapters or appendices.

2nd October 2021

Gergana Daskalova

Пътнико, пътят сам не съществува.
Пътят с ходене се прави.

A road does not exist on its own.
A road is made by walking.

Abstract

Across the globe, the populations of species and the biodiversity of ecological communities are changing, including declines, gains and stable trends over time. Against a backdrop of accelerating global change, a critical research challenge is to disentangle the sources of the heterogeneous patterns of population and biodiversity change over time. In this thesis, I linked population and biodiversity change with species traits like rarity and commonness, and with global change drivers like forest loss. I synthesised global biodiversity databases with gridded driver datasets to quantify how species' populations and biodiversity are being impacted by human activities in the Anthropocene.

The rise of open-access data in ecology has produced databases with millions of records which have launched large-scale syntheses of how Earth's biota is changing over time and space. However, our knowledge of biodiversity change is limited by the available data and their biases. In **Chapter 1**, I tested the representation of three worldwide biodiversity databases (Living Planet, BioTIME and PREDICTS) across geographic and temporal variation in global change over land and sea and across the tree of life. I found that variation in global change drivers is better captured over space than over time and in the marine realm versus on land. I provided recommendations on how to improve the use of existing data, better target future ecological monitoring and capture different combinations of global change.

In **Chapter 2**, I tested whether vertebrate species from specific biomes, taxa or with certain species traits are more likely to increase or decrease in a time of accelerating global change. I analysed nearly 10 000 population abundance time series from over 2000 vertebrate species part of the Living Planet Database. I integrated abundance data with information on geographic range, habitat preference, taxonomic and phylogenetic relationships, and IUCN Red List Categories and threats. I found that 15% of populations declined, 18% increased, and 67% showed no net changes over time. Amphibians were the only taxa that experienced net declines in the analysed data, while birds, mammals

and reptiles experienced net increases. Despite this variation among broad taxonomic groups, surprisingly I did not detect phylogenetic patterns in which species were more likely to decline versus increase. Population trends were poorly explained by species' rarity and global-scale threats. I found that incorporating the full spectrum of population change, including declines, gains and stable trends, will improve conservation efforts to protect global biodiversity.

In **Chapter 3**, I explored land-use change to fill the gap in empirical evidence of how habitat transformations such as forest loss and gain are reshaping biodiversity over time. I quantified how change in forest cover has influenced temporal shifts in populations and ecological assemblages from over 6000 globally distributed time series across six taxonomic groups. I found that local-scale increases and decreases in abundance, species richness, and temporal species replacement (turnover) were intensified by as much as 48% after forest loss. Larger amounts of forest loss did not always correlate with higher population and biodiversity change across sites, highlighting the mediating effects of local context and historical baselines. Temporal lags in population- and assemblage-level shifts after forest loss extended up to 50 years and increased with species' generation time. My findings indicate that forest loss amplified population and biodiversity change, with effects on both short and long temporal scales. A mix of immediate and lagged biodiversity change following land-use change emphasises the need for temporally explicit biodiversity scenarios to accurately estimate progress towards conservation goals.

Together, my thesis findings demonstrate the wide spectrum of population and biodiversity change happening across varying amounts of global change and different realms, taxa and species traits. These heterogeneous impacts of global change on population and biodiversity spanned temporal scales from immediate effects in a couple of years to lagged responses decades after disturbance. The links between global change drivers and shifts in species' abundance, species richness and compositional turnover depended on historical context and species' characteristics like generation time. I documented both immediate and temporally delayed effects of global change drivers on

species' populations abundance and the biodiversity of ecological assemblages which highlights the importance of long-term ecological monitoring. The main implications of my thesis findings are that first, any inferences drawn from biodiversity syntheses reflect the types of species and places represented by the data and the global change that is experienced. To create accurate scenarios, we need biodiversity data that span not only different taxa and locations, but also the spectrum of global change variation around the world. Second, biodiversity predictions should incorporate both positive and negative impacts of global change drivers as well as lagged responses. Finally, ecosystems and the species within them are usually simultaneously exposed to a suite of global change drivers and a key future research step is to test the synergy and/or antagony in the effects and interactions among multiple types of environmental change on populations and biodiversity.

Overall, my thesis research demonstrates that the drivers of biodiversity change in the Anthropocene have both immediate and temporally-delayed effects which depend on species' traits and the sites' historical context. My findings suggest that by incorporating the full spectrum of biodiversity change and the nuance around interacting global change drivers we can improve projections of future ecological shifts and enhance local and international conservation policies.

Lay summary

Life on our planet is incredibly diverse. There are over eight million species across a myriad of habitats, including forests, oceans, coastlands, rivers, deserts and more. From the most stunningly coloured parrots in the Amazon to the incredibly strong willows of the Arctic and the humble house sparrow, together these species make up Earth's biodiversity. This biodiversity underpins the water, air, land and soil upon which our society is built. These species, and millions more, are the culmination of over 4 billion years of evolution. And yet, the last century has brought unprecedented changes. Humans have transformed and continue to transform the planet by cutting down forests, farming land, building cities and burning fossil fuels. Our activities and their consequences for nature have brought a time of rapid global change and we know that biodiversity is shifting in response. What we have not yet disentangled, however, is what kinds of species are most likely to thrive or perish and what are short- and long-term impacts of human activities like the cutting of forests on the planet's biodiversity.

Since beginning my PhD research in 2017, nearly a hundred plants and animals have been declared extinct. Faced with ever-diminishing habitats due to logging and agriculture, the cryptic treehunter, a bird species from Brazil, has disappeared from the canopies of the Atlantic forests. With its island habitat engulfed by rising sea levels, the the Bramble Cay melomys – a small island marsupial from Australia – has similarly perished. But before final extinction from the planet as a whole, comes biodiversity change detectable at smaller scales. It is at these regional or even smaller scales that conservation actions are usually implemented. At sites around the world, the abundance and type of plants and animals – common like the house sparrow or rare as the likely extinct cryptic treehunter – are changing over time. In places like the Amazon, a walk in the forest today might be accompanied by an entirely different soundscape compared to twenty years ago, as global change has reshuffled biodiversity. To understand such biodiversity changes, we need the lens of time — a way to track species presence, abundance and their drivers of change over time. Since biodiversity is naturally variable, I used information on biodiversity over five up to 150 years to be able to tell apart signal

from noise in the data. My thesis aimed to link global change with biodiversity change, focusing on the implications of data biases, the importance of rarity and commonness in predicting species declines and increases, and the short- and long-term impacts of forest loss on biodiversity.

Parallel with global change, an ecological data revolution is also underway. We now have more records of the planet’s biodiversity than ever before, but data collection efforts are not equally distributed around the world or across the tree of life. Birds are the best studied group of animals and the majority of long-term biodiversity data come from Europe and North America. Biodiversity change, however, occurs across the whole planet, creating a mismatch between the universal nature of shifts in biodiversity and the limited samples that we have. We already know that many places and species are understudied. What we were previously lacking was was information about whether biodiversity records come from habitats that are not disturbed by human activities, heavily modified or somewhere in between. I tested how well three worldwide biodiversity databases captured the variety of ways in which humans have altered the planet over land and sea. I found that this variation in global change is better captured over space than over time. Spatial representation of global change was as high as 78% in the marine realm and 31% on land. However, many gaps remain, for example, in places experiencing high rates of climate change like the Arctic or in the areas of the world where human impact has been minimal. By targeting future data collection so that it includes both wild and modified sites, we can improve our ability to predict the future of Earth's biodiversity.

As human impacts continue to accumulate on land, oceans and rivers, it is important to track how the numbers of different species are changing over time to identify those that are threatened with extinction. Among the different animals on Earth, some are rare and found in very few locations, while others persist much more widely. This rarity or commonness has often been used to guide conservation, yet it remains an open question of how rarity relates to changes in the number of animals at sites around the world across globally monitored species. I studied nearly 10 000 populations from over 2000 species including birds, mammals, fishes, sharks, reptiles and amphibians. I found that found that

15% of populations declined, 18% increased, and 67% showed no net changes over time. Surprisingly, common animals were just as likely to increase or decrease over time as rare ones. For example, a population of the common species red deer in Canada declined by more than half, going from 606 down to 194 individuals. In contrast, a population of the rare Hawksbill sea turtle from Barbados showed a nearly three-fold increase, going from 89 to 328 individuals. My findings highlight that looking beyond just rare species, with monitoring efforts across a diversity of species, can improve conservation efforts to protect global biodiversity.

Forests support around 80% of all species living on land. Advances in satellite monitoring have revealed how the area covered by forests on Earth has been changing over time. Simultaneously, large collections of biodiversity records from places where people return year after year to measure biodiversity have also been made available. The next key step was to merge these different types of data to deepen our knowledge of both the immediate and the long-term impact of forest loss on biodiversity. Combining over 5 million records from over 6000 locations around the world, I carried out a global analysis of how forest loss has influenced the biodiversity of plants and animals over the last 150 years. Forests are being lost across the planet. In temperate biomes, forest cover change has persisted for centuries, but in once-secluded wilderness, forest loss is accelerating. I found that forest loss did not always lead to declines in biodiversity. Instead, when forest cover declined, changes in biodiversity intensified, with increases in the abundance of some species and decreases in others. The composition of forest life – the different types of species present – was altered too. The rate at which these changes happened in each location accelerated as forest cover shrank. I discovered that the pace at which forest loss alters biodiversity differs among short-lived animals such as forest beetles and longer-lived species such as red-tailed hawks. The longer species live, the longer it took for the effects of forest loss to manifest themselves, creating ecological lags between the timing of forest loss and biodiversity responses. Such lags can carry across generations. Even if plants and animals manage to survive alongside forest loss, they might not be able to reproduce, or their offspring might be too weak to survive. My findings emphasise both the positive and negative consequences of land-use change on the world's biodiversity and demonstrate how, by combining datasets from around the world, we can assess the state of the world's forests.

My thesis research demonstrates that global change is influencing temporal change in biodiversity in both positive and negative ways. The mix of immediate and delayed changes in biodiversity highlights how important it is to monitor plants and animals over decades to capture their temporal dynamics in continuously shifting landscapes. A single snapshot in time cannot detect the full extent of human impacts on biodiversity. As conservation actions continue to be implemented around the world, we need to track biodiversity change over time to monitor their success be better equipped to conserve Earth's biodiversity not just now, but for decades to come.

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Chapter 1. Introduction

Chapter 1. Introduction

1.1 Aims of thesis

In this thesis, I aimed to advance our understanding of biodiversity change in the Anthropocene (Figure 1.1) In particular, I synthesised worldwide and cross-taxa open-access biodiversity data with information on global change drivers and species traits to uncover the quantitative links between temporal change in populations and ecological assemblages, species traits and forest cover change, a key global change driver in terrestrial ecosystems.

Overarching research questions

I investigated a range of metrics (population change, species richness, community turnover) to quantify differences in temporal biodiversity trends across taxa, biomes, different types of species and anthropogenic drivers. The specific research questions I addressed are:

1) How well do open-access biodiversity datasets capture variation in global change drivers around the world?
2) How do species' population trends vary across biomes, taxa and and do rarity traits drive variation in species' abundance over time?
3) How does forest cover change influence population and biodiversity change over time?

Quantifying the links between the intensities of anthropogenic drivers and temporal biodiversity trends is important for conservation and policy.

I combined global gridded change datasets with population and biodiversity time series to ask:

How well do open-access biodiversity datasets capture variation in global change around the world?

How do species' populations trends vary across biomes, taxa and rarity traits?

How does forest cover change influence population and biodiversity change over time?

What are the mechanisms behind how a mix of positive and negative biodiversity responses to global change can arise?

Figure 1.1 My thesis brought together open-access biodiversity and global change datasets to quantify how biodiversity change in the Anthropocene varied across realms, taxa, different types of species and varying exposures to forest cover change. Such research can help ground truth the scenarios for future biodiversity change that are used in international reports and policies, such as those by IPBES.

1.2 Structure of thesis

First, I reviewed the existing evidence for population and biodiversity change around the world and the possible factors explaining heterogeneous trends (**Chapter 1**). **Chapter 2** quantified marine and terrestrial global change across the locations of records from three open-access biodiversity datasets (Living Planet Database, BioTIME and PREDICTS), with an emphasis on human use intensity, climate change, human population density, pollution and invasive species potential. **Chapter 3** focused on population trends of vertebrate species across the marine, terrestrial and freshwater realms and how they relate to species' geographic range, mean population size, habitat specificity and IUCN Red List status. **Chapter 4** tested how gains and losses in forest cover change over time correspond with temporal shifts in population abundance, species richness and compositional turnover and additionally assesses the influence of historical baselines of forest loss and temporal lags in biodiversity responses. **Chapter 5** presents a synthesis of my research findings and discusses their broader implications, as well as future research directions. All results chapters (**Chapters 2-4**) represent stand-alone research papers and are either published or under review. My work involved collaboration with multiple biodiversity scientists and thus, all chapters represent collaborative work under my leadership. The contribution of each author is listed at the beginning of the chapters.

Chapter 1: **Introduction.** Global change drivers such as climate change and land-use change are reshaping ecosystems around the world (IPBES, 2019), but their magnitudes are not uniform over space (Bowler et al., 2020) and over time (Ellis et al., 2013; Mihoub et al., 2017). Simultaneously with accelerating global change, biodiversity around the world is also shifting in terms of species' abundances, the numbers of species present at local scales and the types of species that ecological communities represent (Blowes et al., 2019; Newbold et al., 2015). My thesis aimed to establish the quantitative links between global change variation around the world, species traits and the temporal trends in abundance, species richness and compositional turnover across taxa and at sites around the world.

***Chapter 2:* Representation of global change drivers across biodiversity datasets.** Ecological communities around the world are under pressure from accelerating global change, yet we lack a quantitative understanding of how well monitoring captures variation in the intensity of different drivers and their effects on biodiversity (De Palma et al., 2018; IPBES, 2019). Trends from large-scale compilations of biodiversity records are often extrapolated to scenarios for the entire globe, but without accounting for how well databases represent the world, such extrapolations will be biased. I found that biodiversity data captured most of the variation in global change, but gaps still remained, particularly in capturing extreme climate change and relatively low intensities of global change. Biodiversity monitoring often started after the peak intensity in environmental change for drivers like primary forest loss, but more closely coincides with the period of rapid climate change. Filling the remaining global change gaps will allow us to better understand ongoing change and predict future trajectories for the Earth's biota. This manuscript is currently in review at the journal Nature Ecology and Evolution.

***Chapter 3:* Rare and common vertebrates span a wide spectrum of population trends.** Population change is not unidirectional across different taxa and regions (Hefley *et al.* 2016; Ceballos *et al.* 2017; Leung *et al.* 2017), and species vary in their sensitivity to global change drivers (Betts et al., 2017; Fritz et al., 2009; Julliard et al., 2004). For example, species' attributes such as rarity, conservation status, distribution and taxon are often assumed to predict variation in population change (Hutchings & Reynolds, 2004; Julliard et al., 2004; Shultz et al., 2005). However, there are very few empirical tests of the influence of rarity and conservation status on population change and extinction risk (Purvis *et al.* 2000b; O'Grady *et al.* 2004; Ripple *et al.* 2017a), and those that exist mostly focus on either specific taxa (Cardillo et al., 2004; Fritz et al., 2009; Jones et al., 2003) or focus on population declines rather than the full spectrum of population change (Purvis et al. 2000a; Fritz et al. 2009; Gilroy et al. 2016; Hefley et al. 2016; Ceballos et al. 2017a). In contrast to a common assumption that rare (or less abundant) species are more likely to be declining under anthropogenic change, I found that population trends cover a wide spectrum of change from losses to gains, which are not related to species rarity. Across six vertebrate taxa, my findings showed that amphibians were the only taxa that experienced net declines over time, as well as the taxa most prone to population fluctuations. Overall, I found a wide spectrum of population declines across latitudes, biomes and taxa that was poorly explained by species rarity. As human activities continue to accelerate, a key research direction is to determine how rarity attributes and species traits interact with global change drivers and together influence biodiversity. This manuscript is published in the journal Nature Communications.

Chapter 4: **Landscape-scale forest loss as a catalyst of population and biodiversity change.** Land-use change is the most important driver of biodiversity change in terrestrial ecosystems (IPBES, 2019; Kehoe et al., 2017; Maxwell et al., 2016; Newbold et al., 2015), but a global attribution of land-use change (e.g., conversion of forests to agricultural fields) to biodiversity change through time is lacking (De Palma et al., 2018). By exploring the temporal dynamics between biodiversity change and forest cover change, we can compare historic baselines and lags in biodiversity responses. In my analyses, I found that responses of biodiversity to land-use change were complex (i.e., not unidirectional) and forest loss was concurrent with amplified gains and losses in population abundance and biodiversity over time. Lags in biodiversity change following large forest loss events were frequent and often extending up to half a century and were longer in taxa with longer generation times. My findings indicated both immediate and delayed biodiversity change following forest loss, highlighting the need for a long-term temporal perspective in biodiversity assessments. This manuscript is published in the journal Science.

Chapter 5: **Synthesis.** Biodiversity responses to global change are heterogeneous, possibly because of cumulative or interactive effects of global change drivers on shifts in the Earth's biota over time. In this chapter, I synthesised the results from my thesis. I discussed possible mechanisms behind how a mix of positive and negative biodiversity responses to global change can arise, including 1) interactions between global change drivers arising from simultaneous exposure to multiple types of environmental change, and 2) sampling and scale effects such as landscape-scale species pool size and dark diversity – species that could inhabit a given area or plot yet have not colonised thus far.

Finally, I highlight future research paths that can build on my thesis findings and further disentangle the complex effects of global change on the planet's biodiversity.

1.3 Global change is reshaping biodiversity worldwide

All across the globe, species' populations and the biodiversity of ecological assemblages are changing in complex ways, including declines, increases and no net changes in abundance and species richness and shifts in composition over time (Bernhardt-Römermann et al., 2015; Biesmeijer, 2006; Blowes et al., 2019; Carvalheiro et al., 2013; Dornelas et al., 2014; Elahi, Connor, et al., 2015; Elahi, O'Connor, et al., 2015; IPBES, 2019; Vellend et al., 2013). Against a backdrop of accelerating global change, we need empirical evidence of the sources of heterogeneous patterns of population and biodiversity change to inform global scale biodiversity policies and their translation into local-scale conservation. Differential exposure to drivers like climate change and land-use change, together with varying vulnerability to threats, likely both influence the direction and magnitude of shifts in population abundance, species richness and community composition (Bowler et al., 2017, 2018, 2019, 2021; Callaghan et al., 2021; Crossley et al., 2021; Dornelas et al., 2014; Fritz et al., 2009; Newbold et al., 2015; van Klink et al., 2020; Williams et al., 2020; Williams & Newbold, 2021). Despite multiple calls for more comprehensive biodiversity attribution analyses (De Palma et al., 2018; IPBES, 2019; Mazor et al., 2018; Sirami et al., 2017), our current knowledge has largely been limited by the paucity of large-scale temporal biodiversity data and planetary-scale information on the intensity of drivers like land-use change and climate change.

More and more open-access biodiversity and population data are accumulating

Recent compilations of long-term population (LPI, 2016; Santini et al., 2018; van Klink et al., 2021) and biodiversity time series (Bruelheide et al., 2019; Dornelas et al., 2018), together with data on species traits (Bjorkman, Myers-Smith, et al., 2018; Jones et al., 2009; Kattge et al., 2020; Wilman et al., 2014) and global layers of human-driven environmental change (e.g., Bowler et al., 2020; Hansen et al., 2013; Karger et al., 2017), allow us to quantitatively test the factors explaining biodiversity change at sites around the world (Franklin et al., 2017; Hampton et al., 2013; Wüest et al., 2020). The rise of open-access ecological data has spearheaded biodiversity assessments, scenario development for future biodiversity trajectories and has launched a new era for data syntheses across temporal, spatial and taxonomic scales (IPBES, 2019; Leclère et al., 2020; Thuiller et al., 2019). Unravelling how global change drivers are reshaping Earth's biota and which types of species are most at risk of declines can provide evidence that can then be used to create scenarios and predictions for ecological changes across the Anthropocene (IPBES, 2019; Mazor et al., 2018; Sirami et al., 2017).

Population and biodiversity change are connected

Biodiversity change is multi-faceted and occurs on multiple inter-connected spatial and temporal scales (Figure 1.2). Shifts in population abundance can lead to changes in the richness and composition of ecological assemblages (Leung et al., 2017). Investigating changes in the abundance of populations around the world can provide valuable insight into the processes that ultimately alter species richness, community composition, functional diversity and genetic diversity (Leung et al. 2017). Community composition can change without directional trends in species richness (Dornelas et al., 2014; Hillebrand et al., 2018; Magurran et al., 2018; Vellend et al., 2013) and following both species richness gains or losses (Baeten et al., 2014). Comprehensive detection and attribution analyses ought to quantify the full spectrum of biodiversity trends (McGill et al. 2015; Magurran et al. 2018; Primack et al. 2018; Yoccoz et al. 2018). Population and biodiversity change impact on the available genetic pool in a given area which can then have implications for future population and biodiversity dynamics (Hastings & Harrison, 1994). Such population and biodiversity changes can lead to shifts in ecosystem functioning through changes in the dominant species traits of a community (Loreau, 2001). In this thesis, I studied temporal trends in both populations and ecological assemblages to gain a better understanding of the drivers of biodiversity change in the Anthropocene.

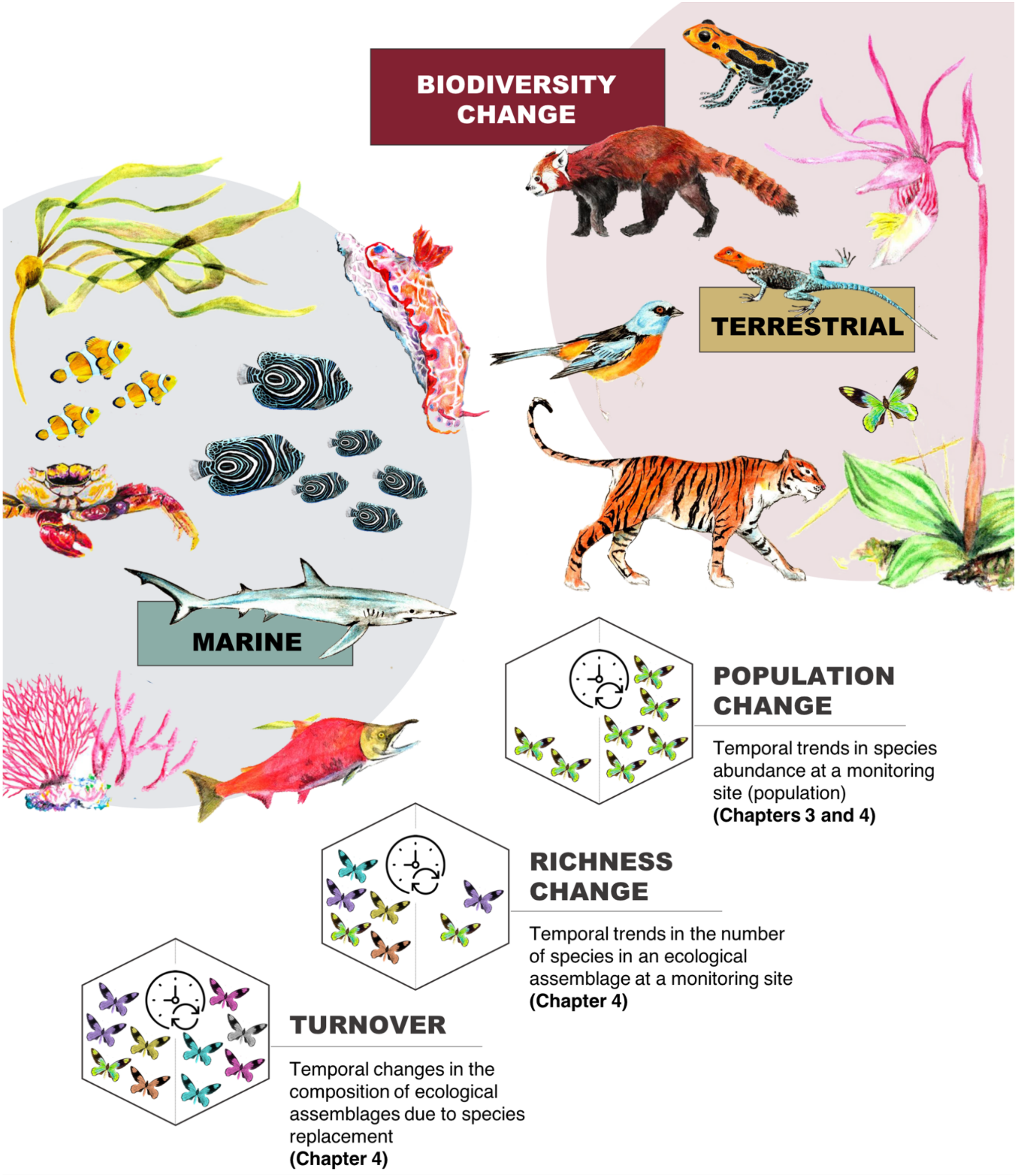

Figure 1.2. Global change is reshaping terrestrial and marine biodiversity, leading to shifts in population abundance, species richness and the composition of ecological assemblages (turnover). Population change, richness change and turnover represent different facets of biodiversity change that together provide more comprehensive insights into the different ways in which biodiversity is being altered across the Anthropocene. Species illustrations by Malkolm Boothroyd.

1.4 Rarity traits might explain heterogeneous biodiversity and population trends

Understanding what factors best explain population change and extinction risk has been a key focus in population ecology and conservation biology and possible measures include species' attributes and traits, such as rarity proxies like geographic range (Cardillo et al., 2004; Collen et al., 2009; Gaston & Blackburn, 1995; O'Grady et al., 2004; Olden et al., 2007; Owens & Bennett, 2000; Purvis et al., 2000; Ripple et al., 2017). Population declines can lead to local extinction of populations and eventually potential global extinction of species (Ceballos *et al.* 2017). Extinction risk, the likelihood that a species will go extinct within a given time frame (Mace et al., 2008), is widely assumed to increase when species are rare (i.e., they have small geographic ranges (Jones et al., 2003), small population sizes (Green, 2003) and are very specialised (Gilroy et al., 2016) or a combination of the three (Rabinowitz, 1981). Rare species with small populations are more likely to undergo stochastic fluctuations that could lead to extinction at any point as per population dynamics theory (Lande, 1993; Melbourne & Hastings, 2008) and are more susceptible to inbreeding (Hanski, 1998; Kareiva, 1990). Allee effects, the positive relationship between population growth rate and population density, further increase the likelihood of declines due to low reproductive output once populations reach a critically low density (Dennis *et al.* 2016b; Sun 2016). Small populations from rare species are thought to be more likely to experience population declines (Hutchings & Reynolds, 2004; Manne & Pimm, 2001; McKinney, 1997; Purvis et al., 2000). Cross-taxa and cross-biome empirical tests of the traits best explaining population declines have yet to be undertaken at global scales.

1.5 Varying exposure to global change could broaden the spectrum of biodiversity and population trends

Spatial and temporal variation in population and biodiversity change might be explained by both past and present local environmental factors and anthropogenic drivers (Betts et al., 2017; Brook et al., 2006; Fritz et al., 2009; Jung et al., 2019; Jung, Rowhani, &

Scharlemann, 2019; Phillips et al., 2017). Biodiversity has been influenced by human activities for millennia and contemporary biodiversity change might be a continuation of trends that first started in the distant past (Ellis et al., 2013; Mottl et al., 2021). Since the start of the Industrial Revolution in the 1800s, the rate of species extinctions has increased relative to the background rate of extinction as estimated based on fossil records (Barnosky et al., 2011; De Vos et al., 2015; Pimm et al., 2014). More recently, both gains and losses in local-scale population abundance and species richness have been observed over time, which were frequently paralleled with changes in community composition (Bowler et al., 2021; Leung et al., 2017, 2020; Rosenberg et al., 2019; Spooner et al., 2018; van Klink et al., 2020; van Strien et al., 2016). Attributing heterogeneous biodiversity change to its drivers is critical to determine the impacts of human activities on the world's ecosystems and on the services that they provide for society (IPBES, 2019).

Human exploitation of natural resources (hereafter, "human use") and climate change are the two main types of global change influencing biodiversity across the terrestrial and marine realms (Bowler et al., 2020; IPBES, 2019; Maxwell et al., 2016; Pereira et al., 2012). In terrestrial ecosystems, land-use change, habitat fragmentation and urbanization have altered the species composition of many communities through local extinctions, recolonizations and changes in community evenness (Marta et al., 2021; Newbold et al., 2015; Supp & Ernest, 2014). Conversion of natural habitats to agricultural land has led to the decline of many common (Donald et al., 2006; Gaston & Fuller, 2007) and rare species (Clark & Tilman, 2008) and has homogenised ecological communities by creating environmental conditions in which only certain kinds of species can survive (Smart et al., 2006; Vellend et al., 2007). The spread of invasive species has similarly been linked to biotic homogenization in both terrestrial and aquatic ecosystems (Kortz & Magurran, 2019; Magurran et al., 2015; Muthukrishnan & Larkin, 2020). Warmer temperatures have been linked with species range shifts (Pecl et al., 2017), vegetation change in high-latitude systems (Myers-Smith et al., 2015), biodiversity declines (Dawson et al., 2011; Parmesan & Yohe, 2003), but also population increases (Bowler et al., 2017). Rising water temperatures, increased nutrient fluxes and pollution have modified marine systems (Crain et al., 2008; Halpern et al., 2008; Tittensor et al., 2010), driving changes in species richness, abundance and composition (Elahi et al., 2015; García Molinos et al., 2015). In both terrestrial and aquatic ecosystems, global change, such as human use of ecosystems and climate change, is restructuring the planet's biodiversity (IPBES, 2019).

The different drivers of population and biodiversity change do not act in isolation (Dawson et al., 2011; de Chazal & Rounsevell, 2009; Findell et al., 2017). One of the biggest challenges in biodiversity research is disentangling biodiversity change caused by multiple simultaneously occurring drivers from naturally occurring variation due to fluctuations in populations and communities (Buschke et al., 2021; De Palma et al., 2018; Magurran & Dornelas, 2010). Furthermore, we do not know how ecosystems will respond to global change drivers in the long term, as there might be lag effects and threshold points (Isbell et al., 2019; Jackson & Sax, 2010; Pardini et al., 2010). Alternatively, communities might adapt, thus leading to decreased impacts of global change drivers with time (García Molinos et al., 2015). Biodiversity syntheses are a key step towards understanding how global change drivers impact biodiversity across spatial and temporal scales (de Chazal & Rounsevell, 2009; IPBES, 2019; Mihoub et al., 2017; Sirami et al., 2017).

1.6 Biodiversity syntheses are challenged by data gaps

The temporal, spatial and taxonomic scales of investigation influence the direction and magnitude of detected biodiversity change (Bernhardt-Römermann et al., 2015; Chase et al., 2018, 2019; Jarzyna & Jetz, 2018; Keil & Chase, 2019; Korell et al., 2021; Levin, 1992; Murphy & Lenoir, 2021; Seabloom et al., 2021; Whittaker et al., 2005). Even though we now have more biodiversity data than ever before, there are still numerous data gaps remaining in the monitoring of species across time, space and taxa. Such missing information challenges the quantification of biodiversity trends in the Anthropocene and can translate into biases in study findings. For example, cross-taxa global syntheses are usually dominated by vertebrate versus invertebrate data. Some gaps in data cannot be filled, for example when it comes to biodiversity monitoring in the more distant past, while spatial and taxonomic coverage is more easily improved. Additionally, even if data for the species or areas of interest are available, the data might be from one spatial or temporal scale, while the impacts of global change might be more evident at a different scale. Biodiversity data collected at small local scales might not capture the effects of drivers that act at larger spatial scales like climate change (Keil et al., 2012). Accounting for data gaps and scale effects by statistically modelling historical baselines, temporal mismatches, geographic and taxonomic gaps can improve biodiversity estimates and provide stronger evidence for policy and conservation actions (Dias et al., 2021; Gomez et al., 2018; Humbert et al., 2009; Isaac et al., 2014; Schrodt et al., 2015).

Historical baselines and temporal mismatches

Biodiversity monitoring often starts after the peak intensity of a global change driver, introducing mismatch between when a driver might have exerted the highest impact and when we monitor its effects (Mihoub et al., 2017). Such mismatches can lead to a false underestimation of the impacts of global change on biodiversity and can hinder conservation efforts, highlighting the importance of incorporating historical baselines (Bjorkman & Vellend, 2010; Mihoub et al., 2017). The non-random selection of study sites can further bias estimates of biodiversity change and its link to global change (Fournier et al., 2019). In a conservation context, species- or assemblage-level monitoring often begins after a species is already declining while for behavioural or evolutionary studies there is a tendency to choose sites with high species abundance. Additionally, long-term monitoring sites are often selected in places with no major threats to ensure the longevity of the monitoring programme, thus excluding sites where major human development is likely in the future. When data collected for different purposes are brought together in global databases, the resulting data compilation will likely include time series with both unnaturally high and low biodiversity, creating a baseline for future comparisons that might not necessarily reflect the long term trajectory of a population or assemblage (Fournier et al., 2019; Wauchope et al., 2019, 2021). Temporal gaps in data are some of the hardest to fill, particularly relating to monitoring in the past, but integrating biodiversity records with historical trajectories of global change can improve research by providing a long-term context to recently collected biodiversity data.

Geographic and taxonomic data gaps

Despite the rise of open-access data in ecology, many regions and taxa are poorly studied, such as the tropics, Arctic, invertebrates in general and species living in the deep sea and below the soil surface. Geographically, there are mismatches between research effort and global change intensity around the world. For example, the Arctic is experiencing the highest rates of climate warming but is understudied due to extreme climate, travel distances and logistical challenges (IPCC, 2021). Studying places like the Arctic is expensive and comes at a time when much of conservation funding is already allocated to monitoring (Buxton et al., 2020). However, concentrating research to the more accessible parts of the world can bias our knowledge of the impacts of global change on biodiversity. Taxonomically, winner and loser species could emerge at the scales of narrow evolutionary units, like individual families, or broad, like entire phyla (Dornelas et al., 2019; Finderup Nielsen et al., 2021; Jarzyna & Jetz, 2017; Jetz, 2002; Jetz et al., 2004; Pecl et al., 2017; Rosauer et al., 2017). However, many taxa such as invertebrates, fungi or belowground biodiversity remain poorly studied with hundreds to thousands of species yet to be identified. Uneven data collection across the tree of life risks missing the early signs of species decline and biodiversity loss or conversely, if monitoring stops once a population is stable, the long-term impacts of conservation interventions could remain unknown. Such geographic and taxonomic gaps in biodiversity monitoring stem from 1) the Linnaean shortfall (the Earth’s biodiversity has yet to be fully sampled and classified and 2) the Wallacean shortfall (we do not have comprehensive distribution data for all known species, Whittaker *et al.* (2005)). Limitations due to data gaps can be at least party addressed using large open-access databases, such as GBIF (GBIF, 2018), the Living Planet Database (LPI, 2016), PREDICTS (Hudson et al., 2017) and BioTIME (Dornelas et al., 2018). However, existing data are of varying quality, potentially introducing noise and error into biodiversity syntheses. When calculating indicators of change using open-access big ecological data, we can partially account for variable data quality using data filtering to remove false records (especially when using GBIF data, Franklin et al. 2017; Serra-Diaz et al. 2017).

1.7 Scale effects in biodiversity change

Gaps in biodiversity data interact with scale effects in biodiversity detection and attribution. For example, global change data are not always available at a resolution fine enough to match the scales at which species might respond to disturbance, particularly for species with small roaming ranges. Additionally, even if on the landscape scale there is habitat change, some species might be able to persist in remaining refugia or suitable microclimates. Spatially, the effects of land-use change on biodiversity are known to decrease as study area increases (Chase *et al.* 2018), whereas the impacts of climate change are likely stronger at larger spatial scales (Keil et al., 2012). Thus, landscape-level habitat changes might not always translate to local-scale biodiversity change. The findings of global loss of species and local no net change are not necessarily in opposition, because at small spatial scales, local extinctions and colonization can be balanced, at regional scales the spread of invasive species could contribute to species richness gain, and at planetary scales, overharvesting and habitat change can lead to species extinction (McGill et al., 2015; Vellend, Dornela et al., 2017). At local scales, biodiversity losses could be balanced with gains over time due to community re-assembly and self-regulation, and as a result, richness and abundance could remain stable (Dornelas et al., 2014; Gotelli et al., 2017; Hill et al., 2016; Magurran et al., 2018; McGill et al., 2015; Sax & Gaines, 2003; Supp & Ernest, 2014; Vellend, Baeten, et al., 2017; Vellend et al., 2013; Yoccoz et al., 2018). At global scales, species are going extinct quicker than the evolutionary scales of speciation, causing biodiversity loss at the planetary scale (Barnosky et al., 2011). The mounting evidence for variation in biodiversity change highlights the need to determine the traits and drivers to which we can attribute variation in biodiversity trends, but such studies have to account for scale effects and possible mismatches between biodiversity-driver relationships at different scales.

1.8 Heterogeneous biodiversity change has implications for international policy and conservation

As society moves forward with the post-2020 Global Biodiversity Framework, we need reliable scenarios for the future of biodiversity and indicators to quantify progress towards conservation goals (Hansen et al., 2021; Jetz et al., 2019; Pereira & Cooper, 2006). Examining the drivers of temporal shifts in individual species' populations and entire ecological assemblages provides evidence for conservation decision-making (Batt et al., 2017; Ehrlén & Morris, 2015; Hefley et al., 2016; O'Grady et al., 2004). Biodiversity indices like the Biodiversity Intactness Index (BII) (Scholes & Biggs, 2005) or the Living Planet Index (LPI) (Lambertini, 2020; McRae et al., 2017) aim to summarise broad trends in biodiversity and are used in global assessments and scenarios for the future (IPBES, 2019). However, indices can mask important heterogeneity in biodiversity trends and are susceptible to bias from the assumptions made when calculating them, random fluctuations and data gaps (Buschke et al., 2021; Leung et al., 2020). Additionally, conservation actions are predominantly implemented on smaller, country-specific, regional or local scales (Guerrero et al., 2013; Mills et al., 2010), while scenarios and indicators are often calculated across taxa and on planetary scales (Agardy, 2005; Pressey et al., 2007). Similarly, overall species' Red List status is determined on a global scale based on multiple criteria (Mace et al., 2008), but species' global status might differ from its national or regional status. On a local scale, populations might vary in the direction and magnitude of experienced abundance change, creating contrasts with Red List statuses (Ehrlén & Morris, 2015; Gilroy et al., 2016; Lawson et al., 2015; Leung et al., 2017; van Strien et al., 2016). Heterogeneous population and biodiversity trends on local scales can be masked by global average trends, thus risking the danger of not noting biodiversity declines early enough to be able to reverse them. By quantifying the nuance and full distribution of the impacts of global change drivers on biodiversity, we can better understand ongoing shifts in Earth's biota and predict future trends and their consequences for ecosystems and humanity.

1.9 Methods

My thesis combined multiple open-access databases which together provided information on population change, biodiversity change, species traits and global change drivers. The key data sources and statistical workflows are listed below, with additional details provided in the Methods sections of each data chapter.

Living Planet Database (**Chapters 2**, **3** and **4**)

The Living Planet Database includes 9284 vertebrate population time series from different taxa across the terrestrial, marine and freshwater realms and between 1970 and 2014 (note that not all populations were monitored across the entire time period, LPI 2016). These time series represented repeated monitoring surveys of the number of individuals in a given area, hereafter called “populations”. The survey methods and study areas varied among time series but were consistent within time series. The Living Planet Database is available at https://livingplanetindex.org/data_portal.

BioTIME database (**Chapters 2** and **4**)

The BioTIME database includes 332 studies of assemblage time series, which together result in over 14 million abundance records of species within ecological communities (Dornelas et al., 2018). There are almost 50 thousand species represented in the database. BioTIME spans over terrestrial, marine and freshwater realms. As with the Living Planet Database, survey methods varied, including plots, transects and more, but were consistent within time series. The studies part of BioTIME vary largely in size which is why I used the rarefied version of BioTIME (see Blowes et al., (2019) for details), where studies were split by cells of approximately 96 km^2, producing 44 532 time series. For example, some marine studies done on ships covered very large areas and were split into multiple time series. If there were two studies within the same cell, their identities were kept separate and data from different studies were not combined. The BioTIME database is available at https://biotime.st-andrews.ac.uk.

The large temporal, geographic and taxonomic scales of the databases I used allowed me to answer key questions about how Earth's ecosystems are changing in the Anthropocene (Table 1.1, Figure 1.3). The Living Planet and BioTIME Databases represent the two largest ecological time series open-source databases currently available. Additionally, in **Chapter 2** I used the PREDICTS database to quantify global change variation across the locations of the Living Planet, BioTIME and PREDICTS databases and provide context for recent findings emerging from biodiversity syntheses (Blowes et al., 2019; Dornelas et al., 2014, 2019; Newbold et al., 2018; Newbold et al., 2015; Vellend et al., 2013). From the PREDICTS database I only used the geographical coordinates of each site and not the biodiversity data themselves, because the goal was to extract the magnitudes of global change drivers at the sites sampled by the database. From the Living Planet and BioTIME databases I used both the site coordinates (**Chapter 2**) and the population and biodiversity information (**Chapters 3-4**). Since the key questions in my thesis revolve around temporal biodiversity change and its drivers, I used time series databases (Living Planet and BioTIME) in **Chapters 3** and **4**. Both the Living Planet and BioTIME databases are living and growing compilations of ecological data. As more data become available and ongoing and future monitoring begins to fill in the taxonomic and geographic gaps in existing datasets, we will be able to re-assess and test the generality of the patterns of population change across biomes and taxa.

Table 1.1 Number of time series per taxa in the Living Planet and BioTIME databases. Note that the sample size for each analysis different depending on the specific research question (see Methods sections in each chapter for details).

Database	Realm	Taxa	Time series
Living Planet (Chapters 2, 3 and 4)	Terrestrial	Amphibians	46
		Birds	3447
		Mammals	1036
		Reptiles	111
	Marine	Ray-finned fish	1120
		Birds	1001
		Sharks and rays	131

		Mammals	289
		Reptiles	160
BioTIME (Chapters 2 and 4)	Terrestrial	Terrestrial plants	177
		Birds	1600
		Mammals	40
		Terrestrial invertebrates	71
		Multiple taxa	30
		Amphibians	273
	Marine	Birds	9438
		Fish	24 297
		Mammals	480
		Marine invertebrates	2044
		Benthos	4383
		Multiple taxa	1538
		Marine invertebrates/plants	161

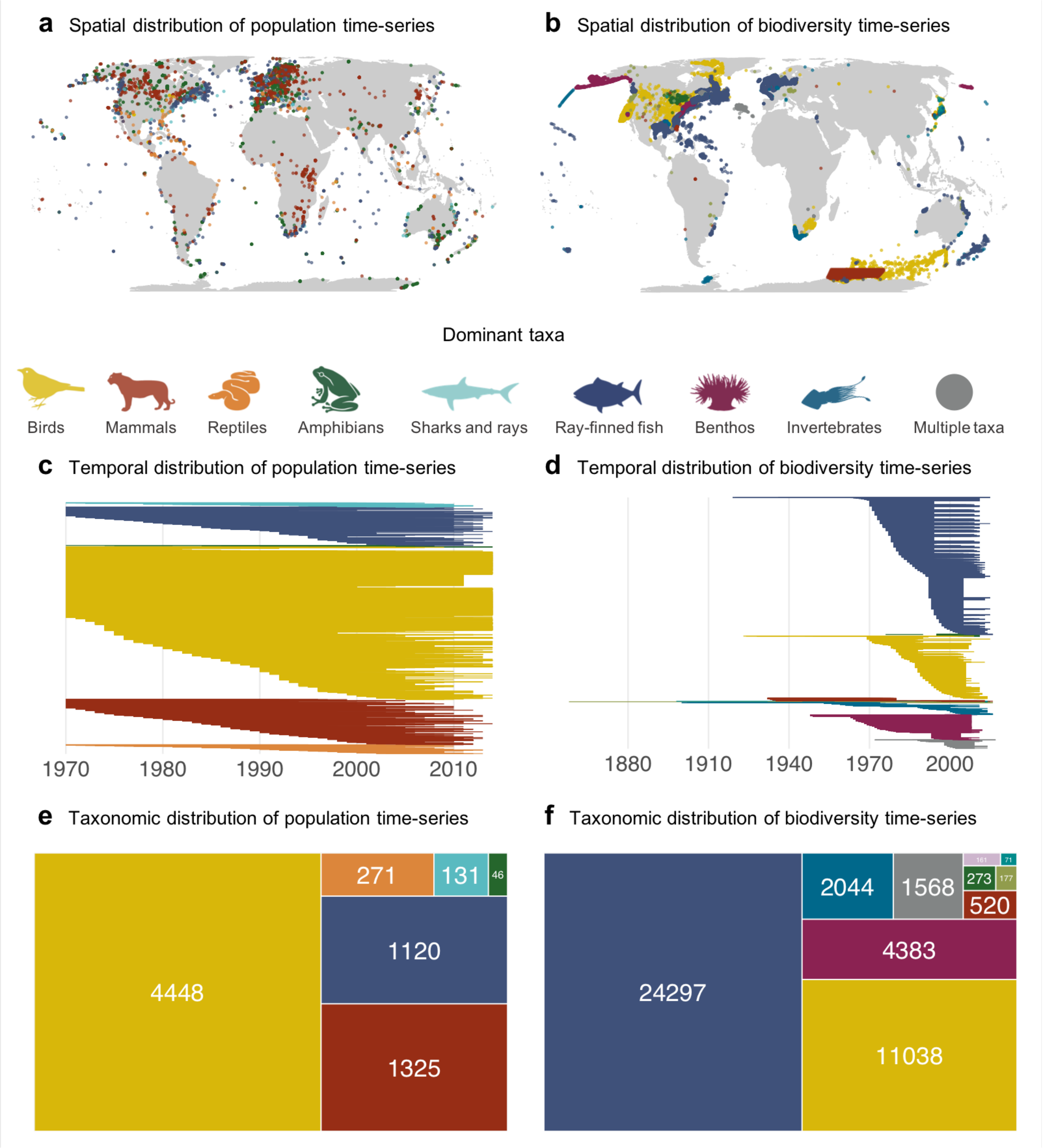

Figure 1.3. My thesis synthesises population and biodiversity time series data across space, time and taxa. The high number of records in Europe from very similar locations obscures some of the records. Please see the original data papers for each database (LPI, 2016 and Dornelas et al., 2019) that offer more detailed visualisations of data points. Note that the time scales on **c** and **d** are different to allow the visualisation of variation in the population time series.

Global change layers

To quantify the magnitude of different global change drivers, I used several global gridded datasets from which I extracted driver magnitude across the locations of biodiversity sites (Figure 1.4).

The marine and terrestrial harmonised layers developed by Bowler et al. (2020) were used in **Chapter 2** (Appendix 1.3). As in Bowler et al. (2020), I grouped the 16 layers into five categories: human use (land-use for the terrestrial realm, and exploitation for the marine realm), climate change, human population density, pollution and invasion potential. The driver data were harmonised to a standard spatial grid with a resolution of 100 km^2 and were aggregated over the time period between 1990 and 2010.

I used the Land Use Harmonisation (LUH, Hurtt et al., 2011) database of reconstructed historical land cover at a 0.25° resolution to extract land cover estimates over a long historic period (from the year 800 to 2014). The LUH database featured in **Chapter 2** (primary forest cover) as well as in **Chapter 4** (primary and secondary forest cover).

I used the CRU TS v4.05 database (Harris et al., 2020) to obtain terrestrial monthly surface air temperature at a spatial resolution of 0.5°. For the marine realm, I extracted sea surface temperature at a spatial resolution of 2° from the NOAA Extended Reconstructed SST v5 database (Huang et al., 2017). These data were used in **Chapter 2** to calculate the magnitude of temperature change over time across the sites part of the Living Planet, BioTIME and PREDICTS databases.

I extracted contemporary forest cover change from the Global Forest Change (GFC) database (2000 – 2016, forest loss and gain at a 30 m resolution, Hansen et al., 2013), also from the ESA Landcover database (1992 – 2015, 300m resolution, (ESA Climate Change Initiative, 2017). I calculated habitat transitions using the MODIS Landcover database (2000 – 2013, 500m resolution, (Channan et al., 2014). These data, together with the LUH dataset, were used in **Chapter 4**.

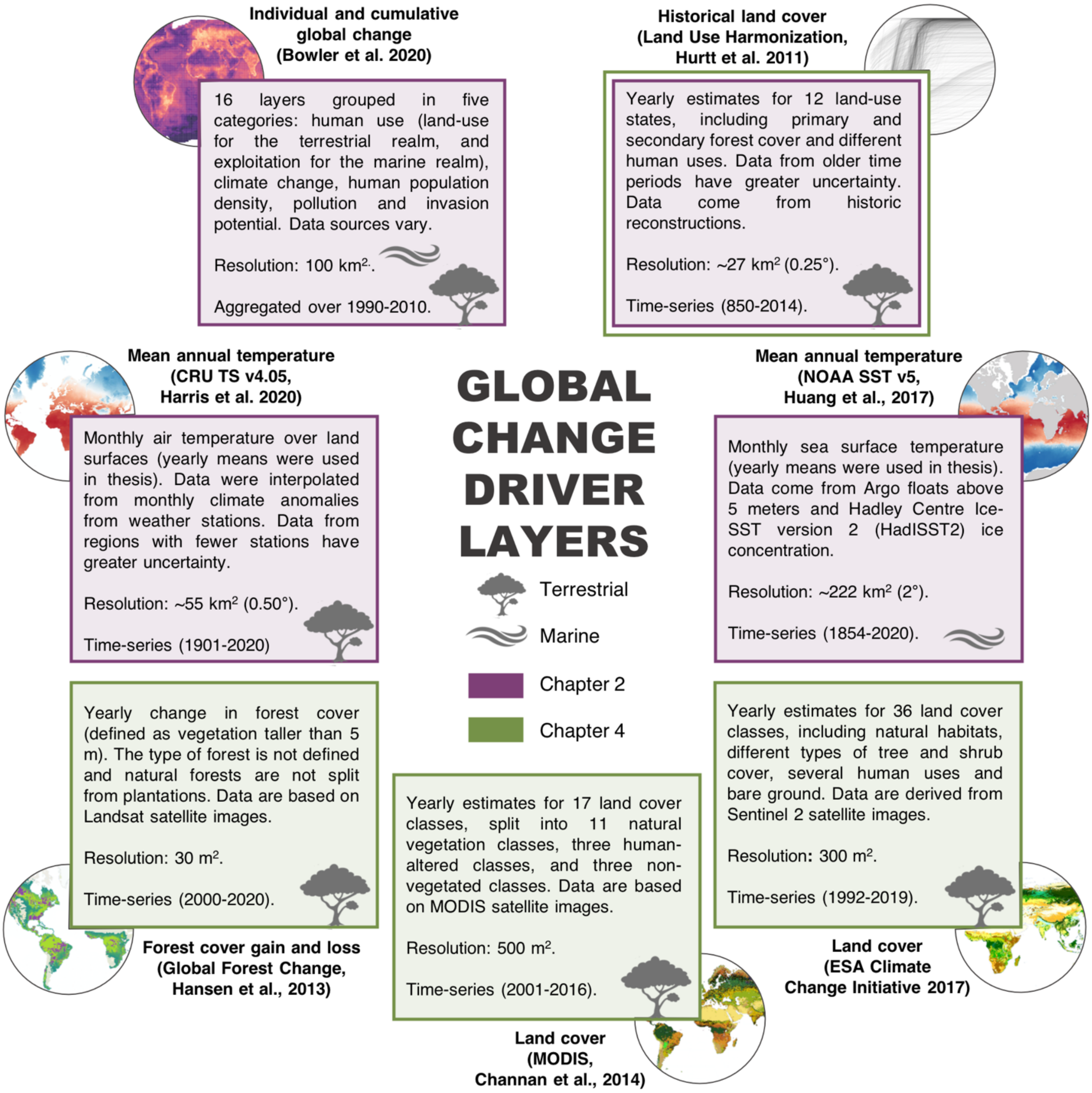

Figure 1.4. My thesis research used different gridded datasets to quantify the intensity of global change drivers across sites with population and biodiversity time series.

Statistical approaches and workflow

In analysing multiple global datasets together, I needed to account for the different data structures and varying replication across space, time and taxonomy. Broadly, the two key statistical approaches that I used were hierarchical models and general linear models, both based on Bayesian inference. The specific details around statistical models are outlined in each results chapter (**Chapter 2-4**). In **Chapter 2**, I extracted the magnitudes of different global change drivers across sites from the Living Planet, BioTIME and PREDICTS databases. In this chapter, I focused only on the global change drivers to test for example whether one database has more disturbed sites than another. The global change magnitudes were the response variable in a general linear model comparing global change across the different biodiversity databases, as well as across a random sampling of global change across the globe (driver magnitude as a function of an interaction term between two categorical explanatory variables – driver type and data source; data source was either Living Planet, BioTIME, PREDICTS or random global sampling). In **Chapters 3** and **4**, I used a two-stage analysis process. First, I calculated population change (trend from state-space models), richness change (slope from linear mixed effect model modelling richness versus year), compositional turnover (the turnover component of beta diversity, partitioned as per (Baselga, 2010) and using Jaccard's dissimilarity comparing assemblage composition at the start and end of time series). Second, I modelled population trends, richness trends and turnover across biomes, taxa and rarity trends in **Chapter 3**, and across forest cover change in **Chapter 4**. Sensitivity analyses using the BioTIME databases have showed that calculating turnover is not biased by using the first versus second year of the time series (Blowes et al., 2019; Dornelas et al., 2014). Overall, my thesis tested the links between the patterns of biodiversity change and the variation in global change around the world, spanning realms, taxa and biomes.

1.10 Additional projects complimentary to PhD research

During my PhD, I also completed two research internships and two Arctic field expeditions, and I also contributed to multiple research collaborations and two working groups. These projects all had biodiversity change at its core and provided different perspectives to the core topic of drivers of biodiversity change in the Anthropocene. The abstracts of the research papers stemming from these projects are included as appendices and summarised below.

Species pools and dark diversity across the tundra biome (National Geographic Early Career Explorer project, International Tundra Experiment (ITEX) network collaboration, Appendix 1.1).

The Arctic is warming at three times the rate of the global average (IPCC, 2021) and tundra plants are responding by increasing in cover, abundance and height (Bjorkman et al., 2020; Bjorkman, Myers-Smith, et al., 2018; Myers-Smith et al., 2011). Much of the evidence behind tundra vegetation change comes from small survey plots, leaving the landscape context of ongoing local-scale changes unknown. To fill this knowledge gap, I co-developed a monitoring protocol with the ITEX network aiming to quantify the species pool size around long-term monitoring tundra sites and their dark diversity (https://osf.io/agdfq/). I defined dark diversity using a temporal perspective as all the species that were present in the species pool but were never recorded inside the long-term plots across the duration of the monitoring. I completed the protocol on Qikiqtaruk-Herschel Island in 2018 and 2019, and other researchers completed it on further 15 tundra research sites, making for a total of 36 plant communities sampled. I found that dark diversity across the tundra varied from zero to nearly 100 species. Sites with higher dark diversity had experienced less compositional changes over time, but as these sites have a high colonization potential, dark diversity might be the fuel for future biodiversity change. Many of the data from the databases I used across my thesis come from plots similar to those in the Arctic, and this project aims to find the sources of biodiversity change observed at local scales (i.e., warmer versus colder, wetter versus drier parts of the landscape). I am leading an in-prep. manuscript based on this project (Daskalova, G.N., and the ITEX species pool consortium. Dark diversity across the tundra biome. In prep for Global Change Biology).

Land abandonment and population change in Europe (Research internship with Prof Henrique M. Pereira, German Centre for Integrative Biodiversity Research (iDiv), Appendix 1.2).

Land-use change processes occur over a wide spectrum, from land-use intensification (e.g., when forests are converted to fields) to land abandonment (when fields are no longer used for agriculture). In Europe, land-use intensification and land abandonment often occur in parallel, despite these two processes representing the extremes of land-use change (e.g., from forest to agricultural field, and from agricultural field to eventually forest, (Donald *et al.* 2006; Rey Benayas 2007; Sanderson *et al.* 2013; Crouzeilles *et al.* 2016). In recent years, rates of land abandonment have outpaced rates of land-use intensification and yet, the effects of land abandonment on biodiversity remain unknown. A major knowledge gap is whether abandoned land supports ecosystems similar to those prior agricultural use, or it creates novel ecosystems with unprecedented species composition. For my internship at iDiv, I asked how land abandonment in Europe varies over space and time, what the dominant land cover trajectories are following abandonment, and how vertebrate population abundance had changed in areas with land abandonment. I found that land abandonment had nearly doubled across Europe between 2009 and 2020. In areas with abandonment, vegetation cover was denser and taller, and vertebrate abundance was higher. By studying the effects of land abandonment and the shift from agricultural to semi-natural land, this project particularly well complements the research in **Chapter 4** which focused on forest loss and biodiversity change. I am leading an in prep. manuscript based on this project (Daskalova, G.N. and Pereira, H.M. Herbivorous mammals and carnivorous birds benefit from land abandonment in EU countries. In prep. for Ecology Letters).

Methods to account for temporal pseudoreplication in biodiversity time series analysis (In collaboration with Dr Isla Myers-Smith and Dr Albert Phillimore, Appendix 1.3).

The rise of open-access data in ecology has facilitated macroecological studies spanning space, time and taxa, but the analysis of such data come with numerous challenges (Wüest et al., 2020). While the implications of spatial pseudoreplication have long been recognised in ecology (Hurlbert, 1984), statistically accounting for temporal pseudoreplication has remained a more contentious issue (Daskalova et al., 2021; Seibold et al., 2021). In both local and regional, and sometimes even larger, studies data from different sites but from the same year are likely correlated. For example, certain years can be exceptionally good or bad for certain species, and particularly when such years occur at the start of a monitoring time series, they can skew overall estimated temporal trend because of a false baseline effect. Such was the case in a regional study in Northern German by Seibold et al. (2021) where the authors accounted for spatial but not for temporal pseudoreplication. I lead a re-analysis of the Seibold et al. (2021) data and demonstrated that after including a year random intercept term in the statistical models analysing invertebrate change over time, five out of six reported declines become non-significant. This reanalysis illustrates that statistical designs can dramatically influence the determined statistical significance of quantitative analyses of population and biodiversity trends over time. More statistically conservative approaches better capture the errors including year effects inherent in population and biodiversity monitoring. This project provides methodological context to all analyses in my thesis and is published as "Daskalova, G. N., Phillimore, A. B., & Myers-Smith, I. H. (2021). Accounting for year effects and sampling error in temporal analyses of invertebrate population and biodiversity change: a comment on Seibold et al. 2019. *Insect Conservation and Diversity*, *14*(1), 149-154".

Highlighting a balanced view of insect trends (In collaboration with Dr Maria Dornelas, Appendix 1.4).

Building on my previous project on analysing invertebrate trends and statistical methods, I also worked together with Dr Maria Dornelas on an invited perspective piece in Science commenting on the analysis of van Klink et al., (2020). van Klink et al. (2020) conducted a meta-analysis of insect abundance and biomass changes over time across the terrestrial and freshwater realms and found declines on land but increases in freshwater ecosystems. Our perspective highlighted the importance of communicating the nuance around biodiversity change, particularly given that insect change has become a standout topic for both the media and policy-makers. By shifting our perspective on the full distribution of biodiversity change instead of focusing solely on mean values and summary indicators, we can understand more about the causes of biodiversity gain and loss and better target conservation actions. This perspective is published as "Dornelas, M., & Daskalova, G. N. (2020). Nuanced changes in insect abundance. *Science*, *368*(6489), 368-369".

Ecosystem change following mammal reintroductions in Australia (Research internship with Prof Richard Hobbs, University of Western Australia, Appendix 1.5).

Species reintroductions are an increasingly popular form of active conservation management, particularly following local extinctions of keystone species (Seddon et al., 2007). In Australia, the reintroduction of digging mammals has been suggested as a way to reverse the ecosystem damage from livestock farming and overgrazing (Palmer et al., 2020). For my internship at UWA, I worked together with Bryony Palmer (PhD student) and Prof Richard Hobbs. Since my PhD used already available data and was conducted at very large spatial scales, the project at UWA was an opportunity to study the impacts of conservation interventions following land-use change in greater detail. The project resulted in the following publication: "Palmer, B. J., Valentine, L. E., Lohr, C. A., Daskalova, G. N., & Hobbs, R. J. (2021). Burrowing by translocated boodie (*Bettongia lesueur*) populations alters soils but has limited effects on vegetation. *Ecology and Evolution*, *11*(6), 2596-2615".

Upscaling of individual species dynamics to community trends in biodiversity and composition using vegetation change data sets (sREplot working group, German Centre for Integrative Biodiversity Research (iDiv), Appendix 1.6)

Changes in the composition of ecological communities are widespread around the world and more common than shifts in species richness (Blowes et al., 2019). One of the remaining unknowns is what types of species are becoming more or less common and what implications that has for ecosystem functions and services. As a member of the sREplot working group, I contributed to an analysis testing how the geographic range of plant species in forest, tundra and grassland habitats relates to their likelihood to persist, go extinct or colonise. By focusing on plants, this project provides a compliment to **Chapter 3** where I studied species' geographic range and vertebrate population trends. The resulting manuscript is published as a preprint and is currently in review at Ecology Letters: "Staude, I., Pereira, H. M., Daskalova, G. N., Bernhardt-Römermann, M., Diekmann, M., ... & Baeten, L. (2021). Consistent replacement of small- by large-ranged plant species across habitats. EcoEvoArxiv. DOI: 10.32942/osf.io/ujky2."

Quantifying temporal change in traits across taxa and the globe (sTeTra working group, German Centre for Integrative Biodiversity Research (iDiv),)

By quantifying changes in functional diversity, we can link local-scale biodiversity change with ecosystem function and determine the wider consequences of changes in community composition. As a member of the sTeTra working group, I will contribute to the synthesis of the BioTIME database with trait databases to test for directional shifts in traits such as body size across taxa and biomes. The first meeting of the sTeTra working group is scheduled for October 2021. The working group builds on my studies of biodiversity change and global change drivers (**Chapters 2** and **4**) and will also explore the interactions between trait change and the intensity of human activities.

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Chapter 2. Representation of global change drivers across biodiversity datasets

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The following chapter "Representation of global change drivers across biodiversity datasets" is in revision at Nature Ecology and Evolution (ID: NATECOLEVOL-210613960A, decision letter 8th Sept 2021) and is available as a preprint on EcoEvoArxiv (https://ecoevorxiv.org/db4s7/).

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Code and data availability: All data and code are publicly available. Population and biodiversity time series data are freely available in the Living Planet and BioTIME Databases (see references for details on data collection). The Living Planet Database can be accessed on http://www.livingplanetindex.org/data_portal. The BioTIME

Database can be accessed on Zenodo (https://doi.org/10.5281/zenodo.1211105) or through the BioTIME website (http://biotime.st-andrews.ac.uk/). PREDICTS can be downloaded from https://www.predicts.org.uk/pages/outputs.html. A GitHub repository (https://github.com/gndaskalova/GlobalChangeSpace) contains the database of biodiversity data locations and associated global change driver magnitudes I compiled, as well as my code. I completed a pre-registration on the Open Science Framework (https://osf.io/qjr27/?view_only=56d98233baa047fcb2d5fe554103f01e) for the global change representation research questions but note that the PREDICTS database was added to the analyses after the pre-registration was submitted.

2.1 Summary

Global change has altered biodiversity and impacted ecosystem functions and services around the planet. Understanding the effects of anthropogenic drivers like land-use change, fishing, human exploitation of natural resources and climate change on biodiversity change has become a key challenge for science and policy. However, our knowledge of biodiversity change is limited by the available data and their biases. Over land and sea, I tested the representation of three worldwide biodiversity databases (Living Planet, BioTIME and PREDICTS) across geographic and temporal variation in global change and across the tree of life. I found that variation in global change drivers is better captured over space than over time around the world and across the previous 150 years. Spatial representation of global change was as high as 78% in the marine realm and 31% on land. Among the five global change drivers I tested, climate change and pollution in marine ecosystems were sampled the most representatively by the Living Planet and BioTIME databases. Across all types of global change that I studied, the mid-range of intensities was the best sampled, leaving intact and heavily impacted areas underrepresented in biodiversity databases. Contemporary warming was better captured in biodiversity time series relative to drivers like forest loss for which the peak disturbance often occurred decades to centuries before the start of biodiversity monitoring. My findings suggest ways to improve the use of existing biodiversity data and better target future ecological monitoring.

2.2 Introduction

Human activities are reshaping the planet from the tropics to the poles and across land and sea (Bowler et al., 2020; Ellis et al., 2013; IPCC, 2014), and the Earth's biodiversity is shifting in response (IPBES, 2019). Parallel with this rapid biotic reorganization, an ecological data revolution is underway with more open-access data available now than ever before (Culina et al., 2018; Hampton et al., 2013). Large-scale data compilations (e.g., Living Planet (WWF, 2018), BioTIME (Dornelas et al., 2018), PREDICTS (Hudson et al., 2017), GBIF (GBIF, 2021), TetraDensity (Santini et al., 2018)) have been analysed to test general patterns of biodiversity change across the world and impacts of anthropogenic drivers, such as land-use change, climate change and human exploitation of natural resources (**Chapter 4**; Antão et al., 2020; IPBES, 2019; McCallen et al., 2019; Millette et al., 2020; Newbold et al., 2015). Such studies have revealed a wide spectrum of biodiversity change, including both increases and decreases of species richness and abundances, with trends quantified over time (Blowes et al., 2019; Dornelas et al., 2014; Macgregor et al., 2019; Vellend et al., 2013), space (Betts et al., 2017; Newbold et al., 2015) and taxa (**Chapter 3**; Outhwaite et al., 2020). The biodiversity data underlying many of these syntheses (e.g., time series, occurrence records and space-for-time surveys) have already been shown to be biased geographically and taxonomically (Amano et al., 2016; Boakes et al., 2010; Gonzalez et al., 2016; Meyer et al., 2015). Surprisingly, much less attention has been given to whether the data are also biased with respect to the overall variation in global change drivers (e.g., human use of ecosystems, climate change, pollution). Yet, knowing to what degree the sampling of biodiversity databases captures global change is vital for interpreting results derived from data syntheses and identifying future data gaps to be filled. The next stage of biodiversity syntheses, scenarios and conservation goals will be brought together in the Convention on Biological Diversity's Post-2020 Global Biodiversity Framework. I argue that, post-2020, biodiversity science needs to move towards improved representation of global change variation in biodiversity data.

Insights from large-scale data syntheses inform trajectories of past, current and future change in the Earth's biota (Hill et al., 2018; IPBES, 2019; Schipper et al., 2019; WWF, 2018), as well as the development of indicators for global conservation policies (OECD, 2019; Xu et al., 2021). To upscale the findings of syntheses of local-scale data to estimates of global or mean biodiversity change, the underlying data should be representative across multiple dimensions: space, time, taxonomic variation, as well as variation in the drivers of biodiversity change (Johnston et al., 2020; Mentges et al., 2021; Mihoub et al., 2017; Troudet et al., 2017). There is already recognition of the biases associated with space and geography (Boakes et al., 2010; Gonzalez et al., 2016; Johnston et al., 2020; Mentges et al., 2021), time and historical baselines (Boakes et al., 2010; Buckland & Johnston, 2017; Gonzalez et al., 2016; Wauchope et al., 2021) and taxonomy (Buckland & Johnston, 2017; Feng et al., 2021; Troudet et al., 2017). In contrast, sampling biases with respect to drivers of change are rarely emphasised in the existing literature (but see Shirey et al., (2021) for spatio-taxonomic biases in North American butterfly occurrence records). At smaller spatial scales, sampling biases are well-documented in national monitoring schemes and citizen science data (e.g., showing over-representation of urban areas (Marsh & Cosentino, 2019) or under-representation of regions undergoing rapid climate change (Shirey et al., 2021)). In contrast, at the larger spatial scales of data syntheses, sampling biases associated with global change drivers remain unknown. Such knowledge gaps compromise our ability to draw broad inferences from the outcomes of syntheses and to quantify the shape of the relationship between driver intensity, such as extent of land-use change, and biodiversity, in order to identify ecological tipping points (Isbell et al., 2019; Mihoub et al., 2017; Moore, 2018; Ritchie et al., 2021). Thus, to interpret the findings of any data synthesis, we need to consider if the underlying data are sampled from sites with the full range of different driver intensities, or rather mostly include heavily impacted sites or wilderness areas (De Palma et al., 2018; IPBES, 2019; Mihoub et al., 2017). Understanding the representativeness of biodiversity data across global change axes is essential to interpret estimates of regional or global-scale biodiversity change from compilations of local-scale data.

Here, I quantify global change representation in biodiversity databases, present my perspective on capturing the representativeness of biodiversity data in large-scale syntheses and discuss implications for interpreting their findings. I focus on four aspects of representativeness – global change intensity over space, global change intensity over time, geography, and taxonomy. Particularly, I highlight the patterns in spatial and temporal sampling of global change drivers as under-explored types of bias. My perspective serves two important purposes: 1) to highlight the variation in global change drivers that is already captured by global datasets and hence the driver impacts that I can quantify in ongoing studies, and 2) to identify the gaps in data representativeness that future studies, monitoring and data mobilization actions should target. By building biodiversity databases that are more representative of multiple axes of natural and anthropogenic variation, we can improve predictions of the global state and trends of biodiversity.

2.3 Methods

Workflow

I combined three of the largest, currently available, open-access biodiversity databases - Living Planet (WWF, 2018) - marine and terrestrial; BioTIME (Dornelas et al., 2018) - marine and terrestrial; and PREDICTS (Hudson et al., 2017) - terrestrial, with maps of the intensities of five global change drivers (Bowler et al., 2020). The drivers I focused on were human use (land use intensity in the terrestrial realm and fishing in the marine realm), climate change (changes in mean temperature and precipitation and their extremes), human population density, pollution and invasive species pressure. To measure how well each database captures variation in global change intensity over space, I first estimated driver variation around the world. I then determined the 'global change space' using the dominant orthogonal axes of change (similar to the concept of trait or niche space, Díaz et al., (2016)). I then mapped the sampling sites within each database onto the global change space to highlight the sampled region, as well as regions with under- or over- representation. To quantify the representation of global change intensity over time, I focused on climate change and land cover change across terrestrial sites with time series data from the Living Planet and BioTIME databases. I chose those two drivers because they have global-scale data available at an annual (or finer) time step for long enough periods to coincide with when the population and biodiversity time series were surveyed. At each site, I compared the amount of change that occurred before relative to during the periods of biodiversity monitoring. To estimate geographic representation, I mapped site locations of the three databases and determined sampling intensity across an ~30° spatial grid covering the planet. Finally, to estimate taxonomic representation, I calculated the percentage of known species included in the three databases, with each species having the same weight.

Databases of ecological monitoring

I combined three of the largest biodiversity databases - Living Planet (7,340 time series spanning 1970-2014), BioTIME (44,532 time series spanning 1858-2017) and PREDICTS (468 studies spanning 1984-2013). The Living Planet database (WWF, 2018) includes time series data of individual species' abundance for vertebrate taxa for the terrestrial, marine and freshwater realms. The BioTIME database (Dornelas et al., 2018) is also a compilation of time series but of ecological assemblages for vertebrate, invertebrate and plant taxa across the terrestrial, marine and freshwater realms. Freshwater realm data were excluded for the purposes of this analysis because of lack of global change driver data for freshwater environments. The PREDICTS database (Hudson et al., 2017) includes space-for-time comparison studies testing the effects of land-use change on vertebrates, invertebrates and plants and thus focuses on the terrestrial realm. For this chapter, I only used the geographical coordinates of the sites within each database and not the biodiversity data collected at each site.

Databases of global change

I used the 16 marine and terrestrial global change driver layers compiled by Bowler et al. (2020; Appendix 2.4). I selected these layers because they had been harmonised across both realms and hence were most suitable for my global analysis. As in Bowler et al. (2020), these layers were grouped into five focal drivers: 1) human use (land-use for the terrestrial realm, and exploitation for the marine realm), 2) climate change, 3) human population density, 4) pollution and 5) invasion potential. The driver data were harmonised to a standard spatial grid with a resolution of 100 km^2 and were aggregated over the time period between 1990 and 2010. The driver data were not available on an annual time step with the exception of the variables forest loss and climate change. Data limitations were particularly pronounced for the marine realm, as it is harder to monitor global change at sea than over land (Bowler et al. 2020). For details on the individual layers forming the global change data, including their resolutions and temporal coverage, see Appendix 1.3. I used the Land Use Harmonisation (LUH) database of reconstructed historical land cover at a 0.25° resolution (Hurtt et al., 2011) to extract primary forest cover estimates over a long historic period (from the year 800 to 2014). For the terrestrial realm, I obtained monthly surface air temperature at a spatial resolution of 0.5° from the CRU TS v4.05 database (Harris et al., 2020) and for the marine realm, I extracted sea surface temperature at a spatial resolution of 2° from the NOAA Extended Reconstructed SST v5 database (Huang et al., 2017). For each of the different metrics, I used the highest resolution data available to improve the precision of land cover and temperature estimates. For both surface air temperature and sea surface temperature, I aggregated the monthly data into yearly averages for time periods matching the timing of biodiversity time series as well as the period of same duration preceding the monitoring (e.g., for a time series from 2000 to 2010, I extracted data from 1990 to 2000 and from 2000 to 2010).

Mapping ecological monitoring in global change space

I combined the geographical coordinates of all spatially-explicit monitoring sites in the Living Planet, BioTIME and PREDICTS databases. For each sampling site, I extracted the intensity of 16 global change layers as well as their cumulative magnitudes. The driver data matching the sites in each database are available in an open-access repository (see Code and Data Availability section). The estimates for the magnitudes of each driver were standardised between 0 and 1 to make them comparable. I used a Principal Component Analysis (PCA) to map global change space within the two dominant orthogonal axes (similar to trait space, Díaz et al., (2016)), which explained 81% of the variation, and visualised the sampled sites in this global change space. I extracted driver intensity for one million simulated random locations spanning the globe to represent an unbiased sample of the marine and terrestrial surface of the world. I used this random sample as a comparison for quantifying the representation of global change variation in biodiversity data. To calculate the percentage overlap between global change space and the area within it occupied by the three databases, I used the package SIBER v.2.1.6.9 (Jackson et al., 2011) and 95% prediction ellipses. The overlap was calculated using ellipses based on the climate change and human use variables, since human population density, pollution and invasion pressure were positively correlated with human use. I visualised marine and terrestrial global change space separately because of known differences in the global change driver variables capturing human impact across realms and suspected differences in the patterns of sampling effort (Bowler et al., 2020).

To statistically compare the intensity of global change drivers around the world and in locations with biodiversity data, I used two Bayesian general linear models (one for the marine and one for the terrestrial realm) with driver intensity as the response and an interaction term between driver type and database as the predictor (see code repository for more details https://github.com/gndaskalova/GlobalChangeSpace). This model tested what types of sites were represented by each biodiversity database but did not include any biodiversity data per se as that was the focus of **Chapters 3-4**. Database represented a four-level categorical variable (Random global sampling, Living Planet, BioTIME or PREDICTS database; in the marine model the PREDICTS database was omitted since it only covers the terrestrial realm). The ‘Random global sampling’ level was used as the reference so the coefficients for the three databases represent differences from the random global sampling. Driver intensity values for each driver were standardised between zero and one to make them comparable. Because of the large sample size, the driver data were not sensitive to outlier values which if present, could have biased the standardisation of the data. I fitted my model using the package brms v.2.15.0 (Bürkner, 2017) and the default weakly informative priors. I considered credible intervals around the effect size (posterior mean) that do not overlap zero to indicate that global change on sites with existing biodiversity data differs from random sampling. When effect sizes are negative this indicates that sites with existing biodiversity data underestimate driver intensity and when effect sizes are positive this indicates that sites with existing biodiversity data overestimate driver intensity.

Quantifying mismatches between peak driver intensity and ecological monitoring

To quantify how well biodiversity datasets captured variation in global change over time, I focused on changes in primary forest cover derived from the LUH database (Hurtt et al., 2011) and in temperature, derived from the CRU TS v.4.05 database (Harris et al., 2020) for the terrestrial realm and from the NOAA Extended Reconstructed SST v5 database (Huang et al., 2017) for the marine realm. I chose these focal drivers because they explain large amounts of the variation in global change in the terrestrial realm (Bowler et al., 2020) and they have long-enough temporal data to allow us to determine the trajectory of change and assess its match with the timing of biodiversity data collection.

I visualised primary forest cover from the year 800 to 2014 for the location of each terrestrial site in the Living Planet and BioTIME databases and indicated when the monitoring began at each site. I was unable to complete a similar analysis for the marine realm because there are no available temporal data for human use drivers like fishing of a sufficiently high temporal and spatial resolution. I extracted monthly mean temperature data for the same locations and summarised it as yearly averages. I then compared the slopes of temperature change during the biodiversity monitoring with the slopes of temperature change in the period preceding the monitoring (the two comparison periods were of equal length and always more than five years). For the comparison, I used general linear models predicting temperature change as a function of period, a two-level categorical variable with the levels of before and during monitoring.

Determining geographic and ecoregion representation

I mapped the location of sampling sites within the Living Planet, BioTIME and PREDICTS databases. Ecoregion polygons were retrieved for the terrestrial (Olson et al., 2001) and marine (Spalding et al., 2007) realms. I then counted the number of ecoregions that were sampled by each database (sampling indicates at least one record in a given ecoregion).

Determining taxonomic representation

To quantify taxonomic representation, I extracted the numbers of known species per taxa (birds, bony fish, mammals, amphibians, sharks, reptiles, terrestrial plants and arthropods) from the 2019 edition of the Catalogue of Life (http://www.catalogueoflife.org) and then compared them to the numbers of distinct species recorded in the Living Planet, BioTIME and PREDICTS databases. I quantified taxonomic representation as percentages of species which have at least one record in the respective databases.

2.4 Results and discussion

2.4.1 Biodiversity data capture spatial variation in global change space at sea, but not on land

Overall, I found that biodiversity data from the Living Planet, BioTIME and PREDICTS databases capture a surprisingly high amount of the spatial variation in global change intensity around the planet, especially in the marine realm (Figure 2.1). There was between 1 (Figure 2.1). Among the five global change drivers I tested, climate change and pollution in the marine realm were sampled the most representatively, suggesting that we can test the effects of these drivers with higher confidence and the underlying data could be used when creating global scenarios for the future (Figure 2.2, Appendix 2.3). The terrestrial global change space was less well sampled and the highest overlap with global change was 31% for the Living Planet Database (Figure 2.1). In fact, all three databases predominantly sampled places with medium to high human use and lacked data from regions with low land-use change and pollution. Similarly, across both realms, but particularly strongly over land, all databases were lacking sites that have experienced high amounts of climate change, reflecting geographic gaps in data collection in places like the Arctic (Figure 2.4). Following experimental design principles, manipulative studies to determine treatment effects often include a range of treatment levels from low to high in order to have sufficient statistical power (Osenberg et al., 1994). I propose extending experimental design thinking to syntheses of observation studies that aim to attribute change to a driver by ensuring data are included from sites experiencing a range of driver intensities.

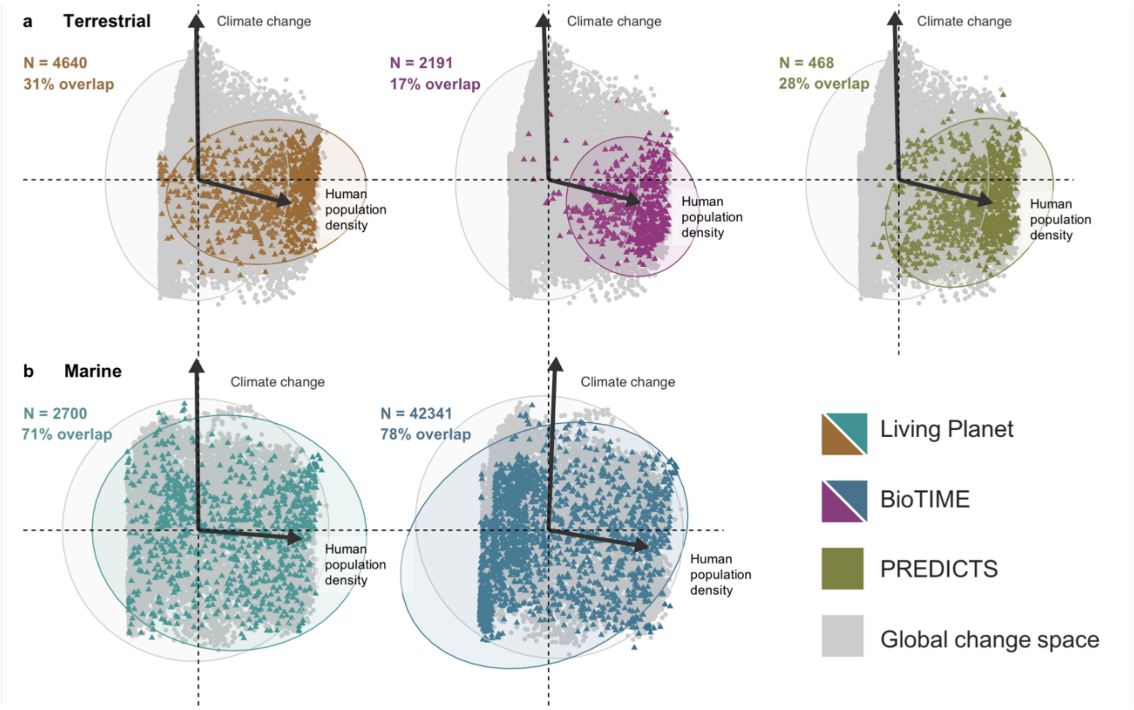

Figure 2.1. Biodiversity data capture spatial variation in global change space better in the marine versus terrestrial realm. Figure shows Principal Component Analysis of the terrestrial (panel **a**) and marine (panel **b**) magnitudes of human use, climate change, human population density, pollution and invasion potential across the locations of the Living Planet, BioTIME and PREDICTS databases as well as one million randomly sampled locations across the full extent of the globe (in grey). PCA axes omitted for visual clarity. Arrows show direction and magnitude of PCA scores for climate change and human population density. Human use, pollution and invasion potential were correlated with human population density (see Figure S11 in the supplementary information of Bowler et al. 2020). Thus, climate change and human population density together capture the two dominant axes of global change variation. For details on the global change driver layers, see Bowler et al. 2020. For latitudinal variation in global change space, see Appendix 2.2. Annotations show sample size (N) and the percentage overlap between the 95% prediction ellipses covered by random sampling of global change space and the variation in global change sampled by the different databases.

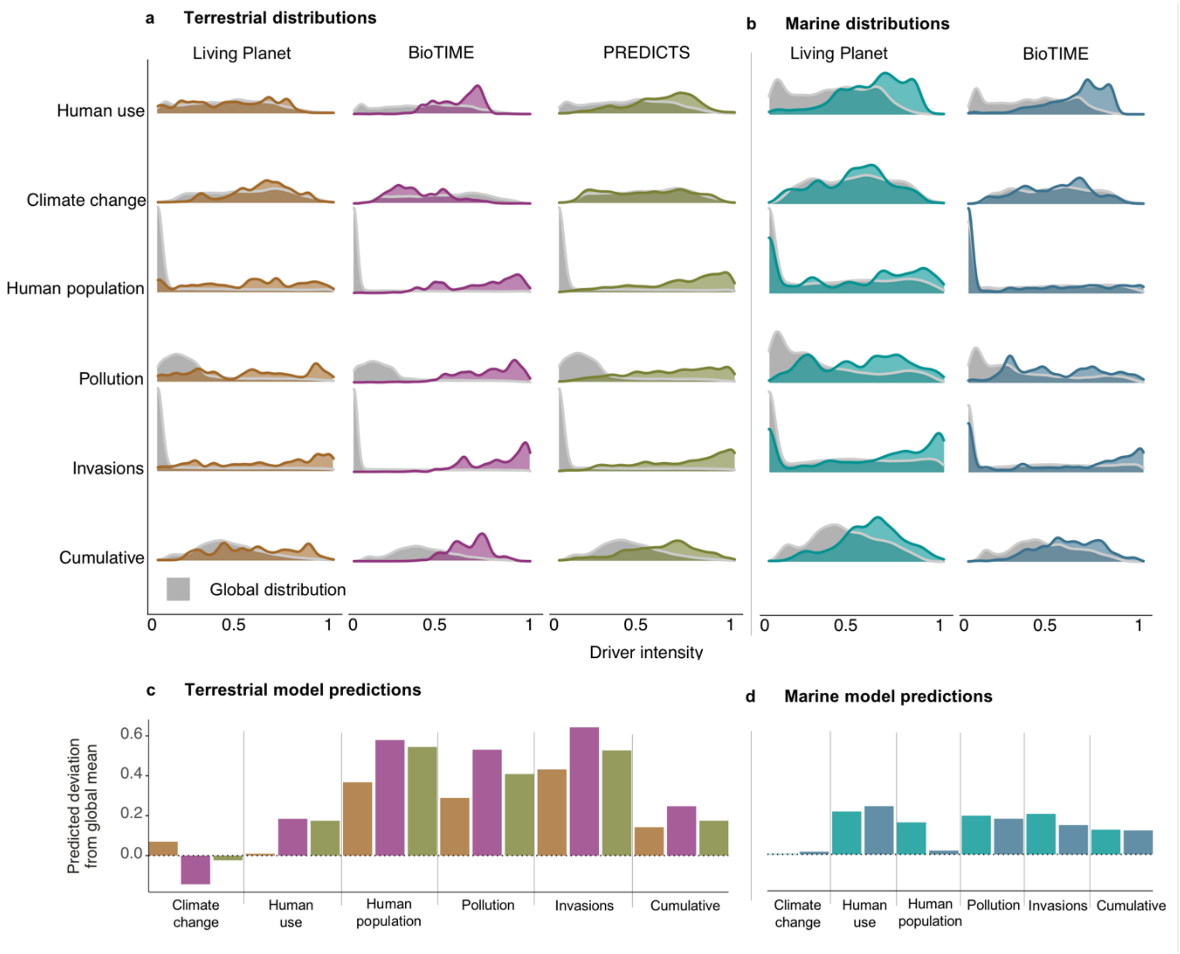

Figure 2.2. Higher magnitudes of global change drivers are overrepresented in biodiversity data. Panels **a** and **b** show distributions of the raw global change driver data from random sampling spanning the globe and sites from existing biodiversity databases. Panels **c** and **d** show effect sizes of general linear models comparing the magnitude of global change drivers (response variable) across the Living Planet, BioTIME and PREDICTS databases and a random sampling of the planet (categorical explanatory variable). Positive effect sizes indicate higher average magnitudes at the sampled sites within databases than in the random global sampling, and negative effect sizes indicate lower average magnitudes. Because of the large sample sizes included in the statistical models, the 95% credible intervals around the effect sizes were too small to be visualised in the figure. See Appendix 2.3 for all outputs from statistical models.

2.4.2 Biodiversity data often miss the temporal peaks of land cover change, but capture those of climate change

I found mismatches between when global change occurred and the timing of biodiversity data collection, which were more frequent for land-use change than for climate change (Figure 2.3). While it is well-known that peak land-use conversion often predates ecological monitoring by centuries to millennia (e.g., Ellis et al., 2013; Hurtt et al., 2011; Klein Goldewijk et al., 2017), studies rarely quantify the magnitude of this mismatch or account for the long-term trajectory or historic baseline (but see **Chapter 2**; Betts et al., 2017). For drivers such as forest loss, the peak often occurred decades to centuries before the start of most biodiversity monitoring, particularly in Europe (Figure 3a-b in the present chapter, **Chapter 2**). In contrast, for climate warming, a driver that is more pronounced in more recent decades, I found that the majority of the Living Planet and BioTIME time series (76% and 56% of terrestrial time series, and 64% and 59% of marine time series, respectively) have experienced larger magnitudes of warming during the period of monitoring when compared to the same length of time preceding data collection. Thus, biodiversity data better captured contemporary warming relative to other global change drivers (Figure 2.3c-f). My results suggest that weaker or stronger relationships between biodiversity time series and drivers such as forest loss and climate change likely reflect differences in the time periods when each driver was most intense.

The sampled variation in global change driver intensity over time can influence the strength of relationships detected in attribution analyses (**Chapter 4**; Isbell et al., 2019; Mihoub et al., 2017) and can obscure assessment of biodiversity trends in ecosystems with tipping points (Dakos et al., 2019). Monitoring schemes that start well after the peak magnitude of a global change driver will likely underestimate that driver's impact on biodiversity (Mihoub et al., 2017). Equally, lagged biodiversity change might mean that the effects of land-use drivers like forestry or agriculture persist decades after harvest or farming has ceased (**Chapter 4**; Isbell et al., 2019). These interactions between lagged biodiversity responses to disturbance and temporal variability of global change have produced heterogeneous and often non-linear biodiversity trends, as have been reported for many taxa, including birds (Jarzyna & Jetz, 2018), moths (Macgregor et al., 2019) and wasps (Jönsson et al., 2021). Additionally, analyses of observational datasets with both short durations and little variation in global change intensity over time have reduced statistical power and thus might fail to detect the effect of global change drivers (Jennions, 2003). The temporal mismatch of ecological monitoring and global change drivers is hard to alleviate because new data collection cannot fill historic data gaps. To move forward, ecologists should mobilise as much existing data as possible, improve data accessibility and develop methods to account for variation in driver intensity over time in statistical models.

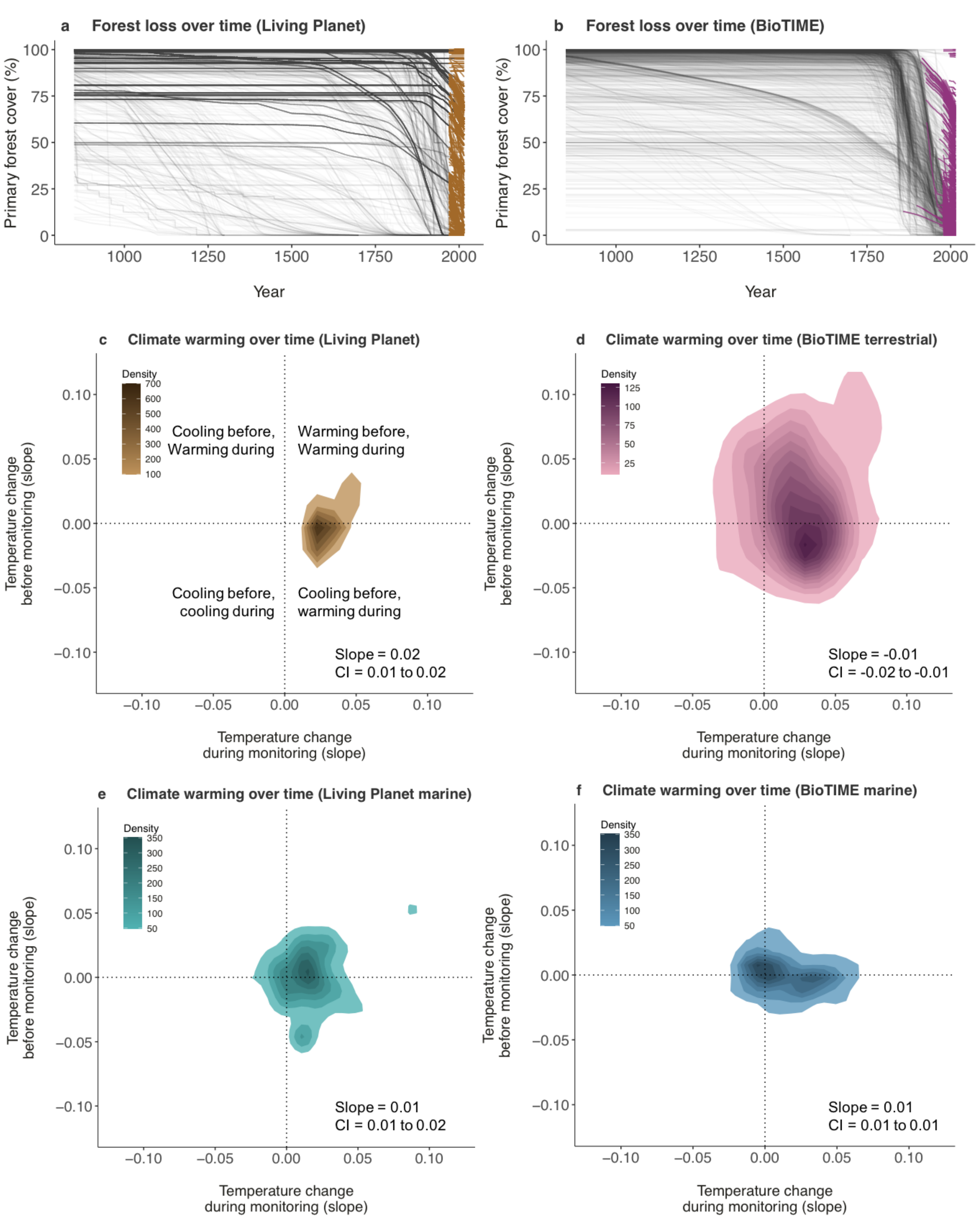

Figure 2.3. The majority of primary forest was lost by the time ecological monitoring began whereas high magnitudes of climate warming predominantly occurred during the time series. Panels **a** and **b** show the temporal trajectory of primary forest loss across sites part of the Living Planet (N = 4640) and BioTIME (N = 2191)

databases. The primary forest cover estimates show proportions based on the LUH database (Hurtt et al., 2011) and were calculated for cells of approximately ~96 km^2 around the centre point of each site. Historic human use time series data of sufficient duration were not available for the marine realm. The periods for comparison in panels **c**-**e** were the same as the duration of each time series and were always more than five years (for example for a time series starting in 2000 and ending in 2010, I used 1990-2000 as the comparison period). Slope values on the axes of panels **c**-**e** show changes in temperature in degrees Celsius per year, derived from general linear models estimating temperature as a function of year. For the terrestrial realm, surface air temperature was obtained from the CRU TS v4.05 database (Harris et al., 2020) and for the marine realm, the sea surface temperature data was extracted from the NOAA Extended Reconstructed SST v5 database (Huang et al., 2017). Slope and credible interval annotations on panels **c**-**e** show the posterior mean for the average temperature change in the period during monitoring relative to before monitoring. See Appendix 2.3 for all outputs from statistical models.

2.4.3 Geographic gaps in biodiversity data do not always result in gaps in global change space

Underrepresentation in geographic space did not directly translate into gaps in global change space and thus an incomplete geographic sample can capture a surprising amount of variation in global change driver intensity (Figures 2.1-2.2, 2.4). Geographic gaps exist across all three databases I tested, particularly in tropical and high latitudes and in the deep sea. Regions including Northern Asia, Africa and South America had fewer sample sites than Europe and North America across all three databases. For example, there were twice as many European records as there were South American ones in the PREDICTS database, despite South America being almost twice the size of Europe. Europe and North America not only had more sampling across space, but repeat sampling was also more frequent (Figure 2.4a-e). Ecoregions in the marine realm were better represented than those in the terrestrial realm, with data sampled in 69% and 48% of marine ecoregions in the Living Planet and BioTIME databases, compared with the same in 16%, 30% and 32% of terrestrial ecoregions in the Living Planet, BioTIME and

PREDICTS databases, respectively (Figure 2.4). Geographic biases are well-known caveats of biodiversity data (e.g., Boakes et al., 2010; Gonzalez et al., 2016; Titley et al., 2017) and can be particularly problematic when extrapolating from patchy local-scale data to broad macroecological patterns (IPBES, 2019). For example, studies of insect biodiversity trends from a limited sample of geographic locations have found steep declines (e.g. 63 sites in Germany and 73 sites in predominantly North America and Europe in Hallmann et al. (2017); Sánchez-Bayo & Wyckhuys (2019), respectively), whereas studies from larger and more geographically representative datasets have found no net change (van Klink et al., 2020). This nuance around the source locations of biodiversity data is often lost in media and public communication of population and biodiversity change, sometimes leading to misinterpretation of local declines as ubiquitous worldwide (Daskalova et al., 2021; Didham et al., 2020; Dornelas & Daskalova, 2020; Montgomery et al., 2019). Ecologists should target future ecological monitoring that fills in the gaps in not just geographic but also in global change space, particularly places with high climate change and less disturbed ecosystems, to better capture and communicate biodiversity change.

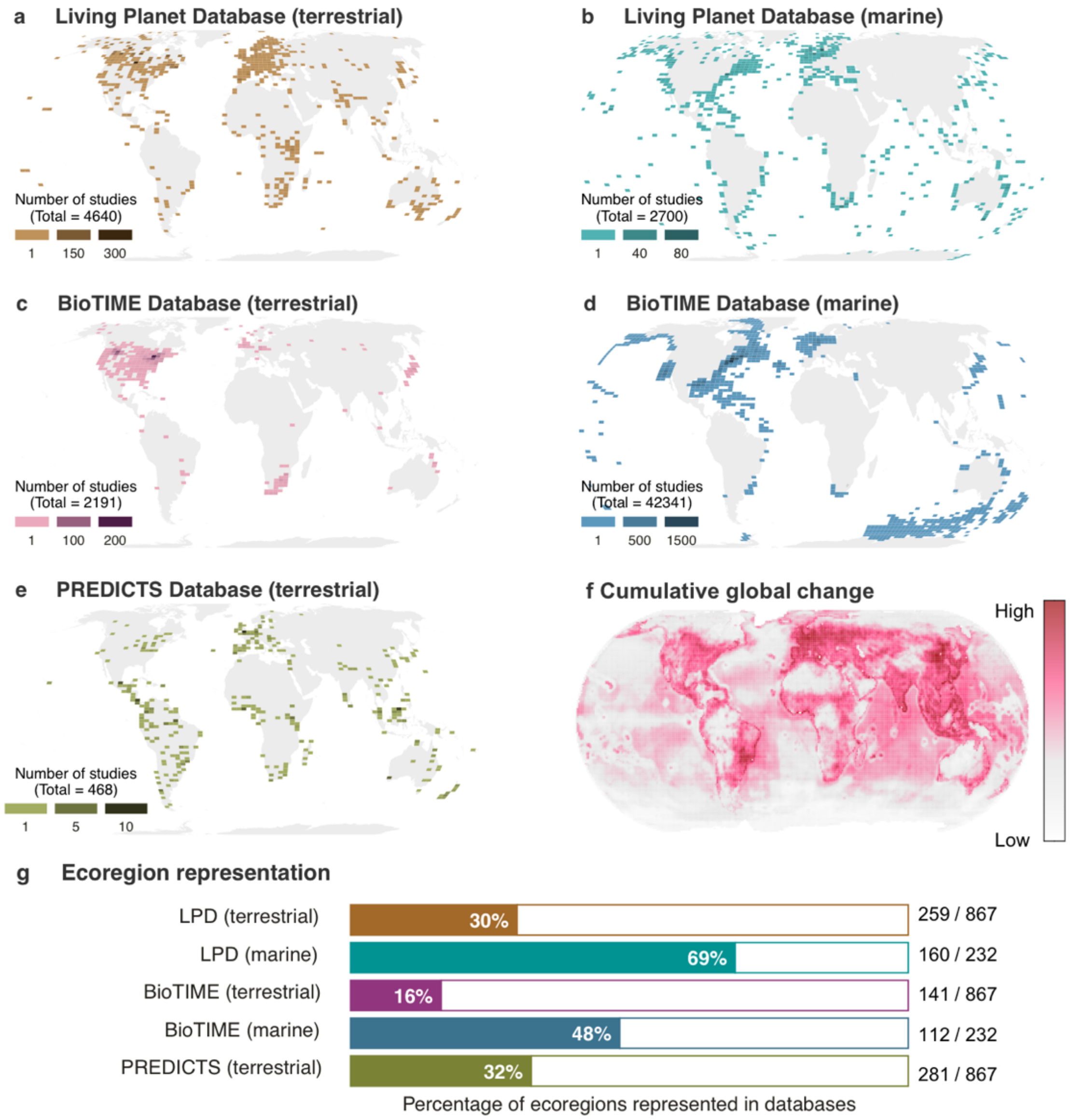

Figure 2.4. Geographic and ecoregion gaps in biodiversity data exist in both the marine and terrestrial realms but they do not directly translate to gaps in global change variation. Maps on panels **a-e** show locations of sites from the Living Planet, BioTIME and PREDICTS databases with darker colours indicating higher numbers of sites. Panel **f** shows the intensity of cumulative global change (climate change, human use, human population density, pollution and invasion pressure combined) across the terrestrial and marine realms, based on Bowler et al., 2020. Ecoregions are based on the classification of Olson & Dinerstein (2002). Number annotations on panel **f** show the number of ecoregions represented by at least one record and the total number of marine and terrestrial ecoregions on Earth.

2.4.4 More and less well represented taxa may respond differently to global change drivers

Taxonomic representation in biodiversity analyses could influence the detected global change responses, with certain taxa being more or less sensitive to global change (Barnagaud et al., 2012; Frishkoff et al., 2016; Isaac & Cowlishaw, 2004; Rocha-Ortega et al., 2021). For example, longer-lived species may have greater lagged responses to global change drivers such as land-use change when compared with species with shorter generation times (**Chapter 4**). I found that birds were the best-, and arthropods the worst-represented taxa across the Living Planet, BioTIME and PREDICTS databases (Figure 2.5), as commonly found in ecological datasets (Dornelas et al., 2018; Hudson et al., 2017; Rocha-Ortega et al., 2021). Recently, invertebrates and in particular insects have been highlighted as a taxon experiencing potential steep declines in abundance and biomass (Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019), yet such findings are confounded by the general paucity of invertebrate data (Daskalova et al., 2021; Didham et al., 2020; Montgomery et al., 2019; but see van Klink et al., 2021 for a recent effort in compiling insect data). In contrast, birds are the focus of many national and international monitoring schemes and for many species, research has established how populations are changing over time (Brlík et al., 2021).

There are frequent calls for better sampling across the tree of life to capture the variety of ways in which species from the smallest ant to the biggest sequoias are being impacted by the Anthropocene (e.g.,Bardgett & van der Putten, (2014); Cameron et al., (2018, 2019); Collen et al., (2008); Geijzendorffer et al., (2016); Pereira et al., (2013); Wetzel et al., (2018)). Without representative taxonomic coverage, ecologists could be failing to characterise the full balance between the winners and losers of a particular global change driver (Dornelas et al., 2019). While my findings show that the spatial variation in global change is broadly well-sampled by the three databases I tested (Figure 2.1), it is important to highlight that the majority of those biodiversity records are for mammals, birds and plants. Consequently, global change space remains poorly represented for less studied taxa like terrestrial invertebrates for which representation was only 3.2% for time series data (BioTIME) and 29.4% for space-for-time data, despite invertebrates representing 97% of all known species (PREDICTS, see Appendix 2.1 for global change space across all studied taxa). Extending findings from the limited representation of the planet's diversity to cross-taxa scenarios of future change should be done with caution and placed in the context of which species have the most records within the database (Leclère et al., 2020; Mace et al., 2018; L. M. Pereira et al., 2020).

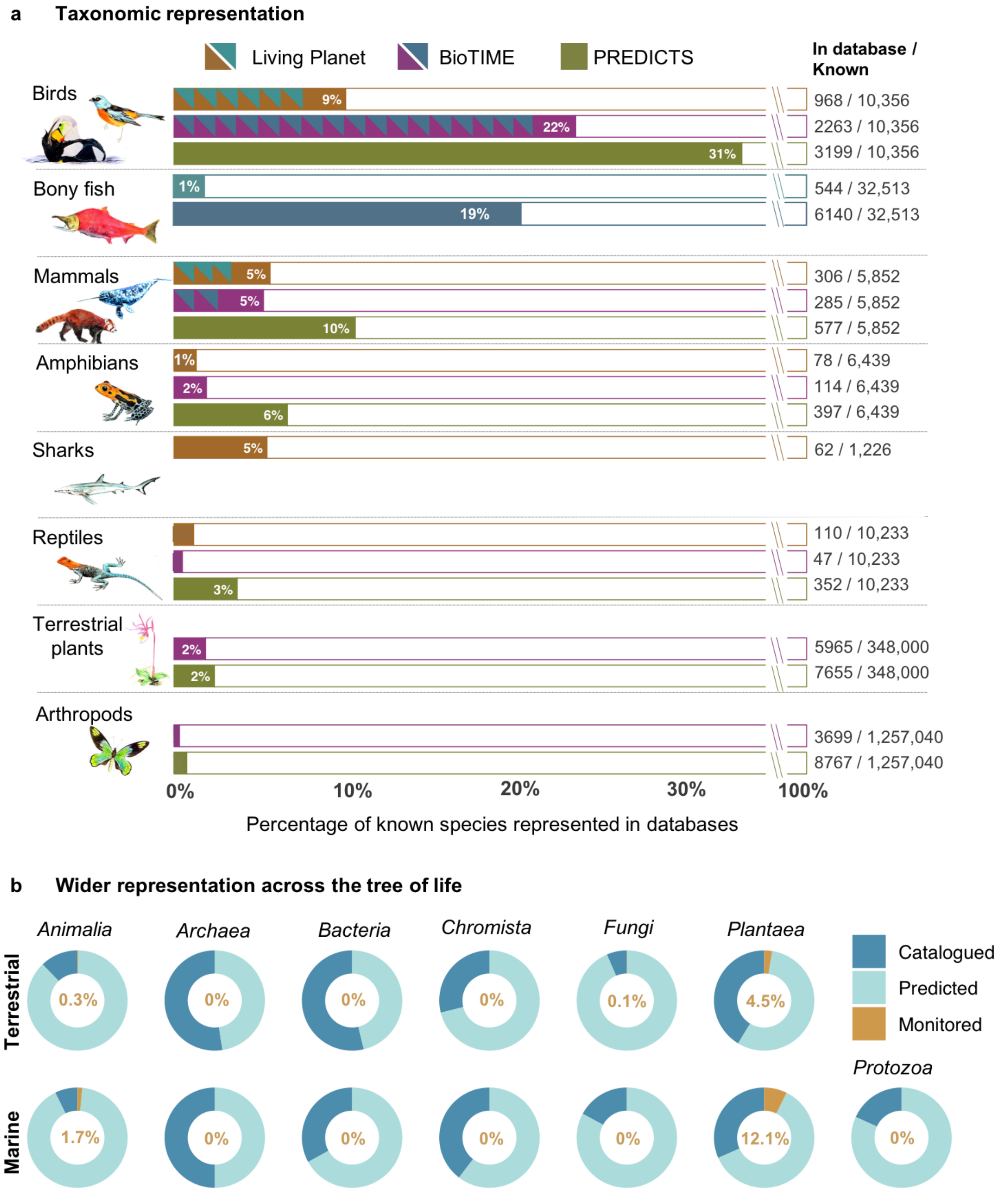

Figure 2.5. Taxonomic representation of biodiversity data is highest for birds and mammals and lowest for arthropods. The data available across biodiversity databases do not reflect the taxonomic diversity of the tree of life and millions of species are not represented by even a single record (**b**). Percentages in **a** show how many of the known species in each taxon are represented by at least one record in the Living Planet, BioTIME and PREDICTS databases. Panel **b** shows how monitored species fit within the larger

tree of life and is based on catalogued and predicted species in (Mora et al., 2011). The "Monitored" category combines the species represented in the Living Planet, BioTIME and PREDICTS databases and the percentages show how many of the predicted species feature at least once in biodiversity databases. The numbers of known species per taxa were extracted from the 2019 edition of the Catalogue of Life (http://www.catalogueoflife.org). The values for the birds and mammals in the Living Planet and BioTIME database include both marine and terrestrial species. Note that the BioTIME database additionally include records for marine invertebrates, benthos, marine plants, freshwater plants, freshwater invertebrates and freshwater fish.

2.4.5 Recommendations for capturing the spectrum and distribution of global change across space, time and the tree of life

Understanding ongoing and future biodiversity change can be improved by quantitatively accounting for the representation of biodiversity data across global change space, over the temporal trajectory of drivers, across geographic regions and across the tree of life. Together, my four recommendations provide guidance on using existing observational data, determining where to locate future ecological monitoring and designing experimental studies of novel global change space without modern day analogues.

Recommendation 1: Test the global change representation of databases and syntheses

Extending our thinking beyond just geographic, temporal and taxonomic bias to include global change variation can contextualise research findings from biodiversity data. The different relative positions of the current forms of global biodiversity databases within global change space might explain some of the differences in research findings. For example, predominantly negative impacts of intensifying land-use change have been found using PREDICTS (Newbold et al., 2015), both negative and positive influences of forest loss based on Living Planet and BioTIME (**Chapter 4**) and stronger impacts of temperature change on richness, composition and abundance trends in BioTIME (Antão et al., 2020). In this study, I present a way to test data representation across different global change drivers over space and time that can be applied to other datasets. I recommend that future syntheses explicitly include tests of the representation of their data for the global change drivers being tested in addition to highlighting other data gaps (Boakes et al., 2010; Cameron et al., 2018; Collen et al., 2008; Feng, X. et al., 2021; Geijzendorffer et al., 2016; Rocha-Ortega et al., 2021; Troudet et al., 2017; Wetzel et al., 2018).

Recommendation 2: Account for data representation across multiple axes in existing syntheses of observational data

Beyond testing for global change representation, studies should ideally account for the representation of their data for the global change driver (s) of interest. A variety of approaches could be used, including the following: 1) Randomised subsampling can help balance uneven data where certain types of global change are overrepresented while others are underrepresented (Buckland & Johnston, 2017), however, this has the disadvantage of discarding potentially valuable data. 2) Statistical weightings have been used to adjust the representativeness of the data sample e.g., by up-weighting under-represented regions or taxa (e.g., as employed by the Living Planet Index, McRae et al. (2017) and often with citizen science data (Geijzendorffer et al., 2016; Xu et al., 2021) but this approach can over emphasise the effect of very small portions of the overall data (Leung et al., 2020) and potentially inflate errors associated with those data (Buschke et al., 2021; Didham et al., 2020; Leung et al., 2020; Wauchope et al., 2021). 3) Bias can be explicitly modelled using fixed effects for continuous variables of driver intensity and random effects to represent geographic, temporal and taxonomic structure (e.g., as in Palma et al. (2018), but care must be taken to ensure all uncertainties are propagated through to the global mean estimate (Bennington & Thayne, 1994; Sánchez-Tójar et al., 2020; Tessarolo et al., 2021; Wintle et al., 2003)). 4) Baselines, time since disturbance and changing intensity of impact of global change drivers can be explicitly incorporated into analyses of time series data (**Chapter 4**; Isbell et al., 2019). Analyses that account for global change representation will provide more accurate attribution of biodiversity change to global change drivers.

Recommendation 3: Prioritise new data collection for underrepresented parts of the global change spectrum

A lot of the focus in the literature is on filling geographic (Boakes et al., 2010; Gonzalez et al., 2016; Johnston et al., 2020; Mentges et al., 2021), temporal (Boakes et al., 2010; Buckland & Johnston, 2017; Gonzalez et al., 2016; Wauchope et al., 2021), and taxonomic (Buckland & Johnston, 2017; Feng et al., 2021; Troudet et al., 2017) biodiversity data gaps, but this focus should be shifted towards prioritising regions that undersample global change. For example, biodiversity data are currently lacking from places with high magnitudes of climate change including Arctic and boreal forest regions, as well as tropical regions that are currently entering non-analogue climate space (Fitzpatrick & Hargrove, 2009). These data are important not just for understanding current effects of climate change, but also as sentinels of future change around the world (Fitzpatrick & Hargrove, 2009; Mahony et al., 2018; Pfeiffer et al., 2020). Another underrepresented part of the global change spectrum is sites with low human impact (Figures 1-2), which provide a necessary comparator for testing the impacts of human use, pollution and other global change drivers. Such sites, however, by definition tend to be more difficult to access. Remote sensing monitoring of biodiversity in such places could achieve a balance between collecting data and minimising human impact (Vihervaara et al., 2017). The gaps above refer to marine and terrestrial environments, but for the freshwater realm, we have yet to collect enough data to be able to quantify global change space. Collecting large-scale information of the disturbance levels across rivers and lakes can reveal the freshwater global change space. We would then be able to test how representative the locations of freshwater biodiversity monitoring sites are of the wider global change spectrum. Although ecologists cannot achieve greater global change representation of historic and current data, the monitoring programs of the future can prioritise global change representation, while also filling geographic and taxonomic gaps.

Recommendation 4: Design experiments to study novel global change space

Global change space is not static and to make scenarios for future biodiversity trends, ecologists need to sample not only current variation in global change drivers, but also future combinations of global change drivers (Zurell et al., 2012). I suggest that using projections for climate change and human impact, such as IPCC (IPCC, 2014) and HYDE (Klein Goldewijk et al., 2017), we can compute future global change space and determine novel environments without current-day analogues and where those novel environments will most likely occur. Designing lab and field experiments that test novel combinations and magnitudes of global change drivers can provide a preview of biodiversity responses to future environmental conditions. Prioritising biodiversity monitoring where novel environments will likely develop will ensure that future biodiversity syntheses and impact assessments will represent future as well as current global change.

2.5 Conclusion

Predicting future biodiversity change and its consequences for ecosystem functions and services to society is an urgent scientific challenge. Global biodiversity monitoring needs to capture a representative sample of the world over both space and time, as well as the full spectrum of global change drivers. In this study, I quantified four types of representativeness - global change intensity over space, global change intensity over time, geography, and taxonomy (Figures 2.1-2.5). Together, my findings demonstrate that global biodiversity datasets capture a large proportion of the intensity of global change, but not uniformly. Over space, existing data capture up to 78% of the spatial variance in global change drivers, but more so at sea than on land (78% versus 31%). Over time, monitoring often starts after the peak intensity in environmental change for drivers like primary forest loss (**Chapters 2** and **4**), but more closely coincides with the period of rapid climate change (Figure 2.3). I identify four recommendations to test and account for current and future global change representation: 1) Test the global change representation of databases and syntheses, 2) Account for data representation across multiple axes in existing syntheses of observational data, 3) Prioritise new data collection for underrepresented parts of the global change spectrum, and 4) Design experiments to study novel global change space.

The biodiversity synthesis literature must progress beyond merely discussing bias to instead quantify and account for the global change representation of biodiversity data. By considering all axes of the global change spectrum, ecologists can strengthen the empirical evidence for the next stage of IPBES global biodiversity assessments and the global biodiversity indicators for the Post-2020 Global Biodiversity Framework. With continued calls for more biodiversity data (e.g., IPBES, 2019; Jetz et al., 2019; Kissling et al., 2018), I especially advocate for future biodiversity monitoring to target not just geographic and taxonomic gaps, but to also ensure improved representation of global change by focusing on the under-represented areas in global change rather than geographic space.

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Chapter 3. Rare and common vertebrates span a wide spectrum of population trends

Chapter 3. Rare and common species span a wide spectrum of population trends

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The following chapter “Rare and common vertebrates span a wide spectrum of population trends” has been published in Nature Communications:

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Author contributions: IMS, my supervisor, and I conceived the idea. I conducted the statistical analyses. JLG contributed to the calculation of geographic range estimates. All authors contributed to the integration of the LPI, GBIF and IUCN databases, which I led. I created all figures with input from IMS. I wrote the first draft of the manuscript and all authors contributed to revisions.

Code and data availability: Raw data are available from the following websites: for population time series (LPI, 2016) - http://www.livingplanetindex.org/data_portal, GBIF occurrences (GBIF, 2017) - https://www.gbif.org, bird geographic ranges (BirdLife International, 2018) - http://datazone.birdlife.org, mammal geographic ranges (Jones et al., 2009) - http://esapubs.org/archive/ecol/E090/184/, species' habitat preferences, threat types and IUCN Red List Categories (IUCN, 2017) - https://www.iucnredlist.org, and phylogenies (Jetz et al., 2012; Jetz & Pyron, 2018; Tonini et al., 2016) - https://vertlife.org and https://birdtree.org. Code for all data processing and analyses and summary datasets are publicly available on GitHub and archived on Zenodo (DOI: 10.5281/zenodo.3817207) (Daskalova, G.N., 2020).

3.1 Summary

The Earth’s biota is changing over time in complex ways. A critical challenge is to test whether specific biomes, taxa or types of species benefit or suffer in a time of accelerating global change. I analysed nearly 10 000 abundance time series from over 2000 vertebrate species part of the Living Planet Database. I integrated abundance data with information on geographic range, habitat preference, taxonomic and phylogenetic relationships, and IUCN Red List Categories and threats. I found that 15% of populations declined, 18% increased, and 67% showed no net changes over time. Against a backdrop of no biogeographic and phylogenetic patterning in population change, I uncovered a distinct taxonomic signal. Amphibians were the only taxa that experienced net declines in the analysed data, while birds, mammals and reptiles experienced net increases. Population trends were poorly captured by species’ rarity and global-scale threats. Incorporation of the full spectrum of population change will improve conservation efforts to protect global biodiversity.

3.2 Introduction

Ecosystem-level change is currently unfolding all around the globe and modifying the abundances of the different species forming Earth’s biota. As global change continues to accelerate (Ehrlén & Morris, 2015; Hefley et al., 2016), there is a growing need to assess the factors explaining the variation in ecological changes observed across taxa and biomes (IPBES, 2018). However, existing empirical studies of the predictors of the abundance of individuals of different species over time (hereafter, population change) mostly focus on either specific taxon (Gilroy et al., 2016) or on population declines alone (Ceballos et al., 2017; Hefley et al., 2016). A critical research challenge is to disentangle the sources of heterogeneity across the full spectrum of population change for available population data. Recent compilations of long-term population time series, extensive occurrence, phylogenetic, habitat preference and IUCN Red List Category data (Jetz et al., 2012; Jetz & Pyron, 2018; Tonini et al., 2016) provide a unique opportunity to test which species- and population-level attributes explain variation in population trends and fluctuations among vertebrate species monitored around the world. Such population change is the underlying process leading to community reassembly (Batt et al., 2017) and the resulting alterations to biodiversity are vitally important for ecosystem functions and services (Oliver et al., 2015).

The distributions of global change drivers such as land-use change, habitat change, pollution, invasion by non-native species and climate change show distinct clustering across space (Bowler et al., 2020; Halpern et al., 2015; Hansen et al., 2013). Biodiversity trends derived from assemblage time series have also been shown to vary, with the marine realm emerging as a hotspot for rapid changes in community composition (Blowes et al., 2019). Since assemblages are made up of populations, the biogeographic patterns at the assemblage level suggest similar clustering might occur at the population level as well (Dornelas et al., 2019). In addition to geographic patterns in exposure to anthropogenic activities, species' vulnerability and traits can moderate population responses to natural and anthropogenic environmental change (Isaac & Cowlishaw, 2004), both across evolutionary time (Jetz et al., 2012; Jetz & Pyron, 2018; Tonini et al., 2016) and in the modern day (Newbold et al., 2018; Sykes et al., 2020; Vincent et al., 2020). Building on known variability in species' vulnerability (Isaac & Cowlishaw, 2004; Khaliq et al., 2014; Morrison et al., 2018), I expected taxonomic and phylogenetic signals in population trends and fluctuations (e.g. greater declines, increases or fluctuations in abundance for specific taxa and among specific clades). Understanding which biomes, taxa and types of species are experiencing the most acute changes in abundance over time could provide key insights for conservation prioritization.

Conservation efforts often focus on protecting rare species - those with restricted geographic extents, small population sizes or high habitat specificity - as they are assumed to be more likely to decline and ultimately go extinct (Gaston & Fuller, 2008; Longton & Hedderson, 2000; Pigott & Walters, 1977). Species with a smaller geographic range might have more concentrated exposure to environmental change, with less opportunities to find refugia or disperse, thus increasing the likelihood of declines (Batt et al., 2017; Ehrlén & Morris, 2015). As per population dynamics theory (Lande, 1993; Melbourne & Hastings, 2008) and Taylor's power law (Kilpatrick & Ives, 2003), species with small populations are more likely to undergo stochastic fluctuations that could lead to pronounced declines, local extinction and eventually global extinction (Ceballos et al., 2017). Small populations are also more likely to decline due to inbreeding, but there are also instances of naturally small and stable populations (Hanski, 1998; Kareiva, 1990). Allee effects, the relationship between individual fitness and population density, further increase the likelihood of declines due to lack of potential mates and low reproductive output once populations reach a critically low density (Dennis et al., 2016; Sun, 2016). Furthermore, environmental change might have disproportionately large effects on the populations of species with high habitat specificity, as for these species persistence and colonization of new areas are limited by strict habitat preferences (Bowler et al., 2018; Ehrlén & Morris, 2015). The fossil record indicates that on millennial time scales, rare species are more likely to decline and ultimately go extinct (Harnik et al., 2012), but human actions have pushed Earth away from traditional geological trajectories (Steffen et al., 2007), and the relationships between rarity and population change across the planet have yet to be tested for the time from the 1970s onwards.

On a global scale, species are exposed to a variety of threats, among which habitat change, resource exploitation and hunting dominate as key predictors of extinction risk (Maxwell et al., 2016). Species' IUCN Red List Categories are often used in conservation prioritisation and more threatened species tend to be the focus of conservation initiatives (Martín-López et al., 2011). At more local scales, there might be variation in how populations are changing over time in different locations, in isolation from their overall conservation status (Gilroy et al., 2016; van Strien et al., 2016). Testing population change across species' IUCN Red List Category allows us to link contemporary changes in abundance with long-term probability of extinction (Mace et al., 2008). Determining how local-scale population trends vary across species' IUCN Red List Categories has practical applications for assessing species' recovery which is useful for the proposed IUCN Green List of Species (Akçakaya et al., 2018).

Here, I asked how the trends and fluctuations of vertebrate populations vary with biogeography, taxa, phylogenetic relationships and across species' rarity metrics and IUCN Red List Categories and threat types from the species' IUCN Red List profiles. I tested the following predictions: 1) There would be biogeographic patterns in population trends and fluctuations across the planet's realms and biomes, in line with particular regions of the world experiencing high rates of environmental change (e.g., tropical forests (Barlow et al., 2007)). 2) Populations of rare species would be more likely to decline and fluctuate than the populations of common species. 3) Populations of species with a higher IUCN Red List Category and higher number of threats would be more likely to decline and fluctuate than the populations of least concern species and those exposed to a lower number of threats. I quantified differences in population trends and fluctuations across latitudes and biomes within the freshwater, marine and terrestrial realms to test the presence of distinct hotspots of declines and increases. Additionally, I used data from the VertLife and BirdLife Databases (Jetz et al., 2012; Jetz & Pyron, 2018; Tonini et al., 2016) to assess taxonomic and phylogenetic signals. I measured rarity using three separate metrics – geographic range derived from GBIF records, mean population size (number of individuals that were recorded during monitoring for each population in the Living Planet Database) and habitat specificity derived from the species' IUCN Red List profiles. In a *post-hoc* analysis, I compiled threat types and number of threats derived from the species' IUCN Red List profiles to determine how threats influence local-scale population change. Using the largest currently available compilation of population records over time, I conducted a global synthesis of population trends and fluctuations to provide key empirical evidence for the management, conservation and prediction of ecological changes during the Anthropocene.

3.3 Methods

Workflow

I focused on two aspects of population change – overall changes in abundance over time (population trend, μ) and abundance variability over time (population fluctuations, σ^2). In the first stage of my analyses, I quantified trends and fluctuations for each population using state-space models that account for observation error and random fluctuations (Humbert et al., 2009, Appendix 3.1). In the second stage, I modelled the population trend and fluctuation estimates from the first stage across latitude, realm, biome, taxa, rarity metrics, phylogenetic relatedness, species' IUCN Red List Category and threat type using a Bayesian modelling framework (Appendix 3.2). I included a species random intercept effect to account for the possible correlation between the trends of populations from the same species (see Appendix 3.21 for sample sizes). As sensitivity analyses, I additionally used variance weighting of the population trend estimates (μ) by the observation/measurement error around them (τ^2) and population trend estimates from linear model fits (slopes instead of μ) as the input variables in the second stage models, as well as several different fluctuations estimates. I also repeated my analyses on a single-country scale, using only populations within the United Kingdom, where monitoring efforts are particularly rigorous and extensive. All different analytical approaches yielded very similar results. Effect sizes plotted on graphs were standardized by dividing the effect size by the standard deviation of the corresponding input data. All data syntheses, visualization and statistical analyses were conducted using R version 3.5.1 (R Core Team, 2017).

Population data

To quantify vertebrate population change (trends and fluctuations), I extracted the abundance data for 9286 population time series from 2084 species from the publicly available Living Planet Database (LPI, 2016) (http://www.livingplanetindex.org/data_portal) that covered the period between 1970 and 2014 (Appendix 3.1). These time series represented repeated monitoring surveys of the number of individuals in a given area, hereafter called "populations". The time series sampled geographic locations around the world and represented a broad range of global change, from relatively intact to disturbed sites (Chapter 1). Nevertheless, there were still biases in the data (Chapter 1, see Appendix 3.19 for a discussion of the possible implications of data biases). Monitoring duration differed among populations, with a mean duration of 23.9 years and a mean sampling frequency of 23.3 time points (Appendix 3.3, see Appendices 3.6 and 3.7 for effects of monitoring duration on detected trends). In the

Living Planet database, 17.9% of populations were sampled annually or in rare cases multiple times per year. The time series I analysed include vertebrate species that span a large variation in age, generation times and other demographic-rate processes. For example, in Chapter 4 I found that when generation time data were available (approximately 50.0% or 484 out of 968 bird species, and 15.6% or 48 out of 306 mammal species), the mean bird generation time is 5.0 years (min = 3.4 years, max = 14.3 years) and the mean mammal generation time is 8.3 years (min = 0.3 years, max = 25 years). Thus, most vertebrate time series within the LPD captured multiple generations.

In my analysis, I omitted populations which had less than five time points of monitoring data, as previous studies of similar population time series to the ones I have analysed have found that shorter time series might not capture biologically meaningful directional trends in abundance (Wauchope et al., 2019). Populations were monitored using different metrics of abundance (e.g., population indices vs. number of individuals). Before analysis, I scaled the abundance of each population to a common magnitude between zero and one to analyse within-population relationships to prevent conflating within-population relationships and between-population relationships (van de Pol & Wright, 2009). Scaling the abundance data allowed us to explore trends among populations relative to the variation experienced across each time series.

Phylogenetic data

I obtained phylogenies for amphibian species from https://vertlife.org[4], for bird species from https://birdtree.org (Jetz et al., 2012), and for reptile species from https://vertlife.org (Tonini et al., 2016). For each of the three classes (*Amphibia*, *Aves* and *Reptilia*), I downloaded 100 trees and randomly chose 10 for analysis (30 trees in total). Species-level phylogenies for the classes *Actinopterygii* and *Mammalia* have not yet been resolved with high confidence (Foley et al., 2016; Tarver et al., 2016).

Rarity metrics, IUCN Red List Categories and threat types

I defined rarity following a simplified version of the ‘seven forms of rarity’ model (Rabinowitz, 1981), and thus consider rarity to be the state in which species exist when they have a small geographic range, low population size, or narrow habitat specificity. I combined publicly available data from three sources: 1) population records for vertebrate species from the Living Planet Database to calculate mean population size, 2) occurrence data from the Global Biodiversity Information Facility (GBIF, 2017) (https://www.gbif.org) and range data from BirdLife (BirdLife International, 2018) (http://datazone.birdlife.org) to estimate geographic range size, and 3) habitat specificity and Red List Category data for each species from the International Union for Conservation (IUCN, 2017) (https://www.iucnredlist.org). The populations in the Living Planet Database (LPI, 2016) do not include species that have gone extinct on a global scale. I extracted the number and types of threats that each species is exposed to globally from their respective species' IUCN Red List profiles (IUCN, 2017).

Quantifying population trends and fluctuations over time

In the first stage of my analysis, I used state-space models that model abundance (scaled to a common magnitude between zero and one) over time to calculate the amount of overall abundance change experienced by each population (μ, Humbert et al., 2009). State-space models account for process noise (σ^2) and observation error (τ^2) and thus deliver robust estimates of population change when working with large datasets where records were collected using different approaches, such as the Living Planet Database (Knape et al., 2011; Leung et al., 2017; Pedersen et al., 2011). Previous studies have found that not accounting for process noise and measurement error could lead to over-estimation of population declines (Rueda-Cediel et al., 2018), but in my analyses, I found that population trends derived from state-space models were similar to those derived from linear models. Positive μ values indicate population increase and negative μ values indicate population decline. State-space models partition the variance in abundance estimates into estimated process noise (σ^2) and observation or measurement error (τ^2) and population trends (μ):

$$X_t = X_{t-1} + \mu + \varepsilon_t, \text{ (1)}$$

where X_t and X_{t-1} are the scaled (observed) abundance estimates (between 0 and 1) in the present and past year, with process noise represented by $\varepsilon_t \sim \textit{gaussian}\ (0, \sigma^2)$. I included measurement error following:

$$Y_t = X_t + F_t, \text{ (2)}$$

where Yt is the estimate of the true (unobserved) population abundance with measurement error:

$$F_t \sim \text{gaussian}(0, \tau^2). \quad (3)$$

I substituted the estimate of population abundance (Y_t) into equation 1:

$$Yt = Xt-1 + \mu + \varepsilon t + Ft, \quad (4)$$

Given $Xt-1 = Yt-1 - Ft-1$ (5), then:

$$Y_t = Y_{t-1} + \mu + \varepsilon_t + F_t - F_{t-1}. \quad (6)$$

For comparisons of different approaches to modelling population change, see Appendix 3.20 Sensitivity analyses.

Quantifying rarity metrics

I tested how population change varied across rarity metrics – geographic range, mean population size and habitat specificity – on two different but complementary scales. I quantified rarity metrics for species monitored globally and in the UK. In the main text, I presented the results of my global scale analyses, whereas in the appendices, I included the results when using only populations from the UK, a country with high monitoring intensity.

Quantifying geographic range

To estimate geographic range for bird species monitored globally, I extracted the area of occurrence in km^2 for all bird species in the Living Planet Database that had records in the BirdLife Data Zone (BirdLife International, 2018). For mammal species' geographic range, I used the PanTHERIA database (Jones et al., 2009) (http://esapubs.org/archive/ecol/E090/184/). To estimate geographic range for bony fish, birds, amphibians, mammals and reptiles monitored in the UK (see Appendix 3.25 for species list), I calculated a km^2 occurrence area based on species occurrence data from GBIF (GBIF, 2017). Extracting and filtering GBIF data and calculating range was computationally intensive and occurrence data availability was lower for certain species. Thus, I did not estimate geographic range from GBIF data for all species part of the Living Planet Database. Instead, I focused on analysing range effects for birds and mammals globally, as they are a very well-studied taxon and for species monitored in the UK, a country with intensive and detailed biodiversity monitoring of vertebrate species. I did not use IUCN range maps, as they were not available for all of my study species, and previous studies using GBIF occurrences to estimate range have found a positive correlation between GBIF-derived and IUCN-derived geographic ranges (Phillips et al., 2017).

For the geographic ranges of species monitored in the UK, I calculated range extent using a minimal convex hull approach based on GBIF (GBIF, 2017) occurrence data. I filtered the GBIF data to remove invalid records and outliers using the *CoordinateCleaner* package (Zizka et al., 2019). I excluded records with no decimal places in the decimal latitude or longitude values, with exactly the sample values for both latitude and longitude, and those within a one-degree radius of the GBIF headquarters in Copenhagen, within 0.0001 degrees of various biodiversity institutions and within 0.1 degrees of capital cities. This filtering helps exclude instances of the location of museum specimens falsely being noted as the museum itself versus the place from where the specimen was collected. For each species, I excluded the lower 0.02 and upper 0.98 quantile intervals of the latitude and longitude records to account for outlier points that are records from zoos or other non-wild populations. I drew a convex hull to most parsimoniously encompass all remaining occurrence records using the *chull* function, and I calculated the area of the resulting polygon using *areaPolygon* from the *geosphere* package .

Quantifying mean population size

I calculated mean size of the monitored population, referred to as population size, across the monitoring duration using the raw abundance data, and I excluded populations which were not monitored using population counts (e.g., I excluded indexes).

Quantifying habitat specificity

To create an index of habitat specificity, I extracted the number of distinct habitats a species occupies based on the IUCN habitat category for each species' profile, accessed through the package *rredlist* (Chamberlain, 2017). I also quantified habitat specificity by surveying the number of breeding and non-breeding habitats for each species from its online IUCN species profile (the 'habitat and ecology' section). The two approaches yielded similar results (Appendix 3.10, Appendix 3.23, key for the profiling method is presented in Appendix 3.26). I obtained global IUCN Red List Categories and threat types for all study species through the IUCN Red List profiles (IUCN, 2017).

Testing the sources of variation in population trends and fluctuations

In the second stage of my analyses, I modelled the trend and fluctuation estimates from the first stage across latitude, realm, biome, taxa, rarity metrics, phylogenetic relatedness, species' IUCN Red List Category and threat type using a Bayesian modelling framework through the package *MCMCglmm* (Hadfield, 2010). I included a species random intercept effect in the Bayesian models to account for the possible correlation between the trends of populations from the same species (see Appendix 1.21 for sample sizes). The models ran for 120 000 iterations with a thinning factor of ten, a burn-in period of 20 000 iterations and the default one chain. I assessed model convergence by visually examining trace plots. I used weakly informative priors for all coefficients (an inverse Wishart prior for the variances and a normal prior for the fixed effects):

$$Pr\ (\mu) \sim N\ (0,\ 10^8)\ (7)$$

$$Pr\ (\sigma^2) \sim Inverse\ Wishart\ (V = 0,\ nu = 0)\ (8)$$

Testing population trends and fluctuations across latitude, biomes, realms and taxa

To investigate the geographic and taxonomic patterns of population trends and fluctuations, I modelled population trends (μ) and population fluctuations (σ^2), derived from the first stage of my analyses (state-space models), as a function of 1) latitude, 2) realm (freshwater, marine, terrestrial), 3) biome (as defined by the 'biome' category in the Living Planet Database, e.g., 'temperate broadleaf forest' (Olson & Dinerstein, 2002) and 4) taxa (*Actinopterygii*, bony fish; *Elasmobranchii*, sharks and rays; *Amphibia*, amphibians; *Aves*, birds; *Mammalia*, mammals; *Reptilia*, reptiles). I used separate models for each variable, resulting in four models testing the sources of variation in trends and four additional models focusing on fluctuations. Each categorical model from this second stage of my analyses was fitted with a zero intercept to determine if net population trends differed from zero for each of the categories under investigation. The model structures for all models with a categorical fixed effect were identical except for the identity of the fixed effect, and below I describe the taxa model:

$$\mu_{i,j,k} = \beta_0 + \beta_{0j} + \beta_1 * taxa_{i,j,k}, \text{ (9)}$$

$$y_{i,j,k} \sim gaussian(\mu_{i,j,k}, \sigma^2), \text{ (10)}$$

where $taxa_{i,j,k}$ is the taxa of the *ith* time series from the *jth* species; β_0 and β_1 are the global intercept (in categorical models, $\beta_0 = 1$) and the slope estimate for the categorical taxa effect (fixed effect), β_{0j} is the species-level departure from β_0 (species-level random effect); $y_{i,j,k}$ is the estimate for change in population abundance for the *ith* population time series from the *jth* species from the *kth* taxa.

Testing population trends and fluctuations across amphibian, bird and reptile phylogenies

To determine if there was a phylogenetic signal in the patterning of population change within amphibian, bird and reptile taxa, I modelled population trends (μ) and fluctuations (σ^2) across phylogenetic and species-level taxonomic relatedness. I conducted one model per taxa per population change variable – trends or fluctuations using Bayesian linear mixed effects models using the package *MCMCglmm* (Hadfield, 2010). I included phylogeny and taxa as random effects. The models did not include fixed effects. I assessed the magnitude of the random effects (phylogeny and species) by inspecting their posterior distributions, with a distribution pushed up against zero indicating lack of effect, since these distributions are always bounded by zero and have only positive values. I used parameter-expanded priors, with a variance-covariance structure that allows the slopes of population trend (the μ values from the first stage analysis using state-space models) to covary for each random effect. The prior and model structures were as follows:

$$Pr(\mu) \sim N(0, 10^8), \text{ (11)},$$

$$Pr(\sigma^2) \sim Inverse\ Wishart\ (V = 1, nu = 1), \text{ (12)},$$

$$\mu_{i,k,m} = \beta_0 + \beta_{0k} + \beta_{0m}, \text{, (13)}$$

$$y_{i,k,m} \sim gaussian(\mu_{i,k,m}, \sigma^2), \text{(14)}$$

where β_0 is the global intercept ($\beta_0 = 1$), β_{0l} is the phylogeny-level departure from β_0 (phylogeny random effect); $y_{i,k,m}$ is the estimate for change in population abundance for the *ith* population time series for the *kth* species with the *mth* phylogenetic distance.

To account for phylogenetic uncertainty, for each class, I ran ten models with identical structures but based on different randomly selected phylogenetic trees. I reported the mean estimates and their range for each class.

Testing population trends and fluctuations across rarity metrics

To test the influence of rarity metrics (geographic range, mean population size and habitat specificity) on variation in population trends and fluctuations, I modelled population trends (μ) and fluctuations (σ^2) across all rarity metrics. I conducted one Bayesian linear models per rarity metric per model per scale (for both global and UK analyses) per population change variable – trends or fluctuations. The response variable was population trend (μ values from state-space models) or population fluctuation (σ^2 *values from state-space models*), and the fixed effects were geographic range (log transformed), mean population size (log transformed) and habitat specificity (number of distinct habitats occupied). The model structures were identical across the different rarity metrics and below I outline the equations for population trends and geographic range:

$$\mu_{i,k,n} = \beta_0 + \beta_{0k} + \beta_1 * geographic\ range_{i,k,n}, \text{(15)}$$

$$y_{i,k,n} \sim gaussian(\mu_{i,k,n}, \sigma^2), \text{(16)}$$

where *geographic range*$_{i,k,n}$ is the logged geographic range of the *kth* species in the *ith* time series; β_0 and β_1 are the global intercept and slope estimate for the geographic range effect (fixed effect), β_{0j} is the species-level departure from β_0 (species-level random effect); $y_{i,k,n}$ is the estimate for change in population abundance for the *ith* population time series from the *jth* species with the *nth* geographic range.

Testing population trends across species' IUCN Red List Categories

To investigate the relationship between population change and species' Red List Categories, I modelled population trends (μ) and fluctuations (σ^2) as a function of Red List Category (categorical variable). I conducted one Bayesian linear model per population change metric per scale (for both global and UK analyses). To test variation in population trends and fluctuations across the types and number of threats to which species are exposed, I conducted a *post-hoc* (i.e., conducted after the results of the initial hypothesis testing was done) analysis of trends and fluctuations across threat type (categorical effect) and number of threats that each species is exposed to across its range (in separate models). The model structures were identical to those presented above, except for the fixed effect which was a categorical IUCN Red List Category variable.

3.4 Results

3.4.1 Vertebrate population change spanned declines, increases and no net change over time

I found a broad spectrum of population trends across vertebrate populations within the Living Planet Database. Across the time series I analysed, 15% (1381 time series) of populations were declining, 18% (1656 time series) were increasing, and 67% (6249 time series) showed no net changes in abundance over time, in contrast to a null distribution derived from randomised data (Appendix 3.5b). Trends were considered statistically different from no net change when the confidence intervals around the population trend estimates did not overlap zero. My results were similar when I weighted population trends by the state-space model derived observation error (Figures 3.1-3.4 and Appendices 3.2-3.3).

3.4.2 There were weak biogeographic patterns of population change

I found that globally, population increases, declines and fluctuations over time occurred across all latitudes and biomes within the freshwater, marine and terrestrial realms, with no strong biogeographic patterning and no specific hotspots of population declines (Figure 3.1, Appendix 3.22). Across realms, monitored vertebrate populations experienced net population increases (freshwater slope = 0.005, CI = 0.002 to 0.01;

marine slope = 0.004, CI = 0.002 to 0.01; terrestrial slope = 0.003, CI = 0.001 to 0.005, Figure 3.1d-e). In the freshwater and terrestrial realms, there was a bimodal distribution of population trends, driven largely by terrestrial bird species showing small increases and decreases over time (Hartigans' dip test, D = 0.04, $p < 0.01$). Across biomes, populations in Mediterranean forests, montane grasslands, polar freshwaters, temperate wetlands, tropical forests and tropical coral biomes were more likely to increase, whereas populations from the remaining studied biomes experienced no net changes (Figure 3.1h, Appendix 3.22). Population fluctuations were less pronounced in the terrestrial realm (slope = 0.02, CI = 0.018 to 0.021, Figure 3.1f-g), but those populations were also monitored for the longest duration across systems (average duration – 28 years for terrestrial, 18 years for marine and 21 years for freshwater populations, Appendices 2.3, 2.6 and 2.22).

3.4.3 Amphibians declined on average but there were no phylogenetic patterns across any of the studied taxa

I found taxonomic, but not phylogenetic patterns, in population trends and fluctuations over time among nearly 10 000 populations from over 2000 vertebrate species, with amphibians emerging as the taxa experiencing pronounced declines (Figure 3.2, Appendix 3.21). Amphibians experienced net declines over time (slope = -0.01, CI = -0.02 to -0.005), whereas birds, mammals and reptiles experienced net increases (slope = 0.004, CI = 0.003 to 0.01; slope = 0.01, CI = 0.01 to 0.01; slope = 0.02, CI = 0.01 to 0.02), with birds having a bimodal trend distribution indicating greater numbers of increasing and decreasing trends (Hartigans' dip test, D = 0.04, $p < 0.01$, Figure 3.1a, see Appendices 3.5, 3.6 and 3.12). Bony fish population trends were centred on zero (slope = -0.001, CI = -0.004 to 0.002, Figure 3.1a-b) and sharks and rays showed net declines, but the credible intervals overlapped zero (slope = -0.01, CI = -0.02 to 0.01). Fluctuations were most common for amphibian populations (slope = 0.04, CI = 0.036 to 0.049, Figure 3.2d), which were monitored for the shortest time period on average (11 years, Appendix 3.3, Appendix 3.21). I did not detect finer scale species-level phylogenetic clustering of population change (both trends and fluctuations) within amphibian, bird and reptile classes (Figure 3.2, Appendices 3.15 and 3.24). Similarly, species identity within amphibian, bird and reptile classes did not explain variation in population trends or fluctuations (Figure 3.2, Appendices 3.15 and 3.24). There were no distinct clusters of specific clades that were more likely undergo increases, decreases or fluctuations in population abundance (Figure 3.2).

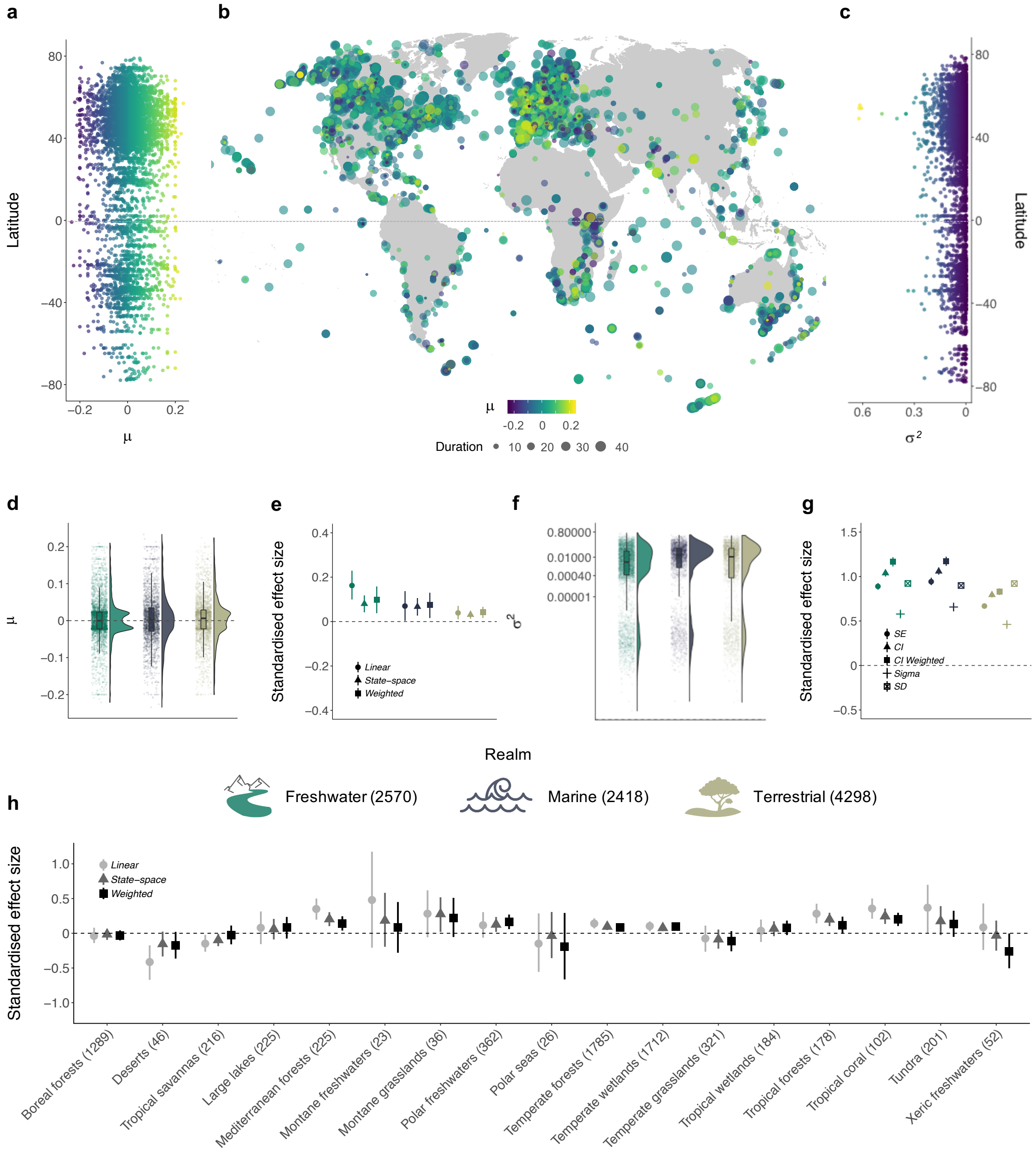

Figure 3.1. Population declines, increases and fluctuations over time occurred across all latitudes and biomes within the freshwater, marine and terrestrial realms. Results include 9286 populations from 2084 species. The lack of strong biogeographic differences in vertebrate population trends among realms and biomes was also apparent on a UK scale (Appendix 3.23 and Appendix 3.23). The numbers in the legend for plots **d**-**g** and on the x axis in plot c show the sample sizes for realms and biomes, respectively. The μ values of population trend (plots **a**-**b**, **d**-**e**, **h**) and the σ^2 values of population fluctuation (plots **c**, **f**-**g**) are from state-space models of changes in abundance over time for each population. Plots **d** and **f** show the distribution of population trends across realms including raw values (points) and boxplots (including the mean, first and third quartiles and boxplot whiskers that cover 1.5 times the interquartile range). Plots **e**, **g** and **h** show the effect sizes (centre of error bars) and the 95% credible intervals of population trends (**e**, **h**) across realms and biomes, and fluctuations across realms (**g**). For variation in fluctuations across biomes, see Appendix 3.8. The three estimates in plots **e** and **h** refer to different analytical approaches: population trends calculated using linear models (circles), state-space models (μ, triangles), and population trends (μ) weighted by τ^2, the observation error estimate from the state-space models (squares). The five estimates in plot **g** refer to different analytical approaches, where the response variables in the models were: 1) the standard error around the slope estimates of the linear models of abundance versus year (circles), 2) half of the 95% confidence interval around the μ value of population change (triangles), 3) half of the 95% confidence interval around μ weighted by τ^2, (full squares), 4) the process noise (σ^2) from the state-space models, and 5) the standard deviation of the raw data for each population time series (empty squares). The process noise is the total variance around the population trend minus the variance attributed to observation error. See Appendix 3.21 for model outputs. Icon credits: tree by FayraLovers, wave by Setyo Ari Wibowo, mountain and stream by Nikita Kozin.

2.4.4 Both rare and common species experience the full spectrum of population change

Species-level metrics, such as rarity and global IUCN Red List Category, did not explain the heterogeneity in trends of monitored populations in the Living Planet Database. Both rare and common species experienced declines, increases and fluctuations in population abundance over time (Figures 3.3 and 3.4). Across these time series, species with smaller ranges, smaller population sizes, or narrower habitat specificity (i.e., rare species) were not more prone to population declines than common species (Figure 3.3, Appendix 3.21). Populations that experienced more fluctuations had smaller mean population sizes on average (slope = -0.001, CI = -0.001 to -0.001, Figure 3.3f). I found increasing, decreasing and stable populations across all IUCN Red List Categories (Figure 3.4a). For example, a population of the Least concern species red deer (*Cervus elaphus*) in Canada declined by 68% over seven years going from 606 to 194 individuals and a population of the critically endangered Hawksbill sea turtle (*Eretmochelys imbricate*) from Barbados increased by 269% over seven years going from 89 to 328 individuals. I found more fluctuations (Least concern: slope = 0.022, CI = 0.021 to 0.023; Critically endangered: slope = 0.035, CI = 0.028 to 0.041), but not more population declines, with increasing IUCN Red List Category (Figure 3.4, Appendix 3.21). Populations from species with a higher number of threats from the species' IUCN Red List profiles did not experience greater declines when compared to those categorized with a smaller number of threats (Figure 3.4f). There were no distinct signatures of threats from the species' IUCN Red List profiles that were associated with predominantly declining local trends of monitored populations (Figure 3.4e) and there were increasing, decreasing and stable trends across all threat types.

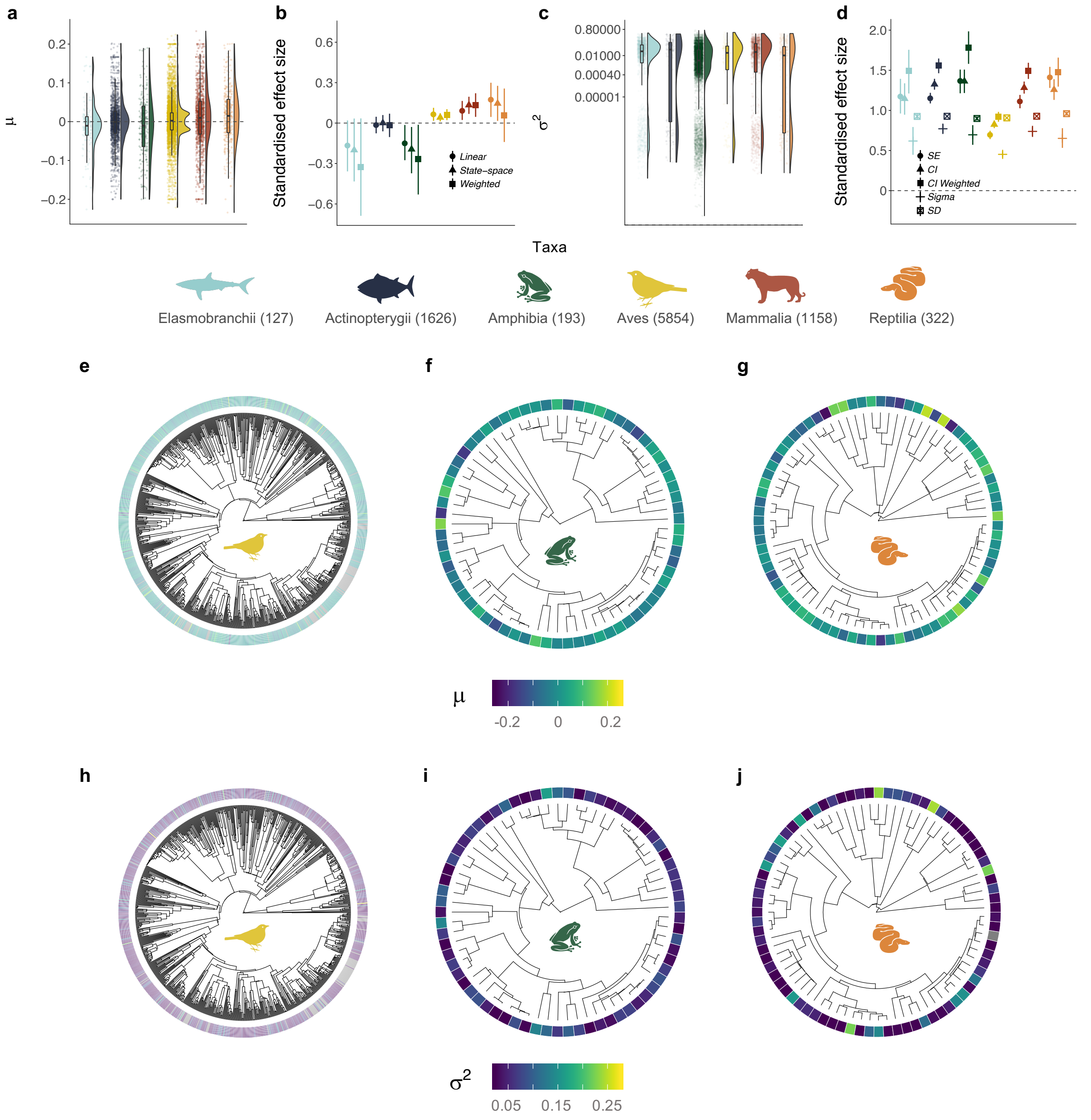

Figure 3.2. Population trends and fluctuations varied more among, rather than within, taxa, with amphibians being the only group showing pronounced declines over time. There were no distinct phylogenetic patterns in population trends and fluctuations (plots **e**-**j**). For details on phylogenetic models, see methods. Grey colour in the heatmap in plot **h** shows species for which no population trend data were available. The numbers in the legend for plots **a**-**d** show sample size for each taxon. The *μ* values of population trend (plots **a**-**b**, **e**-**g**) and the σ^2 values of population fluctuation (plots **c**-**d**, **h**-**j**) were derived from state-space model fits of changes in abundance over the

monitoring duration for each population. Plots **a** and **c** show the density distribution of population trends across taxa, the raw values (points) and boxplots (including the mean, first and third quartiles and boxplot whiskers that cover 1.5 times the interquartile range). Plots **b** and **d** show the standardised effect sizes (centre of error bars) and the 95% credible intervals of population trends (**b**) and fluctuations (**d**) across the five studied taxa. See Figure 3.1 caption for further details on effect sizes and Appendices 3.21 and 3.24 for model outputs. Icon credits: bird by Hernan D. Schlosman, snake and frog by parkjisun, fish by Julia Söderberg.

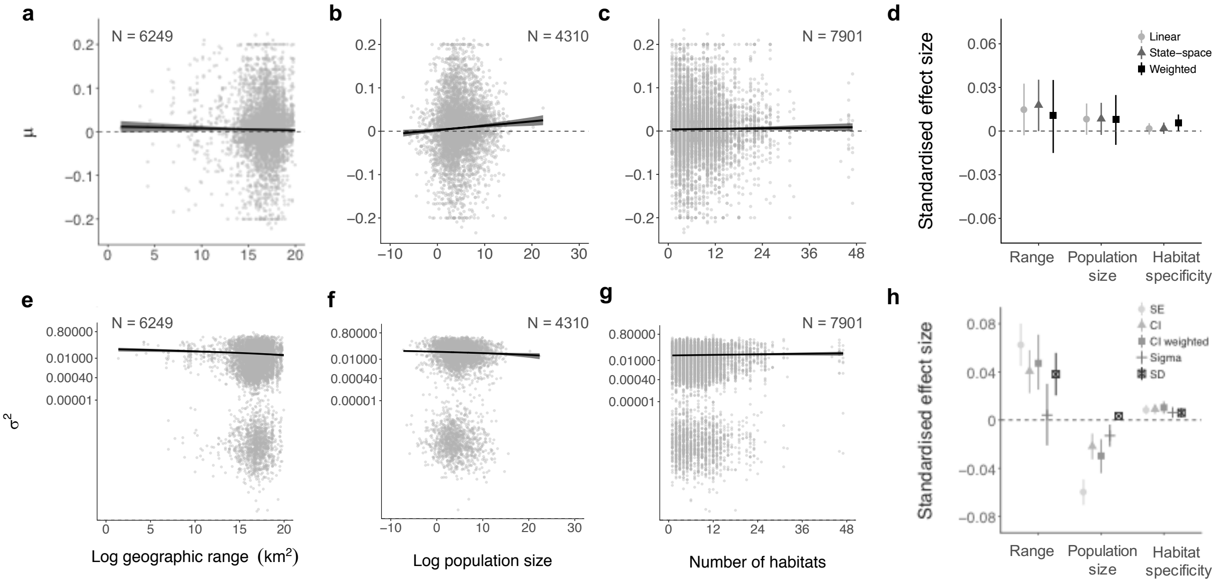

Figure 3.3. Rarity metrics did not explain heterogeneity in local population trends, and both rare and common species experienced declines and increases over time, whereas smaller populations fluctuated more over time. Numbers on plots show sample size for each metric. Rarity metrics were calculated for all species for which information was available and cover all taxa represented in the Living Planet Database, except for geographic range, which refers to the global range of only bird and mammal species in the global Living Planet Database (plots **a**-**e**). The μ values of population trend (plots **a**-**d**) and the σ^2 values of population fluctuation (plots **e**-**h**) were derived from state-space model fits of changes in abundance over the monitoring duration for each population. Plots **d** and **h** show the standardized effect sizes (centre of error bars) and the 95% credible intervals of three rarity metrics on population trends (**d**) and fluctuations

(**h**). Lines on **a**-**c** and **e**-**g** show model fits and 95% credible intervals. See Figure 3.1 caption for further details on effect sizes and Appendix 3.22 for model outputs.

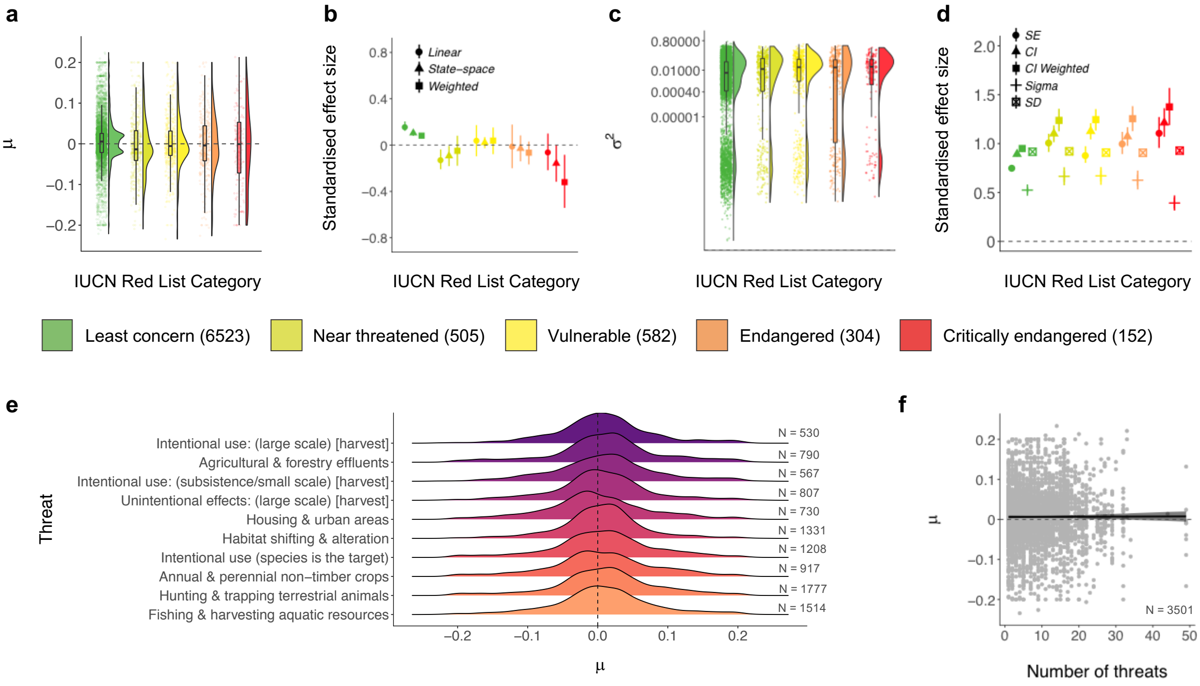

Figure 3.4. On local scales, there were increasing, decreasing and stable populations across the full spectrum of the globally determined species' IUCN Red List Category and anthropogenic threat type from the species' IUCN Red List profiles. Numbers in the legend for plots **a**-**d** and in plots **e**-**f** show sample size for each metric. Plots **a** and **c** show the density distribution of population trends across Red List status, the raw values (points) and boxplots with the mean, first and third quartiles and boxplot whiskers that indicate the distance that covers 1.5 times the interquartile range. Plots **b** and **d** show the standardized effect sizes (centre of error bars) and the 95% credible intervals of population trends (**b**) and fluctuations (**d**) across Red List status categories. The μ values of population trend (plots **a**, **e**-**f**) and the σ^2 values of population fluctuation (plot **c**) were derived from state-space model fits of changes in abundance over the monitoring duration for each population. For the relationships between type and number of threats and population fluctuations, see Appendix 3.18. Plot **e** shows the distributions of population trends across different threats that the species face globally, with the central tendencies of all distributions overlapping with zero. Lines in plot **f** show

model fit and 95% credible intervals, where “number of threats” refers to the number of different threats that each species, whose populations are locally monitored, are exposed to on a global scale. See Figure 3.1 caption for further details on effect sizes, Methods for details on deriving the number and types of threats and Appendix 3.21 for model outputs.

3.5 Discussion

Taken together, my analysis of nearly 10 000 vertebrate population time series using a state-space modelling approach demonstrated ubiquitous alterations in vertebrate abundance over time across all biomes on Earth. I revealed that population change includes both increasing and decreasing populations and spans a wide spectrum of magnitudes, and while anthropogenic impacts have accelerated in recent decades, my results highlight that vertebrate species span a wide spectrum of population change across variation in the number and types of threats to which species might be exposed. Against a backdrop of no biogeographic patterning of population trends and fluctuations (Figure 3.1), I uncovered distinct taxonomic signals, with amphibians representing the only taxa that exhibited pronounced net declines, while birds, mammals and reptiles on average became more abundant over time (Figure 3.2). Within amphibian, bird and reptile taxa, there was no distinct phylogenetic clustering of closely related species experiencing similar population trends or fluctuations (Figure 3.2). I found that both rare and common species experienced the full spectrum of population change, from declines to no net changes and increases. Species’ geographic range, mean population size and habitat specificity did not explain variation in population trends, but species with smaller population sizes were nevertheless more likely to fluctuate, potentially increasing their extinction risk (Figure 3.3. There was no consistent pattern of greater population declines with increasing IUCN Red List Category (Figure 3.4). On a global scale, the vertebrate species in the Living Planet Database are exposed to a variety of threats according to the species' IUCN Red List profiles, but on more local scales, none of the threats were characterized by predominantly declining populations (Figure 3.4), testifying to the diverse ways in which populations are likely responding to threats during the Anthropocene.

Contrary to my initial predictions, I did not find a distinct geographic patterning of population change around the world, nor a consistent trend of increasing declines in population abundance with increasing IUCN Red List Category (Figures 1 and 4). Similar lack of biogeographic signal has been documented in regional studies of population change from the Netherlands (van Strien et al., 2016) and in temperate North America and Europe (Leung et al., 2017). Coarsely represented biogeographic regions and global-scale species' IUCN Red List Categories and threat types might not capture the drivers acting in the locations of the specific populations I studied (Brook et al., 2006; Fritz et al., 2009; Maxwell et al., 2016; Pereira et al., 2012). Furthermore, the same driver can have opposing effects on population abundance at different sites (Chapter 4). A lack of biome-specific directional trends in population change, despite a spatial clustering of human pressure around the world (Bowler et al., 2020), can also arise due to differences in species traits and vulnerability to environmental change within biomes (Isaac & Cowlishaw, 2004; Khaliq et al., 2014; Morrison et al., 2018). Accounting for divergent responses of species to global change is key when translating global policy, such as the upcoming post-2020 planetary biodiversity strategy (CBD, 2010), into conservation actions implemented on scales much finer than biogeographic realms (Hill et al., 2016; Stevenson et al., 2021).

My results highlight variation in population change among taxa, with amphibians emerging as the taxa experiencing the most pronounced declines in the Living Planet Database. The remaining taxa showed either stable or increasing net changes in abundance over time (Figure 3.2). Such taxonomic patterns could be driven by different taxon-specific factors including reproductive strategy, trophic level, generation time and life history traits (Cardillo et al., 2004; Purvis et al., 2000). For amphibians, population declines have been linked to the spread of a fungal disease (chytrid fungus, *Batrachochytrium dendrobatidis*), facilitated by global warming (Pounds et al., 2006), as well as habitat loss and Allee effects in small populations (Green, 2003). Within bird, amphibian and reptile taxa, phylogenetic relatedness and species-level taxonomic classification did not explain variation in population trends and fluctuations. A similar lack of phylogenetic dependencies has been detected for the population growth rates of migratory birds (Moller et al., 2008). While phylogenetic clustering might be lacking in contemporary trends, there is evidence that phylogenetic relatedness predicts extinction, a process occurring over much longer time scales (Jetz & Pyron, 2018; Tonini et al., 2016). Over shorter time periods, species' traits and ability to persist, reproduce and disperse in ever changing landscapes might be influencing local abundance (Isaac & Cowlishaw, 2004), which has created a mix of winners and losers across all taxa (Dornelas et al., 2019). I demonstrated ongoing alterations in the abundances of six vertebrate taxa which over time, may lead to shifts in community composition and ultimately alter ecosystem function as some species become locally extinct whilst others become more abundant (Batt et al., 2017; Oliver et al., 2015).

Surprisingly, my results indicated that despite decades of conservation focus on rare species (Gaston & Fuller, 2008; Longton & Hedderson, 2000; Pigott & Walters, 1977), both rare and common species in the Living Planet Database experienced declines and increases in population abundance over the period of monitoring. The lack of rarity effects on population trends can be explained by theory and empirical evidence demonstrating that small populations do not necessarily have a higher likelihood of experiencing declines and some species are able to persist in small, but stable populations (Caughley, 1994). The power of rarity metrics to predict population trends could also be mediated by whether species are naturally rare or have become rare due to external drivers in recent years (Harrison et al., 2008; Robbirt et al., 2006). Naturally rare species might be more likely to persist over time, whereas species that have more recently become rare might be more likely to decline in response to environmental disturbance (Newbold et al., 2018). Furthermore, the timing and magnitude of past and current disturbance events influence population trends (Chapter 4, Mihoub et al., 2017) and there could be temporal lags in both positive and negative abundance changes over time (Chapter 4; Vellend et al., 2006). However, disentangling the processes leading to rarity over time remains challenging, and across the 2084 species I studied, there are likely cases of both natural and human-driven vertebrate population change. I found that species with small populations were, nevertheless, more likely to fluctuate (Figure 3.3f), which may increase their probability of extinction, a process that could play out over longer time-scales than found for most population monitoring time series to date (Fagan & Holmes, 2006; Lande, 1993; Melbourne & Hastings, 2008). My results highlight that rarity metrics alone do not capture the heterogeneity in local population change over time, and common species should not be overlooked in conservation prioritization decisions as they could be as likely to decrease in abundance over time as rare species.

My finding that declines are not universal, or even predominant, for vertebrate populations monitored for longer than five years in the Living Planet Database contrasts with reports of an overall decline in the Living Planet Index (WWF, 2018b), a weighted summary of population change across all abundance time series in the Living Planet Database. Consistent with my results, the Living Planet Reports (McRae et al., 2012, 2016; WWF, 2018b) also document that the numbers of declining and increasing species are similar across this database, but the Living Planet Reports document a larger magnitude of population declines relative to increases. The calculation of the Living Planet Index involves differential weighting of population trends derived using logged abundance data, geometric means and generalized additive models, which could explain the discrepancies between my study findings and those of the Living Planet Reports (WWF, 2018a). The Living Planet Index is hierarchically averaged from populations to species, taxa and realm and is also weighted by the estimated and relative number of species within biomes, which influences the direction and magnitude of the Living Planet Index (McRae et al., 2017; WWF, 2018a). In contrast, my analysis explores the heterogeneity in local trends and fluctuations of monitored species from the raw population abundance data, and thus, I did not use an index with weightings, and I did not aggregate population trends to a species-level. Rather than summarising trends with an index, my goal was to explain variability in abundance over time across better monitored vertebrates around the world. I detected net population declines at local scales over time only in the amphibian taxa, in contrast with the overall negative trend of the aggregate weightings of the Living Planet Index (WWF, 2018b). I caution that distilling the heterogeneity of local population change at sites around the world into a simple metric might hide diverging trends at local scales, such as the increases and declines I found.

The magnitude of population trends could be influenced by how long populations are monitored (Wauchope et al., 2019), random population fluctuations (Buschke et al., 2021), as well as whether monitoring began during a population peak or a population trough (Daskalova et al., 2021; Fournier et al., 2019). While overall, I did not find a strong effect of duration on the detected population trends in the Living Planet Database (Appendices 3.6, 3.7 and 3.21), my findings demonstrated that for reptiles, time series with longer durations are more likely to capture declines (Appendix 3.21). I also found a bimodal pattern of weak population increases and decreases in time series with longer durations particularly for terrestrial bird species with the monitoring unit being an index (Appendix 3.12). Seven key challenges have been identified when drawing robust inference about population trends over time: establishment of the historical baseline, representativeness of site selection, robustness of time series trend estimation, mitigation of detection bias effects, and ability to account for potential artefacts of density dependence, phenological shifts and scale-dependence in extrapolation from sample abundance to population-level inference (Didham et al., 2020). New methods to rigorously account for different sources of uncertainty in time series and filling in data gaps will allow the analyses of available population data to better inform global estimates of net trends across taxa (Hochkirch et al., 2021; Rowland et al., 2021).

The strength of documented relationships between population dynamics and global change could be influenced by how well-monitored populations capture the full range of variation in driver intensity. To attribute population trends and fluctuations to site-specific anthropogenic drivers, we need to go beyond previous studies that have focused exclusively on declines and extinctions (Ceballos et al., 2017; Davidson et al., 2017). We require attribution analyses that statistically test the links between observed changes in ecosystems and the experienced extrinsic pressure (IPBES, 2018). Through attribution studies that encompass the full spectrum of population change, including positive, negative and stable trends (Chapter 4; Spooner et al., 2018), we can better understand the variety of ways in which climate change, land-use change and other drivers are altering global biodiversity. For a subset of the bird populations in the Living Planet Database, greater warming of temperatures corresponded with a higher likelihood of population declines over time (Spooner et al., 2018), which could be caused by worldwide and cross-biome phenological mismatches between breeding and resource availability (Keogan et al., 2018). Across terrestrial species represented in the Living Planet Database, peak forest loss was associated with accelerations in both population increases and decreases in the period following habitat alteration (Chapter 4). There is evidence from the marine realm that when species are simultaneously exposed to multiple drivers, the resulting biodiversity effects are antagonistic and could produce patterns of no net biodiversity changes (Dunic et al., 2017). The next critical step is to test how multiple global change drivers together (Bowler et al., 2020) influence populations across both terrestrial and marine realms and determine how these relationships are mediated by species' traits and vulnerability to extrinsic threats (Vinebrooke et al., 2004).

3.6 Conclusion

In summary, my global analysis reveals the ubiquitous nature of population change over time across monitored vertebrate species. I show that in a time of accelerating global change, there were as many increases as there are decreases in population abundance over time. Among this heterogeneity, I uncovered pronounced declines in amphibian abundance as well as net abundance increases for birds, mammals and reptiles in the Living Planet Database. The taxonomic patterning of population change highlights amphibians as a conservation priority, especially as their declines can have further cascading effects across trophic levels within ecosystems. Rarity metrics, specifically geographic range, mean population size and habitat specificity, as well as IUCN Red List Categories, threat types and numbers, and evolutionary history, did not explain the heterogeneity in population change across the data analysed in this study. My findings caution the use of rarity metrics as a proxy for future global population trends, but suggest that such metrics, in particular mean population size, are nevertheless indicators of population fluctuations, which might ultimately be related to increased species extinction risk. On a global scale, both rare and common vertebrate species face numerous threats due to resource exploitation and habitat change. As human activities continue to accelerate, the next key step is to determine how intrinsic factors, such as rarity attributes and threats, interact with extrinsic global change drivers and together influence the persistence of Earth's biota. Capturing the complexity of species' population dynamics will improve our estimates of shifts in community composition and ultimately the impact of altered ecosystem functions and services around the world.

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Chapter 4. Landscape-scale forest loss as a catalyst of population and biodiversity change

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Author contributions: I conceptualised the study together with IMS and MD. I integrated databases and conducted statistical analyses with input from SB, IMS, ADB and MD. I created the figures with input from co-authors. SB, MD and SRS wrote the code for the rarefaction of the BioTIME studies. IMS. was my primary supervisor, MD my co-supervisor and ADB is on my supervisory committee. AM and MD fund the compilation of the BioTIME database. I wrote the first draft and all authors contributed to revisions.

Data and code availability: Code for the rarefaction of the BioTIME Database is available at https://doi.org/10.5281/zenodo.1475218. Code for statistical analyses is available at http://doi.org/10.5281/zenodo.1490144. Population and biodiversity data are freely available in the Living Planet and BioTIME Databases. The Living Planet Database can be accessed on http://www.livingplanetindex.org/data_portal. The BioTIME Database can be accessed on Zenodo (https://doi.org/10.5281/zenodo.1211105) or through the BioTIME website (http://biotime.st-andrews.ac.uk/). The public studies which were included in the version of BioTIME I analysed can be downloaded from http://biotime.st-andrews.ac.uk/BioTIME_download.php. Land-use change data are publicly available in the Land Use Harmonization Database (https://luh.umd.edu), the Forest Cover Change Database (https://earthenginepartners.appspot.com/science-2013-global-forest) and the MODIS Landcover Database (https://modis.gsfc.nasa.gov/data/dataprod/mod12.php).

4.1 Summary

Global biodiversity assessments have highlighted land-use change as a key driver of biodiversity change. However, we are lacking empirical evidence of how habitat transformations like forest loss and gain are reshaping biodiversity over time. Here, I quantified how change in forest cover has influenced temporal shifts in populations and ecological assemblages from 6,090 globally-distributed time series across six taxonomic groups. I found that local-scale increases and decreases in abundance, species richness, and temporal species replacement (turnover) were intensified by up to 48% following

forest loss. Temporal lags in population- and assemblage-level shifts after forest loss extended up to 50 years and increased with species' generation time. My findings show that land-use change catalyses population and biodiversity change, emphasizing the both the positive and negative biotic consequences of land-use change.

4.2 Introduction

Accelerating human impacts are reshaping Earth's ecosystems (IPBES, 2019). The abundance of species' populations (Chapter 3, Dornelas et al., 2019) and the richness (Baeten et al., 2010; Dornelas et al., 2014; Vellend et al., 2013) and composition (Dornelas et al., 2014) of ecological assemblages at sites around the world are being altered over time in complex ways (Hillebrand et al., 2018; Magurran et al., 2018; Yoccoz et al., 2018). However, there is currently only a limited quantitative understanding of how global change drivers, such as land-use change, influence the observed heterogeneous local-scale patterns in population abundance and biodiversity (Bowler et al., 2020; Leung et al., 2017; Yoccoz et al., 2018). In terrestrial ecosystems, much current knowledge stems from space-for-time approaches (Betts et al., 2017; Newbold et al., 2015) and model projections (Newbold, 2018; Newbold et al., 2018) that attribute population and richness declines to different types of land-use change, including reductions in forest cover. Yet, space-for-time methods may not accurately represent the effects of global change drivers, because they do not account for ecological lags (Elmendorf et al., 2015; Mihoub et al., 2017; Yoccoz et al., 2018) and community self-regulation (Gotelli et al., 2017). Furthermore, ongoing controversy about the diverse impacts of habitat fragmentation on biodiversity (Damschen et al., 2019; Fahrig, 2017; Haddad et al., 2017) could be in part attributable to a lack of observational data from sites encompassing the full spectrum of forest fragmentation. Recent global-scale datasets of past land cover reconstructions (Hurtt et al., 2011) and contemporary high-resolution remote-sensing observations (Channan et al., 2014; Hansen et al., 2013) provide an unique opportunity to quantify landscape-scale decreases and increases in forested areas around the world (hereafter, "forest loss and gain"). By integrating forest loss estimates with over five million population and biodiversity observations (Dornelas et al., 2018; LPI, 2016), my analysis provides new insights into the influence of land-use change on local-scale population and biodiversity change around the planet.

In my study, I set out to conduct a global extent attribution analysis of the influence of forest cover change on population and biodiversity change (Figure 1, Appendix 4.1). I quantitatively tested specific predictions of the extent and pace of landscape-scale forest loss impacts on species' populations and ecological assemblages across terrestrial ecosystems around the planet (Figures 1-2). Land-use change, and particularly forest cover loss, alters habitat and resource availability (Elahi et al., 2015; Newbold et al., 2015; Sax & Gaines, 2003) and is a global threat for the persistence of terrestrial species (IUCN, 2017, Figures 2, Appendix 4.12). I thus predicted the greatest impacts on populations and biodiversity when time series monitoring encompasses the 10-year period that included the largest reduction in forested areas at each site (calculated between 850 and 2015, hereafter "all-time peak forest loss"). I also expected greater population and species richness declines and higher turnover after, relative to before, contemporary peak forest loss - the year of the largest reduction in forested area within the duration of each time series. Finally, species with longer generation times typically respond more slowly to environmental change (Krauss et al., 2010). I thus predicted lags in ecological responses to forest loss to increase with longer generation times across taxa.

4.3 Methods

To relate population and biodiversity change to historic forest loss, I quantified the baseline all-time peak forest loss at each site. To relate population and biodiversity change to contemporary forest loss, I compared population and biodiversity change before and after contemporary peak forest loss. To investigate temporal lags, I quantified the time period between contemporary peak forest loss and maximum change in populations and assemblages detected after peak forest loss has occurred at each site (Figure 1B). I calculated population change (μ) using state-space models that account for observation error and random fluctuations (Humbert et al., 2009), and richness change (slopes of rate of change over time) using mixed effects models. I quantified temporal change in species composition as the turnover component of Jaccard's dissimilarity measure (change due to species replacement, Baselga, 2010*)*. Turnover is often independent of changes in species richness (Hillebrand et al., 2018) and is the dominant component of compositional change across time series of ecological assemblages (Blowes et al., 2019). I used a hierarchical Bayesian modelling framework, with individual time series nested within biomes (Olson & Dinerstein, 2002) to account for the spatial structure of the data (see Appendix 4 for further details and sensitivity analyses).

I measured landscape-scale historic and contemporary forest loss by integrating information from the Land Use Harmonization (Hurtt et al., 2011) and Global Forest Change (Hansen et al., 2013) databases I also examined whether my results were consistent across land-use change data sources using the ESA Landcover (ESA Climate Change Initiative, 2017) and KK09 (Kaplan et al., 2009) databases. I compared historic and contemporary forest loss with temporal population change (trends in the numerical abundance of species) and biodiversity change (trends in species richness and turnover in assemblage composition, Figures 1-2). I analysed 2729 populations of 730 species and biodiversity change in 3361 ecological assemblages (Figures 2A-3). I measured population change using the Living Planet Database that includes 133,092 records of the number of individuals of a species in a given area over time (LPI, 2016), and biodiversity change using the BioTIME database that comprises 4 970 128 records of the number and abundance of species in ecological assemblages over time (Dornelas et al., 2018). Together, these time series represent a range of taxa including amphibians (388), birds (5090), mammals (266), reptiles (76), invertebrates (80) and plants (187) and 2,157 sites which cover almost the entire spectrum of forest loss and gain around the world (Figure 2B). I used a standardised cell size of 96 km^2 to match response variables (population change, richness change and turnover) to landscape-scale forest change but note that analyses were robust to the spatial scale over which I calculated forest change (Appendices 4.13-4.14).

I did not predetermine sample size and instead worked with all available temporal population, biodiversity and forest cover change data that met my duration criteria. For analyses of population change, I included time series with five or more survey points. For analyses of biodiversity change, I included time series with five or more data points when analyzing the full time series (using forest loss estimates from the Land Use Harmonisation (LUH) database), and time series with two or more data points when matching the duration of time series comparisons to the 16-year duration of the Global Forest Change (GFC) Database from 2000 to 2016. I calculated forest loss on a standardised landscape scale (~96 km^2). Both the LUH and GFC databases are measured on an annual time step. All statistical models were fitted in a Bayesian framework using the *brms* package v2.1.0 (Bürkner, 2017) in R v3.5.1 (R Core Team, 2017). Models were run for 6000 iterations, with a warmup of 2000 iterations and four chains. Convergence was assessed visually by examining trace plots and using *Rhat* values (the ratio of the effective sample size to the overall number of iterations, with values close to one indicating convergence). See Appendix 4 for details on each database and statistics.

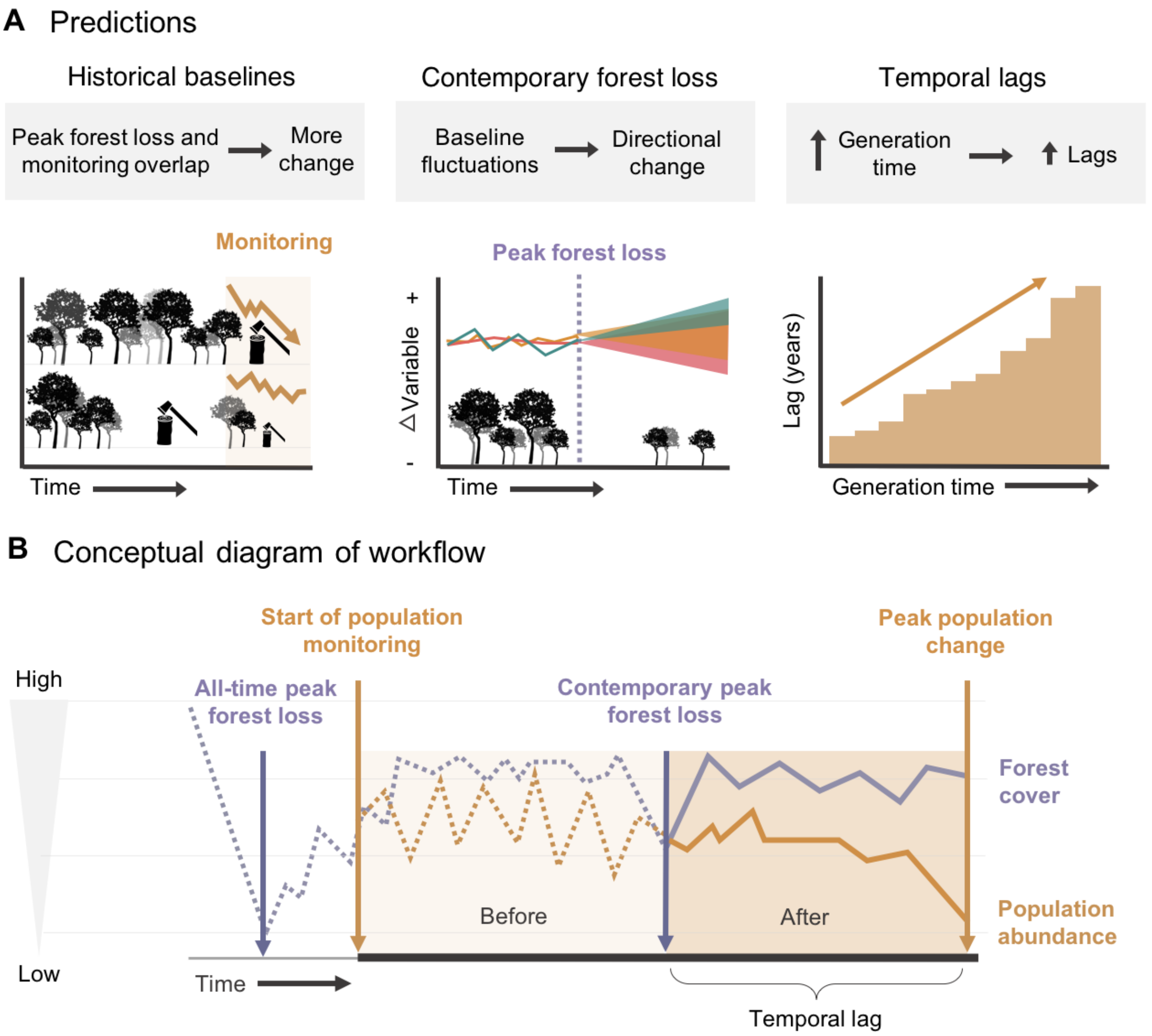

Figure 4.1. Influence of forest loss on population and biodiversity change. I tested three pathways through which forest loss can influence the population abundance of species and the richness and turnover of ecological assemblages: historical baselines of forest loss, timing of contemporary forest loss and temporal lags in population and biodiversity responses. **A**, Conceptual diagram of my predictions outlined with respect to population change, richness change and turnover (temporal species replacement). **B**, Analytical workflow for determining all-time and contemporary peak forest loss and temporal lags.

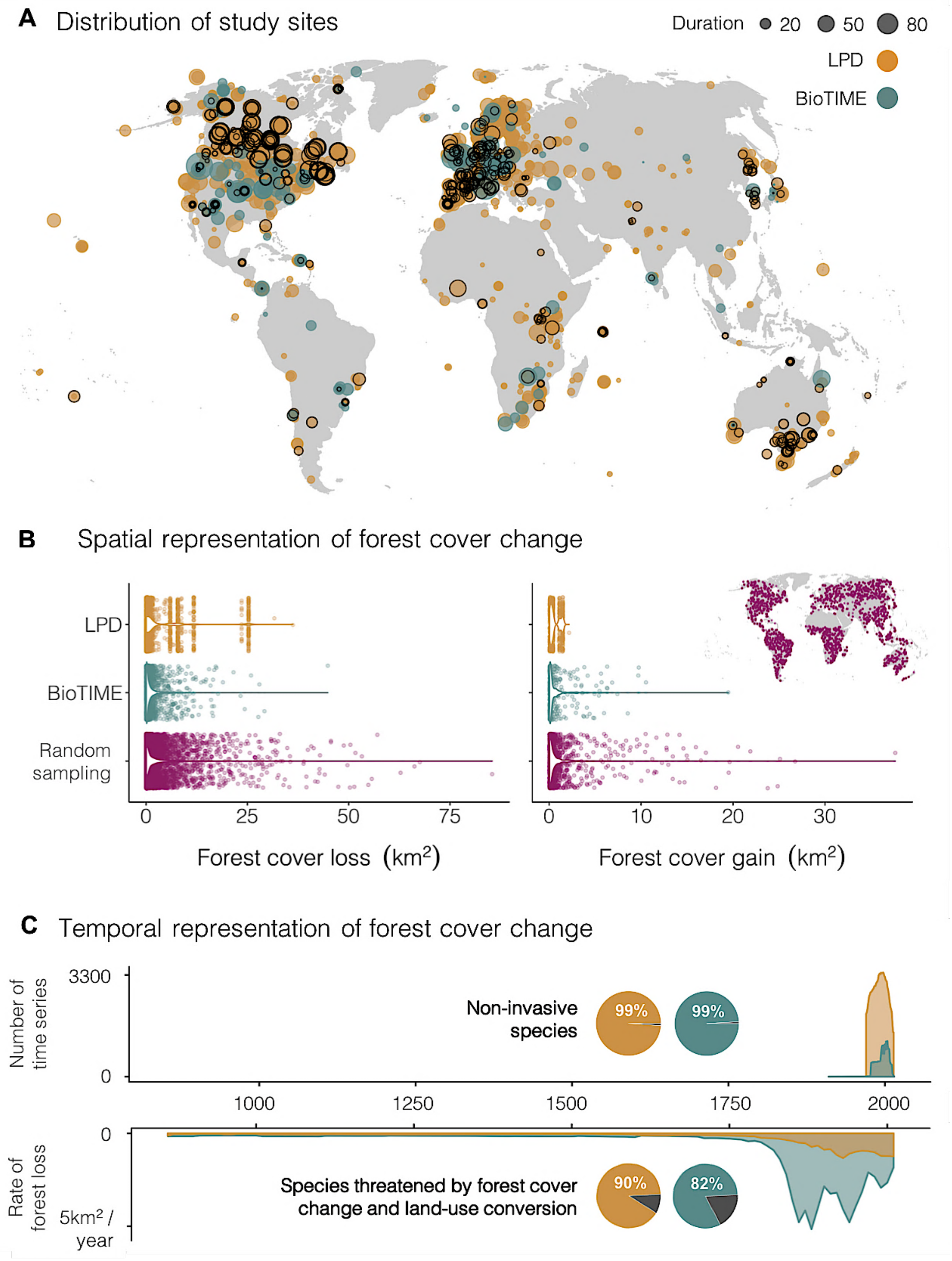

Figure 4.2. Population and biodiversity monitoring over time broadly spans the global variation in forest cover change. A, Locations and duration of 542 Living Planet

Database (LPD) and 199 BioTIME studies, containing 6,090 time series from 2,157 sites (black outline shows sites that were forested at the start of the monitoring (1,247 sites); see Appendix 4.18 for sample size in each woody biome). **B**, 44% of all time series experienced historic or contemporary forest loss of comparable magnitude to forest cover change across a simulated random sample of geographical locations (shown on map inset in **B**) from the global distribution of forest cover loss and gain. I did not detect directional effects of the magnitude of forest gain across monitored sites (Appendices 4.4-4.6). **C**, the number of time series increases over time (top), but the rates of forest loss were often higher before the start of monitoring (bottom, for variation in monitoring periods among time series, see Appendices 4.2-4.3). Insets in panel **C** show the proportion of study species that are not classified as invasive (top) and that are threatened by land-use change, based on species' IUCN threat assessments (bottom, see Appendix 4.12 for details).

4.4 Results and discussion

4.4.1 Historical baselines influenced forest loss effects on population and biodiversity change

In line with my first prediction ("historical baselines"), I found that local-scale population declines were most pronounced when the monitoring occurred during the period of all-time peak forest loss (Figures 4.1B and 4.3B-C). For many of the sites represented by the time series I studied, dramatic changes in forest cover occurred in the last two centuries, with all-time peak forest loss in regions like Europe and North America typically in the early 1800's, before biodiversity, population and satellite monitoring had begun (Figures 4.2C and 4.3B). These time series captured over half of the spectrum of contemporary forest cover change around the world, in contrast to previous criticisms of these data underrepresenting areas with anthropogenic impact (Gonzalez et al., 2016) Figure 4.2B-C and 4.3B). Yet, in only approximately 5% of monitored time series forest loss led to a conversion in the dominant habitat type (e.g., from primary forest to urban areas). Habitat conversions corresponded with both gains and losses in populations and biodiversity, with the highest rates of turnover when primary forests were converted to agricultural and urban areas, or to secondary forests (Appendix 4.17). The links between historical baselines, the timing of all-time peak forest loss and resulting ecological change emphasise the need for a long-term perspective to quantify the full breadth of biodiversity change in the Anthropocene (Bowler et al., 2020; Mihoub et al., 2017).

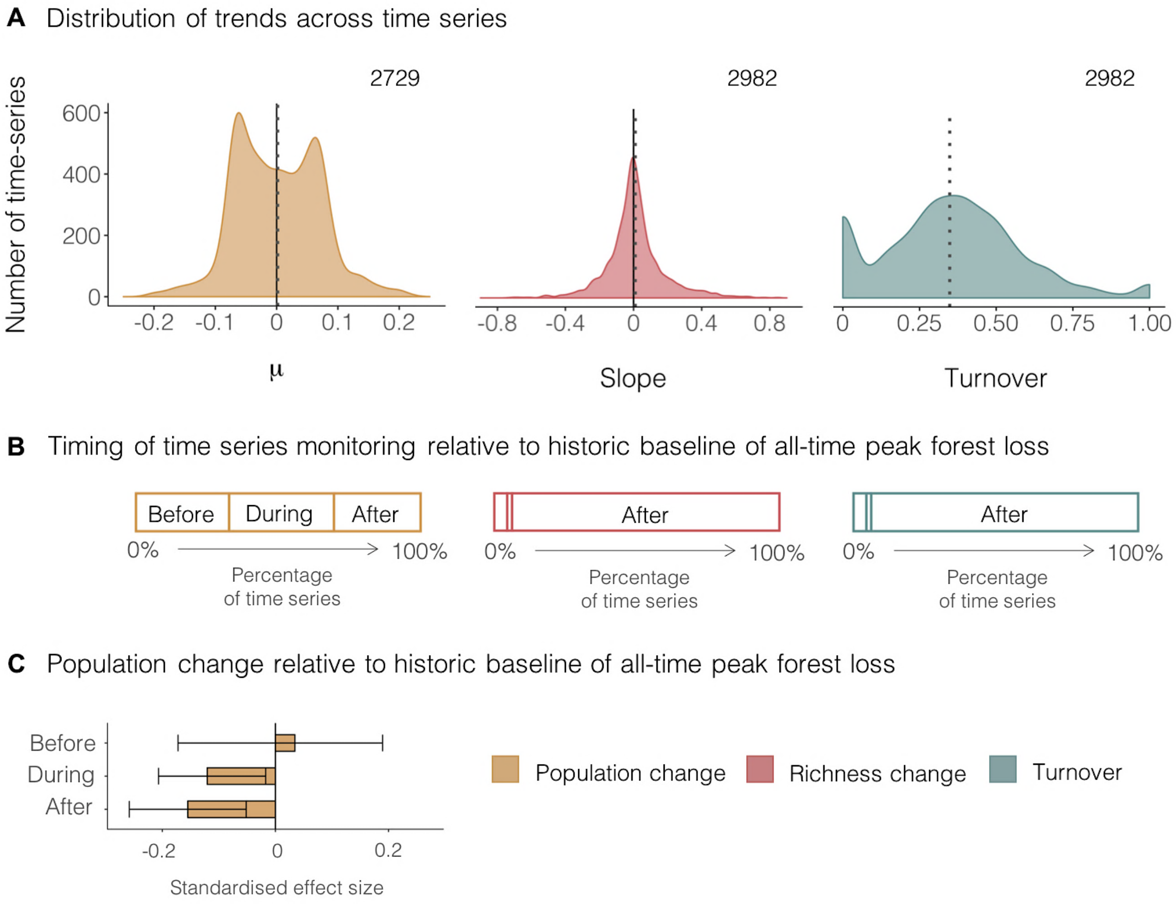

Figure 4.3. Heterogeneity in population and biodiversity trends and land-use histories from sites around the world. A, All three metrics of ecological change (population change, richness change and turnover) show heterogeneous distributions across sites. **B**, Population monitoring occurred at different time periods relative to all-time peak forest loss (for 33% of sites before, for 37% during and for 30% of sites after), whereas biodiversity monitoring predominantly started after all-time peak forest loss had occurred (94% of sites). **C**, Population declines were most acute when all-time peak forest loss occurred during the population monitoring period (slope = -0.01, CI = -0.01 to -0.01; see Appendix 4.19 for model outputs). Low sample size for the ‘before’ (101) and ‘during’

(38) categories precluded a similar analysis for richness change and turnover. Numbers on **A** show sample size (*i.e.*, number of time series).

4.4.2 Contemporary forest loss amplified population and biodiversity change

Contrary to my second prediction ("contemporary forest loss"), I found that forest loss acted as a catalyst amplifying both increases and decreases in local-scale populations and assemblages over time (Figures 4.3-4.4 and Appendices 4.4-4.6, 4.9-4.10). Across time series, more than half of all populations and assemblages (61%) experienced higher rates of change after the largest forest loss event within each time series. Contemporary peak forest loss intensified population declines, population increases and richness losses, but not richness gains, relative to the period before peak forest loss (Figure 4.4). In nearly a third of time series (32%), more than 10% of the species in the assemblage at the time of contemporary peak forest loss were replaced by new species by the end of the time series (Figure 4.4G-H). The assemblages that experienced the most richness change also experienced the most turnover (Pearson's correlation = 0.37, 95% confidence intervals = 0.31 to 0.43). The influence of contemporary peak forest loss on population and biodiversity change was not strongly correlated to the magnitude of the specific forest loss event (Appendices 4.4-4.6). My findings indicate a wide spectrum of population and biodiversity responses to forest loss that might be overlooked without accounting for temporal dynamics and lagged responses (Betts et al., 2017; Ceballos et al., 2017; Newbold et al., 2015, 2018).

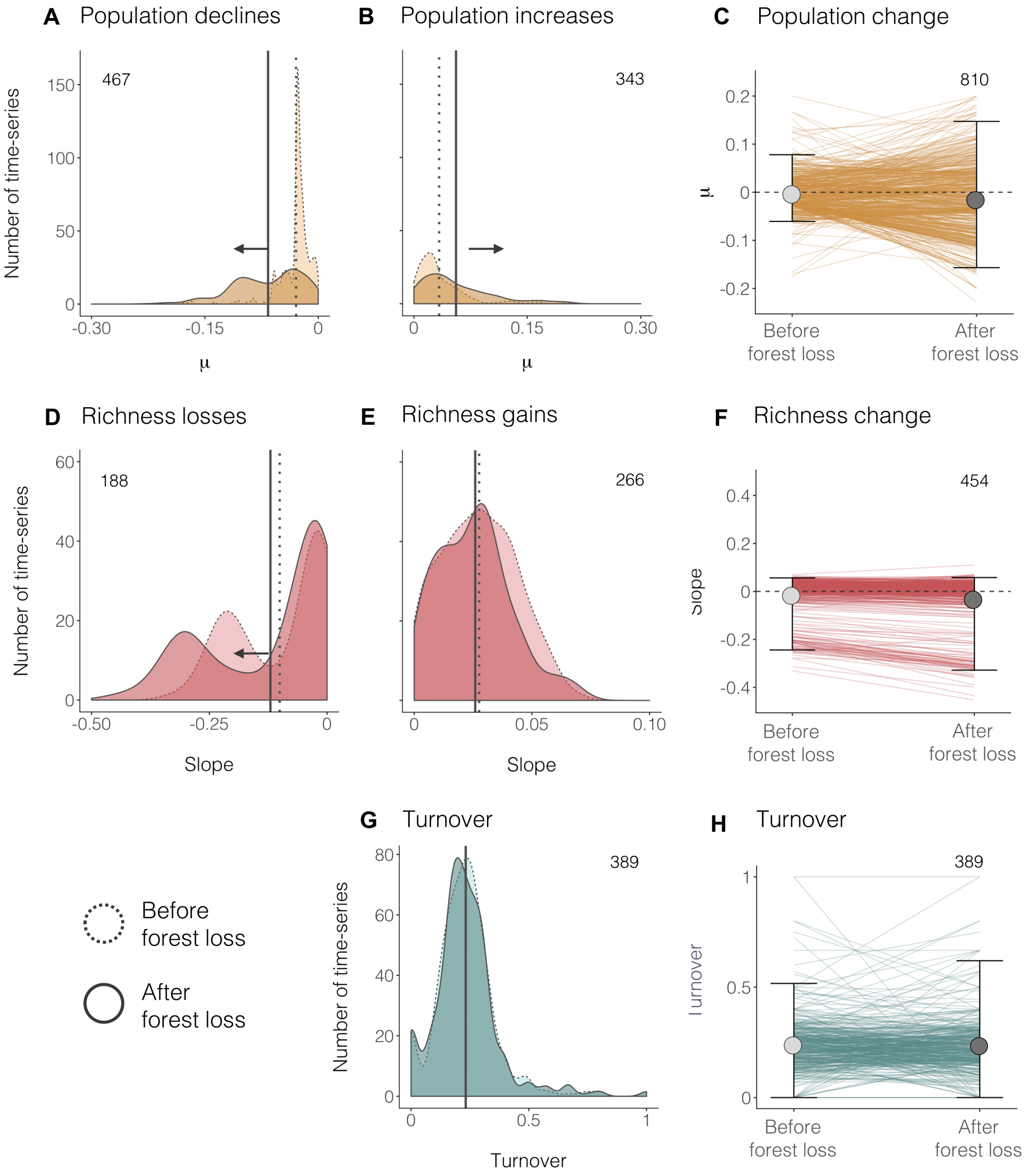

Figure 4.4. At the site level, population and biodiversity change increase after contemporary peak forest loss. In total, population and richness change increased across 61% and decreased across 39% of the 1653 time series for which baseline comparisons were possible (i.e., the time series were long enough to include at least five years before and after forest loss). Only turnover included instances of no difference in the amount of change before and after peak forest loss (6% of time series). Distributions compare **A**, population declines (μ), **B**, population increases (μ), **D**, richness losses

(slopes), **E**, richness gains (slopes) and **G**, turnover (Jaccard's dissimilarity) in the periods before and after contemporary peak forest loss, the largest forest loss event during the monitoring of each site. Vertical lines over distributions show the mean for each category (dotted – before; solid – after). Temporal trends before and after peak forest loss (**C**, **F**, **H)** are indicated with lines for individual time series. Light and dark grey points and error bars show mean values and 2.5 and 97.5% quantiles. Duration varied among time series but was consistent for each individual time series (*i.e.*, *n* years before forest loss = *n* years after forest loss, n ≥ 5 years; see Figure S8 for relationship between duration and number of survey points). Numbers on plots indicate sample size. See Appendix 4.19 for model outputs.

4.4.3 Temporal lags spanned from six years to half a century

In line with my third prediction ("temporal lags"), I found evidence for up to half-century ecological lags in local-scale changes in population abundance, species richness and turnover following contemporary peak forest loss (Figure 4.5). On average, I documented maximum change in populations and ecological assemblages six to 13 years after forest loss across taxa. Yet, nearly half of population and biodiversity change (40%) happened within three years of peak forest loss, demonstrating that rapid shifts in populations and assemblages occur frequently after habitat change (Figure 4.5, Appendix 4.7). Consistent with my prediction, the period between peak forest loss and peak change in populations and biodiversity was longer for taxa with longer generation times (*e.g.*, large mammals and birds, Figure 4.5B, Appendix 4.19). Population declines and increases occurred on similar timescales (Figure 4.5C). Losses in species richness lagged behind gains by approximately half a year (slope = 0.5, CI = 0.1 – 1.05), indicating that extinction debts and immigration credits accumulated at roughly the same speed across taxa. The similar pace and temporal delay of population declines and increases, and richness gains and losses could help to explain previous findings of community self-regulation (Gotelli et al., 2017) and no net population change (Chapter 3, Dornelas et al., 2019; Leung et al., 2017) and richness change (Dornelas et al., 2014; Vellend et al., 2013) at local scales. Temporal lags in biodiversity change have also been observed in post-agricultural forests (Baeten et al., 2010; Vellend et al., 2006) and fragmented grasslands (Krauss et al., 2010), where agricultural activity has ceased decades to centuries ago, yet richness and assemblage composition change continue to the modern-day. Overall, my results indicate that increasing rates of land-use change in the Anthropocene (De Palma et al., 2018; Egli et al., 2018) will alter ecosystems on both short- and long-term timescales that need to be captured in ongoing and future biodiversity monitoring.

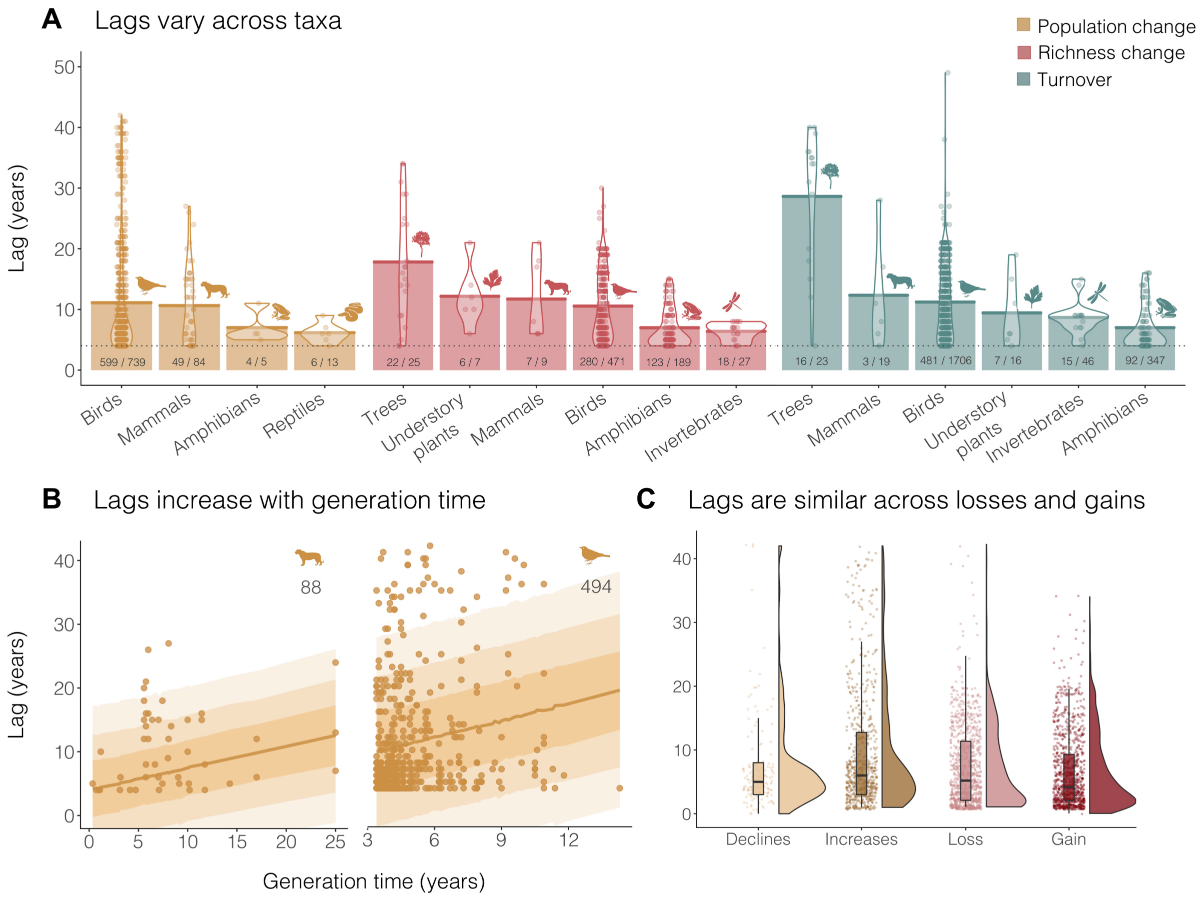

Figure 4.5. Temporal lags in population and biodiversity change following contemporary peak forest loss. Population and assemblage change after contemporary peak forest loss may be delayed by up to half a century, with taxa and species with long generation times showing the longest temporal lags. **A**, I categorised lags as time periods of three (dashed horizontal line) or more years between peak forest loss during the monitoring for each time series, and peak population/biodiversity change (Figure 2B, sample size was 841 time series for population change, 728 for richness change and 2,157 for turnover). Bars show mean lag for each taxon; violins show the distribution of lag values and the points are lag values for each time series. Numbers on

bars indicate how many time series experienced lags out of the total sample size for each taxon. **B**, Temporal lags in mammal and bird population change increased with longer species' generation times. **C**, Temporal lags were similar across population declines and increases, and species richness losses and gains. See Appendix 4.19 for model outputs.

Heterogeneity in responses to forest cover loss could be due to a number of factors, including: i) temporal lags in population or assemblage responses as observed in my study and elsewhere (Krauss et al., 2010; Mihoub et al., 2017), ii) context specific responses to forest loss, such as the same amount of habitat change corresponding to biodiversity declines at one site, but increases at another (Betts et al., 2017, 2018, 2019), and iii) interactions with other drivers occurring simultaneously with forest loss (Bowler et al., 2020; Fridley & Wright, 2018; Spooner et al., 2018). My finding that forest loss was concurrent with both declines and increases in populations and assemblages is consistent with the varied and often positive effects of habitat fragmentation on biodiversity metrics such as species richness (Fahrig, 2017). However, forest loss occurring outside of the period of population or biodiversity monitoring, as well as the type of woody vegetation being gained and lost, might influence my ability to detect a causal link between forest loss and biodiversity change (Isbell et al., 2019; Mihoub et al., 2017). Increases in woody vegetation caused by agroforestry or plantations might not reflect ecosystem recovery such as with natural succession after forest cover loss (Curtis et al., 2018; Potapov et al., 2008; Veldman et al., 2019). My finding that forest cover gain did not directly correspond with gains in population abundance and species richness highlights the need for high-resolution temporal data of the specific vegetation types constituting forest cover changes around the world. The heterogeneity of forest cover change effects on biodiversity (Banks-Leite et al., 2014; Betts et al., 2017, 2019; Orme et al., 2019) demonstrate that caution is warranted with recent calls for global afforestation as a climate change mitigation tool (Bastin et al., 2019).

Variation in species' vulnerability to forest cover loss (Betts et al., 2019; Orme et al., 2019) may be contributing to the wide spectrum of population and biodiversity responses to shifts in forest cover. Species that have experienced frequent habitat disturbance during their evolutionary history might be more resilient to land-use change, whereas novel habitat alterations could have a greater influence on species' persistence and abundance (Betts et al., 2017, 2019; Figure 3). In a *post-hoc* test, I found that in forest-dominated sites, where past disturbances were likely less frequent, declines in species' abundance were more frequent than increases, whereas richness change and turnover did not show directional trends (Appendix 4.16). Additionally, in my study, rare and common species, as defined by their range size, mean population size and habitat specificity (Rabinowitz, 1981), responded in similar ways to forest loss (Appendices 4.11-4.12). In contrast to this result, space-for-time comparisons that do not account for temporal dynamics and lagged responses have found that land-use change impacts rare species more negatively than common species (Sykes et al., 2019). Accounting for both inter- and intraspecific heterogeneity in species' vulnerability to forest cover change is key when scaling from localised impacts of human activities to global-scale biodiversity patterns and attribution of change (Betts et al., 2019; Ceballos et al., 2017; Damschen et al., 2019; Fahrig, 2017; Haddad et al., 2017; IPBES, 2019; Orme et al., 2019).

Taxonomic, spatial and temporal imbalances in sampling can make large-scale attribution analyses of biodiversity trends and global change drivers challenging and influence the inferences I draw from such studies (Appendices 4.2, 4.3, 4.9, 4.11-4.19). For this reason, I explored in greater detail three specific challenges of my terrestrial biodiversity attribution analyses. First, tropical species and locations are under-represented in current open-source temporal biodiversity databases (Figure 2A, Gonzalez et al., 2016, Chapter 2). In a *post-hoc* test, I found that in the tropics, where there is intense, often unprecedented forest loss, the effects of forest loss were stronger and more negative across sites with available data, relative to the rest of the globe (Appendices 4.9, 4.10, 4.18, 4.19). Second, the spatial scales at which biodiversity is monitored (from 1 m^2 to 25 x 10^8 km^2) and the resolution of forest cover datasets (from 30 m to ~20 km, Appendices 4.13, 4.14) could introduce spatial mismatches between the driver and response. Nevertheless, I found that the heterogeneous relationships between richness change, turnover and forest loss were consistent across forest loss calculated on scales from 10 km^2 to 500 km^2 (Appendices 4.16A-B). Third, temporal mismatches and lags (Figures 1C and 5) can obscure relationships between forest loss and population and biodiversity change. I found that attribution signals were strongest when a peak in forest loss occurred during the time series monitoring (Figures 3 and 4). My results indicate that biodiversity assessments and global change attribution analyses will be improved by better spatial and temporal matching of biodiversity and environmental impact data.

4.5 Conclusion

In summary, my analysis reveals an intensification of both increases and decreases of populations and biodiversity by up to 48% after forest loss at sites around the planet. This finding demonstrates heterogeneity in the influence of forest cover change on populations and ecological assemblages and challenges the assumption that land-use change predominantly leads to population declines and species richness loss (Ceballos et al., 2017; Newbold, 2018; Newbold et al., 2015). A current assumption underlying existing projections of biodiversity responses to land-use change (Newbold, 2018; Newbold et al., 2015) is that space-for-time approaches accurately reflect longer-term population and biodiversity dynamics (De Palma et al., 2018). In contrast, I found temporal lags of up to half of a century in population and biodiversity change following forest loss that differed across taxa and generation times. My analyses highlight that the local-scale responses of populations and assemblages to forest cover loss and gain are complex and variable over time. Incorporating the full spectrum of population and biodiversity responses to land-use change will improve projections of the future impacts of global change on biodiversity and thus contribute to the conservation of the world's biota during the Anthropocene.

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Chapter 5. Synthesis

Chapter 5. Synthesis

5.1 Summary of key findings and synthesis

The main aim of my thesis was to quantify the patterns and drivers of population and biodiversity change observed across taxa, realms and sites around the world (**Chapter 1**). The key finding from my research is that global change drivers are leading to both gains and losses in population abundance and species richness, as well as shifts in composition (Figure 5.1). This change is complex and nuanced and no single species' trait or driver on its own can explain the wide range in biodiversity trends across the Anthropocene.

In the thesis, I focused on three themes:

1) Quantifying the types of global change that have occurred across the locations represented by global biodiversity databases (**Chapter 2**).
2) Capturing the variation of vertebrate population trends across biomes, taxa, rarity traits and species' IUCN Red List status (**Chapter 3**).
3) Comparing the historic and contemporary effects of forest cover change on temporal shifts in population abundance, species richness and compositional turnover across vertebrates, invertebrates and plants (**Chapter 4**).

Together, the three data chapters spanned the terrestrial, marine and freshwater realms, tens of thousands of locations around the world and records from over 50,000 different species.

KEY FINDINGS

Chapter 2.

Biodiversity datasets capture between 17% and 78% of the global change spectrum.

Chapter 3.

Rarity did not explain the heterogeneous population trends observed across taxa and at sites around the world.

Chapter 4.

Local-scale increases and decreases in abundance, species richness, and turnover intensified by up to 48% following forest loss, with lags up to 50 years.

Chapter 5. Synthesis

Interactions between species' traits, community self-regulation and simultaneous exposure to multiple global change drivers could broaden the spectrum of biodiversity change.

DIRECTIONS FOR FUTURE RESEARCH

Land abandonment as an underexplored driver of change

Simultaneous exposure to multiple types of global change

Landscape context of biodiversity change

Figure 5.1. Global change drivers are leading to both gains and losses in population abundance and species richness, as well as shifts in composition.

My main findings were:

1. **Biodiversity datasets span different gradients of the spectrum of global change including human use of natural resources and climate change.**

In **Chapter 2**, I quantified what types of survey sites were represented by global biodiversity datasets, with a focus on variation in global change over space and time. My starting hypothesis was that compilations of biodiversity data would capture only a limited sample of the variation of global change intensity around the world. Surprisingly, I found that three worldwide ecological databases – Living Planet, BioTIME and PREDICTS – occupy high proportions of global change space (between 71% and 78% in the marine realm and between 17% to 31% in the terrestrial realm). All three databases included sites with moderate to high human use intensity. There were, however, differences in representation when it came to intact sites. The Living Planet database included both relatively intact sites as well as sites with high human use, pollution and climate change, whereas the BioTIME and PREDICTS databases overrepresented sites with high global change and underrepresented those with low values of human impact. This heterogeneity in global change intensity across population and biodiversity monitoring could contribute to the wide distribution of population trends found in global biodiversity and population datasets (**Chapter 3**).

For nearly a decade, a debate has been ongoing around the contrasting findings of no net richness change based on time series data and richness declines from space-for-time data (Dornelas et al., 2014; Gonzalez et al., 2016; Newbold et al., 2015; Vellend et al., 2013, 2017). My thesis demonstrates that the global change variation captured by population and biodiversity monitoring can vary nearly two-fold within the terrestrial realm (*e.g.*, 17% for the BioTIME versus 31% for the Living Planet database). Such data compilations represent different combinations of global change drivers such as climate change and human use. For example, amphibian time series from the Living Planet Database come from sites with predominantly heavy human use, and perhaps unsurprisingly, amphibians were also the only taxon found to be declining in abundance over time (Leung et al., 2017, 2020, **Chapter 3**).

I found that there were frequent mismatches between the timing of peak global change and that of biodiversity monitoring (**Chapter 4**). This type of mismatch is frequently hypothesised and discussed as a major issue in ecology which can lead to underestimating the impacts of global change on biodiversity (De Palma et al., 2018; Essl et al., 2015; Mihoub et al., 2017). In **Chapter 4**, I compared vertebrate population trends before, during and after peak forest loss at each study site between the years 850 and 2014. I found that declines in vertebrate abundance tended to occur when all-time peak forest loss happened during the period of species' population monitoring (**Chapter 4**). In the instances when all-time peak forest loss had occurred decades to centuries before the first species' abundance records were collected, I found a wide spectrum of population trends, including declines, increases and no net change over time (**Chapter 4**). My results highlight the importance of considering historical legacies in biodiversity analyses and accounting for the different temporal trajectories of global change driver intensity around the world.

2. Global change space varies across latitudes with greater climate change at high latitudes and greater human use nearer to the equator.

In **Chapter 2**, I quantified the amount of human use, climate change, human population density, pollution and invasion pressure across the locations of three worldwide biodiversity databases. Biogeographic patterning of global change occurs at the planetary scale (Bowler et al., 2020; Crain et al., 2008; Halpern et al., 2015; Sanderson et al., 2002), thus I hypothesised that there will be differences in the types and amounts of global change estimated for sampling sites across biodiversity datasets. My findings showed that Arctic and tropical latitudes occupy the extremes of the global change space (**Chapter 2,** Appendix 2.2) and those were also the regions for which I found different global change impacts relative to the rest of the planet. In contrast, global change at temperate latitudes spanned a wide spectrum from relatively intact to more disturbed sites. Low tropical latitudes, on the other hand, will likely be entering non-analogue climate space in the future that might be beyond the boundaries of the current global change space (Fitzpatrick & Hargrove, 2009; Ribeiro et al., 2016; Tovar et al., 2013). My results demonstrate that population and biodiversity monitoring unevenly samples global change drivers (**Chapter 2**). Thus, population and biodiversity trends derived from global databases may not represent the full magnitude and combination of biodiversity drivers across the planet.

In **Chapter 3**, I compared trends and temporal fluctuations in population abundances of vertebrate species across nearly 10,000 sites from different regions around the world. My hypothesis was that there would be differences in population change across biomes because of the uneven distribution of global change around the world (**Chapter 2**, Bowler et al., 2020; Halpern et al., 2015) and because of differences in species' vulnerability and traits (e.g., terrestrial species could migrate from unfavourable habitats more easily than freshwater species, Chichorro et al., 2018; Coll et al., 2012; Concepción et al., 2015; Howard et al., 2020; Marini et al., 2010; Morrison et al., 2018). I found that vertebrate populations in polar freshwaters, tropical forests, and tropical coral biomes were more likely to increase in abundance between 1970 and 2014 (but note that not all species were monitored for this entire period). In contrast, populations from the remaining studied biomes experienced no net changes during the same study period. Additionally, I found that montane and tropical biomes had more pronounced vertebrate population fluctuations compared to other biomes (**Chapter 3**). Many latitudinal bands and biomes, however, did not have distinct patterns in population trends and fluctuations. Bringing together my findings from **Chapters 2** and **3**, a possible explanation of the similar distributions of population change across most biomes is that in each biome, species' populations are likely experiencing a mix of beneficial and detrimental environmental conditions (Bowler et al., 2018; Crain et al., 2008; Darling et al., 2010; Radinger et al., 2016). Simultaneous exposure to different types of global change driver is likely producing a mix of population increases and declines across biomes, mediated by whether or not species' vulnerability to threats is correlated (Vinebrooke et al., 2004). The presence of a wide distribution of population trends across biomes suggests that global biodiversity maps might obscure local-scale heterogeneity and thus hinder conservation (Wyborn & Evans, 2021, but see Schmidt-Traub, 2021).

In **Chapter 4**, I quantified the effects of forest loss on population and biodiversity change at sites around the world. My hypothesis was there would be greater population and biodiversity change when big forest loss events had occurred during the temporal span of each time series, because they impact resource and habitat availability (Elahi et al., 2015; Newbold et al., 2015; Sax & Gaines, 2003). As seen in **Chapter 2**, these sites represented a range of global change conditions which were then reflected in the heterogeneous forest loss impacts I detected on species' populations and the biodiversity of ecological assemblages (**Chapter 4**). I found that the effects of forest loss on changes in population abundance and species richness were up to three times more negative in the tropical regions, whereas across the rest of the planet there was a balance of positive and negative effects (**Chapter 4**). Additionally, when forest loss occurred in forest-dominated areas, there were nearly twice as many population declines as there were in intact forest habitats. My results highlight that the landscape context of biodiversity monitoring sites is key in interpreting detected trends.

3. The magnitude and pace of global change impacts on biodiversity varies across the vertebrate tree of life.

Discovering common patterns of change across organisms from the same taxa is one of the cornerstones of macroecology and biogeography (Dornelas et al., 2019; McGill, 2019). Certain taxa, like amphibians, have been found to be relatively vulnerable to diseases, climate change and anthropogenic disturbance (Hof et al., 2011; Jetz & Pyron, 2018). In **Chapter 3,** I found that across six vertebrate taxa — birds, mammals, reptiles, amphibians, sharks and bony fishes — amphibians were the only taxon experiencing net declines in abundance over time. I had additionally hypothesised that such declines would be clustered for species that share a closely related evolutionary history and are vulnerable to similar threats (González-del-Pliego et al., 2019). Surprisingly, across the phylogenies of amphibians, but also reptiles and birds, I found that evolutionary relatedness did not explain variation in abundance trends over time. However, the data rarely included more than three separate populations from the same species and a broader population sampling might reveal more phylogenetic patterns. The lack of phylogenetic patterning could relate to the distribution of global change across sites with population monitoring (**Chapter 2**) as both closely and distantly related species are likely exposed to a suite of global change drivers (Howard et al., 2020; Isaac & Cowlishaw, 2004; Maxwell et al., 2016; Tulloch et al., 2015). Particularly, if species have evolved through niche divergence, versus niche conservatism, then their resource and habitat requirements, and their sensitivity to threats, might differ, despite close evolutionary relatedness (Ahmadzadeh et al., 2013; Buckley et al., 2010; Pearman et al., 2010; Wiens et al., 2010). Local-scale changes in population abundance might thus be decoupled from the likelihood of evolutionary extinction on a planetary scale (Brook et al., 2006; Fritz et al., 2009; Maxwell et al., 2016; Pereira et al., 2012).

I also explored how the impacts of forest loss on population and biodiversity change vary across different vertebrate and invertebrate taxa (**Chapter 4**). My hypothesis was that species' traits would moderate the effects of forest loss on biodiversity, creating taxonomic patterns. I did not detect differences in the trends of different taxa following reductions in forest cover (**Chapter 4**). However, cross-taxa differences do not always relate only to broad classifications like order or class and can instead be more linked to life history traits of different species. In a *post-hoc* test of temporal lags between big forest loss events and population and biodiversity change, I found the greatest lags for groups with longer generation times, like trees, larger birds and mammals (**Chapter 4**). Temporal lags need to be incorporated in biodiversity scenarios that currently assume constant rates of biodiversity change over time to fully capture the impact of global change on species (IPBES, 2019; Isbell et al., 2019).

4. Rarity cannot explain the heterogeneous trends of population change observed across taxa and at sites around the world.

Species' vulnerability to global change is related to metrics like geographic range, mean population size and habitat specificity, which together capture a continuum from rarity to commonness (Isaac & Cowlishaw, 2004; Newbold et al., 2018; Rabinowitz, 1981). My prediction was that the rarity status of vertebrate species would be related to their abundance trends over time, with more declines for rarer species. Surprisingly, I found that rare species (those with smaller geographic ranges, smaller mean population sizes and narrower habitat specificity) were not more likely to decline in abundance over time than common species (**Chapter 3**). Species' IUCN Red List status, which is determined across the species' range, was similarly unrelated to the abundance trends of individual populations. This decoupling further highlights the heterogeneity in local-scale population trends. My findings demonstrate that common species should not be overlooked in conservation and reinforce the importance of monitoring species locally, regardless of their global status.

Rarity metrics could be interacting with global change drivers and together influencing species' abundance (Newbold et al., 2018; Williams & Newbold, 2021). To test this interaction in the context of vertebrate species and forest loss, in **Chapter 4** I explored whether species with smaller geographic ranges, smaller mean population sizes and narrower habitat specificity have more negative abundance trends when forest cover is reduced. I found that regardless of whether species were rare or common, they experienced the full spectrum of forest loss effects (**Chapter 4**). Rarity and commonness were poor predictors of population responses to forest loss over time. Species are frequently exposed to more than one global change driver, for example to both climate change and forest loss simultaneously. As a result, species' abundance could be negatively affected by one driver (*e.g.*, forest loss) and positively affected by another (*e.g.*, climate warming), producing complex interactions and heterogeneous trends in the planet's biodiversity (Bowler et al., 2018; Vinebrooke et al., 2004; De Laender, 2018; IPBES, 2019).

5. **The effects of global change drivers on population and biodiversity change are rarely unidirectional and instead produce a combination of gains and losses.**

Global change drivers like land-use change, climate change and human exploitation of natural resources influence the habitat and persistence of Earth's biodiversity (IPBES, 2019). Such interactions are most often hypothesised to have negative effects on the abundance of individual species' populations and the richness and composition of entire ecological communities (IPBES, 2019). In Chapter 4, I expected that forest loss would be correlated with population declines and biodiversity loss. I focused on large reductions in forest cover that occurred over the duration of population and biodiversity time series from around the world. I found that after peak forest loss, declining populations declined at even greater rates. In contrast to my expectations, my results also showed that increasing populations increased more rapidly following forest loss, leading to an amplification of both positive and negative change (**Chapter 4**). Forest loss intensified losses in species richness, but not in species richness gains (**Chapter 4**). In around 35% of studied time series, species turnover was higher following a decline in forest cover (**Chapter 4**). My findings of both positive and negative population and biodiversity trends associated with forest loss highlight that to accurately predict how global change will impact biodiversity in the future, we need to allow predictive models and scenarios to include biodiversity gains as well as losses.

Different magnitudes of forest loss occurred across the sites represented by population and biodiversity time series (**Chapter 1**). The influence of the landscape context of forest loss is likely important, because the same amount of forest loss could produce very different ecological impacts at different sites (Betts et al., 2017, 2018). For example, forest loss might reduce the total amount of forest in an area, without dramatically altering species richness, alternatively if the forest that was lost was the last remaining patch of a particular habitat in a region, species might disappear locally. Changes in dominant habitat type were rare in the locations represented in the Living Planet and BioTIME time series (< 5% of time series, **Chapter 4**), in line with the temporal mismatch between the intensity of global change and locations where biodiversity monitoring occurs (**Chapter 1**). However, when habitat transitions did occur, for example from primary forests to human-dominated uses, there was high compositional turnover and newly colonising species frequently replaced over 50% of the existing species (**Chapter 4**).

Global change drivers like forest loss can have both immediate as well as temporally delayed effects on species' populations and biodiversity. In addition to Key finding 3, I used a *post-hoc* analysis to examine whether lag times for abundance and species richness declines were shorter than for gains. I found that lags were similar across gains and losses in population abundance and species richness, suggesting that positive and negative changes in populations and ecological assemblages are occurring at similar paces (**Chapter 4**). The simultaneous occurrence and pace of extinctions and colonisations at local scales can contribute to the reported trends of no net changes in total abundance and species richness detected in global data syntheses (Blowes et al., 2019; Dornelas et al., 2014; Jones & Magurran, 2018).

Together, my findings demonstrate that global change drivers are influencing temporal trends in biodiversity in both positive and negative ways. Instead of a common directional response in species' abundance, species richness and turnover, I found a wide distribution of biodiversity gains and losses, some of which can take decades to become apparent in monitoring data. The mix of immediate and delayed changes in biodiversity highlights the importance of long-term ecological monitoring that can capture the temporal dynamics of species and assemblages in continuously shifting landscapes. Incorporating temporal estimates of the full spectrum of biodiversity change, not just the extreme declines or increases, in scenarios of shifts in the Earth's biota is important to ensure a representative picture of how the planet is changing in the Anthropocene.

In the sections that follow, I discuss the possible mechanisms behind the heterogeneous biodiversity responses to global change that I documented in my thesis, with a focus on interactions between multiple global change drivers. I then consider the implications of my thesis findings for ecological monitoring, biodiversity assessments and scenario development. Finally, I recommend directions for future research and conclude by summarising the new insights gained from my thesis and how they advance the field of global change ecology.

5.2 Possible mechanisms behind heterogeneous biodiversity responses to global change

Global change is reshaping the planet and in response, biodiversity is shifting in varying ways, including declines, gains and stable trends (IPBES, 2019). Declines of primary forest cover have been linked with biodiversity loss (Betts et al., 2017), but also with amplification of both gains and losses in biodiversity (Chapter 4). Climate warming has increased plant species richness on mountain summits (Steinbauer et al., 2018), but when looking across different plant, vertebrate and invertebrate taxa, has had weak effects on richness and abundance in terrestrial ecosystems (Antão et al., 2020). At tropical latitudes, greater exposure to climate change for species living closer to their upper thermal limits corresponds with increased physiological constraints (Deutsch et al., 2008; Sunday et al., 2011). Habitat fragmentation has similarly had mixed effects on biodiversity, including no detected effects as well as biodiversity increases (Fahrig, 2017). Although variation in the impacts of global change drivers on biodiversity is common, understanding how and why this mix of ecological responses arises has remained largely unquantified.

There are several, likely interacting factors, that could explain the heterogeneous biodiversity responses to global change observed at sites around the world. First, species have different traits, allowing some to thrive in a given set of environmental conditions while others perish (Chichorro et al., 2018; Poff, 1997; Spooner et al., 2012; Verberk et al., 2013). Large-scale biodiversity syntheses usually combine data on hundreds to thousands of different species and as a result, when testing the effects of global change drivers, the data will likely include species with both positive, negative or null responses to the specific type of change. Second, natural ecological processes like community self-regulation (Gotelli et al., 2017), local extinction and colonisation (Hanski, 1998), and population cycles (Krebs & Myers, 1974) can produce a mix of positive, negative and stable trends, regardless of global change. Biodiversity is not static and thus, the impacts of global change drivers should be evaluated against a baseline of naturally changing biodiversity (Dornelas et al., 2013). Third, species and ecological assemblages are usually simultaneously exposed to multiple types of global change, creating cumulative effects (Burton et al., 2014; Christensen et al., 2006; Crain et al., 2008; Vinebrooke et al., 2004). These cumulative effects could be synergistic (the drivers together have greater effect on biodiversity than the sum of their effect), antagonistic (one driver has positive effects, the other has negative effects, producing no net impact), or additive (the effects of the multiple drivers represent the sum of their individual effects, (Vinebrooke et al., 2004; Darling et al., 2010; Radinger et al., 2016; Rillig et al., 2019, 2021). The magnitudes and combinations of global change vary around the world (Blowes et al., 2019; Halpern et al., 2015), creating a wide distribution of biodiversity change, likely moderated by species traits, natural ecological processes and their interactions with different global change drivers (Betts et al., 2017; De Frenne et al., 2013; IPBES, 2019; Isaac & Cowlishaw, 2004; Mantyka-Pringle et al., 2012; Suggitt et al., 2018).

5.3 Interactions between global change drivers arising from simultaneous exposure to multiple types of environmental change

Ecosystems and the species that form them are usually simultaneously exposed to a suite of global change drivers, such as climate change, human use, population density, pollution and invasion pressure. When conducting data syntheses of observational data, as I did in my thesis, it is very likely that multiple types of environmental change have occurred across the duration of the different time series that were part of the analyses. In **Chapter 4** I found that after peak forest loss, there were negative, positive and stable trends in species' populations and assemblage biodiversity. This heterogeneity could be driven by interactions between forest loss and other global change drivers present across the sites that I studied. For example, land-use change, specifically forest clearing, can lead to a loss of cooler microhabitats across the landscape (De Frenne et al., 2019), thus making warm-intolerant species more vulnerable to climate warming (Betts et al., 2018; De Frenne et al., 2013; González del Pliego et al., 2016; Lawrence & Vandecar, 2015; Nowakowski et al., 2017; Suggitt et al., 2018). In contrast, rising temperatures can facilitate forest growth by lifting physiological constraints on tree seedling growth across latitudes, thus accelerating secondary succession (Fridley & Wright, 2018). Warming and alterations in precipitation regimes have also been linked with both increases and decreases in species' vulnerability to land-use change (Mantyka-Pringle et al., 2012). Such interactions among global change drivers could produce antagonistic, additive and/or synergistic effects on population and biodiversity change (Figure 5.2).

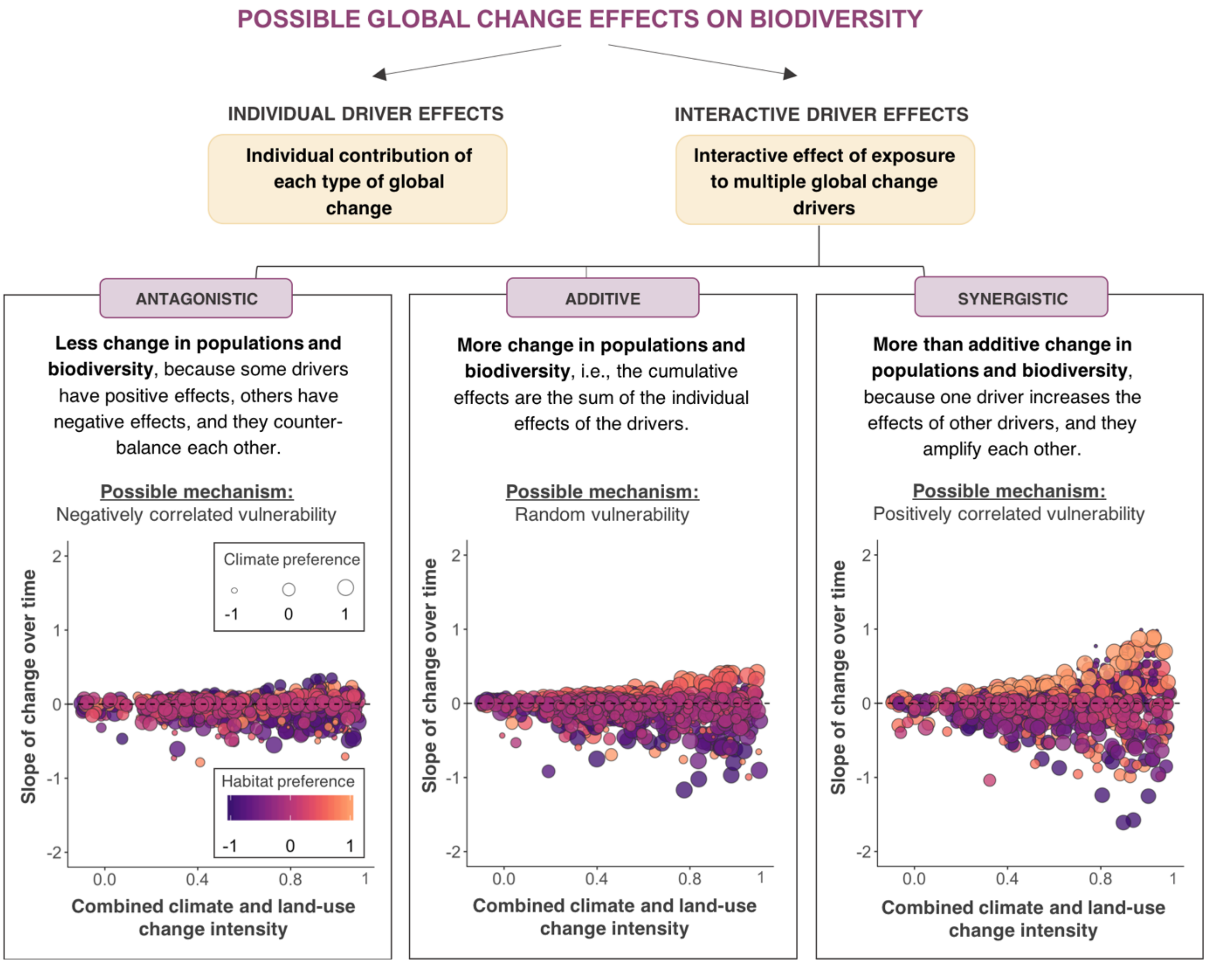

Figure 5.2. Exposure to global change drivers alters ecosystems in a variety of ways, and the possible interactive effects of multiple types of drivers can be antagonistic, additive or synergistic. One possible mechanism through which such interactions arise is the possible correlation among species traits' and their vulnerability to different types of global change. Bubble plots show outputs of simulation models, where each site experienced different amounts of climate and land-use change, and species responses were regulated based on their climate and habitat preferences. When

species vulnerability to the two drivers is correlated, I found more change over time (synergy), whereas if a species responds positively to land-use change, but negatively to climate change, I found less change in population abundance over time (antagony). Figure based on Daskalova *et al.* (in prep.) “Interactive effects of multiple global change drivers on population and biodiversity change across the marine and terrestrial realms” (see Appendix 1.7 for abstract).

5.4 Implications of thesis findings for ecological monitoring, biodiversity assessments and scenario development

The key finding of my thesis is that there is a lot of nuance around the population and biodiversity change that is driven by different types of global change around the world. Such heterogeneity has three key implications for ecological monitoring, biodiversity assessments and scenarios for future shifts in the Earth’s biota.

1. The mix of immediate and delayed global change impacts on biodiversity (**Chapter 4**) highlights the value of long-term ecological monitoring to capture the temporal dynamics of how ecosystems are changing and accurately reflect that in policy and conservation. Often monitoring stops once a species has stabilised or once a species has become locally extinct, but continued monitoring will produce more accurate and precise estimates of biodiversity change. In addition to continuing existing monitoring, my research suggests a new way to target the establishment of future monitoring by aiming to fill in the gaps in global change space (**Chapter 2**). To understand ongoing biodiversity change and create representative scenarios for future trajectories, we need data that span not only geographic and taxonomic space, but also the variation of global change impacts around the world. Establishing long-term ecological monitoring sites that together form a network that is representative of the different magnitudes and combinations of global change can help bridge small-scale observational studies and planetary-scale scenarios and international policies. If ample funding and research effort is dedicated to

monitoring biodiversity in a more representative way, we are more likely to make informed, evidence-driven decisions and achieve better conservation outcomes.

2. We need to statistically account for the structures and properties of biodiversity data to produce better estimates of how species and ecological assemblages are changing under the impacts of global changes. The rise of open-access data in ecology has facilitated large-scale syntheses across realms, biomes and taxa, but such data are also associated with biases, pseudoreplication and correlation over time and space. Analytical methods in ecology are continuously advancing, allowing us to better reflect data hierarchy, structure and biases in statistical models. In **Chapter 4**, I developed a method to incorporate historical forest loss baselines when analysing the effects of forest loss and population and biodiversity change. In a side project to this thesis, I showed that after accounting for temporal pseudoreplication in biodiversity data whereby records from the same year are correlated, significant trends in biodiversity change over time can become non-significant (Daskalova et al., 2021). Concepts like pseudoreplication, historical baselines and geographic or taxonomic bias and spatial and temporal autocorrelation are well-established in ecology (Boakes et al., 2010; Diniz-Filho et al., 2003; Rousset & Ferdy, 2014; van de Pol & Wright, 2009; Wolkovich et al., 2014) and we can improve biodiversity assessments by incorporating them into statistical analyses. By advancing data syntheses methods and developing improved ways to quantify global change space and incorporate historical baselines, my research provides strong evidence that can be used in assessments like those by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

3. The context of findings from large-scale biodiversity syntheses like the ones in my thesis is key for interpreting and using such studies as scientific evidence in conservation and policy-making. Over the four years of my PhD there were numerous debates centred around biodiversity change. From the trends of insects (Crossley et al., 2020; Daskalova et al., 2021; Didham et al., 2020; Hallmann et

al., 2017; Seibold et al., 2019; Thomas et al., 2019; van Klink et al., 2020) to the value of global conservation priority maps (Jung et al., 2021; Schmidt-Traub, 2021; Tulloch et al., 2015; Wyborn & Evans, 2021), the impacts of habitat fragmentation (Fahrig, 2017; Fahrig et al., 2019; Fletcher et al., 2018; Haddad et al., 2015), and the role of tree planting in mitigating climate change (Bastin et al., 2019; Grainger et al., 2019; Lewis et al., 2019; Veldman et al., 2019), these discourses have questioned the status-quo of global change ecology and though their topics vary, a common theme has emerged. Without context, a summary indicator or a mean of a distribution of trends risks being misused or miscommunicated by the media. My global change space framework (**Chapter 2**) suggests a way to put the findings of biodiversity syntheses in perspective by quantifying the types of locations represented by the underlying data in terms of human use, climate change and other types of disturbance. Monitoring the entirety of Earth's biodiversity is not achievable but by quantifying and communicating the ecological context of the data we do have, be it in terms of the global change space occupied (**Chapter 2**), types of sites surveyed (**Chapter 2**) or the types of species monitored (**Chapter 3**), we can increase the value and use of the millions of open-access biodiversity records.

5.5 Directions for future research

5.5.1 Land abandonment as an underexplored driver of change

Global change drivers like conversion of natural habitats to agricultural land and climate warming are the most frequently studied types of global change (de Chazal & Rounsevell, 2009; Mazor et al., 2018), but other types of anthropogenic pressure are increasingly altering ecosystems too (IPBES, 2019). The less-studied extreme of land-use change, land abandonment, is set to outpace the rates of land conversion in the next 50 years (Figure 5.3, Baumann et al., 2011; Li & Li, 2017), yet its ecological consequences remain poorly understood, particularly at broader scales. There is evidence of increased biotic homogenisation following loss of traditional farming practices and a decline in human density in rural areas (Amici et al., 2015). In terms of species' abundance in areas with land abandonment, there are findings of both increases and decreases for bird species

(Herrando et al., 2014). For herbaceous plants, land abandonment can lead to a decline in species richness because of an increase in tree cover density that limits nutrients and light (Amici et al., 2015). During a research internship at the German Centre for Integrative Biodiversity Research (iDiv), I developed a project to quantify the amount of abandoned land has changed between 2006 and 2018 across the EU and the resulting shifts in vegetation cover and species' abundance (see Appendix 1.2 for abstract). I found that there were nearly equal instances of abandoned land transitioning to forests as there were of abandoned land remaining as grasslands. Overall, the abundance of bird and mammal species was higher in areas with land abandonment, particularly for carnivorous birds and herbivorous mammals (Figure 5.3). The frequency of land abandonment is projected to keep increasing in the next century (Li & Li, 2017). Land abandonment is a key part of the global change reshaping the planet's biota and thus should be incorporated into biodiversity assessments and scenarios (Beilin et al., 2014; Katayama et al., 2015; Queiroz et al., 2014).

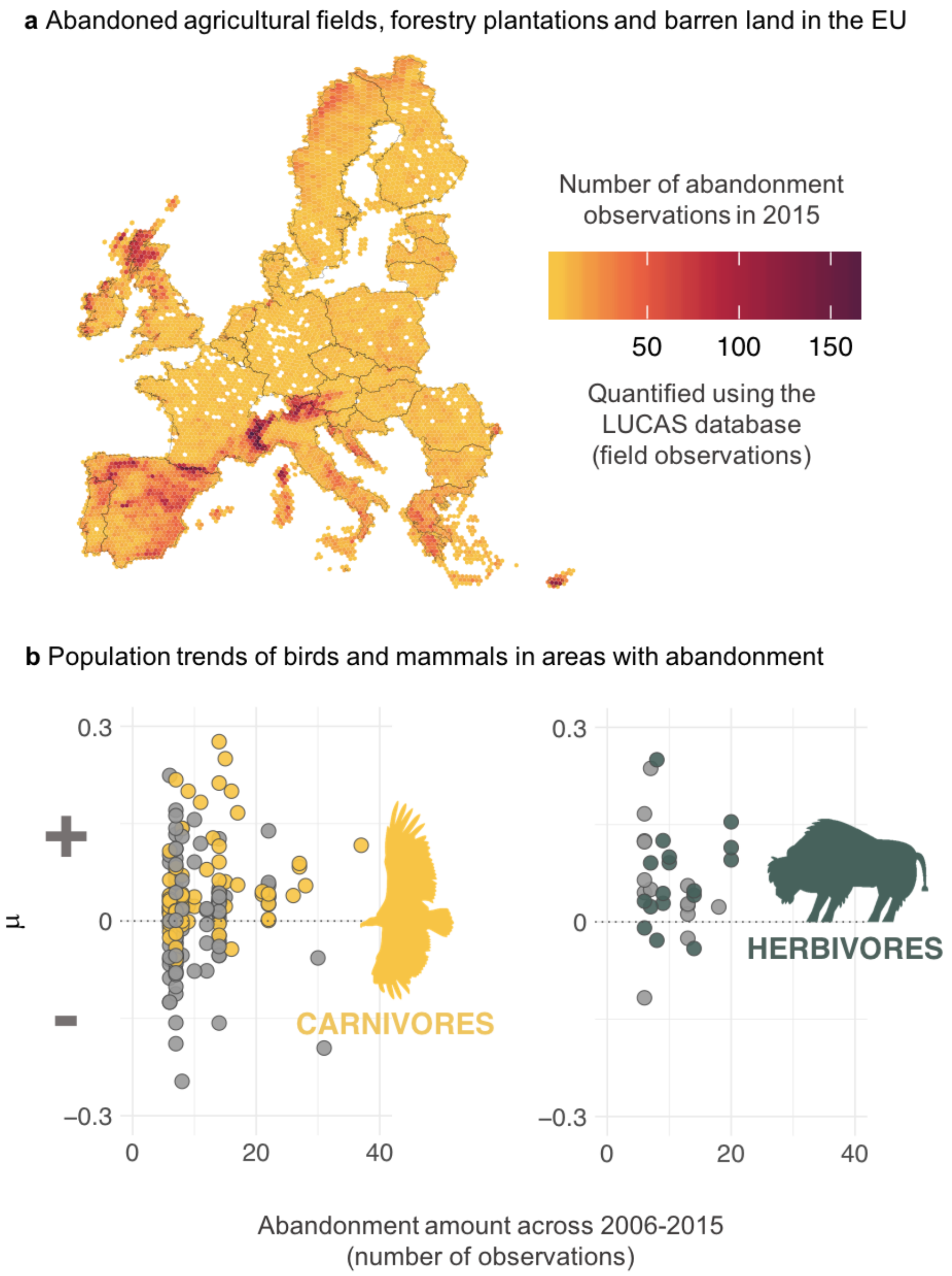

Figure 5.3. Land abandonment occurs across Europe, influencing the population abundance of birds and mammals. Map on **a** shows the number of *in-situ* (field) observations of land abandonment during the EU-wide monitoring done for the LUCAS database. White areas on the map show places with no abandonment. Points on **b** show population trends (μ values from state-space models) of birds and mammals. Grey points indicate non-carnivorous birds and non-herbivorous mammals, whereas yellow shows

carnivorous birds and teal shows herbivorous mammals. Population increases were more likely for carnivorous birds. For mammals, there were more increases than declines in areas with abandonment, but diet did not explain heterogeneity in trends. Figure based on Daskalova and Pereira*.* (in prep.) “Population change across Europe’s land abandonment hotspots” (see Appendix 1.2 for abstract).

5.5.2 Simultaneous exposure to multiple types of global change

Understanding how different global change drivers together influence the Earth’s biodiversity is a key priority for conservation and both international and national policy (IPBES, 2019; Mazor et al., 2018; Schmidt-Traub, 2021). The cumulative and potentially interactive effects of different stressors are frequently the focus of experimental and manipulative studies (Birk et al., 2020; Blake & Duffy, 2010; Townsend et al., 2008) but extending such research to observational data has been challenging. Cumulative and interactive effects have remained poorly defined, but there are recent suggestions for unified frameworks for defining the effects of multiple global change drivers (Orr et al., 2020; Rillig et al., 2021, Figure 5.2). A lack of data with high enough temporal and spatial resolution, as well as difficulties associated with isolating confounding factors (De Palma et al., 2018), have hindered large-scale syntheses of biodiversity change and multiple types of global change. Thanks to recent advances in remote sensing and statistics as well as the rise of open-access data in ecology, we can now bring together diverse data streams (*e.g.*, biodiversity time series, species’ traits, magnitudes of global change) to better understand biodiversity change during a time of complex changes in ecosystems around the world. For example, we now know that changes in climate influence biodiversity responses to land-use change (Williams & Newbold, 2020). Future research can explore the interactions not only between climate change and land-use change, but also among other important, yet understudied drivers like pollution, abandonment and human depopulation (Figure 5.3), marine exploitation and the spread of invasive species.

In a collaboration with Diana Bowler, Anne Bjorkman, Amanda Bates, Shane Blowes, Laura Antão, Anne Magurran, Maria Dornelas and Isla-Myers-Smith, I am building on my PhD research and particularly Chapter 4 to explore how multiple drivers influence population and biodiversity change. I am focusing on cumulative driver intensity (combined intensities of human use, climate change, human population density, pollution and invasive species pressure) and the possible interactive effects of human use and climate change on biodiversity trends. From my preliminary analyses, I have found that higher cumulative driver intensity does not correlate with higher magnitudes of population change, richness change or turnover in neither the terrestrial realm, nor the marine realm. My findings further showed that interactive effects between human use and climate change were most often synergistic in tropical and polar zones across both land and sea. At those latitudes, higher intensity of both human use and climate change was associated with greater population and biodiversity change. Such interactive effects were lacking from temperate regions. This project is pre-registered on the Open Science Framework (https://osf.io/qjr27/?view_only=56d98233baa047fcb2d5fe554103f01e) and I am continuing to work with our co-authorship team to explore the effects of multiple drivers on biodiversity change in greater detail. By showing how human activities, both singly and in combination, are altering biodiversity, this project could contribute to filling key research gaps for policy and global biodiversity assessments (IPBES, 2019; Mazor et al., 2018).

5.5.3 Landscape context of biodiversity change

Linking local-scale estimates of biodiversity change with landscape-scale ecological processes and environmental variation can provide insights into the mechanisms of the ongoing reorganisation of ecological communities (de Chazal & Rounsevell, 2009; De Palma et al., 2018; Elmhagen et al., 2015; IPBES, 2019, Chapter 4, Figure 5.4). Much of the knowledge we have about how biodiversity is being altered by global change comes from data collected at small spatial scales, bringing issues of scale and precluding us from understanding processes that occur at larger scales, like species colonisation and extinction (Batary et al., 2011; Chase et al., 2018, 2019; Hanski, 1998, Chapter 1 section 1.5). Additionally, by focusing on quadrats, plots or small study areas, we might be excluding species which occur in close proximity to the sampling areas but not within them. Thus, biodiversity monitoring undersamples the actual biodiversity represented within landscapes. This landscape-scale diversity where species which are not found within a given survey area but could potentially colonise the habitat if the conditions become suitable is sometimes referred to as “dark diversity” (Lewis et al., 2016; Pärtel, 2014; Pärtel et al., 2011; Trindade et al., 2020). Dark diversity is also a term used to mean species absent from a study site but present in the surrounding region and potentially able to inhabit particular ecological conditions (Partel et al. 2011). Here, I refer to the diversity in the species pool that is absent in sampling plots.

During my PhD, I established a project with the International Tundra Experiment network and conducted my own Arctic fieldwork across three summers from 2017 – 2019 (Rixen et al., 2019) to test how landscape-scale biodiversity influence measured biodiversity trends (Appendix 1.1), I extended the dark diversity concept to include a temporal element (Figure 5.4). First, I quantified how many plant species occur at the landscape-scale (within 100-meter radius of the 1x1 m monitoring plots) across 15 sites in the alpine and Arctic tundra. In this study, I defined as dark diversity the species which are part of the species pool but have never been recorded inside the long-term monitoring plots over the duration of plot-scale surveys at each site (between 10 and 20 years). I found that species pool size varied by an order of magnitude, from around 10 species to over a hundred (Figure 5.4). The amounts of dark diversity were similarly variable, suggesting that there is colonisation potential and over time, new species might become present in the monitoring plots (Figure 5.4). These findings demonstrate that though all of these tundra sites would be classified as from the same biome in a global analysis, they each have different landscape contexts and varying temporal dynamics when it comes to species extinction and colonisation. I am continuing to explore biodiversity change through collaborative data synthesis among the ITEX network. To quantify landscape-scale biodiversity and better understand the impacts of localised biodiversity change on larger-scale biodiversity trends, future research can link biodiversity data with information on microclimate and landscape heterogeneity (sometimes termed “geodiversity”), species pool size and dark diversity (Alahuhta et al., 2020; De Frenne et al., 2013, 2013; Hjort et al., 2012; Lembrechts et al., 2020; Parks & Mulligan, 2010; Trindade et al., 2020; Zellweger et al., 2020).

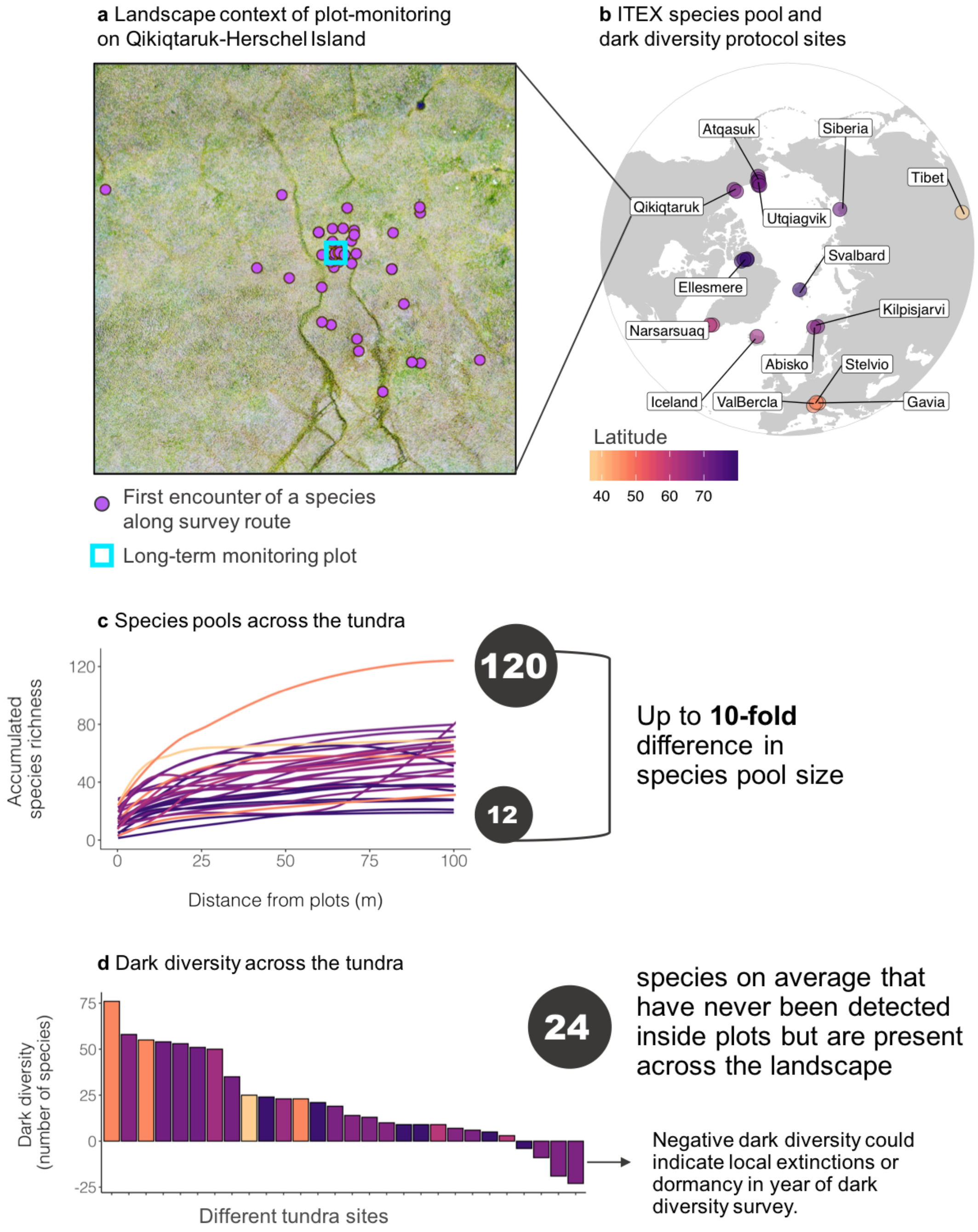

Figure 5.4. Species pool sizes of vascular plants vary across the tundra and there is high dark diversity around the long-term monitoring plots part of the International Tundra Experiment (ITEX) network. Plot **a** shows the landscape on Qikiqtaruk-Hershel Island (derived from drone images) together with the locations of the first individual of each new species encountered during the species pool survey. The same protocol was also conducted on 14 other sites (plot **b**). Accumulated species richness (plot **c**) was calculated over a 100-meter radius, with the centre of the middle

1x1 m long-term monitoring plot as the starting point for the survey. Dark diversity (**d**) was defined as the number of species which occur within 100 meters of the long-term monitoring plots but have not been detected inside the plots across the duration of the monitoring. Figure based on Daskalova et al. (in prep) “Plant species pools and dark diversity across the tundra biome” (see Appendix 1.1 for abstract).

5.6 Conclusion

Global change drivers are reshaping biodiversity around the world, creating a mix of gains, losses and stable trends (IPBES, 2019). Such shifts in the Earth’s biota influence the functioning of ecosystems around the world and the services they provide for humanity (Benayas et al., 2009; Elmhagen et al., 2015; Isbell et al., 2011; Rosa et al., 2020; Smale et al., 2019). Understanding how and why biodiversity is changing over time, around the world and across the tree of life is key for conservation decision-making and can help link local-scale changes with global-scale policies and scenarios for the future (Agardy, 2005; Geijzendorffer et al., 2016; Mazor et al., 2018). The upcoming Convention on Biological Diversity’s Post-2020 Global Biodiversity Framework will set the direction for international policy and goals in the coming decade. Quantifying biodiversity change over time can help track short-term progress towards conservation targets and improve long-term scenarios for plants, animals and other organisms around the planet (Di Marco et al., 2019; Nicholson et al., 2019; Pereira et al., 2020; Rosa et al., 2020).

The aim of my thesis was to determine how population and biodiversity change varied across taxa, realms and sites around the world. Each of the over 50,000 locations included in my PhD research represents a diversity of species, each with its own traits, threats and vulnerabilities, and multiple environmental changes brought by the accelerating global change in the Anthropocene. Across all of them, a common theme of heterogeneous impacts of global change on both short and long timescales emerged. Biodiversity projections often assume that the impacts of global change are constant over time and frequently extrapolate estimates from space-for-time data to project future trajectories of change. Broadly, my thesis findings highlight the need to incorporate the full distribution of global change impacts on biodiversity into future scenarios, including lagged and temporally-variable shifts in species' abundance, species richness and community composition.

My key findings were: 1) Biodiversity datasets span different gradients of the global change spectrum, helping us to interpret heterogeneous results (**Chapters 2**, **3** and **4**). 2) Ecosystems at different latitudinal bands around the world occupy different parts of the global change space, providing context for biogeographic patterns in population and biodiversity change (**Chapters 2, 3** and **4**). 3) The magnitude and pace of global change impacts on biodiversity varies across the vertebrate tree of life (**Chapters 3** and **4**). 4) Rarity cannot explain the heterogeneous trends of population change observed across taxa and at sites around the world (**Chapters 3** and **4**). 5) The effects of global change drivers on population and biodiversity change are rarely unidirectional and instead produce a combination of gains and losses (**Chapter 4**). My PhD research indicates that just as ecosystems and the biodiversity within them are complex, so are the drivers of biodiversity change in the Anthropocene. My findings suggest that by embracing the nuance around biodiversity change following land-use change, climate change and other transformations of the planet and by reflecting this nuance in biodiversity assessments and conservation actions, we will better protect global biodiversity under increasing anthropogenic pressure.

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Appendices

Appendix 1. Supporting information for Chapter 1. Introduction.

Appendix 1.1 Abstract for "Species pools and dark diversity across the tundra biome" project.

Title: Dark diversity in the tundra: the source of future biodiversity change?

Authors: Gergana N Daskalova, Isla Myers-Smith, Christian Rixen, Anne Bjorkman, Toke Høye, Mats Björkman, Ingibjörg Svala Jónsdóttir, Isabel Barrio, Sonja Wipf, Greg Henry, Elise Gallois, Zoe Panchen, Sofie Agger, Anne Tolvanen, Hans Cornelissen, Rien Aerts, Jake Harris, Nicoletta Cannone, Petr Macek, Francesco Malfasi, Signe Normand

Abstract: Tundra plant communities are responding as the climate continues to warm, with shifts in community composition and traits observed across many tundra sites. However, from where across the landscape new species come and how the larger species pool influences local-scale biodiversity change remains unknown. Traditional plant surveys often capture scales of only several square meters, leaving many unmonitored species that by chance could be absent in small plots. This so-called "dark biodiversity" could be a hidden source of future plant biodiversity change. Here, we bring together decades of monitoring observations with the first findings from the International Tundra Experiment Species Pool Protocol to reveal the magnitude of dark biodiversity in tundra ecosystems and the links between local compositional changes and the larger species pool.

Across 15 sites including over 30 vegetation types, we found that on average there are 30 species present within 100 m radius of long-term monitoring plots, which have never been recorded inside the plots. The amount of dark diversity varied considerably among sites (sd = 21 species), as did the rate of species accumulation with distance across different landscapes (Figure 5.4 in Chapter 5). We are currently integrating the ground-based species pool and plot-scale community composition data with information on topography and microhabitats derived from aerial drone imagery. This combination will allow us to determine which parts of the tundra landscape this dark diversity occupies – environmentally similar or more variable habitats, or the warmest microclimates. Understanding the relationships between the species pool, dark diversity and plot-scale diversity can help us find the hotspots of plant biodiversity across tundra landscapes and will improve predictions of future changes in the richness and composition of tundra ecosystems with warming.

Appendix 1.2 Abstract for "Land abandonment and population change in Europe" project.

Title: Accelerating land abandonment is reshaping ecosystems and biodiversity across Europe

Authors: Gergana N. Daskalova, Henrique M. Pereira

Abstract: Land-use change is altering terrestrial ecosystems globally, but most of our knowledge focuses on intensification, leaving the effects of abandonment unknown. We asked how land abandonment in Europe varies over space and time, what the dominant land cover trajectories are following abandonment, and how vertebrate population abundance changes in areas with land abandonment. We found that land abandonment has nearly doubled across Europe over the last decade, leading to shifts in land cover and ecosystem structure. In the mid-latitudes (~45-55° N), abandoned land transitioned into grassland and shrublands, while post-abandonment woodlands occurred across the whole continent. In areas with abandonment, we found more net population increases than in places without abandonment, particularly for herbivorous mammals and carnivorous birds (Figure 5.3 in Chapter 5). As urbanisation and rural depopulation are predicted to increase, land abandonment will likely alter habitats and biodiversity on even larger scales and influence the functioning of ecosystems in Europe and beyond.

Appendix 1.3 Abstract for "Methods to account for temporal pseudoreplication in biodiversity time series analysis" project.

This project has been published as:

Daskalova, G. N., Phillimore, A. B., & Myers-Smith, I. H. (2021). Accounting for year effects and sampling error in temporal analyses of invertebrate population and biodiversity change: a comment on Seibold et al. 2019. *Insect Conservation and Diversity*, *14*(1), 149-154. **https://doi.org/10.1111/icad.12468**

Abstract

1. An accumulating number of studies are reporting severe insect declines. These studies aim to quantify temporal changes in invertebrate populations and community composition and attribute them to anthropogenic drivers.
2. Seibold *et al*. 2019 (Nature, 574, 671–674) analysed arthropod biomass, abundance and species richness from forest and grassland plots in a region of Germany and reported declines of up to 78% between 2008 and 2018. However, their analysis did not account for the confounding effects of temporal pseudoreplication.
3. We show that simply by including a year random effect in the statistical models and thereby accounting for the common conditions experienced by proximal sites in the same years, four of the five reported declines become non-significant out of six tests overall.
4. To place recent estimates of insect trends in a broader context, we analysed invertebrate biomass, abundance and richness from 640 time series from 1167 sites around the world. We found that the average trends across the terrestrial and freshwater realms were not significantly distinguishable from no net change. Shorter time series that are likely most affected by sampling error variance – such as those in Seibold *et al*. 2019 (Nature, 574, 671–674) – yielded the most extreme decline and increase estimates.

5. We suggest that the media uptake of negative trends from short time series may be serving to exaggerate the ‘insect Armageddon’ and could undermine public confidence in research. We advocate that future research uses appropriate model structures to build a more robust understanding of biodiversity change.

Appendix 1.4 Abstract for "Highlighting a balanced view of insect trends" project.

This project has been published as:

Dornelas, M., & Daskalova, G. N. (2020). Nuanced changes in insect abundance. *Science*, *368*(6489), 368-369. https://www.science.org/lookup/doi/10.1126/science.abb6861

Abstract: Drastic declines in insect biomass, abundance, and diversity reported in the literature have raised concerns among scientists and the public (*1–3*). If extrapolated across Earth, biomass losses of ~25% per decade (*1*) project a potential catastrophe developing unnoticed under our noses. The phrase "insect Armageddon" has captured the collective attention and shined a spotlight on one of the most numerous and diverse groups of organisms on the planet. Yet, insects are critically understudied. For example, the BioTIME database (*4*)—a compilation of biodiversity time series—contains records for 22% of known bird species but only 3% of arthropods (the phylum that includes insects and spiders). On page 417 of this issue, van Klink *et al.* conduct a thorough global assessment of insect abundance and biomass trends and paint a more nuanced picture than that predicted by extrapolations (*5*).

References for abstract:

1. C.A.Hallmann *et al.*,*PLOS ONE* 12,e0185809(2017).
2. B. C. Lister, A. Garcia, *Proc. Natl. Acad. Sci. U.S.A*. 115, E10397 (2018).
3. S. Seibold *et al.*, *Nature* 574, 671 (2019).
4. M. Dornelas *et al.*, *Glob.Ecol.Biogeogr*. 27,76(2018).
5. R. van Klink *et al.*, *Science* 368, 417 (2020).

Appendix 1.5 Abstract for “Ecosystem change following mammal reintroductions in Australia” project.

This project has been published as:

Palmer, B. J., Valentine, L. E., Lohr, C. A., Daskalova, G. N., & Hobbs, R. J. (2021). Burrowing by translocated boodie (Bettongia lesueur) populations alters soils but has limited effects on vegetation. *Ecology and Evolution*, *11*(6), 2596-2615. https://doi.org/10.1002/ece3.7218

Abstract: Digging and burrowing mammals modify soil resources, creating shelter for other animals and influencing vegetation and soil biota. The use of conservation translocations to reinstate the ecosystem functions of digging and burrowing mammals is becoming more common. However, in an increasingly altered world, the roles of translocated populations, and their importance for other species, may be different. Boodies (*Bettongia lesueur*), a commonly translocated species in Australia, construct extensive warrens, but how their warrens affect soil properties and vegetation communities is unknown. We investigated soil properties, vegetation communities, and novel ecosystem elements (specifically non-native flora and fauna) on boodie warrens at three translocation sites widely distributed across the species’ former range. We found that soil moisture and most soil nutrients were higher, and soil compaction was lower, on warrens in all sites and habitat types. In contrast, there were few substantial changes to vegetation species richness, cover, composition, or productivity. In one habitat type, the cover of shrubs less than 1 m tall was greater on warrens than control plots. At the two sites where non-native plants were present, their cover was greater, and they were more commonly found on boodie warrens compared to control plots. Fourteen species of native mammals and reptiles were recorded using the warrens, but, where they occurred, the scat of the non-native rabbit (*Oryctolagus cuniculus*) was also more abundant on the warrens. Together, our results suggest that translocated boodie populations may be benefiting both native and non-native flora and fauna. Translocated boodies, through the

construction of their warrens, substantially alter the sites where they are released, but this does not always reflect their historic ecosystem roles.

Appendix 1.6 Abstract for “Upscaling of individual species dynamics to community trends in biodiversity and composition using vegetation change data sets” project.

This project is published as a preprint and is in revision at Ecology Letters.

Staude, I., Pereira, H. M., Daskalova, G. N., Bernhardt-Römermann, M., Diekmann, M., Pauli, H., ... & Baeten, L. (2021). Consistent replacement of small-by large-ranged plant species across habitats. EcoEvoArxiv preprint. https://ecoevorxiv.org/ujky2/

Abstract: The direction and magnitude of long-term changes in local plant species richness are highly variable among studies, while species turnover is ubiquitous. However, it is unknown whether the nature of species turnover is idiosyncratic or whether certain types of species are consistently gained or lost across different habitats. To address this question, we analysed the trajectories of 1827 vascular plant species over time intervals of up to 78 years at 141 sites in three habitats in Europe – mountain summits, forests, and lowland grasslands. Consistent across all habitats, we found that plant species with small geographic ranges tended to be replaced by species with large ranges, despite habitat-specific trends in species richness. Our results point to a predictable component of species turnover, likely explained by aspects of species’ niches correlated with geographic range size. Species with larger ranges tend to be associated with nutrient-rich sites and we found community composition shifts towards more nutrient-demanding species in all three habitats. Global changes involving increased resource availability are thus likely to favor large-ranged, nutrient-demanding species, which are typically strong competitors. Declines of small-ranged species could reflect not only abiotic drivers of global change, but also biotic pressure from increased competition. Our study highlights the need to consider the traits of species such as the geographic range size when predicting how ecological communities will respond to global change.

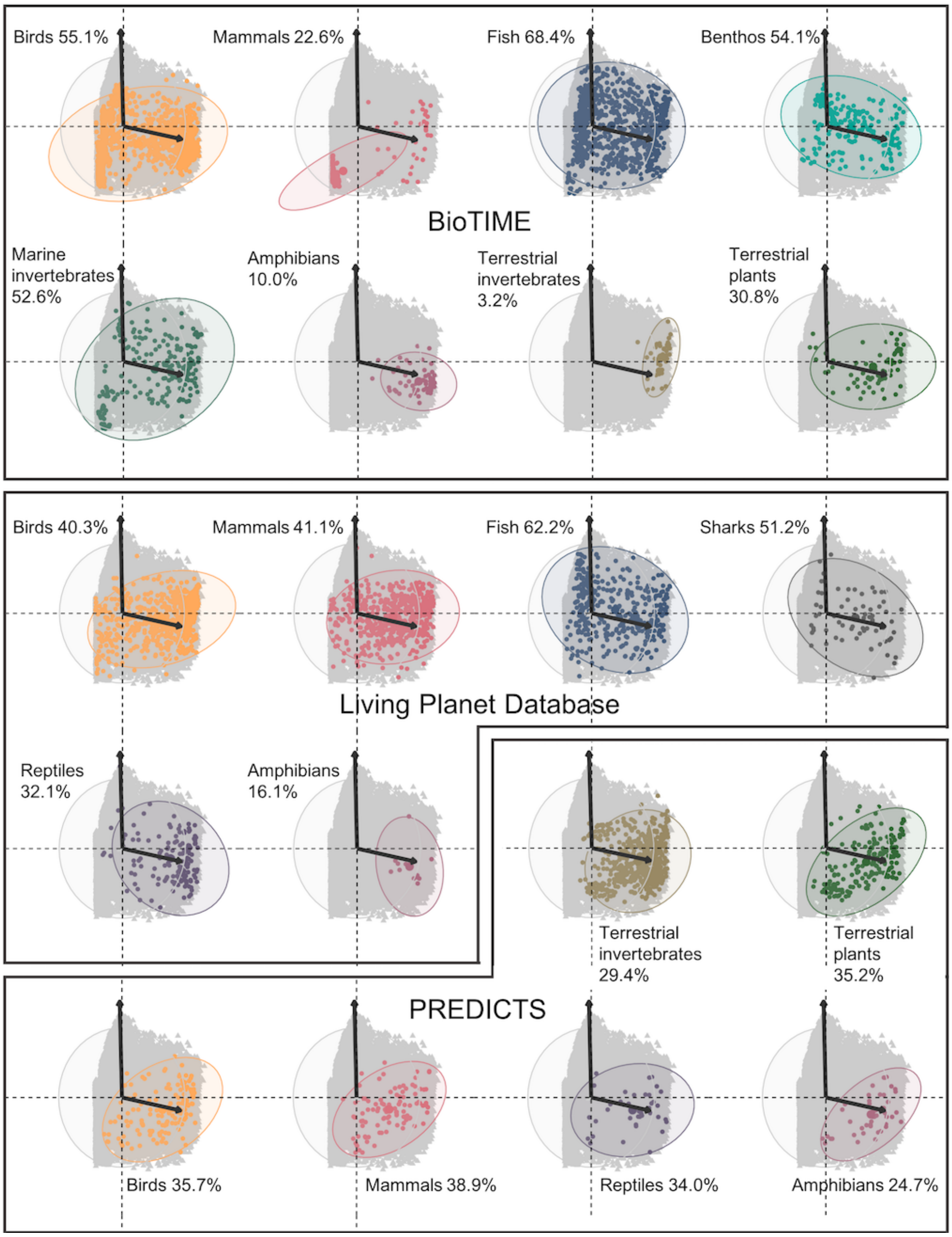
Appendix 1.7 Abstract for "Cumulative effects of global change drivers are stronger at latitudinal extremes". This project is pre-registered on the Open Science Framework (https://osf.io/qjr27/?view_only=56d98233baa047fcb2d5fe554103f01e).

Authors:

Gergana Daskalova, Diana Bowler, Anne Bjorkman, Amanda Bates, Shane Blowes, Laura Antão, Anne Magurran, Maria Dornelas, Isla-Myers-Smith

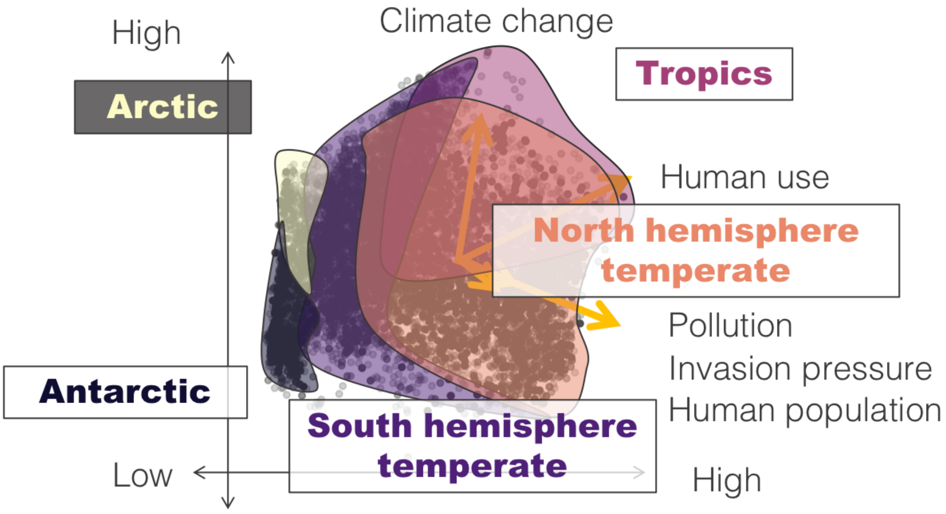
Abstract: Marine and terrestrial ecological communities are under pressure from accelerating global change, yet we lack quantitative attribution of simultaneous exposure to different drivers. We tested the relationships between cumulative intensity of climate change, human use, pollution and invasion risk, and changes in over 7300 species populations and 44 500 communities using the largest available time series databases (Living Planet and BioTIME). Correspondence between global change and population and biodiversity shifts was greater in marine versus terrestrial areas. We found synergistic driver effects in tropical and polar zones across both land and sea, where higher intensity of multiple anthropogenic impacts was associated with greater population and biodiversity change. In contrast, in temperate zones, we found antagonistic effects, whereby drivers act in opposing directions, potentially producing no net population and biodiversity change. By showing how human activities, both singly and in combination, are altering biodiversity, these results could contribute to policy and global assessments.

Appendix 2. Supporting information for Chapter 2. Representation of global change drivers across biodiversity datasets.



Appendix 2.1. Global change representation varies across taxa. Figure shows Principal Component Analysis of the magnitudes of human use, climate change, human population density, pollution and invasion potential across the locations of the Living

Planet, BioTIME and PREDICTS databases, split by taxa, as well as one million randomly sampled locations across the full extent of the globe (in grey). PCA axes omitted for visual clarity. Upwards PCA arrow shows climate change, arrow pointing right shows human population density. Arrows show direction and magnitude of PCA scores. Human use, pollution and invasion potential were correlated with human population density (see Figure S11 in the supplementary information of Bowler et al. 2020). Thus, climate change and human population density together capture the two dominant axes of global change variation. For details on the global change driver layers, see Bowler et al. 2020. Annotations show the percentage overlap between the 95% prediction ellipses covered by random sampling of global change space and the variation in global change sampled by the different databases across taxa.



Appendix 2.2. Ecosystems at different latitudes occupy distinct parts of global change space. Figure shows Principal Component Analysis of the magnitudes of human use, climate change, human population density, pollution and invasion potential. The PCA is based on one million simulated random locations spanning the globe to represent an unbiased sample of the marine and terrestrial surface of the world. Colours indicate different latitudes. Places in the Arctic, for example, are characterised with high climate change and low human use and human population density. The tropics, in contrast, occupy a larger area and thus have more variable global change conditions, including moderate to high human use and moderate to high climate change.

Appendix 2.3. Model outputs for all statistical analyses. Term names starting with "b" refer to fixed effects and sigma indicates the residual variance. Continuous variables (intensities of global change drivers) were scaled between zero and one to make them comparable. I used Bayesian general linear models and I analysed the terrestrial and marine data separately.

Model	**Term**	**Estimate**	**Lower 95% CI**	**Upper 95% CI**	**Rhat**
Terrestrial global change drivers across databases and the world	b_intercept	0.518	0.507	0.528	1.002
	b_samplinglivingplanet	0.070	0.058	0.081	1.001
	b_samplingbiotime	-0.144	-0.157	-0.131	1.002
	b_samplingpredicts	-0.024	-0.038	-0.010	1.001
	b_drivercumulative	-0.109	-0.123	-0.094	1.002
	b_driverhuman_population	-0.379	-0.393	-0.365	1.002
	b_driverhuman_use	-0.113	-0.127	-0.098	1.001
	b_driverinvasions	-0.350	-0.365	-0.336	1.001
	b_driverpollution	-0.290	-0.305	-0.276	1.001
	b_samplinglivingplanet.drivercumulative	0.072	0.056	0.089	1.001
	b_samplingbiotime.drivercumulative	0.391	0.372	0.409	1.002
	b_samplingpredicts.drivercumulative	0.199	0.179	0.218	1.001
	b_samplinglivingplanet.driverhuman_population	0.298	0.282	0.315	1.001
	b_samplingbiotime.driverhuman_population	0.723	0.706	0.742	1.002
	b_samplingpredicts.driverhuman_population	0.568	0.549	0.588	1.001
	b_samplinglivingplanet.driverhuman_use	-0.061	-0.077	-0.044	1.001
	b_samplingbiotime.driverhuman_use	0.328	0.311	0.347	1.001
	b_samplingpredicts.driverhuman_use	0.198	0.179	0.219	1.001
	b_samplinglivingplanet.driverinvasions	0.362	0.345	0.378	1.001
	b_samplingbiotime.driverinvasions	0.787	0.767	0.805	1.002
	b_samplingpredicts.driverinvasions	0.551	0.531	0.571	1.000
	b_samplinglivingplanet.driverpollution	0.219	0.204	0.236	1.000
	b_samplingbiotime.driverpollution	0.675	0.657	0.693	1.001
	b_samplingpredicts.driverpollution	0.432	0.413	0.453	1.000
	sigma	0.231	0.230	0.232	1.000

Marine global change drivers across databases and the world	b_intercept	0.484	0.460	0.507	1.000
	b_samplinglivingplanet	0.002	-0.024	0.027	1.000
	b_samplingbiotime	0.013	-0.010	0.037	1.000
	b_drivercumulative	-0.030	-0.064	0.004	1.001
	b_driverhuman_population	-0.194	-0.226	-0.157	1.001
	b_driverhuman_use	-0.110	-0.144	-0.076	1.000
	b_driverinvasions	-0.133	-0.168	-0.101	1.000
	b_driverpollution	-0.155	-0.188	-0.121	1.000
	b_samplinglivingplanet.drivercumulative	0.121	0.085	0.160	1.001
	b_samplingbiotime.drivercumulative	0.107	0.073	0.141	1.001
	b_samplinglivingplanet.driverhuman_population	0.158	0.123	0.196	1.001
	b_samplingbiotime.driverhuman_population	0.006	-0.028	0.041	1.001
	b_samplinglivingplanet.driverhuman_use	0.212	0.175	0.248	1.001
	b_samplingbiotime.driverhuman_use	0.228	0.194	0.262	1.000
	b_samplinglivingplanet.driverinvasions	0.201	0.165	0.236	1.000
	b_samplingbiotime.driverinvasions	0.134	0.100	0.168	1.000
	b_samplinglivingplanet.driverpollution	0.192	0.156	0.229	1.000
	b_samplingbiotime.driverpollution	0.166	0.132	0.199	1.000
	sigma	0.274	0.273	0.274	1.000
Terrestrial temperature change (Living Planet Database)	b_intercept	0.011	0.009	0.013	1.000
	b_periodduringmonitoring	0.017	0.015	0.020	1.000
	sigma	0.080	0.080	0.081	1.000
Marine temperature change (Living Planet Database)	b_intercept	0.004	0.001	0.007	1.000
	b_periodduringmonitoring	0.013	0.009	0.017	1.000
	sigma	0.050	0.048	0.051	1.000
Terrestrial temperature change (BioTIME)	b_intercept	0.027	0.024	0.031	1.000
	b_periodduringmonitoring	-0.011	-0.017	-0.007	1.000
	sigma	0.104	0.102	0.105	1.000
Marine temperature change (BioTIME)	b_intercept	0.010	0.009	0.012	1.000
	b_periodduringmonitoring	0.008	0.007	0.010	1.000
	sigma	0.058	0.057	0.058	1.000

Appendix 2.4. Metadata and web links for each variable dataset included in the global change driver layers used to quantify global change space and extract driver information for the sites represented by the Living Planet, BioTIME and PREDICTS databases. The table is extracted from Bowler et al., 2020 where there are additional driver data details. T denotes "Terrestrial" and M – "Marine".

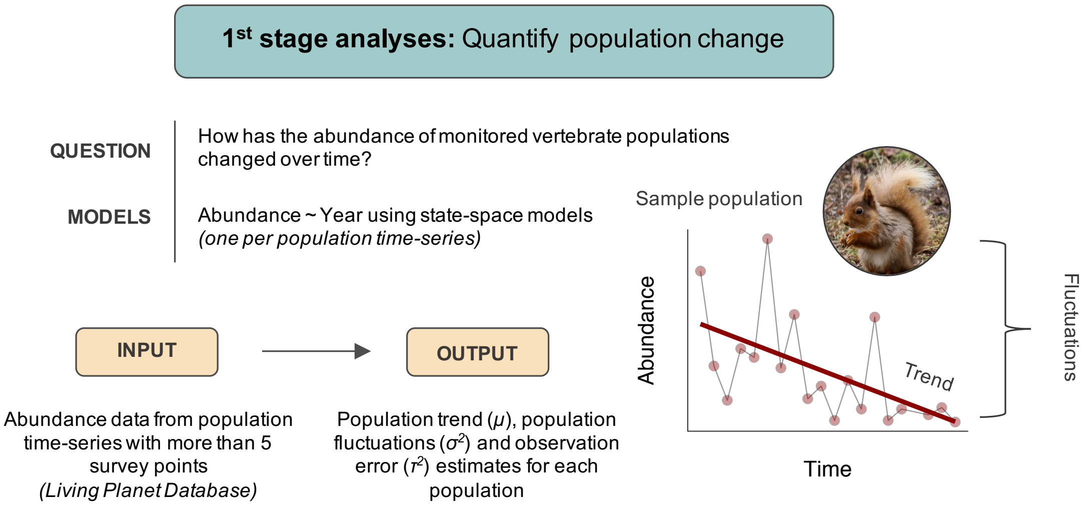
Variable	Realm	Best Data Layer	Time series	Resolution	Description/Url/Reference
Temperature	T	CRU v 4.02	Yes	0.5°	mean monthly and yearly temperatures (°C) https://crudata.uea.ac.uk/cru/data/hrg/ (Harris *et al.* 2014)
Aridity change	T	CRU v 4.02	Yes	0.5°	ratio of mean monthly and yearly pet (mm day^{-1}) and precipitation (mm) https://crudata.uea.ac.uk/cru/data/hrg/ (Harris *et al.* 2014)
Sea surface temperature	M	HadISST	Yes	1°	mean monthly and yearly sea surface temperatures (°C) https://www.metoffice.gov.uk/hadobs/hadisst/data/download.html (Rayner *et al.* 2003)
Ocean acidification	M	Ocean Acidification	Yes* (2000-2009 vs 1870)	1 km^2	change in aragonite saturation state https://www.nceas.ucsb.edu/globalmarine/impactbyactivity (Halpern *et al.* 2008)
Pasture	T	Pasture fraction	No (2000)	5'	fraction of cell area (0-1) based on agricultural inventory data and satellite-derived land cover data http://www.earthstat.org/ (Ramankutty *et al.* 2008)
Cropland	T	Cropland fraction	No	5'	fraction of cell area (0-1) based on national and subnational agricultural data and satellite-derived land cover data

			(2005)		(Fritz *et al.* 2015)
Cattle density		Gridded Livestock of the World	No (2005)	1 km	FAOSTAT national estimates and modelled downscaling (Robinson *et al.* 2014)
Forest loss	T	Land-Use Harmonization 2 (primary forest cover)	Yes	0.25°	fraction of cell area (0-1) using FAO national wood harvest volume data and an ecosystem model http://luh.umd.edu/ (Hurtt *et al.* 2013)
Urban cover	T	MODIS	No (2001)	5'	Urban cover (0 or 1) based on satellite-derived land cover data http://glcf.umd.edu/data/lc/ (Friedl *et al.* 2010)
Fishing	M	Commercial fishing layers	No (1999-2003)	1 km^2	tons of caught fish per ton of carbon https://www.nceas.ucsb.edu/globalmarine/impactbyactivity (Halpern *et al.* 2008)
Population density	T	SEDAC population data v4	No (2000)	30”	UN-adjusted population density http://sedac.ciesin.columbia.edu/data/set/gpw-v4-population-density/data-download (Center for International Earth Science Information Network - CIESIN - Columbia University 2017)
Coastal population	M	Coastal population	No (1992-2002)	1 km^2	number of people within 25 km radius https://www.nceas.ucsb.edu/globalmarine/impactbyactivity (Halpern *et al.* 2008)

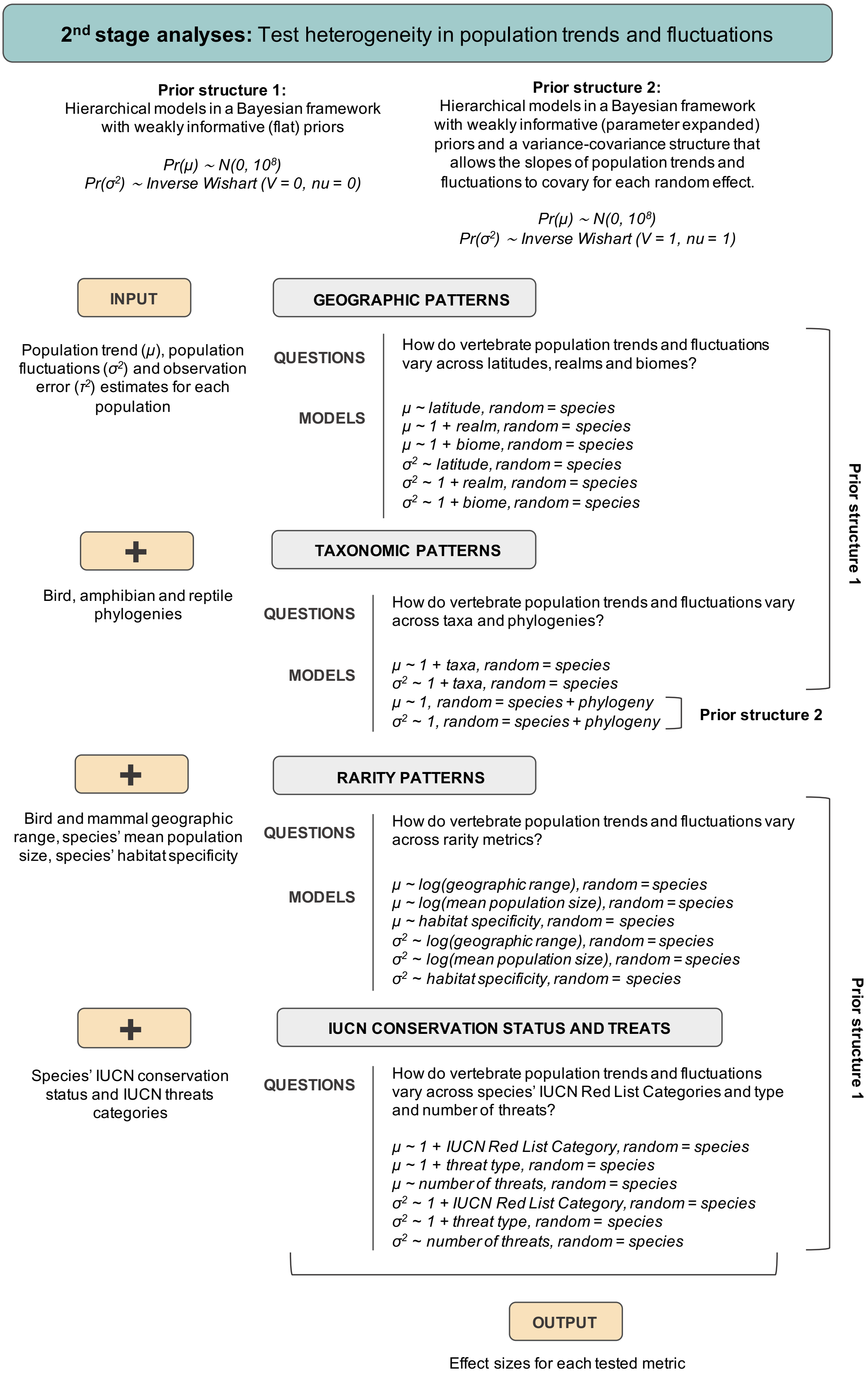
N deposition	T	Atmospheric nitrogen deposition	No (1993)	5° x 3.75°	mg N/m^2 of total inorganic nitrogen (N), NHx (NH3 and NH4+), and NOy http://webmap.ornl.gov/ogcdown/dataset.jsp?ds_id=830 (Dentener 2006)
Fertilizer application	T	Nitrogen fertilizer application (v1)	No (1994-2001)	0.5°	kg of Nitrogen fertilizer per hectare of cropland http://sedac.ciesin.columbia.edu/data/set/ferman-v1-nitrogen-fertilizer-application (Potter *et al.* 2010)
Pesticides	T	Riverthreat.net: Pesticide loading	No (2000)	0.5°	kg of pesticide per hectare of cropland http://www.riverthreat.net/data.html (Vorosmarty *et al.* 2010)
Light pollution	T/M	NOACC NGDC stable night lights	No (2006)	1 km	radiance values https://knb.ecoinformatics.org/#view/doi:10.5063/F15718ZN (Halpern *et al.* 2008)
Coastal pollution	M	Pesticide, Fertilizer	No (1993-2002)	1 km^2	average annual use in agricultural land https://knb.ecoinformatics.org/#view/doi:10.5063/F15718ZN (Halpern *et al.* 2008)
Shipping pollution	M	Shipping pollution	No (2004-2005)	1 km^2	ship activity (number of ships) https://knb.ecoinformatics.org/#view/doi:10.5063/F15718ZN (Halpern *et al.* 2008)
Invasions	T	Accessibility (Travel time)	No (2000)	30”	travel time to major cities (in hours and days) http://forobs.jrc.ec.europa.eu/products/gam/ (Nelson 2008)
Invasions	M	Port volume	No (1999-2003)	1 km^2	amount of cargo traffic at ports https://knb.ecoinformatics.org/#view/doi:10.5063/F15718ZN

(cargo volume at ports)	(Halpern *et al.* 2008)

Appendix 3. Supporting information for Chapter 3. Rare and common vertebrates span a wide spectrum of population trends



Appendix 3.1. Conceptual diagram of the first stage of my analyses where I calculated population trends and fluctuations. I analysed vertebrate population time series from the Living Planet Database (133,092 records) covering the period between 1970 and 2014. These time series represent repeated monitoring surveys of the number of individuals in a given area (species' abundance over time), to which I refer as "populations". Diagram shows one sample population of Red squirrel (*Sciurus vulgaris*). I quantified two aspects of population change – overall change in abundance over time (population trends) and abundance variability over time (population fluctuations). I used state-space models that account for observation error and random fluctuations (Humbert et al., 2009). The input abundance data for the state-space models were scaled to a common magnitude between zero and one to analyse within-population relationships to prevent conflating within-population relationships and between-population relationships (van de Pol & Wright, 2009). Squirrel photo by author.



2nd stage analyses: Test heterogeneity in population trends and fluctuations

Prior structure 1:
Hierarchical models in a Bayesian framework
with weakly informative (flat) priors

$Pr(\mu) \sim N(0, 10^8)$
$Pr(\sigma^2) \sim$ *Inverse Wishart (V = 0, nu = 0)*

Prior structure 2:
Hierarchical models in a Bayesian framework
with weakly informative (parameter expanded)
priors and a variance-covariance structure that
allows the slopes of population trends and
fluctuations to covary for each random effect.

$Pr(\mu) \sim N(0, 10^8)$
$Pr(\sigma^2) \sim$ *Inverse Wishart (V = 1, nu = 1)*

INPUT

Population trend (μ), population fluctuations (σ^2) and observation error (τ^2) estimates for each population

GEOGRAPHIC PATTERNS

QUESTIONS How do vertebrate population trends and fluctuations vary across latitudes, realms and biomes?

MODELS
$\mu \sim$ *latitude, random = species*
$\mu \sim$ *1 + realm, random = species*
$\mu \sim$ *1 + biome, random = species*
$\sigma^2 \sim$ *latitude, random = species*
$\sigma^2 \sim$ *1 + realm, random = species*
$\sigma^2 \sim$ *1 + biome, random = species*

+

Bird, amphibian and reptile phylogenies

TAXONOMIC PATTERNS

QUESTIONS How do vertebrate population trends and fluctuations vary across taxa and phylogenies?

MODELS
$\mu \sim$ *1 + taxa, random = species*
$\sigma^2 \sim$ *1 + taxa, random = species*
$\mu \sim$ *1, random = species + phylogeny*
$\sigma^2 \sim$ *1, random = species + phylogeny*

Prior structure 1

Prior structure 2

+

Bird and mammal geographic range, species' mean population size, species' habitat specificity

RARITY PATTERNS

QUESTIONS How do vertebrate population trends and fluctuations vary across rarity metrics?

MODELS
$\mu \sim$ *log(geographic range), random = species*
$\mu \sim$ *log(mean population size), random = species*
$\mu \sim$ *habitat specificity, random = species*
$\sigma^2 \sim$ *log(geographic range), random = species*
$\sigma^2 \sim$ *log(mean population size), random = species*
$\sigma^2 \sim$ *habitat specificity, random = species*

+

Species' IUCN conservation status and IUCN threats categories

IUCN CONSERVATION STATUS AND TREATS

QUESTIONS How do vertebrate population trends and fluctuations vary across species' IUCN Red List Categories and type and number of threats?

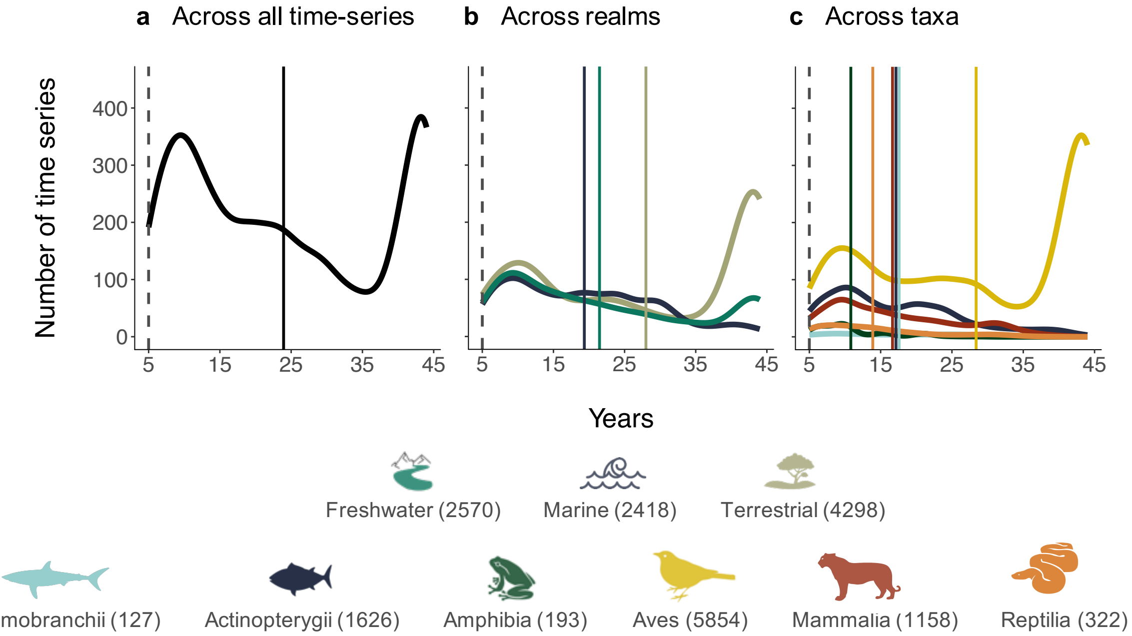
$\mu \sim$ *1 + IUCN Red List Category, random = species*
$\mu \sim$ *1 + threat type, random = species*
$\mu \sim$ *number of threats, random = species*
$\sigma^2 \sim$ *1 + IUCN Red List Category, random = species*
$\sigma^2 \sim$ *1 + threat type, random = species*
$\sigma^2 \sim$ *number of threats, random = species*

Prior structure 1

OUTPUT

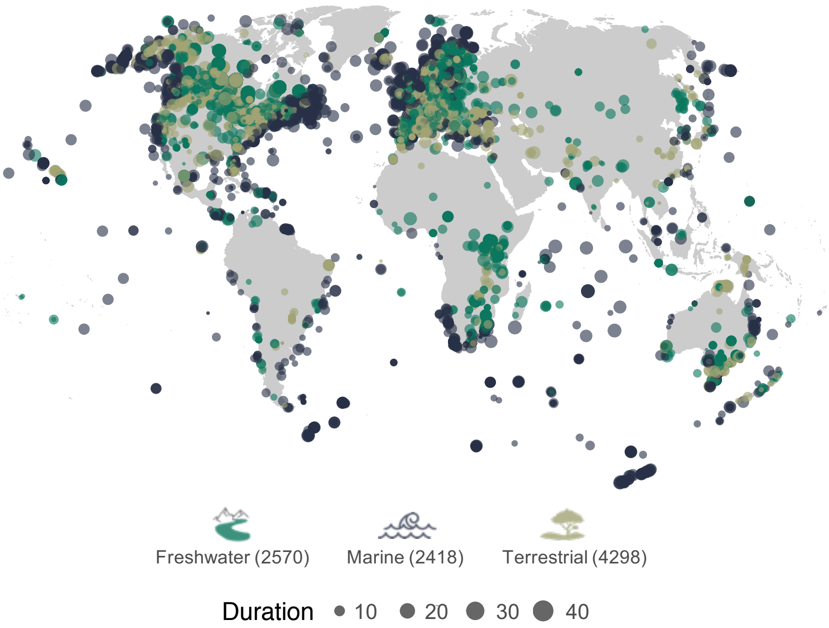
Effect sizes for each tested metric

Appendix 3.2. Conceptual diagram of the second stage of my analyses where I quantified the geographic, taxonomic, rarity and threat patterns within vertebrate population trends and fluctuations. I modelled the trend and fluctuation estimates from the first stage (Appendix 3.1) across latitude, realm, biome, taxa, rarity metrics, phylogenetic relatedness, species' conservation status and threat type using a Bayesian modelling framework (Hadfield, 2010). Each model included a species random intercept effect to account for the possible correlation between the trends of populations from the same species. The prior structure (weakly informative priors) was identical across all models except the phylogeny models from the taxonomic patterns section, where the prior structure allowed for an additional phylogeny random effect. See methods for additional details.

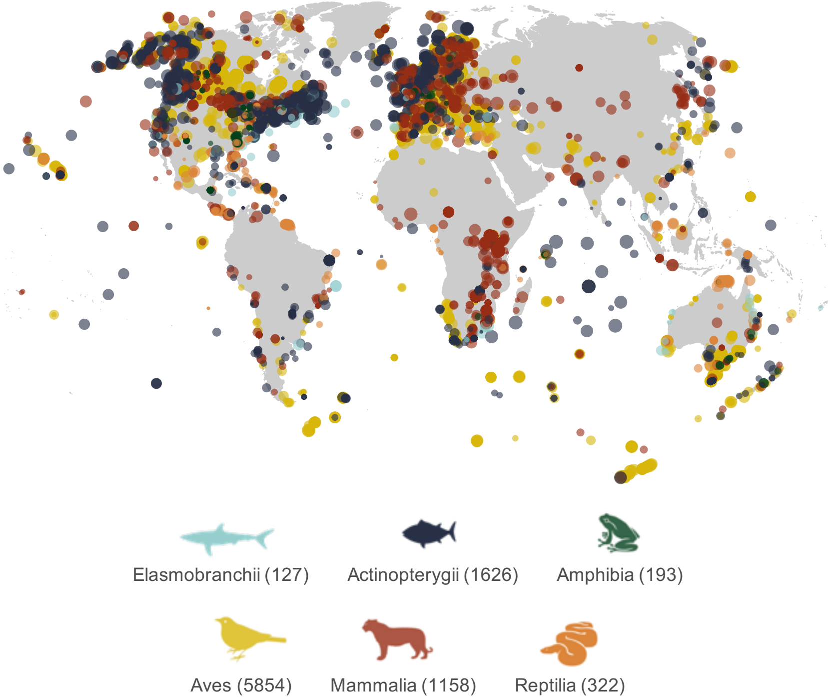


Appendix 3.3. The duration of monitoring varied by realm and taxa. Distribution of monitoring duration across (a) all time series, (b) realms and (c) taxa. In my study, I included time series with more than five survey points in time, with the dashed line representing five years and solid lines showing the mean duration for each category. Numbers in legend correspond to sample size in each category.

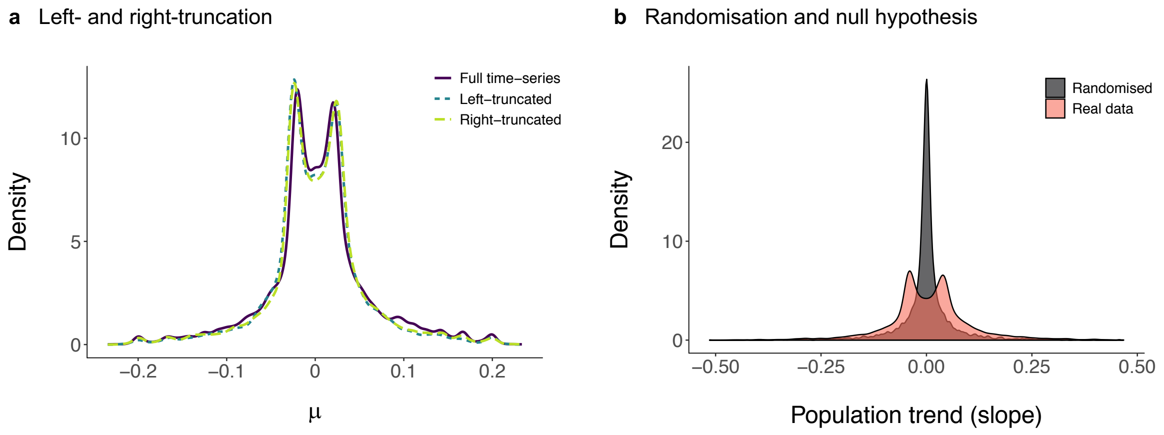
a Distribution of population time-series across realms



b Distribution of population time-series across taxa

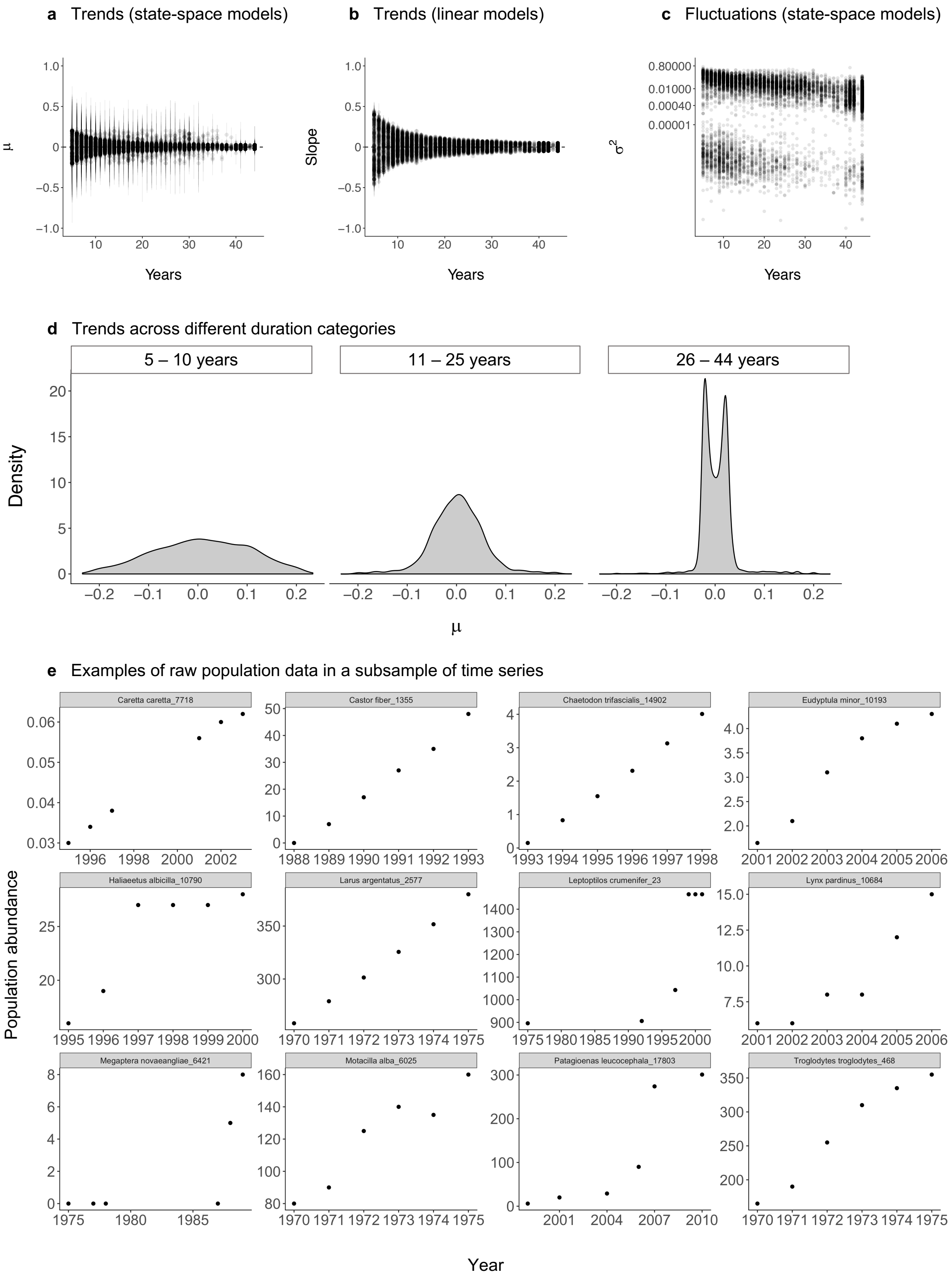


Appendix 3.4. The Living Planet Data represent a broad range of geographic locations, ecological settings and taxonomic groups. My analysis of the patterns in vertebrate population trends and fluctuations includes time series across realms (a) and different taxa (b), with a global geographic distribution of records. Numbers in legend correspond to sample size in each category.


a Left- and right-truncation

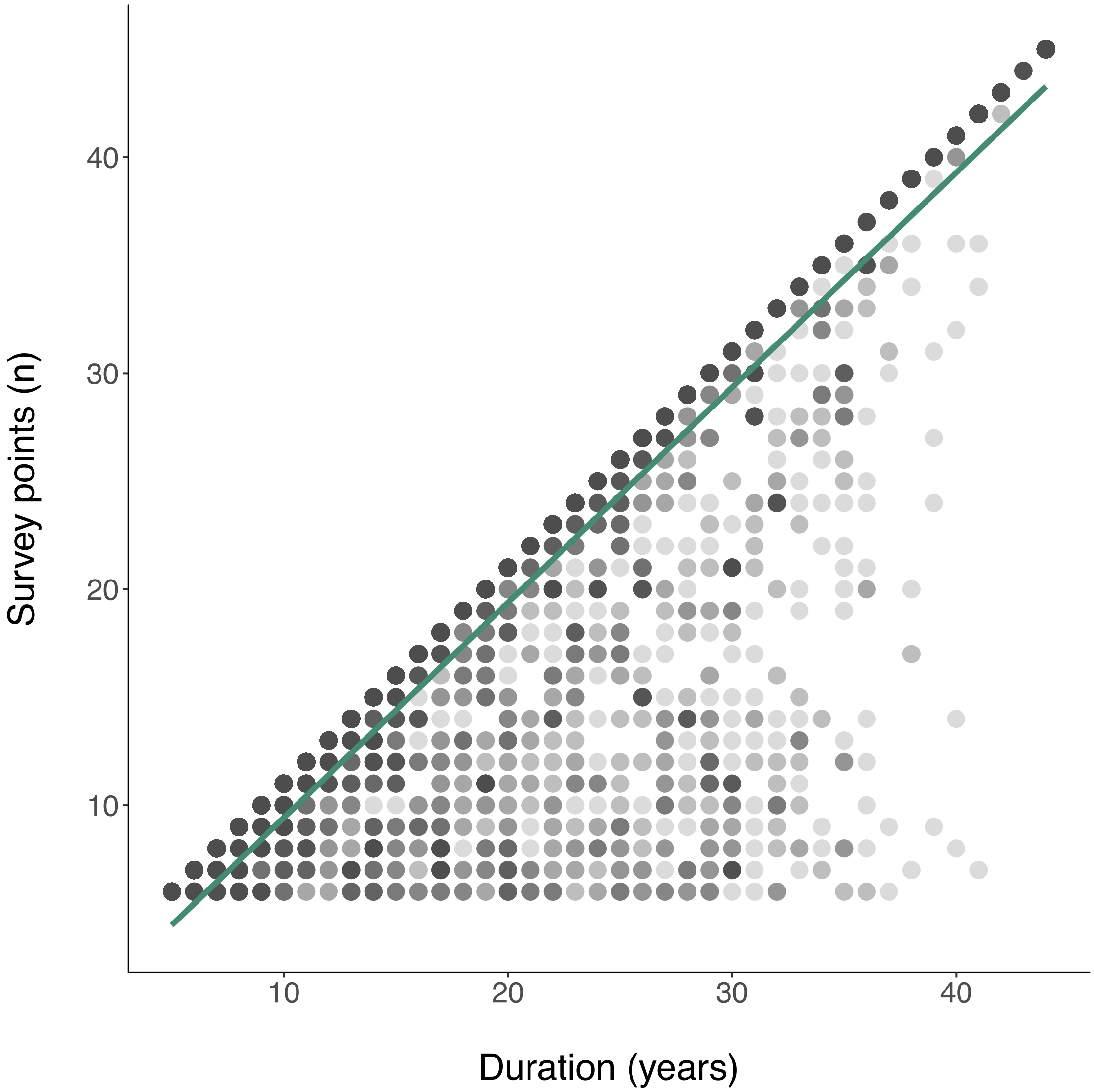
b Randomisation and null hypothesis

Appendix 3.5. The distribution of population trend values across time series was not sensitive to the omission of the first five (left-truncation) or the last five years (right-truncation) of population records and it differed from a null distribution derived from randomised data. Following Fournier et al., 2019, I tested the time series that I analysed for site-selection bias. Removing the first five survey points reduces the bias stemming from starting population surveys at points when individual density is high, whereas removing the last five years reduces the bias of starting surveys when species are very rare. There were slightly fewer trends centred on zero (no net change in abundance over time) when I left- and right-truncated the data, suggesting that longer time series are more likely to show no net changes in abundance (see Appendix 3.6 for a visualization of population trends versus monitoring duration. I also compared the distribution of estimated population trends against a null hypothesis (b). To derive a null distribution, I used a randomisation approach. Within each time series, I randomised the abundance data, keeping the overall range of the original data. The two peaks of μ are apparent in the overall distribution of time series data. These peaks are created by many weakly positive and negative population trends from longer time series that often are bird species from terrestrial systems. I hypothesised that there might a publication bias against no net change studies, or a bias against including such studies in global databases.

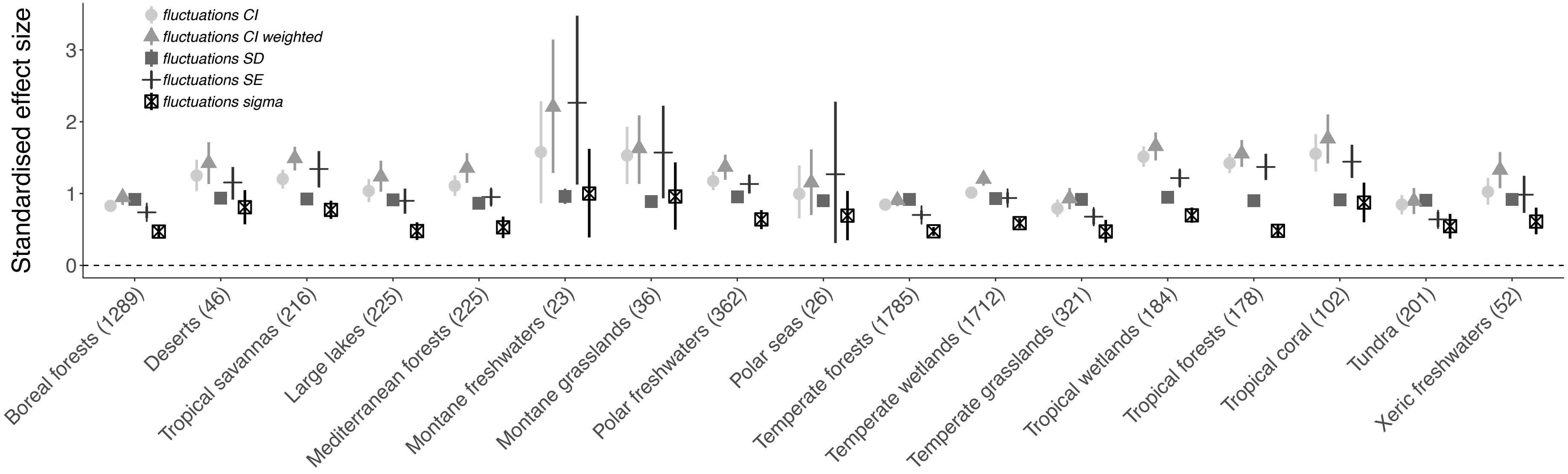


Appendix 3.6. Both positive and negative vertebrate population trends were smaller in magnitude for longer time series of data. Monitoring duration results are for 9286 populations from 2084 species. Population trends (μ) were estimated for all

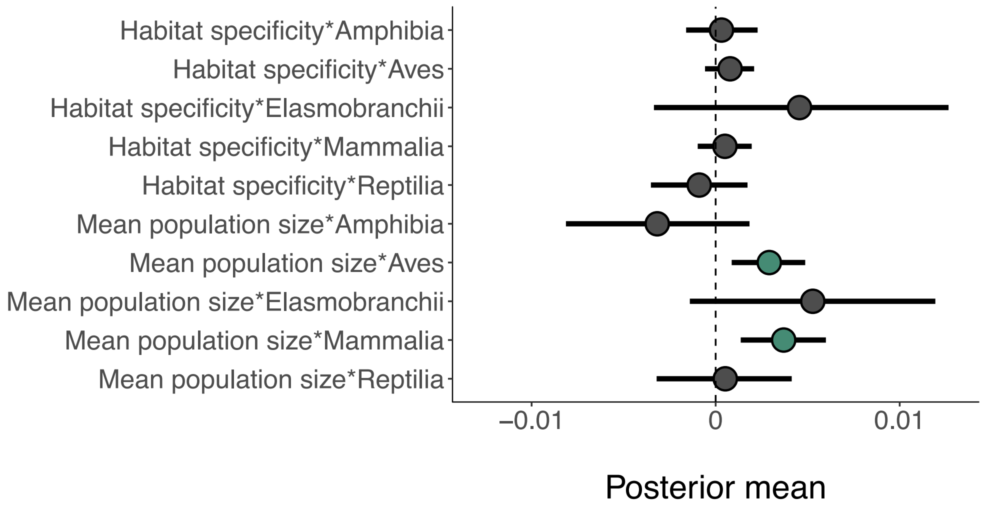
populations monitored for more than five time points using state-space models (a, d) and linear models (b). Population fluctuations (c) are plotted on a log10 y axis and represent the estimates for process noise (σ^2, the process noise is the total variance around the population trend minus the variance attributed to observation error) derived from state-space models. Error bars on (a) and (b) show 95% confidence intervals and their centres show population trends from state-space models (a) and linear models (b). The sample sizes for the duration categories were as follows 5 - 10 years: 2084 time series; 10 - 25 years: 3358 time series; 25 - 44 years; 3844 time series. Plot (e) shows the raw population trend data behind 12 time series which had the same population trend values ($\mu = 0.20$). These time series are part of a "band" of time series which had very similar population trend estimates. Eighty, or approximately 1% of the time series I analysed form linear relationships over time with errors around the slopes of <0.001, such that I suspect these data might be modelled rather than measured population data. The presence of modelled data within the dataset may help partially explain the low variance bands of σ^2 values (c) and the pattern of two peaks in weak population increases and decreases for longer time series (d). Please see Appendix 3.19 sections "Time series with low variation" and "Clustering in the values of population trends and fluctuations" for further details.



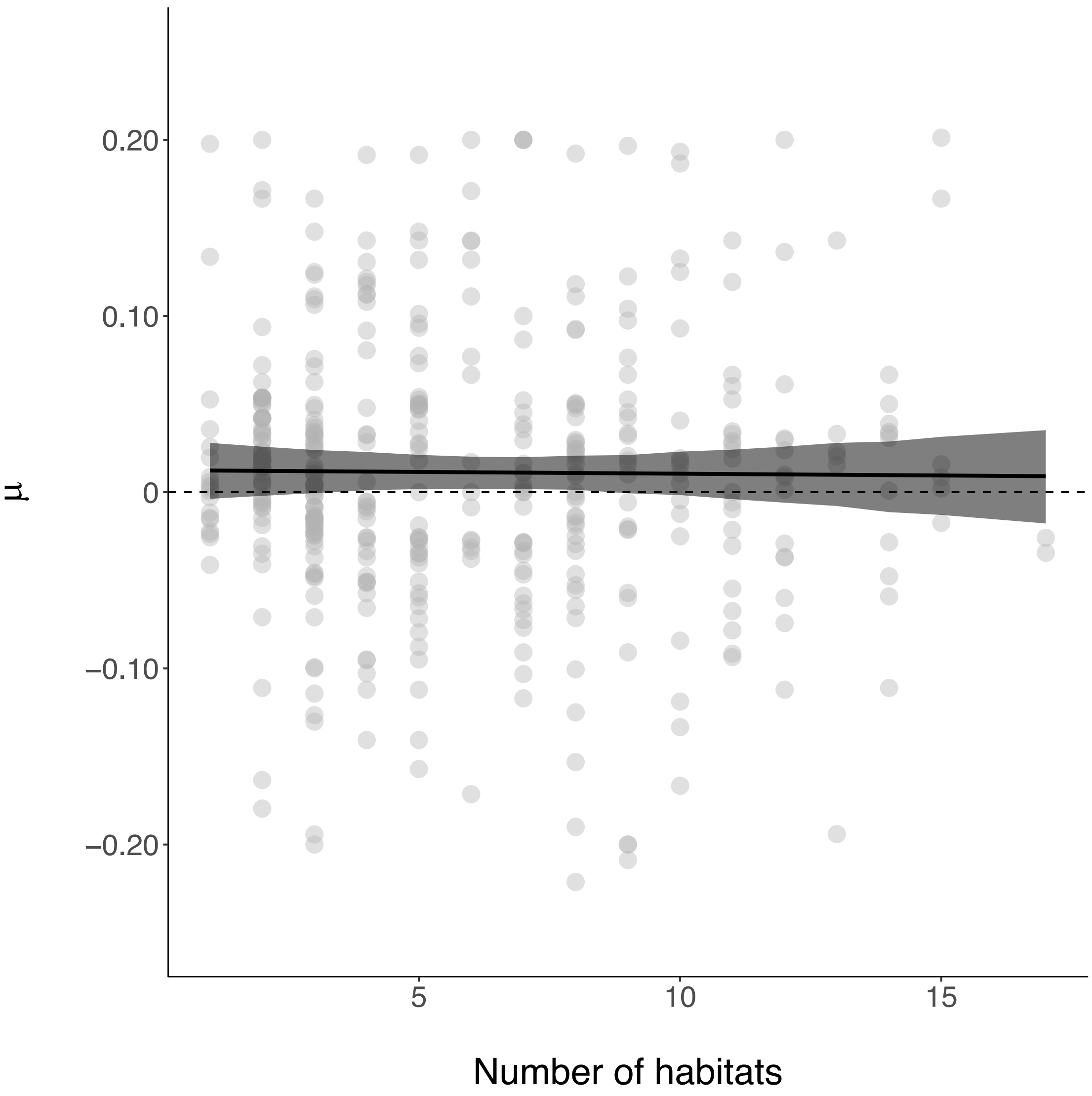
Appendix 3.7. Number of survey points within time series positively correlated with time series duration. I included time series with more than five survey points in time in my analyses, but populations were not always monitored in each intervening year. Green line shows a linear model fit of survey points versus duration. There was a minimum of six time points for each time series. Among the time series I analysed, 18% had a duration of less than 10 years, 30% had a duration between 10 and 20 years, 18% had a duration between 21 and 30 years, and 33% had a duration between 31 and 44 years. See Appendix 3.3 for the density distribution of monitoring duration for the studies I included in my analyses.



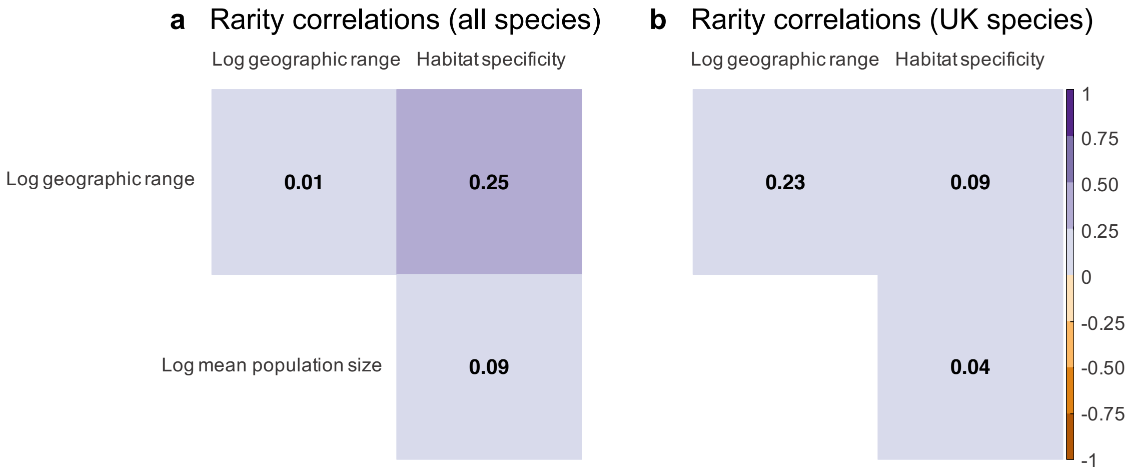
Appendix 3.8. Population fluctuations did not show distinct biome-specific patterns, except for montane and tropical biomes where fluctuations were more pronounced compared to the rest of the biomes I studied. The five estimates (centre points of error bars) for each category refer to different analytical approaches, where the response variables in the models were: 1) the standard error around the slope estimates of the linear model fits of abundance versus year (circles), 2) half of the 95% confidence interval around the μ value of population change (triangles), 3) half of the 95% confidence interval around μ weighted by τ^2, (full squares), 4) the process noise (σ^2) from the state-space models, and 5) the standard deviation of the raw data for each population time series (empty squares). The process noise is the total variance around the population trend minus the variance attributed to observation error. The effect sizes were standardized by dividing the effect size by the standard deviation of the corresponding input data. Error bars show 95% credible intervals.



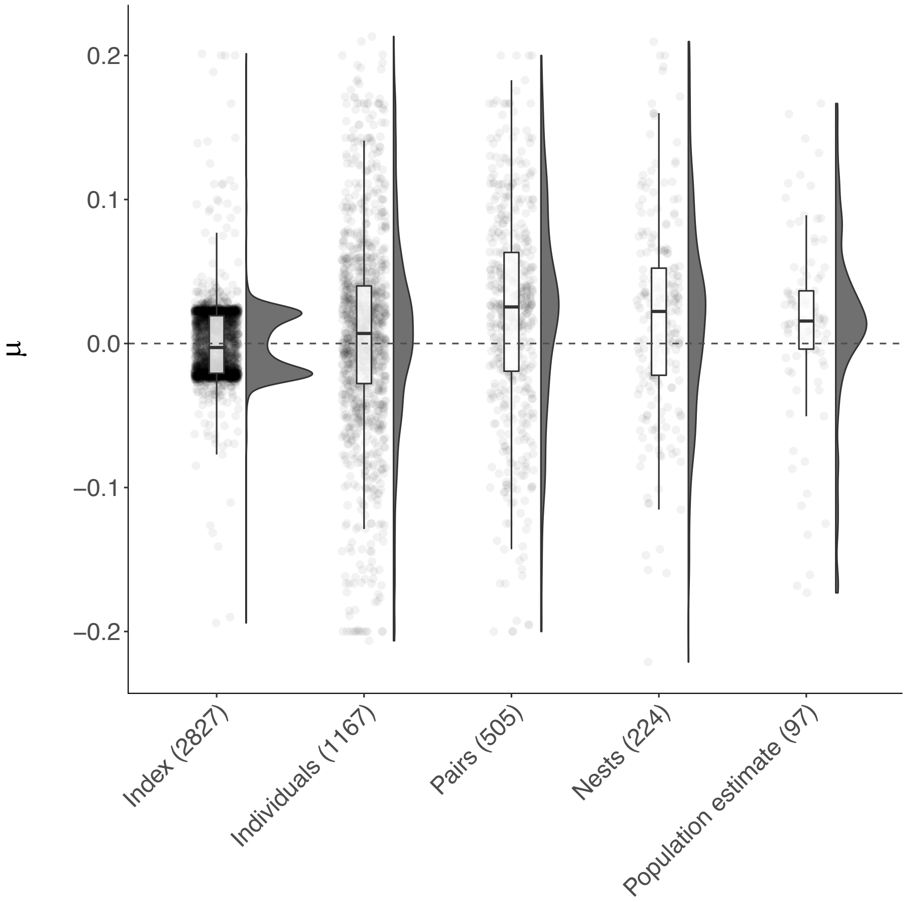
Appendix 3.9. Birds and mammals with larger mean population sizes were more likely to experience population increases. I tested for interaction effects of rarity and taxa on population trends and, except for mean population size for mammals and birds, rarity traits were not significant predictors of population change. Teal colour indicates posterior means where the 95% credible intervals did not overlap zero, grey colour indicates the opposite. Error bars show 95% credible intervals, and their centres show effect sizes. The sample size was 7901 population time series for the habitat specificity model and 4310 population time series for the mean population size model.



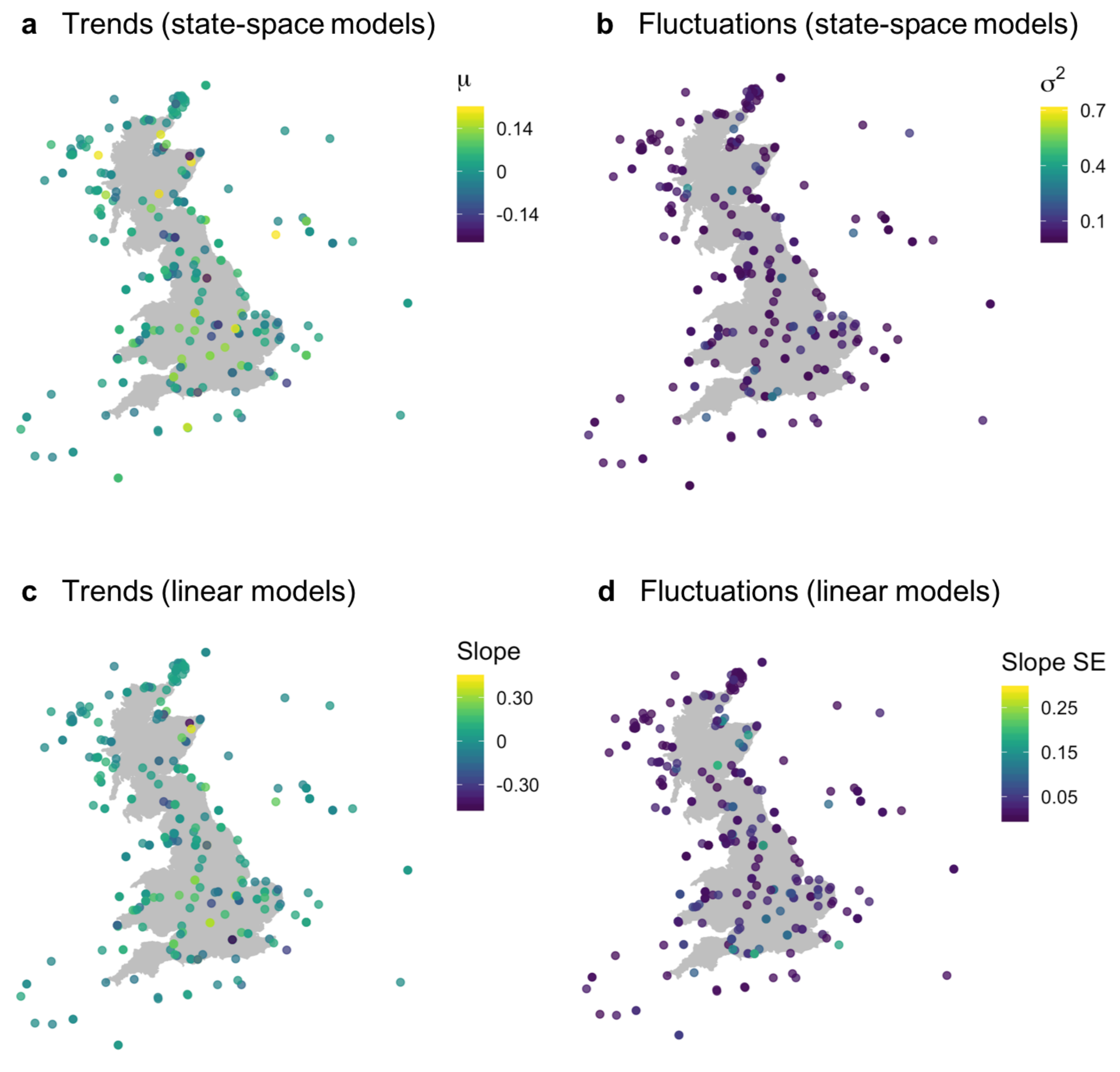
Appendix 3.10. Variation in vertebrate population trends was not explained by habitat specificity. Habitat specificity was calculated as the number of different habitats occupied by each species which I derived by surveying the 'Habitat and Ecology' profile for each species on the IUCN Red List website. The μ values of population change are derived from state-space model fits of changes in abundance over the monitoring duration for each population. Line shows model fit and shaded area shows 95% credible intervals. See Appendix 3.22 for full model outputs. This figure is based on populations monitored in the UK, see Figure 3.3c for the effects of habitat specificity on population trends across bird and mammal species globally.



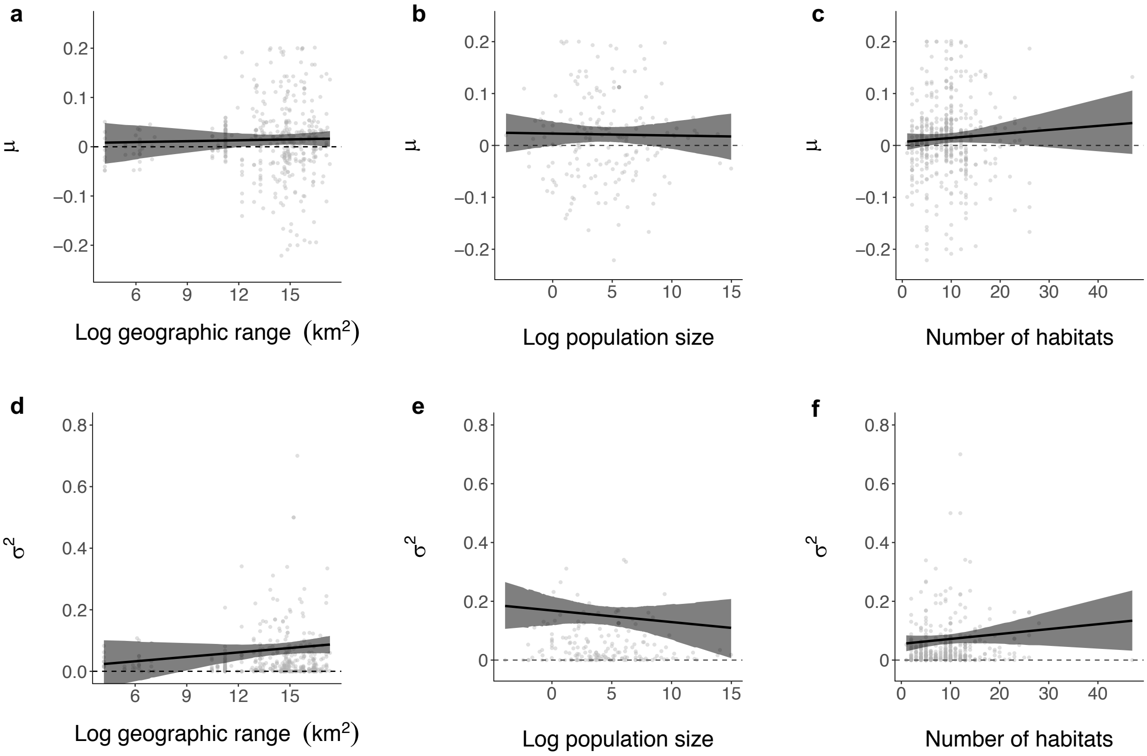
Appendix 3.11. The three rarity metrics used in this study were weakly correlated at both UK and global scales. See Appendix 3.21 for sample sizes on each geographic scale.



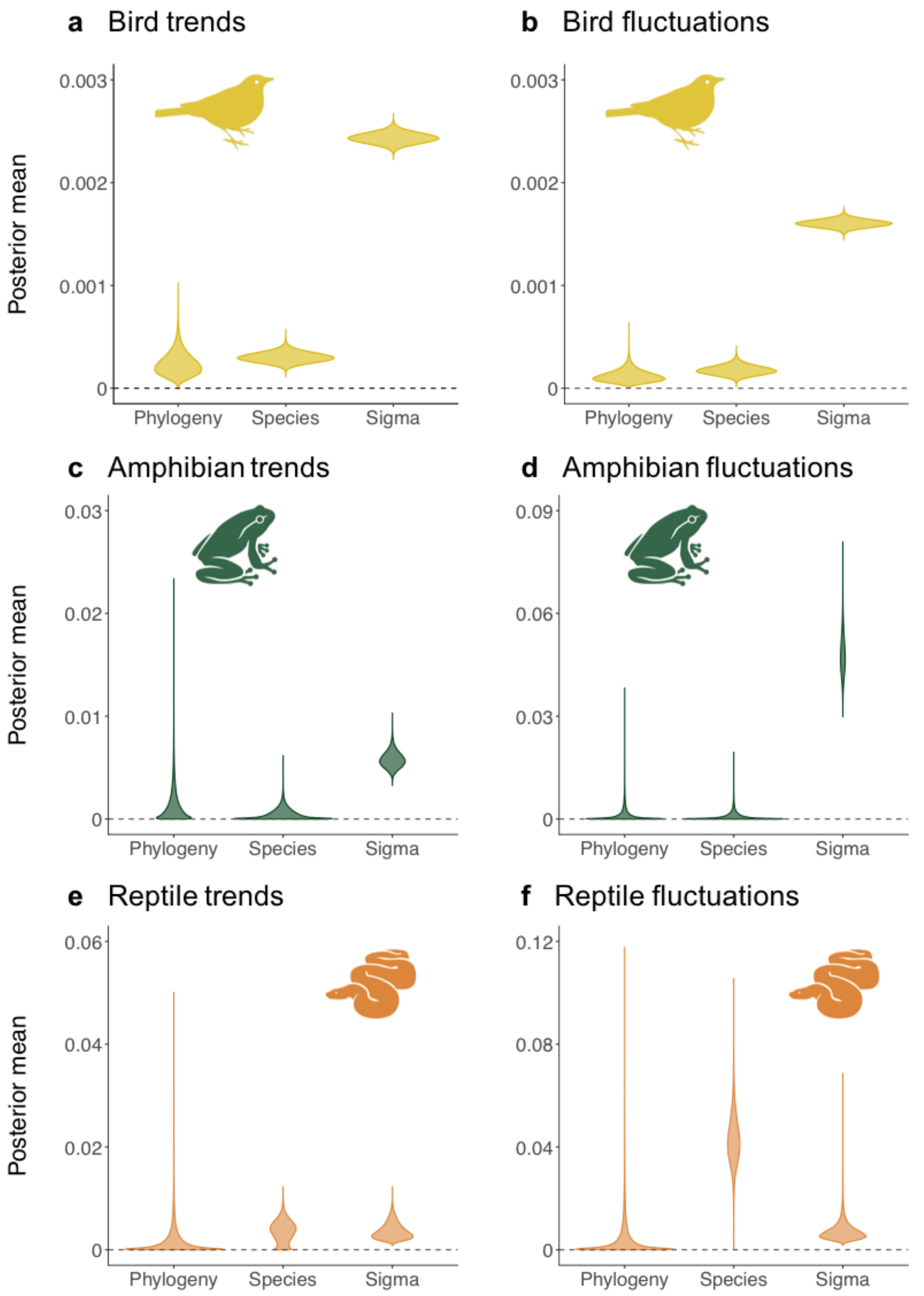
Appendix 3.12. There was no systematic difference in the distribution of population trends across commonly used abundance metrics in the Living Planet Database. Population trends represent *μ* values from state-space Numbers on the x axis correspond to sample size in each category. Density plots show the density distribution of population trends across sampling units, points show the raw values and boxplots show the mean, first and third quartiles and boxplot whiskers that cover 1.5 times the interquartile range. Population data where the units are an index were more likely to have weakly increasing or decreasing trends with many populations with *μ* values around 0.025 and -0.025. These *μ* estimates are reasonable trend estimates for these time series; however, there seem to be population within the Living Planet Database that are modelled, particularly for studies with longer duration which could partially explain these peaks in the population trend estimates near zero (see Figures 3.1, 3.2 and Appendices 3.5 and 3.6).



Appendix 3.13. Population trends and fluctuations did not show geographic patterning within the UK. Results include 508 populations from 237 species in the UK. See methods for additional details on the different ways I quantified trends and fluctuations.



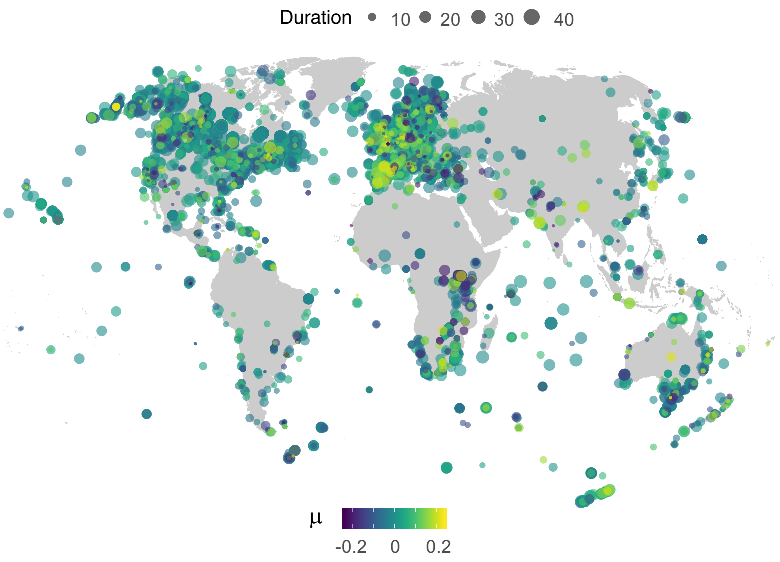
Appendix 3.14. The effects of rarity on population trends and fluctuations were consistent at both UK (pictured here) and global scales (Figure 3.3. Rare species were not more likely to decline than common species. Populations from species with smaller mean population sizes and populations from habitat generalist species were more likely to fluctuate. The *μ* values of population trend (plots a-c) and the σ^2 values of population fluctuation (d-f) were derived from state-space model fits of changes in abundance over the monitoring duration for each population. The population fluctuations represent the process noise from the state-space models which is the total variance around the population trend minus the variance attributed to observation error. Lines on plots a-f show model fits and 95% credible intervals. See Appendix 3.21 for sample sizes for each analysis and Appendices 3.22 and 3.23 for model outputs.



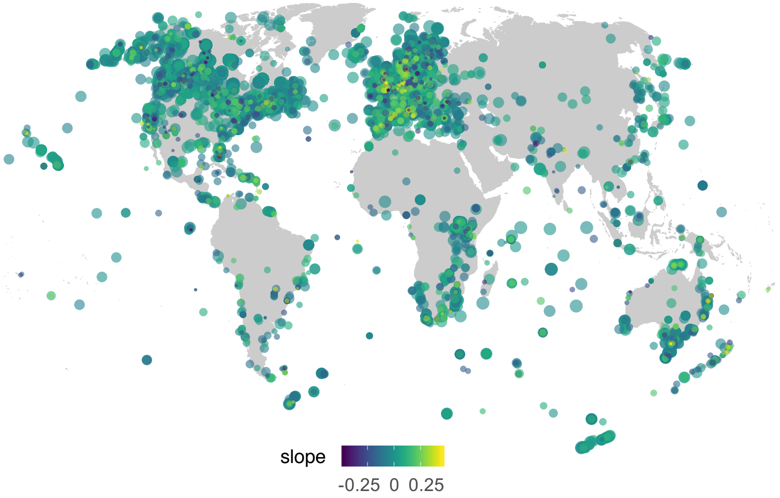
Appendix 3.15. There were no phylogenetic patterns in the population trends and fluctuations of birds, amphibians and reptiles. Phylogeny refers to variance explained by phylogenetic relationships, species refers to variance explained by within-species differences (some species were represented by more than one population, thus introducing species-level variance), and residual variance refers to the variance not explained by phylogeny and species effects. The figure shows violin

plots of the distributions of posterior means for phylogenetic, species and residual variance across taxa (the wider the violin, the more records there are with that value). The distributions are based on ten models for each taxon for each type of population change using 10 random trees to account for phylogenetic uncertainty. Phylogeny effects were calculated based on a branch length covariance matrix. See Appendix 3.24 for full model outputs.

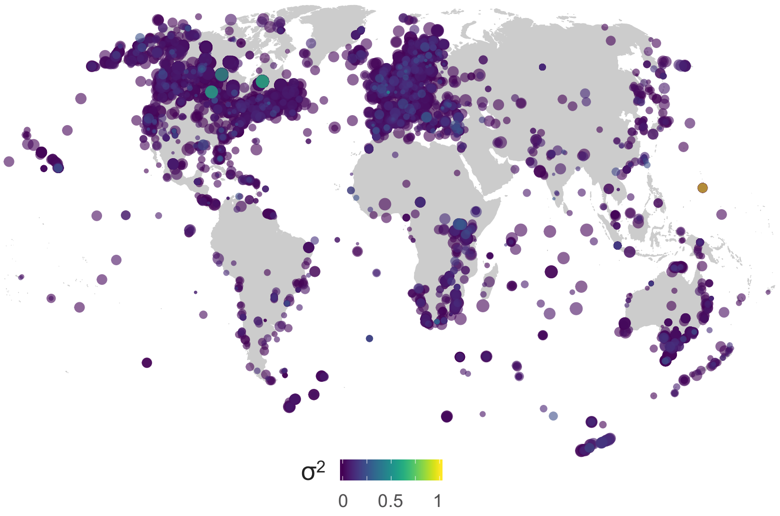
a Population trends from state-space models



b Population trends from linear models

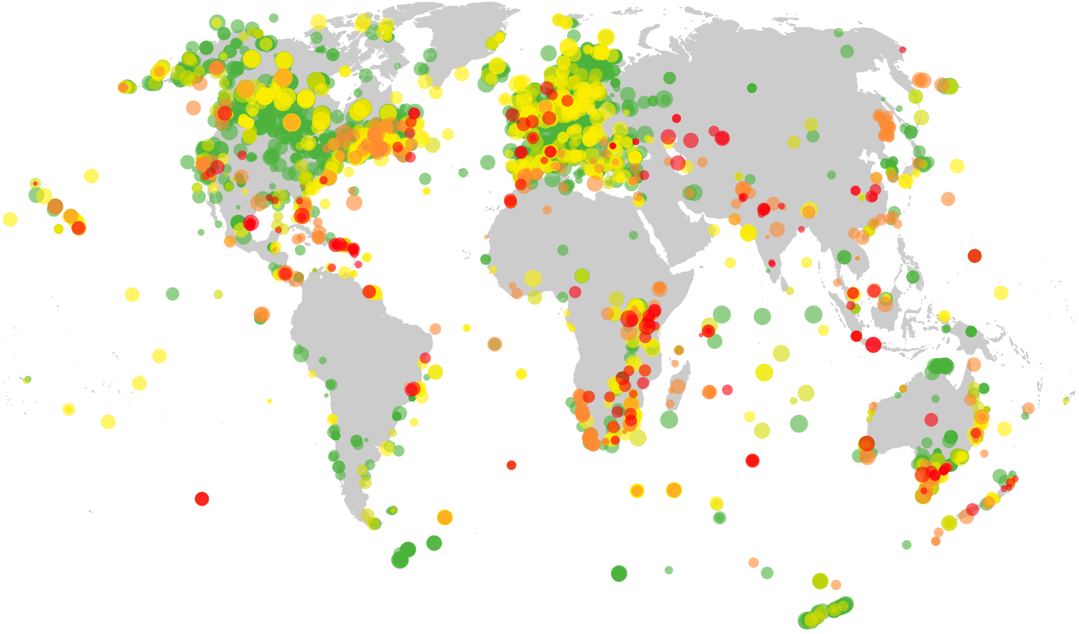


c Population fluctuations from state-space models



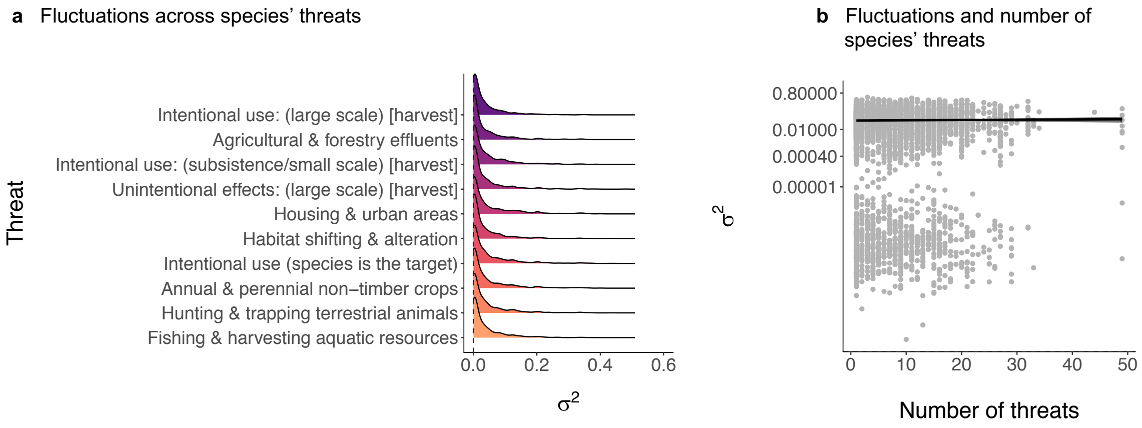
Appendix 3.16. Population change is ubiquitous across the planet, with no distinct hotspots of declines, increases or fluctuations. Maps show geographic distribution of time series colour-coded by the magnitude of change experienced. The population fluctuations represent the process noise from the state-space models which is the total variance around the population trend minus the variance attributed to observation error. See Methods for additional details on calculating trends and fluctuations.

a Distribution of population time-series across IUCN Red List Categories



b Time-series duration across IUCN Red List Categories

Appendix 3.17. Species across the whole spectrum of the IUCN Red List Categories are distributed around the world, with a concentration of least concern species in Northern America and Europe. In my study, I included time series with more than five survey points in time (b), with the dashed line five years and solid lines showing the mean duration for each category. Populations from least concern species were monitored for longer durations. Numbers next to each category show sample size.



Appendix 3.18. Population fluctuations did not differ based on the type and number of threats based on species' IUCN Red List profiles. Fluctuations were estimated using the process noise (σ^2) values from state-space model fits of changes in abundance over the monitoring duration for each population. Densities in (a) show distributions of fluctuation estimates across different threats. Line in (b) shows model fit and shaded area shows 95% credible intervals, where "number of threats" refers to the number of different threats that each species, whose populations are locally monitored, could be exposed to throughout their distribution range, based on species' IUCN Red List profiles. See Methods for how the types of threats were derived and Appendix 2 for model outputs. The sample sizes in (a) (number of population time series) were as follows: Intentional use: (large scale) [harvest] – 530, Agriculture and forestry effluents – 790, Intentional use: (subsistence/small scale) [harvest] – 567, Unintentional effects: (large scale) [harvest] – 807, Housing & urban areas – 730, Habitat shifting and alteration – 1331, Intentional use (species is the target) – 1208, Annual & perennial non-timber crops – 917, Hunting & trapping terrestrial animals – 1777, fishing & harvesting aquatic resources – 1514. The sample size in (b) was 3501 population time series.

Appendix 3.19 Data limitations

Taxonomic and geographic gaps

My analysis is based on 9286 monitored populations from 2084 species from the largest currently available public database of population time series, the Living Planet Database (LPI, 2016). Nevertheless, the data are characterized by both taxonomic and geographic gaps that can influence my findings. For example, there are very few population records from the Amazon and Siberia (Figure 3.1b) – two regions currently undergoing rapid environmental changes due to land-use change and climate change respectively. Additionally, birds represent 63% of all population time series in the Living Planet Database, whilst there were fewer records for taxa such as amphibians and sharks that were undergoing declines (Figure 3.2 and Appendix 3.4). On a larger scale, the Living Planet Database under-represents populations outside of Europe and North America and over-represents common and well-studied species (McRae et al., 2017). I found that for the populations and species represented by current monitoring, rarity does not explain variation in population trends, but I note that the relationship between population change and rarity metrics could differ for highly endemic specialist species or species different to the ones included in the Living Planet Database (Newbold et al., 2018). As ongoing and future monitoring begins to fill in the taxonomic and geographic gaps in existing datasets (Hochkirch et al., 2021), we will be able to re-assess and test the generality of the patterns of population change across biomes, taxa, phylogenies, species traits and threats.

Monitoring extent and survey techniques

The Living Planet Database combines population time series where survey methods were consistent within time series but varied among time series. Thus, among populations, abundance was measured using different units and over varying spatial extents. There are no estimates of error around the raw population abundance values available and detection probability likely varies among species. Thus, it is challenging to make informed decisions about baseline uncertainty in abundance estimates without prior information. I used state-space models to estimate trends and fluctuations to account for these limitations as this modelling framework is particularly appropriate for analyses of data collected using disparate methods (Knape et al., 2011; Leung et al., 2017a; Pedersen et al., 2011). Another approach to partially account for observer error that has been applied to the analysis of population trends is the use of occupancy models (van Strien et al., 2016). Because the precise coordinates of the polygons where the individual populations were monitored are not available, I was not able to test for the potential confounding effect of monitoring extent, but my sensitivity analysis indicated that survey units do not explain variation in the detected trends (Appendix 3.12).

Temporal gaps

The population time series from the Living Planet Database that I used cover the period between 1970 and 2014, with both duration of monitoring and the frequency of surveys varying across time series. I omitted populations which had less than five time points of monitoring data, as previous studies of similar population time series data have found that shorter time series are less likely to capture directional trends in abundance (Wauchope et al., 2019). In Chapter 4, I found significant lags in population change following disturbances (forest loss) and that population monitoring often begins decades to centuries after peak forest loss has occurred at a given site. The findings of Chapter 4 suggest that the temporal span of the population monitoring does not always capture the period of intense environmental change and lags suggest that there might be abundance changes that have not yet manifested themselves. Thus, the detected trends and the baseline across which trends are compared might be influenced by when monitoring takes place and at what temporal frequency. Challenges of analysing time series data are present across not just the Living Planet Database that I analysed, but more broadly across population data in general, including invertebrate datasets (Didham et al., 2020). Nevertheless, the Living Planet Database represents the most comprehensive compilation of vertebrate temporal population records to date, allowing large-scale analyses possible into the patterns of vertebrate trends and fluctuations around the world (Buschke et al., 2021; Leung et al., 2017b, 2020).

Time series with low temporal variation

Eighty populations (<1% of the 9286 time series) had very little variance (see Appendix 3.27 for full references for those studies). The majority of those studies are for bird species and come from the North American breeding bird survey with a measurement unit of an index (USGS, 2011). I have also observed some time series that appear to show logistic relationships with little natural variance (e.g., time series 468, 10193, 17803, see Appendix 3.28 for full references). Inspecting the raw data showed that some populations have abundances which follow an almost perfect linear or logarithmic increase over time, as could be the case for modelled, versus raw field data. I provide the references for these studies and cannot definitively attribute the low variance to a particular cause across all studies. Some of these studies are reported in units that are an index which may not capture variation in the same way as other raw units of population data. Some of these time series may represent modelled population data based on demographic information rather than only direct observations of populations (e.g., time series 1355 Nolet & Baveco, 1996). I chose to not remove studies that may not be raw observation time series based on visual inspection of trends to avoid introducing bias against populations with naturally low variation into my analysis.

Clustering in the values of population trends and fluctuations

I found a clustering of population trend and fluctuations values in some parts of the population change spectrum. For example, I found two peaks – in small increases and in small decreases over time – which were most prevalent in terrestrial bird studies and species which were monitored using an index (Figure 3.2, Appendix 3.12). Overall, 11.4% of time series had trend values between 0.02 and 0.03 and 11.6% of time series had trend values between -0.03 and -0.02. There was also a similar, but smaller, clustering around trends of 0.25 and -0.25. All reported population trends are from models that converged successfully, and visual inspection indicated to us that the μ values are appropriate estimates for the individual time series (Appendix 3.6e). I investigated the population time series where the value of the population trends over time were estimated to be the same value and found that they came from a variety of taxa, locations and survey methods (Appendix 3.6e). I hypothesised that there might be a publication bias against publishing no net change studies, which could explain the trough in μ values of around zero in long-term studies. The clustering of values for some time series may sometimes be associated with the same time series that also have low variance (Appendix 3.6e, see discussion above). With the information available in the Living Planet Database metadata, I cannot fully explain the clustering in population trends. I advocate for more detailed metadata in future versions of the Living Planet Database to allow researchers to filter the database appropriately for individual analyses.

Challenges in estimating geographic range

Estimating geographic range across taxa, and specifically for species that are not birds or mammals, remains challenging due to data limitations. I used a static measure of geographic range, which does not account for changes in species distributions over time. Furthermore, species could naturally have a small range or the small range size could be due to historic habitat loss (Magurran & Henderson, 2003). The UK populations included in the Living Planet Database are predominantly from species with wide geographic ranges (Appendix 3.25), and my global scale analysis of the relationship between population change and geographic range is based on mammal and bird data. As data availability improves, future research will allow us to test the effect of geographic range on the trends of other taxa, such as amphibians and sharks.

Appendix 3.20 Sensitivity analyses

Trends relative to null expectation

I tested whether the number of increasing and decreasing populations trends differed from a null expectation using a data randomisation approach (Appendix 3.5b). I used linear models to estimate trends in the data and randomised data with identical structure to the Living Planet Database. I found that there were over 10 times more population declines and increases in the real data relative to the randomised data (2.29% of trends were declining and 2.30% were increasing in the randomised data, versus 28.9% and 32.5% of time series which had significant negative and positive slopes in the real data, respectively).

Monitoring duration, sampling methods and site-selection bias

To assess the influence of monitoring duration on population trends, I used a Bayesian linear model. I modelled population trend (μ) as a function of monitoring duration (years) for each population, fitted with a zero intercept, as when duration is zero, no population change has occurred. Monitoring duration was weakly positively related to vertebrate population trends, with slightly greater population increases found for longer duration studies (Appendix 3.6, Appendix 3.22). There was a similar weakly positive effect of number of time points within time series (Appendix 3.22). Additionally, I tested if monitoring duration influenced the relationships between population trends across systems, and population trends across taxa. I found that duration did not influence those relationships, except for reptiles, where declines were more frequent as monitoring duration increased (Appendix 3.22). Variation in population trends was not explained by sampling method across the five most used abundance metrics (population index, number of individuals, number of pairs, number of nests and population estimate, Appendix 12). Following Fournier *et al.* 2019, I tested the time series that I analysed for site-selection bias. Removing the first five survey points reduces the bias stemming from starting population surveys at points when individual density is high, whereas removing the last five years reduces the bias of starting surveys when species are very rare. The distribution of population trend values across time series was not sensitive to the omission of the first five (left-truncation) or the last five years (right-truncation) of population records (Appendix 3.5a). Additionally, I used a data randomisation approach to compare the distribution of trends from the real data to a null distribution and found different patterns (Appendix 3.5b). Overall, my sensitivity analyses suggest that my findings are robust to the potential confounding effects of differences in monitoring duration, sampling method and site-selection.

Comparison of modelling approaches

I conducted the following supplementary analyses: in the second-stage Bayesian models estimating population trends across systems, biomes, taxa and rarity metrics, 1) I weighted μ values by the square of τ^2, the observation error estimate derived from the state-space models (Humbert et al., 2009), 2) I used slopes of linear model fits of abundance (scaled at the population level, centred on zero and with a standard deviation of one) (van de Pol & Wright, 2009) instead of the μ estimates from state-space models, 3) I modelled the standard error around the slope values of the linear models, the error around μ (half of the 95% confidence interval) and the standard deviation of the raw population data for each time series as additional metrics of population variability. To allow comparison, I scaled the different metrics of population variability to be centred on zero and with a standard deviation of one before they were used as response variables in models. All different analytical approaches yielded very similar results (see main text and Appendices 3.5, 3.6, 3.9 and 3.22).

Appendix 3.21. Number of species and populations included in analyses.

Scale	**Analysis**	**Number of species**	**Number of populations**	**Number of species with >3 populations**
Global	System	2074	9286	834
	Biome	2074	9286	834
	Taxa			
	- *Actinopterygii*	544	1626	151
	- *Amphibia*	78	193	21
	- *Aves*	968	5852	538
	- *Mammalia*	306	1158	94
	- *Reptilia*	110	322	16
	Red List status	1702	8064	708
	Latitude	2074	9286	834
	Duration	2074	9286	834
UK	Geographic range	167	381	32
	Population size	112	253	19
	Habitat specificity	144	289	29
	Red List status	153	364	31

Appendix 3.22. Model outputs from global analyses. Sigma is the overall model residual variance. Net population change was estimated using μ values derived from state-space models of population abundance versus time and slopes of linear models of population abundance versus time. The weighted μ models included μ as a response variable, weighted by τ, the observation error estimate derived from the state-space models. The fluctuation models included the process noise (σ^2) values from state-space models, half of the 95% confidence interval around the μ value of population change, the standard error around the slopes of linear models of population abundance versus time, and the standard deviation of the raw time series data for each population. The process noise is a metric of population fluctuations, whereas the rest of the metrics show population variability. The weighted fluctuation models were weighted by τ, the observation error estimate derived from the state-space models.

Model name	Variable	Post. mean	Lower 95% CI	Upper 95% CI	Eff. sample size	pMCMC	Effect
Latitude - μ	(Intercept)	0.003	0.0002	0.005	18,000	0.037	fixed
	Decimal.Latitude	0.00001	-0.00004	0.0001	18,000	0.687	fixed
	sigma	0.003	0.003	0.003	15,774		residual
Realm - μ	Freshwater	0.003	-0.001	0.006	18,000	0.146	fixed
	Marine	0.004	0.0003	0.007	18,597	0.029	fixed
	Terrestrial	0.003	0.0002	0.005	18,000	0.035	fixed
	sigma	0.003	0.003	0.003	16,324		residual
Realm - weighted	Freshwater	0.004	-0.001	0.009	18,000	0.156	fixed
	Marine	0.003	-0.002	0.008	18,000	0.168	fixed
	Terrestrial	0.003	0.00001	0.007	18,000	0.053	fixed
	sigma	0.003	0.003	0.003	13,851		residual
Realm - slope	Freshwater	0.006	-0.0002	0.012	18,000	0.067	fixed
	Marine	0.003	-0.002	0.009	18,000	0.263	fixed
	Terrestrial	0.004	-0.001	0.008	18,000	0.114	fixed
	sigma	0.008	0.008	0.008	15,950		residual
Realm - fluctuations σ	Terrestrial	0.022	0.020	0.024	16,584	0.0001	fixed
	Marine	0.028	0.026	0.030	21,131	0.0001	fixed
	Freshwater	0.028	0.025	0.030	17,579	0.0001	fixed

	sigma	0.002	0.002	0.002	15,086		residual
Realm - fluctuations CI	Freshwater	0.144	0.136	0.152	18,000	0.0001	fixed
	Marine	0.148	0.140	0.155	18,000	0.0001	fixed
	Terrestrial	0.118	0.111	0.124	18,000	0.0001	fixed
	sigma	0.012	0.011	0.012	17,555		residual
Realm - fluctuations CI weighted	Terrestrial	0.130	0.122	0.138	18,000	0.0001	fixed
	Marine	0.169	0.159	0.180	18,000	0.0001	fixed
	Freshwater	0.170	0.159	0.181	16,896	0.0001	fixed
	sigma	0.011	0.010	0.011	18,000		residual
Realm - fluctuations SE	Freshwater	0.135	0.126	0.143	18,000	0.0001	fixed
	Marine	0.139	0.131	0.148	18,000	0.0001	fixed
	Terrestrial	0.109	0.102	0.115	18,440	0.0001	fixed
	sigma	0.012	0.011	0.012	18,000		residual
Realm - fluctuations SD	Freshwater	0.563	0.557	0.569	18,000	0.0001	fixed
	Marine	0.568	0.562	0.573	18,000	0.0001	fixed
	Terrestrial	0.547	0.542	0.552	18,000	0.0001	fixed
	sigma	0.008	0.008	0.008	16,850		residual
Biome - μ	Boreal forests/taiga	0.002	-0.002	0.006	18,664	0.235	fixed
	Deserts and xeric shrublands	-0.006	-0.023	0.012	18,000	0.526	fixed
	Trop. and subtrop. grasslands savannas and shrublands	-0.009	-0.019	0.0004	18,000	0.061	fixed
	Large lakes	0.003	-0.005	0.012	18,000	0.405	fixed
	Mediterranean forests woodlands and scrub	0.005	-0.003	0.014	18,000	0.188	fixed
	Montane freshwaters	0.011	-0.028	0.051	18,000	0.574	fixed
	Montane grasslands and shrublands	0.030	0.010	0.050	18,000	0.003	fixed
	Polar freshwaters	0.004	-0.003	0.012	18,000	0.258	fixed
	Polar seas	-0.011	-0.035	0.014	18,000	0.397	fixed
	Temperate forests	0.002	-0.002	0.005	18,000	0.318	fixed
	Temperate wetlands and rivers	0.002	-0.002	0.007	18,000	0.226	fixed
	Temperate grasslands savannas	-0.004	-0.011	0.003	18,000	0.247	fixed

	and shrublands						
	Tropical wetlands and rivers	0.002	-0.007	0.011	18,000	0.725	fixed
	Tropical and subtropical forests	0.018	0.009	0.027	18,000	0.0001	fixed
	Tropical coral	0.024	0.012	0.037	18,000	0.0001	fixed
	Tundra	0.007	-0.002	0.015	19,239	0.111	fixed
	Xeric freshwaters and endorheic basins	-0.002	-0.017	0.013	18,000	0.831	fixed
	sigma	0.003	0.003	0.003	15,790		residual
Biome - slope	Boreal forests/taiga	0.002	-0.004	0.007	18,000	0.523	fixed
	Deserts and xeric shrublands	-0.027	-0.050	-0.002	18,000	0.031	fixed
	Trop. and subtrop. grasslands savannas and shrublands	-0.017	-0.030	-0.004	18,000	0.014	fixed
	Large lakes	0.002	-0.010	0.015	18,781	0.792	fixed
	Mediterranean forests woodlands and scrub	0.010	-0.002	0.023	17,610	0.109	fixed
	Montane freshwaters	0.021	-0.034	0.074	18,000	0.445	fixed
	Montane grasslands and shrublands	0.021	-0.005	0.046	17,224	0.115	fixed
	Polar freshwaters	0.003	-0.009	0.014	18,000	0.660	fixed
	Polar seas	-0.016	-0.046	0.015	17,196	0.320	fixed
	Temperate forests	0.003	-0.001	0.008	17,408	0.165	fixed
	Temperate wetlands and rivers	0.004	-0.001	0.010	18,000	0.123	fixed
	Temperate grasslands savannas and shrublands	-0.001	-0.010	0.007	18,000	0.780	fixed
	Tropical wetlands and rivers	0.003	-0.011	0.016	18,000	0.713	fixed
	Tropical and subtropical forests	0.025	0.012	0.038	17,560	0.0002	fixed
	Tropical coral	0.036	0.019	0.052	18,000	0.0001	fixed
	Tundra	0.013	-0.0003	0.026	17,563	0.048	fixed

	Xeric freshwaters and endorheic basins	0.014	-0.010	0.038	18,257	0.265	fixed
	sigma	0.003	0.003	0.003	13,753		residual
Biome - weighted	Boreal forests/taiga	0.003	-0.003	0.010	18,000	0.334	fixed
	Deserts and xeric shrublands	-0.019	-0.049	0.011	18,000	0.208	fixed
	Trop. and subtrop. grasslands savannas and shrublands	-0.004	-0.021	0.013	18,000	0.635	fixed
	Large lakes	0.007	-0.007	0.021	18,000	0.336	fixed
	Mediterranean forests woodlands and scrub	0.006	-0.008	0.020	19,170	0.402	fixed
	Montane freshwaters	0.023	-0.044	0.094	18,000	0.521	fixed
	Montane grasslands and shrublands	0.037	0.003	0.071	20,405	0.033	fixed
	Polar freshwaters	0.012	-0.001	0.025	18,000	0.069	fixed
	Polar seas	-0.023	-0.066	0.018	18,000	0.292	fixed
	Temperate forests	0.003	-0.003	0.009	18,000	0.265	fixed
	Temperate wetlands and rivers	0.005	-0.002	0.012	17,585	0.169	fixed
	Temperate grasslands savannas and shrublands	-0.008	-0.019	0.004	18,000	0.161	fixed
	Tropical wetlands and rivers	0.006	-0.010	0.022	18,000	0.473	fixed
	Tropical and subtropical forests	0.014	-0.001	0.029	18,000	0.068	fixed
	Tropical coral	0.039	0.018	0.060	18,000	0.0003	fixed
	Tundra	0.013	-0.001	0.027	18,000	0.071	fixed
	Xeric freshwaters and endorheic basins	-0.021	-0.048	0.003	18,000	0.099	fixed
	sigma	0.008	0.007	0.008	16,533		residual
Biome - fluctuations σ	Boreal forests/taiga	0.018	0.015	0.021	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.044	0.031	0.057	18,000	0.0001	fixed

	Trop. and subtrop. grasslands savannas and shrublands	0.044	0.037	0.051	18,000	0.0001	fixed
	Large lakes	0.024	0.018	0.030	18,000	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.022	0.016	0.028	18,000	0.0001	fixed
	Montane freshwaters	0.047	0.018	0.075	18,000	0.001	fixed
	Montane grasslands and shrublands	0.031	0.016	0.046	18,000	0.0001	fixed
	Polar freshwaters	0.027	0.021	0.033	17,652	0.0001	fixed
	Polar seas	0.037	0.019	0.055	17,689	0.0001	fixed
	Temperate forests	0.019	0.017	0.022	17,789	0.0001	fixed
	Temperate wetlands and rivers	0.024	0.022	0.027	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.015	0.010	0.020	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.046	0.039	0.054	18,000	0.0001	fixed
	Tropical and subtropical forests	0.041	0.035	0.048	17,508	0.0001	fixed
	Tropical coral	0.029	0.020	0.038	18,000	0.0001	fixed
	Tundra	0.020	0.014	0.026	18,497	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.039	0.028	0.052	18,845	0.0001	fixed
	sigma	0.002	0.002	0.002	14,440		residual
Biome - fluctuations CI	Boreal forests/taiga	0.091	0.083	0.100	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.210	0.173	0.247	17,389	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.200	0.178	0.222	18,000	0.0001	fixed
	Large lakes	0.112	0.095	0.130	18,000	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.132	0.115	0.150	18,000	0.0001	fixed

	Montane freshwaters	0.197	0.108	0.286	18,000	0.0001	fixed
	Montane grasslands and shrublands	0.163	0.121	0.206	18,000	0.0001	fixed
	Polar freshwaters	0.147	0.132	0.164	18,000	0.0001	fixed
	Polar seas	0.146	0.096	0.204	17,894	0.0001	fixed
	Temperate forests	0.099	0.091	0.107	18,000	0.0001	fixed
	Temperate wetlands and rivers	0.132	0.123	0.141	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.092	0.077	0.106	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.219	0.198	0.239	18,000	0.0001	fixed
	Tropical and subtropical forests	0.197	0.178	0.215	18,405	0.0001	fixed
	Tropical coral	0.161	0.135	0.189	18,000	0.0001	fixed
	Tundra	0.107	0.090	0.124	18,338	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.177	0.146	0.211	18,000	0.0001	fixed
	sigma	0.011	0.011	0.011	17,482		residual
Biome - fluctuations CI weighted	Boreal forests/taiga	0.104	0.092	0.115	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.239	0.190	0.288	18,524	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.248	0.220	0.274	18,431	0.0001	fixed
	Large lakes	0.134	0.111	0.158	16,663	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.162	0.137	0.187	18,000	0.0001	fixed
	Montane freshwaters	0.276	0.161	0.393	18,000	0.0001	fixed
	Montane grasslands and shrublands	0.173	0.121	0.222	17,341	0.0001	fixed
	Polar freshwaters	0.172	0.149	0.193	18,386	0.0001	fixed
	Polar seas	0.169	0.103	0.237	18,368	0.0001	fixed
	Temperate forests	0.107	0.097	0.116	18,000	0.0001	fixed

	Temperate wetlands and rivers	0.156	0.144	0.169	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.107	0.090	0.124	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.239	0.211	0.267	18,000	0.0001	fixed
	Tropical and subtropical forests	0.216	0.190	0.242	18,000	0.0001	fixed
	Tropical coral	0.183	0.147	0.218	18,000	0.0001	fixed
	Tundra	0.114	0.091	0.137	18,000	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.230	0.186	0.273	18,000	0.0001	fixed
	sigma	0.010	0.010	0.011	16,732		residual
Biome - fluctuations SE	Boreal forests/taiga	0.086	0.077	0.096	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.204	0.162	0.242	18,000	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.126	0.102	0.150	18,000	0.0001	fixed
	Large lakes	0.095	0.076	0.114	17,101	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.149	0.131	0.167	17,283	0.0001	fixed
	Montane freshwaters	0.184	0.091	0.283	18,000	0.0002	fixed
	Montane grasslands and shrublands	0.110	0.065	0.156	18,000	0.0001	fixed
	Polar freshwaters	0.152	0.134	0.169	18,000	0.0001	fixed
	Polar seas	0.076	0.019	0.137	18,000	0.011	fixed
	Temperate forests	0.094	0.086	0.103	18,000	0.0001	fixed
	Temperate wetlands and rivers	0.123	0.113	0.133	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.096	0.080	0.111	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.229	0.207	0.251	18,000	0.0001	fixed

	Tropical and subtropical forests	0.154	0.133	0.174	18,000	0.0001	fixed
	Tropical coral	0.187	0.158	0.218	18,580	0.0001	fixed
	Tundra	0.111	0.092	0.129	18,663	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.129	0.095	0.163	18,000	0.0001	fixed
	sigma	0.012	0.011	0.012	17,110		residual
Biome - fluctuations SD	Boreal forests/taiga	0.523	0.517	0.530	18,000	0.0001	fixed
	Deserts and xeric shrublands	0.585	0.556	0.614	18,000	0.0001	fixed
	Trop. and subtrop. grasslands savannas and shrublands	0.602	0.585	0.619	18,000	0.0001	fixed
	Large lakes	0.540	0.527	0.555	18,000	0.0001	fixed
	Mediterranean forests woodlands and scrub	0.574	0.560	0.587	18,300	0.0001	fixed
	Montane freshwaters	0.605	0.537	0.671	18,000	0.0001	fixed
	Montane grasslands and shrublands	0.583	0.549	0.616	18,000	0.0001	fixed
	Polar freshwaters	0.570	0.557	0.582	18,000	0.0001	fixed
	Polar seas	0.548	0.504	0.588	18,000	0.0001	fixed
	Temperate forests	0.536	0.531	0.542	18,000	0.0001	fixed
	Temperate wetlands and rivers	0.557	0.551	0.564	18,000	0.0001	fixed
	Temperate grasslands savannas and shrublands	0.526	0.515	0.537	18,000	0.0001	fixed
	Tropical wetlands and rivers	0.608	0.593	0.625	18,000	0.0001	fixed
	Tropical and subtropical forests	0.614	0.600	0.629	18,000	0.0001	fixed
	Tropical coral	0.609	0.588	0.629	18,264	0.0001	fixed
	Tundra	0.539	0.525	0.553	18,000	0.0001	fixed
	Xeric freshwaters and endorheic basins	0.556	0.530	0.580	18,000	0.0001	fixed

	sigma	0.007	0.007	0.008	17,425		residual
Taxa - *μ*	Actinopterygii	0.00004	-0.004	0.004	18,851	0.986	fixed
	Amphibia	-0.012	-0.022	-0.002	17,369	0.027	fixed
	Aves	0.003	0.001	0.006	18,000	0.007	fixed
	Elasmobranchii	-0.010	-0.022	0.002	17,095	0.097	fixed
	Mammalia	0.010	0.005	0.015	19,689	0.0001	fixed
	Reptilia	0.010	0.001	0.020	18,000	0.029	fixed
	sigma	0.003	0.003	0.003	16,346		residual
Taxa - weighted	Actinopterygii	-0.001	-0.007	0.004	18,000	0.744	fixed
	Amphibia	-0.016	-0.032	-0.001	18,000	0.046	fixed
	Aves	0.005	0.002	0.008	18,000	0.003	fixed
	Elasmobranchii	-0.017	-0.035	0.002	18,000	0.077	fixed
	Mammalia	0.011	0.004	0.017	18,490	0.001	fixed
	Reptilia	0.004	-0.010	0.018	18,000	0.578	fixed
	sigma	0.003	0.003	0.003	14,129		residual
Taxa - slope	Actinopterygii	-0.001	-0.008	0.005	18,000	0.664	fixed
	Amphibia	-0.020	-0.037	-0.002	16,874	0.026	fixed
	Aves	0.006	0.001	0.010	18,000	0.009	fixed
	Elasmobranchii	-0.018	-0.039	0.002	17,613	0.083	fixed
	Mammalia	0.011	0.003	0.020	18,000	0.012	fixed
	Reptilia	0.022	0.006	0.038	18,000	0.007	fixed
	sigma	0.008	0.008	0.008	16,177		residual
Taxa - fluctuations *σ*	Actinopterygii	0.032	0.030	0.035	17,489	0.0001	fixed
	Amphibia	0.040	0.033	0.047	18,000	0.0001	fixed
	Aves	0.018	0.017	0.020	18,000	0.0001	fixed
	Elasmobranchii	0.030	0.022	0.039	18,000	0.0001	fixed
	Mammalia	0.035	0.032	0.038	17,868	0.0001	fixed
	Reptilia	0.034	0.028	0.041	18,000	0.0001	fixed
	sigma	0.002	0.002	0.002	13,289		residual
Taxa - fluctuations CI	Actinopterygii	0.163	0.155	0.171	18,000	0.0001	fixed
	Amphibia	0.208	0.186	0.231	18,000	0.0001	fixed
	Aves	0.094	0.089	0.099	17,127	0.0001	fixed
	Elasmobranchii	0.152	0.125	0.177	18,000	0.0001	fixed
	Mammalia	0.182	0.172	0.193	18,000	0.0001	fixed
	Reptilia	0.195	0.176	0.216	18,476	0.0001	fixed
	sigma	0.012	0.011	0.012	18,000		residual
Taxa - fluctuations CI weighted	Actinopterygii	0.191	0.180	0.202	18,000	0.0001	fixed
	Amphibia	0.272	0.242	0.304	17,535	0.0001	fixed

	Aves	0.105	0.098	0.112	18,000	0.0001	fixed
	Elasmobranchii	0.197	0.160	0.232	18,434	0.0001	fixed
	Mammalia	0.212	0.198	0.226	19,200	0.0001	fixed
	Reptilia	0.229	0.201	0.257	18,000	0.0001	fixed
	sigma	0.011	0.011	0.012	17,175		residual
Taxa - fluctuations SE	Actinopterygii	0.159	0.150	0.168	18,000	0.0001	fixed
	Amphibia	0.224	0.199	0.247	17,493	0.0001	fixed
	Aves	0.080	0.074	0.086	18,000	0.0001	fixed
	Elasmobranchii	0.151	0.124	0.179	18,000	0.0001	fixed
	Mammalia	0.157	0.145	0.169	18,000	0.0001	fixed
	Reptilia	0.233	0.211	0.255	18,000	0.0001	fixed
	sigma	0.011	0.011	0.012	18,000		residual
Taxa - fluctuations SD	Actinopterygii	0.572	0.566	0.579	18,000	0.0001	fixed
	Amphibia	0.612	0.596	0.630	18,000	0.0001	fixed
	Aves	0.530	0.526	0.534	18,000	0.0001	fixed
	Elasmobranchii	0.563	0.542	0.582	18,000	0.0001	fixed
	Mammalia	0.603	0.595	0.611	18,000	0.0001	fixed
	Reptilia	0.610	0.595	0.625	18,000	0.0001	fixed
	sigma	0.008	0.007	0.008	18,000		residual
Number of time points - μ	points	0.00002	-0.00004	0.0001	18,000	0.464	fixed
	sigma	0.003	0.003	0.003	16,697		residual
Number of time points – σ (fluctuations)	points	0.0002	0.0001	0.0003	16,224	0.0001	fixed
	sigma	0.002	0.002	0.002	16,816		residual
Duration	duration	0.0001	0.00003	0.0001	18,398	0.001	fixed
	sigma	0.003	0.003	0.004	18,000		residual
Duration * System interaction	Freshwater	0.006	0.002	0.010	17,386	0.008	fixed
	Marine	0.009	0.004	0.014	18,000	0.001	fixed
	Terrestrial	0.009	0.006	0.013	18,000	0.0001	fixed
	duration	-0.0001	-0.0002	0.0001	18,025	0.532	fixed
	Marine:duration	-0.0002	-0.001	0.0001	18,000	0.162	fixed
	Terrestrial:duration	-0.0002	-0.0004	0.00004	17,941	0.113	fixed
	sigma	0.003	0.003	0.004	18,062		residual
Duration * Taxa interaction	Actinopterygii	0.0005	-0.006	0.007	18,000	0.890	fixed
	Amphibia	-0.019	-0.039	0.002	18,000	0.077	fixed
	Aves	0.010	0.006	0.014	18,000	0.0001	fixed

	Mammalia	0.011	0.003	0.019	18,000	0.009	fixed
	Reptilia	0.023	0.010	0.038	18,000	0.001	fixed
	duration	-0.00003	-0.0004	0.0003	18,000	0.879	fixed
	Amphibia:duration	0.001	-0.001	0.002	18,000	0.444	fixed
	Aves:duration	-0.0002	-0.001	0.0001	18,000	0.242	fixed
	Mammalia:duration	-0.00001	-0.001	0.001	18,000	0.956	fixed
	Reptilia:duration	-0.001	-0.002	-0.0001	18,000	0.026	fixed
	sigma	0.003	0.003	0.003	16,297		residual
Sampling units - *μ*	(Intercept)	-0.0001	-0.003	0.003	18,000	0.918	fixed
	Individuals (1167)	0.006	0.002	0.010	18,000	0.003	fixed
	Pairs (505)	0.015	0.009	0.020	18,000	0.0001	fixed
	Nests (224)	0.015	0.007	0.023	18,000	0.0002	fixed
	Population estimate (97)	0.017	0.007	0.027	18,000	0.001	fixed
	sigma	0.002	0.002	0.002	15,983		residual
Geographic range birds/mammals - *μ*	(Intercept)	0.012	-0.002	0.026	18,000	0.082	fixed
	log(Geographic range)	-0.0005	-0.001	0.0004	18,000	0.278	fixed
	sigma	0.003	0.003	0.003	17,575		residual
Geographic range birds/mammals - *μ* * taxa interaction	(Intercept)	0.068	0.031	0.107	18,000	0.0002	fixed
	log(Geographic range)	-0.004	-0.007	-0.002	18,000	0.001	fixed
	Aves	-0.076	-0.119	-0.031	18,000	0.001	fixed
	log(Geographic range):Aves	0.005	0.002	0.008	18,000	0.001	fixed
	sigma	0.003	0.003	0.003	16,888		residual
Geographic range birds/mammals - weighted	(Intercept)	0.013	-0.011	0.038	18,000	0.295	fixed
	log(Geographic range)	-0.0004	-0.002	0.001	18,000	0.564	fixed
	sigma	0.003	0.003	0.003	16,791		residual
Geographic range birds/mammals - slope	(Intercept)	0.010	-0.020	0.041	18,433	0.515	fixed
	log.range	-0.0002	-0.002	0.002	18,408	0.813	fixed
	sigma	0.008	0.007	0.008	16,986		residual
Geographic range	(Intercept)	0.046	0.032	0.060	18,000	0.0001	fixed

birds/mammals - fluctuations *σ*							
	log(Geographic range)	-0.001	-0.002	-0.001	18,000	0.001	fixed
	sigma	0.002	0.002	0.002	15,577		residual
Geographic range birds/mammals - fluctuations CI	(Intercept)	0.180	0.137	0.226	18,000	0.0001	fixed
	log(Geographic range)	-0.004	-0.007	-0.001	18,769	0.003	fixed
	sigma	0.011	0.011	0.011	18,000		residual
Geographic range birds/mammals - fluctuations CI weighted	(Intercept)	0.173	0.117	0.233	18,000	0.0001	fixed
	log(Geographic range)	-0.003	-0.006	0.001	18,000	0.122	fixed
	sigma	0.011	0.010	0.011	18,000		residual
Geographic range birds/mammals - fluctuations SE	(Intercept)	0.082	0.037	0.126	17,605	0.0001	fixed
	log(Geographic range)	0.001	-0.002	0.004	17,534	0.512	fixed
	sigma	0.011	0.011	0.011	18,000		residual
Geographic range birds/mammals - fluctuations SD	(Intercept)	0.605	0.571	0.638	17,938	0.0001	fixed
	log(Geographic range)	-0.004	-0.006	-0.002	17,306	0.0004	fixed
	sigma	0.008	0.007	0.008	18,000		residual
Mean population size - *μ*	(Intercept)	0.001	-0.003	0.005	18,000	0.794	fixed
	log(Mean population size)	0.001	0.001	0.002	18,000	0.0004	fixed
	sigma	0.004	0.004	0.004	15,837		residual
Mean population size - *μ* * taxa interaction	(Intercept)	0.007	-0.003	0.018	18,000	0.161	fixed
	log(Mean population size)	-0.001	-0.003	0.001	18,000	0.197	fixed
	Amphibia	-0.006	-0.027	0.017	18,000	0.615	fixed
	Aves	-0.009	-0.021	0.003	18,000	0.133	fixed
	Elasmobranchii	-0.025	-0.050	0.0004	18,000	0.055	fixed

	Mammalia	-0.009	-0.022	0.006	18,000	0.211	fixed
	Reptilia	0.007	-0.011	0.025	18,000	0.434	fixed
	log(Mean population size):Amphibia	-0.003	-0.008	0.002	19,145	0.215	fixed
	log(Mean population size):Aves	0.003	0.001	0.005	18,000	0.003	fixed
	log(Mean population size):Elasmobranchii	0.005	-0.001	0.012	18,428	0.127	fixed
	log(Mean population size):Mammalia	0.004	0.001	0.006	18,000	0.002	fixed
	log(Mean population size):Reptilia	0.001	-0.003	0.004	18,000	0.772	fixed
	sigma	0.004	0.004	0.004	16,486		residual
Mean population size - weighted	(Intercept)	0.002	-0.005	0.008	18,000	0.611	fixed
	log(Mean population size)	0.001	0.0003	0.002	18,000	0.014	fixed
	sigma	0.005	0.004	0.005	13,784		residual
Mean population size - slope	(Intercept)	-0.0002	-0.007	0.006	18,000	0.946	fixed
	log(Mean population size)	0.002	0.001	0.003	18,000	0.0002	fixed
	sigma	0.011	0.010	0.012	15,825		residual
Mean population size - fluctuations *σ*	(Intercept)	0.034	0.032	0.037	18,000	0.0001	fixed
	log(Mean population size)	-0.001	-0.001	-0.0002	18,000	0.003	fixed
	sigma	0.002	0.002	0.002	6,763		residual
Mean population size - fluctuations CI	(Intercept)	0.222	0.212	0.232	18,000	0.0001	fixed
	log(Mean population size)	-0.004	-0.006	-0.003	18,000	0.0001	fixed
	sigma	0.026	0.025	0.027	14,178		residual
Mean population size - fluctuations CI weighted	(Intercept)	0.262	0.249	0.275	18,000	0.0001	fixed

	log(Mean population size)	-0.007	-0.009	-0.004	18,000	0.0001	fixed
	sigma	0.026	0.025	0.028	13,162		residual
Mean population size - fluctuations SE	(Intercept)	0.228	0.218	0.238	18,000	0.0001	fixed
	log(Mean population size)	-0.010	-0.012	-0.008	18,000	0.0001	fixed
	sigma	0.023	0.022	0.024	15,480		residual
Mean population size - fluctuations SD	(Intercept)	0.001	-0.001	0.003	17,324	0.454	fixed
	log(Mean population size)	0.00000	-0.00001	0.00002	18,000	0.556	fixed
	sigma	0.00000	0.00000	0.00000	18,000		residual
Habitat specificity - *μ*	(Intercept)	0.002	-0.001	0.006	18,000	0.176	fixed
	Habitat specificity	0.0002	-0.0002	0.001	18,000	0.321	fixed
	sigma	0.003	0.003	0.003	15,647		residual
Habitat specificity - *μ* * taxa interaction	(Intercept)	0.003	-0.004	0.011	18,000	0.443	fixed
	Habitat specificity	-0.0004	-0.002	0.001	18,187	0.538	fixed
	Amphibia	-0.015	-0.035	0.004	17,354	0.130	fixed
	Aves	-0.002	-0.011	0.007	18,000	0.652	fixed
	Cephalaspidomorphi	0.016	-0.103	0.132	18,000	0.796	fixed
	Elasmobranchii	-0.027	-0.055	0.001	17,291	0.059	fixed
	Holocephali	-0.105	-0.224	0.013	18,000	0.082	fixed
	Mammalia	0.008	-0.003	0.018	18,000	0.168	fixed
	Myxini	-0.063	-0.145	0.022	18,000	0.146	fixed
	Reptilia	0.015	-0.007	0.036	18,000	0.176	fixed
	Habitat specificity:Amphibia	0.0003	-0.002	0.002	17,509	0.753	fixed
	Habitat specificity:Aves	0.001	-0.001	0.002	18,000	0.261	fixed
	Habitat specificity:Elasmobranchii	0.005	-0.003	0.013	18,000	0.264	fixed
	Habitat specificity:Mammalia	0.001	-0.001	0.002	19,769	0.494	fixed
	Habitat specificity:Reptilia	-0.001	-0.004	0.002	18,000	0.503	fixed

	sigma	0.003	0.003	0.003	16,057		residual
Habitat specificity - weighted	(Intercept)	0.002	-0.003	0.006	18,000	0.443	fixed
	Habitat specificity	0.0004	-0.0001	0.001	18,000	0.128	fixed
	sigma	0.003	0.003	0.003	13,856		residual
Habitat specificity - slope	(Intercept)	0.003	-0.003	0.009	18,000	0.317	fixed
	Habitat specificity	0.0003	-0.0003	0.001	18,000	0.321	fixed
	sigma	0.008	0.008	0.009	16,422		residual
Habitat specificity - fluctuations *σ*	(Intercept)	0.023	0.021	0.025	16,596	0.0001	fixed
	Habitat specificity	0.0002	-0.0001	0.0005	17,782	0.123	fixed
	sigma	0.002	0.002	0.002	14,047		residual
Habitat specificity - fluctuations CI	(Intercept)	0.126	0.118	0.134	18,000	0.0001	fixed
	Habitat specificity	0.001	-0.0002	0.002	18,000	0.117	fixed
	sigma	0.012	0.011	0.012	18,411		residual
Habitat specificity - fluctuations CI weighted	(Intercept)	0.140	0.129	0.151	18,000	0.0001	fixed
	Habitat specificity	0.001	-0.0001	0.002	18,000	0.065	fixed
	sigma	0.011	0.011	0.012	18,131		residual
Habitat specificity - fluctuations SE	(Intercept)	0.117	0.108	0.126	18,000	0.0001	fixed
	Habitat specificity	0.001	-0.0002	0.002	18,000	0.138	fixed
	sigma	0.012	0.012	0.012	17,484		residual
Habitat specificity - fluctuations SD	(Intercept)	0.555	0.549	0.561	18,000	0.0001	fixed
	Habitat specificity	0.0003	-0.0004	0.001	16,414	0.349	fixed
	sigma	0.008	0.008	0.008	18,000		residual
IUCN Red List Categories - *μ*	Least concern	0.005	0.003	0.008	18,000	0.0001	fixed
	Near threatened	-0.004	-0.012	0.004	18,000	0.319	fixed
	Vulnerable	0.003	-0.005	0.010	18,000	0.427	fixed
	Endangered	-0.004	-0.013	0.006	18,000	0.452	fixed
	Critically endangered	-0.007	-0.020	0.005	18,541	0.259	fixed
	sigma	0.003	0.003	0.003	15,497		residual

IUCN Red List Categories - weighted	Least concern	0.007	0.004	0.010	18,000	0.0001	fixed
	Near threatened	0.001	-0.010	0.011	18,241	0.852	fixed
	Vulnerable	0.003	-0.008	0.013	18,000	0.626	fixed
	Endangered	-0.007	-0.020	0.006	18,000	0.291	fixed
	Critically endangered	-0.014	-0.032	0.004	18,000	0.114	fixed
	sigma	0.003	0.003	0.003	14,285		residual
IUCN Red List Categories - slope	Least concern	0.009	0.005	0.012	18,905	0.0001	fixed
	Near threatened	-0.011	-0.024	0.003	18,000	0.121	fixed
	Vulnerable	0.003	-0.010	0.016	16,528	0.684	fixed
	Endangered	-0.007	-0.023	0.009	18,000	0.423	fixed
	Critically endangered	-0.013	-0.034	0.009	18,000	0.254	fixed
	sigma	0.008	0.008	0.009	15,931		residual
IUCN Red List Categories - fluctuations σ	Least concern	0.023	0.022	0.025	16,756	0.0001	fixed
	Near threatened	0.028	0.023	0.033	17,565	0.0001	fixed
	Vulnerable	0.027	0.022	0.032	20,081	0.0001	fixed
	Endangered	0.032	0.026	0.039	18,000	0.0001	fixed
	Critically endangered	0.039	0.031	0.048	18,000	0.0001	fixed
	sigma	0.002	0.002	0.002	13,906		residual
IUCN Red List Categories - fluctuations CI	Least concern	0.124	0.118	0.129	18,000	0.0001	fixed
	Near threatened	0.152	0.134	0.171	18,000	0.0001	fixed
	Vulnerable	0.151	0.134	0.169	17,076	0.0001	fixed
	Endangered	0.168	0.146	0.189	20,476	0.0001	fixed
	Critically endangered	0.178	0.150	0.208	18,000	0.0001	fixed
	sigma	0.012	0.012	0.012	17,734		residual
IUCN Red List Categories - fluctuations CI weighted	Least concern	0.140	0.133	0.147	18,000	0.0001	fixed
	Near threatened	0.172	0.147	0.196	17,244	0.0001	fixed
	Vulnerable	0.171	0.148	0.195	18,589	0.0001	fixed
	Endangered	0.194	0.165	0.222	18,000	0.0001	fixed

	Critically endangered	0.193	0.155	0.231	18,000	0.0001	fixed
	sigma	0.012	0.011	0.012	17,086		residual
IUCN Red List Categories - fluctuations SE	Least concern	0.119	0.113	0.125	18,000	0.0001	fixed
	Near threatened	0.135	0.114	0.156	18,000	0.0001	fixed
	Vulnerable	0.127	0.107	0.147	18,000	0.0001	fixed
	Endangered	0.143	0.119	0.167	18,000	0.0001	fixed
	Critically endangered	0.149	0.116	0.180	17,444	0.0001	fixed
	sigma	0.012	0.012	0.012	18,000		residual
IUCN Red List Categories - fluctuations SD	Least concern	0.550	0.546	0.554	18,000	0.0001	fixed
	Near threatened	0.575	0.561	0.589	18,000	0.0001	fixed
	Vulnerable	0.573	0.559	0.586	17,618	0.0001	fixed
	Endangered	0.596	0.580	0.613	18,000	0.0001	fixed
	Critically endangered	0.604	0.582	0.625	17,544	0.0001	fixed
	sigma	0.008	0.008	0.008	17,153		residual
IUCN threat type - *μ*	Fishing / harvesting aquatic resources	0.005	-0.0005	0.010	18,000	0.085	fixed
	Hunting / trapping terrestrial animals	0.005	-0.0003	0.010	18,000	0.068	fixed
	Annual / perennial non-timber crops	0.005	-0.0004	0.012	18,000	0.080	fixed
	Intentional use (species is the target)	0.005	-0.001	0.011	18,000	0.092	fixed
	Habitat shifting / alteration	0.005	-0.001	0.011	18,000	0.098	fixed
	Housing / urban areas	0.004	-0.002	0.011	17,916	0.210	fixed
	Unintentional effects: (large scale) [harvest]	0.004	-0.002	0.010	19,228	0.205	fixed
	Intentional use: (subsistence /small scale) [harvest]	0.005	-0.002	0.012	18,423	0.192	fixed
	Agricultural / forestry effluents	0.005	-0.002	0.011	18,000	0.153	fixed

	Intentional use: (large scale) [harvest]	0.004	-0.003	0.011	17,575	0.257	fixed
	sigma	0.004	0.004	0.004	18,000		residual
IUCN threat number - μ	(Intercept)	0.004	-0.001	0.009	18,000	0.145	fixed
	Number of threats	0.0001	-0.0004	0.001	18,000	0.726	fixed
	sigma	0.004	0.004	0.004	16,084		residual
IUCN threat type - fluctuations σ	Fishing / harvesting aquatic resources	0.033	0.028	0.037	17,468	0.0001	fixed
	Hunting / trapping terrestrial animals	0.033	0.029	0.038	17,547	0.0001	fixed
	Annual / perennial non-timber crops	0.033	0.029	0.038	17,225	0.0001	fixed
	Intentional use (species is the target)	0.033	0.029	0.038	18,000	0.0001	fixed
	Habitat shifting / alteration	0.032	0.028	0.037	17,548	0.0001	fixed
	Housing / urban areas	0.034	0.029	0.039	18,000	0.0001	fixed
	Unintentional effects: (large scale) [harvest]	0.033	0.028	0.037	17,134	0.0001	fixed
	Intentional use: (subsistence/small scale) [harvest]	0.033	0.028	0.038	18,000	0.0001	fixed
	Agricultural / forestry effluents	0.033	0.028	0.037	17,571	0.0001	fixed
	Intentional use: (large scale) [harvest]	0.032	0.027	0.037	18,000	0.0001	fixed
	sigma	0.002	0.002	0.002	18,000		residual
IUCN threat number - fluctuations σ	(Intercept)	0.029	0.026	0.032	17,078	0.0001	fixed
	Number of threats	0.0001	-0.0002	0.0004	18,000	0.475	fixed
	sigma	0.002	0.002	0.002	7,021		residual

Appendix 3.23. Model outputs from UK-scale analyses. Sigma is the overall model residual variance. Net population change is estimated using μ values derived from state-space models of population abundance versus time and slopes of linear models of population abundance versus time. The weighted μ models included μ as a response variable, weighted by τ, the observation error estimate derived from the state-space models. The fluctuation models included the process noise (σ^2) values from state-space models, half of the 95% confidence interval around the μ value of population change, the standard error around the slopes of linear models of population abundance versus time, and the standard deviation of the raw time series data for each population. The process noise is a metric of population fluctuations, whereas the rest of the metrics show population variability. The weighted fluctuation models were weighted by τ, the observation error estimate derived from the state-space models.

Model name	Variable	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample size	pMCMC	Effect
Realm - μ	Terrestrial	0.011	-0.003	0.023	18,000	0.105	fixed
	Marine	0.007	-0.006	0.020	18,000	0.297	fixed
	Freshwater	0.030	0.010	0.049	17,098	0.002	fixed
	sigma	0.003	0.003	0.004	13,565		residual
Realm - weighted	Terrestrial	0.015	0.0004	0.030	18,000	0.038	fixed
	Marine	0.008	-0.008	0.024	18,000	0.303	fixed
	Freshwater	0.027	0.005	0.050	18,000	0.021	fixed
	sigma	0.003	0.002	0.004	10,568		residual
Realm - slope	Freshwater	0.062	0.025	0.098	18,000	0.0003	fixed
	Marine	0.007	-0.018	0.031	18,000	0.601	fixed
	Terrestrial	0.020	-0.004	0.045	18,380	0.114	fixed
	sigma	0.011	0.009	0.012	15,525		residual
Realm - fluctuations σ	Terrestrial	0.085	0.062	0.105	18,000	0.0001	fixed
	Marine	0.056	0.034	0.079	18,000	0.0001	fixed
	Freshwater	0.051	0.019	0.083	18,000	0.002	fixed
	sigma	0.005	0.004	0.006	16,954		residual
Realm - fluctuations CI	Terrestrial	0.193	0.165	0.220	18,000	0.0001	fixed
	Marine	0.118	0.090	0.146	18,000	0.0001	fixed
	Freshwater	0.139	0.100	0.181	18,000	0.0001	fixed

	sigma	0.011	0.009	0.013	15,777		residual
Realm - fluctuations CI weighted	Terrestrial	0.191	0.157	0.224	18,000	0.0001	fixed
	Marine	0.134	0.098	0.172	18,000	0.0001	fixed
	Freshwater	0.164	0.115	0.217	18,001	0.0001	fixed
	sigma	0.010	0.007	0.012	15,014		residual
Taxa - μ	Actinopterygii	-0.003	-0.020	0.014	16,879	0.744	fixed
	Amphibia	-0.0002	-0.051	0.052	18,000	0.995	fixed
	Aves	0.012	0.001	0.022	18,000	0.027	fixed
	Elasmobranchii	0.006	-0.045	0.056	17,998	0.811	fixed
	Mammalia	0.046	0.023	0.069	17,742	0.0001	fixed
	Reptilia	0.044	-0.018	0.108	18,000	0.181	fixed
	sigma	0.004	0.003	0.004	10,343		residual
Taxa - weighted	Actinopterygii	-0.010	-0.033	0.011	18,000	0.374	fixed
	Amphibia	-0.002	-0.065	0.061	18,000	0.947	fixed
	Aves	0.017	0.005	0.029	18,000	0.005	fixed
	Elasmobranchii	0.002	-0.089	0.086	18,000	0.972	fixed
	Mammalia	0.043	0.015	0.069	18,000	0.002	fixed
	Reptilia	0.030	-0.039	0.103	18,000	0.404	fixed
	sigma	0.003	0.002	0.004	9,676		residual
Taxa - slope	Actinopterygii	-0.009	-0.042	0.024	17,082	0.593	fixed
	Amphibia	0.004	-0.095	0.111	18,000	0.931	fixed
	Aves	0.020	0.0001	0.040	18,434	0.046	fixed
	Elasmobranchii	-0.014	-0.106	0.078	18,000	0.766	fixed
	Mammalia	0.099	0.053	0.145	18,000	0.0001	fixed
	Reptilia	0.069	-0.048	0.185	19,449	0.241	fixed
	sigma	0.011	0.009	0.013	14,664		residual
Taxa - fluctuations σ	Actinopterygii	0.051	0.019	0.082	18,000	0.001	fixed
	Amphibia	0.083	-0.023	0.182	18,000	0.117	fixed
	Aves	0.073	0.053	0.091	18,000	0.0001	fixed
	Elasmobranchii	0.072	-0.010	0.154	18,000	0.083	fixed
	Mammalia	0.054	0.012	0.098	18,000	0.014	fixed
	Reptilia	0.123	0.014	0.222	18,000	0.021	fixed
	sigma	0.005	0.004	0.006	17,207		residual
Taxa - fluctuations CI	Actinopterygii	0.113	0.074	0.153	18,891	0.0001	fixed
	Amphibia	0.230	0.107	0.358	18,000	0.0004	fixed
	Aves	0.166	0.143	0.190	18,000	0.0001	fixed
	Elasmobranchii	0.186	0.078	0.290	18,000	0.001	fixed
	Mammalia	0.150	0.095	0.204	18,761	0.0001	fixed
	Reptilia	0.275	0.146	0.410	18,000	0.0002	fixed
	sigma	0.011	0.009	0.013	15,974		residual
Taxa - fluctuations CI weighted	Actinopterygii	0.138	0.088	0.190	18,000	0.0001	fixed
	Amphibia	0.287	0.134	0.448	18,000	0.001	fixed
	Aves	0.169	0.142	0.197	18,255	0.0001	fixed
	Elasmobranchii	0.266	0.097	0.432	17,623	0.003	fixed

	Mammalia	0.156	0.090	0.222	18,000	0.0001	fixed
	Reptilia	0.311	0.158	0.474	18,000	0.0001	fixed
	sigma	0.009	0.007	0.012	14,900		residual
Geographic range (all) - *μ*	(Intercept)	0.006	-0.052	0.063	18,000	0.850	fixed
	log(km2_range)	0.001	-0.003	0.005	18,000	0.762	fixed
	sigma	0.004	0.003	0.004	14,513		residual
Geographic range (all) - weighted	(Intercept)	-0.012	-0.077	0.050	18,000	0.710	fixed
	log.range	0.002	-0.002	0.006	18,000	0.346	fixed
	sigma	0.003	0.002	0.004	13,236		residual
Geographic range (all) - slope	(Intercept)	0.009	-0.105	0.120	18,239	0.870	fixed
	log.range	0.001	-0.006	0.009	18,257	0.755	fixed
	sigma	0.011	0.009	0.013	16,452		residual
Geographic range (all) - fluctuations *σ*	(Intercept)	0.004	-0.101	0.115	18,000	0.939	fixed
	log(km2_range)	0.005	-0.003	0.012	18,000	0.198	fixed
	sigma	0.005	0.004	0.006	18,000		residual
Geographic range (all) - fluctuations CI	(Intercept)	0.045	-0.086	0.177	18,000	0.494	fixed
	log.range	0.008	-0.001	0.017	18,000	0.079	fixed
	sigma	0.011	0.009	0.013	16,713		residual
Geographic range (all) - fluctuations CI weighted	(Intercept)	0.059	-0.104	0.221	18,000	0.472	fixed
	log.range	0.008	-0.003	0.019	18,000	0.162	fixed
	sigma	0.010	0.008	0.013	15,715		residual
Geographic range (all) - fluctuations SE	(Intercept)	0.050	-0.104	0.206	18,000	0.528	fixed
	log.range	0.008	-0.003	0.018	18,000	0.159	fixed
	sigma	0.009	0.007	0.010	18,000		residual
Geographic range (all) - fluctuations SD	(Intercept)	0.171	0.039	0.294	18,000	0.008	fixed
	log.range	0.016	0.007	0.025	18,000	0.0002	fixed
	sigma	0.017	0.014	0.020	15,395		residual
Mean population size - *μ*	(Intercept)	0.023	0.0001	0.047	1,207	0.051	fixed
	log(Mean population size)	-0.0004	-0.004	0.004	2,374	0.860	fixed
	sigma	0.006	0.005	0.008	411		residual
Mean population size - weighted	(Intercept)	0.021	-0.002	0.045	852	0.066	fixed
	log(Mean population size)	-0.0001	-0.004	0.004	1,950	0.964	fixed
	sigma	0.007	0.005	0.009	222		residual
Mean population size - slope	(Intercept)	0.035	-0.006	0.075	1,274	0.071	fixed
	log(meanpop)	-0.001	-0.008	0.006	6,788	0.832	fixed
	sigma	0.022	0.016	0.027	593		residual

Mean population size - fluctuations *σ*	(Intercept)	0.169	0.118	0.216	18,000	0.0001	fixed
	log(Mean population size)	-0.004	-0.013	0.005	18,000	0.389	fixed
	sigma	0.034	0.023	0.045	200		residual
Mean population size - fluctuations CI	(Intercept)	0.298	0.242	0.357	18,000	0.0001	fixed
	log(Mean population size)	-0.009	-0.019	0.001	18,000	0.080	fixed
	sigma	0.026	0.018	0.035	11,283		residual
Mean population size - fluctuations CI weighted	(Intercept)	0.298	0.240	0.354	18,305	0.0001	fixed
	log(Mean population size)	-0.009	-0.019	0.001	18,000	0.077	fixed
	sigma	0.026	0.018	0.035	10,953		residual
Mean population size - fluctuations SE	(Intercept)	0.354	0.293	0.411	18,000	0.0001	fixed
	log(meanpop)	-0.024	-0.034	-0.014	18,099	0.0001	fixed
	sigma	0.014	0.009	0.018	16,950		residual
Mean population size - fluctuations SD	(Intercept)	0.519	0.473	0.565	17,529	0.0001	fixed
	log(Mean population size)	-0.007	-0.016	0.001	17,123	0.086	fixed
	sigma	0.030	0.019	0.039	83		residual
Habitat specificity - *μ*	(Intercept)	0.007	-0.010	0.024	18,000	0.449	fixed
	Habitat specificity	0.001	-0.001	0.002	18,000	0.340	fixed
	sigma	0.004	0.003	0.005	13,436		residual
Habitat specificity (profiling) - *μ*	(Intercept)	0.013	-0.005	0.030	18,000	0.173	fixed
	Habitat specificity	-0.0002	-0.003	0.002	18,000	0.864	fixed
	sigma	0.005	0.004	0.005	8,201		residual
Habitat specificity - weighted	(Intercept)	0.009	-0.012	0.030	18,441	0.381	fixed
	Habitat specificity	0.001	-0.001	0.003	18,000	0.424	fixed
	sigma	0.003	0.002	0.004	10,360		residual
Habitat specificity - slope	(Intercept)	0.013	-0.020	0.046	17,956	0.434	fixed
	Habitat specificity	0.001	-0.002	0.004	17,589	0.434	fixed
	sigma	0.011	0.009	0.014	13,969		residual
Habitat specificity (profiling) - slope	(Intercept)	0.015	-0.020	0.049	18,509	0.394	fixed
	Habitat specificity	0.0004	-0.004	0.005	17,454	0.852	fixed
	sigma	0.013	0.011	0.016	12,446		residual
Habitat specificity - fluctuations *σ*	(Intercept)	0.055	0.027	0.085	18,000	0.0003	fixed
	Habitat specificity	0.002	-0.001	0.004	17,598	0.221	fixed
	sigma	0.005	0.004	0.006	17,516		residual
Habitat specificity (profiling) - fluctuations *σ*	(Intercept)	0.022	0.008	0.038	18,947	0.004	fixed

	Habitat specificity	0.002	-0.0003	0.004	18,000	0.092	fixed
	sigma	0.002	0.001	0.002	12,444		residual
Habitat specificity - fluctuations CI	(Intercept)	0.138	0.101	0.176	18,800	0.0001	fixed
	Habitat specificity	0.003	-0.001	0.006	18,000	0.137	fixed
	sigma	0.011	0.009	0.014	15,996		residual
Habitat specificity - fluctuations CI weighted	(Intercept)	0.146	0.098	0.192	18,046	0.0001	fixed
	Habitat specificity	0.003	-0.001	0.007	19,218	0.205	fixed
	sigma	0.010	0.008	0.013	15,033		residual
Habitat specificity - fluctuations SE	(Intercept)	0.155	0.114	0.198	18,000	0.0001	fixed
	Habitat specificity	0.001	-0.003	0.004	18,000	0.772	fixed
	sigma	0.009	0.007	0.010	18,000		residual
Habitat specificity - fluctuations SD	(Intercept)	0.400	0.360	0.438	17,592	0.0001	fixed
	Habitat specificity	0.0004	-0.003	0.004	18,000	0.844	fixed
	sigma	0.017	0.014	0.020	15,211		residual
IUCN Red List Categories - μ	Least concern	0.013	0.003	0.023	17,332	0.011	fixed
	Near threatened	0.020	-0.014	0.053	18,436	0.259	fixed
	Vulnerable	0.014	-0.028	0.059	18,000	0.516	fixed
	Endangered	-0.038	-0.186	0.114	18,000	0.621	fixed
	Critically endangered	0.070	-0.024	0.166	17,353	0.148	fixed
	sigma	0.004	0.003	0.004	14,117		residual
IUCN Red List Categories - weighted	Least concern	0.017	0.006	0.029	17,546	0.003	fixed
	Near threatened	0.025	-0.017	0.064	16,702	0.222	fixed
	Vulnerable	0.001	-0.046	0.048	18,000	0.964	fixed
	Endangered	-0.038	-0.181	0.102	18,000	0.598	fixed
	Critically endangered	0.044	-0.200	0.283	16,964	0.713	fixed
	sigma	0.003	0.002	0.004	10,497		residual
IUCN Red List Categories - slope	Least concern	0.026	0.007	0.046	18,000	0.009	fixed
	Near threatened	0.016	-0.053	0.079	18,000	0.635	fixed
	Vulnerable	0.017	-0.069	0.102	18,000	0.689	fixed
	Endangered	-0.011	-0.289	0.275	18,091	0.934	fixed
	Critically endangered	0.053	-0.129	0.235	18,475	0.566	fixed
	sigma	0.011	0.009	0.013	15,903		residual
IUCN Red List Categories - fluctuations σ	Least concern	0.073	0.056	0.090	19,089	0.0001	fixed
	Near threatened	0.052	-0.012	0.113	18,000	0.099	fixed
	Vulnerable	0.061	-0.018	0.141	18,461	0.139	fixed
	Endangered	0.173	-0.072	0.417	18,000	0.165	fixed
	Critically endangered	0.003	-0.159	0.166	18,000	0.976	fixed
	sigma	0.005	0.004	0.006	17,270		residual

IUCN Red List Categories - fluctuations CI	Least concern	0.165	0.144	0.187	18,000	0.0001	fixed
	Near threatened	0.134	0.057	0.211	18,000	0.001	fixed
	Vulnerable	0.140	0.041	0.240	18,000	0.005	fixed
	Endangered	0.237	-0.089	0.541	18,433	0.140	fixed
	Critically endangered	0.105	-0.103	0.314	17,573	0.321	fixed
	sigma	0.011	0.009	0.013	16,778		residual
IUCN Red List Categories - fluctuations CI weighted	Least concern	0.175	0.148	0.201	18,000	0.0001	fixed
	Near threatened	0.166	0.071	0.263	18,000	0.001	fixed
	Vulnerable	0.148	0.034	0.264	18,000	0.013	fixed
	Endangered	0.236	-0.100	0.568	18,000	0.176	fixed
	Critically endangered	0.070	-0.256	0.420	18,493	0.690	fixed
	sigma	0.010	0.008	0.012	15,655		residual
IUCN Red List Categories - fluctuations SE	Least concern	0.165	0.141	0.190	18,376	0.0001	fixed
	Near threatened	0.134	0.048	0.227	14,776	0.004	fixed
	Vulnerable	0.113	-0.002	0.228	17,971	0.051	fixed
	Endangered	0.071	-0.281	0.409	18,000	0.692	fixed
	Critically endangered	0.079	-0.156	0.315	18,000	0.516	fixed
	sigma	0.009	0.007	0.010	18,000		residual
IUCN Red List Categories - fluctuations SD	Least concern	0.408	0.386	0.429	18,770	0.0001	fixed
	Near threatened	0.358	0.287	0.432	18,000	0.0001	fixed
	Vulnerable	0.319	0.223	0.418	18,000	0.0001	fixed
	Endangered	0.243	-0.085	0.586	18,000	0.157	fixed
	Critically endangered	0.331	0.129	0.536	18,000	0.002	fixed
	sigma	0.016	0.015	0.016	18,000		residual

Appendix 3.24. Phylogeny model outputs. To account for phylogenetic uncertainty, I ran the phylogenetic models for amphibian, bird and reptile species using 10 different trees for each class, and here I present the mean, min and max values from the different model runs. Sigma is the overall model residual variance. Net population change is estimated using μ values derived from state-space models of population abundance versus time and slopes of linear models of population abundance versus time. The fluctuation models were based on the process noise (σ^2) values from state-space models.

Model name	Variable	Mean pMCMC	Max pMCMC	Min pMCMC	Mean effective sample size	Mean post. mean	Max post. mean	Min post. mean	Mean lower 95% CI	Max lower 95% CI	Min lower 95% CI	Mean upper 95% CI	Max upper 95% CI	Min upper 95% CI
Amphibian population trends	(Intercept)	0.587	0.621	0.558	10047	-0.009	-0.008	-0.009	-0.051	-0.046	-0.054	0.031	0.035	0.027
	Phylogeny				7037	0.001	0.001	0.001	0	0	0	0.004	0.005	0.004
	Sigma				9856	0.006	0.006	0.006	0.004	0.004	0.004	0.007	0.007	0.007
	Species				7912	0.001	0.001	0	0	0	0	0.002	0.002	0.002
Amphibian population fluctuations	(Intercept)	0	0	0	9947	0.155	0.156	0.155	0.104	0.105	0.102	0.208	0.211	0.206
	Phylogeny				9778	0.001	0.001	0.001	0	0	0	0.005	0.006	0.005
	Sigma				10172	0.048	0.048	0.048	0.037	0.038	0.037	0.059	0.06	0.059
	Species				9817	0.001	0.001	0.001	0	0	0	0.003	0.003	0.003
Bird population trends	(Intercept)	0.449	0.63	0.305	10233	0.005	0.005	0.004	-0.009	-0.005	-0.014	0.018	0.021	0.016
	Phylogeny				3770	0	0	0	0	0	0	0	0.001	0
	Sigma				9992	0.002	0.002	0.002	0.002	0.002	0.002	0.003	0.003	0.003
	Species				6682	0	0	0	0	0	0	0	0	0
Bird population fluctuations	(Intercept)	0.001	0.006	0	10183	0.02	0.02	0.019	0.01	0.013	0.007	0.029	0.032	0.027

	Phylogeny				3995	0	0	0	0	0	0	0	0	0
	Sigma				9221	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
	Species				5322	0	0	0	0	0	0	0	0	0
Reptile population trends	(Intercept)	0.832	0.856	0.812	10030	0.004	0.005	0.003	-0.038	-0.033	-0.047	0.048	0.056	0.043
	Phylogeny				3971	0.002	0.002	0.001	0	0	0	0.007	0.01	0.005
	Sigma				3562	0.004	0.004	0.004	0.001	0.001	0.001	0.007	0.007	0.007
	Species				3419	0.004	0.004	0.004	0	0	0	0.007	0.007	0.007
Reptile population fluctuations	(Intercept)	0.003	0.004	0.001	9839	0.151	0.152	0.151	0.074	0.078	0.07	0.23	0.236	0.225
	Phylogeny				2958	0.004	0.005	0.004	0	0	0	0.017	0.019	0.016
	Sigma				3888	0.007	0.007	0.007	0.003	0.003	0.002	0.014	0.015	0.014
	Species				6057	0.043	0.043	0.043	0.025	0.026	0.024	0.062	0.064	0.061

Appendix 3.25. List of species included in the UK scale analysis of population change across rarity metrics.

Species name	Number of populations
Acrocephalus schoenobaenus	1
Acrocephalus scirpaceus	1
Agonus cataphractus	1
Alca torda	4
Anarhichas lupus	1
Anas acuta	1
Anas crecca	1
Anas platyrhynchos	2
Anser albifrons	4
Anser fabalis	1
Anthus pratensis	2
Ardea cinerea	1
Arenaria interpres	1
Argentina silus	1
Argentina sphyraena	1
Arnoglossus laterna	1
Asio flammeus	1
Aythya ferina	4
Aythya fuligula	2
Botaurus stellaris	14
Branta bernicla	54
Branta canadensis	1
Branta leucopsis	3
Brosme brosme	1
Bucephala clangula	1
Bufo bufo	1
Burhinus oedicnemus	1
Buteo buteo	1
Calidris alba	1
Calidris alpina	1
Calidris canutus	2

Calidris maritima	2
Callionymus maculatus	1
Capreolus capreolus	3
Carduelis cannabina	2
Cepphus grylle	2
Cervus elaphus	2
Cetorhinus maximus	1
Cettia cetti	1
Charadrius hiaticula	1
Chelidonichthys lucerna	2
Circus aeruginosus	1
Circus cyaneus	1
Clupea harengus	2
Columba oenas	1
Coronella austriaca	1
Corvus corax	1
Corvus corone	1
Corvus monedula	1
Crex crex	1
Cyclopterus lumpus	1
Cygnus columbianus	3
Cygnus cygnus	1
Cygnus olor	1
Delphinus delphis	2
Echiichthys vipera	1
Egretta garzetta	1
Emberiza cirlus	1
Emberiza citrinella	1
Emberiza schoeniclus	3
Eptesicus serotinus	1
Esox lucius	2
Falco peregrinus	1
Falco tinnunculus	1
Fulica atra	1
Fulmarus glacialis	7
Gadus morhua	7

Glyptocephalus cynoglossus	1
Haematopus ostralegus	2
Haliaeetus albicilla	1
Halichoerus grypus	52
Hippoglossus hippoglossus	1
Lagopus lagopus	3
Larus argentatus	1
Larus canus	1
Larus fuscus	1
Larus melanocephalus	1
Lepidorhombus whiffiagonis	2
Lepus timidus	1
Limosa lapponica	2
Limosa limosa	2
Lissotriton vulgaris	5
Lophius budegassa	1
Lophius piscatorius	2
Lullula arborea	1
Melanogrammus aeglefinus	9
Meles meles	1
Mergus serrator	1
Merlangius merlangus	8
Merluccius merluccius	2
Micromesistius poutassou	1
Milvus milvus	3
Molva molva	1
Morus bassanus	4
Muscicapa striata	1
Myotis nattereri	1
Natrix natrix	1
Netta rufina	1
Numenius arquata	2
Nyctalus noctula	1
Oenanthe oenanthe	1
Orcinus orca	1
Oriolus oriolus	1

Oryctolagus cuniculus	6
Oxyura jamaicensis	2
Pandion haliaetus	1
Parus major	2
Passer domesticus	1
Passer montanus	1
Perca fluviatilis	3
Perdix perdix	1
Phalacrocorax aristotelis	8
Phoca vitulina	28
Phrynorhombus norvegicus	1
Pipistrellus pipistrellus	1
Pipistrellus pygmaeus	1
Platichthys flesus	1
Plecotus auritus	1
Plectrophenax nivalis	2
Pleuronectes platessa	6
Pluvialis apricaria	2
Pluvialis squatarola	1
Podiceps cristatus	1
Pollachius pollachius	1
Pollachius virens	3
Prunella modularis	1
Puffinus mauretanicus	2
Pyrrhula pyrrhula	1
Raja brachyura	1
Raja clavata	1
Raja microocellata	1
Raja montagui	1
Rhinolophus ferrumequinum	2
Rhinolophus hipposideros	4
Rissa tridactyla	9
Salmo salar	1
Salmo trutta	1
Scomber scombrus	2
Scyliorhinus canicula	1

Sitta europaea	1
Sprattus sprattus	1
Stenella coeruleoalba	1
Stercorarius parasiticus	3
Sterna dougallii	5
Sterna hirundo	1
Sterna paradisaea	1
Sternula albifrons	1
Streptopelia turtur	1
Strix aluco	1
Sturnus vulgaris	1
Sylvia communis	1
Syngnathus rostellatus	1
Tachybaptus ruficollis	1
Tadorna tadorna	1
Thalasseus sandvicensis	2
Trachurus trachurus	2
Tringa nebularia	1
Tringa totanus	1
Trisopterus esmarkii	2
Trisopterus luscus	1
Trisopterus minutus	1
Triturus cristatus	5
Turdus philomelos	1
Tursiops truncatus	4
Uria aalge	10
Vanellus vanellus	3
Xiphias gladius	1

Appendix 3.26. Profiling method for estimating habitat specificity for 144 species with populations in the UK in the LPD. I extracted the habitats in which each species occurs from their IUCN Red List profiles (http://www.iucnredlist.org/) and I followed this key for consistency.

Habitat	Considered to be the same as:	Considered to be different to:
Rural park	Suburban park, urban park, rural garden, suburban garden, urban garden	
Lake	Big lake, small lake, pond, pool, dam, oxbow lake, reservoir	
Bog	Swamp, bogland	Lagoon
Coastal cliff	Island cliff	
Shingle beach	Pebble beach, rock beach	Sandy beach
Stream	River	Weir
Fruit Tree Plantation	Fruit Garden, orchard	
Thicket	Copse, grove, small stand	
Forest		Woodland
Glade	Forest Clearing	
Broadleaf	Deciduous	
Urban	Suburban	
River margin	Various types of river margins	
Tidal Creek		Estuary
Harbour	Dock, jetty, pier	
Bush lands	Shrublands	
Irrigation channel	Ditch	
Heath	Moorland	
Sandy beach	Spit, dune	Shingle beach, pebble beach, rock beach
Crag	Rocky outcrop, cliff, rocky slope	
Marsh	Wet meadow	
Islet	Island	

Appendix 3.27. References for eighty time series (or 1% of analysed time series) which had very little variance (error < 0.001). See Appendix 6e for a visualisation of the data from a subsample of those time series.

Time series id	Data source citation
4178	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
13773	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3697	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
18118	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
13797	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4218	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4220	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3725	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
2916	Sauer, J. R., J. E. Hines, et al. (2012). The North American Breeding Bird Survey, Results and Analysis 1966 - 2011, USGS Patuxent Wildlife Research Center, Laurel, MD.
13846	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3771	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
2987	Sauer, J. R., J. E. Hines, et al. (2012). The North American Breeding Bird Survey, Results and Analysis 1966 - 2011, USGS Patuxent Wildlife Research Center, Laurel, MD.
4236	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4237	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3803	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3808	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.

3816	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3813	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3821	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
13944	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
11350	KeiÅÁs, O. (2005). Impact of changes in agricultural land use on the Corncrake Crex crex population in Latvia. Acta Universitatis Latviensis 691: 93-109.
13976	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3997	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3995	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3998	Environment Canada (2014). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2012. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
13694	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
13520	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3018	Sauer, J. R., J. E. Hines, et al. (2012). The North American Breeding Bird Survey, Results and Analysis 1966 - 2011, USGS Patuxent Wildlife Research Center, Laurel, MD.
13687	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14076	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14074	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3326	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14095	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14093	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
13584	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.

3883	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
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2632	Fylkesmannen i Vestfold (2004). Hekketakseringer, sjÌüfugl i Vestfold, MiljÌüvernavdelingen.
3360	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14286	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4245	Environment Canada (2014). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2012. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4247	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
18111	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4229	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
1037	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14728	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14208	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3947	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4254	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4253	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14217	Environment Canada (2014). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2012. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3958	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3245	Sauer, J. R., J. E. Hines, et al. (2012). The North American Breeding Bird Survey, Results and Analysis 1966 - 2011, USGS Patuxent Wildlife Research Center, Laurel, MD.
14249	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.

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14327	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3674	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
13636	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4051	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4069	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4086	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4088	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4083	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
3119	Sauer, J. R., J. E. Hines, et al. (2012). The North American Breeding Bird Survey, Results and Analysis 1966 - 2011, USGS Patuxent Wildlife Research Center, Laurel, MD.
4085	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4087	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4093	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
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14807	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.

14801	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
14804	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4132	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4143	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4139	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
4151	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.
18190	Environment Canada (2015). North American Breeding Bird Survey - Canadian Trends Website. Data-version 2014. from http://www.ec.gc.ca/ron-bbs/P001/A001/?lang=e.

Appendix 3.28. References for time series which appear to show logistic growth with little variance (see Appendix 3.6e for visualisation of data).

Time series id	Data source citation
468	NERC Centre for Population Biology (1999). The Global Populations Dynamics Database. http://cpbnts1.bio.ic.ac.uk/gpdd/, Imperial College,.l Batten, L. A. and J. H. Marchant (1977). Bird Population Changes for Years 1974-75. Bird Study 24(1): 55-61.
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Appendix 4. Supporting information for Chapter 4 “Landscape-scale forest loss as a catalyst of population and biodiversity change”

Supplementary methods

Databases

Forest cover change databases

I extracted historic forest loss and habitat transitions from the LUH database (850 – 2015, 0.25° degree resolution which is around 27 km, Hurtt et al., 2011), contemporary forest cover change from the GFC database (2000 – 2016, forest loss and gain at a 30 m resolution, Hansen et al., 2013), also from the ESA Landcover database (1992 – 2015, 300m resolution, ESA Climate Change Initiative, 2017) and habitat transitions from the MODIS Landcover database (2000 – 2013, 500m resolution, Channan et al., 2014).

By synthesising information from scenario data based on Earth Dynamics Models (LUH) and remote-sensing databases (GFC, ESA, MODIS), I estimated historic baselines for forest loss across sites, as well as contemporary forest cover change (gain and loss) and habitat transitions. I calculated overall forest cover change rather than using an annual rate, because I considered total habitat change that better captures cumulative effects to be more meaningful for comparison with long-term population and biodiversity trends. GFC and MODIS detect forest cover, with no distinction between primary and secondary forests, thus I derived information on transitions from primary to secondary forest from the LUH database. Together, the four databases (GFC, MODIS, LUH, ESA) encompass two different elements of land-use change: 1) land cover types and long-term historical reconstructions of past land-use and habitat conversions and 2) high-resolution satellite data from recent years of forest cover change and habitat conversions.

Population time series (Living Planet Database)

I analysed 2729 population time series with records distributed around the world. These time series represent repeated monitoring surveys of the number of individuals in a given area (species' abundance over time), to which I refer as "populations". Geographic representation is variable with, for example, an under-representation of tropical regions (Figure 2A). In the LPD, some populations have precise coordinates, whereas the location of others are approximate. Because of the extent over which I calculated forest cover change (96 km^2), I included both populations with precise and approximate coordinates in my analysis. I only included populations with at least five survey points and duration varied across time series ranging between five to 44 years covering the period between the years 1970 and 2014 (Appendices 4.2, 4.11).

Biodiversity time series (BioTIME Database)

I analysed 3361 time series from 190 studies from terrestrial biomes across the globe that make up a part of the BioTIME database (Dornelas et al., 2018, download link available at http://biotime.st-andrews.ac.uk/BioTIME_download.php and list of non-public studies is included in Appendix 4.20). Similarly to the LPD, tropical regions and some taxa such as amphibians and reptiles were under-represented in BioTIME. To account for the different spatial extents of the BioTIME database, studies with multiple locations and extents > 71.7 km^2 were partitioned into 96 km^2 grids (studies with extents < 71.7 km^2 were assigned to the grid cell in which they were centred), and then sample-based rarefaction was applied to standardise sampling within each time series (Blowes et al., 2019). The identity of each study was always kept intact, and I did not combine data from different studies, e.g., if there were data from two studies in the same cell, those represented separate time series. When analysing forest loss across the whole duration of each time series, I included assemblage time series with at least five survey points and duration varied across time series ranging between five to 158 years covering the period between the years 1858 and 2016 (Appendices 4.2, 4.11). When analysing forest loss between 2000 and 2016 (the duration of the GFC database), I included time series with two or more data points. Protected areas contained 63 of 199 (32%) study locations, but because those studies covered smaller sampling areas, overall only 1% of the analysed and rarefied time series were located inside protected areas.

Calculating population change

I calculated population change using state-space models which are particularly appropriate when quantifying change in data with varying collection methodology, as they take into account observation error and process noise (Knape et al., 2011; Pedersen et al., 2011). For more details on state-space model calculations, see Humbert *et al.* 2009 (Humbert et al., 2009) and Chapter 3. I scaled the population size data to be between 0 and 1 to analyse within-population relationships and to make sure that I were not conflating within-population relationships and between-population relationships (van de Pol & Wright, 2009). State-space models partition the variance in abundance estimates into process error (σ^2) and observation or measurement error (τ^2) and estimate population trends (μ):

$$X_t = X_{t-1} + \mu + \varepsilon_t, (1)$$

where X_t and X_{t-1} are the scaled (observed) abundance estimates (between 0 and 1) in the present and past year, with process noise represented by $\varepsilon_t \sim gaussian(0, \sigma^2)$. I included measurement error following:

$$Y_t = X_t + F_t,$$

where Yt is the estimate of the true (unobserved) population abundance with measurement error:

$$F_t \sim \text{gaussian}(0, \tau^2).$$

I substituted the estimate of population abundance (Y_t) into equation 1:

$$Y_t = X_{t-1} + \mu + \varepsilon_t + F_t .$$

Given $X_{t-1} = Y_{t-1} - F_{t-1}$, then:

$$Y_t = Y_{t-1} + \mu + \varepsilon_t + F_t - F_{t-1} .$$

For each time series, I calculated overall population change (μ) experienced over different periods matching the questions in Figure 1: 1) across the periods before and after contemporary peak forest loss, 2) across the full duration of the time series, 3) from 2000 to 2016 (matching the temporal scale of the GFC database), and 4) from 2000 to 2013 (matching the temporal scale of the MODIS database). I standardised the number of years over which I calculated population change before and after peak forest loss on the population-level, meaning that the number of years before and after (five or more) was the same within populations, but might differ among populations.

Calculating richness change

To estimate richness change, I modelled species richness versus time (year, mean centred) with random slopes and intercepts for each rarefied cell and a Poisson error distribution with a log link.

$$log(\mu_{j,i,t}) = \beta_0 + \beta_{0j} + \beta_{0j,i} + (\beta_1 + \beta_{1j} + \beta_{1j,i})year_{j,i,t},$$
$$y_{j,i,t} \sim poisson(\mu_{j,i,t}) ,$$

where $year_{j,i,t}$ is the time in years, β_0 and β_1 are the global intercept and slope (fixed effects), β_{0j} and β_{1j} are the biome-level departures from β_0 and β_1 (respectively; biome-level random effects), $\beta_{0j,i}$ and $\beta_{1j,i}$ are the (nested) cell-level departures from β_0 and β_1 (cell-level random effects); $y_{j,i,t}$ is the (rarefied) species richness within the *jth* biome in the *ith* cell in year *t*.

From the richness over time model, I extracted the posterior means for richness change for each time series (i.e., the cell-level slope estimates), which then became the response variable in the second stage of my analyses where I tested richness change versus forest cover change.

For time series with five or more years of monitoring records, I calculated overall richness change experienced 1) across the periods before and after contemporary peak forest loss, and 2) across the full duration of the time series. For time series with two or more years of monitoring records, I calculated overall richness change experienced 3) from 2000 to 2016 (matching the temporal scale of the GFC database), and 4) from 2000 to 2013 (matching the temporal scale of the MODIS database). The GFC and MODIS databases cover shorter time periods, thus I included biodiversity time series with shorter durations than the five-year cut off point that was used in the rest of my analyses using datasets with longer durations (but note that 76% of biodiversity time series had a duration of three or more years). When I calculated slopes of richness change over time, I included a time series ID random effect. Most time series (72%) were from separate studies and 28% included more than one time series per study because these studies covered very large areas (e.g., with time series located across the continental US). Calculating richness slopes with a model including a nested random effect (time series ID within study) produced very similar estimates.

Calculating turnover

To determine changes in community composition, I calculated the turnover component of beta diversity. Turnover quantifies the changes due to species replacement rather than changes in species abundances (Baselga, 2010; Blowes et al., 2019). I calculated turnover between the end of each time period (outlined above) and the first year of observation in the same period. Turnover is bound between zero and one, where zero is no change in species composition and one indicates that all of the original species of a community have been replaced with new species. I calculated turnover for the same time periods as for richness change (outlined above). Previous studies using the BioTIME database have found that calculating turnover relative to the second or the last year of observation produces similar results (Dornelas et al., 2014).

Statistical analyses

I matched the temporal scales of the forest cover change data and the population and biodiversity data when investigating attribution signals (i.e., evidence that a predictor variable is a potential driver of population or biodiversity change). For example, when testing the effects of forest cover change and land-use transitions as detected by GFC (2000 to 2016) and MODIS (2000 to 2013), I calculated population and biodiversity change for the matching time periods. Because of the longer duration of the LUH database, I was also able to extract forest and land cover information for the full duration of the LPD and BioTIME time series and to calculate the peak and overall forest loss during the period from 850 to 2015. For my analyses of all-time and contemporary peak forest loss and overall forest loss, I excluded locations which had less than 5% (0.05 out of maximum 1) forest cover loss (using the LUH database over a time period matching the duration of each time series). For my analyses of contemporary forest loss, I excluded locations which had less than 0.5 km^2 forest cover change (using the GFC database over a time period matching the duration of GFC from 2000 to 2016). For my cross-scale analysis, I excluded locations which had no forest cover across the duration of the time series in both the 96 km^2 cells and the 500 km^2 larger landscape cells from my analyses of population and biodiversity change versus forest cover gain and loss from 2000 to 2016 (using the GFC database). See Appendix 4.19 for the outputs of all statistical models and their respective sample sizes.

Prior specification

I used weakly regularizing normally-distributed priors for the global intercept and slope for all statistical models except the model of turnover versus overall forest cover change (which was a zero one inflated model):

$$\beta_0 \sim gaussian(0, 6),$$
$$\beta_1 \sim gaussian(0, 6).$$

For the turnover models that had a zero one inflated beta distribution, I used the following priors:

$$\beta_0 \sim gaussian(0, 6),$$
$$\beta_1 \sim gaussian(0, 6),$$
$$zoi \sim gaussian(0, 0.5),$$
$$coi \sim gaussian(0, 0.5),$$

where *zoi* is the probability of being a zero or a one and *coi* is the conditional probability of being a one (given an observation is a zero or a one).

Group-level parameters (the rarefied cell random effect in the species richness over time model, *i*, and the biome random effect in all models, *j*) were all assumed to be *gaussian*(0, σ), and priors on the σ were the same for all models:

$$\sigma\beta_{0j} = \sigma\beta_{0j,i} \sim half\ Cauchy(0, 2).$$

Historical baselines

To estimate the historic baseline of forest cover change, I calculated change in % forest cover across 10-year periods for each site from 850 to 2015 from the LUH database. I then determined all-time peak forest loss as the period when the most forest loss occurred (calculated using the difference in forest area at the start and end of standardised 10-year blocks). Here, I asked the question:

- *Are populations more likely to experience declines when the monitoring includes the period of all-time peak forest loss (the largest reduction in forest area between 850 and 2015)?*

To determine if population change differed based on whether population time series were recorded before, during, or after the period of all-time peak forest loss, I modelled μ (population change) as a function of when monitoring started. I defined all-time peak forest loss as the timing of the largest forest loss event at the location of each time series between the years 850 and 2015. I used a categorical variable with three levels – before, during or after peak forest loss – and time series duration (numeric) as fixed effects, with a biome random effect to account for the spatial clustering of the data. Low sample size precluded a similar analysis for richness change and turnover (Appendix 4.3B). The model was as follows:

$$\mu j,i,m = \beta 0 + \beta 0j + \beta 1 * duration j,i,m + \beta 2 * monitoring\ start j,i,m,$$

$$y j,i,m \sim gaussian(\mu j,i,m,\sigma 2),$$

where $duration_{j,i,m}$ is the duration of the time series in years of cell i within biome j for monitoring start m, and $monitoring\ start_{j,i,m}$ is an indicator variable denoting when monitoring started; β_0, β_1 and β_2 are the global intercept and slope estimates for duration and the categorical monitoring start variable respectively (fixed effects), β_{0j} is the biome-level departures from β_0 (respectively; biome-level random effects); $y_{j,i,m}$ is the estimate for change in population size or species richness for the *i*th cell in the *j*th biome for the *m*th monitoring start.

Contemporary forest loss

To determine contemporary peak forest loss for each time series of monitoring data, I used the LUH database to calculate yearly changes in forest cover across the duration of each time series and determined the year when the most change had occurred (contemporary peak forest loss). I compared biodiversity change across equal durations before and after the year of contemporary peak forest loss. E.g., if a time series included seven years of biodiversity data before the peak in recent forest cover change and 10 years of data after that peak, I included only the first seven years of biodiversity data after the forest cover change peak (making for a total of 14 years of data included in the analysis for this example time series). The v2h release of LUH includes annual gridded fractions of land-use states for the period from 850 to 2013 at 0.25° x 0.25° resolution. The estimates are based on historical reconstructions using Earth System models, with inputs such as regional and national rates of wood harvest and potential biomass density. The accuracy and precision of LUH increases towards the modern day, when there are more available data to inform the Earth System models. Note that unlike GFC, LUH estimates forest cover as a proportion (bounded between zero and one). I asked:

- *Are population abundance, richness and turnover trends stronger in the period after, relative to before, contemporary peak forest loss?*

To test if temporal population and biodiversity change differed before and after peak forest loss at the site-level, I split each time series into two periods – before and after peak deforestation – and estimated population change, richness change and turnover for each period separately. Then, to infer if population and biodiversity change differed following peak forest loss, I modelled μ (population change), richness change (cell-level random slopes) and turnover as a function of period (categorical with two levels – before or after forest loss) and time series duration (numeric) as fixed effects, with a biome random effect to account for the spatial clustering of the data. For population and richness change, I modelled the positive and negative components of the distributions of change separately, e.g., one model for populations with positive μ values and one model for populations with negative μ values. This approach allowed me to test if the effects of forest loss differ across the positive and negative dimensions of population and biodiversity change. The models were as follows:

$$\mu_{j,i,p} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i,p} + \beta_2 * period_{j,i,p},$$

$$y_{j,i,p} \sim gaussian(\mu_{j,i,p}, \sigma^2),$$

where $duration_{j,i,p}$ is the duration of the time series in years of cell i within biome j for period p, and $period_{j,i,p}$ is an indicator variable for the period (before or after forest loss); β_0, β_1 and β_2 are the global intercept and slope estimates for duration and the categorical period effect, respectively (fixed effects), β_{0j} is the biome-level departures from β_0 (biome-level random effects); $y_{j,i,p}$ is the estimate for change in population size or species richness for the ith cell in the jth biome for the pth period.

To model the change in turnover before and after contemporary peak forest loss, I followed the same conceptual framework as outlined above, but I used a zero one inflated beta distribution to account for the properties of turnover (bounded between zero and one, inclusive, where one is a complete change in species composition). The probability density function for the zero one inflated beta distribution is:

$$betainf(y; \alpha, \gamma, \mu, \phi) = \begin{cases} \alpha(1-\gamma), & y = 0 \\ \alpha\gamma, & y = 1 \\ (1-\alpha)\gamma f(y; \mu, \phi), & 0 < y < 1, \end{cases}$$

where α is the probability that a zero or one occurs, γ is the probability that a one occurs (given an observation is a zero or a one), and μ and ϕ are the mean and precision of the beta distribution, respectively. In the parameterisation approach that I used (Bürkner, 2017) ϕ is inversely related to the variance. Beta parameterisation is also sometimes expressed through the parameters p and q that can be derived from my framework following $\phi = p + q$ (Ferrari & Cribari-Neto, 2004). Because only 7% of time series did not experience any change in species composition (y = 0) in the time period after contemporary forest loss, and less than 1% of time series had a completely new set of species (y = 1) occupying the ecological communities, for y = 0 and y = 1, α and γ were modelled assuming a Bernoulli distribution and logit-link function, and models were fit with only an intercept. For $0 < y < 1$, I assumed a beta error distribution and a logit-link function:

$$logit(\mu_{j,i,p}) = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i,p} + \beta_2 * period_{j,i,p},$$
$$y_{j,i,p} \sim Beta(\mu_{j,i,p}, \phi),$$

where $duration_{j,i,p}$ is the duration of the time series in years of cell *i* within biome *j* for period *p,* and $period_{j,i,p}$ is an indicator variable for the period (before or after forest loss); β_0, β_1 and β_2 are the global intercept and slope estimates for duration and the categorical period variable respectively (fixed effects), and β_{0j} are the biome-level departures from β_0 (biome-level random intercepts); $y_{j,i,p}$ is the estimate of turnover for the *i*th cell in the *j*th biome for the *p*th period.

Additionally, I investigated the relationships between the magnitude of contemporary forest loss and gain experienced during each time series and the population and biodiversity trends at each site. I asked:

- *Do higher magnitudes of forest loss correspond with more population and biodiversity losses over time, and higher magnitudes of forest gain with more population and biodiversity gains?*

I used two databases (LUH, GFC) to calculate the magnitude of forest cover change across sites. First, to estimate forest cover change across a time period matching the full duration of the biodiversity observations, I derived the change in primary forest cover from the LUH database (Hurtt et al., 2011) for 96 km^2 cells around the location of each population in the LPD database and for the standardised grid cells of the BioTIME database (~ 96 km^2 each,). For my analyses, I focused on time series from locations that have experienced at least 5% (0.05 out of maximum 1) forest loss. To calculate total forest cover change over the period of a given population or biodiversity time series, I subtracted the proportion of forest cover in the first year of biodiversity monitoring from the proportion of forest cover in the last year. The type of forest cover change detected by the LUH database was predominantly forest loss, with forest gain occurring infrequently and at very small magnitudes (<0.001 out of maximum 1), thus I focused on forest loss when using this database.

Second, I derived overall forest loss and forest gain across the 2000 to 2016 period for 96 km^2 cells around the location of each population in the LPD database and for the standardised grid cells of the BioTIME database (~ 96 km^2 each) from the GFC database using the Google Earth Engine (Gorelick et al., 2017). The GFC database provides high resolution forest cover change data, derived from Landsat satellite observations at a 30-meter spatial resolution. I calculated the total area of forest cover gain and loss separately (measured in km^2) for each 96 km^2 cell on a yearly time step. I then summed the yearly values for the period that coincided with population and biodiversity monitoring to estimate overall forest cover gain and loss (two separate metrics). For example, for a biodiversity time series spanning 2002 to 2009, my forest cover gain and loss metrics included the total amount of forest cover gained and lost during that same period. For my analyses, I focused on time series from locations that have experienced at least 0.5 km^2 of forest gain or loss. GFC does not distinguish between primary forest, secondary forest and plantations, but it does provide a very high-resolution measure of general forest cover (Curtis et al., 2018; Hansen et al., 2013). The drivers of the forest loss detected by GFC across my study sites are predominantly forestry, changes in agricultural practices and wildfires (Curtis et al., 2018). Note that the GFC database spans from 2000 to 2016, with forest gain data available up to 2014, whereas the earliest terrestrial biodiversity record in BioTIME is from 1858.

To test the effect of forest cover change on population and biodiversity change among sites, I modelled population and biodiversity change versus overall forest cover change (calculated as forest cover gain and forest cover loss (GFC database, 2000 to 2016) and forest loss (LUH database, across the duration of the time series). Models of population and richness change versus forest cover change were fitted assuming Gaussian error.

$$\mu_{j,\,i} = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,\,i} + \beta_2 * forest\ change_{j,i},$$

$$y_{j,\,i} \sim gaussian(\mu_{j,\,i}, \sigma^2),$$

where *duration*$_{j,i}$ is the duration of the time series in years of cell *i* within biome *j*, *forest change*$_{j,i}$ is the forest cover change in cell *i* within biome *j*; β_0, β_1 and β_2 are the global intercept and slope estimates for duration and forest cover change respectively (fixed effects), and β_{0j} are the biome-level departures from β_0 (biome-level random intercepts); $y_{j,i}$ is the population or richness change metric (a separate model for population declines, population increases, richness losses and richness gains) in the ith cell within the jth biome.

Models of turnover versus forest cover change were fit with a zero one inflated beta distribution to account for the properties of turnover (bounded between zero and one). I used the same probability density function for the zero one inflated beta distribution as in the model for turnover before and after contemporary peak forest loss. For y = 0 and y = 1, α and γ were modelled assuming a Bernoulli distribution and logit-link function, and I fit models with only an intercept. For 0 < y < 1, I assumed a beta error distribution and a logit-link function:

$$logit(\mu_{j,i}) = \beta_0 + \beta_{0j} + \beta_1 * duration_{j,i} + \beta_2 * forest\ change_{j,i},$$

$$y_{j,i} \sim Beta(\mu_{j,i}, \phi),$$

where $duration_{j,i}$ is the duration of the time series in years of cell i within biome j, $forest\ change_{j,i}$ is the forest cover change in cell i within biome j; β_0, β_1 and β_2 are the global intercept and slope estimates for duration and forest cover change respectively (fixed effects), and β_{0j} are the biome-level departures from β_0 (biome-level random intercepts); $y_{j,i}$ is turnover in the ith cell within the jth biome.

Temporal lags

To test for temporal lags in population and biodiversity responses to contemporary peak forest loss, I first calculated when population and biodiversity change were greatest following peak forest loss for each time series. Rates of population change were calculated using state-space models and a Kalman filter (Humbert et al., 2009; Leung et al., 2017). Peak richness change and peak turnover were calculated as the maximum value of the absolute differences between consecutive observations of species richness and turnover, relative to the species richness and composition before contemporary peak forest loss. I then quantified lag as the number of years between contemporary peak forest loss and peak population/biodiversity change. I asked:

- *Do temporal lags in population and biodiversity change following contemporary peak forest loss increase with higher generation time across taxa?*

I modelled lag as a function of taxa, as I expect that species with longer generation times will respond to disturbance more slowly.

$$\mu_{j,i} = \beta_{0j} + \beta_1 * taxa_{j,i},$$
$$y_{j,i} \sim gaussian(\mu_{j,i}, \sigma^2),$$

where $taxa_{j,i}$ is the taxa of the cell i in the biome j time series, β_1 is the slope for taxa effect (fixed effect), and β_{0j} are the biome-level random intercepts; $y_{j,i}$ is the temporal lag in the population or biodiversity change metric (a separate model for population change, richness change and turnover) for the ith cell within the jth biome.

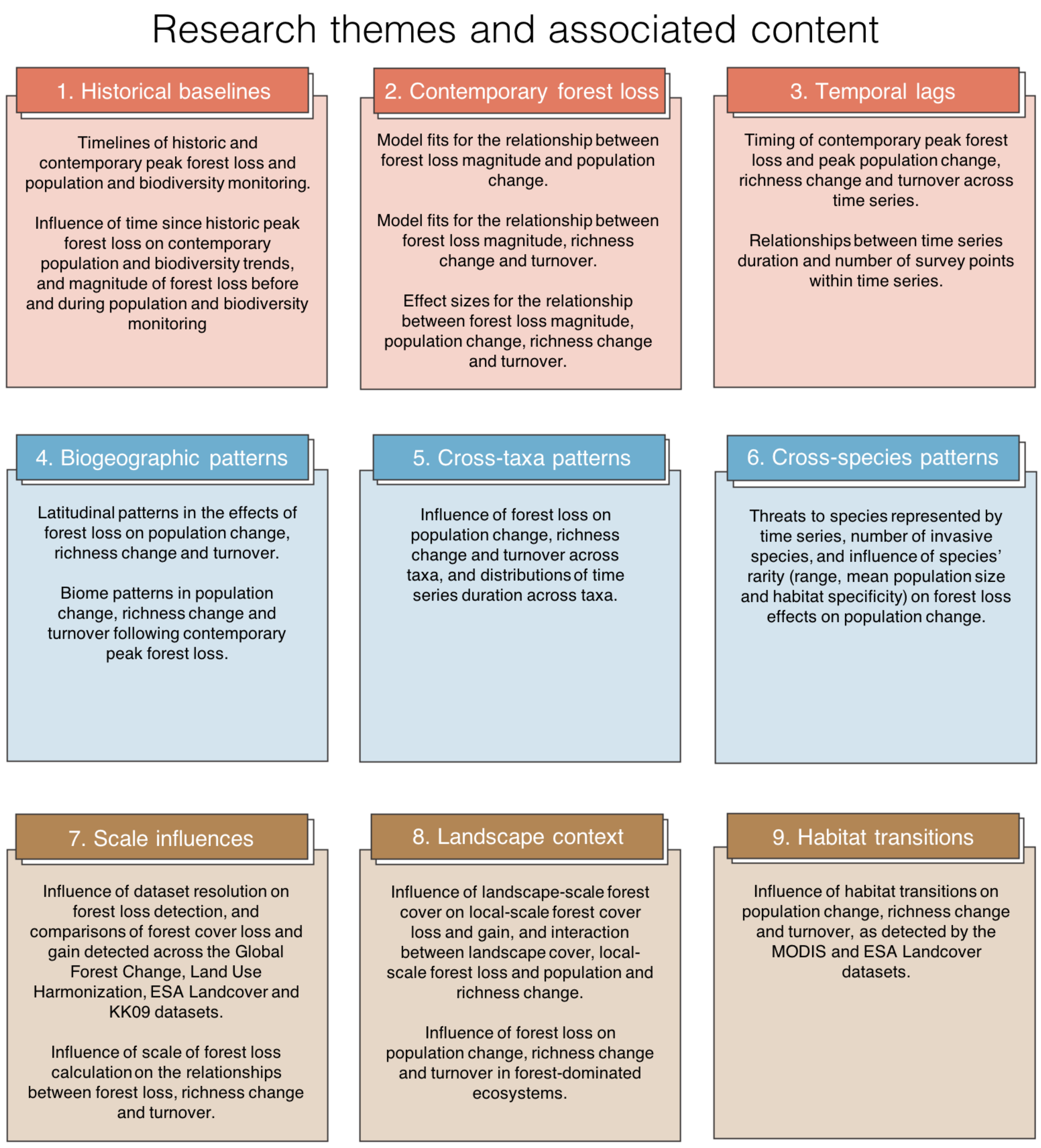
I extracted mammal generation times from the Pacifici *et al.* 2013 Database (Pacifici et al., 2013) N = 88) and bird generation times from the BirdLife Database (BirdLife International, 2018) N = 494). To test lagged responses to forest loss in greater detail, I asked:

- *Within bird and mammal taxa, do species with longer generation times experience longer lags in population change following contemporary peak forest loss?*

I modelled lag as a function of generation time in birds and mammals, the taxa for which generation time data were freely available (BirdLife International, 2018; Pacifici et al., 2013).

$$\mu g = \beta 0 + \beta 1 * generation\ timeg,$$
$$yg \sim gaussian(\mu g, \sigma^2),$$

where generation $time_g$ is the mammal generation time in years, β_0 and β_1 are the global intercept and slope (fixed effect); y_g is the temporal lag in population change for a species with generation time g.



Research themes and associated content

1. Historical baselines

Timelines of historic and contemporary peak forest loss and population and biodiversity monitoring.

Influence of time since historic peak forest loss on contemporary population and biodiversity trends, and magnitude of forest loss before and during population and biodiversity monitoring

2. Contemporary forest loss

Model fits for the relationship between forest loss magnitude and population change.

Model fits for the relationship between forest loss magnitude, richness change and turnover.

Effect sizes for the relationship between forest loss magnitude, population change, richness change and turnover.

3. Temporal lags

Timing of contemporary peak forest loss and peak population change, richness change and turnover across time series.

Relationships between time series duration and number of survey points within time series.

4. Biogeographic patterns

Latitudinal patterns in the effects of forest loss on population change, richness change and turnover.

Biome patterns in population change, richness change and turnover following contemporary peak forest loss.

5. Cross-taxa patterns

Influence of forest loss on population change, richness change and turnover across taxa, and distributions of time series duration across taxa.

6. Cross-species patterns

Threats to species represented by time series, number of invasive species, and influence of species' rarity (range, mean population size and habitat specificity) on forest loss effects on population change.

7. Scale influences

Influence of dataset resolution on forest loss detection, and comparisons of forest cover loss and gain detected across the Global Forest Change, Land Use Harmonization, ESA Landcover and KK09 datasets.

Influence of scale of forest loss calculation on the relationships between forest loss, richness change and turnover.

8. Landscape context

Influence of landscape-scale forest cover on local-scale forest cover loss and gain, and interaction between landscape cover, local-scale forest loss and population and richness change.

Influence of forest loss on population change, richness change and turnover in forest-dominated ecosystems.

9. Habitat transitions

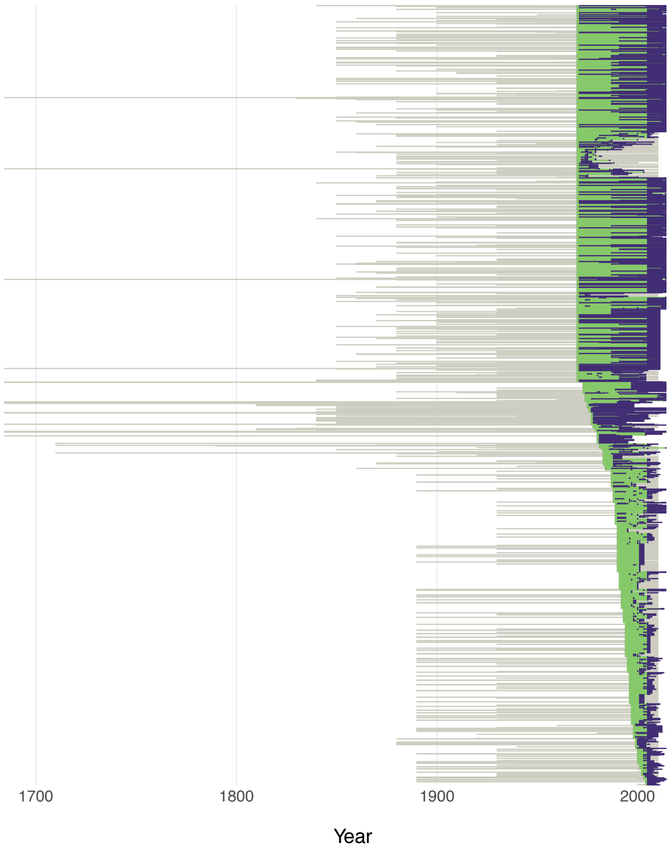
Influence of habitat transitions on population change, richness change and turnover, as detected by the MODIS and ESA Landcover datasets.

Appendix 4.1. Index of key research themes and their associated sections in Appendix 4. See Appendix 4.19 for model outputs and sample sizes. For details on each step of my analyses, see correspondingly numbered sections in the text below. The methods and key results for themes 1-3 are covered in the main text of Chapter 4.

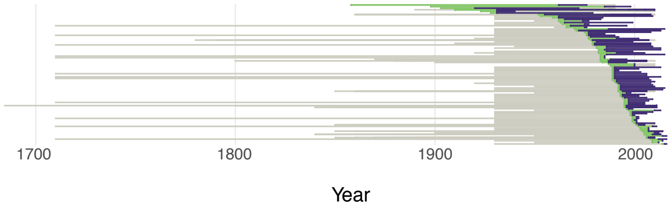
1. Historical baselines

All-time peak forest loss occurred at variable time points across the population and biodiversity time series (Appendix 4.2), but the time since all-time peak forest loss was not directly related to contemporary trends in population abundance, species richness and turnover (Appendix 4.3). I found that local-scale population declines were most pronounced when the monitoring occurred during the period of all-time peak forest loss (see Chapter 4 for further details).

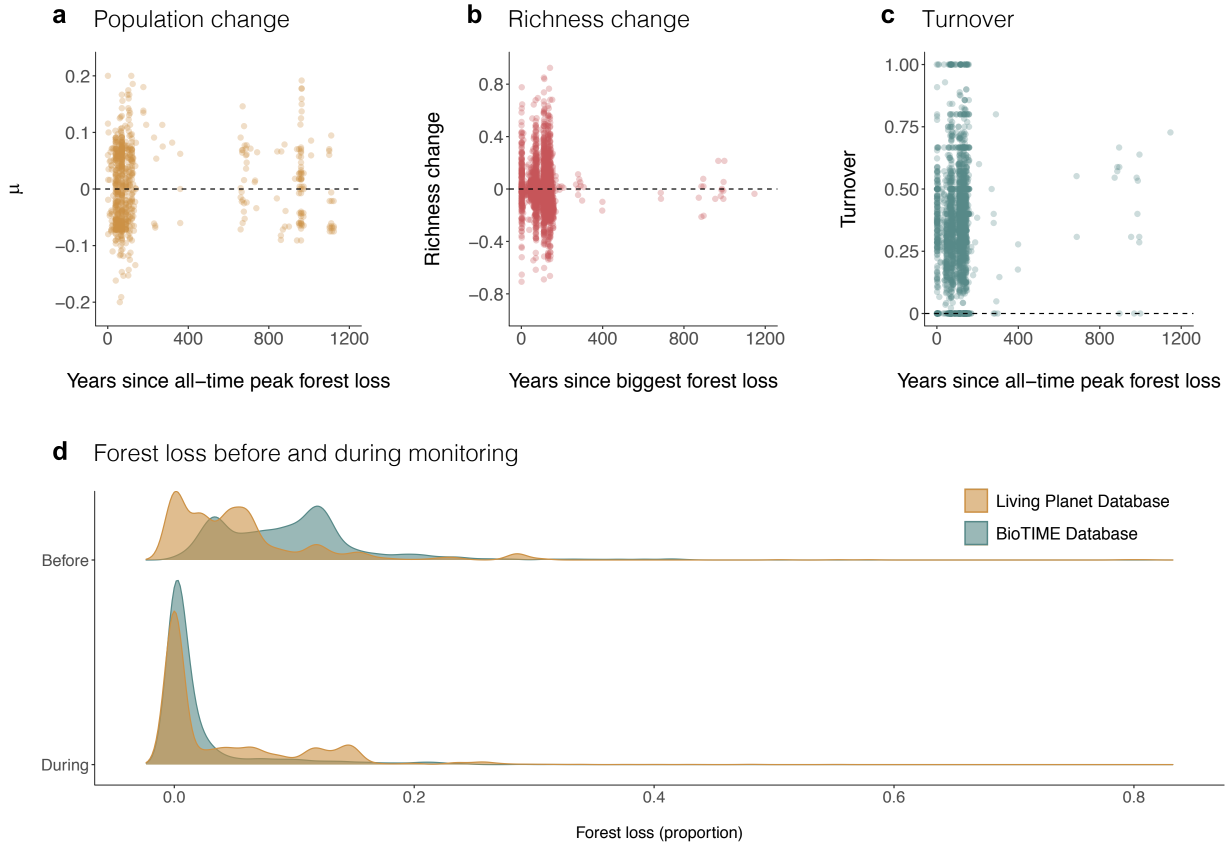
a Population time series from the Living Planet Database



b Biodiversity time series from the BioTIME Database



Appendix 4.2. Historic peaks of forest cover change often occurred decades to centuries before population monitoring starts (38% of time series), with some instances (23% of time series) of peaks in forest cover change occurring after population monitoring has ceased. All-time peak forest occurred before biodiversity monitoring started in 78% of cases. Each line represents a single population time series (out of 2,729), part of the Living Planet Database (a) (LPI, 2016) or the BioTIME Database (b), which included 190 studies (Dornelas et al., 2018). Note that the BioTIME studies were rarefied into equally sized cells (~96 km^2), resulting in 3,361 time series and peaks in forest cover change were calculated on the time series level for analysis, but because of the large number of cells (> 3,000), here I visualised study-level data. Grey lines start at the historic peak of forest cover change for each time series. The detected forest cover change constituted declines in forest cover, calculated based on the LUH database (Hurtt et al., 2011). Green and purple lines show the duration of biodiversity monitoring, with the break between green and purple indicating the largest forest cover change event across the duration of each time series.

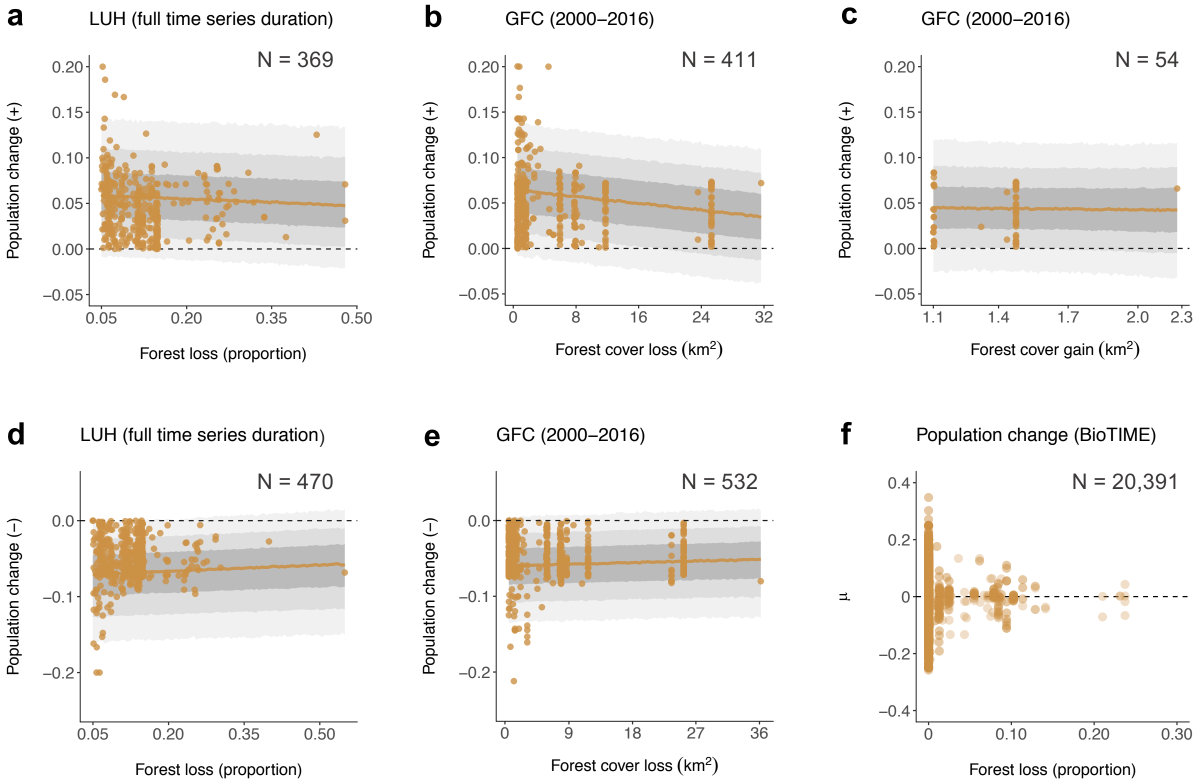


Appendix 4.3. Time since all-time peak forest loss was a poor predictor of the variation in contemporary population and biodiversity change, and for many of the locations represented by the time series in my study, there was more forest loss before monitoring began, relative to during the monitoring period.

2. Contemporary forest loss

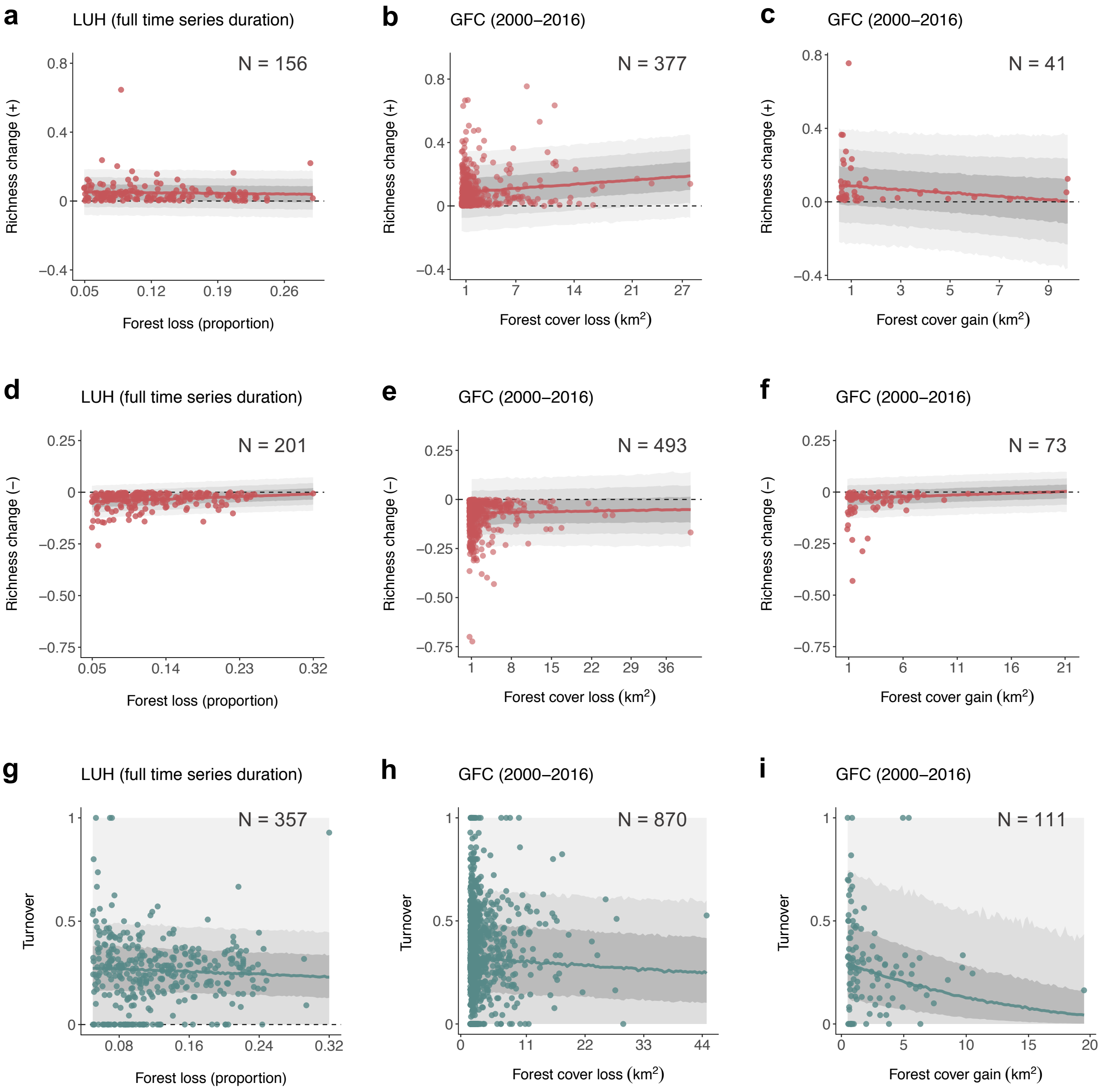
I found that local-scale increases and decreases in abundance, species richness, and temporal species replacement (turnover) were intensified by up to 48% following forest loss (see Chapter 4). I did not detect an effect of the magnitude of forest change on population and biodiversity losses. Greater magnitudes of forest loss did not correspond with larger increases in turnover or greater declines in populations and richness, and richness gains increased with forest loss (Appendix 4.4-4.6). Similarly, gains in forest cover did not correspond with gains in population abundance and species richness

(Appendix 4.4-4.6). When shorter time series were included in the analyses, larger forest cover loss corresponded with larger species richness gains (slope = 0.10, CI = 0.02 to 0.06, see Appendix 4.19 for outputs of models using time series with two or more survey points, and using time series with five or more survey points). I also quantified population change using the BioTIME database (following the same state-space modelling framework as with the LPD) and found similar lack of directional patterns in the relationships between population change and overall forest loss (Appendix 4.4**f**).



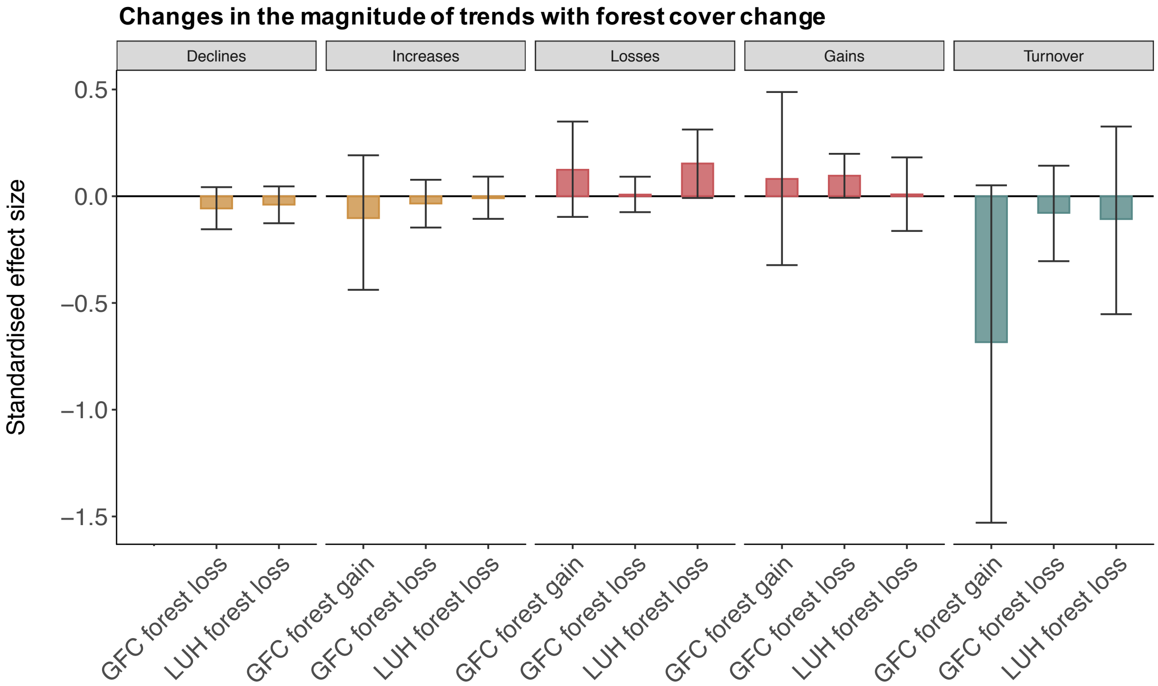
Appendix 4.4. Model visualisations for forest cover change and population change. Among time series, there were no directional trends between negative population change and forest cover change, quantified from both the GFC (Hansen et al., 2013) and LUH (Hurtt et al., 2011) databases. Sample size was too low for the convergence of a model testing negative population change versus forest cover gain. **f**, Similar lack of directional trends between population change and forest loss were apparent when using population change, calculated based on the terrestrial vertebrate and invertebrate species population time series within the BioTIME Database. Model fits on **a**-**e** are mixed effects models with

a biome random effect and a Gaussian error distribution. Grey shades indicate the 95%, 80% and 50% credible intervals. See Appendix 4.19 for model outputs.



Appendix 4.5. Model visualisations for forest cover change and biodiversity change (species richness and turnover). Among time series, greater forest loss corresponded with lower species richness loss, though note that the effect size was small (slope = 0.01, CI = 0.01 to 0.01) and increases in forest cover were related to lower turnover (slope = -0.26, CI = -0.47 to -0.07). **d**, **e**, **f**, There were no directional trends between species richness losses and forest cover gain, and between turnover and forest cover loss.

Asterisks indicate relationships where the 95% credible intervals for the slope did not overlap zero (**a**, **e**, **j**). Richness change was calculated using a mixed effects model with a Poisson error distribution. Turnover refers to changes in species composition due to species replacement in the final year of the time series relative to the start of the time series. Model fits on **a-f** are mixed effects models with a biome random effect and a Gaussian error distribution. Model fits in **h-j** are zero-one-inflated beta models with a logit link function. Grey shades indicate the 95%, 80% and 50% credible intervals. See Appendix 4.19 for model outputs.

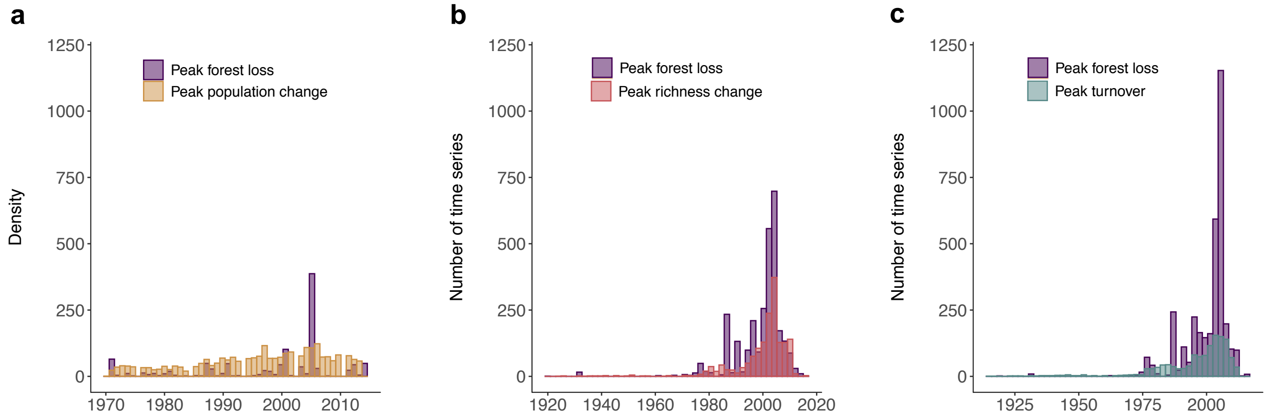


Appendix 4.6. Population change, richness change and turnover across sites experiencing forest loss span a spectrum from increases to no net changes and declines. The magnitude of forest loss experienced across sites over the duration of the GFC database (2000-2016) or the whole population and biodiversity time series duration

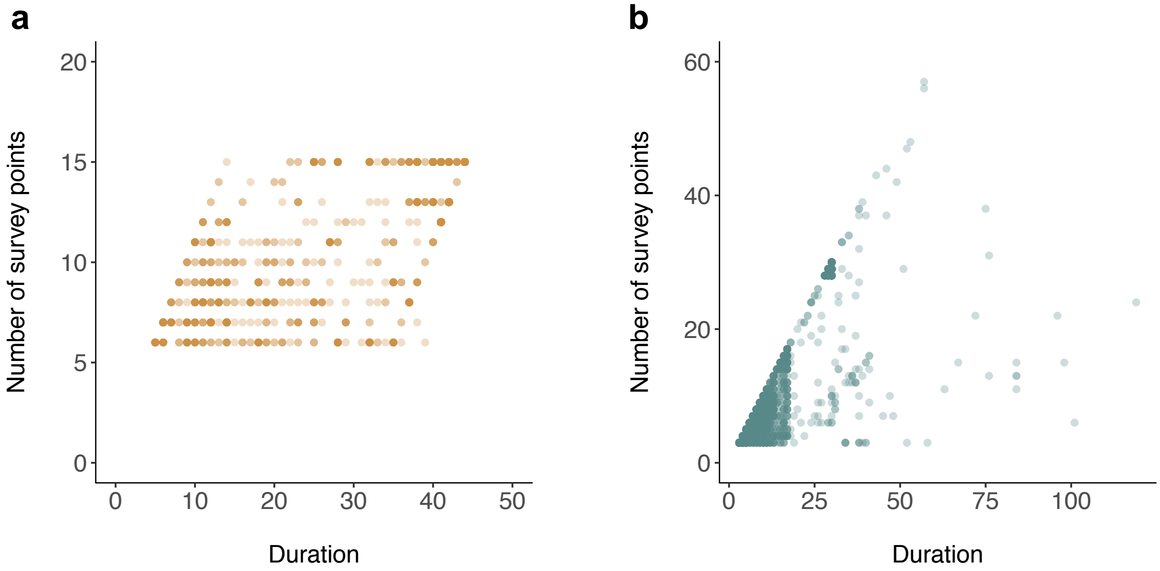
(forest loss calculated using LUH database) did not influence population declines and increases, richness losses, or turnover. Standardised effect sizes were calculated by dividing the model slopes by the standard deviation of the dependent variable. Numbers indicate sample size. For model visualisations, see Appendices 4.4-4.5.

3. Temporal lags

Temporal lags in population- and assemblage-level shifts after forest loss extended up to 50 years and were longer for species with longer generation times (see main text for further detail). Broadly across time series, the years in which forest loss peaked also coincided with peaks in population change, richness change and turnover, but there were also temporal delays in population and biodiversity change (Appendix 4. 7 and see Figure 5 in Chapter 4). The duration and number of survey points in population and biodiversity monitoring (Appendix 4.8) can influence my ability to detect responses to global change drivers, thus reinforcing the importance of frequent and long-term monitoring (Mihoub et al., 2017). I included duration as a fixed effect in my statistical models to test whether time series duration influenced the detected trends in population abundance, species richness and turnover. The trends often did not vary based on duration, with a general tendency for longer-duration time series to have more stable trends (See Appendix 4.19 for further details). As continued monitoring encompasses longer temporal spans with more frequent surveys, we will improve my ability to detect and attribute shifts in the Earth's biota.



Appendix 4.7. Generally, the years in which peak forest loss occurred across sites coincided with the most population and biodiversity change, but there were also lags in time (a-c).



Appendix 4.8. The duration of time series is broadly positively correlated with the number of survey points in each time series. Yellow shows the Living Planet database, blue shows BioTIME.

4. Biogeographic patterns

Methods

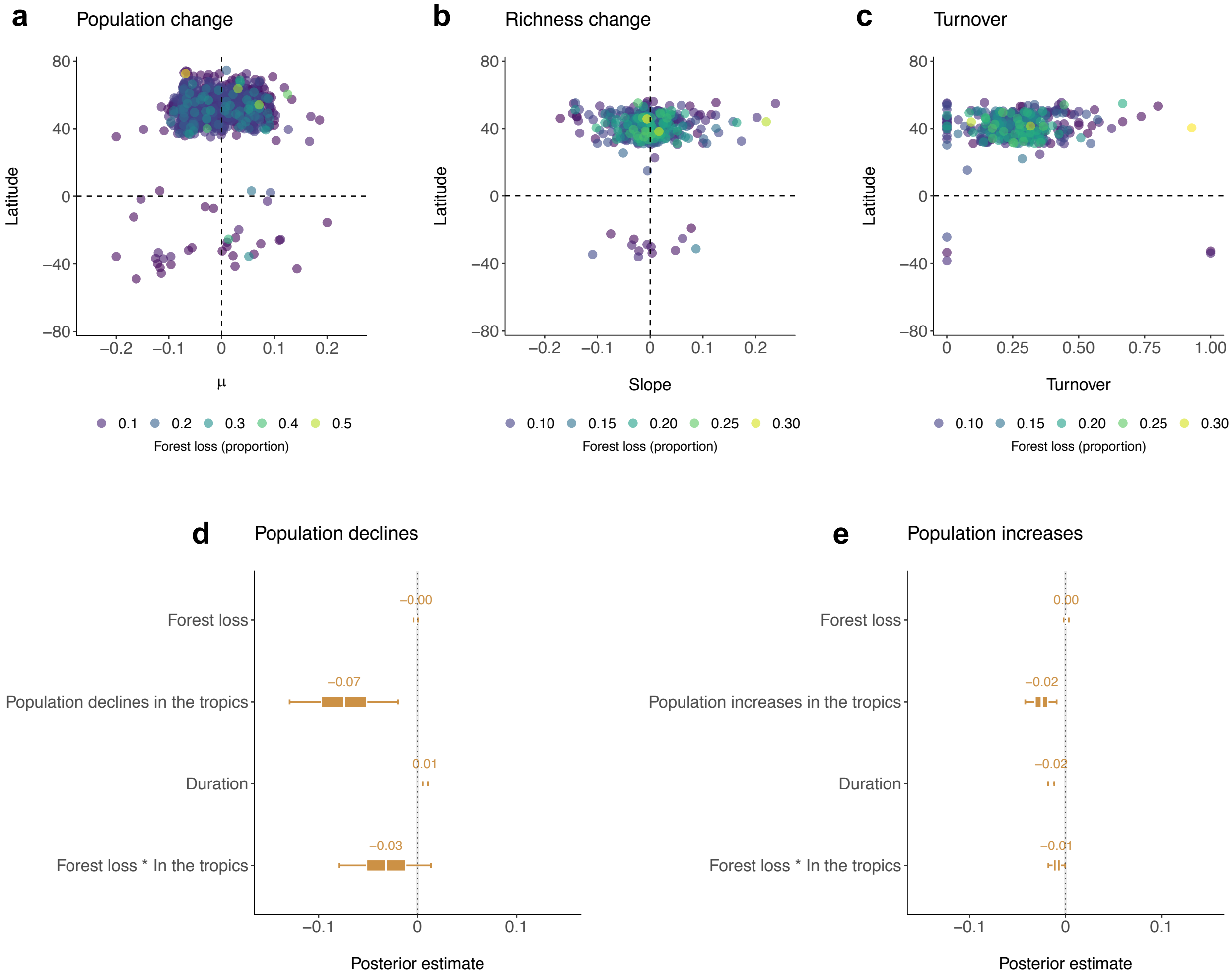
The effects of forest loss on populations and ecological assemblages are likely heterogeneous around the world. Thus, I asked:

- Do forest loss effects vary across latitude and specifically, are the effects of forest loss on population and biodiversity change in the tropics different relative to the rest of the world?
- Do forest loss effects on population change, richness change and turnover vary across biomes?

To investigate differences in how forest loss influences populations in different latitudes, and specifically in the tropics relative to the rest of the world, I included an interaction term between amount of forest loss and a categorical variable (in the tropics/not in the tropics) in a model of population trends versus magnitude of forest loss across the duration of each time series. A similar analysis was not possible for biodiversity change because of low sample size in tropical relative to non-tropical locations. Additionally, I visualised the posterior mean distributions per biome from my models comparing population change, richness change and turnover after contemporary peak forest loss, relative to the period before the forest loss event occurred.

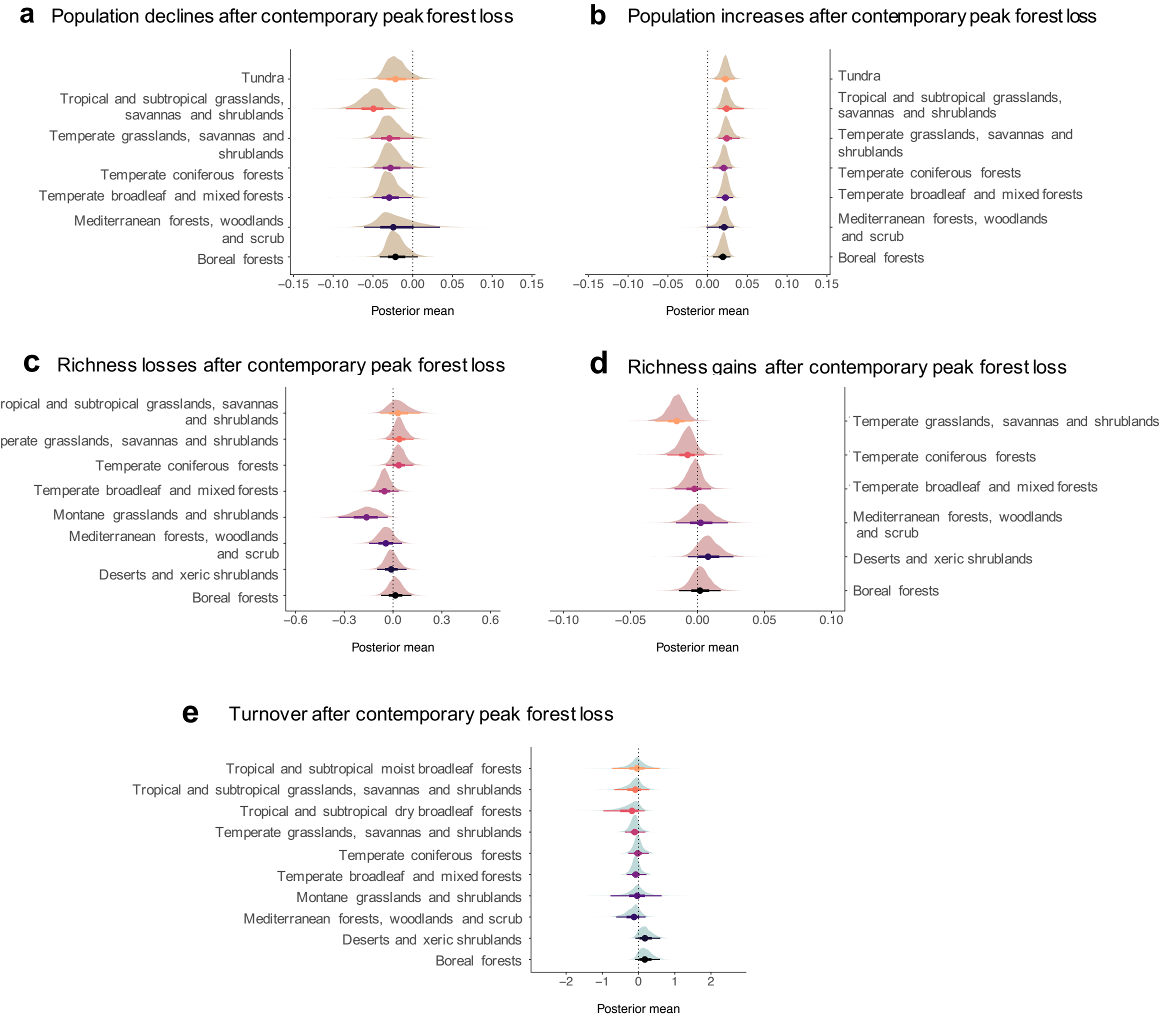
Results

I did not detect overall directional patterns in forest loss effects on populations and ecological assemblages across latitudes (Appendix 4.9**a**-**c**). However, I found that the effects of forest loss were more likely to be negative in the tropics relative to the rest of the globe. In particular, population increases were less frequent at tropical sites where higher amounts of forest have been lost (Appendix 4.19**d**-**e**). Population declines after contemporary peak forest loss were also more pronounced in tropical biomes (Appendix 4.10**a**). Richness losses after peak forest loss were more pronounced in montane biomes (Appendix 4.10**b**), whereas all biomes experienced varying amounts of turnover (Appendix 4.10**c**). The geographic gaps in the Living Planet and BioTIME databases reflect current differences in survey effort and public availability of data. With future monitoring targeted to places where forest loss effects are stronger, such as the tropics and places currently experiencing peaks in forest loss, we will be better able to capture the variety of ways in which human activities are transforming ecosystems.



Appendix 4.9. I detected little latitudinal patterning in the relationships between forest loss, population and biodiversity change, with the exception of tropical latitudes, where the effects of forest loss on population change were more negative in the tropics compared to the rest of the planet. Plots show population change, richness change and turnover over time across latitude (a, b, and c) for time series that experienced at least 5% loss in forest cover across their duration. Model summary graphs (d-e) show effect sizes and 95% credible intervals from models which included a binary categorical variable (in the tropics or not; for population declines there were 453 time series non-tropical and 17 tropical time series, and for population increases there were 351 non-tropical and 18 tropical time series). I categorised time series based on whether or not they fall within the Tropics of Capricorn and Cancer. Forest loss was calculated

using the LUH database as proportions bounded between zero and one across the same duration as that of each individual time series. See Appendix 4.19 for full model outputs.



Appendix 4.10. Biome differences in shifts in population change, richness change and turnover after contemporary peak forest loss, relative to the period before the forest loss event. Distributions show the posterior means extracted from mixed effects model comparing trends before and after peak forest loss, with biome as a random effect. See Appendix 4.19 for model outputs.

5. Cross-taxa patterns

Methods

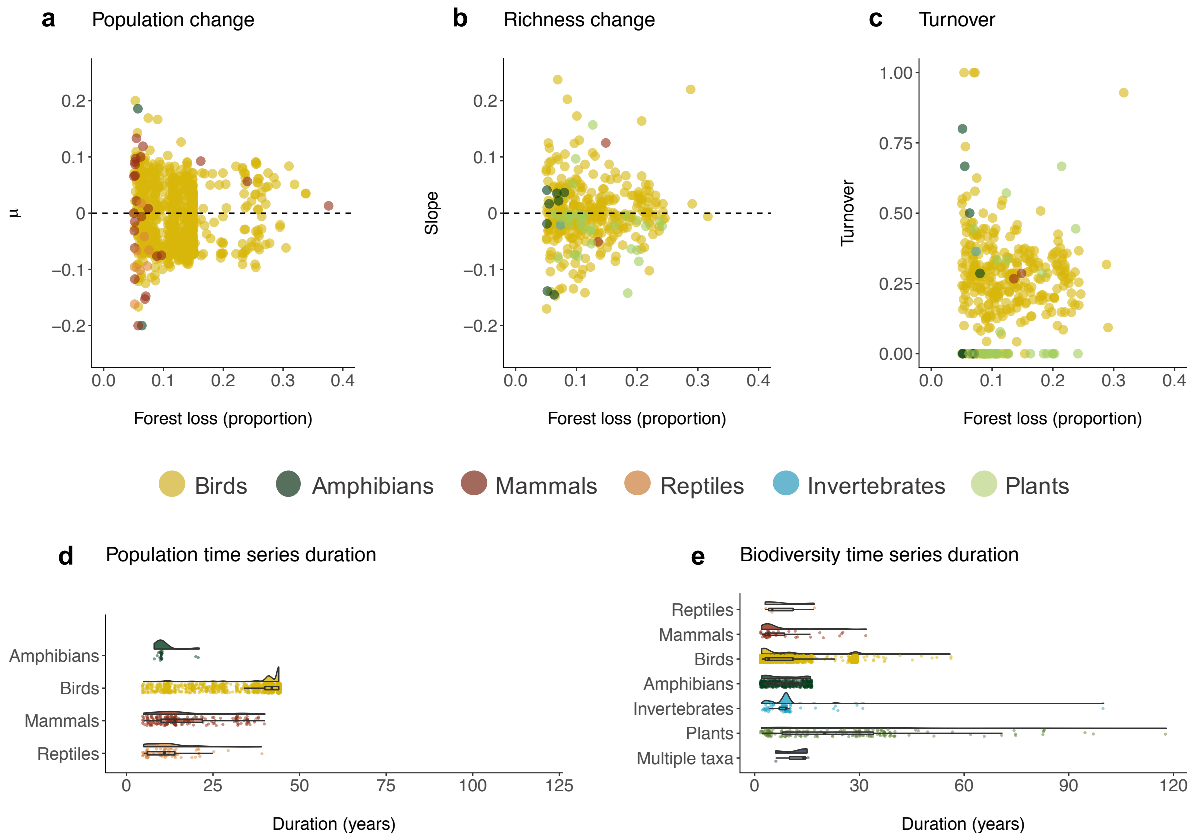
To determine if different groups of organisms are influenced by forest loss in varying ways, I asked:

- *Is there a taxonomic signal in the relationships between forest loss and population change, richness change and turnover?*

I thus visualised taxon-specific associations with forest loss.

Results

I did not find distinct taxonomic patterning in the relationships between population change, biodiversity change and forest cover loss (Appendix 4.11**a**-**c**). The sampling effort and time series duration differed across taxa. Birds, trees and mammals were better sampled with a greater number of longer time series (Appendix 4.11**d**-**e**). Filling in taxonomic gaps in population and biodiversity monitoring can provide further insights into potential taxon-specific responses to land-use change. Note that while there were no directional relationships between the amount of forest loss and population and biodiversity trends across taxa, I did find clear differences among taxa in the pace at which the abundance and biodiversity changed following contemporary peak forest loss (see temporal lags section and Figure 5 in Chapter 4 for further detail).



Appendix 4.11. Lack of taxonomic patterning in the relationships between forest loss, population and biodiversity change. Plots show population change, richness change and turnover over time across different taxa (**a**-**c**) for time series that experienced at least 5% loss in forest cover across their duration. Forest loss was calculated using the LUH database as proportions bounded between zero and one across the same duration as that of each individual time series. Population **d** and biodiversity **e** monitoring duration varied across taxa, with taxa like birds and plants usually monitored for longer time periods.

6. Cross-species patterns

Methods

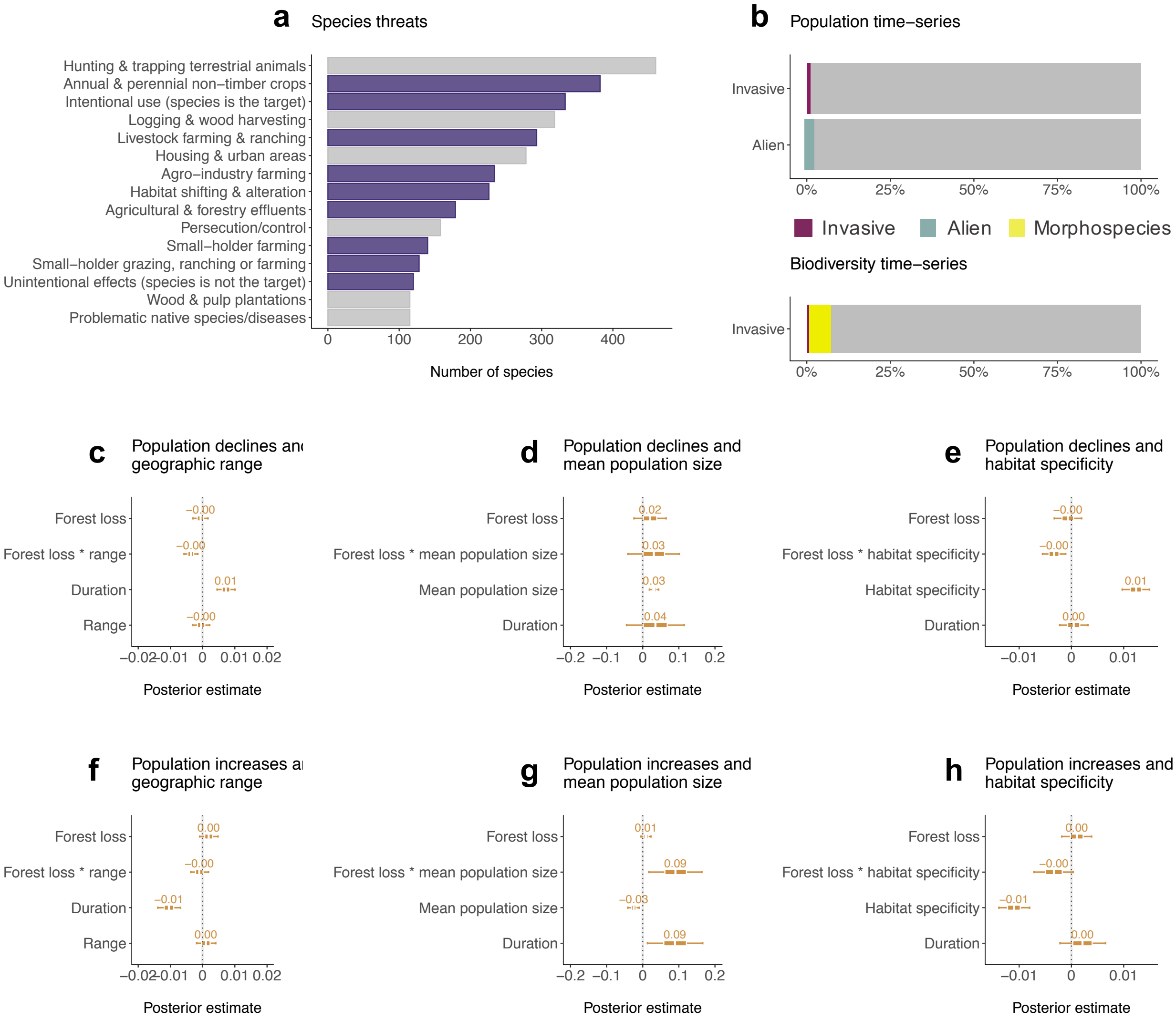
The patterns I detect in how forest loss influences populations and ecological assemblages can also be influenced by the types of species which are represented. To test this, I asked:

- *What are the threats commonly associated with the species represented in the population and biodiversity time series I studied?*
- *What proportion of the species represented in the population and biodiversity time series are classified as invasive or non-native?*
- *Are rare species more likely to respond negatively to forest loss compared to common species?*

I extracted species' threats from the IUCN Red List Database (IUCN, 2017) using the package *rredlist* v0.5.0 (Chamberlain, 2017) for the 755 species for which global threat assessments were available. Alien and invasive categorizations were available from the Living Planet Database. To classify the species from the BioTIME database, I used the Global Invasive Species Database (Invasive Species Specialist Group, 2019). I tested if rare species (based on species' geographic range, mean population size and habitat specificity) were more likely to be negatively influenced by forest loss by including a forest loss * rarity metric interaction term in my models. For full details on methods to determine rarity, see Chapter 3. Similar *post-hoc* analysis was not possible for the biodiversity time series because habitat preference and rarity data were not available for many of the species included in the BioTIME database.

Results

The dominant threats to the species represented in the databases were related to land-use change (Appendix 4.12**a**). A very small proportion (around 1%) of the species represented in my analyses were classified as invasive or alien (based on the Global Invasive Species Database, (Invasive Species Specialist Group, 2019), with around 3% of species identified as only morphospecies for which I cannot attribute species status (Appendix 4.12**b**). Because such a small proportion of species were alien or invasive, I was not able to test if such species respond differently to forest loss. I found that regardless of whether species were rare or common, they experienced the full spectrum of forest loss effects (Appendix 4.12**c**-**h**). Species' geographic range, mean population size and habitat specificity were poor predictors of population responses to forest loss over time (Appendices 4. 12**c**-**h**, 4.19).



Appendix 4.12. Many of the species I studied face threats related to land-use change, but there were no distinct responses to forest loss based on species' rarity and very few of the species were classified as invasive or alien. All species in the Living Planet Database were identified to the species level, whereas in the BioTIME Database, 7% of species were recorded as morphospecies. I found that regardless of whether species were rare or common, they experienced the full spectrum of forest loss effects (see Appendix 4.19 for full model outputs).

7. Scale influences

Methods

Ecological processes, including changes in biodiversity like richness increases and decreases, vary across spatial scales (Chase et al., 2019). In my analyses, I focused on local-scale population and biodiversity change. However, there are also scale influences in the driver which I tested, and specifically the scale over which forest cover change is calculated, as well as the resolution of the forest databases themselves. To test for the influence of scale in calculating forest cover change and subsequently, the relationships between population change, biodiversity change and shifts in forest cover, I asked:

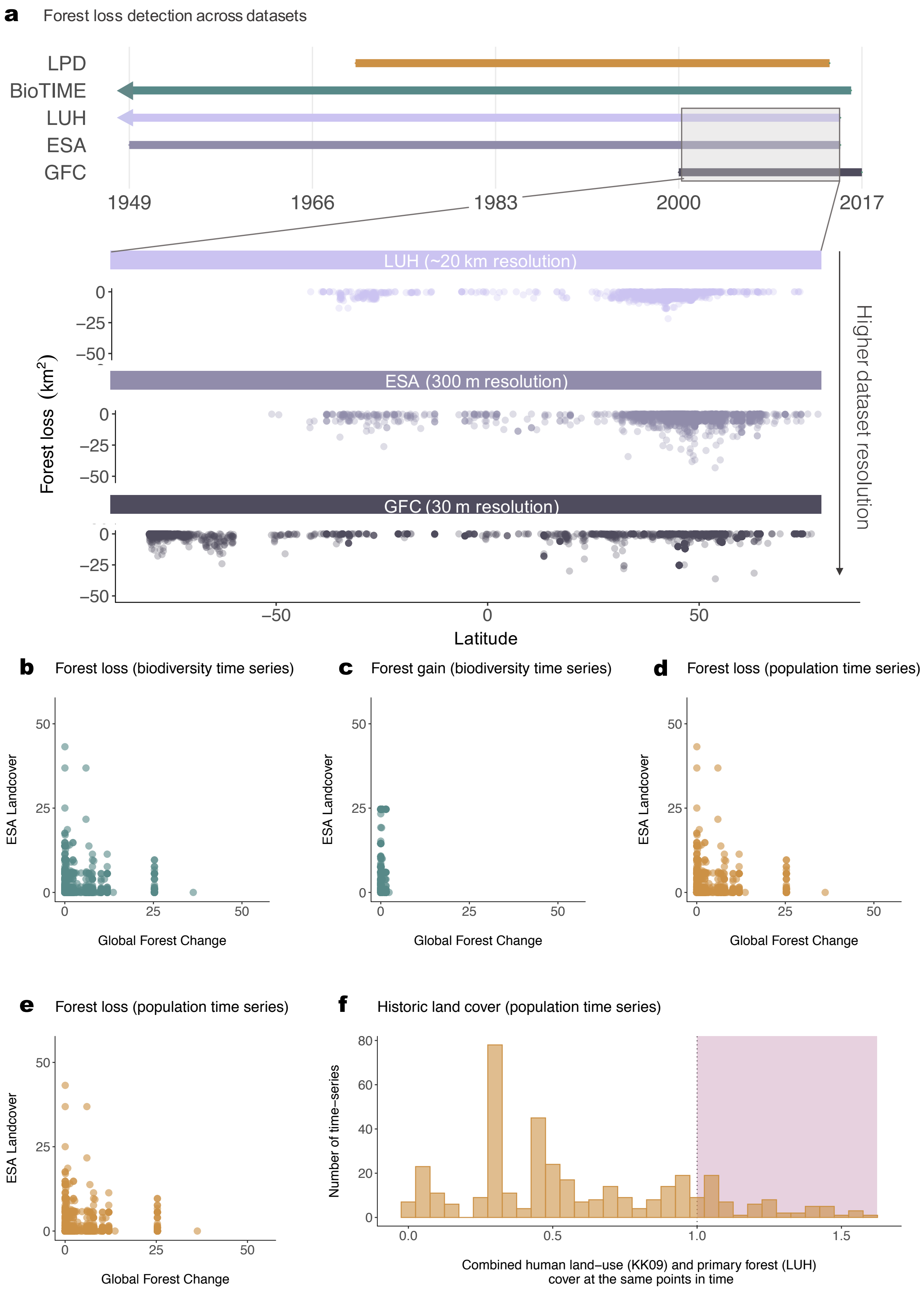
- *Does the amount of detected forest cover change vary depending on data sources?*
- *Does the spatial scale over which I quantify forest cover change influence its detected effects on population and biodiversity change?*

I tested how the amount of detected forest loss varies across two remote-sensing databases (GFC and ESA Landcover) for the time period over which they overlap (2000-2015). Uncertainty in forest cover estimates derived from the LUH database increases for records further back in time. On a European scale, I was able to compare historic land cover estimates as quantified by the LUH and KK09 databases. Additionally, I visualised the relationships between population change, richness change, turnover and forest loss across different spatial scales of calculating forest loss – from 10 to 500 km^2. Note that the scale over which I calculated biodiversity change (~96 km^2) remained constant as this is the scale for which I rarefied the biodiversity data based on study area (i.e., larger studies were split into smaller ones, but samples from different studies were never mixed together, for more details see Blowes et al. (2019).

Results

I found frequent mismatches in the magnitude of detected forest cover change detected at sites, but the broad variation in forest cover change across sites was similar (Appendices 5.4A-D, 4.5). I found that historic land cover estimates extracted from the LUH and KK09 databases were broadly consistent (Appendix 4.13f). I found low correspondence between the GFC and ESA Landcover databases. While GFC focuses exclusively on forests, ESA Landcover provides estimates for 37 different land cover classes. Thus, the potential explanations for the mismatches between the two databases include: 1) different definitions of a forest, 2) a ten-fold difference in resolution (30 m for GFC versus 300 m for ESA Landcover, and 3) differences in satellite data sources and processing methods. Previous studies comparing field observations to estimates from remote-sensing databases have found that the GFC performs better relative to other remote-sensing data sources (Andreacci & Marenzi, 2020), and I found that the GFC detects the most forest cover change (Appendix 4.13a), so I focused out magnitude of forest cover change analyses on estimates derived from the GFC.

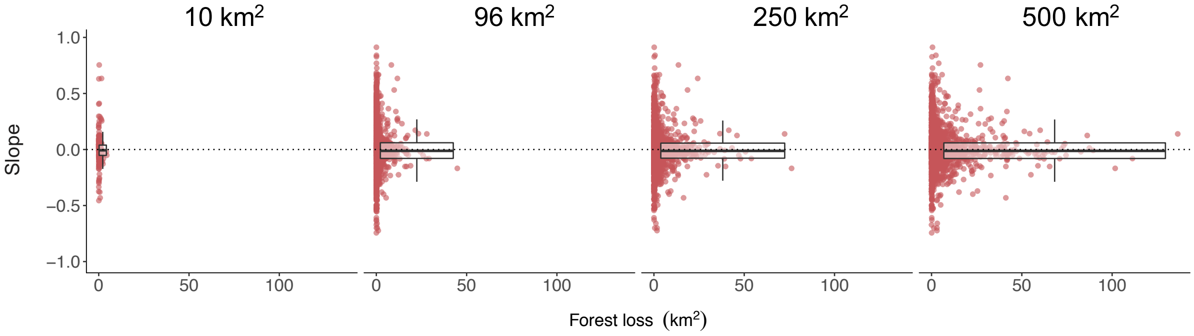
In my analyses, I focused on using the Land Use Harmonization database because it includes the longest possible temporal records of forest loss, and the GFC database, because it provides the highest spatial resolution for forest cover change currently available. My findings of both positive and negative associations of population and biodiversity change with forest cover change were broadly consistent regardless of the database with which forest cover was calculated.


a
Forest loss detection across datasets
LPD
BioTIME
LUH
ESA
GFC
1949
1966
1983
2000
2017
LUH (~20 km resolution)
ESA (300 m resolution)
GFC (30 m resolution)
Forest loss (km²)
0
–25
–50
Higher dataset resolution
–50
0
50
Latitude
b
Forest loss (biodiversity time series)
c
Forest gain (biodiversity time series)
d
Forest loss (population time series)
ESA Landcover
Global Forest Change
0
25
50
e
Forest loss (population time series)
f
Historic land cover (population time series)
Number of time–series
0
20
40
60
80
0.0
0.5
1.0
1.5
Combined human land–use (KK09) and primary forest (LUH)
cover at the same points in time

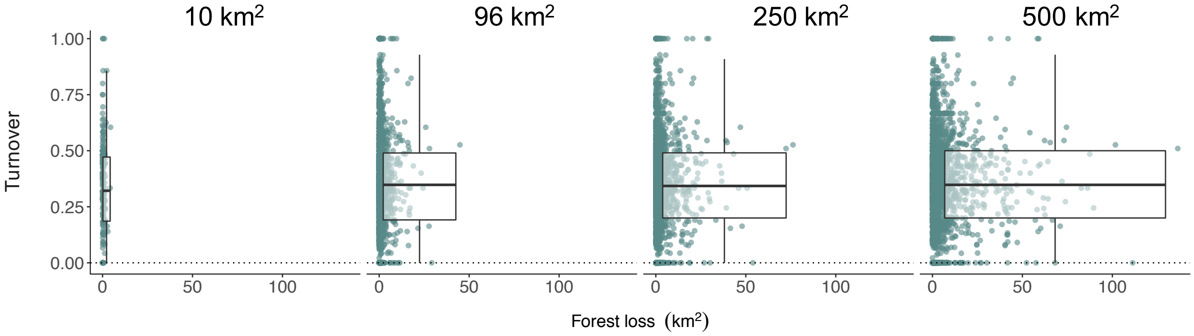
Appendix 4.13. Population, biodiversity and forest cover databases cover different periods in time and the amount of detected forest loss increases with higher resolution of the spatial data. Note that the LUH database starts in 850 and the first record in BioTIME is in 1858. The forest databases used to calculate forest loss were the LUH database*,* the ESA Landcover database and the GFC database. Direct comparisons of detected forest loss and gain across sites are shown in b-e. I derived historic anthropogenic land cover in Europe from the KK09 database (Kaplan et al., 2009) and primary forest cover derived from the LUH database (Hurtt et al., 2011) for the first year of each population time series for the same sized cells (~96 km^2) and combined them. This combined measure is shown on the x-axis of plot f. It is possible for the two estimates to be below one (suggesting at a given location there is some land under anthropogenic land use, some primary forest, but also another land cover type). Estimates above a value of one indicate instances where there might be an error in either of the two databases as the combined area of anthropogenic and forest cover in a cell should sum to one.

The cell size over which I calculated forest cover change (from 10 km^2 to 500 km^2) did not influence overall findings, as detected forest cover change scaled proportionately with cell size across locations and the slopes of model comparisons with richness change and turnover remained centred on zero (Appendix 4.14).

a Richness change and forest loss (GFC dataset) calculated across different scales



d Turnover and forest loss (GFC dataset) calculated across different scales



Appendix 4.14. The detected forest loss increased with larger cell sizes, but regardless of the cell size, I found both positive and negative richness trends associated with forest loss. Figure shows amount of forest cover loss based on GFC database (Hansen et al., 2013) across different cell sizes and how that relates to richness change slopes and turnover (Jaccard's dissimilarity). Boxplots show that the mean richness slopes and turnover did not vary substantially depending on the scale of calculating forest loss.

8. Landscape context

Methods

Landscape context, i.e., how much forest cover there is across larger spatial scales surrounding the location of each time series, can mediate the effects of forest loss on populations and biodiversity over time. Additionally, places where forests are the dominant habitat type might support more forest specialists (Betts et al., 2017). Populations and biodiversity are also always variable over time following natural community processes (Gotelli et al., 2017). Thus, I compared population and biodiversity trends on sites with intact and dominating forest cover with previously intact but now disturbed sites which have experienced forest loss. I asked:

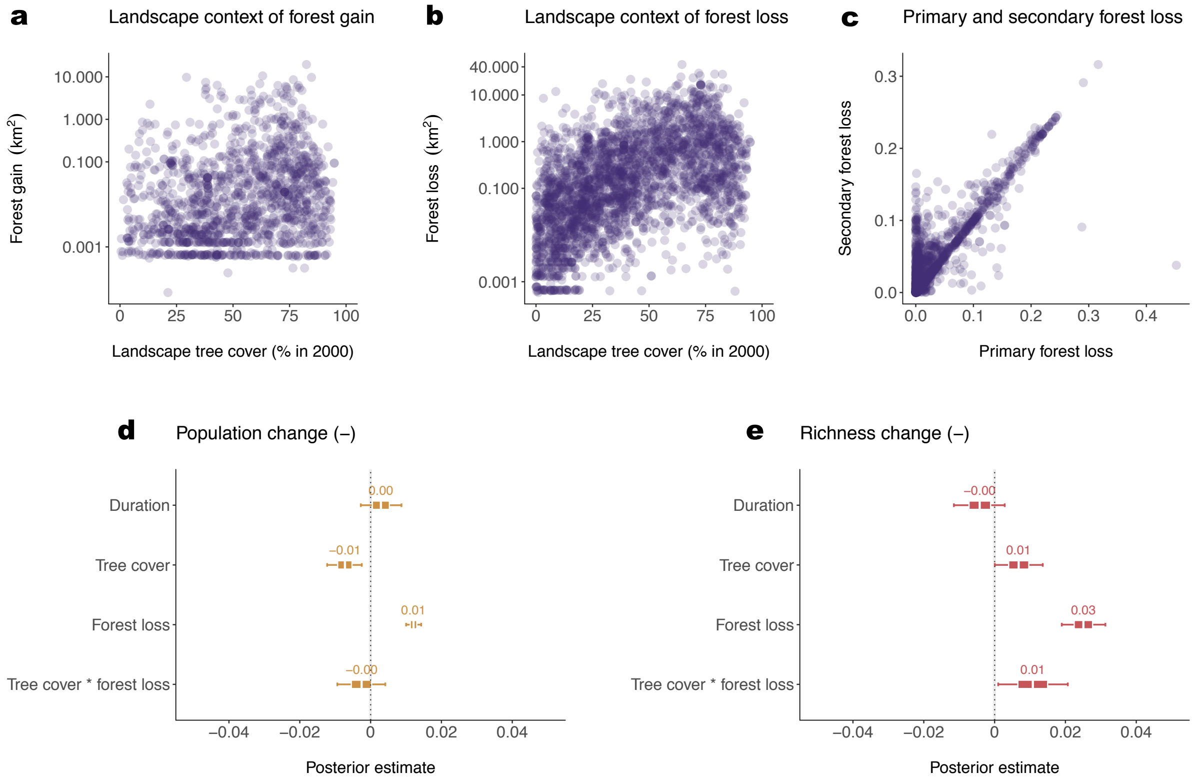
- *Does the landscape context of forest loss (amount of forested area in 500 km^2 cell around each time series location) influence the relationships between forest loss and population and biodiversity change?*
- *Does the type of forest (primary vs. secondary forest) influence the amount of detected forest cover change?*
- *What are the effects of forest loss on population change, richness change and turnover in forest-dominated sites?*

I included an interaction term forest loss * wider landscape forest cover in my models of population declines and richness losses versus magnitude of forest loss over the whole duration of each time series to test if higher forest cover in the wider landscape buffers the localised effects of forest loss. I visualised the relationship between losses in primary and secondary forest cover. I filtered for the time series where forests were the dominant habitat type at the start of the monitoring and categorised them as having remained relatively intact over time (<5% forest loss) or disturbed (>5% forest loss). I then visualised the distributions of population change, richness change and turnover across those two categories.

Results

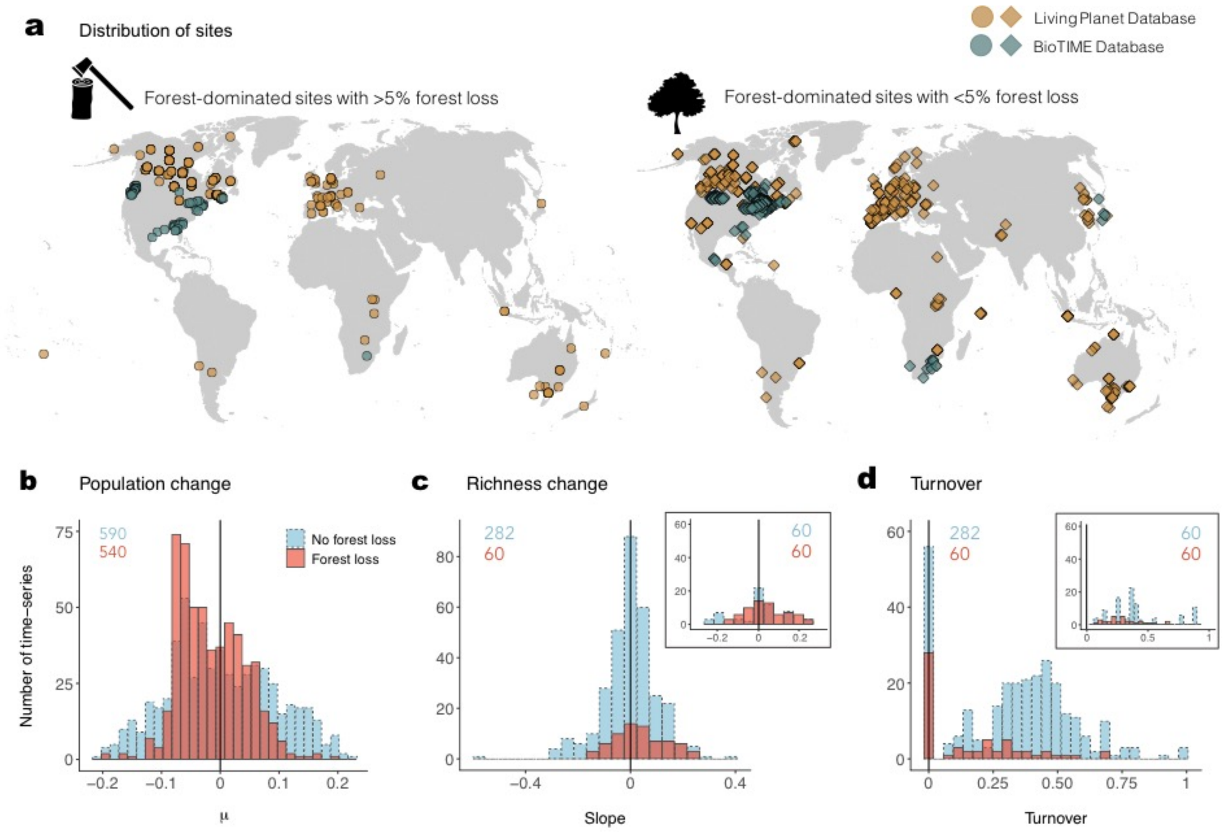
My findings were not influenced by the type of forest cover (primary vs secondary), as loss of secondary forest cover scaled proportionately to primary forest loss (Appendix 4.15a-c). Landscape context did not influence the relationship between forest cover change and population declines (Appendix 4.15d-e), but richness losses were lower when the landscape-scale forest cover was higher.

I found that in forest-dominated sites, where past disturbances were likely less frequent, declines in species' abundance were more frequent than increases, whereas richness change and turnover did not show directional trends (Appendix 4.16). The wide variety of richness trends and turnover on intact forested sites could potentially be explained by the presence of other global change drivers instead of forest loss present there, such as climate change or pollution.



Appendix 4.15. The amount of forest cover gain and loss broadly increases as tree cover within a 500 km^2 cell around each site increase, and the effects of forest loss

on species richness over time were less negative in places with higher tree cover. I calculated tree cover using the GFC database (a-b). Secondary forest loss scaled positively with primary forest loss (as captured by the LUH database). Forest loss on c was measured as a proportion between zero and one. I did not detect a significant interaction between tree cover and forest loss on population declines. See Appendix 4.19 for full model outputs.



Appendix 4.16. Forest-dominated sites which experienced forest loss were associated with more population declines relative to intact forested sites. The forest-dominated sites were predominantly in North America and Europe. x-axes on b-d show population trends (μ), slopes of richness change, and turnover (Jaccard's dissimilarity). Insets on c and d show a comparison of North American time series where for the "no forest loss" category I bootstrapped samples (we took the means of 100 random selections of the 282 available richness slopes) to achieve a more balanced sample distribution between the two categories.

Methods

Land-use change can lead to shifts in the dominant habitat type across ecosystems. Such habitat transitions from one state to another could represent a drastic change influencing the persistence of species and ecological communities (Betts et al., 2017). Thus, I asked:

- *How do habitat transitions relate to population change, richness change and turnover?*

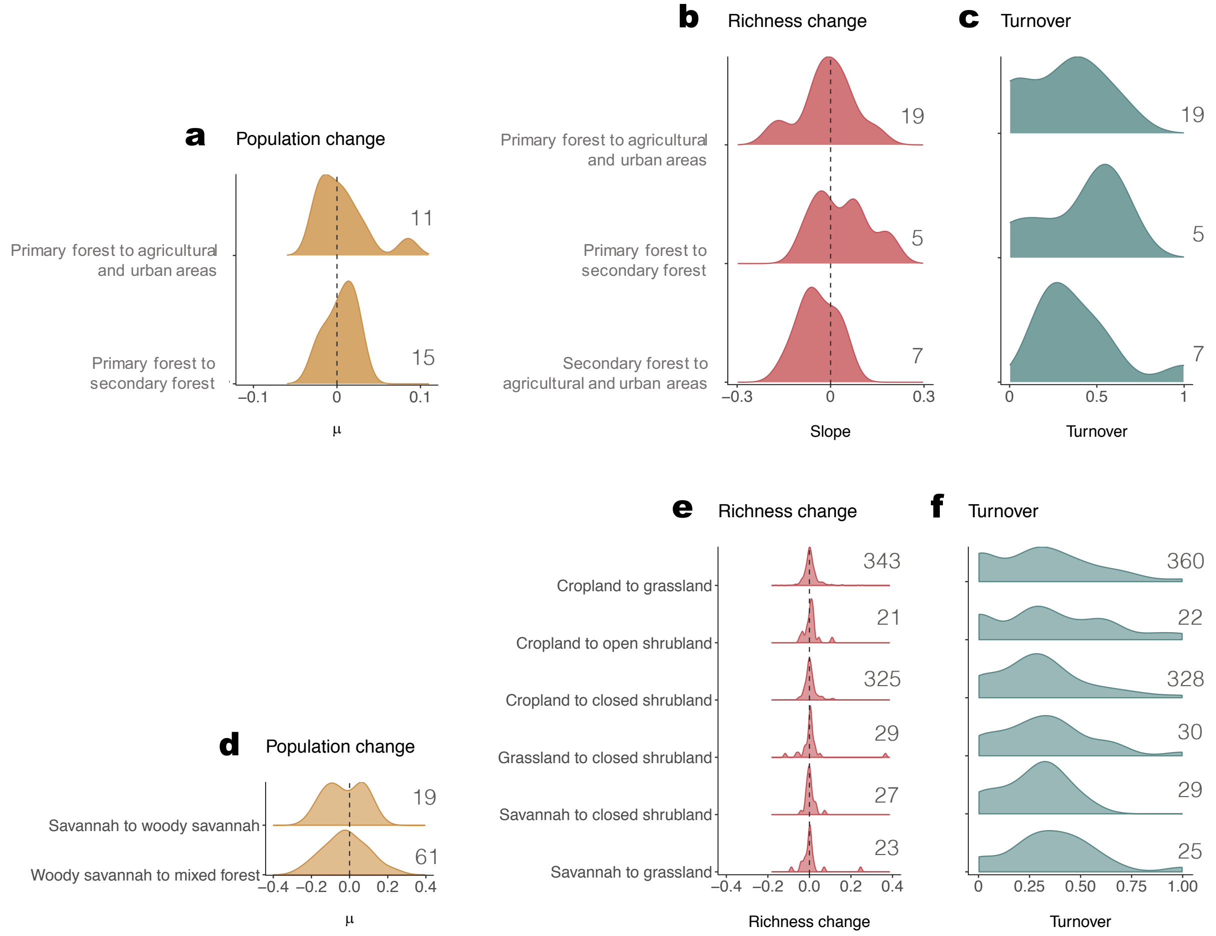
To quantify habitat conversion for locations where I had population and biodiversity monitoring data, I used the MODIS Landcover database (Channan et al., 2014). The MODIS database has a resolution of 500 m, and it uses satellite-derived reflectance data to classify land cover around the world. To determine the types of habitat conversion between 2000 and 2013 (the time span of available MODIS data) across all monitoring locations, I calculated the dominant land cover type at the start and end of each population and biodiversity time series and split time series into categories such as “no habitat conversion” and “grassland to woody savannah”. I focused on the eight most frequent types of habitat conversion.

To determine the influence of the type of habitat transitions on population and biodiversity change, I compared the distributions of population and biodiversity change across transitions types (from primary forest to secondary forest, from primary forest to non-natural habitat, and from secondary forest to non-natural habitat, to which I refer as habitat conversion). Small sample sizes (on average 10 time series per transition type) precluded statistical analysis, thus I report findings from a visual inspection of distributions of population and biodiversity change across habitat conversion types.

Results

In approximately 5% of monitored time series, forest loss consisted of a conversion in the dominant habitat type (*e.g.*, from primary forest to urban areas). Habitat conversions corresponded with both gains and losses in population abundance and species richness

(Appendix 4.17a-b, d-e). Turnover was high when primary forests were converted to agricultural and urban areas and to secondary forests (Appendix 4.17c), as well as when sites underwent transitions in dominant habitat types (Appendix 4.17f). While land-use and habitat transitions were not common across the time series I studied, when they did occur, they were associated with shifts in populations and biodiversity, particularly replacement of species (turnover).



Appendix 4.17. Population and biodiversity change following land-use transitions as detected by the LUH database (Hurtt et al., 2011) and following habitat transitions as detected by the MODIS Landcover database (Channan et al., 2014). Population and biodiversity change following land-use and habitat transitions included instances of declines, increases and no net changes across sites. Both land-use and habitat transitions were associated with high turnover (e.g., around 50% of original species replaced by the end of the time series which has experienced the transition).

Distributions show *μ* values for population change, posterior means (slopes) for richness change and Jaccard's dissimilarity for turnover under different habitat conversions. The y-axis refers to the probability density function for the kernel density estimation per unit on the x-axis, and the distributions are relative to one another. Numbers in plots indicate number of time series for each category.

Appendix 4.18. Number of time series in this study across woody biomes, as defined by Olson and Dinerstein (Olson & Dinerstein, 2002).

Database	Biome	Number of time series
Living Planet Database (total 2729 time series)	Boreal forests/taiga	919
	Deserts and xeric shrublands	20
	Flooded grasslands and savannas	3
	Mediterranean forests woodlands and scrub	128
	Montane grasslands and shrublands	2
	Temperate broadleaf and mixed forests	853
	Temperate coniferous forests	301
	Temperate grasslands savannas and shrublands	241
	Tropical and subtropical coniferous forests	1
	Tropical and subtropical dry broadleaf forests	5
	Tropical and subtropical grasslands savannas and shrublands	70
	Tropical and subtropical moist broadleaf forests	58
	Tundra	128
BioTIME (total 3361 time series)	Boreal forests/taiga	232
	Deserts and xeric shrublands	45
	Flooded grasslands and savannas	4
	Mangroves	5
	Mediterranean forests woodlands and scrub	49
	Montane grasslands and shrublands	69
	Temperate broadleaf and mixed forests	2,020
	Temperate conifer forests	695
	Temperate grasslands savannas and shrublands	147
	Tropical and subtropical dry broadleaf forests	3
	Tropical and subtropical grasslands savannas and shrublands	23

	Tropical and subtropical moist broadleaf forests	57
	Tundra	12

Appendix 4.19. Model outputs for all analyses. Scaled variables were mean centred on zero. Term names starting with "b" refer to fixed effects and term names starting with "r" refer to random intercepts. Sigma indicates the residual variance. For turnover models, "zoi" refers to the probability of being a zero or a one, "coi" refers to the conditional probability of being a one (given an observation is a zero or a one), and "phi" is the precision parameter of zero-one inflated beta distribution. "Scaled" indicates variables which were centred with a mean of zero. Numbers (N) refer to the sample size for each model and are presented as number of time series out of the overall number of population (2729) and biodiversity (3361) time series I analysed. The sample sizes for each model were determined based on the aim of the model (e.g., testing specifically time series where populations declined, and the sites experienced more than 5% forest loss). See methods for details on analyses. The differences in sample size for the different statistical models stem from the nature of each research question and data availability. See section 4.3 Methods in Chapter 4 for details of models.

Model	Term	Estimate	Std. error	Lower 95% CI	Upper 95% CI
Population declines before/after forest loss (N = 467 / 2,729)	b.intercept	-0.040	0.011	-0.061	-0.025
	b.after.forest.loss	-0.037	0.002	-0.041	-0.033
	b.duration.scaled	0.010	0.001	0.008	0.012
	sigma	0.033	0.001	0.032	0.035
	biome.boreal.forests.taiga	0.016	0.011	0	0.036
	biome.flooded.grasslands.and.savannas	-0.036	0.033	-0.083	0.006
	biome.mediterranean.forests.woodlands.and.scrub	0.013	0.021	-0.017	0.056
	biome.temperate.broadleaf.and.mixed.forests	0.008	0.011	-0.009	0.027
	biome.temperate.coniferous.forests	0.009	0.011	-0.008	0.029
	biome.temperate.grasslands.savannas.and.shrublands	0.008	0.012	-0.011	0.031
	biome.tropical.and.subtropical.coniferous.forests	-0.004	0.016	-0.032	0.027
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.012	0.014	-0.038	0.009
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.026	0.023	-0.060	0.006
	biome.tundra	0.015	0.013	-0.003	0.036
	b.intercept	0.034	0.004	0.028	0.041

	b.after.forest.loss	0.022	0.003	0.017	0.027
Population increases before/after forest loss (N = 343 / 2,729)	b.duration.scaled	-0.010	0.002	-0.013	-0.008
	sigma	0.038	0.001	0.036	0.040
	biome.boreal.forests.taiga	-0.002	0.003	-0.010	0.002
	biome.flooded.grasslands.and.savannas	0	0.004	-0.008	0.012
	biome.mediterranean.forests.woodlands.and.scrub	-0.001	0.004	-0.013	0.008
	biome.temperate.broadleaf.and.mixed.forests	0	0.003	-0.006	0.006
	biome.temperate.coniferous.forests	-0.001	0.003	-0.010	0.005
	biome.temperate.grasslands.savannas.and.shrublands	0.001	0.004	-0.005	0.012
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.001	0.004	-0.007	0.013
	biome.tundra	0	0.003	-0.008	0.008
Population change before/during/after peak deforestation (N = 1,941 / 2,729)	b.intercept	0.002	0.006	-0.010	0.011
	b.periodduring	-0.007	0.003	-0.012	-0.001
	b.after.forest.loss	-0.009	0.004	-0.015	-0.003
	b.duration.scaled	-0.006	0.002	-0.009	-0.003
	sigma	0.057	0.001	0.056	0.059
	biome.boreal.forests.taiga	0.002	0.007	-0.009	0.014
	biome.deserts.and.xeric.shrublands	-0.030	0.012	-0.049	-0.012
	biome.flooded.grasslands.and.savannas	-0.011	0.017	-0.040	0.016
	biome.mediterranean.forests.woodlands.and.scrub	0.010	0.008	-0.003	0.023
	biome.montane.grasslands.and.shrublands	0.013	0.016	-0.012	0.039
	biome.temperate.broadleaf.and.mixed.forests	0.009	0.007	-0.002	0.020
	biome.temperate.coniferous.forests	0.001	0.007	-0.011	0.013
	biome.temperate.grasslands.savannas.and.shrublands	-0.004	0.008	-0.017	0.009
	biome.tropical.and.subtropical.coniferous.forests	0.003	0.016	-0.023	0.033
	biome.tropical.and.subtropical.dry.broadleaf.forests	-0.022	0.015	-0.048	0.001
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.003	0.008	-0.016	0.010
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.018	0.009	0.004	0.032
	biome.tundra	0.011	0.008	-0.002	0.025

Richness losses before/after peak deforestation (N = 188 / 3,361)	b.intercept	-0.100	0.033	-0.163	-0.043
	b.after.forest.loss	-0.018	0.011	-0.036	-0.001
	b.duration.scaled	0.035	0.006	0.026	0.044
	sigma	0.097	0.004	0.091	0.103
	biome.boreal.forests.taiga	0.032	0.042	-0.039	0.105
	biome.deserts.and.xeric.shrublands	0.007	0.039	-0.065	0.071
	biome.mediterranean.forests.woodlands.and.scrub	-0.026	0.046	-0.105	0.048
	biome.montane.grasslands.and.shrublands	-0.146	0.076	-0.268	-0.031
	biome.temperate.broadleaf.and.mixed.forests	-0.035	0.033	-0.091	0.029
	biome.temperate.conifer.forests	0.053	0.037	-0.011	0.116
	biome.temperate.grasslands.savannas.and.shrublands	0.056	0.035	0	0.124
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.048	0.059	-0.041	0.154
Richness gains before/after peak deforestation (N = 266 / 3,361)	b.intercept	0.030	0.005	0.020	0.039
	b.after.forest.loss	-0.002	0.001	-0.004	0
	b.duration.scaled	0.002	0.001	0	0.003
	sigma	0.016	0.001	0.015	0.017
	biome.boreal.forests.taiga	0.004	0.007	-0.008	0.015
	biome.deserts.and.xeric.shrublands	0.010	0.008	-0.002	0.024
	biome.mediterranean.forests.woodlands.and.scrub	0.004	0.009	-0.009	0.020
	biome.temperate.broadleaf.and.mixed.forests	0	0.005	-0.010	0.010
	biome.temperate.conifer.forests	-0.005	0.006	-0.016	0.004
	biome.temperate.grasslands.savannas.and.shrublands	-0.013	0.006	-0.024	-0.003
Turnover before/after peak deforestation (N = 389 / 3,361)	b.intercept	-1.009	0.095	-1.219	-0.831
	b.zoi.intercept	-1.266	0.076	-1.392	-1.146
	b.coi.intercept	-2.553	0.235	-2.937	-2.190
	b.after.forest.loss	-0.036	0.043	-0.105	0.031
	b.duration.scaled	-0.121	0.044	-0.195	-0.052
	phi	13.448	0.684	12.352	14.551
	biome.boreal.forests.taiga	0.211	0.174	-0.026	0.493
	biome.deserts.and.xeric.shrublands	0.210	0.171	-0.023	0.500
	biome.mediterranean.forests.woodlands.and.scrub	-0.088	0.168	-0.450	0.164

	biome.montane.grasslands.and.shrublands	-0.001	0.204	-0.467	0.486
	biome.temperate.broadleaf.and.mixed.forests	-0.042	0.094	-0.214	0.165
	biome.temperate.conifer.forests	0.010	0.104	-0.165	0.243
	biome.temperate.grasslands.savannas.and.shrublands	-0.069	0.104	-0.273	0.133
	biome.tropical.and.subtropical.dry.broadleaf.forests	-0.142	0.225	-0.671	0.160
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.050	0.172	-0.434	0.268
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.005	0.194	-0.463	0.432
Population change and magnitude of peak forest loss (N = 618 / 2,729)	b.intercept	0.028	0.006	0.017	0.039
	b.max.loss.scaled	-0.002	0.002	-0.005	0.001
	b.duration.scaled	-0.021	0.002	-0.024	-0.018
	sigma	0.043	0.001	0.041	0.045
	biome.boreal.forests.taiga	-0.001	0.006	-0.013	0.010
	biome.flooded.grasslands.and.savannas	0.009	0.014	-0.010	0.043
	biome.mediterranean.forests.woodlands.and.scrub	-0.001	0.010	-0.024	0.022
	biome.temperate.broadleaf.and.mixed.forests	0.008	0.007	-0.002	0.021
	biome.temperate.coniferous.forests	0.001	0.007	-0.011	0.014
	biome.temperate.grasslands.savannas.and.shrublands	0	0.008	-0.016	0.015
	biome.tropical.and.subtropical.coniferous.forests	0.001	0.011	-0.023	0.027
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.017	0.018	-0.049	0.005
	biome.tropical.and.subtropical.moist.broadleaf.forests	0	0.011	-0.025	0.024
	biome.tundra	-0.002	0.008	-0.017	0.011
Richness change and magnitude of peak forest loss (N = 386 / 3,361)	b.intercept	0.028	0.005	0.019	0.040
	b.max.loss.scaled	-0.003	0.001	-0.005	-0.001
	b.duration.scaled	-0.002	0.002	-0.006	0.001
	sigma	0.027	0.001	0.025	0.028
	biome.boreal.forests.taiga	0.007	0.008	-0.003	0.021
	biome.deserts.and.xeric.shrublands	-0.005	0.007	-0.020	0.006
	biome.mediterranean.forests.woodlands.and.scrub	0	0.006	-0.014	0.012
	biome.montane.grasslands.and.shrublands	0.013	0.018	-0.006	0.058

	biome.temperate.broadleaf.and.mixed.forests	-0.001	0.005	-0.013	0.007
	biome.temperate.conifer.forests	-0.003	0.006	-0.016	0.005
	biome.temperate.grasslands.savannas.and.shrublands	-0.006	0.006	-0.019	0.002
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.002	0.009	-0.027	0.015
Turnover and magnitude of peak forest loss (N = 386 / 3,361)	b.intercept	0.220	0.115	0.013	0.425
	b.max.loss.scaled	0.005	0.007	-0.006	0.016
	b.duration.scaled	-0.010	0.004	-0.017	-0.003
	sigma	0.091	0.003	0.087	0.096
	biome.boreal.forests.taiga	-0.153	0.117	-0.355	0.059
	biome.deserts.and.xeric.shrublands	-0.121	0.118	-0.327	0.087
	biome.mediterranean.forests.woodlands.and.scrub	-0.070	0.118	-0.278	0.138
	biome.montane.grasslands.and.shrublands	0.699	0.141	0.473	0.957
	biome.temperate.broadleaf.and.mixed.forests	-0.125	0.115	-0.333	0.080
	biome.temperate.conifer.forests	-0.122	0.116	-0.322	0.090
	biome.temperate.grasslands.savannas.and.shrublands	-0.125	0.116	-0.333	0.080
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.004	0.142	-0.223	0.254
Population declines and overall forest loss (N = 470 / 2,729)	b.intercept	-0.052	0.003	-0.062	-0.047
	b.forest.loss.scaled	-0.001	0.001	-0.003	0.001
	b.duration.scaled	0.012	0.001	0.009	0.014
	sigma	0.026	0.001	0.025	0.028
	biome.boreal.forests.taiga	0.001	0.003	-0.004	0.013
	biome.deserts.and.xeric.shrublands	-0.003	0.007	-0.031	0.007
	biome.mediterranean.forests.woodlands.and.scrub	-0.001	0.005	-0.018	0.007
	biome.temperate.broadleaf.and.mixed.forests	0	0.003	-0.006	0.010
	biome.temperate.coniferous.forests	0.001	0.004	-0.006	0.012
	biome.temperate.grasslands.savannas.and.shrublands	0.001	0.004	-0.007	0.012
	biome.tropical.and.subtropical.coniferous.forests	-0.001	0.005	-0.021	0.011
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.003	0.006	-0.024	0.006

	biome.tropical.and.subtropical.moist.broadleaf.forests	0.002	0.005	-0.008	0.022
	biome.tundra	0.006	0.009	-0.003	0.024
Population increases and overall forest loss (N = 369 / 2,729)	b.intercept	0.047	0.003	0.042	0.054
	b.forest.loss.scaled	0	0.002	-0.003	0.002
	b.duration.scaled	-0.012	0.002	-0.015	-0.009
	sigma	0.029	0.001	0.027	0.031
	biome.boreal.forests.taiga	0	0.002	-0.008	0.006
	biome.mediterranean.forests.woodlands.and.scrub	0.001	0.003	-0.005	0.017
	biome.temperate.broadleaf.and.mixed.forests	0	0.002	-0.008	0.004
	biome.temperate.coniferous.forests	0	0.002	-0.009	0.006
	biome.temperate.grasslands.savannas.and.shrublands	0	0.002	-0.010	0.005
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.001	0.003	-0.017	0.006
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.001	0.003	-0.006	0.023
	biome.tundra	-0.001	0.003	-0.011	0.005
Population declines and forest cover loss (2000-2016) (N = 532 / 2,729)	b.intercept	-0.052	0.002	-0.057	-0.046
	b.forest.loss.scaled	-0.002	0.001	-0.004	0.001
	b.duration.scaled	0.012	0.001	0.009	0.014
	sigma	0.027	0.001	0.025	0.028
	biome.boreal.forests.taiga	0	0.002	-0.006	0.006
	biome.mediterranean.forests.woodlands.and.scrub	0	0.003	-0.007	0.009
	biome.temperate.broadleaf.and.mixed.forests	0	0.002	-0.006	0.005
	biome.temperate.coniferous.forests	0.001	0.003	-0.004	0.009
	biome.temperate.grasslands.savannas.and.shrublands	0	0.003	-0.008	0.009
	biome.tropical.and.subtropical.dry.broadleaf.forests	-0.001	0.003	-0.014	0.008
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.001	0.004	-0.007	0.017
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.003	0.004	-0.017	0.003
	b.intercept	0.051	0.003	0.047	0.057
	b.forest.loss.scaled	-0.001	0.002	-0.004	0.002

Population increases and forest cover loss (2000-2016) (N = 411 / 2,729)	b.duration.scaled	-0.015	0.002	-0.018	-0.012
	sigma	0.032	0.001	0.030	0.034
	biome.boreal.forests.taiga	-0.002	0.003	-0.009	0.003
	biome.deserts.and.xeric.shrublands	0	0.003	-0.009	0.008
	biome.mediterranean.forests.woodlands.and.scrub	0	0.003	-0.009	0.006
	biome.temperate.broadleaf.and.mixed.forests	0.001	0.002	-0.004	0.007
	biome.temperate.coniferous.forests	0	0.003	-0.005	0.007
	biome.temperate.grasslands.savannas.and.shrublands	0.001	0.003	-0.006	0.009
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0	0.003	-0.006	0.011
	biome.tropical.and.subtropical.moist.broadleaf.forests	0	0.003	-0.008	0.008
	biome.tundra	0	0.003	-0.011	0.007
Population increases and forest cover gain (2000-2016) (N = 54 / 2,729)	b.intercept	0.049	0.048	-0.064	0.266
	b.forest.gain.scaled	-0.003	0.005	-0.012	0.005
	b.duration.scaled	0.002	0.012	-0.014	0.028
	sigma	0.027	0.003	0.023	0.032
	biome.temperate.broadleaf.and.mixed.forests	-0.005	0.049	-0.233	0.103
	biome.temperate.coniferous.forests	0.019	0.062	-0.109	0.238
	biome.tundra	-0.013	0.045	-0.197	0.109
Richness losses and overall forest loss (N = 201 / 3,361)	b.intercept	-0.036	0.005	-0.045	-0.027
	b.forest.loss.scaled	0.006	0.003	0.001	0.011
	b.duration.scaled	0.003	0.003	-0.002	0.008
	sigma	0.039	0.002	0.036	0.042
	biome.boreal.forests.taiga	0	0.005	-0.013	0.016
	biome.deserts.and.xeric.shrublands	0.002	0.005	-0.008	0.015
	biome.mediterranean.forests.woodlands.and.scrub	0	0.005	-0.015	0.012
	biome.montane.grasslands.and.shrublands	0	0.005	-0.016	0.013
	biome.temperate.broadleaf.and.mixed.forests	0	0.004	-0.009	0.009
	biome.temperate.conifer.forests	-0.004	0.006	-0.017	0.004
	biome.temperate.grasslands.savannas.and.shrublands	-0.001	0.005	-0.013	0.010

	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.001	0.005	-0.012	0.017
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.001	0.006	-0.011	0.018
Richness gains and overall forest loss (N = 156 / 3,361)	b.intercept	0.045	0.009	0.026	0.063
	b.forest.loss.scaled	0.001	0.006	-0.009	0.009
	b.duration.scaled	-0.015	0.006	-0.024	-0.006
	sigma	0.063	0.004	0.057	0.068
	biome.boreal.forests.taiga	-0.002	0.014	-0.043	0.028
	biome.deserts.and.xeric.shrublands	0.009	0.016	-0.013	0.049
	biome.mediterranean.forests.woodlands.and.scrub	-0.004	0.013	-0.040	0.019
	biome.montane.grasslands.and.shrublands	-0.003	0.013	-0.040	0.022
	biome.temperate.broadleaf.and.mixed.forests	-0.001	0.009	-0.020	0.020
	biome.temperate.conifer.forests	0.013	0.017	-0.007	0.042
	biome.temperate.grasslands.savannas.and.shrublands	-0.003	0.011	-0.026	0.019
	biome.tropical.and.subtropical.dry.broadleaf.forests	-0.003	0.014	-0.042	0.028
Richness losses and forest cover loss (2000-2016) (N = 493 / 3,361)	b.intercept	-0.070	0.012	-0.088	-0.048
	b.forest.loss.scaled	0.001	0.004	-0.005	0.006
	b.duration.scaled	0.027	0.004	0.021	0.033
	sigma	0.079	0.003	0.075	0.083
	biome.boreal.forests.taiga	-0.012	0.016	-0.041	0.010
	biome.deserts.and.xeric.shrublands	0.001	0.020	-0.039	0.043
	biome.mediterranean.forests.woodlands.and.scrub	0.010	0.018	-0.019	0.044
	biome.montane.grasslands.and.shrublands	0.006	0.020	-0.027	0.047
	biome.temperate.broadleaf.and.mixed.forests	-0.021	0.013	-0.043	0
	biome.temperate.conifer.forests	-0.004	0.012	-0.027	0.016
	biome.temperate.grasslands.savannas.and.shrublands	-0.002	0.019	-0.037	0.033
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.003	0.020	-0.034	0.043
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.020	0.018	-0.008	0.048
	b.intercept	0.095	0.015	0.065	0.121
	b.forest.loss.scaled	0.012	0.006	0.002	0.022

Richness gains and forest cover loss (2000-2016) (N = 377 / 3,361)	b.duration.scaled	-0.033	0.006	-0.042	-0.023
	sigma	0.114	0.004	0.108	0.122
	biome.boreal.forests.taiga	0.044	0.028	0	0.087
	biome.deserts.and.xeric.shrublands	0.004	0.027	-0.045	0.063
	biome.flooded.grasslands.and.savannas	-0.001	0.028	-0.066	0.050
	biome.mediterranean.forests.woodlands.and.scrub	-0.007	0.024	-0.056	0.033
	biome.montane.grasslands.and.shrublands	-0.011	0.028	-0.074	0.034
	biome.temperate.broadleaf.and.mixed.forests	0.008	0.017	-0.019	0.041
	biome.temperate.conifer.forests	-0.006	0.016	-0.035	0.023
	biome.temperate.grasslands.savannas.and.shrublands	0.003	0.023	-0.039	0.048
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.014	0.029	-0.076	0.032
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.012	0.025	-0.065	0.028
Richness losses and forest cover gain (2000-2016) (N = 73 / 3,361)	b.intercept	-0.041	0.021	-0.074	0.003
	b.forest.gain.scaled	0.009	0.008	-0.004	0.022
	b.duration.scaled	0.027	0.009	0.012	0.042
	sigma	0.068	0.006	0.059	0.078
	biome.boreal.forests.taiga	0.012	0.025	-0.028	0.072
	biome.mediterranean.forests.woodlands.and.scrub	0.007	0.027	-0.044	0.074
	biome.montane.grasslands.and.shrublands	0.004	0.027	-0.053	0.066
	biome.temperate.broadleaf.and.mixed.forests	-0.016	0.023	-0.064	0.017
	biome.temperate.conifer.forests	-0.025	0.028	-0.076	0.010
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.011	0.022	-0.025	0.061
Richness gains and forest cover gain (2000-2016) (N = 41 / 3,361)	b.intercept	0.070	0.040	-0.001	0.133
	b.forest.gain.scaled	0.012	0.028	-0.035	0.056
	b.duration.scaled	-0.075	0.026	-0.115	-0.031
	sigma	0.128	0.016	0.102	0.153
	biome.boreal.forests.taiga	-0.014	0.042	-0.103	0.063
	biome.mediterranean.forests.woodlands.and.scrub	-0.004	0.047	-0.108	0.093
	biome.montane.grasslands.and.shrublands	-0.014	0.047	-0.120	0.064

	biome.temperate.broadleaf.and.mixed.forests	0.056	0.051	-0.011	0.138
	biome.temperate.conifer.forests	0.014	0.042	-0.055	0.109
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.009	0.049	-0.124	0.081
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.017	0.046	-0.122	0.068
Turnover and overall forest loss (N = 357 / 3,361)	b.intercept	-0.891	0.057	-0.993	-0.775
	b.zoi.intercept	-1.652	0.138	-1.877	-1.434
	b.coi.intercept	-1.533	0.296	-1.998	-1.044
	b.forest.loss.scaled	-0.018	0.036	-0.076	0.042
	b.duration.scaled	-0.156	0.071	-0.265	-0.037
	phi	12.932	1.013	11.364	14.591
	biome.boreal.forests.taiga	0.011	0.057	-0.122	0.225
	biome.deserts.and.xeric.shrublands	-0.003	0.055	-0.164	0.133
	biome.mediterranean.forests.woodlands.and.scrub	-0.004	0.058	-0.194	0.153
	biome.montane.grasslands.and.shrublands	0	0.058	-0.201	0.183
	biome.temperate.broadleaf.and.mixed.forests	-0.015	0.046	-0.142	0.080
	biome.temperate.conifer.forests	0.010	0.049	-0.092	0.145
	biome.temperate.grasslands.savannas.and.shrublands	0.011	0.051	-0.091	0.160
	biome.tropical.and.subtropical.dry.broadleaf.forests	0.001	0.057	-0.170	0.195
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.002	0.058	-0.159	0.202
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.017	0.064	-0.280	0.120
Turnover and forest cover loss (2000-2016) (N = 870 / 3,361)	b.intercept	-0.524	0.104	-0.728	-0.373
	b.zoi.intercept	-1.705	0.092	-1.841	-1.548
	b.coi.intercept	-1.308	0.192	-1.636	-1.021
	b.forest.loss.scaled	-0.018	0.026	-0.061	0.023
	b.duration.scaled	-0.274	0.030	-0.321	-0.227
	phi	7.298	0.361	6.747	7.886
	biome.boreal.forests.taiga	0.054	0.116	-0.133	0.288
	biome.deserts.and.xeric.shrublands	0.045	0.168	-0.228	0.498
	biome.flooded.grasslands.and.savannas	-0.063	0.172	-0.538	0.237

	biome.mediterranean.forests.woodlands.and.scrub	0.034	0.151	-0.267	0.384
	biome.montane.grasslands.and.shrublands	0.001	0.171	-0.419	0.414
	biome.temperate.broadleaf.and.mixed.forests	0.054	0.101	-0.094	0.274
	biome.temperate.conifer.forests	0.135	0.122	-0.025	0.353
	biome.temperate.grasslands.savannas.and.shrublands	0.037	0.133	-0.191	0.330
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.196	0.251	-0.681	0.109
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.118	0.154	-0.422	0.082
Turnover and forest cover gain (2000-2016) (N = 111 / 3,361)	b.intercept	-0.924	0.283	-1.616	-0.366
	b.zoi.intercept	-1.382	0.216	-1.720	-1.033
	b.coi.intercept	-0.552	0.348	-1.126	0.012
	b.forest.gain.scaled	-0.150	0.090	-0.297	-0.010
	b.duration.scaled	-0.393	0.093	-0.542	-0.234
	phi	10.729	1.647	8.198	13.400
	biome.boreal.forests.taiga	0.411	0.431	-0.172	1.206
	biome.mediterranean.forests.woodlands.and.scrub	-0.002	0.499	-1.299	1.151
	biome.montane.grasslands.and.shrublands	0	0.500	-1.179	1.365
	biome.temperate.broadleaf.and.mixed.forests	0.067	0.286	-0.512	0.746
	biome.temperate.conifer.forests	0.116	0.291	-0.377	0.897
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.637	0.658	-1.816	0.148
	biome.tropical.and.subtropical.moist.broadleaf.forests	-0.019	0.334	-0.723	0.694
Population change lags across taxa (N = 841 / 2,729)	b.classmammals	6.684	1.369	4.429	8.916
	b.classbirds	9.136	1.087	7.193	10.944
	b.classamphibians	7.900	3.819	1.893	13.935
	b.classreptiles	2.357	2.679	-1.893	6.608
	sigma	8.137	0.197	7.830	8.464
	biome.boreal.forests.taiga	-0.225	1.174	-2.260	1.695
	biome.flooded.grasslands.and.savannas	-0.648	2.476	-4.770	3.849
	biome.mediterranean.forests.woodlands.and.scrub	-1.707	2.168	-5.133	1.891
	biome.temperate.broadleaf.and.mixed.forests	-2.251	1.157	-4.068	-0.184

	biome.temperate.coniferous.forests	-0.843	1.350	-3.148	1.348
	biome.temperate.grasslands.savannas.and.shrublands	5.008	1.398	2.702	7.240
	biome.tropical.and.subtropical.coniferous.forests	0.033	2.682	-4.539	4.665
	biome.tropical.and.subtropical.dry.broadleaf.forests	-2.146	2.534	-6.585	2.077
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	2.528	1.746	-0.297	5.370
	biome.tropical.and.subtropical.moist.broadleaf.forests	1.796	1.987	-1.342	5.050
	biome.tundra	-1.318	1.535	-3.772	1.270
Richness change lags across taxa (N = 728 / 3,361)	b.taxa.amphibians	9.691	2.065	6.142	13.057
	b.taxa.invertebrates	-1.536	2.430	-5.687	2.300
	b.taxa.birds	8.370	2.029	4.812	11.588
	b.taxa.mammals	6.937	2.407	3.041	11.038
	b.taxa.otherplants	9.207	2.647	5.159	13.557
	b.taxa.trees	17.389	2.526	13.379	21.693
	sigma	4.585	0.122	4.387	4.779
	biome.map.boreal.forests.taiga	2.581	2.879	-2.134	7.321
	biome.map.deserts.and.xeric.shrublands	-0.649	2.101	-3.914	2.991
	biome.map.multiple.ecoregions	-4.292	2.047	-7.532	-0.694
	biome.map.temperate.broadleaf.and.mixed.forests	6.755	2.257	3.076	10.476
	biome.map.temperate.coniferous.forest	-6.899	2.614	-11.178	-2.646
	biome.map.temperate.grasslands..savannas.and.shrublands	2.136	2.032	-1.121	5.758
	biome.map.tropical.and.subtropical.dry.broadleaf.forests	-2.233	3.527	-7.837	3.680
	biome.map.tropical.and.subtropical.grasslands..savannas.and.shrublands	4.577	2.564	0.213	8.611
	biome.map.tropical.and.subtropical.moist.broadleaf.forests	-1.601	3.243	-7.023	3.518
Turnover lags across taxa (N = 2,157 / 3,361)	b.taxa.trees	18.493	2.876	13.600	23.276
	b.taxa.otherplants	12.571	2.724	7.872	17.129
	b.taxa.mammals	11.017	2.708	6.457	15.569
	b.taxa.birds	8.341	2.476	4.159	12.557
	b.taxa.amphibians	10.042	2.500	6.098	14.552

	b.taxa.invertebrates	11.500	2.584	7.214	15.858
	sigma	4.662	0.069	4.551	4.773
	biome.map.boreal.forests.taiga	-0.647	3.328	-6.219	4.794
	biome.map.deserts.and.xeric.shrublands	-3.153	2.494	-7.478	0.989
	biome.map.multiple.ecoregions	-5.443	2.465	-9.816	-1.399
	biome.map.temperate.broadleaf.and.mixed.forests	-4.990	2.504	-9.266	-0.785
	biome.map.temperate.coniferous.forest	-9.358	2.703	-13.802	-4.656
	biome.map.temperate.grasslands..savannas.and.shrublands	3.057	2.485	-1.238	7.187
	biome.map.tropical.and.subtropical.dry.broadleaf.forests	4.616	4.323	-2.065	12.130
	biome.map.tropical.and.subtropical.grasslands..savannas.and.shrublands	13.696	3.059	8.664	18.792
	biome.map.tropical.and.subtropical.moist.broadleaf.forests	-6.432	2.801	-11.174	-1.780
	biome.map.tundra	8.372	2.566	3.894	12.843
Mammal generation time and population change temporal lags (N = 83 / 117)	b.intercept	4.047	1.228	2.131	6.003
	b.generation.time	0.336	0.137	0.110	0.551
	sigma	6.448	0.494	5.687	7.251
Bird generation time and population change temporal lags (N = 545 / 599)	b_Intercept	6.976	1.151	4.683	9.228
	b_mean_gentime	0.842	0.223	0.411	1.291
	sigma	9.158	0.279	8.644	9.723
Population declines, overall forest loss and species' geographic range (N = 359 / 2,729)	b.intercept	-0.060	0.012	-0.087	-0.042
	b.forest.loss.scaled	-0.001	0.001	-0.003	0.002
	b.range.scaled	-0.004	0.001	-0.006	-0.001
	b.duration.scaled	0.007	0.002	0.005	0.010
	b.forest.loss.scaled.range.scaled	0	0.002	-0.003	0.002
	sigma	0.024	0.001	0.023	0.025
	biome.boreal.forests.taiga	0.011	0.013	-0.008	0.038
	biome.temperate.broadleaf.and.mixed.forests	0.007	0.012	-0.013	0.033
	biome.temperate.coniferous.forests	0.003	0.012	-0.017	0.029
	biome.temperate.grasslands.savannas.and.shrublands	0.004	0.013	-0.018	0.031
	biome.tropical.and.subtropical.coniferous.forests	-0.011	0.019	-0.045	0.022

	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.044	0.030	-0.086	0.001
	biome.tundra	0.026	0.016	0	0.051
Population increases, overall forest loss and species' geographic range (N = 302 / 2,729)	b.intercept	0.050	0.008	0.037	0.076
	b.forest.loss.scaled	0.002	0.002	-0.001	0.005
	b.range.scaled	-0.001	0.002	-0.004	0.002
	b.duration.scaled	-0.010	0.002	-0.014	-0.007
	b.forest.loss.scaled.range.scaled	0.001	0.002	-0.002	0.004
	sigma	0.029	0.001	0.027	0.031
	biome.boreal.forests.taiga	-0.003	0.008	-0.028	0.013
	biome.mediterranean.forests.woodlands.and.scrub	0.009	0.013	-0.010	0.038
	biome.temperate.broadleaf.and.mixed.forests	-0.005	0.008	-0.032	0.008
	biome.temperate.coniferous.forests	-0.003	0.008	-0.030	0.011
	biome.temperate.grasslands.savannas.and.shrublands	-0.004	0.009	-0.031	0.011
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.004	0.013	-0.042	0.019
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.035	0.046	-0.005	0.101
	biome.tundra	-0.009	0.013	-0.039	0.006
Population declines, overall forest loss and species' mean population size (N = 36 / 2,729)	b.intercept	0.014	0.041	-0.050	0.082
	b.forest.loss.scaled	0.020	0.027	-0.022	0.066
	b.meanpop.scaled	0.031	0.044	-0.044	0.099
	b.duration.scaled	0.031	0.008	0.019	0.044
	b.forest.loss.scaled.meanpop.scaled	0.035	0.049	-0.045	0.115
	sigma	0.040	0.006	0.031	0.050
	biome.boreal.forests.taiga	-0.005	0.024	-0.055	0.036
	biome.deserts.and.xeric.shrublands	-0.014	0.026	-0.067	0.025
	biome.mediterranean.forests.woodlands.and.scrub	-0.016	0.023	-0.056	0.018
	biome.temperate.broadleaf.and.mixed.forests	-0.015	0.018	-0.046	0.012
	biome.temperate.coniferous.forests	0.031	0.030	-0.009	0.079
	biome.temperate.grasslands.savannas.and.shrublands	-0.010	0.020	-0.050	0.021
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.005	0.020	-0.046	0.030

	biome.tundra	0.037	0.032	-0.007	0.083
Population increases, overall forest loss and species' mean population size (N = 43 / 2,729)	b.intercept	0.038	0.022	0.002	0.077
	b.forest.loss.scaled	0.009	0.009	-0.005	0.023
	b.meanpop.scaled	0.091	0.044	0.012	0.158
	b.duration.scaled	-0.025	0.010	-0.041	-0.010
	b.forest.loss.scaled.meanpop.scaled	0.089	0.047	0.011	0.163
	sigma	0.049	0.006	0.040	0.059
	biome.boreal.forests.taiga	0	0.015	-0.036	0.036
	biome.mediterranean.forests.woodlands.and.scrub	0.006	0.014	-0.017	0.040
	biome.temperate.broadleaf.and.mixed.forests	0	0.011	-0.024	0.024
	biome.temperate.grasslands.savannas.and.shrublands	-0.009	0.017	-0.055	0.016
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.001	0.014	-0.026	0.041
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.006	0.015	-0.019	0.050
	biome.tundra	-0.007	0.014	-0.045	0.013
Population declines, overall forest loss and species' habitat specificity (N = 376 / 2,729)	b.intercept	-0.054	0.004	-0.065	-0.047
	b.forest.loss.scaled	-0.001	0.002	-0.003	0.002
	b.habspec.scaled	-0.003	0.001	-0.006	-0.001
	b.duration.scaled	0.012	0.002	0.010	0.015
	b.forest.loss.scaled.habspec.scaled	0	0.002	-0.002	0.003
	sigma	0.026	0.001	0.025	0.028
	biome.boreal.forests.taiga	0.002	0.004	-0.006	0.013
	biome.deserts.and.xeric.shrublands	-0.006	0.011	-0.035	0.007
	biome.mediterranean.forests.woodlands.and.scrub	-0.001	0.006	-0.018	0.012
	biome.temperate.broadleaf.and.mixed.forests	0	0.004	-0.007	0.011
	biome.temperate.coniferous.forests	-0.001	0.005	-0.011	0.009
	biome.temperate.grasslands.savannas.and.shrublands	0.001	0.005	-0.009	0.014
	biome.tropical.and.subtropical.coniferous.forests	-0.002	0.008	-0.025	0.013
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.006	0.009	-0.028	0.006
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.004	0.008	-0.009	0.027

	biome.tundra	0.012	0.012	-0.002	0.029
Population increases, overall forest loss and species' habitat specificity (N = 316 / 2,729)	b.intercept	0.047	0.003	0.041	0.054
	b.forest.loss.scaled	0.001	0.002	-0.002	0.004
	b.habspec.scaled	-0.003	0.002	-0.007	0
	b.duration.scaled	-0.011	0.002	-0.014	-0.008
	b.forest.loss.scaled.habspec.scaled	0.002	0.003	-0.002	0.006
	sigma	0.029	0.001	0.027	0.031
	biome.boreal.forests.taiga	0	0.003	-0.009	0.006
	biome.mediterranean.forests.woodlands.and.scrub	0.002	0.004	-0.004	0.020
	biome.temperate.broadleaf.and.mixed.forests	-0.001	0.003	-0.009	0.004
	biome.temperate.coniferous.forests	0	0.003	-0.010	0.006
	biome.temperate.grasslands.savannas.and.shrublands	-0.001	0.003	-0.011	0.006
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.001	0.004	-0.017	0.006
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.002	0.005	-0.007	0.024
	biome.tundra	0	0.003	-0.012	0.007
Population declines, overall forest loss in the tropics and elsewhere (N = 470 / 2,729)	b.intercept	-0.050	0.003	-0.057	-0.044
	b.forest.loss.scaled	-0.002	0.001	-0.004	0
	b.tropicaltrue	-0.074	0.034	-0.127	-0.018
	b.duration.scaled	0.008	0.002	0.005	0.010
	b.forest.loss.scaled.tropicaltrue	-0.032	0.029	-0.078	0.014
	sigma	0.026	0.001	0.024	0.027
	biome.boreal.forests.taiga	0.001	0.003	-0.005	0.009
	biome.deserts.and.xeric.shrublands	-0.002	0.006	-0.022	0.009
	biome.mediterranean.forests.woodlands.and.scrub	-0.002	0.005	-0.017	0.006
	biome.temperate.broadleaf.and.mixed.forests	-0.001	0.003	-0.008	0.005
	biome.temperate.coniferous.forests	0	0.003	-0.008	0.007
	biome.temperate.grasslands.savannas.and.shrublands	0.001	0.004	-0.006	0.013
	biome.tropical.and.subtropical.coniferous.forests	-0.001	0.005	-0.018	0.009
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	-0.001	0.004	-0.014	0.009

	biome.tropical.and.subtropical.moist.broadleaf.forests	0.003	0.006	-0.007	0.023
	biome.tundra	0.004	0.006	-0.003	0.018
Population increases, overall forest loss in the tropics and elsewhere (N = 369 / 2,729)	b.intercept	0.049	0.004	0.044	0.061
	b.forest.loss.scaled	0.001	0.002	-0.002	0.003
	b.tropicaltrue	-0.025	0.010	-0.041	-0.009
	b.duration.scaled	-0.015	0.002	-0.018	-0.012
	b.forest.loss.scaled.tropicaltrue	-0.009	0.005	-0.018	-0.001
	sigma	0.029	0.001	0.027	0.031
	biome.boreal.forests.taiga	0	0.003	-0.012	0.006
	biome.mediterranean.forests.woodlands.and.scrub	0.002	0.005	-0.005	0.020
	biome.temperate.broadleaf.and.mixed.forests	-0.002	0.004	-0.015	0.004
	biome.temperate.coniferous.forests	-0.001	0.004	-0.013	0.006
	biome.temperate.grasslands.savannas.and.shrublands	-0.001	0.004	-0.014	0.006
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0	0.004	-0.012	0.015
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.004	0.007	-0.006	0.039
	biome.tundra	-0.002	0.005	-0.019	0.004
Population declines, overall forest loss and starting tree cover (N = 481 / 3,361)	b.intercept	-0.050	0.003	-0.055	-0.045
	b.forest.loss.scaled	0.003	0.004	-0.002	0.009
	b.sum.area.scaled	-0.007	0.003	-0.012	-0.002
	b.duration.scaled	0.012	0.001	0.010	0.014
	b.forest.loss.scaled.sum.area.scaled	-0.003	0.004	-0.009	0.004
	sigma	0.026	0.001	0.025	0.028
	biome.boreal.forests.taiga	-0.001	0.002	-0.007	0.002
	biome.mediterranean.forests.woodlands.and.scrub	0	0.002	-0.006	0.006
	biome.temperate.broadleaf.and.mixed.forests	0	0.002	-0.003	0.005
	biome.temperate.coniferous.forests	0	0.002	-0.004	0.006
	biome.temperate.grasslands.savannas.and.shrublands	0	0.002	-0.006	0.006
	biome.tropical.and.subtropical.dry.broadleaf.forests	0	0.002	-0.008	0.005
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0	0.002	-0.005	0.010

	biome.tropical.and.subtropical.moist.broadleaf.forests	0	0.002	-0.006	0.006
Richness losses, overall forest loss and starting tree cover (n = 493 / 3,361)	b.intercept	-0.069	0.013	-0.090	-0.044
	b.forest.loss.scaled	-0.004	0.005	-0.011	0.003
	b.sum.area.scaled	0.007	0.004	0	0.013
	b.duration.scaled	0.025	0.004	0.019	0.031
	b.forest.loss.scaled.sum.area.scaled	0.011	0.006	0.002	0.021
	sigma	0.079	0.003	0.075	0.083
	biome.boreal.forests.taiga	-0.016	0.018	-0.047	0.011
	biome.deserts.and.xeric.shrublands	0.001	0.023	-0.043	0.046
	biome.mediterranean.forests.woodlands.and.scrub	0.012	0.020	-0.018	0.048
	biome.montane.grasslands.and.shrublands	0.009	0.022	-0.032	0.047
	biome.temperate.broadleaf.and.mixed.forests	-0.025	0.015	-0.050	-0.002
	biome.temperate.conifer.forests	-0.005	0.014	-0.029	0.019
	biome.temperate.grasslands.savannas.and.shrublands	-0.001	0.021	-0.040	0.034
	biome.tropical.and.subtropical.grasslands.savannas.and.shrublands	0.003	0.022	-0.036	0.048
	biome.tropical.and.subtropical.moist.broadleaf.forests	0.022	0.018	-0.007	0.053

Appendix 4.20. Citation sources and associated links for the studies part of the BioTIME Database for which I do not have permission to republish the data. The data from the remaining BioTIME studies in my analysis can all be collectively downloaded from the following link http://biotime.st-andrews.ac.uk/BioTIME_download.php.

Study Id	Citation	Link
42	Gaston, K.J. & Blackburn, T.M. (2000) Pattern and process in macroecology. In. Wiley-Blackwell, Oxford, England.	http://ecologicaldata.org/wiki/eastern-wood
42	Beven, G. (1976) Changes in breeding bird populations of an oak-wood on Bookham Common, Surrey, over twenty-seven years. London Naturalist, 55, 23-42.	http://ecologicaldata.org/wiki/eastern-wood
42	Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993) The new atlas of breeding birds in Britain and Ireland: 1988-1991. T & AD Poyser London.	http://ecologicaldata.org/wiki/eastern-wood
42	Lack, P. (2010) The atlas of wintering birds in Britain and Ireland. A&C Black.	http://ecologicaldata.org/wiki/eastern-wood
42	Standley, P., Bucknell, N., Swash, A. & Collins, I. (1996) The Birds of Berkshire. Berkshire Atlas Group. Reading, UK,	http://ecologicaldata.org/wiki/eastern-wood
42	Stone, B., Sears, J., Cranswick, P., Gregory, R., Gibbons, D., Rehfisch, M., Aebischer, N. & Reid, J. (1997) Population estimates of birds in Britain and in the United Kingdom. British Birds, 90, 1-22.	http://ecologicaldata.org/wiki/eastern-wood
42	Williamson, M. (1987) Are communities ever stable? Symposium of the British Ecological Society (ed by).	http://ecologicaldata.org/wiki/eastern-wood
44	Halpern, C.B. & Lutz, J.A. (2013) "Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions.". Available at: Dryad DigitalRepository doi:10.5061/dryad.1q88j, accessed 2013.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP073
44	Halpern, C.B. & Dyrness, C. (2010) "Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3, 1962-Present". Long-Term Ecological Research. Forest Science Data Bank, Corvallis. Available at:	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP073

	http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP073, accessed 2012.	
44	Halpern, C.B. & Lutz, J.A. (2013) Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecological Monographs, 83, 221-237.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP073
215 – 220 instructions	Click on the link and select the study from the below descriptions to download, leave the 'by species, by location, by date and within coordinates' blank (unless dates are specified on the study information below), i.e., choose Ontario Breeding Bird Atlas (2001-2005) from the 'by dataset' dropdown menu, leave other options blank and click 'Search data' button at foot of page and then read and agree to the data sharing policy outlined before clicking download.	https://www.birdscanada.org/birdmon/default/searchquery.jsp
215	HMANA - Hawk Migration Association of North America (HMANA). Available at: http://www.hmana.org/, accessed 2012. Please select all sites for full study data.	http://hawkcount.org/ http://hawkcount.org/month_summary.php?rsite=
216	NatureCounts - Ontario Breeding Bird Atlas (2001-2005): point count data. NatureCounts, a node of the Avian Knowledge Network. Bird Studies Canada. Available at: http://www.birdscanada.org/birdmon/, accessed 2012.	http://www.birdscanada.org/birdmon/
218	NatureCounts - Maritimes Breeding Bird Atlas (2006-2010): point count data. NatureCounts, a node of the Avian Knowledge Network. Bird Studies Canada. Available at: http://www.birdscanada.org/birdmon/, accessed 2012.	http://www.birdscanada.org/birdmon/
219	Bird Studies Canada (2012) -Marsh Monitoring Program. NatureCounts, a node of the Avian Knowledge Network. Available at: http://www.birdscanada.org/birdmon/, accessed 2012.	http://www.birdscanada.org/birdmon/
220	Bird Studies Canada (2012) -Marsh Monitoring Program. NatureCounts, a node of the Avian Knowledge Network. Available at: http://www.birdscanada.org/birdmon/, accessed 2012.	http://www.birdscanada.org/birdmon/

244	Bird Studies Canada (2012) -BC Coastal Waterbird Survey (2004). NatureCounts, a node of the Avian Knowledge Network. Available at: http://www.birdscanada.org/birdmon/, accessed 2012.	http://www.birdscanada.org/birdmon/
277	Halpern, C.B. & Lutz, J.A. (2013) "Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions.". Available at: Dryad DigitalRepository doi:10.5061/dryad.1q88j, accessed 2013.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP073
277	Halpern, C.B. & Dyrness, C. (2010) "Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3, 1962-Present". Long-Term Ecological Research. Forest Science Data Bank, Corvallis. Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP073, accessed 2012.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP073
277	Halpern, C.B. & Lutz, J.A. (2013) Canopy closure exerts weak controls on understory dynamics: a 30-year study of overstory-understory interactions. Ecological Monographs, 83, 221-237. Available at: Dryad DigitalRepository doi:10.5061/dryad.1q88j, accessed 2013.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP073
279	Halpern, C.B. & Dyrness, C. (2010) "Plant succession and biomass dynamics following logging and burning in the Andrews Experimental Forest Watersheds 1 and 3, 1962-Present". Long-Term Ecological Research. Forest Science Data Bank, Corvallis. Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP073, accessed 2012.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP073
293	Rothamsted Park Grass Experiment, Over 100 years of Park Grass, Accessed 2016	http://rothamsted.ac.uk/long-term-experiments-national-capability/classical-experiments http://www.era.rothamsted.ac.uk/eradoc/article/Williams-1-87
309	Pollard, E., Hall, M.L. & Bibby, T.J. (1986) Monitoring the Abundance of Butterflies 1976-1985. Research & survey in nature conservation.	http://jncc.defra.gov.uk/page-2614

	Available at: http://jncc.defra.gov.uk/page-2614, accessed 2016.	
318	SANParks (2011) "Karoo National Park Census Data. 1994 - 2009-. Available at: http://datadryad.org/handle/10255/dryad.13079?show=full, accessed 2016.	https://www.sanparks.org/parks/tankwa/conservation/ff/mammals.php
331	Halpern, C.B. & McKenzie, D. (2001) Disturbance and post-harvest ground conditions in a structural retention experiment. Forest Ecology and Management, 154, 215-225.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP108&topnav=135
331	Halpern, C. (2015) "DEMO: Vegetation Data - Post-Harvest." Demonstration of Ecosystem Management Options. Forest Science Data Bank, Corvallis, OR. Available at: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TP108, accessed 2016.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP108&topnav=135
331	Halpern, C.B., Halaj, J., Evans, S.A. & Dovčiak, M. (2012) Level and pattern of overstory retention interact to shape long-term responses of understories to timber harvest. Ecological Applications, 22, 2049-2064.	http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TP108&topnav=135
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518	D. H. Maphisa, H. Smit-Robinson, L. G. Underhill, R. Altwegg, Drivers of Bird Species Richness within Moist High-Altitude Grasslands in Eastern South Africa. PLOS ONE 11, e0162609 (2016).	https://datadryad.org/stash/dataset/doi:10.5061/dryad.m9p07
521	M. Valeix, H. Fritz, S. Chamaillé-Jammes, M. Bourgarel, F. Murindagomo, Fluctuations in abundance of large herbivore populations: insights into the influence of dry season rainfall and elephant numbers from long-term data. Animal Conservation 11, 391-400 (2008).	https://zslpublications.onlinelibrary.wiley.com/do
522	J. Mundava et al., Factors influencing long-term and seasonal waterbird abundance and composition at two adjacent lakes in Zimbabwe. Ostrich 83, 69-77 (2012).	https://www.tandfonline.com/doi/pdf/10.2989/003065
523	E. Haplet, SANParks, "Monthly bird lists and bird arrival dates, Birmingham Timbivati". Available at:	https://www.sanparks.org/conservation/scientific_new/sava

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524	SANParks, "Northern Plains Ecological Aerial Census data 1993-1998". Available at: http://dataknp.sanparks.org/sanparks/, accessed 2018. (2009). This dataset is available on request.	https://www.sanparks.org/conservation/scientific_new/savannah_arid/data_resources/data_repository.php

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