Planning for future climate and land-use change in the protection of global avian and mammalian biodiversity

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Planning for future climate and land-use change in the protection of global avian and mammalian biodiversity

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Abstract

Global biodiversity is deteriorating, largely due to habitat loss, but increasingly because of climate change. To stop and reverse this trend, we must anticipate how climate change is likely to affect the natural world, understand how climate impacts interact with other major pressures such as land-use, and identify conservation strategies that will safeguard biodiversity amid dramatic global change. In this thesis, I make use of recent advances in data availability and modelling techniques to contribute towards this challenge.

I use best-practice statistical models to project how the distributions of terrestrial mammals and birds will change by 2070 under different socioeconomic development scenarios. Impacts are severe under high emissions scenarios, but the worst impacts can be avoided if we limit greenhouse gas emissions in line with the Paris Agreement. I also show that the biogeographic properties of species' distributions can be used to predict which species will be most affected. In subsequent chapters, I explore important contextual information that will influence how species respond to climate change, or influence our ability to protect them.

First, I show that without rapid emissions cuts, climate impacts on nature will be inequitably distributed between countries, and demonstrate the importance of collaboration across political borders as many species shift across them. Next, I show that the expansion of human land-use over nearly half the planet is a key constraint for species on the move, since large areas of habitat they would otherwise have been expected to colonise have been lost. When considering future land-use change projections, stark contrasts appear between future development scenarios, and if we are to stop biodiversity loss, stringent emissions reductions need to be coupled with a declining land-use footprint to help species cope. Finally, it's not just the availability but also the connectivity of habitats that is important. I reveal where a lack of habitat connectivity between protected areas is most likely to impact range-shifting species, and where conservation efforts should be targeted to preserve and restore this connectivity.

Together, my research shows that severe biodiversity losses this century are not inevitable – but to avoid them, we will need to coordinate ambitious conservation action at broad spatial scales and tackle multiple interacting pressures at once.

Author's Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

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Chapter 1

General Introduction

Glittering-throated Emerald (*Amazilia fimbriata*), central Guyana

Biodiversity loss and the global extinction crisis

Earth is the only place in the universe known to harbour life – the most striking feature of which is its diversity. Beyond its enormous intrinsic value, this biodiversity brings productivity and stability to ecological systems and underpins vital ecosystem functions and processes, ranging from nutrient cycling to carbon sequestration (Cardinale *et al.* 2006; Gonzalez & Loreau 2009; Cardinale 2012; Duffy *et al.* 2017; IPBES 2019). From a more anthropocentric perspective, biodiversity contributes to food and water security, generates opportunities for recreation and tourism, and provides important economic, cultural, spiritual and mental health benefits (Fuller *et al.* 2007; Turner *et al.* 2007; Balmford *et al.* 2015). Placing a total economic value on these benefits is controversial and comes with caveats, but one conservative estimate arrived at the figure of $145 trillion annually – more than twice the value of global Gross Domestic Product (GDP) (Costanza *et al.* 2014).

Despite its ecological, economic and cultural significance, a broad set of indicators reveal that biodiversity is in an alarming decline across the planet (IPBES 2019). Vertebrate populations have fallen by 68% since 1970 (WWF 2020), extinction rates are 100-1000 times higher than the “background” rate (Pimm *et al.* 1995), more than a million species are estimated to be threatened with extinction (many within decades) (IPBES 2019), and their disappearance would be enough to constitute the sixth mass extinction event in Earth’s history (Barnosky *et al.* 2011).

Through several decades of conservation research, the magnitude of biodiversity loss, its impacts, and the factors driving it have become increasingly clear (IPBES 2019). Today, understanding how human activity will continue to affect biodiversity, and the identification and implementation of strategies to reverse these declines, remain amongst the most important challenges facing humanity. In this thesis, by considering key drivers of biodiversity loss, anticipating their future impacts on global biodiversity, and revealing opportunities for conservation action, I aim to contribute towards tackling those challenges.

The drivers of biodiversity loss

At present, the greatest threats to terrestrial biodiversity (in decreasing order of importance) are habitat loss (via land- and sea-use change), direct exploitation, climate change, pollution, and invasive species (IPBES 2019). In this thesis, I will pay special attention to the first and third of these pressures, since habitat loss has been the greatest threat historically, while climate change is set to become an increasingly prominent driver of extinction this century (IPCC 2022). I’ll also consider ways in which these two pressures interact, which is important to understand their impacts accurately, and to correctly identify the places and species most at risk.

Land-use change and biodiversity

Humans have been changing the terrestrial landscape for millennia, particularly since the agricultural revolution around 10,000 years ago (Ellis 2011). In the last few centuries, however, the combination of human population expansion, soaring consumption and increasingly globalised supply chains have driven more drastic changes in land use across the planet, primarily via demand for agricultural land (Vitousek *et al.* 1997; Tilman *et al.* 2011; Steffen *et al.* 2015). Cropland and pasture now encompass 40% of Earth's surface (Foley 2005), and 10% of wilderness areas have been lost in the last two decades alone (Watson *et al.* 2016b). Tropical forests, home to the majority of Earth's species (Barlow *et al.* 2018; Pillay *et al.* 2022), were the main source of new agricultural land in the 1980s and 1990s (Gibbs *et al.* 2010), and remotely sensed data reveal that between 2000 and 2012 a further 2.3 million km^2 of forest was lost globally (Hansen *et al.* 2013). The situation may be worse given that conventional remote sensing techniques largely fail to capture more insidious forest degradation by fire, overhunting and selective logging (Nepstad *et al.* 1999). Furthermore, remaining habitat patches are often highly fragmented, exposing their inhabitants to detrimental 'edge effects'; a recent analysis revealed that 70% of forest now lies within 1km of the forest's edge, reducing biodiversity by 13-75% and impairing key ecosystem functions (Haddad et al. 2015). Although forests have received the most conservation attention, land-use change threatens biodiversity in biomes across the planet, including grasslands, savannas, shrublands and wetlands (Bond & Parr 2010; Overbeck *et al.* 2015; de Carvalho & Mustin 2017).

Primarily, land-use change precipitates biodiversity loss by directly destroying it, replacing complex natural systems with simplified human-dominated ones, such as agricultural monocultures, that are incapable of fulfilling the ecological niches of most species. A global synthesis of studies comparing levels of biodiversity in different land-use types estimated that local abundance and species richness have fallen by 11% and 14% globally on average as a result of land-use change (Newbold *et al.* 2015), although impacts in the worst-affected regions have been much more severe. Furthermore, land use is estimated to have driven biodiversity below its proposed planetary boundary ("safe limit") across 58% of the world's land surface (Newbold *et al.* 2016). Reversing these impacts – or 'bending the curve of biodiversity loss' – will be an enormous challenge, although ensembles of land-use and biodiversity models suggest that it is possible by mid-century, if we can enact transformative change to our food production systems, involving sustainable intensification, reduced food waste and the global uptake of more plant-based diets (Leclère *et al.* 2020). However, as well as this significant challenge, land-use change is occurring against a backdrop of other threats. Of these, climate change is likely to become particularly significant over the next few decades.

Climate change and biodiversity

Human influence on Earth's climate system has triggered a period of rapid warming, at rates not seen for at least the last 2000 years (IPCC 2021). The last four decades have each been warmer than any preceding decade on record since 1850; the ten hottest years on record have all occurred since 2005; and average surface temperatures in 2011-2020 were 1.09˚C above the 1850-1900 average (IPCC 2021). This warming is unequivocally attributable to anthropogenic greenhouse gas (GHG) emissions (Solomon *et al.* 2009; IPCC 2021). The atmospheric concentration of carbon dioxide is now higher than at any time in at least the last two million years, while methane and nitrous oxide are at higher levels than any time in at least the last 800,000 years (IPCC 2021). The severity of future climate change depends greatly on the world's socioeconomic trajectory: under a very low GHG emission scenario it's possible to keep warming to below 1.5°C by 2100 in line with the aspirational goal of the Paris Agreement, while under the highest emission scenario considered by the IPCC, 3.3-5.7 ˚C is very likely (IPCC 2022).

To date, the impacts of climate change have been felt most acutely in arctic ecosystems, where the warming has progressed at twice the global average rate over the past 50 years (Pithan & Mauritsen 2014; IPBES 2019). However, increased temperatures, changes to patterns of precipitation, and increases to the frequency and intensity of extreme climate and weather events are having widespread and pervasive impacts on ecosystems on every continent (IPCC 2022). Climate change impacts can affect biodiversity on a range of scales, from the genetic, up through the organismal (affecting physiology and phenology), population (distribution and dynamics), and community levels, right up to changes on the scale of ecosystems and biomes (affecting functioning, productivity, resilience and integrity) (Bellard *et al.* 2012). At the genetic and organismal level, documented impacts include evolutionary adaptation to temperature extremes; loss of genetic diversity; shifts in temperature-dependent sex ratios; shrinking body sizes and increasing metabolic costs (Scheffers *et al.* 2016a). The majority of impacts, however, have been investigated at the population or species level.

A variety of species-level responses to climate change are possible: they may persist *in situ* and tolerate or adapt to the change; adjust their habitat preference; move elsewhere to track their climate niche ('range shift'); or go locally or globally extinct (Dawson *et al.* 2011). So far, only a handful of modern-day extinctions have been directly attributed to climate change, although warming has been implicated in multiple amphibian extinctions by facilitating the spread of the chytrid fungus (Pounds *et al.* 2006). Much more widely documented, however, are changes to species distributions, abundance, and phenology. Warming has been linked to upslope range shifts and range contractions in many montane species – including birds (Freeman *et al.* 2018), moths (Chen *et al.* 2009) and plants (Steinbauer *et al.* 2018; Zu *et al.* 2021) – while poleward shifts have been documented in British and North American birds (la Sorte & Thompson 2007; Massimino *et al.* 2015). Although poleward and upslope shifts are expected to be most common, long-term data from Australia suggests that interactions between temperature, precipitation and species-specific tolerances may produce more complex and idiosyncratic responses (Vanderwal *et al.* 2012). One modelling study that used species traits to predict climate change impacts estimated that 47% of threatened non-volant mammal species and 23% of threatened birds may have already been negatively impacted in at least part of their distribution (Pacifici *et al.* 2017). Long-term data from North America and Europe have shown that the increasing frequency of temperatures that exceed historically observed tolerances is an important predictor of widespread bumble bee declines (Soroye *et al.* 2020). As climate change continues to unfold and longer-term datasets become available for more taxonomic groups, it is likely that many more examples of climate impacts on species and populations will be documented.

At the community level, assemblages are undergoing a process termed *thermophilization,* whereby climate change has caused declines in cold-adapted species and increases in warm adapted species (Gottfried *et al.* 2012). Across Europe and North America, bird and butterfly communities have been shifting in favour of species from warmer areas (Devictor *et al.* 2008, 2012; Stephens *et al.* 2016), although these shifts still lag behind climate warming. As different species respond at different rates, species interactions are changing and novel communities are emerging (Williams & Jackson 2007) – for example, tropical and boreal species are increasingly being found in temperate and polar communities, respectively (Scheffers *et al.* 2016a). At even broader scales, multiplicative and interacting effects of climate change have triggered ecosystem-level regime shifts to alternative states, such as from coral- to algae-dominated reefs around the world (Graham *et al.* 2015), and even biome-level transitions, such as from tundra to boreal forest in Alaska (Beck *et al.* 2011). Hence, although global temperatures have risen by only ~1˚C relative to pre-industrial levels, climate change is already having a widespread impact on nature, on scales that range from the molecular to the planetary (Scheffers *et al.* 2016a).

Though already significant, these documented impacts are likely to be dwarfed by the effects of continued climate change in the future. Widespread changes to patterns of biodiversity are likely as species distributions change, and global extinction rates are projected to increase significantly in the next few decades (Thomas *et al.* 2004; Foden *et al.* 2013; Urban 2015). Swift and dramatic cuts to global greenhouse gas emissions are needed to avoid these impacts: a global synthesis of many studies estimates that the fraction of species at risk of climate-related extinction grows from 2.8% at present to 5.3% per cent at 2°C warming, but rises to 16% at 4.3°C warming (Urban 2015).

Negative impacts and extinctions appear more likely in montane regions, where upslope shifts force species into increasingly restricted areas of suitable climate, which has been described as an ‘escalator to extinction’ and already documented in tropical bird species, among others (Freeman *et al.* 2018; Urban 2018). Comparisons between biomes suggest that tropical and Mediterranean species also appear most at-risk in the future, as species are adapted to low climatic variability in these regions and are already close to their upper thermal limits (Newbold *et al.* 2020). Species may also struggle to cope with climate change in areas of low topographic heterogeneity, since the velocity of climate change – velocity at Earth’s surface needed to maintain a constant temperature – will be higher in such areas, and may outpace species’ dispersal abilities. However, the relative importance of these considerations, and the impacts of climate change on biodiversity more generally, remain highly uncertain.

Interactions between climate change and land-use change

A key factor shaping the impacts of climate change on biodiversity – and bringing added uncertainty to species responses – is its interaction with other pressures (Mantyka-Pringle *et al.* 2012; Pacifici *et al.* 2015). Here, and elsewhere in this thesis, I focus on the interactions between climate change and land-use, given that land-use is the major present-day cause of extinction risk. However, it’s important to note that interactions between climate change, land-use change and other pressures exist, for example climate change facilitating the spread of pathogens and invasive species (Pounds *et al.* 2006; Hellmann *et al.* 2008; Mainka & Howard 2010), and habitat fragmentation making populations more susceptible to exploitation (Peres 2001).

The processes of climate change and land-use change are inherently interlinked: land-use associated with agriculture and forestry accounts for 24% of global greenhouse gas emissions, for example (IPCC 2014). This kind of interaction (the contribution of land use change to climate change) is now well understood, and is routinely incorporated into future climate and land use scenarios (Reid *et al.* 2005; Moss *et al.* 2010; IPCC 2014). The reciprocal relationship has been given much less attention – that climate change may drive further land use change due to shifts in agriculture and urbanisation as humans adapt (Jones *et al.* 2016).

However, the interactions I explore later in this thesis concern the interacting *effects* of land-use and climate change on biodiversity, as opposed to the interacting processes of change themselves. The combined additive effects of land-use and climate change are sometimes referred to as interactions, for example where the places impacted by multiple pressures coincide. A study of the threats to global amphibian diversity found that areas of high amphibian richness, for example, are disproportionately affected by overlapping threats from climate change and land-use change, and so this interaction is likely to accelerate biodiversity loss beyond that expected from mono-causal assessments (Hof *et al.* 2011).

Other interactions could be considered interactions in the true sense, whereby the combined effect of land use and climate change is disproportionately more severe than would be predicted from summing each pressure's individual impacts. As an important example, land-use is likely to constrain species abilities to cope with climate change. The fragmentation of natural landscapes is likely to prevent species from tracking their climatic niche into new areas in the future, as many species have done during historical periods of rapid climate change (Dawson *et al.* 2011). As another example, populations respond more negatively to climate-change induced drought in more fragmented landscapes (Oliver *et al.* 2012). This kind of interaction can also be seen at the community level; recent evidence shows that intensive agricultural land in the UK has prevented adaptive community reorganisations of butterflies and birds in response to climate change, by exacerbating losses of cold-adapted species and preventing increases in warm-adapted ones (Oliver *et al.* 2017).

In addition to exacerbating population declines, or inhibiting range shifts, land use change may also inhibit *adaptation* to climate change. As discussed by Oliver & Morecroft (2014), land use change often happens disproportionately to regions on biome boundaries (such as the rainforest-Cerrado boundary in Brazil), where many species have their range edges. These range-edge populations, however, may be more adapted to climatic extremes, and have the most potential to evolve under climate change. Therefore, land use change may be eroding species' evolvability in the face of climate change (Rehm *et al.* 2015).

As well as land-use limiting species responses to climate change, the reverse relationship to may also be true: species stressed by climate change, for example because of their physiological tolerances or changed species interactions, may be less resilient to land-use change. A recent study synthesising vertebrate responses to land-use change found that the impact of land-use on abundance was strongly influenced by populations' thermal position within their climatic niche: where temperature extremes were closer to species' thermal limits, abundance was more negatively affected by land-use change (Williams & Newbold 2021). Finally, as well as one pressure aggravating the other, in some circumstances both pressures will exacerbate each other's impacts simultaneously. For example, the stochastic extinction of metapopulations may be more likely in smaller, fragmented populations (impacted by land-use), especially so when populations are suppressed by climate change impacts or subjected to more frequent extreme events (Verboom *et al.* 2010; Oliver & Morecroft 2014). These interactions can be complex and difficult to model, but an understanding of how these drivers of extinction interact is essential if we are to design effective conservation strategies that can protect nature as dramatic environmental changes continue to unfold.

Strategic global conservation in the 21st century

The modern conservation movement has evolved over time, taking an increasingly global perspective and becoming more firmly embedded into and coordinated with the broader sustainable development agenda. This reflects the broadening scope and scale of the challenges that conservation must tackle; conservation policy that is restricted to a national focus is likely to be less effective at protecting biodiversity, due to major efficiency gaps between national and global priorities (Pouzols *et al.* 2014) and shifting priorities as species distributions change (Titley *et al.* 2021).

A key moment for global environmental policy was the 1992 'Earth Summit' in Rio de Janeiro, in which the United Nations defined 'biological diversity' for the first time and the nations of the world agreed on two treaties that, three decades on, still form the backbone of international climate and conservation policy: the United Nations Framework Convention on Climate Change (UNFCCC), and the Convention on

Biological Diversity (CBD). Since then, the CBD has overseen successive, but largely unsuccessful, efforts to curb biodiversity loss through multilateral instruments. The most recent was the *Strategic Plan for Biodiversity 2011-2020* (CBD 2010a) – a global strategy that aimed to stop biodiversity loss, implemented at the national level via individual countries' 'National Biodiversity Strategies and Action Plans' (NBSAPs). At the core of this were 20 'Aichi Biodiversity Targets', detailing more specific goals to be achieved in what was declared the 'UN Decade on Biodiversity'.

However, multiple global-level analyses have concluded that insufficient progress was made on the majority of Aichi Targets, (Butchart *et al.* 2019; IPBES 2019). A national-level analysis concluded that countries had made little or no progress on the majority (53.5%) of indicators considered, and in 22.4% of cases countries were in fact moving in the wrong direction (Buchanan *et al.* 2020). Part of this failure relates to the nature of the targets themselves. Seventy percent of the Aichi Targets were unquantifiable, and most were complex, containing multiple elements, ambiguities and redundancies (Butchart *et al.* 2016). Supporting the idea that the formulation of these targets was partially responsible for their failure, the targets that were perceived to be more measurable, realistic, unambiguous, and scalable were more likely to be achieved (Green *et al.* 2019). The next phase of the CBD's global agenda, the *Post-2020 Biodiversity* Framework, is due to be agreed in Kunming, China, in spring 2022; a first draft has already been written (CBD Secretariat 2021). It remains to be seen whether its suite of 21 targets will be both ambitious and achievable enough to fulfil their purpose. Lessons learned from the Aichi Targets will help, but to ensure their success, mechanisms to ensure national-level compliance and accountability will also need to be strengthened (Xu *et al.* 2021). Moreover, the setting of deliverable biodiversity targets is further complicated by climate change, which may demand greater flexibility in conservation outcomes and may even leave the majority of proposed Post-2020 targets unachievable (Arneth *et al.* 2020).

The challenges facing conservation policy today are exemplified well by area-based conservation targets – an important topic given that protected areas (PAs) are considered a cornerstone of conservation efforts worldwide (Maxwell *et al.* 2020). One of the Aichi Targets often hailed as more successful was Target 11:

> *"By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems*

> *of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes."* (CBD 2010b)

The target galvanized action to expand PA coverage, and the 17% terrestrial target was met (UNEP-WCMC & IUCN 2021). Furthermore, there are signs that PA management and representativeness are generally improving (Tittensor *et al.* 2014). However, despite these successes, it is clear that the global PA network is not fit to safeguard biodiversity both now and into the future. Forty per-cent of protected areas are reported to have 'major deficiencies' in management (Leverington *et al.* 2010); only half of tropical PAs appear to be effective (Laurance 2012); and PA coverage has been deemed inadequate for the majority of ecoregions, important sites for biodiversity and assessed species (Butchart *et al.* 2015). A 2014 analysis found that only 15% of threatened vertebrates, for example, had adequate coverage, and that reaching the 17% area target using the cheapest available land would increase threatened species coverage by just 6% (Venter *et al.* 2014). Meeting coverage targets for all countries, ecoregions, important sites and species in a cost-effective manner would in fact require a near doubling of global PA coverage (Butchart *et al.* 2015). In the Post-2020 framework, it's encouraging that the coverage target for area-based conservation measures has been ambitiously set at 30% by 2030 (CBD Secretariat 2021). However, these improvements need to be targeted strategically to secure genuine biodiversity benefits, rather than simply meeting area targets in themselves (Watson *et al.* 2016a); there has been criticism that the target (or indeed any ambitious area target) presents a perverse incentive that emphasises quantity over quality (Barnes *et al.* 2018).

Climate change further complicates the picture for designing effective area-based conservation strategies (Hannah 2008; Araújo *et al.* 2011; Maxwell *et al.* 2020). A reliance on static protected areas may undermine biodiversity protection in a more dynamic world in which species distributions are changing, since priority areas that maximise ecological representation are likely to change with them (Hannah *et al.* 2007). Where climatic suitability declines for many species, some protected areas may become obsolete, or at least become a poor use of limited conservation funds (Alagador *et al.* 2014). Furthermore, the current focus on PA representativity and area coverage may miss other crucial factors that determine the performance of protected areas under climate change, such as connectivity. The fate of range-shifting species depends on the spatial configuration of habitats and PAs, and the hostility of intervening land-use, as much as the actual area of habitat under protection. Connectivity considerations are alluded to in the Post-2020 area-based target, as they were in Aichi Target 11 before it, but have received much less attention than the more easily-quantified area figure.

It has now been 30 years since the first major multilateral attempt to coordinate environmental policy and action at the global scale, and biodiversity remains in a deteriorating condition. A significant expansion of area-based conservation measures is likely to form a core part of the global biodiversity strategy in the next decade. The challenge will be to do so in a way that balances ecological representation, cost-effectiveness, management effectiveness, enforceability, and outcomes for local communities – and does so in a way that is both flexible and forward-looking, given the uncertain influence of climate change. Despite the enormity and complexity of this task, there are a variety of tools conservationists can take advantage of to identify opportunities. One tool is macroecological modelling, which can help explore the impacts of future climate and land-use scenarios and identify conservation opportunities.

Using macroecology to inform climate-smart conservation

Three broad approaches, and combinations thereof, have been used to estimate the future impacts of climate change on biodiversity at broad scales: trait-based approaches, mechanistic models, and correlative models (Pacifici *et al.* 2015; Foden *et al.* 2019). These approaches can be applied to specific species, and combined across many species to understand patterns of climate vulnerability and biodiversity change under future scenarios. These patterns can reveal groups of species that might warrant particular conservation attention as the climate changes, or places where conservation actions like PA expansion or habitat restoration could benefit the most species, especially when combined with approaches such as systematic conservation planning (Venter *et al.* 2014).

Trait-based assessments use information about species characteristics to determine how sensitive and adaptable they will be, based on *a priori* assumptions of how these traits relate to climate vulnerability (Foden *et al.* 2019). For example, species with high habitat specificity and low dispersal capability could be considered more sensitive to change. Trait-based scoring is relatively straightforward and has the advantage of not relying on more complex modelling techniques (which may be less transparent, difficult to parameterise, and more difficult to communicate). However, it often depends on arbitrary thresholds, is not spatially explicit in itself, and for many species is limited by data availability (Pacifici *et al.* 2015; Foden *et al.* 2019).

Alternatively, mechanistic modelling can potentially offer process-based, spatially explicit projections that are able to be extrapolated into novel conditions (Kearney & Porter 2009). For example, mechanistic models can be used to predict species' responses to climate change by simulating processes of habitat patch colonisation and extinction, given knowledge of climatic tolerances, life history, demography and dispersal parameters, competition and predation, and future land-use scenarios (Pacifici *et al.* 2015). Such models, however, are highly data-intensive and therefore difficult or even impossible to parameterise for many species. Therefore, they have typically been used for a few well-understood focal species (Amstrup *et al.* 2007; Jenouvrier *et al.* 2009).

By far the most commonly used methods are correlative approaches, often known as bioclimatic envelope models or species distribution models (SDMs). These rely on the associations between species' current distributions and environmental variables to predict the distribution of their climatic niches under future environmental scenarios. These predictions may then be combined with assumptions about dispersal to estimate future species distributions. Changes to species ranges can be translated into changes to extinction risk (Bellard *et al.* 2012) via species-area-relationships (Thomas *et al.* 2004) or by applying criteria such as those used by the IUCN Red List (Thuiller *et al.* 2005).

The correlative approach is spatially explicit and is applicable to a wide range of species and spatial scales, as long as their distribution is known and current and future climate and land use predictions are available. It has, however, often been used inappropriately or with unrealistic assumptions, producing inaccurate and misleading predictions (Pearson & Dawson 2003). When using SDMs, an important distinction must be made between the projected distribution of suitable climate, and the predicted 'realised' distribution of the species in question (Araújo & Peterson 2012). Equating the two effectively makes the unrealistic assumption of unlimited dispersal and habitat availability and will underestimate species losses; consequently many analyses have instead assumed no dispersal is possible whatsoever (Jetz *et al.* 2007) – also an unrealistic notion. Reality will lie somewhere in-between, with dispersal mediated by intrinsic species traits (related to demography and population dynamics) and extrinsic barriers to dispersal (the landscape context). In addition to demography and dispersal, SDMs have rarely taken into account other important factors affecting species distributions, including biotic interactions (such as presence of competitors); physiological responses; land use projections at the appropriate scale; and evolutionary responses (Urban *et al.* 2016). Furthermore, SDMs may perform poorly when projecting to novel climates, and contentiously assume species are currently at equilibrium with their current climate (which is unlikely to be true where recent habitat loss, past persecution or natural dispersal barriers prevent species from occupying climatically suitable areas). SDMs may also offer unreliable predictions for species with very narrow ranges or few occurrence records. Finally, the approach also tends to ignore the potential interactions between drivers of extinction discussed above. Despite these caveats, when implemented appropriately, SDMs have been shown to generally perform well when validated with observed abundance changes (Green *et al.* 2008; Stephens *et al.* 2016; Foden *et al.* 2019) and in predicting, for example, introduction success and failure (Hill *et al.* 2002).

All three of these methods have shortfalls, but it is possible to generate a more accurate understanding of the biodiversity impacts of climate change by combining elements of the different approaches (Willis *et al.* 2015). Species trait data on dispersal or adaptive capacity, for example, can be incorporated into a correlative approach to improve range shift projections (e.g. Visconti et al. 2015). Mechanistic elements could also be included to incorporate more realistic processes of dispersal or metapopulation dynamics (e.g. Anderson et al. 2009) .

Key conservation challenges and knowledge gaps under climate change

Despite a surge in research interest over recent years, we still have a relatively poor understanding in general of how species are likely to respond to climate change and what this means for conservation policy. This is essential knowledge if we are to implement the Post-2020 Biodiversity Framework in a way that will meet its mid- (2030) and longer-term (2050) goals. Where global projections have been carried out, data constraints have meant that they have often failed to include important interactions with other threats like land-use change, relied on overly simplistic dispersal assumptions, and ignored important considerations like changing interactions between species. For example, a major global synthesis of biodiversity models used projected future scenarios to explore how we can ‘bend the curve of biodiversity loss’, but focussed only on land-use change, without incorporating climate impacts (Leclère *et al.* 2020). These omissions are difficult, but important, to address, given they have important implications for the priorities and feasibility of conservation options.

Related to this, a major knowledge gap is how land-use is likely to affect the abilities of species to undergo range shifts as the climate changes. Range shifts in response to historical climate changes may have been facilitated by much higher availability and connectivity of suitable habitat (Lagerholm *et al.* 2017). Today, with much of the biosphere transformed for agriculture, it is highly uncertain how land-use will constrain species abilities to cope. Another poorly-understood consideration is how the changes brought about by climate change – on species distributions for example – fit into the human conservation context. The fate of biodiversity depends not only on species exposure and sensitivity to climate change, but also on the abilities of humans to enact and enforce effective conservation measures. There is therefore a need to explore climate impacts on nature in their socio-political context. Finally, given the importance of area-based conservation measures, both in terms of policy and practice, a major knowledge gap relates to how we can future-proof the global PA network and expand it most strategically.

Thesis objectives and outline

Taking terrestrial mammals and birds as focal groups – owing to the availability of appropriate data and their ability to perform well as surrogates for other facets of biodiversity (Larsen *et al.* 2012) – the aims of this thesis are to explore how climate change is likely to shape patterns of biodiversity at the global scale; understand why these impacts vary between different species and different places; and use this information to identify conservation opportunities. Responding to the knowledge gaps identified above, I also aim to explore important contextual information that will mediate climate impacts on species, such as sociopolitical circumstances, the impacts of land-use on the availability of suitable habitat, and how connectivity in the protected area network can be preserved or enhanced as species ranges shift. The specific objectives of my four data chapters are outlined below.

Chapter 2: Modelled climate impacts on terrestrial mammals and birds: understanding range shifts across latitudes and elevations

I begin by introducing my modelling framework, making use of best-practice ensemble species distribution models (SDMs) to simulate range shifts for terrestrial mammals and birds globally, and explore how patterns of species richness and community composition are projected to change. I then dig deeper into these global patterns, investigating the biogeographical factors that explain why responses vary between species. These results provide a more nuanced view as to which species and places are most likely to be affected by climate change, have important implications for conservation strategies around the world, and provide a useful lens through which to view the subsequent chapters in this thesis.

Chapter 3: The human context of climate impacts on biodiversity: global inequities, political borders and the future of transboundary conservation

Next, I explore the important (but often overlooked) human context of these projected changes. I investigate how climate impacts on biodiversity are distributed between nations, and consider how the unequal burden of biodiversity loss may complicate global conservation efforts and further substantiate concerns of international climate justice. I then consider the importance of transboundary conservation under climate change, as many species ranges are projected to move across political borders. I highlight places where cross-border collaboration may be most useful for conservation, and where border barriers, such as walls and fences, may be most detrimental.

Chapter 4: Land-use constraints on range shifts under future development scenarios

Species have coped with dramatic climate change in the past by shifting their ranges, but in a biosphere transformed by humanity, the limited availability of natural habitats casts doubt on whether species will be able to do so today. In this chapter, I combine my SDMs with global land-use projections to investigate how land-use change, past and future, is likely to constrain range shifts in coming decades, and identify places where this land-use is likely to be most harmful for species on the move. I then show the dramatic biodiversity benefits of choosing a more sustainable future development trajectory, taking into account both climate and land-use impacts on species. This chapter considers the importance of tackling multiple pressures on biodiversity together, and highlights how the combination of swift emissions cuts, targeted habitat restoration, and transformative change to our food production systems could begin to reverse global biodiversity declines.

Chapter 5: Climate change, range shifts and habitat connectivity in the global protected area network

Protected areas are likely to play an important role in facilitating range shifts, but a lack of connectivity between them could limit the benefits they provide. However, the magnitude of this problem is poorly understood at the global scale, despite being an important consideration for the Post-2020 Framework if we are to safeguard biodiversity in the medium- and long-term. In my final data chapter, I combine range shift projections, species-specific and fine-resolution habitat suitability data, and dispersal modelling to explore whether a lack of habitat connectivity could limit species' abilities to colonise protected areas under climate change. I identify places and species most impacted by this lack of connectivity, and identify globally important habitat corridors between protected areas that should be preserved to ensure as many species as possible can fulfil their projected range shifts.

Chapter 2

Modelled climate impacts on terrestrial mammals and birds: understanding range shifts across latitudes and elevations

Alexander von Humboldt's influential "Tableau physique" (1807), detailing the plant communities found at different elevations in the Andes. His work was the first to connect climate, geography and species distributions at broad scales, pioneered the use of maps to form and test hypotheses, and was the first to appreciate the impacts of land-use and climate change on an interconnected web of life. *Source: A. de Humboldt, Essai sur la géographie des plantes (1805), Vème partie (Public domain image)*

Abstract

Climate change is expected to cause a major redistribution of biodiversity. In this chapter, I model the climatic niches of the word's terrestrial mammals and birds to understand how their distributions might change under different emissions trajectories. These distribution models will become the starting point for subsequent chapters, but first, I use them here to generate novel insight into how and why species are expected to respond to a changing climate, and what this means for patterns of global biodiversity. Even under a low emissions scenario, by 2070 more than two-thirds (68%) of the planet will become less hospitable for birds and mammals than at present, rising to 84% under a worst-case emissions scenario. Under higher emissions scenarios, losses are particularly severe in sub-Saharan Africa and tropical South America, emphasising the need for rapid cuts to greenhouse gas emissions to avoid significant disruption to some of Earth's most biodiverse regions. Following this distribution modelling, I use generalised additive models to relate species-level climate impacts to some key biogeographic variables, showing how tropical, arctic, montane and specialised species are most at risk. These results provide a more nuanced view as to which species and places are most likely to be affected by climate change, have important implications for designing successful conservation strategies around the world, and provide a useful lens through which to view the subsequent chapters in this thesis.

Introduction

Ongoing biodiversity loss – already suggested to be the sixth mass extinction event in Earth's history (Barnosky *et al.* 2011) – is likely to be exacerbated by climate change (Hannah *et al.* 2002; Thomas *et al.* 2004; Bellard *et al.* 2012; Diaz *et al.* 2019). Concern is mounting that climate change will push many more species towards extinction and significantly re-shape global conservation priorities. As a result, efforts to anticipate how climate change might affect the natural world have developed into a major field of ecology (Scheffers *et al.* 2016a). However, despite this surge in research interest, and proliferating evidence that climate impacts are already being felt by species (Scheffers *et al.* 2016a; IPBES 2019; IPCC 2022), it remains unclear which species and places will be most affected by rising temperatures, and which conservation strategies will be most likely to succeed in this era of rapid change (Dawson *et al.* 2011; Pacifici *et al.* 2015).

Although climate change will have a broad range of impacts, ranging from the genetic level up to that of whole ecosystems (Scheffers *et al.* 2016a), among the most conceptually simple and well-documented impacts are changes to species' geographical distributions, such as range shifts, expansions and contractions (Lenoir & Svenning 2015). For example, warming has been linked to upslope range shifts in many montane species – including birds (Freeman *et al.* 2018), moths (Chen *et al.* 2009) and plants (Steinbauer *et al.* 2018) – while poleward shifts have been documented in British and North American birds (la Sorte & Thompson 2007; Massimino *et al.* 2015). The combination of distribution changes across many species leads to broader changes in species richness and community composition, with knock-on effects for ecosystem functioning and the provision of ecosystem services. Therefore, to understand how climate change might affect not just species-level extinction risk but also broader-scale biodiversity impacts, it's important to understand how individual species will respond, and why.

Species distribution models (SDMs) underpin much of our understanding of how range shifts might unfold – an approach which statistically relates species geographical distributions to environmental variables. Modelled changes in these environmental variables can then be used to project species' changing distributions under future climate scenarios. However, attempts to use SDMs to forecast global scale biodiversity change are rare, and such efforts are often presented with relatively little attempt to interrogate the spatial patterns that emerge, or unpick why responses vary among species.

In this chapter, I address these gaps by using SDMs to simulate range shifts for the majority of the world's terrestrial mammal and bird species. By combining these together, I explore how species richness and community composition are likely to change around the world. Then, I interrogate the species-level responses that drive these global biodiversity changes, asking which biogeographic properties of species' current distributions predispose them to range contractions, expansions and displacements under climate change. Specifically, I focus on two key dimensions of species ranges that underpin their climatic niche – latitude and elevation – asking to what extent we can predict species' responses to climate change from these fundamental properties.

Main questions and hypotheses

1. How will the combination of species-level range shifts affect species richness and community composition around the world? Where will existing species be

most likely to disappear from, and where are novel species assemblages most likely to arise?

2. Can we explain why these patterns emerge by looking at the latitudinal and altitudinal properties of species' ranges? Specifically:
    a. Both high-latitude species (where the magnitude of climate change is greater (Pithan & Mauritsen 2014; IPCC 2021)) and low-latitude species (where climatic niches are narrower and species may be more sensitive to change (Tewksbury *et al.* 2008; Newbold *et al.* 2020)) have been hypothesised to be more impacted by climate change. What is the relative importance of these two hypotheses? Can I find evidence that either group (or both) are more likely to see range size losses and/or see their ranges shift into new areas?
    b. Both high-altitude and lowland species may face threats from climate change. Is there evidence for high altitude species being likely to see a widespread 'escalator to extinction' (Urban 2018) – or are low altitude species more likely to be impacted because of high climate velocity in lowland areas (Loarie *et al.* 2009)? If both are true, what is the relative importance of these two hypotheses?
    c. Finally, I hypothesise that species that currently occupy narrow elevation and latitude bands will see greater range losses and displacement, because their more specialised environmental niches are more prone to shifting elsewhere or disappearing.

Methods

Note: Part 1 of the Methods section of this chapter details my species distribution modelling approach, which has already been published in Titley et al. 2021 (PNAS), since this analysis (which forms the following chapter in this thesis) also depended on outputs from this same SDM work. The remaining methods detailed below (and the rest of this chapter) are novel and have not yet been submitted for peer review and publication.

The overall approach of this chapter was first to generate SDMs – which relate species present distributions to climate variables – and then, using future climate data, use the models to project how species distributions around the world are likely to change under different climate change scenarios. When used appropriately the SDM approach has been shown to simulate accurately responses to climate change for mobile species (Araújo *et al.* 2005; Watling *et al.* 2013; Stephens *et al.* 2016). Next, I used these projections to build a global picture of biodiversity change under climate change. Finally, to understand these patterns, I used a second modelling step to relate the projected impacts on species back to the latitudinal and altitudinal properties of their current ranges, enabling me to ask to what extent, and in what direction, latitude and elevation play a role in shaping species' responses to climate change.

1. Species distribution models

Species distribution data

Species distribution data were obtained from the IUCN Red List (IUCN 2016b) for 5,381 species of terrestrial mammals, and BirdLife International and Handbook of the Birds of the World (BirdLife International and Handbook of the Birds of the World 2017) for 10,930 species of birds. The range polygons were filtered to keep only 'Extant' or 'Probably Extant' polygons ('Presence' code 1 or 2) where the species was native ('Origin' code 1), for the species' breeding and resident ranges ('Seasonality' code 1 or 2). The resulting range polygons were then rasterized to a grid with 0.5˚ resolution. Grid cells were classed as 'presence' where they had at least 10% overlap with the range polygon. To avoid the inherent problems when modelling the climatic niches of range-restricted species (where climate is less likely to be an important determinant of the species distribution), I excluded species classified as being present in fewer than ten grid cells. This resulted in a final set of 3,840 mammal and 8,918 bird species – 78.2% of the original species. All modelling was done in a cylindrical equal area projection to avoid biasing the models by oversampling high latitudes (Budic *et al.* 2016). For each species, 1000 pseudo-absence points were randomly sampled from the same zoogeographic realm(s) (Holt *et al.* 2013) in which the species was found. Points were sampled from the same zoogeographic realm to minimise sampling from regions that are climatically suitable but where the species is not found because of geographical barriers such as oceans and large mountain ranges. I chose a relatively coarse scale (0.5°) to model species climatic niches because climate is ecologically relevant for species distributions at broader scales and because climatologists often caution about the accuracy of climate data derived from General Circulation Models at finer spatial scales (Baker *et al.* 2016).

Predictor variables

Despite the significant body of research employing species distribution models, the bioclimatic predictor variables used vary widely, with little consensus on the best approach to select them. One common approach is to use all 19 bioclimatic variables provided by the *Worldclim* dataset (Hijmans *et al.* 2005; Fick & Hijmans 2017), although high inter-correlations between the variables can lead to model instability (and issues with assigning causality), and is particularly problematic when projecting to future climate scenarios and/or different geographic regions (Dormann *et al.* 2013). A preferable approach is to select variables that are ecologically relevant to the species being modelled based on expert knowledge of causal relationships (mac Nally 2000; Elith & Leathwick 2009). However, this option was unfeasible on a global scale, since there is no obvious set of predictors of ecological relevance to all species, and a lack of species-specific knowledge prevents the identification of relevant variables for every species individually. Consequently, I used a systematic approach to select a set of predictor variables that are broadly ecologically relevant, non-collinear and that produce high performing models when tested on a random subset of species.

First, I pre-selected eight bioclimatic variables from the *WorldClim* dataset (Fick & Hijmans 2017) that have been widely used in niche modelling and have been used to model species distributions accurately under a changing climate (e.g. Stephens et al. (2016)). These included: mean annual temperature and precipitation, temperature seasonality, precipitation seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the wettest month, and precipitation of the driest month. For both temperature and precipitation, these eight variables capture the annual typical conditions, variability (seasonality) and extremes. I then generated all possible combinations of these eight variables, in combinations of between 3-8 variables. This resulted in 219 possible combinations (1 combination of 8, 8 combinations of 7, 28 combinations of 6, and so on). Of these 219, 10 sets were discarded because they did not contain both temperature and precipitation variables. The remaining 209 sets of variables were then tested for collinearity; if any variables in the set had pairwise correlations of $r > 0.7$ (Dormann *et al.* 2013), the set was discarded. This left a final selection of 38 candidate combinations of predictor variables that are biologically relevant at a coarse scale and sufficiently uncorrelated to avoid producing unstable models. These 38 combinations were then used to build Generalised Additive Models (GAMs), using the R package *mcgv* (Wood 2017), for a random subset of 200 bird and 200 mammal species (for more detail, see GAM modelling methods below in section 1.4). The 38 candidate combinations were then ranked according to model performance (using AIC) to identify the best set of predictor variables by tallying the number of times that set appeared in the top quartile of candidate sets. The final set included the following five predictors: mean annual temperature, temperature seasonality, precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality. This set was in the highest performing quartile of candidate variable combinations for >90% of mammal and bird species. When projecting future climate variables, I used downscaled General Circulation Model (GCM) data from CMIP5, downloaded from *WorldClim* (Hijmans *et al.* 2005). To take into account variation in climate projections between different climate models, I used outputs from three different GCMs (HadGEM2-ES, CCSM4, and MIROC-ESM-CHEM). These were selected based on the availability of future projections across the four RCPs (Fick & Hijmans 2017) and demonstrated ability to perform well at simulating climate regimes in multiple world regions (McSweeney *et al.* 2015).

Spatial autocorrelation

Spatial autocorrelation (the higher similarity of closer samples) is a pervasive phenomenon in ecological data. If present and unaccounted for in model development, spatial autocorrelation can lead to inaccurate estimation of model coefficients, inflation of significance values, and inappropriate spatial inference and prediction (Segurado *et al.* 2006; Dormann 2007a; Miller 2012). To account for the spatial dependence in the models, I split the gridded presence/absence data for each species into ten spatially disaggregated blocks (Bagchi *et al.* 2013). Non-contiguous portions of the world's terrestrial ecoregions were used as the sampling units to divide the data; these units were then grouped into 10 blocks using the *blockTools* package in R (Moore & Schnakenberg 2016) such that the total area and mean bioclimate was approximately equal in each block, and that each block contained the full range of bioclimates (Bagchi *et al.* 2013).

Model validation

By splitting the data into ten blocks, I was able to use 10-fold cross-validation to assess model performance. Each block was left out in turn to be used as a testing dataset, and models were trained on the remaining 90% of data. Model performance was then assessed using the area under the receiver operator characteristic (ROC) curve (AUC), which tests for discrimination ability.

Ensemble climatic niche models

Here, my focus is not on projecting realised distribution changes but rather on exploring the potential for species climatic niches to shift into novel regions. For this purpose, I considered that simple species distribution models are adequate. The potential limitations of species distribution models in projecting actual range shifts for species are widely recognised and have been comprehensively discussed elsewhere (Pearson & Dawson 2003; Dormann 2007b; Elith & Leathwick 2009). Future model development could incorporate species traits, land-use and biotic interactions. However, currently we lack sufficient data for almost all species in relation to limiting biotic interactions and their roles in determining species' realised niches. Similarly, global projections of future land use and land cover are currently available only at very coarse spatial scales, and for such broad habitat classifications, so as to be inappropriate for inclusion in modelling future scenarios for most species.

Adapting the methods of Bagchi et al. (2013), I used an ensemble of four different model types for each species: generalised linear models (GLMs); generalised additive models (GAMs), random forests (RFs) and boosted regression trees (BRTs). Combining an ensemble of models has been demonstrated to reduce overfitting and improve predictive performance, especially for rare species (Lomba *et al.* 2010; Breiner *et al.* 2015). The four model types were selected to provide contrast between regression-based and machine learning techniques. This methodology has previously been shown to model accurately species' distributions (Elith *et al.* 2006; Bagchi *et al.* 2013; Stephens *et al.* 2016). Models were fitted on training data leaving one block out in turn, resulting in 40 models per species (10 blocks x 4 model types). These were then used to project future climatic niches across the same and adjacent zoogeographic realms (Holt *et al.* 2013) using future climate variables from the 3 selected GCMs. This resulted in 120 projections per species (40 models x 3 GCMs) for each emissions scenario. Projected probability of occurrence was converted into a binary presence-absence value using a threshold that maximised sensitivity plus specificity (Liu *et al.* 2005). The final projected distribution was determined by taking the mean presence/absence value for each grid cell, weighted by AUC to give greater influence to better performing models in the ensemble. The models had good discrimination ability, with mean AUC (±SD) of 0.942 (±0.052) for mammals and 0.941(±0.049) for birds. Details of model formulation for each model type are given in more detail below; all modelling was done using R (R Core Team 2017).

Generalised Linear Models: When fitting GLMs, I optimised the combination of polynomial model terms to maximise model performance in terms of AUC for each species, as follows. GLMs were used to fit up to and including third-order polynomials for the five predictor variables, resulting in 243 candidate model formulations. Models were fitted to nine blocks of data, with the remaining block used as a testing dataset to evaluate AUC. This was then repeated for each of the ten data blocks. The combination of polynomial terms that maximised AUC across the ten model fittings was used to fit a final set of 10 models.

Generalised Additive Models: I used thin-plate regression splines to fit GAMs using the *mgcv* package in R (Wood 2017). These regressions were fitted as a Bernoulli response using a logit link function. Once again, models were fitted on 90% of the data, leaving one block out as a testing dataset to assess model performance using AUC.

Random Forests: Random forest modelling was done using the package *randomForest* in R (Liaw *et al.* 2014). The number of variables ('mtry') randomly sampled at each split was allowed to vary between one and three. The number of trees was then set initially to 1000, and a random forest was fitted to the data, sequentially omitting one block of data for cross-validation so that performance could be assessed using AUC. The number of trees was then increased by 500 and the procedure repeated until the increased performance (from the addition of 500 new trees) measured using AUC was <1%. The values of mtry and the number of trees that maximised model performance (averaged across the ten blocks of omitted data) were used to fit the final set of 10 models.

Boosted Regression Trees: Boosted regression trees were generated using the *gbm* R package(Ridgeway 2019). A similar cross-validation approach was used to parameterise the BRT models. Learning rate (also known as the shrinkage parameter) was set at 0.001; the number of trees was set at 5000; and tree complexity was allowed to vary between 1 and 4. The tree complexity that minimised summed error across the testing data blocks was used to fit a final set of 10 models.

Dispersal assumptions

I also included a dispersal constraint in species projected distributions since failing to do so is likely to overestimate range shifts and underestimate climate impacts for species whose dispersal capabilities lag behind the velocity of climate change. I did this by 'clipping' species' projected ranges to a plausible dispersal distance from their current range, excluding regions from their projected ranges that they would be unlikely to reach by 2070. Plausible dispersal distances were estimated by multiplying the species natal dispersal distance by its expected number of generations between now and 2070. Natal dispersal estimates were obtained from Santini et al. (2013) for mammals and Santini et al. (2019) for birds, while average generation lengths were obtained from the Pantheria database (Jones *et al.* 2009) for mammals and Bird et al. (2020) for birds.

Sources of uncertainty

The results presented below use state-of-the-art distribution modelling techniques to project the impacts of climate change on biodiversity, but should not be interpreted as a prediction of likely global biodiversity change. There are several important additional considerations that are likely to affect how species respond to rising temperatures – some of which I address in later chapters, while others are beyond the scope of this thesis and remain to be tackled. Key sources of uncertainty include the influence of biotic interactions between species; uncertainty over how climate change will interact with other pressures on nature (see Chapter 4 for an exploration of how human land-use in particular complicates the picture); the poorly understood capacity for species to acclimate to new climates; the importance of factors at finer spatial scales, such as how microclimatic buffering may or may not help species adapt; and uncertainty in the global climate system, especially with regard to feedback loops, regional climatic effects, and major tipping points not captured in the GCMs (Lenton *et al.* 2008a).

2. Mapping global patterns of biodiversity change

By combining individual range shift projections for many species, I mapped how grid-cell level biodiversity is likely to change around the world. Here, I focussed on three measures of biodiversity change:

1. Species richness change, calculated by comparing the species richness under current climate conditions with the expected richness under 2070 climate conditions.
2. Proportion of current assemblage in a given grid cell that still has suitable climate in 2070, hereafter referred to as ‘community persistence’.
3. Proportion of the 2070 assemblage that is new for a given grid cell, hereafter referred to as ‘community novelty’.

Note that persistence and novelty are not the direct inverse of one-another; it is possible for a cell to have both high persistence and novelty, if for example most of the present species still have suitable climate in 2070, but the grid cell may also be colonised by many species in the future. These two measures complement species richness change by taking into account the identities of species, enabling me to capture important shifts in the species assemblages that might not be captured by the net change in number of species alone.

3. Two species-level metrics of climate impact

As I have used a ‘bottom-up’ approach, starting at the species level to build up a picture of global biodiversity change, it is most appropriate to try to understand what is driving these global biodiversity changes by examining what is shaping range shifts at the species level. Therefore, from the modelled range shifts, I have calculated two species-level metrics that capture key dimensions of species distribution changes:

1. Range size ratio: the size of the species’ 2070 climatic niche divided by the size of its present day niche, in terms of number of climatically suitable grid cells. A value above 1 therefore indicates that this species’ range is projected to expand under climate change. A value less than 1 indicates that this species’ range is expected to shrink. The lowest possible value is zero, which would indicate that this species no longer has any suitable climate by 2070 that resembles the climate in its present distribution.
2. Range overlap: the proportion of a species’ 2070 range that overlaps with its present range. If a species had no suitable climate in 2070, this value was set to NA (to differentiate from species where there was still suitable climate and a true lack of overlap).

4. Understanding the role of latitude and elevation in driving these patterns

Latitude and elevation as predictor variables

I used the two species-level metrics of climate impact defined above as response variables in a second modelling step, in which I tried to tease apart the roles of latitude and elevation in driving these range shift responses. To do this, I derived the following four predictor variables from species present distributions, which capture the average and breadth of latitudes and elevations that a species inhabits: mean latitude, latitude range, mean elevation and elevation range.

Mean latitude was calculated by taking the mean latitude, in degrees, across all half-degree grid cells presently occupied by the species, while latitude range was obtained by subtracting the minimum from the maximum latitude values. Latitude degrees south of the equator were treated as negative values. To calculate the elevation variables (mean and range), I first tried to obtain elevation data for each species from the IUCN Red List API (IUCN 2020), which details the minimum and maximum elevation suitable for each species as determined by experts, enabling me to calculate the elevation range directly from these values. Where these elevation limits were not available (37% of species), I calculated the elevation variables by overlaying species ranges with a global digital elevation model (DEM) layer, GMTED2010 (Danielson, J.J., Gesch 2011)

A potential problem with this approach is that the species distribution maps represent the distributional boundaries, rather than the area of habitat (AOH) or area of occupancy (AOO) (Brooks *et al.* 2019). This means that areas unoccupied by the species (such as mountain peaks above the species' typical elevational limits) were likely to be included and give an overestimation of the species' upper altitudinal limit. To minimise this, I first aggregated the 1km resolution DEM raster to a 10km resolution, effectively smoothing out fine-scale topographic variation. I then estimated an upper elevation limit by taking the 90th percentile elevation value across that species' range. This meant that if a small number of high-elevation cells were originally included in the species' range polygon (which are unlikely to be occupied in reality) they would be excluded, but high-altitude adapted species - whose range polygons are largely drawn around mountainous areas - would still show an appropriately high upper elevation limit. To calculate the mean elevation for each species, areas outside of the elevation limits determined above (either from the IUCN Red List API where available, or derived from the DEM data) were excluded and the mean elevation was calculated across the remaining cells. The correlation between elevation values obtained from the IUCN Red List data and for those derived from the DEM data was 0.951 (Pearson's product-moment correlation) suggesting that this approach was a reasonable proxy where direct estimates were not available.

Modelling approach

The response and predictor variables described above were used to build generalised additive mixed models (GAMMs), using the package *gamm4* in R (Wood & Scheipl 2020). This approach has two key advantages over alternative methods. First, the flexibility of generalised additive models allows for non-linear effects, whilst retaining the more straightforward interpretability of a linear modelling approach where the marginal effect of individual variables is easy to deduce. Second, by using a mixed model framework, I was able to consider the nested taxonomic structure in the data by including taxonomic groupings as nested random effects. I built separate models for each of the two response variables (range size ratio and range overlap), using the same predictor variables. In addition to the four latitude / elevation variables described above, which were included as smooth terms using REML smoothing (Wood & Scheipl 2020), I also included range size (the area of its present range polygon in km^2) and number of Level 1 habitat categories listed as 'suitable' for the species by the IUCN Red List (IUCN 2020) as linear fixed effects, to account for and measure any effect of range size or habitat specialisation. The degree of smoothing was calculated in the gamm4 model fitting procedure (Wood & Scheipl 2020). Finally, the taxonomic groupings of class, order and family were included as nested random effects to control for phylogenetic autocorrelation.

Results

Global patterns of projected biodiversity change

Although there is considerable spatial variation, the species richness of terrestrial mammals and birds is projected to decline across the 68-84% of the Earth's land area by 2070, depending on the climate change scenario (Figure 1). Even under the most benign climate change scenario, RCP 2.6, in which emissions reductions go beyond current policies in order to keep warming to less than 2°C above preindustrial levels, grid-cell species richness is projected to decline by -6.4% on average globally. This loss, however, is approximately half of the average loss projected to occur under RCP 4.5 (-11.1%), a climate scenario that would likely involve 2-3°C of warming by 2100 and therefore resembles a world in which the pledges made at COP26 in Glasgow are achieved. A worst case scenario, in which global development is achieved via rapid extraction of fossil fuels (RCP 8.5), has an average projected grid cell richness change of -18.9%.

Several regions in particular are likely to see significant net losses in species richness, regardless of the climate scenario followed. These include central Brazil, encompassing south-eastern Amazonia and the north-western Cerrado biome; parts of sub-Saharan Africa and Madagascar; parts of the Middle East; and Australia (Fig 1). Despite losses in these places, some regions are projected to become hospitable for more species than at present. Shaded in blue in Figure 1, these include the northernmost parts of the North America, central and northern Siberia, the Sahel, much of Argentina, along with the Andes and Tibetan plateau. Under scenarios with greater levels of radiative forcing (Fig 1b-d) these patterns become increasingly exaggerated but the hotspots of loss or gain remain largely consistent – with the exception of Africa, which appears disproportionately impacted by species richness loss in the worst-case scenario (Fig 1d).

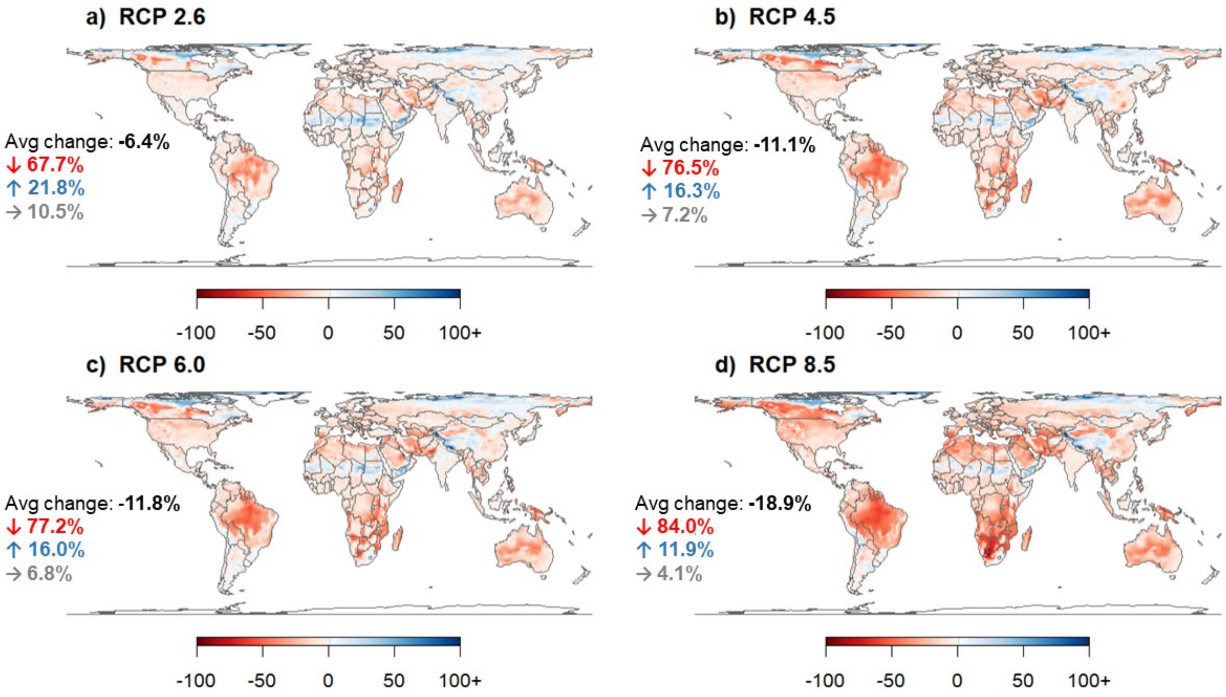


Figure 1: Percentage species richness change by 2070 for terrestrial mammals and birds, under four climate scenarios: RCP 2.6 (a), RCP 4.5 (b), RCP 6.0 (c) and RCP 8.5 (d). All four panels are plotted on the same colour scale for direct comparison. Red colours, where percentage change is negative, indicate a net loss of mammal and bird species under climate change, while blue colours indicate a net gain of species. The global average richness change is labelled for each scenario, along with the area of Earth's landmass projected to see a decline (↓), increase (↑), or no change (→) in species richness.

As well as net species richness change, I also investigated how species assemblages are likely to change, in case species richness changes were obscuring shifts in species identities within communities. Under a low emissions scenario (RCP 2.6), community persistence – the proportion of the current species assemblage in each grid cell that still has suitable climate in 2070 – is below 0.75 for around 11% of Earth's land area (11.4% for mammals, 11.7% for birds). Under RCP 4.5, this percentage of land rises to 22.6% (mammals) and 22.5% (birds). Under RCP 8.5, the equivalent figures are 46.9% and 47.7%. Therefore, achieving the Paris Agreement goal of limiting warming to 2°C (RCP 2.6) would cut the area of land affected by persistence scores <0.75 by around half, compared to only achieving the pledges made at COP26 in Glasgow (similar to RCP 4.5). Under a less likely worst-case climate scenario (RCP 8.5), around half of land becomes inhospitable for more than a quarter of its current inhabitants.

Mapping these scores globally, persistence scores are generally high under RCP 2.6 (Figure 2a and c), but tend to be lower in the Brazilian Amazon, Madagascar (particularly eastern Madagascar for mammals), central Australia and parts of

Canada. Under the moderate emissions scenario (RCP 4.5), the outlook is noticeably worse (Fig 2b and d), with larger areas of tropical South America, southern Africa and Canada in particular are projected to become inhospitable for the majority of species that currently live there. These patterns are broadly consistent for birds and mammals. See the supplementary material for the two higher emissions scenarios, RCP 6.0 and RCP 8.5.

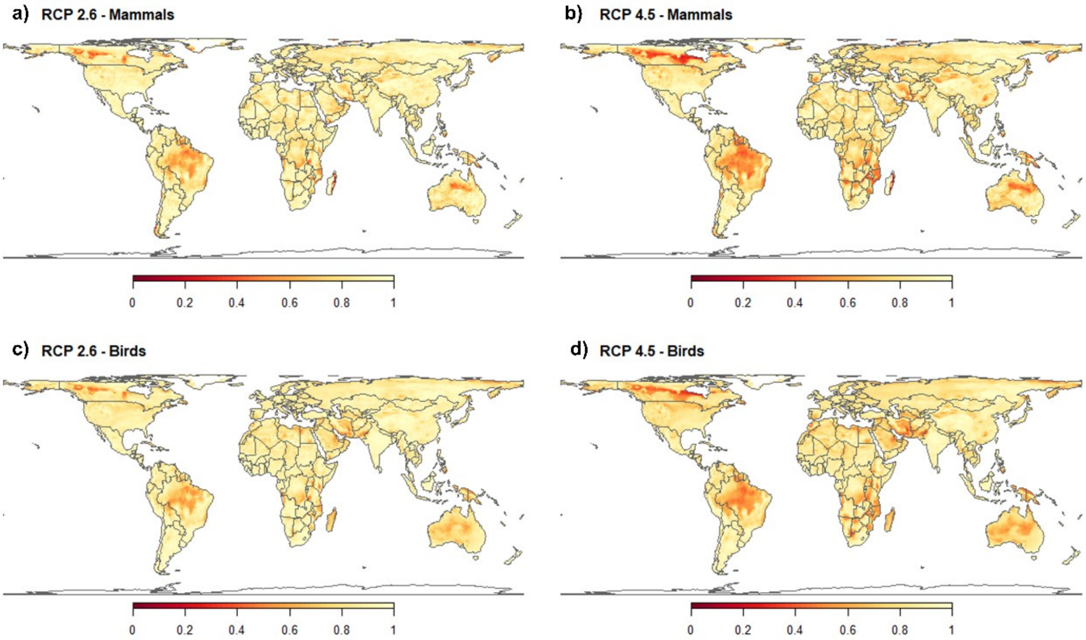


Figure 2: Community persistence (proportion of current community that still have suitable climate) in 2070. Top two panels, a) and b), show mammals only, under two relevant climate scenarios (RCP 2.6, likely less than 2°C warming by 2100, and RCP 4.5, likely 2-3°C warming by 2100). The bottom two panels, c) and d), show birds under the same two scenarios. Darker colours indicate a lower proportion of species able to persist in 2070. All four panels use the same colour scheme to enable direct comparison.

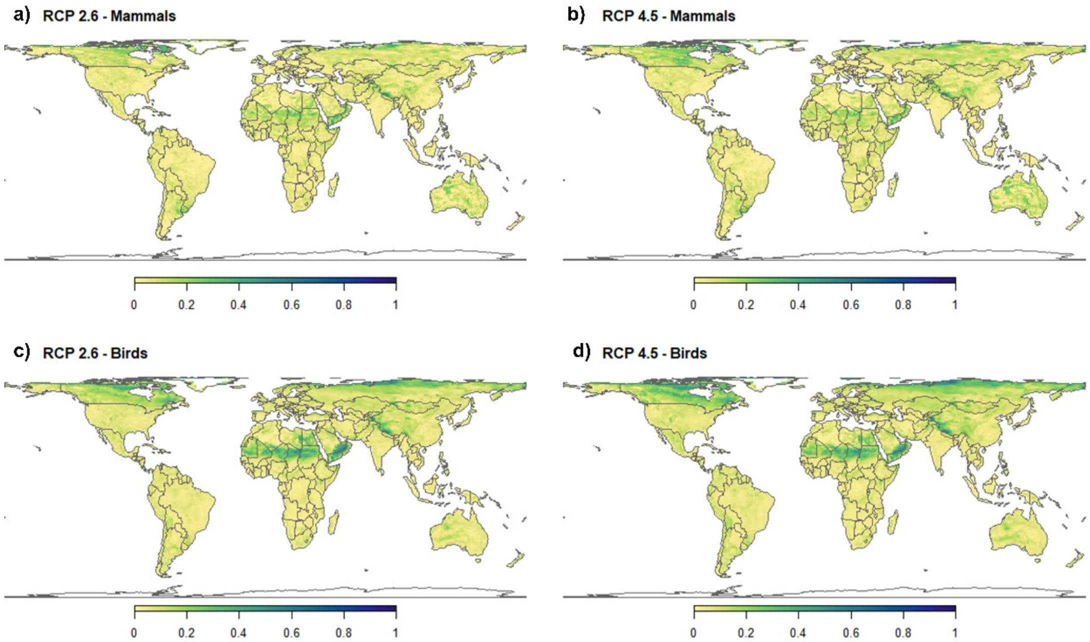


Figure 3: Community novelty (proportion of future community that are new to a particular grid cell). Top two panels, a) and b), show mammals only, under two climate scenarios (RCP 2.6 and RCP 4.5). The bottom two panels, c) and d), show birds under the same two scenarios. All four panels use the same colour scheme to enable direct comparison.

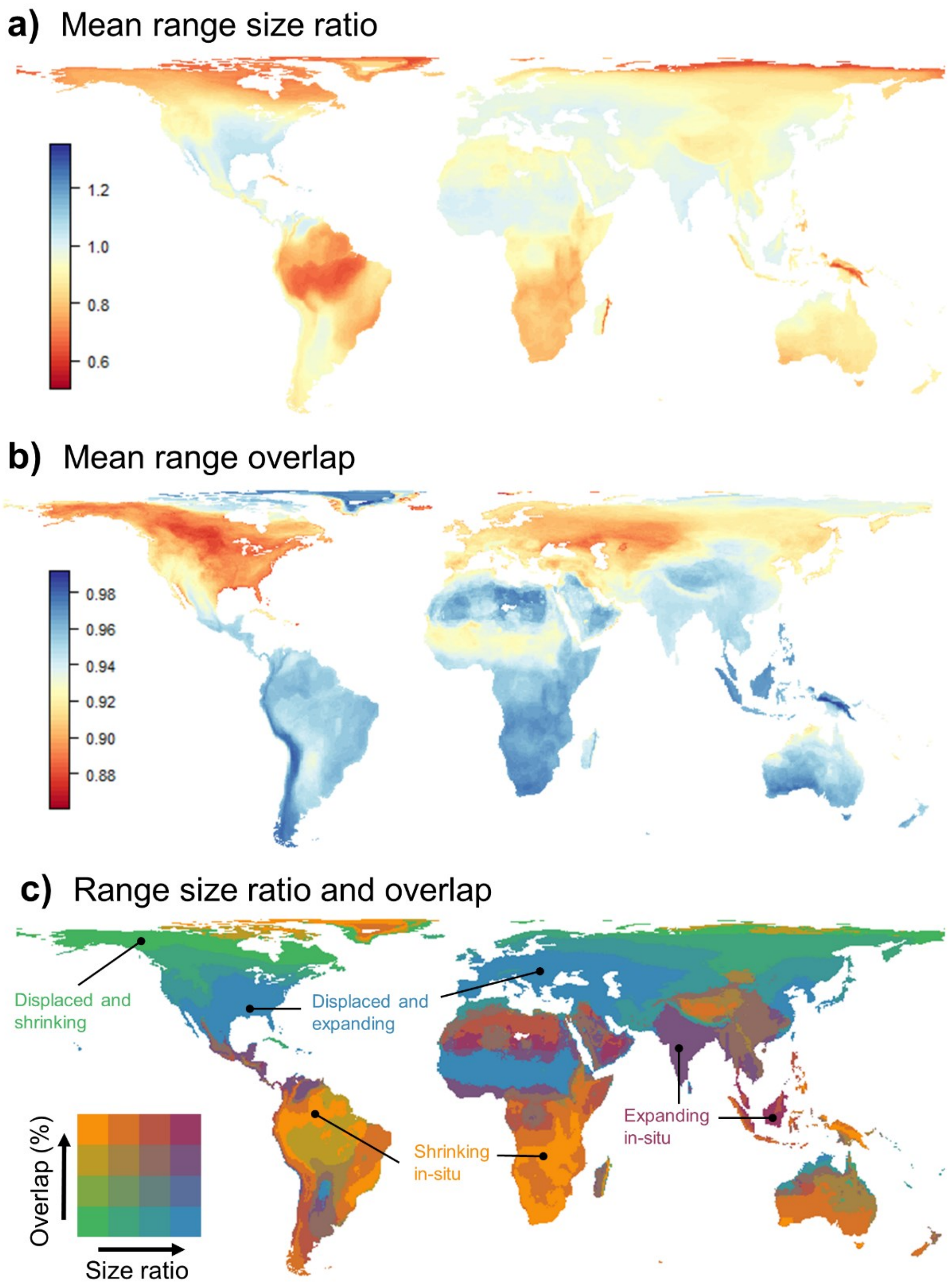
The other dimension of community change that I explored was community novelty – the proportion of species in a grid cell in 2070 that are new. Under RCP 2.6, novelty scores are above 0.25 for 2.5% (mammals) and 6.19% (birds) of land. This rises to 3.5% (mammals) and 8.4% (birds) under RCP 4.5, and 6.4% and 12.9% under RCP 8.5. Highly novel communities seem more likely to arise for birds than for mammals, although both see relatively high novelty scores in artic regions, the Himalayas, and particularly for birds, the Sahel (Figure 3). Under RCP 4.5, the distribution of novelty is similar to RCP 2.6 but the magnitude slightly greater, with species assemblages in Canada, much of Russia, the Andes, Himalayas, and Sahel all seeing higher proportions of the projected assemblage being made up of species not currently present in those grid cells. See the supplementary material for equivalent maps under the two higher emissions scenarios (RCP 6.0 and RCP 8.5).

Species-level responses to climate change

The biodiversity changes described above are the combined responses of many individual species. At the species-level, under RCP4.5 the average species is projected to see a range size ratio (it’s projected future range size relative to its present range size) of 0.79 (standard deviation 0.28), equivalent to a decline of 21%. In total, 78% of species (9315) are projected to see a decline in range size (ratio < 1) and 19% of species (2352) see an expansion in range size (ratio > 1). Around a fifth of species (21%, 2532) see little change to their range size (within +/- 5%). Mapping these results globally (taking the mean across the species currently found in each grid cell), ranges appear most likely to shrink in tropical South America, sub-Saharan Africa, eastern Madagascar, parts of SE Asia (especially New Guinea) and the Arctic (Fig 4a). Range sizes are most likely to increase in the south-eastern USA, temperate Eurasia and India.

Range overlap (the percentage of a species' future projected range that overlaps with its present range) is generally high (mean 0.94), reflecting the fact that many species ranges are projected to become restricted to a smaller region but largely within their current distribution. Overlap is highest in the global South and also Arctic, with mountainous areas in SE Asia and South America standing out (Fig 4b). Overlap is projected to be lowest in North America and Eurasia, suggesting this is where species are most likely to colonise or be displaced into other areas.

Mapping mean range size ratio and range overlap together, its possible to categorise four combinations of these two variables that describe patterns of range changes across much of the planet (Fig 4c). Range changes in many of the world's most biodiverse areas (including Amazonia and much of sub-Saharan Africa) and also the high Arctic could be described as "shrinking in-situ", typified by declining range sizes and relatively high overlap (orange regions on map). In contrast, in much of the USA, temperate Eurasia and the Sahel, ranges tend to see the opposite fate, with both range expansions but low overlap, suggesting that here, many species will expand their ranges into new areas (blue areas). Further north, in Canada, Scandinavia and Russia, both range overlap and range size ratios are relatively low, meaning that species here are more likely to be displaced into new areas but also see decreasing availability of areas with suitable climate (green). Finally, in parts of SE Asia, India, West Africa and Central America, ranges are projected to see relatively high overlap and range expansion, which could be described as 'expanding in-situ', or a localised enlargement of their current distribution (purple).


a) Mean range size ratio

b) Mean range overlap

c) Range size ratio and overlap

Figure 4: Maps show the average range size ratio (a) and range overlap (b) of species presently found in each grid cell. Range projections are for the RCP 4.5 climate scenario in which global mean temperature rises by 2-3 degree this century. In (c), (a) and (b) are combined to produce a bivariate map to reveal how range size ratio and range overlap co-vary. Grid cells are categorised into quartiles of each variable. Examples of the key combinations of the two variables are annotated.

The role of latitude and elevation in shaping species responses

Range size ratio

All four predictors fitted as smoothing terms in the models were significantly related to range size ratio (the ratio between a species' future and present range size) (Table 1 and Figure 5). In addition, I found that range area (km^2) had a positive effect on range size ratio, although the effect size was very close to zero (coefficient estimate = 2.03×10^{-9}, t = 2.924 p = 0.003). The number of habitat categories suitable for a species was also a predictor of higher range size ratios (i.e. associated with range expansion) (coefficient estimate = 0.0134, t = 6.46, p < 0.0001). For the smoothing terms, I describe the relationship of each one in more detail below (shown by the blue shaded curves in Figure 5).

Table 1: The relationship between species' range size ratios and mean latitude, latitude range, mean elevation and elevation range of present day distributions. Relationships are derived from GAMM modelling using the smoothing terms of the four variables presented.

Smooth term	Effective degrees of freedom	F statistic	P value
Mean latitude	8.818	141.60	<0.0001
Latitude range	6.155	27.17	<0.0001
Mean elevation	7.528	102.48	<0.0001
Elevation range	8.322	47.80	<0.0001

Firstly, the effect of mean latitude on range size ratio (Fig 5a, blue curve) varied greatly depending on the latitude. In tropical regions between around 20°S and 5°N, and high northern latitudes above around 50°N, latitude had a negative effect on range size ratio, meaning it was more likely to be associated with range contractions. Conversely, between approximately 5°N and 50°N, mean latitude had a positive effect on range size ratio, meaning it was associated with range expansions. At southern latitudes below around 20°S, the effect of mean latitude was slightly negative, but close to zero.

Secondly, low values of latitude range (i.e. species that occupy narrow latitude bands), in particular those smaller than a 20° latitude range, had a negative effect on range size ratio (Fig 5b, blue). Above this value, the effect of latitude range turned positive, up to a peak at around 60°. Above this value, even greater latitude ranges started to have a less strongly positive effect (though note the increasing sparsity of data points here).

Third, mean elevation also had a significant and variable effect on range size ratio (Fig 5c, blue). Having a mean elevation close to sea level tended to have a positive influence, but this effect quickly and quite linearly drops away with increasing elevation, with the effect of becoming negative around 700m. The curve then flattens off around 1000m, with the effect staying negative but not getting any more strongly negative until mean elevation reaches a second inflexion point around 4000m. The relationship then becomes more negative once again, though note again the sparsity of data points at this end of the distribution.

Finally, elevation range showed a qualitatively similar pattern to latitude range, with low values (i.e. narrow elevation bands) associated with a negative effect on range size ratio (Fig 5d, blue). Above an intermediate value, around 1500m of elevation range, the effect turns positive with these species more likely to see higher range size ratios. This increasing positive effect peaks around 4000m before beginning to drop back towards zero.

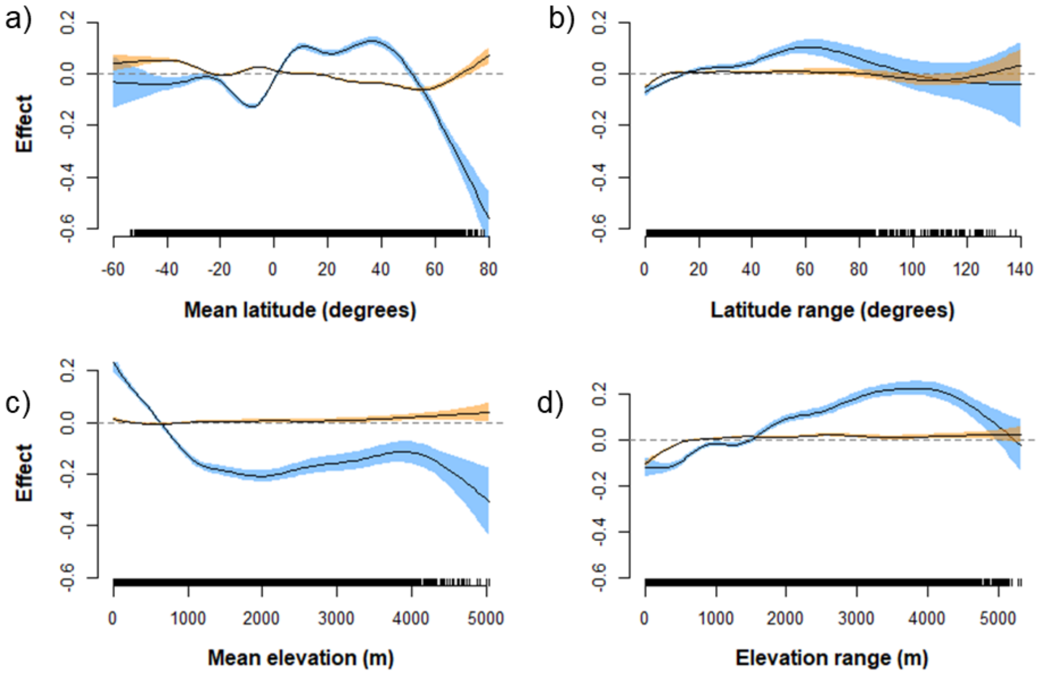


Figure 5: Smooth terms showing the effects of latitude (in degrees) and elevation above sea level (m) on projected range size ratio (blue) and range overlap (orange). Shaded regions indicated 95% confidence bands. Values above zero (grey dotted line) indicate that the variable had a positive influence on range size ratio or range overlap. Negative latitude values indicate the southern hemisphere. The ‘rug’ of black tick marks along the x-axes illustrate the distribution of data points along the axes.

Range overlap

Once again, all four smooth terms were significantly associated with the response variable, this time range overlap (Table 2). In addition, as with range size ratio, species range area was positively associated with greater range overlap, although once again the effect size was very small (coefficient estimate = 1.4×10^{-9}, t = 6.32, p < 0.0001). Unlike with range size ratio, the number of habitat categories suitable for a species was not associated with the degree of range overlap (estimate = 8.2×10^{-4}, t = 1.248, p = 0.212).

Table 2: GAMM model results showing how range overlap (the proportion of a species 2070 range that overlaps its present range) can be predicted from its current mean latitude, latitude range, mean elevation and elevation range.

Smooth term	Effective degrees of freedom	F statistic	P value
Mean latitude	8.835	92.999	<0.0001
Latitude range	8.316	26.985	<0.0001
Mean elevation	5.917	5.517	<0.0001
Elevation range	8.435	33.096	<0.0001

Mean latitude had a positive effect on range overlap at high southern latitudes, around or just below the equator, and arctic latitudes, but an increasingly negative effect between the equator and northern high latitudes (Fig 5a, orange). This suggests that species in the northern hemisphere are likely to see increasing displacement to new regions with increasing distance from the equator (with the exception of very high northern latitudes, where the relationship with range overlap becomes positive again).

The effect of latitude range and elevation range was close to zero for the majority of values of these variables, with the exception of low values (species restricted to narrow latitude and elevation bands) (Fig 5b and d, orange). This shows that these latitudinally or altitudinally restricted species were more likely to be displaced to new areas. Finally, whilst statistically significant (Table 2), the effect of mean elevation on range overlap was close to zero for all values of mean elevation (Fig 5c, orange).

Discussion

These results corroborate and expand upon earlier research predicting that climate change is likely to drive major changes to global biodiversity patterns and present significant challenges for nature conservation (Hannah *et al.* 2002; Jetz *et al.* 2007; Pecl *et al.* 2017). In particular, they reveal which places are likely to become more or less hospitable for terrestrial bird and mammal species in future, and provide a more detailed and nuanced view of the biogeographic factors underpinning these patterns.

Global patterns of projected biodiversity change

The shifting geographies of birds and mammals – beyond impacting the species themselves – will have major repercussions for ecosystem function, for the provision of ecosystem services and for human wellbeing (Pecl *et al.* 2017). These impacts are likely to be greatest in the places projected to see large relative losses in species richness. Concerningly, these include the Brazilian Amazon and Cerrado – one of the most biodiverse regions of the planet – and sub-Saharan Africa, where ecological changes could have damaging impacts on people due to the particularly strong dependence of people on nature to meet basic human needs in this region (Fedele et al. 2021). The greatest relative increases in species richness are projected to be the far northern latitudes and parts of the Sahel region in northern Africa. It's worth noting that these areas currently have relatively low species richness of birds and mammals, so relatively few net colonisations are likely responsible for these high percentage increases. In the Arctic, these increases are explained by the poleward spread of species from more biodiverse lower latitudes and resulting 'borealization' of tundra communities (Fossheim *et al.* 2015; Myers-Smith *et al.* 2020), while in the Sahel, these increases may be explained by higher precipitation associated with the strengthening of the west African monsoon (Pausata *et al.* 2017), making conditions more suitable for current species of higher-richness sub-Saharan areas.

In addition to species richness, I also examined changes to community composition, to ensure I didn't overlook areas that may see changes to the identities but not the net number of species. Palaeontological evidence shows that novel species assemblages with no present-day analogue were widespread during the last glacial cycle (Jackson & Williams 2004), and the reshuffling of species under future climate change is likely to result in the appearance similar no-analogue communities and generate 'ecological surprises' (Williams & Jackson 2007). This will have knock-on effects for ecosystem function and service provision (Evers *et al.* 2018). My modelling suggests that future communities are likely to contain a high proportion of novel species at high altitudes, high latitudes, and also across the southern Sahara/Sahel. This analysis also provides further context for the species richness results – for example, novelty is projected to be high across much of northern Canada, but species richness is only forecast to increase in the northernmost regions; elsewhere the low persistence of species is likely to drive net losses in richness by 2070. Put another way, in a given grid cell, many of the species in this region are likely to disappear and be replaced by new ones, albeit fewer of them such that the net effect is a loss in richness.

The spatial distribution of impacts – on species richness, novelty and persistence – are broadly consistent among climate scenarios, although the magnitude of these impacts is considerably greater under high emissions scenarios. Large contrasts between emissions scenarios can be seen on every continent, but this contrast in biodiversity impacts from climate change is particularly stark in sub-Saharan Africa, which sees minor changes to species richness in RCP 2.6 but dramatic losses of species richness, particularly in southern regions, under RCP 8.5. This underscores the critical importance of reducing greenhouse gas emissions in line with the 2015 Paris Agreement if we are to safeguard biodiversity under climate change. Although the RCP 8.5 scenario is now considered unlikely (Hausfather & Peters 2020), the more likely scenario of RCP 4.5 (similar to the pledges made at COP26 in Glasgow) still results in considerable biodiversity loss (-11.1% richness change globally, and over 20% of grid cells becoming inhospitable for a >25% of their inhabitants). These average impacts on species richness and community persistence under RCP 4.5 are roughly twice as severe as a more sustainable future in line with the Paris Agreement (RCP 2.6), highlighting the significant benefit for global biodiversity of continuing to ratchet up ambition in pursuit of the Paris Agreement goal.

Range shifts across latitudes and elevations

My results reveal the extent to which the predicted variation among species responses to future climate change, and resulting patterns described above, can be explained by some simple but fundamental biogeographic properties of species present distributions.

Mean latitude had a negative effect on range size change at low latitudes, especially just south of the equator, but also at high northern latitudes. This provides support for *both* of the latitude-related hypotheses mentioned in the Introduction: first, that the worst-affected species may be found in tropical regions, where species have narrower climatic niches and are more sensitive to change (Tewksbury *et al.* 2008), and second, at high latitudes where climatic changes are set to be particularly dramatic (IPCC 2014). The approach I have used here, taking advantage of generalised additive models to fit non-linear responses, therefore complements and expands on other recent work that used categorical biome classifications (e.g. temperate, tropical) to compare climate impacts on species in different regions of the world (e.g. Newbold et al. 2020).

Two questions emerge from the relationship between mean latitude and range size change. First, why is the negative effect at low latitudes not symmetrical about the equator, with the 'trough' instead being shifted southwards? Second, why is the negative effect at high northern latitudes, and positive effect at northern mid-latitudes, not mirrored in southern hemisphere, where instead the effect of latitude is close to zero? The first question may be answered by the distribution of tropical forest: the largest expanse of this, the Amazon (a megadiverse region projected to see large losses in species richness under climate change) is largely found south of the equator. This result is therefore likely to be the signal of tropical forest species being particularly sensitive to changes in climatic conditions (Bazzaz 1998; Newbold *et al.* 2020). The second question is most easily explained by the layout of the continents. In the northern hemisphere, mid-latitudes were associated with a positive effect on range size change, particularly around 40°N. However, in the southern hemisphere, this latitude mainly bisects ocean, except for relatively limited stretches in Chile/Argentina and New Zealand. Therefore, the lack of a positive signal at southern hemisphere temperate latitudes may be the result of any species here having their potential range expansions constrained by geography. Furthermore, the magnitude of climate change is forecast to be smaller in the southern hemisphere than the northern hemisphere (IPCC 2014). These factors, combined with the paucity of terrestrial bird and mammal species at high southern latitudes, would also explain why further south towards the pole we do not see the strong negative effect mirrored from northern latitudes.

A final thing to note in regard to latitude is the relationship between the two response variables that I used. Negative effects on range size ratio are often associated with *positive* effects on range overlap. I showed that range shifts for tropical (especially Amazonian and African) and Arctic species - which tend to see low range size ratios and high overlap – tend to follow a pattern of 'shrinking in situ'. In tropical regions, this is probably explained by narrow/specialised climatic tolerances, while in the arctic it is probably another geographic constraint: species have no land area at higher latitudes to move to. This arctic effect is therefore analogous to the 'escalator to extinction' effect documented in montane species (Freeman *et al.* 2018; Urban 2018), but concerning latitude rather than elevation. In contrast, in the northern hemisphere where latitude has a positive effect on range size ratio, we see an increasingly negative effect of latitude on range overlap. This shows that although mid-northern latitudes favour range expansions, they also increasingly favour range displacement into new areas that don't overlap with species current distributions.

The effect of elevation on range size change was also non-linear but more straightforward. Low elevations had a positive effect on range size ratio, but this quickly became negative and remained quite strongly negative for all higher elevations. This is consistent with the 'escalator to extinction' effect (Urban 2018), whereby montane species are more likely to see range size losses or even extinctions because they become restricted to increasingly limited upslope areas as temperatures rise. I did not find evidence to support an alternative hypothesis – that there may (alternatively or additionally) be a negative signal for lowland species, which are less likely keep up with the pace of climate change (Loarie *et al.* 2009). It would be interesting to further test this hypothesis more rigorously with alternative dispersal assumptions, which was beyond the scope of this analysis.

The effects of latitude range and elevation range were quite consistent for both range size change and range overlap. Narrow latitude and elevation bands were negatively associated with range size change and range overlap, confirming the hypothesis set out in the Introduction that these species, which are likely adapted to specialised climatic niches, are most likely to see range losses and range displacement.

In addition to the non-linear responses discussed here, I also considered two linear fixed effects in my models: current range size and the number of level 1 IUCN habitat categories (IUCN 2020) classed as 'suitable' for the species (e.g. 'Forest', 'Savannah', 'Grassland' etc). For both range size change and range overlap, current range size had a positive effect, but a very weak one. This should be interpreted cautiously, given that species with the smallest ranges were excluded from this analysis, but does allow for better interpretation of the above results (e.g. of the effect of latitude range) as the analyses had accounted for range size. The number of habitat categories was positively associated with range size change, suggesting that habitat generalist species are likely to fare better under climate change than specialists. Combined with the result that more specialised species with narrow elevation and latitude tolerances are more likely to see range losses, climate change is likely to contribute to the global biological homogenisation already underway as a result of land-use change, with 'widespread winners and narrow-ranged losers' (Newbold *et al.* 2018).

Conservation implications

The contrast in severity of impacts between climate scenarios shows that curbing greenhouse gas emissions remains the most effective option to safeguard biodiversity from the impacts of climate change. Following RCP 2.6 (similar to Paris Agreement goals) over RCP 4.5 (similar to current trajectory) would approximately halve the impacts of climate change on species richness and community persistence.

My analyses also highlight both the importance and plight of montane ecosystems: mountain chains are likely to provide refuge for many of the world's lowland species, as shown by their projected high community novelty and increases in species richness. However, species that currently live in high altitude areas are associated with range size losses as they are pushed to increasingly limited upslope areas. This suggests that already-documented examples of montane range contractions and mountaintop extinctions (e.g. Freeman et al. 2018) are likely to become a widespread global phenomenon, even if local species richness tends to increase in these regions as they are colonised from lower altitudes. In some cases, assisted colonisation of species to higher neighbouring mountains may help high-altitude species to persist, but this is unlikely to be possible for large numbers of species or across broad areas. In these critically important regions for global biodiversity, the greatest conservation 'gains' will be made by avoiding emissions in the first place, and ensuring montane ecosystems are adequately protected and connected to the broader landscape.

Besides montane species, two other categories of species appear to be particularly at risk. These include arctic species, and climate specialists found in narrow latitudinal and elevation bands. Conservation options may be limited for these species if hospitable climates disappear. Identifying the prevalence and potential benefit of local climatic refugia may help identify places where these at-risk species could continue to survive in a warmer world.

Conclusions

These analyses highlight the risk of dramatic changes to the distributions of bird and mammal species if we do not make deep and swift cuts to global greenhouse gas emissions. Species' idiosyncratic responses to climate change – determined in part by the altitudinal and latitudinal properties of their ranges – will cause both losses and gains in local species richness around the world, but negative impacts are by far the most widespread. Exploring the non-linear relationships of climate impacts with biogeographic variables revealed that these negative impacts are most likely for species found in the tropics, at high northern latitudes, high altitudes, and those specialised to particular habitat types and narrow elevation and latitudinal bands. For such species, improved systematic monitoring will be particularly useful for proactively identifying range shifts or contractions and implementing adaptation actions before it is too late. Such efforts are also particularly needed in tropical montane regions, where our understanding of species' distributions is especially poor (Lenoir & Svenning 2015) and where species-level impacts may be particularly acute. However, as well as revealing where ecological monitoring and conservation action could be targeted, this analysis also makes clear that tackling the root cause – i.e. greenhouse gas emissions – and not only the symptoms of climate change is likely to give the best prognosis for Earth's imperilled bird and mammal biodiversity.

Chapter 3

The human context of climate impacts on biodiversity: global inequities and political borders

The US-Mexico border near Campo, California. *Photo credit: Greg Bulla*

This chapter has already been published (see citation below) and is reproduced here in full, with some minor formatting changes. There is therefore some repetition in the SDM methods already described in Chapter 2.

Citation:

Titley, M.A., Butchart, S.H.M., Jones, V.R., Whittingham, M.J., Willis, S.G., (2021) Global inequities and political borders challenge nature conservation under climate change, PNAS, 118 (7) e2011204118; DOI: 10.1073/pnas.2011204118

Abstract

Underlying socio-political factors have emerged as important determinants of wildlife population trends and the effectiveness of conservation action. Despite mounting research into the impacts of climate change on nature, there has been little consideration of the human context in which these impacts occur, particularly at the global scale. We investigate this in two ways. First, by modelling the climatic niches of terrestrial mammals and birds globally, we show that projected species loss under climate change is greatest in countries with weaker governance and lower GDP, with loss of mammal species projected to be greater in countries with lower CO_2 emissions. Therefore, climate change impacts on species may be disproportionately significant in countries with lower capacity for effective conservation and lower greenhouse gas emissions, raising important questions of international justice. Second, we consider the redistribution of species in the context of political boundaries, since the global importance of transboundary conservation under climate change is poorly understood. Under a high emissions scenario, we find that 35% of mammals and 29% of birds are projected to have over half of their 2070 climatic niche in countries in which they are not currently found. We map these transboundary range shifts globally, identifying borders across which international coordination might most benefit conservation, and where physical border barriers, such as walls and fences, may be an overlooked obstacle to climate adaptation. Our work highlights the importance of socio-political context and the utility of a supranational perspective for 21st century nature conservation.

Main text

Earth’s biodiversity is set to face major disruption under climate change, with substantial implications for natural ecosystems and human societies that depend on them (IPCC 2014; Scheffers *et al.* 2016b; Pecl *et al.* 2017; Díaz *et al.* 2019). However, the fate of biodiversity depends not only on the severity and distribution of climate impacts, but also on the human context in which they occur (Segan *et al.* 2015). For example, socioeconomic factors such as governance, corruption and conflict frequency are important predictors of wildlife population trends and the effectiveness of conservation efforts (Miller *et al.* 2015; Amano *et al.* 2018; Daskin & Pringle 2018; Schulze *et al.* 2018). Political borders, too, have important conservation implications where they fragment policy and legislation across species ranges (Dallimer & Strange 2015), or where they present physical barriers to movement (Linnell 2016; Linnell *et al.* 2016; Trouwborst *et al.* 2016; Peters *et al.* 2018). Here, we use ensemble niche modelling to investigate climate-induced biodiversity change in the context of these two key human considerations: socioeconomic factors of relevance for biodiversity conservation, and the political borders that bound and delineate their influence.

National socio-political context of climate impacts

We modelled the climatic niches of >12,700 species (around 80%) of terrestrial mammals and birds – two groups whose distributions are well-characterised – excluding species with highly restricted ranges whose distributions are likely determined by factors other than climate (see *Materials and Methods*). We projected species' climatic niches to 2070 under the four emissions scenarios adopted by the IPCC for CMIP5 (RCP2.6, RCP4.5, RCP6.0 and RCP8.5) (IPCC 2014). For our first strand of analysis, we aggregated our projections from a half-degree resolution to the national level, and related the projected changes in species richness to national level data on governance, per-capita Gross Domestic Product (GDP) and CO_2 emissions. As an indicator of governance, we used a score derived from six World Bank governance indicators (World Bank, 2019), which has been shown to predict conservation success globally (Amano *et al.* 2018). This score reflects survey respondents views on dimensions of governance such as control of corruption, government effectiveness, and political stability (World Bank, 2019). Under medium (RCP 4.5 & RCP 6.0) and high (RCP 8.5) emissions scenarios, relative loss of bird and mammal richness is greater in countries with lower governance scores and lower per-capita GDP (Fig 1; see Annex, Fig S1, for RCP 4.5 & RCP 6.0). Therefore, birds and mammals may be most threatened by climate change in the countries currently with potentially lowest capacity to implement effective conservation. We also found that loss of mammal species is projected to be greater in countries with lower per-capita CO_2 emissions – the countries least responsible for climate change in the first place (Fig 1 and Annex Fig S1).

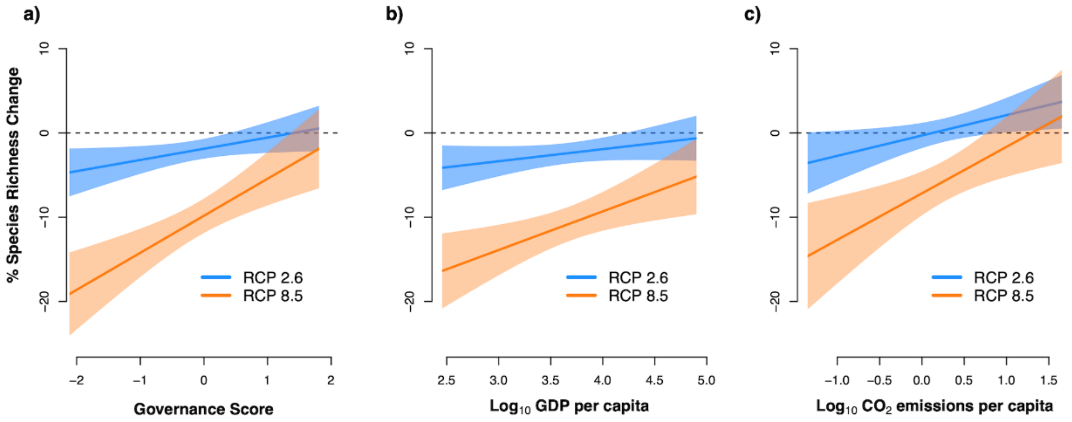


Figure 6. National context of projected climate impacts on birds and mammals. Modelled relationships between mean percentage change in species richness for each country (projected to 2070) and national-level socioeconomic datasets: (a) governance score, (b) per capita GDP, and (c) per capita CO_2 emissions. In each case, results are shown for a low (RCP 2.6) and high (RCP 8.5) emissions scenario – see Annex Fig. S1 for two intermediate scenarios (RCP 4.5 and RCP 6.0). For (a) and (b), relationships shown are for birds and mammals combined, while (c) shows the relationship for mammals only (since bird % species richness change was not significantly related to CO_2 emissions in either RCP scenario). For full GLM results, coefficient estimates and significance values, refer to Annex, Table S1. Shaded areas illustrate 95% confidence bands. Governance score is the mean value of the six national-level worldwide governance indicators provided by the World Bank for the year 2018, which are standardized scores that range from -2.5 to 2.5, where a lower score indicates weaker governance, and which capture government effectiveness; control of corruption; political stability and absence of violence; rule of law; regulatory quality; and voice and accountability.

These patterns reflect a tendency towards greater impacts from climate change in low-latitude countries, which also tend to rank lower for governance, GDP and CO_2 emissions. Although the magnitude of climatic changes are projected to be greatest at higher latitudes (IPCC 2014), climate impacts on nature may be greater in tropical areas because they are more likely to see the emergence of novel climates (Williams *et al.* 2007) and are also where species have narrower climatic niches, making them more sensitive to change (Tewksbury *et al.* 2008). These global inequities in climate impacts on nature reignite questions surrounding the morality of climate inaction in developed nations, which have benefitted disproportionately from fossil fuel consumption – and which continue to benefit from global biodiversity conservation – but face fewer of the associated impacts and costs (Balmford & Whitten 2003). Our results further strengthen the case for substantial and urgent climate change mitigation action, which would minimise these inequities in climate impacts on nature (Fig 1).

Conserving birds and mammals across political borders

In our second strand of analysis, we examined the distributions of birds and mammals in relation to political borders, considering both their present distributions and their projected distributions under climate change. Political borders demarcate the spatial extent of territory ownership and governance, and, by extension, influence the distribution of threats to biodiversity (Dallimer & Strange 2015). Consequently, populations of the same species occurring either side of a political border can be exposed to different threats and pressures, with different implications for conservation and management. Borders can also reduce the efficiency and effectiveness of conservation by impeding coordinated conservation action on either side, especially in areas of conflict (Dallimer & Strange 2015; Thornton *et al.* 2018). These concerns, combined with an increasing appreciation for the broad scale at which ecological processes operate, have led to the growth of the 'transboundary conservation' paradigm in recent decades (Linnell *et al.* 2016). For example, the Convention on the Conservation of Migratory Species of Wild Animals (CMS), or Bonn Convention, was established to coordinate international conservation strategies across the ranges of migratory species (UNEP / CMS 2020g). Under climate change, however, the ranges of many non-migratory species are likely to shift across international borders too, requiring supranational conservation strategies that are similarly coordinated between nations for perhaps a much larger suite of species (Pinsky *et al.* 2018; Scheffers & Pecl 2019; Thornton & Branch 2019).

Despite this growing impetus for internationally coordinated conservation, there has been limited effort to characterize the importance of transboundary conservation globally (Mason *et al.* 2020a), or to identify places where it would be most beneficial in the context of climate change. To address this gap, we first intersected the current distribution maps of all of the world's terrestrial mammals and birds with maps of the world's political borders to calculate the number of species ranges that each border currently bisects. This highlights borders across which transboundary conservation would benefit the most species, such as in the western Amazon and central Africa (Fig 2a). We repeated this for threatened species, to reveal borders where cross-border conservation effort might be prioritised (Fig 2b). By dividing transboundary richness by the total number of species found in the countries either side of each boundary, we also highlight regions where a disproportionate number of species ranges intersect political borders (see Annex Fig S2). This emphasises areas such as western and southern Africa and central Europe, where a high proportion of the species found there span multiple countries. We also calculated that the majority of mammals (60.03%) and birds (71.63%) are ‘transboundary’, in the sense that their ranges span multiple countries and cross international boundaries, underscoring the importance of cross-border collaboration if conservation is to succeed in reversing biodiversity declines.

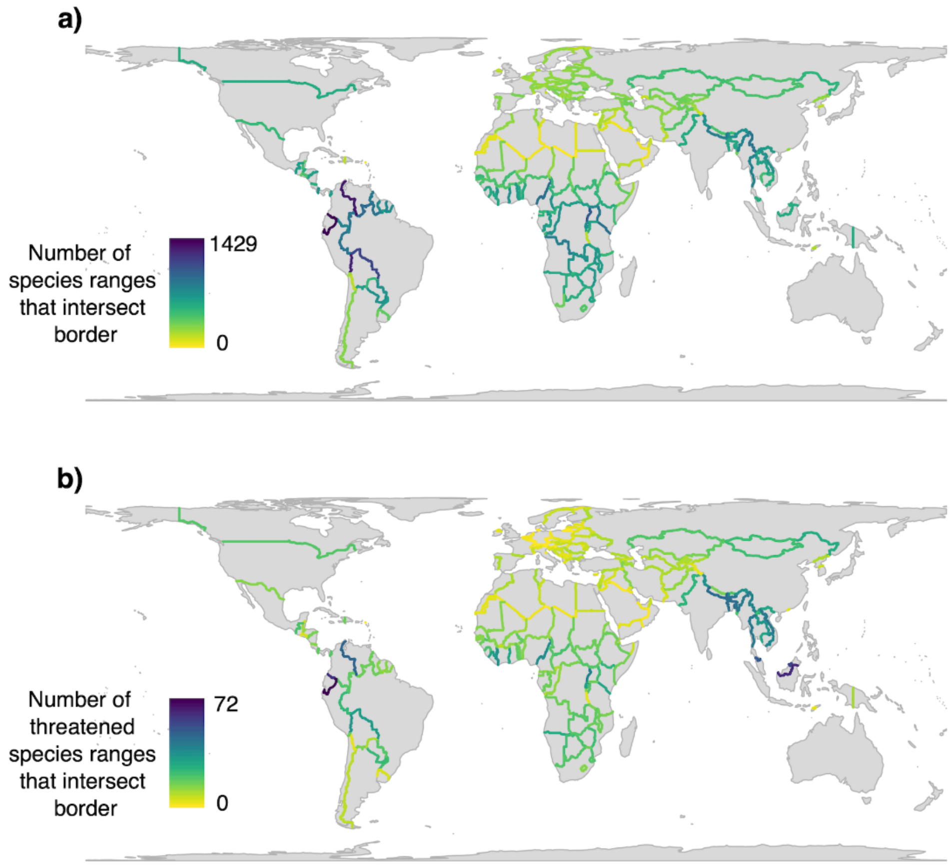


Figure 7. Global transboundary species richness. Maps of the number of species (a) and threatened species (b) whose ranges intersect with political borders. Darker borders indicate a greater number of species that have their ranges bisected by that border.

Climate change increases the importance of transboundary conservation efforts because many species’ ranges may shift across political borders to track their climatic niche, with important implications for international biodiversity governance (Pinsky *et al.* 2018; Scheffers & Pecl 2019; Thornton & Branch 2019). In tracking their climatic niche into new countries, species may be afforded more or less effective conservation across their range owing to differences in conservation policy between countries (Runge *et al.* 2015; Thornton & Branch 2019). To explore this possibility, we combined our projections of species climatic niches with spatial data on the world’s political borders. This revealed that, under a high emissions scenario (RCP 8.5), our models project 35.0% (1343) of mammals and 28.7% (2559) of birds to have more than half of their future (2070) climatic niche in countries in which they are not currently found (Fig 3). Furthermore, over half of modelled mammals (60.8%, 2336) and birds (55.0%, 4904) have at least one fifth of their future climatic niche in such 'new' countries (Fig 3; see Annex, Fig S3, for moderate emissions scenario RCP 4.5).

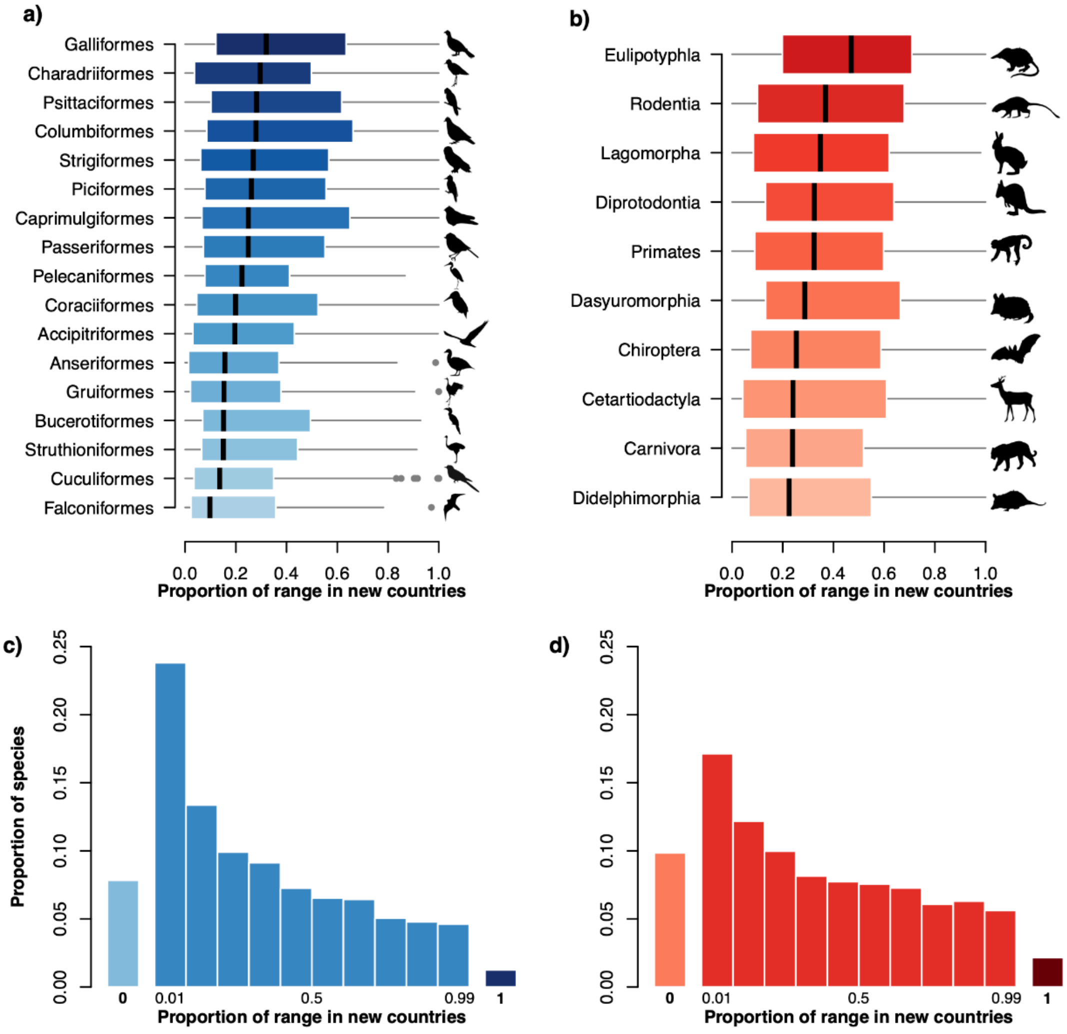


Figure 8. Proportion of species whose ranges move into 'new' countries. Boxplots illustrate the proportion of species ranges that are projected to be found in 'new' countries (countries in which the species isn't currently known to occur) under a high emissions scenario (RCP 8.5) in 2070. Results are broken down by taxonomic order for birds (a) and mammals (b). For clarity, only orders with 50 or more modelled species are shown. Beneath, histograms show the proportion of all modelled birds (c) and mammals (d) with a given proportion of their 2070 range in 'new' countries, under RCP 8.5. Bars are plotted separately (labelled 0 and 1) for the special cases in which species are projected to have none or all of their future niche in new countries. See Annex, Fig. S3 for the equivalent results under a lower-emissions scenario, RCP 4.5.

By summing the number of species whose climatic niches move into adjacent countries for each political border, we were able to map transboundary range shifts globally (Fig. 4 and Annex Fig S4). For mammals, key regions where species may move into new countries under climate change are the USA-Mexico border, western Amazonia, the Andes, central and eastern Africa, the Himalayan region, and the China-Russia border. For birds, western Amazonia emerges as the focus of transboundary range movement. Our results highlight how species-rich regions with political borders that cut across latitudinal or altitudinal climatic gradients are likely to be hotspots for transboundary range shifts, and suggest that, under climate change, this is where proactive cooperation on nature conservation will be most beneficial. In some regions, particularly where governance and cross-border collaboration are already weak and human pressures are high, this will be challenging. The projections are perhaps therefore more troubling for mammals, given the higher numbers of projected transboundary shifts in regions recently identified as having low feasibility for transboundary conservation (Mason *et al.* 2020a), such as central and eastern Africa, parts of the Middle East and borders around the Bay of Bengal. We also repeated this analysis controlling for species richness (by dividing the number of transboundary shifts by the total species richness across the two countries involved). This highlighted areas with high transboundary movement relative to their species richness, for example the Argentina-Chile border, eastern Africa and the Middle East (see Annex, Fig S5). Together, our results indicate that transboundary conservation efforts, while already important for many species, will be of increasing value under climate change. Bilateral or multilateral cooperation will be needed, particularly across borders that we project to be crossed by many range shifts (Fig 4), or where range shifts are projected to be particularly large (see Annex, Fig S6a). As priorities in these areas, we suggest preserving or augmenting habitat connectivity across such borders; expanding and updating the identification of Key Biodiversity Areas for species (IUCN 2016a); coordinating transboundary protected area network design and management to account for the needs of range-shifting species; coordinating appropriate legislation (such as hunting controls for targeted species); expanding the identification and monitoring of range-shifting species; and using or creating means of sharing knowledge, resources and skills between nations.

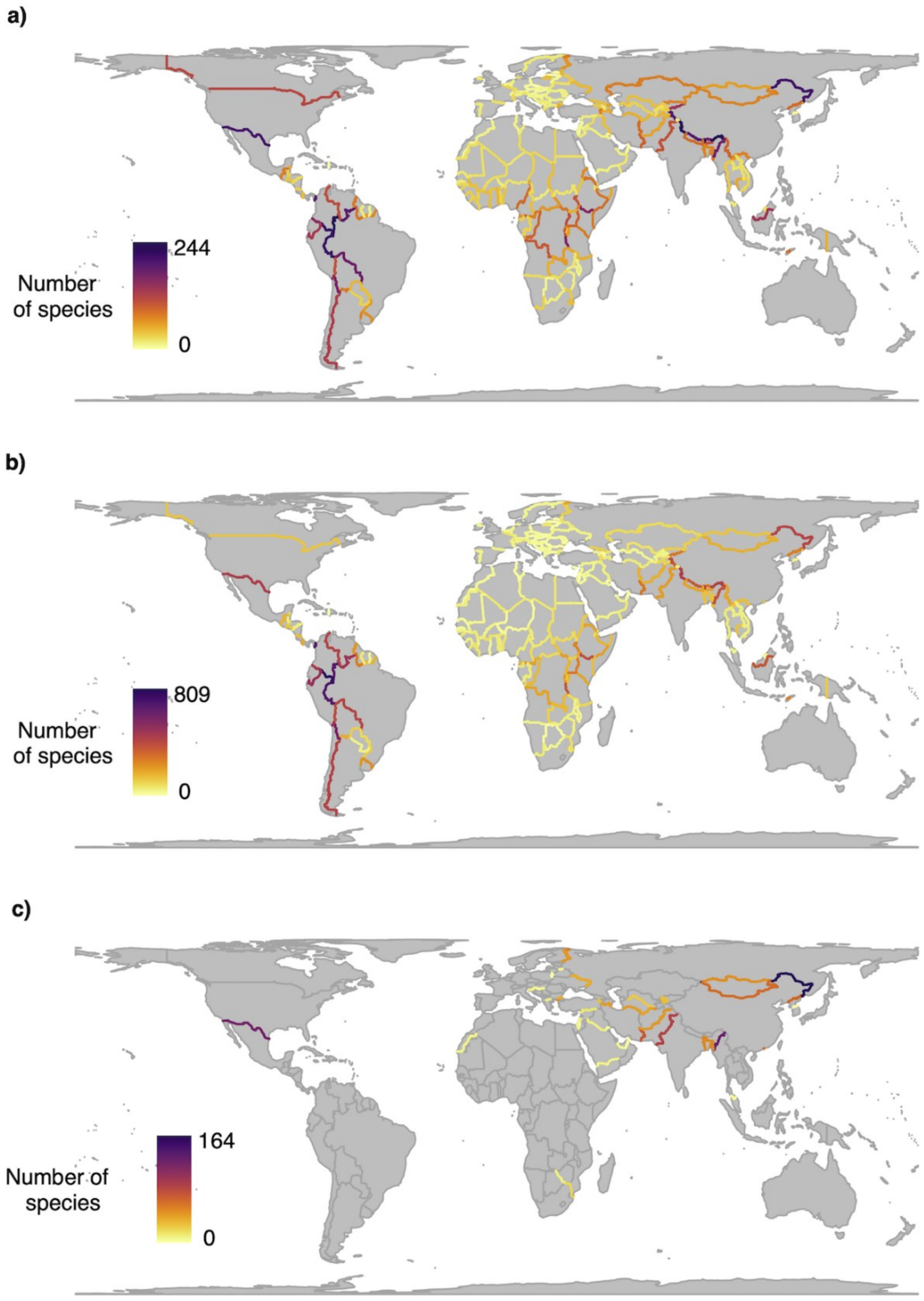


Figure 9. Projected transboundary range shifts for terrestrial mammals and birds under climate change (RCP 8.5). Maps of the world's political borders coloured according to the number of (a) mammals and (b) birds whose ranges are projected to cross that border by 2070 (in either direction). For mammals, transboundary range movement is highest in western Amazonia, the USA-Mexico border, central and east Africa, the China-Russia border and the Himalayan region. For birds, western Amazonia is the focus of transboundary range shifts. For a moderate emissions scenario, RCP 4.5, see Annex, Fig S3.

Transboundary range shifts are likely to have socioeconomic and management implications for the countries involved (Madin *et al.* 2012; Pecl *et al.* 2017). Range shifts of key 'charismatic' species, for example, could make countries more or less appealing for wildlife tourism, with economic consequences for countries that rely on wildlife tourism as a significant source of income. Our models suggest that transboundary range shifts of such species are most likely in central Africa, the western Amazon and Himalayas (see Annex, Fig S6b). For species threatened by wildlife trade, such as those listed under CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora), transboundary range shifts may be especially important, since they may move into countries that offer more or less protection by domestic legislation. This may particularly affect species in the Americas (see Annex, Fig S6c).

The prospect of significant species redistributions has led to calls for new multilateral conservation treaties to meet the demands of biodiversity governance in the 21st century. However, establishing bilateral and multilateral transboundary conservation initiatives takes considerable time and financial resources, and is likely to be particularly challenging where current national-level conservation capacity is weak or lacking (Hannah 2010; Scheffers & Pecl 2019; Mason *et al.* 2020b). Fortunately, many structures are already in place to coordinate conservation policy between multiple governments. The Convention on the Conservation of Migratory Species and Wild Animals (CMS), for example, sets out the legal basis for coordinating conservation strategies across migratory species ranges. Agreements or less formal instruments within CMS require signatories to take into account the need for collaborative transboundary measures with adjacent states (CMS Secretariat 2020; UNEP / CMS 2020a); to cooperate regionally and internationally to remove barriers to migration (UNEP / CMS 2020d, b); identify transboundary habitats that could be considered 'transfrontier conservation areas' (UNEP / CMS 2020f, c) and ensure physical and ecological connectivity between sites now and under climate change (UNEP / CMS 2017, 2020e). Building upon or making innovative use of existing mechanisms such as these to consider explicitly species whose ranges shift across political borders under climate change, for a broader suite of species, may enable more rapid progress. Furthermore, strengthening coordination across borders need not be restricted to top-down legislative action. Particularly in regions where international relations are poor, or where national-level governance and conservation capacity are weak, less formal and locally-established approaches may be more successful at enhancing cooperation and protecting species and habitats that span international borders (Martin *et al.* 2011; Schoon 2013; Mason *et al.* 2020a).

Border barriers and conservation under climate change

Political borders present a more tangible conservation challenge where they are fortified with a physical barrier, such as a wall or fence. As of 2012, 13.2% (by length) of the world's borders are marked with a physical barrier of some form, totalling over 32,000km (Rosière & Jones 2012), and the last two decades have seen a surge in the planning and construction of fortified political borders (Vallet & David 2012). However, the ecological implications of these barriers have not been investigated on a global scale. The construction of such barriers can disturb or destroy habitats, fragment populations, prevent dispersal and migration, and directly or indirectly increase mortality via entanglement, poaching and predation (Flesch *et al.* 2010; Dallimer & Strange 2015; Linnell 2016; Trouwborst *et al.* 2016; Jakes *et al.* 2018; Peters *et al.* 2018). For example, border security fencing in Central Asia is likely to be impeding ungulate migrations (Linnell *et al.* 2016; UNEP / CMS 2019), while recently-erected razor-wire security fencing along the Slovenia-Croatia border has increased mortality in herons and ungulates (Pokorny *et al.* 2017). Barriers along stretches of the USA-Mexico border were found to decrease the abundance of puma (*Puma concolor)* and coati (*Nasua narica*) (McCallum *et al.* 2014), and the planned extension of this barrier is likely to prevent the re-establishment of dwindling or recently extirpated populations of endangered species in the US, such as the Mexican grey wolf (*Canis lupus baileyi*) and Sonoran pronghorn (*Antilocapra americana sonoriensis*) (Peters *et al.* 2018). Under climate change, border barriers may present an additional threat if they prevent species from tracking and filling their shifting climatic niche, but to our knowledge this possibility remains unexplored.

To explore the global ecological implications of border barriers, now and under climate change, we compiled a list of border barriers around the world that are built or under construction (see Annex, Fig S7). By intersecting these fortified borders with species' distribution data, we calculated that they intersect the ranges of – and so may be an obstruction to dispersal for – 775 species (18.5%) of non-flying mammals. The USA-Mexico border wall alone would bisect the ranges of 120 non-flying mammals. While fortified borders similarly intersect the ranges of 264 species of bats and 2337 species of birds, we assume that most are capable of dispersing over border barriers, but note that some terrestrial and understorey forest specialist bird species have very low dispersal ability across roads, rivers and other linear clearings

(Laurance *et al.* 2004a, 2009). A radio-telemetry study of ferruginous pygmy owls (*Glaucidium brasilianum*) near the USA-Mexico border, for example, revealed that their reluctance to fly far above the ground would cause a border wall combined with vegetation gaps to obstruct transboundary movement (Flesch *et al.* 2010). Furthermore, although our analysis has focused on mammals and birds, the implications of political borders and border barriers for nature conservation extend to other taxonomic groups too. Amphibians and reptiles may be negatively affected, while low-flying insect species may be affected by less permeable structures such as walls (Peters *et al.* 2018).

Considering projected range shifts under climate change, under RCP 8.5, our models show that 696 species (16.24%) of non-flying mammal may be unable to track their climatic niche into new countries because of existing (or under-construction) border barriers. These are species whose current climatic niche is found on one side of a fenced or fortified border, and their 2070 climatic niche is projected to cross it. The USA-Mexico border barrier, as a noteworthy example, would prevent 122 species from tracking their climatic niche into the adjacent country. The potential ecological impacts on regional biodiversity that the USA-Mexico border wall may inflict have been previously highlighted (Flesch *et al.* 2010; Peters *et al.* 2018). However, our analysis suggests that its impacts could be more damaging still under climate change, and that, from this ecological standpoint, it may be one of the worst international borders on the planet along which to build such a wall (Fig 4 and Annex, Fig S8). Along with the USA-Mexico border, two other fortified borders are of particular ecological concern: the India-Myanmar border fence, which is under construction, and the China-Russia border. These three border barriers rank top for the number of species whose climatic niches are projected to cross them (Fig 4c), and remain top of the list when the proportion of species' ranges that cross them are taken into account (see Annex, Fig S8). In the case of the USA-Mexico and China-Russia borders, this is likely to be because these are long E-W oriented barriers that could intercept latitudinal range shifts under climate change. The India-Myanmar border would likely impact many species due to its position perpendicular to an elevation gradient in an important biodiversity hotspot (Myers *et al.* 2000a). We also examined which groups of species may be most affected by border barriers by breaking down the results by taxonomic order (see Annex, Fig S9). This revealed carnivorans, ungulates and lagomorphs to have the highest proportion of species whose ranges are projected to cross a border barrier – a third or more of modelled species in these orders. This is concerning given that these groups are known to be amongst the most vulnerable to border fencing impacts (Trouwborst *et al.* 2016). To mitigate these impacts, barriers should be made as permeable to wildlife as possible, enabling smaller animals to pass though or underneath, and strategically placed openings can allow larger animals to cross between countries (Olson 2014; Linnell *et al.* 2016). When and where necessary, assisted translocation of species across borders could be considered to help facilitate range shifts under climate change. Ecologists must participate in the debates surrounding border fortification to ensure the full costs and benefits of this infrastructure can be taken into account.

Conclusions

We highlight three broad insights from our analysis combining macroecological modelling with global socio-political considerations. First, climate impacts on biodiversity are skewed towards the countries with potentially lower capacity for effective conservation and less culpability for climate change in the first place. This is morally and practically important for global biodiversity governance given that similar inequities in the causes and impacts of climate change have been a key obstacle in multilateral climate negotiations (Held & Roger 2018). Second, the pervasiveness and magnitude of projected transboundary shifts among bird and mammal species mean that safeguarding Earth's biodiversity under climate change will demand much greater cross-border collaboration from local communities, conservation organisations and national governments than is needed at present. To facilitate this at the supranational level, expanding or drawing lessons from existing multilateral mechanisms such as CMS, where international cooperation is already a central tenet, may be a pragmatic way forward. Finally, maintaining and enhancing habitat connectivity across borders between area-based conservation measures will be critical to enable range shifts under climate change, and this effort should be targeted to the regions in it will have the most impact. We've shown that this is likely to be where borders cut across broad climatic gradients in species-rich areas, such as around the tropical Andes and Amazon, the Himalayas, and long E-W borders such as the USA-Mexico border. Where border security barriers are a threat to this ecological connectivity, particularly along the USA-Mexico border and parts of Asia, we must ensure that appropriate measures are in place to mitigate their impacts. As climate change drives the displacement of both wild species and humans (IPCC 2014; UNDP 2017), barriers intended to constrain the movement of people must not have unintended adverse outcomes for the natural world.

Materials and Methods

Modelling climatic niches

Our approach focused on ensemble species distribution modelling. Also known as bioclimatic envelope or niche modelling, this method depends on statistical associations between species distributions and environmental variables. Projected changes in environmental variables (due to climate change, for example) can then be used to infer changes in the distributions of species' climatic niches. When used appropriately the approach has been shown to accurately simulate responses to climate change for mobile species (Araújo *et al.* 2005; Watling *et al.* 2013; Stephens *et al.* 2016).

Species distribution data

Species distribution data were obtained from the IUCN Red List (IUCN 2016b) for 5381 species of terrestrial mammals and BirdLife International and Handbook of the Birds of the World (BirdLife International and Handbook of the Birds of the World 2017) for 10930 species of birds. The range polygons were filtered to keep only 'Extant' or 'Probably Extant' polygons ('Presence' code 1 or 2) where the species was native ('Origin' code 1), for the species' breeding and resident ranges ('Seasonality' code 1 or 2). The resulting range polygons were then rasterized to a grid with 0.5˚ resolution. Grid cells were classed as 'presence' where they had at least 10% overlap with the range polygon to avoid the inclusion of cells with only very small areas of overlap with the range polygon (Voskamp *et al.* 2017). To avoid the inherent problems when modelling the climatic niches of range-restricted species (where climate is less likely to be an important determinant of the species distribution), we excluded species classified as being present in fewer than ten grid cells. This resulted in a final set of 3,840 mammal and 8918 bird species – 78.2% of the original species. All modelling was done in a cylindrical equal area projection to avoid biasing the models by oversampling high latitudes (Budic *et al.* 2016). For each species, 1000 pseudo-absence points were randomly sampled from the same zoogeographic realm(s) (Holt *et al.* 2013) in which the species was found. Points were sampled from the same zoogeographic realm to minimise sampling from regions that are climatically suitable but where the species is not found because of geographical barriers such as oceans and large mountain ranges. We chose a relatively coarse scale (0.5°) to model species climatic niches because climate is ecologically relevant for species distributions at broader scales and because climatologists often caution about the accuracy of climate data derived from General Circulation Models at finer spatial scales (Baker *et al.* 2016). Moreover, at this scale we can be reasonably confident that range margins are broadly accurate for species, even in less well recorded regions.

Predictor variables

Despite the significant body of research employing species distribution models, the bioclimatic predictor variables used vary widely, with little consensus on the best approach to select them. One common approach is to use all 19 bioclimatic variables provided by the *Worldclim* dataset (Hijmans *et al.* 2005; Fick & Hijmans 2017), although high inter-correlations between the variables can lead to model instability (and issues with assigning causality), and is particularly problematic when projecting to future climate scenarios and/or different geographic regions (Dormann *et al.* 2013). A preferable approach is to select variables that are ecologically relevant to the species being modelled based on expert knowledge of causal relationships (mac Nally 2000; Elith & Leathwick 2009). However, this option was unfeasible on a global scale, since there is no obvious set of predictors of ecological relevance to all species, and a lack of species-specific knowledge prevents the identification of relevant variables for every species individually. Consequently, we use a systematic approach to select a set of predictor variables that are broadly ecologically relevant, non-collinear and that produce high performing models when tested on a random subset of species.

First, we pre-selected eight bioclimatic variables from the *WorldClim* dataset (Fick & Hijmans 2017) that have been widely used in niche modelling and have been used to model species distributions accurately under a changing climate (e.g.(Stephens *et al.* 2016)). These included mean annual temperature and precipitation, temperature seasonality, precipitation seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the wettest month, and precipitation of the driest month. For both temperature and precipitation, these eight variables capture the annual typical conditions, variability (seasonality) and extremes. We then generated all possible combinations of these eight variables, in combinations of between 3-8 variables. This resulted in 219 possible combinations (1 combination of 8, 8 combinations of 7, 28 combinations of 6, and so on). Of these 219, 10 sets were discarded because they did not contain both temperature and precipitation variables. The remaining 209 sets of variables were then tested for collinearity; if any variables in the set had pairwise correlations of $r > 0.7$ (Dormann *et al.* 2013), the set was discarded. This left a final selection of 38 candidate combinations of predictor variables that are biologically relevant at a coarse scale and sufficiently uncorrelated to avoid producing unstable models. These 38 combinations were then used to build Generalised Additive Models (GAMs), using the R package *mcgv* (Wood 2017), for a random subset of 200 bird and 200 mammal species (for more detail, see GAM modelling methods below in section 1.4). The 38 candidate combinations were then ranked according to model performance (using AIC) to identify the best set of predictor variables by tallying the number of times that set appeared in the top quartile of candidate sets. The final set included the following five predictors: mean annual temperature, temperature seasonality, precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality. This set was in the highest performing quartile of candidate variable combinations for >90% of mammal and bird species. When projecting future climate variables, we used downscaled General Circulation Model (GCM) data from CMIP5, downloaded from *WorldClim* (Hijmans *et al.* 2005). To take into account variation in climate projections between different climate models, we used outputs from three different GCMs (HadGEM2-ES, CCSM4, and MIROC-ESM-CHEM).

Spatial autocorrelation

Spatial autocorrelation (the higher similarity of closer samples) is a pervasive phenomenon in ecological data. If present and unaccounted for in model development, spatial autocorrelation can lead to inaccurate estimation of model coefficients, inflation of significance values, and inappropriate spatial inference and prediction (Segurado *et al.* 2006; Dormann 2007a; Miller 2012). To account for the spatial dependence in our models we split the gridded presence/absence data for each species into ten spatially disaggregated blocks (Bagchi *et al.* 2013). Non-contiguous portions of the world's terrestrial ecoregions were used as the sampling units to divide the data; these units were then grouped into 10 blocks using the *blockTools* package in R (Moore & Schnakenberg 2016) such that the total area and mean bioclimate was approximately equal in each block, and that each block contained the full range of bioclimates (Bagchi *et al.* 2013).

Model validation

By splitting the data into ten blocks, we were able to use 10-fold cross-validation to assess model performance. Each block was left out in turn to be used as a testing dataset, and models were trained on the remaining 90% of data. Model performance was then assessed using the area under the receiver operator characteristic (ROC) curve (AUC), which tests for discrimination ability.

Ensemble climatic niche models

Here, our focus is not on projecting realised distribution changes but rather on exploring the potential for species climatic niches to shift into novel regions. For this purpose, we considered that simple species distribution models are adequate. The potential limitations of species distribution models in projecting actual range shifts for species are widely recognised and have been comprehensively discussed elsewhere (Pearson & Dawson 2003; Dormann 2007b; Elith & Leathwick 2009). Future model development could incorporate species traits, land-use and biotic interactions. However, currently we lack sufficient data for almost all species in relation to limiting biotic interactions and their roles in determining species' realised niches. Similarly, global projections of future land use and land cover are currently available only at very coarse spatial scales, and for such broad habitat classifications, so as to be inappropriate for inclusion in modelling future scenarios for most species.

Adapting the methods of (68), we used an ensemble of four different model types for each species: generalised linear models (GLMs); generalised additive models (GAMs), random forests (RFs) and boosted regression trees (BRTs). Combining an ensemble of models has been demonstrated to reduce overfitting and improve predictive performance, especially for rare species (Lomba *et al.* 2010; Breiner *et al.* 2015). The four model types were selected to provide contrast between regression-based and machine learning techniques. This methodology has previously been shown to model accurately species' distributions (Elith *et al.* 2006; Bagchi *et al.* 2013; Stephens *et al.* 2016). Models were fitted on training data leaving one block out in turn, resulting in 40 models per species (10 blocks x 4 model types). These were then used to project future climatic niches across the same and adjacent zoogeographic realms (Holt *et al.* 2013) using future climate variables from the 3 selected GCMs. This resulted in 120 projections per species (40 models x 3 GCMs) for each emissions scenario. Projected probability of occurrence was converted into a binary presence-absence value using a threshold that maximised sensitivity plus specificity (Liu *et al.* 2005). The final projected distribution was determined by taking the mean presence/absence value for each grid cell, weighted by AUC to give greater influence to better performing models in the ensemble. The models had good discrimination ability, with mean AUC (±SD) of 0.942 (±0.052) for mammals and

0.941(±0.049) for birds. Details of model formulation for each model type are given in more detail below; all modelling was done using R (R Core Team 2017).

Generalised Linear Models

When fitting GLMs, we optimised the combination of polynomial model terms to maximise model performance in terms of AUC for each species, as follows. GLMs were used to fit up to and including third-order polynomials for the five predictor variables, resulting in 243 candidate model formulations. Models were fitted to nine blocks of data, with the remaining block used as a testing dataset to evaluate AUC. This was then repeated for each of the ten data blocks. The combination of polynomial terms that maximised AUC across the ten model fittings was used to fit a final set of 10 models.

Generalised Additive Models

We used thin-plate regression splines to fit GAMs using the *mgcv* package in R (Wood 2017). These regressions were fitted as a Bernoulli response using a logit link function. Once again, models were fitted on 90% of the data, leaving one block out as a testing dataset to assess model performance using AUC.

Random Forests

Random forest modelling was done using the package *randomForest* in R (Liaw *et al.* 2014). The number of variables ('mtry') randomly sampled at each split was allowed to vary between one and three. The number of trees was then set initially to 1000, and a random forest was fitted to the data, sequentially omitting one block of data for cross-validation so that performance could be assessed using AUC. The number of trees was then increased by 500 and the procedure repeated until the increased performance (from the addition of 500 new trees) measured using AUC was <1%. The values of mtry and the number of trees that maximised model performance (averaged across the ten blocks of omitted data) were used to fit the final set of 10 models.

Boosted Regression Trees

Boosted regression trees were generated using the *gbm* R package(Ridgeway 2019). A similar cross-validation approach was used to parameterise the BRT models. Learning rate (also known as the shrinkage parameter) was set at 0.001; the number of trees was set at 5000; and tree complexity was allowed to vary between 1 and 4.

The tree complexity that minimised summed error across the testing data blocks was used to fit a final set of 10 models.

National-level socioeconomic and emissions data

To investigate the socio-political context of our projections, we first generated grid-cell level projections of species richness under current climate and 2070 climate for each RCP scenario, by summing for each grid cell the number of species for which it contains suitable climate. We then calculated the projected percentage change (present to 2070) in species richness for each grid cell. To aggregate these grid-cell level projections to the national level, we took the mean across all grid cells in a country. We then related this measure of national-level richness change to three socioeconomic datasets of relevance to wildlife conservation and climate change: governance, per capita Gross Domestic Product, and per capita CO_2 emissions.

To generate a national level measure of governance quality, we used the six Worldwide Governance Indicator datasets provided by the World Bank (The World Bank 2019). These included indicators of *Political Stability and Absence of Violence*, *Control of Corruption*, *Government Effectiveness*, *Rule of Law*, *Regulatory Quality*, and *Voice and Accountability*. These governance indicators are based on a range of underlying data and are aggregate scores that combine the views of enterprise, citizen and expert survey respondents; for full methodology see (Kaufmann *et al.* 2011). Since these six measures of governance are highly correlated with one another (see Annex, Fig. S10 for a Principal Components Analysis (PCA) of the six variables), we took the mean across all six to produce a single national-level governance metric. This aggregate score has previously been shown to be the strongest predictor of population declines and conservation success in waterbird populations globally (Amano *et al.* 2018).

For all variables, 2018 data were used as the most recent complete dataset, with the exception of CO_2 emissions data, for which 2014 data were the most recently available. To model global patterns of biodiversity change with these socioeconomic factors, we used generalized linear models in R. See supporting Table S1 for detail of GLM formulations and parameters.

Political borders analysis

We obtained spatial data on the world's political borders using the R package *rworldmap* (R Core Team 2017; South 2019). To calculate the number of species' ranges that intersect with the world's political borders, we intersected species' range polygons with the political borders dataset using the *raster* R package (Hijmans *et al.* 2014). To map projected transboundary niche movement, we identified borders across which 'new' species may appear from adjacent countries because their climatic niche is projected to cross the border. To identify political borders that have physical barriers along their length, we first used those listed in (Linnell *et al.* 2016) and (Rosière & Jones 2012) and updated the list with an internet search to identify those added since the date of publication (2012). We also included barriers currently under construction or proposed, since they have the potential to affect biodiversity in the time period of our modelling (present - 2070).

Data Availability

Species distribution data are available from the IUCN Red List, and BirdLife International and the Handbook of the Birds of the World (IUCN 2016b; BirdLife International and Handbook of the Birds of the World 2017). Bioclimatic data, including future projections, are available to download from WorldClim (wordclim.org/data/index.html). World bank governance indicators are available to download at https://info.worldbank.org/governance/wgi/.

Chapter 4

Land-use constraints on avian and mammalian range shifts under future development scenarios

Coquerel's Sifaka (*Propithecus coquereli*) in a forest fragment near Mariarano, NW Madagascar, where it is critically endangered by land-use change

Abstract

Biodiversity has responded to global climate change in the past, in part through major changes to species distributions. However, human land-use may prevent species from shifting or expanding their ranges as the planet warms. Although recent studies have begun to address this interaction, it is poorly understood to what degree both existing and future land-use may inhibit range shifts, where this effect will be most significant, or how this will shape global biodiversity projections under climate change. Here, I address these gaps by combining range shift projections for most of the world's terrestrial mammals and birds (~12,000 species), species-specific habitat data and spatially explicit land-use projections. I show that the expansion of human land-use over the last millennium has limited the potential for 77% of species to fulfil their anticipated range shifts over the next 50 years. Existing land-use reduces future range shift potential by 15.1% on average, but for more than 1600 species, it more than halves the area with suitable climate that they could shift to. By comparison, the impact of projected future land-use change on potential range shifts is relatively small, and in the most sustainable development scenario, future land-use change could facilitate range shifts for many more species than it restricts. From these findings, I highlight areas where habitat restoration should be targeted to help species adapt. I also identify species that I expect to be pushed towards extinction by the combination of future land-use and climate change that could be overlooked if the two pressures are considered separately. Finally, I consider how land-use, in combination with range shifts, affects global biodiversity projections under climate change. Under a fossil-fuelled development scenario, not only are climate impacts severe, but future land-use change continues to exacerbate these impacts on every continent. However, by following a more sustainable development trajectory, future land-use change could be a force for good, making climate impacts on biodiversity less severe than they would be if land-use was paused in its contemporary state. My results hint that combining this more sustainable pathway with targeted restoration to help facilitate range shifts under climate change could begin to reverse global biodiversity loss by 2070. This analysis underscores the importance of considering multiple interacting pressures on biodiversity, reveals the places that should be targeted for protection and restoration to help species on the move, and highlights the enormous value of pursuing a more sustainable development trajectory if we are to slow down and reverse biodiversity loss in the 21st century.

Introduction

Species have responded to major changes to Earth's climate in the past, in part by altering their distributions to stay within the environmental conditions to which they are adapted (Davis & Shaw 2001). However, two key features of contemporary climate change call into question species' abilities to cope via this strategy. First, the unusually rapid pace of modern climate change is likely to outpace many species' dispersal abilities, causing them to lag behind their climatic niche (Devictor *et al.* 2008, 2012). Second, today's climate change is occurring against a backdrop of other pressures that are likely to exacerbate its impacts on nature. Of these pressures, habitat loss driven by land-use change may be the most concerning in the context of terrestrial range shifts, as it could prevent species from tracking their climatic niches into new areas. However, the magnitude of this problem at a global scale is poorly understood, and the areas and species that may be worst affected have not yet been identified.

Land-use change is currently the leading cause of biodiversity loss globally (Díaz *et al.* 2019), and the conversion of natural habitats for human land-use is estimated to have pushed biosphere integrity below a "safe limit" over the majority of Earth's land surface (Newbold *et al.* 2016). Cropland, pasture and urban areas now cover more than half of Earth's ice-free land (Ellis *et al.* 2010), and pressure on biodiversity seems likely to increase further in coming decades as the human population size continues to increase and, more importantly, as consumption and demand for agricultural commodities continue to soar (Foley *et al.* 2011; Tilman *et al.* 2011).

The loss of natural habitats to land-use may be more problematic still under climate change if it interferes with species' abilities to cope with rising temperatures (Mantyka-Pringle *et al.* 2012). Recent work has shown how species that have undergone major range shifts following the last glacial maximum in Europe may have only been able to do so because of uninterrupted habitat availability across the continent (Lagerholm *et al.* 2017). Today, areas of intensive land-use in England appear to be already limiting adaptive community reorganisation of birds and butterflies in response to warming (Oliver *et al.* 2017). Other work on invertebrates in Britain has shown how habitat availability was more important than changes in climatic suitability for explaining between-species variation in recently observed range shifts (Platts *et al.* 2019). In the future, a major redistribution of species is anticipated as climate change unfolds (Scheffers *et al.* 2016a; Pecl *et al.* 2017). Despite growing interest in how both land-use change and climate change may affect biodiversity (Jetz *et al.* 2007; Newbold

2018; Powers & Jetz 2019), no study has assessed how land-use may hinder this redistribution on a global scale.

Here, I address this gap by using a novel approach that combines range shift projections for the majority of the world's terrestrial mammals and birds with species-specific habitat information and land-use change projections. This enables me to explore how land-use may constrain range shifts over the next 50 years, reveal the places where land-use may be an obstacle for the most species, identify species for which this interaction between land-use and climate change may be most significant, and consider how this inhibiting effect of land-use on range shifts may shape global biodiversity projections under climate change. Such information is essential for understanding the full costs of human impacts on nature, for correctly identifying conservation priority species in the face of multiple threats, and for identifying places where the conservation or restoration of habitats could help species adapt to a rapidly changing world.

Methods

Overall approach

The overall approach of this analysis was first to use species distribution models (SDMs) to identify the broad areas where species' climatic niches are projected to shift to under climate change. Then, I used global land-use projections to ask to what extent these anticipated range shifts will not be possible because of the spread of human land use. Importantly, the land-use projections cover both future and historical land-use change. Future land-use projections enabled me to consider how further land-use change this century is likely to impact the potential for species to range-shift. Historical land-use projections, on the other hand, are also important because they enabled me to directly compare anticipated range shifts against a historic reference point before the widespread conversion of ecosystems to agricultural land. This is necessary for the correct attribution of impacts to land-use change: areas could be unsuitable for species for entirely natural reasons (such as natural grasslands being unsuitable for range-shifting forest species). Therefore, a historical baseline enables me to identify places that have specifically *lost* their potential to facilitate range shifts for species over recent centuries as the spread of agricultural land has transformed the biosphere. I emphasise that despite my use of past land-use projections, I was not attempting to recreate species' past distributions or historical patterns of biodiversity, which would involve back-casting SDMs to a historical time period.

Instead, the past land-use projections provide the reference scenario to understand how land-use is likely to constrain *future* range shifts.

With this in mind, in this chapter I set out to do the following (each of which is explained in more detail below):

1. Explore species-level impacts of land-use change on potential range shifts, and map places where land-use is likely to constrain range shifts for the most species. I considered the impacts of both existing land-use (i.e. past land-use change) and future land-use change separately.
2. Identify species for which the combination of future land-use change and climate-driven range shifts is likely to cause particularly severe declines in range size, when either threat in isolation wouldn't be as detrimental.
3. Consider how the loss of range shift potential due to habitat loss from land-use change affects global biodiversity projections under climate change.

Mapping species range shifts under climate change

The starting point for my approach was to use species distribution models (SDMs) to identify the areas climatically suitable for each species now and in the future (2070). SDMs relate the present-day distributions of species to environmental variables. By projecting the models with future climate data, it is possible to infer how the climatic niches of those species are likely to shrink, expand or move under future climate scenarios.

I used ensemble modelling to simulate the climatic niches of 11,912 terrestrial mammal and bird species – two groups whose distributions are well understood. I excluded range-restricted species that occupy fewer than ten 0.5-degree grid cells since these species' distributions are likely strongly influenced by finer-scale factors such as land-cover and habitat availability, and so using broader scale climatic variables would be inappropriate for reliably projecting their ranges. I also excluded bats, since reliable dispersal data isn't available (see discussion of dispersal constraints below). The resulting set of species was composed of 8,918 bird species and 2,994 non-volant mammals. The full methodology for the SDMs can be found in Chapter 2, and is summarised more briefly below.

Species presence-absence data were generated by rasterizing present-day range polygons provided by the IUCN Red List (IUCN 2016b) and BirdLife International (BirdLife International and Handbook of the Birds of the World 2017) to a half-degree grid, classifying cells as ‘presence’ where they have at least 10% overlap with the range polygon. Models were trained to predict these presence-absence data using five non-collinear bioclimatic variables from WorldClim (Fick & Hijmans 2017) (mean annual temperature, temperature seasonality, precipitation of the wettest month, precipitation of the driest month, and precipitation seasonality) – see Titley et al. (2021) for predictor variable justification. For each species, I used four model types (generalised additive models, generalised linear models, random forests and boosted regression trees), to include a mix of machine-learning and parametric approaches. Data for each species were split into ten spatially disaggregated blocks (with each block containing the full range of climate data) to perform ten-fold cross-validation and control for spatial autocorrelation. The four model types were applied to each of the ten blocks of data, leaving one block out each time as a testing dataset and retaining the other nine blocks as training data, producing 40 models per species. Models showed very high predictive ability on species current distributions, with mean (±SD) AUC scores of 0.942 (± 0.052) for mammals and 0.941 (± 0.049) for birds.

When projecting into the future, I used climate projections for 2070 (2061-2080 average) from three general circulation models (HadGem2-ES, MIROC-ESM-CHEM and CCSM4), resulting in an ensemble of 120 projections per species for each climate scenario. I produced these projections for four climate scenarios (representative concentration pathways, hereafter RCPs) used by the IPCC: RCP2.6, RCP 4.5, RCP 6.0 and RCP8.5. The final range projection for a given climate scenario was obtained by taking an AUC-weighted mean (to give more weight to better-performing models in the ensemble) across the 120 projected probabilities of occurrence, with the probabilities converted to a binary presence or absence score according to a threshold set by maximising their predictive ability (sensitivity plus specificity (Liu *et al.* 2005)) on present-day presence-absence data.

I also included a dispersal constraint, since failing to do so is likely to underestimate climate impacts for species whose dispersal capabilities lag behind the velocity of climate change. I did this by limiting species’ projected range changes to only be able to occur within a plausible dispersal distance from their current range, excluding regions that they would be unlikely to reach by 2070. Plausible dispersal distances were estimated by multiplying the species’ natal dispersal distance by its expected number of generations between now and 2070. Natal dispersal estimates were obtained from Santini et al. (2013) for mammals and Santini et al. (2019) for birds, while average generation lengths were obtained from the Pantheria database (Jones *et al.* 2009) for mammals and Bird et al. (2020) for birds. Where data were missing for a particular species, data were taken from the most closely related species with data available.

Mapping species-specific land-use suitability

The objective of this step was to generate 'land-use suitability rasters' for each species: gridded spatial data that details the land-use suitability of grid cells for a particular species, based on their specific habitat requirements. These rasters could then be used to determine how range shifts may be inhibited by unsuitable land use, and how this has changed (or will change) over time because of land-use change.

To do so, I identified the habitat requirements for each species, matched these to land-use categories from spatially explicit land-use projections, and then used these projections filter out parts of their ranges that are of an unsuitable land-use type. This approach is explained more fully below.

Habitat data

Species-specific habitat preference information was obtained from the IUCN Red List API (Version 3) (IUCN 2020). This was downloaded for each species at the finest resolution of habitat classification available ('level 2'), to include specific habitat sub-categories (for example 'Forest – Temperate'). Habitats not classed as 'Suitable' for a given species were excluded, for example those deemed only of marginal importance, following IUCN guidelines. Because the land-use categories that I ultimately needed to match with the habitat data are focused on how humans *use* the land (as opposed to the physical state of the land, or land cover), I then retained only the broad level 1 habitat categories (e.g 'Forest' or 'Savanna') for natural habitats but retained level 2 detail for 'artificial' habitats (e.g. 'Artificial – Arable land' or 'Artificial – Pastureland'). This also avoids over-constraining species range shifts to specific sub-categories, allowing, for example, some 'tropicalization' of temperate regions where the SDMs predict this should occur and where the broader habtiat category (e.g. forest) remains the same. These IUCN habitat categories were then matched to corresponding categories in the land-use data, using the approach described below.

Land-use projections

Land-use projections, both past and future, were obtained from Land Use Harmonisation[2] (LUH2) (Hurtt *et al.* 2020). These consist of 0.25 x 0.25 degree global gridded data with each grid cell giving the fractional area of 12 different land-use classes, and provide a continuous time series of land-use data for the period 850-2100. For my analysis, I used land-use projections from three time periods: 2015 (the first year in the future land-use dataset, to approximate ‘present day’ conditions), 2070 (to match the projected future ranges from the SDMs) and 1000 (a historical baseline reference year, chosen because it well-predates the spread of extensive conversion of land around the world in the last few centuries – see Goldewijk et al. (2017)). For the future projections, I used four contrasting socioeconomic development scenarios that are paired with the RCPs used in the SDM modelling. These scenarios, or shared socioeconomic pathways (SSPs) were SSP1-RCP2.6, SSP2-RCP4.5, SSP4-RCP6.0, SSP5-RCP8.5. The narratives and key land-use implications of each scenario can be found in Table 1.

Table 3: The four SSP-RCP scenarios used for future climate and land-use projections. Descriptions adapted from (Hurtt *et al.* 2020) and (Riahi *et al.* 2017).

SCENARIO	HEADLINE	MAIN NARRATIVE	LAND-USE IMPLICATIONS
SSP1-RCP2.6	Sustainable development - ‘Taking the green road’	Shift to a more sustainable economy, and management of the global commons improves. Warming doesn’t exceed 2 degrees.	Forest area increases, and despite expansion of biofuel cropland, total global agricultural footprint decreases.
SSP2-RCP4.5	‘Middle of the road’	Social, economic and technological trends similar to historical trends. Progress towards the SDGs is unequal and slow.	Forest loss continues up to 2050, followed by gains in forest cover.
SSP4-RCP6.0	Global inequality - ‘A road divided’	Gap widens between middle/high income societies and poorly educated low-income regions. Environmental issues focussed on local issues in wealthier countries.	Modest expansion of cropland and pasture; global forest area increases slightly but this is concentrated in high- and middle-income countries.
SSP6-RCP8.5	Fossil-fuelled development - ‘Taking the highway’	Development is coupled to the continued exploitation of fossil fuels; global economy and consumption grow rapidly.	Rapid expansion of cropland into forest and pastureland.

Matching IUCN habitat data to land-use categories

Having obtained information on which habitats were suitable for each species, I then used these to identify which of the land-use classes were unsuitable, via a ‘crosswalk’ to match the two datasets together. Previous efforts to match the two schemes have relied on expert judgement and have often classified species into a few very broad groups (Powers and Jetz 2019). Here I used a more data-driven approach to minimise subjectivity and retain as much detail as possible in the land-use classifications.

I first obtained a global map of the IUCN habitats from (Jung *et al.* 2020), and spatially overlaid this with the present-day LUH2 land-cover classes. I then used generalised linear regression models to identify which LUH2 category or categories best predict the occurrence of a given IUCN habitat category. Effect sizes for each of the LUH2 predictor categories were compared, and the LUH2 class(es) that most strongly predicted the presence of a particular habitat were selected. Where there was doubt, I erred on the side of including LUH2 categories as suitable matches for a given IUCN category, to avoid overestimating land-use impacts and overstating my conclusions. This means that my results are likely to be conservative estimates of the impacts of land-use, particularly for non-forest species where land-use and habitat categories are less straightforwardly matched. For example, savannah species (as identified by the IUCN habitat classification scheme) were allocated to the LUH2 land-use classes of primary non-forest, secondary non-forest, rangeland and pastureland, all of which were positively associated with the presence of savannah habitat in the (Jung *et al.* 2020) data. For these species, *unsuitable* land-use classes include primary forest, secondary forest, all cropland types and urban areas; any parts of their range covered by these land-uses were subsequently filtered out (see below). Although this is likely to underestimate the impacts of certain instances of land-use change, this approach avoids classifying all rangeland and pasture as inhospitable for savannah species, for example, which would likely overstate the impacts of land-use change. For the full crosswalk between the IUCN habitats and LUH2 categories, including justifications for the matches, see the supplementary material.

Additionally, I used two extra rules when creating the crosswalk. First, if species were identified as only occurring in forest habitats in the IUCN habitat data, then secondary forest (from LUH2) was only classified as suitable where it was over 30 years old. This is likely to be generous for some forest specialist species that live only in mature habitat that resembles primary forest. In the LUH2 data, once primary forest has been converted it can never be restored to ‘primary’ status and is classified as secondary forest regardless of the time of conversion. Therefore it was necessary to allow forest specialist species to occur in some secondary forest habitats to avoid overestimating habitat loss. The 30-year threshold was chosen, again, to err on the conservative (generous) side, and for consistency with other work using LUH2 to assess biodiversity impacts of land-use change, for example Newbold et al. (2015) where forest under 30 years old was classified as ‘young’. A second rule was that species that have ‘Subtropical/Tropical Heavily Degraded Former Forest’ as a suitable IUCN habitat category were allowed to occur in young (< 30 years old) secondary forest, even if other types of forest were not listed as suitable.

Producing land-use suitability rasters

Having identified which land-use categories are likely to be hospitable for each species, I then produced a land-use suitability raster for each species. To do so, I summed together the individual land-use layers deemed suitable for a particular species to produce a final raster layer where the value of each cell represented the total fractional area of land-use that is suitable for that species. In order to understand how this suitability has changed over time, these rasters were produced using land use from the year 1000 (historical baseline), 2015 (“present day”), and 2070 (under the four different socioeconomic scenarios).

Understanding the impacts of land-use on range shift potential

Species level-impacts

In my first strand of analysis, I explored how land-use may limit species’ range shift potential by mapping the area for each species where human land-use is likely to limit the area it could colonise under climate change. This approach is illustrated in Figure 1.

1 Identify a species’ present and projected future ranges using SDMs. Future range is already ‘clipped’ to a plausible dispersal distance that the species can reach by 2070

2 Identify the non-overlapping region that the species is expected to colonise by 2070, (= ‘**new range**’)

3 Combine with species-specific **land-use suitability raster** to calculate area of suitable land-use in new range

4a Compare with **historical land-use baseline** to see how existing land-use will limit new range

4b Compare with **future land-use projection** to see how future land-use change will limit new range

Figure 10: Schematic to illustrate approach for quantifying and mapping the impact of land-use change on individual species’ potential range shifts.

The first step was to identify climatically suitable and plausibly reachable (in terms of dispersal distance) areas that species would be expected to colonise by 2070 in the absence of any land-use constraints. I hereafter refer to these areas of expected colonisation as species' "new ranges". I did this by comparing species present and future projected ranges (the latter had already been 'clipped' to a plausible dispersal distance – see SDM methods above), and the non-overlapping areas were identified (Figure 1, steps 1 & 2).

These "new ranges" were then combined with the land-use suitability rasters produced in the previous stage, to estimate the suitability of land-use in the areas I project species to colonise (Figure 1, steps 3 & 4). As each grid cell in the new range now gives the proportion of that cell containing suitable habitat, sum of these suitability values is equivalent to the area of the species' new range that is suitable. To understand the impacts of existing land use (i.e. past land-use change), I compared this range area given present-day (2015) land-use with the same area given a historical land-use baseline (year 1000) (Fig 1, step 4a). As here I was assessing the role of past-land use change on future range shifts, for simplicity I chose a single future climate scenario for the range shift projections, RCP 4.5 – a scenario likely involving 2-3 degrees of warming this century, resembling a world in which the Glasgow COP26 climate pledges are met.

A similar approach was used to explore the impacts of *future* land-use change (Fig 1, step 4b), by first identifying each species' new range under each future climate scenario, and then combining this with land-use suitability data to calculate the area of each species' new range given 2070 land-use (for each of the four future scenarios) and comparing this with a present day (2015) land-use baseline. All species-level results are presented in the form of a percentage change in the area each species can colonise, relative to the baseline year (i.e. 1000 for historical land-use change; 2015 for future land-use change).

The goal of this analysis was to estimate the extent of climatically suitable habitat that is available for species to colonise, under different assumptions of human land-use. As just described, I estimated this by summing the proportions of colonisable grid cells (i.e. those that are both close enough and climatically suitable for a species) with suitable habitat. Note that in doing so, I am not attempting to measure the probability of persistence or extinction for a species, which will respond to habitat loss in a cumulative and non-linear manner, and also will depend on other factors such as the extent and changing suitability of its present range. Here I have taken the simpler approach of focussing on the changing extent of climatically suitable habitat that it could colonise (rather than exploring persistence probability) to aid communication and avoid overcomplicating the analysis but this could potentially be advanced upon in future work.

Mapping the areas where land-use constrains range shifts for many species

To build up a global picture of places where land-use is likely to prevent the most range shifts, I first summed the new range suitability rasters (the data used in steps 3 & 4 in Figure 1) across all species to calculate the expected richness of colonists in each grid cell under a given land-use assumption (past, present or future). Because the new range suitability rasters give the proportion of each grid cell that is suitable for a species, this summed richness is effectively weighted by the proportion of each cell that is suitable for each species. This was done as a preferable alternative to arbitrarily classifying cells into suitable or unsuitable based on a threshold, which would unnecessarily discard detail. By subtracting the suitability-weighted richness of colonists with 2015 land-use from the equivalent values with 1000 land-use, I calculated the number of colonisations prevented by the land-use change between 1000 and 2015.

A similar approach was taken to assess the impact of future land-use change. Here, for each of the four linked climate and land-use scenarios, the SDM projections were again combined with land-use suitability rasters to calculate the expected colonist richness under assumptions of 2015 land use and 2070 land-use. These were then compared to see how future colonist richness differs with 2070 land-use relative to a 2015 land-use baseline.

Finally, as well as exploring the *number* of species unable to colonise grid cells because of land-use change, I also calculated the *proportion* of species affected, by dividing the number of prevented colonisations in each grid cell by the expected richness of colonists in the land-use baseline (i.e. land use from the year 1000 for past LUC, and 2015 land-use for future LUC). This would highlight areas where a large proportion of the species expected to colonise a region under climate change are unable to do so because land-use change has made them inhospitable, regardless of the total number of anticipated colonisations.

Identifying species affected by the interaction of climate change and future land-use change

For my second set of analyses, I identified species that are projected to undergo an extreme decline (>90%) in range size by 2070 due to future land-use change and climate change, but that would not see a decline this severe (i.e. >90%) if land-use change or climate change were considered in isolation. In other words, these are species for which land-use change appears to be a particularly serious problem when the species' range shift is considered too.

First I produced a list of species expected to see a range size decline of >90% due to land-use change combined with climate change (by comparing its present range size given 2015 land-use with its future range size given 2070 land-use). I then produced a second list of species expected to see range size loss of >90% due to climate change alone (by comparing each species' present range given 2015 land-use with its 2070 range given 2015 land-use) or land-use change alone (by comparing its present range given 2015 land-use with its present range given 2070 land-use). Finally, I identified species that were in the first list but not the second – i.e. species that are projected to undergo such drastic declines only when the combination of land-use change and climate change is considered. This was then repeated for each of the four SSP-RCP scenarios.

Projecting global biodiversity under future land-use and climate scenarios

In my final analysis, I explored how the land-use constraint on range shifts affects global biodiversity projections. To do this, I calculated the mean projected species richness change across all grid cells caused by climate change (i.e. comparing richness calculated using species' future projected ranges to richness calculated using species' present ranges). Crucially, when calculating future richness, I used three different land-use 'treatments':

1. In the first – an entirely hypothetical reference scenario – species were 'allowed' to fulfil their projected range shifts as if land-use had somehow been restored to its state in the year 1000 by 2070. The enhanced availability of suitable habitat would, I hypothesise, help to facilitate species' range shifts around the world, and enable species to expand their ranges more readily as the climate changes. I am not suggesting this as a plausible or desirable conservation goal, but it serves as an illuminating reference point.
2. In the second land-use 'treatment', I calculated future richness if land-use stayed exactly as it was in 2015, revealing the biodiversity loss we'd expect to see from climate change if land-use was frozen in its current state.

3. Finally, in the third ‘treatment’, I calculated future richness using projected 2070 land-use, revealing how the inclusion of future land-use change affects global biodiversity projections under climate change.

This procedure was repeated for each of the four SSP-RCP development scenarios, and continent-level results were also calculated alongside the global average. This novel approach makes it possible to isolate the effect that future land-use change is likely to have on global biodiversity while taking into account expected range shifts due to climate change. It also reveals how choosing alternative socio-economic development scenarios shapes patterns of global biodiversity around the world, and exposes the components of those changes caused by climate change and land-use change.

Results

By how much, and where, will land-use prevent range shifts under climate change?

I first estimated the extent to which *existing* land-use will limit range shifts under climate change. I found that compared with a historical baseline of year 1000 land-use, 2015 land-use restricts range shifts for 8034 (or 77.2% of) species, with the average (median) species having lost 15.1% of the habitat it would be expected to colonise (Fig 2). For 1639 (15.8% of) species, existing land-use is estimated to reduce this potential new range area by more than half. This suggests that, for a sizeable minority of birds and mammals, existing land-use will greatly restrict their abilities to shift their ranges in response to climate change. Although land-use has a negative impact for more than three quarters of the species modelled, I estimate that it makes no difference for 1464 (14.1% of) species and is actually likely to help facilitate greater range shifts for 903 (8.68% of) species.

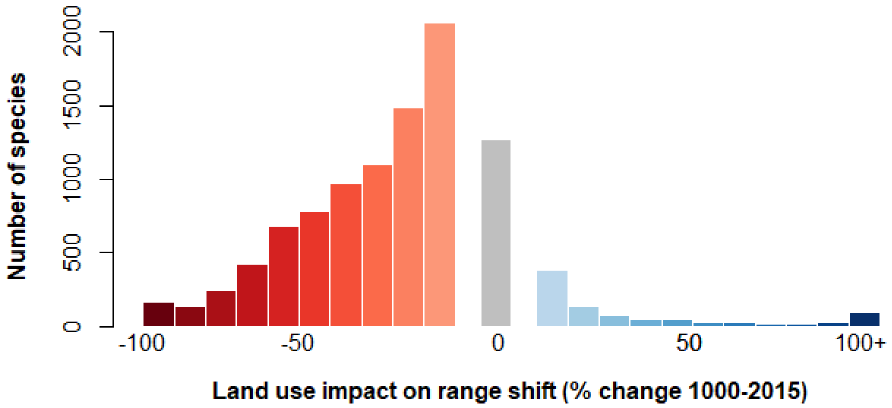


Figure 11: Histogram showing the number of species whose future range shifts are likely to be restricted (red), unaffected (grey) or facilitated (blue) by 2015 land-use, relative to a historical 1000 land-use baseline. Land-use is expected to be a constraint on range shifts for the majority (77.2%) of terrestrial mammals and birds, and more than halve the range shifting potential of more than 1600 species (15.8%).

Mapping these impacts globally, I found that the negative impacts of current land-use on future range shifts are spatially concentrated around the world, with many range shifts likely to be constrained by land-use in the tropical Andes, and particularly in Colombia and Ecuador (Fig 3a). Relatively high numbers of species will also be unable to shift their ranges into parts of central America, the South American Atlantic Forest region, West and East Africa, China, and South-East Asia. I also considered the *proportion* of species expected to shift into each grid cell that would be affected by land-use change, to identify places that may not see large numbers of range shifts or may not be particularly species-rich, but where a large proportion of the community will be affected by land-use (Fig 3b). This highlights heavily impacted regions including Madagascar, the American Midwest, and southern Australia, in addition to the regions identified above.

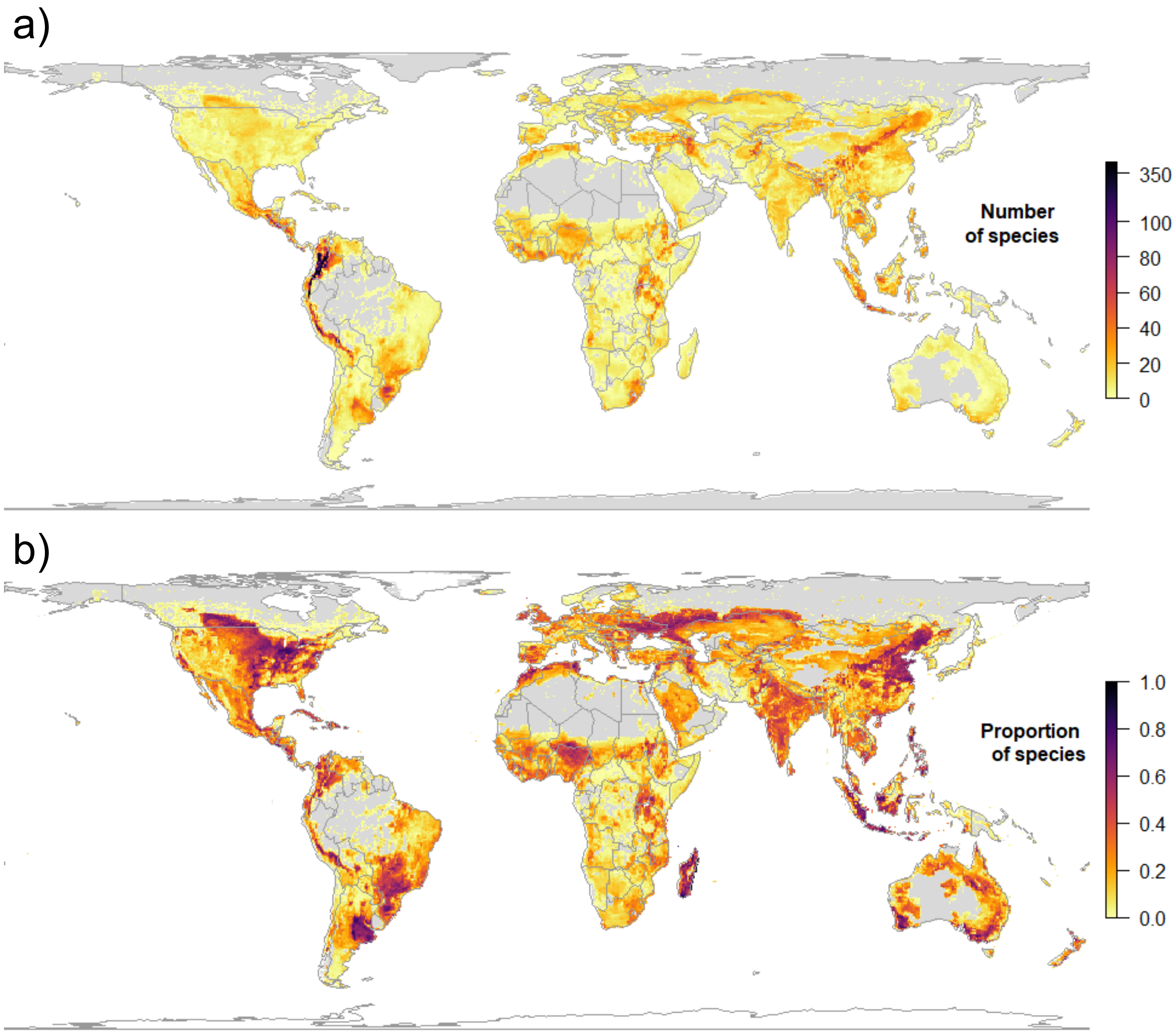


Figure 12: The number (a) and proportion (b) of species prevented from colonising each grid cell because of 2015 land-use (compared to a historical baseline of land-use in the year 1000).

The impact of *future* land-use change on range shifts is projected to be small in comparison to the impact of land that has already been converted, regardless of the future development scenario (Fig 4). However, there is still significant variation among the four future scenarios that I considered. In SSP1-RCP2.6, in which the world follows a more sustainable development trajectory, 27.4% of species still see their range shifts restricted to some degree by further land-use change, mostly by a small amount (Fig 4a). In this more sustainable scenario, the largest category (41.3%) is of species whose range shifts will be facilitated by land-use change – meaning future land-use change will enable them to colonise more areas

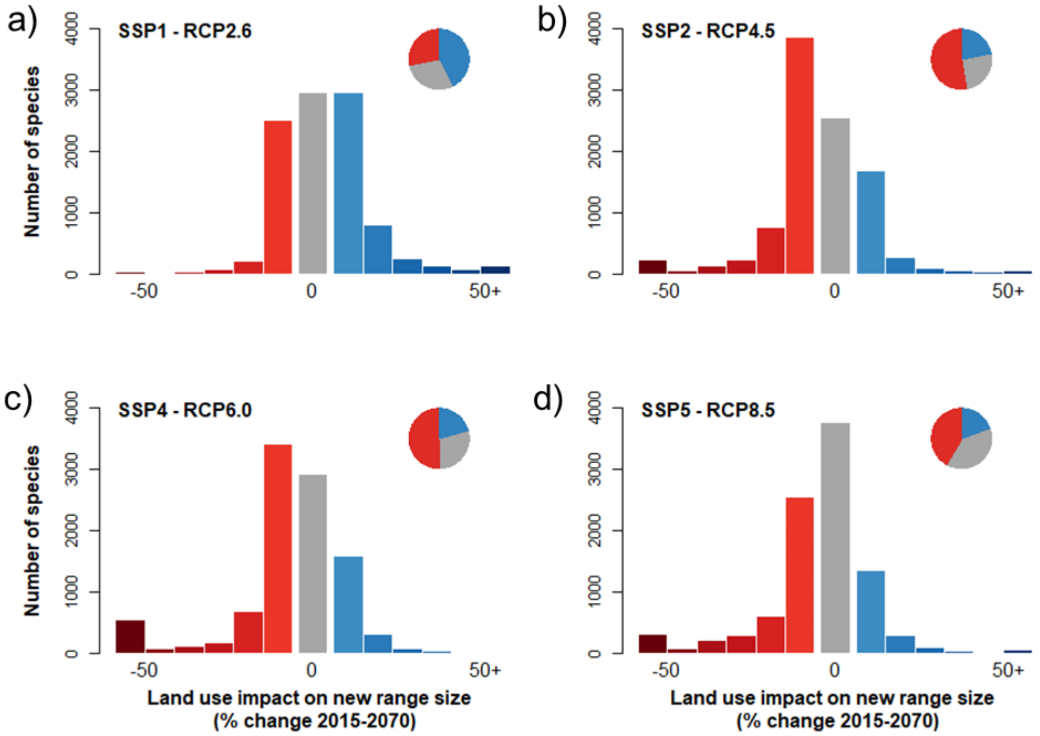


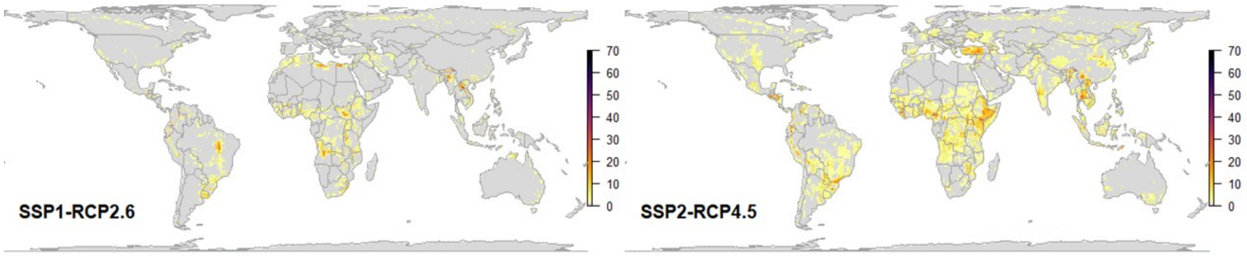
Figure 13: Histograms showing the number of species whose range shifts to new areas will be affected by *future* land-use change under four socioeconomic development scenarios. Bars are coloured according to the direction of land-use impact, with those restricted by future land-use in shades of red; species unaffected by land-use in grey, and those whose range shifts will be facilitated by future land-use change shown in shades of blue. The overall proportion of species belonging to each of these three categories is shown in the corresponding pie charts.

than they could if current land-use persisted to 2070. However, under the other three future scenarios, these 'beneficiaries' of land-use change make up a much smaller proportion of species (21.3%, 19.8% and 18.7%, in Figs 4b, 4c, and 4d respectively). Instead, the largest category of species are those for which future land-use change will further restrict range shifts, making up 50.8%, 48.7% and 40.2% of species in the three scenarios (Figs 4b, 4c and 4d respectively). Although greatest number of species see their range shifts restricted by land-use change in the middle-of-the-road SSP2 – RCP4.5 scenario, the number that are *severely* affected (for example where land-use change will cause >50% declines in their new range size) is highest in the latter two scenarios, SSP4 – RCP6.0 and SSP5 – RCP8.5.

The spatial impacts of future land-use change on range shifts vary considerably for the four future scenarios that I considered (Fig 5), although notably sub-Saharan Africa in particular sees negative impacts in all scenarios other than the most sustainable. In SSP1-RCP2.6, although the negative impacts are considerably less severe than for the other scenarios, land-use change is likely to be a problem for some species in parts of Brazil, tropical Africa, and some parts of mainland Southeast

Asia. In SSP2-RCP4.5, the middle-of-the-road scenario in which historical consumption trends continue, the impacts are similarly distributed but larger in magnitude and more widespread across South America and sub-Saharan Africa (Fig 5b). In SSP4-RCP6.0 – the scenario in which progress towards sustainable development is particularly slow in low income countries – the negative impacts of land-use change are notably concentrated in sub-Saharan Africa, where the highest numbers of prevented range shifts are expected to be found (Fig 5c). Finally, in SSP5-RCP8.5, in which development goals are achieved via rapid fossil fuel consumption, future land-use change is projected to most severely affect range shifts in the Atlantic forest region of Brazil, and West, central and East Africa (Fig 5d).

a) Sustainability b) Middle-of-the-road



c) Inequality d) Fossil-fueled development

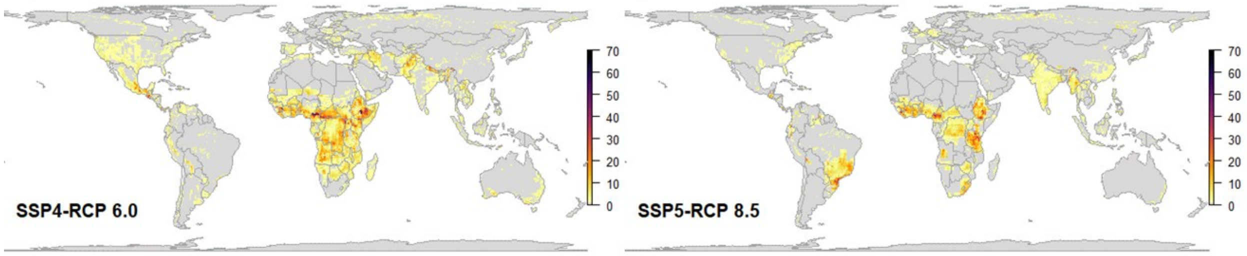


Figure 14: The number of species in each grid cell whose range shifts will be limited by future land-use change. The four panels correspond to the four global development scenarios considered in the analysis. All four are shown on the same scale to enable direct comparison.

Species pushed toward extinction by the interaction of land-use and climate change

In the most sustainable scenario, SSP1-RCP2.6, considering land-use and climate change separately would miss just 6 (3.85% of 152) species expected to see severe (>90%) declines in range size from the combination of land-use change and climate change. However, this number increases with the increasing intensity of the pressures. Under SSP2-RCP4.5, 33 (7.97% of 414) severely affected species would be missed; under SSP4-RCP6.0, 91 (16.88% of 539) severely affected species would be missed; and under SSP5-RCP8.5, the number of missed species is 150 (13.2% of 1,140).

In Figure 6, I map the future land-use change that is responsible for these declines – i.e. the land-use change that will disproportionately affect species' future ranges rather than their present ranges. Impacts are minor in SSP1-RCP2.6, but affect many more species in the other scenarios, notably in south-eastern Brazil, parts of the Andes, tropical Africa (especially upland parts of East Africa), and Madagascar. These are places where many species ranges may shift to or become restricted to, but will also be hotspots for future land-use change in those three development scenarios.

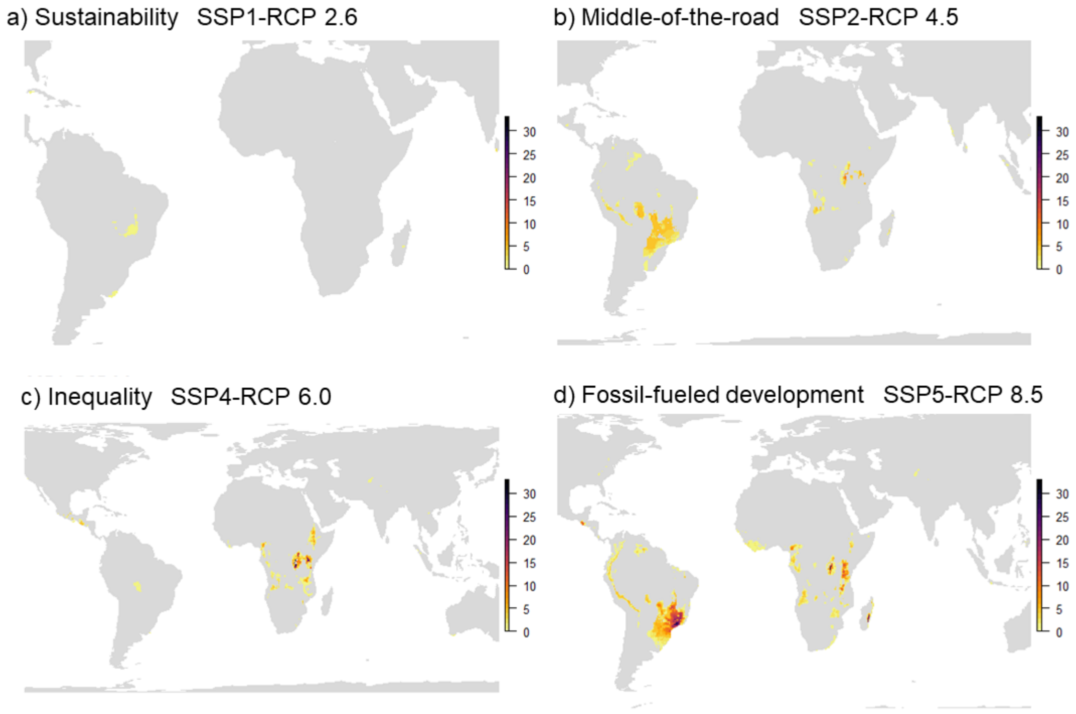


Figure 15: Maps highlighting the regions of land-use change that are responsible for severe (>90%) declines in range size for species that would not be as severely affected by either land-use change or climate change alone. In other words, these maps show areas of projected future land-use change that disproportionately affects species once their range shifts have been taken into account. All four maps are plotted on the same scale to enable direct comparison. Values correspond to the summed number of species unable to colonise a grid cell because of future land-use change (weighted by the proportion of that grid cell that undergoes the land-use change in question).

How does land-use affect global biodiversity projections under climate change?

Even under the most sustainable development scenario with the greatest climate mitigation (SSP1-RCP2.6), average grid-cell level richness is projected to decline slightly by 2070, by approximately 3% (Fig 7, black circle, lighter shade). However, this is a marginally better outcome than if land-use remained in its current (2015) state (black triangle), demonstrating that in this scenario, in which the global agricultural footprint decreases, future land-use change is a global force for good. In SSP1-RCP2.6, only in two regions – Africa and West Asia – does future land-use change exacerbate the losses expected from climate change. If species underwent the climate change induced range shifts expected in SSP1-RCP2.6 and land-use was (implausibly) configured the same as 1000 years ago, grid-cell species richness would increase by more than 10% on average globally. This hints that following SSP1-RCP2.6, combined with targeted restoration efforts in the most critical places to facilitate range shifts, could begin to reverse global biodiversity loss by 2070.

In contrast, SSP5-RCP8.5 has strong negative impacts on biodiversity globally, and future land-use change would exacerbate climate-induced losses on every continent (circles compared to triangles, dark shading), most notably in Latin America and Africa. Even if land-use was hypothetically restored to its state in the year 1000, species' range shifts and expansions would not be enough to push average species richness above its present day levels (black square, dark shading).

The benefit of choosing SSP1-RCP2.6 over SSP5-RCP8.5 is considerable in every region, and globally is similar in magnitude to restoring all habitats to their 1000 land-use state (black circle, light shading compared to black square, dark shading). The greatest benefit of choosing the more sustainable pathway will be felt in Africa, which sees very large declines in biodiversity owing to land-use and climate change in SSP5-RCP8.5 (around 25% loss on average across African grid cells), but only modest declines of around 5% under SSP1-RCP2.6.

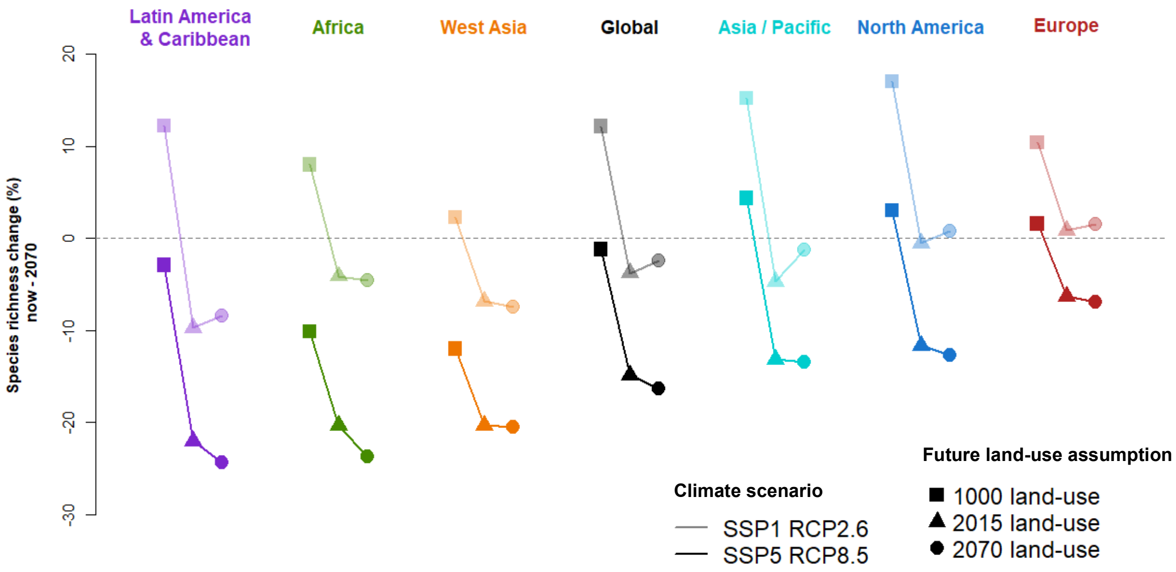


Figure 16: Projections of species richness change around the world (averaged across grid cells in each region) relative to present day conditions. Results are shown for two contrasting development scenarios: a sustainable development scenario (SSP1 RCP2.6, lighter shade) and a fossil-fuelled development scenario with significant climate change and increased agricultural expansion (SSP5 RCP8.5, darker shade). For each, the expected richness change is shown under three future land-use 'treatments' to reveal the land-use component of these changes. Squares show an implausible reference scenario in which land-use was restored to its state in 1000, helping to facilitate range shifts. Triangles show expected richness change if land-use was frozen in its 2015 state. Circles show expected richness change when we include the land-use projections to 2070 under that development scenario.

Discussion

Existing land-use as a range shift constraint

My results reveal how the expansion of human land-use over the past millennium and into the future will limit the abilities of the majority of terrestrial mammals and birds to shift their ranges as the climate crisis unfolds. This is despite conservative (generous) assumptions about which land uses are inhospitable for species, and so the actual impact of land-use on future range shifts may be even greater. For around 15% of species, the area they would be expected to shift to with a historical land-use baseline is more than halved by present day land-use. This highlights how habitat loss presents further challenges for species in the context of climate change, and how the legacy of land-use change continues to affect species many decades after that change occurred.

Land-use is likely to limit the greatest number of future range shifts in the tropical Andes, especially Colombia and Ecuador. I suspect this region stands out in particular because upland areas are characterised by high human population densities and large urban areas – including major cities like Bogota, Medellin and Quito – which are surrounded by highly biodiverse lowland ecosystems. Therefore, upslope range shifts from these lowland regions are likely to encounter large tracts of inhospitable agricultural land and urban areas. However, the global significance of the tropical Andes is, in part, simply due to the high species richness and large number of anticipated range shifts here. Controlling for the expected number of range shifts to each grid cell revealed that land use has a much wider influence across the planet for species on the move. Places like Madagascar, the American Midwest, south eastern Brazil and NE China, for example, see a very high proportion of expected range shifts prevented by land-use, even though the absolute number of prevented range shifts is lower than in other parts of the globe.

In identifying where land-use might pose the biggest problem for species on the move, this analysis also identifies places where restoration effort could benefit the greatest number of species when taking climate change into account. Restoring and connecting habitats together could have considerable benefits for species by facilitating range shifts that would not be possible under the current configuration of land-use. Importantly, many of these places – for example the tropical Andes, Southeast Asia, Madagascar and the Atlantic Forest region of Brazil – have already been identified as priority areas for restoration from the joint perspectives of conserving existing biodiversity, carbon sequestration potential, and cost minimisation (Strassburg *et al.* 2020). This suggests that focussing restoration efforts to these places will not only help to maximise species range shift potential, but also secure other important environmental benefits in a cost-effective manner. In other regions highlighted by my analysis, large scale restoration efforts are likely to be less feasible, for example due to high opportunity costs of restoring productive agricultural land to natural habitats. Such places include parts of North America, southern Australia, parts of Argentina and north-eastern China. In these regions, global efforts to tackle greenhouse gas emissions and minimise the need for range shifts in the first place might be the most important option for protecting biodiversity.

Future land-use as a range shift constraint

Compared with the impact of past land-use change, the impact of *future* land-use change on range shifts is relatively modest – as would be expected from the much shorter timeframe. However, the differences between the four development trajectories is stark, with considerable impacts in some regions under SSP4-RCP6.0

(a world of high global inequality) and SSP5-RCP8.5 (fossil-fuelled development). Therefore, even though it is existing, rather than future, land-use that will be the major constraint on range shifts, my results show the value of following the most sustainable land-use and climate trajectory (SSP1-RCP2.6) to help species cope with climate change. This trajectory is especially important to reduce the number of severely affected species (such as those where future land-use change could make >50% of their new ranges inhospitable). It seems this benefit would be particularly felt in tropical Africa, where future land use change is projected to obstruct range shifts for many species under all but the most sustainable scenario.

To limit future habitat loss resulting from land-use change, and ensure that as many species can track their climatic niches as possible, expansion of the global protected area (PA) estate may be an important conservation strategy. Targets for increased PA coverage are likely to be a feature of the global post-2020 biodiversity strategy, echoing ambitious calls to protect 30% or even 50% of the terrestrial biosphere (e.g. Dinerstein et al. 2017). To maximise the number of mammals and birds able to adapt to climate change, my results suggest this expansion should be prioritised across tropical Africa, south-eastern Brazil, and southern Asia: places where future land-use change is projected to limit the most range shifts.

However, although protected land tends to experience lower rates of conversion (Nagendra 2008; Geldmann *et al.* 2013) and higher levels of biodiversity (Gray *et al.* 2016) than comparable non-protected land, area-based conservation methods are not a silver bullet. Where management capacity and effective enforcement are lacking, so-called ‘paper parks’ may fail to protect biodiversity (di Minin & Toivonen 2015), and ambitious goals to set aside large areas of land for nature conservation must be sensitive to concerns of environmental justice and potential socioeconomic impacts on local peoples and communities (Büscher *et al.* 2017; Schleicher *et al.* 2019). Therefore, as well as legally protecting land from conversion, transformative changes are needed across the global economy, particularly with regards to food production systems, in order to tackle the drivers of land-use change in the first place. To feed a larger population with higher per-capita consumption on the same or smaller agricultural footprint (Tilman *et al.* 2011), it will require a combination of increased yields, shifts towards more plant-based diets, and reduced waste (Foley *et al.* 2011; Springmann *et al.* 2018).

Recent developments in due diligence legislation and zero-deforestation commitments (from European governments for example), as well as pledges to end deforestation by 2030 by more than 100 countries at COP26, offer hope that both ambitions and action to tackle habitat loss are advancing. It remains to be seen whether this increased ambition will be enough to move beyond previous unsuccessful attempts to curb habitat loss, such as the 2014 New York Declaration on Forests. Furthermore, policymakers must ensure that a) *all* habitats are conserved, given a risk of widespread 'leakage' of impacts to important non-forest ecosystems; b) that policies are ambitious enough to tackle the problem, for example targeting all deforestation and not just illegal clearance; and c) transparency is increased in global commodity supply chains to ensure that governments, companies and consumers can be held accountable for both their commitments and for their land-use impacts.

Species affected by the interaction of land-use and climate change

I also considered how a disproportionate impact of land-use change in species future ranges could cause range losses that would otherwise be unforeseen if climate change or land-use change were considered separately. My modelling showed this consideration to affect just a handful of species under SSP1-RCP2.6, but could cause 13-17% of severely affected species (those expected to see >90% decline in range size) to be missed for SSP4-RCP6.0 and SSP5-RCP8.5. I found a considerable amount of spatial variation in these impacts under the different future scenarios, but Madagascar, Atlantic Forest and East African Rift Valley were all highlighted in more than one scenario. In these places, the synergistic effects of land-use and climate change are expected to be particularly damaging for biodiversity. This analysis highlights the importance of considering multiple interacting threats together to avoid the under-appreciation of biodiversity impacts and the misidentification of conservation priority places and species.

Land use and global biodiversity projections under climate change

In the final section of my analysis, I spatially overlaid range shift projections across all modelled species, and explored the resulting global biodiversity change under contrasting development trajectories and also with historical (1000), present-day (2015) and future (2070) land-use snapshots. This analysis revealed how the most sustainable scenario that sees the global agricultural footprint decrease (SSP1-RCP2.6) would be markedly advantageous for bird and mammal biodiversity: not just because it avoids the seriously big losses caused by climate change, but because future land-use change becomes a force for good, helping recoup some of the biodiversity losses we'd see if land-use was frozen in its contemporary state. By contrast, under the fossil-fuelled development scenario which also sees continued agricultural expansion, (SSP5-RCP8.5), not only are the climate impacts much more severe but future LUC will continue to exacerbate biodiversity loss on every continent. This scenario would most harm biodiversity in Latin America and Africa, both because the climate impacts are greater, and also because future land-use change particularly aggravates these impacts (in Africa especially) by curtailing range shifts. Overall, the biodiversity benefit of choosing SSP1 over SSP5 would be similar in magnitude to reversing the last 1000 years of LUC over the next fifty years.

Even under the sustainable development scenario (SSP1-RCP2.6) it’s worth noting that relative to today, global biodiversity change is still projected to be slightly negative by 2070 – although less negative than if land-use was frozen in its contemporary state. However, the data hints that combining this scenario with targeted restoration of important habitats for range shifting species (i.e. restoring historical land cover in the most critical places, where this is complementary and not antagonistic to the broader sustainable development agenda) could push global bird & mammal biodiversity change into the positive by 2070 – a goal that appears far out of reach under a less sustainable development pathway.

Conclusions

The impact of future climate change on Earth’s terrestrial mammal and bird diversity is likely to be severe without rapid emissions cuts. By comparison, the impact of future land-use change is projected to be relatively modest; however, part of the reason that climate impacts will be so severe is because the loss of natural habitats over the last millennium has limited the potential for more than three quarters of terrestrial mammal and bird species to shift their ranges to new places. Future land-use change could either restrict or facilitate range shifts, depending on the global development trajectory we follow. To help the most species cope with climate change, habitat restoration should be targeted to the tropical Andes, Atlantic Forest, East African Rift and Southeast Asia. Efforts to protect of existing habitat from future land-use change will be particularly critical in sub-Saharan Africa.

More generally my results highlight the enormous benefit for biodiversity of choosing a more sustainable development pathway, not just because this avoids the significant losses we might see from climate change, but also because a shrinking agricultural footprint would help many species to shift their ranges. Choosing this trajectory, involving drastic and swift emissions cuts and transformative change to food production systems, along with ambitious but targeted habitat restoration, could enable many more species to cope with climate change and begin to reverse global biodiversity declines. My analysis shows that the cost of not doing so – of continuing to exploit fossil fuels and pursue economic development at the expense of the natural world – will be felt on every continent by biodiversity and the human societies that depend upon it.

Chapter 5

Climate change, range shifts and habitat connectivity in the global protected area network

Te Papakura o Taranaki, New Zealand: an IUCN category II protected area surrounded by agricultural land. *Image credit: Ian Clothier (CC BY-SA 4.0)*

Abstract

Species distributions are changing as the climate warms, and protected areas (PAs) are likely to play a crucial role in facilitating these changes by preserving the habitats species need to colonise. However, a lack of habitat connectivity between PAs may limit their ability to enable range shifts. The severity of this problem, and the places and species most affected, remain poorly understood – despite its importance for global conservation strategies under climate change. By combining range shift simulations, fine-scale and species-specific habitat data, and dispersal modelling for over 11,000 species of terrestrial mammals and birds, I explore for the first time how a lack of habitat connectivity is likely to constrain PA colonisations under climate change globally. I show that a lack of connecting suitable habitat leaves 17.3% of species unable to fulfil the majority (>50%) of their anticipated PA colonisations. On average globally, PAs are not connected by suitable habitat for 21.2% of the species projected to colonise them, but with significant spatial variation: a lack of connectivity is likely to particularly constrain PA colonisations in Europe, the American Midwest, the Brazilian Atlantic forest, southern South America, mainland Southeast Asia, southern Australia and New Zealand. PA connectivity remains relatively high for range-shifting species across Amazonia, parts of North America and sub-Saharan Africa. Poor connectivity is especially associated with species already threatened with extinction, habitat specialists, and species dependent on wetlands or rocky areas. Finally, using an approach based on electrical circuit theory, I simulate dispersal between connected protected areas, identifying valuable yet currently unprotected habitats that are likely to provide between-PA connectivity for many species as their ranges shift. Forests and savannas provide a large and disproportionate amount of this connectivity benefit, and habitats in Central America, the northern Andes, East Africa, and SE Asia should be prioritised for proactive climate-wise conservation. These findings underscore the importance of PA connectivity to help species adapt to climate change, highlight which species and habitat types are most at risk from a lack of connectivity, and shine a spotlight on places to be targeted to preserve or restore climate-resilient landscapes for global bird and mammal conservation.

Introduction

Protected areas (PAs) underpin nature conservation strategies around the world (Dudley 2008; Maxwell *et al.* 2020) by reducing pressure on local biodiversity, particularly from habitat loss, hunting and poaching (Nepstad *et al.* 2006; Andam *et* *al.* 2008; Gaveau *et al.* 2009; Geldmann *et al.* 2013; Hill *et al.* 2020). Consequently, PAs have played an important role in averting recent bird and mammal extinctions (Bolam *et al.* 2021), and harbour greater local biodiversity than comparable unprotected lands (Gray *et al.* 2016). However, despite these benefits, the global PA network remains inadequate for protecting Earth's biodiversity now and into the future: one-third of global "protected" land is under intense human pressure (Jones *et al.* 2018), forty percent of protected areas are reported to have "major deficiencies" in management (Leverington *et al.* 2010), only half of tropical PAs appear to be effective (Laurance et al., 2012) and PA coverage has been deemed inadequate for the majority of (i) ecoregions, (ii) important sites for biodiversity and (iii) assessed species (Butchart *et al.* 2015). Therefore, despite the partial achievement of the Convention on Biological Diversity's Aichi Target 11, which aimed for 17% terrestrial PA coverage by 2020, these shortcomings are likely contributing to the sustained loss of biodiversity globally. More ambitious efforts to expand PA coverage (for example to 30% by 2030 (Dinerstein *et al.* 2019; CBD 2021) or even 50% (Locke 2015; Dinerstein *et al.* 2017)) risk emphasising quantity over quality (Barnes *et al.* 2018), especially if they do not also address the important qualitative components of Aichi Target 11 that remain unfulfilled: that PAs should be "effectively and equitably managed", "ecologically representative", and – crucially in the context of climate change – "well-connected".

As climate change unfolds, a well-connected network of global protected areas is likely to be particularly important as species distributions change (Hannah *et al.* 2007; Alagador *et al.* 2014; Scheffers *et al.* 2016b). Range-shifting species preferentially colonise protected areas (Thomas *et al.* 2012), and increased PA coverage is associated with higher bird colonisation rates (Peach *et al.* 2019), showing that PAs are likely to play an important role in facilitating adaptive responses to climate change. However, protected areas must be sufficiently interconnected to allow species to move between them (Foden & Young 2016). Poor connectivity may occur for entirely natural reasons – for example where regional topography leaves montane PAs isolated from one another. However, connectivity loss is increasingly driven by the modification of landscapes by humans: thanks to agricultural expansion, more than 70% of global forest habitats are now found within 1km of the forest's edge (Haddad *et al.* 2015), and tropical forest PAs are becoming more isolated over time as land-use change continues around them (DeFries *et al.* 2005). Therefore, a lack of between-PA connectivity may be a major constraint for species on the move under climate change, but the severity of this problem is poorly understood (Correa Ayram *et al.* 2016) and it remains unclear which species, places and habitat types should be prioritised at the global scale for climate-smart conservation.

This important knowledge gap is especially true when considering broad spatial scales, or when considering connectivity from the perspective of multiple species and habitat types. Several studies have considered *functional connectivity* (i.e. connectivity from the perspective of species, individuals or genes) for specific species at local to regional scales (e.g. Bauduin et al., 2020), or taken a species-agnostic approach and examined the *structural connectivity* (the physical layout of habitat patches) of particular habitat types (usually forest) (Keeley *et al.* 2018). Few studies have explicitly factored in the range shifts that connectivity needs to facilitate under climate change (Littlefield *et al.* 2019), or considered species-specific habitat requirements for a broad suite of species.

For example, one study investigating PA connectivity at the global scale (Saura *et al.* 2018) concluded that globally only half of protected land is also connected, using a simple indicator that assumed that connectivity can be approximated by a negative exponential relationship with distance between PAs. However, this approach is likely to miss important connectivity constraints caused by the layout or fragmented nature of habitats between PAs, and, by not explicitly considering climate, is unable to identify particularly important regions for range-shifting species. Other studies have considered climate connectivity between spatially explicit habitat patches by assessing whether the climatic gradients encompassed by individual habitat patches exceed projected temperature changes (which would theoretically enable their inhabitants to reach analogous climates in the future) (McGuire *et al.* 2016; Senior *et al.* 2019). But these either considered patches of simply 'natural habitat' (not discriminating between habitat types) or focussed only on tropical forest patches, and didn't explore connectivity from a PA-perspective. Furthermore, this approach to measure climate connectivity assumes that only mean annual temperature is relevant (and is consistently relevant among species); in reality species' climatic niches, and therefore range shifts, are likely to be more complex and idiosyncratic.

Consequently, research to date on PA connectivity has been limited in at least one of the following ways: it has a narrow geographic or taxonomic focus, ignores climate change, uses overly simplistic assumptions of habitat constraints, or fails to account for the species-specific nature of habitat connectivity and responses to climate change. Here, I attempt to address these gaps by combining range shift projections, fine-resolution and species-specific habitat information, and spatial data on the world's protected areas to estimate, for as many species of terrestrial mammal and bird as possible, the extent to which their projected PA colonisations will be possible via connected suitable habitat. This approach is sensitive to, but does not discriminate between, the different habitat requirements of each species, enabling me to move beyond the forest focus of previous research. My approach unites and expands the fields of range-shift modelling and habitat connectivity modelling, advancing simplistic assumptions about dispersal and colonisation in niche models, whilst explicitly considering species distribution changes and species-specific habitat requirements in connectivity analysis. It also brings the advantages of structural connectivity modelling (reduced uncertainty and fewer assumptions (Keeley *et al.* 2018)) whilst taking advantage of species-specific habitat data to keep the species perspective of functional connectivity analysis.

Key research questions

1. Are protected areas sufficiently well-connected to enable species to colonise them under climate change? Where are PAs likely to be most easily colonised as species ranges shift, and where might a lack of connectivity be a major obstacle?
2. Which species will most struggle to colonise new protected areas because of a lack of habitat connectivity? I hypothesise that threatened species will be more affected, since they are more likely to be habitat specialists and more likely to occur in fragmented landscapes.
3. Are species from certain habitats predisposed to high or low PA connectivity, and is there evidence that habitat generalist species are more likely to be able to colonise PAs under climate change?
4. Where should we target habitat conservation to preserve connectivity in the wider landscapes between protected areas? Which habitat types around the world will be most helpful for species colonising new protected areas?

Methods

1. Overview

First, I identified the protected areas of suitable habitat that species would be expected to colonise in the absence of any habitat connectivity constraints, by combining range shift simulations with species-specific habitat data and spatial data on protected areas. Next, I calculated the proportion of these "future PAs" that are connected, via continuous stretches of suitable habitat, to PAs in which that species is presently found. Finally, using an approach based on electrical circuit theory, I simulated dispersal pathways between these connected present and future PAs to identify places and habitats that are most likely to provide this connectivity under climate change and facilitate PA colonisations in the future.

2. Identifying potential protected area colonisations

Projected range shifts

First, I identified the broad area each species was projected to colonise by 2070 due to anticipated range shifts. This was done using the species distribution model (SDM) projections at 0.5 degree resolution described in earlier chapters (see Chapter 2 for methodological detail), taking the mid-range warming scenario RCP4.5 as the focal future scenario. RCP4.5 was chosen because it is likely to result in warming of between 2-3°C by 2100 and therefore resembles a future in which the pledges made at COP26 in November 2021 are fulfilled. Each species' "new range" was determined by identifying the parts of its projected 2070 range that did not overlap with its present range polygon. A fairly simple dispersal constraint was also applied, based on species' generation lengths and natal dispersal distances (see Chapter 2 for detail) to exclude parts of species new ranges that couldn't plausibly reached by 2070 even without habitat considerations. All spatial analyses were done in R (R Core Team 2021) using a cylindrical equal area (Berhmann) projection.

Protected area data

In the next step, species new ranges (see above) were overlain with protected area data taken from the World Database on Protected Areas (WDPA) (UNEP-WCMC & IUCN 2021), to produce a layer of expected PA colonisations for each species. However, the protected area data were first processed and cleaned as follows, following standard procedure for the WDPA data (e.g. Garnett et al., 2018). First, the WDPA datasets, which comprise both point and polygon vector data, were projected to the same cylindrical equal area projection as the species distribution data. Second, any PAs with 'Status' listed as 'Proposed' or 'Not reported' were filtered out. Third, those listed as UNESCO-MAB Biosphere Reserves were also excluded, due to issues concerning geospatial accuracy and the inability to distinguish between core areas and large buffer zones, with only the former meeting the IUCN protected area criteria. Next, the point data were converted into circular polygons by buffering each point with a radius equal to the square root of A/pi, where A was the point's reported area. These buffered points (i.e. now circular polygons) were then combined with the polygon data into a single protected area dataset. This was used to produce two final protected area datasets for each species: the PAs it is expected to colonise by 2070 (by intersecting with a species' new ranges, hereafter referred to as a species' *future PAs*) and the PAs it is assumed to presently occupy (by intersecting with species present ranges, hereafter referred to as *current PAs*). Ultimately, areas of these current and future PAs of that were unsuitable habitat were filtered out using species-specific habitat data (see next section below) such that the final PA data for each species consisted of its present and future PAs that were of a suitable habitat type.

3. Assessing habitat connectivity to future protected areas for each species

Species-specific habitat data

The purpose of this step was to determine the degree to which a lack of between-PA habitat connectivity might limit future PA colonisations for each species. To do this, I combined each species' current and future PAs (see above) with two sets of information: species-specific habitat suitability data, taken from the IUCN Red List API (IUCN 2020), and a global spatial dataset on the distribution of these IUCN habitat classes at a 1km resolution (Jung *et al.* 2020). These were used to produce a 1x1km raster of habitat suitability for each species as follows. First, for a given species, the 'Level 2' (i.e. sub-category level, such as 'Forest – Temperate') habitat classification codes corresponding to 'Suitable' habitat categories were obtained from the IUCN Red List. Next, the matching habitat layers from Jung et al., (2020) were summed together to produce a layer giving the fraction of each 1x1km grid cell that consists of suitable habitat for that species. Cells with less than 30% suitable habitat were excluded (to avoid including cells with only small amounts of fragmented habitat, which would be unlikely to be colonised in reality and unlikely to provide significant connectivity benefits; the analysis was also initially tested with a 10% suitability threshold but found to identify small fragments of the 1km grid cells that were mostly unsuitable anyway and therefore likely not functionally relevant).

Generating species' PA connectivity rasters

To determine which of a species' future PAs were connected to its current PAs, I identified each individual (i.e. non-touching) habitat patch in the species' habitat suitability raster and allocated them a unique identifier. By identifying which habitat patch each protected area was found in, I was then able to determine which future PAs are in separate habitat patches from any of the species' current PAs, and use this to produce a binary PA connectivity raster indicating whether future PA grid cells were connected (1) or unconnected (0) to its current PAs. For each species, I also used this to calculate a ‘species PA connectivity score’: the proportion of its future PA grid cells that are structurally connected to its current PAs via suitable habitat. Two hypothetical examples of how this species PA connectivity score was calculated are shown in Figure 1. From these PA connectivity rasters I also calculated, for each protected grid cell, the proportion of species expected to colonise it that are unable to do so without crossing stretches of unsuitable habitat – i.e. the proportion of species for which that PA is unconnected to their current PAs. This was done by summing the PA connectivity rasters across all species to calculate the total number of colonisations possible via connected habitat for each protected area, and then subtracting from and dividing by the total expected number of species colonisations of each PA to give the proportion *not* possible via connected habitat.

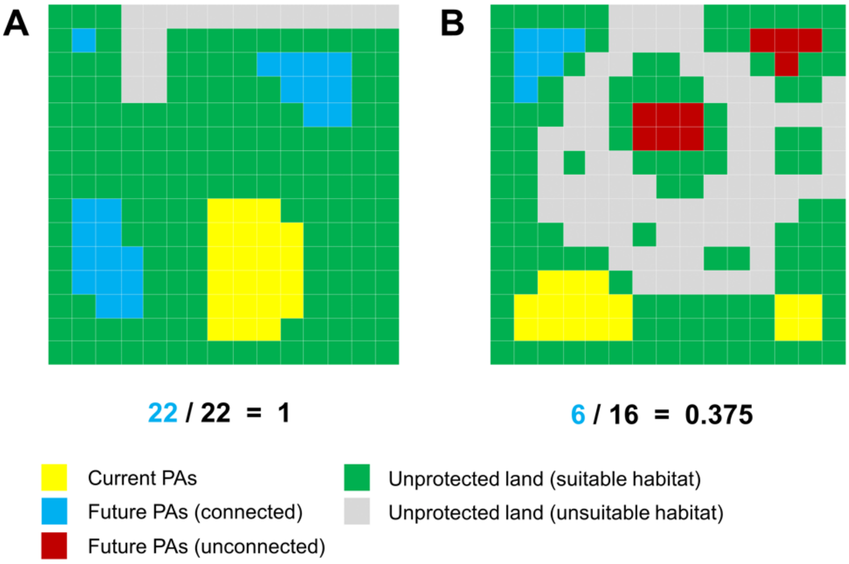


Figure 17: Schematic to illustrate the calculation of species PA connectivity scores from their PA connectivity rasters. In **A**, all expected future PA colonisations are possible (blue shading) via suitable habitat (green) from the species’ present PAs (yellow), resulting in a score of 1. This could result from a species being a habitat generalist, the landscape being largely homogenous and unmodified by humans, or some combination of the two. In **B**, two of the three protected areas this species is expected to colonise (from the range shift projections) are in isolated habitat patches that are not connected (red) to the species’ present PAs, resulting in a lower overall PA connectivity score for this species.

Assumptions and caveats

One potential problem with the above method of connectivity calculation is that it assumes any lack of connectivity (i.e. protected areas being in separate habitat patches) is due solely to the spatial configuration of habitats. However, it may be that this is due to the configuration of *land* rather than habitats *per se* – for example where a species is projected to colonise a PA on a nearby island, and it would be unfair to label such PAs as unconnected by suitable habitat when it would be unconnected even for a species tolerant of all terrestrial habitat types. Therefore I compared the analysis above to a 'reference' scenario in which I assumed all land areas were suitable but non-land was impassable (meaning that each island was identified as an individual patch). This meant I could identify and exclude PAs that were only unconnected because of their geographical isolation, rather than a true lack of habitat connectivity.

A second caveat with this method is that I implicitly assume that any stretch of unsuitable habitat detectable at a 1x1km resolution is impassable for a species. While this is unlikely to be true for every species, many species are reluctant to cross even very narrow stretches of unsuitable habitat (Laurance *et al.* 2004b) and, since I have already factored in species individual habitat requirements, my method is still sensitive to the habitat specificity of species (e.g. generalist species would be 'permitted' to reach PAs that specialist species could not). The focus on my modelling here, in any case, was to provide a first assessment of the connectivity of habitats and its implications for range-shifting species under climate change; not to accurately forecast the realised colonisations for every species. Future work that incorporates more detail on the abilities of individual species to cross stretches of unsuitable habitat would be a useful advance on the analysis presented here, but at present we know very little of species abilities to travel across unsuitable habitat, or which habitats they may tolerate temporarily as they travel to other areas, and so this is not currently possible. The approach I have taken is consistent across species and therefore more transparent, but it should be remembered that it may underestimate connectivity for any species that are habitat specialists, e.g. only having forest habitat categories listed as suitable, but may in fact be able to travel temporarily across stretches of unsuitable habitats.

A final caveat is that I assume habitats will not change between now and 2070. Whilst habitat conversion, restoration and habitat changes brought about by climate change will undoubtedly affect the spatial distribution of habitats (for example the spread of the boreal zone into tundra habitats) these effects will be fairly minor on this 50-year timescale, are highly uncertain and difficult to model at usefully fine resolutions, and so a lack of available data makes connectivity analysis with fine-scale future habitat data impossible at the present time.

Visualising PA connectivity under climate change globally

In order to visualise the connectedness of protected areas for range-shifting species at regional and global scales, the 1x1km PA connectivity rasters for each species (which detail whether a species' future PAs are connected or not to its current PAs) were coarsened to a 10km resolution. To do so, 10x10km protected grid cells were allocated 'connected' or 'unconnected' status for each species according to the status of any 1km protected cells within them. Where a 10km cell contained both connected and unconnected 1km PA cells, the modal value was taken. It should be noted that this approach was adopted purely for ease of visualisation of figures, not for analysing the PA connectivity data (for which I retained the 1km resolution).

Understanding among-species variation in connectivity scores

I explored variation in species connectivity scores in two ways: first, comparing scores between IUCN Red List categories, and second, by investigating whether this variation could be explained by species' habitat affiliations. To investigate whether species more threatened with extinction are more likely to have low PA connectivity scores (as hypothesised), I downloaded species' current IUCN Red List categories (IUCN 2020) and compared species' PA connectivity scores between categories using an ANOVA. To see if habitat variables could explain variation in species PA connectivity, I used the data from Jung et al., (2020) to calculate the proportion of species' present area of habitat (AOH) that is composed of different Level 1 IUCN habitat categories (e.g. Forest, Savanna, Grassland etc), and used these proportions as predictor variables in a generalised linear model (GLM). I also included as predictors the number of habitat categories suitable for a species (as a proxy for habitat specificity / niche breadth) and the area (number of grid cells) a species was expected to colonise. The response variable was logit transformed to better handle proportion data.

4. Dispersal simulations to identify habitat corridors that are important for providing connectivity to protected areas under climate change

Approach: simulating random walks with electrical circuit theory

Having identified which future PAs are structurally connected to present PAs for each species, I then simulated the dispersal of species between their connected current and future PAs to identify places that are likely to help facilitate PA colonisations for many species under climate change. To do so, I modelled species movements through a landscape as a random walk, using an approach based on electrical circuit theory. A random walk through a landscape can be represented by electrical current flowing through a network of nodes connected by resistors (McRae *et al.* 2008). For the purpose of this analysis, a key property of this network is the resistance (or its inverse, conductance) between nodes, which can be interpreted as the ability of a species to move between two grid cells, and which I parameterised using species-specific habitat suitability data (further detail is given below). The goal of this analysis, to continue with the electrical circuit analogy, was to identify areas of high current flow: ‘pinch points’ where the probability of range-shifting species passing through is particularly high. Such places may serve as important habitat corridors that help species to colonise protected areas and persist under climate change.

This random walk approach, based on circuit theory, has several advantages over common alternative methods to model connectivity such as least-cost paths or stepwise dispersal kernels (McRae *et al.* 2008). Firstly, it represents much more realistic dispersal behaviour, given that species don’t have complete knowledge of their landscape and destination from the outset (as is assumed with least-cost paths). Secondly, it better deals with interconnectedness and network redundancy, since the probability of a species using various alternative dispersal pathways is evaluated simultaneously rather than a single pathway being sought. Third, it avoids the need to parameterise highly uncertain dispersal kernels or more complicated analytical models. Lastly, well-developed and computationally efficient algorithms already exist that can be applied to large landscapes.

Dispersal simulation methods

These simulations were implemented using the R package *gdistance* (van Etten 2017) . First, I generated a conductance layer from habitat suitability data (coarsened to 10km for computational reasons, given that future PAs connected at the 1km level had already been identified, and the aim was to identify connectivity hotspots at much broader regional scales). This conductance layer gives the probability of transition between any two adjacent cells (including diagonally adjacent cells such that movement in eight directions was possible from a given focal cell). To generate the conductance layer, I make the assumption that species are likely to move more easily between grid cells containing large amounts of suitable habitat than into or between cells with only small amounts of suitable habitat. Therefore, for each possible movement between two grid cells, the conductance value was derived from the product of the two cells’ habitat suitability for that species, meaning that 1) the transition probability into or from a cell with a habitat suitability of zero was always zero, and 2) transitions were strongly favoured between adjacent cells where both cells had high habitat suitability values.

As my goal was to highlight the habitats most important for ensuring connectivity to each future PA, I took each future PA as the starting point and simulated random walks back through the landscape to the 10 nearest current PA grid cells. Ten cells were selected after initial investigations found this to strike a suitable balance between capturing the nearest current PA(s), allowing other PA cells to be included if the nearest PA was very small, and not including PAs that are far away and therefore less relevant from a connectivity perspective. The random walk simulations were implemented using *gdistance* (van Etten 2017) by calculating the net number of passages between the ‘origin’ and ‘destination’ cells – net meaning the number of passages not cancelled out by passages in the opposite direction. This effectively gives the probability of the “last forward” passage going through any two adjacent cells (McRae *et al.* 2008; van Etten 2017). The outcome of this step was to produce, for each future PA that a species was projected to colonise, a raster of passage probabilities through every cell in the landscape from the nearest current PA cells.

By summing these probability scores up across all the future PAs for a species, I generated a final raster for each species indicating the importance of each grid cell for providing habitat connectivity between the species’ current PAs and future PAs. Finally, to capture broad patterns across many species, I summed these scores for all the modelled species to produce a final global dataset of passage probabilities for all species. This summed passage probability metric captures the number of species that see a PA connectivity benefit from the habitat in a given grid cell, in a way that is sensitive to the relative importance of the cell for each species, and also the number of future PA colonisations that it facilitates for those species.

Comparing the importance of different habitat types

I also investigated the relative importance of different habitat types for providing this inter-PA connectivity under climate change. I did this by summing the passage probability scores described above for all the grid cells of each habitat type (with the grid cell scores weighted by the proportion of those cells made up of the habitat type in question). I also calculated what the ‘expected’ total score for each habitat type would be based solely on the extent of that particular habitat – i.e. if passage probabilities were distributed homogenously across the landscape regardless of habitat type. This meant it was possible to not only identify the most important habitat types for providing inter-PA connectivity, but also say whether connectivity was *disproportionately* concentrated in certain types of habitat. This analysis was done at the global level, and repeated separately for each continent.

Results

Colonisations and connectivity in the global PA network under climate change

In the absence of any habitat connectivity constraints (but requiring that protected areas be of suitable habitat), protected area colonisations by birds and mammals under a mid-range climate scenario (RCP 4.5) by are projected to be widespread globally by 2070 (Fig 1A). The greatest numbers of PA colonisations by birds and mammals are expected where high species richness intersects altitudinal climatic gradients, in protected areas around the tropical Andes, East Africa and southern Asia.

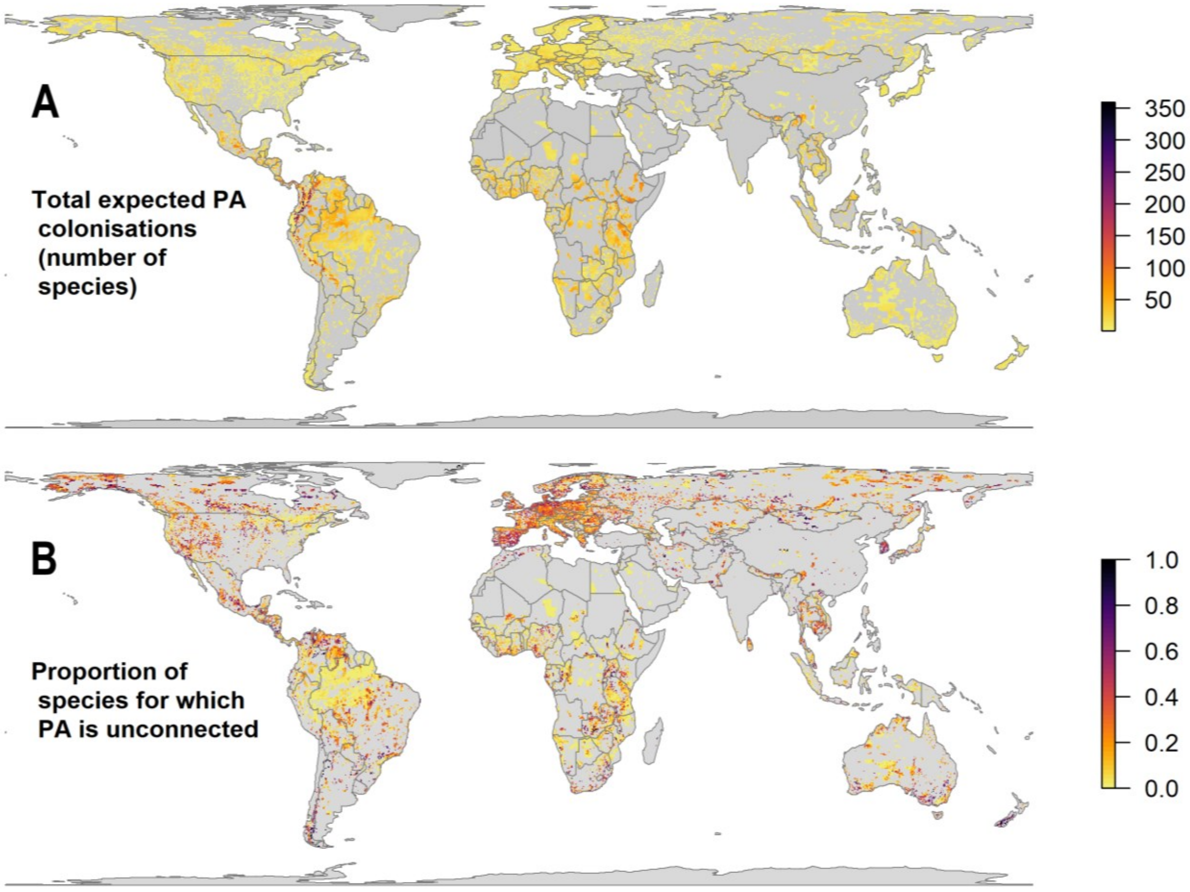


Figure 18: **(A)** The total number of expected bird and mammal colonisations of protected areas globally by 2070 under a moderate warming scenario (RCP 4.5). **(B)** The proportion of these colonisations that are not possible via dispersal through continuous suitable habitat from protected areas in a species current range – in other words, the proportion of species for which each PA is unconnected to their present ranges.

However, in many cases, these colonisations may be hindered by a lack of structural habitat connectivity with species' current protected areas (Fig 1B). Taking the average across all protected grid cells globally, I calculate that PAs are unconnected for 21.2%

of the species expected to colonise them. These patterns of connectivity can be highly spatially heterogeneous within even quite small regions, owing to the structure of habitat in the local landscape, but some broad regional patterns emerge from the global perspective I have taken. As the climate warms in South America, a lack of connectivity between protected areas is unlikely to be a problem for most species in Amazonia. However, poor connectivity may be a significant constraint for species expected to colonise PAs in the Atlantic Forest region of Brazil; northern parts of Venezuela and Colombia; and in mountainous regions of the southern Andes in Chile and Argentina. In Africa, PA connectivity for range shifts is generally high but with a few exceptions - for example, species may struggle to colonise PAs in Uganda around Lake Victoria and in the fragmented montane forests along the border with the Democratic Republic of the Congo. Similarly, species may be unable to reach protected forest habitats in central Kenya, eastern South Africa, parts of Zambia, and some West African PAs. In Europe, a lack of habitat connectivity is likely to be a widespread constraint for PA colonisation, with future PAs often unconnected for around 40% of species, although there is greater connectivity around the Alps, particularly northern Italy and Switzerland, and also in south eastern European countries. Across Southeast Asia, PAs seem moderately well connected to facilitate colonisations under climate change, although species may struggle in the southern Malay Peninsula near Kuala Lumpur and Singapore, and to a lesser degree but more broadly across Cambodia and Thailand. Across the rest of Asia, colonisation may be difficult for some isolated protected areas in central Mongolia and fragmented forests in South Korea. In Australia a lack of connectivity is likely to be a problem for many species projected to colonise PAs in the southwest and southeast where forest patches are surrounded by agricultural land. A very high proportion of expected colonisations may impossible via structurally connected habitat in New Zealand. Finally, in North America, there is high connectivity for species projected to colonise forests in the Northeast USA and in forests stretching from the northern Sierra Nevada up to Canada. Inter-PA connectivity is lower in other parts of the Rocky Mountains, where protected habitats tend to be in more isolated high elevation patches. Protected areas also appear to be poorly connected in northern Canada, likely due to the naturally fragmented nature of wetland habitats, and also in central Mexico, particularly for montane forests along the trans-Mexican volcanic belt.

Understanding between-species variation in PA connectivity

To understand how and why impacts vary between species, I calculated the proportion of expected PA colonisations (number of grid cells) that are possible via structurally connected suitable habitat for each species – hereafter termed a species' PA connectivity score. The average species had a PA connectivity score of 0.77, meaning that around three-quarters of the protected grid cells it was expected to colonise are connected to its current PAs by suitable habitat (although this was highly variable, SD = 0.30), and 17.2% of species had a PA connectivity score below 0.5, meaning that the majority of their expected PA colonisations are not possible via connected suitable habitat.

There was no evidence to suggest that PA connectivity scores differed overall between birds and mammals (t-test, t = -1.5781, df = 4276.6, p = 0.115). However, when breaking down the results by IUCN Red List category, Endangered, Vulnerable and Near Threatened species had significantly lower connectivity scores than Least Concern species (ANOVA, F=16.6, df=5, p < 0.0001, see Supplementary Table 1 for post-hoc pairwise comparisons with Tukey's Honest Significant Differences test), meaning that species already at a higher risk of extinction might also struggle to colonise new protected areas under climate change due to a lack of suitable connecting habitat. Although these differences were statistically significant, the amount of variance explained by Red List category was low ($R^2 = 0.01$).

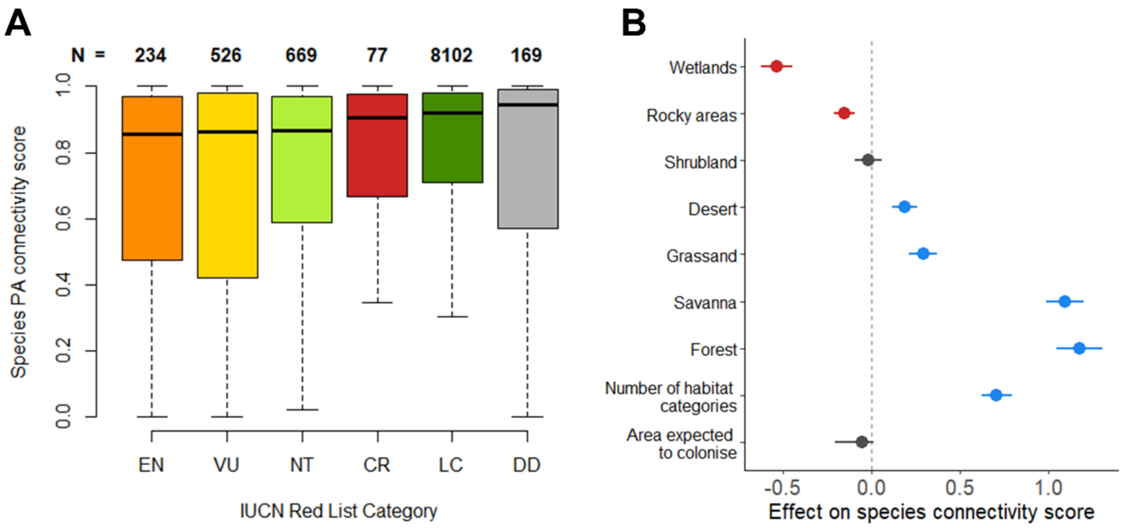


Figure 19: (A) Species' PA connectivity scores broken down by IUCN Red List category. Connectivity scores are significantly lower for Endangered, Vulnerable and Near-Threatened species than for Least Concern species; other pairwise comparisons are not significantly different. **(B)** Standardised effects of the modelled relationship between habitat variables and species' PA connectivity scores. For the habitat categories, the explanatory variables used were the proportion of a species' Area of Habitat made up of that habitat. Blue colours highlight a significant positive effect on species PA connectivity, while red colours indicate a significant negative effect. Black indicates that the effect of that variable was not significantly different from zero. Horizontal lines indicate 95% confidence intervals.

I also considered how the habitat composition of a species' range affected their PA connectivity scores. Having a high proportion of a species' area of habitat (AOH) consisting of wetlands or rocky areas was associated with lower connectivity scores. In contrast, species whose AOH contain higher proportions of forest and savannah habitats tended to have higher connectivity scores. High proportions of grassland and desert also had a positive effect, albeit less strong. The number of habitat categories suitable for a species also had a positive on connectivity scores, showing that habitat generalists tend to suffer less from a lack of connectivity. The effects of shrubland cover, and the area of land species are expected to colonise, were not significantly different to zero. See Supplementary Table 2 for model parameters and significance values.

Identifying globally important habitat corridors between protected areas under climate change

Having quantified the degree to which PA connectivity might affect species' abilities to colonise them under climate change, I explored which unprotected habitats between these PAs were important for providing connectivity and facilitating PA colonisations. To do so, I estimated the probabilities of species passing through landscapes to the protected areas they're projected to colonise under climate change (RCP 4.5), and summed these probability layers together across species to build a global picture (Fig 3). The global distribution of these scores is shown in Fig 3A; I also present selected regions of interest which illustrate important places for providing connectivity between protected areas under climate change. These include unprotected forests in and adjacent to the northern Andes (Fig 3B), montane forests along the Sierra Madre Oriental in Mexico and trans-Mexican volcanic belt (Fig 3C), forest habitats between PAs in West Africa, particularly between Ghana and Nigeria (Fig 3D), and forests at lower elevations in Nepal, Bhutan and NE India, with other important habitats stretching down to the Bay of Bengal around India's borders with Myanmar and Bangladesh (Fig 3E). Finally, Fig 3F uses Madagascar to illustrate how habitats that seem unimportant for providing connectivity for many species at the global scale can be revealed on a more local scale, with the narrow band of remaining humid forest along Madagascar's eastern side, as well as areas of dry forests in the south west, flagged as locally important for providing inter-PA habitat connectivity under climate change.

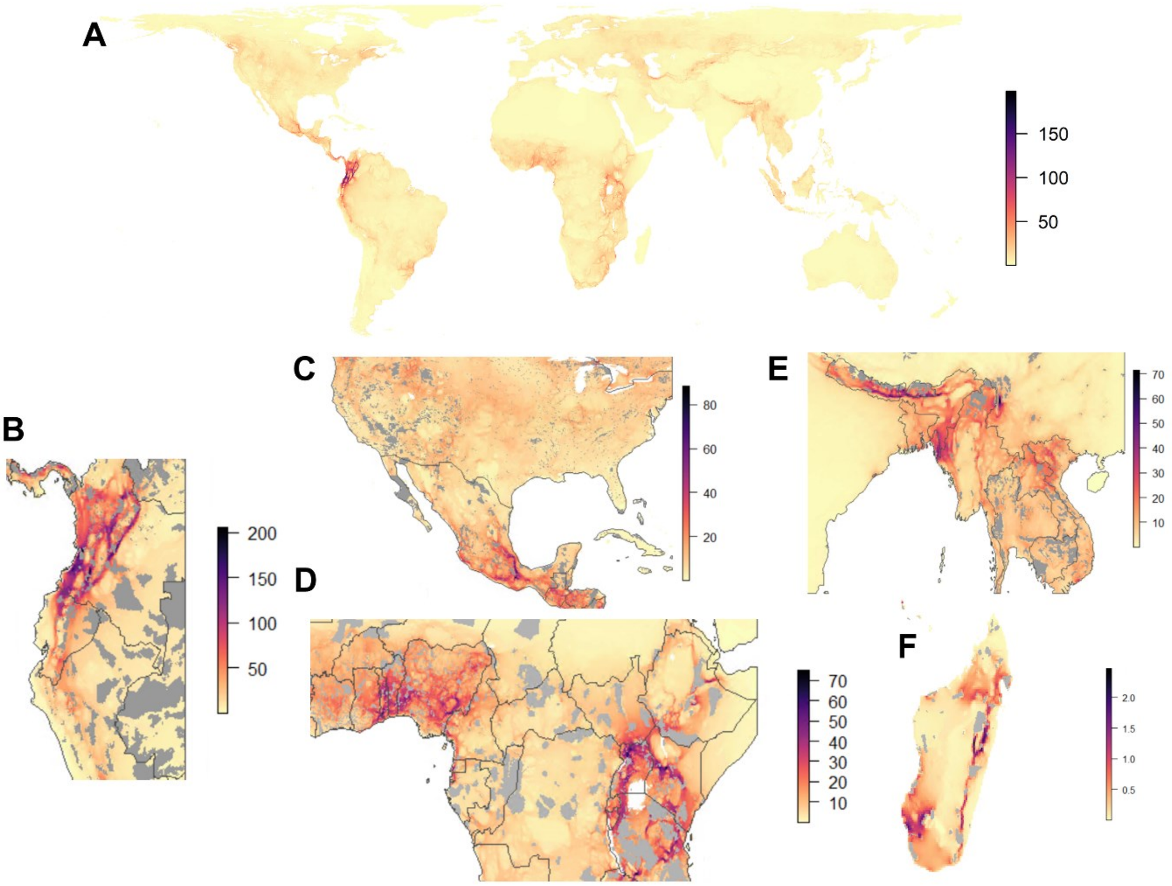


Figure 20: Maps of passage probability scores globally **(A)** and in selected regions **(B-F)**. Grid cells are coloured according to their scores, with darker areas likely to facilitate inter-PA connectivity for more species of birds and mammals under climate change. Grey patches represent protected areas. See Fig 4 for a breakdown of these results by habitat type.

The most important habitat types on each continent for providing these inter-PA connectivity benefits is summarised in Figure 4, where I have summed the scores shown in Fig 3 for each major habitat type. Globally, forest habitats provide the greatest amount of connectivity benefit (in terms of summed species passage probabilities) between protected areas, and are also over-represented given what would be expected from their extent. Savanna habitats are about half as important globally, but provide an even more disproportionate amount of inter-PA connectivity than would be expected from the area they cover. The breakdown of results by continent (Fig 4B-G) reveals that this is largely due to African savanna habitats providing a very large connectivity benefit for species on this continent. On every other continent, forests provide the greatest amount of connectivity for species.

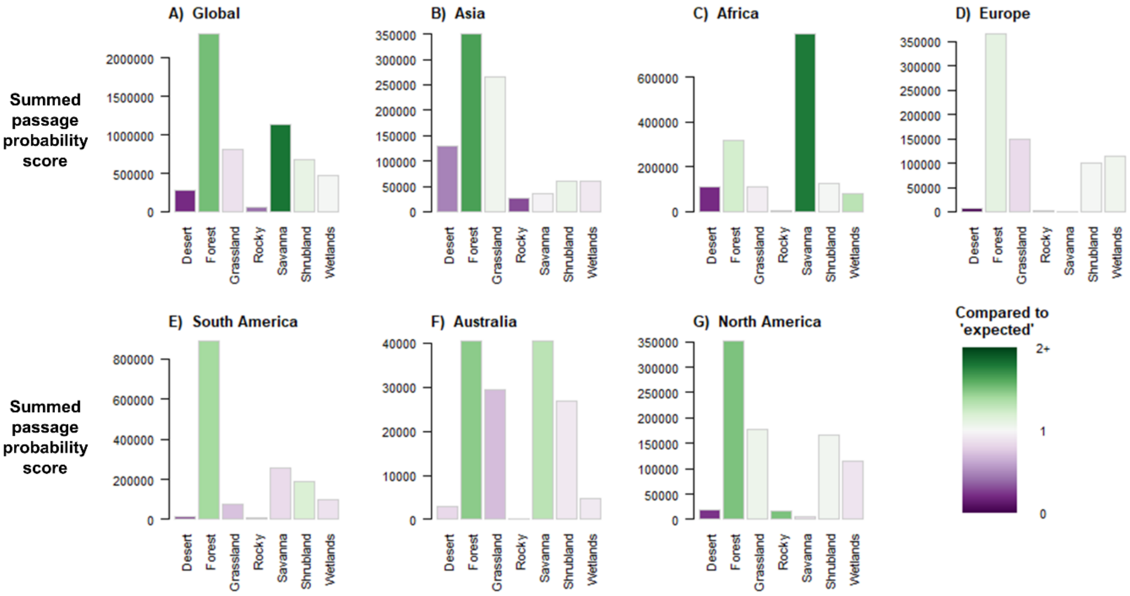


Figure 21: Sum of passage probability scores across grid cells for each habitat type, globally (A) and on each continent (B-G). Bar shading (green to purple) indicates whether a habitat is over- or under-represented compared to a null expectation in which the total summed passage probabilities were distributed evenly among habitats according to their area on each continent. A value of 2 indicates that the habitat type provides twice as much connectivity than would be expected from the extent of that habitat alone; a value of 0.5 indicates that it provides half as much. Globally, forests are the most important habitat type for facilitating PA colonisations under climate change for birds and mammals. Forests and savannas, as well as being the two most important habitat types for connectivity, are also both over-represented compared to their 'expected' importance, while deserts, grasslands and rocky areas are under-represented.

Discussion

This study is the first to map global patterns of PA connectivity under climate change, taking into account the individual habitat requirements of many species. Taking a species-perspective, I have shown that for nearly one-fifth (17.2%) of species, the majority of the protected grid cells they are expected to colonise are unreachable via suitable habitat. Taking a PA perspective, protected grid cells are unreachable for a 21.2% of the species expected to colonise them, on average globally. However, there was significant spatial and inter-species variation in these patterns. The potential sources of this variation are discussed below.

Places and species most affected by poor PA connectivity

My results make it clear that habitat connectivity between PAs can vary greatly across regions, and the reasons behind this lack of connectivity are likely to vary around the world too. In some places, it is likely that habitat fragmentation by agricultural land is the leading culprit – for example in the Atlantic Forest region of South America, mainland Southeast Asia, southern Australia, the American Midwest, and Western Europe. In other places, the climatic or geographic isolation of habitat patches is more likely to play a role, such as in Mongolia and Patagonia. For many regions, it may well be some combination of both natural and artificial fragmentation – for example around the African Rift Valley, where high human population densities and stretches of agricultural land sit at the intersection of a variety of ecosystem types. A similar combination of climatic/topographic and anthropogenic factors may explain poor connectivity in northern Venezuela and New Zealand. Further research and contextual information in these regions may offer more insight and inform conservation options that will be most effective at safeguarding species on the move in these areas. In contrast, PA connectivity is high for range shifting species in much of the Amazon basin, where the forest remains largely intact (Watson *et al.* 2016b); connectivity is also relatively high for many PAs in north-eastern North America and across sub-Saharan Africa.

My analysis also sheds light on which groups of species are likely to be most affected by a lack of PA connectivity under climate change. I showed that poor connectivity is likely to particularly constrain range shifts for species already threatened with extinction, with endangered species having the lowest PA connectivity scores of any IUCN Red List category. This is alarming from a conservation perspective, but perhaps not surprising: threatened species may be more likely to be found in fragmented habitats, and more likely to be habitat specialists (Howard *et al.* 2020), imposing greater constraints on their movement between PAs. Even where their climatic niches are not projected to shrink, this finding suggests that climate change is likely to intensify pressure on threatened species, as it will be particularly difficult for them to find refuge in other protected areas as their climatic niche shifts across the landscape. In general, I observed that the higher the threat level, the lower species' PA connectivity scores, although this trend had one exception: critically endangered species did not have significantly different connectivity scores to any other category. This likely reflects the much smaller sample size of critically endangered species compared with other threat categories, and should be interpreted with caution given that I excluded the most highly range-restricted species from the analysis (because their climatic niches are unlikely to be well-captured by an SDM approach).

As well as comparing Red List categories, my approach enabled me to compare impacts between species according to their habitat affiliations. Species that had high proportions of their AOH being forest or savanna were associated with higher PA connectivity scores, while greater dependence on rocky areas and wetlands had a negative effect. This likely follows from the natural layout of these habitat types, with both wetlands and rocky areas having a naturally patchy distribution separated by different habitat types and strongly defined by topography: rocky areas are typically high altitude and separated by lower elevations with more vegetated habitats, while wetlands have a naturally fragmented distribution determined by watersheds and local elevation minima. Forests and savannas, by contrast, tend to form larger continuous tracts of habitat according to broad climatic patterns, possibly explaining why species in these habitats tend to have higher PA connectivity scores. This does not mean, however, that we should worry less about forest species; many forest habitats are highly fragmented by human land-use (Haddad *et al.* 2015) and indeed many of regions identified in my analysis as having low PA connectivity appear to be fragmented forest regions such as in south-eastern Brazil, Central America, and southern Australia. It has been suggested that tropical forest species may be more prone to fragmentation-derived edge effects, due to their lack of previous exposure to fragmented habitats (Betts *et al.* 2019). Furthermore, it is likely that fragmented forest regions owe their poor connectivity to human landscape modification (unlike naturally isolated rocky areas, for example), and so this is where conservation action may have the most benefit.

Identifying habitat corridors for range shifting species

The uneven spatial distribution of habitats, protected areas, and species themselves mean that the connectivity benefit provided by unprotected habitat patches is likely to vary enormously across landscapes and regions. I showed how the expected flow of species through landscapes as they colonise PAs under climate change is likely to be highly concentrated into specific corridors of unprotected habitat. I found that particularly important broad-scale corridors can be found in Ecuador and Colombia, notably in the montane forests flanking the Andes but also in lowland forest nearer the Pacific coast. Other regions that stand out as being important for connectivity at the global scale include parts of central and southern Mexico, East Africa, West Africa (especially between Ghana and Cameroon), Himalayan subtropical forest in Nepal, Bhutan and India, and in forests stretching between the Himalayas and bay of Bengal around the borders shared between India, Myanmar and Bangladesh.

By identifying the habitat types associated with high passage probabilities, I showed that globally and on every continent other than Africa, forest habitats provide the greatest amount of connectivity benefit between PAs under climate change, and provide a disproportionate amount given their extent. This result partially reflects the fact that forests contain the most species, many of which will be habitat specialists, and therefore many species will be dependent on forest patches between protected areas to provide connectivity under climate change. Inspecting the distribution of passage scores more closely, montane forests seem particularly important for providing inter-PA connectivity under climate change. This may reflect a number of underlying factors. For example, they may provide important connections to higher elevation PAs and upslope climate refugia. Alternatively, montane forest habitats may provide disproportionate connectivity by virtue of being the most intact in a region, since mountainous terrain is less suitable for agriculture. Furthermore, since montane forests are often restricted to a specific altitudinal band, they tend form linear habitat features running perpendicular to the elevation gradient that could actually might help species 'traverse' to other latitudes, rather than necessarily just providing connectivity between protected areas at different altitudes. None of these hypotheses are mutually exclusive; understanding the role of forests and particularly montane forests in providing habitat connectivity under climate change should be a priority for further research. In Africa, the greater importance of savanna (as opposed to forest) than on other continents may reflect Africa's particularly high savanna biodiversity, a greater number of savanna PAs, and possibly the lack of a major elevation gradient bordering most of the Congo, limiting the potential for forest species to colonise higher elevation PAs here.

Conservation implications

Expansion of the global protected area network

The first draft of the post-2020 global biodiversity framework calls for the protection of at least 30% of Earth's land areas and sea areas by 2030 (CBD Secretariat 2021), inheriting language from Aichi Target 11 that these should be "effectively and equitably managed, ecologically representative and well-connected… and integrated into the wider landscapes and seascapes". Although this target need not be exclusively met via strict protected area expansion, since there will be a role for 'other effective area-based conservation measures' (OECMs), it seems likely that expansion of the global protected area estate will form a core part of global conservation policy over the next decade and beyond. To avoid the failings of previous decades (Butchart *et al.* 2015), this PA expansion must be highly strategic

– targeting places that most improve ecological representation and connectivity – and not just continuing historical trends whereby expansion takes place into cheaper land that minimises conflict with agriculture (Venter *et al.* 2018). By identifying places where unprotected habitats are likely to provide high levels of climate connectivity, this chapter contributes to this conversation.

One priority should be the protection of highly diverse "wilderness" areas where connectivity remains very high, such as the Amazon basin, where I assessed almost all projected PA colonisations to be possible via connected habitat. At the global scale, this is rare, and should be protected – especially given that by one estimate, the Amazon has seen significant losses (30%) of wilderness areas in the last two decades alone (Watson *et al.* 2016b). Perhaps more urgent priorities, however, are the unprotected places highlighted as important for connectivity in the dispersal analysis, since these are likely to act as conduits for many species that undergo range shifts between protected areas in the future. These were often forests, especially montane forests that connect PAs across elevation gradients. Habitats in the northern Andes, central America, East Africa, and Himalayas were flagged as particularly critical from a global perspective. It's important however, that other habitats aren't overlooked when identifying areas to protect; savanna habitats, for example, seem likely to provide large and disproportionate amounts of inter-PA connectivity for birds and mammals in Africa and Australia.

Beyond connectivity, many other factors need to be considered when prioritising places for PA expansion. These include areas of particularly high importance for present-day biodiversity, such as Key Biodiversity Areas (Eken *et al.* 2004), and other considerations of ecological representativeness that capture different dimensions of biodiversity and ecosystem service provision. Considering transaction, management and opportunity costs of conservation is also important (Balmford *et al.* 2003; Naidoo & Ricketts 2006); a return-on-investment framework to incorporate these costs may be useful (Tear *et al.* 2014). PA expansion, to enhance connectivity or otherwise, must also factor in potential impacts on people's livelihoods, especially for indigenous peoples and communities with insecure land rights, and must be sensitive to concerns of green colonialism (Domínguez & Luoma 2020). Beyond needing to take these other considerations into account, some have even cautioned against considerations of habitat connectivity altogether, which is inherently complex and uncertain, citing concerns that it may direct resources away from actions that would have more concrete benefits (Hodgson *et al.* 2009). However, my analysis shows that many of the places where PA expansion could most benefit connectivity are already highly biodiverse global conservation priorities – suggesting that targeting action to these places could deliver substantial biodiversity benefits today whilst also helping to future-proof conservation under climate change. More in-depth analysis into the overlap of priorities areas for habitat connectivity and other ecological benefits would be a useful avenue for further research.

Other conservation approaches: restoration, rewilding and species-specific interventions

In places where connectivity is already poor, there is the potential for habitat restoration and rewilding to improve the situation. My results suggest this may be most beneficial in places such as the Atlantic forest of Brazil, Western Europe, the American Midwest and Southeast Asia. Although it remains uncertain whether such initiatives would provide benefits in time to help species cope with climate change, degraded ecosystems can recover quickly (Rozendaal *et al.* 2019) and there is likely to be a delay in species responding to climate change and tracking their shifting climatic niches. Restoration and rewilding initiatives that are targeted to improve connectivity may therefore be a wise use of funds raised for nature-based climate solutions, tackling both the cause and effects of climate change by simultaneously storing carbon and creating habitat corridors for range-shifting species.

In some cases, conservation action may need to be targeted to specific species and habitats. Results from this analysis suggest that special consideration should be paid to species already threatened with extinction and habitat specialists, along with species from rockier habitats (e.g. those adapted to mountain tops) and wetlands, which may most struggle to colonise new PAs as their climatic niches shift. Where geographic barriers are the problem, or where restoration is financially or ecologically most challenging (Strassburg *et al.* 2020), assisted colonisation could be considered, although such efforts are likely to be controversial and expensive and therefore only useful in a minority of cases. Given the scale of the problem, limited conservation funds may be better directed towards actions that can benefit many species at once.

Possible downsides of connectivity

So far, I have implicitly assumed that connectivity is always a desirable outcome for species now and under climate change. However, it is important to consider any downsides that increased connectivity could bring, such as facilitating the spread of invasive species, pests, pathogens, predators and fires that might further endanger, rather than bolster, vulnerable populations (Haddad *et al.* 2011). At the global scale, and in the face of rapid climate change, such risks are likely to be outweighed by the benefits, but remain an important consideration nonetheless. Any potential negative impacts are likely to be very context-dependent and an assessment of the likely benefits and costs should be carried out before efforts to enhance or restore connectivity are undertaken.

Scaling up conservation to the landscape scale and rethinking the role of protected areas

Climate change raises broader questions about the role of protected areas – challenging, for example, typically western notions that nature is a static entity separate from humans that can be preserved in specific places (Vining *et al.* 2008). The purpose of protected areas is likely to become even more varied in future, for example providing stepping stones between important habitat patches in a landscape. As species distributions change, some PAs may become unhelpful and need to be 'retired' if the conservation benefits they provide no longer justify the expenditure of limited funds (Fuller *et al.* 2010; Alagador *et al.* 2014).

More generally, area-based conservation action – be it the preservation of existing habitat through PAs, or the restoration and rewilding of degraded habitats – needs to be framed at the temporal and geographic scales relevant for ecological processes under climate change. This will not be straightforward, as it necessarily implicates a wide variety of stakeholders in ensuring that regional landscapes remain (or become) interconnected enough to protect biodiversity, both now and as the climate crisis continues to unfold. These stakeholders will vary in different regional contexts, but are likely to include local communities and indigenous peoples, protected area managers, conservation organisations, local to national government actors, smallholders, and members of the private sector such as the producers and traders of agricultural commodities. Given the complexities involved with broad-scale conservation efforts, and the challenges of facilitating constructive dialogue between varied stakeholders, it would be pragmatic to learn from existing ambitious conservation initiatives, such as the 2000-mile long Yellowstone to Yukon initiative (Chester 2015) where both habitat connectivity and multi-stakeholder collaboration are central tenets.

Conclusions

A lack of habitat connectivity is likely to be a significant barrier for species colonising protected areas under climate change. Species may be most affected in places where habitats have become highly fragmented by humans, such as in Western Europe or Brazil's Atlantic Forest, or where they are specialists of naturally patchy habitats, such as wetlands and montane habitats. Species already threatened with extinction are also likely to be particularly affected. Future research is needed to better characterise species abilities to disperse across unsuitable habitat areas, to improve our understanding of where these impacts will be more or less acute. PA expansion should be targeted to places that provide high levels of climate-wise connectivity to the PA network, such as in the tropical Andes, African Rift Valley and in forests in the Himalayan region. These regions represent areas where unprotected habitat corridors exist that will facilitate PA colonisations for many species, often because continuous stretches of habitat span elevation gradients. Here, the designation of new PAs to secure important "stepping stone" habitats along these corridors is likely to be more useful than simply expanding existing PAs. More broadly, as PA expansion continues to form a core component of the post-2020 biodiversity framework, PAs must be considered from a broader landscape perspective that also takes into account the matrix of habitats between PAs as a fundamental and complementary part of PA design. To ensure conservation funds are deployed effectively amid disruptive climate change, PAs should be routinely integrated into ambitious, broad-scale and multi-stakeholder conservation initiatives that enable landscapes to fulfil human needs while protecting biodiversity today and into the future.

Chapter 6

General Discussion

Mixed-use landscape near Surama, Guyana

Summary

Rapid climate change is driving changes to the distributions of species worldwide (Scheffers *et al.* 2016a; IPBES 2019). In this thesis, I have advanced our understanding of how climate change will continue to affect the distributions of terrestrial mammals and birds at the global scale, and have explored possible challenges and opportunities that this brings for conservation in a world where other pressures, particularly land-use, already threaten over a million species with extinction (IPBES 2019).

I found that dramatic changes to biodiversity patterns are likely by 2070. Even under the most benign climate scenario I considered, in which temperature rises are likely kept below 2°C, bird and mammal richness is likely to decline across two-thirds of the planet, with increasingly severe impacts under higher emissions trajectories. These biodiversity declines are the combined result of thousands of species' individual responses, since each is adapted to its own climatic niche. However, biogeographic variables can help predict which species will be most affected. I showed how both high latitude species, where the magnitude of climate change is greatest, and low latitude species, where species are most sensitive to change, are most likely to see their ranges shrink. I also showed how an 'escalator to extinction' effect (Urban 2018) is likely to cause range contractions and increase the extinction risk of high altitude-adapted species worldwide, and predicted an analogous situation at the highest latitudes, where limited land availability makes further poleward shifts impossible. Species were also most likely to be affected where their niche spans a narrow range of latitudes, elevations, and habitats.

Because these impacts are distributed unevenly across the planet, biodiversity losses are inevitably biased towards certain nations of the world. I showed that countries with potentially lower capacity to enforce conservation action, and also lower culpability for the emissions driving climate change in the first place, are most likely to see significant biodiversity loss. Considering projected range shifts through the lens of international borders, I showed how transboundary conservation for species on the move is likely to be particularly important around the Amazon basin, the Himalayas and East Africa, where many species are projected to shift across borders. As border walls and fences continue to proliferate (Rosière & Jones 2012; Linnell *et al.* 2016; Jaroszewicz *et al.* 2021), this infrastructure could pose an overlooked barrier to dispersal and I highlighted which borders pose the greatest biodiversity risks.

However, it’s not just border infrastructure that could inhibit range shifts; much more widespread changes to landscapes have been underway for centuries as agricultural land has spread over more than a third of the planet (Foley 2005). In Chapter 4 I showed that this land-use is likely to constrain 77% of species’ abilities to colonise new areas as their ranges shift over the next 50 years, often to a significant degree. The combined effects of climate change and land-use change are likely to continue to erode global biodiversity unless a swift transition to a more sustainable development trajectory, involving the sustainable intensification of food production and rapid cuts to greenhouse gas emissions, is combined with targeted restoration that enables species to fulfil broader range shifts than is currently possible.

Finally, it’s not just the availability of suitable habitat that matters for range-shifting species, but also the connectivity of that habitat. Taking the perspective of protected areas – which underpin conservation efforts worldwide, are a key focus of multilateral environmental policy, and play an important role in facilitating range shifts (Thomas *et al.* 2012; Maxwell *et al.* 2020) – I showed how a lack of between-PA connectivity is likely to leave nearly a fifth of species unable to fulfil more than half of their expected PA colonisations. Mapping the places most impacted, I showed how this lack of connectivity was most likely in landscapes fragmented by humans – Brazil’s Atlantic Forest and parts of Western Europe, for example – and also naturally patchy habitats such as rocky areas and wetlands. I also mapped important connectivity bottlenecks for range shifting species around the world that deserve particular conservation attention, showing that forest and savanna habitats in East Africa, the northern Andes, Central America and bordering the Himalayas may be most critical to protect from conversion if we are to maintain PA connectivity for species whose distributions are changing.

In the remainder of this chapter, I’ll synthesise these findings in more detail, discussing how we can use this information to best protect biodiversity from climate change. I’ll do so by considering key themes that have emerged repeatedly throughout the thesis. I’ll then consider some of the major sources of uncertainty, and areas where I believe future research could be most useful. I’ll conclude with some recommendations for policymakers and conservation practitioners that my research has shown are likely to help safeguard global biodiversity in the face of further land-use and climate change.

Common patterns and themes

Recurring hotspots of loss and opportunity

Throughout this thesis, I have identified regions of the world that are likely to see particularly severe impacts of climate change on bird and mammal biodiversity, or that are likely to be targets for proactive conservation. It's striking, if perhaps unsurprising, that many of these places identified in separate chapters overlap. To some degree, this is to be expected given that each chapter took the same SDM projections as its foundation, and also given that the considerations in question may be correlated in space, such as large areas of human land-use (Chapter 4) and the isolation of protected areas (Chapter 5). Although they may highlight similar places, each of my chapters provide fresh insight into the nature of the different challenges that these hotspots will face, and together provide a more complete picture of how conservation might best proceed in these places.

For example, East Africa, the Himalayas, and tropical Andes were all flagged as important regions for climate-smart transboundary conservation in Chapter 3, and also important places that provide between-PA habitat connectivity for range shifting species in Chapter 5. This shows they are likely to be important places where PA expansion should be coordinated between countries, for example when neighbouring countries are designing and implementing their national biodiversity strategies (NBSAPs) within the CBD's Post-2020 Biodiversity Framework. This coordination is needed to ensure that meeting protected area expansion targets does so in a way that protects important cross-border habitat corridors and meets the needs of species moving through the regions under climate change, rather than just expanding PAs in ways that prioritise present-day, national scale biodiversity (Pouzols *et al.* 2014) (although even this would be an improvement on historical PA designation trends, which have typically involved the protection of land that least conflicts with agriculture (Venter *et al.* 2018). A second example of overlap concerns the American Midwest, Atlantic Forest, parts of Europe, SE Asia and Southern Australia: all are places where land use is likely to prevent a particularly high proportion of range shifts (Chapter 4), and also where a lack of habitat connectivity is likely to limit PA colonisations (Chapter 5). In these places, restoration could provide suitable habitat for many species to colonise, as well as providing "stepping stones" or corridors that enable them to pass through the landscape to reach more hospitable areas further afield.

These correlations amongst impacts can be both reassuring and challenging for conservation. On one hand, conservation funds could be spent more pragmatically in fewer places and tackle several issues at once – for example it's possible to imagine a landscape-scale cross-border initiative to protect and restore habitat in a way that improves habitat connectivity and land-use suitability for range-shifting species, and simultaneously improves cross-border collaboration. By targeting such efforts to key areas that I have identified (for example in East Africa, tropical Andes and near the Himalayas) many of the challenges I have identified for conservation under climate change could be addressed together. On the other hand, these overlapping challenges might complicate conservation. I highlighted the importance of preserving habitat connectivity between protected areas south of the Himalayas, but I also found that this is a region where border infrastructure is being expanded and may obstruct movement for less mobile mammal species – for example along India's borders with Myanmar, Pakistan, and Bangladesh. This again reinforces my conclusion from Chapter 3 that socio-political context is critical, and if these overlapping impacts occur in places where governance and control of corruption are weaker, for example (and therefore where conservation action is less likely to be successful (Amano *et al.* 2018)), opportunities may have a high probability of failure or low return on investment even if the conservation benefits look good on paper.

In addition to these recurrent spatial patterns, there are some non-spatially explicit patterns in the data worth highlighting, where impacts are correlated amongst species rather than amongst places. For example, in Chapter 2, I showed that habitat generalists (specifically, species that occupy more types of IUCN habitat category) are less likely to see range contractions under climate change – probably because they are tolerant of a broader range of climatic conditions and therefore less prone to seeing their climatic niche shrink or disappear. In Chapter 5, I also showed that habitat generalists tended to have higher PA connectivity scores. Together, these findings suggest that not only are habitat generalists less prone to range contractions but also that they'll find their expected range shifts and expansions easier to fulfil. These processes corroborate and expand on other work showing how processes of global change are likely to homogenise biodiversity assemblages around the world by favouring widespread generalists over narrow-ranged specialists (Newbold *et al.* 2018).

The importance of spatial scale

A recurrent broad theme in this thesis is the importance of spatial scale. A systematic assessment of threatened species found that 20% of terrestrial birds and 10% of terrestrial mammals currently depend on broad (landscape) scale conservation (Boyd *et al.* 2008). Under climate change, this is likely to become increasingly important as species distributions change. In Chapter 3, I showed how thinking beyond the national scale will be essential to protect nature under climate change, since around a third of species' climatic niches are projected to shift into other countries. In Chapter 5, the importance of broad-scale thinking was emphasised again – particularly the need to think beyond species current distributions when designing protected area policy, and think beyond PAs themselves to include the broader landscape, which I demonstrated to be crucial for understanding species abilities to colonise PAs.

Chapters 4 and 5 also demonstrated the importance of refining coarser-scale SDM projections with information that is more relevant at finer scales, such as land-use, land cover and habitat connectivity (Pearson & Dawson 2003). In Chapter 4, including a more locally-relevant land-use constraint revealed how this is likely to limit range shifts for more than three-quarters of species. Scale was particularly important in Chapter 5, in which I combined broad scale range shift projections with fine scale (1km^2) habitat data to understand how the more granular consideration of habitat connectivity will enable or impede the broader-scale process of PA colonisation. Although I didn't explore it in this thesis, an emerging area of research concerns fine-scale climatic considerations such as the ability of microclimate to buffer broader scale climate changes or provide local climatic refugia (Senior *et al.* 2018). Including microclimatic information has the potential to improve biodiversity projections under climate change by reducing discrepancies between the climate data used in modelling, and the climate actually experienced by the study organisms (Bütikofer *et al.* 2020). This information will be important to integrate into broader-scale projections of climate impacts as data and methods become available.

More generally, this thesis has taken a global perspective, in an attempt to assess how conservation can best protect Earth's terrestrial mammal and bird diversity in the face of global processes of change. Inevitably, this global perspective may come at the cost of accuracy in a given locality or for a given species, where local or species-specific circumstances will partially determine climate change outcomes and conservation options. Some have recently challenged the utility of global mapping for conservation in general (Wyborn & Evans 2021), on the grounds that it "erases local context and difference" and that most conservation decisions do not occur at the global scale. However, this framing has been argued to constitute a false dichotomy between local and global scale methods (Chaplin-Kramer *et al.* 2021), when in fact information at a variety of scales is useful and should instead be better integrated. Global scale analyses, like the ones I have presented in this thesis, remain useful for several purposes, such as providing broader context for local decisions; to inform agendas and target setting that take place at supranational scales such as under the CBD or by international conservation organisations; for understanding trade-offs between local, national and global priorities; and identifying knowledge gaps in finer-scale information (Chaplin-Kramer *et al.* 2021). For example, my global-scale analyses have revealed important biogeographical predictors of species responses to climate change that wouldn't have been detectable at finer scales (Chapter 2); have directly demonstrated the importance of thinking beyond the national level for climate-smart conservation (Chapter 3); and shown how more locally relevant and species-specific information can be incorporated in global analyses to better understand conservation challenges and priorities globally (Chapters 4 & 5). The global perspective I have taken should be seen as complementary to – and by no means a replacement for – more locally-focussed research, which remains important to add nuance and rich contextual information, empower those with agency to enact change, and amplify the voices of those affected by conservation on the ground.

Key sources of uncertainty & future research priorities

Uncertainty in climate and land-use projections

A key challenge in modelling biodiversity change is the large uncertainty surrounding how climate change, land-use change and their interactions will unfold. Climate change is typically modelled as a gradual process, but climatic variability on annual or decadal timescales is likely to play an important role in shaping species range shifts and other biodiversity outcomes (Early & Sax 2011). On even shorter timescales, extreme weather events that interact with longer-term climatic trends are likely to be very important too (Smith 2011; Sanz-Lázaro 2016; Harris *et al.* 2018), but are inherently unpredictable and difficult to incorporate into long term and broad scale climate projections. Fortunately, our understanding of the causes and patterns of extreme weather is improving, frameworks exist to incorporate both 'presses' and 'pulses' into our understanding of climate impacts (Harris *et al.* 2018), and the increasing availability of remotely sensed data at fine spatial and temporal resolutions may help (Ummenhofer & Meehl 2017). The development of more mechanistic models to understand how ecosystems respond to extreme events, and improved long-term monitoring of ecosystems to capture the before-and-after of extreme weather, should be research priorities.

In addition to the uncertainties arising from climate impacts, land-use change projections are also highly uncertain, and in general land-use-and-biodiversity models are less numerous than those assessing climate impacts (Titeux *et al.* 2017). This partly arises from a lack of land-use projections that are suitable for modelling biodiversity responses. The best available land-use projections at broad scales, such as those used in Chapter 4, have a coarse spatial resolution and relatively few land-use classes (e.g. pasture, forest, cropland), which are more concerned with vegetation types relevant to the climate system rather than being as useful as possible from a biodiversity modelling perspective (Titeux *et al.* 2017). A broader range of models, at finer spatial resolutions, designed with the biodiversity community in mind is an important area for future research.

Furthermore, we need a better understanding of how human responses to climate change interact with land-use. The areas climatically suitable to grow specific crops are likely to change, driving new frontiers of land-use change and habitat loss. Tropical montane ecosystems could be impacted by coffee needing to be grown at higher elevations to maintain yields, for example (Magrach & Ghazoul 2015), while threatened Mediterranean ecosystems could be impacted by the shifting and expanding footprint of viniculture as climate change causes declining grape yields in existing areas of production (Hannah *et al.* 2013). There is also uncertainty surrounding how climate change will affect the feasibility of habitat restoration. This was one of the caveats of Chapter 5, in which I relied on present-day habitat data to model climate connectivity and identify restoration and PA-expansion priorities. Fortunately, recent work using dynamic global vegetation models projected to 2100 concluded that climate impacts will likely not hinder tropical reforestation efforts under any of the IPCC climate scenarios (Koch & Kaplan 2022). Further research into how climate change is likely to drive land-use and land-cover change, incorporating more realistic human decision making, is needed to identify conservation challenges and opportunities more accurately.

Another key source of uncertainty for both climate and land-use projections is the presence of abrupt tipping points: thresholds determined by feedback loops within the Earth system, beyond which dramatic and irreversible changes may suddenly occur (Lenton *et al.* 2008b; Lenton 2011). One of the most well studied examples involves sudden changes to Atlantic thermohaline circulation in response to freshwater forcing (Stocker & Wright 1991; Rahmstrof *et al.* 2005), linked to melting of the Greenland Ice Sheet – itself another climate tipping point (Toniazzo *et al.* 2004; Lenton *et al.* 2008b). As another example, there are signs that large areas of the Amazon forest, especially areas that are drier and close to human activity, are approaching a tipping point at which an irreversible transition to a savanna biome may occur (Lovejoy &

Nobre 2018; Boulton *et al.* 2022). Biodiversity loss itself is likely to constitute a planetary-scale tipping point, or “planetary boundary” (Rockström *et al.* 2009), although it is not obvious what components of biodiversity determine this threshold and at which point it may be transgressed at various spatial scales (Mace *et al.* 2014). Many of these tipping points are poorly understood, add considerable uncertainty to the trajectory of climate and land-use change, and are difficult to account for in conservation planning. Advances in earth system modelling, for example making use of deep learning algorithms to provide early warning signals that detect critical thresholds before they are breached (Bury *et al.* 2021), may offer our best hope.

Improving predictions of biodiversity responses

Beyond the uncertainty in projections of climate and land-use change, there are also important gaps in our understanding of biodiversity impacts. In this thesis I have taken correlative SDMs as a starting point, and refined these SDMs with a more mechanistic understanding of how range shifts will unfold, for example by modelling dispersal between protected areas in Chapter 5. The increasing availability of species-specific trait data (e.g. Tobias et al. 2022) offer hope that range shift projections can be made even more realistic through better parameterisation of more mechanistic and process-based models. Beyond range shifts, there is a need to better understand other responses too, such as the role of evolutionary adaptation, phenotypic plasticity, and the potential benefit of climatic and microclimatic refugia (Keppel *et al.* 2012; Michalak *et al.* 2018; Oostra *et al.* 2018; Labisko *et al.* 2022).

In this thesis, I have focussed on modelling the responses of terrestrial mammals and birds, based on the availability of data on their distributions, habitat requirements and dispersal abilities. These groups are widespread, sensitive to change, and may perform well as surrogates for other taxonomic groups (Larsen *et al.* 2012). Although I found generally consistent responses between birds and mammals, it’s important to remember that they represent a very small fraction of Earth’s biodiversity, and an understanding of how climate change affects other taxonomic groups is desperately needed. In a similar vein, I have tended to rely on richness-based measures of biodiversity, but an appreciation of how climate change affects other facets of biodiversity would be a useful complement to this thesis – for example functional diversity (Stewart *et al.* 2022), phylogenetic diversity (Voskamp *et al.* 2017), and abundance (Howard *et al.* 2015).

Five recommendations for conservation under climate change

I have made more specific recommendations in the context of each chapter, but here I pull out some overarching themes and insights that can be gained from this thesis as a whole.

Consider range-shifting species in PA expansion and habitat restoration targets

Significant expansion of the global protected area estate, and more ambitious efforts to restore degraded lands, are likely to form quantified targets in the CBD's Post-2020 Biodiversity Framework (CBD Secretariat 2021). This action must bring benefits to biodiversity outcomes, rather than just meeting area targets in themselves (Barnes *et al.* 2018; Jetz *et al.* 2021), and must factor in climate change related risks (Arneth *et al.* 2020). I've highlighted several regions where PA expansion may be most beneficial for species on the move, because it will help proactively secure habitats that are suitable for many range-shifting species but are likely to be threatened by future land-use change (parts of tropical Africa, south eastern Brazil and southern Asia). In other places, PA expansion could help to preserve habitat corridors that are important for connectivity between existing PAs (tropical Andes, East Africa, and southern Himalayas). Restoration may be most beneficial where I showed land-use impacts to be a significant constraint on range shifts and where PA connectivity is lower, such as Brazil's Atlantic Forest, SE Asia, American Midwest, Western Europe, Madagascar and southern Australia. Importantly, many of the places that I've highlighted as priorities for protection and restoration are present-day biodiversity hotspots (Myers *et al.* 2000b) or places where restoration would also benefit present-day biodiversity in a cost-effective manner (Strassburg *et al.* 2020), suggesting that better resourcing in these areas could bring substantial benefits both now and in the future.

For example, several of my analyses highlighted the importance of protecting montane habitats and species, which are likely to be particularly threatened by climate change and provide important refuge for range shifting species from lower elevations. This was especially true where mountain ranges coincide with biodiversity hotspots, such as in the tropical Andes, East African Rift and southeastern Himalayas. These are already places where there have been recent calls to increase conservation attention: tropical cloud forests, for example, occupy 0.4% of Earth's land surface but harbour more than 15% of global diversity of birds, mammals, amphibians and tree ferns – but 2.4% of these critically important forests were lost between 2001-2018, a large proportion of which occurred despite formal protection (Karger *et al.* 2021).

Prioritising the (effective) protection of these places is essential to protect biodiversity both today and under climate change. More generally, my research shows that incorporating climate change into the Global Biodiversity Framework need not necessarily conflict with existing conservation priorities, but instead reinforces the need for better resourcing in critical conservation hotspots.

Tackle the cause as well as the symptoms

Expanding PA coverage and habitat restoration are both important, but I have repeatedly shown that the greatest "gains" (relative to the counterfactual) will be made by deep, rapid cuts to greenhouse gas emissions to prevent dangerous levels of climate change in the first place. For example, in Chapter 2, I showed how grid cell level bird and mammal richness was expected to decline by 6.4% under RCP2.6, but 18.9% under RCP 8.5. In Chapter 3, I showed that medium and high scenarios (RCP 4.5, RCP 6.0, and RCP 8.5) result in the greatest climate impacts on biodiversity affecting the poorest countries, but this relationship disappears under a low emissions scenario (RCP 2.6) because the worst impacts are avoided. In Chapter 4, I showed that the combined effects of climate change and land-use change under a fossil-fuelled development scenario would lead to dramatic biodiversity declines on every continent, while a sustainable development trajectory that limits warming to less than 2°C greatly reduces these impacts and puts the possibility of positive biodiversity change within reach. This was most clear in Africa, where climate and land-use change would cause richness declines of around 25% by 2070 under a fossil-fuelled development scenario, but less than 5% under a more sustainable trajectory.

The impacts of even moderate emissions scenarios (similar to current pledges) are severe enough that ratcheting up climate ambition to limit warming to below 2°C in line with the Paris Agreement should be seen as essential, or else meeting the long-term goals of the post-2020 biodiversity framework will be very difficult indeed (Arneth *et al.* 2020). However, adaptation and mitigation can be tackled simultaneously through the adoption of nature-based solutions (Seddon *et al.* 2020). In Chapter 5, I highlighted places where restoration to enhance climate connectivity between protected areas might be most useful – an example action that would both sequester carbon and help facilitate range shifts to enable species to cope with climate change.

Consider multiple and interacting pressures together

It's important to consider how multiple pressures on biodiversity may act synergistically to cause biodiversity loss. Research in this area has been lacking; in a synthesis of over 44,000 articles on the drivers of biodiversity loss, only 12%

considered more than one driver (Mazor *et al.* 2018). In Chapter 4, I showed that climate change is likely to be a greater driver of loss in the future than land-use change, but this is partly because land-use will restrict the abilities of 77% of birds and mammals to colonise new places. Taking the example of species projected to see a 90% decline in range size, I also found that considering climate change or land-use change in isolation is likely to miss between 4-17% of these severely impacted species (depending on the future socioeconomic scenario), because for some species future land-use change is projected to particularly affect their future range. In Chapter 5, I showed that habitat connectivity between PAs is an important consideration for range shifting species, and that many of the places with low PA connectivity were areas affected by severe habitat fragmentation, such as Brazil's Atlantic Forest and Western Europe, underscoring the importance of considering how different pressures on biodiversity interact. Failing to do so is likely to miss places and species threatened by global change, give an inaccurate picture of the impacts of human activity, and potentially lead to the mis-prioritisation and misallocation of conservation funds.

Improve monitoring of species distributions

Highly variable detectability and sampling effort make detecting and documenting range shifts for many species challenging (Bates *et al.* 2015). Systematic and standardised monitoring networks should be established to facilitate early detection of range shifts (Shoo *et al.* 2006; Amorim *et al.* 2014), and these could be prioritised to places where range shifts are expected to be most numerous. This may be particularly important to identify range contractions, in order to respond to rapid declines with timely conservation interventions. Furthermore, as species distributions continue to change, and these changes become increasingly well documented, there will be important opportunities to validate and refine predictions of range shifts and extinction risk with real world data.

Scale up conservation – but stay locally relevant

In the face of climate change, conservation action needs to balance scaling up (to address broad-scale biodiversity changes) with remaining sensitive to local contextual information. Planning conservation at the landscape scale, involving a variety of stakeholders, may be an effective way to do this (Donaldson *et al.* 2016; Baldwin *et al.* 2018; von Holle *et al.* 2020). Climate change will require greater collaboration between protected area managers and within a landscape, including across national borders. At a higher level, as the establishment and expansion of PAs continues in the Post-2020 Biodiversity Framework, neighbouring countries should be encouraged to coordinate their national implementation strategies to jointly maximise conservation gains and preserve or restore climate connectivity. This will be particularly important for smaller countries, or in regions highlighted in my analysis of important regions for transboundary conservation in Chapter 3. Encouragingly, transboundary conservation efforts are on the rise, with increasingly numerous examples of cross-border initiatives resulting in positive outcomes for biodiversity (Liu *et al.* 2022). Under the demands placed on landscapes by climate change, the role of protected areas may need to be reframed: PAs will remain of fundamental importance to conservation, but should be considered a necessary but not sufficient component of a landscape's biodiversity strategy.

Scaling up conservation action to meet the challenge of climate change need not come at the expense of local knowledge and fine-scale contextual considerations. Rather, embracing initiatives at the landscape scale is an important opportunity to bring more voices to the table from diverse stakeholders, ranging from local communities, conservation organisations, government actors, and private sector representatives. This diverse set of perspectives will be essential if the conservation is to meet the ambitious but critically important goals in the Post-2020 Framework in a way that is equitable, embedded into the broader development agenda, and effective at slowing biodiversity loss in the face of broad-scale and powerful processes of change.

Conclusions

In this thesis I have provided fresh insight into the patterns of terrestrial mammal and bird biodiversity loss from climate change, and the drivers behind those patterns; the socio-political context of these impacts; how climate change interacts with land-use change; and how global conservation can help species adapt to climate change as a global redistribution of species is underway. Meeting the long-term goals of the drafted Post-2020 Biodiversity Framework in world affected by climate change will be a formidable challenge, but I have shown that for terrestrial mammals and birds it is not an insurmountable one. Swift emissions reductions in line with the Paris Agreement must be combined with the sustainable intensification of food production and a decreasing agricultural footprint, and complemented by ambitious, broad-scale and collaborative conservation initiatives to protect and restore landscapes in which human societies, and the natural world in which they are embedded, can both flourish.

Appendix A: Supporting Material for Chapter 2

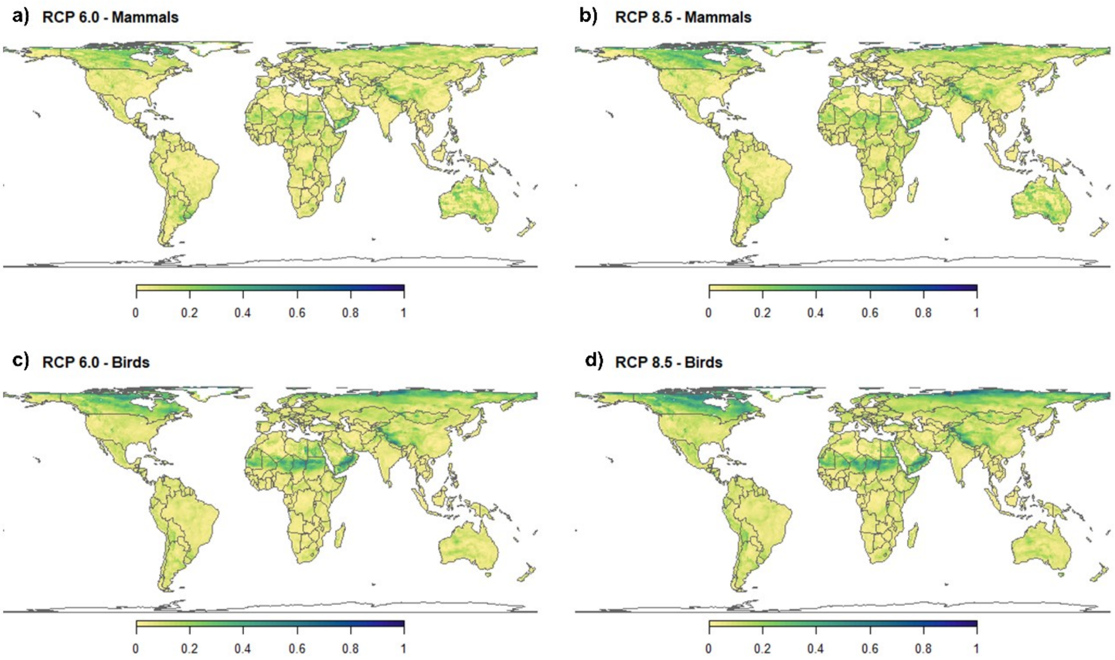


Figure S1: Community novelty (proportion of future species that are new to each grid cell) for mammals (a & b) and birds (c & d) under the two higher-emissions climate scenarios, RCP 6.0 (a & c) and RCP 8.5 (b & d)

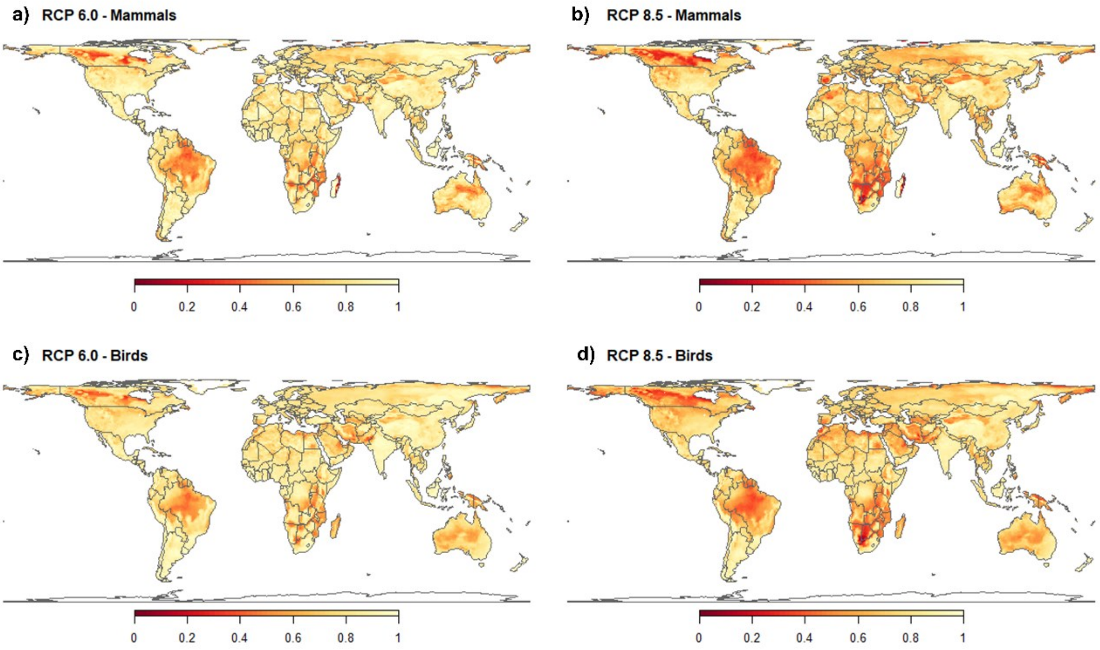


Figure S2: Community persistence (proportion of species able to persist in 2070) under the two higher emissions scenarios, RCP 6.0 (a & c) and RCP 8.5 (b & d). Results are shown separately for mammals (a & b) and birds (c & d).

Appendix B: Supporting Material for Chapter 3

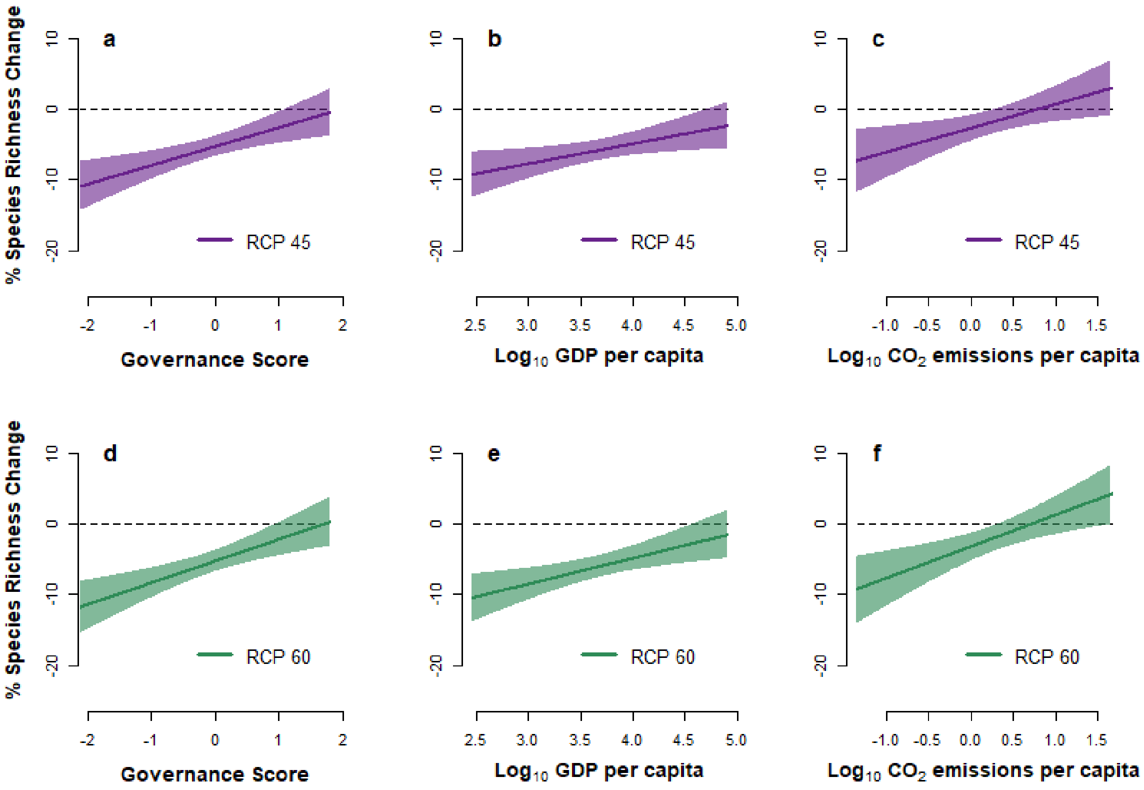


Figure S1. National context of projected changes to terrestrial mammal and bird richness for RCP 4.5 and RCP 6.0. Lines show modelled linear relationships between mean percentage change in species richness across all grid cells in each country and the country's governance score (a and d), GDP (b and e), and CO_2 emissions (c and f). a-c are under RCP 4.5 and d-f under RCP 6.0. As with Fig 1, relationships for bird richness change with CO_2 emissions were not statistically significant (see Table S1) so panels c and f show relationships with mammal richness change only. All others are for combined mammal and bird richness change. Shaded areas indicate 95% confidence bands.

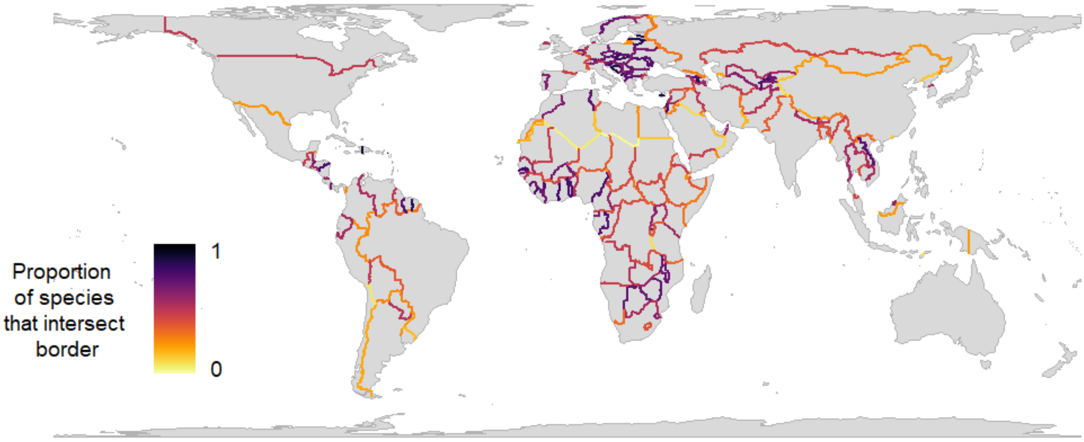


Figure S2. Relative transboundary species richness*.* Borders are coloured according to the proportion of species found in the two countries either side of the border whose ranges intersect the border. This highlights areas where many of the species are 'transboundary', such as western and southern Africa and central Europe. In such areas, transboundary conservation efforts may benefit a disproportionate number of species.

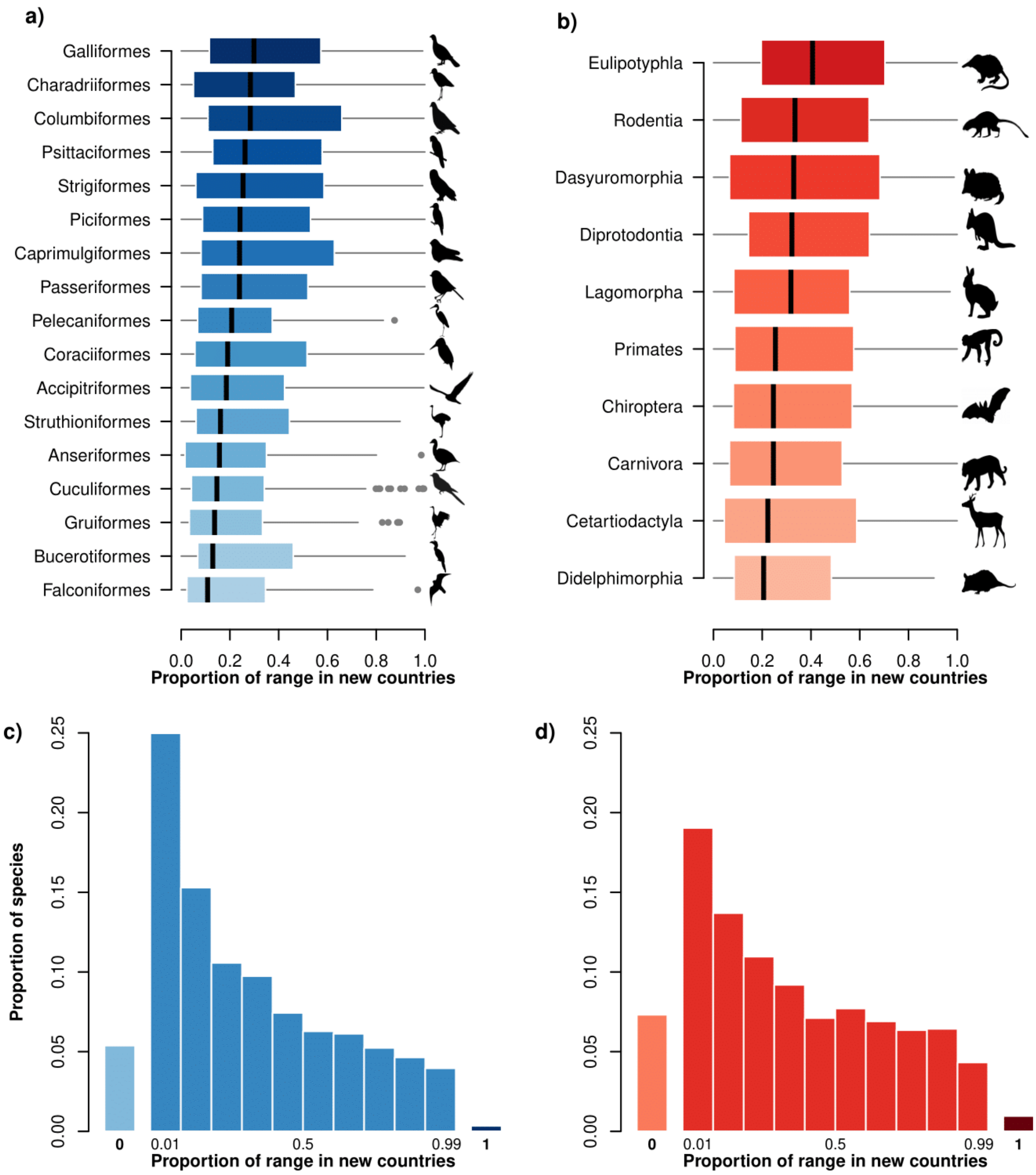
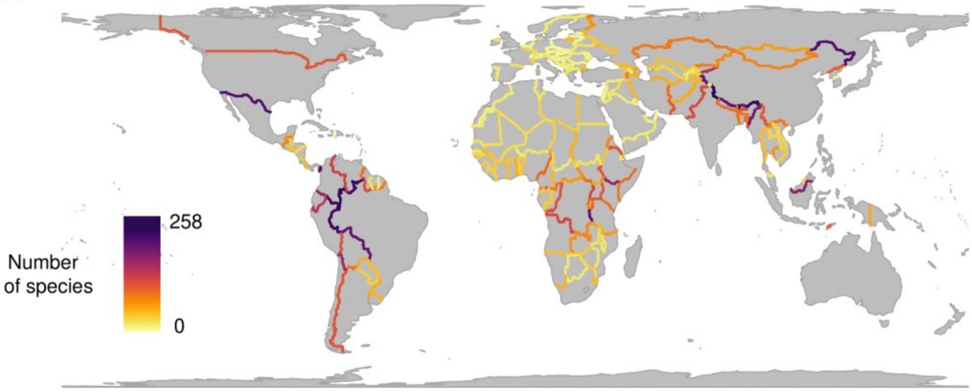


Figure S3: Proportion of species ranges found in ‘new’ countries in 2070 under a moderate emissions scenario (RCP 4.5). Boxplots show the proportion of species ranges in ‘new’ countries (countries in which the species is not currently found) for birds (a) and mammals (b) broken down by taxonomic order. For clarity, only orders with 50 or more modelled species are shown. Beneath, histograms show the proportion of all modelled birds (c) and mammals (d) with a given proportion of their 2070 range in ‘new’ countries, under RCP 4.5. Bars are plotted separately (labelled 0 and 1) for the special cases in which species are projected to have none or all of their future niche in new countries

(a) Mammals – RCP 4.5



(b) Birds – RCP 4.5

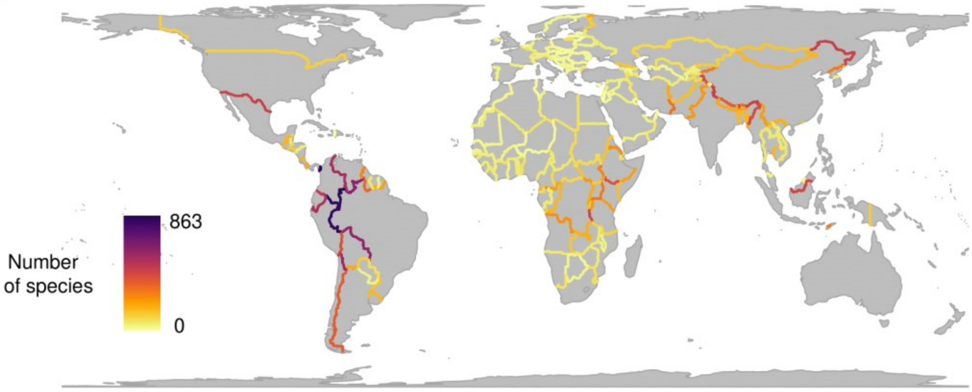
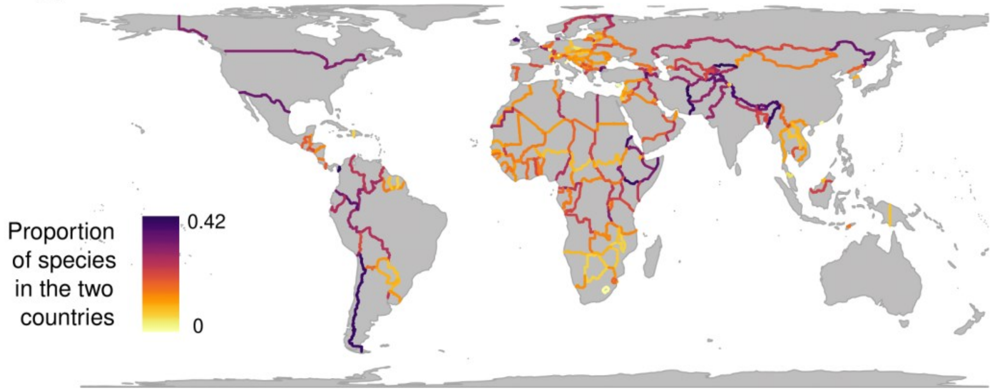


Figure S4. Projected transboundary range shifts for terrestrial mammals and birds under climate change under a moderate emissions scenario (RCP 4.5). National political borders are coloured according to the number of mammal or bird species whose ranges are projected to cross that border under RCP 4.5.

(a) Mammals



(b) Birds

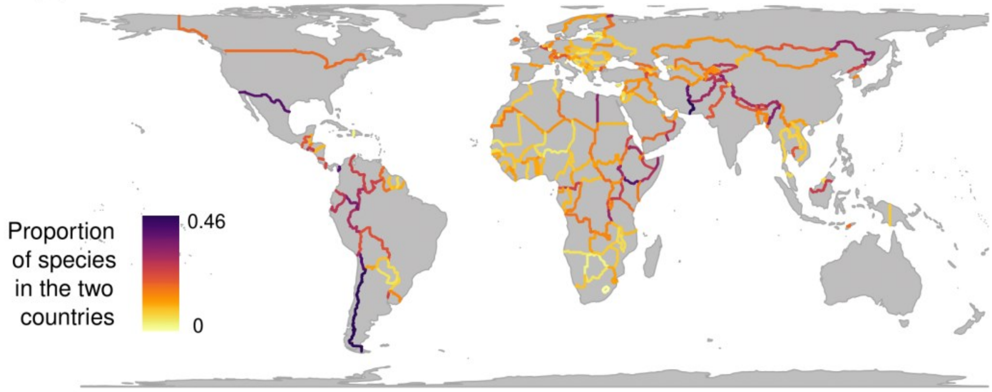
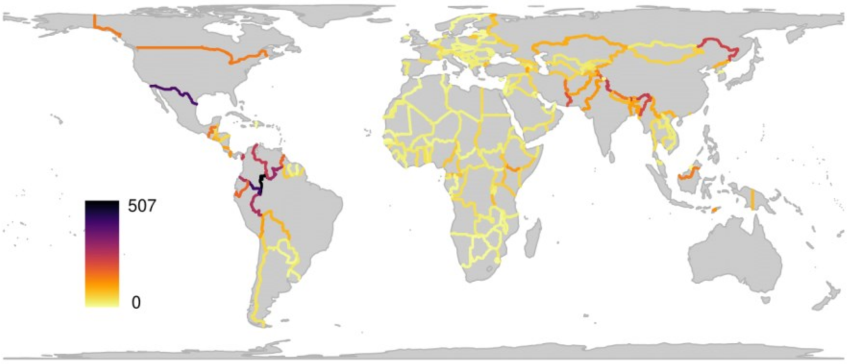
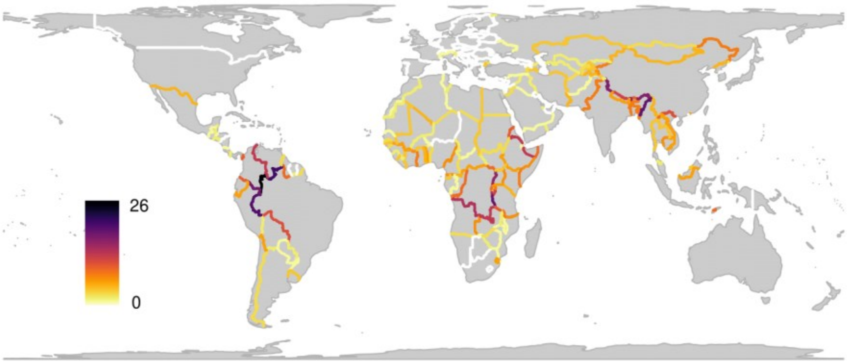


Figure S5. Transboundary range shifts relative to species richness. Borders are coloured according to the number of species' of (a) mammal and (b) bird whose ranges are projected to move across each political border under RCP 8.5, relative to the total number of species of bird or mammal in each country pair.

a) Species with >50% range in new countries



b) 'Charismatic' species



c) CITES species

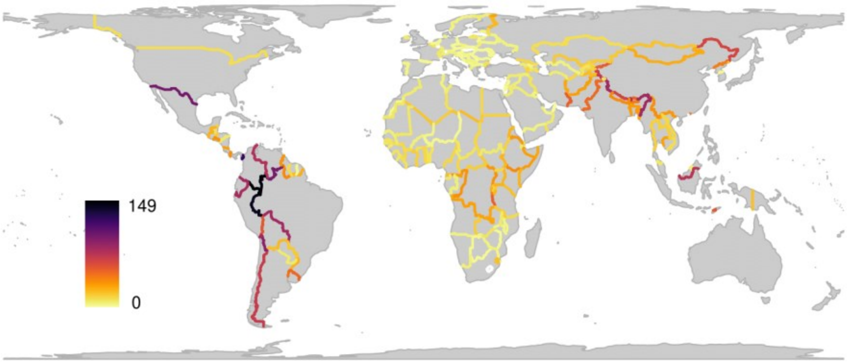


Figure S6: Transboundary range shifts for selected subsets of species. Projected transboundary range shifts (2070, RCP 8.5) are shown for three subgroups of species of particular conservation interest: species that have the majority of their range in new countries (a), ‘charismatic’ groups of mammals species that are likely to be economically valuable for wildlife tourism (b), and species listed under the appendices of CITES (Convention on International Trade in Endangered Species) (c). The ‘charismatic’ species considered in (b) include mammals Felidae (cats), Ursidae (bears), Hyaenidae (hyeanas), Rhinocerotidae (rhinoceroses), Elephantidae (elephants), and Canidae of the genera *Canis* and *Lycaon* (wolves and painted dogs), along with the common hippopotamus, giraffe, African buffalo and the three zebra species (di Minin *et al.* 2013; Maciejewski & Kerley 2014; Albert *et al.* 2018). We also included primates from the families Hominidae (great apes), Cebidae (capuchins and squirrel monkeys), Atelidae (howler, spider and woolly monkeys), Cercopithecidae (Old World monkeys) and Hylobatidae (gibbons)

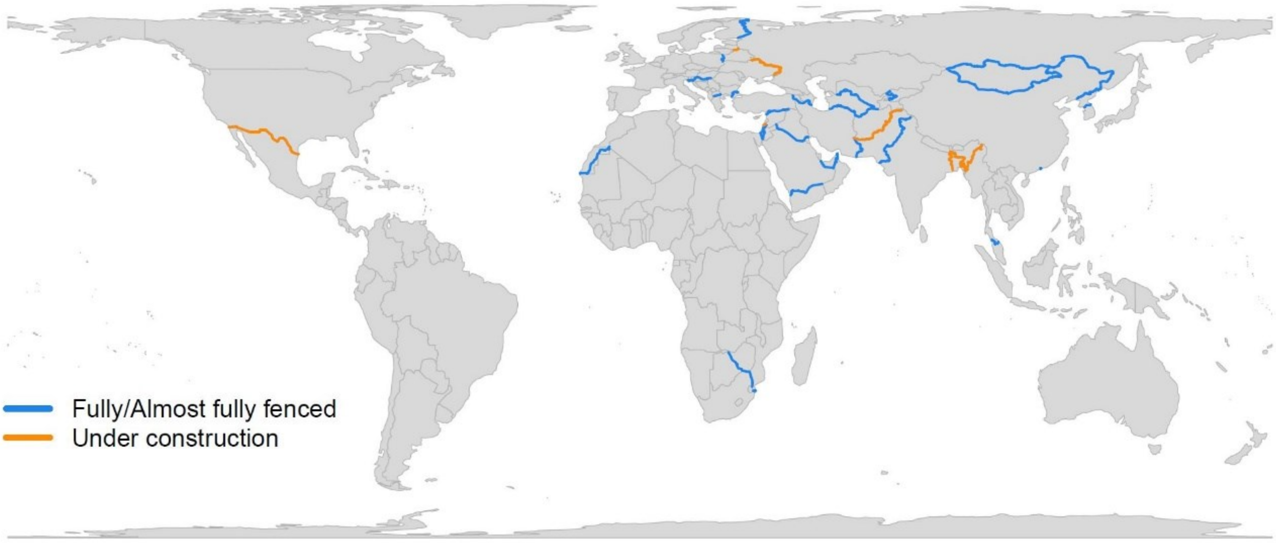


Figure S7: Global map of national borders that have physical barriers such as walls and fences across their entire length (blue) and borders where physical barriers are under construction (orange).

Figure S8: Projected range shifts of non-flying mammals (2070, RCP8.5) across borders that are fortified with walls or fences (including those under construction). The proportional range shift score sums together, for all species that cross that border, the proportion of their range that crosses it. As with the number of species projected to cross each border (Fig 4c), the USA-Mexico border, the India-Myanmar border and the China-Russia border rank highest.

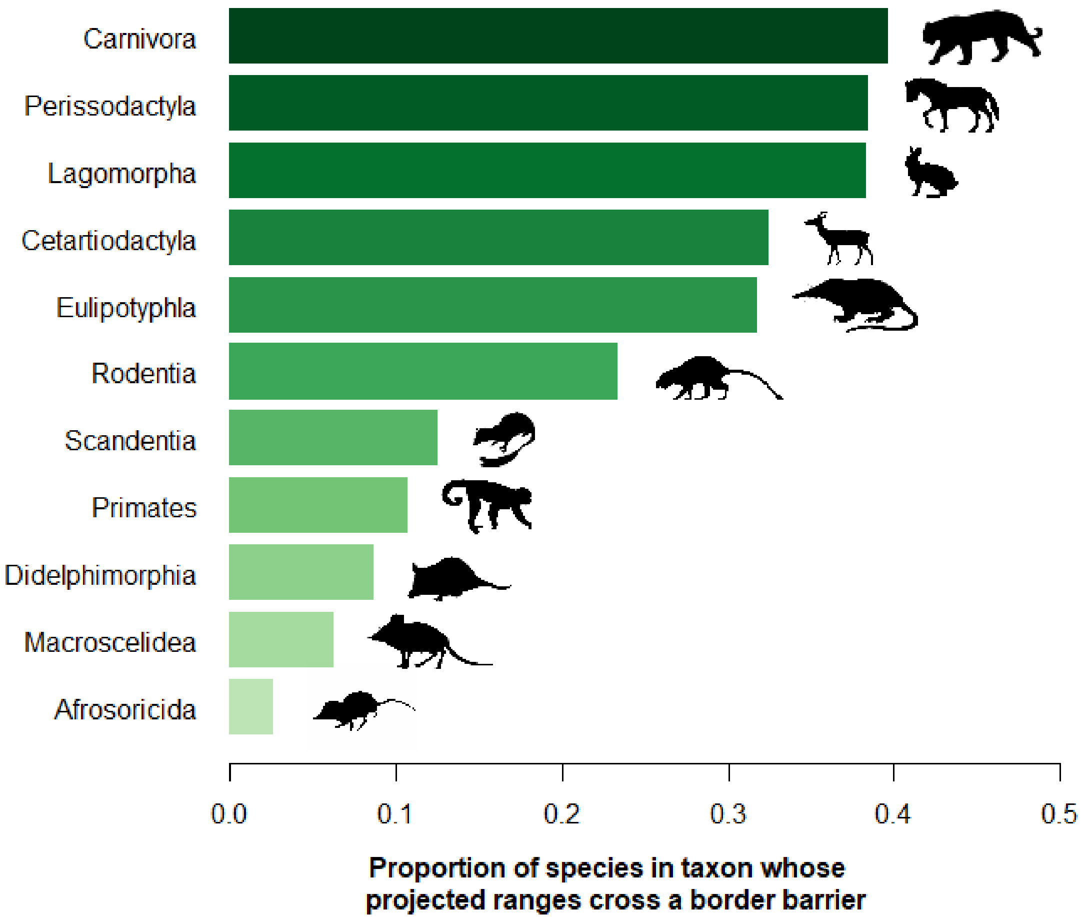


Figure S9: Proportion of species in mammalian orders whose ranges are projected to cross a border barrier under climate change (projecting to 2070 under RCP 8.5). The order Chiroptera (bats) was excluded, as well as orders that contained fewer than 10 modelled species.

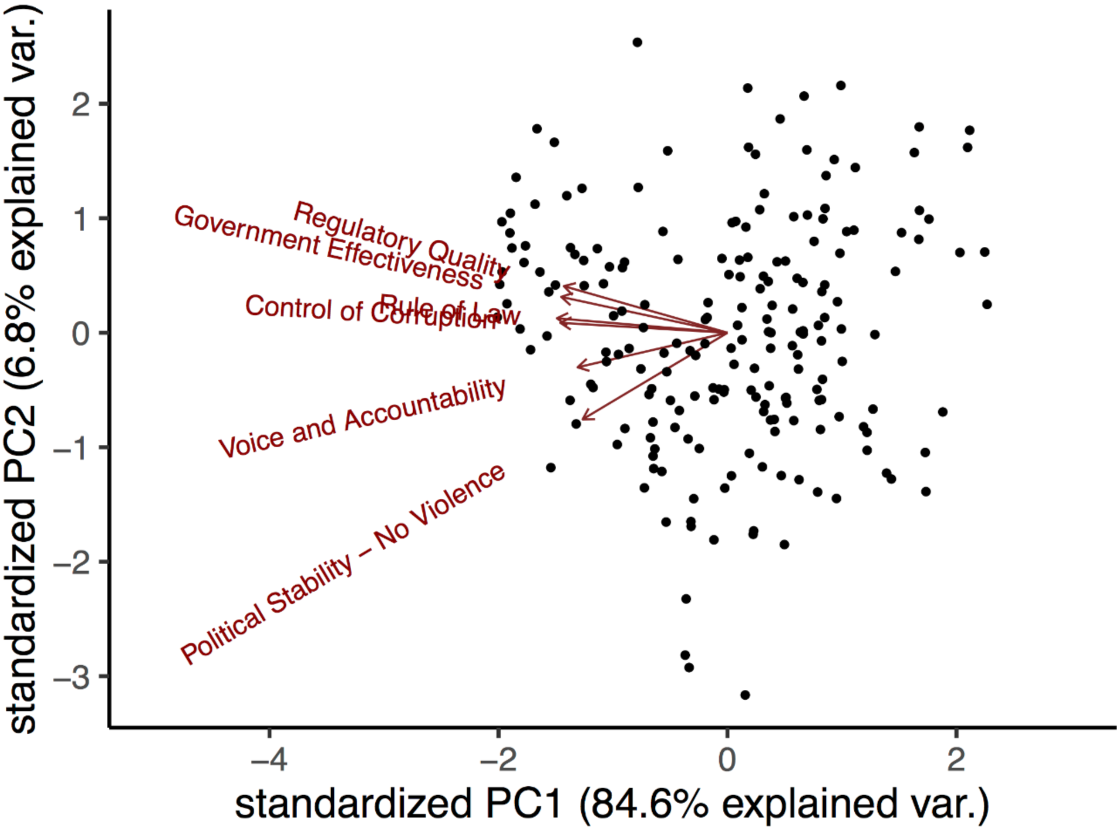


Figure S10. Principal Components Analysis (PCA) of the six governance scores provided by the World Bank (The World Bank 2019) showing a high level of inter-correlation, supporting our decision to follow (Amano *et al.* 2018) and aggregate them into a single indicator of governance quality by taking the mean of all six for each country. Each data point represents a country.

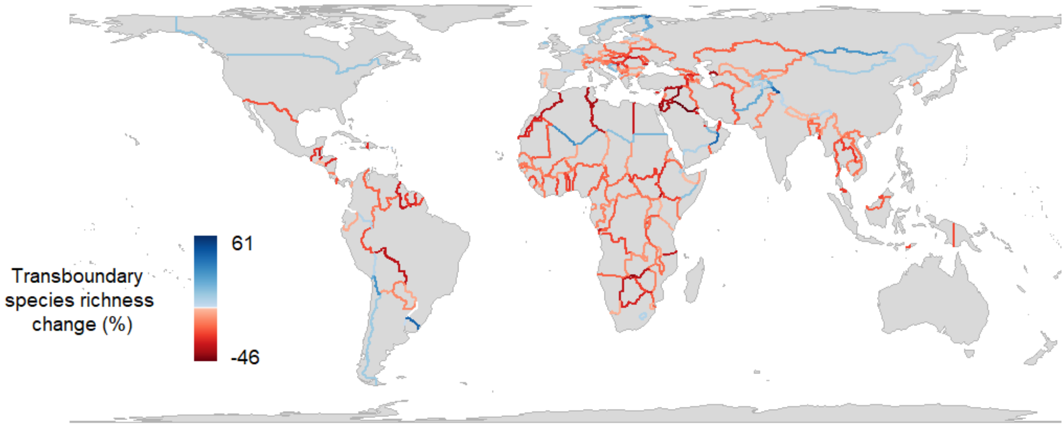


Figure S11: Projected percentage change in transboundary species richness (the number of species whose ranges intersect each political border), comparing present day to 2070 under RCP 8.5.

Table S1. GLM model coefficient estimates and significance values. In each case the response variable is national level percentage change in species richness by 2070 (averaged across all half-degree grid cells within a country). P values and t values shown are for the slope estimate. · P < 0.1, * P<0.5, ** P < 0.01, *** P < 0.001.

Taxon	**Predictor variable**	**Scenario**	**Intercept**	**Slope**	**t value**	**P value**
Both	Governance score	RCP 2.6	-1.876	1.330 *	2.056	**0.0413**
		RCP 4.5	-5.268	2.642 **	3.332	**0.00105**
		RCP 6.0	-5.256	3.082 ***	3.701	**0.000288**
		RCP 8.5	-9.827	3.904 ***	3.904	**0.000135**
Both	Log$_{10}$ GDP per capita	RCP 2.6	-7.664	1.435	1.464	0.1452
		RCP 4.5	-16.137	2.813 *	2.374	**0.018819**
		RCP 6.0	-19.472	3.660 **	2.942	**0.00375**
		RCP 8.5	-27.633	4.582 **	2.790	**0.00592**
Both	Log$_{10}$ CO$_2$ emissions per capita	RCP 2.6	-2.411	0.742	0.846	0.398751
		RCP 4.5	-5.800	1.498	1.341	0.182
		RCP 6.0	-6.213	2.212 ·	1.881	**0.0617**
		RCP 8.5	-10.844	2.403	1.472	0.143
Mammals	Governance score	RCP 2.6	1.060	2.580 ***	3.386	**0.000886**
		RCP 4.5	-1.041	4.227 ***	4.656	**6.56x10^{-6}**
		RCP 6.0	-1.210	4.704 ***	4.799	**3.54x10^{-6}**
		RCP 8.5	-4.697	6.724 ***	5.324	**3.26x10^{-7}**
Mammals	Log$_{10}$ GDP per capita	RCP 2.6	-14.011	3.881 ***	3.304	**0.00118**
		RCP 4.5	-23.424	5.806 ***	4.189	**4.64x10^{-5}**
		RCP 6.0	-28.136	7.009 ***	4.750	**4.54x10^{-6}**
		RCP 8.5	-40.086	9.246 ***	4.938	**1.99x10^{-6}**
Mammals	Log$_{10}$ CO$_2$ emissions per capita	RCP 2.6	-0.301	2.416 *	2.308	**0.0222**
		RCP 4.5	-2.700	3.421 **	2.661	**0.00855**
		RCP 6.0	-3.297	4.474 **	3.258	**0.00136**
		RCP 8.5	-7.165	5.518 **	3.036	**0.00279**
Birds	Governance score	RCP 2.6	-2.771	0.950	1.419	0.158
		RCP 4.5	-6.393	2.388 **	2.887	**0.00441**
		RCP 6.0	-6.475	2.660 **	3.065	**0.00254**
		RCP 8.5	-11.448	3.860 **	3.241	**0.00144**
Birds	Log$_{10}$ GDP per capita	RCP 2.6	-5.363	0.543	0.537	0.592
		RCP 4.5	-13.289	1.660	1.367	0.17343
		RCP 6.0	-16.333	2.429 ·	1.918	**0.056978**
		RCP 8.5	-23.101	2.846 ·	1.702	**0.090801**
Birds	Log$_{10}$ CO$_2$ emissions per capita	RCP 2.6	-3.175	0.070	0.077	0.939
		RCP 4.5	-6.922	0.664	0.577	0.565
		RCP 6.0	-7.297	1.305	1.084	0.280
		RCP 8.5	-12.277	1.132	0.679	0.498

Appendix C: Supporting Material for Chapter 4

IUCN / LUH2 crosswalk

IUCN name	IUCN code	LUH2 categories	Additional notes / justification
Forest	1	primf, secdf	Plus additional rule that secdf >30yrs if species is forest specialist
Savanna	2	primn, secdn, pastr, range	Models supports including pasture and rangeland
Shrubland	3	primn, secdn,range	Model supports including rangeland
Grassland	4	primn, secdn, range	Model supports including rangeland
Wetlands	5	primn, secdn	
Rocky areas	6	primn, secdn	
Caves and subterranean habitats	7	primn, secdn	
Deserts	8	primn, secdn	
Arable land	14.1	c3ann, c4ann, c3per, c4per, c3nfx	Model actually only supports annual and nfx crops but best to include all crops for completeness (IUCN documentation says orchards / perennial crops included in this classification)
Pastureland	14.2	pastr, range	Model supports including rangeland here - makes sense given lack of rangeland classification in IUCN scheme
Plantations	14.3	c3per	This had the most support by far.
Rural gardens	14.4	c3ann, c4ann	These two strongly supported by the regression – supported by IUCN description of rural gardens
Urban areas	14.5	urban	
Subtropical tropical heavily degraded former forest	14.6	secdfu30	Additional rule that secondary forest must be under 30 years old

LUH2 categories: primary forest (primn), secondary forest (secdf), primary non-forest (primn), secondary non-forest (secdn), managed pasture (pastr), rangeland (range), urban areas (urban), c3ann (c3 annual crops), c4ann (c4 annual crops), c3per (c3 perennial crops), c4per (c4 perennial crops), c3nfx (c3 nitrogen fixing crops).

Appendix D: Supporting Material for Chapter 5

Table 1: Results of Tukey's Honest Significant Differences test showing pairwise comparisons of species' PA connectivity scores between different IUCN Red List categories. Differences with adjusted P-values lower than 0.05 are highlighted in bold. This analysis was performed post-hoc following an ANOVA revealing that there were statistically clear differences between the Red List categories (ANOVA, F=16.6, df=5, p < 0.0001).

Pairwise Comparison	Difference	Adjusted P value
VU-EN	0.000404	1
NT-EN	0.04056	0.526728
CR-EN	0.062132	0.649812
LC-EN	**0.095513**	**6.47×10^{-5}**
DD-EN	0.042911	0.772368
NT-VU	0.040157	0.22489
CR-VU	0.061728	0.575587
LC-VU	**0.095109**	**6.05×10^{-11}**
DD-VU	0.042507	0.670056
CR-NT	0.021571	0.992422
LC-NT	**0.054952**	**0.000148**
DD-NT	0.00235	0.999999
LC-CR	0.033381	0.935651
DD-CR	-0.01922	0.997838
DD-LC	-0.0526	0.300561

Table 2: Coefficients for GLM estimating the effect of habitat variables (proportion of a species' AOH made up of different habitat types, as well as number of habitat categories suitable for that species) on species' PA connectivity scores. P values lower than 0.05 are highlighted in bold.

Explanatory variable	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-0.41651	0.091569	-4.54865	**5.47E-06**
Forest	1.494696	0.083266	17.95088	**7.30E-71**
Savanna	2.487133	0.125499	19.818	**1.19E-85**
Shrubland	-0.05082	0.104624	-0.48576	0.627152
Grassland	0.733192	0.102657	7.14215	**9.88E-13**
Wetlands	-1.92772	0.159904	-12.0555	**3.20E-33**
Rocky Areas	-1.4071	0.278546	-5.0516	**4.46E-07**
Desert	0.803369	0.148567	5.407455	**6.55E-08**

Number of habitat categories	0.289165	0.018066	16.00608	**6.61E-57**
Area expected to colonise	-1.36E-08	1.05E-08	-1.29457	0.1955

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