Future-proofing conservation: applying systematic conservation planning to prevent extinction under climate and land use change

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Future-proofing conservation: applying systematic conservation planning to prevent extinction under climate and land use change

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Contents

Acknowledgements

This thesis is the product of three and a half years of work. Looking back on where I started, in the depths of a global pandemic, and with everything that has happened since, I realise that my PhD has taken in some very turbulent times on both a global and a personal level. I certainly couldn’t have reached this stage without the help and support of many of the most important people in my professional and personal life.

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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.

Thomas Smart

March 2024

Dedication

To Grandma, and the wonderful life you led.

Abstract

Humans have been reshaping the environment of Earth for thousands of years. However, the intensity of anthropogenic pressures has rapidly increased in recent decades, pushing an ever-greater number of species towards extinction. The primary driver of modern extinctions is habitat loss, while climate change is projected to become the leading cause of biodiversity loss in the future. To mitigate these impacts and reverse these trends, nations have committed to halt the extinction of threatened species by mid-century, and to protect 30% of global land and sea by 2030 (known as the ‘30 by 30’ target). There is now an urgent need to understand how such targets can be achieved in a way that is deliverable, effective, and resilient to future climate and land use change. To answer this question, my thesis considers how systematic conservation planning approaches can optimise conservation interventions both *in situ* (such as protected area planning) and *ex situ* (such as conservation of threatened species in zoos). I show that both existing protected areas and current zoo collections must evolve significantly if they are to avoid being outpaced by anthropogenic environmental change.

First, I model the impact of climate change on most of the world’s terrestrial vertebrate species (n = 24,598), and identify spatial and phylogenetic shifts in the distribution of threatened biodiversity globally. Using these data, I highlight spatial priorities for area-based conservation, achieving 30 by 30 in a manner that maximises the long-term conservation of threatened evolutionary history under environmental change. I then turn to *ex situ* conservation in zoos, finding that collections must adapt significantly if they are to conserve the taxa most threatened by climate and land use change. As zoos must house appealing species that drive visitation rates, I then investigate the traits that underpin species attractiveness to zoo visitors, with highly active, visible mammals proving the most attractive. I use these results to highlight opportunities to leverage species appeal and maximise investment in conservation. Finally, I bring this information together and apply, for the first time, conservation optimisation algorithms to zoo collection planning at global and regional scales. Such approaches can increase the protection of threatened evolutionary history by approximately an order of magnitude, both *in situ* and *ex situ*, relative to existing protected areas and zoo collections, respectively. These results pose both a challenge and an opportunity to the conservation community, highlighting both the scale of adaptation required, but also the huge potential conservation benefits that could be achieved, even as anthropogenic climate and land use change intensify.

Chapter 1

General Introduction

AI-generated artwork created in the ‘dream’ WOMBO app (https://dream.ai/), using the prompt ‘Climate and land use change intensify and exacerbate a Sixth Mass Extinction’ and the ‘Daydream’ art style.

Global biodiversity in crisis

Humans have fundamentally changed the biotic and abiotic environment of the Earth (Goudie, 2018). Our activities are so widespread and environmentally impactful that they may be ushering in a new geological era, ‘the Anthropocene’, equivalent to some of the greatest natural upheavals in the Earth’s deep history (Steffen et al., 2011). One of the most striking human impacts on the environment is vertebrate biodiversity loss, with evidence of human-induced extinctions stretching back tens of thousands of years on all the world’s land masses beyond Africa and Antarctica (Andermann et al., 2020). While co-evolution with hominins meant sub-Saharan Africa suffered fewer extinctions induced by early humans (Andermann et al., 2020), modern anthropogenic pressures are now pushing African biodiversity into decline as well (Ceballos et al., 2017). Extinction rates have rapidly accelerated in recent centuries (Dirzo et al., 2014), especially in the post-industrial period (Pimm et al., 2014; Steffen et al., 2015). We now live in a world where vertebrate extinction rates may be over 100 times the background average (Pimm et al., 1995; Ceballos et al., 2015), where the combined biomass of humans and domesticated mammal livestock is around 50 times that of all wild mammals on the planet (Greenspoon et al., 2023), and where vertebrate populations have declined by an estimated 69%, on average, in the last 50 years alone (WWF, 2022).

This fundamental restructuring of vertebrate life on Earth has major implications for the stability and functioning of natural processes and the ecosystem services that these provide to humans. As generally larger-bodied, mobile taxa, vertebrate communities exert a strong influence on their environment, for example through predation and herbivory (Jefferies et al., 1994; Mooney et al., 2010), carbon and nutrient cycling (Otero et al., 2018; Berzaghi et al., 2019; Tuo et al., 2024), pollination (Fleming and Muchala, 2008; Ratto et al., 2018), and bioturbation and ‘ecosystem engineering’ (Mallen-Cooper et al., 2019; Beca et al., 2022). Disruption of these natural processes therefore threatens some of the vital ecosystem services that nature provides to humans. Humans rely on wild terrestrial vertebrate biodiversity for a range of direct and indirect ecosystem services, including as a direct food source (Green and Elmberg, 2013; Valencia-Aguilar et al., 2013), pollination of cultivated and commercially profitable crops (Trejo-Salazar et al., 2016), biological control of pests and zoonotic disease vectors (Young et al., 2014; Keesing and Ostfeld, 2021; Díaz-Siefer et al., 2022), and the development of ecotourism opportunities (Balmford et al., 2015; Arbieu et al., 2018). Precipitous declines in vertebrate biodiversity therefore not only threatens the resilience of wild ecosystems, but also human health, food security, and wellbeing.

Significant research attention now focuses on identifying the drivers of biodiversity declines globally, highlighting spatial and phylogenetic hotspots of vulnerability and exposure to anthropogenic threats (Harfoot et al., 2021; Jaureguiberry et al., 2022; Munstermann et al., 2022; Gumbs et al., 2023). While the specific drivers of decline in individual species are highly variable (Munstermann et al., 2022), the macroecological drivers of vertebrate biodiversity loss at the global scale are now increasingly well-defined and understood (IPBES, 2019). In 2019 the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) brought together the best available evidence and identified habitat destruction, primarily through agricultural expansion and urbanisation, as the number one driver of biodiversity loss globally (IPBES, 2019). This was followed by direct exploitation (for food, medicine and the illegal wildlife trade), climate change, pollution, and invasive species (IPBES et al., 2019). While anthropogenic climate change currently threatens a relatively small proportion of terrestrial vertebrates relative to habitat loss (Harfoot et al., 2021; Jaureguiberry et al., 2022; Munstermann et al., 2022), climate change is intensifying and represents a rapidly growing threat to global biodiversity (Urban, 2015; IPCC, 2022; Luedtke et al., 2023).

In this thesis, I focus on the twin threats of future climate and land use change on the distribution, diversity, and extinction risk of terrestrial vertebrates globally, and how conservation action can be prioritised in response. My thesis considers the impact of environmental change on two key pillars of global conservation: the spatial prioritisation protected areas to maximise the effectiveness of *in situ* conservation under future conditions; and the optimisation *ex situ* conservation to maximise the conservation of unique and threatened evolutionary history in global zoo collections. To do so, I first assess the current composition of global zoos collections and discuss how future climate and land use change could impact their conservation value in the absence of collection optimisation. I then use a best-practice ensemble species distribution modelling framework (Araújo et al., 2019) to project the impact of environmental change on the distribution and composition of threatened vertebrate biodiversity, and then combine this information with studies on species attractiveness, identifying ‘Cinderella’ species (Smith et al., 2012) that can elicit support for *in situ* and *ex situ* conservation, acting as conservation flagships and drivers of zoo visitation.

Twin threats of climate and land use change

In February 2024 the European Union’s Copernicus climate-tracking service announced that, for the first time, surface temperatures on Earth had exceeded the pre-industrial average by more than 1.5 °C for the preceding 12-month period (Copernicus, 2024a). While natural annual variation coinciding with the El Niño Southern Oscillation event means that data from a single year should not be over-interpreted, recent research has shown that at current emission rates, long-term warming trends could exceed the COP21 Paris Agreement target of 1.5 °C warming by 2029 (Lamboll et al., 2023). Atmospheric concentrations of CO_2 have increased from around 285 ppm in 1850 to 410 ppm in 2019, an increase that is ‘unequivocally’ caused by human activities that have brought about a faster rate of warming than at any time in at least the last 2,000 years (IPCC, 2021). While the Paris targets are still achievable, the window for doing so is closing (Lamboll et al., 2023). More likely future scenarios in line with current international commitments and pledges (Shared Socioeconomic Pathway [SSP] 2-4.5) are predicted to increase global temperatures by 2.7 °C above pre-industrial levels, with a ‘very likely’ range of 2.1-3.5 °C (IPCC, 2021).

Even the relatively modest levels of warming experienced on Earth so far are already having profound impacts on humanity (Carlton and Hsiang, 2016; Coronese et al., 2019) and biodiversity (Chen et al., 2011; Wiens, 2016). Climate change has already impacted biodiversity globally across all scales, from the scale of genes to entire ecosystem functions (Scheffers et al., 2016). One of the most commonly observed impacts of climate change on biodiversity is distributional shifts, including range contractions (Pacifici et al., 2017), localised extinctions (Wiens, 2016), and colonisation of novel habitats (Chen et al., 2011). Typically, these shifts occur in poleward direction (Chen et al., 2011; Vergés et al., 2014), with tropical species increasingly colonising temperate biomes and temperate species moving into boreal and polar regions (Scheffers et al., 2016), or along elevational gradients from lower to higher elevations (Chen et al., 2011; Mamantov et al., 2021). This can lead to the loss of polar or montane endemics either directly through the loss of climatically suitable habitat (the so-called ‘escalator to extinction’; Urban, 2015; Freeman et al., 2018) or indirectly through competitive exclusion by novel colonisers (Watts et al., 2022). Habitat specialists (Socolar and Wilcove, 2019), island endemics (Leclerc et al., 2021), rare species (Pearson et al., 2014), and species with small ranges (Ohlemüller et al., 2008) and limited dispersal capability (Foden et al., 2013) also face elevated vulnerability to climate change.

While climate change will become a leading threat to biodiversity in the future, habitat loss is already pervasive and the number one cause of recent species extinctions (IPBES, 2019). The primary driver of habitat loss is conversion of natural habitats towards agricultural land use, especially for the production of animal products and feed (Alexander et al., 2015; Mair et al., 2021). Today, only a quarter of the world's land mass can be considered 'wilderness', with nearly three-fifths (58%) under considerable human pressure (Williams et al., 2020). While annual rates of land conversion globally may be slowing (Winkler et al., 2021), an area the size of Mexico (1.9 million km^2) of intact land came under significant human pressure between 2000 and 2013 (Williams et al., 2020).

The direct effects of land use change on biodiversity, for example through altering species richness and abundance patterns, extinction risk, community composition, and ecosystem functions, are well documented (Gaston et al., 2003; Newbold et al., 2015; Newbold et al., 2016; Powers and Jetz, 2019; IPBES, 2019; Newbold et al., 2019; Baisero et al., 2020). However, habitat loss and climate change do not impact biodiversity independently (Hof et al., 2018; Williams et al., 2022), rather, they are intrinsically interlinked. A recent study estimated that land use change is responsible for a third of cumulative greenhouse gas emissions since 1750, and was responsible for 13% of emissions over the past twenty years, despite the vast increases in the burning of fossil fuels over the 20th and 21st centuries (Friedlingstein et al., 2022). Equally, accelerating climate change can induce biome-shifts such as the desertification of dry grasslands and pastures (Burrell et al., 2020), or conversion of tropical forests to shrublands and savannah (Salazar and Nobre, 2010; Dobrowski et al., 2021).

Land use and climate change interact not only on at the macro-, but also the microclimatic level. For example, conversion from primary forest to cropland in the Tropics has been shown to increase local temperatures by, on average, 7.6 °C (Senior et al., 2017). Primary forests can also provide effective buffers from macroclimatic temperature extremes, and this buffering effect is greatest as temperatures anomalies increase in intensity (Santos et al., 2024). This buffering capacity can be lost even under moderate logging (Santos et al., 2024), although some research using different methodologies has suggested that selectively logged forests can still provide significant buffering from macroclimatic temperature extremes (Senior et al., 2017; Senior et al., 2018). However, there is agreement that even minor human modification of habitats can expose species to more extreme microclimatic conditions and push organisms beyond their thermal limits more regularly. Recent research (Williams and Newbold, 2021; Williams et al., 2022) has found that when populations are closer to the species' thermal limits, population abundance in human-modified land uses (relative to natural habitats) declines more strongly than for populations closer to the centre of their thermal niche. This is concerning as species are likely to face extreme temperatures more often in a warming climate, especially in human-modified landscapes, highlighting the acute, interacting effects of climate and land use change on terrestrial biodiversity.

Projecting the impacts of climate and land use change is a key focus of research, and several techniques have been devised to do this, including correlative, trait-based, and mechanistic models, and combinations thereof (Pacifici et al., 2015). In this thesis, I use correlative species distribution models (Araújo et al., 2019), combined with data on species dispersal capabilities and habitat preferences to predict the impacts of climate and land use change on species distributions based on a range of future climate (Riahi et al., 2017) and land use change scenarios (Hurtt et al., 2020). In the following section, I describe the theory, usage, and limitations of this technique in more detail.

Species distribution modelling: theory, practice and limitations

Species distribution modelling (SDM) is a well-established technique for understanding the impact of climate change on biodiversity distributions, and has been applied to estimations of extinction risk (Thomas et al., 2004), protected area planning (Hannah et al., 2008; Bagchi et al., 2013), assessing vulnerability to species invasion (Barbet-Massin et al., 2018), phylogeography (Yannic et al., 2014), conservation translocations (Willis et al., 2009), and the discovery of previously undescribed populations (Rhoden et al., 2017). The most common forms of SDM are correlative models (Araújo et al., 2019), which exploit the statistical relationship between species occurrences and environmental variables to predict species distributions in time and space. SDMs are increasingly used to model species responses to climate change, such as climate-induced range shifts (Araújo et al., 2019), and have been applied to a great variety of taxa including mammals (Lawler et al., 2009; Hidasi-Neto et al, 2019), birds (Howard et al., 2020; Titley et al., 2021), reptiles and amphibians (Mi et al., 2023), fish and marine invertebrates (Jones and Cheung, 2015), and plants (Benito Garzón et al., 2011). The limitations of SDM in this context are well-documented and have been discussed extensively (Pearson and Dawson, 2003; Elith and Leathwick, 2009; Santini et al., 2021). Below, I briefly summarise the limitations of SDM to predict species range shifts under climate change, focusing on three key themes: theoretical and methodological limitations, biotic factors such as species interactions and plasticity, and uncertainty in the magnitude and nature of future climate change itself.

Theoretical and methodological issues

The theoretical basis for SDM is derived from Hutchinson's definition of the 'fundamental niche' of a species as an *n*-dimensional hypervolume in 'niche space', where *n* refers to the environmental variables that delimit the species' niche (Hutchinson, 1957). By contrast, the 'realised niche' of the species defines its actual distribution in geographic space, when factors such as inter-specific competition are accounted for (Hutchinson, 1957). Given correlative SDMs are based only on observed species occurrences, SDMs are generally agreed to model the realized niche of a species (Pearson and Dawson, 2003; Guisan and Thuiller, 2005; Araújo and Guisan, 2006; c.f. Soberón and Peterson, 2005). This is a limitation of SDM as it can lead to violation of the key assumption that species are in equilibrium with current climate, and that species occurrences completely describe the climatic niche of a species, which may be constrained by other biotic or abiotic factors (Araújo and Guisan, 2006).

Another source of uncertainty in SDMs is in the selection of model algorithms (Araújo et al., 2019). To mitigate some uncertainty surrounding model selection, ensemble modelling approaches have been devised, which use model averaging to find consensus in predictions and are thought to produce more reliable results (Marmion et al., 2009; Hao et al., 2019). Uncertainty in model building also arises from the inclusion of inappropriate and/or collinear environmental variables (Dormann et al., 2013; Barbet-Massin and Jetz, 2014), spatial autocorrelation (Roberts et al., 2017), selecting the number and distribution of pseudo-absence data (Valavi et al., 2022), and the statistical thresholds used to convert occurrence probabilities into binary presence/absence maps (Nenzen and Araújo, 2011; Steen et al., 2017).

Biotic factors

Biotic factors, such as inter-specific interactions, are often unaccounted for (Guisan and Thuiller, 2005; Dormann et al., 2017). While biotic interactions are thought to have weak effects on species distributions at coarse scales (Pearson and Dawson, 2003), several studies have found evidence to the contrary (Araújo and Luoto, 2007; Wisz et al., 2013; Araújo and Rozenfeld, 2014). Recent advances in joint species distribution modelling (jSDM; Wilkinson et al., 2021) improve researchers' ability to incorporate species interactions into SDM frameworks, but computational requirements can be prohibitive for macroecological studies modelling several thousand species at global or continental scales.

Species' vulnerability and responses to climate change can be complex and influenced by a range of physiological, evolutionary and life history traits (Foden et al., 2019). Some species exhibit high levels of plasticity, allowing them to adapt their behaviour or physiology in response to changing conditions and persist in areas beyond their current climatic niche. These can include, for example, shifts in diet (Bestion et al., 2019), phenology (Cohen et al., 2018), migratory patterns (Kauffman et al, 2021), and the selection of genetic traits that maximise fitness in novel conditions (Gardner et al., 2019). Another key element moderating species vulnerability to climate change is their dispersal capability (Foden et al., 2013), which is often overlooked in favour of binary 'no dispersal'/'unlimited dispersal' scenarios (Thomas et al., 2004; Urban, 2015). Where species traits are available, these have been incorporated into predictions of range shifts as a function of natal dispersal distance and generation time (Barbet-Massin et al., 2012; Baker et al., 2015; Titley et al., 2021; Voskamp et al., 2021).

Trait-based (Foden et al., 2013; Böhm et al., 2016) and mechanistic models can provide more detailed insights into species responses to climate change (Kearney and Porter, 2009; Franklin 2010; Howard et al., 2024), especially when used in combination with correlative methods (Willis et al., 2015; Foden et al., 2019). However, such approaches can require large amounts of physiological trait data, which are often based on expert opinion and therefore not always reliable (Willis et al., 2015), and which are unavailable for many species, even well-studied taxa like mammals (Paniw et al., 2021).

Uncertainty in future climate change

Considerable uncertainty exists around future climate change itself, both between and within the various Representative Concentration Pathways (RCPs) and Global Circulation Models (GCMs) used to predict future climates (Bagchi et al., 2013; Meehl et al., 2020). These uncertainties can have profound effects on SDM outputs, highlighting once more the need to include multiple potential GCMs in an ensemble modelling framework (e.g. Titley et al., 2021). For example, the choice of GCM was largest source of uncertainty in a SDM study for 29 wetland birds under a severe (RCP8.5) climate change scenario (Steen et al., 2017). However, perhaps the greatest uncertainty with regards to future climate change is the degree to which nations can deliver long-term emissions reductions. The latest Coupled Model Intercomparison Project (CMIP6) includes a range of 'Shared Socioeconomic Pathway' (SSP) scenarios (Riahi et al., 2017) based on different scenarios of global economic development, with 'very likely' projected warming under different SSPs ranging from 1 °C to 5.7 °C by the 2100 (IPCC, 2021). At a time of mounting geopolitical tension between world powers, the ability of the international community to tackle global issues such as climate change remains in the balance.

The above discussion provides a summary of the major theoretical and methodological limitations of SDM in predicting species responses to climate change. While these limitations create several sources of uncertainty in predictions, if these are properly recognised, discussed and, where possible, mitigated (Araújo et al., 2019), SDM can still be a useful tool in strategic conservation planning (Hannah et al., 2008; Bagchi et al., 2013; Mi et al., 2023).

Strategic conservation planning

Given the intensity and scale of the climate and biodiversity crises, global action is required to 'bend the curve' of biodiversity loss and move towards a more sustainable future (Leclère et al., 2020). To this end, in December 2022 the UN Convention on Biological Diversity (CBD) signed the landmark Kunming-Montréal Global Biodiversity Framework (GBF), committing nations to a set of 23 ambitious targets and four overarching goals to protect global biodiversity (CBD, 2022). Goal A of the agreement aims to protect and restore natural ecosystems and halt human-induced extinction of known threatened species altogether by the year 2050 (CBD, 2022). To achieve this, area-based conservation, such as the establishment of protected areas (PAs) and other effective conservation measures (OECMs) that promote biodiversity within a geographically defined area (CBD, 2018), will be central to global conservation efforts (Maxwell et al., 2020). Indeed, Target 3 of the Kunming-Montréal Framework includes the commitment to protect 30% of land and sea by the year 2030, dubbed the ‘30 by 30’ target (CBD, 2022).

Delivering 30 by 30 will require a near-doubling of global protected area coverage in just eight years following the signing of the GBF. However, if area-based conservation is to deliver on the stated goal of restoring biodiversity and preventing human-induced extinctions by mid-century, careful consideration must be given to the nature, distribution and management of both current and new protected areas to ensure that they remain effective under climate and land use change (Hannah et al., 2008; Maxwell et al., 2020; Wauchope et al., 2022; Zeng et al., 2022). Existing protected areas can be effective in mitigating climate change by acting as refugia and important stepping stones that facilitate climate-induced range shifts (Thomas and Gillingham, 2015; Cooke et al., 2023; Mi et al., 2023). However, many protected areas are projected to be highly exposed to novel climatic conditions in future, potentially undermining their ability to protect threatened biodiversity long-term (Hoffman et al., 2019; Asamoah et al., 2021; Dobrowski et al., 2021). Therefore, there is an urgent need to increase not only the quantity but also the quality of protected areas, to maximise the resilience of the overall global network to climate and land use change.

A key tool in effectively delivering 30 by 30 is ‘systematic conservation planning’ (Margules and Pressey, 2000), which is a quantitative, evidence-based decision-making framework to optimise the allocation of limited resources between different conservation priorities, such as the funding of conservation projects (Bennett et al., 2015; Hanson et al., 2019) or design of protected area systems (Yang et al., 2020; Jung et al., 2021). The approach has already been used in a range of conservation contexts, such as the rezoning of the Great Barrier Reef Marine Protected Area (Fernandes et al., 2005) and the design of transboundary protected area systems in southern Africa (Smith et al., 2008). The allocation of protected areas has historically been biased towards areas that are cheap – with relatively low potential for agricultural or economic development – rather than areas that are most important for biodiversity (Venter et al., 2018). However, recent research has demonstrated that systematic conservation planning can greatly improve biodiversity outcomes while still minimising costs (Strassburg et al., 2020; Yang et al., 2020). For example, increasing global protected area coverage by less than 0.5% of global land area could conserve the entire range of 816 habitat-limited species of mammal, bird, and amphibian, including 53 species in a 330 km^2 area of Indonesia alone (0.02% of the country's land area; Zeng et al., 2022).

The recent proliferation of exact integer linear programming techniques and computational advancements, conservationists can now apply such optimisation approaches to much larger and more complex conservation prioritisation problems (Hanson et al., 2019; Hanson et al., 2020; Schuster et al., 2020). Climate-induced spatial shifts in the distribution of species ranges and niches are now increasingly incorporated into national- and global-scale protected area prioritisation studies (e.g. Lawler et al., 2020; Stralberg et al., 2020; Condro et al., 2021; Liang et al., 2024). However, few studies incorporate non-spatial impacts of future environmental change into protected area prioritisation, such as the shifting threat status of constituent species themselves, representing a key knowledge gap that will be addressed in this thesis.

Ex situ conservation planning

Area-based conservation will rightly be at the core of international efforts to halt extinctions (Maxwell et al., 2020), but these efforts alone will be insufficient to protect all species. While spatial prioritisation to inform the establishment of new protected areas is a vital field of research, there is no guarantee that nations will deliver on their commitments to achieve 30 by 30 (Xu et al., 2021). For example, it is noteworthy that none of the previous CBD Aichi targets for 2020 were fully met (CBD, 2020). Protected areas face significant funding shortfalls (Coad et al., 2019), are often poorly managed (Wauchope et al., 2022) and are not always ecologically representative (Venter et al., 2014). In this context, *ex situ* institutions such as zoos and aquaria (hereafter, 'zoos') are likely to play an increasingly important role in the conservation of a growing number of species, especially as anthropogenic climate and land use change threatens species' native ranges (Condé et al., 2013; IUCN, 2023a). In the following chapter, I assess the current composition of global zoo collections in relation to the IUCN Red List, and investigate whether threatened species representation has improved significantly in the approximate decade since a previous global assessment (Condé et al., 2013). I also discuss how future climate and land use change may threaten any recent progress if zoo collections are unable to adapt in response to shifting conservation priorities under environmental change.

Target 4 of the GBF explicitly references the role of *ex situ* conservation to reduce extinction risk and maintain the genetic diversity of threatened species (CBD, 2022). Given their expertise in *ex situ* management of populations of threatened species (Frandsen et al., 2020), and of conservation reintroductions and translocations (Condé et al., 2011; Gilbert et al., 2017), zoos are ideally placed to help address this target (Moss et al., 2023). Historically, zoos housed exotic species to provide opportunities for public recreation (McCann and Powell, 2019; Brereton and Brereton, 2020), but modern zoos now perform a multi-faceted role in society, contributing not only to public recreation, but also to science and research, public health and wellbeing, local and regional economies, and influencing policy (Spooner et al., 2023), with implications for collection planning (Fa et al., 2014). For example, balancing the representation of conservation priority species with those that attract the public is a difficult balancing act (Fa et al., 2014; Bowkett, 2014). This is because charismatic species (*sensu* Lorimer, 2007) are typically large-bodied mammals, which can be expensive to maintain but are not always highly threatened (Martin et al., 2014). Here, systematic conservation planning approaches (Margules and Pressey, 2000), including novel optimisation algorithms (Hanson et al., 2019), can assist curatorial decision making by balancing potential trade-offs using best available evidence.

Zoos have long recognised the need for strategic collection planning that recognise the broader contribution of zoo species to conservation (Hutchins et al., 1995). Despite this, a 2009 study showed that less than half (48%) of sampled zoo populations were breeding to replacement – that is, birth rates were too low to maintain stable population sizes (Lees and Wilcken, 2009). Zoos have systematically reduced the number of species in their collections over several decades (Brereton and Breton, 2020) and some argue that there is ‘literally not enough space’ to increase conservation breeding programmes sustainably (Alroy, 2015). This is concerning when viewed in the light of recent analysis, which showed that to achieve truly self-sustaining populations, conservation breeding programmes in North American Zoos alone would require space for another 100,000 individual animals (Powell, 2019). Almost 30 years on from the initial call for strategic collection planning, zoos have a much greater awareness of issues around the long-term sustainability of their collections. Progress towards sustainability itself, however, has been more limited, and will only become more challenging as climate and land use change threaten ever more species in their native ranges (Junhold and Oberwemmer, 2011).

Knowledge gaps, challenges, and opportunities

This thesis focuses on how the effectiveness of both *in situ* and *ex situ* conservation can be maximised under future environmental change. In the sections above I outlined the significant contributions that systematic conservation planning can make, and in many cases has already made, towards achieving the goals and targets of the Kunming-Montréal GBF (CBD, 2022). However, significant gaps remain. Specifically, in an *in situ* conservation context, spatial and non-spatial impacts of future environmental change have not yet been integrated into protected area prioritisation studies to inform 30 by 30. Maximising the conservation of threatened and unique evolutionary history is a priority for modern conservation (Gumbs et al., 2023). Protected area prioritisation should therefore not only incorporate geographic shifts in the distribution of threatened species, but also phylogenetic shifts in the distribution of extinction risk across the tree of life. In an *ex situ* context, despite growing awareness of the challenges facing zoo collections under environmental change (Junhold and Oberwemmer, 2011), and the proliferation of powerful optimisation tools and software (Schuster et al., 2020), systematic conservation planning has yet to be tested in a global zoo collection planning context. The results of such novel studies have significant potential to inform long-term, strategic collection planning that can future-proof *ex situ* conservation against anthropogenic environmental change. This knowledge gap is addressed, for the first time, in Chapter 7 of this thesis.

By filling these knowledge gaps, the research presented here can also highlight how *in situ* and *ex situ* conservation efforts can be better integrated to maximise impact. In 2013 the World Association of Zoos and Aquaria (WAZA) adopted the ‘One Plan’ approach to species conservation proposed by the IUCN (Byers et al., 2013). Under the ‘One Plan’ approach, zoos aim to integrate *in situ* and *ex situ* population management and conservation interventions, and foster collaborative partnerships with local conservation organisations in species’ native ranges (Byers et al., 2013; Traylor-Holzer et al., 2019). Working alongside these stakeholders, the One Plan approach promotes the joint development of comprehensive conservation plans that align *in situ* and *ex situ* actions to maximise the chances of success (Traylor-Holzer et al., 2019). Identifying which species are the optimal candidates for *ex situ* conservation in zoos, as well as spatial hotspots of threatened evolutionary history and priorities for *in situ* protection, represents a significant opportunity to further our understanding of the evolving role of zoos in global conservation efforts under climate and land use change. Such insights can demonstrate how zoos might proactively establish *in situ* conservation projects and partnerships, in line with their *ex situ* collection plans and activities, and get ahead of the curve of climate and land use change. This would maximise the effectiveness of the One Plan approach and zoos' contribution to both Targets 3 and 4 of the Kunming-Montréal GBF.

Thesis outline

In this thesis, I combine systematic conservation planning approaches (Margules and Pressey, 2000) with ensemble species distribution models to identify spatial and phylogenetic priorities for conservation, under a range of future climate and land use change scenarios. Specifically, I model how climate and land use change will impact the diversity of the world's threatened vertebrate evolutionary history, and identify priorities for extending protected area coverage to meet the 30 by 30 targets in a manner that is resilient to future environmental change. I also present a first-of-its-kind application of conservation optimisation algorithms (Hanson et al., 2019; Schuster et al., 2020) to global zoo collection planning, demonstrating how collection composition must evolve to keep pace with changing environmental conditions.

In Chapter 2, I set out the theoretical basis and motivation for why future climate and land use change must be better incorporated into zoo collection planning. Previous research has shown that species in zoos tend to be less endemic and less threatened than close relatives not currently held in zoos (Martin et al., 2014; Biega et al., 2017). As endemic species are more vulnerable to environmental change than generalists (Leclerc et al., 2020), I therefore predict that this situation is likely to be exacerbated in future, with zoos disproportionately housing species less likely to be threatened by future climate and land use change.

In the following chapter, I apply ensemble species distribution models to 24,598 terrestrial vertebrate species to identify those most likely to be impacted by environmental change. I provide a broad overview of predicted macroecological shifts in species diversity patterns, and apply my projections to IUCN Red List Criteria to project shifts in species' Red List status (IUCN, 2022). Finally, I use these Red List status projections to predict, for the first time, future changes in species' EDGE (evolutionarily distinct, globally endangered) scores under environmental change, using the latest EDGE2 metric (Gumbs et al., 2023).

In Chapter 4 I apply my projections of spatial and phylogenetic shifts in conservation priorities to a spatial conservation optimisation framework (Hanson et al., 2020). Specifically, I highlight 30 by 30 could be achieved in a manner that maximises long-term conservation of the greatest amount of threatened evolutionary history under environmental change. I show the importance of international co-operation and the equitable delivery of global protected area coverage targets, and highlight how the burden of conservation falls disproportionately on low-income nations with the least ability to directly fund protected area expansion (Shen et al., 2023).

In the remaining chapters, I turn my attention towards *ex situ* conservation in zoos. In Chapter 5 I assess how results from my SDMs (Chapter 3) are likely to impact the conservation value of existing zoo collections globally. In Chapter 6 I investigate the traits that underpin species attractiveness to the public, a key driver of investment in species conservation (for better or worse) and of taxonomic bias in global zoo collections (Fa et al., 2014; Bellon, 2019; Mooney et al., 2020; Mammola et al., 2020). Using zoos as a ‘natural laboratory’ to test visitors’ preferences for different species, I build trait-based predictive models of species attractiveness and identify both ‘Cinderella species’ (Smith et al., 2012) – which are attractive to the public but are so far overlooked as candidates for flagship species campaigns (Veríssimo et al., 2011) – and ‘Cinderella Zones’, a novel concept highlighting spatially explicit areas where there is a high richness in Cinderella species but a relative paucity of existing flagships. Such zones again fall disproportionately in low-income nations, highlighting opportunities to drive investment where it is needed most, both for conservation and improving human livelihoods.

Finally, in Chapter 7 I bring together my results from all previous chapters and apply them to novel conservation prioritisation algorithms that simulate ‘optimal’ zoo collections under current and future environmental conditions, at a global and regional (British and Irish) scale. My optimisations simultaneously maximise both collection attractiveness and the representation of threatened evolutionary history, after correcting for species persistence probabilities, and without requiring significant increases in zoo capacity. I show that zoos could increase the amount of threatened evolutionary history conserved in their collections under climate and land use change by more than an order of magnitude, relative to existing collections, while also significantly increasing the overall attractiveness of zoo collections worldwide.

Chapter 2

Zoos risk being outpaced by climate and land use change

The African painted dog (*Lycaon pictus*) is a charismatic species widely held in Species360 zoo collections, and is particularly threatened by anthropogenic climate change in its native range, as well as habitat loss, disease, and conflict with humans. *Photo credit: Derek Keats (Flickr, CC BY 2.0 DEED).*

Abstract

Current extinction rates far exceed the background average, and the Earth may be entering a Sixth Mass Extinction event. Target 4 of the recently agreed Kunming-Montréal Global Biodiversity Framework explicitly highlighted, for the first time, *ex situ* conservation as a means to prevent species extinctions. In this context, zoos are presented with both a considerable opportunity but also a formidable challenge. Given finite resources, how can the conservation value of their collections be maximised? Zoos already face criticism from some quarters around the representation of threatened biodiversity in their collections, a situation which is likely to be complicated by the dynamic situation brought about by climate and land use change, as an ever-increasing number of species require *ex situ* conservation. In this chapter, I propose a novel application of Systematic Conservation Planning to maximise the conservation value of zoo collections under current and projected future environmental conditions. By harnessing newly available exact integer linear programming tools and advances in optimisation software, conservation prioritisation algorithms can inform evidence-based curatorial decisions under environmental change. These novel tools can balance trade-offs between threatened species representation and the housing of key attractor species that drive zoo visitation and revenues, and fund zoos' wider contributions to biodiversity conservation.

Zoos and the challenge of climate change

Terrestrial vertebrates are threatened by human activities worldwide (Harfoot et al., 2021), with some researchers arguing that the Earth is undergoing a 'Sixth Mass Extinction' event (Ceballos et al., 2020; Cowie et al., 2022). Anthropogenic climate change is already a growing threat to biodiversity, and is predicted to become a dominant driver of global biodiversity loss in the coming decades (IPBES, 2019). Preserving the remaining viable habitat within species' native ranges, such as through the establishment of protected areas, is central to global conservation efforts (Maxwell et al., 2020) and has the potential to conserve a huge number of species (Shen et al., 2023; Chapter 4). However, variable funding and management of existing protected areas leads to inconsistent outcomes (Coad et al., 2019; Wauchope et al., 2022), while climate change threatens their long-term resilience and viability (Asamoah et al., 2021; Dobrowski et al., 2021). For example, they are often established where land is cheapest rather than the highest biodiversity priority (Venter et al., 2018), and uneven representation of climatic conditions in the global protected area network is likely to be exacerbated under climate change (Elsen et al., 2020). It is therefore imprudent to assume all species can be insulated from the threats of environmental change through purely *in situ* conservation measures.

In recognition of this fact, Target 4 of the Kunming-Montréal GBF explicitly references the need for *ex situ* conservation, such as the management of threatened species populations outside their native ranges, to prevent further extinctions (CBD, 2022). With their wealth of experience in *ex situ* population management of threatened species (Frandsen et al., 2020), cryopreservation of genetic material (Bolton et al., 2022), and conservation breeding and reintroduction programmes (Gilbert et al., 2017), zoos are uniquely placed to help address this Target. The IUCN Species Survival Commission recently published a position statement highlighting the role of zoos and botanic gardens in preventing species extinctions, representing a significant vote of confidence in zoos' ability to deliver on Target 4 of the GBF (IUCN, 2023a). However, zoos face a formidable challenge: given finite resources, how can they maximise their contribution to global conservation?

Zoos are cultural institutions (Powell, 2019) which have evolved from places of public entertainment to 'conservation hubs' that provide a wealth of services to species, communities, science and policy (Spooner et al., 2023). Worldwide, zoos receive an estimated 700 million visits per year and contribute around US $350 million to conservation funding, making them a major financial contributor to global conservation (Gusset and Dick, 2011). However, maintaining this high level of funding and attendance is dependent upon zoos providing an attractive collection of species that appeal to the public and drive revenue (Mooney et al., 2020; Brereton and Brereton, 2020). Unfortunately, not all endangered species appeal to the public, whereas many non-threatened species are major attractors (Colléony et al., 2017). Zoos therefore face a dilemma in balancing these potentially competing priorities, which will only be complicated by an ever-growing list of species that become threatened by anthropogenic environmental change (IPBES, 2019).

In other contexts, such as reserve selection and spatial conservation prioritisation, systematic conservation planning (Margules and Pressey, 2000) has been applied to guide objective, evidence-based decisions. A suite of tools are now available to prioritise spatially optimal investments in *in situ* conservation, such as Marxan (Watts et al., 2009), Zonation (Moilanen, 2007, and more recent packages such as *prioritizr* (Hanson et al., 2020). Here, I propose a novel application of SCP to zoo collection planning, to increase the resilience of zoos and secure their contribution to global conservation under climate change. Species distribution modelling (SDM), if combined with global datasets on current zoo collections (https://zims.species360.org), could highlight climate-threatened taxa that are currently under-represented in zoos. Combining these models with trait data that define species' charisma (Lorimer, 2007) and their attractiveness to zoo visitors would permit the optimisation of collections, considering both conservation priorities and species attractiveness. This would provide insight into how zoos can optimise the composition of their collections to both maximise *ex situ* conservation value and attract visitors, driving revenues that can then be directed towards both *ex situ* and *in situ* projects (Mooney et al., 2020).

An Imperfect Ark: Biases in Current Zoo Collections

As public attitudes towards animal welfare and cognition evolve, the zoo community must continually justify its existence (Patrick and Tunnicliffe, 2013) by empirically demonstrating their value to conservation and society (Powell, 2019; McCann and Powell, 2019; Spooner et al., 2023). However, several studies have called into question zoos' ability to manage sustainable populations that adequately represent threatened biodiversity (Lees and Wilcken, 2009; Condé et al., 2013; Martin et al., 2014; Alroy, 2015; Powell, 2019; McCann and Powell, 2019), leading to a 'sustainability crisis' in modern zoos (Lees and Wilcken, 2009; Powell, 2019). For example, one study found that threatened species were significantly more represented in zoos than expected by chance for only two of 59 vertebrate orders (Condé et al., 2013; see Box 1 for an updated summary of global zoo collection composition). Similarly, previous research has shown that species held in zoos are less likely to be threatened than close relatives not held in zoos (Martin et al., 2014), and were also less likely to be endemic, be habitat specialists, or have a restricted range (Martine et al., 2014; Biega et al., 2017). Such findings are concerning when one considers that endemic species with restricted ranges, in particular island or mountain endemics (Leclerc et al., 2020; Manes et al., 2021), are more vulnerable to climate change than their more generalist counterparts (De la Fuente et al., 2022). It stands to reason,

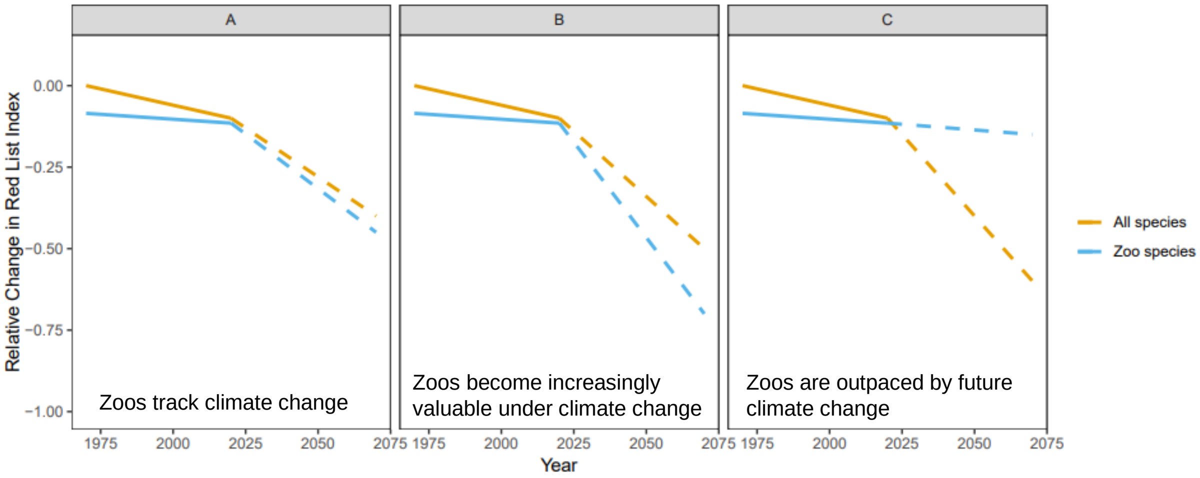


Figure 1. Hypothetical projection of how resilient current zoo collections may be to anthropogenic environmental change. Here, I use the Red List Index ('RLI'; Butchart et al., 2007) as a metric of overall extinction risk for terrestrial vertebrates. RLI is an aggregate measure of endangerment for a clade, with values of 1 indicating all species are Least Concern and a value of 0 indicating all species are extinct. Falling RLI therefore indicates increasing overall endangerment. Orange lines indicate hypothetical RLI for all species globally, while blue lines represent hypothetical RLI Index for species currently held in zoos. Dashed lines represent possible future trends under different scenarios: **A** species currently held in zoos are equally as threatened by environmental change as all species generally, meaning RLI of zoo collections roughly tracks global trends; **B** zoos disproportionately house species likely to become threatened by climate change, meaning RLI declines for zoo species more rapidly than species generally; **C** species most likely to become threatened by climate change are under-represented in zoos, with global RLI overtaking zoo RLI, thereby eroding the conservation value of zoo collections.

therefore, that if zoos already preferentially house generalist species over specialised endemics, they likely house species that will be less vulnerable to environmental change in future ('Scenario C', Figure 1).

Given zoos have such limited space, and are under such pressure to demonstrate conservation impact, why is it that non-threatened species remain so widespread in zoos? Clearly, zoos do not exist in a vacuum where collection managers can focus solely on species of maximum conservation concern (Bowkett, 2014). Zoos are constrained by their unique position at the interface between biodiversity conservation and public recreation, meaning collections must be attractive to the public to remain viable (Mooney et al., 2020). The need to house charismatic species is perhaps the strongest driver of bias in zoo collections (Moss and Esson, 2010; Fa et al., 2014), and mediates not only zoo attendance but also financial contributions to *in situ* projects (Mooney et al., 2020). Other constraints include: financial considerations – rare endemics can be expensive to maintain (Bowkett et al., 2014), logistical issues around the importing of exotic species (Martin et al., 2014; Tapley et al., 2015; Brady et al., 2017), specialist husbandry requirements (Bowkett, 2014; Brady et al., 2017), institutional preferences (Martin et al., 2014; ,Bardy et al., 2017), and architectural constraints related to the built environment and heritage of the zoo estate (Krause and Robinson, 2022).

How zoos should allocate finite resources between charismatic attractor species and *ex situ* conservation priorities remains an open area of debate (Martin et al., 2014; Bowkett, 2014; McCann and Powell, 2019; Mooney et al., 2020). However, relatively little attention is paid to the dynamic situation brought about by climate change (IPBES, 2019). Current threat status may be a poor indicator of future vulnerability to extinction (Luedtke et al., 2023), and climate change may disrupt the delicate balance struck by zoos when planning their collections (Junhold and Oberwemmer, 2011; Mooney et al., 2020; Spooner et al., 2023). Systematic conservation planning could therefore represent a powerful tool to prevent zoos being outpaced by environmental change (Chen et al., 2011; Ceballos et al., 2017).

Identifying Climate-Threatened Species

Several methods, from complex mechanistic models to simple bioclimatic envelopes, can be applied to quantify species vulnerability to climate change. Species distribution modelling (SDM) is a well-established technique for understanding the impact of climate change on biodiversity. The most common forms of SDM are correlative models (Araújo et al., 2023), which exploit the statistical relationship between species occurrences and environmental variables to predict species distributions in time and space, including under future climate change (e.g. Titley et al., 2021; Mi et al., 2023). SDM is subject to several limitations, which have been discussed extensively in the literature and in Chapter 1, which I will not replicate here (e.g. Elith and Leathwick, 2009). However, a great strength of SDM is that it does not require large amounts of species-specific data on physiological and ecological traits on which more complex, mechanistic models rely, but which are unavailable for many species (Foden et al., 2013; Briscoe et al., 2019). Consequently, SDM allows for predictions of climate-induced range shifts to be generated relatively rapidly for large numbers of species, and information on species dispersal capabilities and future habitat availability can complement these correlative approaches. Uncertainties can be mitigated, or at least explicitly quantified, through ensemble

Box 1: Current Composition of Global Zoo Collections

Species360 (https://zims.species360.org) holds data on the collections of over 1,300 *ex situ* institutions worldwide. Here I briefly assess global terrestrial vertebrate collections in 1,128 global zoos, aquaria and other visitor attractions in relation to species' IUCN Red List status (IUCN, 2021). Overall, Species360 zoos house 5,154 terrestrial vertebrates, including 1,003 mammals, 2,220 birds, 1,401 reptiles and 530 amphibians. This equates to 17.5%, 20.2%, 13.2%, and 7.4% of all terrestrial mammals, birds, reptiles and amphibians recognised by the IUCN Red List, respectively. South American zoos typically hold the most species per institution (median = 93 species) while Australasian zoos held the least species on average (median = 57 species).

Figure 2 shows the proportion of species in zoo collections in each IUCN Red List threat category, broken down by continent and class. Across all taxa, 79.6% of species in zoos are not in a threatened Red List category (Extinct in the Wild/Critically Endangered/Endangered/ Vulnerable; Mace et al., 2008). Mammals have the highest representation of threatened species (32.6%) compared to the global mammalian Red List (22.5%), with Australian zoos housing a particularly high proportion of threatened mammals. There is also a marginally higher percentage of threatened reptiles in zoos compared to the global reptilian Red List (Figure 2). This somewhat contradicts earlier findings (Martin et al., 2014), which suggest that species in zoos are less likely to threatened than close relatives not in zoos. This difference may be due to updates in the Red List, the increased number of institutions now recognised by Species360, and the phylogenetic pairwise approach used by Martin et al. (2014).

Strikingly, 87.7% of bird species in zoos are non-threatened. While this is only marginally higher than the percentage of non-threatened birds globally (86.5%), and there may be sound reasons for keeping non-threatened species in zoos (Bowkett, 2014), it is unlikely that nearly 90% of zoo resources need to be committed to such species. However, this represents some level of progress in the last decade, before which only 8% of birds in zoos were classed as threatened, compared to 12.6% of birds globally at the time (Condé et al., 2013). Regardless, given the scale of the biodiversity crisis, one could argue that zoos should aim to significantly exceed, rather than simply match, patterns in the Red List generally.

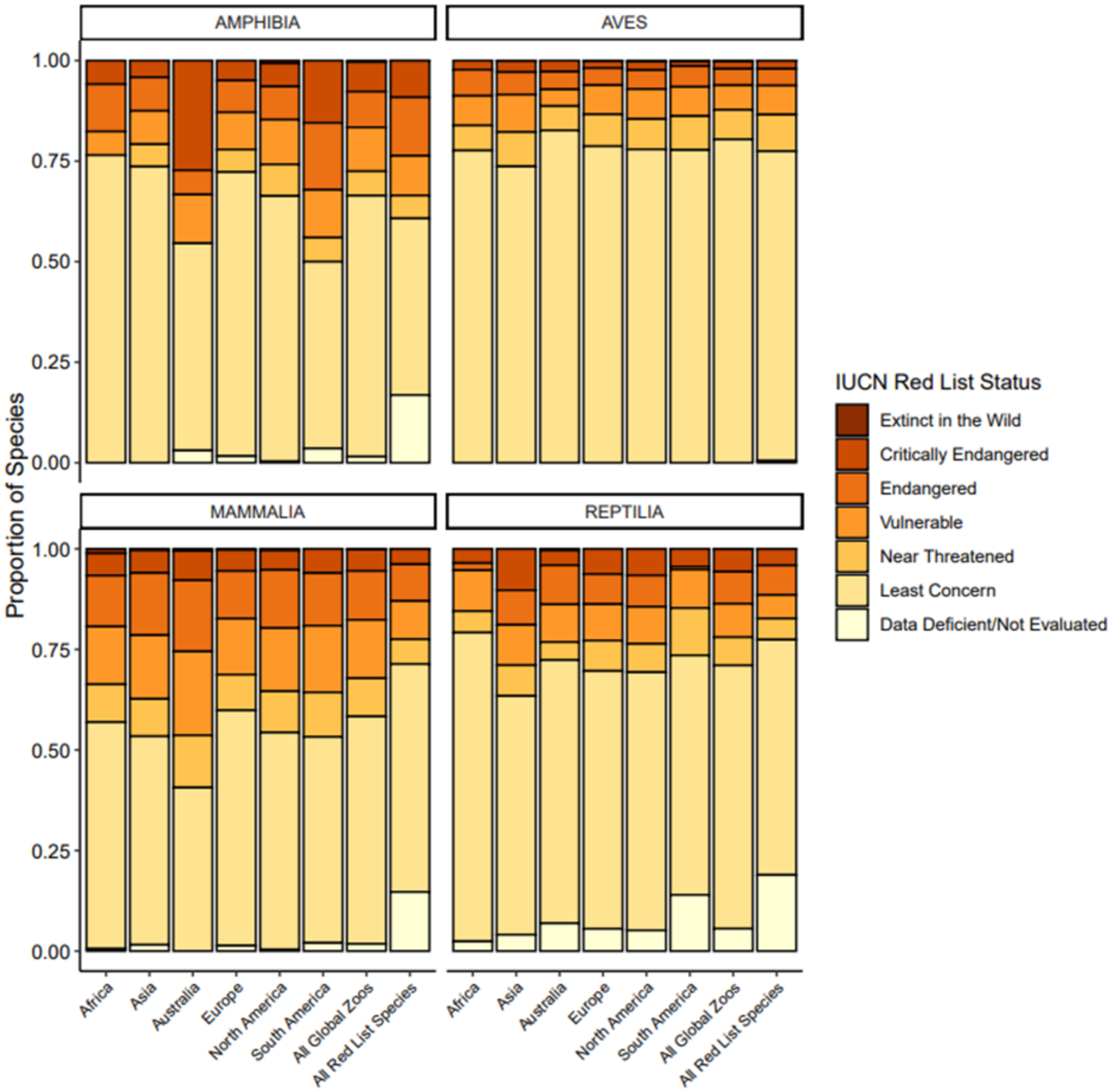


Figure 2. Composition of global zoo collections in relation to the IUCN Red List. Stacked bar charts show the proportion of terrestrial mammal, bird, reptile, and amphibian species held in zoos on each continent by IUCN Red List category. For each chart, the stacked bar second from the right shows the aggregated composition of global zoo collections, and the bar on the extreme right shows the proportion of all species of that class in each IUCN Red List category, for comparison.

For amphibians, the picture is more complicated. Australian and South American zoos protect a greater percentage of threatened amphibian species than the global amphibian Red List generally (Figure 2). However, Australian zoos hold relatively low absolute numbers of amphibian species, and the South American case is largely driven by a single specialist institution in Quito. Similarly, when considering the overall abundance (number of individual animals) of amphibians in zoos, 61.1% of individuals in North American zoos are threatened, including 8,658 (20.3%) from Extinct in the Wild species, but 7,392 (85.4%) of these individuals are concentrated in just two zoos in New York and Toledo, which considerably skews these aggregate results.

modelling approaches to find consensus in predictions (Hao et al., 2019), and following ‘gold standard’ guidelines as recommended in (Araújo et al., 2019).

For global zoo collection optimisation, requiring estimates of climate threat for vast numbers of species, SDM therefore represents an attractive proposition provided the limitations and uncertainties are dealt with explicitly and appropriately (Araújo et al., 2019). SDM projections can also be produced for multiple time horizons to provide zoo collection planners with a timeframe in which species are likely to become threatened. Population declines often lag behind climate impacts (Howard et al., 2023), and identifying climate-threatened species before wild populations begin to decline could be of great utility for strategic collection planning. SDM may not be the appropriate method for assessing climate threat for some species, particularly rare endemics with highly restricted ranges, and alternative approaches should be explored for these species. These may include trait-based vulnerability assessments (TVAs; Foden et al., 2013), regional SDMs modelled at finer spatial scales or higher taxonomic levels (Foden et al., 2019), or Multivariate Environmental Similarity Surfaces (Jarvie and Svenning, 2018) which quantify the dissimilarity between present and future conditions in species current ranges. For a review of approaches for tackling these ‘problematic’ species, see (Foden et al., 2019). However, correlative SDM has been shown to be of great value for macroecological studies assessing climate impacts on many thousands of species globally (Biber et al., 2020; Titley et al., 2021; Mi et al., 2023), and non-climatic factors such as biotic interactions, habitat specialisation or human persecution may all be more important limiting factors on the narrow-ranged species that are unsuitable for correlative SDM.

Quantifying Zoo Capacity

Any algorithmic approach to systematic conservation planning requires robust information on the study system, such that clear, transparent targets can be defined for the optimisation process (Margules and Pressey, 2000). It is therefore crucial to understand the resource constraints that limit options available to decision-makers. In a zoo setting, such constraints may be equivalent to the carrying capacity of the global zoo community. Lack of space, staffing, and financial resources have all been identified as factors limiting the number of threatened species held in zoo collections (Bowkett, 2014; Brady et al., 2017), and it is likely that any evolution in the composition of zoo collections will have to occur with the constraints of current zoo capacity (Powell, 2019).

One way to quantify zoo carrying capacity would be to estimate the overall exhibit space available to collection planners globally. National and regional zoo accreditation bodies such as the Association of Zoos and Aquaria in North America (AZA, aza.org/animal-care-manuals) and the European Association of Zoos and Aquaria (EAZA, eaza.net/conservation/programmes/#BPG), alongside professional organisations like the Australian Society of Zookeeping (ASZK, aszk.org.au/resources) already provide publicly available guidelines on recommended spatial requirements for housing a wide range of species in zoo exhibits. Such data could be complemented with information gleaned from grey literature, expert and professional opinion, and data sources such as the Species360 Zoological Information Management System (ZIMS, zims.species360.org) to collate all available information on species' spatial requirements. However, such data are biased towards a few well studied clades of mammals and birds (especially primates, carnivores, ungulates, and raptors), and are unable to capture some of the non-areal elements such as vertical structure and three-dimensional exhibit arrangement, as well as heating, lighting, and other environmental elements of exhibit design. Such knowledge gaps could be filled by eliciting expert input from zoo practitioners (e.g. Brady et al., 2017), or through entirely non-spatial proxy measures such as species energetic requirements, which can be estimated with some confidence using allometric equations of body mass and metabolic rates (McNab, 2008).

Optimising the Ark

Systematic conservation planning has yet to be applied to zoo collection planning using optimisation algorithms. Here, I describe how optimisation algorithms, already widely used in spatial conservation prioritisation, can be adapted and applied to zoo collection planning (Figure 3). In spatial systematic conservation planning, the study system is often divided into 'planning units', which may take the form of gridded cells or discrete units based on some administrative or ecological boundary (Margules and Pressey, 2000; Moilanen, 2007). In a non-spatial zoo collection planning framework, the planning units would be represented by individual species, each with associated features including, for example, conservation value (including present and future threat status), phylogenetic distinctiveness, educational value, or

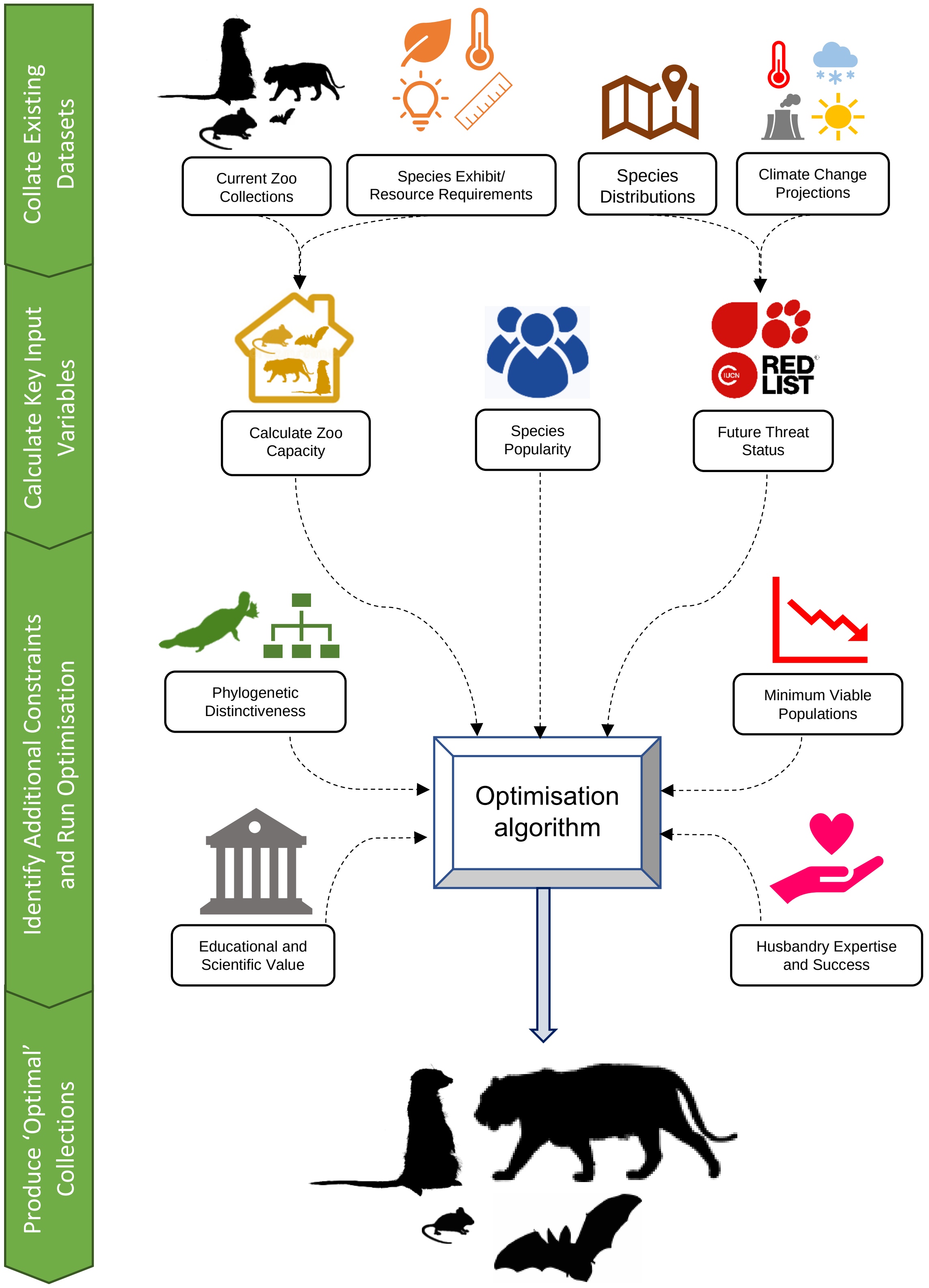


Figure 3. Schematic diagram of optimisation approach. Zoo collections signified by four species: meerkats, which represent popular but non-threatened species; tigers (popular and threatened species); bats (unpopular but threatened species); and mice (unpopular and non-threatened species). Note that the size of the icon indicates population size, such that current zoo collections have many 'meerkat' species but few 'bats', whereas an optimal collection may have relatively fewer 'meerkats' and 'mice' and increased numbers of 'bat' and 'tiger' species.

species charisma. In spatial prioritisation algorithms, each planning unit is associated with an 'opportunity cost', which is typically defined as the revenues foregone when land parcels are set aside for protected areas rather than agricultural or other economic use (Margules and Pressey, 2000; Strassburg et al., 2020; Brito-Morales et al., 2022). The opportunity cost of committing fewer zoo resources to charismatic attractor species in favour of threatened non-charismatics could be defined as the reduction in collection popularity, with its associated effects on zoo visitation and revenues (Mooney et al., 2020).

Quantifying these opportunity costs requires an index of species attractiveness, or 'non-human charisma' (Lorimer, 2007). Several studies (Ward et al., 1998; Moss and Esson, 2010; Carr, 2016) have quantified species attractiveness through the 'attraction power', the proportion of visitors who stop at an exhibit, and 'hold time', how long they spend viewing a species. These observational studies provide a simple and efficient metric of species popularity, but are of course limited to species already held in any given zoo, and therefore require rigorous species selection to maximise coverage of species trait-space and minimise bias in training data when building trait-based models of attractiveness. Alternative methods include assessments of species' online prevalence as a proxy for charisma (Wong and Rosindell, 2022), their use in promotional material for NGOs, zoos, and even children's animated film posters (Albert et al., 2018), and image-based surveys of respondents' preferences between species (MacDonald et al., 2015; Haukka et al., 2023). While these methods can be less constrained by collection composition in any given zoo, they rely on 'static' materials such as photographs of species rather than real-world encounters with species in the physical environment, and may therefore be less appropriate for predicting visitor behaviour and preferences in the context of a zoo visit.

Armed with indices on species endangerment, attractiveness, and resource requirements, researchers could then produce optimised hypothetical zoo collections under current and future climate scenarios, recognising that no model will be able to fully capture the complexity of curatorial decision making at an individual zoo level. So far, I have described zoo collection optimisations in a similar framework to well-established and popular spatial optimisation software such as Marxan (Watts et al., 2009) and Zonation (Moilanen, 2007), which use heuristic algorithms and simulated annealing to approximate an optimal solution. Optimisation algorithms have also been applied to non-spatial conservation problems in recent years, such as the allocation of funding between conservation projects based on their respective costs, benefits, and likelihood of success (Brazill-Boast et al., 2018; Hanson et al., 2020). These problems are now often solved using ‘exact algorithms’, which unlike heuristics are guaranteed to find a true optimal solution (Hanson et al., 2019; Beyer et al., 2016; Schuster et al., 2020). While heuristics have traditionally been favoured for solving complex problems, a category which the allocation of global zoo resources would certainly fall into, in recent years computational advances have allowed for ever more complex problems to be solved using exact algorithms. Some researchers (Beyer et al., 2016; Schuster et al., 2020) have called for the wider use of exact algorithms in systematic conservation planning, while recognising that such approaches can require specialist mathematical and programming skills compared to heuristic algorithms (Hanson et al., 2019). While the idiosyncrasies of individual institutions and species means that optimisation outputs could not be considered prescriptive, such optimisations would provide a valuable evidence base, highlighting potential options for curators to collectively work towards a more sustainable future for their collections.

Conclusions

Global biodiversity is in crisis. Species extinction rates far exceed the background average, and are only likely to increase as anthropogenic climate and land use change place further strain on natural ecosystems (IPBES, 2019; Ceballos et al., 2017; Harfoot et al., 2021). Zoos already make significant contributions to global conservation (Gilbert et al., 2017; Frandsen et al., 2020; Bolton et al., 2022; IUCN, 2023a), but the pace of climate change and biodiversity loss may hamper their potential contribution to Target 4 of the Kunming-Montréal GBF (CBD, 2022; Figure 1). This is where the systematic conservation planning framework (Margules and Pressey, 2000) can add value to zoo collection planning. Here, I have outlined how exact algorithms could be deployed as a decision-support tool to zoo curators and managers. As with any model, optimal zoo collection simulations will have inherent limitations, and must work alongside input from expert zoo staff with specialist knowledge in species requirements and institutional objectives. However, given the urgency of the climate and biodiversity crises, the need for quantitative evidence on which species zoos could and should conserve has never been more pressing.

Chapter 3

Impacts of future climate and land use change on terrestrial vertebrates, and implications for in situ and ex situ conservation

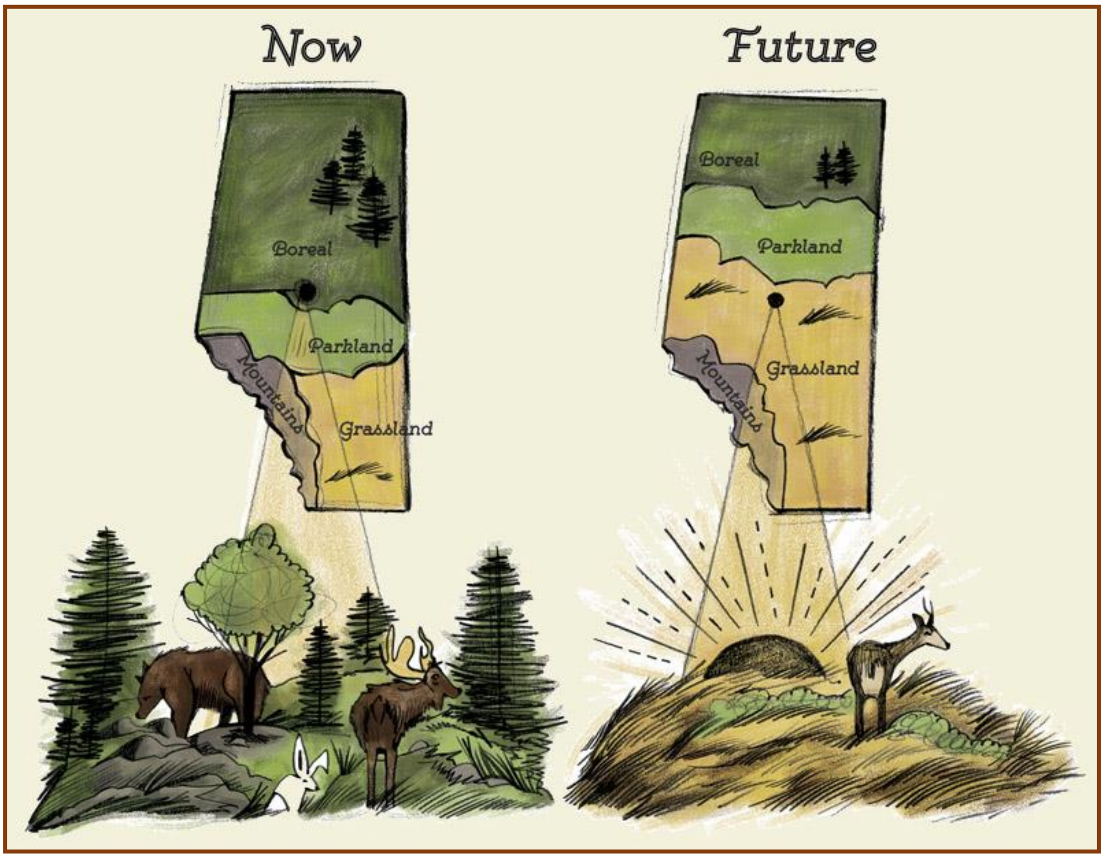


Illustration from the Alberta Biodiversity Monitoring Institute (ABMI) describing predicted climate-induced shifts in forest and grassland biomes, and associated changes in species distributions and community assemblages. *Illustration credit: Amanda Schutz, Woodward Design. Source: ABMI, https://abmi.ca/home/biodiversity/biodiversity-climate-change.html.*

Abstract

Anthropogenic climate and land use change are among the most severe pressures on terrestrial biodiversity globally, driving losses and pushing the Earth towards a ‘Sixth Mass Extinction’ event. If nations are to tackle the twin crises of biodiversity loss and environmental change, understanding how species are likely to respond to these pressures will be vital. In this chapter, I use an ensemble species distribution modelling framework to predict the impacts of future climate and land use change on the majority of the world’s terrestrial vertebrate species (n = 24,598). I use these projections to predict changes in: species distributions and community composition, species’ future IUCN Red List status, and future changes to evolutionary distinct and globally endangered (EDGE) species. To represent the latter category, I use the new EDGE2 metric that estimates the amount of unique threatened evolutionary history expected to be lost should the species go extinct. I show that climate and land use change will have profound effects on terrestrial vertebrate biodiversity, inducing widespread range shifts and novel communities, particularly in high latitude and elevation regions. I highlight spatial and phylogenetic hotspots of extinction risk, and identify 2,753 species projected to lose all their climatically suitable habitat by 2070 under a middle-of-the-road warming scenario, in line with current international commitments and pledges to reduce emissions. My findings highlight the need for climate-smart *in situ* conservation planning, promoting both physical and climatic connectivity between protected areas to facilitate climate-induced range shifts, and the need for heterogeneous habitats that support a diversity of ecological and climatic niches, especially in montane areas projected to see increasing colonisation by lowland species.

Introduction

June 2024 was the hottest June on record, marking a 13-month streak of record-breaking global temperatures (Copernicus, 2024b). At the same time, land use change affects over 600,000 km^2 of land area annually, on average (Winkler et al., 2021). These high rates of habitat loss currently represent the primary driver of terrestrial extinctions (IPBES, 2019), while climate change is a growing threat to many species (IPCC, 2022; Luedtke et al., 2023). Such intense and rapid changes in the Earth’s environment is already having observable impacts on biodiversity, ecosystems, and nature’s services to people across a broad range of spatial, temporal, and ecological scales (Scheffers et al., 2016). Indeed, climate and land use change often interact, exacerbating impacts on biodiversity and potentially undermining mitigation efforts (Hof et al., 2018; Newbold, 2018; Williams and Newbold, 2020).

Species may respond to a changing environment in myriad ways, some of which may infer fitness advantages while others may be maladaptive (Radchuk et al., 2019). These can include, for example, behavioural plasticity such as shifts in diet (Bestion et al., 2019), phenology (Cohen et al., 2018), and migratory patterns (Kauffman et al, 2021), and evolutionary changes through selection of traits that maximise fitness in novel conditions (Gardner et al., 2019). One of the most widely documented responses to environmental change, however, is shifting species distributions as species track spatial shifts in their climatic niche (Chen et al., 2011; Lenoir and Svenning, 2015; Scheffers et al., 2016). While these shifts often lag behind a warming climate (Howard et al., 2023), they typically occur along latitudinal (Vergés et al., 2014) or elevational (Sekercioglu et al., 2008) gradients, resulting in novel species assemblages and interactions that can lead to biotic homogenisation (Hidasi-Neto et al., 2019), loss of rare endemics (de la Fuente et al., 2022), and disrupted ecosystem processes (Newbold et al., 2019).

With global greenhouse gas emissions continuing to increase (UNEP, 2023) and rates of land use change remaining high (although decelerating since 2005; Winkler et al., 2021), understanding how environmental change impacts species distributions, community assemblages, and conservation priorities will be vital to tackle the twin crises of climate change and biodiversity loss. A well-established method for predicting climate and land use change impacts on species distributions is correlative species distribution modelling (SDM), which models the statistical relationship between species occurrence records and environmental variables such as temperature, rainfall, habitat, and topography (Elith and Leathwick, 2009). While this approach is subject to limitations, as discussed in Chapter 1, intelligent conceptualisation and parameterisation of SDMs can mitigate these limitations and ensure model predictions are robust (Aráujo et al., 2019). While trait-based and mechanistic models can provide more detailed insights into species responses to climate change (Pacifici et al., 2015; Foden et al., 2019), such approaches require large amounts of physiological trait data which are often unavailable, even for well-studied taxa like mammals (Paniw et al., 2021).

In this chapter, I present results from SDMs for the majority of the world's terrestrial vertebrates (n = 24,598 of 31,862 species; 77.2% of all such species). I combine these projections of shifts in species' climatic niches with land use change projections and estimates of species dispersal capabilities, to predict relative changes in climatically suitable Area of *Occupiable* Habitat (AOOH) from the present day to the year 2070. I use AOOH here as an extension of the 'Area of Habitat' (AOH; Brooks et al., 2019) measure of overall habitat available to a species, by explicitly accounting for species' dispersal capabilities to identify habitats that a species could occupy within a given timeframe. I then use these projections to answer three main research questions:

1) How will future climate and land use change impact the spatial distribution of terrestrial biodiversity? Which regions are likely to see disproportionately high levels of local extirpations and/or colonisation by novel species? Which regions are predicted to experience high levels of biotic homogenisation?
2) How will climate and land use change affect species threat status and trends in global vertebrate endangerment? Following published methodologies and IUCN guidelines (IUCN, 2022), I convert predicted abundance changes into Red List categories to characterise trends in future endangerment.
3) How will environmental change affect the phylogenetic distribution of threatened evolutionary history? Using the updated 'EDGE2' metric (Gumbs et al., 2023), I estimate species future EDGE (evolutionary distinct, globally endangered) scores, which represent the expected loss of unique evolutionary history (MY) should the species go extinct.

Methods

Species range data

Spatial data on current species distributions were obtained from the IUCN in December 2021 for mammals, birds, reptiles, and amphibians (IUCN, 2021; Birdlife, 2021), with additional reptile range data obtained from Roll et al. (2017). IUCN range maps are imperfect and can be especially prone to false positive (commission) errors, but they are relatively comprehensive, applied consistently across taxa, and are less sensitive to survey effort when compared with point data from occurrence records such as GBIF (Beck et al., 2014; Maréchaux et al., 2017).

Bats (Chiroptera) were excluded from further consideration due to a lack of reliable dispersal information for these species (see *Accounting for species dispersal capabilities* below). Fully marine mammals (cetaceans and pinnipeds) and reptiles (sea turtles and sea snakes) were also excluded, as were pelagic seabirds such as penguins (Sphenisciformes), and petrels, albatrosses, and shearwaters (Procellariiformes). Range data were filtered to include only resident and breeding ranges where species were known to be native, reintroduced, extant or probably extant. Therefore, non-breeding ranges of migratory species are not considered, potentially underestimating climate threat for these species (Zurell et al., 2018). However, climate exerts stronger influences on summer (breeding) rather than winter (non-breeding) ranges for migratory birds (Zurell et al., 2018), and impacts species population trends more strongly in breeding rather than non-breeding ranges (Howard et al., 2020).

Species range data were projected and rasterised using Behrmann's equal area projection (Budic et al., 2016). Raster resolution was 0.5 degrees (~55 km at the equator), with species deemed 'present' in a grid cell if the range polygon covered at least 10% of the cell. Species with fewer than 10 'presence' cells at this resolution were excluded, resulting in a dataset of (3,248 mammals, 8,861 birds, 2,630 amphibians and 5,194 reptiles). To improve coverage of restricted range species, spatial resolution was reduced to 0.25-degree grid cells and the 10% presence threshold was removed, such that species whose ranges occurred in any part of a grid cell were classed as 'present' in that cell. This approach may marginally increase false-positive rates, but allowed for a further 523 mammals, 938 birds, 1,421 amphibians and 1,783 reptiles to be included, resulting in a total dataset of 24,598 species.

Climate variable selection

Variable selection is a major source of uncertainty in SDM, and should be made with consideration to the known environmental tolerances of the study species (Barbet-Massin and Jetz, 2014; Araújo et al., 2019). Historic climate data were obtained from WorldClim (Fick and Hijmans, 2017), using the 1970-2000 average as the 'baseline' climate. Following Voskamp (2017) and Titley et al., (2021), I selected eight WorldClim bioclimatic variables, representing the annual means, monthly maxima and minima, and seasonality of temperature and precipitation (Titley et al., 2021). All combinations of ≥ 3 variables that included at least one temperature and one precipitation variable were generated, and combinations where variables exceeded a collinearity threshold of $r > 0.7$, were excluded (Dormann et al., 2013). This resulted in 38 candidate variable combinations (Appendix A, Table S1). I divided species by the four taxonomic classes and three latitudinal bands based on current range centroids (boreal: y co-ordinate of centroid > 23.5 degrees; tropical: $23.5 \geq y \geq -23.5$; austral: $y < -23.5$), resulting in 12 species sets. I randomly sampled 100 species from each set and ran SDMs for each of the 38 variable combinations, using regression-based generalised additive models (GAM) and a tree-based algorithm, gradient boosting machines (GBM; methods below). Models were ranked by AUC (area under the receiver operating curve) to quantify model performance. For each of the 12 species sets, the number of times a model was ranked in the top quartile of candidate models was calculated, to find the variable combination best supported for that taxon and latitudinal band (Appendix A, Table S1).

Future climates

Shared Socioeconomic Pathways

The latest projections of future climate change were produced as part of the IPCC 6th Assessment Report (AR6; IPCC, 2021). To account for uncertainty in the intensity of future climate change, I selected four Shared Socioeconomic Pathways (SSPs) ranging from significant and immediate mitigation (SSP1-2.6, ‘Taking the Green Road’), a gradual but delayed shift towards sustainability (SSP2.4-5, ‘Middle of the Road’), an increasingly competitive world which inhibits international co-operation (SSP3.7-0, ‘A Rocky Road’), to a scenario based on continued and increasing fossil fuel dependence (SSP5-8.5, ‘Taking the Highway’; Riahi et al., 2017).

Global Circulation Models

Considerable uncertainty also exists around specific climatic changes that will occur under different greenhouse gas emissions scenarios (Tebaldi et al., 2020). Currently, future climates are predicted using Global Circulation Models (GCMs) produced as part of the Coupled Model Intercomparison Project (CMIP6). A major point of difference between GCMs is in their estimate of Equilibrium Climate Sensitivity (ECS), or the predicted warming impact produced by doubling atmospheric CO_2 concentrations. I selected three CMIP6 global circulation models

(GCMs) with relatively low (BCC-CMS2-MR), moderate (IPSL-CM6-LR) and high (CanESM5) estimates of Equilibrium Climate Sensitivity (Meehl et al. 2020).

Downscaling GCMs

To produce species threat status predictions using the decadal time horizons appropriate for IUCN Red List assessments (IUCN, 2022), I generated future climates for each decadal timestep between 2030 and 2070, following a similar downscaling approach to that used by WorldClim (Hijmans, 2020). Briefly, for each of the three GCMs, four SSPs, and five future timesteps (a total of 60 future climate scenarios), I obtained mean monthly maximum temperature, mean monthly minimum temperature, and monthly precipitation from the Earth System Grid Federation database (https://esgf-index1.ceda.ac.uk/search/cmip6-ceda/). Monthly climate variables were averaged across the prior and following decade, such that the ‘2050’ climate was the average climate for the years 2041-2060, for example. Historic projections for each GCM were also obtained and averaged across the years 1970-2000 to align with WorldClim baseline climate derived from real-world observations.

Historic climate data from WorldClim are available at a fine spatial resolution (30 arc-seconds), whereas GCMs are generally at very coarse scales of 1 degree (60 arc-minutes) or more. GCM projections were therefore resampled to 30 arc-second resolution using bilinear interpolation, and the change in temperature (absolute difference) and precipitation (relative difference) between historic and future climate was calculated for each cell (Hijmans, 2020). Temperature and precipitation changes were calibrated against historic (observed) WorldClim data and were then aggregated back to 0.5-degree (or 0.25-degree) resolution, and projected to Berhrmann’s equal area projection (Hijmans, 2020). Finally, bioclimatic variables were calculated using the biovars function in the *dismo* R package (Hijmans, 2017).

Modelling approach

Pseudoabsence selection

For many species, comprehensive and reliable absence data are either unavailable or are very difficult to obtain, particularly for highly mobile or poorly studied species (Valavi et al., 2022). To overcome the lack of ‘true absence’ data, many SDM approaches rely on generating so-called ‘pseudoabsence’ points sampled from areas outside of the species’ known range (Elith and Leathwick, 2009). Therefore, I randomly sampled 1,000 pseudoabsence points from the biogeographic realms (Holt et al., 2013) where each species currently occurs (Titley et al., 2021). See Appendix A for justification of this approach.

Dealing with spatial autocorrelation

The reliability of SDM outputs can be undermined by improper treatment of spatial autocorrelation (Dormann, 2007; Roberts et al., 2017). Following Bagchi et al. (2013) and using the *blockTools* R package (Moore, 2016), I divided terrestrial ecoregions of the world (Olson et al., 2001) into ten spatially disaggregated blocks, such that the mean bioclimate is similar across each block but each block represents the full variation in terrestrial climatic conditions (Bagchi et al., 2013). These ten spatially disaggregated blocks were then used for model training and testing. In some cases, species only occurred in one spatial block, making this approach inappropriate (n=2,388, 9.7% of modelled species). For these species, I randomly split the presence and absence data into five test and training blocks and performed five-fold cross-validation.

Model algorithms

The choice and parameterisation of model algorithms can have significant impacts on SDM predictions (Araújo et al., 2019). Ensemble modelling approaches have been shown to improve model performance and reduce overfitting, particularly for rare species (Marmion et al., 2009; Hao et al., 2019). Following Titley et al. (2021), I adopted an ensemble modelling approach using four model algorithms representing both regression-based methods (generalised linear models [GLMs] and GAMs) and tree-based methods (random forests [RFs] and GBMs). Model parameterisation was as follows:

GLM

For GLMs, I generated all possible combinations of variables from first to third order polynomials, to account for the possible nonlinear effects of predictors. For all model algorithms, the data were split into up into the ten spatially disaggregated testing and training blocks (see ‘Dealing with spatial autocorrelation’, above). GLMs were fitted to each block and each polynomial term combination, and optimum combination of polynomial terms with the maximum AUC was selected for each of the ten fitted models.

GAM

GAMs were fitted using thin-plate regression splines using the ‘gam’ function in the *mgcv* R package (Wood, 2001). Models were smoothed to a gamma value of 1.4, and ‘k’ was set to -1 to allow the *mgcv* package to automatically set the number of knots at the upper limit of the degrees of freedom for smoothing terms and to avoid excessive computation time.

RF

RFs were fitted using the *randomForest* R package (Liaw and Wiener, 2002) with an initial 1,000 trees. The ‘mtry’ argument, which defines the number of randomly sampled variables that are used at each split was set to vary between one and three. RFs were initially fit to 1,000 trees, then the number of trees increased by increments of 500 until the relative improvement in AUC was less than 1%. The RF model using the optimum number of trees and mtry value was then selected for each of the ten blocks.

GBM

I fitted GBMs using the *gbm* R package (Ridgeway and Ridgeway, 2004) and used an optimisation approach to find the optimum combination of tree complexity, learning rate and number of trees for each block. Tree complexity was allowed to vary between one and four, ranging from additive models to four-way interactions. Learn rate varied between 0.001, 0.01 and 0.05. The number of trees was allowed to increase up to a maximum of 5,000, while bagging fraction was set at 0.5 so that 50% of the data was randomly selected at each step (Elith et al., 2008). Optimum parameter combinations that minimised prediction error were then selected for each block.

Model averaging

The modelling approach described above produced up to 40 optimally tuned and parameterised models for each species (10 blocks x 4 algorithms). For each model, continuous probability of occurrence maps (scaled between 0 and 1) were converted to presence-absence using the true-skill statistic (Allouche et al., 2006). To produce an overall ensemble prediction based on all models produced for each species, a consensus projection of climatically suitable range was produced for both continuous and presence-absence models, by taking the AUC-weighted average of candidate model predictions.

Calculating relative species abundance

Accounting for species dispersal capabilities

I constrained projections of species distributions under climate change to areas where species are likely to be able to reach within a given timeframe. To do this, I gathered data on species age at first reproduction (AFR) and natal dispersal distance (*d*), and estimated the species dispersal capability for each decadal timestep up to the year 2070 (Eqn 1).

Eqn 1: $$D_t = d \times \frac{t - 2020}{AFR}$$

Where D_t represents total dispersal capability by year t, with 2020 set as the baseline timestep.

Data for AFR were obtained from Pacifici et al. (2013) for mammals, Bird et al. (2020) for birds and the AnAge database (de Magalhaes and Costa, 2009) for reptiles and amphibians. Data for *d* were derived from allometric equations from Sutherland et al. (2000) for mammals, models based on hand-wing index (a strong correlate of *d*) for birds (Sheard et al., 2020; Stewart et al., 2022; Weeks et al., 2022), published estimates in Smith and Green (2005) for amphibians and a wider literature search for reptiles (Supplementary Data S1). Missing data were phylogenetically imputed using the *Rphylopars* R package (Goolsby et al., 2017), using phylogenetic trees for mammals (Upham et al., 2019), birds (Jetz et al., 2012), amphibians (Jetz and Pyron, 2018), snakes, lizards, and tuatara (Lepidosauria; Tonini et al., 2016), and turtles and crocodilians (non-avian Archosauromorpha; Colston et al., 2020). As data used to derive *d* varied among taxa, data imputation for each clade are summarised in Appendix A. Dispersal capabilities were constrained to contiguous land masses for all species other than volant birds, for which I allowed trans-oceanic dispersal to land masses within one *d* of the source land mass.

Quantifying land use change impacts

The Land Use Harmonization (LUH2) dataset provides historic and future projections of fractional cover of 12 land use classes at 0.25-degree resolution, harmonised with SSP climate scenarios (Hurtt et al., 2020). I associated each of these 12 broad land use classes to IUCN Level 1 habitat types using a previously developed crosswalk (Titley, 2022; see Appendix A for details). Species habitat preferences were extracted from the IUCN Red List using the *rredlist* R package (Chamberlain, 2020), allowing fractional cover of suitable habitat in each grid cell to be calculated. The LUH2 categories are relatively coarse, and include only two primary and secondary habitat categories (forest and non-forest). As such, this dataset probably provides a conservative estimate of the impact of land use change on biodiversity, particularly for specialist species with narrow habitat requirements (Socolar and Wilcove, 2019).

To match the midpoint of the 1970-2000 baseline climate period, LUH2 fractional land use classes were obtained for the year 1985, and for each decadal timestep between 2030 and 2070, for each SSP. Presence-absence maps of species' climate niches and estimated dispersal capabilities were overlaid with fractional suitable land use maps. The species' total Area of Occupiable Habitat (AOOH) for that timestep was calculated as the summed product of the binary climate niche and dispersal rasters, and the fractional land use raster. This process was repeated for each SSP and decadal timestep such that relative changes in AOOH could be estimated under each scenario. To understand the relative impacts of climate and land use change on species AOOH, in each grid cell I calculated the summed change in both climatic suitability (SDM presence-absence) and habitat suitability (proportion of suitable habitat from LUH2 projections) for all 24,598 modelled species. I present results from these analyses as a bivariate map showing areas of high climate and land use change impacts, and where these impacts overlap, for terrestrial vertebrate biodiversity (Figure 2d).

This approach assumes a linear relationship between AOOH and abundance. While abundance and AOOH is likely to be positively correlated, I accept that the assumption of linearity will not hold true in many cases because, for example, populations may be unevenly distributed or particularly fragmented throughout species ranges, potentially impacting carrying capacity and population viability (Akçakaya et al., 2006). That said, rather than precisely predicting the exact Red List status of each individual species, the purpose of this Chapter (and the subsequent Chapters 4, 5, and 7 that build on these results) is to understand the broad, macroecological impacts of environmental change on global biodiversity, and use these findings to identify priorities for *in situ* conservation in protected areas and *ex situ* conservation in zoos in aggregate terms. Regardless, under the IUCN Red List Guidelines (IUCN, 2022) this assumption of linearity is, after all, deemed allowable in the absence of more detailed information on species population dynamics, as is the case for many thousands of species for which such data are generally lacking (Briscoe et al., 2019; Paniw et al., 2021).

Predicting Future IUCN Red List Status

Setting baseline population sizes

I used my calculations of AOOH as a proxy for abundance and predicted changes in future IUCN Red List status using Criterion A3, where a population reduction is 'projected, inferred or suspected to be met in the future', with population changes calculated over a timeframe of 10 years or three generations, whichever is longer (IUCN, 2022). Under this criterion, species are classified as 'Vulnerable', 'Endangered' and 'Critically Endangered' if they suffer or are projected to suffer a population reduction of 30%, 50% or 80%, respectively (IUCN, 2022). However, three generation lengths often did not round evenly to the decadal timesteps at which I made my SDM projections. Also, the WorldClim baseline climate period of 1970-2000 has a median year of 1985, which would therefore inflate the impacts of climate and land use change on species' Red List status for earlier timesteps, such as the period up to 2030, as more than three decades of past climate and land use change would be condensed into a single timestep. For each Red List status prediction, I therefore calculated a corrected baseline population size (baseline AOOH) to account for these discrepancies and remove bias induced by inappropriate setting of baseline years, using Eqn 2:

Eqn 2: $$P_c = P_t\left(\left(\left(\frac{P_b}{P_t}\right)^{\frac{1}{t-c}}\right)^{g}\right)$$

…where P_c is the corrected baseline population size P for baseline year c. Timestep t represents the decadal timestep (e.g. 2030) for which the Red List projection is being made. The uncorrected baseline (e.g. 1985) population is indicated by P_b and g represents the number of years in three generations, with $g \geq 10$ in all cases. Therefore, $\left(\frac{P_b}{P_t}\right)^{\frac{1}{t-c}}$ represents the annual rate of population change for the time period between t and c, which is then extended for g years to retrospectively estimate P_c based on P_t. Finally, I estimated standardised percentage change in species population size (Δ_p) using Eqn 3:

Eqn 3: $$\Delta_p = 100\left(\frac{P_t - P_c}{P_c}\right)$$

See Appendix A for worked examples demonstrating this approach.

Assigning Red List categories

Species should be classified as ‘Near Threatened’ if population trends are approaching those that would result in a threatened Red List category (Vulnerable or worse). I therefore classified species as Near Threatened if they suffered a projected decline of 20% or more. If species suffered an initial population reduction and were assigned to a threatened category but then stabilised at later timesteps, species could move back towards less threatened categories to reflect the appropriate timeframe of Red List assessments (ten years or three generations). However, as species may be threatened for reasons other than climate and land use change, I limited any recovery to the species’ original threat category. ‘Data Deficient’ (DD) and ‘Not Evaluated’ (NE) species were able to move into threatened categories if they met any of the Δ_p thresholds, which would indicate a minimum level of endangerment under Criterion A3, even if the species is yet to be assessed under other criteria. Predicting species’ future Red List status under a single criterion may underestimate species endangerment, as it does not explicitly account for other criteria relating to fragmentation, small range sizes, or highly restricted population sizes (IUCN, 2022). However, this means that my predictions are likely to be conservative and, if anything, may underestimate the impacts of climate and land use change on species’ future threat status.

EDGE2 Calculations

Armed with these projections of future Red List status, I could then predict, for the first time, species’ future EDGE scores under environmental change. The original ‘EDGE’ (Evolutionarily Distinct and Globally Endangered) metric (Isaac et al., 2007) has recently been improved upon (‘EDGE2’; Gumbs et al., 2023). The EDGE2 metric incorporates uncertainty in species extinction probability (GE2) and phylogenetic complementarity when quantifying evolutionary distinctiveness (ED2), such that a species’ EDGE score is dependent on the probability of extinction of closely related species. To incorporate uncertainty in phylogenetic tree structure, ED2 scores are calculated across a large number of candidate trees ($100 < n \leq 1{,}000$; Gumbs et al., 2023). Published EDGE scores using the EDGE2 metric are available for mammals (Gumbs et al., 2023). Given the considerable computational requirements of computing these scores for over 30,000 terrestrial vertebrate species for current conditions and multiple SSP scenarios, I limited the number of phylogenetic trees in my calculations to 100. I otherwise followed methods outlined by Gumbs et al. (2023).

Briefly, this first involves assigning a probability of extinction *p* to each species based on its IUCN Red List status. *p* is randomly drawn from a range of possible values derived from a quartic curve, whereby the median *p* doubles with each increase in Red List category, such that median *p* for CR = 0.97; EN = 0.485; VU = 0.2425; NT = 0.12125; LC = 0.060625 (Gumbs et al., 2023). *p* for DD/NE species is randomly drawn from the full range of possible values (0.0001 – 0.9999, median = 0.5). These values are then multiplied by ED2, the expected evolutionary distinctiveness of the species given its terminal branch length (unique to the species) plus the number and extinction probabilities of close relatives, such that species with a few highly threatened close relatives will have a higher EDGE score than an equally threatened species with many non-threatened close relatives (Gumbs et al., 2023). These scores are equivalent to the expected amount of unique evolutionary history (MY) that would be lost should the species go extinct. I repeated this process across 100 randomly sampled phylogenetic trees for mammals using species' current Red List statuses.

When comparing my estimated scores for mammals with published data (Gumbs et al., 2023), I found a very strong correlation (Pearson's $r > 0.95$, df = 5,710, $p < .001$) for both raw EDGE estimates and ranked scores, so reducing the number of trees did not qualitatively affect estimated EDGE scores. I repeated this process for each future timestep, SSP scenario and taxonomic group. My estimates of future EDGE scores include species projected to lose all of their climatically suitable habitat. Such species were assigned a future Red List Status of Extinct in the Wild. I fixed *p* for these species at the maximum value of 0.9999, implying near-certain extinction and increasing the ED2 value of close relatives.

Following this process, I estimated EDGE scores for the world's terrestrial vertebrates under current conditions and future SSPs. I then mapped how the distribution of threatened vertebrate evolutionary history shifts in geographical and phylogenetic space (Figure 4), identifying EDGE species hotspots and evolutionary lineages likely to contain the most threatened evolutionary history under environmental change.

Results

Even under the relatively moderate SSP2-4.5, the scenario most in line with current international commitments to reduce greenhouse gas emissions (Hausfather and Peters, 2020), climate and land use change are projected to fundamentally change spatial patterns in terrestrial vertebrate biodiversity (Figures 1-2; Appendix A, Figures S1-4). It will also have profound impacts on species threat status and trends in overall endangerment (Figure 3), and the phylogenetic and spatial distribution of threatened evolutionary history (Figure 4).

How will future environmental change impact the distribution of terrestrial biodiversity?

Richness change

Despite the acute effects of environmental change on terrestrial vertebrate biodiversity, species richness patterns under SSP2-4.5 appear stable for much of the world's land masses, and even trend positively for some regions (Figure 1a). By contrast, species richness is projected to decline most severely in tropical east Africa. Vertebrate richness is also projected to decline in some areas of the Amazon basin and the Atlantic Forest system of Brazil (Figure 1a). However, these aggregate richness patterns conceal much more severe shifts when considering taxonomic classes separately (Appendix A, Figures S1-4). Avian richness is projected to be stable or increasing worldwide, with particular increases in the northern Andes and other high elevation systems such as the Ethiopian highlands, central-southern Mexico, and central Asia (Appendix A, Figure S2). Other taxa show much more negative richness trends globally, with particularly strong decreases in mammal richness in Kenya, Uganda and Tanzania (Appendix A, Figure S1). Ectotherm (reptile and amphibian) richness faces the most precipitous declines in the tropical forests of the Amazon and Congo basins, with particularly strong declines of amphibian richness in the Atlantic Forest (Appendix A, Figure S4).

Community Turnover

As a result, community turnover (the proportion of species in each grid cell that are either lost or gained in 2070, relative to the combined richness of the grid cell across present and future timesteps) is projected to be severe and widespread across the planet (Figure 1b). Turnover is highest in species-poor areas such as the desert systems of Australia, the Sahara and the Middle East, and Arctic regions, where just a few colonisations or extinctions can have profound

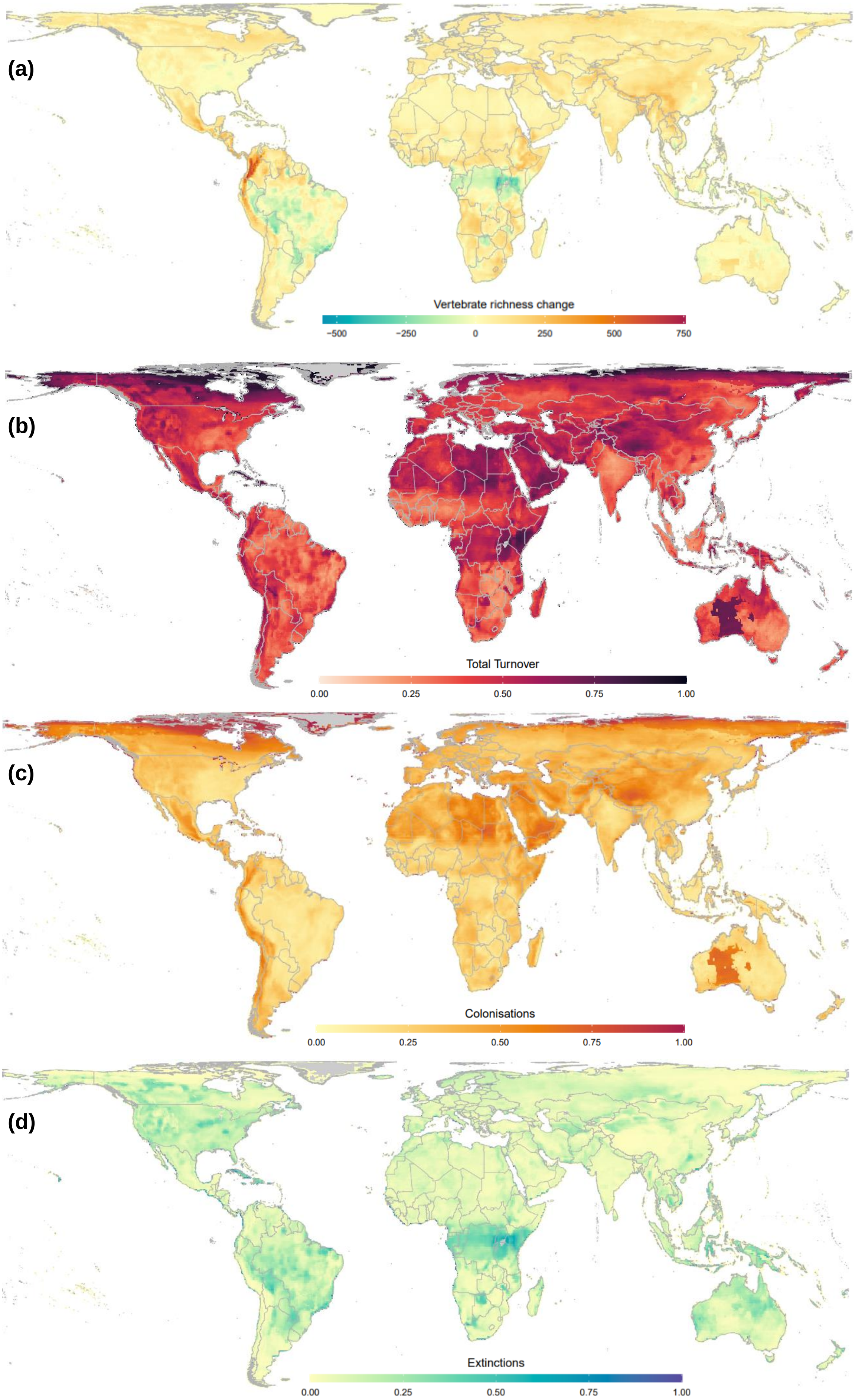

(a)
Vertebrate richness change
−500
−250
0
250
500
750
(b)
Total Turnover
0.00
0.25
0.50
0.75
1.00
(c)
Colonisations
0.00
0.25
0.50
0.75
1.00
(d)
Extinctions
0.00
0.25
0.50
0.75
1.00

Figure 1. Change in terrestrial vertebrate biodiversity patterns under SSP2-4.5, up to the year 2070. (a) Change in overall species richness per ~25 km grid cell, with species classed as ‘present’ if they have at least 1% suitable habitat within the grid cell. **(b)** Overall turnover in terrestrial vertebrate community per grid cell. Turnover is calculated as the proportion of species gained (e.g. through colonisation) or lost (e.g through local extinction) relative to the total number of species that occurs in the grid cell across both current and future (2070) time periods (Hallett et al., 2016). **(c)** Rate of colonisation per grid cell (proportion of novel species in 2070 relative to total species richness across both timesteps). **(d)** Rate of local extinctions per grid cell (proportion of species lost by 2070 relative to total richness across both timesteps).

effects on proportional turnover. However, some biodiversity hotspots (Myers et al., 2000) also face high turnover rates, especially those in the tropical Andes and east Africa (Figure 1b). With the former, turnover is driven almost entirely by colonisation by novel bird (and to a lesser extent mammal) species (Appendix A, Figure S2). With the latter, turnover in is driven almost entirely by localised extinctions (Figure 1d), whereas colonisation rates remain low (Figure 1c). These high local extinction rates in east Africa are common across all taxonomic classes, and are comparable only in island systems in the Caribbean and Oceania (Figure 1d; Appendix A, Figures S1-4).

Drivers of Change

While I did not investigate the precise drivers of localised extinctions explicitly, my data indicate that a combination of abiotic (exposure to anthropogenic climate and land use change) and biotic (species dispersal capabilities) are likely to drive changes in distribution patterns and extinction risk in terrestrial vertebrates. Arctic regions are projected to see the strongest increases in mean temperatures (Figure 2a), aligning with areas of high community turnover driven primarily by colonisation of novel species (Figure 1b-c), creating novel Arctic communities as the climate becomes hospitable for more temperate-adapted species.

Colonisation rates (Figure 1c) were largely driven by birds, whereas other taxa, particularly ectotherms, were rarely able to expand their ranges as new areas became climatically suitable. For example, birds had a median estimated dispersal capability of 8.2 km/yr (inter-quartile range [IQR] = 4–21.9) whereas amphibians and reptiles had a median dispersal capability of just 0.114 km/yr (IQR = 0.07-0.195). Patterns of colonisation and extinction, whereby colonisation by novel avian species maintains or increases local species richness and drives community turnover, while reptilian and amphibian species face localised extinctions across

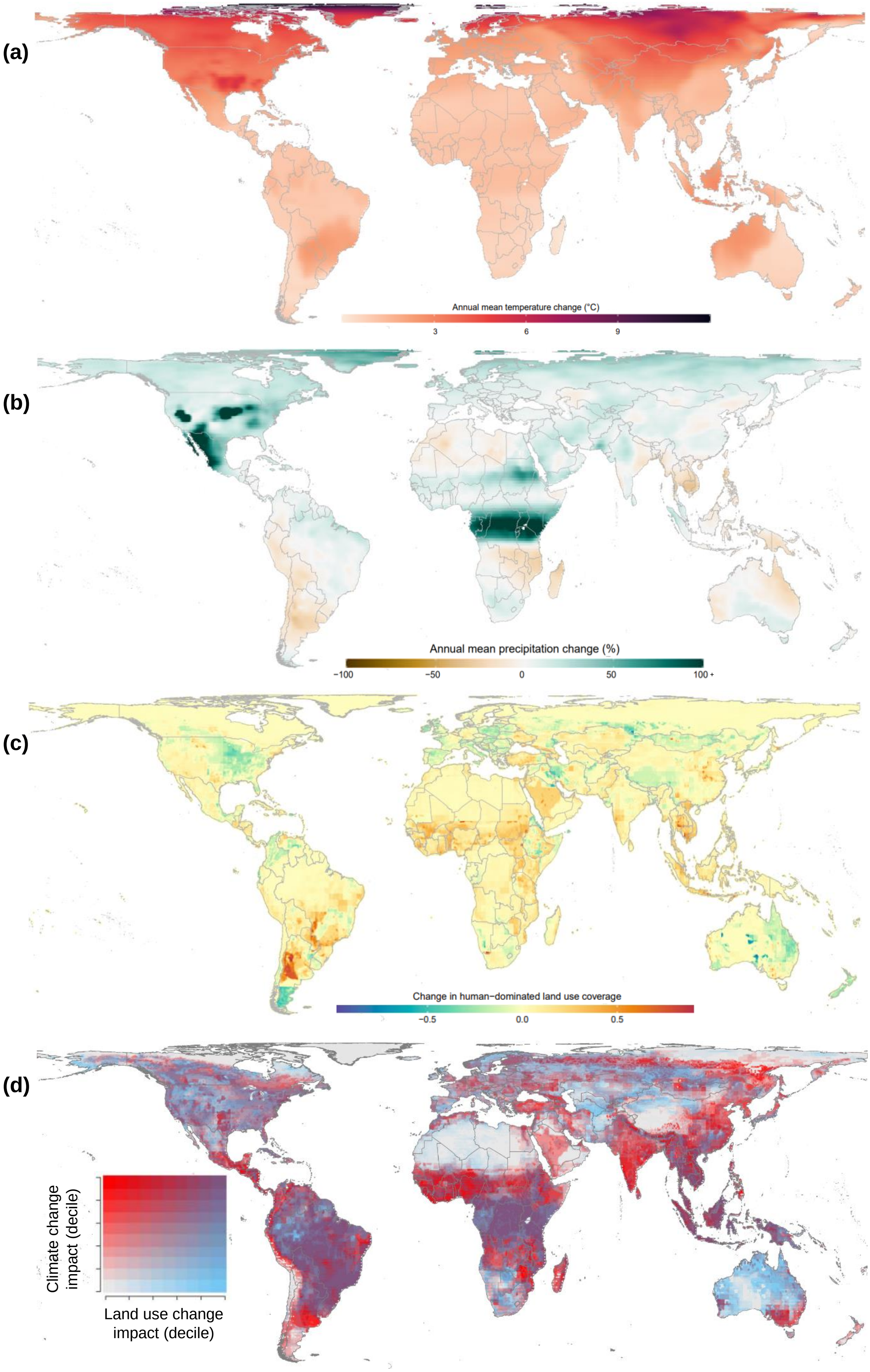

(a)
Annual mean temperature change (°C)
3
6
9
(b)
Annual mean precipitation change (%)
−100
−50
0
50
100 +
(c)
Change in human−dominated land use coverage
−0.5
0.0
0.5
(d)
Climate change impact (decile)
Land use change impact (decile)

Figure 2. Potential drivers of change in terrestrial vertebrate biodiversity patterns under SSP2-4.5, up to the year 2070. (a) Mean absolute change in annual mean temperature (°C) per ~25 km grid cell across the three global circulation models (GCMs) used in species distribution modelling. **(b)** Mean proportional change in total annual precipitation across the three GCMs. Note that the colour bar is capped at a 100% increase to aid visualisation. **(c)** Rate of conversion from primary and/or secondary natural habitats (forest/non-forest) to anthropogenic land uses such as cropland, pasture, and rangeland in the LUH2 projections. Positive values indicate net increase in anthropogenic land use at the expense of natural habitats, while negative values indicate net reduction in anthropogenic land use as natural habitats re-establish. **(d)** Bivariate map showing impacts of climate and land use on species AOOH per grid cell. Red values indicate declines in climate suitability for more species, blue values indicate declines in habitat suitability due to land use change. Purple areas represent concurrent land use and climate impacts. Cells divided into deciles.

much of the planet (Figure 1), therefore suggests that dispersal capability strongly filters species' vulnerability to environmental change (Pacifici et al., 2015; Foden et al., 2019).

Hotspots of localised extinctions correlated with areas projected to have the greatest exposure to both climate and land use change in future (Figure 2). This was particularly the case in the African tropics, which is projected to be exposed to severe changes in rainfall patterns under SSP2-4.5 (Figure 2b). When averaged across GCMs, this region is projected to see a more than doubling in annual rainfall (Figure 2b), largely driven by extreme increases in rainfall predicted under IPSL-CM6A-LR. This region has a highly diverse topography, meaning that accurately predicting changes in rainfall is notoriously challenging (Ayugi et al., 2021), and traditional downscaling of coarse-resolution GCMs may misrepresent the climatic complexity in the region (Hijmans, 2020). However, given these uncertainties, it is prudent to assume that species will face novel and potentially inhospitable climatic conditions in east Africa, aligning with the precautionary principle at the heart of conservation (Cooney and Dickson, 2012). This area is also projected to see relatively high rates of natural habitat conversion towards anthropogenic land uses (Figure 2c), resulting in combined climate and land use change impacts on east African biodiversity (Figure 2d).

Threatened Species and Red List Status Projections

Of the 24,598 species included in my SDMs, 3,150 (12.8%) are currently threatened with extinction (IUCN Red List Categories Vulnerable, Endangered, Critically Endangered, and Extinct in the Wild; Mace et al., 2008). This contrasts with 20.5% of non-Chiropteran terrestrial vertebrates generally, because the species with ranges too small to be included in my SDMs are disproportionately more likely to be threatened (Cardillo et al., 2008). Under the 'middle of the road' SSP2-4.5, the proportion of species projected to be threatened in future more than doubles to 27%, including 2,753 species (11.2%) projected to lose all climatically suitable habitat by the year 2070. Under the most severe scenario, SSP5-8.5, almost two-fifths (39.1%) of modelled vertebrates are threatened by 2070, with one in six species (n=4,354, 17.7%) projected to become Extinct in the Wild through complete loss of climatically suitable habitat within their future occupiable range.

Figure 3 shows projected shifts in species Red List status for each class of terrestrial vertebrate, under SSP2-4.5. Equivalent figures for other SSPs are given in Appendix A. Under mild (SSP1-2.6) or moderate (SSP2-4.5) environmental change, the proportion of modelled species in a threatened category increases sharply up to 2030, but then rises much more slowly up to 2070, reflecting a more gradual increase in endangerment with more concerted international effort to mitigate or prevent climate and land use change (Figures 3 and S6, Appendix A). Under these scenarios, 22.1% (SSP1-2.6) and 27% (SSP2-4.5) of modelled species are projected to be threatened by 2070. By contrast, under the more severe SSP3-7.0 and SSP5-8.5, the proportion of modelled species that are projected to be threatened continues to increase rapidly throughout the period, reaching 37.5% and 39.1% by 2070, respectively (Appendix A, Figures S7 and S8). The direction of these trends is consistent across taxa, but magnitude varies. Endangerment is projected to be most severe for amphibians, with 40.9% of modelled amphibians projected to be threatened by 2070 under SSP2-4.5, compared to just 18.9% of modelled birds (Figure 3).

How will environmental change affect the phylogenetic distribution of conservation priorities and threatened evolutionary history?

Under current conditions, the terrestrial vertebrate with highest EDGE score is the Madagascan big-headed turtle (*Erymnochelys madagascariensis*), with a median estimate of 76.74 MY of threatened evolutionary history expected to be lost should this species go extinct (IQR = 72.27-81.21). The top-ranked amphibian, bird and mammal species are the Bale Mountains frog(*Ericabatrachus baleensis*, 66.05 MY, IQR = 58.41-75.08), the giant ibis (*Thaumatibis gigantea*, 55.44 MY, IQR = 50.7-58.39) and the mountain pygmy possum (*Burramys parvus*, 25.71, IQR = 22.53-27.71), respectively. However, under all four SSP scenarios the species

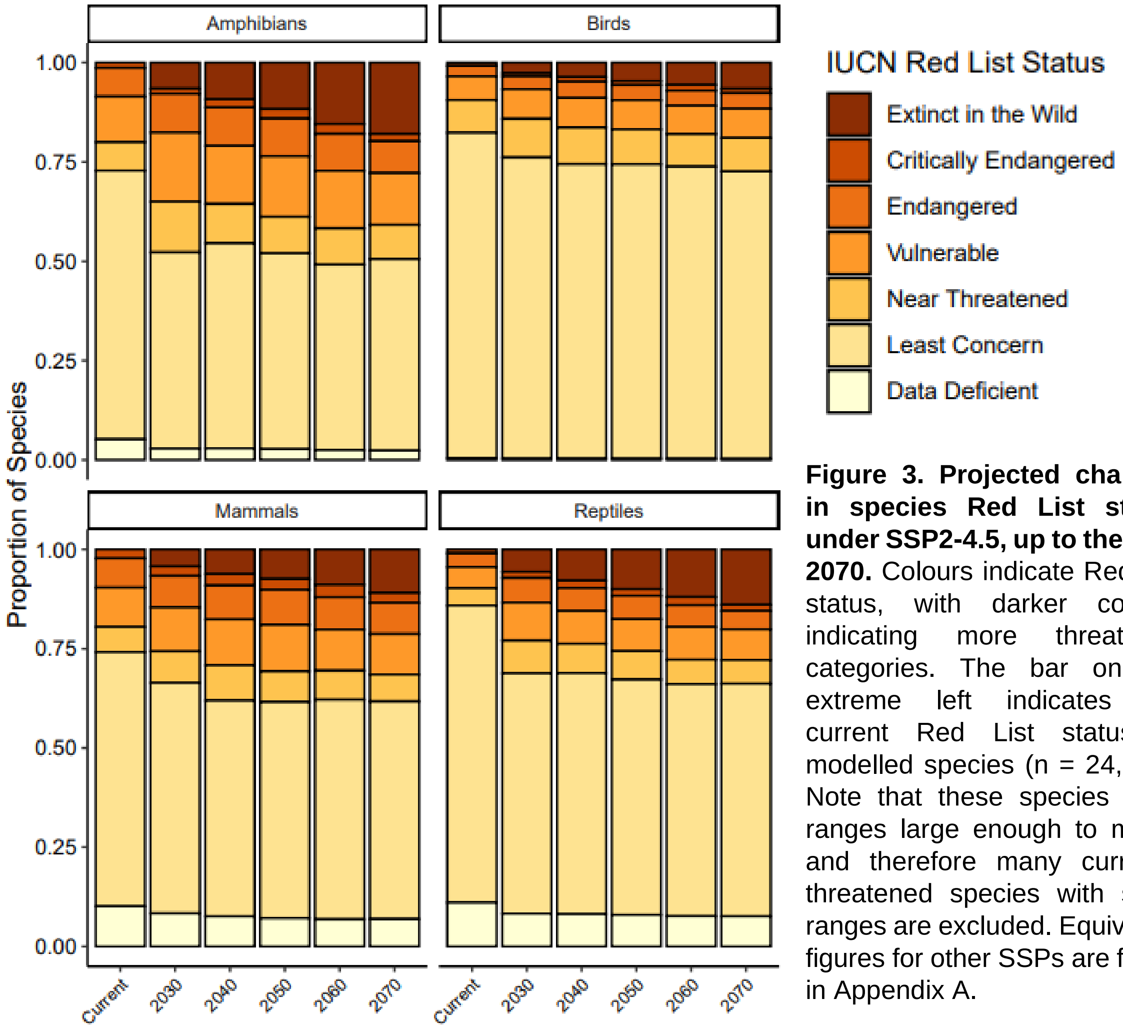


Figure 3. Projected changes in species Red List status under SSP2-4.5, up to the year 2070. Colours indicate Red List status, with darker colours indicating more threatened categories. The bar on the extreme left indicates the current Red List status of modelled species (n = 24,598). Note that these species have ranges large enough to model and therefore many currently threatened species with small ranges are excluded. Equivalent figures for other SSPs are found in Appendix A.

projected to represent the greatest amount of threatened evolutionary history by 2070 are caecilians, specifically Boulenger's caecilian (*Boulengerula boulengeri*, SSPs 1-2.6, 2-4.5 and 3-7.0) and Kirk's caecilian (*Scolecomorphus kirkii*, SSP5-8.5). This reflects a consistent pattern whereby amphibians, and particularly caecilians, face the greatest increases in EDGE scores under environmental change (Figure 4a).

Under the 'middle of the road' SSP scenario (SSP-2.45), the families facing the greatest increase in mean EDGE score are the Diatomyidae (+39.88 MY) and solenodonts (Solenodontidae, +36.53 MY). However, the former is represented by a single species, the Laotian rock-rat (*Laonastes aenigmamus*), a Least Concern species projected to become Extinct in the Wild by 2070 under SSP2-4.5, while the latter is represented by just two species, the Hispaniolan and Cuban solenodons (*Solenodon paradoxus* and *Atopogale cubana*). The

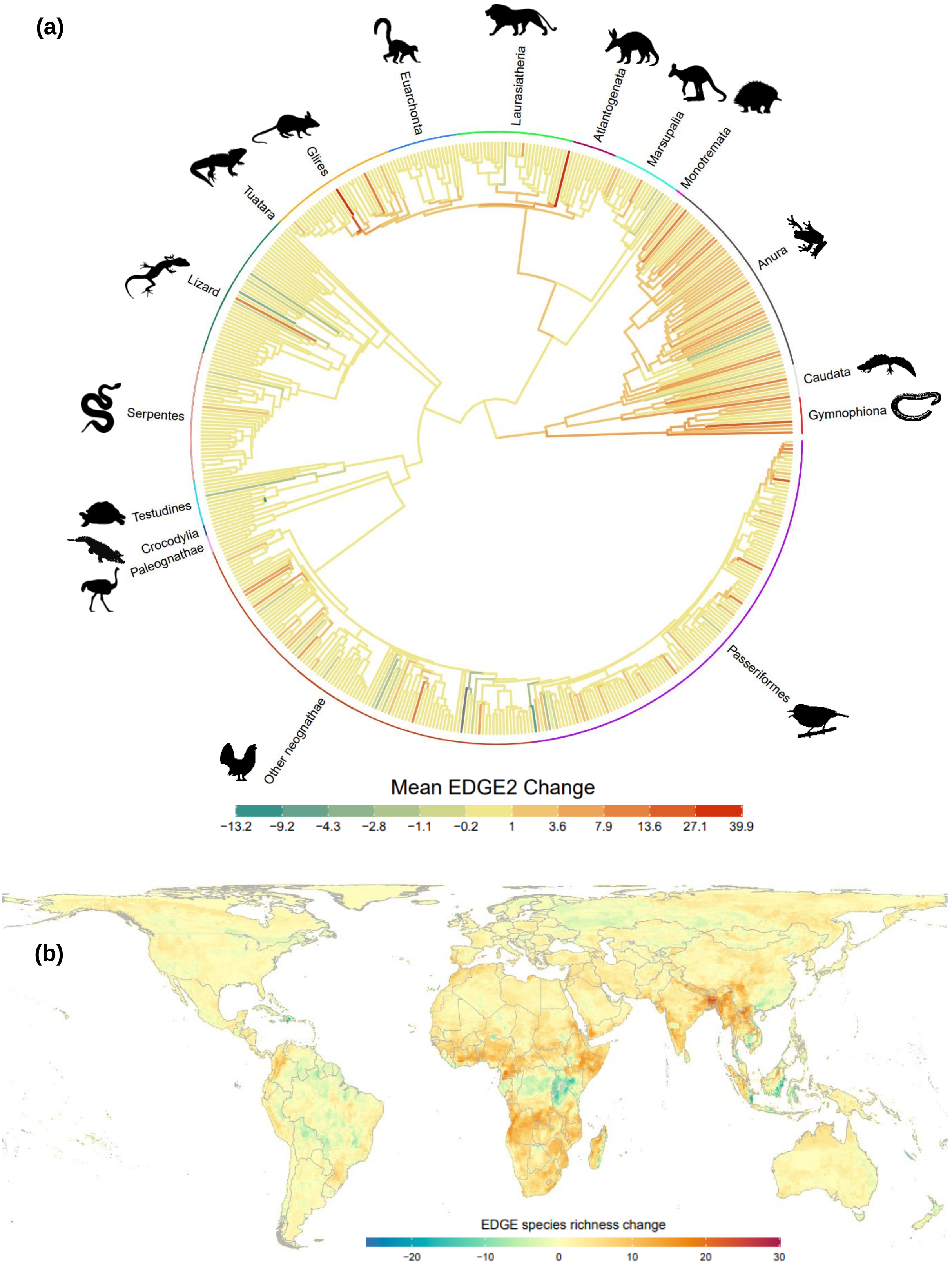


Figure 4. Spatial and phylogenetic shifts in the distribution of threatened evolutionary history under environmental change. (a) Change in mean EDGE score for terrestrial vertebrate families under SSP2-4.5 up to the year 2070. Red branches indicate increases in mean EDGE score, blue branches show decreases in mean EDGE score. Coloured bars represent major taxonomic clades. (b) Change in richness of EDGE species (threatened species with above median EDGE score in ≥ 95% of iterations) richness per ~25 km grid cell, under SSP2-4.5 up to the year 2070. Species classed as ‘present’ if they have at least 1% suitable habitat within the grid cell.

Hispaniolan solenodon is also projected to become Extinct in the Wild, leaving the Cuban solenodon as the sole surviving member of this lineage. The top five families that face the greatest mean increases in EDGE score and are represented by more than five species are all amphibians, specifically African caecilians (Herpelidae, 9 species, +17.7 MY), button frogs (Cycloramphidae, 34 species, +9.35 MY), mudpuppies (Proteidae, 6 species, +8.8 MY), Neotropical tailed caecilians (Rhinatrematidae, 10 species, +6.93 MY), and robber frogs (Brachycephalidae, 37 species, +6.17 MY). Beyond Amphibia, major increases in mean EDGE scores are constrained to just a few families (Figure 4a). The worst-affected avian families are the Cuban warblers (Teretistridae, 2 species, +15.75 MY) and todies (Todidae, 5 species, +11.4 MY), which are both Caribbean island endemics. The avian family with more than five species with the greatest increase in mean EDGE score is the owlet-nightjars (Aegothelidae, 10 species, +5.07 MY). The mammal and reptile families with more than five species with the greatest increase in mean EDGE score are the ring-necked possums (Pseudocheiridae, 18 species, +1.36 MY) and side-necked turtles (Podocnemididae, 8 species +0.5 MY), respectively.

Species are classified as ‘EDGE species’ if they are in a threatened Red List category and their EDGE score is greater than the median for the clade in at least 95% of iterations (Gumbs et al., 2023). Under current conditions, these species are highly concentrated in a few hotspots, such as southeast Asia, northern Madagascar, the Indo-Gangetic plain, and east Africa (Pipins et al., in review). Under environmental change, EDGE species richness is projected to shift considerably (Figure 4b). Consistent with my results for all species (Figure 1a), EDGE species richness is projected to decline markedly in tropical east Africa (Figure 4b), with other notable losses in Hispaniola, Cambodia, and southeastern Borneo and southeastern Sumatra. However, other parts of southeast Asia such as northern Vietnam, Laos and Myanmar see significant increases in EDGE species richness, which also increases in the Ganges river delta, the Sahel, southern Africa, Madagascar, and the Andes (Figure 4b).

Discussion

In this chapter I have explored the implications of future anthropogenic climate and land use change on terrestrial vertebrate biodiversity. Using an ensemble species distribution modelling (SDM) framework (Marmion et al., 2009), I have predicted climate-induced shifts in spatial patterns of species richness, community turnover, local extinction and colonisation dynamics, and investigated potential drivers of these dynamics (Figures 1-2). Applying these SDM outputs to IUCN Red List Criterion A3 has revealed concerning declines in species conservation status, even under relatively mild climate and land use change scenarios (Figure 3). More than a quarter (27%) of modelled species are threatened by 2070 under the moderate SSP2-4.5 scenario, including 2,753 species projected to lose all of their climatically suitable AOOH. While care should be taken in directly inferring IUCN Red List status from SDM outputs (Akçakaya et al., 2006; IUCN, 2022), the precautionary principle would still demand that these species be a particular focus of conservation attention, including through *ex situ* programmes in zoos (CBD, 2022; IUCN, 2023a). I have taken these projections still further, investigating how environmental change threatens the vertebrate tree of life, highlighting phylogenetic hotspots of endangerment and lineages likely to become priorities for conserving threatened evolutionary history in future (Figure 4).

Conservation implications

The range shifts predicted by my SDMs largely agree with predictions elsewhere in the literature – namely, that many species are likely to shift their ranges along latitudinal or elevational gradients in response to a warming climate (Figures 1a and 1c; Chen et al., 2011; Telwala et al., 2013; Hastings et al., 2020); that island systems are likely to see elevated levels of extinction with global loss of island endemics (Figures 1a and 1d; Veron et al., 2019; Leclerc et al., 2020); and that species dispersal capabilities are likely to moderate species vulnerable to environmental change (Pacifici et al., 2015; Foden et al., 2019). Avian species with high dispersal capabilities were much more able to colonise habitats that became newly climatically suitable, maintaining or even increasing local species richness for much of the planet (Figure 1a), while taxa with poor dispersal capabilities such as reptiles and amphibians had extremely low rates of colonisation, with widespread losses of ectotherm species richness globally (Appendix A, Figures S1-4).

Climate-smart connectivity corridors

These results highlight that maintaining and protecting viable corridors of climatically suitable habitat will be vital to facilitate species range shifts and allow species to respond to changing environmental conditions (Hannah et al., 2008; Senior et al., 2019; Parks et al., 2020).

Protected areas can act as refugia for climate-threatened species (Mi et al., 2023) and have higher rates of colonisation by novel species undergoing climate-induced range shifts (Thomas et al., 2012; Cooke et al., 2023). Improving connectivity between existing protected areas should be a key consideration as nations expand protected area coverage in line with the ‘30 by 30’ target of 30% of land and sea being protected by 2030 (CBD, 2022). However, key areas of connectivity between global protected areas are subject to elevated anthropogenic pressure, with nearly a quarter of such areas currently unprotected and potentially vulnerable to future agricultural expansion (Brennan et al., 2022). Similarly, human-constructed barriers (such as border walls) are likely to disrupt the ability of 696 non-volant mammal species to track their climatic niche under future climate change, including 122 species disrupted by the USA-Mexico border wall alone (Titley et al., 2021).

In addition to physical connectivity between species’ current and future climatically suitable ranges, climatic connectivity (the ability of species to range shift without encountering hostile climatic conditions), is also a vital consideration in establishing dispersal corridors for range-shifting species, especially for those with reduced ability to make large-scale dispersal movements in environmentally hostile conditions (McGuire et al., 2016; Senior et al., 2019). For example, only 41% of the natural areas of continental USA are climatically connected, while climatic connectivity can increase to 65% of natural lands through the establishment of climate-smart connectivity corridors that minimise exposure to hostile climates and human-modified land uses (McGuire et al., 2016). In a global study of tropical forest systems, 62% of tropical forest areas had insufficient climatic connectivity to facilitate climate-induced range shifts, with climatic connectivity further threatened by ongoing deforestation (Senior et al. 2019). Therefore, habitat creation, restoration and protection measures must incorporate not only physical connectivity but also climatic gradients, and should be a key consideration in the pathway to achieving 30 by 30 (Senior et al., 2019). In the following chapter, I demonstrate how protected area prioritisation can maximise the conservation of long-term refugia from climate and land use change for terrestrial vertebrate threatened evolutionary history.

Global biotic homogenisation

High rates of colonisation by temperate and/or lowland species in high latitude and high-altitude regions such as the Arctic, Andes and Himalaya (Figure 1c) are likely to produce novel species assemblages (Figure 1b). Given the global scale and extremely broad taxonomic scope of my study, I did not include biotic interactions in my SDM framework. Despite recent advances such as the greater adoption of joint species distribution modelling (jSDM) frameworks to incorporate species associations into SDM predictions (Wilkinson et al., 2021), doing so across a set of 24,598 species globally was not viable. While biotic interactions such as competition and predation can influence species range dynamics, even at continental scales (Araújo and Luoto, 2007), abiotic factors such as climate are theorised to have a greater influence on species distributions at coarse spatial scales (Pearson and Dawson, 2003). Furthermore, negative biotic interactions (e.g. competitive exclusion) are likely to have weaker effects on species distributions at coarse scales (Araújo and Rozenfeld, 2014), while positive interactions manifest across all scales (Araújo and Luoto, 2007), especially in stressful environments such as mountain ranges, deserts, and Arctic systems where my models predict high rates of community turnover (D'Amen et al., 2018; Mod et al., 2020).

Therefore, at the relatively coarse (~25 km or ~50 km grid cell) resolution of my global SDMs, colonisation of hostile mountain, desert, and Arctic environments (Figure 1b-c) by lowland species are unlikely to be prevented by negative biotic interactions, leading to biotic homogenisation through the loss of these unique communities of endemic species (Baiser et al., 2012; Hidasi-Neto et al., 2019). Conservation strategies in these regions must therefore be cognisant of the likely colonisation of these more specialist systems by more generalist colonisers (especially birds) under climate and land use change. Applying conservation interventions that are relevant at different spatial scales will be required to reflect the scales at which these community turnover dynamics apply (Sidemo-Holm et al., 2022). Maintaining high-quality habitat in climatic refugia will be vital for conserving endemic species at local scales, where competitive exclusion by exotic generalists may threaten persistence of local endemics (Hidasi-Neto et al., 2019; Sidemo-Holm et al., 2022). At regional scales, promoting a heterogeneous and connected mosaic of habitats will allow for the partitioning of communities and the persistence of rare endemics, alongside the reintroduction and/or translocation of such species, where appropriate (Holl et al., 2022).

Defaunation of a biodiversity hotspot in east Africa

A striking and somewhat surprising result from my SDMs was the very high extinction rates projected across tropical Africa and especially the East African Rift System (Figure 1a), which was common across all taxonomic groups (Appendix A, Figures S1-4). Previous global SDM studies have not detected this level of potential defaunation of east Africa under climate and land use change (Hof et al., 2018; Biber et al., 2020; Biber et al., 2023). However, these studies have all used the earlier CMIP5 GCM projections, rather than the latest CMIP6 models used here. While I did not explicitly investigate the primary driver of loss of climatic suitability, broad assessment of the magnitude of projected climate and land use change across the globe (Figure 2a-b) show that, in combination with land use change (Figure 2c), these patterns are more likely to be driven by changing rainfall in the region than projected warming (Figure 2a-b). It should be noted, however, that the three GCMs I selected for my SDMs have been shown to perform relatively poorly in predicting both the March-April-May and October-November-December rainy seasons in east Africa (Ayugi et al., 2021) and generally predicted greater than observed increases in rainfall in Uganda 1981-2014 (Ngoma et al., 2021). This is not to invalidate SDM predictions in this region, but it is important to note that SDMs are likely predicting species responses to entirely novel precipitation conditions here. Under the precautionary principle, it is therefore prudent to assume that these conditions will not be suitable for the persistence of a great many east African species.

Given the topographic and climatic diversity of east Africa, and of the East African Rift System in particular (Camberlin, 2018), some species projected to become locally extinct in my SDMs may be able to persist in microclimate refugia that are not picked up by the coarse-resolution GCMs used here (Hijmans, 2020). Providing long-term protection for these refugia will be vital to stem biodiversity loss the East African Rift System. With increasing conversion of natural to anthropogenic land uses in the region (Figure 2c) alongside unpredictable and potential extreme changes in rainfall patterns (Figure 2b), there is a risk that human-wildlife conflict in the region may intensify under future environmental change (Abrahms et al., 2023). Here, developing robust economic incentives to conserve the remaining refugia from climate and land use change, as well as surrounding areas in the habitat matrix to allow for dispersal and healthy metapopulation dynamics, will be crucial (Abrahms et al., 2023). For example, just and equitable sharing of wildlife tourism revenues, and empowerment of local communities in decision-making processes, is central to the long-term sustainability of area-based conservation in the region (Spenceley et al., 2021). With the tourism industry contributing more than 10% of national GDP in east Africa (UNCDAT, 2017), prioritising protection of long-term refugia is necessary not only for conservation, but also to ensure the future prosperity and livelihoods of communities living alongside the iconic biodiversity of east Africa.

An emerging role for ex situ conservation

The most immediate conservation priorities are the up to 4,354 species projected to lose all climatically suitable habitat in my SDM results, thereby becoming Extinct in the Wild. Of these, 1,929 species are projected to become Extinct in the Wild even under the mildest climate and land use change scenario (SSP1-2.6). This includes 12.7% of modelled amphibians and 9.7% of modelled reptiles, further highlighting the elevated vulnerability to climate and land use change faced by these ectothermic species with limited dispersal capabilities. Over the past decade zoos have increasingly moved towards the 'One Plan Approach' for species conservation, whereby *ex situ* and *in situ* populations and conservation actions are planned and managed in an integrated manner (Byers et al., 2013; Traylor-Holzer et al., 2019). This will likely require increased flow of individuals between wild and captive populations to maximise genetic diversity, with an increasing potential role for conservation translocations (Gilbert et al., 2017).

Given the relatively poor dispersal capabilities of threatened Amphibia and Reptilia, these species should be important candidates for conservation translocations under climate and land use change (Hoegh-Guldberg et al., 2008). Conservation translocations can themselves be informed by SDMs to highlight climatically suitable areas of habitat beyond species' dispersal capabilities (Willis et al., 2009). However, only 11.5% of species involved in reintroduction projects with zoo involvement are reptiles and amphibians, while 39.7% are birds and 37.2% are mammals (Gilbert et al., 2017). Addressing this gap in translocation and reintroduction effort will be an important step towards mitigating climate and land use change impacts for these vulnerable species. In Chapter 5, I discuss in more detail the implications of these findings for global zoo collections, highlighting how significant adaptation of zoo collection composition will be required if zoos are to avoid being outpaced by anthropogenic environmental change.

Conclusions

Here, I have demonstrated that projected climate and land use change up to 2070 will have profound impacts on the spatial and phylogenetic distribution of threatened biodiversity. Some impacts are likely to be unavoidable, with many thousands of species predicted to become threatened even under the mildest warming scenarios. My results highlight hotspots of community turnover, localised extinctions, and changes in the spatial and phylogenetic distribution of threatened evolutionary history. This underlines the importance of proactive, strategic conservation planning to mitigate these impacts. Specifically, designing both physically and climatically connected protected area networks that facilitate species range shifts, and effectively managing existing protected areas to conserve climate refugia for endemic species, will be vital to mitigate anthropogenic declines in biodiversity. In doing so, conservation planners must be cognisant of the changing community composition and species interactions predicted by my models. Management strategies that allow novel species undergoing climate-induced range shifts to coexist with native endemics, particularly in high latitude and elevation regions projected to see the greatest levels of turnover, will be paramount for long term, climate-smart conservation.

Chapter 4

Global priorities to protect threatened evolutionary history under climate and land use change *in situ*

Giraffe (*Giraffa camelopardalis*) photographed in Nairobi National Park, Kenya, with the nearby cityscape of Nairobi in the background. *Photo credit: Alexmbogo (Wikimedia Commons, CC BY-SA 4.0 DEED)*

Abstract

Human-induced extinction of phylogenetically and functionally distinct biodiversity leads to the homogenisation of the world's biota and threatens ecosystems and human livelihoods. Nations have committed to protect 30% of the planet by 2030, but as climate and land use change intensify, relatively little attention has been paid to potentially shifting conservation priorities as ever-more irreplaceable evolutionary history becomes threatened with extinction. Here, I present priorities for expanding the global protected area system to maximise protection of evolutionarily distinct and globally endangered (EDGE) terrestrial vertebrates under current and future conditions. I show that optimal protected area systems could provide long-term protection for over 90% of terrestrial vertebrate threatened evolutionary history, and that 70% of these conservation gains can be achieved in just four tropical and subtropical forest biomes. I also compare two prioritisation pathways under differing levels of international cooperation, and find that international co-operation leads to improved conservation outcomes at lower cost when compared with nations acting independently. My findings call for an integrated international strategy to achieve global targets, with the costs and benefits of protected area expansion shared equitably among nations, recognising the fundamental rights and roles of indigenous peoples in delivering this step-change in global conservation.

Introduction

Anthropogenic pressures on biodiversity have never been more intense (Steffen et al., 2011; Harfoot et al., 2021), leading to potentially catastrophic biodiversity losses that threaten ecosystems and human livelihoods (Barnosky et al., 2011; IPBES, 2019). Since extinction risk is not distributed evenly across the tree of life, conserving threatened phylogenetic diversity has become a priority for global conservation (Carmona et al., 2021; Gumbs et al., 2023). Retaining phylogenetic diversity conserves the diversity of form, features and functions that underpin the natural services biodiversity provides to humans (Flynn et al., 2011; Owen et al; 2019; Molina-Vegas et al., 2021). To help achieve this, area-based conservation (Maxwell et al., 2020) – such as the establishment of protected areas (PAs) and other effective area-based conservation measures (OECMs) – is central to global efforts to halt biodiversity loss. In December 2022 the international community signed the Kunming-Montréal Global Biodiversity Framework (GBF), recognising the importance of area-based conservation and committing to increase global coverage of protected land and sea to 30% by 2030, dubbed the ’30 by 30’ target (CBD, 2022).

Protecting 30% of the Earth’s land and sea is ambitious and will require a near-doubling in global protected area coverage in just eight years following the signing of the GBF. The challenge of delivering spatially optimal protected areas is complicated by anthropogenic climate and land use change. Many of the world’s protected areas are exposed to high rates of future climate change (Asamoah et al., 2021) which may reduce the extent and quality of protected habitat (Xi et al., 2021) and result in climate-induced biome shifts, such as transitions from broadleaved forests to savannah grasslands in tropical regions (Dobrowski et al., 2021). In response, many species are shifting their ranges to track changing environmental conditions (Lawler et al., 2009). While current protected areas provide refugia from climate and land use change for many species (Mi et al., 2023), other species are likely to suffer range contractions both inside and outside protected areas (Hoveka et al., 2022), while shifts in community composition (Baker et al., 2015; Voskamp et al., 2022), functional diversity (Stewart et al., 2022), and phylogenetic diversity (Voskamp et al., 2021) may disrupt ecosystem functions and population viability for many species in unpredictable ways.

Effective protected area planning must not only consider potential shifts in species distributions induced by anthropogenic environmental change, but also shifts in species conservation status and relative conservation importance. Although previous studies have accounted for predicted species range shifts when prioritising protected area expansion (Bagchi et al., 2018; Lawler et al., 2020; Mi et al., 2023), very few have integrated spatial and non-spatial impacts of future environmental change, such as the changing threat status and relative conservation priority of species themselves. For example, a recent assessment of the world’s amphibians demonstrated that climate change was the primary driver of 39% of Red List status deteriorations for the period 2004-2022 (Luedtke et al., 2023). This knowledge gap could undermine the significant levels of research effort already committed to protected area prioritisation. Global biodiversity is in a state of disequilibrium in the face of emerging anthropogenic threats (Storch et al., 2022), with conservation priorities becoming something of a moving target. If we fail to fully account for potential changes in conservation priority species in the future, we risk designing protected area systems that are ill-equipped to conserve threatened biodiversity in the long term.

Here I identify priority areas for expanding the global protected area system to maximise the protection of threatened vertebrate evolutionary history under both current and future climate and land use conditions. I use species distribution models (SDMs) for most of the world's terrestrial vertebrates (n = 24,598, of which 3,771 mammals, 9,799 birds, 6,977 reptiles, and 4,051 amphibians) to predict shifts in species distributions and IUCN Red List status. I then estimate species future EDGE (evolutionary distinct, globally endangered) scores using the updated 'EDGE2' metric (Gumbs et al., 2023). These scores represent the expected loss of unique evolutionary history (MY) should the species go extinct, and were used as weightings in my prioritisations. I present results for current conditions and future conditions under Shared Socio-Economic Pathway (SSP) 2-4.5 for the year 2070, prioritising areas that provide consistent refugia from climate and land use change for conservation priority species (see Methods). I also generate prioritisations under an 'international co-operation' pathway where the global 30% target can be met with differing levels of protection in each country, and a 'domestic' pathway where each nation achieves 30% coverage independently (Shen et al., 2023). Results for other future scenarios are presented in Appendix B. I highlight spatial conservation priorities and show how international co-operation provides greater conservation benefits at lower cost than the domestic pathway, and I identify countries and biomes where increased protection would provide the greatest gains for global biodiversity conservation.

Results

Existing Protected Areas

Existing protected areas provide sufficient protection for only 4,687 MY of threatened terrestrial vertebrate evolutionary history (just 12.8% of a possible total of 36,703 MY) under current conditions. However, they provide sufficient protection for 9,076 species (30.6% of the 29,678 species in our prioritisations). Here, I define 'sufficient' protection as per Butchart et al. (2015), whereby species with smaller ranges require greater coverage to be deemed protected (See Methods; Butchart et al., 2015). Therefore, existing PAs disproportionately protect species of lower conservation priority when weighted by species' EDGE scores, failing to provide sufficient protection for 32,016 MY (87.2%) of threatened evolutionary history. This is primarily driven by the disproportionately poor coverage of amphibians. For example, only 1.5% of newt and salamander (Caudata), 6.3% of caecilian (Gymnophiona), and of 8.5% frog (Anura) threatened evolutionary history is sufficiently covered by existing PAs. By contrast, orders of large mammals and birds such as carnivores (Carnivora), odd-toed ungulates (Perissodactyla), storks (Ciconiiformes) and hornbills (Bucerotiformes) are well-represented in existing PAs (which protect 71.2%, 67.8%, 66.5% and 65.7% of threatened evolutionary history, respectively). Individual species in these four orders represent, on average, 0.77 MY (95% CI = 0.60-0.93) of threatened evolutionary history, compared to an average of 2.7 MY (2.6-2.8) for a typical amphibian species.

When species' future range shifts are accounted for, and concurrent phylogenetic shifts in the distribution of threatened evolutionary history are estimated, existing PAs perform even worse. Under these future conditions existing protected area systems will sufficiently protect only 7,945 species (27%), representing just 4,317 MY (10.7%) of the surviving evolutionary history available to protect in future scenarios. If these significant gaps in current area-based conservation coverage are not filled by effective implementation of 30 by 30 targets, tens of billions of years of vertebrate evolutionary history will remain unprotected.

Spatial Priorities for Protection

Protected area prioritisation will conserve the greatest amount of threatened evolutionary history if nations work co-operatively and account for long-term refugia from climate and land use change when delivering on the 30 by 30 targets. Delivering area-based conservation as recommended by this prioritisation would increase the number of species receiving sufficient protection in long-term refugia from climate and land use change refugia from 7,945 (27%) to 27,192 (92.5%), representing a nearly nine-fold increase in threatened evolutionary history (4,317 to 36,258 MY; 10.7 to 90.1% of a total 40,250 MY) protected under this prioritisation when compared with existing protected area systems. This prioritisation resulted in increased protected area coverage concentrated in well-recognised biodiversity hotspots in the tropics and subtropics (Myers et al., 2000), such as Meso-America, the Tropical Andes, the Atlantic Forest, Madagascar and much of southern and south-east Asia (Figure 1d). Prioritisations generated under current conditions achieved similarly impressive results to those generated under future conditions. Indeed, more species are conserved when prioritising under current

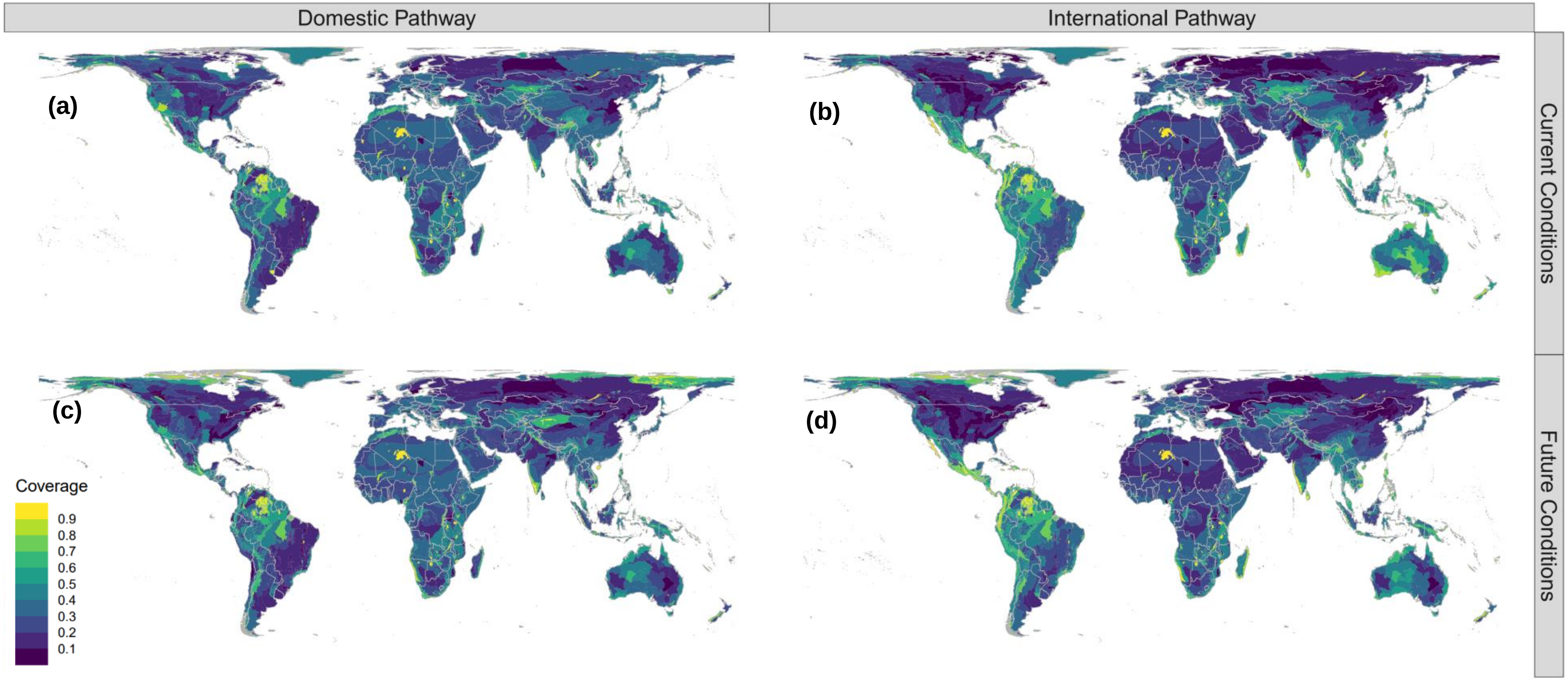


Figure 1. Global distribution of protected areas (PAs and OECMs) across the ecoregions of the world under each optimisation scenario. Prioritisations under current climatic and land use conditions and current EDGE scores (top row, a-b) and under future conditions using harmonic means of species AOOH (Area of Occupiable Habitat, Chapter 3) in each planning unit for all decadal timesteps up to 2070, and projected EDGE scores for 2070, under the SSP2-4.5 representative pathway (bottom row, c-d). Prioritisations generated using the domestic pathway to reaching global targets (per-country coverage bounded between 27.5-32.5% for nations currently below 32.5% coverage, left column, a and c) and using the international co-operation pathway (per-country coverage bounded between 10-67%, right column, b, and d). Results are displayed as the proportion of protected area coverage in each terrestrial ecoregion (Olson et al., 2001) to aid visualisation.

rather than future conditions (Figure 2a), albeit more threatened evolutionary history is conserved when prioritising under future rather than current conditions (Figure 2b). This demonstrates how threatened evolutionary history patterns do not always follow richness patterns, and simply maximising the number of species protected does not necessarily prevent loss of unique phylogenetic diversity. Furthermore, overlaying the outputs of prioritisations generated under current conditions with future species distributions and future EDGE scores markedly reduced their effectiveness (Figure 2a-b). Under the international co-operation pathway, the number of species that would be protected under environmental change fell from 28,073 (94.5%) to 24,311 (82.7%; Figure 3a), with over two billion fewer years of threatened evolutionary history protected (33,694 [91.8%] to 31,441 MY [78.1%]; Figure 2b), underlining the vital importance of accounting for environmental change in protected area prioritisation.

International Cooperation vs Domestic Pathways

When incorporating the impacts of future climate and land use change, the international co-operation pathway outperformed the domestic pathway for all measures (Figure 2). Under this scenario, the international co-operation pathway protects 27,192 species (92.5%), representing 36,258 MY (90.1%) of threatened evolutionary history (Figure 2a-b). This contrasts with 23,998 species (81.6%) representing 31,783 MY (79%) protected under the domestic prioritisation pathway. International co-operation could therefore conserve an additional 3,194 species, representing 4,475 MY of threatened evolutionary history, when prioritising for future climate and land use conditions. International co-operation also resulted in a lower solution cost and a lower proportion of the total global land surface required for protection, under both current and future conditions (Figure 2c-d).

Fortuitously, there are extensive areas of the world selected for protection under all four prioritisation scenarios (i.e. current/future conditions and domestic/international co-operation pathways; ‘Priority Additional PAs’, yellow, Figure 3). These areas are the most pressing priorities and potential ‘low hanging fruit’ for conservation of threatened evolutionary history, as they represent areas that would provide long-term refugia for the greatest proportion of globally important threatened evolutionary history while also allowing nations to achieve domestic coverage targets. The most significant concentrations of these immediate protection priorities occur in the biodiversity hotspots of Madagascar, southern India, Mexico, the Tropical

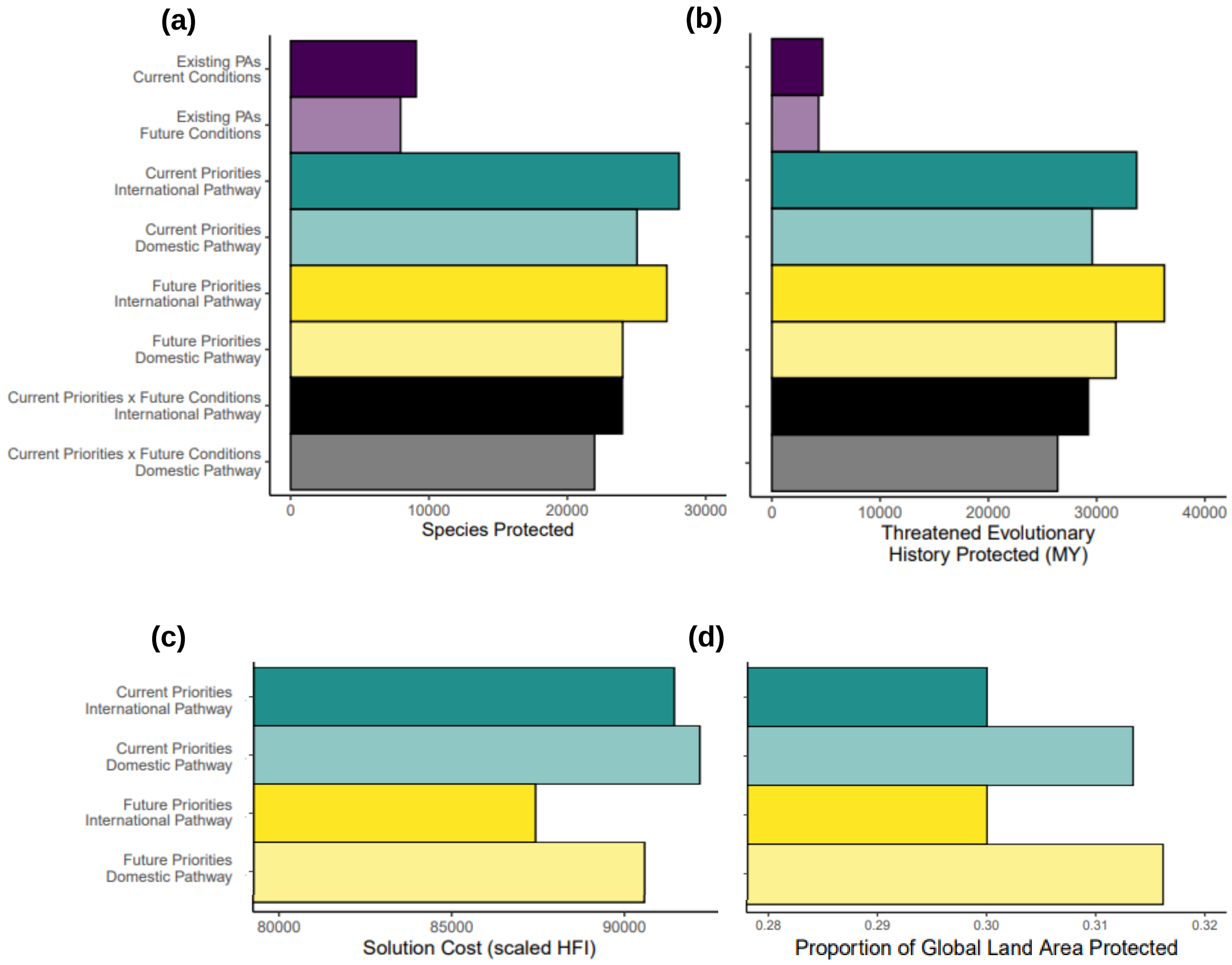


Figure 2. Relative performance of protected area prioritisation scenarios. Number of species protected in each scenario (a), amount of threatened evolutionary history protected (b), relative cost of each scenario using scaled Human Footprint Index (HFI; Venter et al., 2016; Stralberg et al., 2020) as a proxy for land acquisition and restoration costs (c), and overall global coverage of protected areas (d). Note x axis of (c) and (d) do not start at 0. Purple colours indicate existing protected area performance under current (bold) and future (pale) conditions. Teal colours represent prioritisations solved under current conditions under international cooperation (bold) and domestic (pale) pathways. Yellows represent prioritisations solved under future conditions. Black and grey represent the performance of prioritisations under current conditions when overlaid with future species distributions and EDGE scores, under international cooperation and domestic pathways, respectively.

Andes and the island of New Guinea (Figure 3). The next highest priority areas for protection are those that are selected under both current and future conditions under the international co-operation pathway (‘Priorities under International Co-operation, green, Figure 3). Such areas are more thinly dispersed globally, but tend to concentrate in relatively higher latitudes and elevation regions including the Himalaya, central Asia, the Chilean Andes, central Mexico and

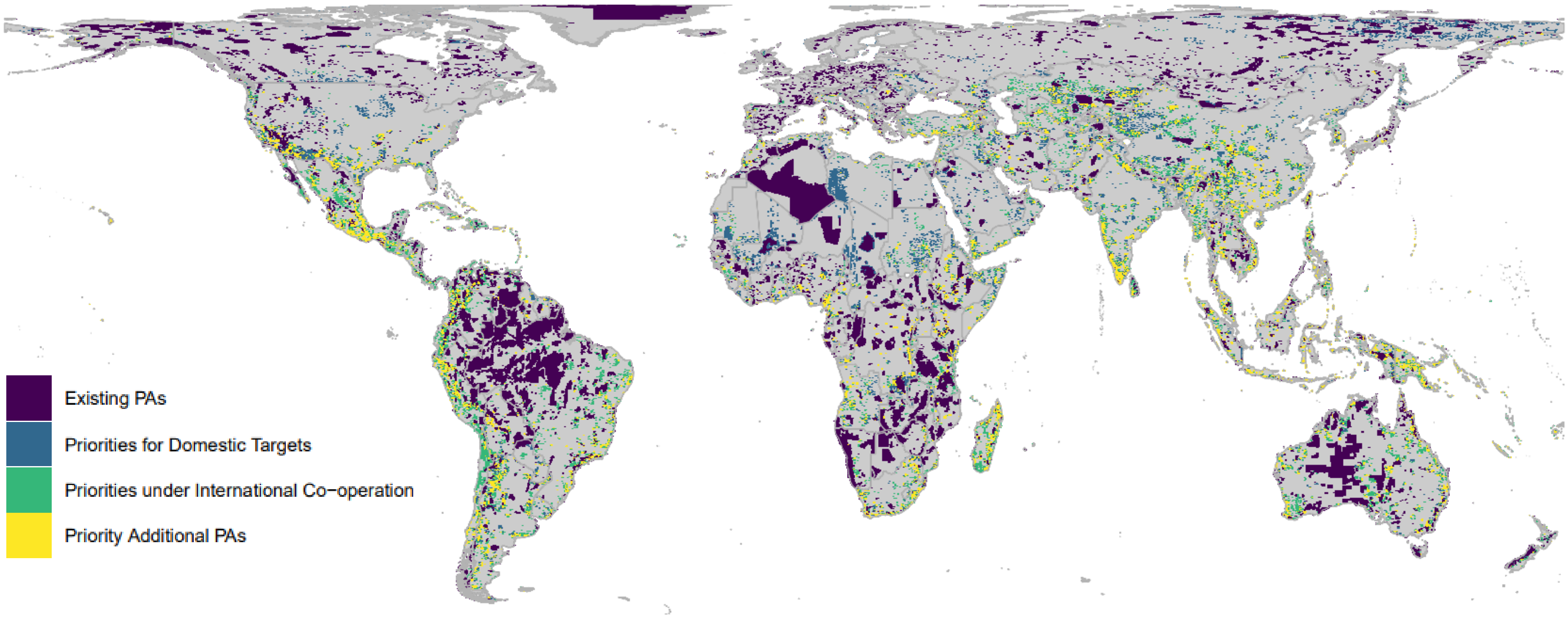


Figure 3 Priority areas for immediate protection that deliver for international and domestic targets under both current and future conditions. Areas of overlap between prioritisations under all four scenarios (Priority Additional PAs, yellow), between current and future conditions under international co-operation pathway (Priorities under International Co-operation, green), and between current and future conditions under domestic pathway (Priorities for Domestic Targets, blue). Overlaps indicate areas of high conservation value for current biodiversity while providing refugia for many species up to the year 2070.

southern Madagascar, perhaps reflecting latitudinal range shifts away from tropical and/or low elevation biodiversity hotspots under climate change (Figures 1-2).

Notwithstanding the areas of overlap in solutions highlighted above, there were still considerable differences between the spatial distribution of selected sites under the international co-operation and domestic prioritisation pathways (Figures 1-2). A major driver of this discrepancy is that high latitude regions of Russia and Canada, and large areas of the Sahara are selected for prioritisation in the domestic pathway, despite these regions having very low vertebrate richness and representing relatively little threatened evolutionary history (Figure 1c, 'Domestic Pathway/Future Conditions'). Despite this, the international co-operation pathway does also select some areas of northern Canada and northeast Russia, potentially highlighting the last key refugia from global heating for climate-threatened Arctic species. However, the extent of protection in these regions is not as pronounced, with greater coverage afforded to biodiversity hotspots such as the tropical forests of Ecuador, Costa Rica, Peru, and Madagascar (Figure 1d, 'International Pathway/Future Conditions').

Key Conservation Opportunities

Biodiversity of conservation importance is unevenly distributed between the political (nations, Figure 4a-b) and ecological (biogeographic realms and biomes, Figure 4c-d) boundaries of the world. The nations with the highest concentrations of threatened evolutionary history under both current and future conditions were Brazil, Colombia, Mexico, Madagascar, India, Indonesia, and China (pale bars, Figure 4a-b). However, the proportion of threatened evolutionary history currently classed as protected in each of these nations is low (dark bars, Figure 4a-b; Table 1). Taken together, these seven countries currently support 16,275 MY of threatened evolutionary history, of which only 1,557 MY (9.6%) has sufficient coverage to be considered protected. However, an international co-operation prioritisation would provide long term refugia up to 2070 for 14,920 MY (92.1%) of threatened evolutionary history in these countries, meaning that 41.15% of the total threatened evolutionary history protected worldwide could be achieved through protected area prioritisation in these seven nations alone. Similar findings were found for other scenarios (Table 1).

When considering ecological boundaries, I divided the world into six biogeographic realms (combining data for Oceania and Australasia and excluding Antarctica) and further subdivided

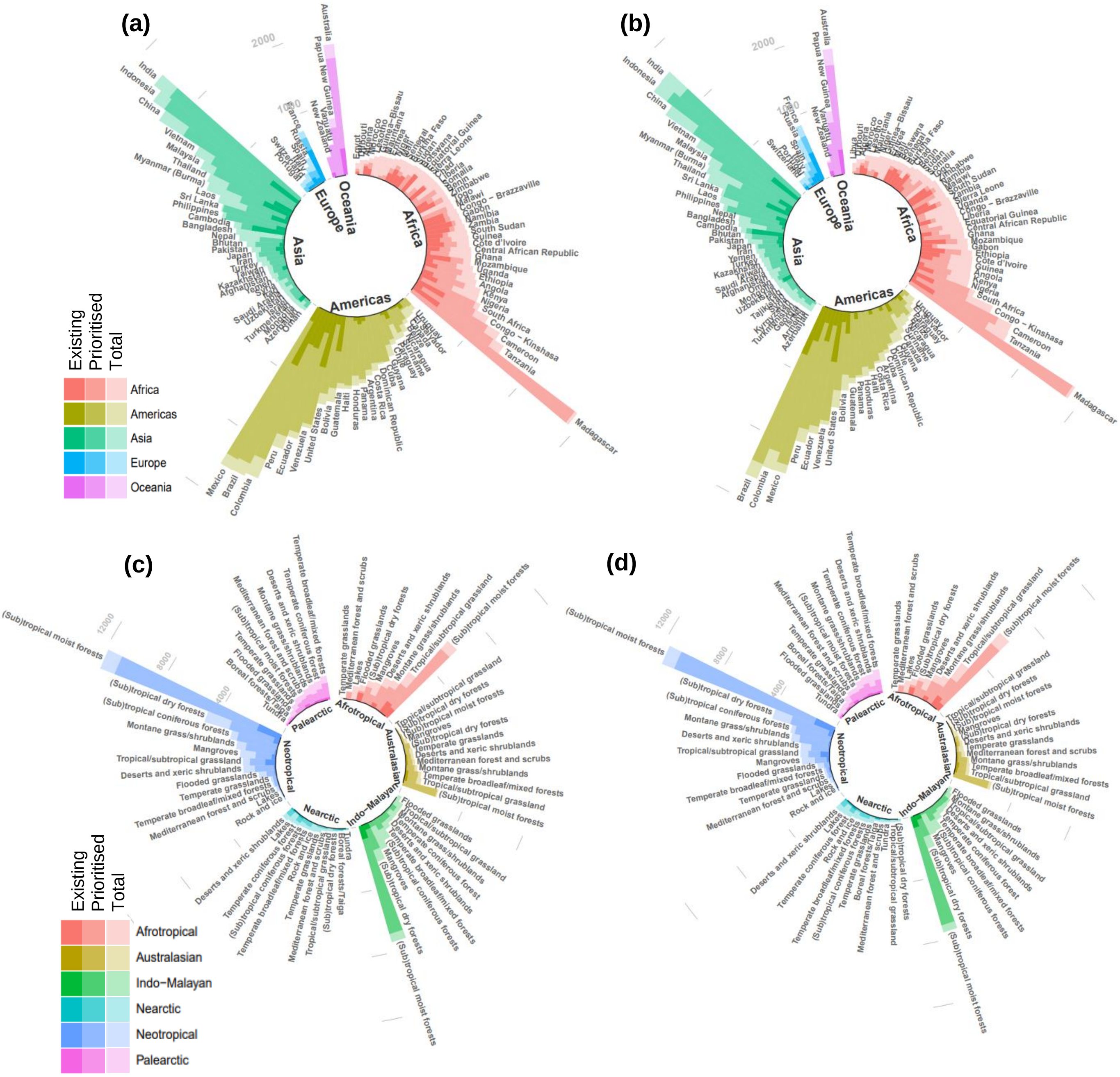


Figure 4. Total threatened evolutionary history in each country and biome, and the proportion that is currently protected or could be protected by additional protected areas. (a-b) Threatened evolutionary history in each country. (c-d) Threatened evolutionary history in each biome. Results presented here are for prioritisations under future conditions and projected EDGE scores for 2070, under the SSP2-4.5 representative pathway. (a and c) International co-operation pathway. (b and d) Domestic pathway. Pale bars represent total threatened evolutionary history occurring in that country/biome. Dark bars represent the threatened evolutionary history currently protected within that country/biome. Medium bars represent the additional threatened evolutionary history protected by in each prioritisation. Colours represent major continents (a-b) and biogeographic realms (c-d; Olson et al., 2001). Only countries/biomes covering at least 50 grid cells at ~25 km resolution and with total threatened evolutionary history > 150 MY are included. Species were designated 'protected' if range-size based thresholds (Butchart et al., 2015) were met in that country/biome alone, independent of the amount of protected range in other countries/biomes. Antarctica was excluded, and data from Australasia and Oceania were combined.

Table 1. Summary of threatened evolutionary history (TEH) currently and potentially protected under each prioritisation scenario in each nation, for the top ten countries ranked by current total evolutionary history. Changes of more than 15 percentage points between prioritisation pathways are in bold.

Country	Current Total TEH (MY)	% Currently Protected	% Protected under Current-International	%Protected under Current-Domestic	Future Total TEH (MY)	% Currently Protected	% Protected under Future-International	% Protected under Future-Domestic
Madagascar	2,880	0.6	98.5	89.3	2,825	0.1	98.5	86.9
India	2,594	0	89.3	92.6	2,605	0	86.3	87.8
Mexico	2,573	8.3	93.5	85.4	2,459	8.5	94.8	87.8
Brazil	2,564	33.7	88.8	76.3	2,664	27.9	**91.5**	**70.9**
Colombia	2520	20.3	**88.9**	**66.2**	2,462	20.6	**89.0**	**69.5**
Indonesia	2,468	18.9	92.3	91.0	2,596	18.4	90.9	93.0
China	2,250	0.5	82.2	89.8	2,261	0.1	78.7	90.2
Peru	2,017	23.5	90.8	79.9	1,962	23.6	89.9	78.9
Australia	1,833	20.1	89.4	88.8	1,813	19.5	87.0	85.0
Ecuador	1,818	15.3	**95.1**	**60.7**	1,799	12.0	**93.9**	**62.0**

Table 2. Summary of threatened evolutionary history (TEH) currently and potentially protected under each prioritisation scenario in each biome, for the top six biomes ranked by current total evolutionary history. Changes of more than 15 percentage points between prioritisation pathways are in bold.

Biome - Realm	Current Total TEH (MY)	% Currently Protected	% Protected under Current-International	%Protected under Current-Domestic	Future Total TEH (MY)	% Currently Protected	% Protected under Future-International	% Protected under Future-Domestic
(Sub)tropical moist forest - Neotropical	11,853	12.9	**92.0**	**73.3**	11,615	11.6)	**(92.8**	**74.1**
(Sub)tropical moist forest - Indo-Malayan	7,394	11.4	92.9	86.7	7,541	9.7)	93.9	87.8
(Sub)tropical moist forest - Afrotropical	5,987	10.8	89.3	82.7	6,230	7.5)	86.3	78.1
(Sub)tropical dry forest - Neotropical	4,734	7.1	**66.7**	**41.6**	3,932	7.0)	**70.1**	**46.7**
(Sub)tropical grassland - Afrotropical	3,024	26.4	70.8	68.8	3,250	22.3)	64.5	62.6
(Sub)tropical coniferous forest - Neotropical	2,950	0.3	85.6	78.8	2,610	0.3)	**89.1**	**71.9**

these by the 14 major biomes (habitat types; Olson et al., 2001; Figure 4c-d). Threatened evolutionary history is highly concentrated in the (sub)tropical moist broadleaved forests of the Neotropical, Afrotropical, Indo-Malayan and Australasian realms, while the Nearctic and Palearctic realms had much less threatened evolutionary history despite their large extent.

The four key forest biomes alone account for 27,287 MY of threatened evolutionary history under current conditions, or 68.6% of the global total. Only 3,024 MY of threatened evolutionary history in these four biomes are currently sufficiently protected. Protected area prioritisation under the international co-operation pathway would provide long-term refugia for 25,284 MY (91.8%) of the threatened evolutionary history surviving to 2070 in these four biomes alone, accounting for 69.7% of the total threatened evolutionary history to be conserved under this prioritisation scenario globally.

Discussion

Here I highlight spatial priorities for extending protected area coverage to meet the ‘30 by 30’ targets agreed in the Kunming-Montréal Global Biodiversity Framework (GBF; CBD, 2022). Specifically, I identify places where protected areas can maximise conservation of threatened evolutionary history under climate and land use change. Building on previous work (Strassburg et al; 2020; Yang et al., 2020; Jung et al., 2021), I incorporate – in addition to spatial shifts in threatened biodiversity - phylogenetic shifts in conservation priorities, as more branches of the vertebrate tree of life become threatened under environmental change. By considering differing levels of international co-operation to achieve global targets, I show that significantly greater conservation benefits can be achieved at reduced cost when 30% coverage targets are integrated across nations rather than achieved at the purely domestic level, agreeing with recent findings elsewhere (Shen et al., 2023). By highlighting areas of overlap where prioritisations under current conditions align with future climate refugia, and identifying the key nations and biomes where protected area prioritisation could have the greatest benefit for biodiversity now and into the future, my findings provide a roadmap to achieving the ambitious targets nations have set themselves by 2030.

Targeting Action to Reach 30 by 30

My results demonstrate that threatened evolutionary history is (and will remain) unevenly distributed across the world (Armstrong et al., 2019). Threatened evolutionary history is particularly concentrated in areas of tropical and subtropical moist forest biomes in nations including Madagascar, Brazil, Mexico and Indonesia (Figure 4, Tables 1-2). These biomes account for 69% of the total threatened evolutionary history of the world's terrestrial vertebrates globally, while 44% is found in just seven tropical and subtropical nations with significant moist broadleaved forest habitats. While global action is required and all nations must contribute to achieve 30 by 30, action must focus on areas with the greatest opportunities for rapid conservation gains. To do this, the global community will need to support these nations in extending protection of their tropical and subtropical forests, through, for example, financial compensation or the development of alternative markets and livelihoods for communities impacted by protected area expansion (Wilting et al., 2017; Shen et al., 2023).

Recognising these global priorities for immediate action, nations will need to decide which areas to protect first on the way to achieving the '30 by 30' targets. While there is inherent uncertainty in projecting climate and land use change and their interacting effects on biodiversity (Rands et al., 2010; Titley et al., 2021), ignoring their impacts on threatened evolutionary history is likely to reduce the future effectiveness of global protected area systems (Asamoah et al., 2021; Xi et al., 2021; Dobrowski et al., 2021). My prioritisations under future conditions take the harmonic mean of species Area of Occupiable Habitat (AOOH; Chapter 3) for each decade from the present day to 2070, adding greater weight to refugial areas that remain stable throughout the period. While this approach may underestimate AOOH for some species in some areas, it is conservative and helps concentrate additional protection in areas most likely to be resilient to environmental change. Overlaying outputs from multiple scenarios highlight the most important and resilient refugia for threatened evolutionary history now and into the future, and should be the immediate priority for enhanced area-based conservation measures ('Priority Additional PAs', Figure 3). Given the clear conservation benefits of an integrated approach to protected area expansion evidenced here and elsewhere (Shen et al., 2023), I recommend that attention should subsequently be focused on the 'International Priority' areas in Figure 3, with protection extended to 'Domestic Priority' areas only when such interventions will not divert conservation effort from areas identified as global conservation priorities.

Delivering 30 by 30 Equitably

My results demonstrate that an efficient and effective global protected area system covering 30% of the world's land mass by 2030 requires significant international co-operation and integrated cross-border actions between nations. Allowing countries to diverge in protected area coverage (international co-operation pathway) conserved an additional 3,194 species representing over 4 billion years of threatened evolutionary history under future conditions, when compared with the domestic prioritisation pathway where each country achieves ~30% protection independently. In addition, these greater conservation benefits under international co-operation simultaneously require less land in total, and a lower overall cost than domestic orientated solutions (Figure 2). Therefore, it is incumbent upon nations to work collaboratively if the conservation benefits of the 30 by 30 targets are to be fully realised (Evans et al., 2012; Shen et al., 2023).

International collaboration to share the burden of effective area-based conservation is not just an ecological imperative, but a moral and ethical imperative, too. Morality in global conservation funding has been distilled into three key questions (Armstrong,2019): Who caused/is causing damage that makes conservation necessary? Who has the capacity to pay for conservation? Who stands to benefit from conservation? To address the first question, habitat loss and climate change are largely driven by consumption of natural resources, and in a globalised economy the sources and impacts of consumption do not always align geographically (Rands et al., 2010; Wilting et al., 2017; Armstrong, 2019; Titley et al., 2021). For example, the per-capita 'biodiversity footprint' of the average citizen in rich nations like Australia can be up to eight times the global average (Wilting et al., 2017). Similarly, climate impacts on mammals are projected to be greatest in nations with lower GDP and lower greenhouse gas emissions per-capita (Titley et al., 2021), meaning the burden of conservation under climate change falls on countries that not only contribute the least emissions, but also have the least ability to finance conservation to mitigate these impacts. Furthermore, conserving biodiversity as a global public good (Rands et al., 2010) and the concurrent ecosystem service benefits such as carbon storage and water quality and provisioning

(Strassburg et al., 2020; Yang et al., 2020; Jung et al., 2021; Zeng et al., 2022; Shen et al., 2023) means that benefits of area-based conservation are felt globally, and are not limited to the nations in with the greatest protected area coverage. While my prioritisations focus on biodiversity and do not explicitly account for other ecosystem service benefits, my results largely align with similar studies which integrate these additional benefits (but do not incorporate future environmental change; Strassburg et al., 2020; Jung et al., 2021; Zeng et al., 2022; Shen et al., 2023). Given my prioritisations largely focus on (sub)tropical forest biomes, protected area expansion in these areas will have concurrent global benefits such as enhanced climate change mitigation.

Equitably delivering conservation not only pertains to co-operation between nations, but also between government bodies, conservation organisations and the Indigenous Peoples and local communities (IPLCs) most directly affected by the establishment of new protected areas. Traditional area-based conservation paradigms have been characterised as 'fortress conservation', whereby protected areas are separate to and devoid of the human societies that have often been responsible custodians of these lands for generations (Rights and Resources Initiative, 2020). Such exclusive approaches to area-based conservation are not only ethically questionable (Rights and Resources Initiative, 2020), but also counter-productive. A wide body of literature has now established that lands managed by IPLCs perform as well or better than publicly- or privately-owned protected areas, in terms of supporting biodiversity and threatened species (Schuster et al., 2019), preventing deforestation (Fa et al., 2020; Pacheco and Meyer, 2022), improved management of fire regimes (Hoffman et al., 2021), and protecting the world's irreplaceable carbon stores (Walker et al., 2020). However, these benefits can be dependent on the level of legal recognition of IPLC land rights (Walker et al., 2020; Pacheco and Meyer, 2022), which is a concern given IPLCs manage around half of the world's land but their ownership rights are recognised on just 11% of land area (Rights and Resources Initiative, 2023). Increasing the legal recognition of indigenous rights and the vital role IPLCs play in conserving biodiversity and natural resources is therefore both ethically and practically vital to achieving 30 by 30 in a just and cost-effective manner.

However, in some contexts, major capital investment from public and private bodies will still be required to achieve conservation targets. Appropriately directing these additional funds from high- to low-income nations will be crucial if the 30 by 30 targets are to be met. Several potential funding mechanisms are available to facilitate the equitable funding of protected area expansion in low-income nations (Evans et al., 2012). Payments for Ecosystem Services (PES) schemes incentivise conservation of natural habitats, including through voluntary carbon markets and the REDD+ (Reduced Emissions from Degradation and Deforestation) mechanism which incentivises lower-income nations to conserve their forest habitats to store and sequester carbon (Hein et al., 2013). Other mechanisms include ‘Debt-for-Nature’ swaps whereby national sovereign debt relief is provided in return for nature conservation. A recent study assessed the potential applicability of Debt-for-Nature swaps in 67 countries at risk of debt distress and found that the total estimated cost of protecting biodiversity priority areas amounted to just 5.02% of the combined sovereign debt of these 67 countries (Nedopil et al., 2023). Furthermore, as high-income nations are often the end-consumers of extractive and ecologically damaging processes such as the trade in endangered wildlife (Liew et al., 2021), these nations could ease the opportunity costs of ending these processes by investing in alternative markets and livelihoods in exporting nations, while encouraging behaviour change among their domestic populace to reduce demand for ecologically damaging practices (Liew et al., 2021).

Conclusions

Achieving the Kunming-Montréal GBF targets by 2030 is a momentous challenge, but in a new age of human-induced extinctions (Steffen et al., 2011; Harfoot et al., 2021) effective area-based conservation has never been more vital. As climate and land use change intensify, the 30 by 30 targets must be achieved in a strategic and evidence-based manner that builds long-term resilience into the global protected area system. Here, I generate global protected area prioritisations that explicitly incorporate multiple impacts of environmental change: species range shifts, expansions, and contractions; how these impacts may change conservation priorities; and uncertainties around long-term refugia for threatened species. While no protected area system is a panacea that will conserve all species, and additional actions will be required beyond area-based conservation, I highlight areas where there is the greatest opportunity for rapid conservation gains and where consensus among different prioritisation scenarios allows us to have the greatest confidence in these gains. My findings demonstrate the critical need for international co-operation, strengthened legal recognition of the rights and roles of indigenous peoples, and robust funding mechanisms to ensure the burdens and benefits of conservation are shared equitably among nations and communities.

Methods

N.B. The section below has been prepared for submission of this chapter to Nature Ecology and Evolution. As such, it repeats some information already described in Chapter 3 methods.

Study System

I formulated global protected area prioritisations using the *prioritizr* R package (Hanson et al., 2020) and the Gurobi optimisation software (version 10.0.2; Gurobi Optimization LLC, 2020). First, I divided global land area into 0.25-degree (~25km at the equator) grid cells, or ‘planning units’, which were then projected to Behrmann’s equal area projection to ensure all planning units were of the same dimensions across all latitudes. The continent of Antarctica was the only land mass removed from the global study system. My prioritisations had a broad taxonomic scope, including almost all terrestrial vertebrate taxa as ‘Features’ to be protected. Fully marine mammals (cetaceans and pinnipeds) and reptiles (sea turtles and sea snakes) were excluded, as were pelagic seabirds such as penguins (Sphenisciformes), and petrels, albatrosses and shearwaters (Procellariiformes). Due to a lack of reliable information on dispersal capabilities, bats (Chiroptera) were excluded from species distribution modelling and therefore from my prioritisations. Also excluded were Extinct in the Wild species with no native range remaining, although these species were retained when estimating species EDGE scores using the EDGE2 metric (see *Species Weights*, below).

Spatial Data

I obtained spatial data on current protected areas from the Word Database on Protected Areas and Other Effective Conservation Measures (WDPA; Protected Planet, 2023). These data were cleaned following standard procedures using the *wdpar* R package (Hanson et al., 2022). Specifically, for protected areas represented only by point localities I drew a circle around the point coordinates, using a radius calculated from the area of the site given in the WDPA data

(Shen et al., 2023). Entirely marine protected areas were excluded. The proportion of each planning unit currently covered by protected areas was ‘locked in’ to maximise the realism of my solutions. I used an adapted version (Stralberg et al., 2020) of the Human Footprint Index (HFI; Venter et al., 2016) as a proxy for land acquisition costs, which has been shown to predict land values more accurately than several other proxies (Nolte, 2020). I aggregated the scaled-HFI values to estimate the total cost of each ~25km planning unit.

Spatial data on terrestrial vertebrate species’ extant, native/reintroduced and resident/breeding ranges were obtained from the IUCN Red List for global terrestrial vertebrates (IUCN, 2021; Birdlife; 2021), with additional reptile range data derived from (Roll et al., 2017). For the purposes of species distribution modelling, species with ranges overlapping fewer than ten ~25 km grid cells were discounted as occurrence data were too limited to produce reliable models of the species’ climatic niche (Chapter 3). The ranges of these excluded species were therefore held constant throughout all five scenarios.

Historic climate data were downloaded from WorldClim (Fick and Hijmans; 2017), using the 1970-2000 average as the ‘baseline’ climate. Future climate data for the SSP2-4.5 and SSP5-8.5 warming scenarios were downloaded from the Earth System Grid Federation database (https://esgf-index1.ceda.ac.uk/search/cmip6-ceda/). Three CMIP6 global circulation models (GCMs) were selected representing a range of with low (BCC-CMS2-MR), moderate (IPSL-CM6-LR) and high (CanESM5) estimates of Equilibrium Climate Sensitivity (ECS), representing the warming impact of a doubling of atmospheric CO_2 (Meehl et al., 2020).

The Land Use Harmonization (LUH2) dataset provides historic and future projections of fractional cover of 12 land use classes at 0.25-degree resolution, harmonised with SSP climate scenarios (Hurtt et al., 2020). Fractional cover of each land use was downloaded for the year 1985 (the mid-point of the 1970-2000 baseline climate period) and for each decadal timestep between 2030 and 2070, for each Shared Socioeconomic Pathway (SSP) scenario representing different possible levels of future global heating due to human activity. Species habitat preferences were extracted from the IUCN Red List using the *rredlist* R package (Chamberlain; 2020). IUCN habitat classes were matched to the LUH2 land use categories using a crosswalk (Titley, 2022; Appendix A). The LUH2 land use categories are relatively coarse – for example, there are only two primary habitat categories (forest and non-forest) -

and as such this dataset probably provides a conservative estimate of the impact of land use change on biodiversity, particularly for specialist species with narrower habitat requirements.

Species Distribution Modelling

For each species, presence data were derived from IUCN range maps and rasterised using Behrmann's equal area projection. All cells at least 10% covered by a species range map were included as presences. 1,000 pseudo-absences were randomly generated for each species from the same biogeographic realms (Holt et al., 2013) where species were known to occur, to minimise sampling of climatically suitable areas where species are absent due to other biotic or abiotic factors such as mountain ranges or oceans acting as barriers to dispersal. I fitted species distribution models using four commonly applied model algorithms: generalised linear models (GLM), generalised additive models (GAM), random forests (RF) and gradient boosting machines (GBM). To reduce spatial autocorrelation, I divided the presence-absence data into ten spatially disaggregated blocks based on terrestrial ecoregions (Olson et al., 2001), such that the mean bioclimate is similar across all blocks but each block samples the full range of climatic conditions (Bagchi et al., 2013). These blocks were then used as spatially independent test and training sets in model validation, with the performance of each model quantified by area under the curve (AUC). Each model was then projected to both current climatic conditions and future conditions. Probability of occurrence projections were binarized to produce projected presence-absence maps using the true-skill statistic (Allouche et al., 2006). For each timestep and SSP, an ensemble projection was produced by taking the average of all projections weighted by model AUC. See Chapter 3 for detailed methodology.

I constrained my projections of species range shifts under climate change to areas where a species is likely to be able to disperse to within a given time frame. To do this, I gathered data on species Age at First Reproduction (AFR) and natal dispersal distance (*d*), and calculated the total dispersal capability of the species for each decadal timestep up to the year 2070 (see Chapter 3). Missing data were phylogenetically imputed using the *Rphylopars* R package (Goolsby et al., 2017; Appendix A). Dispersal capabilities were constrained to contiguous land masses for all species other than some volant birds, for which I allowed trans-oceanic dispersal to islands and land masses within one *d* of the source land mass.

Following this process, I had projections of species climatic niches, projected proportion of suitable land cover per cell based on species habitat preferences, and realistically reachable areas based on species current distributions and estimated dispersal capabilities. Overlaying each of these layers provided an estimate of per-cell Area of Occupiable Habitat (AOOH, see Chapter 3) of each species and each year-SSP combination. These AOOH layers were then used as Feature Data in each of my ten protected area prioritisation scenarios (see *Prioritisation Scenarios*, below). I also used the summed AOOH of each species in each climate change scenario to calculate weightings for species to be used in protected area prioritisation, such that species representing greater levels of threatened evolutionary history were prioritised for protection (see *Species Weights*, below).

Species Weights

EDGE Concept

The original metric for identifying EDGE (Evolutionarily Distinct and Globally Endangered) species was developed by the Zoological Society of London in 2007 (Isaac et al., 2007). The recently published EDGE2 metric (Gumbs et al., 2006) improves on this original iteration by incorporating probabilistic extinction risk measures (GE2) and phylogenetic complementarity in quantification of evolutionary distinctiveness (ED2). Species' EDGE scores are equivalent to the expected loss of unique evolutionary history (MY) should the species go extinct.

Red List Calculation

As GE2 extinction probabilities are still based on IUCN Red List categories, I estimated future Red List Status according to Red List Criterion A3, where a population reduction is 'projected, inferred or suspected to be met in the future', with population changes calculated over a timeframe of 10 years or three generations, whichever is longer (IUCN, 2022). I calculated the proportional change in summed AOOH from the current baseline for each species (see *Species Distribution Modelling*, above), and assigned species to Near Threatened, Vulnerable, Endangered, and Critically Endangered categories at a given decadal timestep they suffered a population reduction of 20%, 30%, 50% or 80%, respectively (IUCN, 2022). This approach assumes a linear relationship between climatically suitable AOOH and abundance, which may not hold true in many cases. However, under the IUCN Red List Guidelines (IUCN, 2022) this is an allowable assumption in the absence of more detailed information - as is the case when modelling for many thousands of species for which detailed demographic data are generally lacking. See Chapter 3 for full details on projecting future Red List status.

EDGE2 Calculations

To incorporate uncertainty in the structure of phylogenetic trees, ED2 scores are calculated across a large number of candidate trees (100 < n ≤ 1,000; Gumbs et al., 2023). Published EDGE scores are available for mammals (Gumbs et al., 2023). Given the considerable computational requirements of computing these scores for over 35,000 terrestrial vertebrate species (including those excluded from SDMs) for current conditions and multiple future projections under different SSP scenarios, I limited the number of phylogenetic trees in my calculations to 100. I otherwise followed methods outlined by Gumbs et al. (2023). When comparing my estimated scores for mammals with published data (Gumbs et al., 2023), I found a very strong correlation (Pearson's $r > 0.95$, df = 5,710, $p < .001$) for both raw EDGE estimates and ranked scores, providing confidence that reducing the number of trees did not qualitatively affect my EDGE score estimates.

I then repeated this process for each future timestep and each SSP scenario for mammals; birds; amphibians; snakes, lizards, and tuatara (Lepidosauria); and crocodiles and turtles (non-avian Archosauromorpha). My estimates of future EDGE scores under climate and land use change includes species that are projected to lose all their climatically suitable habitat, and are therefore assigned a future Red List Status of Extinct in the Wild. The current EDGE2 metric (Gumbs et al., 2023) treats Extinct in the Wild species as Critically Endangered when estimating extinction probability due to their potential for future recovery. While a number of once Extinct in the Wild species have been reintroduced successfully into the wild (Condé et al., 2011), this is a very costly and management intensive conservation intervention, and should not be relied upon for such a large number of potentially Extinct in the Wild species. I therefore fixed the probability of extinction for species projected to become Extinct in the Wild at the maximum value of 0.9999, implying near-certain extinction and thereby increasing the ED2 value of related species under these scenarios.

Following this process, I was able to estimate EDGE scores (the amount of threatened evolutionary history (MY) expected to be lost if the species were to go extinct) for the world's terrestrial vertebrates under current conditions, and estimate future EDGE scores for the year 2070 based on projected changes in the IUCN Red List under two climate and land use change scenarios (SSP2-4.5 and SSP5-8.5). These scores were then used as feature weights in my protected area prioritisation scenarios.

Prioritisation Scenarios

Environmental Conditions and Prioritisation Pathways

I generated prioritisations for a total of ten scenarios representing current and future climatic conditions. The first scenario prioritised protected areas under current conditions, the second and third scenarios prioritised protected areas for the year 2070 under a 'middle-of-the-road' (SSP2-4.5) and a 'worst-case' (SSP5-8.5) warming scenario, respectively. In the fourth and fifth scenarios, I set my feature (species) data using harmonic means of species' Area of Occupiable Habitat (AOOH, Chapter 3) in each cell and for each decadal timestep, from the present baseline (2020) up to 2070 (see *Species Data*, below). These scenarios therefore added additional weight to cells with consistent habitability representing long-term climate refugia.

I repeated these five scenarios under two 'protection pathways'. In the 'international co-operation' pathway the upper and lower bounds of per-country protected area coverage was allowed to vary between 10 and 67%, allowing more optimal coverage of biodiversity but requiring robust financing mechanisms to spread the burden of protection equitably between high-income, biodiversity-poor nations and low-income, biodiversity rich nations. The 10% lower bound was selected as a non-trivial national contribution to the global protected area system, while the 67% upper bound was based on the highest national coverage rates of any nation excluding small island states (Costa Rica, 57.2%), plus an increase of ten percentage points equivalent to the lower bound for national coverage. The 'domestic' pathway constrained per-country protected area coverage to between 27.5 and 32.5% (other than nations already exceeding 32.5% coverage), and represents a situation where each nation achieves the 30% target domestically but has little regard to the uneven spread of threatened biodiversity globally (Shen et al., 2023). In all scenarios, I also set global coverage constraints to ensure overall protected area coverage was at least 30%. In this chapter, I present results for current conditions and the SSP2-4.5 future scenario using harmonic means, with results from other scenarios presented in Appendix B.

Objective function

I generated prioritisations using the ‘minimum shortfall objective’ in the *prioritizr* R package (Hanson et al., 2020). This objective aims to minimise the sum of the species’ target shortfalls (expressed as proportions of the species’ targets), weighted by species weights (EDGE scores), while ensuring that the solution remains within a defined budget. Species-specific representation targets were calculated following Butchart et al. (2015), such that species with ranges ≤ 1,000 km^2 required 100% protected area coverage species with ranges ≥ 250,000 km^2 required only 10% coverage, with loglinear interpolation used to derive targets for species with intermediate range sizes (Butchart et al., 2015). Species coverage targets were capped at 1,000,000 km^2 for species with extremely large ranges (Butchart et al., 2015).

Given the relatively coarse (~25km) resolution of my planning units, I allowed for proportional decisions whereby only a fraction of a grid cell was designated for protection. In these cases, I assumed that the features (species) and costs (scaled-HFI) were evenly distributed within a planning unit, such that if a unit was assigned 50% protection this would contribute 0.5 units towards species representation targets and would cost half the estimated value of the planning unit. All prioritisations were solved to optimality using the Durham University supercomputer and Gurobi optimisation software (version 10.0.2; Gurobi Optimization LCC, 2020).

Species Data

For current conditions and the 2070 conditions prioritisation scenarios, I used the raw AOOH layers as feature data in the optimisation problem formulation. For the two refugia scenarios, I took the harmonic means of species’ AOOH of each grid cell for each decadal timestep from present day to 2070, thereby penalising planning units where AOOH drops to a low level at any point up to 2070. This ensured that additional weight was given to planning units that were consistently able to support species under climate and land use change. Features were weighted according to current EDGE scores for prioritisations under current conditions, or using projected EDGE scores for the year 2070 under SSP2-4.5 and SSP5-8.5 for the future conditions scenarios.

Cost Data

For each scenario I set minimum and maximum budgets (based on scaled-HFI) and ran prioritisations by incrementally increasing the budget by 5% until the maximum budget was reached. For the both prioritisation pathways, the minimum budget was the sum of the scaled-HFI values for current protected areas. For the maximum budget under the international co-operation pathway, I ranked all non-protected cells globally by scaled-HFI and selected the most expensive cells that would allow the solution to reach 30% global protected area coverage. I summed the value of these most expensive cells and added this to the minimum budget. For the domestic pathway I calculated the summed value of the most expensive cells in each country that would allow the country to hit the 30% national target. I then summed these national maximum budgets and added this to the minimum budget as with the international co-operation pathway.

All analyses were conducted using R version 4.2.2 (R Core Team, 2022).

Chapter 5

Implications of climate and land use change for current global zoo collections

Amphibians, such as this red-eyed tree frog (*Agalychnis callidryas*), are the class of terrestrial vertebrates most threatened by climate and land use change, yet remain under-represented in current zoo collections. *Photo credit: Jerry Bauer, USDA Forest Service, CC BY-NC-ND 2.0 DEED.*

Abstract

Target 4 of the Kunming-Montréal Global Biodiversity Framework explicitly mentions, for the first time, *ex situ* conservation as a means of preventing extinction and loss of genetic diversity globally. This represents a considerable opportunity for zoos to contribute to global conservation efforts. However, zoos already face criticism from some quarters for a perceived failure to adequately represent the world's threatened biodiversity, a situation that is likely to become more acute under future climate and land use change. Here, I apply the results from the species distribution models described in Chapter 3 to current global zoo collections, and assess whether current collections adequately represent the terrestrial vertebrate biodiversity that is most likely to become threatened under future environmental change. I show that overall endangerment of species in zoos is lower than that for all terrestrial vertebrates globally, and that this gap is predicted to widen as climate and land use change drive ever more species into threatened Red List categories. These results demonstrate that zoo collections must adapt significantly if they are to maximise their relevance to Target 4 of the Global Biodiversity Framework in the long-term, or zoos risk being outpaced by environmental change.

Introduction

Area-based conservation to preserve habitats and species in their native ranges is central to global conservation efforts (Maxwell, 2020). In the previous chapter, I demonstrated that this has the potential to conserve the majority of terrestrial vertebrate species and the threatened evolutionary history that they represent, even under future climate and land use change. However, this will be dependent on optimal distribution, management, and funding of protected areas, which has not always been the case in area-based conservation efforts to date (Venter et al., 2018; Coad et al., 2019; Wauchope et al., 2022). It would therefore be imprudent to risk the future of global biodiversity on the assumption that *in situ* conservation will be delivered and managed in an optimal way. Indeed, even optimised protected area systems will not be able to conserve all species under environmental change (Shen et al., 2023; Chapter 4).

In this context, the role of zoos, aquaria, and other *ex situ* institutions, such as academic collections and specialist breeding centres (Biega et al., 2017), may become increasingly important to global conservation efforts as climate and land use change threaten species' native ranges. While not all species will be suitable for *ex situ* conservation (Carter et al., 2016), and the success rates of *ex situ* programmes and reintroductions in particular can be highly variable (Condé et al., 2011; c.f. Balmford et al., 2011), the intensity of human-induced environmental change means that for many species, conservationists may be faced with few alternative options (Chapter 3). Given these realities, the importance of *ex situ* conservation in zoos has recently been highlighted by the IUCN (IUCN, 2023a) and, for the first time, has been explicitly mentioned as a means to prevent extinction and loss of genetic diversity in a global target of the UN Convention on Biological Diversity (Kunming-Montréal Global Biodiversity Framework [GBF] Target 4; CBD, 2022).

Despite their increasing importance to global conservation efforts, this may be undermined by taxonomic bias in their collections. (Condé et al., 2013; Brereton and Brereton, 2020). Emerging research suggests that, while current zoo collections perform reasonably well in conserving the most evolutionarily distinct and globally endangered species ('EDGE' species; Gumbs et al., 2023), overall representation of the phylogenetic tree of life for tetrapods is highly uneven (Gumbs et al., in prep.). Conserving and representing phylogenetically distinct biodiversity in particular is an important consideration for zoos for two reasons. First, basic physiological and demographic information are still missing for vast numbers of species (Condé et al., 2019; Paniw et al., 2021), and housing rare, evolutionarily distinct species provides zoos with the opportunity to fill important knowledge gaps of great value to conservation science (Loh et al., 2018; Rose et al., 2019). Second, zoos place great importance on their role as centres of biodiversity and conservation education (Moss and Esson, 2013; Patrick and Caplow, 2018). If zoo collections provide a partial and highly skewed sample of the world's biodiversity and the vast array of evolutionary histories of life on Earth (Gumbs et al., in prep.), can zoos truly claim to be fulfilling their educational role to their maximum potential?

In Chapter 3, I demonstrated how anthropogenic climate and land use change will have profound implications for terrestrial vertebrate biodiversity globally, including on the composition and distribution of threatened vertebrate evolutionary history. These findings could severely impact the representation of threatened biodiversity in zoos. Previous research has shown that, for example, birds and mammals held in zoos are not only less likely to be threatened than close relatives not held in zoos, but are also less likely to be endemic, be habitat specialists, or have a restricted range (Martin et al., 2014). Such findings are concerning when viewed in the light of climate and land use change, as such species are likely to be more vulnerable to environmental change than their more generalist counterparts (Ohlemüller et al., 2008; Foden et al., 2019; de la Fuente et al., 2022). It stands to reason, therefore, that if zoos already preferentially house more generalist species with larger ranges over specialised endemics, they likely house species that will be less vulnerable to future climate and land use change in future.

Here, I consider what these environmental changes mean for the *ex situ* conservation of threatened species in zoos, by cross-referencing my earlier results with data from the Species360 Zoological Information Management System (zims.species360.org), the most comprehensive global dataset on global zoo collections currently available. I show that, just like *in situ* conservation, *ex situ* conservation will be sensitive to changes in species' threat status brought about by anthropogenic climate and land use change. These findings hold true both when considering absolute numbers of threatened species in zoos relative to biodiversity generally, and when considering the representation of EDGE species in particular and the amount of threatened evolutionary history they represent. The results presented here provide quantitative evidence supporting the theoretical arguments put forward in Chapter 2, reinforcing the need for long-term, proactive systematic conservation planning of zoo collections to ensure they remain relevant to conservation under environmental change.

Methods

In this chapter, I build on projections of species Red List status and EDGE scores calculated in Chapter 3, with a specific focus on implications for global zoo collections given their current composition. These projections were based on an ensemble species distribution modelling (SDM) approach, whereby I calculated proportional changes in species' total climatically suitable Area of Occupiable Habitat (AOOH, Chapter 3). AOOH is based on species' projected climatic niche, dispersal abilities, and future land use change projections. I then used these outputs to predict species future Red List status based on Criterion A3, using proportional declines in total AOOH as a proxy for population size, in line with IUCN Red List guidelines (IUCN, 2022). For full details of these methods, see Chapter 3.

Zoo collections data

I obtained data on existing zoo collections globally from the Species360 ZIMS database. The ZIMS database includes collection information for over 1,300 institutions in 102 countries globally, making it the most detailed and extensive database of *ex situ* collections globally (Species360, n.d.). While I recognise the importance of non-zoo institutions for *ex situ* conservation (Biega et al., 2017), here I focus on the conservation value of collections held in visitor attractions such as zoos, aquaria, and safari parks (hereafter ‘zoos’). Conservation of threatened species is central to the self-professed mission and vision statements of international zoo associations (e.g. WAZA, https://www.waza.org/about-waza/), and, crucially, public perceptions of the role of modern zoos in society, including through *ex situ* management of populations of threatened species (Powell, 2019; Spooner et al., 2023). Therefore, I filtered the ZIMS data to remove non-visitor institutions such as research centres, academic institutions, and private collections. This resulted in a final dataset of 1,128 zoos from 92 countries worldwide.

Predicting Changes in the Red List Index

Using species’ predicted future Red List statuses (Chapter 3), I predicted trends in the IUCN Red List Index (RLI; Butchart et al., 2007) for the years 2030-2070. I did this for all terrestrial vertebrates globally, and for species currently held in global zoo collections. The RLI is measured between 0 (all species Extinct or Extinct in the Wild) and 1 (all species are Least Concern), and therefore represents an aggregate measure of the overall endangerment of a set of species at a given point in time, and can reveal temporal trends in overall threat levels (Butchart et al., 2007). The RLI for time t (RLI_t) is calculated as follows:

Eqn 1:
$$RLI_t = 1 - \frac{\sum_s W_{c(t,s)}}{(W_{EX} \times N)}$$

Where $W_{c(t,s)}$ is the Red List category c weighting for species s at time t. Weightings for c range from 0-5: Least Concern = 0, Near Threatened = 1, Vulnerable = 2, Endangered = 3, Critically Endangered = 4, Extinct (EX)/Extinct in the Wild = 5. Therefore, W_{EX} = 5. N represents the total number of species in the sample, excluding those already deemed extinct at the start of the study period (and Data Deficient/Not Evaluated species unless treated as described below).

Following Butchart et al. (2010), I predicted the RLI while accounting for two major sources of uncertainty inherent in RLI calculations: the treatment of Data Deficient/Not Evaluated species, and temporal uncertainty in the true timing of shifts in Red List categories. Because my SDM projections share the same 2030-2070 timeframe for all taxa, I did not have to extrapolate RLI trends for certain taxa to create a temporally consistent aggregate RLI for all groups, the third major source of uncertainty in RLI calculations (Butchart et al., 2010). For each decadal timestep up to 2070, I randomly assigned Data Deficient/Not Evaluated species of each taxonomic class to a Red List category based on the proportion of assessed species of that class in each category at the timestep in question. I then calculated RLI for each class and timestep using Equation 3, above. To estimate RLI for intermediate years between decadal timesteps, I generated linear trend lines between decadal RLI estimates and extracted annual estimates from these trendlines. To account for temporal uncertainty in the 'true' timing of changes in Red List status, I randomly assigned annual RLI estimates to each year based on a moving five-year window (i.e. two years either side of the focal year; Butchart et al., 2010). I repeated this process 10,000 times and calculated the mean RLI for each class and year combination (Butchart et al., 2010). Finally, I repeated RLI calculations for species represented in Species360 zoo collections only.

Assessing EDGE Profile of Current Zoo Collections

In Chapter 3 I generated predictions of species current and future EDGE (Evolutionary Distinct, Globally Endangered) scores under a range of future scenarios of climate and land use change, using the updated EDGE2 metric (Gumbs et al., 2023). The EDGE2 metric allows for the identification of 'EDGE species', which are species in a threatened IUCN Red List category whose expected evolutionary distinctiveness (ED2) values are above the median for the clade in at least 95% of iterations (Gumbs et al., 2023). Using these criteria, I generated EDGE species lists under current conditions and for the year 2070, the latter under the 'middle of the road' SSP2-4.5 scenario and the more severe SSP5-8.5, and calculated the number of these current and future EDGE species that were currently represented in global zoo collections. These lists were then used to assess how well current zoo collections capture conservation priority species under both current and future environmental conditions.

Generating unique species pairs

To assess whether species' raw EDGE scores varied between species in and out of zoo collections, I generated unique pairs of closely related species where one species in each pair is currently held in global zoo collections, following Martin et al. (2014) and Biega et al. (2017). I repeated the following process for each of the 100 phylogenetic trees used to estimate species' EDGE scores for mammals; birds; amphibians; snakes, lizards, and tuatara (Lepidosauria); and crocodiles and turtles (non-avian Archosauromorpha). First, I generated all possible species pairs in the phylogenetic tree using the extractTipPairs function in the R package *patherit* (Mitov and Stadler, 2018), and extracted all pairs that included one species in current zoo collections and one species not included in zoo collections. I then further filtered the dataset to include, for each species, only the most closely related paired species by patristic distance. In cases where multiple paired species were equally closely related to the species of interest, data for related species were averaged to create a single unique species pair (Martin et al., 2014; Biega et al., 2017). The data associated with each species were the estimated EDGE scores from each of the 100 EDGE iterations (see Chapter 3), for current conditions, and for the year 2070 under SSP-2-4.5 and SSP5-8.5. As my approach accounts for uncertainty in the phylogenetic position of species within each tree (and their associated EDGE scores), unlike previous studies (Martin et al., 2014; Biega et al., 2017), the exact number of species pairs for each taxonomic group varied across the 100 iterations. For a summary of sample size ranges for each taxonomic group, see Appendix C.

Statistical analysis

Datasets of unique species pairs for each iteration and taxonomic group were analysed using comparative generalised estimating equations (Paradis and Claude, 2002), using the compar.gee function in the R package *ape* (Paradis et al., 2004), accounting for phylogenetic non-independence in the data (Paradis and Claude, 2002). I modelled species current and future (2070, SSP2-4.5 and SSP5-8.5) EDGE scores separately, with the presence or absence of the species in global zoo collections as a single explanatory variable. These models estimated the expected difference in species EDGE scores (MY of threatened evolutionary history) between species in and out of global zoo collections, under current and future conditions. Negative effects would indicate that species in zoos represent less threatened evolutionary history than expected by chance, and vice versa. Similarly, if effect sizes become increasingly negative under environmental change, this would suggest that current zoo collections are less able to conserve lineages containing evolutionary history most likely to become threatened in future, and vice versa.

Results

Threatened species representation in zoos

In total, 6,988 (20.3%) terrestrial vertebrate species included in my study are considered threatened according to the IUCN Red List (IUCN, 2021). In Chapter 2, I showed that 23.5% of terrestrial vertebrate species currently held in Species360 zoos were threatened, including bats (Chiroptera), although representation of threatened species varies both taxonomically and geographically. Bats were excluded from further analysis due to uncertainties in dispersal capability. After also removing threatened species that had ranges too small to be included in SDMs, this left 3,150 currently threatened species included in my SDMs (Chapter 3). Of these, 24.6% are represented in existing Species360 zoo collections. However, this proportion falls to 16.1% when considering species projected to be threatened by 2070 under SSP2-4.5, and 14.7% under more severe environmental change (SSP5-8.5). Under both SSP2-4.5 and SSP5-8.5 fewer than 10% of species projected to become Extinct in the Wild are currently represented in global zoos. This suggests that if zoos do not proactively adapt the composition of their collections to account for these most threatened species of the future, many thousands of species risk extinction.

Figure 1 shows how projected shifts in species IUCN Red List status affect trends in the IUCN Red List Index (RLI) under each SSP. This is shown separately for ‘all species’ and for species currently held in global Species360 zoo collections. The current RLI for all terrestrial vertebrates is 0.8344, while the current RLI for species in zoos is only very slightly higher at 0.8444. Under mild (SSP1-2.6) or moderate (SSP2-4.5) environmentally change, global RLI for terrestrial vertebrates is projected to decline sharply up to 2030, and then more slowly up to 2070, reflecting a more gradual increase in aggregate endangerment with more concerted international effort to reduce greenhouse gas emissions and land use conversion (Chapter 3). Under these scenarios, the global RLI is projected to fall to 0.7710 and 0.7384, respectively (Figure 1). By contrast, under the more severe SSP3-7.0 and SSP5-8.5, global RLI is projected

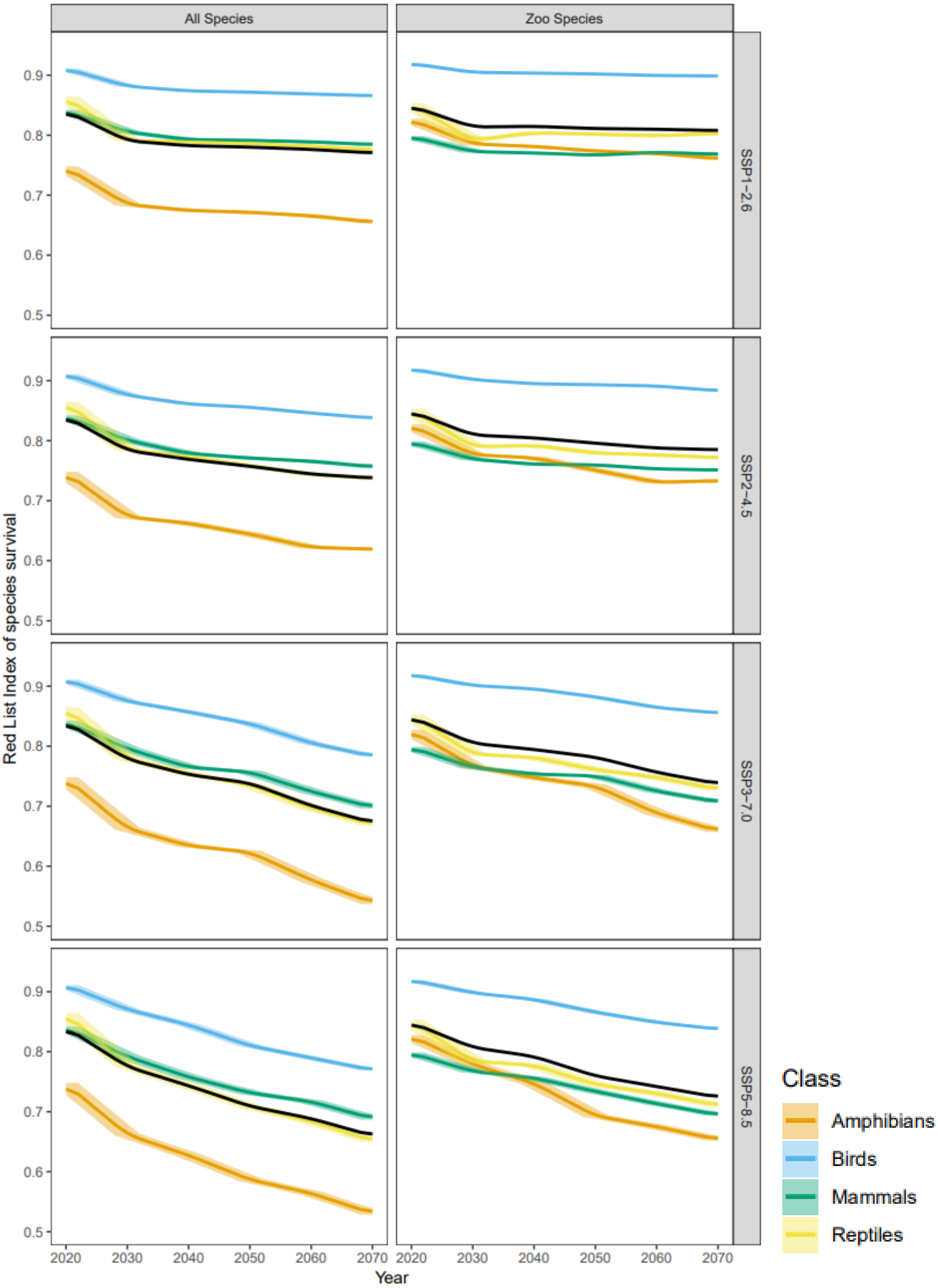


Figure 1. Projected trends in IUCN Red List Index (RLI) from present day to 2070. The RLI represents an aggregate measure of endangerment for a taxonomic clade, with an RLI of 1 indicating all species are Least Concern and an RLI of 0 being all species are Extinct (Butchart et al., 2007). Rows represent different environmental change scenarios (SSPs). The left column is the projected RLI for all species and the right column is the projected RLI for current zoo collections. Colours indicate taxonomic class, with the black line representing aggregate RLI for all classes. Shaded areas indicate 95% confidence intervals, accounting for uncertainty in the status of Data Deficient/Not Evaluated species and the exact timing of shifts in Red List status.

to continue to decline steeply throughout the study period, reaching 0.6755 and 0.6629 by 2070, respectively.

While RLI for global zoo collections is currently close to the global average for terrestrial vertebrates, Figure 1 reveals some potentially concerning biases in the representation of threatened species and those likely to become threatened under environmental change. Firstly, under all SSPs, the initially negligible gap between global and zoo RLI widens from .01 to between .036 (SSP1-2.6) and .064 (SSP3-7.0), meaning that the aggregate endangerment of terrestrial vertebrates will become more severe for species not in zoos compared to those currently in zoos. Furthermore, the only taxonomic class that has a lower current RLI for species in zoos than its global average is mammals, whereas RLI for other classes (particularly Amphibia) in zoos is considerably higher than the global average.

Conservation of threatened evolutionary history

EDGE species representation

Under anthropogenic climate and land use change, the number of EDGE species (Gumbs et al., 2023) is projected to rise markedly, especially for mammals, birds, and amphibians under the more severe SSP5-8.5 warming scenario (Figure 2). In Figure 2, I show whether and to what extent these changes in EDGE species richness globally will be reflected in changes in EDGE species representation in existing global zoo collections. In some circumstances, current EDGE species can lose their EDGE status in future even when the conservation status of the species in question shows no improvement. This is due to changes in the distribution of extinction risk across the phylogenetic tree of life, with associated changes in the expected evolutionary distinctiveness thresholds required to be classed as an EDGE species (ED2; Gumbs et al., 2023; Chapter 3 Methods). Therefore, here I retain all current EDGE species in future EDGE species lists, to reflect the growing number of species requiring conservation attention under climate and land use change. Using my current EDGE score estimates (Chapter 3), I identified 3,374 EDGE species, of which 677 (20%) are currently represented in Species360 collections. Coverage of current EDGE species is greatest for crocodiles and turtles (Archosauromorpha), with 91 of 110 (82.7%) EDGE species represented in Species360 zoo collections. By contrast, only 69 of 1,016 (6.8%) EDGE amphibians are currently

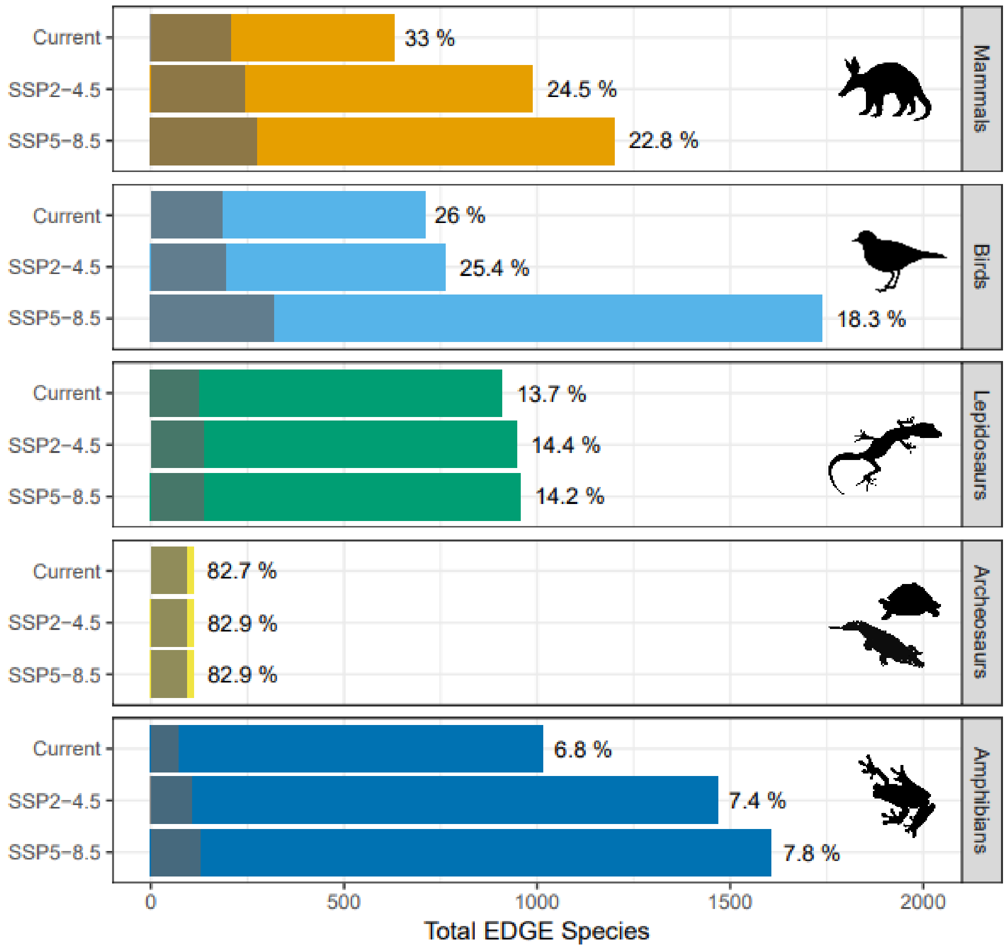


Figure 2. Projected changes in EDGE species richness globally and in current zoo collections under environmental change. Coloured bars indicate the total richness of EDGE species in each class under current conditions and under SSP2-4.5 and SSP5-8.5, for the year 2070. Shaded sections of the bars represent the proportion of these EDGE species that are currently represented in global zoo collections, with representation rates (expressed as a percentage) given at the end of each bar. If current zoo collections already house more of the species projected to become new EDGE species than one would expect by chance, then these percentages would increase (as for Amphibia). By contrast, the percentages would decrease if zoos house fewer new EDGE species than expected by chance (as for birds and mammals).

represented in global zoos (Figure 2). Currently, mammal and bird EDGE species are better represented, with 33% and 26% coverage, respectively. However, these proportional representations are expected to fall by around a third under future climate and land use change, with just 22.8% and 18.3% of EDGE mammals and birds, respectively, represented in zoo collection under the most severe warming scenario. This pattern contrasts with that observed for reptiles, whereby the overall number of global EDGE species, and their proportional representation in existing zoo collections, is projected to remain relatively stable under future climate and land use change scenarios.

Species in zoos have lower EDGE scores than close relatives

Regarding zoo species' raw EDGE scores compared to close relatives not in zoos, results from phylogenetically controlled generalised estimating equations suggested that presence in zoos was negatively associated with species EDGE scores in over 75% of the 100 model iterations, and this pattern was consistent across all climate scenarios and all taxonomic groups other than the crocodiles and turtles (Archosauromorpha; Figure 3). When considering all taxa together, under current conditions presence in zoo collections was associated with a median reduction in EDGE score of 0.137 MY (IQR = 0.014-0.403) relative to species not in zoos, and this gap increased to 0.208 MY (0.041-0.497) and 0.237 (0.033-0.491) under SSP2-4.5 and SSP5-8.5, respectively.

While the smaller number of unique species pairs that could be generated for amphibians and crocodiles and turtles (Archosauromorpha) led to greater uncertainty and variability in effects for these taxa (Figure 3; Appendix C), it is notable that effect sizes for amphibians and snakes, lizards, and tuatara (Lepidosauria) tended to be larger than for endotherms (birds and mammals). This was particularly the case when assessing zoo collections under current environmental conditions (green colours, Figure 3), suggesting that while endotherm species in zoos tend to have lower current EDGE scores than close relatives not in zoos, this discrepancy is even greater for amphibians and lepidosaurs. However, under future conditions, effect sizes for ectotherms (reptiles and amphibians) remain relatively stable, while they increase for endotherms (blue and amber colours, Figure 3). This reinforces the findings in Figure 2 that proportional coverage of EDGE mammals and birds in existing Species360 collections is projected to decline under future environmental change, especially under SSP5-8.5. Mammalian and avian zoo collections are therefore less likely to conserve the evolutionary lineages that are projected to become increasingly threatened under environmental change.

Discussion

Target 4 of the Kunming-Montréal Global Biodiversity Framework (GBF) presents the global zoo community with a unique opportunity to demonstrate their value to biodiversity conservation through *ex situ* management of threatened species (Condé et al., 2011; CBD, 2022; Moss et al., 2023). However, the results presented here are concerning from the

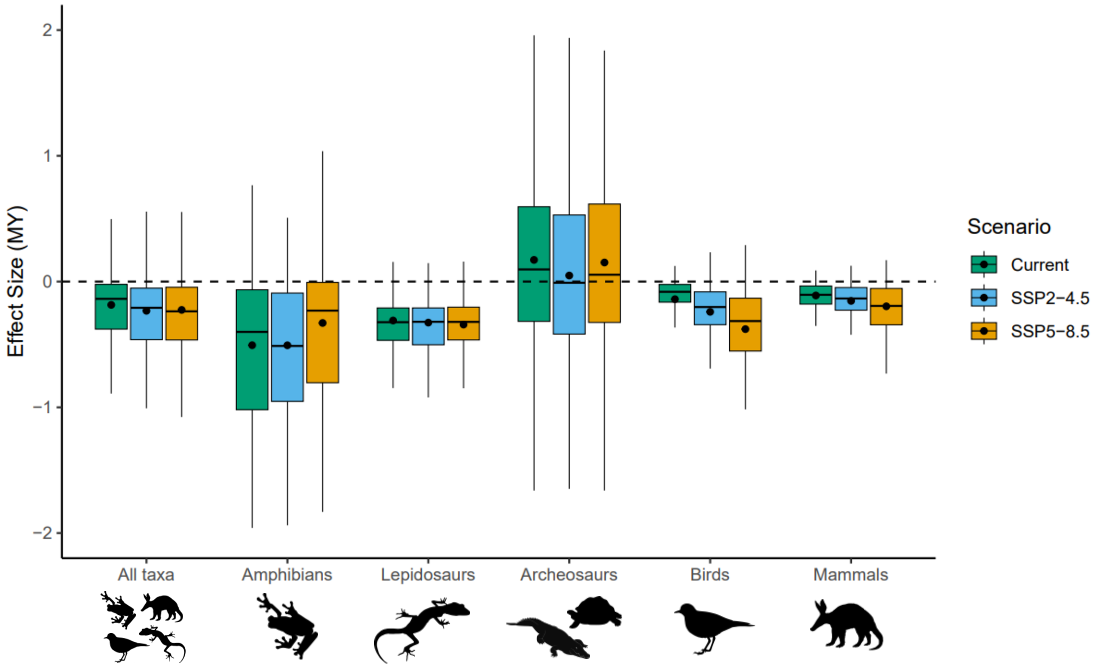


Figure 3. Species in zoos typically have lower EDGE scores than close relatives not in zoos. Boxplot showing effect sizes of phylogenetic linear models with species EDGE scores (MY of threatened evolutionary history) as the dependent variable and presence in current zoo collections as the independent variable. Unique pairs of closely related species were generated for each of the 100 phylogenetic trees used to estimate species EDGE scores. Models were run for each of the 100 trees and 100 EDGE score estimates under current conditions (green) and for the year 2070 under SSP2-4.5 (blue) and SSP5-8.5 (amber). Mean effect sizes are marked by black dots. Presence in current zoo collections was negatively associated with species EDGE scores in at least 75% of cases for all scenarios and all taxa other than crocodiles and turtles (Archosaurs). For birds and mammals in particular, effect sizes were more strongly negative under future environmental change, meaning zoo collections do not currently conserve mammalian and avian evolutionary likely to become threatened in future.

perspective of *ex situ* conservation, as they suggest that zoo collections will have to adapt significantly in response to future environmental change. In Chapter 2, I set out the theoretical basis for the urgent need to better integrate long-term projections of climate and land use change into strategic zoo collection planning, given previous research has hinted that species held in zoos are likely to be less threatened by environmental change (Martin et al., 2014). Here, I have provided quantitative evidence to support these theoretical predictions, further highlighting the utility of systematic prioritisation approaches to optimise zoo collections for conservation under climate and land use change (see Chapter 7).

Current ex situ conservation gaps

When considering the current composition of global zoo collections, I found that for most taxonomic groups, species in zoos were typically less threatened (indicated by a higher RLI) than the global average for the taxon in question. Specifically, only mammal species in zoos had a more severe index of overall endangerment (RLI = 0.795) than the global average (RLI = 0.836), while reptile species' aggregate endangerment was approximately equal for zoo species and all reptiles globally, and birds and amphibians had a higher RLI in zoos (lower overall endangerment) than birds and amphibians globally (Figure 1). Furthermore, these gaps between global and zoo species' overall endangerment are projected to increase under climate and land use change, providing quantitative evidence that zoo collections do indeed house species that are, on average, less likely to become threatened by environmental change. This finding builds on previous research that showed that zoo species were less endemic and more wide-ranging than relatives not in zoos, indicating a likely lower vulnerability to future climate and land use change (Martin et al., 2014; Biega et al., 2017). The fact that gaps in overall endangerment were strongest for amphibians is also of concern, as amphibians are already the most threatened class of terrestrial vertebrate (IUCN, 2023b), are particularly vulnerable to environmental change (Luedtke et al., 2023; Chapter 3), and are currently under-represented in zoos relative to their global endangerment levels (Figure 1; Jacken et al., 2020).

Similarly, for most taxa, species in zoos represented less threatened evolutionary history than their close relatives not in zoos, meaning current zoo collections are likely to perform poorly in conserving unique phylogenetic diversity across the vertebrate tree of life (Figure 3). In this case, the only exception were turtles and crocodilians (Archosauromorpha), with highly variable results from pairwise phylogenetically-controlled models due to the limited number of unique species pairs generated for this less speciose clade. Furthermore, when considering EDGE species richness and their proportional representation in current zoo collections (Figure 2), reptilian EDGE species representation is projected to remain stable under climate and land use change. This is not to suggest that reptiles are not vulnerable to these pressures (quite the opposite – Figure 1; Chapter 3; Appendix A). Rather, it suggests that the composition of EDGE species lists is likely to remain relatively constant, with current EDGE reptiles remaining the highest conservation priorities for conserving threatened reptilian evolutionary history under environmental change.

My results agree to some extent with previous research, albeit from more than a decade ago, that showed that species in zoos were more likely to be threatened than would be expected by random chance for just two of 59 vertebrate orders (carnivorous marsupials and turtles; Condé et al., 2013). The results presented here suggest that, while there has been some progress since this earlier study (see Chapter 2, Box 1), there remain significant gaps in representation for many taxa, particularly threatened Amphibia (Dawson et al., 2016; Biega et al., 2017; Jacken et al, 2020; Brereton and Brereton, 2020). Recent research has shown that only 4.3% of amphibian species recommended for *ex situ* conservation are present in current zoo collections, and a remarkable 44% of amphibian species in zoos were held by just one institution (Jacken et al., 2020). Similarly, I found that only 6.8% of EDGE amphibians are currently represented in Species360 zoos, and despite modest increases in representation under climate and land use change, >92% of future EDGE amphibians are also unrepresented in current zoo collections (Figure 2). Zoos must therefore redouble their recent efforts (Dawson et al., 2016) to better represent amphibian species threatened with extinction, even before the impacts of future environmental change on these species are accounted for.

Environmental Change Poses Risks for Global Zoo Collections

Assessing climate and land use change impacts on the conservation value of current zoo collections is a novel element of this study. While previous studies (e.g. Condé et al., 2013; Martin et al., 2014; Biega et al., 2017; Jacken et al, 2020; Kerr et al., 2023) have examined threatened species representation in global and regional zoo collections, no study has yet applied global projections of future threat status to current zoo collections under environmental change. This new perspective reveals yet more concerning patterns in the representation (or lack thereof) of threatened species in zoos, particularly for reptiles and amphibians. The latter are not only the most threatened terrestrial vertebrate class (IUCN, 2023b), but also the most poorly represented in current zoo collections (Chapter 2; Brereton and Brereton, 2020; Figure 3). Amphibians are also the terrestrial vertebrate class most vulnerable to future environmental change (Figures 1-3; Appendix A; Luedtke et al., 2023).

However, the impacts of climate and land use change on the representation of threatened biodiversity in zoos also extends to the relatively well-represented mammals and birds (Figures 2-3). The proportional representation of EDGE mammals and birds is projected to decline under future climate and land use change scenarios, whereas it is projected to remain stable or even marginally increase for reptiles and amphibians (Figure 2). Phylogenetically controlled models using related species pairs showed that mammals and birds in zoos represented less threatened evolutionary history than close relatives not in zoos, echoing previous findings related to threat status, range size and endemism using similar methods (Martin et al., 2014). While these effects were relatively small for mammals and birds (Figure 3), I found a concerning and consistent trend whereby the gap in threatened evolutionary history representation increased with the intensity of environmental change (Figure 3). Target 4 of the Kunming-Montréal GBF explicitly stresses the need to conserve the genetic diversity and evolutionary potential of species through integrated *in situ* and *ex situ* conservation (CBD, 2022). Therefore, zoos should focus efforts on the irreplaceable threatened evolutionary history represented by phylogenetically distinct branches of the tree of life. My findings suggest that current zoo collections not only perform relatively poorly in representing threatened ectotherm (reptile and amphibian) evolutionary history, but that endotherm (bird and mammal) evolutionary history projected to become threatened in future is also disproportionately under-represented. Zoos' long-term contribution to Target 4 will therefore be conditional upon their ability to adapt their collections and get ahead of the curve of climate and land use change.

Clearly, there is a need for the composition of zoo collections to evolve to reflect shifting conservation priorities. However, zoo collection planning is multi-faceted and curators must balance a range of, at times competing, priorities when making curatorial decisions (Fa et al., 2014). Not least among these is the need to house a collection of species that appeal to the public, drive visitation, and indirectly allow zoos to carry out their wider conservation mission, including through financial contributions to *ex situ* conservation (Moss and Esson, 2010; Fa et al., 2014; Mooney et al., 2020). Similarly, curators are constrained by limited space and the architectural heritage of their institutions (Powell, 2019; Breteon and Brereton, 2020; Krause and Robinson, 2022). Given the findings presented here, this tension at the heart of zoo collection planning is only likely to intensify under anthropogenic climate and land use change. In the following chapters, I investigate on which species are likely to be most attractive to the public, and then combine this information with empirical estimates of species future EDGE scores and spatial exhibit requirements, to simulate optimal collections under climate and land use change that balance these priorities and maximise zoos' contributions to the Kunming-Montréal GBF targets.

Chapter 6

A synthesis of global vertebrate attractiveness reveals hotspots of untapped flagship species

Photograph of a sleeping Fossa (*Cryptoprocta ferox*). In this chapter, I find that the fossa was found to be the most attractive species to the public outside of established flagship species, making it the top-ranked most attractive ‘Cinderella species’ on Earth. *Photo credit: Tambako The Jaguar (Flickr, CC-BY-ND-2.0 DEED)*

Abstract

Biodiversity is declining worldwide, with significant shortfalls in the funding required to reverse this trend. Leveraging the appeal of charismatic ‘flagship species’ can drive investment in conservation. However, such promotions largely focus on a select few species, with many ‘Cinderella’ species – overlooked species with flagship potential – remaining underutilised. Using zoo visitor data, I build trait-based models of species attractiveness and predict the attractiveness of terrestrial vertebrates globally, before investigating the phylogenetic and spatial distribution of attractor species. Attractive species are heavily biased towards mammals, with bright coloration, high activity and visibility, high threat status and forward-facing eyes promoting attractiveness. I identify global hotspots of species attractiveness and ‘Cinderella Zones’ – areas that support many attractive species but have few existing flagships – which represent important opportunities to drive investment in area-based conservation. Importantly, such areas are disproportionately found in low-income with limited ability to bear the costs of conservation. Leveraging flagship potential in these zones could therefore strengthen funding streams and channel investment to where it is most needed, both for biodiversity conservation and to improve human livelihoods.

Introduction

To date, international efforts to halt the global biodiversity declines of the 20th and 21st century have proven ineffective, with 28% (44,000 *spp.*) of species assessed by the IUCN now threatened with extinction (IUCN, 2023b). The overriding cause of biodiversity loss is the ever-increasing impact of human activity on the planet (IPBES, 2019), and changing human behaviour at a global scale is the only viable solution to reverse these trends (Balmford and Cowling, 2006; Nielsen et al., 2021). Both the drivers of and potential solutions to the biodiversity crisis are increasingly well understood (Cowling, 2014), but conservation science has so far failed to elicit change in human behaviour at the scale require to prevent further extinctions (Balmford et al., 2021).

One example of the mismatch between our understanding of the biodiversity crisis and global action to address it can be found in the under-resourcing of biodiversity conservation globally (Coad et al., 2019). The global shortfall in conservation funding has been estimated at $598–

824 billion per annum if nations are to halt global biodiversity loss (Deutz et al., 2020). Finding innovative ways to close this gap in conservation funding is therefore an urgent priority for global conservation science and practice (Karolyi and Tobin-de la Fuente, 2023), and has led to increasing calls for conservationists to integrate ‘conservation marketing’ into their practice (Wright et al., 2015; MacDonald et al., 2017; Veríssimo, 2019). Conservation marketing applies the concepts of social marketing (promoting behaviour change in fields such as public health, safety, and education) to encourage environmentally sustainable behaviours and pro-conservation policies, including public and private investment in species conservation (Balmford and Cowling, 2006; Wright et al., 2015).

A key tool in conservation marketing is the flagship species approach, whereby species that are deemed particularly charismatic or attractive to the public are used as emblems to garner public support and funding (Caro, 2010; Veríssimo et al., 2012). To date, however, the flagship species approach has been non-systematic and is usually limited to a sub-group of charismatic megafauna (Caro, 2010), potentially diverting funds away from species and habitats of greater conservation priority (Andelman and Fagan, 2010). Retaining a narrow taxonomic focus of flagship campaigns can also reinforce cultural norms, whereby the perceived conservation value of flagship species is inflated by their cultural prominence at the expense of less ‘popular’ taxa, creating a cycle of conservation inequality (Davies et al., 2018). Despite these concerns, when combined with spatial prioritisation and planning, the flagship species approach can maximise investment without diverting funds from other conservation priorities (Bennett et al., 2015; McGowan et al., 2020). Given the urgency of the biodiversity crisis and the huge shortfalls in conservation funding, identifying novel candidate species and regions for conservation marketing effort will be vital. Here, for the first time, I model the attractiveness of the world’s terrestrial vertebrates (birds, mammals, reptiles and amphibians), and use these models to map where species attractiveness to humans occurs in both geographic space and phylogenetic space across the vertebrate tree of life.

My models use behavioural observation of zoo visitors to identify the traits that drive species attractiveness to the general public. Zoos exist at the intersection of tourism, conservation, research and public wellbeing (Spooner et al., 2023), and are unique in providing access to a wide diversity of species at a single site. In this ‘marketplace’ of competing stimuli, such as other exhibits (Bitgood et al., 1988), observation of visitor time budgets across exhibits can provide a direct measure of interest in species and is less sensitive to self-reporting biases inherent in commonly-used survey-based methods (e.g. Frynta et al., 2010; MacDonald et al., 2015; Skibins et al., 2017; Haukka et al., 2023), making zoo visitor observations a powerful tool for understanding the drivers of species attractiveness.

In this study, I collected 21,046 observations of zoo visitor interactions with 299 vertebrate species across 42 taxonomic orders at zoos across the UK. I measured species' 'attraction power' (proportion of visitors who stop to view an animal) and 'hold time' (how long they stop for) as proxies for attractiveness (Moss and Esson, 2010). I then collated data on morphometric (body mass and length), ecological (diet, threat status), and evolutionary traits (phylogenetic distance from humans, evolutionary distinctiveness) for the world's terrestrial vertebrates from previously published online data repositories. I supplemented these data with information on species colouration, patterning, facial markings, eye position, and ornamentation gleaned from online photographs, resulting in a final trait dataset for 24,750 species. I fitted generalised linear mixed-effects models associating species traits with attraction power and hold time, accounting for species taxonomy in the random effects error structure. I then generated bootstrapped trait-based predictions of attractiveness for the world's terrestrial vertebrates, and used ancestral state reconstruction to map modelled attractiveness onto the vertebrate tree of life to show the distribution of attractiveness in phylogenetic space.

Smith et al. (2012) introduced the concept of 'Cinderella species' by characterising the typical traits of mammal species that are regularly used as flagship species by conservation NGOs. They then identified, from 1,098 threatened mammal species, those (Cinderella) species that share these traits but which are underutilised as flagships. Here, I applied this approach to the world's terrestrial vertebrates, modelling the attractiveness of 24,750 mammal, bird, reptile, and amphibian species, and mapped 'Cinderella Zones' where a high richness of these attractive but non-flagship species coincide with areas of low existing flagship richness. These zones represent key areas where flagship status could be extended to underpromoted species to maximise investment in conservation (Balmford et al., 2015; Maxwell et al., 2020). To do this, I first collated lists of mammals, birds, reptiles, and amphibians already recognised as flagship species (Roll et al., 2016; Kalinkat et al., 2017; Wong and Rosindell, 2022). I then designated highly attractive species beyond these existing flagships as Cinderella species, and mapped the richness of both existing flagships and Cinderella species globally, to highlight, importantly, where high Cinderella richness coincides with low existing flagship richness. I found that the extent and distribution of Cinderella Zones vary with taxonomic class and are disproportionately concentrated in low-income countries in the tropics. This highlights potential opportunities for greater conservation marketing of Cinderella species to maximise their currently untapped flagship potential, attracting public and private investment from richer nations to meet the 2030 global targets more equitably (Shen et al., 2023).

Results and Discussion

Inter-specific differences in attractiveness

Of 21,046 observed visitors, 11,665 (55.4%) stopped to view animals. Mean attraction power was 69.1% (95% CI = 68.1-70.1) for mammals, 56.9% (55.4-58.4) for reptiles, 44.8% (42.7-46.9) for amphibians, and 42.5% (41.3-43.7) for birds, although these values varied widely among species (Figure 1). Mammals also achieved the highest mean hold time of 67.8 seconds (65.5-70.1), compared to 30.4 seconds (29.0-31.7) for reptiles, 28.9 seconds (27.6-30.3) for birds, and 21.9 seconds (20.6-23.2) for amphibians. The chimpanzee (*Pan troglodytes*) was the most attractive species in my zoo sample, with an attraction power of 98.9% (96.7-99.9) and a mean hold time of 171 seconds (126.9-215.2). The species with the lowest attraction power in my sample was the highly cryptic Chapa bug-eyed frog (*Theloderma bicolor*) with no visitors spotting this species, while mean hold time was lowest for the bearded reedling (*Panurus biarmicus*) at 8.5 seconds (5.7-11.3).

My finding that the most attractive taxa in this study were mammals, particularly elephants, apes and large carnivores, is consistent with previous (albeit more restricted) studies which also found these taxa to be the most charismatic mammals (Smith et al., 2012; Skibins et al., 2017; Albert et al., 2018; Berti et al., 2020). However, most previous studies have relied on relatively ‘static’ proxies, such as zoo promotional material or species image ratings, to assess attractiveness. The fact that my attractiveness predictions correlate strongly with previous

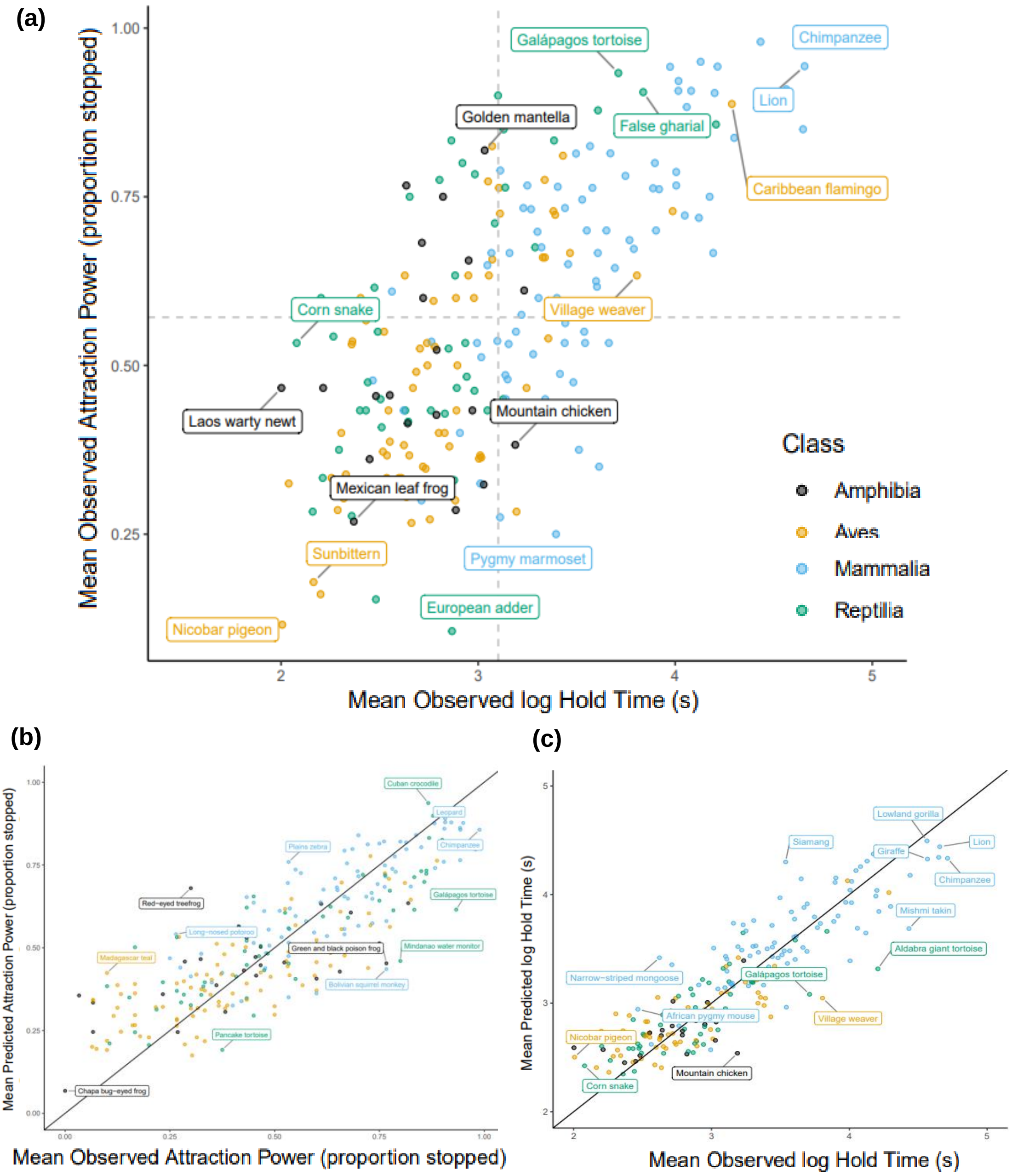


Figure 1. Observed and predicted mean attraction power and hold time per species. Mean observed hold time in seconds (log-scale) and attraction power per species (a). Dashed lines indicate the overall per-species means for hold time and attraction power. Per-species mean observed vs mean predicted attraction power (b) and log hold time (c). Black lines indicate 1-1 diagonal where observed value = predicted value. Species below the 1-1 line were more attractive than predicted by my models, while species above the line were less attractive than predicted. Species with fewer than 30 overall observations were excluded from (a, b, and c) and species with fewer than ten visitor stops (hold time measurements) were additionally excluded from (a and c). Colours indicate taxonomic class.

findings derived from alternate methodologies (Skibins et al., 2017; Albert et al., 2018; Berti et al., 2020) further substantiates the utility of this approach.

Model performance

Following five-fold cross validation, I found a strong correlation between observed and predicted data at the species level (Pearson's $r \geq 0.836$, $p < .001$ for both attraction power and hold time; Figure 1b-c). RMSE and MAE values, based on mean observed and predicted values for each species are, respectively, 0.140 and 0.112 for attraction power and 0.337 and 0.258 for hold time. To demonstrate how well my zoo-based attractiveness measure explains investment in real-world investment in species conservation, I extracted data on EU LIFE investment in species conservation projects and cross-referenced these with my species attractiveness predictions (predicted attraction power x predicted hold time). The original authors (Mammola et al., 2020) used relative Google Search volume from the Google Trends API to conclude that species popularity was the primary driver of conservation effort and investment over species traits such as threat status and body size. However, for the 258 terrestrial vertebrate species present in my dataset, my zoo-based measure correlated more strongly with total funding for species conservation projects (Pearson's $r = 0.367$, df = 269, $p < .001$) than the internet popularity measure used by Mammola et al. (Pearson's $r = 0.292$, df = 268, $p < .001$), reinforcing the strength of my attractiveness measure to act as a proxy for flagship potential.

Drivers of attractiveness

For both dependent variables, only one top model was selected from my model selection process (see Methods), with no other models falling within 2 ΔAICc (Akaike, 1974) of the top-performing model (Burnham and Anderson, 2004). The top-performing attraction power model revealed that attraction power was significantly positively associated with animal visibility and activity levels, bright colouration, forward facing eyes, threatened Red List status and body length, although the quadratic body length term had a negative effect (Figure 2). Attraction power was also negatively associated with body patterning (Figure 2a). The top-performing hold time model also included activity and visibility levels, forward facing eyes, and body length and mass, which all significantly increased hold time, but again the quadratic body length term was negative. Facial patterning also negatively affected hold time (Figure 2b). While increasing body size tended to increase attractiveness, the negative quadratic terms for body

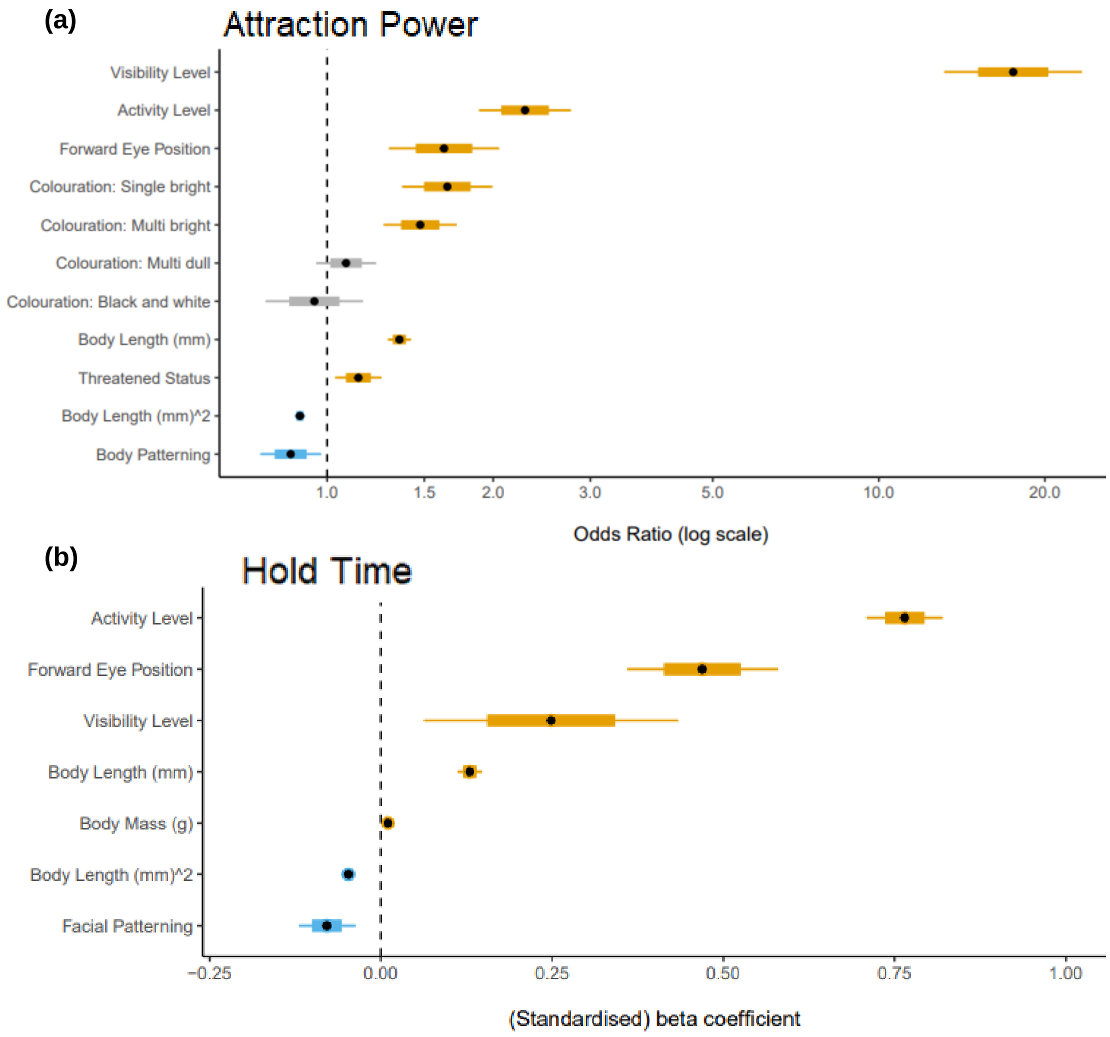


Figure 2. Effects sizes of explanatory variables included in attraction power and hold time models. Odds ratios for fixed effect terms included in models predicting attraction power (a) and (standardised) beta coefficients for hold time (b). The continuous variables of Body Length, Body Mass, and their quadratic terms were standardised using z-transformation prior to modelling. Dots indicate central estimates, with bars and whiskers representing the 67% and 95% confidence intervals, respectively. Orange represents a significant (p < .05) positive effect, and grey represents a non-significant effect. Note that the reference category for Colouration in (a) was 'Single Dull').

length were contrary to my expectations (Berti et al., 2020; Collins et al., 2021). However, while significant, standardised effect sizes for these quadratic terms were small relative to other variables (standardised β = -0.046, 95% CI = -0.53 - -0.038 for hold time, odds ratio = 0.885, 0.876-0.885 for attraction power) and were far outweighed by major drivers such as activity level, visibility level, eye position and species taxonomy, with effect sizes often an order of magnitude greater than these quadratic body length effects (Figure 2a-b). The significant positive effects of forward-facing eyes supports previous research suggesting that human-like features increase species attractiveness (Smith et al., 2012; Skibins et al., 2017), and is a key tenet of the ‘baby schema’ (Lorenz, 1943) that drives perceptions of ‘cuteness’ in non-human species (Borgi and Cirulli, 2016). The negative effect of body and facial patterning on attraction power may be related to cryptic behaviour of some species, with patterning reducing detectability (Endler, 1978). Threat status had a small but significant effect on attraction power, but no effect on hold time. Previous studies have lacked consensus on the relationship between species threat status and attractiveness (Colléony et al., 2017; Davies et al., 2018; c.f. Clucas et al., 2008; Skibins et al., 2017). The public’s understanding of the IUCN Red List and associated extinction risk is quite poor (Courchamp et al., 2018), which might explain why threat status was only a weak driver of attractiveness.

Bright body colouration significantly increased attraction power, in line with previous research on birds (Stokes, 2007; Frynta et al., 2010; Santangeli et al., 2023). Cooney et al. (2022) mapped the brightness of songbird (passerine) plumages globally, and found that brightness peaked in tropical forests in the Amazon, Congo, and southeast Asia. It is surprising, then, that these regions did not have disproportionately high levels of avian attractiveness relative to species richness (Appendix D, Figure S6b). This may be explained by the relatively low attractiveness of (typically smaller) songbirds in my study relative to larger (non-passerine) birds (Appendix D, Figure S2).

While the most attractive species in my study generally agree with previous studies, the traits driving attractiveness and the magnitude of these effects occasionally differed from the consensus. In particular, I found that animal activity levels and their visibility were more important than traits such as body size and colouration, that have been found to be important in other species attractiveness studies (Stokes, 2007; Frynta et al., 2010; Albert et al., 2018; Berti et al., 2020; Santangeli et al., 2023; Figure 2). However, in contrast to most previous studies, I measured visitor responses to real-world encounters with species, which permits activity and visibility to be assessed; something that many other studies could not do. This underlines the potential of zoos to provide richer insights into species attractiveness to the public. Indeed, animal activity and visibility levels have long been recognised as an important driver of positive wildlife-viewing experiences and human attitudes towards species (Skibins et al., 2017; Arbieu et al., 2018; Salas et al., 2021). However, these variables have tended to be overlooked in many previous studies.

Phylogenetic distribution of attractiveness

Complete trait data were available from online image databases for 10,648 of 10,649 (>99.9%) birds globally, 1,289 of 1,602 (81.1%) terrestrial non-volant mammals (excluding Rodentia and Eulipotyphla, which are both highly speciose but generally morphologically similar), 7,452 of 10,588 (70.4%) reptiles and 4,030 of 7,133 (56.5%) amphibians (see Appendix D for sources of trait data). When rodents (Rodentia) and shrews, hedgehogs and allies (Eulipotyphla) are included, complete data were available for 2,620 of 4,413 (59.3%) terrestrial non-volant mammals, resulting in a final set of 24,750 species whose attractiveness to zoo visitors could be estimated, representing 75.5% of all possible species. Ancestral state reconstruction revealed interesting patterns in the phylogenetic distribution of attractiveness across the vertebrate tree of life (Figures 3, S1-5, Appendix D). Elephants, great apes, cats, and bears were particularly attractive (Figure 3), consistently more so than other primate and carnivore families. Carnivores have long been recognised as flagship species for wildlife tourism and area-based conservation. This is especially true for ‘big cats’ such as lions, leopards, tigers (*Panthera spp.*), and cheetah (*Acinonyx jubatus*), where these species exist (Belbachir et al., 2015; Van der Meer et al., 2016; Buckley and Mossaz, 2018).

Non-hominid primates showed highly variable attractiveness between families - from the least attractive night monkeys (Aotidae, mean attractiveness index = 8.97, 8.94-9.00) to the most attractive indris, sifakas and woolly lemurs (Indriidae, mean = 24.83, 22.72-26.94). Among birds, attractiveness was highly concentrated in flamingos (Phoenicopteridae), which were by far the most attractive bird family (mean = 25.12, 21.89-28.35). By contrast, small songbirds (Passeriformes) generally had low predicted attractiveness. Among Amphibia, hotspots of attractiveness were found in tree frogs (Hylidae), leaf frogs (Phyllomedusidae), mantellas (Mantellidae), and glass frogs (Centrolenidae; Figure S5). Among reptiles, crocodilians had the highest predicted attractiveness (Appendix D, Figures S3-4).

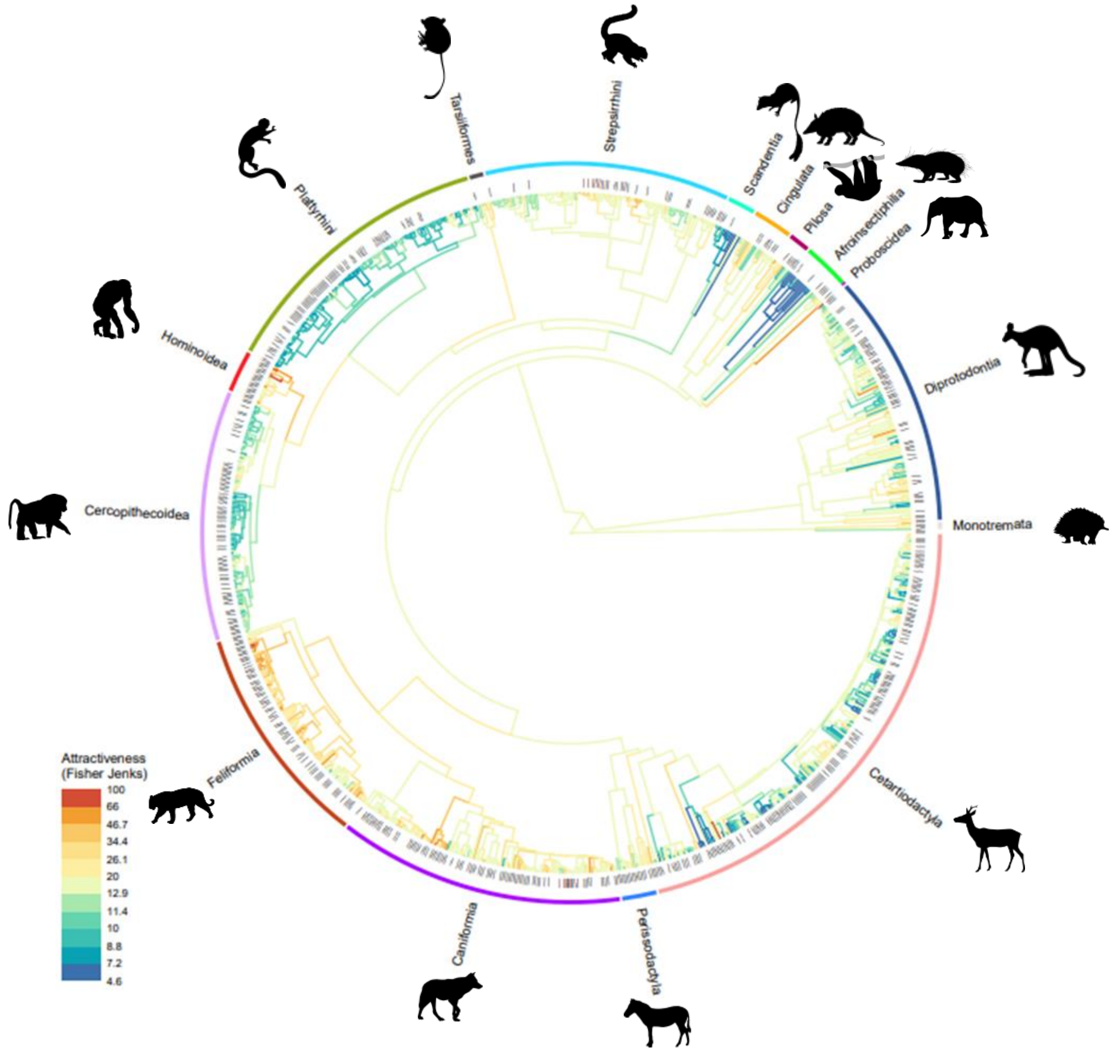


Figure 3. Phylogenetic distribution of predicted species attractiveness for non-volant terrestrial mammals. Phylogenetic tree for mammals (Upham et al., 2019) showing the phylogenetic distribution of predicted species attractiveness. The tree includes only species from orders sampled in at least one zoo and with full trait data available. Rodents are excluded, to show more clearly differences among other taxa. Red colours indicate more attractive species, and blue colours indicate less attractive species. Black dashes at tip labels indicate species currently held in zoos according to the global Species360 (ZIMS) database (zims.species360.org). External coloured lines represent major taxonomic groups. See Figure S1 for full mammal tree, and Figures S2-5 for equivalent trees for other classes (Appendix D).

Spatial distribution of attractiveness

For each class, I used Loess regressions comparing species richness with summed species attractiveness scores to identify hotspots where summed attractiveness was greater than expected given species richness. Tropical regions generally had higher summed attractiveness than high-latitude regions for all classes, given the greater species richness in tropical biomes. However, plotting residuals from models of summed attractiveness against species richness revealed areas of divergence (Appendix D, Figure S6). After accounting for richness, mammal attractiveness is disproportionately high across east Africa and the Sahel region, the Himalaya and the Tibetan Plateau, and the northern Amazon and the Cerrado systems in South America (Appendix D, Figure S6a). This largely aligns with the distribution of large felids like lions, jaguars, and the snow leopard (*Panthera spp.*; Figure 5a). Avian attractiveness is disproportionately high in southern and eastern Africa, but is disproportionately low in high altitude systems such as the Himalaya and central China, directly contrasting patterns seen in mammalian attractiveness (Appendix D, Figure S6b). Reptile attractiveness is disproportionately high in the northern Amazon basin, southern Mexico, continental southeast Asia and Sumatra (Appendix D, Figure S6c), while amphibian attractiveness is high in the northern Amazon, the Congo basin and eastern Madagascar (Appendix D, Figure S6d).

Figure 5a shows the taxonomic classification of the single most attractive species in each 0.25-degree grid cell across the world's terrestrial regions. From this, the predominance of carnivores is apparent, with the most attractive species across almost all of continental Eurasia, Africa, and the Americas being either cat-like (Feliformia) or dog-like (Caniformia) carnivores. Exceptions include pockets of sub-Saharan Africa where great apes (Hominidae) or megaherbivores such as the African elephant (*Loxodonta africana*) and giraffe (*Giraffa camelopardalis*) predominate. The most attractive species in Australia are marsupials such as wallabies, wombats, and quokkas (Diprotodontia) and echidnas (Tachyglossidae). Crocodilians are the most attractive species in Cuba, Jamaica, Haiti, and some parts of Madagascar, Borneo, and Sumatra, while other reptiles were the most attractive species in the Philippines, eastern Indonesia, Oceania, and parts of Australia and New Zealand. Birds were very rarely the top-ranked taxa in a region, while amphibians represented the most popular species in just a few isolated cells. See Figure S8 (Appendix D) for equivalent plots for each class separately.

Cinderella Zones

I classified Cinderella Zones for each vertebrate class (Figure 4) as areas that were in the upper quartile of grid cells for Cinderella species richness but also the lower quartile of grid cells for existing flagship species richness (see Methods). The extent and distribution of

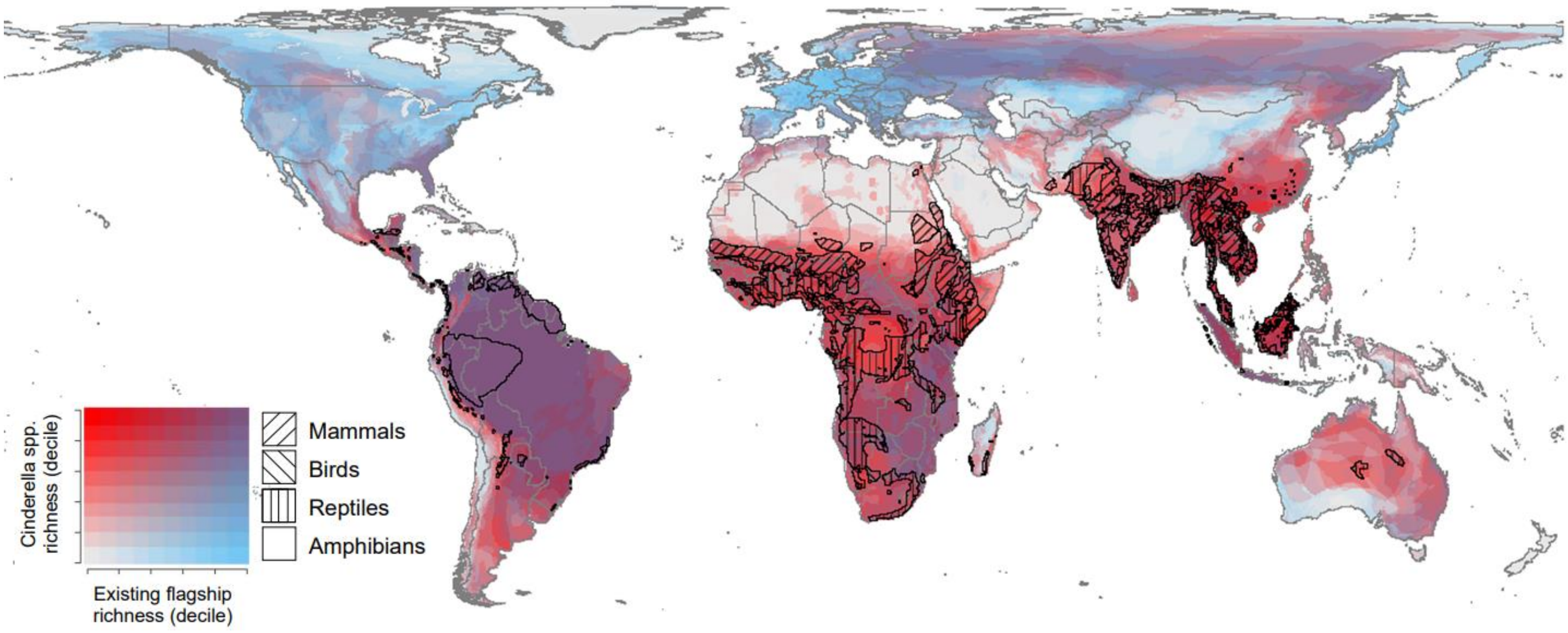


Figure 4. Distribution of Cinderella species, existing flagships, and Cinderella Zones. Bivariate map of Cinderella species richness (reds) and existing flagship species richness (blues) for all terrestrial vertebrates, overlaid with the distribution of Cinderella Zones for each class (black outlines and hatched areas). Cinderella Zones indicate areas where there is a high richness (top quartile of cells) of Cinderella species for a given class but a relative paucity of existing flagships (bottom quartile of cells). Purple areas indicate high richness of both Cinderella and existing flagship terrestrial vertebrate species.

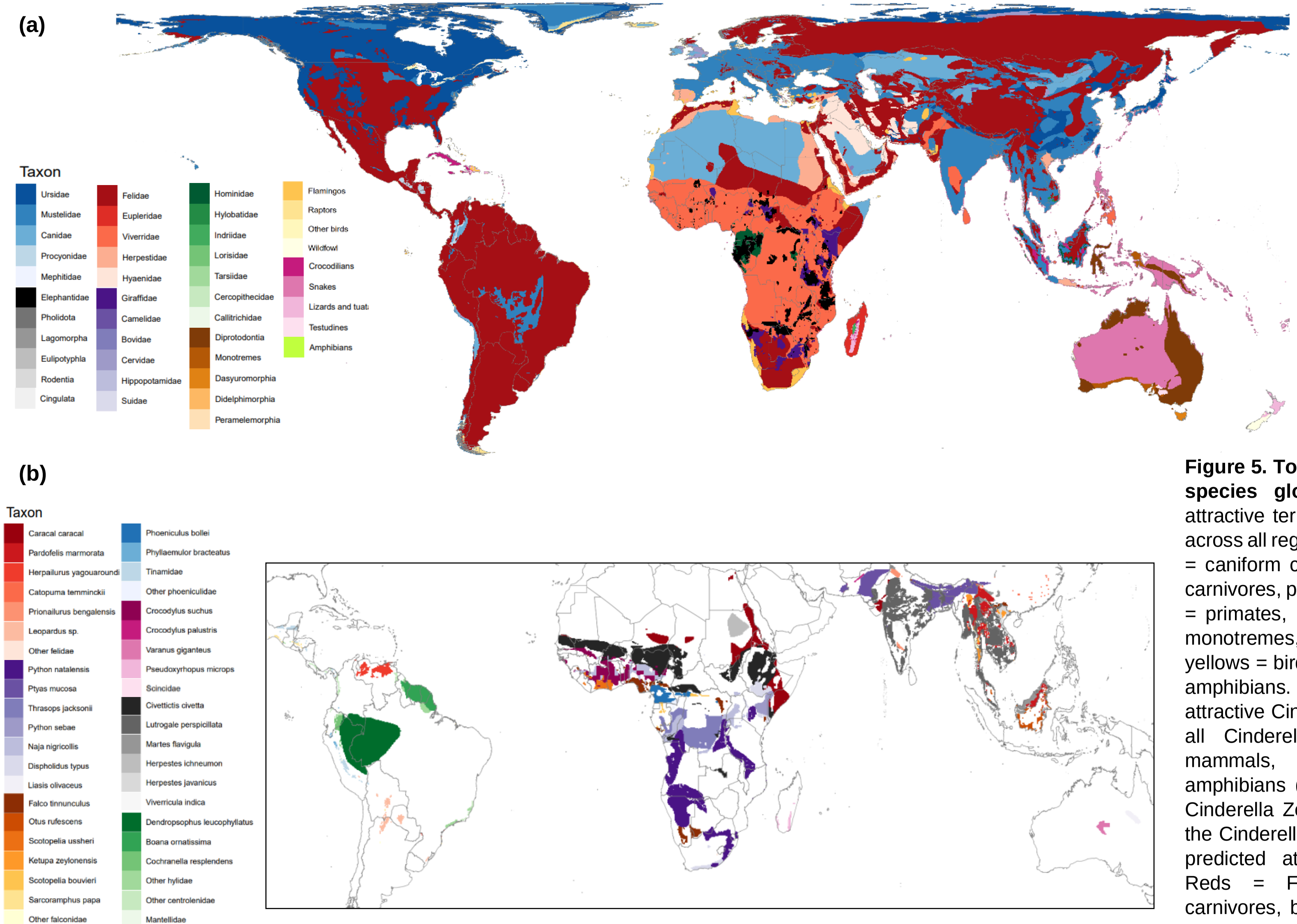


Figure 5. Top-ranked most attractive species globally. Identity of most attractive terrestrial vertebrate species across all regions of the world (a). Blues = caniform carnivores, reds = feliform carnivores, purples = ungulates, greens = primates, browns = marsupials and monotremes, greys = other mammals, yellows = birds, pinks = reptiles, lime = amphibians. Identity of the most attractive Cinderella species present in all Cinderella Zones identified for mammals, birds, reptiles, and amphibians (b). In areas identified as Cinderella Zones for multiple classes, the Cinderella species with the highest predicted attractiveness is mapped. Reds = Felidae, greys = other carnivores, browns = raptors, blues = other birds, pinks = legged reptiles (lizards and crocodilians), purples = snakes, greens = amphibians.

Cinderella Zones varied widely between classes, as did the diversity of key Cinderella species identified for each class (Figures 4, 5b, Appendix D).

For mammals, Cinderella Zones were distributed across a wide range of tropical biomes, including South American tropical forests, the more arid Sahel region of Africa, as well as large portions of India and continental southeast Asia (Figures 4, S7a, Appendix D). Figure 5b shows the top-ranked most attractive Cinderella species in each of the identified Cinderella Zones. The top-ranked Cinderella species in mammalian Cinderella zones were all carnivores, particularly Felidae and other feliform (cat-like) carnivores, including the Asian golden cat (*Catopuma temminckii*) – the Cinderella species with the second highest predicted attractiveness globally, behind only the fossa (*Cryptoprocta ferox*) of Madagascar. Avian Cinderella Zones were largely constrained to pockets of southern and western Africa and southeast Asia (Figures 4, S7b, Appendix D), with raptors (birds of prey) as the top-ranked avian Cinderella species in most areas (Figure 5b). Reptile and amphibian Cinderella Zones were primarily constrained to tropical Africa and South America, respectively (Figures 4, S7c-d, Appendix D). While there was a strong phylogenetic diversity of top-ranked reptilian Cinderella species among Cinderella Zones, top-ranked Cinderella species were identified from just three amphibian families (tree frogs [Hylidae], mantellas [Mantellidae], and glass frogs [Centrolenidae]; Figure 5b).

A striking commonality between Cinderella Zones is that they are primarily found in relatively low-income countries that may be less able to fund and maintain effective area-based conservation measures. When combining the Cinderella Zones identified for each class of terrestrial vertebrates (Figures 4, S7, Appendix D), almost a third (31.7%) of Cinderella Zone area falls within nations in the lowest quintile of nations ranked by GDP per capita adjusted for purchasing power parity (PPP; World Bank, 2023), whereas only 1.4% of Cinderella Zone area falls within nations in the top quintile for GDP-PPP. By contrast, when considering all terrestrial vertebrates together, much of Europe, North America and Japan are relatively saturated with existing flagships (blue colours, Figure 4). Reversing the above analysis, by highlighting areas of high existing flagship richness and low Cinderella species richness, reveals that 47.6% of these areas that are saturated with flagships occur in the top quintile of nations measured by GDP-PPP, with less than 1% occurring in the lowest income quintile. This demonstrates the opportunities for extending the flagship species concept to areas of the world in greatest financial need for support. To effectively meet the UN’s 30% protected area coverage by the year 2030, a much greater burden of protection will fall on low-income countries (Shen et al., 2023). Here, I show that there is great untapped flagship potential in these zones, which also align with areas of greatest need for investment for biodiversity conservation.

Globally, visits to protected areas generate an estimated US $600 billion in direct in-country expenditure (Balmford et al., 2015), although most of these visits and associated expenditure currently occur in Europe and North America. Better accounting of the direct and indirect economic benefits of area-based conservation, plus integration into national economies, could help reduce the perceived economic burden of protected area establishment (Maxwell et al., 2020), particularly in poorer nations that contain many of the areas of highest conservation priority (Brooks et al., 2006; Miller et al., 2013). Focusing greater conservation marketing effort on previously overlooked species can influence both public sector funding and private sector donations (Veríssimo et al., 2017; Bellon 2019), with demonstrable co-benefits for wider biodiversity if this investment is directed in a targeted and efficient manner (Bennett et al., 2015; McGowan et al., 2020). Therefore, leveraging the innate appeal of Cinderella species alongside existing flagships is an important tool to attract investment in times of global economic uncertainty.

Effectively scaling up protected area coverage and equitably distributing the economic costs and benefits of doing so represents a significant challenge to the global community, but is imperative if nations are to meet the Kunming-Montréal GBF targets. The Cinderella zones and species identified here represent novel opportunities for renewed investment in area-based conservation.

Conclusions

My trait-based models predicted the attractiveness of most of the world’s terrestrial vertebrates, significantly broadening the taxonomic and spatial scope of previous studies of wildlife's attraction to people. Intelligent and targeted use of conservation flagships can effectively conserve wider biodiversity while maintaining the funding benefits associated with flagship species (McGowan et al., 2020). Here, I directly quantify the attractiveness (and flagship potential) of the world's terrestrial vertebrates, and identify Cinderella Zones where greater conservation marketing effort can extend the benefits afforded by flagship status to a much greater diversity of species and regions across the globe. These zones fall disproportionately within low-income nations with less ability to finance area-based conservation measures, highlighting both the need for international co-operation in biodiversity conservation and the potential for Cinderella Zones to help overcome these funding challenges. Nations are committed to protecting 30% of the world's land mass and increasing global conservation funding by $200 billion per year by 2030 (CBD, 2022). Leveraging the flagship appeal of the right species in the right places will be vital if these goals are to be achieved in an efficient, equitable and cost-effective manner.

Materials and Methods

Study sites

Zoos were selected to cover a diversity in collection sizes, compositions, geographies, and catchment areas across the UK. The zoos included in the study were Chester Zoo, Paignton Zoo, Newquay Zoo, ZSL London Zoo and Twycross Zoo (Appendix D, Table S1).

Species selection

First, species zoo holdings for terrestrial mammals, birds, reptiles, and amphibians at each institution were obtained from the Species360 ZIMS database (zims.species360.org). Species holdings for terrestrial vertebrates for candidate zoos were downloaded from the Species360 ZIMS database (zims.species360.org). Species housed in off-show exhibits were removed to produce a final list of candidate species. Bats were excluded due to a combination of logistical issues of conducting visitor observations in often darkened free-flight areas, and possible biases related to the Covid-19 pandemic and public attitudes towards bats as common hosts of zoonotic coronaviruses (Banerjee et al., 2019; Lu et al., 2021; Platto et al., 2021).

Next, a set of species traits that may influence species attractiveness was derived based on traits previously associated with attractiveness in the published literature (Appendix D, Table S2). Trait data for all species currently held in the host zoos, excluding bats (Chiroptera), were either extracted from electronic datasets or classified from species images (*Species Image Coding,* below). From this subset of zoo species, I filtered species that occurred in at least one of my study zoos. To maximise the taxonomic representation and breadth of species-trait combinations in the zoo observations analyses, I used a semi-systematic approach in which species were weighted according to the relative uniqueness of their set of traits. Continuous trait variables were binned and converted to factors. Then, for each variable, the proportion of species in each factor level was calculated. These were then summed for each species to produce a score of relative uniqueness u, where higher scores indicate more common traits. To account for some species having identical trait combinations, I counted the number of times each unique combination of traits occurred in the dataset c. I then calculated a weighting w for each species as:

Eqn. 1: $$w = \frac{1}{u \times c}$$

I then took 10,000 weighted random samples of species and counted the number of times each species was sampled. I ranked the species by this count value to produce a priority list of species which represent the maximum diversity of species traits. Pilot studies were then conducted to filter out species where data collection was inappropriate or impractical (for example, when a species had recently been taken off-show), and replacement species representing the same taxonomic group and/or similar trait sets were selected. Trait data were also collated using the same approaches, where possible, for all other terrestrial vertebrate species from the global species pool. This was done for 24,750 species in total, representing 75.5% of all non-Chiropteran terrestrial vertebrates, the omitted species being those for which I could not collect the full complement of focal trait data.

Species image coding

A range of online sources were consulted to obtain high-quality species images from which species traits could be derived. These included: iNaturalist 'Research Grade' observations (inaturalist.org/), Animal Diversity Web (animaldiversity.org/), eBird (ebird.org/), AviBase (avibase.bsc-eoc.org/), Birds of the World (birdsoftheworld.org/bow/home), the Reptile Database (reptile-database.reptarium.cz/), the Australian Reptiles Online Database (arod.com.au/), AmphibiaWeb (amphibiaweb.org/), Threatened Amphibians of the World (Stuart et al., 2008), CalPhotos (calphotos.berkeley.edu/), the Nature Picture Library (naturepl.com/blog/), WikiMedia (commons.wikimedia.org/), Flickr (flickr.com/), the websites of the American Society of Mammologists (mammalsociety.org/), the IUCN Red List (iucnredlist.org/), CITES (cites.org/), the IUCN Afrotheria specialist group (afrotheria.net/), Animalia.bio (animalia.bio/), Biolib (biolib.cz/en/), California Herps (californiaherps.com/), and images published in the scientific and grey literature.

For traits including body colouration, body patterning, facial patterning, eye position and ornamentation I derived a set of rules for trait categorisation. A subset of 50 species were drawn from the species pool, ensuring a relatively even representation of the five traits were included in the subset. A Chester Zoo intern, two additional volunteers and I then categorised the traits of each species in the subset independently according to the initial ruleset. The raters then met to discuss any discrepancies, and any areas of ambiguity in the initial ruleset that were causing discrepancies in trait categorisation were adapted. Raters then categorised the images a second time, again independently of each other, according to the new ruleset. Following this second round of trait categorisation, inter-rater reliability (Cohen's K) was ≥ 0.9 for all five traits and between all four raters. Following this process, I and the Chester Zoo intern proceeded to categorise traits for the rest of the species where high-quality images were available (n = 24,750). Occasional instances where raters were unsure how to categorise a species trait were resolved via email. The final ruleset for categorising species traits based on online images is given in the Table S4 (Appendix D).

Visitor-exhibit sampling

Covert visitor observations followed a well-established method of measuring the 'attraction power' (the proportion of visitors who stop to view a species), and 'hold time' (how long they stop for; Figure 1). This method is unobtrusive, simple to perform, allows for relatively rapid collection of large amounts of data, and is well established in visitor studies research (Serrell, 1997; Moss and Esson, 2010; Schwan et al., 2014). Visitors were selected for observation upon approaching an exhibit, or at the first point at which they might see the focal animal in walkthrough or 'free-flight' areas. A continual selection method was employed, meaning that once an observation was completed, the next visitor to approach the exhibit was selected for observation. Only one visitor from any group was selected for observation. Due to ethical considerations, no evidently vulnerable adults or minors were observed, although adults in groups with children could be selected for observation.

Non-identifiable demographic data, including approximate age, assumed gender, and group type of selected visitors were recorded. Exhibits were classified based on whether visitor areas were ‘functional’ or ‘immersive’ and whether animal areas were ‘functional’ or ‘naturalistic’ (see Appendix D, Table S3 for an explanation of exhibit classification definitions). Walkthrough exhibits were recorded separately to the previous groups, making five exhibit categories in total. Whether the exhibit was indoors or outdoors, weather conditions, and ambient temperature were also recorded. As animal visibility and activity levels can have strong effects on visitor behaviour (Turnock and Moss, 2015; Skibins et al., 2017), these were recorded on a 1-4 scale (Appendix D, Table S2). Activity and visibility levels were recorded twice – when the visitor first approached the exhibit, and the maximum level reached while the visitor was stopped at an exhibit. This accounted for any effects of differing animal activity and visibility on attraction power and hold time.

Attraction power was recorded on a binary scale (0 = did not stop, 1 = stopped). To prevent the time visitors spend searching for an animal inflating the hold time of cryptic species, visitors were recorded as ‘stopped’ only once they had evidently spotted the animal. Instances where animals were not visible were discounted. Species that occurred in multiple collections were sampled in at least two zoos, wherever possible (n= 87, 29% of species). See Supplementary Data S2 for the final species list for zoo observations. Of the 299 species selected for visitor observations, 266 (89%) species had at least 30 visitor observation recordings, with sampling effort spread across different times of day.

Random effects

Data were analysed using generalised linear mixed-effect models in the R package lme4 (Bates et al., 2010). Zoo, recorder ID, season (summer 2021, winter 2021-22; summer 2022), and taxonomic effects of order nested within class, were included as random intercepts for binomial GLMMs of attraction power. Some orders were further sub-divided, where evidence existed in the literature for differing human preferences for clades within orders, as follows. Humans have been shown to have differing empathetic and compassionate responses to apes, monkeys and prosimians within the order primates (Miralles et al., 2019), so the order was split into these three sub-groups. Humans have also been shown to prefer feliform (cat-like) over caniform (dog-like) carnivores, so the order Carnivora was split between suborders

Feliformia and Caniformia (MacDonald et al., 2022). Finally, humans tend to find legless squamates less appealing than legged squamates (Janovcová et al., 2019), so the order Squamata (snakes and lizards) was split accordingly.

Fixed effects

To meet the linear model assumption of normally distributed residuals, hold time (s) was log-transformed. Initial data exploration and plotting revealed visitor demographics, exhibit traits, and weather variables to be only very weakly related to attraction power or hold time. Consequently, I omitted these variables from further analysis. This resulted in a final set of 12 predictor variables as fixed effects in GLMMs (Appendix D, Table S2). There is some evidence that both very small and very large species can be attractive to humans (Berti et al., 2020; Collins et al., 2021), so I included quadratic terms for both body mass and body length as additional fixed effects. Linear and quadratic body mass and length terms were standardised using z-transformation. I converted IUCN Red List status into a binary variable with Least Concern, Near Threatened, Data Deficient and Not Evaluated species classified as ‘Not Threatened’ and Vulnerable, Endangered, Critically Endangered and Extinct in the Wild species classified as ‘Threatened’ (following Mace et al., 2008). This reduced potential bias caused by relatively small numbers of species falling in each category, or zoo visitors being unfamiliar with the Red List grading system and the relative endangerment of, for example, ‘Vulnerable’ versus ‘Endangered’ species.

Model selection

Candidate predictor variable combinations were extracted using the dredge function in the MuMIn R package (Barton and Barton, 2020). To avoid overfitting and reduce computational constraints, I limited the number of fixed effect terms to a maximum of eight, resulting in 22,818 candidate models for each dependent variable. Data were split into five test and training folds for cross-validation. ‘Hold time’ data folds were stratified by date to ensure the nested random effect of date was sufficiently represented across all folds. For attraction power, date was excluded as a random effect and folds were stratified by the outcome variable attraction power, to ensure a balanced sample of outcomes across folds. Each of the 22,818 candidate models were fitted and ranked by AICc (Akaike, 1974), after removing models that failed to converge or that resulted in a singular fit. As no models for either attraction power or hold time fell within 2 ΔAICc of the top-performing model for each dependent variable, only the top-performing model was selected for out-of-sample prediction (Burnham and Anderson, 2004). To assess the predictive accuracy of the selected hold time and attraction power models, five-fold cross-validation was performed and the mean absolute error (MAE) and root-mean square error (RMSE) were calculated for each model.

Predicting to out-of-sample species

For predicting the attraction power and hold time of species for my full dataset (i.e. all terrestrial vertebrates for which trait data were available, including species within and beyond my zoo sample), the random intercepts of zoo, recorder ID, and season (and date) were not relevant, so predictions were made based on fixed effects and the nested random effect of taxonomic class and order only. Across the global terrestrial vertebrate pool of 32,783 species (excluding bats), 24.5% of species were missing some categorical trait data. These species were excluded from out-of-sample predictions. I also lacked data for the activity and visibility levels of out-of-sample species. To account for this, for each species I generated all 16 possible combinations of activity and visibility levels and calculated the relative frequency of each combination for the species included in my sample. For out-of-sample species, I used the mean relative frequencies of each combination from related species in my sample, averaging first by genus, then family, order, and class. To account for uncertainty in model coefficients, I produced 100 bootstrapped predictions for each species and each activity-visibility combination (1,600 predictions per species) using the ‘bootMer’ function in the R package *MerTools* (Knowles and Frederick, 2016). I then took a weighted mean of bootstrapped predictions using the relative frequency of activity-visibility combinations as weights, such that predictions for highly active and visible species were weighted towards higher activity/visibility categories.

Phylogenetic and spatial distribution of attractiveness

To provide a single metric of attractiveness I took the product of predicted hold time (s) and attraction power, and scaled the output between 0 and 100, to provide a relative measure of the attractiveness of each species. This simple metric therefore assumes a species viewed for

10 seconds by 80% of visitors would be equally as attractive as a species viewed for 80 seconds by only 10% of visitors. While some (e.g. Balmford, 2000) argue that the former species should be deemed more ‘popular’, a species visited only very briefly is perhaps unlikely to be a key driver in a visitor’s decision to attend a zoo (or be indicative of flagship potential more broadly), whereas the latter species where relatively few visitors have a keen interest in the animal may be more important in driving visitation and attitudes towards species conservation for some visitors. Given these uncertainties, I did not weight my attractiveness metric towards either attraction power or hold time.

To assess the phylogenetic distribution of species attractiveness, I reconstructed ancestral states using recently published phylogenetic trees and the R package *phytools* (Revell, 2012), and used these trees to visualise the phylogenetic distribution of species attractiveness (Figures 3 and S1-5, Appendix D). To map the global distribution of species attractiveness and identify hotspots with high richness of attractive native species, I downloaded species resident and/or breeding ranges from the IUCN Red List (IUCN, 2021; Birdlife, 2021), with additional range data for reptiles downloaded from the GARD database (Roll et al., 2017). I then rasterised these range maps at 0.25-degree resolution, projected to Behrmann’s cylindrical equal area projection, and summed the rasters to produce richness plots. To highlight areas with unusually high or low levels of summed attractiveness relative to species richness, I fitted a Loess regression between summed species attractiveness and richness in each grid cell, and plotted model residuals.

Cinderella species and Cinderella Zones

I identified potential ‘Cinderella species’, species that possess traits that are attractive to humans but which are not typically recognised as current flagship species, following Smith et al. (2012). To do this, I first gathered information on existing flagship species, then from my pool of 24,750 species I identified the subset of species in each class predicted to be highly attractive beyond the list of current flagships, as described below.

For mammals and birds, I downloaded the top 100 most popular species from the OneZoom project Popularity Index (Wong and Rosindell, 2022). The OneZoom top 100 amphibians and reptiles were highly biased towards a few speciose genera (such as Xenopus and Crotalus, perhaps highlighting biases towards common pet species and North American species, respectively). Therefore, as an alternative metric of attractiveness for these two taxa, I sourced flagship reptiles and amphibians from Kalinkat et al. (2017) and Roll et al. (2016), respectively. I removed any extinct, domesticated and marine species, and then supplemented the OneZoom top 100 lists with some well-established flagship bird and mammal species, using the following criteria. Species that were close congenerics of flagship species already in the list, and which look very similar, such as missing species of orangutan (*Pongo spp.*) or rhinoceros (Rhinocerotidae) were added. Also added were charismatic megafauna with well-established flagship status that appear regularly in animated films (e.g. macaws [*Ara spp*., *Anodorhynchus hyacinthinus*]; Dos Santos Ferreira et al., 2023), and ring-tailed lemurs (*Lemur catta*; Durbin, 1999), company branding (e.g. Common kingfisher [*Alcedo atthis*] and Kingfisher Beers™), and wildlife tourism literature (e.g. Cape buffalo [*Syncerus caffer*], a missing species of the 'Big 5' African safari flagships; Skibins et al., 2016). Species that are particularly evocative of a geographical area and often used as national symbols (e.g. kiwis of New Zealand [*Apteryx spp*.; Bennett et al., 2015] and giant salamanders of China and Japan [*Andrias spp*.; Pan et al., 2016]), were also added to the existing flagship list. Following this process, an additional 20 mammal, 23 bird, 3 amphibian flagships were added to the overall list, which, after these additions, comprised 94 mammal, 122 bird, 64 reptile and 10 amphibian species (for full flagship list and justification of inclusion, see Supplementary Data S3).

To validate my flagship selection, I took 1,000 random samples of 94, 122; 64 and 10 non-flagship mammals, birds, reptiles, and amphibians, respectively, and compared the mean attractiveness score of the randomly sampled species with that of my flagship list. In all 1,000 iterations, the median attractiveness of existing flagships exceeded the median of the random sample, and was, on average, 78.8% (range = 64.3-88.4%) higher. This provides significant confidence that not only is the existing flagship species list likely to be reliable, but also that my attractiveness predictions are strongly related with species already deemed attractive enough to be designated as flagship species.

For each of the 100 bootstrapped predictions of attractiveness for the 24,750 species with full trait data available, I ranked species in order of attractiveness and identified which species occurred in the top decile of most attractive species for each bootstrap iteration. I then classified species as potential Cinderella/Flagship species if they occurred in the top decile in at least 95% of the bootstrap iterations. This approach follows that of Gumbs et al. (2023) when identifying EDGE (Evolutionarily Distinct and Generally Endangered) species, although the authors used a median rather than top decile threshold for the EDGE2 metric. I used the top decile threshold because my attractiveness scores were significantly right-skewed, meaning a median threshold would select far too many species with relatively little value from the perspective of conservation marketing and flagship appeal. I then filtered the list of potential Cinderella/Flagship species to remove any species already listed as an existing flagship. This resulted in a final list of 89 mammal, 330 bird, 176 reptile and 124 amphibian Cinderella species (Supplementary Data S4 for Cinderella species list).

To highlight areas where additional flagship species could be utilised to enhance biodiversity conservation, I mapped the richness of Cinderella species against the richness of existing flagship species using a bivariate chloropleth map (Figures 4, S7, Appendix D). I then derived polygons from these bivariate rasters outlining the boundaries of contiguous Cinderella Zones, which I classified as cells that were in the upper quartile of cells when ranked by Cinderella species richness but the lower quartile of cells when ranked by existing flagship richness, thereby avoiding hotspots of Cinderella richness that were already saturated with existing flagships, whilst highlighting hotspots with the most potentially unexploited flagship space. This methodology was modified slightly for reptiles (Appendix D, Figure S7c) where there was relatively little overlap in areas in the top quartile of Cinderella species richness and bottom quartile flagship richness, with only a few very small areas of overlap in South Africa, southern Asia and central Australia. I therefore extended the Cinderella Zone designation for reptiles to include areas in the upper quartile of Cinderella richness and below median flagship richness.

All data analysis and modelling were conducted using R version 4.2.2 (R Core Team, 2022)

Chapter 7

Climate-proofing global zoo collections through novel conservation prioritisation approaches

A child having a close encounter with a False gharial (*Tomistoma schlegelii*) at the immersive *Monsoon Forest* exhibit at Chester Zoo, UK. © *North of England Zoological Society.*

Abstract

Climate and land use change are intensifying pressures on species' native ranges, meaning that there may be increased demand for *ex situ* conservation of threatened species in zoos in future. However, zoos have finite resources, and some researchers argue that there is no more space to increase conservation breeding programmes. In such situations, systematic conservation planning approaches can inform the optimal allocation of resources and account for trade-offs, such as the need to balance zoo collection attractiveness with threatened species representation. In this final data chapter, I bring together information on species' future threat status under climate and land use change, trait-based predictions of species attractiveness to zoo visitors, and estimates of species' exhibit requirements and population persistence probabilities to simulate optimal zoo collections that maximise both conservation value and collection attractiveness, without requiring significant increases in exhibit space. Exploiting recent advances in exact integer linear programming, I apply, for the first time, conservation optimisation algorithms to both global and regional (British and Irish) zoo collections. I show that while existing collections are highly suboptimal, optimising global collections can conserve over 17 billion years of threatened vertebrate evolutionary history, representing a more than ten-fold increase relative to existing collections, alongside a six-fold increase in total global collection attractiveness. In British and Irish zoos alone, collection optimisation can increase the amount of threatened amphibian evolutionary history conserved more than 15-fold. These results demonstrate a potential pathway for zoos to secure a sustainable future and maximise their conservation impact, which, if achieved, would have profound benefits for global biodiversity conservation under future environmental change.

Introduction

Terrestrial vertebrate biodiversity is already under significant pressure due to human activities (Ceballos et al., 2020; Harfoot et al., 2021), and is projected to become increasingly threatened as climate and land use change intensify in the future (Newbold, 2018; Powers and Jetz, 2019). In this context, *ex situ* institutions such as zoos are likely to play an increasingly prominent role in the preservation of a growing number of species (IUCN, 2023a), a fact that has now been recognised in Target 4 of the Kunming-Montréal Global Biodiversity Framework

(GBF; CBD, 2022), which for the first time explicitly references *ex situ* conservation in a UN Convention on Biological Diversity target (Moss et al., 2023).

In Chapter 2 of this thesis, I set out how zoos are ideally placed to respond to Target 4 of the Kunming-Montréal GBF through the management of *ex situ* populations of threatened species. However, I also showed how this potential may be undermined by the under-representation of threatened taxa, inadequate population sizes and genetic diversity, and limited space to increase zoo capacities in the long term (Lees and Wilcken, 2009; Condé et al., 2013; Powell, 2019). Species currently in zoos tend to be more generalist and less endemic than close relatives not in zoos (Martin et al., 2014; Biega et al., 2017) and, as a result, it might be expected that zoos disproportionately house species less vulnerable to future environmental change (Foden et al., 2019; Manes et al., 2021). In Chapters 3-5, I provided quantitative evidence that this is indeed the case, with climate and land use change projected to increase extinction risk more severely for species outside zoo collections, when compared to those in current zoo collections. I demonstrated that protected area prioritisation to meet 30% global coverage targets by 2030 (GBF Target 3) has great potential to conserve the world's threatened evolutionary history. However, current protected areas are inadequate to achieve this objective, and effective and timely delivery of such targets should not be relied upon (Xu et al., 2021; Wauchope et al., 2022). Indeed, results from my previous chapters suggest that several thousand species are at risk of losing all climatically suitable habitat even under relatively mild climate and land use change scenarios, making *in situ* conservation potentially ineffective for these species in the long term. These conservation gaps will need to be filled by *ex situ* institutions if future extinctions are to be prevented.

The role of zoos in conserving threatened species *ex situ* is well-recognised and long-established (Soulé et al., 1986; IUCN, 2023a). However, early ambitions to retain 90% of founder genetic diversity in *ex situ* populations for 200 years (Soulé et al., 1986), were soon found to be unrealistic, given insufficient space and resources in the global zoo estate (Hutchins, 1995; Lees and Wilcken, 2009; Alroy, 2015; Powell, 2019). Indeed, zoos have been reducing the number of species in their collections in recent decades (Brereton and Brereton, 2020), with some arguing for a more restricted 'Promise List' of species that zoos can be confident that they can conserve *ex situ* for the long-term (Powell, 2019). Currently, decisions on which species are targeted for *ex situ* management are normally made at the regional scale, with Taxon Advisory Groups (TAGs) designing regional collection plans (RCPs) that make *ex situ* management recommendations in line with IUCN guidelines (IUCN, 2014) and the 'One Plan' approach to species conservation (Byers et al., 2013). While these RCPs follow an explicit five-step evaluative process (IUCN, 2014; Traylor-Holzer et al., 2019), decisions at each stage are largely based on expert opinion and may lack empirical data. While not intended to replace valuable expert input, systematic conservation planning approaches based on quantitative data can provide additional insights and assist evidence-based collection planning decisions, and help balance potential trade-offs between collection attractiveness and conservation priorities (Fa et al., 2014).

Here, I apply systematic conservation planning and prioritisation approaches (Margules and Pressey, 2000; Hanson et al., 2019) to zoo collections at global and regional (Britain and Ireland) scales. Using this approach, I show how collections must pro-actively adapt to avoid being outpaced by climate and land use change. However, species attractiveness to zoo visitors is a key concern in collection planning and a driver of zoo visitation, gate receipts and financial contributions to conservation (Fa et al., 2014; Mooney et al., 2020; Chapter 6). By bringing together information on species' projected threat status and phylogenetic distinctiveness (EDGE scores, Gumbs et al., 2023; Chapter 3), estimated attractiveness (Chapter 6), spatial requirements, and probability of persistence in zoos and in the wild, I provide the first application of exact integer linear optimisation algorithms (Schuster et al., 2020) to strategic zoo collection planning. First, I provide a novel application of conservation project prioritisation to simulate optimal collections at a global scale. I then provide more granular optimisations at the level of individual exhibit spaces for a subset of 105 BIAZA (British and Irish Association of Zoos and Aquaria) zoos, using a purpose-built, bespoke R package developed as part of this research (Hanson, unpublished; Appendix E). The findings presented here provide unique and novel insights into strategic zoo collection planning under future environmental change, providing invaluable information to zoo curators and managers to maximise their long-term contributions to international biodiversity conservation targets.

Methods

Global Collection Optimisation

In Chapter 4 I deployed spatial conservation prioritisation algorithms (Hanson et al., 2020) to identify spatial priorities for *in situ* area-based conservation (Maxwell et al., 2020). Here, I optimise global zoo collections under current and future climate and land use conditions, using a non-spatial conservation project prioritisation framework in the R package *oppr* (Hanson et al, 2019). *oppr* uses exact integer linear programming (Schuster et al., 2020) to find truly optimal solutions to problems of resource allocation between large sets of potential conservation projects, balancing trade-offs between project costs, probability of success and potential conservation benefits (Hanson et al., 2019). I adapt the *oppr* framework such that each species is recast as a conservation 'project' at different threshold population sizes, each with an associated probability of population persistence and estimated costs given the spatial requirements of housing the species at each threshold population size. Whereas spatial prioritisation optimises the selection of spatial 'planning units' each with associated costs and features (e.g. species) of conservation value, this approach instead considers zoos as a blank slate to be populated with the optimal combination species to maximise the conservation and attraction value of collections, given current constraints of the global zoo estate.

Candidate species

Pilot testing of zoo collection optimisations in *oppr* revealed that the full dataset (all global zoos, all terrestrial vertebrates) was too large to find an optimal solution, even when using high-performance computing and state-of-the-art Gurobi optimisation software (www.gurobi.com). I therefore divided species into three broad taxonomic clades (mammals, birds, and herpetofauna [reptiles and amphibians]) and optimised each clade separately. While this means that the total zoo exhibit space committed to each clade is fixed at current levels, it also adds a level of realism in that many zoo exhibits cannot be easily adapted to house different taxa. For example, many ectothermic reptiles and amphibians require specialist environmental conditions and cannot simply be exchanged with large, endothermic mammals with large outdoor paddocks. Furthermore, this division reflects the typical curatorial management structure of most zoos, with curatorial teams often divided between mammal, bird and ‘lower vertebrate’ (reptiles, amphibians, fish) sections.

For non-chiropteran terrestrial mammals, I had complete trait data (and therefore attractiveness estimates, see Chapter 5) for 2,620 species, and I did not have to filter this dataset. The highly speciose bird and herpetofauna clades, however, were still too large for efficient optimisation. As a result, I filtered these clades to only include species that were a) currently held in global zoo collections; b) on any of the ‘borderline’, ‘research’, ‘watch’, or ‘EDGE’ lists based on my EDGE calculations (Gumbs et al., 2023; Chapter 3); or c) either a current flagship species or a potential flagship ‘Cinderella’ species based on my trait-based estimates of species attractiveness (Smith et al., 2012; Chapter 6). This resulted in a final set of 5,046 candidate herpetofauna and 5,463 candidate birds to include in my optimisations.

Persistence probabilities

The *oppr* optimisation algorithm accounts for the probability of project success, which in this case is the probability of a species persisting under *ex situ* conservation. It also adjusts for the baseline probability of success, which in this case is the probability of the species persisting in the absence of *ex situ* conservation. For the baseline probability of success, I estimated the probabilities of species persistence for *in situ* populations using the inverse of species extinction probabilities used in the calculation of species EDGE scores (Chapter 3; Gumbs et al., 2023). These *in situ* persistence probabilities therefore represented probability of persistence if species were not to be conserved in zoo collections.

To estimate probabilities of population persistence for species in zoos at different threshold population sizes, I obtained species life history data from the Species360 Demographic Species Knowledge Index (DSKI; Condé et al., 2019). These life history data included: estimates of species’ age at first reproduction (AFR), lifespan (y), adult survival, juvenile survival, litter/brood size, and number of litters per year. Missing data were, where possible, phylogenetically imputed to find estimated means and standard deviations of imputed trait values. Phylogenetic imputation was inappropriate for some traits among less well-studied taxa (e.g. juvenile survival among Amphibia), and traits with fewer than 50 species records were fixed at a typical mean value given the limited data available, with large standard deviations set manually to reflect this uncertainty (see Appendix E for details). For each species I then generated 1,000 estimates of each trait, randomly sampling from a normal distribution based on imputed trait means and standard deviations. I then ran 1,000 population viability analyses (PVAs) for each species in the *popbio* R package (Stubben and Milligan, 2007) using these estimated trait values.

I first simulated a large starting population with 1,000 juvenile and 1,000 adult individuals, and simulated up to 1,000 years into the future until a stable population structure was reached, to find the optimal ratio of juveniles and adults. I then ran each of my 1,000 PVA iterations from this stable state ratio at initial population thresholds of 14, 42, 70, 140, 350, 700 and 1,400 individuals. These thresholds represent the absolute population sizes (N) required for effective population size (N_e) thresholds of 10, 30, 50, 100, 250, 500, and 1,000, respectively, under optimal genetic management and the highest N/Ne ratios reported in the literature (Willis and Wiese, 1993; Frankham et al., 2002; WAZA, 2011). Estimating population persistence thresholds of 140 and below were necessary for exhibit-specific optimisation for BIAZA zoos (see below). However, an N_e of 100 or below incurs limited inbreeding depression (Frankham et al., 2014) and even an N_e of 120 is only sustainable with regular supplementation with wild founders (Lacy, 1987; WAZA, 2011). Only population thresholds of 350, 700, and 1,400 (N_e of 250, 500 and 1,000) were therefore retained for global collection optimisation.

For each species, I then calculated the rate of population failure (populations fall below 10 individuals) across the 1,000 PVA iterations and a 100-year time horizon (Powell, 2019). Following this process, I combined *in situ* and *ex situ* persistence probability estimates, such that if a species had *in situ* and *ex situ* persistence probabilities both of 50%, the ‘probability of success’ for including this species in zoos would therefore be 75%, adjusted for the baseline persistence probability (Hanson et al., 2019). This calculation can be expressed as $P = 1 - p_i p_e$ where P is the total baseline-adjusted probability of persistence, p_i is the probability of population failure (extinction) *in situ* and p_e is the probability of population failure *ex situ.*

Species spatial requirements

Each species at each threshold population size was associated with an estimated overall ‘Project Cost’, which represented the total exhibit space (m^2) required to house a population of the given size in zoos. First, I obtained areal exhibit space requirements from published guidelines from the European Association of Zoos and Aquaria (EAZA), the Association of Zoos and Aquaria (AZA) in North America, the Australian Society of Zookeeping (ASZK), and a thorough search of additional grey literature (Supplementary Data S5). This provided data on spatial requirements for housing species at recommended group sizes at a range of taxonomic levels, from species-level to broad polyphyletic clades, such as Insectivora. Across all taxonomic levels, this process provided spatial requirement estimates for 1,645 mammal, 1,700 birds, 6,392 amphibians (including guidelines for ‘small, terrestrial frogs’, which covered 5,982 species) and 181 reptiles. I then imputed missing data by assigning spatial requirements to closely related species of similar size and ecology (Supplementary Data S6). Given the limited data on reptilian spatial requirements, when imputing missing data I scaled reptile spatial requirements by species’ body length, such that a species’ spatial requirements could still be informed by related species, even if they differed greatly in size.

I obtained existing zoo collection data from the Species360 Zoological Information Management System (ZIMS, zims.species360.org), and extracted the median group size for each species in zoos, which I classed as the number of adult individuals per institution. After filtering some non-zoo institutions such as university collections and research centres, the Species360 ZIMS database included 1,128 institutions across 92 countries holding at least one terrestrial vertebrate species. To estimate the median group sizes that would be necessary to house species that are not currently held in zoos, I used the median group size of species of the same genus, family, order and class, sequentially, until all missing data were filled. I then calculated the overall cost of maintaining a species of a given threshold population size by multiplying the spatial requirements of a typical (median) group size by the required multiplier to reach the threshold population size.

‘Budget’: Total zoo exhibit space

Armed with data on species spatial requirements and median (and, where expressed in published guidelines, maximum) group sizes, I was then able to estimate the overall exhibit area committed to terrestrial vertebrates across all Species360 zoos globally. Some zoos will have multiple exhibit spaces housing the same species, and some of the group sizes in the zoo holdings data (given as per-institution population sizes in Species360) exceeded maxima recommended in published guidelines. Here, I divided such large groups within a single institution into sub-groups (representing separate exhibit spaces) based first on a) maximum recommended group size, where available, followed by b) the median per-institution group size for the species. I therefore assumed exhibit spaces and group sizes for each species were relatively consistent across institutions and were within recommended guidelines (Supplementary Data S5). Following this subdivision of large groups, I recalculated and summed the exhibit space required to house all (sub-)groups of each species in each institution to derive an overall ‘budget’ (total exhibit space) available for mammals, birds and herpetofauna in global zoos.

Species weights and objectives

In *oppr*, I set my optimisations to maximise weighted species richness using the ‘add_max_ richness_objective’ function. This objective aims to maximise the weighted persistence of all species, given the expected additional persistence benefit of inclusion in the solution (relative to baseline) and the weightings assigned to each species, which were either species’ EDGE scores, their estimated attractiveness, or a combined weighting that incorporates both measures at an optimal trade-off threshold value calculated using Cohon’s penalty (Cohon, 1979; see below). For full mathematical formulation of this objective, see Appendix E.

I formulated my optimisations to maximise both the amount of threatened evolutionary history expected to persist due to zoo collection optimisation as well as the overall attractiveness of collections, within the budget (set as the total exhibit space currently available in zoos for each clade). In Chapter 3, I describe the calculation of species EDGE scores under current conditions, and under future climate and land use change scenarios. I therefore ran optimisations based on species’ current estimated EDGE scores and their projected EDGE scores for 2070 under a ‘middle-of-the-road’ warming scenario of SSP2-4.5, as well as the more severe SSP5-8.5 scenario, the latter representing continued fossil fuel-based development (Riahi et al., 2017). A species’ EDGE score represents the amount of threatened evolutionary history that would be expected to be lost should the species go extinct, given its evolutionary distinctiveness and the number and extinction probability of close relatives (Gumbs et al., 2023). In Chapter 6, I developed trait-based predictive models of species attractiveness to zoo visitors, for 24,750 species with full trait data available. The EDGE scores and attractiveness estimates were used as feature weights in collection optimisations.

For each clade (mammals, birds, herpetofauna) and climate scenario (current conditions, SSP2-4.5, SSP5-8.5), I first ran an optimisation maximising EDGE-weighted richness, followed by an optimisation maximising attractiveness-weighted richness, specifying an optimality gap of 0 to ensure the optimal solution was found. To combine these two variables into a single weighting, I then calculated Cohon's penalty (Cohon et al., 1979; Ardron et al., 2010) to produce an overall weighting at the optimum trade-off threshold between both variables. The new weighting W, after accounting for Cohon's penalty C, is calculated as:

Eqn. 1a: $$C = \left|\frac{p_1w_1 - p_2w_1}{p_1w_2 - p_2w_2}\right|$$

Eqn. 1b: $$W = w_1 + Cw_2$$

Where w_1 is the first weighting variable and w_2 is the second weighting variable, and p_1w_1 is the persistence-weighted sum of w_1 under the first prioritisation, p_1w_2 is the persistence-weighted sum of w_2 under the first prioritisation, and so on.

Finally, I ran a third optimisation for each clade/scenario using the combined EDGE and attractiveness weighting W, having calculated the optimum Cohon's penalty trade-off threshold between the two variables. All optimisations were run using the Durham University Hamilton high-performance computer and Gurobi optimisation software (v10.0.2).

Exhibit-Specific Optimisation for BIAZA Zoos

While the optimisation process described above provides a global perspective on what the international zoo community might be able to achieve under systematic optimisation of their collections, a potential weakness of the approach is that it treats each population as a single 'project' or unit, and does not account for the distribution of species and individuals between institutions and specific exhibit spaces. The structural design and architectural heritage of any zoo estate can be a significant constraint on curatorial decision-making (Krause and Robinson, 2022), and *ex situ* populations are more commonly managed at regional rather than global scales through regional global collection plans (WAZA, 2019; Traylor-Holzer et al., 2019). To account for these factors, I produced an additional set of collection optimisations at a more granular, exhibit-specific level, for a limited set of 105 British and Irish (BIAZA) zoos. This approach assumes that the BIAZA zoos cannot exchange individuals with, for example, other

European (EAZA) institutions. We imposed this restriction because the vast number of potential solutions when considering a larger number of zoos made optimisation impractical.

zooptimal formulation

To run these exhibit-specific optimisations, I used a bespoke R package developed by Dr Jeffrey Hanson (https://jeffrey-hanson.com) called *zooptimal*, designed for this exact purpose (Hanson, unpublished). *zooptimal* is a multi-objective mixed integer linear programming algorithm which assigns species to individual exhibits that are of appropriate dimensions to house a typical group size of the species, and calculating the probability of population persistence as the total population size across all zoos incrementally increases. *zooptimal* follows a lexicographic approach to multi-objective prioritisation: first, the prioritisation solves to maximise weighted species richness, accounting for species attractiveness/EDGE weights and persistence probabilities, as described for *oppr*. Next, to prevent excessive numbers of a species amassing in a single zoo, and to ensure a relatively even spread of the attractiveness benefits of housing charismatic species, the prioritisation then solves for a secondary objective that maximises summed per-species richness across all zoos. For a complete description of the mathematical formulation of the *zooptimal* algorithm, see Appendix E.

Persistence probabilities

Species persistence probabilities at the threshold population sizes of 14, 42, 70, 140, 350, 700, and 1,400 were previously calculated using PVAs for global collection optimisation in *oppr*. To estimate species persistence probabilities at intermediate population sizes between these thresholds, I fit asymptotic curves to the threshold estimates using the *aomisc* R package (Onofri, 2020), adding an additional data point of 0 probability of persistence at a threshold population size of 0. While *zooptimal* has the functionality to calculate changes in persistence probability from the addition of one individual to the population, this results in extremely complex calculations that make processing time impractical. Therefore, I retained the threshold population sizes of 0, 14, 42, 70 and 140, and then extracted estimates from the asymptotic curves for further threshold population sizes rising in increments of 140, up to a maximum of 1,400. This resulted in a more granular set of 14 threshold population sizes (and associated persistence probabilities) for each species compared to the global optimisation using *oppr*. The *zooptimal* prioritisation assigns species persistence probabilities based on the highest population size threshold exceeded, such that a population of 150 individuals will be assigned the persistence probability of the 140 population size threshold, and so on.

Assigning appropriate enclosures to species

Earlier analysis using *oppr* provided estimates of species exhibit requirements and exhibit sizes for global zoos, which I filtered to only include BIAZA institutions. Candidate species followed the same selection criteria as defined for the global optimisations. I then identified, for each candidate species, which exhibits in BIAZA zoos were large enough to house the median group size of the species, ensuring exhibits could only be assigned to species of the same clade as their current occupants (e.g. current aviaries can only house birds in alternative scenarios). I further constrained exhibits over 2 m^2 in area to only be assigned to species whose spatial requirements were at least 75% of the exhibit space. This prevented wasted exhibit space by, for example, very small species being placed in large paddocks, while simultaneously constraining the number of unrealistic solutions and reducing processing time.

Optimisation scenarios

I ran exhibit-specific optimisations for BIAZA collections for each clade (mammals, birds, herpetofauna) and climate scenario (current conditions, SSP2-4.5, SSP5-8.5) separately, as per the global collection optimisations. Hence, I first ran optimisations maximising EDGE-weighted richness, followed by an optimisation maximising attractiveness-weighted richness, specifying an optimality gap of 0 to ensure the optimal solution is found. I then found the optimum trade-off threshold between the two weighting variables using Cohon’s penalty (Cohon et al., 1979) and reran a final optimisation maximising both collection attractiveness and threatened evolutionary history across BIAZA collections.

Results

Global Collection Optimisation

Existing collections

Of the 5,104 species included in the 1,128 global institution collections, 1,038 (20.3%) belong to an IUCN Red List threatened category (Vulnerable, Endangered, Critically Endangered, Extinct in the Wild; Mace et al., 2008). 48.8% of global zoo exhibit space is committed to these threatened species, based on species' estimated spatial requirements. Here, I calculate the additional threatened evolutionary history conserved in zoos by multiplying species' EDGE scores by the additional persistence probability provided by *ex situ* populations. That is, the amount of threatened evolutionary history (MY) that would be expected to be lost in the absence of these *ex situ* populations. Existing global zoo collections currently conserve an additional 1,331 MY of threatened evolutionary history, which equates to just 3.2% of total threatened evolutionary history for terrestrial vertebrates. Of the additional 1,331 MY of threatened evolutionary history currently conserved in zoos, the majority (919 MY, 69%) can be deemed 'irreplaceable'. In this context, irreplaceability reflects the proportional role of zoos alone in facilitating a species persistence (Figure 1). For example, if a species had an *in situ* persistence probability of 50%, and a 50% persistence probability in zoos, zoo populations increase overall persistence probability from 50% to 75%, or 25 percentage points. Zoos would therefore contribute one third of the overall persistence probability for the species globally, with zoos providing irreplaceable conservation for one third of the threatened evolutionary history represented by the species.

Optimisation under current conditions

When the global zoo collection was optimised based on species current EDGE scores, this increased the amount of threatened evolutionary history protected almost six-fold to 7,950 MY, or 19.3% of total terrestrial vertebrate threatened evolutionary history. After weighting by persistence probability, global collection attractiveness also increased more than four-fold, from a summed attractiveness score (Chapter 6) of 3,776 in existing collections to 15,694 in optimised collections. Species attractiveness scores are a unitless metric equivalent to the average time (in seconds) zoo visitors are likely to spend viewing the species, including those who do not stop to view the species at all (0 seconds viewing time). See Chapter 6 for details. Therefore, existing global zoo collections do a poor job of approximating the total conservation value and attractiveness of an optimised collection, and significant adaptation of collection composition would be needed if zoos collections were to approach optimality, even before accounting for future environmental change (Figure 1).

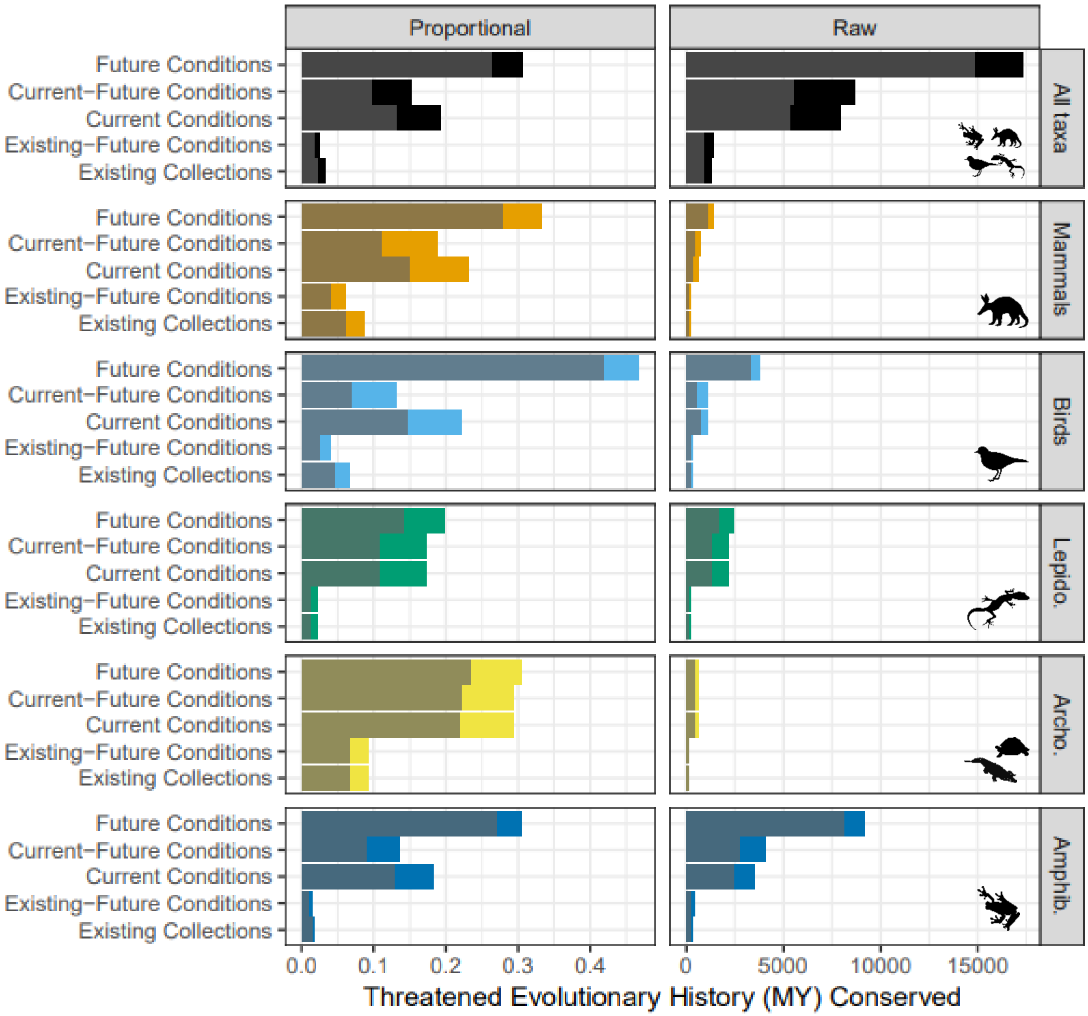


Figure 1. Additional threatened evolutionary history conserved in global zoos under collection optimisation. Bars represent the amount of additional threatened evolutionary history (MY) expected to persist over 100 years given the persistence probability of zoo populations and wild populations. Wild persistence probability is the inverse of the probability of extinction given species Red List status, as calculated for species EDGE scores (Gumbs et al., 2023). Estimates are given for all taxa combined (top panels) and for each clade, with the proportion of evolutionary history conserved in each clade given in the left column, and absolute totals (MY) in the right column. Grey-shaded areas of each bar represent the irreplaceability of zoo collections in terms of their contribution to species overall persistence. Bars represent estimates for existing zoo collections 'Existing Collections', optimised collections using species current EDGE scores 'Current Conditions', and projected future EDGE scores for 2070 under SSP2-4.5 'Future Conditions'. 'Existing-Future Conditions' and 'Current-Future Conditions' represent the change in evolutionary history conserved when species' future EDGE scores are assigned to existing collections and collections optimised under current conditions, respectively.

However, the solution generated under current conditions is also likely to be suboptimal when future impacts of climate and land use change on species extinction risk is considered. After assigning species' projected future EDGE scores (year 2070 under SSP2-4.5) to the solution produced using species current EDGE scores, the proportion of threatened evolutionary conserved falls by more than a fifth (21.2%), despite a modest increase in the absolute amount of threatened evolutionary history conserved (Figure 1). This is because species EDGE scores are generally projected to increase as climate and land use change threatens ever-more branches of the vertebrate tree of life (Chapter 3). The reduction in the *ex situ* conservation value of global zoo collections optimised under current conditions, when considering environmental change, is most stark for birds, amphibians, and mammals, with proportional threatened evolutionary history conserved falling by 40.7%, 25.8% and 18.6%, respectively (‘Current-Future Conditions’, Figure 1). This reaffirms the urgent need to build resilience to projected environmental change into global zoo collection planning.

Climate-proof global zoo collections

When optimising global zoo collections under future conditions (year 2070, SSP2-4.5), the amount of additional threatened evolutionary history conserved in zoo collections rises by more than an order of magnitude relative to existing collections, to 17,379 MY, of which 14,814 MY (85%) would be irreplaceable (‘Future Conditions, Figure 1). Under this scenario, zoos would conserve 30.7% of the projected total of 56,504 MY of threatened evolutionary history for terrestrial vertebrates globally, providing a vital contribution to global biodiversity conservation and directly addressing Target 4 of the Kunming-Montréal GBF. Simultaneously, this optimisation increases the summed attractiveness scores of global zoo collections by more than six-fold to 22,953, relative to existing collections, demonstrating that adapting zoo collections to maximise conservation value in the face of global environmental change need not come at the expense of zoos’ abilities to house charismatic species that drive visitation and gate receipts (Fa et al., 2014; Mooney et al., 2020).

Global zoo collection optimisation under future environmental conditions would require considerable compositional turnover in vertebrate collections (Figures 2 & 3). The most significant compositional changes occur in herpetofauna collections, with increasing coverage of frogs and lizards at the expense of large-bodied crocodilians (Figures 2 & 3). At the family level, there were also significant changes in the number of species represented in some mammal and bird families, ranging from a decrease of 121 species in ducks (Anatidae) to an increase of 285 species in the highly speciose voles, hamsters and allies (Cricetidae; Figure 2a). Considering family representation in zoo collections proportional to species richness (Figure 2b), increases in representation occur most often in mammals, but are common across

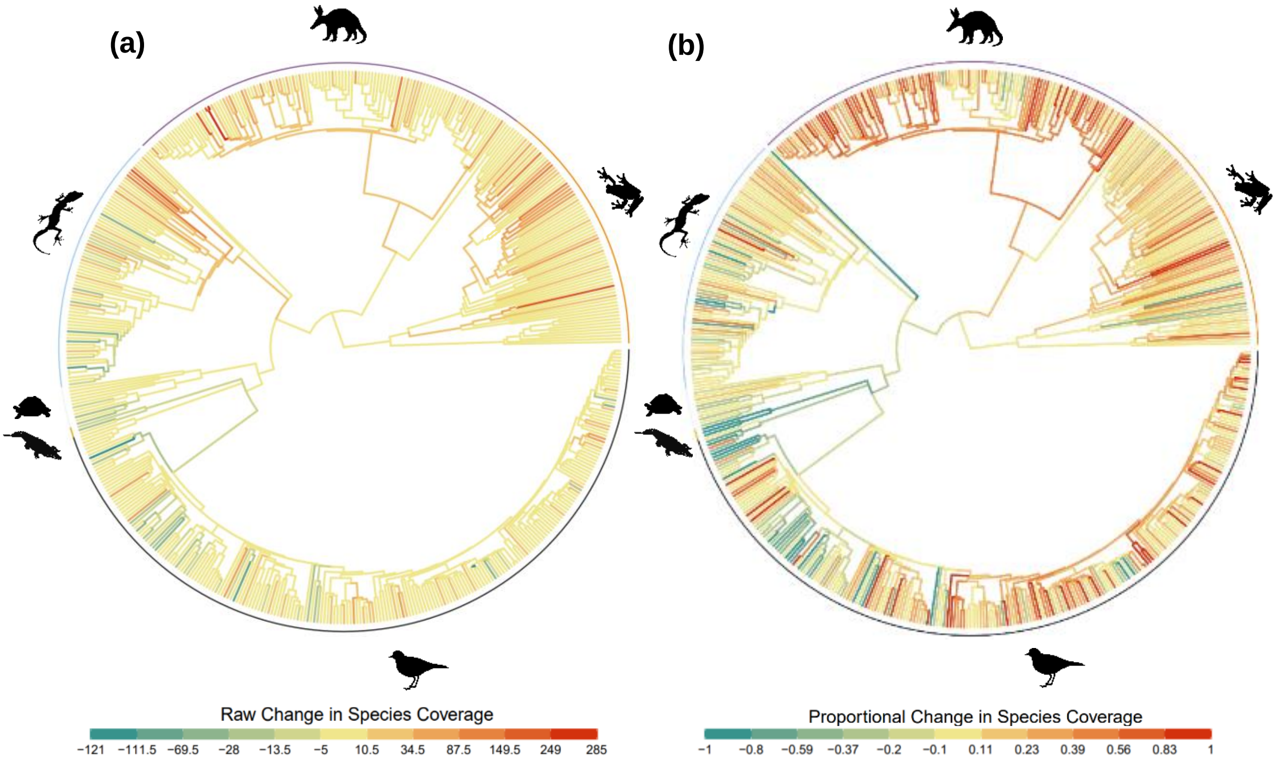
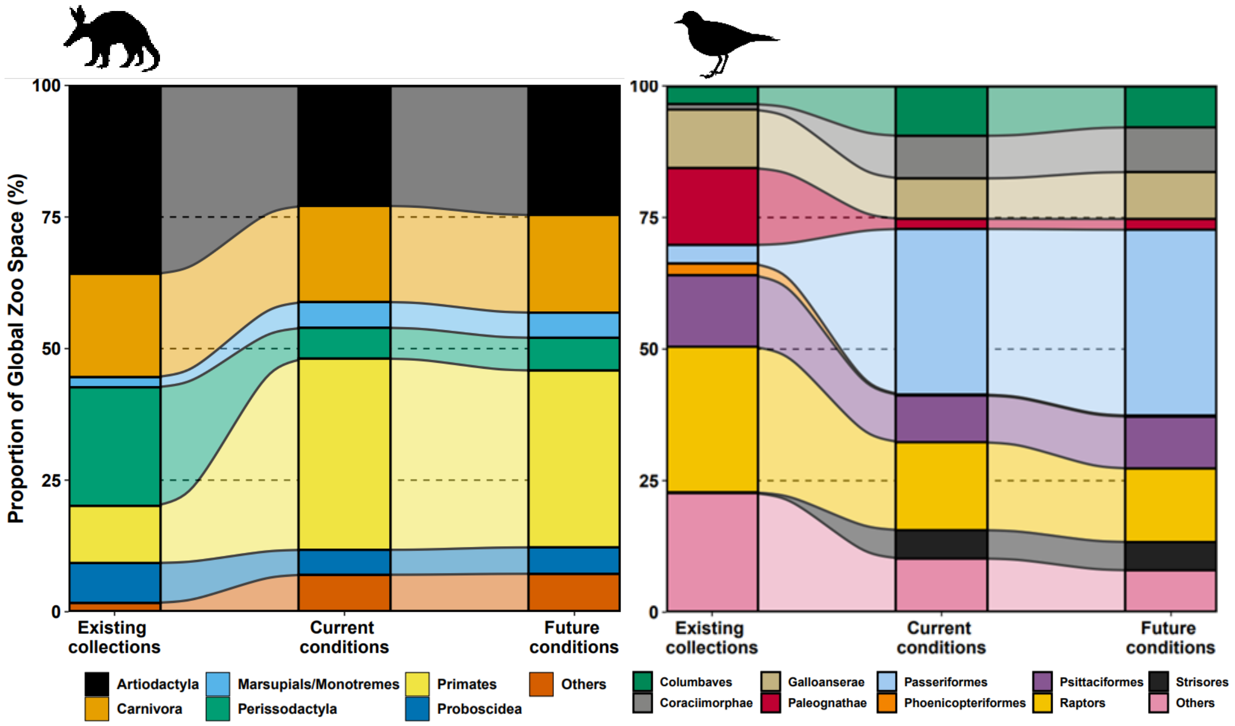


Figure 2. Change in the phylogenetic distribution of species representation in optimised global zoo collections under future environmental conditions. The phylogenetic tree on the left (a) shows the summed change in species coverage (number of species per family represented in global zoo collections) between existing collections and optimised collections under 'middle-of-the-road' warming scenario of SSP2-4.5, for the year 2070. The tree on the right (b) shows the change in the proportional coverage of species under global collection optimisation (0 = no change, -1 = all species removed, +1 = all species added to collections).

the vertebrate tree of life (Figure 2b). Increases in representation were strongest for small-bodied mammal species, whilst the representation of larger-bodied mammal lineages were not adversely affected (Figure 2a). However, this move towards smaller-bodied species significantly reduced the representation of some larger-bodied bird and reptilian lineages (Figure 2b), especially among crocodilians (Crocodylia), pythons (Pythonidae), and monitor lizards (Varanidae), as well as large birds such as cranes (Gruiformes), storks (Ciconiiformes), and ibises and spoonbills (Threskiornithidae). This is despite these larger species generally being more attractive to visitors (Chapter 6).

Changes in the division of global zoo exhibit space between taxonomic clades reveals similar patterns, where the proportion of exhibit space committed to generally large-bodied clades is reduced under global collection optimisation (Figure 3). In line with changes in species representation, there are significant reductions in exhibit space committed to crocodilians and large birds such as ostriches, rheas, and cassowaries (Paleognathae). Significant reductions



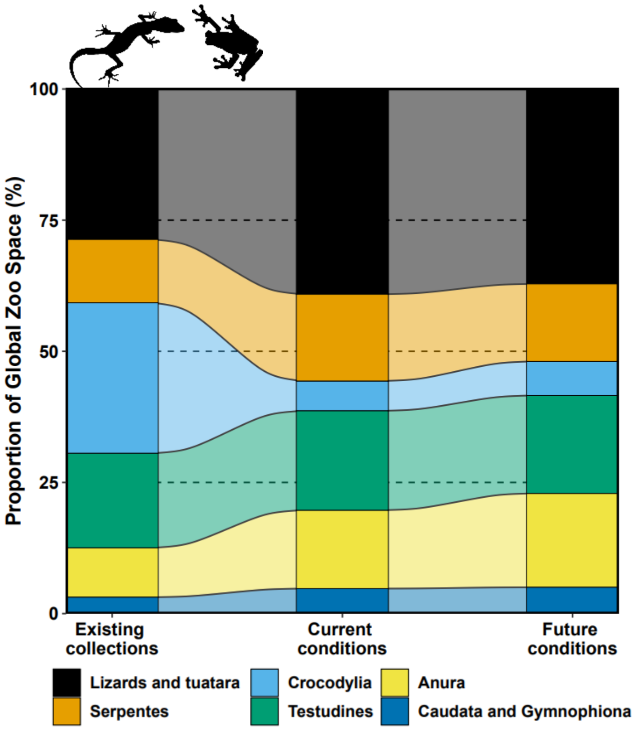


Figure 3. Change in the proportion of zoo exhibit space committed to broad taxonomic clades. Stacked bar charts show the proportion of zoo exhibit space committed to major clades of mammals (top left), birds (top right) and herpetofauna (bottom left) in existing collections (left bars), collections optimised under current conditions (middle bars) and collections optimised under future conditions and a 'middle-of-the-road' warming scenario. (SSP2-4.5; right bars). Shaded areas indicate the trend required to reduce/expand coverage of the clade between scenarios. Dashed lines indicate 25%, 50% and 75% intercepts on the y axis.

in exhibit space are also suggested for odd-toed (Perissodactyla) and even-toed (Artiodactyla) ungulates (Figure 3), a pattern that was not detected by simple measures of species presence/absence in zoos (Figure 2). Using recommended exhibit sizes, I estimate that 49.4% of the 2,952 ha of existing global zoo exhibit space for mammals is currently committed to ungulates, a figure that almost halves (26.2%) following collection optimisation under future conditions. By contrast, the proportion of global mammal exhibit space committed to primates would triple in extent (from 9.2% to 28.5%; Figure 2).

Exhibit-Specific Optimisation of BIAZA Collections

Existing collections

As of 2023, 105 institutions were members of the British and Irish Association of Zoos and Aquaria (BIAZA), according to the Species360 ZIMS database. After correcting for species persistence probabilities, these 105 zoos conserve an additional 797 MY of terrestrial vertebrate evolutionary history that would be expected to be lost in the absence of *ex situ* populations. This is equivalent to just 1.95% of the total threatened evolutionary history for terrestrial vertebrates globally (Figure 4). That said, BIAZA zoos alone conserve more than half of the total threatened evolutionary history in zoos globally, highlighting their value to global *ex situ* conservation. However, this also indicates a potentially high level of redundancy in collections, which may represent opportunities for further optimisation of collections. BIAZA institutions are also taxonomically biased in the threatened evolutionary history currently conserved in their collections, with 6.1% of mammal threatened evolutionary history conserved, compared to just 0.64% of amphibian threatened evolutionary history (Figure 4).

Optimisation under current and future conditions

Exhibit-specific optimisation of BIAZA collections under current conditions more than doubles the amount of additional threatened evolutionary history conserved to 1,770 MY, of which 1,290 MY (73%) is irreplaceable (Figure 4). This level of increase is consistent across all taxonomic groups other than crocodiles and turtles (Archosauromorpha) which sees a more modest increase relative to existing collections. As with global zoo collection optimisation, however, these considerable gains are vulnerable to future climate and land use change. Under future change projections, the proportion of vertebrate threatened evolutionary history conserved in BIAZA zoos falls from 4.32% to 3.18%, a proportional fall of 26.4% (‘Current-Future Conditions’, Figure 4). Bird collections optimised for current conditions were most susceptible to future environmental change, with the proportion of avian threatened evolutionary history conserved falling by almost half (48.2%) when species’ future EDGE scores were assigned to this solution (Figure 4, left column). By contrast, estimates for reptiles

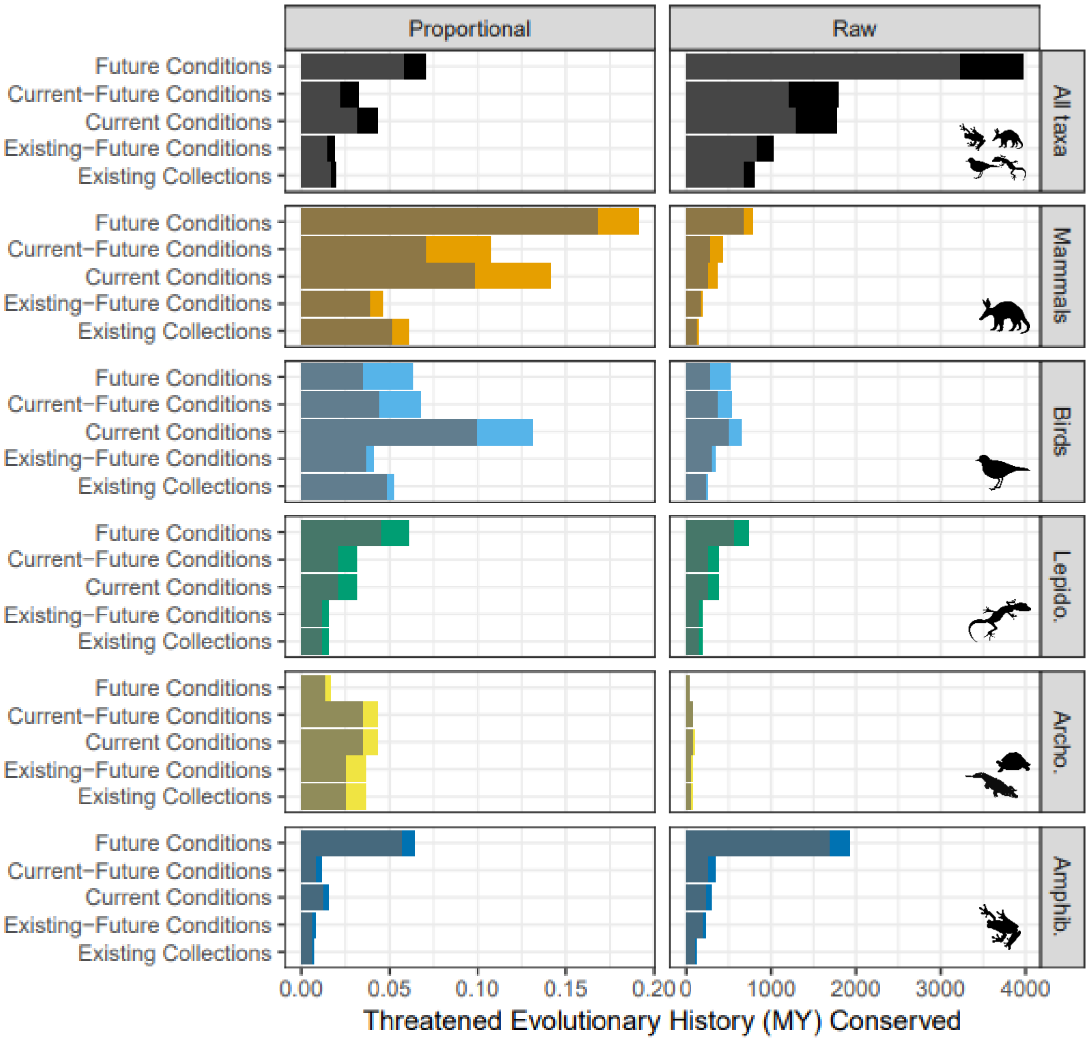


Figure 4. Additional threatened evolutionary history conserved in BIAZA zoos under exhibit-specific zoo collection optimisation. Bars represent the amount of additional threatened evolutionary history (MY) expected to persist over 100 years given the persistence probability of zoo populations and wild populations, and grey-shaded of each bar represent the irreplaceability of zoo collections' contribution to species overall persistence, as per Figure 1. Estimates are given for all taxa combined (top row) and for each clade in subsequent rows, with the proportion of evolutionary history conserved in each clade given in the left column, and absolute totals (MY) in the right column.

(Lepidosauria and Archosauromorpha) remained relatively stable, suggesting a reduced sensitivity to environmental change for reptilian collections optimised under current conditions.

When optimising BIAZA collections while accounting for species' future EDGE scores, total additional threatened evolutionary history conserved in BIAZA zoos increased to almost four billion years (3,977 MY), of which 3,231 MY (81.2%) is considered irreplaceable (Figure 4). This represents a more than five-fold increase relative to existing collections, with future-optimised BIAZA zoos conserving 7% of total vertebrate threatened evolutionary history globally. The greatest gains are seen in mammals (153 MY to 778 MY, a five-fold increase) and amphibians (124 MY to 1,918 MY), which would see a remarkable 15-fold increase in threatened evolutionary history protected, after correcting for population persistence probabilities. By contrast, the absolute and proportional amount of threatened evolutionary history conserved for birds fell when collections were optimised for future conditions relative to current conditions (Figure 4). The only possible explanation for this result is the statistical threshold used to optimise Cohon's penalty between attractiveness and EDGE weightings, which differed for each optimisation scenario. The amount of crocodile and turtle (Archosauromorpha) threatened evolutionary history was also lower than conserved in existing collections following optimisation (Figure 4). This latter result may be explained by the fact that crocodiles and turtles were included alongside amphibians and other reptiles in the herpetofauna collection optimisation, with crocodile and turtle exhibit space largely recommitted to lizards and tuatara and, indirectly, frogs (Figure 6).

Phylogenetic shifts in collection composition

In contrast to global collection optimisation, BIAZA collections optimised for future conditions saw increases in absolute representation of amphibian families more commonly than other taxa (Figure 5a). However, when correcting for species richness of each lineage, the greatest proportional increases in coverage occur in mammals, although there is greater variability among mammal families in the BIAZA optimisation compared to the global optimalisation (Figure 5b). Specifically, in this optimisation, increases in proportional representation are particularly concentrated in marsupial families, while some other mammalian lineages see a reduction in representation. Such reduced representation is observed among camels (Camelidae), horses (Equidae), tapirs (Tapiridae), and even some carnivore lineages, such as bears (Ursidae). Among birds, particular increases in representation were found among tinamous (Tinamidae, +20 species, +42.6 % points) and several families of nightjars and potoos (Caprimulgiformes), owlet-nightjars (Aegotheliformes), frogmouths (Podargiformes), and hummingbirds, swifts and allies (Apodiformes; Figure 5). By contrast, representation of crocodilian and turtle lineages saw considerable declines in coverage in both absolute and proportional coverage (Figure 5), with particular reductions in alligator (Alligatoridae, -7 species, -87.5 % points) and crocodile (Crocodylidae, -9 species, -60 % points) families.

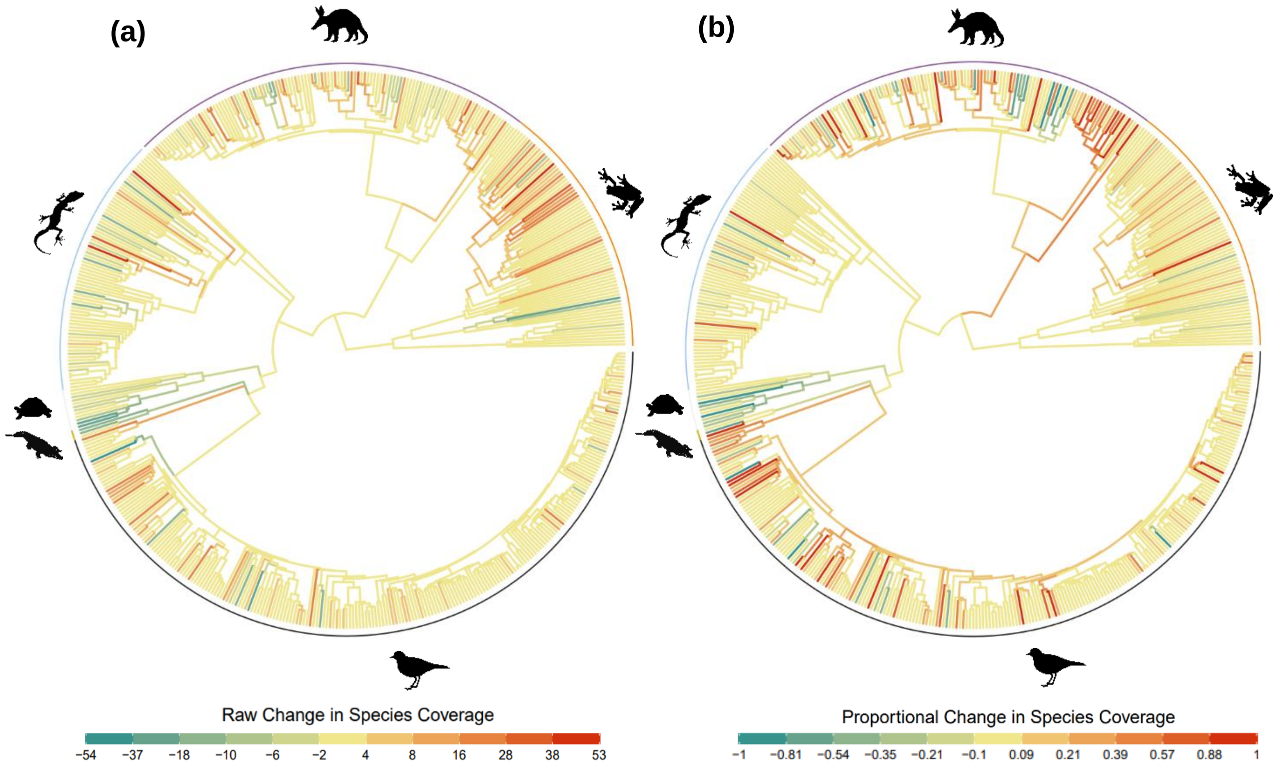


Figure 5. Change in the phylogenetic distribution of species representation in optimised BIAZA zoo collections under future environmental conditions. As per Figure 2, the phylogenetic tree on the left (a) shows the summed change in species coverage (number of species per family represented in global zoo collections) between existing collections and optimised collections under ‘middle-of-the-road’ warming scenario of SSP2-4.5. The tree on the right (b) shows the change in the proportional coverage of species under global collection optimisation (0 = no change, -1 = all species removed, +1 = all species added to collections).

Reallocation of BIAZA exhibit space

Unlike global optimisation in *oppr*, the *zooptimal* outputs allow the explicit identification of species being removed and added from each individual exhibit, revealing patterns not only in overall changes in the proportion of exhibit space assigned to different clades, but also the directionality of these changes (Figure 6). Among mammals, the largest proportional increases in BIAZA exhibit space committed to a clade was for primates, rising from 13.1% to 22.6% of the estimated 146.7 ha of mammal exhibit space in BIAZA zoos, with much of this increase coming from exhibits previously committed to carnivores and even-toed ungulates (Figure 6). This is despite the fact that the most common exchange between existing and optimised collections under future conditions was for exhibits previously committed to lemurs (Lemuridae) to be reassigned to rabbits and hares (Leporidae), with 104 such exchanges in the optimal solution. These apparently contradictory findings are explained by the less frequent

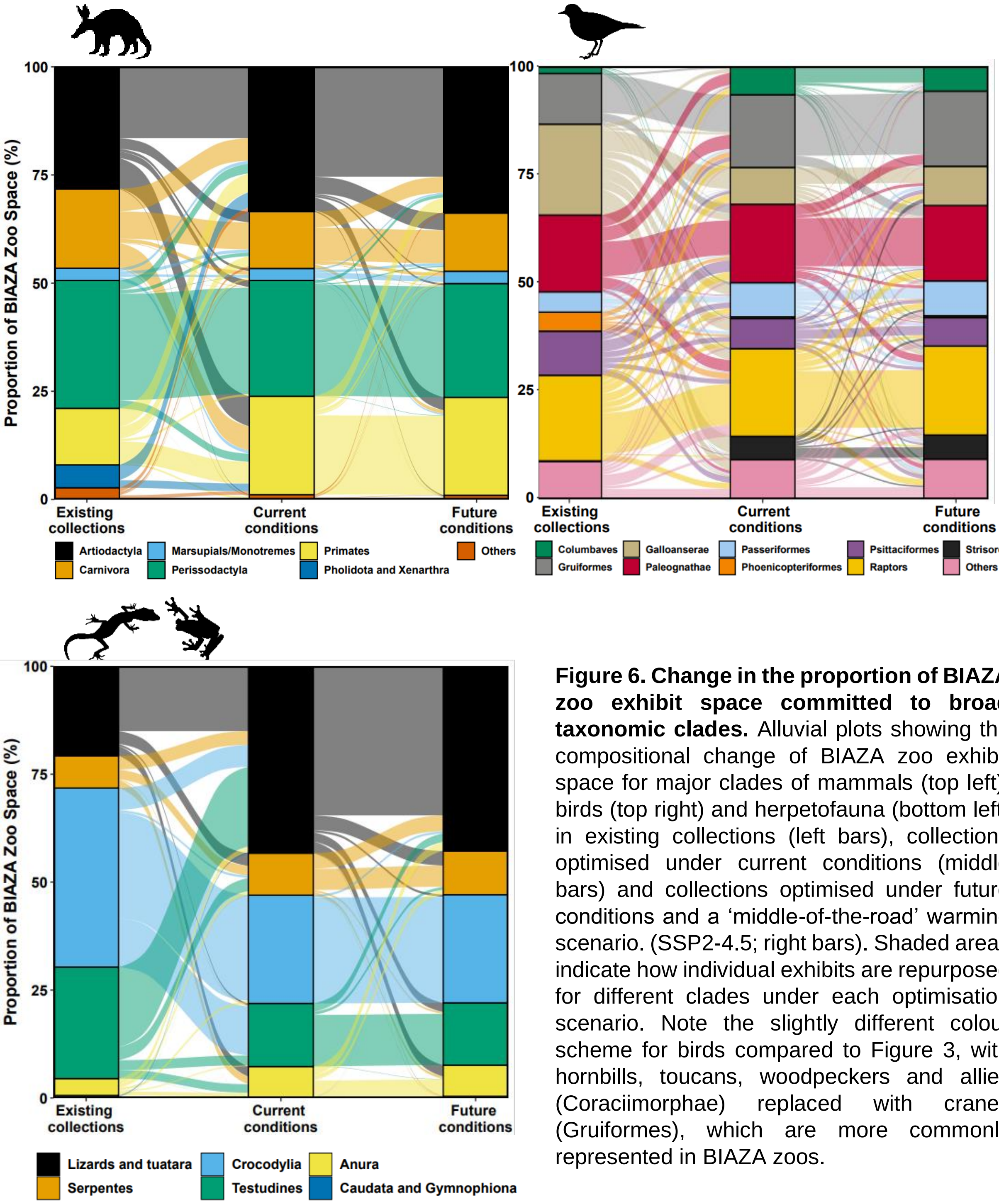


Figure 6. Change in the proportion of BIAZA zoo exhibit space committed to broad taxonomic clades. Alluvial plots showing the compositional change of BIAZA zoo exhibit space for major clades of mammals (top left), birds (top right) and herpetofauna (bottom left) in existing collections (left bars), collections optimised under current conditions (middle bars) and collections optimised under future conditions and a 'middle-of-the-road' warming scenario. (SSP2-4.5; right bars). Shaded areas indicate how individual exhibits are repurposed for different clades under each optimisation scenario. Note the slightly different colour scheme for birds compared to Figure 3, with hornbills, toucans, woodpeckers and allies (Coraciimorphae) replaced with cranes (Gruiformes), which are more commonly represented in BIAZA zoos.

but more consequential (in terms of exhibit space) exchanges towards large-bodied primate families such as apes (Hominidae, +6.8 ha) and old world monkeys (Cercopithecidae, +0.5 ha), in many exhibits currently housing cats (Felidae, 25 exchanges), capybara and other cavies (Caviidae, 19 exchanges), and deer (Cervidae, 15 exchanges).

Optimised bird collections saw particularly strong reductions in the proportion of exhibit space given over to waterfowl (Anseriformes), which saw reductions from 18.6% to just 6% of the estimated 17.8 ha of avian exhibit space in BIAZA zoos (Galloanserae, Figure 6). While waterfowl exhibits were transferred to a wide variety of other avian taxa (Figure 6), the most common exchanges were from ducks (Anatidae) to nightjars (Caprimulgidae, 102 exchanges), owlet-nightjars (Aegothelidae, 67 exchanges), and frogmouths (Podargidae, 64 exchanges). Another very frequent exchange was for exhibits currently housing ducks to be reassigned to parrots (Psittacidae, 93 exchanges). The most common exchanges in herpetofauna exhibits were from mantellas (Mantellidae) to glass frogs (Centrolenidae, 135 species), tortoises (Testudinidae) to tuatara (*Sphenodon punctatus*, Sphenodontidae, 56 exchanges), and colubrid snakes (Colubridae) to anoles (Dactyloidae, 35 exchanges). In terms of overall exhibit space, the general trend was away from crocodilians and turtles (Archosauromorpha) and towards lizards, tuatara, and frogs. Notably, however, there was also a significant transfer of crocodilian exhibit space towards turtles (Testudines), with almost all turtle exhibit space under optimised scenarios derived from exhibits currently housing crocodilians, while most exhibit space currently housing turtles repurposed for lizards and tuatara (Figure 6).

Discussion

My global zoo collection optimisations provide a broad overview of the potential conservation value of global collections under anthropogenic climate and land use change. Of course, to be effective in the real-world, such optimisations would require good genetic management of populations and unhindered transfer of species into zoos and between institutions. In this ‘all else being equal’ scenario, zoos could conserve over 17 billion years (more than 30% of the total) of threatened evolutionary history for terrestrial vertebrates under climate and land use change. Optimising global zoo collections in this manner increases the amount of threatened evolutionary history conserved by more than an order of magnitude (Figure 1), alongside a simultaneous six-fold increase in the total attractiveness of global collections. The regional collection optimisation for 105 BIAZA zoos provides a more granular assessment of how curators could tailor their collections to maximise conservation of threatened species (including those projected to become threatened in future) and key attractor species, taking into account physical constraints of the entire zoo estate (Krause and Robinson, 2022). Even in these

BIAZA zoos alone, collection optimisation would conserve an additional 4 billion years of threatened vertebrate evolutionary history, including a 15-fold increase in the amount of amphibian threatened evolutionary history conserved relative to existing collections. In both global and regional optimisations, more than 80% of the threatened evolutionary history conserved is 'irreplaceable', given the relative projected persistence probabilities of wild and zoo populations (Figures 1 and 4).

Optimal global and regional collection composition

In terms of conserving threatened evolutionary history for terrestrial vertebrates, existing collections perform poorly at both global and regional (BIAZA) scales, especially for highly speciose but highly threatened taxa such as amphibians and, to a lesser extent, snakes, lizards, and tuatara (Lepidosauria; Figures 1 and 4). This echoes previous findings (Condé et al., 2013; Biega et al., 2017; Jacken et al., 2020; Brereton and Brereton, 2020) that such taxa are poorly represented in zoos and that significant representation gaps remain, particularly for threatened Amphibia, despite modest recent advances in this area (Dawson et al., 2016; Chapter 2). Global collection optimisations led to a general move away from large-bodied taxa that demand significant amounts of exhibit space, towards more small-bodied taxa. This is particularly the case in herpetofauna collections, where the proportion of exhibit space committed to crocodilians decreased markedly, in favour of smaller-bodied frogs, lizards and tuatara (Figure 3). Similarly, in bird collections exhibit space for large-bodied paleognaths such as ostriches, rheas, and emus, and raptors (birds of prey) was reduced in favour of smaller-bodied songbirds (Passeriformes) and nightjars, owlet-nightjars, hummingbirds and swifts (collectively termed 'Strisores' in Figures 3 and 6).

These findings validate suggestions by Balmford et al. (1996) and Balmford (2000; c.f. Ward et al., 1998) that *ex situ* conservation breeding programmes could become more efficient with a greater focus on smaller-bodied species with lower spatial requirements. While large mammals are key attractor species for zoo visitors (Moss and Esson, 2010), and mammal body mass and species richness are positively associated with visitation rates (Mooney et al., 2020), my findings are the first to explicitly quantify the trade-off between species attractiveness and conservation priority weightings (EDGE scores) across all terrestrial vertebrate taxa. My results suggest that the current focus on large-bodied charismatics may prevent zoos' from reaching their full conservation potential, at least when considering collections at a global scale.

The more granular, exhibit-specific optimisations of BIAZA collections reveal a more complex situation with regards to species body size, spatial requirements, and collection optimality (Figure 6). For mammals, larger-bodied taxa did not see the same reduction in proportional exhibit space in optimised global collections (Figure 3), with the proportion of BIAZA exhibit space committed to ungulates, for example, increasing under future conditions (Figure 6). Among primates in particular, the net reduction in the number of BIAZA exhibits committed to smaller primate families such as lemurs (Lemuridae) and marmosets and tamarins (Callitrichidae) contrasted with the net increase of 6.84 ha in exhibit space committed to apes (Hominidae). This is despite there being a small overall reduction in ape richness (-2 species), but no reduction in lemur or callitrichid richness in optimised BIAZA collections under future conditions. Similarly, 16 fewer species crocodilian species were present in optimised collections, despite relatively modest reduction in exhibit space committed. This suggests that optimised collections of large mammals and reptiles would concentrate more resources on a reduced diversity of species, maximising population sustainability in BIAZA institutions alone, given these optimisations do not consider supplementation from non-BIAZA institutions or from the wild (McCann and Powell, 2019; Brereton and Brereton, 2020).

In contrast to global collection optimisation (Figure 3), avian BIAZA collections saw large-bodied ostrich-like species (paleognaths) and cranes (Gruiformes) increasing in proportional exhibit space (Figure 6) and species richness (Figure 5). Here, the constraints around exhibit suitability included in the *zooptimal* optimisation may be the underlying cause of this discrepancy, with only a limited number of bird species able to fill large exhibits currently occupied by large-bodied birds (Krause and Robinson, 2022). Discrepancies between optimised global and regional collections under environmental change demonstrates the importance of regional collection planning (Lees and Wilcken, 2009; Condé et al., 2013; Traylor-Holzer et al., 2019) which takes into account the architectural heritage and logistical constraints of individual institutions (Krause and Robinson, 2022). However, it also highlights how greater exhibit versatility - meaning exhibits are suitable for a greater diversity of species - can provide curators with greater flexibility in collection planning, and should be factored in to the exhibit design process. Previous regulatory constraints (such as CITES legislation) have had observable impacts on zoo collection planning in the past (Brereton and Brereton, 2020). Understanding how national and regional collections can be independent and sustainable in an era of increasing logistical and legal constraints around the transfer of live animals (BIAZA, 2023), and how this affects collection priorities, is vital for zoo curators and managers.

Collection redundancy – a double-edged sword

In line with previous research (McCann and Powell, 2019; Powell, 2019), my results hint at a potentially concerning level of redundancy in global zoo collections that may limit zoos' potential to maximise coverage of threatened biodiversity in the long term. It is striking that, based on current collections, the regional subset of BIAZA zoos conserve 60% (797 MY) of the total threatened evolutionary history contained in all Species360 zoo globally, after correcting for population persistence. This implies that the entire collections of the 1,023 other institutions across 90 nations add only an additional 534 MY of threatened evolutionary history not otherwise conserved in BIAZA zoos. Comparison of the taxonomic coverage of different families following collection optimisations (Figures 2 & 5) and the spatial resources committed (Figures 3 & 6) further evidences the high levels of redundancy in collections. For example, in BIAZA collections, optimisation under future conditions led to a net reduction of 199 exhibit spaces housing lemurs (Lemuridae), despite there being no overall loss of lemur representation at the species level after optimisation. This implies that current levels of lemur taxonomic representation may be conserved through more efficient use of resources, freeing up space for other taxa (McCann and Powell, 2019; Powell, 2019).

Of course, redundancy in collections is not necessarily negative. A certain level of redundancy across institutions is required to maintain metapopulations of species across institutions (Condé et al., 2013), and to conserve against stochastic effects of very small populations with limited representation across different institutions (Jacken et al., 2020). An influential study assessing the global representation and population sustainability of threatened species in Species360 zoos (Condé et al., 2013) revealed that maintaining metapopulations of at least 250 individuals would, for most species, require intensive co-operation of up to 24 zoos across a radius of more than 2,000 km. The authors recommended greater trans-national collaboration of zoos in regional clusters with a clear taxonomic focus, in line with the ‘One Plan’ approach to integrated *in situ* and *ex situ* population management (Byers et al., 2013).

My results further support these moves towards regionalised collection management (Byers et al., 2013; Traylor-Holzer et al., 2019), which would likely increase redundancy in regional collections, while decreasing global redundancy as regional collections diverge in taxonomic focus. While this reduction in beta-diversity (*sensu* Whittaker, 1972) between neighbouring institutions may have a modest dampening effect on attendance (Mooney et al., 2020), this could be mitigated by intelligent selection of attractor species (Moss and Esson, 2010; Chapter 5) and the collection optimisation approaches I have demonstrated here. In return, the global conservation value of zoo collections could be maximised, while costs and logistical constraints minimised (Condé et al., 2013). The effectiveness of any subsequent reintroductions could benefit from spatially explicit integration of *ex situ* and *in situ* population management close to or within species’ native ranges, which has been shown to improve the probability of reintroduction success (Byers et al., 2013; Biega et al., 2017; Biega et al., 2019).

Limitations

While my novel optimisation approaches have clear applications to long-term, climate-smart zoo collection planning, both global and regional optimisation approaches are subject to inherent limitations and uncertainties. While such uncertainties do not invalidate my findings, it is important that curators and managers bear these in mind when interpreting my results.

The primary limitation of any modelling-based study of this kind is the uncertainty inherent in the input data itself. In Chapters 2 and 3 I discussed limitations inherent in the use of correlative SDM to predict the impacts of climate change on biodiversity and on species’ extinction risk, in particular (see Elith and Leathwick, 2009 for an overview). Equally, my trait-based predictive models of species attractiveness to zoo visitors (Chapter 5) are also subject to uncertainties, especially for taxa poorly represented in the 299 species where visitor observations were sampled, although my models had good predictive performance at the species level. Given the gaps in life history traits data available in the Demographic Species Knowledge Index (Condé et al., 2019), especially for poorly-studied taxa, my estimates of species persistence probabilities necessarily relied on phylogenetic imputation and relatively simple matrix-based population viability analyses. These models did not explicitly incorporate genetic effects such as inbreeding depression, although it should be noted that recent research has not detected genetic declines as severe as expected in most zoo populations (Che-Castaldo et al., 2021). While all the above inputs may be suboptimal for any given species, I explicitly incorporated uncertainty into my estimates of species EDGE scores, attractiveness estimates, and persistence probabilities, and more complex methodologies relying on more detailed data would be inappropriate or impossible for a study incorporating all terrestrial vertebrates (Paniw et al., 2021).

One limitation of the global collection optimisation approach, specifically, is that it treats all populations as single, discrete units, and does not account for the spatial distribution of species between institutions. This is a necessary limitation given the vast number of potential solutions, and even then, optimisation was only possible by dividing mammal, bird and herpetofauna collections, despite using cutting-edge Gurobi optimisation software (Schuster et al., 2020) and a high-performance computer cluster. This optimisation effectively assumes all global zoo space as a single, empty area to be filled with any combination of candidate species, with no regard to ‘real-world’ spatial structure of the zoo estate. Results should therefore be interpreted as an ‘all-else-being-equal’ case, where logistical constraints such as collaboration and transfer between international zoos are entirely removed. By contrast, the regional optimisation approach considers BIAZA zoo populations as entirely isolated, with no exchange with non-British and Irish institutions. While this is an unrealistic scenario, it provides the additional benefit of showing how BIAZA collections would need to adapt to be completely ‘self-sufficient’ (Lees and Wilcken, 2009) at a time of growing regulatory barriers to live animal transfer (BIAZA, 2023). Furthermore, the exhibit-specific approach increases the number of potential solutions exponentially, and the computational power required to run such a study at a global scale is not currently available.

Finally, my optimisation approaches consider four variables: species EDGE scores, species attractiveness, spatial requirements, and persistence probabilities. These variables can all be quantified with a level of certainty. However, there are many additional reasons why species may be kept in zoos, many of which are not quantifiable in the same way (Bowkett, 2014). For example, the development and trialling of vaccines for elephant endotheliotropic herpesvirus

(EEHV) at Chester Zoo, UK (Maehr et al., 2023) could have game-changing consequences for elephant conservation *in situ* and *ex situu*, but the ‘potential’ research value and conservation impact of any future research cannot be incorporated into such approaches. How individual species contribute to the educational missions of zoos (Patrick and Caplow, 2018), visitors’ physical and mental well-being (Coolman et al., 2020; Spooner et al., 2023), and connection to nature (Howell et al., 2019; Rose et al., 2022) are all intangibles that are not accounted for in my optimisations, and could be fruitful lines of future research.

Recommendations

Given the limitations discussed above, my results should not be interpreted as a prescriptive instruction manual on which species to keep at which zoo. Rather, this research provides an indicative pathway, highlighting the extent of what is possible if global and regional zoo communities work collectively to mitigate the impacts of climate change on the conservation value of their collections. Here I have used threatened evolutionary history (species’ EDGE scores) as a weighting to prioritise *ex situ* conservation of threatened and phylogenetically distinct species, and as measure of the overall conservation value of zoo collections. However, conserving threatened evolutionary history *per se* is not the end-goal of *ex situ* conservation, and must be tied with appropriate, targeted, and effective *in situ* and *ex situ* measures to conserve species and prevent further extinctions, in line with the One Plan approach. Below, I provide four key recommendations for zoo curators, managers, and the wider conservation community based on these findings.

First, zoos must consider the long-term sustainability of their regional or national collections. The legal and regulatory landscape for zoos already constrains collection planning (Brereton and Brereton, 2020; BIAZA, 2023) and this situation may not ease in the coming years. It is therefore prudent to consider the sustainability of populations at regional or even national scales. Regional collection optimisation suggested that there may be a need to focus greater resources on a more limited number of taxa that can be sustainably and independently managed without supplementation from wild populations or more geographically distant collections (Condé et al., 2013; Powell, 2019).

Second, zoo collection planning must consider diversity and redundancy in their collections at the alpha (institutional), beta (regional) and gamma (global/continental) scales. The occasionally divergent findings in regional and global optimisations presented here, in contrast to existing collection compositions, highlights how regional and global priorities may differ. Working within the framework of the One Plan approach (Byers et al., 2013), continuing moves towards regional collection planning with zoo clusters taking on a particular taxonomic focus is recommended (Condé et al., 2013; Traylor-Holzer et al., 2019). When these can be aligned with species native ranges and local *in situ* conservation organisations, results are likely to improve (Biega et al., 2019). Incorporating regionalised collection optimisation into regional collection planning therefore presents a useful tool for zoo curators and managers in future.

Third, despite modest increases in amphibian representation over the past two decades (Dawson et al., 2016), there remain significant gaps in conservation of threatened amphibians. Collection optimisation can massively increase the conservation of threatened evolutionary history for amphibians, and acting on this information is all the more pressing given amphibians are simultaneously the most threatened vertebrate class (IUCN, 2023a), the class most threatened by climate change (Luedtke et al., 2023; Chapter 3), and are currently under-represented in global zoo collections (Jacken et al., 2020).

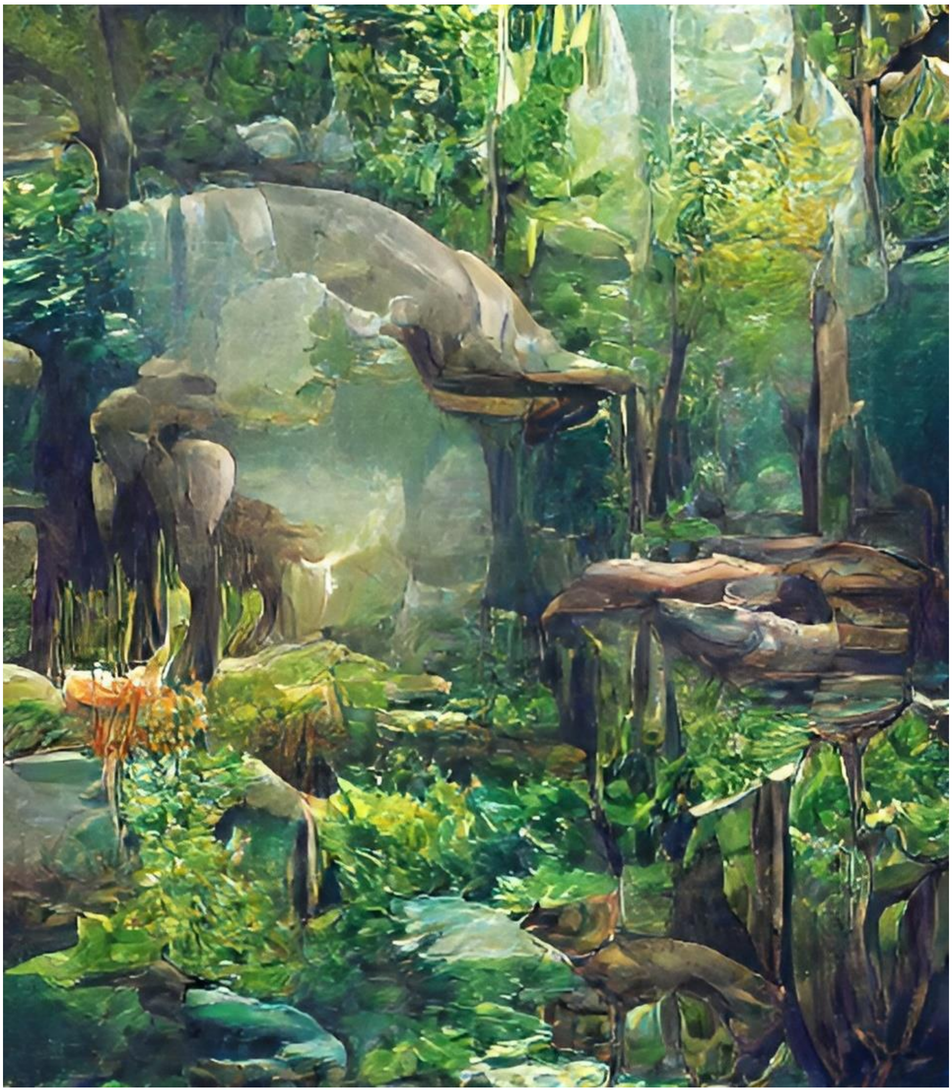
Fourth, and finally, action needs to be taken now. My results show that existing collections are not able to provide long-term protection for species threatened by future environmental change. While optimising collections under current conditions can have significant short-term benefits for the conservation of threatened evolutionary history in zoos, these benefits are short-lived and will be eroded by future environmental change if collections do not continue to adapt (Figures 1 & 4). Therefore, projected future impacts on biodiversity must be ‘priced in’ to collection planning now. This includes recognising when *ex situ* conservation programmes need to be established, before wild populations decline to such an extent that collecting a large enough pool of genetically diverse founders would threaten the security of wild populations. Conservationists should exploit lags in the impacts of climate change on wild populations (Howard et al., 2023), identifying species that are vulnerable to environmental change before population declines begin to be observed.

Conclusions

Applying systematic conservation planning approaches to global and regional zoo collections can massively increase both the conservation value and the attractiveness value of zoo collections, particularly under future environmental change. Existing zoo collections conserve just 3.2% of total threatened evolutionary history for terrestrial vertebrates, after correcting for persistence probability. This can be increased to 30.7% while simultaneously increasing global collection attractiveness six-fold. Amphibians alone would see a fifteen-fold increase in the amount of threatened evolutionary history conserved in BIAZA collections. I show that incorporating future environmental change in this way will not be straightforward and requires major changes to collection composition, but will be vital if zoos are to keep pace with a changing world. While recognising the inherent limitations and uncertainties of any model-based optimisation approach, this study is the first to apply exact integer linear programming to zoo collection planning, explicitly balancing trade-offs in species conservation priority, attractiveness, and resource requirements while accounting for environmental change. These findings therefore provide invaluable information for zoo curators and managers as they deliver on Target 4 of the Kunming-Montréal Global Biodiversity Framework.

Chapter 8

General discussion



AI-generated artwork created in the ‘dream’ WOMBO app (https://dream.ai/), using the prompt ‘Optimal conservation protects biodiversity in the future’ and the ‘Daydream’ art style.

Summary

Anthropogenic pressures are already having acute effects on the Earth's natural systems and threaten vertebrate biodiversity globally (Steffen et al., 2011; Gouldie, 2018; Harfoot et al., 2021). In particular, the loss of suitable habitat due to land use change and, increasingly, changing climatic conditions are primary drivers of biodiversity loss (IPBES, 2019; IPCC, 2022). The Kunming-Montréal Global Biodiversity Framework (GBF; CBD, 2022) will form the basis of global efforts to reverse this trend and 'bend the curve' towards a future where biodiversity can stabilise and begin to recover (Leclère et al., 2020), with nations signing up to ambitious goals including the halting of anthropogenic extinction of threatened species by 2050. In this thesis, I have demonstrated how systematic conservation planning approaches (Margules and Pressey, 2000) will be vital to achieve these goals. Specifically, I focused on how GBF Target 3 (protecting 30% of land and sea by 2030, or '30 by 30') and Target 4 (halt species extinction and protect genetic diversity) can be delivered in the face of environmental change. I have shown that climate and land use change are likely to have profound impacts on the distribution, extinction risk, and phylogenetic diversity of vertebrates globally, and highlight how both *in situ* (e.g. area-based [Maxwell et al., 2020]) and *ex situ* conservation (e.g. in zoos) must adapt to avoid being outpaced by these rapid environmental changes.

Impacts of climate and land use change on biodiversity and conservation

In Chapter 3 I developed ensemble species distribution models to predict the impact of future climate and land use change on the world's terrestrial biodiversity, and showed that even under relatively moderate future warming scenarios, anthropogenic environmental change will have profound impacts on the distribution and conservation status of the world's terrestrial vertebrates. In the following chapter, I applied these results to highlight spatial priorities for conserving the world's threatened evolutionary history under climate and land use change (see '*Spatial Priorities for 30 by 30'*, below).

In Chapter 5, I provided quantitative evidence to support the arguments I made in Chapter 2. Namely, that systematic conservation planning approaches will likely be required to maintain the conservation value of global zoo collections under environmental change. As threatened species are currently under-represented in global zoo collections (Condé et al., 2013) and tend to be less endemic and more generalist than related species not held in zoos (Martin et al., 2014), zoos likely house species less vulnerable to climate and land use change. Using IUCN Red List Criterion A3 (an observed, inferred, or projected population decline), I found that even under a relatively moderate warming scenario (SSP2-4.5) more than a quarter (27%) of modelled species are likely to be threatened by 2070, including 2,753 species that are projected to lose all of their climatically suitable habitat and are therefore at risk of becoming Extinct in the Wild.

Given Goal A of the Kunming-Montréal GBF requires human-induced extinctions of threatened species to be halted by 2050, such species must therefore be immediate priorities for conservation action, including the establishment of *ex situ* conservation breeding programmes where appropriate (Condé et al., 2011). However, the effectiveness of current *ex situ* conservation strategies is also threatened by environmental change, with the aggregate threat status (Butchart et al., 2007) of species in zoos declining less rapidly than for species generally. Furthermore, species in zoos tended to have lower EDGE2 scores – equivalent to the expected loss in unique evolutionary history (MY) should a species go extinct – than close relatives not in zoos. Concerningly, this latter discrepancy is projected to strengthen under more severe climate change scenarios, especially for mammals and birds. Taken together, these findings suggest that future climate and land use change may exacerbate existing issues around threatened species representation in zoos (Condé et al., 2013; Martin et al., 2014).

Spatial Priorities for 30 by 30

In Chapter 4, I provided novel insights into how nations could achieve Target 3 of the Kunming Montréal GBF in a manner that maximises the conservation of threatened evolutionary history (Gumbs et al., 2023). Using projected species range shifts and future EDGE scores derived from my SDM outputs, I showed that spatially optimised protected area networks can provide long-term refugia from climate and land use change for over 27,000 species representing over 36 billion years of threatened evolutionary history, a near nine-fold increase relative to existing protected areas. This study is the first to explicitly integrate the spatial (range shifts) and non-spatial (phylogenetic distribution of extinction risk) impacts of climate and land use change into spatial prioritisation of the world's protected areas. Importantly, my results demonstrate that conservation priorities are disproportionately concentrated in low-income nations in the

Tropics, with the least capacity to fund the expansion and maintenance of effective area-based conservation measures (Maxwell et al., 2020; Titley et al., 2021; Shen et al., 2023). My findings call for an integrated, international approach to share the burden of conservation equitably among nations (Leclère et al., 2020), and establishing robust funding mechanisms that direct conservation finance from high- to low-income nations will be vital to achieve positive outcomes for biodiversity and local communities (Evans et al., 2012).

Leveraging species attractiveness to catalyse conservation funding

Expanding global protected area networks will require significant funding, while existing protected areas are already hampered by funding shortfalls (Coad et al., 2019). In Chapter 6, I identified 'Cinderella species' (Smith et al., 2012), which share traits with existing flagship species but are so-far overlooked in traditional flagship campaigns. Using zoos as a natural laboratory for investigating public preferences between a wide diversity of taxa, I modelled 'attraction power' (proportion of visitors who stop to view an animal) and 'hold time' (how long they stop for) against a set of species morphological and ecological traits, producing trait-based predictive models of species attractiveness that I could then apply to 24,750 species with full trait data available. I found a strong preference for mammals (Moss and Esson, 2010), particularly cats (Felidae), elephants (Elephantidae), and apes (Hominidae), with attractiveness largely driven by species activity and visibility levels.

Using these trait-based attractiveness estimates, I furthered the Cinderella species concept (Smith et al., 2012) by highlighting spatial priority areas where high richness of such species coincides with a paucity of existing flagships, thereby representing spatially explicit hotspots of previously unexploited flagship potential. These 'Cinderella Zones' can therefore be used in conjunction with protected area prioritisation (Chapter 4) to highlight where increased funding opportunities coincide with areas most in need of area-based conservation (McGowan et al., 2020). Importantly, I found that 31.7% of Cinderella Zones occurred in low-income nations, including much of the Sahel region and other (sub)tropical nations with a high conservation burden as identified in Chapter 4, whereas only 1.4% occurred in high-income nations. Therefore, these findings provide important new information on how finance can be raised and directed towards conservation priorities in parts of the world most in need of financial assistance to support area-based conservation.

Optimising ex situ collections conservation under climate change

In Chapter 7, my final data chapter, I brought together my findings from Chapters 3, 5, and 6, alongside additional data on species husbandry requirements and life history traits, to simulate optimal zoo collection compositions that maximise both collection attractiveness and representation of threatened evolutionary history. I applied, for the first time, conservation prioritisation algorithms (Hanson et al., 2019) to global zoo collections, including a bespoke algorithm for exhibit-specific collection optimisation at a regional (British and Irish) scale.

As with spatial prioritisation of area-based conservation to meet 30 by 30, I demonstrated how such systematic conservation planning approaches (Margules and Pressey, 2000) can dramatically increase the *ex situ* conservation of threatened evolutionary history under anthropogenic climate and land use change. When accounting for *ex situ* population persistence, global zoo collection optimisation under a ‘middle-of-the-road’ warming scenario of SSP2-4.5 can conserve an additional 17,379 MY of terrestrial vertebrate threatened evolutionary history, a more than ten-fold increase relative to existing collection composition. This could simultaneously increase the total attractiveness of collections more than six-fold. These findings demonstrate that current global zoo collections are suboptimal, but also that increasing the conservation value of global zoo collections need not come at the expense of collection attractiveness, on which zoos rely to maintain visitation rates, gate receipts, and *in situ* conservation contributions (Fa et al., 2014; Bowkett et al., 2014; Mooney et al., 2020).

Synthesis

Anthropogenic climate and land use change will dramatically alter the distribution of species and conservation priorities, and these changes carry profound implications for global conservation efforts. Existing *in situ* and *ex situ* conservation measures are currently suboptimal and have been unable to arrest the continuing declines in terrestrial vertebrate biodiversity (IPBES, 2019). In this thesis I have demonstrated that without significant adaptation to the world’s protected areas and *ex situ* collections, these conservation shortfalls are likely to become increasingly severe, even under relatively mild scenarios of future climate and land use change. While these findings are concerning, my research has also demonstrated that much more positive outcomes for biodiversity are still possible, and that evidence-based, strategic delivery of Targets 3 and 4 of the Kunming-Montréal GBF can provide long-term protection from anthropogenic climate and land use change, be it in *in situ* protected areas or *ex situ* zoo collections, for tens of thousands of species and billions of years of threatened evolutionary history. Goal A of the Framework, to prevent human induced extinction of threatened species by 2050, is therefore still achievable, but will require a concerted international response (Leclère et al., 2020) and truly integrated *in situ* and *ex situ* conservation interventions (Byers et al., 2023).

Focal areas for in situ conservation

Projections from my species distribution models highlight hotspots of localised extinctions, colonisations, and community turnover for terrestrial vertebrates globally (Chapter 3). My results add further evidence of a potential ‘escalator to extinction’ effect (Urban, 2015; Freeman et al., 2018), whereby lowland areas (particularly in the Tropics) see net losses of species whereas high elevation and/or high latitude areas see an increase in colonisation by more warm-adapted species, producing novel community assemblages (Telwala et al., 2013; Hastings et al., 2020). Such areas will require significant conservation attention for two main reasons. First, the high rates of projected colonisation by lowland species indicate that these areas could provide important climatic refugia for many species as their lowland ranges become increasingly inhospitable. Second, native species in these montane or high latitude systems will likely face increased competition for resources and novel interactions with colonising species, even if they retain enough climatically suitable habitat to persist in the absence of these interactions. Intelligently designed protected areas can simultaneously provide climatic refugia for native species and facilitate climate-induced range shifts at the warm edge of species ranges (Cooke et al., 2022; Mi et al., 2023), especially areas with high levels of structural and topographic diversity (Stein et al., 2014; Thomas and Gillingham, 2015).

One such area highlighted in my research is the tropical Andes, an existing biodiversity hotspot (Myers et al., 2020) which is projected to see the highest levels of colonisation by novel species globally, particularly by lowland birds tracking an elevational gradient in their climatic niche (Chapter 3). At the same time, the tropical Andes was consistently picked out as a priority for the establishment of additional protected areas in both domestic and international co-operation pathways in my protected area prioritisations (Chapter 4). Given this biodiversity hotspot is projected to become of increasing importance to a large number of species undergoing climate-induced range shifts, extending area-based conservation to currently unprotected areas of the tropical Andes will be of paramount importance for the conservation of neotropical biodiversity. Encouragingly, protected area coverage in the Andes has increased substantially in recent decades, although ecological and taxonomic representativeness is still uneven (Fajardo et al., 2023). Increasing the representation of heterogeneous, high-quality habitats increases the diversity of ecological niches available to species, thereby increasing the diversity of trophic guilds and habitat specialisations that can persist in a protected area (Quito et al., 2020). Establishment and, crucially, management (Wauchope et al., 2022) of protected areas in the Andes should therefore promote heterogeneous habitats and microclimates to maximise the niche space available to species, to facilitate species range shifts and the coexistence of novel and native species. This equally applies to other upland and montane systems that also see high levels of colonisation and are selected for protected area prioritisation, such as southern-central Mexico and the western Himalaya. However, promotion of heterogeneity alone can reduce the overall extent of contiguous habitats that may support more wide-ranging species at higher trophic levels, and careful consideration must be given to balance these priorities, where appropriate (Thomas and Gillingham, 2015).

Another area of alignment in the results I have presented across this thesis is in the highlands of Ethiopia. In a similar mode to the tropical Andes, this region is projected to see an increase in overall species richness under future environmental change, driven by high colonisation rates by equatorial species and lowland species (Hastings et al., 2020; Chapter 3). The Ethiopian highlands were also identified as major Cinderella Zones for mammals in my study of the global distribution of species attractiveness (Chapter 6), and had significant areas picked out as priorities for new or expanded protected areas to conserve threatened evolutionary history under environmental change (Chapter 4). Economically, Ethiopia is currently ranked 160th of 202 global nations, with a GDP per capita (corrected for purchasing power parity) just 13.5% of the global average (World Bank, 2023). The region therefore has both significant potential, and significant need, for external finance to fund and maintain area-based conservation and improve livelihoods (Evans et al., 2012; Maxwell et al., 2020).

One method by which this could be achieved could be to promote sustainable and responsible wildlife tourism opportunities focused around novel flagships (e.g. the Ethiopian wolf, *Canis simensis*, Figure 1). Global visits to protected areas are estimated at 8 billion visits per year, generating up to $600 billion US in direct and indirect in-country expenditure, albeit the majority of these visits and associated spending are currently concentrated in Europe and North America (Balmford et al., 2015). While wildlife tourism is established in Ethiopia, it is small relative to neighbouring countries like Kenya and Tanzania, and sustainably scaling up community-based tourism infrastructure remains a challenge (Amare, 2015). Exploiting the flagship potential of its many Cinderella mammal species could promote the unique wildlife viewing opportunities of the region, releasing pressure on more established destinations in east Africa. This is especially pertinent given my finding that the Albertine Rift systems of east Africa are likely to see some of the highest rates of localised extinctions globally (Chapter 3). If distributed equitably and efficiently among local communities and conservation initiatives, wildlife tourism revenues could contribute to economic development, human wellbeing, and help overcome existing challenges such as human-wildlife conflict and land use pressure on protected areas (Amare, 2015).

Aligning in situ and ex situ conservation

Systematic conservation planning and zoo collection optimisation can, in and of itself, markedly increase the long-term conservation value of global zoo collections under climate and land use change, especially for currently under-represented taxa such as threatened amphibians (Condé et al., 2013; Biega et al., 2017; Jacken et al., 2020; Chapter 7). However, zoo-based *ex situ* conservation can be most effective when integrated with *in situ* conservation projects and partnerships, under the 'One Plan' approach to species conservation (Byers et al., 2013; Traylor-Holzer et al., 2019). To briefly recap, the One Plan approach encourages the integrated management of *ex situ* and *in situ* populations, and joint development of species conservation plans through collaboration between zoos and *in situ* partners (Traylor-Holzer et al., 2019). The research I have presented here has direct applications to the One Plan approach, and provides novel insights into how future environmental change can inform the establishment, development, and prioritisation of these partnerships and strategic conservation plans.

Specifically, bringing together information on priority species for *ex situ* conservation, spatial priorities for *in situ* protected areas, and hotspots of Cinderella species with flagship potential, spatially and taxonomically explicit priorities for *in situ*-*ex situ* conservation plans can be identified. Here, I set out five criteria that can be used to identify such opportunities, and provide examples of species and spatial focus areas selected under these criteria.

1) Is the species currently under- or unrepresented in zoo collections, and is it identified as a priority for bringing into *ex situ* conservation under zoo collection optimisation? Such species are therefore priorities for additional *ex situ* conservation effort.
2) Is the species considered a 'Cinderella' species, which could act as attractor species for zoo visitors and a potential flagship for conservation in its native range?
3) Where is the species expected to persist under future climate and land use change? Such information is vital when considering spatially explicit *in situ* conservation interventions.
4) Where does the species' current and future distribution overlap with 'Cinderella Zones', where relatively low richness of existing flagship species means that additional flagship species campaigns could be most effective?
5) Does the remaining distribution in Cinderella Zones also overlap with areas selected as priorities for additional protected areas under spatial conservation prioritisation? This ensures that species-specific conservation plans have the greatest potential to benefit wider biodiversity and the conservation of threatened evolutionary history beyond the focal species.

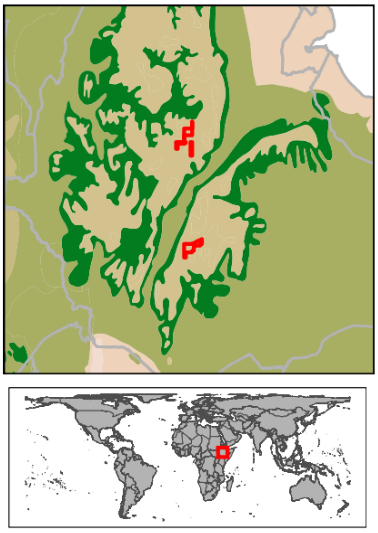
Under these criteria, 87 species are selected as candidates for new *in situ*-*ex situ* conservation plans in spatially explicit focus areas that are both prioritised for protected areas under environmental change (Chapter 4) and overlap with Cinderella Zones (Chapter 6). Of these, 10 are mammals, 41 are birds, 34 are amphibians and two are reptiles. Table 1 provides summary information of the top-six candidate mammals and the top bird, amphibian and reptile species selected under these criteria, ranked by estimated attractiveness, alongside information on the geography and ecology of the spatial focus areas in question. In Figure 1, I provide further information including maps of potential focus areas for future conservation projects for the top-ranked mammal (Ethiopian wolf, *Canis simensis*), bird (Rufous fishing owl, *Scotopelia ussheri*) and herpetofauna species (spikethumb frogs, *Plectrohyla spp*.). For the full list of candidate species and areas, see Appendix F. Below, I discuss in more detail the opportunities and challenges for establishing a One Plan approach to conservation planning for the top-ranked of all 87 candidate species, the Ethiopian wolf.

According to its most recent IUCN Red List assessment (Marino and Sillero-Zubiri, 2011), fewer than 200 mature Ethiopian wolves may remain, spread across seven isolated populations in the Ethiopian highlands (Figure 1). Approximately 2,000 km^2 of currently unprotected land in the Ethiopian highlands provides long-term refugia from environmental change for the Ethiopian wolf. This area coincides with identified Cinderella Zones and is a priority for establishing new protected areas (Table 1). Establishing new protected areas here could provide long-term conservation benefits for at least an additional 228 MY of threatened evolutionary history under future climate and land use change (Figure 1), and the Ethiopian wolf would be an ideal candidate species to act as a conservation flagship to drive financial and political support for such interventions in Ethiopia, a low-income nation that may be in greatest need of such support (Evans et al., 2012; Shen et al., 2023). As the Ethiopian wolf was also identified as a priority for *ex situ* conservation in my global zoo collection optimisations, it represents a key opportunity for zoos to contribute to species conservation in line with the One Plan approach (Byers et al., 2013) while simultaneously helping to deliver 30 by 30 and driving investment in area-based conservation (Maxwell et al., 2020).

Zoos have long recognised the potential benefits of establishing *ex situ* populations of Ethiopian wolves as an insurance against stochastic extinction and limited geneflow between isolated wild populations, but efforts to bring the species into zoo collections were abandoned in 2004 due to opposition from the Ethiopian government (Traylor-Holzer et al., 2018). Given these constraints, and the fact that conservation breeding and reintroduction programmes are more likely to be successful when established in or near species' native or historic ranges (Byers et al., 2013; Biega et al., 2019), establishing *ex situ* populations in-country, in partnership with local/regional organisations such as the Pan-African Association of Zoos and Aquaria (PAAZA) and the Ethiopian Wolf Conservation Programme, has already been identified as the greatest opportunity for the global zoo community to contribute directly to Ethiopian wolf conservation (Traylor-Holzer et al., 2018). My finding that the Ethiopian wolf

(a)

Photo © David Castor



Species: Ethiopian wolf *Canis simensis*	**Attractiveness** 58.5

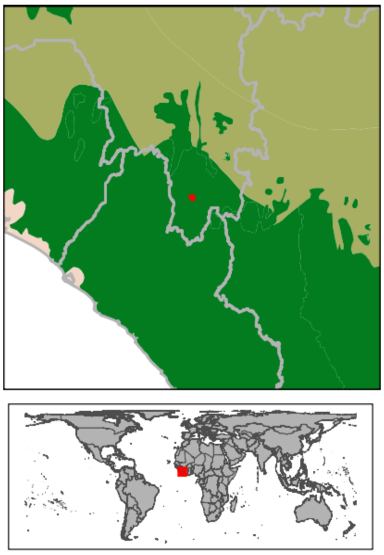
Red List Status		
Current	*SSP2-4.5*	*SSP5-8.5*
EN	EN	EN

Countries	**Ecoregions**
🇪🇹	Ethiopian montane forests, moorlands, grasslands and woodlands. Sahelian Acacia savanna

EDGE2 Estimate (MY)			**Total Threatened Evolutionary History (MY)**		
Current	*SSP2-4.5*	*SSP5-8.5*	*Current*	*SSP2-4.5*	*SSP5-8.5*
0.99	1.11	1.09	274.6	228.2	244.3

(b)

Photo © Francesco Veronesi



Species Rufous fishing owl *Scotopelia ussheri*	**Attractiveness** 21.4

Red List Status		
Current	*SSP2-4.5*	*SSP5-8.5*
VU	VU	VU

Countries	**Ecoregions**
🇬🇳	Western Guinean lowland forests.

EDGE2 Estimate (MY)			**Total Threatened Evolutionary History (MY)**		
Current	*SSP2-4.5*	*SSP5-8.5*	*Current*	*SSP2-4.5*	*SSP5-8.5*
0.80	0.71	0.79	295.6	423.0	345.7

(c)

Photo of congeneric *P. exquisita*, © Tom Kennedy

Species	**Attractiveness**
Greater spikethumb frog *Plectrohyla avia* &	29.3
Rio Sananja spikethumb frog *Plectrohyla pokomchi*	28.7

Red List Status

Current		*SSP2-4.5*		*SSP5-8.5*	
P. avia	*P. pokomchi*	*P. avia*	*P. pokomchi*	*P. avia*	*P. pokomchi*
EN	EN	EN	EN	EN	EN

Countries	**Ecoregions**
	Central American montane, pine-oak, and Atlantic moist forests. Sierra Madre de Chiapas and Petén-Veracruz moist forests. Motagua Valley thornscrub

EDGE2 Estimate (MY)

Current		*SSP2-4.5*		*SSP5-8.5*	
4.49	4.26	4.49	4.69	4.49	4.43

Total Threatened Evolutionary History (MY)

Current	*SSP2-4.5*	*SSP5-8.5*
377.4	227.7	220

🟩 (Sub)tropical moist broadleaved forests
🟩 (Sub)tropical dry broadleaved forests
🟩 (Sub)tropical coniferous forests
🟩 (Sub)tropical grasslands/savanna/shrublands
🟫 Flooded grasslands/savanna
🟫 Montane grasslands/shrublands
🟫 Deserts/xeric shrublands
🟫 Mangroves

Figure 1. Information factsheet for the top-ranked mammal (Ethiopian wolf, *Canis simensis*, **a**), bird (rufous fishing owl, *Scotopelia ussheri*, **b**), and herpetofauna (spikethumb frogs, *Plectrohyla spp*., **c**) that are candidates for future *in situ-ex situ* conservation projects and partnerships in line with the 'One Plan' approach to integrated species conservation (Byers et al., 2013). Species ranked by estimated attractiveness. All candidate species are 'Cinderella' species, are found in 'Cinderella Zones' (Chapter 6), are currently absent from zoo collections, are selected under future global collection optimisations (Chapter 7), and their range persists in areas prioritised for protected area expansion under current and future (SSP2-4.5) conditions, and both domestic and international co-operation pathways (Chapter 4). The left side includes information on species estimated attractiveness, current and future Red List status, and current and future EDGE2 estimates (MY of unique evolutionary expected to be lost should the species go extinct). The right side includes spatial information on focus areas for *in situ* projects, including a map, countries and ecoregions overlapping the focus area, and the total threatened evolutionary history (summed EDGE2 scores (MY)) of species that occur in the focus areas.

is a priority for *ex situ* conservation is not in itself new. However, by combining this information with spatial priorities for delivering 30 by 30 and opportunities for driving investment in area-based conservation, I provide novel, empirical evidence of the value of a One Plan approach to Ethiopian wolf conservation, which can support future efforts to establish such projects and partnerships in Ethiopia.

Beyond the Ethiopian wolf, the 87 candidate species and focus areas provide a combined 178,459 km^2 of opportunities for *in situ*-*ex situ* projects and partnerships following the One Plan approach (Appendix F). Some candidate species, such as the giant armadillo (*Priodontes maximus*), which has never successfully bred in zoos (Carter et al., 2016), pose particular challenges for conservation breeding programmes. Here, *ex situ* interventions may be limited to providing expertise and financial and technical support for existing *in situ* projects such as the ICAS Giant Armadillo project (https://www.icasconservation.org.br), which zoos already significantly support (Desbiez, 2024). Establishing *ex situ* populations may be of existential importance for other candidate species, such as Durrell's glass frog (*Espadarana durrellorum*), which is currently classed as Least Concern (and projected to remain so under SSP2-4.5) but is projected to lose all its climatically suitable habitat under the more severe SSP5-8.5 (Appendix F). In partnership with specialist organisations in its native Ecuador (Biega et al., 2017; Appendix F) zoos should work to establish sustainable *ex situ* populations of this species, while wild populations are still sufficiently robust for a large enough number of founders to be collected to establish genetically sustainable *ex situ* populations. My decadal SDM projections can inform such timelines for the establishment of *ex situ* programmes. Simultaneously, *in situ* projects that can mitigate the potential impacts of the most severe climate and land use change scenarios should be devised, such as establishing protected areas that conserve microclimatic refugia from macroclimatic change (Senior et al., 2017).

Caveats and Data Limitations

Throughout this thesis I have shown that systematic conservation planning (Margules and Pressey, 2000) will be a vital tool to inform both *in situ* and *ex situ* conservation under future climate and land use change, if Targets 3 and 4 of the Kunming-Montréal GBF are to be achieved effectively. However, given the predicted intensity of future climate and land use change, and the urgency of the biodiversity crisis (IPBES, 2019; IPCC, 2021), I have necessarily relied on predictive modelling approaches and at times incomplete datasets, the limitations of which must be carefully considered when interpreting my results. Here, I highlight

Table 1: Summary information for the candidate species for *in situ-ex situ* conservation partnerships, in line with the ‘One Plan’ conservation approach. Table includes information on geographic distribution of species long-term climatic refugia, as well as their projected Red List Status and EDGE2 scores (Chapter 3). These areas coincide with priorities for protected area expansion under all current, future, domestic and international prioritisations (Chapter 4), and ‘Cinderella Zones’ (Chapter 6). All species are themselves ‘Cinderella’ species, are not currently housed in a Species360 zoo, and are selected in all global zoo collection optimisations for current and future (year 2070, SSP2-4.5/SSP5-8.5) environmental conditions (Chapter 7). The top-six candidate mammal species, ranked by estimated attractiveness, and the top bird, reptile, and amphibian species, are shown here. See Appendix F for full shortlist.

Species	**Countries**	**Ecoregions**	**Area (km^2)**	**Current Status**	**Future Status (SSP2-4.5/ SSP5-8.5)**	**EDGE2 Score**	**Future Score (SSP2-4.5)**	**Future Score (SSP5-8.5)**	**Attractiveness Estimate**
Canis simensis	Ethiopia	Ethiopian montane grasslands, woodlands, forests, & moorlands	2,017	EN	EN	0.99	1.11	1.09	58.49
Caracal aurata	Congo, DR Congo, Angola, Cameroon, Nigeria, Cent. Afr. Rep..	Forest-savanna mosaics; Lowland, Highlands & swamp forests	9,858	VU	VU	0.87	0.9	0.86	43.76
Priodontes maximus	Venezuela, Argentina, Brazil, Bolivia.	Wetlands; Delta swamp, montane, coastal & dry forests; Cordillera de Merida páramo; Llanos; Yungas; mangroves; xeric scrub and shrublands	9,161	VU	VU	3.58	3.47	3.53	41.39
Viverra tangalunga	Malaysia, Indonesia, Brunei	Montane & lowland rain forests; Peat & freshwater swamp forests; heath forests; mangroves; montane alpine meadows	32,284	LC	LC	0.16	0.14	0.14	37.84
Genetta servalina	DR Congo, Cent. Afr. Rep.	Forest-savanna mosaics	613	LC	VU/CR	0.05	0.5	1.97	34.82
Genetta maculata	Ethiopia, Nigeria, Somalia, Eritrea, DR Congo, Cameroon, Cent. Afr. Rep., Chad	Ethiopian montane grasslands, woodlands, forests, & moorlands; forest-savanna mosaics; savanna; xeric & Hobyo grasslands and shrublands; bushlands and thickets; Highlands forests	46,592	LC	LC/NT	0.06	0.05	0.12	33.99
Plectrohyla avia	Guatemala, Mexico	Moist, montane & pine-oak forests	1,627	EN	EN	4.49	4.5	4.78	29.33
Scotopelia ussheri	Guinea	Lowland forests	20	VU	VU	0.8	0.71	0.79	21.45
Liopholis kintorei	Australia	Central Ranges xeric scrub	984	VU	VU	1.18	1.08	1.07	17.44

three key sources of uncertainty and caveats that are of particular importance when considering my findings in an applied context, such as real-world zoo collection planning.

Spatial and temporal resolution of species distribution models

Underlying my prioritisations of *in situ* and *ex situ* conservation under future environmental change are the outputs from correlative species distribution modelling (SDM) for the world's terrestrial vertebrates (Chapter 3). Given the broad taxonomic scope and global spatial scale of my study, these models were necessarily produced at a relatively coarse resolution (0.5-degree or 0.25-degree grid cells). My models were therefore unable to capture many finer-scale environmental variations and ecological processes, such as the existence and persistence of microclimatic refugia under macroclimatic change (Senior et al., 2018), species interactions that may facilitate or prevent niche partitioning and species coexistence at finer spatial scales (König et al., 2021), and the fine-scale structure and configuration of habitats that may mediate dispersal at the scale of individuals and populations (Årevall et al., 2018).

Temporally, I projected SDM outputs to decadal timesteps from the present day, then each decade between 2030 and 2070, to align my projections with the minimum 10-year timescale required for Red List assessments (IUCN, 2022). This represents a significant improvement on typical SDM studies that project species range shifts typically to one or two future timesteps, such as the year 2050 and/or 2070 (Thomas et al., 2004; Thuiller et al., 2019; Titley et al., 2021). However, individual species responses to environmental change may occur at much finer temporal scales, especially in response to extreme events that may not be well represented by the annual or monthly bioclimatic variables used in my SDMs (Feldmeier et al., 2018). Relatedly, my Red List assessments also cannot factor in extinction debts driven by climate and land use change, whereby extinction lags behind changing environmental conditions (Dullinger et al., 2012; Howard et al., 2023). This could in fact be somewhat beneficial in a conservation planning context, however, by highlighting species and regions that are likely to suffer extinction debts before population declines are observed in reality.

Data limitations relevant to ex situ conservation

When optimising zoo collections under future climate and land use change, I relied on species' *in situ* extinction risk based on SDM outputs, and *ex situ* population persistence probabilities based on incomplete life history trait data (Condé et al., 2019). With regards to *in situ* extinction risk, I followed published IUCN guidelines for assigning species Red List status from these outputs (IUCN, 2022), and then derived a probability of extinction following the widely accepted and established methodology used in the EDGE2 protocol (Gumbs et al., 2023). My estimates of species' future Red List status assumed a linear relationship between population trends and changes in species' Area of Occupiable Habitat (AOOH, Chapter 3). Such assumptions are unlikely to hold for many species but are justifiable in the absence of alternative data, as was the case here (IUCN, 2022). *Ex situ* population persistence probabilities were based on relatively simplistic population viability analyses, and required significant amounts of data imputation to fill data gaps (Condé et al., 2019). While I adjusted species population thresholds to account for imperfect population management (an N/Ne ratio of 1.4, Willis and Wiese, 1993), more complex modelling could explicitly incorporate genetic effects such as inbreeding depression, such as through the VORTEX population simulation software (Lacy, 1993).

I also found a real paucity of comprehensive information on the costs of keeping various taxa in zoos. While some financial cost estimates have been made for a very limited number of taxa, such as elephants in UK zoos (Sach et al., 2019), such information is simply unavailable for the vast majority of species, and should be a priority for future research to inform global and regional zoo collection planning. The spatial estimates of species exhibit requirements I present here are therefore the best available information for a study of this kind. However, I recognise that these do not incorporate the additional costs in terms of environmental regulation (e.g. heating and lighting), welfare and enrichment requirements, staffing, and veterinary costs that contribute significantly to the overall cost of keeping species in zoos (Brady et al., 2017; Sach et al., 2019). While there will also be up-front costs in converting exhibit spaces to house different species, my exhibit-specific optimisations of British and Irish zoos largely accounted for this by constraining candidate species to those of the same section (mammals, birds, herpetofauna) and with similar spatial requirements.

Implications for collection planning

In this thesis I presented the first application of conservation optimisation algorithms (Hanson et al., 2019) to zoo collection planning at global and regional (British and Irish) scales. However, it is vital that my results are not considered prescriptive or in any way an instruction manual on exactly which species should be housed in which zoos, at what time. Rather, my research highlights a direction of travel that may be achievable if other logistical and/or technical barriers (such as around the international exchange of animals between zoos) were not a factor in decision-making. There are many ‘immeasurable’ factors that will influence curators’ decision-making that cannot be captured in this quantitative optimisation framework (Fa et al., 2014; Bowkett et al., 2014). For example, the value of applied research, such as the development of vaccines for diseases that threaten both *in situ* and *ex situ* populations, is difficult to quantify (Woodroffe, 2021; Maehr et al., 2023). With regards to species attractiveness, the extent to which species attractiveness is inherent (i.e. driven by species traits) or culturally reinforced (Courchamp et al., 2018), remains uncertain. Similarly, whether the species identified as attractive are the result of enhanced conservation marketing (Veríssimo et al., 2017) and/or promotion by zoos themselves (Rose et al., 2018), remains unknown. Resolving such questions would provide valuable lines of inquiry for future research.

Here, I provide a snapshot of what ‘could’ be possible under future climate and land use change, highlighting the benefits that could be achieved in terms of collection attractiveness and the conservation of threatened evolutionary history in zoos. Curators and managers should consider how their collections, and those of their partner institutions, might be able to contribute to this collective move towards a more optimal collection composition in future.

Future Directions

My findings have provided novel insights into the potential for systematic conservation planning and conservation prioritisation to inform biodiversity conservation both *in situ* and *ex situ*. Specifically, I show that pro-active planning and optimisation is going to be vital if nations are to halt anthropogenic extinctions of threatened species by mid-century (Goal A of the Kunming-Montréal GBF), and effectively deliver 30% protected area coverage (Target 3) and conserve species and genetic diversity (Target 4) by 2030. Below, I outline five overarching recommendations that can help achieve these aims, based on the findings of this thesis.

1) **Integrate non-spatial and spatial impacts of environmental change into conservation planning.** Significant research focus is now committed to prioritising and designing climate-proofed global protected areas that can facilitate species range

shifts under climate change and conserve refugia and remaining species niche space (Hannah et al., 2008; Lawler et al., 2020; Mi et al., 2023). However, my research has demonstrated that significant shifts in the phylogenetic distribution of extinction risk are likely to occur under climate and land use change, and some species represent more unique evolutionary history than others (Gumbs et al., 2023). While we should aim to prevent all anthropogenic extinctions (CBD, 2022), the loss of some species will therefore have a greater conservation impact than others, especially when viewed from the perspective of evolutionary history and phylogenetic diversity. Systematic conservation planning should not only be a question of *where* we conserve, but also *what* we conserve, and why.

2) **Fill data gaps to improve ecological forecasting.** The fields of species distribution modelling and conservation prioritisation are rapidly expanding and developing, with a suite of complex tools, such as mechanistic modelling frameworks (Briscoe et al., 2019) now available to inform predictive modelling under climate and land use change. However, such models still rely on detailed life history, ecological and physiological trait data, which is often unavailable for many species, even in well-studied taxa such as mammals (Paniw et al., 2019). Another important data gap that could improve ecological forecasting would be a more comprehensive understanding of microclimate buffering in response to climate change (De Frenne et al., 2021), especially in non-forest biomes, which could greatly improve the accuracy of SDM-based estimates of future extinction risk under climate change (Lembrechts et al., 2019).
3) **Improve knowledge sharing among *ex situ* institutions.** The Species360 Zoological Information Management System (ZIMS) is an excellent tool that is central to zoo activities, including studbook maintenance and genetic management of populations, collection planning, and recording of veterinary histories of individual animals. However, the system is reliant on zoo staff uploading information in an accurate, timely, and comprehensive manner, and some gaps remain. For example, information on exhibit dimensions and characteristics is often lacking, and such information could be useful to collection planning and future optimisation studies following similar methods to those used here. Furthermore, while the Species360

Demographic Species Knowledge Index (Condé et al., 2019) is an excellent resource on species life history traits, data are missing on key traits for many species, including those currently held in zoos. Filling these gaps would be beneficial not only to the global zoo community but also to the conservation science community in general, especially given zoos are uniquely placed to provide vital information on species life histories that are difficult to study in the wild (Loh et al., 2018).

4) **Prevent climate and land use change at source.** Taking a 'bigger picture' view of my findings, a key takeaway message is that even moderate future climate and land us change scenarios are likely to incur significant losses for biodiversity and make achieving Kunming-Montréal GBF goals considerably more challenging. In Chapter 3, I showed that even under the mildest warming scenario of SSP1-2.6 there will be some increase in overall endangerment of terrestrial vertebrate biodiversity, but that this largely stabilises by mid-century, in line with Goal A of the Framework. By contrast, under more severe climate and land use change endangerment continues to increase, with almost 40% of modelled species threatened with extinction by 2070 under SSP5-8.5. While the window for achieving the Paris targets is closing (Lamboll et al., 2023), defeatism must not be allowed to set in, because each fraction of a degree of warming carries implications for biodiversity and humanity (IPCC, 2022). Limiting anthropogenic habitat loss and climate change will be the most effective ways to conserve biodiversity into the future (IPBES, 2019; IPCC, 2022).

5) **Get ahead of the curve through action rather than reaction.** We can, and must, prevent the worst excesses of climate and land use change in the coming decades (IPCC, 2022). However, success on this front is not guaranteed and global conservation (including both *in situ* and *ex situ* measures) could be increasingly undermined by anthropogenic environmental change. Proactive measures should be implemented now to get ahead of the curve of biodiversity loss induced by climate and land use change (Hannah et al., 2008; Maxwell et al., 2020; Leclère et al., 2020). My research has demonstrated that there are significant gaps in threatened biodiversity representation in both *in situ* protected areas and *ex situ* zoo collections, and that climate and land use change are likely to exacerbate this issue in the absence of significant adaptation. Effective conservation under environmental change will rely on strategic, evidence-based decisions made today to adequately conserve the threatened biodiversity of tomorrow.

Conclusions

In this thesis I have shown that ongoing anthropogenic climate and land use change is likely to exacerbate the extinction crisis that the Earth is already experiencing. Specifically, I demonstrate how climate and land use change will impact terrestrial vertebrate biodiversity globally, and identify spatial priorities for area-based conservation to maximise the long-term conservation of threatened evolutionary history under environmental change. I highlight spatial and phylogenetic hotspots of species attractiveness where additional flagship campaigns could be most effective, driving external investment into area-based conservation in low-income nations with high conservation burdens, where such investment is most needed. Finally, I show how zoos can adapt their collections to maximise the representation of threatened evolutionary history under climate and land use change, and highlight key candidate species and spatial focus areas for delivering climate-smart conservation under the ‘One Plan’ approach. In the absence of major, proactive adaptation to both *in situ* and *ex situ* conservation practices, the world risks missing internationally agreed targets to halt biodiversity loss and prevent the anthropogenic extinction of threatened species, with potentially devastating implications for ecosystems and ecological processes on which human wellbeing and prosperity rely. My research provides novel, important, and timely insights into how such future scenarios could be avoided.

Appendices

Appendix A. Supporting information for Chapter 3

Supplementary Methods S1

Pseudoabsence selection

For many species, comprehensive and reliable absence data are either unavailable or are very difficult to obtain, particularly for highly mobile or poorly studied species (Valavi et al., 2022). To overcome the lack of 'true absence' data, many SDM approaches rely on generating so-called 'pseudoabsence' points sampled from areas outside of the species' known range (Elith and Leathwick, 2009). For regression-based methods such as generalised linear models (GLMs) and generalised additive models (GAMs) a very large number of pseudoabsences has been recommended (>10,000; Barbet-Massin et al., 2012). However, when using global rasterised climate models at 0.5-degree resolution, 10,000 pseudoabsence points would cover approximately 1/6th of global land surface, including many cells that are too distant from the species range to provide meaningful information. Therefore, I randomly sampled 1,000 pseudoabsence points from the biogeographic realms (Holt et al., 2013) where each species currently occurs (Titley et al., 2021).

LUH2-IUCN habitat crosswalk

Here, I provide brief details on the crosswalk approach developed by Titley (2022) for converting LUH2 land use categories to IUCN Level 1 habitat classifications. Whereas previous studies (e.g. Powers and Jetz, 2019) have relied on expert opinion to determine crosswalk relationships, this quantitative approach ensures the crosswalk matches are best supported by published data. First, a global map of IUCN Level 1 habitat types was obtained from Jung et al. (2020), and overlaid with the LUH2 map of fractional cover for the 12 land use classes for the year 2015, approximating present conditions. Generalised linear models were fitted for each IUCN habitat category, with the 12 LUH2 classes used as predictor variables. The LUH2 class(es) that had the strongest positive association (quantified by model effect size) with each IUCN habitat category were then matched in the crosswalk.

The crosswalk (Titley, 2022) also contained two additional rules: species classed as forest-dependent (associated with forest habitat types only) by the IUCN data were constrained to primary forest and secondary forest greater than 30 years old (Newbold, 2015) under the LUH2 data, while species associated with the IUCN Habitat category 'Subtropical/Tropical Heavily Degraded Former Forest' were assumed to be able to persist in young (< 30 years old) secondary forest, even if the species was not associated with other forest types in the IUCN data.

Calibrating species population declines: worked example

I used species' total Area of Occupiable Habitat (AOOH) within their climatically suitable range as a proxy for overall population size, and predicted changes in Red List status using IUCN Criterion A3, with population changes calculated over a timeframe of 10 years or three generations, whichever is longer (IUCN, 2022). Under this criterion, species are classified as Vulnerable, Endangered, and Critically Endangered if they suffer or are projected to suffer a population reduction of 30%, 50%, or 80%, respectively (IUCN, 2022). However, three generation lengths did not always round evenly to the decadal timesteps of my SDMs. For each Red List status prediction, I therefore calculated a corrected baseline population size (baseline AOOH) to account for these discrepancies and remove bias induced by inappropriate setting of baseline years, using Eqn 2:

Eqn 2:
$$P_c = P_t\left(\left(\left(\frac{P_b}{P_t}\right)^{\frac{1}{t-c}}\right)^{g}\right)$$

…where P_c is the corrected baseline population size P for baseline year c. Timestep t represents the decadal timestep (e.g. 2030) for which the Red List projection is being made. The uncorrected baseline (e.g. 1985) population is indicated by P_b and g represents the number of years in three generations, with $g \geq 10$ in all cases. Therefore, $\left(\frac{P_b}{P_t}\right)^{\frac{1}{t-c}}$ represents the annual rate of population change for the time period between t and c, which is then extended for g years to retrospectively estimate P_c based on P_t. Finally, I estimated standardised percentage change in species population size (Δ_p) using Eqn 3:

Eqn 3:
$$\Delta_p = 100\left(\frac{P_t - P_c}{P_c}\right)$$

As a worked example, let Least Concern species S have a 'current' (1985) population of 100 and a 2030 projected population of 80, and a generation length of five years such that g = 15 and the adjusted baseline year b is 2015. The annual rate of population change $\left(\frac{P_b}{P_t}\right)^{\frac{1}{t-c}}$ therefore equals $\left(\frac{100}{80}\right)^{1/45}$ or 1.005. Over 15 years the overall proportional change in P is therefore 1.005^{15} or 1.078, meaning the corrected baseline P_{2015} is 80 x 1.078 = 86.24. Therefore, $\Delta_p = 100\left(\frac{80-86.24}{86.24}\right)$ or a standardised percentage population change from the adjusted baseline year of -7.24%. At this stage, the species would not be facing a severe enough decline to be moved towards a threatened IUCN Red List category. To calculate Δ_p for the same species S for the year 2070, we would round up g to the nearest decade (20 years) to find the uncorrected baseline population year P_{2050}. Let P_{2050} = 50 and P_{2070} = 20. The annual rate of population change $\left(\frac{P_b}{P_t}\right)^{\frac{1}{t-c}}$ in this case therefore equals $\left(\frac{50}{20}\right)^{1/20}$ or 1.0469. Over 15 years the overall proportional change in P is therefore 1.0469^{15} or 1.988, meaning the corrected baseline P_{2055} is 20 x 1.988 = 39.76. Therefore, $\Delta_p = 100\left(\frac{20-39.76}{39.76}\right)$ or a standardised percentage population change from the adjusted baseline year of -49.7%. In this case, species S would be moved to the Vulnerable Red List category, and is very close to the 50% reduction threshold for being categorised as Endangered.

Trait data imputation details

Mammals

Estimates of mammal natal dispersal distance *d* were derived from allometric equations given by Sutherland et al., 2000. First, body mass (g) estimates for 5,400 mammal species were obtained from the EltonTraits dataset (Wilman et al., 2014), and body length (mm) estimates for 1,941 species were obtained from the PanTHERIA database (Jones et al., 2009). Linear equations associating log10 body mass and log10 body length were fitted for placental (R^2 = 0.9705) and non-placental (R^2 = 0.9307) mammals, to fill in gaps in body length and mass data. Estimates of generation length for 5,426 species and age at first reproduction (AFR) for 1,053 species were obtained from Pacific et al. (2015). Missing mammal body mass, body length, generation length and AFR were then phylogenetically imputed using the *Rphylopars*

R package (Goolsby et al., 2017). Using these imputed data, I then applied the allometric equations given in Sutherland et al. (2000) to estimate *d* for carnivorous (> 80% diet made up of animal matter; Wilman et al., 2014) and herbivorous/omnivorous mammal species.

Birds

I obtained bird body mass (g) data for 9,993 species from Wilman et al. (2014). Comprehensive AFR and generation length estimates for 11,126 were obtained from Bird et al. (2020). Species dispersal estimates based on hand-wing index and other morphometric traits (Sheard et al., 2020) were available for 8,270 species from Stewart et al. (2022). These data were then merged, and missing data were phylogenetically imputed using *Rphylopars* for volant and non-volant birds separately.

Reptiles

Reptile body mass (g) data were obtained from Meiri et al. (2021), which provided comprehensive mass estimates covering 11,133 species. Body length (mm) estimates for 9,824 snakes, lizards, and tuatara (Lepidosauria), alongside allometric equations for converting length to mass, were obtained from Feldman et al. (2016). These allometric equations were used to fill gaps in body length data, using the mass data from Meiri et al. (2021). The dataset was then merged with the IUCN taxonomy, and data for species present in the IUCN taxonomy but missing from the morphological dataset (n = 175) had their length and mass estimates phylogenetically imputed in *Rphylopars.* Turtle (Testudines) carapace length data were obtained for 255 species from Regis and Meik (2017), and simple linear models were fitted associating carapace length estimates with body mass, for turtles (R^2 = 0.864) and tortoises (Testudinidae; R^2 = 0.775) separately. As with snakes, lizards, and tuatara, missing morphometric data were phylogenetically imputed for 38 species after matching to IUCN taxonomy. Crocodilian body length data were derived from allometric equations given in Slavenko et al. (2016), which were then applied to mass data from Meiri et al. (2021).

Estimates of *d* for 56 reptile species were gathered from a literature search (Supplementary Data S1). Given the sparse data available, phylogenetic imputation resulted in spurious results. Therefore, simple linear models associating log(*d*) with logged body mass (g) were fitted (R^2 = 0.5495) to fill in missing data. While this model had relatively low explanatory power, it was the best model available given the limited data. Regardless, relatively low dispersal capabilities of reptiles meant that errors would rarely qualitatively impact my results at the 0.5/0.25-degree resolution of my SDMs. Estimates of AFR and total longevity were obtained from the AnAge database (de Magalhaes and Costa, 2009) for 74 and 522 reptile species, respectively. Estimates of annual survival were obtained for 108 species from Pike et al. (2008). Missing data for AFR, longevity and annual survival were filled by taking the family average, then the order average, and finally the average across the entire taxonomic class until no missing data remained. Reptilian generation length was then estimated by calculating half of the species productive lifespan using AFR, annual survival, and longevity estimates (Pacifici et al., 2015).

Amphibians

Estimates of body length (snout-vent length, mm) and body mass (g) were obtained for 5,227 and 591 amphibian species, respectively, from the AmphiBIO database (Oliveira et al., 2017). Linear models associated body length with body mass were fitted separately for frogs (Anura; R^2 = 0.688), newts and salamanders (Caudata; R^2 = 0.709) and caecilians (Gymnophiona; R^2 = 0.722). These models were used to fill in missing length and mass data, where possible. Mass and length estimates for the remaining 1,539 amphibians with missing data were then phylogenetically imputed in *Rphylopars*. Estimates of d for 89 amphibian species were obtained from Smith and Green (2005), and fitted to species body mass estimates using a simple linear model as described for reptiles. The amphibian model had very low explanatory power (R^2 = 0.0813). Again, the very low dispersal capabilities of most amphibians means that these uncertainties are unlikely to qualitatively impact my results, given the spatial resolution of my SDMs. Data on amphibian longevity (n = 78 species) and AFR (n = 174 species) were extracted from AnAge and imputed as described for reptiles. Annual survival was set at a constant of 0.67 (a typical figure based on the very limited data available on AnAge), and these data were then used to estimate amphibian generation length as described for reptiles.

Table S1. Summary of variables included in best performing models for each taxon-latitudinal band species subset. Dots indicate that the variable is included in the best supported model.

Species Subset	bio_1	bio_4	bio_5	bio_6	bio_12	bio_13	bio_14	bio_15
Boreal mammals	▪	▪				▪	▪	▪
Tropical mammals	▪	▪				▪	▪	▪
Austral mammals	▪	▪				▪	▪	▪
Boreal birds	▪	▪				▪	▪	▪
Tropical birds		▪	▪			▪	▪	▪
Austral birds	▪	▪				▪	▪	▪
Boreal reptiles	▪	▪				▪	▪	▪
Tropical reptiles	▪	▪				▪	▪	▪
Austral reptiles	▪	▪				▪	▪	▪
Boreal amphibians	▪	▪				▪	▪	▪
Tropical amphibians		▪	▪			▪	▪	▪
Austral amphibians		▪	▪			▪	▪	

bio_1 = Mean annual temperature (°C)
bio_4 = Temperature seasonality (sd x 100)
bio_5 = Max. temperature of warmest month (°C)
bio_6 = Min. temperature of coldest month (°C)
bio_12 = Annual precipitation (mm)
bio_13 = Precipitation of wettest month (mm)
bio_14 = Precipitation of driest month (mm)
bio_15 = Precipitation seasonality (CV)

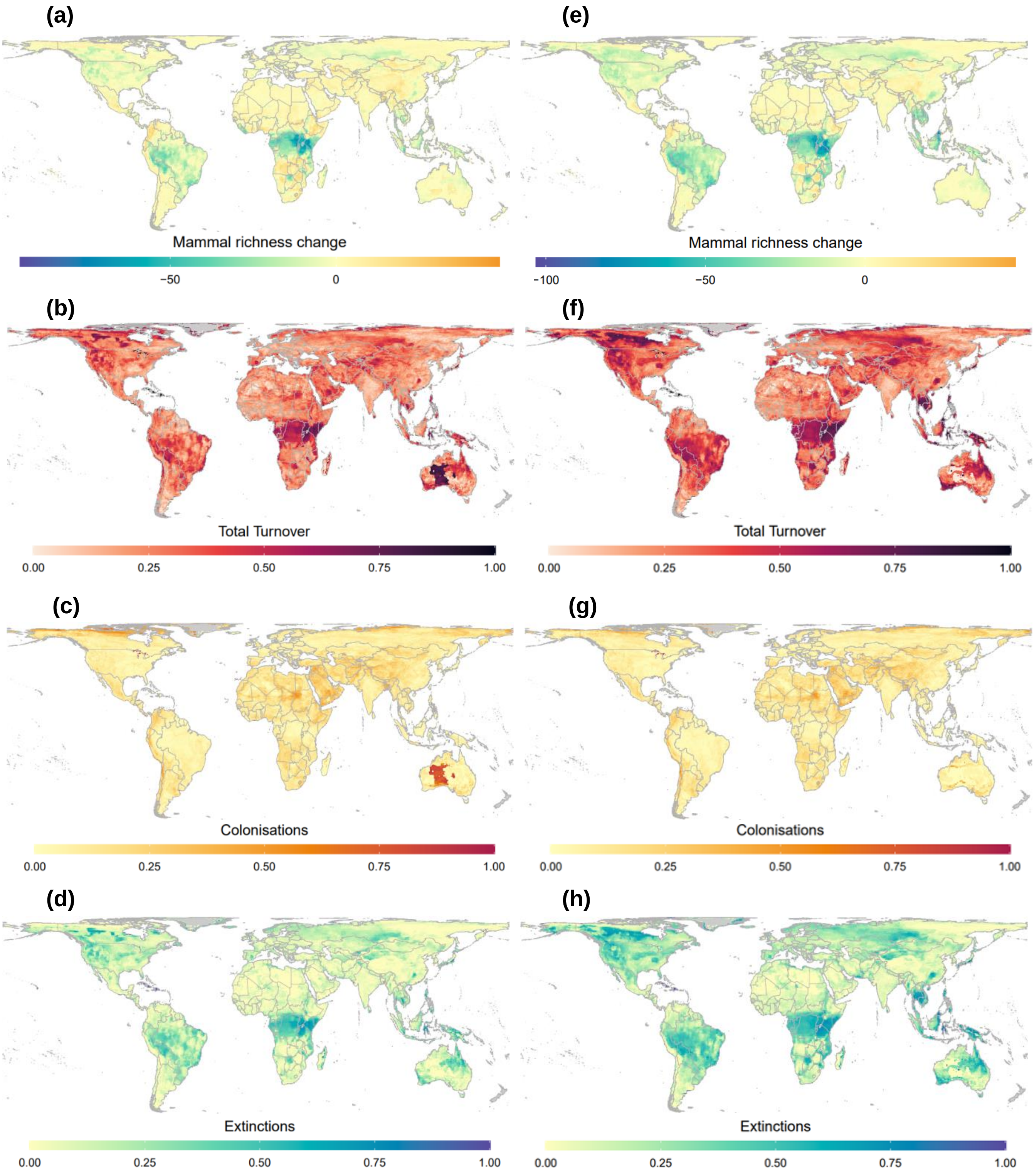


Figure S1. Change in terrestrial mammal biodiversity patterns under SSP2-4.5 (a-d) and SSP5-8.5 (e-h), up to the year 2070. (a, e) Change in overall species richness per ~25 km grid cell, with species classed as ‘present’ if they have at least 1% suitable habitat within the grid cell. (b, f) Overall turnover in terrestrial mammal community per grid cell. Turnover is calculated as the proportion of species gained (e.g. through colonisation) or lost (e.g. through local extinction) relative to the total number of species that occur in the grid cell across both current and future (2070) time periods (Hallett et al., 2016). (c, g) Rate of colonisation per grid cell (proportion of novel species in 2070 relative to total species richness across both timesteps). (d, h) Rate of local extinctions per grid cell (proportion of species lost by 2070 relative to total richness across both timesteps).

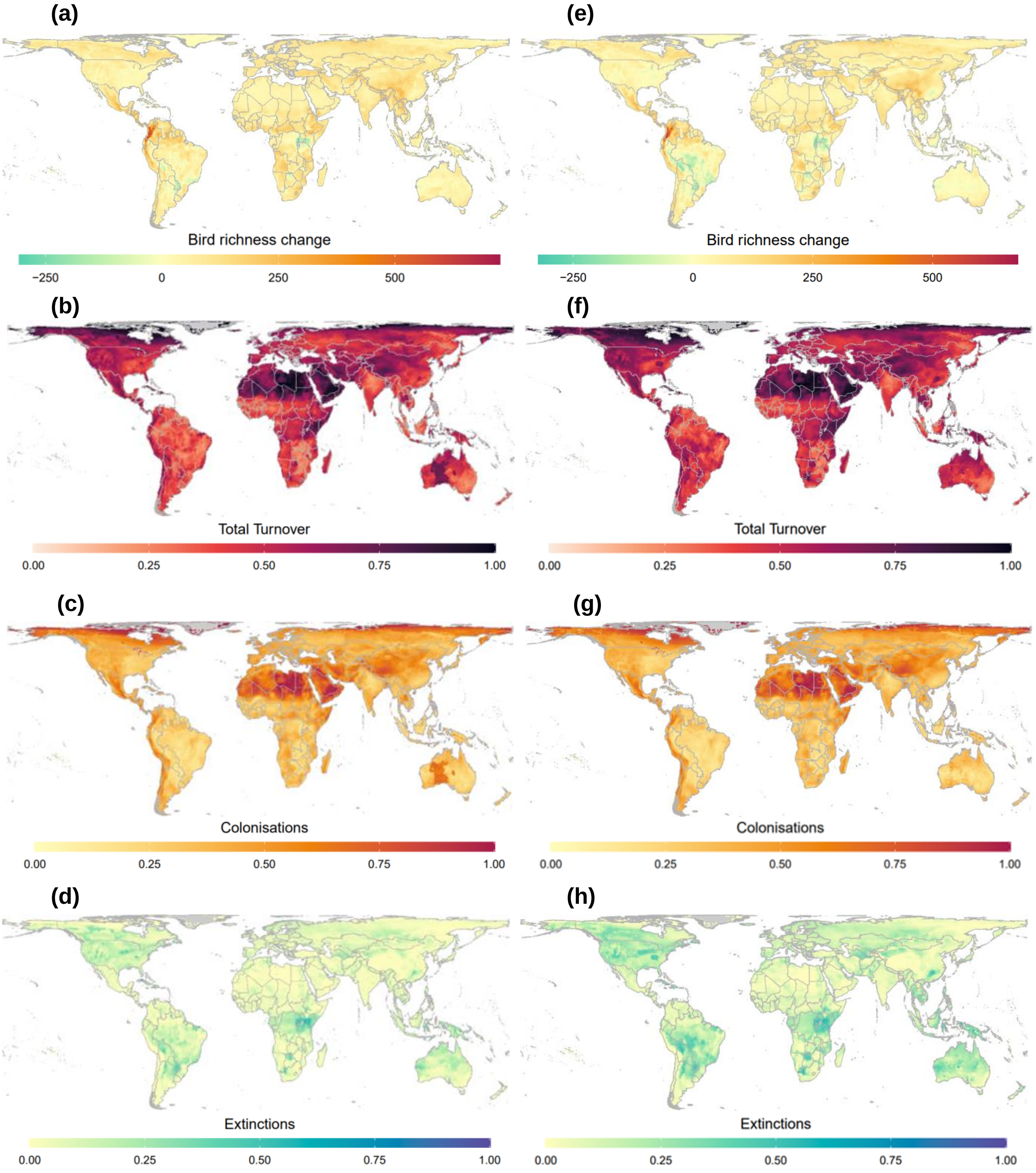


Figure S2. Change in terrestrial bird biodiversity patterns under SSP2-4.5 (a-d) and SSP5-8.5 (e-h), up to the year 2070. (a, e) Change in overall species richness per ~25 km grid cell, with species classed as 'present' if they have at least 1% suitable habitat within the grid cell. (b, f) Overall turnover in terrestrial bird community per grid cell. Turnover is calculated as the proportion of species gained (e.g. through colonisation) or lost (e.g. through local extinction) relative to the total number of species that occur in the grid cell across both current and future (2070) time periods (Hallett et al., 2016). (c, g) Rate of colonisation per grid cell (proportion of novel species in 2070 relative to total species richness across both timesteps). (d, h) Rate of local extinctions per grid cell (proportion of species lost by 2070 relative to total richness across both timesteps).

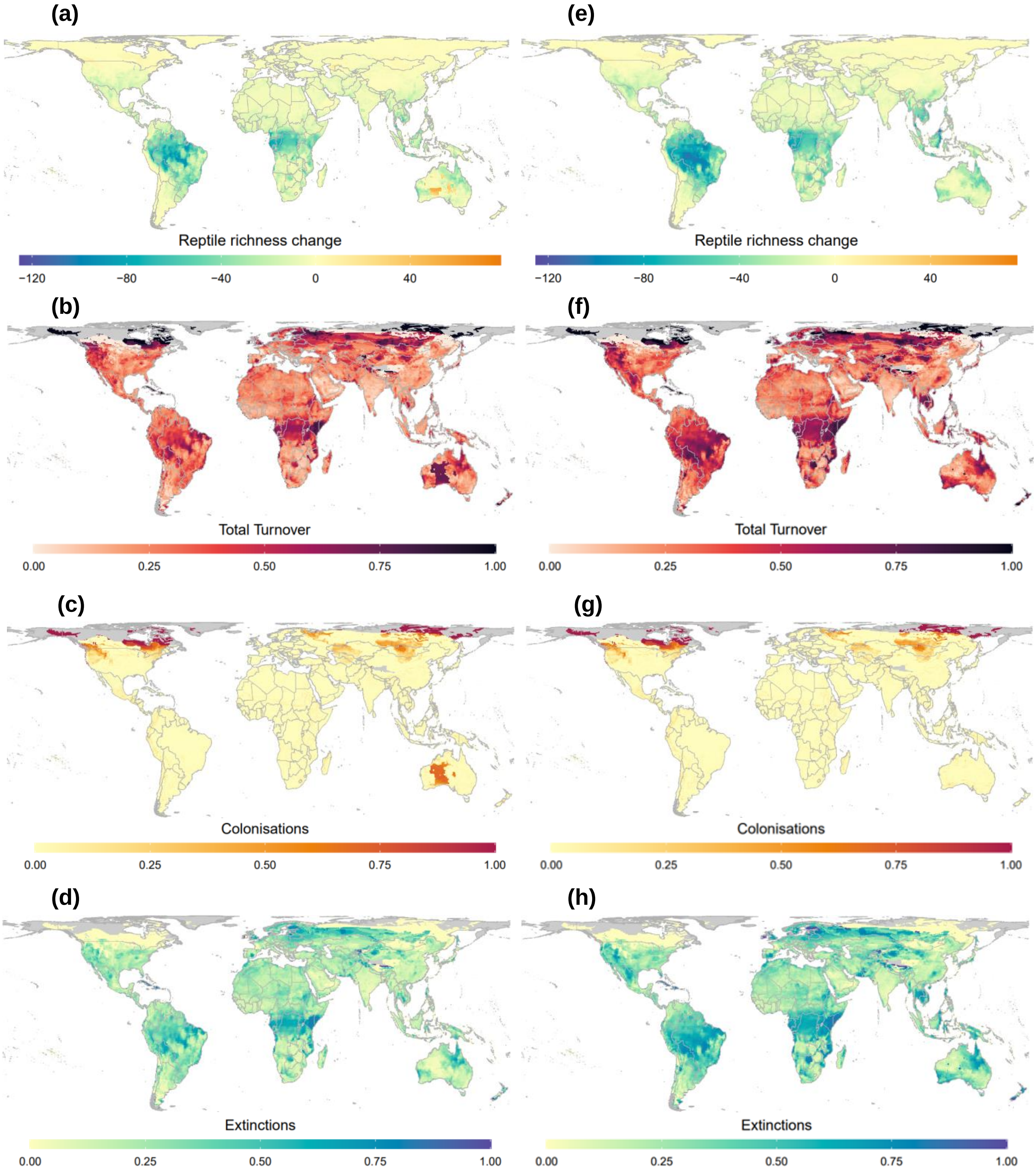


Figure S3. Change in terrestrial reptile biodiversity patterns under SSP2-4.5 (a-d) and SSP5-8.5 (e-h), up to the year 2070. (a, e) Change in overall species richness per ~25 km grid cell, with species classed as 'present' if they have at least 1% suitable habitat within the grid cell. (b, f) Overall turnover in terrestrial reptile community per grid cell. Turnover is calculated as the proportion of species gained (e.g. through colonisation) or lost (e.g. through local extinction) relative to the total number of species that occur in the grid cell across both current and future (2070) time periods (Hallett et al., 2016). (c, g) Rate of colonisation per grid cell (proportion of novel species in 2070 relative to total species richness across both timesteps). (d, h) Rate of local extinctions per grid cell (proportion of species lost by 2070 relative to total richness across both timesteps).

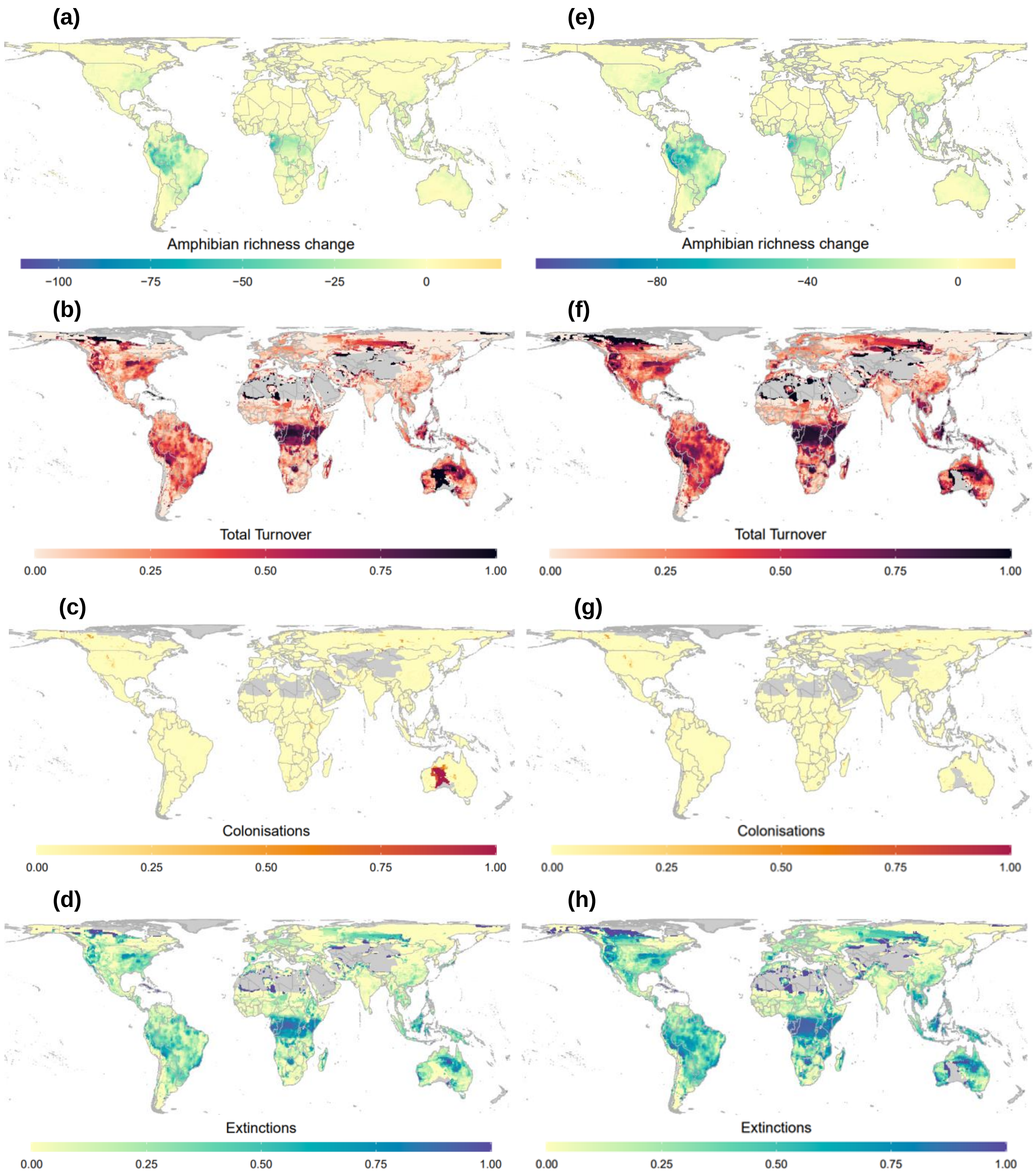


Figure S4. Change in terrestrial amphibian biodiversity patterns under SSP2-4.5 (a-d) and SSP5-8.5 (e-h), up to the year 2070. (a, e) Change in overall species richness per ~25 km grid cell, with species classed as ‘present’ if they have at least 1% suitable habitat within the grid cell. (b, f) Overall turnover in amphibian community per grid cell. Turnover is calculated as the proportion of species gained (e.g. through colonisation) or lost (e.g. through local extinction) relative to the total number of species that occur in the grid cell across both current and future (2070) time periods (Hallett et al., 2016). (c, g) Rate of colonisation per grid cell (proportion of novel species in 2070 relative to total species richness across both timesteps). (d, h) Rate of local extinctions per grid cell (proportion of species lost by 2070 relative to total richness across both timesteps).

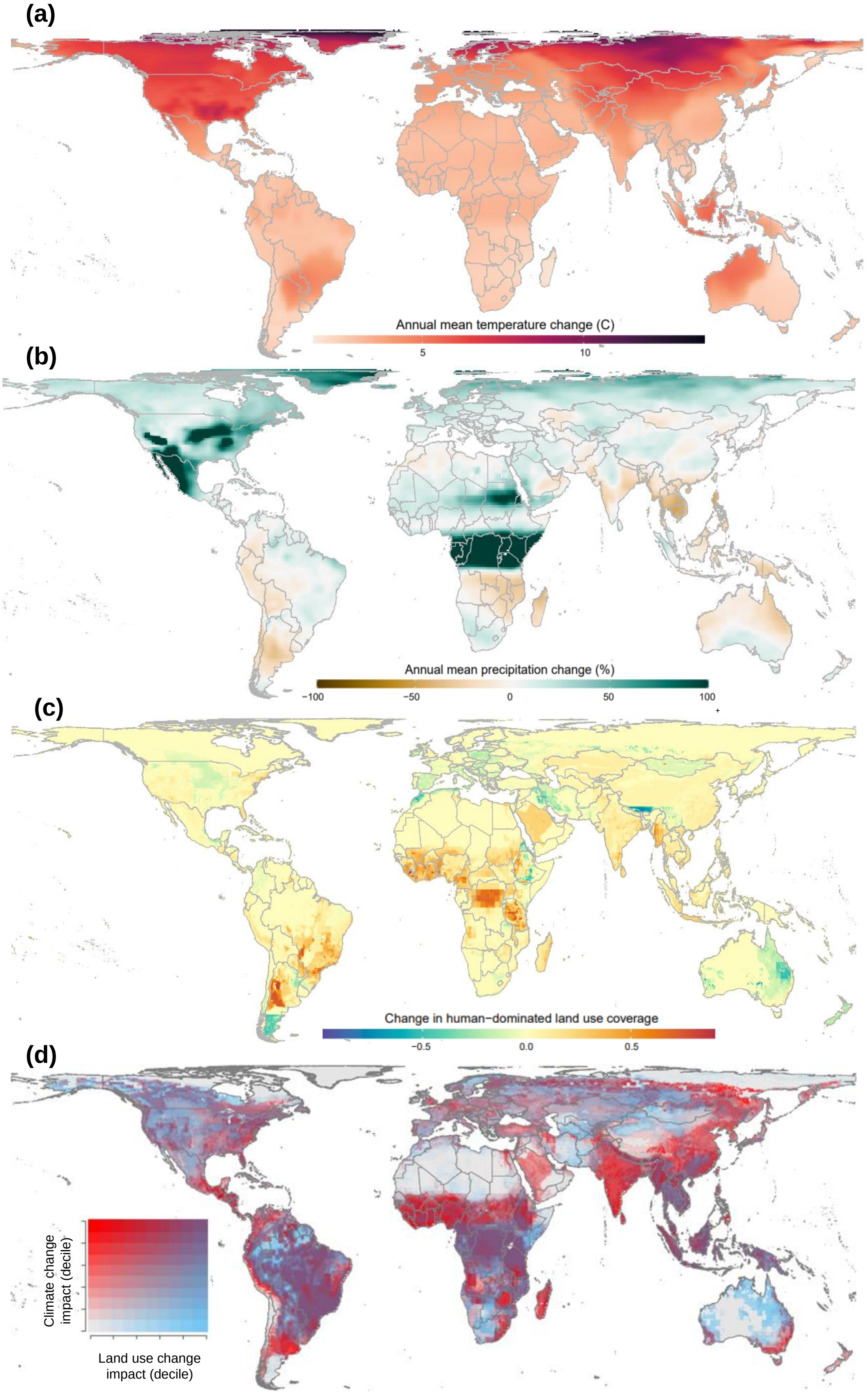


Figure S5. Potential drivers of change in terrestrial vertebrate biodiversity patterns under SSP5-8.5, up to 2070. (a) Mean absolute change in annual mean temperature (°C) per across the three global circulation models (GCMs) used in SDM. (b) Mean proportional change in total annual precipitation across the three GCMs. Colour bar capped at a 100% increase to aid visualisation. (c) Rate of conversion from natural habitats to anthropogenic land uses in LUH2 projections. Positive values indicate net conversion of natural habitats to human-dominated land use, and vice versa. (d) Bivariate map showing impacts of climate and land use on species Area of Occupiable Habitat (AOOH) per grid cell.

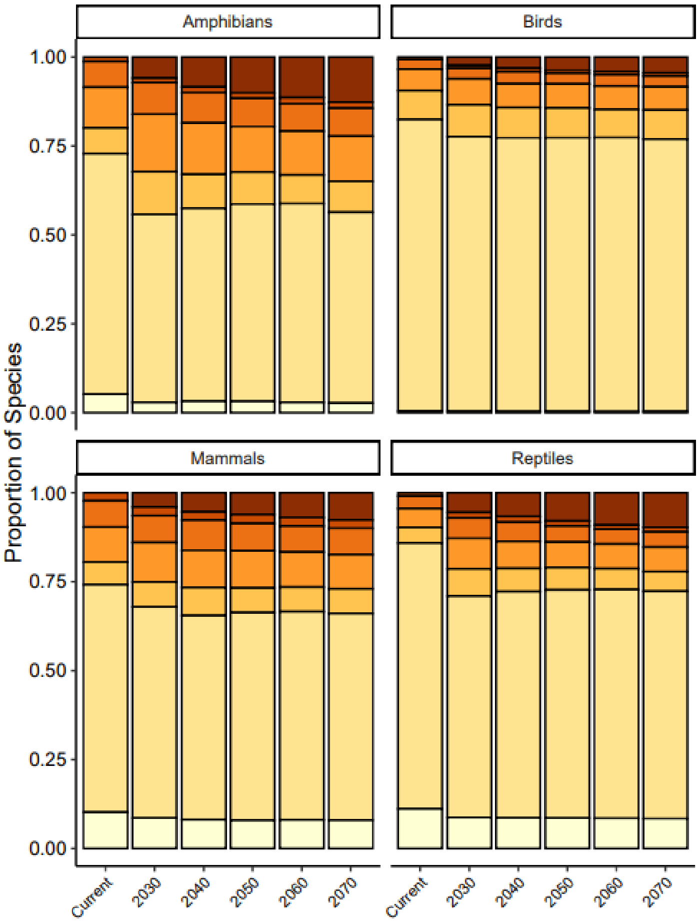


Figure S6. Projected changes in species Red List status under SSP1-2.6, up to the year 2070. Colours indicate Red List status, with darker colours indicating more threatened categories. The bar on the extreme left indicates the current Red List status of modelled species (n = 24,598). Note that these species have ranges large enough to model and therefore many currently threatened species with small ranges are excluded.

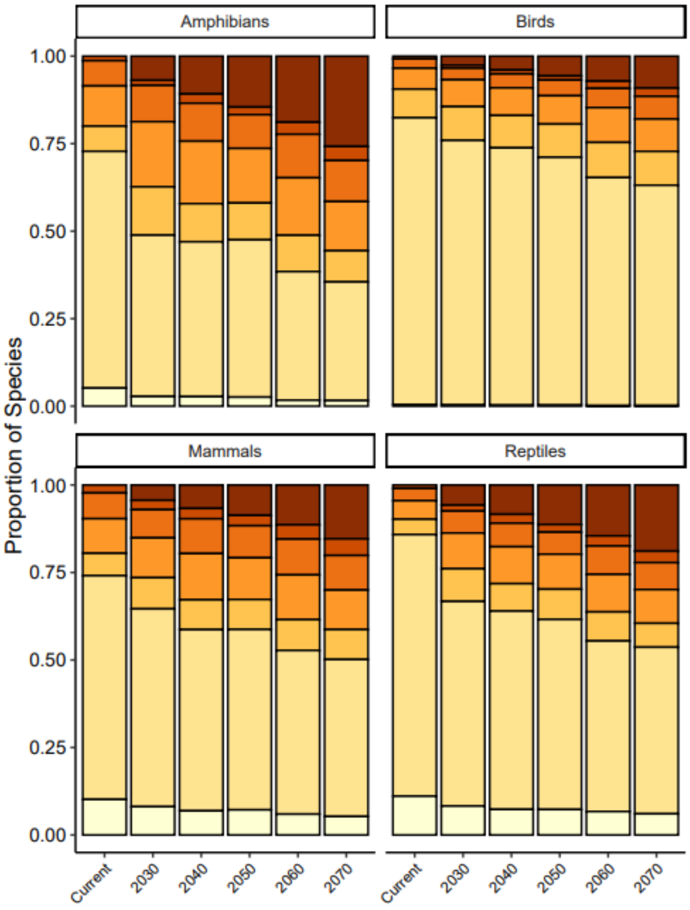


Figure S7. Projected changes in species Red List status under SSP3-7.0, up to the year 2070. Colours indicate Red List status, with darker colours indicating more threatened categories. The bar on the extreme left indicates the current Red List status of modelled species (n = 24,598). Note that these species have ranges large enough to model and therefore many currently threatened species with small ranges are excluded.

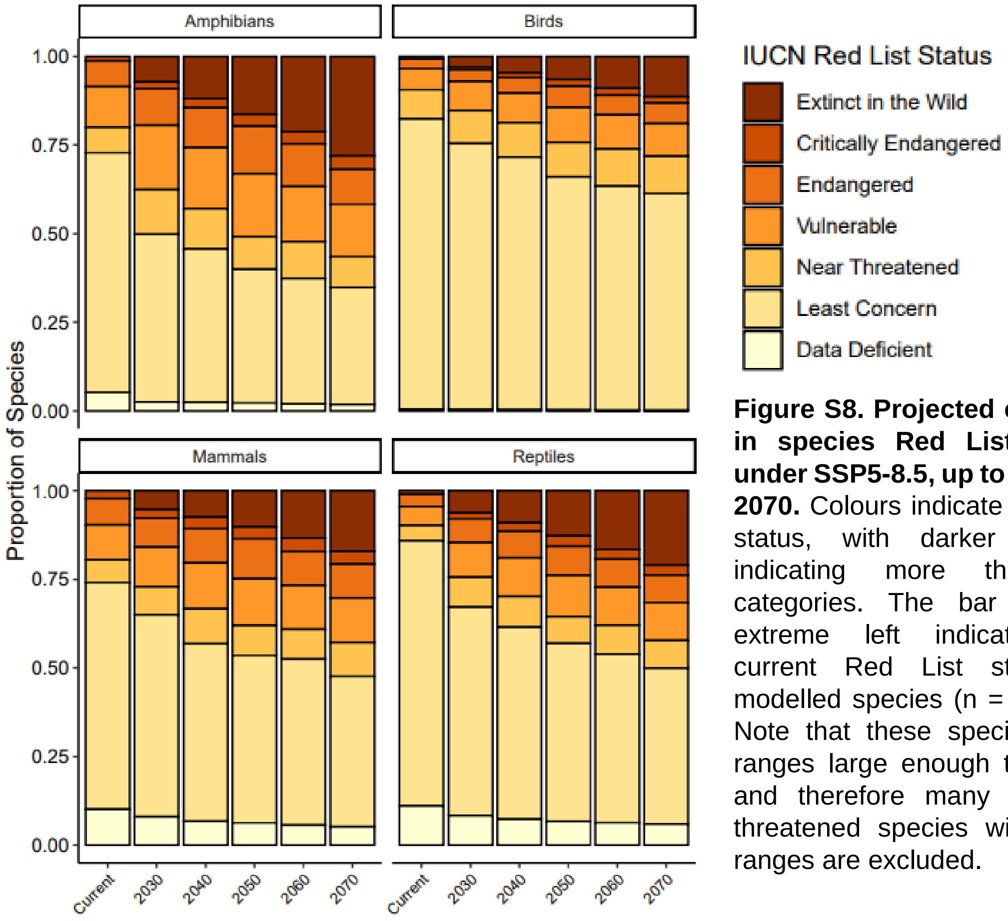


Figure S8. Projected changes in species Red List status under SSP5-8.5, up to the year 2070. Colours indicate Red List status, with darker colours indicating more threatened categories. The bar on the extreme left indicates the current Red List status of modelled species (n = 24,598). Note that these species have ranges large enough to model and therefore many currently threatened species with small ranges are excluded.

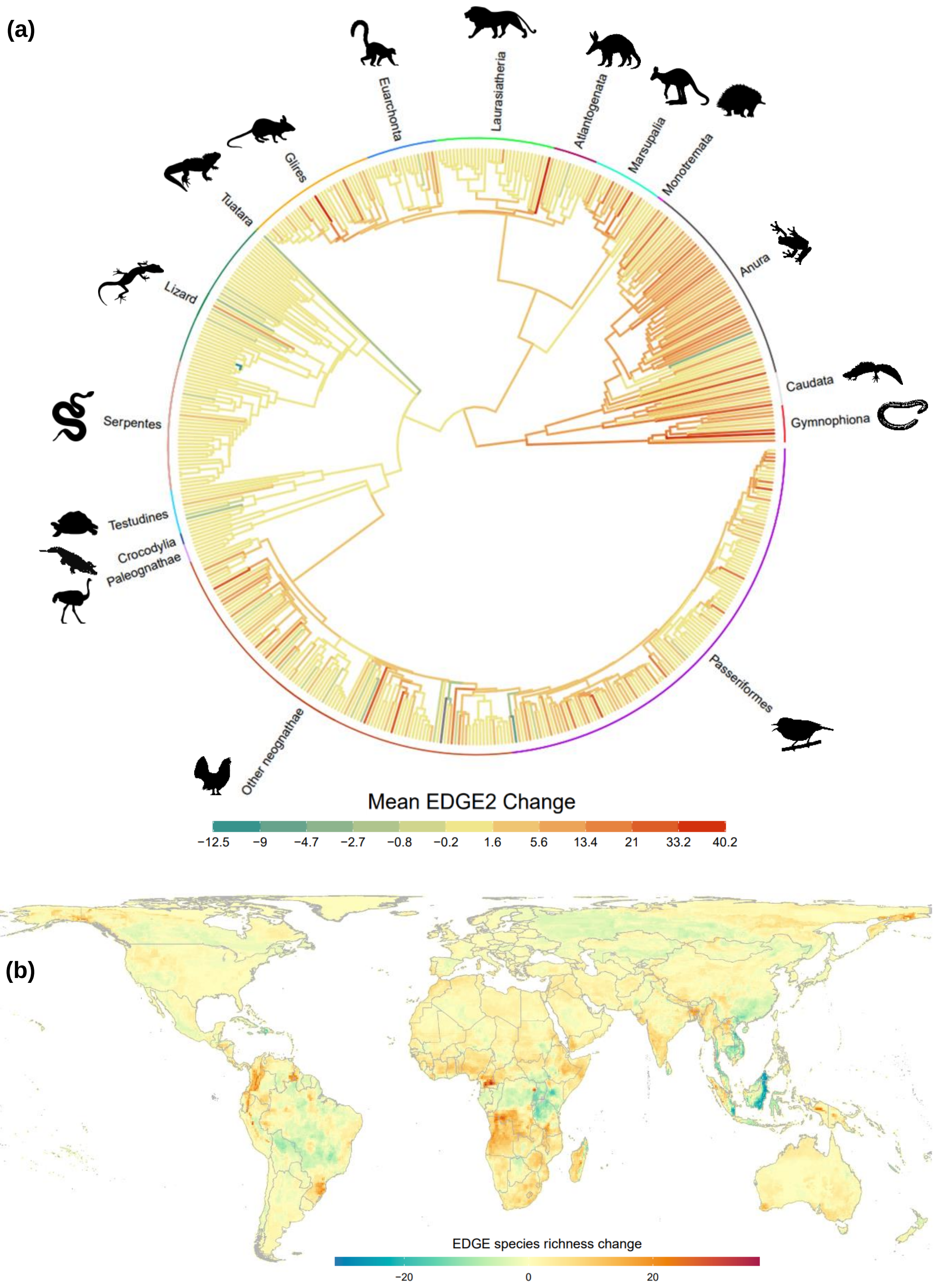


Figure S9. Spatial and phylogenetic shifts in the distribution of threatened evolutionary history under environmental change. (a) Change in mean EDGE score for terrestrial vertebrate families under SSP5-8.5 up to the year 2070. Red branches indicate increases in mean EDGE score, blue branches show decreases in mean EDGE score. Coloured bars represent major taxonomic clades. (b) Change in richness of EDGE species (threatened species with above median EDGE score in ≥ 95% of iterations) richness per ~25 km grid cell, under SSP5-8.5 up to the year 2070. Species classed as 'present' if they have at least 1% suitable habitat within the grid cell.

Appendix B. Supporting information for Chapter 4

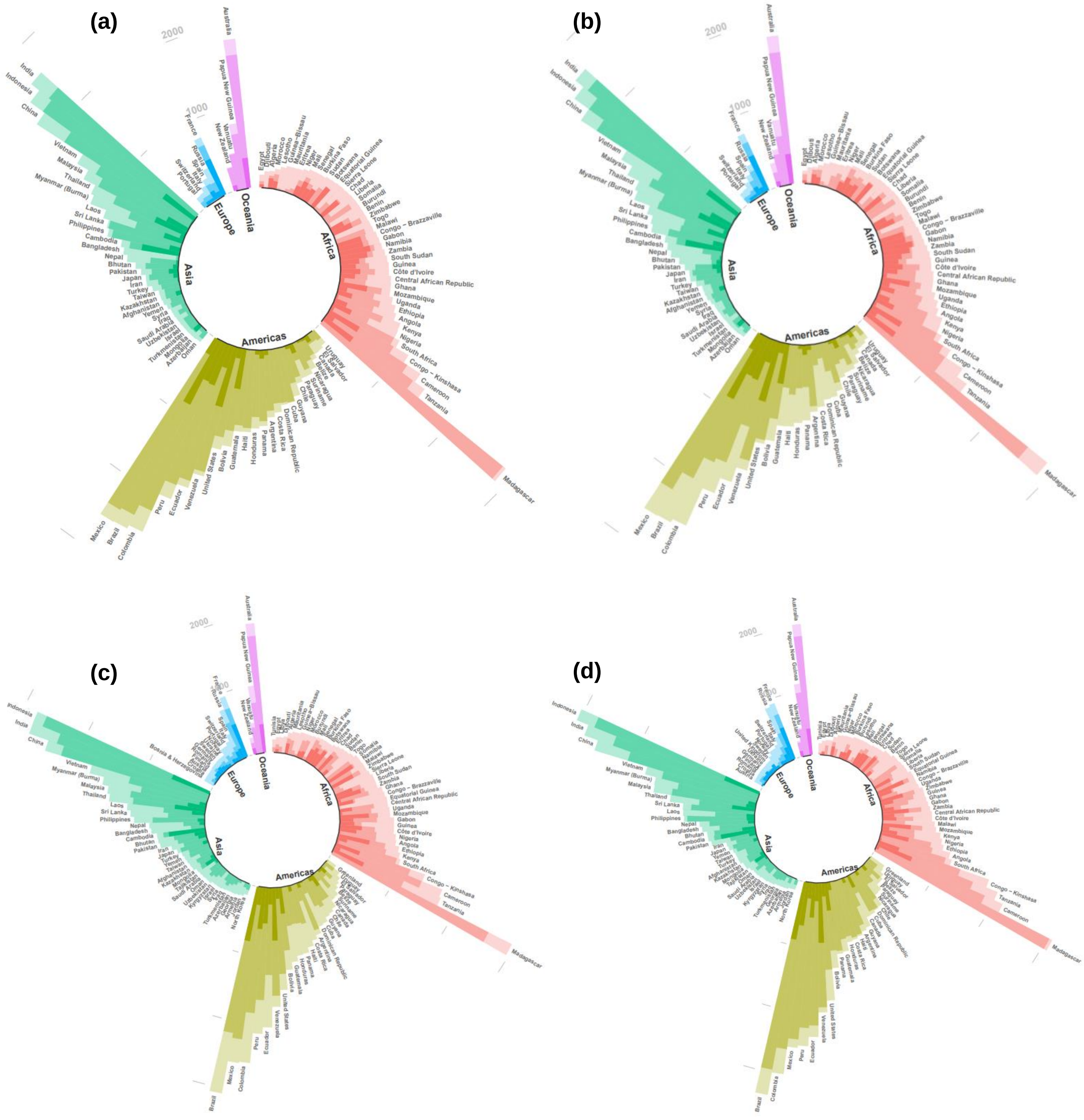


Figure S1. Total threatened evolutionary history in each country, and the proportion that is currently protected or could be protected by additional protected areas. Threatened evolutionary history in each country protected in prioritisations using species' current distributions and current EDGE scores (a-b), and under future conditions using species distributions and projected EDGE scores for the year 2070 under the SSP2-4.5 representative pathway (c-d). (a and c) International co-operation pathway. (b and d) Domestic pathway. Pale bars represent the total threatened evolutionary history occurring in that country. Dark bars represent the threatened evolutionary history currently protected within that country. Medium bars represent the additional threatened evolutionary history protected in each prioritisation scenario. Colours represent major continents. Only countries covering at least 50 grid cells at ~25 km resolution and with total threatened evolutionary history > 150 MY are included. Species were designated 'protected' if range-size based thresholds (Butchart et al., 2015) were met in that country alone, independent of the amount of protected range in other countries.

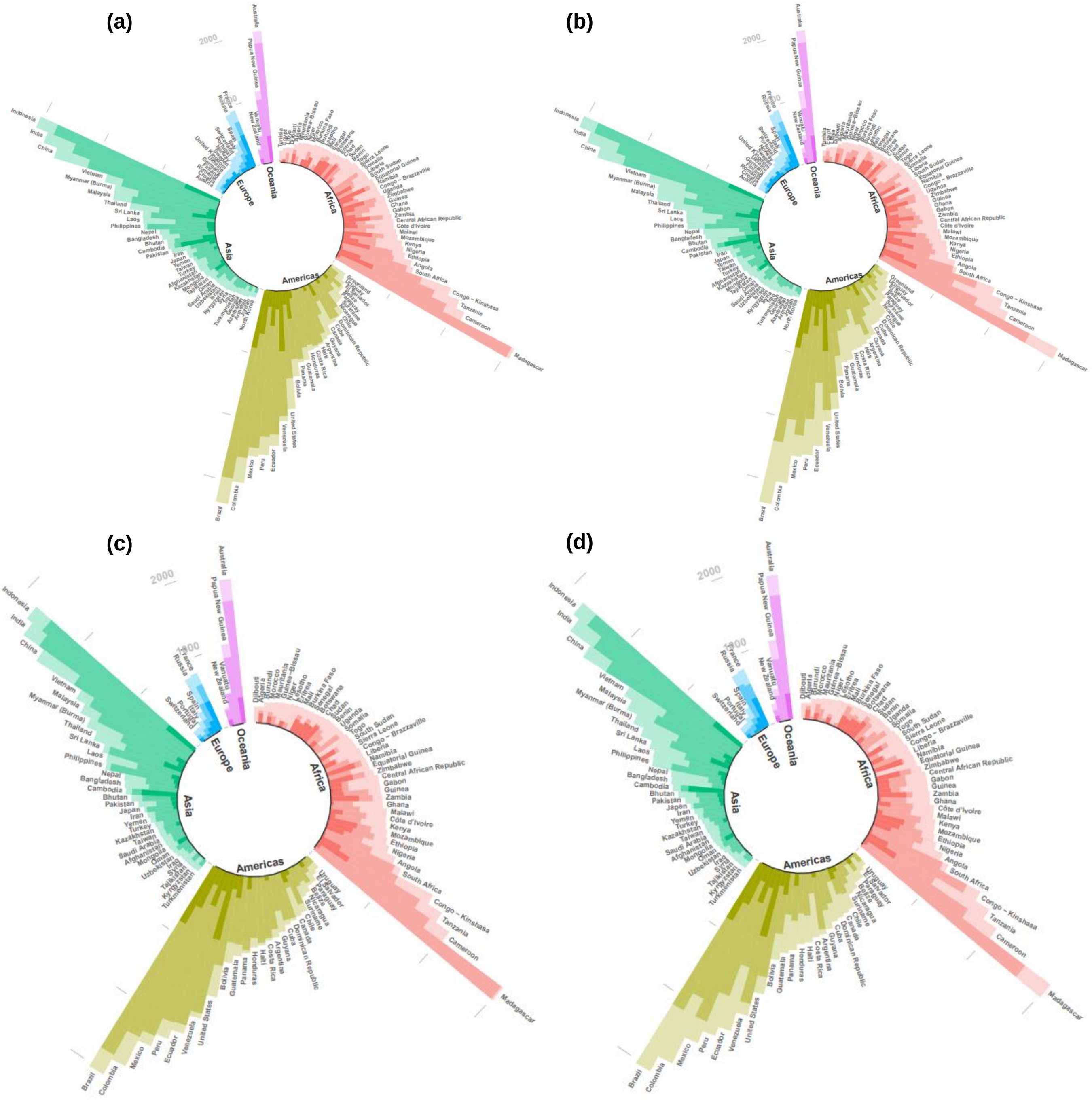


Figure S2. Total threatened evolutionary history in each country, and the proportion that is currently protected or could be protected by additional protected areas. Threatened evolutionary history in each country for prioritisations using species' future distributions and projected EDGE scores for the year 2070 (a-b), and harmonic means of species' Area of Occupiable Habitat (AOOH, Chapter 3) for each decade up to 2070 (c-d), under the SSP5-8.5 representative pathway. (a and c) International co-operation pathway. (b and d) Domestic pathway. Pale bars represent the total threatened evolutionary history occurring in that country. Dark bars represent the threatened evolutionary history currently protected within that country. Medium bars represent the additional threatened evolutionary history protected in each prioritisation scenario. Colours represent major continents. Only countries covering at least 50 grid cells at ~25 km resolution and with total threatened evolutionary history > 150 MY are included. Species were designated 'protected' if range-size based thresholds (Butchart et al., 2015) were met in that country alone, independent of the amount of protected range in other countries.

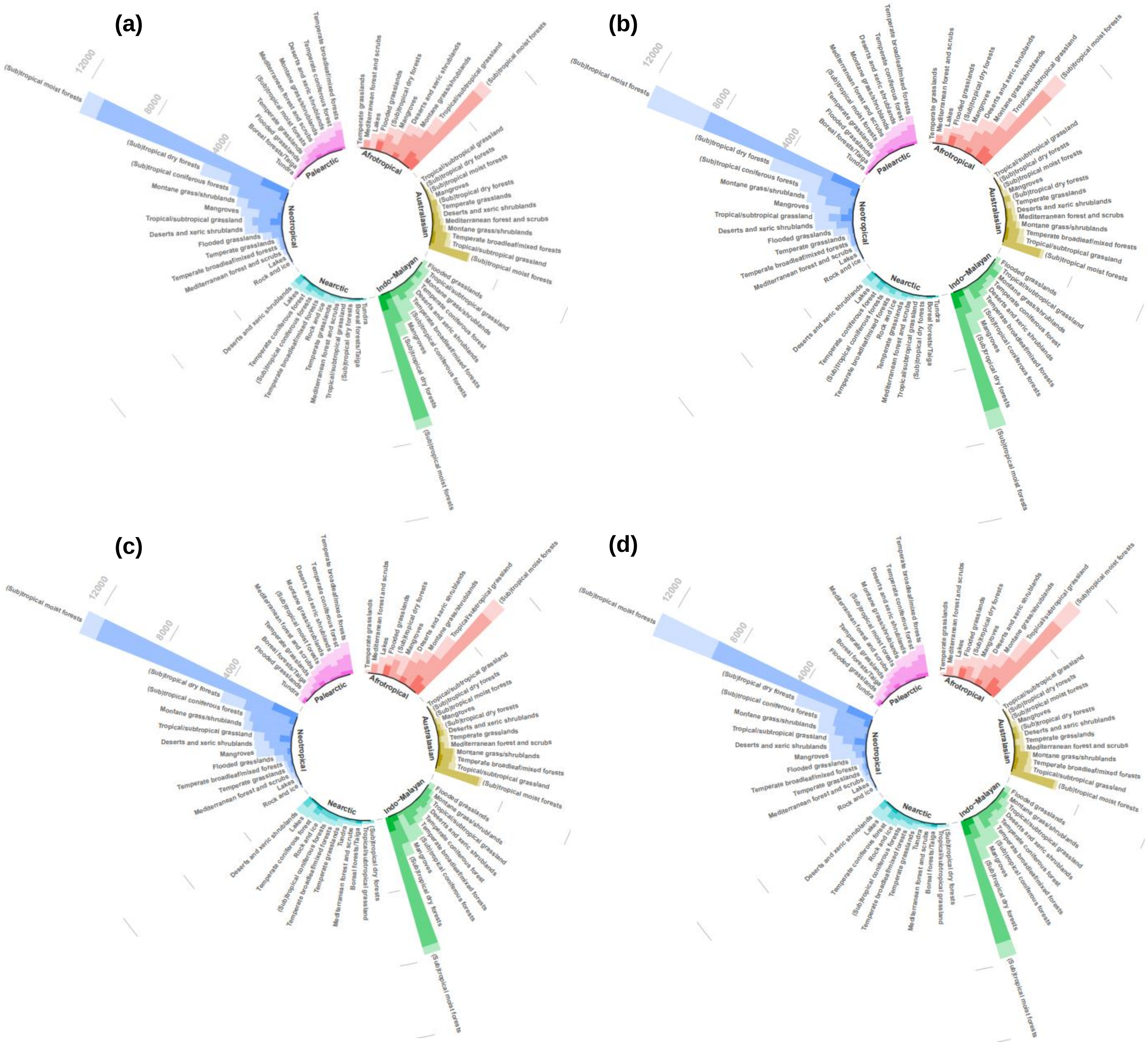


Figure S3. Total threatened evolutionary history in each biome, and the proportion that is currently protected or could be protected by additional protected areas. Threatened evolutionary history in each biome for prioritisations using species' current distributions and current EDGE scores (a-b), and under future conditions using species distributions and projected EDGE scores for the year 2070 under the SSP2-4.5 representative pathway (c-d). (a and c) International co-operation pathway. (b and d) Domestic pathway. Pale bars represent total threatened evolutionary history occurring in that biome. Dark bars represent the threatened evolutionary history currently protected within that biome. Medium bars represent the additional threatened evolutionary history protected in each prioritisation scenario. Colours represent biogeographic realms (Olson et al., 2001). Only biomes covering at least 50 grid cells at ~25 km resolution and with total threatened evolutionary history > 150 MY are included. Species were designated 'protected' if range-size based thresholds (Butchart et al., 2015) were met in that biome alone, independent of the amount of protected range in other biomes. Antarctica was excluded, and data from Australasian and Oceanian realms were combined.

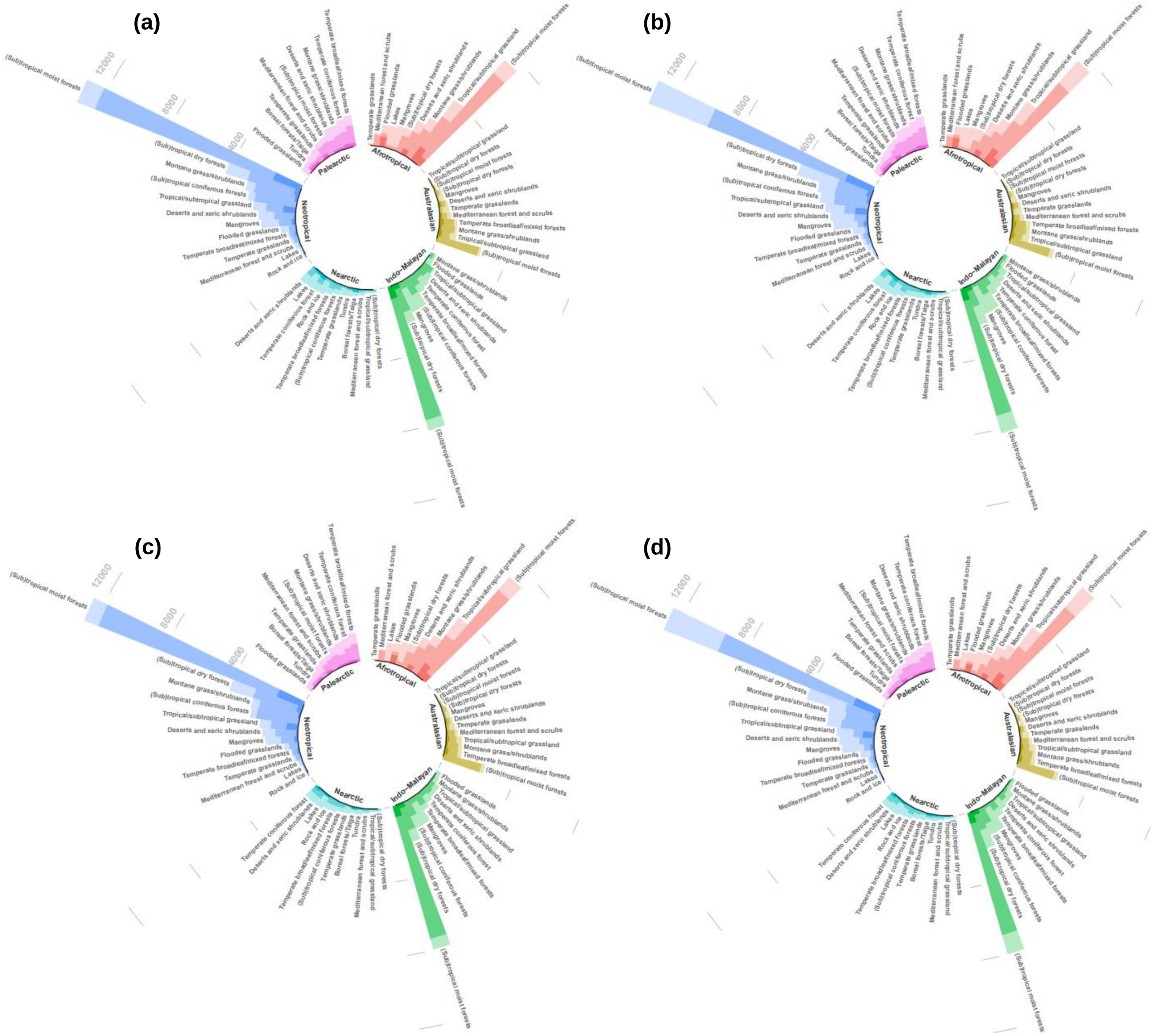


Figure S4. Total threatened evolutionary history in each biome, and the proportion that is currently protected or could be protected by additional protected areas. Threatened evolutionary history in each biome for prioritisations using species' future distributions and projected EDGE scores for the year 2070 (a-b), and harmonic means of species' Area of Occupiable Habitat (AOOH, Chapter 3) for each decade up to 2070 (c-d), under the SSP5-8.5 representative pathway. (a and c) International co-operation pathway. (b and d) Domestic pathway. Pale bars represent total threatened evolutionary history occurring in that biome. Dark bars represent the threatened evolutionary history currently protected within that biome. Medium bars represent the additional threatened evolutionary history protected in each prioritisation scenario. Colours represent biogeographic realms (Olson et al., 2001). Only biomes covering at least 50 grid cells at ~25 km resolution and with total threatened evolutionary history > 150 MY are included. Species were designated 'protected' if range-size based thresholds (Butchart et al., 2015) were met in that biome alone, independent of the amount of protected range in other biomes. Antarctica was excluded, and data from Australasian and Oceanian realms were combined.

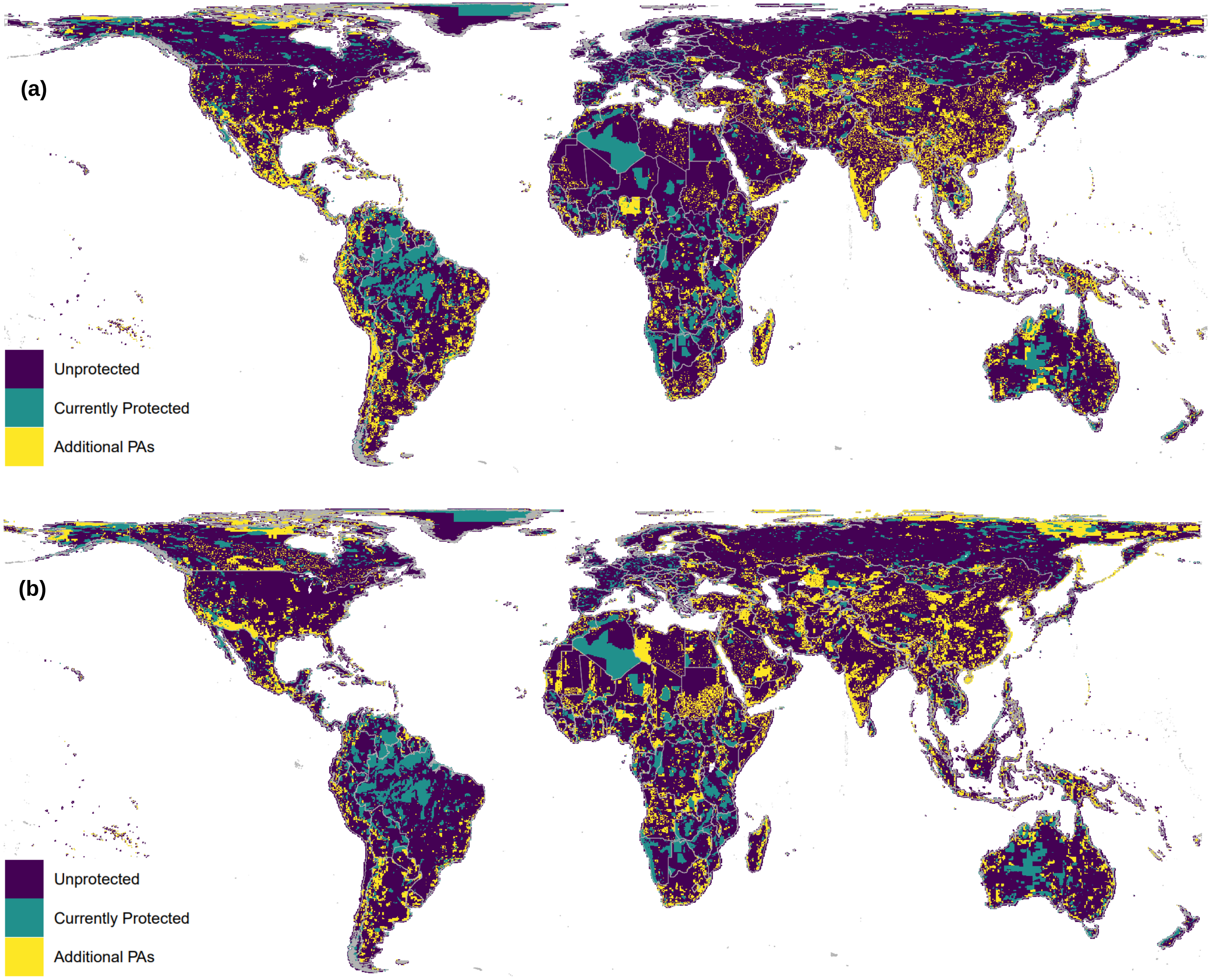


Figure S5. Global distribution of current protected areas and priorities for additional protected areas. Prioritisations under future conditions species' Area of Occupiable Habitat (AOOH, Chapter 3) in each planning unit and projected EDGE scores for the year 2070 under SSP2-4.5. Prioritisations using the international co-operation (a) and the domestic pathway (b).

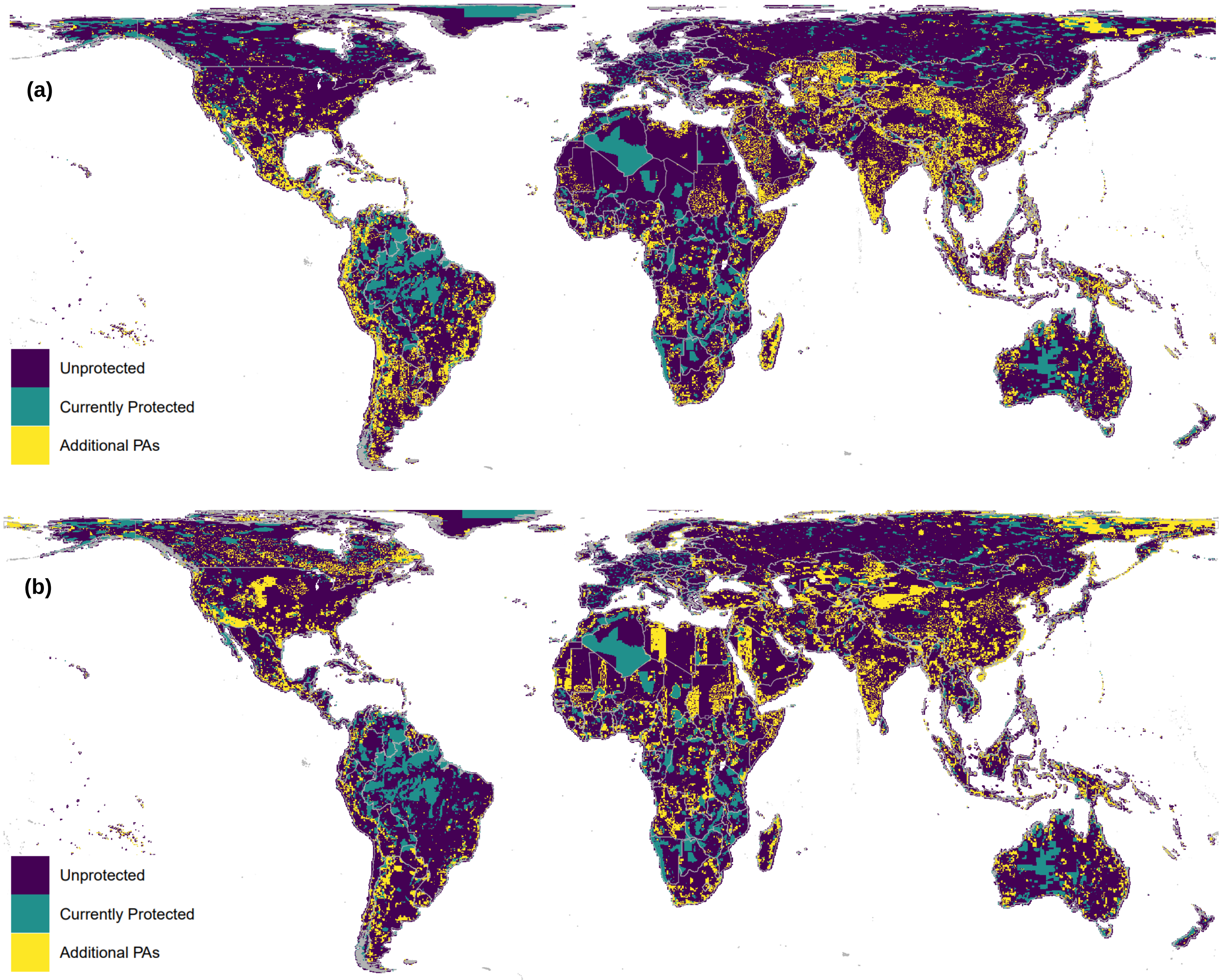


Figure S6. Global distribution of current protected areas and priorities for additional protected areas. Prioritisations under future conditions species' Area of Occupiable Habitat (AOOH, Chapter 3) in each planning unit and projected EDGE scores for the year 2070 under SSP5-8.5. Prioritisations using the international co-operation (a) and the domestic pathway (b).

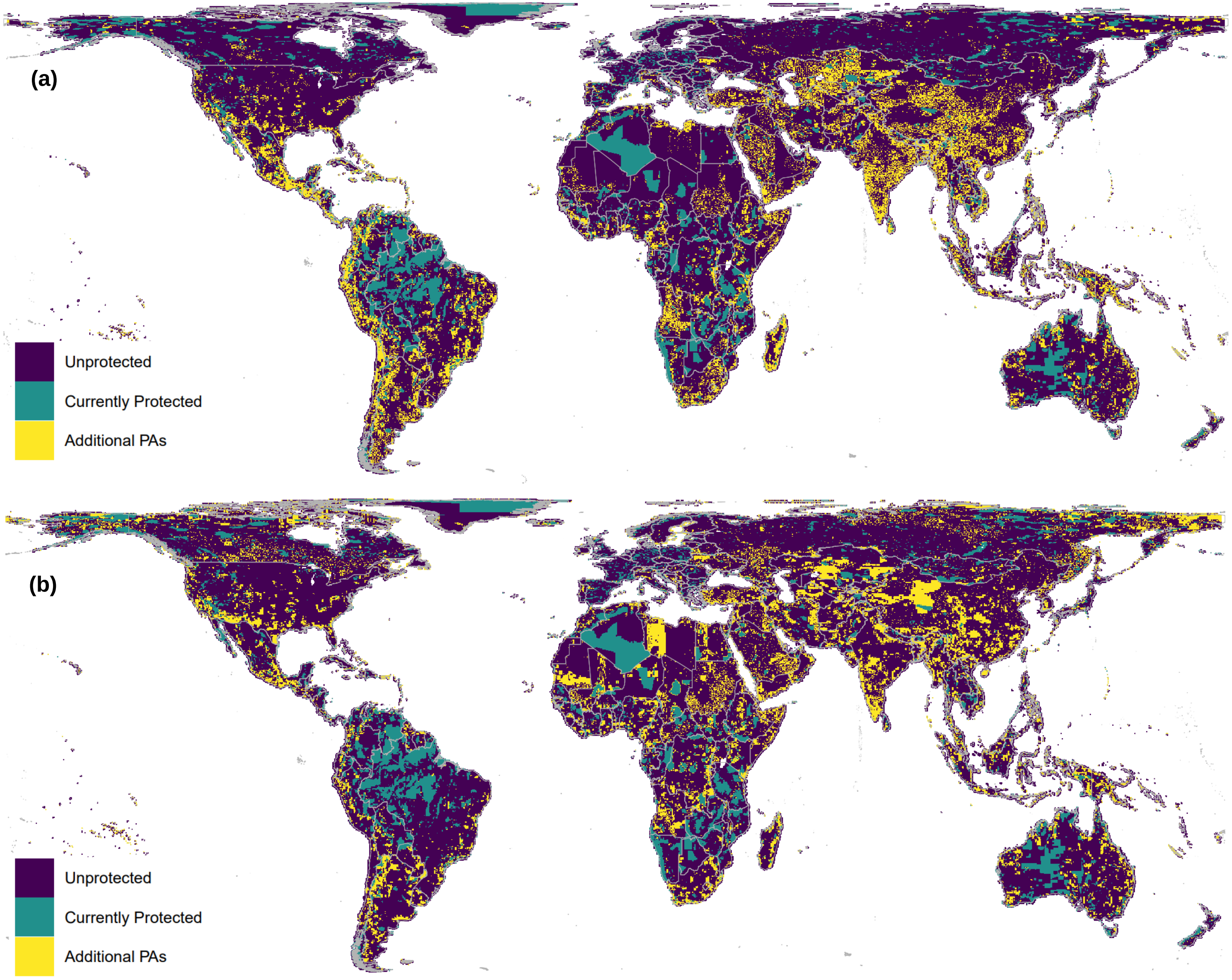


Figure S7. Global distribution of current protected areas and priorities for additional protected areas. Prioritisations under future conditions using harmonic means of species' Area of Occupiable Habitat (AOOH, Chapter 3) in each planning unit for all decadal timesteps up to 2070, and projected EDGE scores for 2070, under SSP5-8.5. Prioritisations using the international co-operation (a) and the domestic pathway (b).

Appendix C. Supporting information for Chapter 5

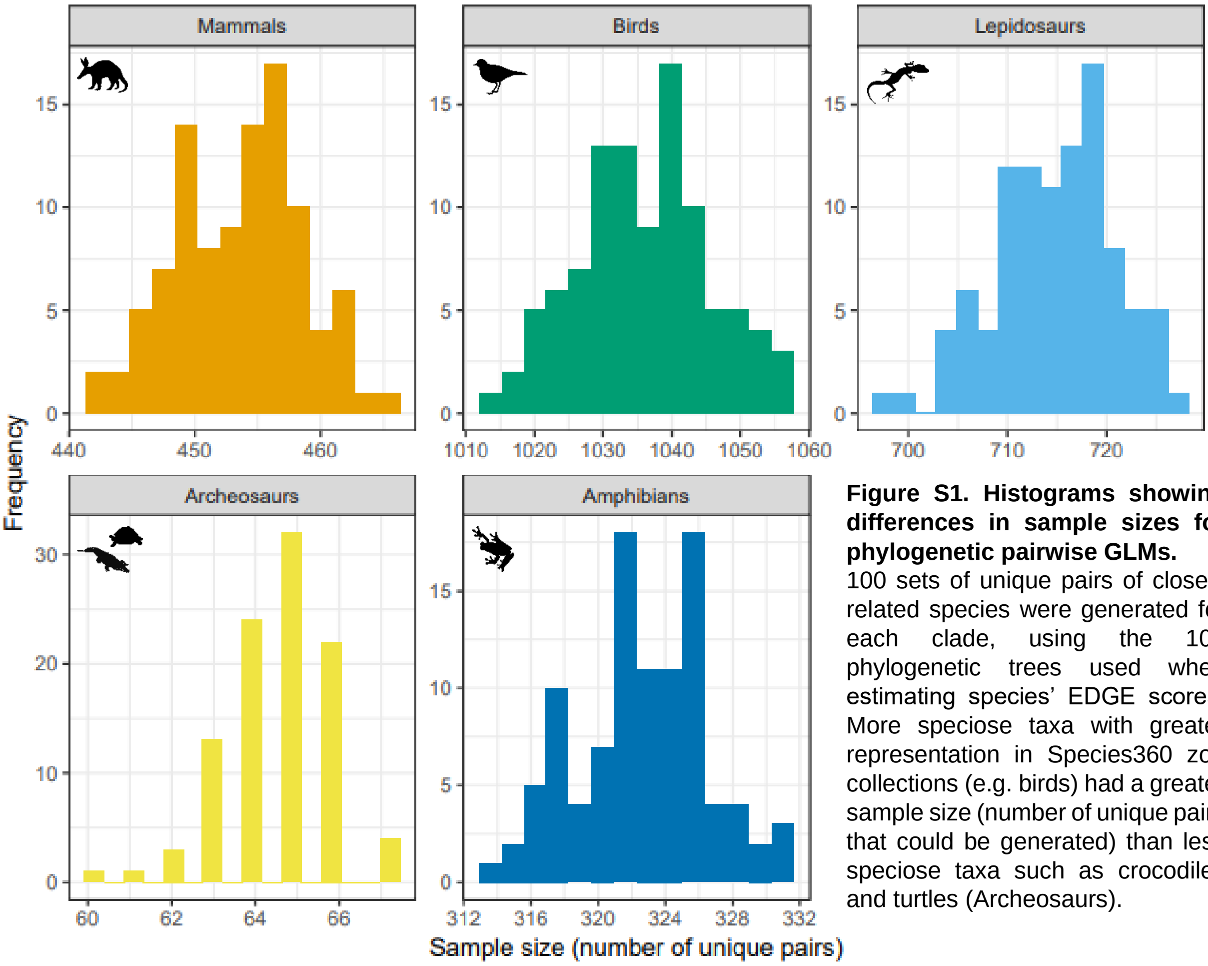


Figure S1. Histograms showing differences in sample sizes for phylogenetic pairwise GLMs. 100 sets of unique pairs of closely related species were generated for each clade, using the 100 phylogenetic trees used when estimating species' EDGE scores. More speciose taxa with greater representation in Species360 zoo collections (e.g. birds) had a greater sample size (number of unique pairs that could be generated) than less speciose taxa such as crocodiles and turtles (Archeosaurs).

Appendix D. Supporting information for Chapter 6

Supplementary Methods S1

Visitor observations followed a well-established method of measuring the ‘attraction power’ (the proportion of visitors who stop to view a species), and ‘hold time’ (how long they stop for) for each of the species selected for sampling (Moss and Esson, 2010).

Attraction power was calculated on a binary scale (0 = did not stop, 1 = stopped). To prevent the time visitors spend searching for an animal inflating the hold time of cryptic, perhaps less popular species, visitors were recorded as ‘stopped’ only once they had evidently spotted the animal. When visitors stopped scanning the exhibit and fixed their gaze on the animal for more than 2 seconds, they were recorded as ‘stopped’. Additional body language cues, such as pointing, also indicated visitors had successfully spotted an animal. Hold time was recorded using a stopwatch, starting from the time a visitor spotted an animal. Instances where animals were not visible were discounted.

I conducted most visitor observations, with some additional observations conducted by a Chester Zoo intern and a Master’s student following training in the data collection protocol. To minimise ‘social desirability bias’, in which visitors alter their behaviour according to perceived social norms or expectations (Grimm et al., 2010), observers always wore plain clothes. If an observed visitor or a member of their party approached the observer, data for that observation were omitted. Cases where uniformed members of staff were present in the exhibit were also excluded.

Data collected in summer 2021 were intended for use in a study focused on identifying inter-species differences in attractiveness at a single zoo. Consequently, more data were collected per species in this period (120 observations for the 60 species sampled). Subsequent data collection aimed for 30 observations per species per zoo to maximise taxonomic coverage and the different exhibit contexts among institutions. To avoid overly biasing models towards the summer 2021 dataset, observations from this period were down-weighted with a value of 0.25. Species sampled in summer 2021 were resampled in 2022 to further reduce this bias.

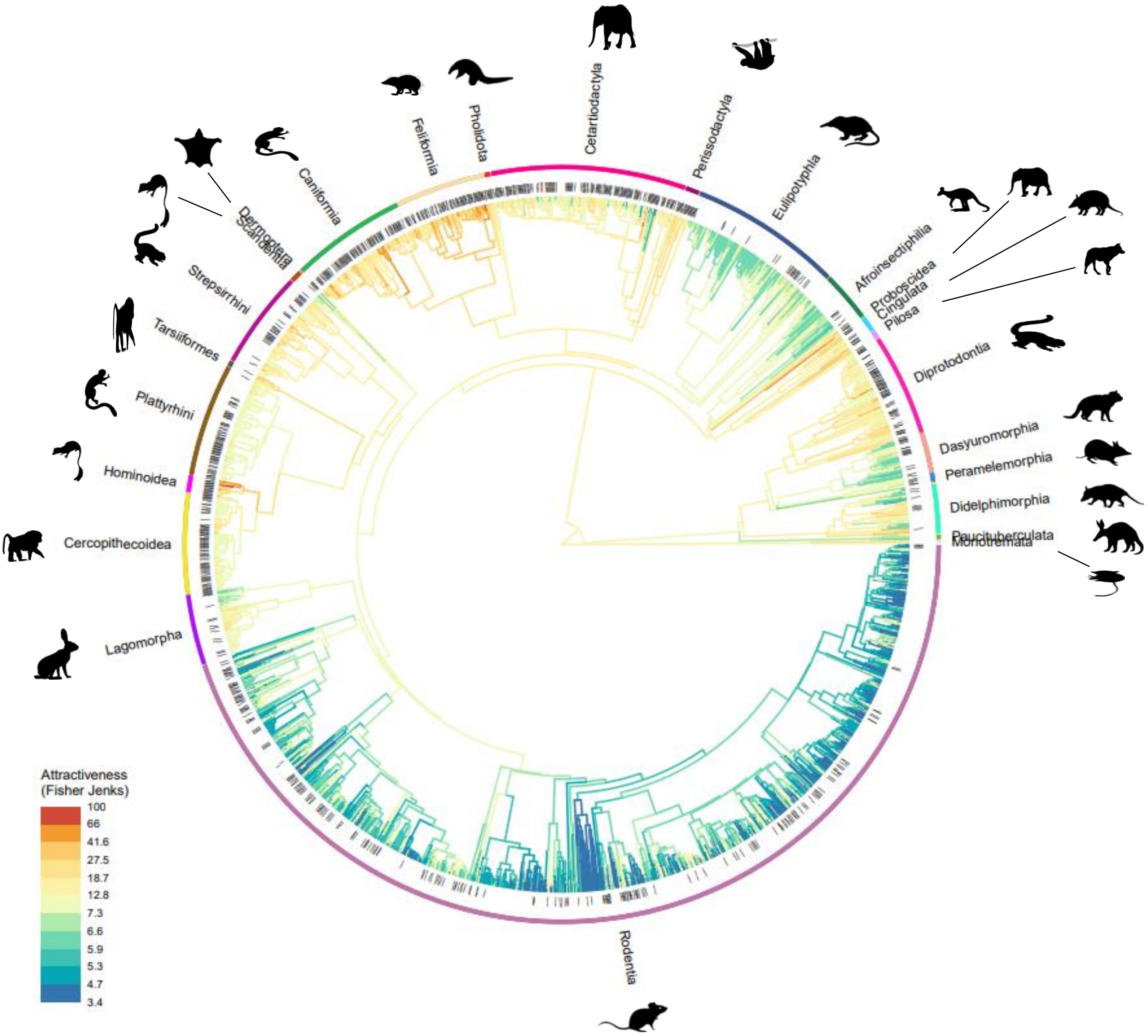


Figure S1. Phylogenetic tree for all non-volant mammals (Upham et al., 2019) with full trait data available showing the phylogenetic distribution of predicted species attractiveness. Red colours indicate more attractive species, and blue colours indicate less attractive species. Black dashes at tip labels indicate species currently held in Species360 zoo collections. Coloured bars represent major taxonomic groups.

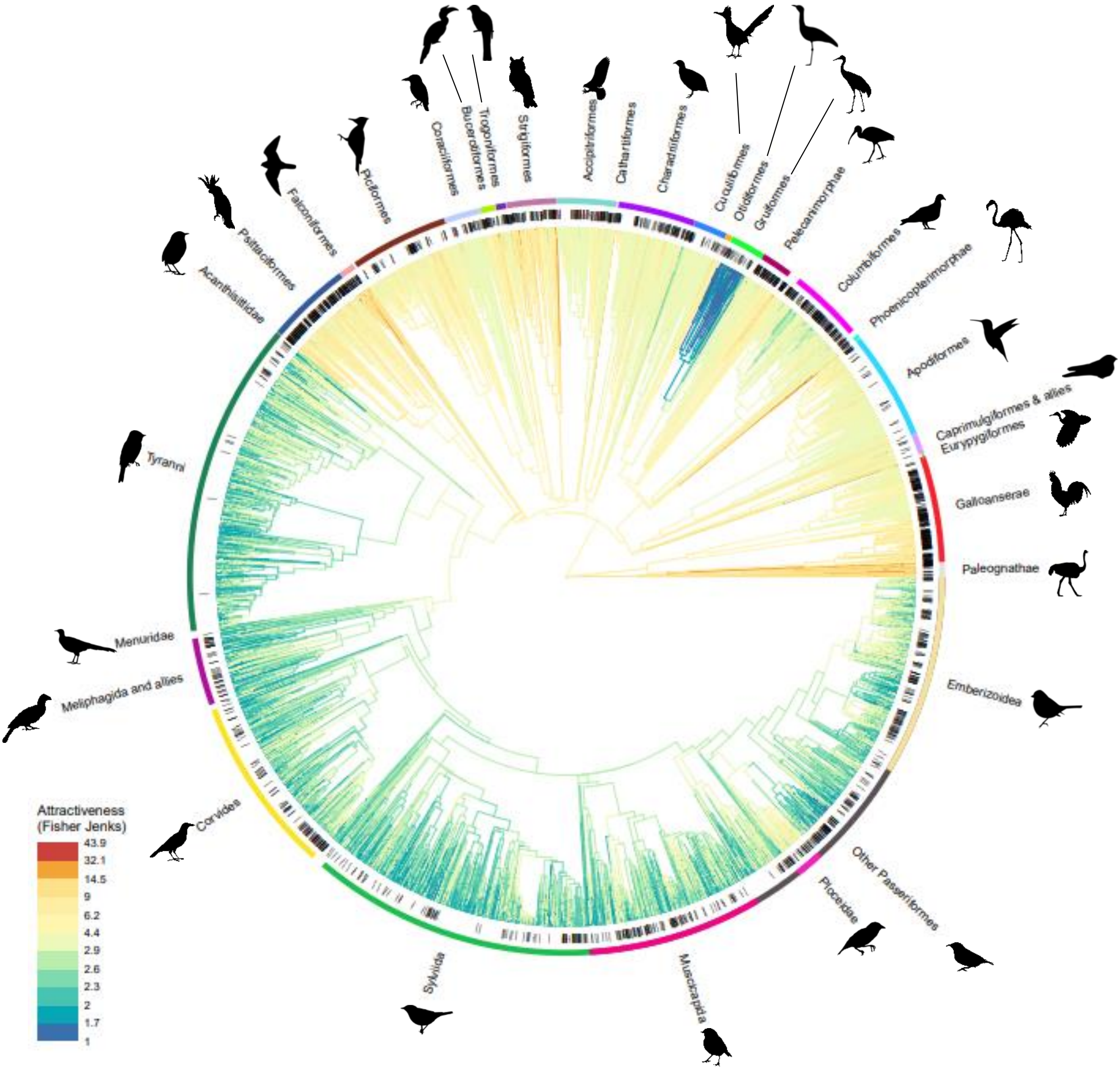


Figure S2. Phylogenetic tree for terrestrial birds (Jetz et al., 2012) with full trait data available. Pelagic seabirds are excluded here. Red colours indicate more attractive species, and blue colours indicate less attractive species. Black dashes at tip labels indicate species currently held in Species360 zoo collections. Coloured bars represent major taxonomic groups.

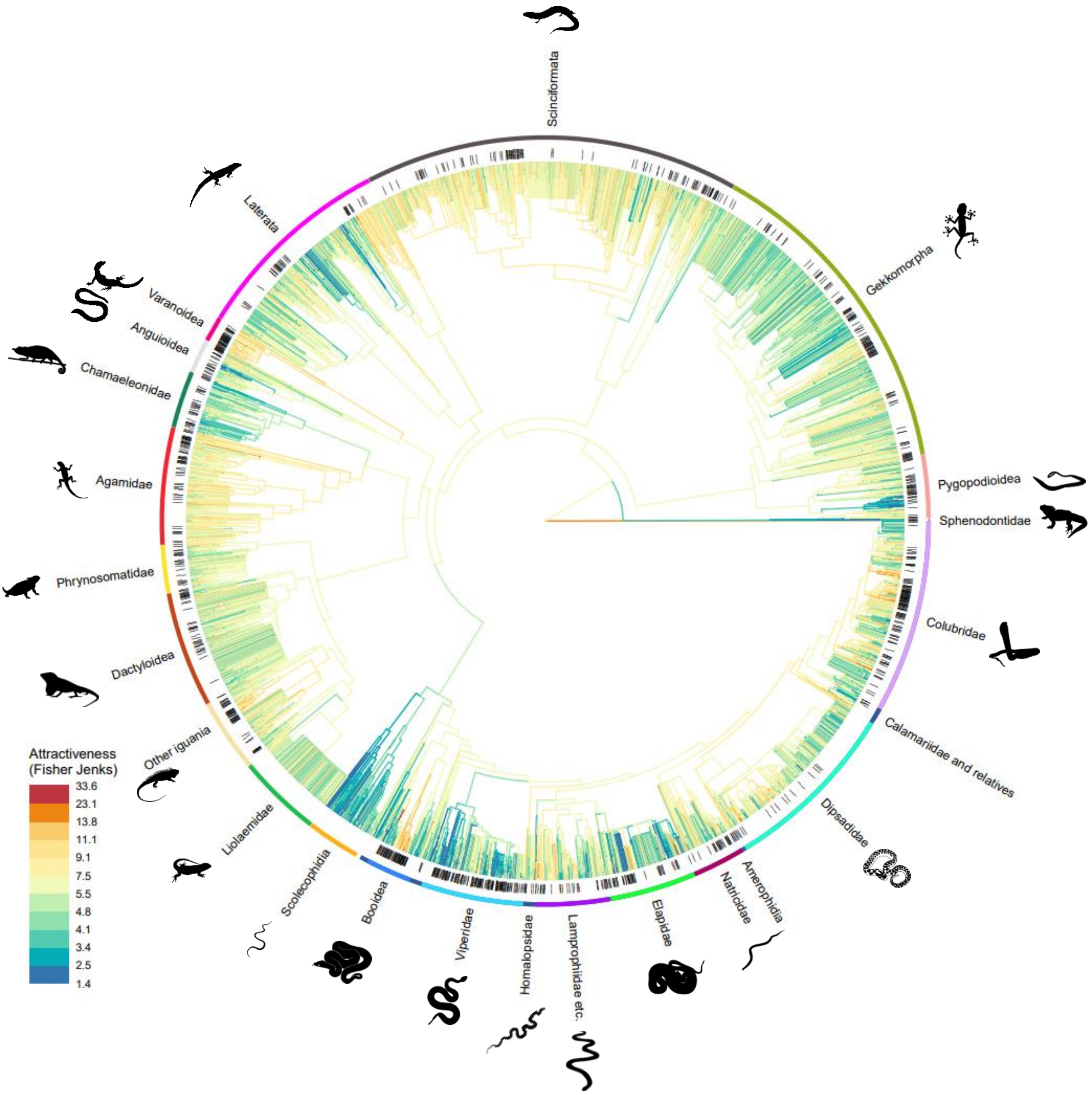


Figure S3. Phylogenetic tree for terrestrial snakes, lizards, and tuatara (Lepidosauria; Tonini et al., 2016) with full trait data available. Red colours indicate more attractive species, and blue colours indicate less attractive species. Black dashes at tip labels indicate species currently held in Species360 zoo collections. Coloured bars represent major taxonomic groups.

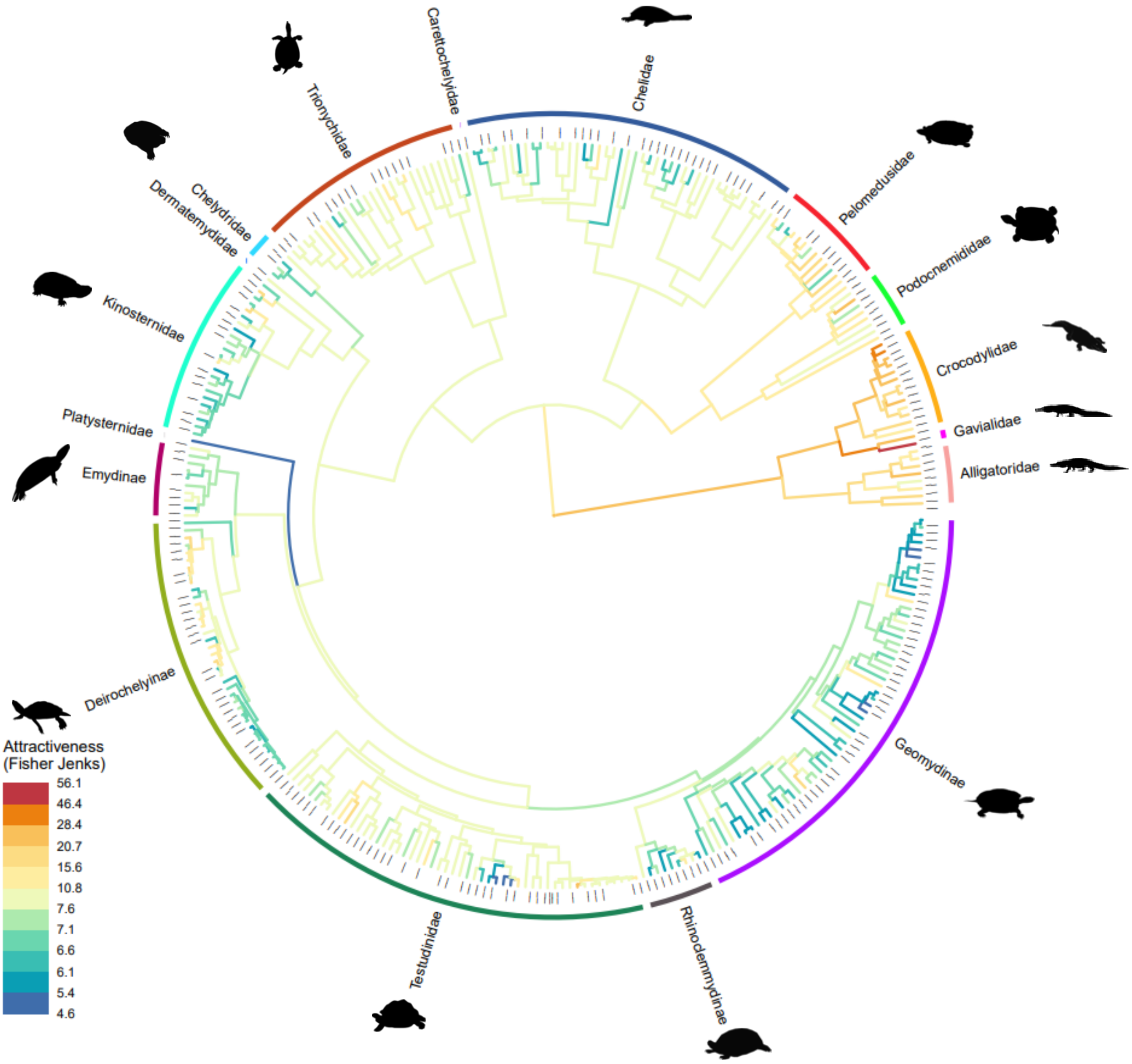


Figure S4. Phylogenetic tree for terrestrial crocodiles and turtles (non-avian Archosauromorpha; Colston et al., 2020) with full trait data available. Red colours indicate more attractive species, and blue colours indicate less attractive species. Black dashes at tip labels indicate species currently held in Species360 zoo collections. Coloured bars represent major taxonomic groups.

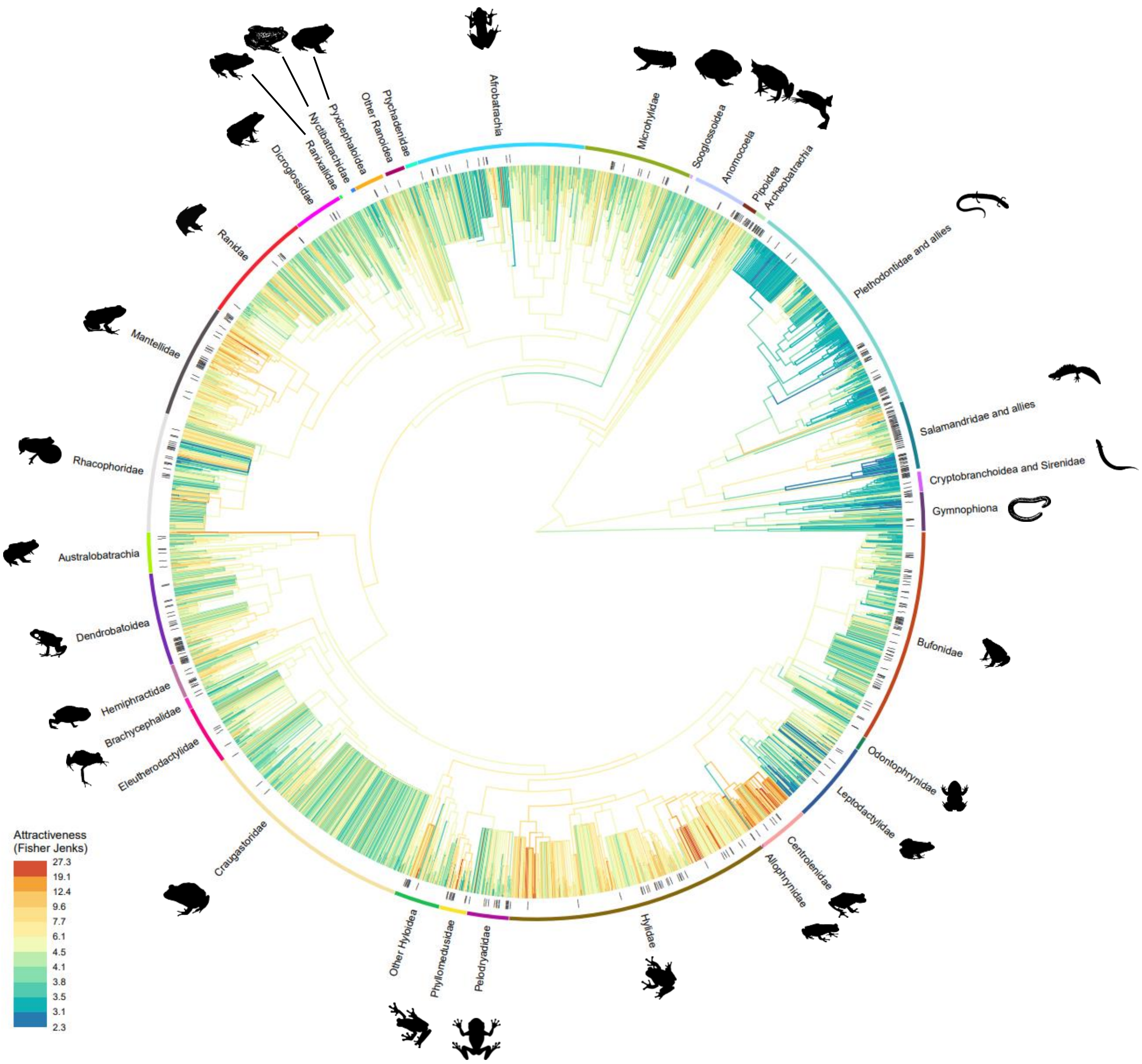


Figure S5. Phylogenetic tree for amphibians (Jetz and Pyron, 2018) with full trait data available. Red colours indicate more attractive species, and blue colours indicate less attractive species. Black dashes at tip labels indicate species currently held in Species360 zoo collections. Coloured bars represent major taxonomic groups.

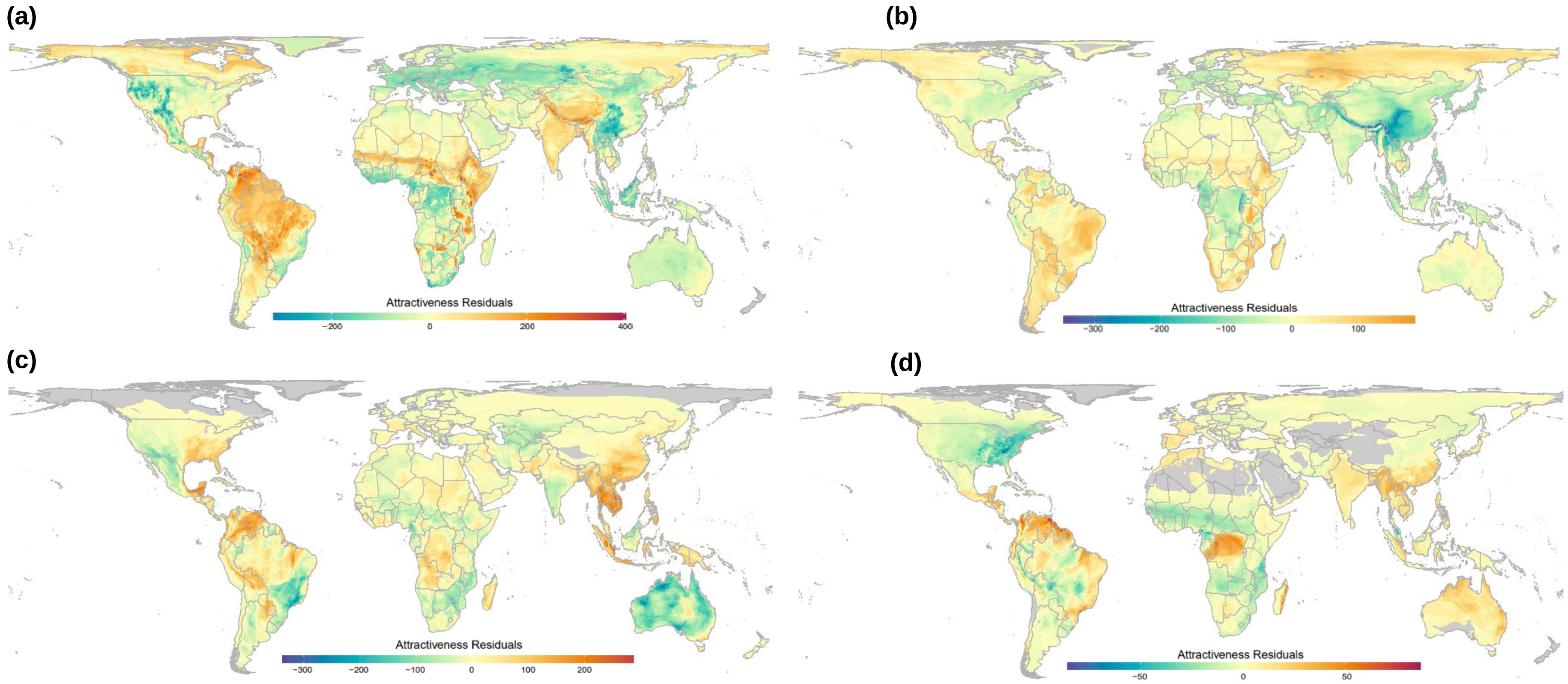


Figure S6. Residuals of a Loess regression between species richness and summed species attractiveness for (a) terrestrial non-volant mammals, (b) terrestrial birds, (c) reptiles and (d) amphibians. Positive residuals (red) indicate regions where summed species attractiveness is higher than expected relative to species richness, while negative (blue) residuals indicate regions where attractiveness is lower than expected relative to species richness. Grey areas indicate regions with no native species of this class resident or breeding in the area.

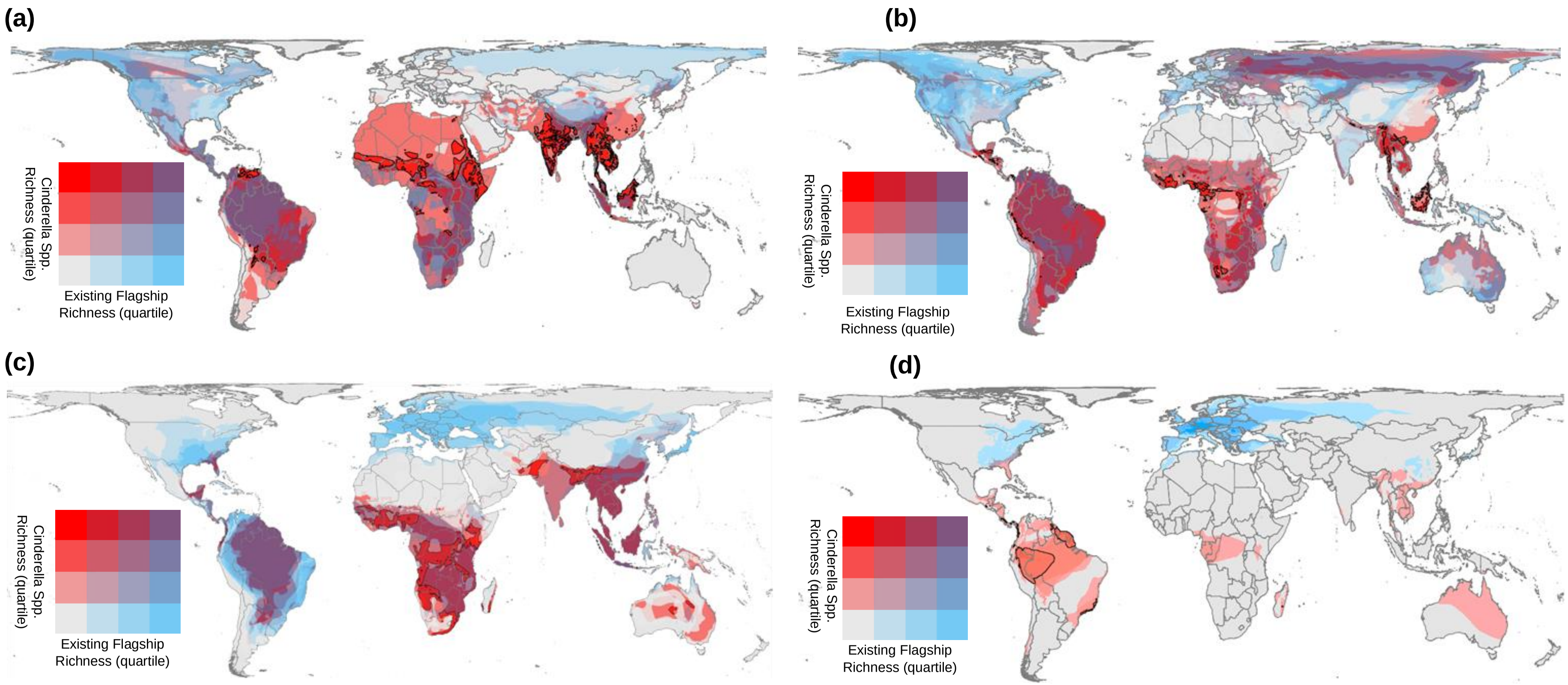


Figure S7. Bivariate maps of ‘ Cinderella species’ richness (reds) and existing flagship species richness (blues) for (a) terrestrial non-volant mammals, (b) terrestrial birds, (c) reptiles and (d) amphibians. Purples indicate areas where richness of both Cinderella species and existing flagships is high. Bright red areas outlined in black indicate ‘ Cinderella Zones’ where there is a high richness (top quartile of cells) of Cinderella species for each class but a relative paucity of existing flagships (bottom quartile of cells for mammals, birds, amphibians, below median cells for reptiles).

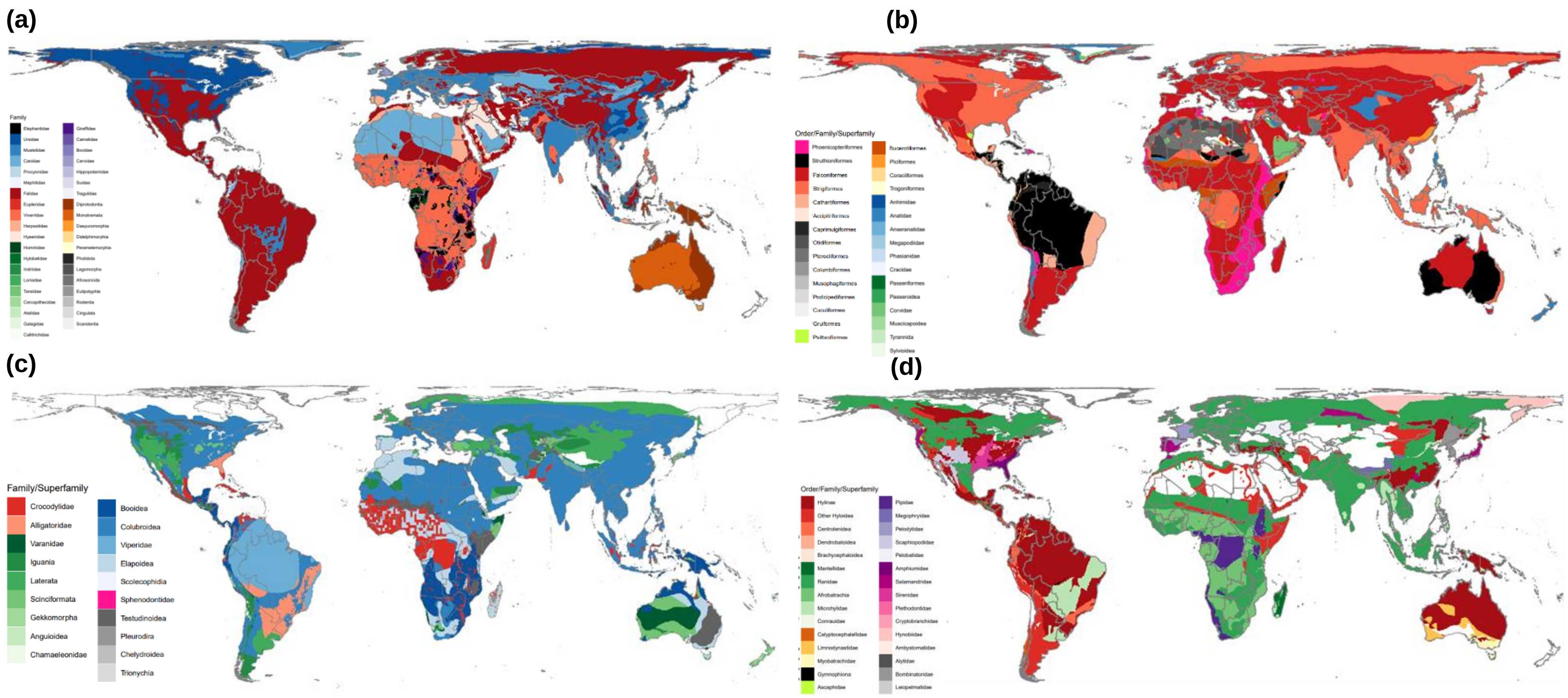


Figure S8. Taxonomic group of the top-ranked most attractive species in each area of the world for (a) mammals, (b) birds, (c) reptiles and (d) amphibians. Species range maps were downloaded from the IUCN Red List (2021-v2) with additional reptile ranges taken from the GARD database (Roll et al., 2017). Major taxonomic groups within each class are assigned to a colour, with different shades indicating the different families/superfamilies/orders within each major taxonomic group.

Table S1: Summary information on five host zoos (all data taken from the latest International Zoo Yearbook (ZSL, 2020), data provided to IZY in 2019)

Institution	**Size (ha)**	**Annual Attendance**	**N Species**	**N Individuals**	**Notes**
Chester Zoo	50.6	1,969,768	Mammals: 90 Birds: 142 Reptiles: 58 Amphibians: 31	Mammals: 1203 Birds: 1912 Reptiles: 138 Amphibians: 540	Largest and most attended zoo in the UK. Most attended tourist attraction in England outside London and the South East[2]. Subject of popular documentary series *The Secret Life of the Zoo*, aired on terrestrial television. Situated in northwest England approx. 3.6 km from the centre of the city of Chester (pop. 80,000). Highly populated region with two major cities within one hour's journey by private car (Liverpool City Region, pop. 1.55 million; Greater Manchester, pop. 2.82 million).
Paignton Zoo	34.4	399,143	Mammals: 56 Birds: 130 Reptiles: 41 Amphibians: 26	Mammals: 254 Birds: 1010 Reptiles: 126 Amphibians: 192	Large zoo in the coastal town of Paignton in Devon, southwest England (pop. 49,000). Domestic tourism hotspot around 30 km from the city of Exeter (pop. 130,000) and 40 km from the city of Plymouth (pop. 265,000). Owned by the charity Wild Planet Trust, which also owns Newquay Zoo.
Newquay Zoo	4	160,000	Mammals: 40 Birds: 78 Reptiles: 15 Amphibians: 25	Mammals: 167 Birds: 392 Reptiles: 73 Amphibians: 390	Small zoo in coastal town of Newquay in Cornwall, a hotspot of domestic tourism in the far southwest of England (pop. 23,600). Located around 65 km from the nearest major city (Plymouth). Owned by Wild Planet Trust, which also owns Paignton Zoo.
ZSL London Zoo	15	1,073,545	Mammals: 57 Birds: 87 Reptiles: 44 Amphibians: 18	Mammals: 414 Birds: 595 Reptiles: 128 Amphibians: 432	Medium sized zoo in the Richmond Park area of London, the largest city in western Europe (pop. 8.8 million) and a hotspot of international tourism, with 21 million visits to the city in 2019[3]. Established in 1828, it is the oldest scientific zoo in the world[4] and opened its doors to the public in 1847. A plaque in the Reptile House commemorates the filming of a famous scene in *Harry Potter and the Philosopher's Stone* (Warner Bros, 2001). The Zoo is owned by the scientific charity the Zoological Society of London, which also owns ZSL Whipsnade Zoo and publishes four scientific journals: *Journal of Zoology*, *Animal Conservation*, *International Zoo Yearbook*, and *Remote Sensing in Ecology and Conservation.*
Twycross Zoo	17	580,076	Mammals: 54 Birds: 33 Reptiles: 12 Amphibians: NA*	Mammals: 40 Birds: 78 Reptiles: 15 Amphibians: NA*	Medium-sized zoo in a relatively rural area of the East Midlands of England, although within around 30 km of the major cities of Birmingham (pop. 1.15 million) and Leicester (pop. 367,000). Twycross Zoo has a long-established specialism in primates and has one of the largest primate collections in Europe, and is the only UK zoo to house all four great apes (chimpanzees, bonobos, orangutans, gorillas)[5].

* No amphibian data was provided by Twycross for Amphibia, however at the time of data collection one amphibian species (Chapa bug-eyed frog *Theloderma bicolor*) was on show (one individual).

Table S2: Summary of variables included in modelling model selection process.

Trait	Scale/ Categories	Definition	Source	Justification
Threat Status[ap,ht]	Threatened EW, CR, EN, VU Non-threatened NT, LC, DD, NE.	See IUCN Red List Categories and Criteria: IUCN. (2012). *IUCN Red List Categories and Criteria: Version 3.1*. Second edition. Cambridge, UK: IUCN.	IUCN Red List[6]	7,8,9
Evolutionary Distinctiveness	ED Scores	Calculated per segment of phylogenetic tree as time covered by segment (myr) divided by number of species in the subtree that the segment forms. Species ED = sum of segment scores to tree root.	EDGE of Existence[10]	7,11
Phylogenetic distance from humans	Divergence time (myr)	Estimated time (myr) since evolutionary divergence between common ancestor of humans and species in question.	TimeTree[12]	8,13,14
Body Mass[ht]	Grams	Linear and quadratic terms included.	15,16,17	7,18,19,20
Body Length[ap,ht]	mm	Mammals: head-base of tail length. Birds: beak tip-base of tail. Amphibians and Reptiles (snout-vent length (SVL)). Linear and quadratic terms included.	15,16,17,21,22	23
Diet	% Carnivory	'Carnivory' refers to the summed percentage of animal matter in total diet.	15,24	7,25
Colouration[ap]	Single dull	Single dull colour e.g. greys, browns.	Coded from online images.	26,27,28
	Multi dull	More than one dull colour.		
	Single bright	Single body colour which is bright or iridescent. Greens, yellows, reds etc.		
	Multi bright	As 'Multi dull', but at least one colour qualifies as 'bright'.		
	Black and white	Self-explanatory.		
Patterned[ap]	No	No distinctive pattern on the body of the animal. There may be discrete blocks of colour, but no consistent pattern.	Coded from online images.	27,29,30
	Yes	Main body of animal is patterned, such as spots, stripes, blotches. Pattern can be 'irregular', like a domestic cow.		
Facial[ht]	Yes	Colouration or pattern on the head, face or throat that is distinct from that on the body. For example, eye patches,rings, distinct colouration, throat markings.	Coded from online images.	7
	No	None of the above		
Eye Position[ap,ht]	Forward	Forward facing eyes	Coded from online images.	7,19
	Side	Eyes positioned on side of head		
Ornamentation	Yes	Any form of armour (e.g. spikes, shell, horns, tusks, large claws), unusual appendage (e.g. trunk, throat sack) or distinctive display feature (e.g. unusual tail, crest, mane or facial ruff).	Coded from online images.	7,28
	No	None of the above		
Activity Level[ap,ht,*]	1	Animal sleeping.	Recorded at time of observation.	23,31
	2	Animal awake (eyes open), not moving.		
	3	Animal moving around exhibit.		
	4	Intense activity: running, leaping, flying.		
Visibility Level[ap,ht,*]	1	Animal barely visible – requires active searching to find.	Recorded at time of observation.	32-35
	2	More than 50% of the animal obscured, e.g. by foliage, water, shadow, exhibit features.		
	3	Mostly visible, less than 50% obscured.		
	4	Fully visible, 0% obscured.		

[ap] Variable included in attraction power model. [ht] Variable included in hold time model.

* Set at the activity/visibility level of the animal when visitors entered the 'in-zone' for attraction power, and at the maximum level reached during visitor stay for hold time.

Table S3: Summary of variables excluded from modelling due to insufficient explanatory power.

Variable	Scale/ Categories	Definition	Source	Justification
Ambient temperature	° Celsius	Self-explanatory	Accu Weather	36
Weather	Rain Cloudy Part cloudy Sunny	Rain falling 100-90% cloud cover 90-30% cloud cover, indirect sunlight < 30 % cloud cover, direct sunlight	Determined visually	36
Exhibit type	Functional-Functional	Animal exhibit area functional in design and lacking naturalistic features. Visitor areas also functional in design.	Determined visually.	32,37,38,39
	Naturalistic-Functional	Animal exhibit areas include naturalist features evocative of species native ranges (e.g. plants, topography). Visitor areas still functional in design.		
	Functional-Immersive	Animal areas functional but visitor areas include immersive features such as plants, temperature, humidity, sound and lighting evocative of species native ranges.		
	Naturalistic-Immersive	Both animal areas naturalistic and visitor areas immersive. Overall exhibit space provides multisensory stimuli and evokes species native range.		
	Walkthrough	Free-flight aviaries or exhibits with no barrier separating visitors and animals.		
Indoor/ Outdoor	Indoor/ Outdoor	Is the visitor area housed in a self-contained structure with at least two walls covered by a roof, providing shelter from adverse weather conditions?	Determined visually	32,36
Multispecies	Single species Multispecies	Multispecies exhibits contain >1 species in same exhibit space.	Determined visually	23,32
Gender	Male Female	The perceived gender of the visitor in each group selected for observation.	Determined visually	40,41
Age	18-30 31-45 46-60 61+	The estimated age (in years) of the visitor in each group selected for observation.	Determined visually	40,41
Group Type	Adults and children	Group contains at least one adult (18+) and one child (under 18).	Determined visually	40,41
	Adults only	Group contains more than one adult but no children.		
	Solo adult	Single adult visitor.		

Table S4. Ruleset for classifying traits from species images

Trait	Option	Definition	Additional Notes
Colouration	Single dull	Single body colour, relatively dull e.g. greys, browns, black. Many species have slightly paler underside, but unless this is a distinctly different colour, this still counts as 'single' colour. Colouration refers to the main body of the animal, and does not include any facial patterning under the 'Facial' trait. For example, a spectacled bear is black all over with some facial markings. This would still be classed as 'Single dull'.	Colouration and patterning refer to the main body of the animal, this is to avoid double counting of distinctive colour/pattern on the head or tail.
	Multi dull	As above, but more than one dull colour on the main body of the animal. Low contrast between the colours.	'Multi' colouration only refers to distinct colours. Gradations of the same tone, such as colours becoming paler towards the chest of the animal don't count.
	Single bright	As 'Single dull' except the main body colour is bright or striking. Greens, blues, yellows, reds etc.	
	Multi bright	As 'Multi dull', however AT LEAST ONE of the colours would be considered 'bright'.	
	Black and white	Self explanatory.	
Patterning	No	No distinctive pattern on the body of the animal. There may be stand-alone patches of colour, but no discernable or consistent pattern	Colouration and patterning refer to the main body of the animal, this is to avoid double counting of distinctive colour/pattern on the head or tail. Patterns must be *consistent* and *repeated*.
	Yes	Main body of animal is patterned, such as spots, stripes, blotches. Pattern can be 'irregular', like a domestic cow, but discrete colour blocks that do not form a consistently repeated pattern do not count.	
Facial	Yes	Colouration or pattern on the head or face that is distinct from any colouration or pattern on the body. For example, a tiger's stripes continue onto the face, but this is not distinct from the body pattern so wouldn't count. Can include eye patches, eye rings, throat markings, or distinct colour for the face or head of the animal	
	No	None of the above	
Eye Position	Forward	Forward facing eyes to improve depth perception	
	Side	Eyes positioned on side of head to maximise peripheral vision	
Ornamentation	Yes	The animal has some form of armour (e.g. spikes, shell, horns, tusks, large claws), unusual appendage (e.g. trunk, throat sack) or distinctive display feature (e.g. unusual tail, crest, mane or ruff around the face etc).	Tails with particularly distinct colouration, patterning or shape (e.g. particularly long and whip-like, spiky, decoy appendage) are classed as *ornamentation*.
	No	None of the above	

Reference List S1 (For Tables S1-S3)

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Appendix E: Supporting information for Chapter 7

Supplementary Methods S1: Mathematical Formulation for the oppr ‘max_richness_objective’ algorithm

N.B. The formulation described here is taken from the oppr reference guide https://prioritizr.github.io/oppr/reference/add_max_richness_objective.html (Hanson et al., 2020). This is a previously published R package that I provided no input into, and is entirely the work of Dr Jeffrey Hanson and colleagues. Here, I provide the mathematical formulation for the max_richness_objective function purely for reference. Only cosmetic edits are made to ensure consistency of language with the main text, where necessary.

A problem objective is used to specify the overall goal of the project prioritization problem. Here, the maximum richness objective seeks to find the set of actions that maximizes the total number of features (e.g. populations, species, ecosystems) that is expected to persist within a pre-specified budget. Let I represent the set of conservation actions (indexed by i). Let C_i denote the cost for funding action i, and let m denote the maximum expenditure (i.e. the budget). Also, let F represent each feature (indexed by f), W_f represent the weight for each feature f (defaults to one for each feature unless specified otherwise), and E_f denote the probability that each feature will go extinct given the funded conservation projects.

To guide the prioritization, the conservation actions are organized into conservation projects. Let J denote the set of conservation projects (indexed by j), and let A_{ij} denote which actions $i \in I$ comprise each conservation project $j \in J$ using zeros and ones. Next, let P_j represent the probability of project j being successful if it is funded. Also, let B_{fj} denote the probability that each feature $f \in F$ associated with the project $j \in J$ will persist if all of the actions that comprise project j are funded and that project is allocated to feature f. For convenience, let Q_{fj} denote the actual probability that each $f \in F$ associated with the project $j \in J$ is expected to persist if the project is funded. If the argument to `adjust_for_baseline` in the `problem` function was set to `TRUE`, and this is the default behaviour, then $Q_{fj} = (P_j \times B_{fj}) + ((1 - (P_j B_{fj})) \times (P_n \times B_{fn}))$, where `n` corresponds to the baseline "do nothing" project. This means that the probability of a feature persisting if a project is allocated to a feature depends on (i) the probability of the project succeeding, (ii) the probability of the feature persisting if the project does not fail, and

(iii) the probability of the feature persisting even if the project fails. Otherwise, if the argument is set to `FALSE`, then $Q_{fj} = P_j \times B_{fj}$.

The binary control variables X_i in this problem indicate whether each project $i \in I$ is funded or not. The decision variables in this problem are the Y_j, Z_{fj}, and E_f variables. Specifically, the binary Y_j variables indicate if project j is funded or not based on which actions are funded; the binary Z_{fj} variables indicate if project j is used to manage feature f or not; and the semi-continuous E_f variables denote the probability that feature f will go extinct.

Now that we have defined all the data and variables, we can formulate the problem. For convenience, let the symbol used to denote each set also represent its cardinality (e.g. if there are ten features, let F represent the set of ten features and also the number ten).

$$\text{Maximize} \sum_{f=0}^{F} (1 - E_f) W_f \text{ (eqn 1a)}$$

$$\text{Subject to} \sum_{i=0}^{I} C_i \leq m \text{ (eqn 1b)}$$

$$E_f = 1 - \sum_{j=0}^{J} Z_{fj} Q_{fj} \; \forall \; f \in F \text{ (eqn 1c)}$$

$$Z_{fj} \leq Y_j \; \forall \; j \in J \text{ (eqn 1d)}$$

$$\sum_{j=0}^{J} Z_{fj} \times \text{ceil}(Q_{fj}) = 1 \; \forall \; f \in F \text{ (eqn 1e)}$$

$$A_{ij} Y_j \leq X_i \; \forall \; i \in I, j \in J \text{ (eqn 1f)}$$

$$E_f \geq 0, E_f \leq 1 \; \forall \; b \in B \text{ (eqn 1g)}$$

$$X_i, Y_j, Z_{fj} \in [0, 1] \; \forall \; i \in I, j \in J, f \in F \text{ (eqn 1h)}$$

The objective (eqn 1a) is to maximize the weighted persistence of all the species. Constraint (eqn 1b) limits the maximum expenditure (i.e. ensures that the cost of the funded actions do not exceed the budget). Constraints (eqn 1c) calculate the probability that each feature will go extinct according to their allocated project. Constraints (eqn 1d) ensure that feature can only be allocated to projects that have all of their actions funded. Constraints (eqn 1e) state that each feature can only be allocated to a single project. Constraints (eqn 1f) ensure that a project cannot be funded unless all of its actions are funded. Constraints (eqns 1g) ensure that the probability variables (E_f) are bounded between zero and one. Constraints (eqns 1h) ensure that the action funding (X_i), project funding (Y_j), and project allocation (Z_{fj}) variables are binary.

Supplementary Methods S2: Mathematical formulation for the zooptimal algorithm

N.B. The formulation described here was written and developed by Dr Jeffrey Hanson. While I provided conceptual input and feedback, credit for the mathematical formulation and R package development are entirely his. I present Dr Hanson's formulation here verbatim, for reference, with only cosmetic edits made to correct typing errors and ensure consistency of language with the main text.

The optimisation problem is formulated as a multi-objective mixed integer programming problem. To describe its mathematical formulation, I begin by defining the concepts and variables that underpin the optimization problem. Broadly speaking, the optimisation problem aims to cost-effectively allocate animal populations to zoo enclosures. Let Z denote a set of zoos (indexed by z), and let E denote the set of enclosures (indexed by e) that exist across all zoos. To indicate the location of each enclosure, let L_{ez} denote if enclosures $e \in E$ are present in zoos $z \in Z$ or not (using values of ones and zeros, respectively). Since different types of enclosures can support animal populations of different sizes for different species, let T denote the set of enclosure types (indexed by t) and Q_{et} indicate if enclosures $e \in E$ belong to types $t \in T$ or not (using values of ones and zeros, respectively).

The optimization problem considers a set of species. Let S denote the set of species (indexed by s). Since species are typically housed in zoos at standard group sizes (e.g. individuals are typically housed as solitary individuals, pairs, or large family groups), let g_s denote the standard group size for each species. To account for the fact that different species have different enclosure requirements, let R_{st} indicate if species $s \in S$ can persist – given their standard group size – in enclosures that belong to types $t \in T$ or not (using ones and zeros, respectively). Additionally, to account for the fact that it is more important to maintain some groups of species in zoos than other species, let w_s denote a weight for each species. For example, the w_s values could be parametrized using scores describing trait-based attractiveness or evolutionary distinctiveness.

Since the overall aim is to maximize the overall persistence of species, we define a mathematical function for estimating the probability that a given species will persist given a total population size across all zoo collection. To define this function, let N denote a set of total population numbers (indexed by n with cardinality m) for evaluating the probability that each species will persist (e.g., $N = \{0,70,350,700,1400\}$). Next, let ψ_{sn} denote the probability that species $s \in S$ will persist given the total population numbers $n \in N$ (e.g., with values between zero and one). Note that, if desired, it is possible to account for wild populations by ensuring that $\psi_{sn} > 0$ where $N_n = 0$. Given parameters denoting (s) the relevant species and (x) its population size, the mathematical function is defined as follows.

$$f(s,x) = \begin{cases} \psi_{s,1}, \text{if } N_1 \leq x < N_2 \\ \psi_{s,2}, \text{if } N_2 \leq x < N_3 \\ \psi_3, \text{if } N_3 \leq x < N_4 \\ \dots \\ \psi_{s,m}, \text{if } N_m \leq x < \infty \end{cases} \qquad \text{(eqn 1)}$$

Here, eqn 1 defines a step function. For a given species (s), it will return the probability of persistence (ψ_{sn}) associated with the greatest total population number (per N_n) that is exceeded by the given population size (x). To linearize this function, it is implemented using a series of piece-wise linear constraints.

$$\begin{aligned} X_{se} &= \begin{cases} 1, \text{if species } s \text{ allocated to enclosure } e, \\ 0, \text{else} \end{cases} && \text{(eqn 2a)} \\ H_{sz} &= \begin{cases} 1, \text{if species } s \text{ allocated to an enclosure in zoo } z, \\ 0, \text{else} \end{cases} && \text{(eqn 2b)} \\ y_s &= \text{total population size for species } s && \text{(eqn 2c)} \\ z_s &= \text{probability of persistence for species } s && \text{(eqn 2d)} \\ \lambda_1 &= \text{weighted sum probability of all species persisting} && \text{(eqn 2e)} \\ \lambda_2 &= \text{total number of species present in each zoo} && \text{(eqn 2f)} \end{aligned}$$

The decision variables are the binary X_{se} and H_{sz} variables and the continuous y_s, z_s, λ_1, and λ_2 variables. The X_{se} variables indicate if each species is allocated to each enclosure (at the standard group size). The y_s variables denote the total population size of each species across all zoos. The z_s variables denote the expected probability of each species persisting given the total population sizes. The λ_1 and λ_2 variables denote metrics for multi-objective optimization. Specifically, the λ_1 variable denotes the weighted sum probability of all species persisting and the λ_2 variables denotes the total number of species present in each zoo.

Given all the previously defined variables, the optimisation problem is formulated as the following lexicographic multi-objective mixed integer programming problem.

$$
\begin{array}{lll}
\text{lex max } \lambda_1, \lambda_2 & & \text{(eqn 3a)} \\
\text{subject to } \lambda_1 = \sum_{s \in S} z_s w_s & & \text{(eqn 3b)} \\
\lambda_2 = \sum_{z \in Z} \sum_{s \in S} H_{sz} & & \text{(eqn 3c)} \\
z_s = f(s, y_s) & \forall s \in S & \text{(eqn 3d)} \\
y_s \leq \sum_{e \in E} X_{se} g_s & \forall s \in S & \text{(eqn 3e)} \\
X_{se} \leq \max_{t \in T} (R_{st} Q_{et}) & \forall s \in S, e \in E & \text{(eqn 3f)} \\
H_{sz} \leq \sum_{e \in E} X_{se} l_{ez} & \forall s \in S, z \in Z & \text{(eqn 3g)} \\
\sum_{s \in S} X_{se} \leq 1 & \forall e \in E & \text{(eqn 3h)} \\
X_{se} \in \{0, 1\} & \forall s \in S, e \in E & \text{(eqn 3i)} \\
H_{sz} \in \{0, 1\} & \forall s \in S & \text{(eqn 3j)} \\
0 \leq z_s \leq 1 & \forall s \in S & \text{(eqn 3k)} \\
0 \leq y_s \leq \infty & \forall s \in S & \text{(eqn 3l)} \\
0 \leq \lambda_1, \lambda_2 \leq \infty & & \text{(eqn 3m)}
\end{array}
$$

Here (eqn 3a), the objective is to lexicographically (hierarchically) maximize the λ_1 variable and, subsequently, the λ_2 variable. Constraint (eqn 3b) defines the λ_1 variable as the weighted sum of the probability of each species persisting. Constraint (eqn 3c) defines the λ_2 variable as the total number of species present in each zoo. Since the λ_2 only counts each species once per zoo (if assigned to one of the zoo's enclosures) – and does not count a given species multiple times if present in multiple enclosures in the same zoo – maximizing this variable helps spread out populations of species across multiple zoos. Thus, the objective for the problem is to first maximize the overall weighted probability of persistence for the species and then, subsequently, maximize the total number of species present in each zoo. Constraints (eqn 3d) define each species' probability of persistence, based on their total population sizes (per eqn 1). Constraints (eqn 3e) ensure that the total population size for each species is calculated based on each species' group size and the number of enclosures to which they are assigned. Constraints (eqn 3f) ensure that a given species can only be assigned to an enclosure if the enclosure belongs to one of the enclosure types that can house the species. Constraints (eqn 3g) ensure that the variables used to determine if each species is present or absent from each zoo (i.e. H_{sz}) are calculated correctly based on which species are assigned to each enclosure. Constraints (eqn 3h) ensure that, at most, only a single species can be assigned to each enclosure. Constraints (eqn 3i and eqn 3j) specify that the X_{se} and H_{sz} variables are binary. Constraints (eqn 3j) ensure that the z_s probability variables range between zero and one. Constraints (eqn 3k and 3l) ensure that the total population size variables, λ_1 and λ_2 variables contain positive values.

Table S1. Summary of sample sizes (n), means, and standard deviations (sd) for life history data used in population viability analyses (PVAs) for each class. All data taken from the Demographic Species Knowledge Index (DSKI, Condé et al., 2019). Values in bold italics were manually assigned due to insufficient data for phylogenetic imputation (n < 50).

		AFR (d)[1]	**Juv. Surv.[2]**	**Ad. Surv.[2]**	**Lifespan (y)[1]**	**Litter size[1]**	**Litters/y[1]**
Mammalia	n	2,003	12	161	2,606	3,381	1,198
	mean	1.30	***0.67***	0.70	11.22	2.90	2.15
	sd	1.84	***0.1***	0.11	11.82	2.09	1.33
Aves	n	1,277	128	385	1,668	6,732	633
	mean	1.53	0.42	0.64	12.27	3.22	1.63
	sd	1.17	0.15	0.1	7.76	2.03	0.51
Reptilia	n	757	0	109	1,430	3,338	845
	mean	2.11	***0.5***	0.55	9.73	8.14	2.36
	sd	1.01	***0.2***	0.09	5.55	23.81	2.90
Amphibia	n	199	13	17	225	694	2
	mean	2.22	***0.33***	***0.67***	10.36	972	***1.25***
	sd	0.65	***0.2***	***0.2***	3.42	2,169	***0.25***

[1] Values bounded at 0.
[2] Values bounded at 0 and 1.
Juv./Ad. Surv = Juvenile/adult annual survival rate.

Sample sizes (n) indicate the number of species in each class with data available for the given trait. Means and standard deviations are based on mean values across the entire class following phylogenetic imputation. However, species-specific means and standard deviations were actually used in PVAs, with both means and variance in each trait estimated for each species during phylogenetic imputation. Using these species-specific means and variances, 1,000 viable values within the relevant bounds[1,2] were randomly generated from a normal distribution for each trait. These 1,000 combinations of life history traits were then used in 1,000 PVA iterations for each species.

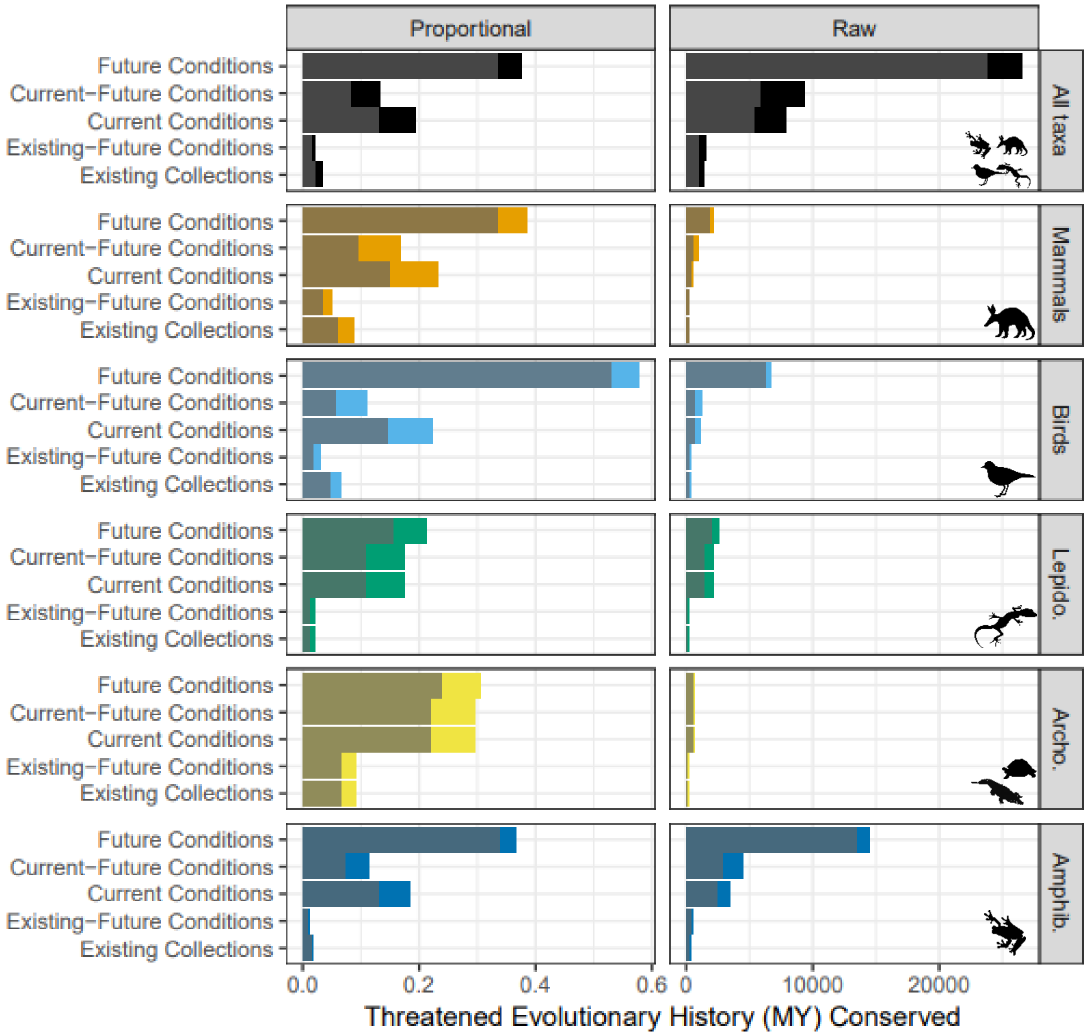


Figure S1. Additional threatened evolutionary history conserved in global zoos under collection optimisation, under SSP5-8.5. Bars represent the amount of additional threatened evolutionary history (MY) expected to persist over 100 years given the persistence probability of zoo populations and wild populations. Wild persistence probability is the inverse of the probability of extinction given species Red List status, as calculated for species EDGE scores (Gumbs et al., 2023). Estimates are given for all taxa combined (top panels) and for each clade, with the proportion of evolutionary history conserved in each clade given in the left column, and absolute totals (MY) in the right column. Grey-shaded areas of each bar represent the irreplaceability of zoo collections in terms of their contribution to species overall persistence. Bars represent estimates for existing zoo collections ‘Existing Collections’, optimised collections using species current EDGE scores ‘Current Conditions’, and projected future EDGE scores for 2070 under SSP5-8.5 ‘Future Conditions’. ‘Existing-Future Conditions’ and ‘Current-Future Conditions’ represent the change in evolutionary history conserved when species’ future EDGE scores are assigned to existing collections and collections optimised under current conditions, respectively.

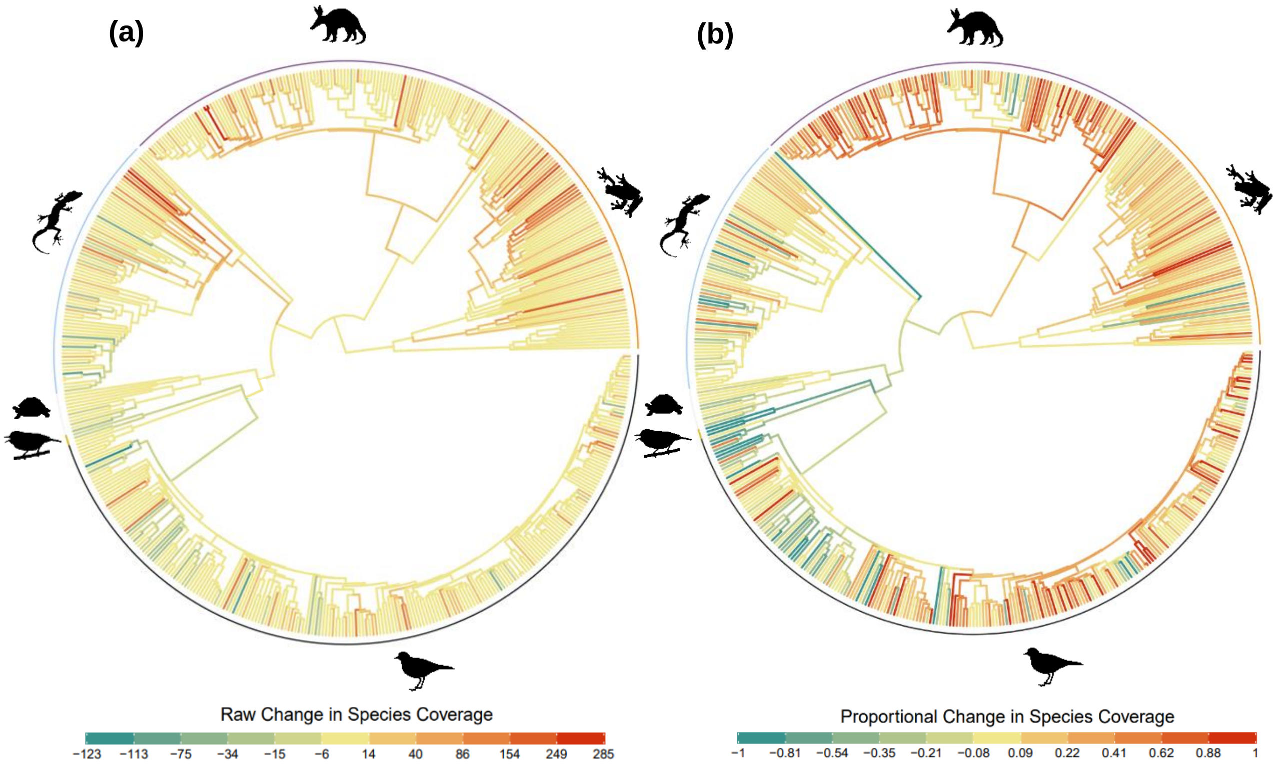
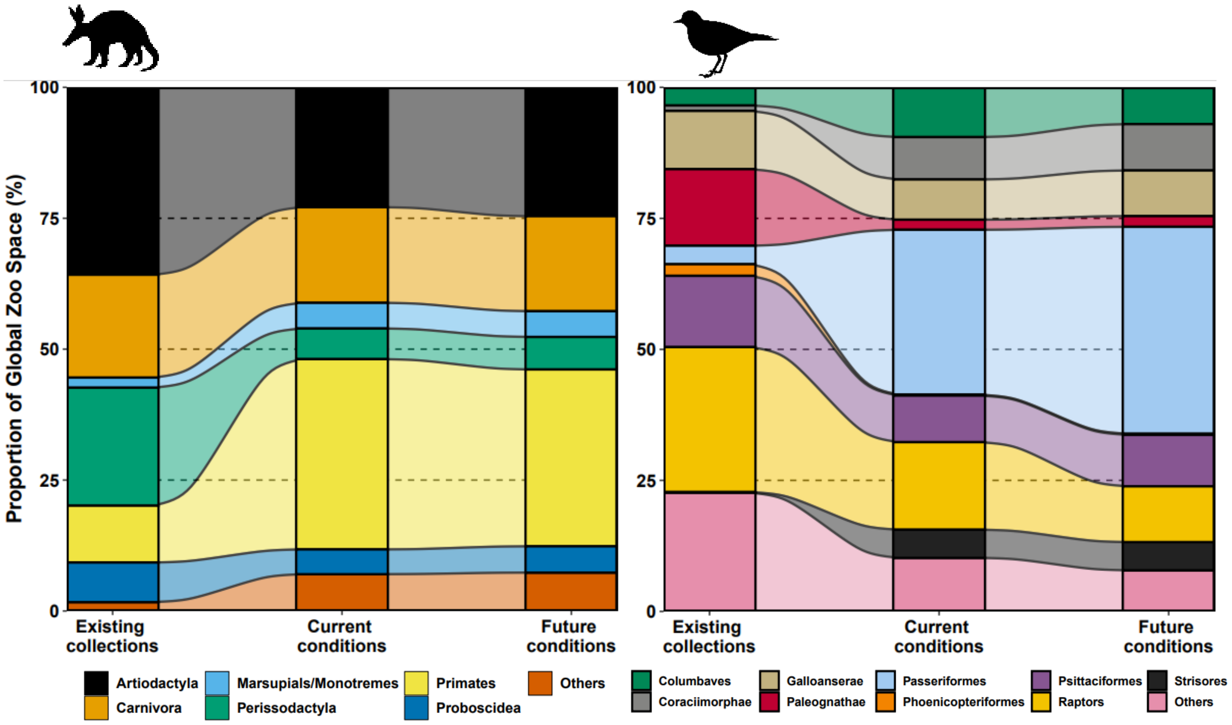


Figure S2. Change in the phylogenetic distribution of species representation in global zoo collections under collection optimisation and SSP5-8.5. The phylogenetic tree on the left (a) shows the summed change in species coverage (number of species per family represented in global zoo collections) between existing collections and optimised collections under a severe warming scenario of SSP5-8.5, for the year 2070. The tree on the right (b) shows the change in the proportional coverage of species under global collection optimisation (0 = no change, -1 = all species removed, +1 = all species added to collections).



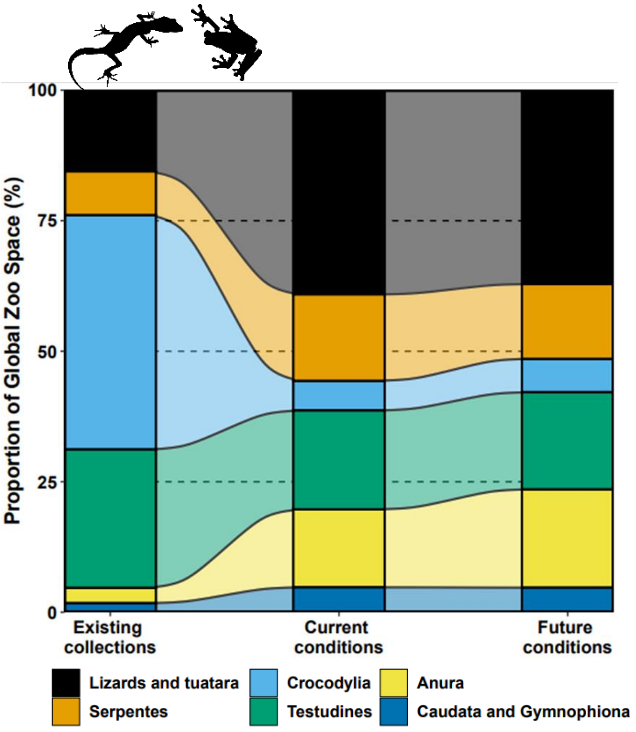


Figure S3. Change in the proportion of zoo exhibit space committed to broad taxonomic clades, under SSP5-8.5. Stacked bar charts show the proportion of zoo exhibit space committed to major clades of mammals (top left), birds (top right) and herpetofauna (bottom left) in existing collections (left bars), collections optimised under current conditions (middle bars) and collections optimised under future conditions and a severe warming scenario. (SSP5-8.5; right bars). Shaded areas indicate the trend required to reduce/expand coverage of the clade between scenarios. Dashed lines indicate 25%, 50% and 75% intercepts on the y axis.

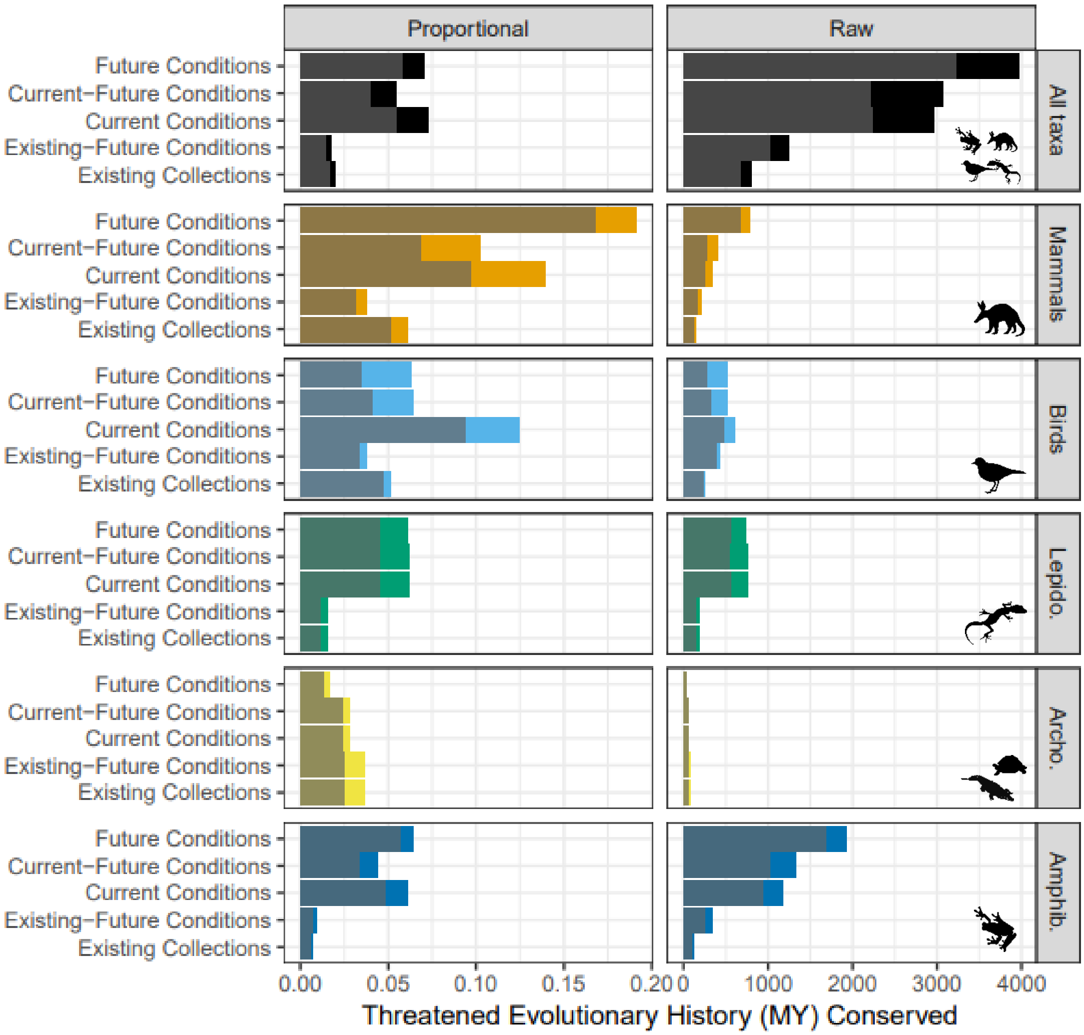


Figure S4. Additional threatened evolutionary history conserved in BIAZA zoos under exhibit-specific zoo collection optimisation, under SSP5-8.5. Bars represent the amount of additional threatened evolutionary history (MY) expected to persist over 100 years given the persistence probability of zoo populations and wild populations, and grey-shaded areas of each bar represent the irreplaceability of zoo collections' contribution to species overall persistence, as per Figure S1. Estimates are given for all taxa combined (top row) and for each clade in subsequent rows, with the proportion of evolutionary history conserved in each clade given in the left column, and absolute totals (MY) in the right column.

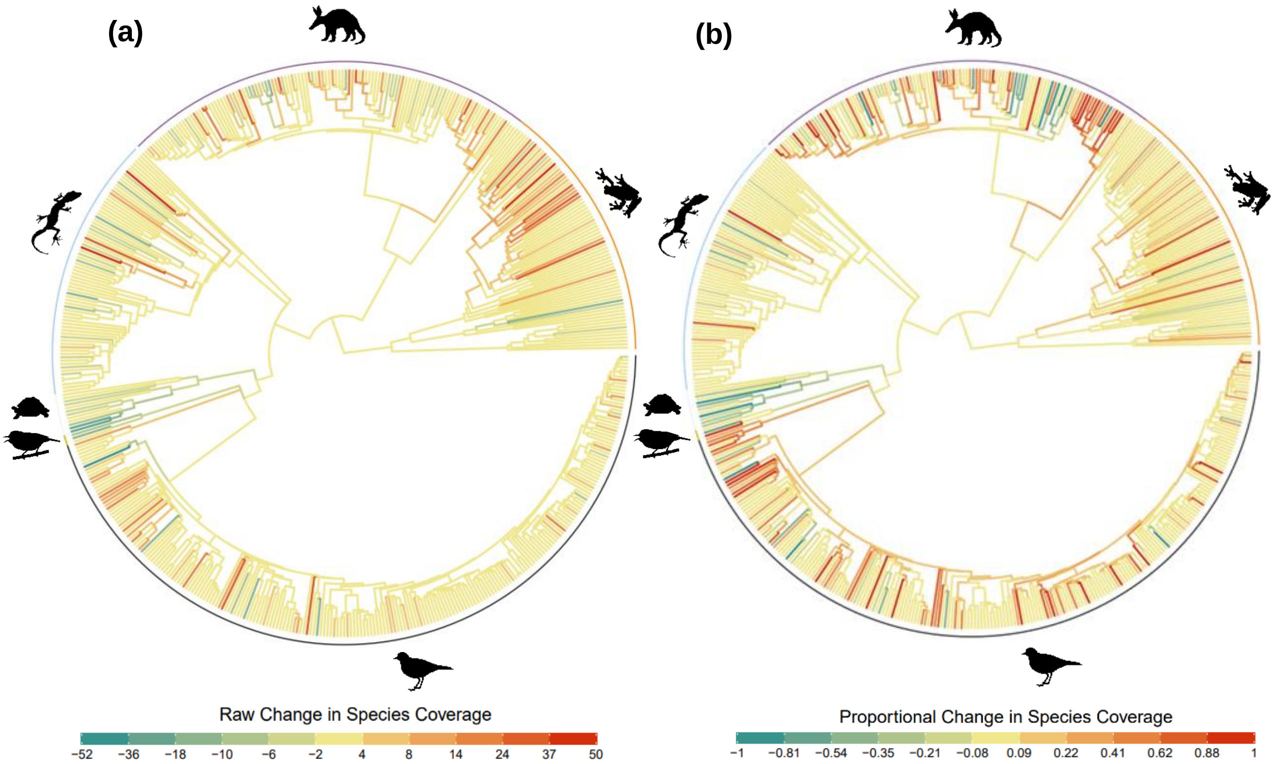
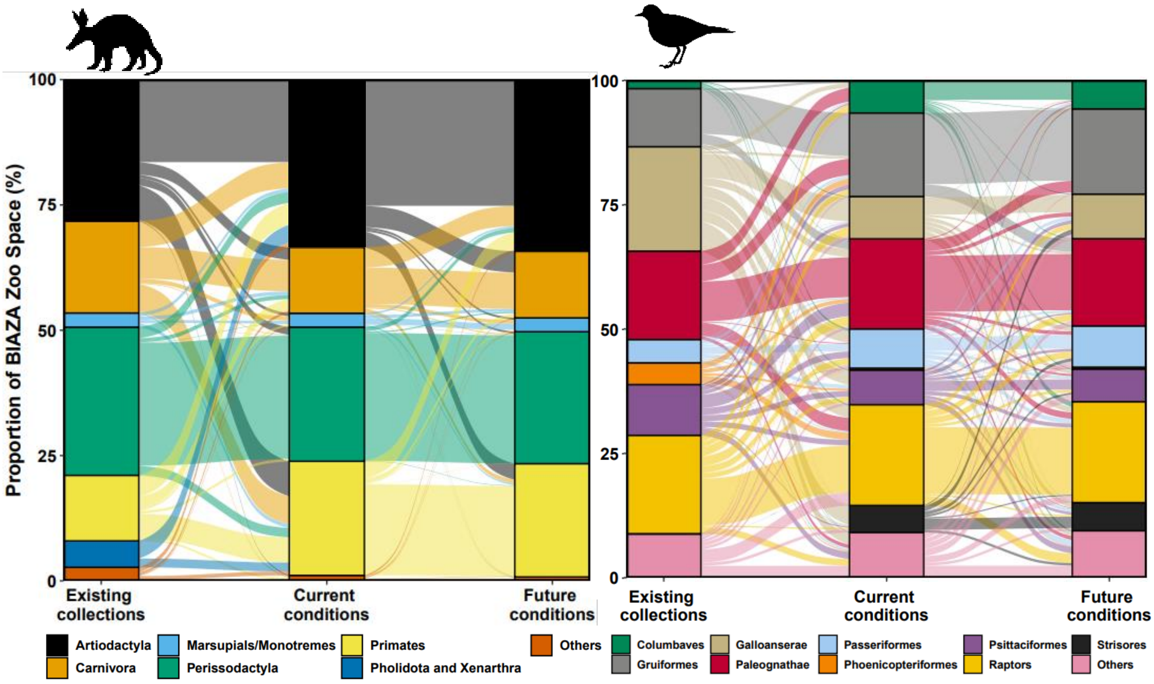


Figure S5. Change in the phylogenetic distribution of species representation in BIAZA zoo collections under collection optimisation and SSP5-8.5. As per Figure S2, the phylogenetic tree on the left (a) shows the summed change in species coverage (number of species per family represented in BIAZA zoo collections) between existing collections and optimised collections under severe warming scenario of SSP5-8.5. The tree on the right (b) shows the change in the proportional coverage of species under global collection optimisation (0 = no change, -1 = all species removed, +1 = all species added to collections).



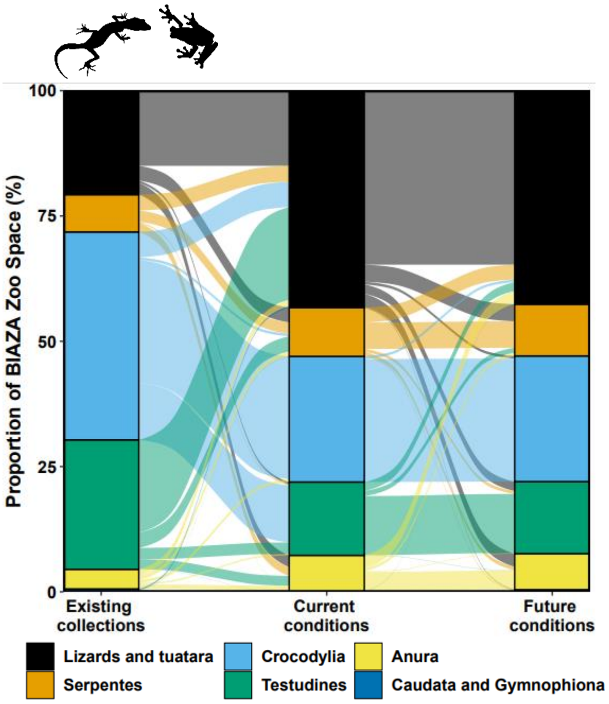


Figure S6. Change in the proportion of BIAZA zoo exhibit space committed to broad taxonomic clades, under SSP5-8.5. Alluvial plots showing the compositional change of BIAZA zoo exhibit space for major clades of mammals (top left), birds (top right) and herpetofauna (bottom left) in existing collections (left bars), collections optimised under current conditions (middle bars) and collections optimised under future conditions and a severe warming scenario. (SSP5-8.5; right bars). Shaded areas indicate how individual exhibits are repurposed for different clades under each optimisation scenario. Note the slightly different colour scheme for birds compared to Figure S3, with hornbills, toucans, woodpeckers and allies (Coraciimorphae) replaced with cranes (Gruiformes), which are more commonly represented in BIAZA zoos.

Appendix F: Supporting information for Chapter 8

Table S1: Summary information for the 87 shortlisted species identified as candidates for *in situ-ex situ* conservation partnerships, in line with the ‘One Plan’ conservation approach. The table includes information on geographic distribution of species long-term climatic refugia, as well as their projected Red List Status and EDGE scores (Chapter 3). These areas coincide with priorities for protected area expansion under all current, future, domestic and international prioritisations (Chapter 4), and ‘Cinderella Zones’ (Chapter 6). All species are themselves ‘Cinderella’ species, are not currently housed in a Species360 zoo, and are selected in all global zoo collection optimisations for current and future (year 2070, SSP2-4.5/SSP5-8.5) environmental conditions (Chapter 7).

Species	Countries	Ecoregions	Area (km^2)	Current Status	Future Status (SSP2-4.5/ SSP5-8.5)	EDGE2 Score	Future Score (SSP2-4.5)	Future Score (SSP5-8.5)	Attractiveness Estimate
Mammals									
Bdeogale nigripes	Cameroon, Congo, Central African Rep, DR Congo, Nigeria	Forest-savanna mosaics; Highlands forests	4,362	LC	LC/EN	0.04	0.05	0.47	28.56
Cabassous unicinctus	Venezuela, Bolivia	Montane,dry & delta swamp forests; mangroves; wetlands; Cordillera de Merida páramo; Bolivian Yungas; Llanos; xeric scrub & shrubland.	7,590	LC	LC	0.17	0.18	0.14	32.89
Canis simensis	Ethiopia	Ethiopian montane grasslands, woodlands, forests, & moorlands	2,017	EN	EN	0.99	1.11	1.09	58.49
Caracal aurata	Congo, DR Congo, Angola, Cameroon, Nigeria, Central African Rep	Forest-savanna mosaics; Lowland forests, Highlands & swamp forests	9,858	VU	VU	0.87	0.9	0.86	43.76
Genetta maculata	Ethiopia, Nigeria, Somalia, Eritrea, DR Congo, Cameroon, Central African Rep, Chad	Ethiopian montane grasslands, woodlands, forests, & moorlands; forest-savanna mosaics; savanna; xeric & Hobyo grasslands and shrublands; bushlands and thickets; Highlands forests	46,592	LC	LC/NT	0.06	0.05	0.12	33.99
Genetta servalina	DR Congo, Central African Rep	Forest-savanna mosaics	612.8	LC	VU/CR	0.05	0.5	1.97	34.82
Leopardus jacobita	Bolivia, Argentina, Peru	Montane dry forests; puna; Yungas; Dry Chaco; High Monte	727.7	EN	EN	0.47	0.46	0.48	25.43
Paradoxurus jerdoni	India	Moist deciduous & montane rain forests; moist, dry deciduous & thorn scrub forests	11,483	LC	LC	0.05	0.05	0.06	28.26

Priodontes maximus	Venezuela, Argentina, Brazil, Bolivia	Wetlands; Delta swamp, montane, coastal & dry forests; Cordillera de Merida páramo; Llanos; Yungas; mangroves; xeric scrub and shrublands	9,161	VU	VU	3.58	3.47	3.53	41.39
Viverra tangalunga	Malaysia, Indonesia, Brunei	Montane & lowland rain forests; Peat & freshwater swamp forests; heath forests; mangroves; montane alpine meadows	32,284	LC	LC	0.16	0.14	0.14	37.84
Birds									
Asio abyssinicus	DR Congo	Montane & lowland forests	1,802	LC	LC	0.18	0.19	0.2	7.44
Batrachostomus auritus	Malaysia, Indonesia	Freshwater swamp, lowland rain & heath forests; mangroves	1,042	NT	NT	2.07	2.28	3.23	9.49
Batrachostomus stellatus	Indonesia	Mangroves; Borneo peat & freshwater swamp forests	874.2	NT	NT	1.37	1.63	1.78	8.79
Bubo leucostictus	Nigeria	Nigerian lowland forests	0.04	LC	LC	0.15	0.17	0.2	7.92
Bubo shelleyi	Nigeria	Central African mangroves	19.74	VU	VU	1.1	0.99	1.11	7.60
Ciccaba albitarsis	Peru, Ecuador	Real montane forests	121.6	LC	LC	0.12	0.15	0.12	7.38
Colaptes atriceps	Peru	Peruvian Yungas	102.1	LC	LC	0.07	0.07	0.08	8.48
Colaptes cafer	Mexico	Pine-oak forests	19.63	LC	LC	0.1	0.12	0.11	11.11
Colaptes mexicanoides	Honduras, Guatemala	Central American montane, pine-oak, moist & dry forests	300	LC	LC/VU	0.07	0.07	0.44	11.10
Colaptes rivolii	Peru, Ecuador	Real montane forests	121.6	LC	LC	0.13	0.15	0.12	12.74
Euplectes hartlaubi	Cameroon	Forest-savanna mosaic	19.64	LC	LC	0.12	0.1	0.11	8.50
Nothoprocta taczanowskii	Peru, Bolivia	Bolivian Yungas	121.1	VU	VU	2.16	2.11	2.27	10.58
Otus rufescens	Malaysia, Indonesia	Heath, lowland rain & freshwater swamp forests; mangroves	1,042	NT	NT	0.5	0.46	0.65	16.44
Otus sagittatus	Thailand, Burma	Lowland moist deciduous & semi-evergreen rain forests	594	VU	VU	0.83	1.04	1.07	11.61
Otus spilocephalus	China, Vietnam	Subtropical evergreen forests	1,921	LC	LC	0.27	0.41	0.44	10.29
Phoeniculus bollei	DR Congo	Lowland forests	19.64	LC	LC	0.54	0.55	0.53	13.76

Phyllaemulor bracteatus	Panama	Isthmian-Atlantic & Chocó-Darién moist forests	19.64	LC	LC	3.36	3.41	2.98	20.93
Picus erythropygius	Burma	Subtropical forests	19.63	LC	LC	0.14	0.15	0.13	8.03
Picus guerini	China, Vietnam	Subtropical evergreen forests	1,921	LC	LC	0.1	0.1	0.11	8.02
Picus vittatus	China, Laos	Subtropical forests	3,115	LC	LC/NT	0.07	0.07	0.17	11.09
Ploceus batesi	Cameroon	Coastal forests & lowland forests	2,952	EN	EN	0.62	0.78	0.8	8.25
Ploceus dorsomaculatus	Cameroon	Northwestern Congolian lowland forests	984.1	LC	VU/CR	0.07	0.33	1.65	7.81
Ploceus luteolus	Ghana	West Sudanian savanna	19.64	LC	LC	0.07	0.11	0.08	8.00
Ploceus preussi	DR Congo	Lowland forests	19.64	LC	LC	0.06	0.05	0.07	7.81
Ploceus vitellinus	Kenya	Bushlands and thickets; coastal forest mosaic	0.05	LC	LC	0.07	0.08	0.09	7.81
Pogoniulus coryphaea	DR Congo	Lowland & montane forests	325.62	LC	LC/VU	0.3	0.31	2.34	12.52
Pogonornis bidentatus	Central African Rep	Northwestern Congolian lowland forests	0.01	LC	LC	0.1	0.09	0.12	8.35
Polihierax insignis	Burma	Subtropical & moist deciduous forests	73.88	NT	NT	0.84	0.79	0.78	21.05
Prodotiscus insignis	Guinea, Sierra Leone	Lowland & montane forests; forest-savanna mosaic	1,266	LC	LC	0.25	0.26	0.27	11.87
Psilopogon faiostrictus	Vietnam, China	Northern Indochina subtropical forests	6,655	LC	LC/VU	0.13	0.14	0.79	12.87
Psilopogon virens	China, Vietnam	Subtropical evergreen forests	1,921	LC	LC	0.18	0.21	0.26	12.87
Psilopogon zeylanicus	Nepal	Savanna and grasslands	19.64	LC	LC	0.12	0.16	0.16	8.61
Rhinopomastus castaneiceps	Cameroon	Atlantic Equatorial coastal forests	0.09	LC	LC	0.2	0.19	0.21	13.65
Rhinopomastus cyanomelas	Namibia	Namib desert, Namibian savanna woodlands	121.6	LC	LC	0.3	0.28	0.24	14.86
Scotopelia bouvieri	Benin	Lowland forests; forest-savanna mosaic	0.05	LC	LC	0.12	0.11	0.68	13.59
Scotopelia ussheri	Guinea	Lowland forests	19.64	VU	VU	0.8	0.71	0.79	21.45
Steatornis caripensis	Peru	Moist forests; Yungas, wet puna	879.6	LC	LC	4.59	4.59	4.57	9.96
Tinamus osgoodi	Peru	Yungas & moist forests	492.1	VU	VU	2.58	2.63	2.63	15.80
Tinamus tao	Bolivia, Peru	Bolivian Yungas	43.87	VU	VU	2.67	2.84	2.55	14.01

Touit surdus	Brazil	Serra do Mar coastal forests	19.69	VU	VU/EN	0.68	0.68	1.53	11.91
Verreauxia africana	Cameroon	Coastal forests	0.04	LC	VU/EN	0.7	3	5.52	10.80
Reptiles									
Eurylepis poonaensis	India	Dry deciduous, thorn scrub & moist deciduous forests	1,781	EN	EN	5.12	5.18	4.9	15.84
Liopholis kintorei	Australia	Central Ranges xeric scrub	984.1	VU	VU	1.18	1.08	1.07	17.44
Amphibians									
Agalychnis buckleyi	Ecuador	Real montane & moist forests	1,031	LC	LC/VU	0.5	0.66	3	20.02
Boana dentei	French Guiana	Moist forests & mangroves	940	LC	LC	0.58	0.68	0.85	15.91
Boana nympha	Ecuador	Real montane & moist forests	0.04	LC	LC/EN	0.64	1.06	9.58	12.68
Boana ornatissima	Suriname	Freshwater swamp & moist forests	2,946	LC	LC	0.93	0.99	0.76	16.79
Bokermannohyla ahenea	Brazil	Coastal forests, & montane savanna	453.3	DD	DD	1.78	2.73	2.38	23.90
Bokermannohyla astartea	Brazil	Atlantic forests & coastal forests	0.04	LC	NT/LC	0.32	1.05	0.36	16.28
Bokermannohyla hylax	Brazil	Serra do Mar coastal forests	0.05	LC	VU/NT	0.16	1.66	0.82	24.75
Boophis boehmei	Madagascar	Lowland & subhumid forests	2,170	EN	EN	3.45	3.51	3.39	17.45
Boophis microtympanum	Madagascar	Lowland & subhumid forests	714.6	LC	LC/VU	0.84	0.87	4.39	14.01
Boophis narinsi	Madagascar	Lowland & subhumid forests	1,225	EN	EN	3.55	3.69	4.04	17.02
Centrolene buckleyi	Ecuador	Real montane & moist forests	0.08	VU	VU	0.91	0.94	0.97	17.23
Chimerella mariaelenae	Ecuador	Eastern Cordillera real montane forests, Napo moist forests	0.04	LC	LC/VU	0.38	0.41	1.84	22.05
Cochranella erminea	Peru	Várzea & moist forests	55.33	LC	LC/VU	0.17	0.22	1.04	22.13
Cochranella resplendens	Ecuador	Eastern Cordillera real montane forests, Napo moist forests	826.8	LC	LC/EN	0.23	0.29	3.25	22.19
Dendropsophus minusculus	Guyana	Guianan moist forests	492.1	LC	LC	0.52	0.47	0.45	15.56

Duellmanohyla uranochroa	Costa Rica	Talamancan & Isthmian-Atlantic moist forests	266	VU	VU	3.43	3.23	3.61	14.99
Espadarana durrellorum	Ecuador	Eastern Cordillera real montane forests, Napo moist forests	0.04	LC	LC/EW	0.29	0.26	6.05	24.68
Hyalinobatrachium pellucidum	Peru	Peruvian Yungas, Ucayali moist forests	82.95	NT	NT	1.79	1.74	1.67	24.62
Isthmohyla xanthosticta	Costa Rica	Talamancan montane forests	19.63	DD	DD	2.44	2.07	3.18	12.62
Isthmohyla zeteki	Costa Rica	Talamancan & Isthmian-Atlantic moist forests	0.01	VU	VU	3.87	3.54	4.23	24.65
Nymphargus grandisonae	Colombia	Northwestern Andean montane forests	223.6	LC	LC/VU	0.51	0.47	2.09	22.24
Nymphargus posadae	Ecuador	Real montane & moist forests	0.08	LC	LC	0.25	0.18	0.21	24.82
Nymphargus prasinus	Colombia	Montane & moist forests	121.7	VU	VU	1.28	1.4	1.45	17.24
Phyllomedusa venusta	Colombia	Chocó-Darién moist forests	594.1	LC	LC	0.25	0.28	0.29	20.64
Plectrohyla avia	Guatemala, Mexico	Moist, montane & pine-oak forests	1,627	EN	EN	4.49	4.5	4.78	29.33
Plectrohyla hartwegi	Guatemala	Moist, montane & pine-oak forests; thornscrub	832.3	EN	EN	3.76	3.66	3.99	25.38
Plectrohyla matudai	Mexico, Guatemala	Moist, montane & pine-oak forests	1,775	LC	LC	0.38	0.39	0.42	24.49
Plectrohyla pokomchi	Guatemala	Moist, montane & pine-oak forests; thornscrub	602.3	EN	EN	4.26	4.69	4.43	28.71
Plectrohyla quecchi	Guatemala	Moist, montane & pine-oak forests; thornscrub	730.4	EN	EN	4.27	4.22	4.13	22.84
Plectrohyla sagorum	Guatemala, Mexico	Moist, montane & pine-oak forests	1,730	VU	VU	2.02	2	2.15	22.92
Rulyrana flavopunctata	Ecuador	Napo moist forests, Eastern Cordillera real montane forests	487.9	LC	LC/NT	0.14	0.14	0.34	16.46
Rulyrana saxiscandens	Peru	Moist forests & Yungas	1,047	EN	EN	0.61	0.59	0.67	25.74
Sachatamia ilex	Colombia	Chocó-Darién moist forests	1,004	LC	LC	0.61	0.58	0.69	16.57
Vitreorana uranoscopa	Brazil	Alto Paraná Atlantic forests, Serra do Mar coastal forests	0.04	LC	LC/VU	1.14	1.09	4.89	23.78

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