The Global Drivers of Wildlife Tourism and its Future Potential in a Changing World

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The Global Drivers of Wildlife Tourism and its Future Potential in a Changing World

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Declaration

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

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Abstract

Nature tourism is tourism with the primary aim of experiencing and enjoying nature, often in protected areas (PAs). Wildlife is a key attraction within the nature tourism industry, with many tourists visiting PAs to view and interact with free-roaming animals. This form of non-consumptive wildlife tourism can generate revenue for conservation, local communities, and national economic development. Accordingly, wildlife tourism has been heralded as a powerful tool that can help countries protect their biodiversity, while also growing and diversifying their economies, contributing to multiple international conservation and development goals simultaneously. In light of this, the lack of quantitative information on where tourists chose to go to watch wildlife, and why, has been identified as a major research gap. This study aims to determine the drivers of global wildlife tourism by identifying species' traits and PA features that attract wildlife tourists, and to explore the potential of wildlife tourism in the future.

I start by using phylogenetic comparative methods to predict the attractiveness of the world's birds and terrestrial non-volant mammals. I define a species' attractiveness based on the frequency with which species are cited by wildlife tourism resources (i.e., global and regional wildlife tourism guidebooks, brochures, websites) aimed predominantly at generalist, Western and/or English-speaking tourists, a large subset of the wildlife tourism market. In combination with data on species' traits and range attributes, I model this index of *attractiveness* at a global scale. I repeat these analyses at a national scale, focussing on the United Kingdom, to explore whether the drivers of species *attractiveness* differ at these two scales. I go on to predict the popularity of PAs, based on the frequency of their occurrences within the same wildlife tourism literature mentioned above. To model this index of *popularity*, I consider predictor variables such as the *attractiveness* of the constituent species pool, as well as other PA features (such as size, remoteness, and land cover present at a site). I use ensemble species distribution models to assess the potential impact of future climate change on the ranges of the world's birds and terrestrial mammals, taking into account uncertainty in climate models and species dispersal, and consider how this might influence global patterns of wildlife tourism.

At the larger scale, species *attractiveness* was determined by a number of traits, including body mass, extinction risk, time partitioning (i.e., nocturnal vs. diurnal), and sociality/coloniality. Another important feature was the habitat in which a species occurs. The study also shows, for the first time, the significant impact of evolutionary distinctiveness, migratory behaviour in birds, and political stability (of the country in which a species is found) on species *attractiveness*. In the United Kingdom, *attractiveness* was influenced by a similar suite of traits, but slight variations indicated heterogeneous tourist preferences that differ between international globe-trotting tourists vs. mostly domestic tourists visiting the United Kingdom. The presence of *attractive*, as well as rarer, species assemblages was a key determinant enhancing PA *popularity* globally. PA *popularity* was also influenced by landscape features, age, size, accessibility and designation/management category. The observed connections between different components of biodiversity values supports the notion that managing PAs for both biodiversity and wildlife tourism simultaneously is possible. Strong relationships between PA *popularity*, as determined by citation frequency within wildlife tourism resources, and PA visitor numbers, suggest that wildlife tourism literature can serve as a proxy for human use of PAs.

The results of my research indicate significant and untapped financial opportunities available to countries in sub-Saharan Africa, South America and South East Asia that protect, market, and develop their wildlife assets in the right way. PAs located in East and Southern Africa, the Peruvian Amazon, and Patagonia were predicted to be most *popular*. Despite possessing slightly less *attractive* species assemblages, PAs in India, the Iberian Peninsula and the western portions of the United States were also *popular*. These PAs should be prioritised for wildlife tourism investment, as well as management efforts to maximise tourist interest but reduce the risk of over-visitation, in order to capitalise on wildlife tourism opportunities and the benefits they offer for biodiversity conservation and local people. In East Africa, the Amazon basin, and the Guianas, robust, proactive adaptation is needed to help managers mitigate projected climate-induced declines in species *attractiveness*. The tropical Andes, the Himalayas, and Russia's Northern Taiga, may benefit from colonisation by *attractive* species as a result of climate change, but environmental impacts of increased visitation may need to be addressed.

List of Abbreviations

AICc corrected Akaike information criterion. 138, 142, 143

BAP Biodiversity Action Plan. 135, 136, 139, 142, 143, 150

BCI Bright Colour Index. 135, 136

CBD Convention on Biological Diversity. 6

CCI Climate Change Initiative. 72

CES cultural ecosystem services. 9

CEs choice experiments. 17

CV contingent valuation. 17, 23

ES ecosystem services. 7–9, 65, 90, 95

ESA European Space Agency. 72, 183

GCM global climate model. 105, 106

GLM generalised linear model. 137, 138

GLMM generalised linear mixed model. 44, 67, 69, 73, 74, 178

GMTED Global Multi-resolution Terrain Elevation Data. 68, 71, 72

HBW Handbook of the Birds of the World. 38

HDI Human Development Index. 68, 72, 78, 83

HMW Handbook of the Mammals of the World. 38, 40

IPBES Intergovernmental Platform on Biodiversity and Ecosystem Services. 8, 10

IUCN International Union for Conservation of Nature. 40, 68, 72, 73, 80, 83, 92, 136, 183

MA Millennium Ecosystem Assessment. 8, 9

NCP nature's contributions to people. 8

NRMSE normalized root mean square prediction error. 43

PA protected area. iii, iv, 6–8, 10, 12–21, 23, 24, 26, 29, 31, 34, 35, 56, 57, 59–62, 64–86, 89–98, 102, 107, 119, 122, 127, 130, 131, 138, 139, 145, 147, 148, 152, 153, 157, 159–161, 164–169, 183, 184, 208, 209

POIs Points of Interest. 72

RCP Representative Concentration Pathway. 105–108, 115, 119, 122, 128

RSPB Royal Society for the Protection of Birds. 131, 139, 145, 151

SDGs Sustainable Development Goals. 34, 62

SDM species distribution model. 103, 104, 106, 124

TCM travel cost method. 17, 23

TEEB The Economics of Ecosystems and Biodiversity. 8, 16

TEV total economic value. 16

UNESCO United Nations Educational, Scientific and Cultural Organization. 72

VIFs Variance Inflation Factors. 43, 73, 137

WDPA World Database of Protected Areas. 72, 79

WTP willingness-to-pay. 17

Contents

Chapter 1

General Introduction

1.1. CONSERVATION AND THE GLOBAL BIODIVERSITY CRISIS

The current loss of global biodiversity is a critical environmental problem that is reaching a crisis point. Despite the adoption of numerous international agreements aimed at conserving biodiversity, such as those laid out by the Convention on Biological Diversity (CBD, 2010), biodiversity continues to be lost (Ament et al., 2019; Butchart, Walpole, et al., 2010; Tittensor et al., 2014). The CBD articulated five strategic goals to be achieved by 2020, known as the Aichi Biodiversity Targets, which, among other things, reasserts the role of protected areas (PAs) in conserving nature. The definition of a PA is "*a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values*" (IUCN, 2015). PAs are considered the cornerstone of *in situ* biodiversity conservation (Chape et al., 2005), and now represent one of the most significant forms of human land-use, covering $>$ 15% of the Earth's land and inland freshwater and 7% of its oceans (UNEP-WCMC et al., 2019). Beyond setting a target for PA coverage in the marine and terrestrial realms, the latest CBD targets also call for PAs to be effectively managed (CBD, 2018). Recent reviews concluded that well-managed PAs reduce rates of habitat loss (considered the primary threat to biodiversity) (Butchart, Scharlemann, et al., 2012; Edgar et al., 2014; Geldmann et al., 2013) and maintain species population levels better than other management approaches (Laurance et al., 2012; Lester et al., 2009). However, while there has been an overall increase in the total area covered by the global PA network, insufficient management budgets have, in many cases, precluded effective conservation, indicating that the goal of effective PA management is not being met (Butchart, Walpole, et al., 2010; Ceballos et al., 2015).

The ubiquitous under-financing of conservation efforts worldwide can be attributed, in part, to the high costs of conservation. The direct costs of management and opportunity costs of setting aside land for protection means that governments often favour alternative land-uses (Wilkie, Carpenter, and Zhang, 2001). Competition over limited government resources from more immediate social needs, such as education and health, means that government funding for conservation is less reliable in lower income countries, which encompass many high priority conservation areas (Emerton et al., 2006).

On top of the costs to governments, substantial costs are felt by local people living adjacent to PAs. These costs can broadly be categorized as visible or hidden (Barua et al., 2013). The former refers to direct material losses such as livestock depredation and spread of disease, crop raiding, and property damage by wildlife spilling over from PAs. The latter includes the removal of traditional land rights and restrictions on livelihood activities. The exclusion and repression of Indigenous or rural peoples forms the basis of ‘fortress’ conservation, a prominent component of colonisation (Domínguez and Luoma, 2020; Sand, 2012). When PAs were first established during the era of broad colonial conquest and exploration, native people were pushed off their traditional lands and only uses with the potential to benefit colonisers, whose own natural areas may already been developed for other economic purposes, were permitted – i.e., tourism and scientific research (Laltaika and Askew, 2018). Under the fortress conservation paradigm, colonial legacies persist today in the form of insecure land tenure for local people, the military culture of PA administration, and economic leakage of tourism revenue, whereby revenue is lost to outside economies via foreign companies (Sène-Harper and Séye, 2019).

Previous studies have reported that living close to PAs incurs costs of $> 84\%$ of household income (Bush et al., 2013; Poudyal et al., 2018; Vedeld et al., 2012). The repressive policies of PAs also bring with them social costs for local people, who may experience fear, trauma, anxiety, and other negative experiences and feelings (Barua et al., 2013; Thondhlana et al., 2020). These tremendous costs have spurred hostility among local people towards conservation efforts, and provided economic incentive to engage in illegal activities, such as logging or poaching, creating challenges for PA management and driving continued degradation of wildlife resources (Balmford and Whitten, 2003; Campbell et al., 2008; Karanth and DeFries, 2011; Watson et al., 2014). PAs that fail to integrate local livelihoods therefore typically do not achieve their conservation goals, simultaneously failing to support the people that depend upon their natural resources (Leverington et al., 2010; Watson et al., 2014).

Alongside the high and inequitable costs associated with conserving biodiversity is a lack of recognition of both the market and non-market value of biodiversity. PAs generate a variety of ecosystem services (ES) (Chen et al., 2017), which local people can use for subsistence and income generation (Braber et al., 2018; Bray et al., 2008; Putz et al., 2012; Sebele, 2010) and can help PAs 'pay their way'. In light of the ongoing threats to global biodiversity, recognizing PAs as human-natural systems and the natural resources they harbour as economic assets that can generate sustainable streams of revenue and employment opportunities that benefit not only nature, but also the local people living alongside these areas, is becoming especially important (Balmford, Beresford, et al., 2009; Liu, Dietz, et al., 2007; Naughton-Treves et al., 2005).

1.2. THE ECOSYSTEM SERVICES FRAMEWORK

The objectives of biodiversity conservation are broadening to encompass the preservation of goods and services that people derive from ecosystems e.g., crop pollination, food provisioning, water purification, and carbon sequestration. ES could be instrumental in making a case for biodiversity conservation, if their benefits are made explicit. Consequently, and advanced by various global initiatives, the ES concept is being increasingly used as a framework for guiding scientific research and decision-making, to support conservation and environmental management (Weyland and Laterra, 2014). Spatial assessments of different ES may be of particular importance when designing conservation strategies and identifying an efficient and effective network of priority areas. Indeed, the Aichi targets, laid out by the Strategic Plan for Biodiversity 2011–2020, included ES as an element to be considered in the global expansion of PAs (Target 11) and a priority for protection and restoration (Target 14).

Initiated in 2001, the Millennium Ecosystem Assessment (MA) documented the importance of ES, defined as the benefits people obtain from ecosystems, to human well-being, and showed that the continued supply of these services is threatened by unsustainable human activities (UNEP, 2005). The MA framework categorizes ES as provisioning, regulating, cultural, and supporting ES, and splits human well-being into the basic materials for life, security of resources, good health, social relations, and freedom and choice. ES and human well-being components are influenced by direct anthropogenic and natural drivers and indirect institutional, governance and other drivers. The Economics of Ecosystems and Biodiversity (TEEB, 2010) framework brought an economic perspective of ES to the debate, recognizing, demonstrating, and capturing the economic value of biodiversity, as well as the costs arising from biodiversity loss and ecosystem degradation

Building on the MA and TEEB frameworks, in 2012, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) was established (Biodiversity and Services, 2021). The IPBES framework includes nature (biodiversity and ecosystems) and nature's benefits (i.e., ES) as two separate components, and links the latter with the quality of life (or human well-being), without categorizing services or well-being. The direct and indirect drivers, including anthropogenic assets, such as built infrastructure, technology, knowledge, financial assets, have an impact on nature and its benefits to people, and therefore on the quality of people's lives. A key element of the IPBES framework is the notion of nature's contributions to people (NCP) (Díaz, Pascual, et al., 2018), akin to the TEEB definition of ES as the direct and indirect contributions of ecosystems to human well-being. The NCP approach recognizes the influence of culture on defining links between people and nature and emphasises the central role of Indigenous and other knowledge systems (Díaz, Demissew, et al., 2015).

Although substantial progress has been made in assessing and mapping ES, least attention has been paid to what the MA defines as cultural ecosystem services (CES), despite rising public demand for these types of services (Daniel et al., 2012). CES are the non-material benefits people obtain from ecosystems and include spiritual experiences, cognitive development, cultural identity, recreation, and aesthetic inspiration (UNEP, 2005). The importance of CES is well recognized, but their integration into the ES framework has been hindered by the difficulty in quantifying them in biophysical or monetary terms and their dependence on subjective human values. To a degree, all ES depend on subjective human values (e.g., not everything that is potentially nutritious is viewed as food by all cultures), and these values may change over time, but, CES may depend on them to a greater degree (e.g., the aesthetic appeal of a landscape depends on the experiences, knowledge and uses of landscapes by people).

Because ES are based on biological and non-biological attributes of ecosystems, as well as human values, the relationship between biodiversity and ES flows is likely to be complex for a wide variety of systems. There is evidence that some forms of ES depend on biodiversity and the ecological processes it comprises (Fagan et al., 2008) but it is essential that the ES concept is not viewed as a ‘silver bullet’ that provides ‘win-win’ scenarios for people and conservation (see Vira and Adams, 2009). Justifying biodiversity conservation primarily in terms of ES is risky, and policy makers and conservationists need to be careful not to promote ES at the expense of biodiversity. However, growing knowledge and recognition about ES may expand the potential for biodiversity conservation that simultaneously benefits people and promotes human well-being.

1.3. NATURE TOURISM

The fastest growing CES in today’s society is tourism and recreation. In ES classifications, everyday short-term recreation in nearby green spaces and tourism are often lumped together. However, while tourism is defined as “*the activities of persons travelling to and staying in places outside their usual environment for not more than one consecutive year for leisure, business and other purposes*” (UNWTO, 2013), recreation is an activity done for enjoyment outside of work, such as walking, camping, and wildlife watching, which can form important components of tourism. These, and other recreational activities, provide opportunities for people to experience the benefits of ES directly, including physical exercise, aesthetic experiences, and intellectual stimulation. They also generate substantial economic benefits. As a whole, the tourism industry contributes to 10.4% of global Gross Domestic Product and supports one in ten jobs (319 million), representing a key driver of economic growth and development (UNWTO, 2019; WTTC, 2019).

The enjoyment of nature is considered an important, and growing, motivation for tourism and a major co-benefit of conservation. Precise definitions of nature tourism do not exist, but for the purpose of this study, I define it broadly as tourism with the primary aim of enjoying nature (Balmford, Beresford, et al., 2009). From the 1960s, growth in nature tourism has been stimulated by growing interest in the natural world, more affordable travel and greater accessibility of natural areas, better knowledge of destinations through the internet, new source markets, and product innovation (Novelli, Barnes, et al., 2006). The term nature tourism is often used interchangeably with eco-tourism, but eco-tourism typically has a narrower definition that requires a direct contribution to conservation and the well-being of local people (Fig. 1.1) (IES, 2000). Under the IPBES framework, tourism operations can be conceptualised as anthropogenic assets that together with nature, co-create benefits for people.

PAs are popular destinations for nature tourism. Many were set up with the dual mandates of biodiversity protection and public use, which, during the colonial period, meant they were to be enjoyed by foreign tourists, but it was not until around the middle of the 20th century that tourism inside PAs accelerated (Zeiger et al., 1992). PAs are visited for their various natural and cultural attractions e.g., geology in Yosemite National Park, US; lakes in Jasper National Park, Canada; archaeological ruins in Parque Nacional Palenque, Mexico. In some regions, wildlife is the major attraction drawing visitors to PAs, and the single biggest driver of tourism growth (UNWTO, 2018). The revenue generated from wildlife tourism through e.g., fees and prices for entry, activities, accommodation and purchases, is now of national significance for some countries, such as Rwanda, where revenue from visits to see mountain gorillas *Gorilla beringei beringei* inside Volcanoes National Park is the country's largest source of foreign exchange, raising US$200 million annually (Maekawa et al., 2013). The most detailed, up-to-date study on wildlife tourism's economic impact comes from the World Travel & Tourism Council, which estimated that, in 2018, it directly contributed $120.1 billion to the global economy (4.4% of the total contribution the entire tourism industry) (WTTC, 2019). If multiplier effects across the global economy are included, the total economic contribution of wildlife tourism came to $343.6 billion. In the same year, it sustained an estimated 21.8 million jobs (equal to 6.8% of total jobs sustained by global travel and tourism).

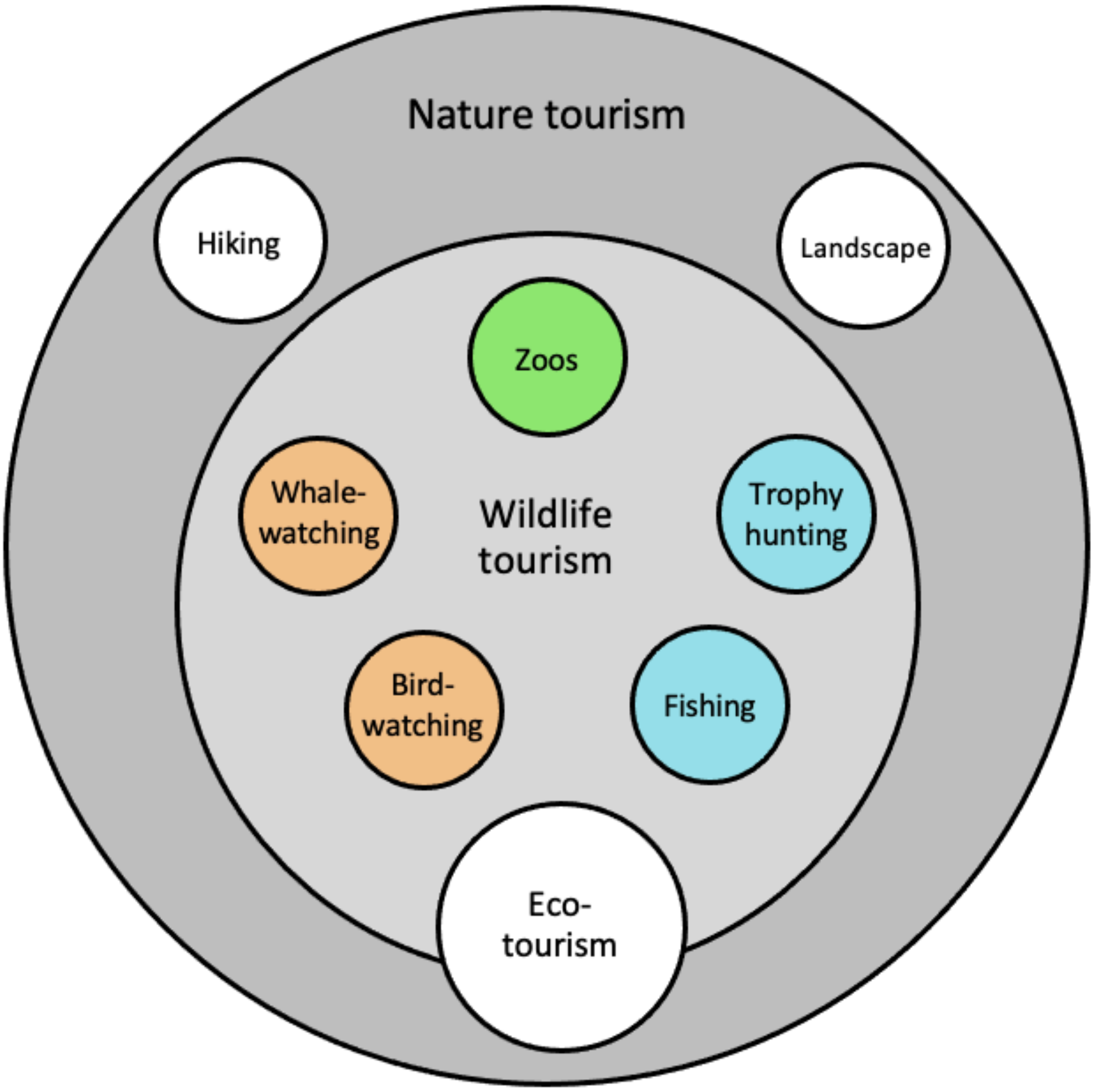

Figure 1.1: Relative position of wildlife tourism within the larger nature tourism industry, showing examples of non-consumptive wildlife tourism activities (orange), consumptive activities (blue), and *ex situ* activities (green), based on information from Newsome, Dowling, et al. (2005), Reynolds and Braithwaite (2001), and Wearing and Neil (2009).

The focus of this thesis is non-consumptive wildlife tourism, which involves viewing and often photographing free-ranging animals in their natural habitat, and includes activities such as whale-watching and birdwatching (Fig. 1.1) (Higginbottom, 2004). Wildlife tourism can also involve the consumptive use of wildlife, such as trophy hunting or sport fishing (Mbaiwa, 2003; Novelli, Barnes, et al., 2006; Winterbach et al., 2015). *Ex situ* wildlife tourism occurs where animals are observed outside of their natural habitat in captive or semi-captive settings like zoos (Skibins et al., 2013).

1.4. BENEFITS OF WILDLIFE TOURISM

Wildlife tourism is being promoted as a powerful tool that can help countries grow and diversify their economies by generating income and employment opportunities, while simultaneously protecting their biodiversity. Although not the focus of my thesis, nature tourism, more generally, is also thought to contribute to human well-being, including improving physical and mental health (Sandifer et al., 2015). Accordingly, wildlife tourism has been heralded for its potential to help nations meet multiple ambitious international targets, such as those laid about by the Aichi Targets, as well as the United Nations Sustainable Development Goals (Eagles, 2014; Imran et al., 2014; Job and Paesler, 2013; UN, 2015).

Wildlife tourism can help promote biodiversity conservation in myriad ways, but perhaps most importantly through generating funds. PA agencies in many developing countries now receive most of their recurrent funding from tourism, through the various fees charged to visitors (Buckley, Castley, et al., 2012; Rylance et al., 2017). For some PAs, the proportion is $> 80\%$. The relationship between tourism revenue and the conservation of threatened species in PAs globally has been demonstrated for mammals, birds, and frogs (Buckley, Castley, et al., 2012; Morrison et al., 2012; Steven, Castley, et al., 2013). For some threatened species, $> 80\%$ of remaining global habitat (Morrison et al., 2012) or $> 60\%$ of remaining global populations (Buckley, 2009; Buckley, Castley, et al., 2012; Steven, Castley, et al., 2013) is protected through funding raised from tourism.

Indirect conservation benefits of wildlife tourism come from educating the public and promoting pro-conservation behaviours, including philanthropy, volunteering and consumer habits, through exposure to nature (Bentz et al., 2016; Schuhmann et al., 2016; Skibins et al., 2013). Even tourism based on a few charismatic species (i.e., species with widespread popular appeal) may lead to greater appreciation of other threatened wildlife at larger scales, supporting broader conservation goals (Skibins et al., 2013). Tourists seeking to experience nature are often in favour of regulations and infrastructure that minimise any negative environmental impacts of their activities, facilitating the implementation of sustainable tourism practices (Avila-Foucat et al., 2013; Ziegler et al., 2012). Private tourism operators themselves may also be actively engaged in conservation efforts to preserve the wildlife attractions that they depend on, including funding and/or operating breeding and translocation programmes; invasive species controls; anti-poaching measures; conservation concessions or land easements (Biggs et al., 2016; Buckley and Mossaz, 2018; Nelson et al., 2010).

The more successful wildlife tourism operations provide economic benefits to gateway communities, which are those that live alongside natural areas and other tourism sites (Karanth and DeFries, 2011; Mearns, 2012; Nyaupane and Chhetri, 2009). Employment in hotel, airline, safari and other tourism-related ventures has diversified and increased income opportunities for rural people and the use of locally-sourced goods and services in wildlife tourism ventures supports small-scale industries and agriculture, which has been shown to improve standards of living by allowing families to pay school fees, purchase foods and clothes, and construct houses (Job and Paesler, 2013; Lindsey, Nyirenda, et al., 2014; Newsome and Hassell, 2014; Richardson, Fernandez, et al., 2012; Sebele, 2010). In certain communities, earnings from wildlife tourism have been re-invested in development, such as improving road networks, schools and other infrastructure (Mbaiwa, 2003; Mbaiwa and Stronza, 2010; Newsome and Hassell, 2014; Nielsen and Spenceley, 2011). Where local people see the benefits of wildlife through tourism, it provides an economic alternative to less sustainable activities such as hunting and logging (Mbaiwa, 2003; Thapa et al., 2017; Walpole and Goodwin, 2001) and fosters more positive attitudes towards conservation efforts (Krüger, 2005; Spenceley et al., 2010; Wilson, Hayward, et al., 2017). If a tourism icon is a source of human-wildlife conflict, such as a crop raiding or livestock predating species, income from tourism can also compensate for these losses and discourage retaliatory hunting (Lepp, 2007; Walpole and Leader-Williams, 2002).

1.5. CHALLENGES OF WILDLIFE TOURISM

Following a global meta-analysis of eco-tourism, encompassing wildlife tourism operations, from 188 case studies, Krüger (2005) concluded that only $\sim$18% made measurable positive contributions to conservation. Several known issues and challenges, discussed below, have been associated with wildlife tourism that may account for its sometimes-limited role in nature conservation.

On its own, wildlife tourism may not be able to generate the funding for effective conservation without other forms of public and political support. Indeed, few examples exist where tourism has generated sufficient revenue to cover the full costs of PA management (Baral et al., 2008; Lindsey, Nyirenda, et al., 2014). Preferences for charismatic species (e.g., large-bodied mammals) are sometimes criticised for directing conservation funds away from wider biodiversity (Clucas et al., 2008). This has been countered with the argument that focal species may serve as ‘flagship species’, which capture public support and funding that can be used to conserve general biodiversity (Lindsey, Alexander, et al., 2007; McGowan et al., 2020;

Meer et al., 2016; Williams, Burgess, et al., 2000) or 'umbrella species', whereby conserving the focal species' habitat may conserve other species that occur within that species' habitat (Andelman and Fagan, 2000; Li and Pimm, 2016). Of course, tourism can have adverse environmental effects, exposing vulnerable species and habitats to new threats. This can be particularly problematic for rare species that may be disproportionately impacted if they are perceived as more interesting or attractive (Courchamp, Angulo, et al., 2006; Reynolds and Braithwaite, 2001). In the aforementioned meta-analysis, as many as 36% of all tourism programs were considered unsustainable due to negative impacts on target species, usually resulting from large numbers of poorly regulated or managed tourists (Krüger, 2005).

The direct impacts of tourism activities on wildlife can include injury, stress or death of animals, and disruption of crucial behaviours such as feeding or breeding (Macdonald, Gallagher, et al., 2017). Development of infrastructure and accommodation, as well as pollution, can also lead to the loss or deterioration of habitat and wildlife corridors. Improved access to remote areas, where popular wildlife tourism destinations are often located, and increased habituation of animals, also make them more vulnerable to poaching. Stocking charismatic species at high densities or introducing extralimital species (i.e., species introduced outside their natural geographic range within a geopolitical area), as occurs in many African PAs, can lead to hybridization and competitive exclusion of native species, habitat degradation, and the low survival rate of extralimital species (Castley et al., 2001; Maciejewski and Kerley, 2014a,b).

If well-managed, tourism has the potential to mitigate conflict between conservation and the rights of Indigenous and rural peoples through e.g., revenue generation and job creation. However, if managed poorly, tourism can have the opposite effect. Indeed, examples of conflict between people and wildlife e.g., crop and livestock depredation and the loss of human life, have been linked to tourism operations. High tiger *Panthera tigris* densities, for example, in a few heavily visited sites in India, where more revenue allows for greater ranger enforcement, have increased human fatalities, leading to negative consequences for both people and tigers (Macdonald, Gallagher, et al., 2017). This highlights the importance of considering cultural and local contexts when selecting flagships species on which tourism is focussed (Bowen-Jones and Entwistle, 2002). The well-established risk of aggression associated with provisioning and habituation of animals for tourism purposes can also increase risks to human safety (as well as ecological instability).

The example above of rising human fatalities reflects an extreme concern regarding the impacts that wildlife tourism has on local people. More prevalent is the unequal distribution of revenue in foreign-dominated industries, which tend to employ few local people, the latter mostly in poor-quality, low-skilled and low-paid seasonal positions, hence producing only marginal economic benefits for local people (He et al., 2008; Mbaiwa and Stronza, 2010). There are few cases of successful or profitable community-based projects, where local people are more involved in decision-making (Mbaiwa, 2003). Leakages of financial revenue overseas through the import of tourism-related goods and services have also limited the benefits that local industries and agriculture receive from wildlife tourism (Walpole and Goodwin, 2000, 2001). Even in PAs with high tourism revenue, such as from gorilla *Gorilla* spp. tracking, the economic rewards do not always compensate for the losses felt by the local people (Adams and Infield, 2003). Infrastructural development costs and increased land prices means that wildlife tourism can also put pressure on local economies (Karanth and DeFries, 2011). Tourism can lead to the commodification and exploitation of local people, threatening their culture, Indigenous identities, and religious traditions (Stelios and Melisidou, 2007). Where wildlife tourism fails to create enough revenue for local communities, or conservation is prioritised over people, local attitudes can become hostile, undermining conservation efforts (Krüger, 2005).

1.6. WILDLIFE TOURISM DRIVERS

Difficulties in access, lack of well-developed infrastructure, political instability, inadequate involvement of local communities, and an absence of natural attractions, including preferred species, are all thought to limit the benefits of tourism (Funston et al., 2013; Krüger, 2005). However, especially important in determining the success of tourism ventures is thorough planning, management, and marketing. The lack of assessment into the role of species and site features in influencing tourists' decision-making, and with it a strategic plan on how to attract tourists, is thought to contribute to the unsustainability of many wildlife tourism projects (Krüger, 2005).

Awareness of the drivers of wildlife tourism is needed to quantify a site's tourism potential, enabling investment to be directed towards priority areas that are better suited to wildlife tourism, where tourism operations are more likely to succeed, and to develop effective marketing strategies and sustainable management plans that incorporate tourists' needs, interests, and preferences (Grünewald et al., 2016; Veríssimo, MacMillan, et al., 2011; Willemen et al., 2015). The valuation of wider biodiversity for wildlife tourism is also needed to determine its role in providing economic incentive for conservation, especially in PAs where biodiversity value is high but traditional charismatic megafauna are absent.

With a better understanding of the species and site features that attract tourists, managers could maximise visitation (within sustainable levels), and possibly charge higher fees to visitors, through targeted management and marketing that conserves and promotes key attractions, thereby maximising tourism revenue. New opportunities for tourism development could be created by identifying and marketing attractive species that are currently overlooked by the general public, so-called ‘Cinderella species’ (Balmford, Green, et al., 2015; McGowan et al., 2020; Smith et al., 2012). Capitalising on such opportunities would not only open up untapped sources of revenue for biodiversity conservation and local communities, but also relieve pressure on some of the more heavily exploited regions receiving unsustainable visitor numbers. If managers can identify the species that are preferred by tourists, and therefore those that are likely to experience greatest pressure, they will be better informed to minimize negative ecological impacts and by enhancing visitor satisfaction, they may be able to strengthen the connection between tourists and nature, promoting more environmentally responsible behaviours. In light of global change, understanding wildlife tourist preferences can ultimately help ensure tourism operations remain viable, and enable managers to exploit any future opportunities that emerge e.g., from climate change (Williams and Polunin, 2000).

1.6.1. Current research methodologies

The factors influencing tourists’ decision-making in nature tourism have been assessed using PA visitor counts, visitor surveys, and/or spatial proxies for visitation e.g., social media data. Following the TEEB valuation framework, this research often includes some well-established economic valuation methods. Measuring the tourism value of PAs in monetary terms can demonstrate tangible economic benefits attributable to these areas and their natural assets that are comparable to those of commercially traded components such as timber, oil, and agricultural products and can therefore present an economic justification for the continued use of these areas as conservation tools. Environmental economics usually assesses natural assets, such as wildlife, within the framework of total economic value (TEV) (Tisdell and Wilson, 2003; Turner et al., 2003). TEV includes all values that relate to the asset, with the main components being use and non-use values (Tamayo et al., 2018). The former is the value obtained from the actual use of the asset, either directly or indirectly (Alves et al., 2017). The latter refers to the value that people assign to assets, even if they never have and never will use it (Liu, Liu, et al., 2019; Tamayo et al., 2018; Xiao, Wang, et al., 2021), and includes the value assigned to the existence of environmental resources (existence value), the option of using the good at some point in the future (option value), and preserving a good or service for use by future generations (bequest value).

The direct use value of a PA's natural assets can be calculated using PA visitor numbers and expenditure on entrance fees, accommodation, guides, and so on. Perhaps the most notable study assessing PA visitation is the study by Balmford, Green, et al. (2015), in which they predicted visitation to the world's terrestrial PAs and estimated its global economic value at ∼US$600 billion/year (in terms of direct in-country expenditure). Similarly, at a continental level, Schägner, Brander, et al. (2016) explored the factors that influence national park visitation across Europe, and estimated a recreational value of €14.5 billion annually for 449 parks in the study area. The travel cost method (TCM) is an approach that uses the distance people have travelled to estimate direct use values. Heagney et al. (2018) undertook one of the few, more extensive TCM studies, exploring the use of a PA network across the state of New South Wales in Australia, using phone surveys.

Measuring direct use values, which are more likely to be traded on commercial markets, can be a more straightforward process than measuring other values, because the markets have already done the work of calculating these values, but tourists may place value on natural assets on top of their obvious market value. The majority of research eliciting this non-market values from tourists has involved the use of 'stated preference' techniques, such as contingent valuation (CV) and choice experiments (CEs), to assess respondents' willingness-to-pay (WTP) for non-market goods and services and have been used to capture both use and non-use value (Di Minin et al., 2013; Lindsey, Alexander, et al., 2007; Naidoo and Adamowicz, 2005a). The CV method involves asking respondents directly for their WTP for a clearly defined good (e.g., seeing their preferred or favourite animal). CEs provide the respondents with choice alternatives where the different goods are defined by their attributes, the cost of the good being one of them. Information about the WTP of respondents for changes in attribute levels (e.g., population densities of preferred species) is then obtained by observing the choices made.

Crowdsourced and remote-sensing data, such as Flickr (`https://www.flickr.com/`) and Instagram (`https://www.instagram.com/`) are emerging as a potential cost-effective source of information on tourists' behaviours, preferences, and values. Hausmann, Toivonen, Fink, et al. (2019) and Hausmann, Toivonen, Slotow, et al. (2017) used social media data to explore the recreational value of Important Bird and Biodiversity Areas globally and the factors attracting tourists to PAs in sub-Saharan Africa, respectively, while Willemen et al. (2015) used social media to quantify the attractiveness of species to tourists visiting African PAs. When tested against actual visitor numbers, social media data have been found to be a robust indicator or proxy for visitation (Hausmann, Toivonen, Slotow, et al., 2017; Wood et al., 2013), and therefore direct use value (Sonter et al., 2016)

1.6.2. Key concepts underlying tourism consumer psychology

Various terms have been used when discussing tourist preferences for species and other aspects of the wildlife tourism experience, including "charisma" (Albert et al., 2018; Berti et al., 2020; Lorimer, 2007; Macdonald, Burnham, et al., 2015), "popularity" (Clucas et al., 2008; Hausmann, Toivonen, Fink, et al., 2019; Neuvonen et al., 2010; Norman and Pickering, 2019; Reynolds and Braithwaite, 2001; Veríssimo, Vaughan, et al., 2017; Willemen et al., 2015), "attractiveness" (de Castro et al., 2015; Garnett et al., 2018; Hausmann, Slotow, Fraser, et al., 2017; Siikamäki et al., 2015; Veríssimo, Fraser, et al., 2009; Willemen et al., 2015), "appeal" (Smith et al., 2012; Steven, Smart, et al., 2017), and "value" (Farr et al., 2014; Guimarães et al., 2015; Maciejewski and Kerley, 2014b; Pires et al., 2016). These terms refer to highly complex and inter-connected concepts, and some have been used interchangeably in the literature e.g., attractive species being described as charismatic and popular and charismatic species being defined as attractive, appealing, and preferred. The term "value" stands out, with its economic connotations, and is more closely linked to the benefits a species conveys to people.

The current research into wildlife tourist preferences can be divided into two main parts, discussed in detail below, which include the 1) key species and 2) site features that attract tourists to particular wildlife watching destinations. Throughout this thesis, I use the term "attractiveness" when discussing tourists' preferences for species, which more accurately describes a species ability to draw tourists to a site, without assigning them an economic value, but acknowledge that this term likely encapsulates the above concepts. Furthermore, some researchers separate charisma (i.e., charm or appeal) from endangered status or rarity (Arbieu, Grünewald, Martín-López, et al., 2018; Colléony et al., 2017), such that the term "attractiveness" may be more effective at encompassing both affect-related (i.e., related to emotions and feelings) and scientific considerations. I discuss PA "popularity" as a proxy for PA visitation, which may be influenced by the "attractiveness" of its natural assets (e.g. wildlife, landscape), but also by other factors.

1.6.3. Which species are attractive to people?

Mounting research has begun to reveal particular species that attract public interest. In line with the aesthetic and ecological facets of species charisma, proposed by Lorimer (2007), various commonalities have been identified amongst the species that are attractive to people. For example, people show a strong attraction to large-bodied, 'cuddly' or 'cute' vertebrates with forward-facing eyes and human-like attributes species (Berti et al., 2020; Lindsey, Alexander, et al., 2007; Lorimer, 2007; Macdonald, Burnham, et al., 2015). For marine and bird species especially, colouration has also been identified as an important feature, adding to a species' attractiveness (Jefferson et al., 2014; Veríssimo, Fraser, et al., 2009). The perceived cognitive and emotional capacity of an animal, as well as its behaviour, has been recognised as important (Curtin, 2006). For instance, part of the draw of large felids is thought to be the thrill of observing the animals actively hunting their prey (Clucas et al., 2008; Okello et al., 2008). Likewise, birds that display unique courtship rituals, feeding activities, and nest-building skills have been found to be more attractive to birdwatchers (Veríssimo, Fraser, et al., 2009). Breeding groups have also been found to be more attractive to tourists than individual animals, perhaps because of the opportunities to view interesting behaviours between individuals e.g., grooming, parental care, mating (Di Minin et al., 2013). Threat status and endemism have been found to be particularly important, with rare, endangered, and endemic species being more attractive to people than more common, widepsread species (Di Minin et al., 2012; Grünewald et al., 2016; Macdonald, Burnham, et al., 2015; Maciejewski and Kerley, 2014b; Steven, Smart, et al., 2017; Veríssimo, Fraser, et al., 2009). For tourism purposes, the attractiveness of rare species may apply to species that are locally rare within specific PAs (Grünewald et al., 2016; Maciejewski and Kerley, 2014b; Okello et al., 2008).

The above features could be considered 'aesthetic' features. The detectability or visibility of a species is also thought to be important in determining species attractiveness. This could be considered part of the 'ecological' facet of charisma, as coined by Lorimer (2007), and may be particularly influential in tourism, which depends on reliable opportunities to view animals in the wild. Indeed, it has been suggested that the best tourism attractions are: predictable in activity or location; approachable; tolerant of human intrusion; present in open habitats; local abundant; and/or are diurnally active (Reynolds and Braithwaite, 2001). This has been demonstrated for African safaris, with species that can be easily spotted in the open savannas attracting more attention than those that occur in areas with dense vegetation (Grünewald et al., 2016; Maciejewski and Kerley, 2014b; Okello et al., 2008). The size and social system of a species might also be an important component of ecological charisma, as larger, group-living species are generally more visible. Technological and methodological developments have overcome some of the obstacles associated with observing animals in the wild, making a wider range of species more accessible, and therefore potentially attractive, to tourists – safari and birdwatching tours operate in the early hours of the morning, whilst night-time safaris and sea turtle walks are popular, permitting observations of nocturnal and crepuscular species (Wilson and Tisdell, 2001).

The final facet of species charisma is ‘corporeal’ charisma (Lorimer, 2007), which relates to a deeper emotional attachment that can be influenced by encounters or interactions with a species over time. This might be influenced by the publicity that a species has enjoyed in the media (Lorimer, 2006; Reynolds and Braithwaite, 2001). Emphasis of marketing strategies towards large-bodied mammals has raised the public profile of these species and likely raised their perceived attractiveness (Macdonald, Burnham, et al., 2015). Linked with this is the symbolic depiction of some animals e.g., lions *Panthera leo* and eagles in various cultures and mythologies (Okello et al., 2008).

1.6.4. What destination features make them popular for wildlife tourism?

Numerous studies have revealed various site features, with a strong focus on PAs, that influence their popularity as wildlife tourism destinations. The most obvious attractions for wildlife tourists are charismatic species. The Komodo dragon *Varanus komodoensis* is the main reason for visiting the Komodo National Park in Indonesia (Walpole and Goodwin, 2001); large marine species such as cetaceans, sharks, rays and turtles attract tourists to coastal destinations (Bentz et al., 2016; Farr et al., 2014; Uyarra et al., 2005); felids are important species for the African safari industry (Grünewald et al., 2016; Maciejewski and Kerley, 2014b; Okello et al., 2008; Winterbach et al., 2015); and the mountain gorilla *G. b. beringei* is the main focus of tourism activities in Volcanoes National Park in Rwanda (Nielsen and Spenceley, 2011). Tourists have also been found to appreciate wider biodiversity, particularly experienced and domestic tourists, both within the terrestrial (Di Minin et al., 2012; Lindsey, Alexander, et al., 2007; Loureiro et al., 2012; Naidoo and Adamowicz, 2005a) and marine realm (Biggs et al., 2016; Uyarra et al., 2005). This has sometimes, though not always, been reflected in higher visitation rates in more biodiverse PAs (Chung et al., 2018; Naidoo and Adamowicz, 2005b; Siikamäki et al., 2015).

The landscape is another key element of the wildlife tourism experience (Lindsey, Alexander, et al., 2007; Loureiro et al., 2012). PAs at high elevations and with diverse land cover, but open vegetation, have been found to be more heavily visited (Balmford, Green, et al., 2015; Chung et al., 2018; Hausmann, Toivonen, Slotow, et al., 2017; Schägner, Brander, et al., 2016). These PAs may be more popular among tourists because of their wildlife viewing opportunities and other natural attractions, and their recreational opportunities. PAs at higher elevations may also encompass relatively pristine ecosystems resulting from low development pressure. The same may be true of old PAs, which have been found to be more heavily visited than more recently designated PAs (Balmford, Green, et al., 2015; Chung et al., 2018), but older PAs may also be better known. Climate is also important, and PAs with cool temperatures and low rainfall have been found to be more heavily visited (Chung et al., 2018; Richardson and Loomis, 2004). Some studies have found that the management category of a PA might be important, and that particular designations, such as national park or World Heritage site, as well as stricter protection, could increase the number of visitors (Balmford, Green, et al., 2015; Chung et al., 2018; Neuvonen et al., 2010; Willemen et al., 2015; Xiao, Aultman-Hall, et al., 2018). This might reflect a combination of perceived 'prestige', and more pristine and diverse natural attractions in such PAs.

No matter how appealing the natural setting, the potential of wildlife tourism depends on a range of socio-economic factors (Willemen et al., 2015). Several studies have found that PAs with more amenities e.g., roads, trails, and hotels, and a higher local human population are typically more heavily visited (Balmford, Green, et al., 2015; Hausmann, Toivonen, Fink, et al., 2019; Hill and Courtney, 2006; Schägner, Brander, et al., 2016). Large PAs have recorded higher visitation rates (Balmford, Green, et al., 2015; Chung et al., 2018; Neuvonen et al., 2010), possibly because they support more natural attractions, but also because they can host a greater number of visitors than smaller PAs. PAs in richer countries have also been found to receive more visitors than those in poorer countries, reflecting the higher number of citizens who can afford to travel and recreate, and/or better-developed infrastructure (Balmford, Green, et al., 2015; Chung et al., 2018; Hausmann, Toivonen, Slotow, et al., 2017).

The reliability and convenience of transport links should have an impact on tourists' decisions, since many wildlife tourism sites are located in remote areas. This is reflected in higher visitation rates in PAs that are more accessible and have higher densities of amenities, which include transportation and parking, making them relatively easy and cheap to reach (Balmford, Green, et al., 2015; Chung et al., 2018; Schägner, Brander, et al., 2016). Perceptions of safety and security are of high importance for tourists' decision-making, deterring visitors from countries with high levels of conflict and unstable political climates (Akama and Kieti, 2003; Newsome and Hassell, 2014). The Congo Basin is a good example of how civil unrest, as well as high travel costs and long journey times, have so far limited tourism levels in a region with an abundance of charismatic mammals, such as gorillas *Gorilla* spp. and forest elephants *Loxodonta cyclotis* (Wilkie and Carpenter, 1999; Wilkie, Carpenter, and Zhang, 2001). On a local level, tourists visiting Kruger National Park in South Africa were found to be reluctant to stay in village accommodation, which may reflect concerns over safety (Chaminuka et al., 2012).

1.6.5. Heterogeneous preferences

Peoples' preferences for species, and other components of the wildlife tourism experience, are diverse, with marked differences between tourists and the local people. When discussing the idea of flagship species, Leader-Williams and Dublin (2000b, p. 69) question *"to whom are they* (flagships) *charismatic*"?, arguing that the qualities that might attract Westerners, such as large body size, may make these species "uncharismatic" to the local people living among them. For example, a review by Inskip and Zimmermann (2009) shows that for animal groups such as felids, conflict with humans increases with body mass. The importance of cultural context and the inclusion of local needs and values in the development of tourism operations, as well as the preferences of wildlife tourists, could play a key role in encouraging greater support from those who ultimately underlie the success of many conservation initiatives – i.e., the local communities.

Wildlife tourists themselves represent a heterogeneous population, consisting of different typologies categorized by different experiences, demographic factors, preferences, and requirements, despite being driven by the same overarching motivation. Duffus and Dearden (1990) proposed a conceptual framework for classifying wildlife tourist typologies into a broad continuum of experience level and involvement in or dedication to certain wildlife watching-related activities, which captures the sequential change in the type of visitors to a site. According to this framework, initially, a wildlife tourism site attracts exploratory, specialist, enthusiasts e.g., avid birdwatchers. These tourists are more knowledgeable and environmentally conscious, fewer in number, and require little infrastructure or interpretative facilities. Then, with growing awareness, marketing, and development of the site, less ambitious, more generalist tourists will dominate the visitor profile, visiting the site in greater numbers and putting greater pressure on the site. Whale shark tourism at Ningaloo Marine Park, Western Australia appears to have developed according to this trajectory (Catlin and Jones, 2010; Catlin, Jones, et al., 2010).

The position of an individual along this continuum is clearly dependent on factors such as knowledge and awareness of environmental issues, as well as income, age, occupation, and nationality, and, crucially, wildlife viewing preferences (Di Minin et al., 2012; Lindsey, Alexander, et al., 2007). For generalist, first time, international, and/or wealthier tourists, charismatic species are thought to be preferred (Di Minin et al., 2013; Kerley et al., 2003), whereas domestic, lower-income and experienced or specialist tourists show greater interest in wider biodiversity (including less charismatic species), landscapes, and scenery (Di Minin et al., 2012; Lindsey, Alexander, et al., 2007). For a site to extract the greatest benefit from tourism, managers must understand which tourists are visiting the site and cater to diverse preferences to ensure increased visitor numbers, satisfaction, and loyalty. In line with the above framework, studies that have simultaneously evaluated the preferences and profiles of wildlife visitors show that they are often generalist, international and/or Western, well-educated with a high level of disposable income (Catlin and Jones, 2010; Di Minin et al., 2012; Guimarães et al., 2015; Lindsey, Alexander, et al., 2007), though in some PAs, domestic, non-Western visitors dominate (Hausmann, Slotow, Fraser, et al., 2017; Karanth and DeFries, 2011).

1.7. TOURISM LITERATURE AS A NOVEL DATA SOURCE

Although there is substantial economic potential for exploiting wildlife resources for non-consumptive wildlife tourism, it is important to note that there are limits to approaching conservation via common economic valuations. Critics argue that monetary values assigned to the level of individual or groups of animals (Di Minin et al., 2012; Meer et al., 2016) are often derived from poor methods and/or provide misleading or unreliable figures (see Catlin, Hughes, et al., 2013). For example, the values of species at specific locations have sometimes been extrapolated to animals outside of that area, which may not always be appropriate. Furthermore, Indigenous people, who value an animal as part of their cultural heritage, may not feel that its value can be captured monetarily.

Whether stated preference techniques adequately reflect revealed preferences and behaviours is also debated (Loomis and Richardson, 2006). Comparisons have revealed that estimates of use value from CV and the TCM may differ considerably, particularly if the experience being studied is part of a bundle of experiences, between which the TCM cannot distinguish (Armbrecht, 2014; Wood et al., 2013). Stated preference and travel cost methods are also limited by costly and time-consuming data collection via visitor surveys, providing limited spatial and temporal coverage (Wood et al., 2013). Our current understanding of wildlife tourist preferences is therefore skewed to certain sites and species (e.g., charismatic megafauna) on which research has been focussed. The use of single-site surveys (or surveys from a small number of sites) means that they are restricted in their ability to explore additional contextual factors that may influence tourists' decisions.

The use of PA visitation data to explore tourism patterns is hindered by the lack of long-term statistics regarding visitor numbers, which are missing or not accessible for many PAs. Where visitor numbers have been estimated, the methods used for these calculations vary considerably across PAs and include gate receipts, car counts and trail use. This makes direct comparisons difficult (Balmford, Green, et al., 2015; Tenkanen et al., 2017). PA visitation has therefore mostly been explored at the national level (visitor data collated at the national level are more likely to have been collated using comparable methods), precluding insights into visitation patterns at a large scale. In the context of wildlife tourism, an important limitation of assessing PA visitation is that visitor numbers provide no indication of the specific motivations of tourists visiting PAs, some of whom may visit PAs in order to participate in physical activities, such as canoeing, mountain-biking or hiking, whilst others may visit PAs to participate in observational activities, such as watching wildlife or viewing attractive landscapes/scenery (Lindsey, Alexander, et al., 2007). Problems of using social media data as a proxy for visitation arise from uneven, clustered and unreliable data, due to biases and errors inherent in internet usage and geo-tagged data (Hausmann, Toivonen, Slotow, et al., 2017; Levin et al., 2015; Mancini et al., 2019; Richards and Friess, 2015; Willemen et al., 2015; Wood et al., 2013).

The lack of reliable quantitative assessments of the factors that influence tourists' behaviour and decision-making globally, including their choice of destination, expectations, satisfaction, intentions to revisit, amount of money spent, duration of the stay, and word-of-mouth recommendation, remains a major research gap (Catlin, Jones, et al., 2010; Reynolds and Braithwaite, 2001). There are a two particularly important avenues for further enquiry. First, our current knowledge of wildlife tourist preferences is limited in spatial scale and skewed to a small number of (often well-known) PAs and species (Hausmann, Toivonen, Slotow, et al., 2017; Lindsey, Alexander, et al., 2007; Maciejewski and Kerley, 2014b; Okello et al., 2008), but little is known about wildlife tourists' attitudes more generally. Second, no study has directly assessed wildlife tourism potential across the global PA network. Here, I use wildlife tourism literature as a potential novel source of information on wildlife tourist preferences and the drivers of wildlife tourism in PAs globally.

Before, during, and even after their travels, tourists often refer to a variety of travel-related literature, including glossy souvenir picture books, tourist brochures, guidebooks and tour operator websites (referred to collectively throughout this thesis as 'guides') (Therkelsen and Sørensen, 2005). Millions of tourists use guides as their key resource in order to choose a destination and plan a vacation, imagine and fantasise in anticipation of a trip, develop a cultural and environmental understanding of the destination, and to reflect back on a trip afterwards (Eagles and McCool, 2002; Muhoho-Minni and Lubbe, 2017; Nishimura et al., 2006; Young, 2009). Guidebooks make up a significant portion of the travel-related literature (Catlin and Jones, 2010). Lonely Planet, one of the world's largest and most popular publishers of travel guidebooks, sells over six million books annually (Boone and Kurtz, 2008). Tour operators have also begun to take advantage of the growing popularity of electronic sources used by travellers and have developed websites and online brochures that contain up-to-date travel information and itineraries. These resources are used by many tourists in place of traditional travel agents, with brands such as Lonely Planet and Rough Guide being particularly popular. Thanks, in part, to the wealth of tourism literature available, destinations that were once remote, unknown or difficult to reach have now been opened up to travellers.

The extent of coverage of guides varies from the entire globe to individual cities, and some focus on specific activities, including wildlife watching. Their aims and objectives also vary, with some designed to inform tourists on what destinations to visit and what sights or species to see, as well as providing transport and accommodation information for a particular country, city, or region. Others aim to inform the traveller about culture, customs, the environment, and behavioural expectations. Different guides are also targeted towards different audiences. Picture or coffee table books tend to be aimed at beginner or less experienced and/or international tourists (who also tend to be more heavily influenced by such promotional material than more specialist or expert tourists) (Catlin, Jones, et al., 2010; Curtin and Wilkes, 2005), whereas brochures, field guides, and online resources tend to cater towards more specialist tourists.

The 42 guides from which data were collated for the bulk of this thesis have been published since 1996 (Table 1.1). The guides were chosen to, either individually, or as part of a series of regional guides, provide global coverage of wildlife tourism destinations. However, lack of access to certain resources (e.g., guides published in specific languages and for specific countries) left gaps in some areas (Fig A.1). The majority of guides (and tour operators) included in this study originate from Western and/or English-speaking countries and are directed towards more generalist tourists. Inferences made from the subsequent analyses should therefore be limited to this unknown, but undoubtedly important, proportion of the global wildlife tourism market

(Goodwin, Kent, et al., 1997; Guimarães et al., 2015). The inclusion of a greater range of resources in future research would expand the current coverage and provide insight into the preferences of a wider subset of tourists.

The destinations and focal species cited in guides can be expected to reflect pre-existing preferences, where representations reinforce the attractiveness of iconic species and the popularity of particular destinations, and also play an important role in shaping tourist preferences (Reynolds and Braithwaite, 2001; Young, 2009). Zillinger (2006) demonstrated that the presentation of a site in a guidebook was directly related to its success as a tourist destination, and McGregor (2000) found that guidebooks strongly influence tourist behaviour. I add to this research by testing the citation frequency of PAs within guides against visitor numbers, in order to explore whether information from guides can be used as a proxy for human use of PAs. Questions regarding the extent to which wildlife tourism literature *reflects* or *influences* preferences should be explored in future research. By consulting numerous resources, potential biases associated with author preferences were reduced, but the factors leading to the selection or exclusion of attractions by authors, or publishers, should also be investigated.

Table 1.1: Guidebooks, online brochures and websites from which data were extracted for this thesis and whether they cited birds and/or mammals as attractions.

Source	Birds	Mammals
Global guidebooks		
Beletsky, L. (2010) *Global Birding: Travelling the World in Search of Birds*. Washington, DC: National Geographic.	✓	X
Brodowsky, P.K. & the National Wildlife Federation (2009) *Destination Wildlife*. New York City, NY: TarcherPerigee.	✓	✓
Burrard-Lucas, W. & Burrard-Lucas, N. (2015) *Top Wildlife Sites of the World*. London, UK: New Holland Publishers Pty Ltd.	✓	✓
Carwardine, M. (2011) *Ultimate Wildlife Experiences*. London, UK: Wanderlust Publications Ltd.	✓	✓
Couzens, D. (2013) *Top 100 Birding Sites of the World*. London, UK: New Holland Publishers Pty Ltd.	✓	X
Garbutt, N. (2007) *100 Animals to see before they die*. Chalfont St Peter, UK: Bradt Travel Guides.	X	✓
Gray, W. (2012) *Wildlife Travel*. Bath, UK: Footprint Travel Guides.	✓	✓
Holing, D. & Baker, C. (1996) *Nature Journeys*. Glasgow, UK: Harper Collins.	✓	✓
Lukas, D. (2009) *A Year of Watching Wildlife*. Franklin, TN: Lonely Planet.	✓	✓
Parry, J. (2007) *Global Safari*. London, UK: Carlton Books Ltd.	✓	✓
Riley, L. & Riley, W. (2005) *Nature's Strongholds: The World's Great Wildlife Reserves*. Princeton, NJ: Princeton University Press.	✓	✓
Santolalla, F. (2006) *Parques y Reservas del Mundo. Guia de los Mejores Espacios Naturale*. Barcelona, Spain: Lynx Ediciones.	✓	✓

Source	Birds	Mammals
Wilson, S. (2016) *Ultimate Wildlife Destination*. London, UK: New Holland Publishers Pty Ltd.	✓	✓
Wood, S. (2012) *Swimming with Dolphins, Tracking Gorilla*. Chalfont St Peter, UK: Bradt Travel Guides Ltd.	✓	✓
Regional guidebooks		
Bennet, J., Harley, D., Worley, M., Donaldson, B., Andrew, D., Geering, D., Povey, A. & Cohen, M. (2000) *Watching Wildlife Australia*. Carlton, Australia: Lonely Planet Publications Pty Ltd.	✓	✓
Hunter, L. & Andrew, D. (2002) *Watching Wildlife Central America*. Carlton, Australia: Lonely Planet Publications Pty Ltd.	✓	✓
Hunter, L., Rhind, S. & Andrew, D. (2002) *Watching Wildlife Southern Africa*. Carlton, Australia: Lonely Planet Publications Pty Ltd.	✓	✓
Firestone, M.D., Fitzpatrick, M., Karlin, A., Thomas, K. (2009) *Watching Wildlife East Africa*. Carlton, Australia: Lonely Planet Publications Pty Ltd.	✓	✓
Briggs, P. & van Zandbergen, A. (2016) *East African Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Chesire, G., Walker, B. & Lloyd, H. (2007) *Peruvian Wildlife: A Visitors Guide to the Central Andes*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Wijeyeratne, G. (2007) *Sri Lankan Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Gorman, G. (2008) *Central and Eastern European Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Walters M. (2008) *Chinese Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Fitter, J. (2009) *New Zealand Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Martin, S. (2010) *Australian Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Unwin, M. (2011) *Southern African Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Soper, T. (2012) *The Arctic: A Guide to Coastal Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Soper, T. (2015) *Antarctica: A Guide to the Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	X	✓
Austin, D. & Garbutt, N. (2015) *Madagascar Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.	✓	✓
Brochures		
Exodus Wildlife Encounters (2017/2018)	✓	✓
Heatherlea Birding and Wildlife Holidays (2017)	✓	✓
Natural Habitat Adventures & WWF (2017-2018)	✓	✓
Natural World Safaris (2017)	✓	✓
Naturetrek Birdwatching, Botanical & Natural History Holidays (2017)	✓	✓
Naturetrek Tailormade Bespoke wildlife and cultural holidays crafted by experts (2017)	✓	✓
Ornitholidays (2017)	✓	✓
Rockjumper Worldwide Birding Adventures (2017)	✓	✓
The Travelling Naturalist Birdwatching and Wildlife Holidays Worldwide (2017/18)	✓	✓
Wildlife Worldwide Winter/Spring (2017)	✓	✓
Speyside Wildlife (2017)	✓	✓
Websites		
Exsus (available at www.exsus.com)	✓	✓
Wildwings (available at www.wildwings.co.uk)	✓	✓

1.8. BIRDS AND TERRESTRIAL MAMMALS AS TOURISM ATTRACTIONS

I focus on the potential role of birds and mammals as wildlife tourism attractions, as these taxa are known to be major components of the wildlife tourism experience (Arponen et al., 2014; Callaghan et al., 2018; Clucas et al., 2008; Lindsey, Alexander, et al., 2007; Maciejewski and Kerley, 2014a; Smith et al., 2012; Veríssimo, Fraser, et al., 2009), as well as being two of the best-known, most widely studied taxa, with intensive monitoring resulting in geographically diverse and robust datasets (Bonnet et al., 2002; Titley et al., 2017). I focus on terrestrial mammals, because the factors driving marine wildlife tourism are expected to differ from those of terrestrial-based activities (Farr et al., 2014; Uyarra et al., 2005; Williams and Polunin, 2000). I chose to include all birds, because marine species can often be viewed from land e.g., at nesting colonies.

1.9. CLIMATE & ENVIRONMENTAL CHANGE

Since 1880, global average temperatures have risen by 0.85°C (IPCC, 2013). According to the latest report from the Intergovernmental Panel on Climate Change, the likely global average temperature increase between the baseline period of 1986–2005 and 2081–2100 varies between 0.3 and 4.8°C (IPCC, 2007). This temperature rise has been attributed largely to the increase of atmospheric carbon dioxide (CO_2), which is principally driven by anthropogenic greenhouse gas emissions (IPCC, 2001). Consequences of global climate change include sea level rise, ocean acidification, and increases in extreme weather conditions. According to the report by the IPBES (2019), climate change is projected to become increasingly important as a driver of changes in nature and its contributions to people, including by threatening many species with global extinction, over the next decades.

The relationship between climatic conditions and tourism, and in particular those activities related to nature and wildlife, means that the industry is highly sensitive to climate change. Exactly how climate change will affect future tourism patterns remains uncertain (IPCC, 2007), but it will likely cause shifts in climatically suitable areas for tourism, and therefore visitation patterns, resulting in 'winners' and 'losers', where climate change might have beneficial or negative effects on tourism operations, respectively. The dependence of some economies on tourism means that economic and environmental repercussions of climate change could be severe. The changes in policy, investment, and management needed for tourism destinations to effectively adapt to climate change may take decades to implement. An understanding of potential changes in visitation based on future patterns of climatic changes is needed to anticipate, plan for, and proactively influence future visitation.

In light of this, increasing research is focusing on identifying the climatic drivers of tourism, and predicting climate change impacts (Amelung et al., 2007; Fisichelli et al., 2015; Pröbstl-Haider et al., 2015). Previous research has mostly focussed on the direct role of temperature on tourism patterns. For example, studies looking at visitation to national parks in the Rocky Mountains found that an extended warm-weather season might increase the number of hikers visiting the parks (Loomis and Richardson, 2006; Richardson and Loomis, 2004; Scott, Jones, et al., 2007). In addition, some studies have looked at indirect effects of climate change on tourism through e.g., glacier retreat, natural disasters, forest fires, changing animal abundances (Richardson and Loomis, 2004; Scott, Jones, et al., 2007). Lower mammal abundances and glacial retreat could mean that visitation to the Rocky Mountains will eventually decrease, even if there is an initial rise in visitor numbers resulting from warmer temperatures (Scott, Jones, et al., 2007).

The initial response of many species to climatic changes will be to shift their ranges to new locations with more suitable climates, and there is already documented evidence of this occurring (Pecl et al., 2017). In general, projections suggest that species will move poleward and towards higher elevation, where conditions are typically cooler and moister (Hof et al., 2018). Given the fact that wildlife represents a major tourist attraction, the lack of research into the impacts of this global 're-shuffling' in species distributions on tourism patterns is surprising. Forecasting future ranges of attractive species will help shed light on how global patterns of wildlife tourism might look as a result of climate change. This information could inform prioritisation of conservation and management efforts, in order to ensure tourism operations remain viable, and enable managers to exploit novel opportunities, where climate change forces attractive species to move into climatically suitable areas (Williams and Polunin, 2000). Mapping key sites that fall outside of the current PA network or important migration corridors could also advise the expansion of the PA network, as called for in the Aichi Targets (CBD, 2018; McCook et al., 2009; Struebig et al., 2015), or the improvement of conservation efforts outside the current network.

As well as being a highly climate-sensitive sector, tourism is a growing contributor to climate change. The United Nations held the Second International Conference on Climate Change and Tourism, in Davos, Switzerland, in 2007, which estimated that tourism accounts for roughly ∼5% (with a high estimate of 12.5%) of CO_2 emissions, through transportation, accommodation, and other tourism-related activities and infrastructure (Scott, Hall, et al., 2019; UNWTO, 2008). Low-carbon forms of tourism (e.g., rail travel, short- to medium-haul flights, longer stays, domestic tourism, 'green' accommodation) and are therefore vital to decouple future tourism growth from increasing greenhouse gas emissions.

Tourism has been shown to contribute (and be impacted) by other major areas of global environmental change, which should be addressed to minimise the negative impacts of tourism operations (Gössling, 2005). For example, it can exacerbate water problems in countries facing water scarcity due to increasing demand for water, and waste from tourism may also decrease water quality. Land use change may be less of an issue for wildlife or nature tourism, which can create an economic argument for preserving natural areas, but land may still need to be converted for e.g., campsites, airports, trails, and the production of food and other items needed by this industry. As a minimum estimate, tourism-related land use may account for ∼515,000km^2, representing 0.34% of the terrestrial surface of the earth. Travel also brings with it the risk of disease, where tourists are at risk of both acquiring diseases and also spreading them across the globe (potentially in a matter of hours with the rise of air travel). This is particularly true where tourists engage in nature-based activities in remote areas, where they may be exposed to a larger variety of (potentially unknown) species and pathogens, that could lead to outbreaks of novel zoonotic diseases.

1.10. THESIS AIMS

Several important gaps remain in our knowledge regarding the drivers of wildlife tourism. Below, I outline those that form the basis of my thesis and describe the structure and aims of the following chapters:

2. **Identify the traits that make birds and terrestrial mammals attractive to tourists and highlight hotspots of wildlife tourism based on attractive species assemblages**

   In the next chapter, I identify the traits that make birds and terrestrial mammals attractive to tourists using data from wildlife tourism literature (see Table 1.1). I predict the attractiveness of all birds and terrestrial mammals based on these traits and then model spatial patterns of summed attractiveness across the world's land mass. I identify hotspots where tourism potential is high by highlighting regions with the highest summed species attractiveness. I also identify possible overlooked species, which are those whose observed attractiveness was lower than predicted based on their traits, and highlight potentially under-exploited hotspots where these species are most abundant.

3. **Identify the factors that influence PA popularity as wildlife tourism destinations and explore whether popularity correlates with visitation**

   I focus on PAs as wildlife tourism destinations and explore the factors that influence their popularity using the same wildlife tourism literature data. I then predict the popularity of the world's terrestrial and coastal PAs based on these factors. I use a subset of PAs for which visitor data are available and explore how well my models predict PA visitation.

4. **Predict climate change impacts on future patterns of wildlife tourism based on species range shifts**

   I use current and projected bird and terrestrial mammal ranges to identify changes in cumulative species attractiveness worldwide. I flag areas that are projected to increase or decrease in species attractiveness and explore how these areas relate to current wildlife tourism potential, to identify hotspots that are projected to benefit or be at risk from climate change, due to emigration or colonisation by attractive species.

5. **Explore tourist preferences for wildlife within the United Kingdom**

   I repeat the global analysis of the traits that make species attractive to tourists at a finer scale within the United Kingdom. I compare how the traits that influence citation frequency of species in wildlife tourism guides, at this national scale, differ from, or mirror, global patterns. Owing to the smaller scale of this analysis, I am able to include additional physical traits (e.g., colouration, unusual adornments/appendages), for which data are not available at the global scale, which have been found to be important in influencing species attractiveness. Finally, I identify important hotspots for British wildlife tourism.

Chapter 2

Global Assessment of the Tourism Potential of Birds and Terrestrial Mammals

2.1. ABSTRACT

Wildlife tourism is recognised as a valuable cultural ecosystem service that can promote biodiversity conservation and improve the livelihoods of local people. However, due to the presence of preferred species, some sites may be better suited to wildlife tourism than others. Comprehensive and robust global assessments of which species attract tourists, and why, remain limited. Here, I use wildlife tourism literature to assess the attraction of birds and terrestrial mammals as potential wildlife tourism draws. In total, 58% (n = 5,756) of all bird species and 23% (n = 1,209) of non-volant terrestrial mammals were cited as attractions in a series of guidebooks, online brochures, and websites. Combining this information with species trait data, I produce the first global synthesis of the drivers of species *attractiveness* for wildlife tourism. Overall, *attractiveness*, measured as the number of guides citing a species as a wildlife tourism attraction, was determined by a number of key traits, including body mass, extinction risk, time partitioning, and sociality/coloniality. Another important feature related to the habitat in which a species occurs. The study also demonstrates, for the first time, the *attractiveness* of evolutionary distinct species and migratory birds, and provides the first empirical evidence for the role of political stability (in the country in which a species is found) in determining species *attractiveness*.

I use this information, together with species ranges maps, to map wildlife tourism hotspots around the world, including those whose tourism potential is potentially being under-exploited, based on a high richness of *attractive* species. The spatial framework developed in this study represents a key step in prioritising investment towards the most important wildlife tourism sites globally. The findings can help enhance existing wildlife tourism operations and create new opportunities for wildlife tourism development by informing management and marketing of *attractive* species.

2.2. INTRODUCTION

The viewing of free-roaming animals in the wild, often in protected areas (PAs), is a popular global pastime and an increasingly important component of the global tourism industry. This form of non-consumptive wildlife tourism has been heralded for its role in supporting conservation activities and providing income opportunities for local communities (Karanth, Gopalaswamy, et al., 2012; Nielsen and Spenceley, 2011). However, due to the presence of preferred species, some sites may be better suited to wildlife tourism than others. In general, wildlife tourism has been focussed on charismatic megafauna (e.g., large-bodied mammals with popular appeal) (Okello et al., 2008; Winterbach et al., 2015). Yet, it is not known to what extent these species are preferred by tourists, or which other species are important when the former are absent. This has been identified as a major issue limiting wildlife tourism potential (Krüger, 2005; Okello et al., 2008). Presently, there is significant scope for the development and improvement of wildlife tourism operations around the world (Green and Higginbottom, 2000; Lindsey, Alexander, et al., 2007; Okello et al., 2008; Tortato and Izzo, 2017), which, if capitalised on, could contribute to the achievement of international conservation goals and Sustainable Development Goals (SDGs) simultaneously (Buckley, 2012; CBD, 2018; Saarinen, Rogerson, et al., 2011).

In order to help decision-makers prioritise investment towards key sites with high wildlife tourism potential, and to effectively advertise and manage these sites to accommodate and maximise tourist interest, a better understanding of wildlife tourist preferences is needed (Okello et al., 2008). Market forces dictate the success of specific localities as wildlife tourism destinations, so it is essential that opportunities to view preferred species are advertised effectively to draw tourists in the first place (potentially also allowing managers to charge higher prices). Tourists often express frustration, disappointment, and dissatisfaction when they do not see their preferred species (Andersen and Miller, 2006; Prakash et al., 2019). Conserving key species and maximising opportunities to view them would therefore help ensure that tourists are satisfied enough to repeat the visit and/or give positive recommendations to other potential tourists, an important channel through which information on destinations is shared. The identification of the most sought-after species would also allow managers to monitor the health or status of their populations and mitigate tourism pressures, such as disruptions to important behaviours and/or habitats (Castley et al., 2001; Macdonald, Gallagher, et al., 2017). Thus, important questions remain: which species are most attractive to wildlife tourists?, what factors contribute to their attractiveness?, and where do these species occur?

Previous studies have, to some extent, highlighted some of the species that are attractive to people (Albert et al., 2018; Clucas et al., 2008; Macdonald, Burnham, et al., 2015). Many of these studies have focused on those that attract tourists specifically, and have identified commonalities amongst these species. Size and conservation status have been identified as key factors influencing species attractiveness, with large, rare and endangered species being particularly attractive (Clucas et al., 2008; Di Minin et al., 2012; Lindsey, Alexander, et al., 2007; Maciejewski and Kerley, 2014b). There is also evidence that carnivores are more attractive, though mega-herbivores are known to attract substantial numbers of tourists as well (Clucas et al., 2008; Lindsey, Alexander, et al., 2007; Okello et al., 2008; Veríssimo, Fraser, et al., 2009). In addition, endemism and uniqueness have been shown to make species more attractive (Grünewald et al., 2016; Okello et al., 2008; Veríssimo, Fraser, et al., 2009; Winterbach et al., 2015). Beyond these more aesthetic features, tourists have also been found to be attracted to groups of animals, more so than to individuals (Di Minin et al., 2012). Diurnal species are also thought to make better tourism attractions than nocturnal ones (Reynolds and Braithwaite, 2001), and those that occur in open habitats have been found to attract greater attention, likely due to reasons of increased visibility (Grünewald et al., 2016; Okello et al., 2008).

These studies have provided valuable information that has enhanced our understanding of which species tourists are interested in seeing and why, which can help inform local management efforts e.g., flagship selection, vegetation management, and species reintroductions (Arbieu, Grünewald, Schleuning, et al., 2017; Maciejewski and Kerley, 2014b; Veríssimo, Fraser, et al., 2009). Most of these studies have relied on costly and time-consuming stated preference techniques, such as contingent valuation methods and choice experiments, or visitor counts, and have therefore focussed on a small number of (often well-known) PAs and species (Lindsey, Alexander, et al., 2007; Maciejewski and Kerley, 2014b; Okello et al., 2008). Moreover, many have assessed respondents willingness-to-pay for features of the wildlife tourism experience, thereby assigning a monetary value to individual species. Although wildlife tourism undoubtedly offers substantial economic potential, such economic valuations can be based on poor methods that lead to unreliable and possibly misleading figures (see Catlin, Hughes, et al., 2013). Comprehensive assessments of wildlife tourism, at cross-county or global levels, are therefore lacking. As a result, large-scale spatial assessments (increasingly used to map and value priority sites for ecosystem services) of wildlife tourism are also lacking (but see Willemen et al., 2015).

Against this backdrop, I develop a novel approach to assess tourists' preferences for birds and mammals on a global scale. Rather than commodify species in monetary terms or define a species' intrinsic appeal, I quantify the attractiveness of species as a measure of tourism potential i.e., a species' potential to draw wildlife tourists to a particular site (Willemen et al., 2015). I do this using data collated from wildlife tourism resources, including guidebooks, brochures, and websites, which I refer to collectively as 'guides'. These resources are increasingly used by tourists to obtain information on potential tourism destinations (Catlin and Jones, 2010; Nishimura et al., 2006; Young, 2009; Zillinger, 2006), and therefore contain a wealth of information on the types of species that are being used to attract wildlife tourists. The number of guides in which a species was cited served as a proxy or index of *attractiveness*, assuming that more attractive species would be mentioned in more guides. Note that *attractiveness* (and the term *attractive*) is italicised throughout this thesis when referring to my index of *attractiveness*, based on citation frequency by guides, to differentiate it from the definitions used by others (e.g., to refer to physical or aesthetic attractiveness) (Reynolds and Braithwaite, 2001; Veríssimo, Fraser, et al., 2009). I use this information to identify where the most *attractive* species occur around the world, producing the first global spatial assessment of wildlife tourism. The main aims of this chapter are to:

1. examine whether citation frequency by wildlife tourism guides can be predicted by features relating to species' aesthetic appeal, visibility, and accessibility,
2. predict the *attractiveness* of birds and mammals on the basis of their features and test this against citation frequency, and
3. map spatial patterns in wildlife tourism potential, including identifying which areas are potentially overlooked as wildlife tourism destinations, based on their constituent species pool.

2.3. METHODS

2.3.1. Wildlife tourism literature

I collected data from 42 wildlife tourism guides published over the last 30 years that provided (near) global overviews of key species at wildlife tourism destinations (see Chapter 1 Table 1.1). Guides were chosen through a general search on Amazon and Google, using different combinations of the following keywords: "wildlife", "tourism", "destination", "site", "guidebook", "brochure", "tour". This was supplemented with searches using the keywords "birding" and "birdwatching", to incorporate the preferences of more specialist wildlife tourists.

In order to be included in the analysis, a guide had to be focussed primarily on wildlife watching and promote birds and/or terrestrial mammals as tourism attractions. I excluded field guides, which tend to list the species present at a site without consideration for which species are more or less attractive to tourists. Information about the sales figures of guides was not accessible, so I selected guides from international publishers known for their best-selling wildlife guides (e.g., Lonely Planet and Bradt) to guarantee that the guides reached a large number of people. I also included guides from other publishers and tour operators that were among the top results returned by the search engines. I sought to obtain global coverage of wildlife tourism destinations, but challenges in the guide selection process left gaps in some areas (Fig A.1). The guides chosen predominantly captured the preferences of the large subset of wildlife tourists that consists of Western, English-speaking, first-time or inexperienced tourists.

I used the avian taxonomy of Jetz, Thomas, Joy, Hartmann, et al. (2012) and the mammalian taxonomy of Wilson and Reeder (2005) to compile global datasets of extant birds and non-volant terrestrial mammals (excluding species known from only one or two specimens). I aligned these taxonomies to those used by BirdLife International (2017a) and the International Union for Conservation of Nature IUCN (2016), respectively. The final datasets included 3,814 mammal species and 9,968 bird species. Every time a species was mentioned in a guide, it was recorded, along with details of the site with which it was associated. This methodology was based on the assumption that more attractive species will be mentioned more often. I initially derived an *attractiveness* index using the total number of times a species was cited in the guides as an attraction at a unique site (i.e., the total number of unique site-species combinations). This index, however, was biased towards wide-ranging species, which are present at a greater number of sites. I therefore used the number of guides a species was mentioned in as a proxy or index for *attractiveness*, which was expected to more accurately capture preferences towards range-restricted species. Species that were not mentioned in any guide were assigned an *attractiveness* index of zero. Where non-specific names for species were used, I attempted to identify the species using published and online literature. Higher order classifications (e.g., monkeys, lemurs, waders) that could not be identified to the species level were recorded, but excluded from analyses.

2.3.2. Trait data

I collated data for birds and mammals on a comprehensive number of trait and ecological attributes that had been suggested in the scientific literature as possible determinants of species attractiveness. These included 1) body mass; 2) range size; 3) evolutionary distinctiveness; 4) extinction risk; 5) social grouping; 6) trophic level; 7) time partitioning; 8) habitat association; 9) range remoteness; 10) political stability of a species range; and, for birds, 11) migration habits. These data were obtained from existing published datasets (see Table 2.1), referenced in full below. Taxonomic mismatches between datasets were resolved using BirdLife International (2017a) and IUCN (2016) checklists. Although other traits have also been found to be important (see Section 1.7.1), a lack of data available on these traits for most species precluded their inclusion in this analyses. Nevertheless, some of these are explored at a smaller, national scale within the UK in Chapter 5 e.g., colouration.

I included body size as a potential predictor of species *attractiveness*, based on evidence that larger species are preferred by tourists over smaller ones (Clucas et al., 2008; Di Minin et al., 2012; Maciejewski and Kerley, 2014b; Okello et al., 2008). I obtained mean body mass from BirdLife International (2017b), the CRC handbooks (Dunning, 2007; Silva and Downing, 1995), and the Handbook of the Mammals of the World (HMW) series (Wilson, Mittermeier, et al., 2009-2019). If a range was provided, or if multiple estimates of body mass were given, the mid-range or mean values were calculated. The thrill of observing predators hunting their prey has been found to attract tourist interest (Clucas et al., 2008; Lindsey, Alexander, et al., 2007; Okello et al., 2008), so I included trophic level as a predictor. I categorized species as herbivorous, omnivorous or carnivorous using data from BirdLife International (2017b), the Handbook of the Birds of the World (HBW) Alive (del Hoyo, Elliot, et al., 2017), Kissling et al. (2014a,b) and Wilman et al. (2014). I included time partitioning (also referred to as activity pattern) as a predictor, based on suggestions that diurnal species make better tourism attractions than nocturnal species because they are easier to see in the wild (Reynolds and Braithwaite, 2001). I categorized birds as nocturnal or diurnal, primarily using family descriptions from the HBW Alive, though Stephen Willis from the Durham University Conservation Ecology Group noted activity patterns individually for species when activity patterns within a family group were not uniform. I used the dataset of Bennie et al. (2014) to classify mammals as diurnal, nocturnal, cathemeral, or crepuscular.

Table 2.1: **Species' traits and range attributes that have been suggested by studies to influence their attractiveness to tourists.**

Trait	Description	Sources	Links
Log$_{10}$ body mass	Mean body mass in kg for mammals and g for birds	BirdLife International (2017b); the CRC handbooks (Dunning, 2007; Silva and Downing, 1995); the HMW series (Wilson, Mittermeier, et al., 2009-2019)	http://www.birdlife.org/
Log$_{10}$ range size	Size of species' breeding range in km^2	BirdLife International and Handbook of the Birds of the World (2016) and IUCN (2016)	https://www.iucnredlist.org/; http://www.birdlife.org/
Extinction risk	Continuous measure of extinction risk ranging from 'Least Concern' (1), to 'Critically Endangered' (5)	IUCN (2016)	https://www.iucnredlist.org/
Trophic level	Categorical variable describing whether a species is herbivorous, omnivorous, or carnivorous	BirdLife International (2017b), del Hoyo, Elliot, et al. (2017), Kissling et al. (2014a,b), and Wilman et al. (2014)	http://www.birdlife.org/; https://birdsoftheworld.org/bow/home; https://datadryad.org/stash/dataset/doi:10.5061/dryad.6cd0v; https://figshare.com/collections/EltonTraits_1_0_Species-level_foraging_attributes_of_the_world_s_birds_and_mammals/3306933
Evolutionary uniqueness	The amount of unique evolutionary history a species represents	The EDGE of Existence programme (Jetz, Thomas, Joy, Redding, et al., 2014)	https://www.edgeofexistence.org/
Habitat type	Main habitat associated with each species (see Appendix Tables B.1 & B.2)	BirdLife International (2017b), del Hoyo, Elliot, et al. (2017), and Global Mammal Assessment programme (2017)	https://globalmammal.org/; http://www.birdlife.org/; https://birdsoftheworld.org/bow/home
Social grouping	Binary variable describing whether a species is solitary or lives in groups/colonies	PanTHERIA (Jones et al., 2009); HMW (Wilson, Mittermeier, et al., 2009-2019); del Hoyo, Elliot, et al. (2017), Fisher et al. (2003), and Pearce, Carbone, et al. (2013)	http://esapubs.org/archive/ecol/E090/184/; https://birdsoftheworld.org/bow/home
Time partitioning	Categorical variable describing whether a species is nocturnal or diurnal (as well as cathemeral or crepuscular for mammals)	Bennie et al. (2014) and del Hoyo, Elliot, et al. (2017)	https://birdsoftheworld.org/bow/home; https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4183310/
Remoteness	The shortest straight-line distance, in km, between a species range margin and the closest large airport	*OpenFlights database* (2019)	https://openflights.org/data.html
Political stability	Mean political stability estimates across a species range over a twenty-year period	World Bank Group (2018)	https://databank.worldbank.org/databases
Migratory behaviour	Continuous measure of bird migratory behaviour ranging from residents (1) to full migrants (4)	BirdLife International (2017b)	http://www.birdlife.org/

Veríssimo, Fraser, et al. (2009) found that endemism and unique characteristics and behaviours are important attributes for birders. I expanded upon this and explored the potential effect of range size on *attractiveness* of both birds and mammals. I used spatial range maps from BirdLife International and Handbook of the Birds of the World (2016) and the IUCN (2016) and the 'rgeos' and 'rgdal' packages in R (Bivand, Keitt, et al., 2020; Bivand, Rundel, et al., 2020) to estimate species' breeding range sizes. The Zoological Society of London's EDGE of Existence programme provides a comprehensive dataset that scores species according to the amount of unique evolutionary history they represent (Jetz, Thomas, Joy, Redding, et al., 2014), allowing me to conduct the first global assessment of the role of evolutionary distinctiveness in determining species *attractiveness*. I used the IUCN Red List status as a measure of extinction risk, transforming it from a six category factor variable to a continuous scale, ranging from 'Least Concern' (1), to 'Critically Endangered' (5) (Jetz and Freckleton, 2015). If a species had not been evaluated by the IUCN because it was either considered a subspecies, race, or conspecific, I used the status of the parent or sister taxon. 'Data Deficient' species were treated as missing values. This variable was included based on extensive existing literature suggesting that rare or endangered species are preferred by tourists over more common species (Di Minin et al., 2012; Grünewald et al., 2016; Macdonald, Burnham, et al., 2015; Maciejewski and Kerley, 2014b; Steven, Smart, et al., 2017; Veríssimo, Fraser, et al., 2009).

I included social grouping as a predictor variable to confirm past findings that groups of animals are of greater interest to tourists than individual animals (Di Minin et al., 2013). I used the dataset from Lukas and Clutton-Brock (2013) to categorize mammals as either solitary or group living. I re-classified socially monogamous species that are pair-bonded as group living. For species not categorised by Lukas and Clutton-Brock (2013), missing data were filled in using group size data on marsupials from Fisher et al. (2003) and primates from Pearce, Carbone, et al. (2013). Any remaining data gaps were then filled in using group size information from PanTHERIA (Jones et al., 2009), followed by categorizations in the HMW (Wilson, Mittermeier, et al., 2009-2019). For group size data, species with mean group sizes ≥ 1.5 were categorized as group living. Data on the colonial habits of birds had previously been collated by the Conservation Ecology Group at Durham (primarily by S. Willis), extracting data principally from del Hoyo, Elliot, et al. (2017) to designate birds known to nest colonially, semi-colonially or loosely colonially as colonial, and all others as non-colonial.

Beyond species' intrinsic traits, destination features have been found to be influence tourists' decisions, which are likely to be reflected in how attractive the species are that occur there.

I included political stability and remoteness, two critical elements that tourists take into consideration when making decisions, as predictor variables. I first transformed polygons to an equal-area Behrman projection and determined species' range sizes from the total area of species' range polygons. I calculated mean political stability scores across species' ranges by intersecting species' range maps with political stability data for individual nations published by the World Bank Group (2018) across a twenty-year period, weighting species' political stability scores by the proportion of a species' range within each country. Each species was also assigned a remoteness value (representing notional accessibility of species' ranges to non-local tourists) by calculating the shortest straight-line distance, in Robinson projection, between a species' range margin and the closest large airport, the latter defined in the *OpenFlights database* (2019).

I included habitat as a predictor variable to explore the suggestion that species in open habitats are preferred by tourists due to increased visibility (Gray and Bond, 2013; Kiss, 2004). The Global Mammal Assessment programme (2017) provided data on habitat associations in mammals. The primary habitat was calculated as that which made up the largest proportion of a species' range. I obtained habitat associations for birds from BirdLife International (2017b), which was supplemented with information in the text descriptions from del Hoyo, Elliot, et al. (2017). For analyses, I combined similar habitats that offer comparable visibility of wildlife into single categories (see Appendix Tables B.1 & B.2). I included migratory behaviour in birds as a predictor variable, as mass migrations are well known to be popular wildlife tourism spectacles (Curtin and Wilkes, 2005; Okello et al., 2008), converting BirdLife International (2017b) categories to a continuous scale, ranging from residents (1), to nomads (2), which move "*in response to resources that are sporadic in time and distribution*", to altitudinal migrants (3), which regularly or seasonally make "*cyclical movements to higher/ lower elevations with predictable timing and destinations*", to full migrants (4), which make "*regular or seasonal cyclical movements beyond the breeding range, with predictable timing and destinations*". I did not explore migrations by mammals because of a lack of data on mammal migrations globally and the rarity of mass migrations among terrestrial mammals.

2.3.3. Data imputation

Sixteen percent (n = 1,581) of bird species and 57% (n = 2,168) of mammal species had missing values for at least one trait. The trait with the most amount of missing data was sociality in mammals, with 40% (n = 1,540) of species missing information on this trait. The remaining traits were $> 80\%$ complete (see Appendix Table B.3 for patterns in missing data). Usually, researchers handle missing data by omitting individuals for which all observations are not available. This reduces the available sample size and is known to introduce biases in model estimates (Nakagawa and Freckleton, 2008).

I used phylogenetic imputation to fill in gaps in the trait dataset and hence minimise biases created by missing data. Before performing imputation, I used the 'geiger' and 'phytools' packages in R to measure phylogenetic signal in continuous and categorical traits, respectively, that had missing data (Harmon et al., 2020; Revell, 2020). I did this across a random selection of 10 bird and 10 mammal putative phylogenies – phylogenies for both birds and mammals are not fully resolved, so are typically presented as a large number of potential trees. I sampled phylogenetic trees from the posterior distribution of a recent bird phylogeny generated under a Bayesian inference framework by Jetz, Thomas, Joy, Hartmann, et al. (2012), based on the topology of orders from Hackett et al. (2008), and from the 10,000 individual mammal trees constructed by Kuhn et al. (2011), which comprise one resolution of the polytomies of a supertree published initially by Bininda-Emonds et al. (2007) and updated by Fritz et al. (2009), treating these as equivalent to a Bayesian posterior distribution. I adopted a maximum-likelihood approach to find the best-fitting Pagel's lambda (λ), which simultaneously calculates the phylogenetic signal in the data and adjusts the internal branch lengths of the tree to better fit the data, assuming a Brownian model of evolution (Freckleton et al., 2002; Pagel, 1997). I compared models with the observed maximum-likelihood values of λ to models assuming no phylogenetic signal ($\lambda = 0$), using likelihood ratio tests approximated by a chi-squared distribution. The tests showed significant phylogenetic signal in traits with missing values (all $P < 0.0001$, see Appendix Table B.4), supporting the use of an imputative approach that incorporated phylogeny to fill in gaps in species trait data.

I used the R package 'Rphylopars' to impute missing values through maximum-likelihood estimation based on a covariance matrix determined by phylogenetic and phenotypic correlations (Goolsby et al., 2017). Following recommendations in the imputation literature, I used all variables (i.e., traits and range attributes) that would go into the main analysis to impute missing values, ensuring that the imputation model preserved the relationships between the variables of interest (Moons et al., 2006). I performed phylogenetic imputations across five bird and five mammal phylogenies, using the best fitting λ, producing a total of five imputed datasets for each taxon (Penone et al., 2014).

I tested the accuracy of the imputation procedure by cross-validating imputed values with observed values. I did this by first removing species with missing values for a particular trait, thereby producing datasets that contained complete observations for that trait, and then randomly removing 40% of these complete observations, which represents the maximum percentage of missing values in a single trait in my bird and mammal datasets (see Appendix Table B.3). I then imputed missing values five times using five different phylogenies, resulting in a total of 25 datasets with imputed values. I iterated this process for both birds and mammals by cycling through each trait that required imputation. The predictive power of my imputation models was measured as the percentage of (in)correct classifications of categorical traits and the normalized root mean square prediction error (NRMSE) for continuous traits, which is calculated as:

$$NRMSE = \frac{(\sqrt(mean(\hat{y}_i - y_i))^2}{y_{max} - y_{min}}$$

where $\hat{y}_i$ is the predicted value and y_i is the observed value of a trait for species i and y_{min} and y_{max} are the minimum and maximum values for that trait, respectively. The results suggested accuracy of the imputation procedure was high; imputed data resembled observed values, producing an average of 75.39% correct classifications of categorical variables and an average NRMSE of 0.017 for covariates (Appendix Table B.5). Although the proportion of misclassifications was relatively high for mammal habitat associations (57.12%), $< 1\%$ of mammals were missing these data.

2.3.4. Data analysis

I explored the influence of species traits and range attributes on their *attractiveness* in a series of multiple regression models. I expected an interaction between range size and both accessibility and extinction risk, presuming tourists might be more willing to travel to more remote sites in search of endangered, endemic or otherwise range-restricted species than they would to see widespread species. No significant interaction was found between range size and extinction risk for mammals ($P > 0.05$), so this interaction was removed from analyses. The number of guides a species was cited in (i.e., its *attractiveness* index and my measure of potential attractiveness to wildlife tourists) served as the response variable. Log_{10}-transformations were applied to body mass and range size to adjust for non-linear relationships. Covariates were centred and standardised to a mean of zero and a standard deviation of one to improve the interpretability of parameter estimates. Variance Inflation Factors (VIFs), calculated using the 'car' package in R (Fox et al., 2020), were less than three, suggesting multicollinearity was not a concern (Zuur et al., 2010).

I used Bayesian phylogenetically-informed comparative analyses to account for the non-independence of species data points arising from their common ancestry. Specifically, I used Markov Chain Monte Carlo generalised linear mixed models (GLMMs), using the R package 'MCMCglmm' (Hadfield, 2010). These methods allow error structures of the models to incorporate the degree of relatedness between species as estimated by a phylogenetic tree. Phylogeny is treated as a random effect, with the proportion of residual variance that can be attributed to it estimated using heritability (h^2), which is equivalent to Pagel's λ in a phylogenetic generalised least squares model (see Freckleton et al., 2002), such that values close to zero indicate a negligible effect of phylogeny and values close to one suggest there is strong phylogenetic signal in the data. Taxonomic order was included as a second random effect, to account for any between taxa-variance that is not due to phylogeny.

I used zero-altered (or hurdle) Poisson models to account for zero-inflation. The first part of this model explores the probability that the response variable is non-zero (i.e., the probability of a species being selected as a tourism attraction by guides, hereafter 'binomial model'). The second part is equivalent to a zero-truncated Poisson model, exploring the number of guides each species was cited in, using data from only those species cited at least once (hereafter referred to as the 'frequency model'). I used diffuse normal priors with a mean of zero and a large variance around the mean (10^{10}) for the fixed effects (Hadfield and Nakagawa, 2010; Hadfield, 2012). The residual variance cannot be estimated in a model with a binary response, as it is wholly described by the mean, so I fixed this to one (de Villemereuil, Wells, et al., 2012; Hadfield, 2010). I used an inverse-gamma prior for the residual variance of the frequency model, which captures over-dispersion (V = diag(2), $\nu = 0.002$) (Hadfield, 2010). I used a chi-squared prior for the random effect in the binomial model, which best approximates a uniform prior distribution of h^2 for binary data (Capellini et al., 2015; de Villemereuil, Gimenez, et al., 2013; Hadfield, 2010), and a parameter expanded prior for the frequency model (V = 1, $\nu = 1$, $\alpha\mu$ = 0, αV = 255) (Sakamoto et al., 2016; Street et al., 2017).

Any tree is unlikely to be an accurate representation of the true phylogenetic relationships between species. I therefore fitted models across a sample of 100 bird and 100 mammal phylogenetic trees. This number reflects a compromise between the need to capture phylogenetic uncertainty and the high memory requirements of fitting Bayesian phylogenetic models over multiple trees. I sampled trees from the posterior distribution of bird phylogenies generated by Jetz, Thomas, Joy, Hartmann, et al. (2012) and the 10,000 mammal trees constructed by Kuhn et al. (2011). I ran models across each imputed dataset and each tree, resulting in a total of 500 bird and 500 mammal models from which I was able to extract average model parameters that incorporated uncertainty in both phylogenetic relationships and the imputation procedure.

After pilot studies, the models were run for 3.5 million iterations, with a burn-in of 10,000 and a thinning interval of 3,000, resulting in an effective sample size of $>$ 1,000 for all variables for each chain. I checked for adequate convergence of chains through visual inspection of trace plots and Gelman-Rubin's potential scale reduction factors ($\hat{R}$) and found that most chains converged well ($\hat{R} \leq 1.1$). However, chains for the crepuscular ($\hat{R} = 1.28$) and group living ($\hat{R}$ $= 1.12$) components in the binomial part of the mammal models showed some convergence problems (Gelman and Rubin, 1992). Increasing the number of iterations did not improve chain convergence. I therefore re-ran the mammal models without time partitioning and sociality as predictors to confirm that remaining model parameters were not sensitive to the inclusion of these problematic predictors. I confirmed independence of samples using diagnostics plots and tests for autocorrelation. The liability matrices for the binomial part did not reveal numerical problems associated with a high degree of zero response values.

In order to maximise explanatory power, all variables were kept in the model (i.e., no model selection was performed) (Balmford, Green, et al., 2015; Richards, Whittingham, et al., 2011; Whittingham et al., 2006). I used the percentage of posterior β coefficient estimates crossing zero to assess the strength of evidence for fixed effects. I assumed the posterior distributions for non-influential predictors to be centred on or substantially overlapping with zero, and 95% of posterior distributions shifted substantially away from zero in either a positive or negative direction to indicate support for a positive or negative effect of predictor variables, respectively. A pseudo-R^2 measure, estimated as the squared Pearson's correlation between predicted *attractiveness* and the observed number of guides citing each species, was used to estimate the explanatory power of models. Statistical analyses were performed in R Version 3.4.0 (R Development Core Team, 2018).

2.3.5. Model predictions

I predicted the *attractiveness* of species based on their traits and range attributes using the results of both the binary and frequency parts of the hurdle models (i.e., the probability of a non-zero response and the posterior mean of the Poisson distribution). I calculated residual values for each species by subtracting predictions from the actual number of guides a species was mentioned in. Positive residuals were interpreted as overlooked tourism potential, whereby a species was cited as an attraction in less guides than would be expected based on its traits.

Visual inspection of diagnostic plots was used to confirm that extreme trait values were not driving the highest residuals (i.e. that the model was not just under-predicting at the low end and over-predicting at the high end of trait values). Species polygons were extracted onto a global grid of 48.25 x 48.25 km cells ($\sim$0.5° at 30° North/South), which I transformed to a Mollweide projection. If a species' polygon overlapped by $\geq$ 10% with the underlying grid cell, it was considered present in that cell. I highlighted global hotspots for wildlife tourism by summing predicted *attractiveness* of all species occurring in each grid cell, using the 'rgeos' and 'rgdal' packages in R (Bivand, Keitt, et al., 2020; Bivand, Rundel, et al., 2020) and breeding range data from BirdLife International and Handbook of the Birds of the World (2016) and the IUCN (2016). I similarly summed the residuals of only those species with positive residuals in a cell, revealing hotspots with potentially under-exploited wildlife tourism potential. I did this separately for birds and mammals to highlight the congruence (or non-congruence) among hotspots of both taxa.

Besides the presence of attractive species, actual tourism levels will depend of a range of factors. Of particular concern for tourism is the threat of terrorism, crime, or war, which may negatively impact countries' reputations as tourism destinations and may deter all but the most committed tourists, regardless of their wildlife tourism product (Akama and Kieti, 2003; Novelli, Morgan, et al., 2012). Politically unstable countries may invest less in the development infrastructure and amenities, which may further impede tourism growth. I attempted to account for this when predicting species *attractiveness*, but due to the transboundary nature of many species, my models may not have captured its full effect on destination attractiveness. That is, the tourism potential of a country undergoing political turmoil may have been over-estimated if it shares many of the same species as a neighbouring, relatively stable country, and vice-versa. I therefore identified hotspots that are best positioned for wildlife tourism development using a spatial threshold approach. First, I pooled predicted bird and mammal *attractiveness* indices to explore tourism potential based on combined wildlife assets of both taxa. I then overlayed species *attractiveness* and residuals with national political stability indices from the World Bank Group (2018), with each index classified into $\frac{1}{3}$ quantiles.

2.4. RESULTS

Fifty eight percent (n = 5,756) of bird and 23% (n = 1,209) of mammal species were cited by at least one guide. Forty percent (n = 2,731) of birds and 27% (n = 331) of mammals mentioned in guides were only cited in one guide. The mean observed *attractiveness* of birds and mammals (i.e., the mean number of guides a species was cited in) was 1.73 (SD = 2.65) and 1.42 (SD = 3.52), respectively. h^2 (i.e., the proportion of residual variance that can be attributed to phylogeny) of the bird and mammal frequency models were 0.97 and 0.67, and h^2 of the binomial models were 0.70 and 0.82, respectively, indicating strong phylogenetic signal in model residuals. Pseudo-R^2 values indicated excellent model fit for the bird (0.64) and mammal (0.77) models. For a global list of species *attractiveness* indices and residuals, see `https://github.com/mairekirkland/thesis_datasets`.

2.4.1. Determinants of species *attractiveness*

The binomial part of the phylogenetically-informed hurdle models revealed a number of traits and range attributes that influenced whether a species was selected by guides as a tourism attraction or not (Fig. 2.1A & 2.1C). The primary habitat in which a species is found had a relatively strong effect among mammals, with those using all other habitats (except artificial habitats) being less likely to be selected by guides than those in open habitats (the reference level in Fig. 2.1). In contrast, habitat was not found to be influential in the bird binomial models. Body mass, political stability across a species range, and evolutionary distinctiveness all had positive effects on the likelihood of species from both taxa being selected as tourism attractions. Overall, range size had a positive effect among both taxa as well, but the interaction term in the bird models indicated that its effect was stronger among more remote birds than more accessible birds (Appendix Fig. B.1). Migratory behaviour, which was only explored for birds, also had a positive effect, such that migrants were more likely to be selected as tourism attractions than resident species. Extinction risk was only found to be influential in the mammal binomial models, with endangered species more likely to be selected than those at lower risk of extinction (Fig. 2.1A & 2.1C). Diurnality and social grouping/coloniality were not influential in the binomial models, but convergence issues in the mammal models could be creating erroneous results.

The results of the frequency models were quantitatively similar to those of the binomial models (Fig. 2.1B & 2.1D). In these models, body mass was the most influential trait, having a strong positive effect on the number of guides citing a species. Contrasting the binomial models, however, diurnality and coloniality/sociality were influential in the frequency models of both taxa, the effects of which were positive. Furthermore, the effect of different habitats differed from the binomial models and between taxa; mammals from bare habitats were cited in less guides, while birds occurring in aquatic or bare habitats were cited in more guides, than those in open habitats. The interaction terms between range size and accessibility this time indicated that the direction of the effect of range size depended on accessibility, switching from positive to negative with reduced accessibility (Appendix Fig. B.1). In other words, species with more accessible ranges were cited by more guides if they were more widespread, whereas those with more remote ranges were cited more often if they were range-restricted. There was also an interaction between the effects of range size and extinction risk on the number of guides citing birds, with a positive effect of extinction risk switching to a negative effect with an increase in range size (Appendix Fig. B.2). This meant that widespread species were cited by more guides if they were at lower risk of extinction, and range-restricted species were cited by more guides if they were at greater risk of extinction. Although influential in the binomial mammal models, extinction risk had no effect on the number of guides a mammal was cited in (Fig. 2.1B & 2.1D).

2.4.2. Geographic patterns in wildlife tourism potential

The main hotspots identified for wildlife tourism were located in sub-Saharan Africa, South America, and South East Asia, based on high cumulative species *attractiveness* (Fig. 2.2A & 2.2C) and residuals (Fig. 2.2B & 2.2D). Polar regions, deserts, and the western coasts of Chile and Argentina had low *attractiveness* indices for both taxa (Fig. 2.2A & 2.2B). The majority of the Northern Hemisphere, as well as South America's west coast and New Zealand, had low residual scores for both taxa (Fig. 2.2B & 2.2D). The rest of Oceania and Madagascar also had low residual scores for mammals (Fig. 2.2D).

The hotspots shown in Fig. 2.2 include some of the best-known wildlife watching destinations globally, but also other regions that are less well-known for their attractive fauna. The most prominent areas of high bird *attractiveness* in South America were Amazonia, the Guianas, the Pantanal, the Atlantic forest of Brazil, and the tropical Andes (Fig. 2.2A). East African hotspots for *attractive* birds included the Eastern Arc mountains, the Albertine Rift Valley, the Ethiopian Highlands, the Eastern African Highlands and northeastern South Africa. The Euro-Siberian region and central Asian mountains, including the Himalayan foothills and adjoining areas in Bhutan, were also highlighted as top sites for *attractive* birds, as was Australia's eastern seaboard and adjoining interior, and smaller isolated hotspots such as Albany on the southwest coast (Fig. 2.2A). The hotspots of high mammal *attractiveness* that emerged differed slightly from those identified for birds, though there was substantial overlap (Fig. 2.2C). East Africa was identified as a particularly prominent hotspot for *attractive* mammals. The North American

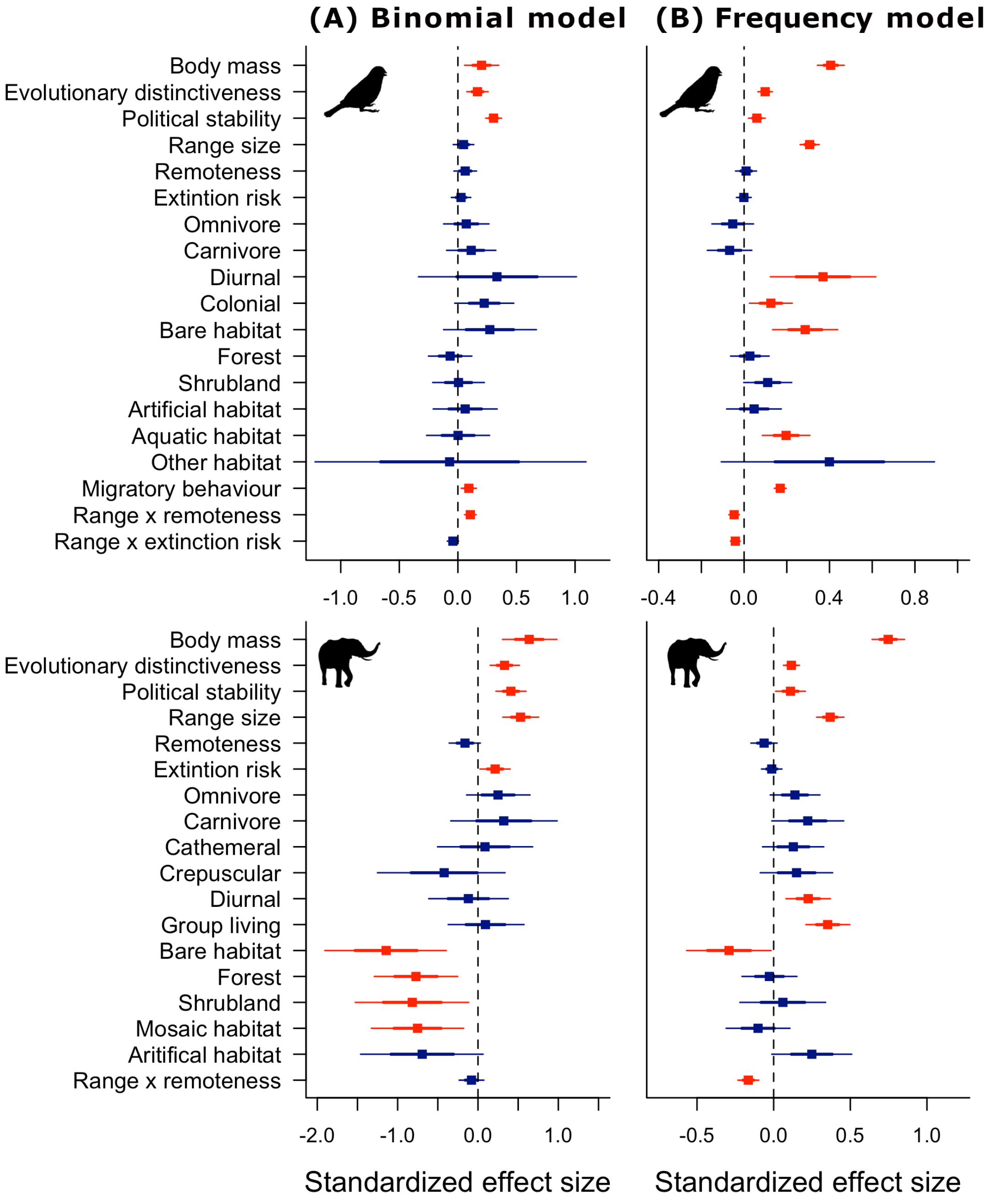

Figure 2.1: Coefficients plots for the Markov Chain Monte Carlo GLMMs explaining the *attractiveness* of birds (n = 9,968) and non-volant terrestrial mammals (n = 3,814), exploring the effects of predictor variables on **A** whether a species was selected by guides or not (binomial model) and **B** the number of guides a species was cited in (frequency model). The centre point denotes the mean, the thick bar denotes the posterior standard deviations (equivalent to the standard errors) and the thin bar denotes the 95% lower and upper credibility limits, as calculated by averaging 500 separate GLMMs, using the package MCMCglmm in R, 100 different phylogenetic trees and five imputed datasets for each taxon. Variables highlighted in red are considered influential. Full model coefficients can be found in Appendix Table B.6.

Rocky Mountains were highlighted as a top potential site for viewing *attractive* mammals as well. South American hotspots for *attractive* mammals coincided with those for birds. India and the Himalayan foothills, and the Greater Mekong biodiversity hotspot of Southeast Asia, were also highlighted for their mammal *attractiveness* (Fig. 2.2C).

The distribution of species with positive residuals highlighted regions with higher wildlife tourism potential, based on *attractiveness* of the assemblages present, than was reflected in the guides. The patterns that emerged when looking at these residuals were similar to species *attractiveness* patterns, although sites in the Northern Hemisphere were notable exceptions where high *attractiveness* was not mirrored by high residuals. The largest area of high bird residuals occurred in Brazil (Fig. 2.2B). However, residuals of birds were high throughout much of South America, including in Amazonia, the tropical Andes, the Guianas, the Pantanal, and the Atlantic forest of Brazil, extending into the Brazilian-Uruguayan savanna. In Africa, the Rwenzori mountain range on the border between Uganda and the Democratic Republic of Congo in Africa was flagged as having very high bird residuals. The rest of sub-Saharan Africa, with the exception of the heart of the Congo basin and the arid zones of southern Africa, also had high, though slightly lower, residual scores for birds. South East Asia also had high avian residuals, which were highest in the Mekong biodiversity hotspot, New Guinea, the Himalayas, and Australia's eastern seaboard (Fig. 2.2B). The distribution of mammal residual hotspots globally was similar to those for birds, with the exception of Australia, where positive residuals of mammals were low (Fig. 2.2D). Sub-Saharan Africa, specifically the East African Rift Valley, the Atlantic Equatorial coastal forests, the Guinean forests of West Africa, and the Miombo eco-region, emerged as the major hotspot of high mammal residuals. Amazonia was the prominent feature in the Americas with the highest residual scores for mammals. In Asia, it was the Mekong biodiversity hotspot (Fig. 2.2D).

2.4.3. Relationship between species richness and *attractiveness*

General linear models revealed that there was a strong, significant relationship between species richness of each grid cell and the sum of the predicted *attractiveness* of species occurring in the cell, for both birds (β = 1.886, 95% CI = 1.876-1.896, P < 0.001, R^2 = 0.764) and mammals (β = 4.554, 95% CI = 4.535-4.573, P < 0.001, R^2 = 0.650). Nevertheless, after controlling for species richness, substantial variation in cumulative *attractiveness* exists, particularly among birds (Fig. 2.3). In general, residuals from the linear models were high, suggesting higher *attractiveness* than expected based on richness alone, across much of the polar and sub-polar regions of the Northern Hemisphere and the savanna ecosystems of sub-Saharan Africa. Temperate zones of the United States, Europe, and Asia, also had positive residuals, and residuals were particularly high across the Euro-Siberian region and the central Asian mountains. Amazonia, the Pantanal, the Guianas, and the Indian sub-continent, stretching to the Tibetan Plateau, had higher residuals for mammals, while Amazonia exhibited negative residuals for birds, indicating that bird *attractiveness* was predicted to be lower in this region than expected based on species richness. The remaining portions of the terrestrial land mass predominantly had negative residuals, which were especially low in the islands of South East Asia, New Guinea, and the tropical Andes, and also, in the case of mammals, in the tropical rainforests of West and Central Africa and Madagascar (Fig. 2.3).

2.4.4. Overlap between wildlife tourism potential and political stability

The mean political stability of countries worldwide, between 1996 and 2015, ranged from -2.61 in Afghanistan to +1.72 in Greenland, with a mean of 0.03 (SD = 0.94), whereby higher values reflect greater stability. Areas of both high species *attractiveness* and residuals, based on combined values for birds and mammals, that are also politically stable included: Southern African countries, predominantly Botswana, Namibia, Zambia, Malawi; West African countries such as Benin, Ghana, and Gabon; much of Australia; Bhutan; some South East Asian countries, including Vietnam, Laos, Malaysia, and Singapore; and, in South America, Uruguay, French Guiana, and parts of Chile (Fig. 2.4). The regions of Eastern Europe and the middle to northern portion of the Rocky Mountain ecoregion that were highlighted for their high species *attractiveness* also fall within regions of high stability (Fig. 2.4A). Amazonia, as well as East and remaining parts of Southern Africa, the West Sudanian savanna, and South-eastern China contained large proportions of land with high *attractiveness* and residual values, but political stability in these regions was lower than in the aforementioned areas (Fig. 2.4). Northern Mongolia also covered a large area of high species *attractiveness* but relatively low political stability (Fig. 2.4A). Regions of high *attractiveness* and residual values, where political stability was lowest, included: much of Africa, particularly countries in Central and West Africa and the Horn of Africa; Colombia; Nepal; Russia; and much of South East Asia (Fig. 2.4).

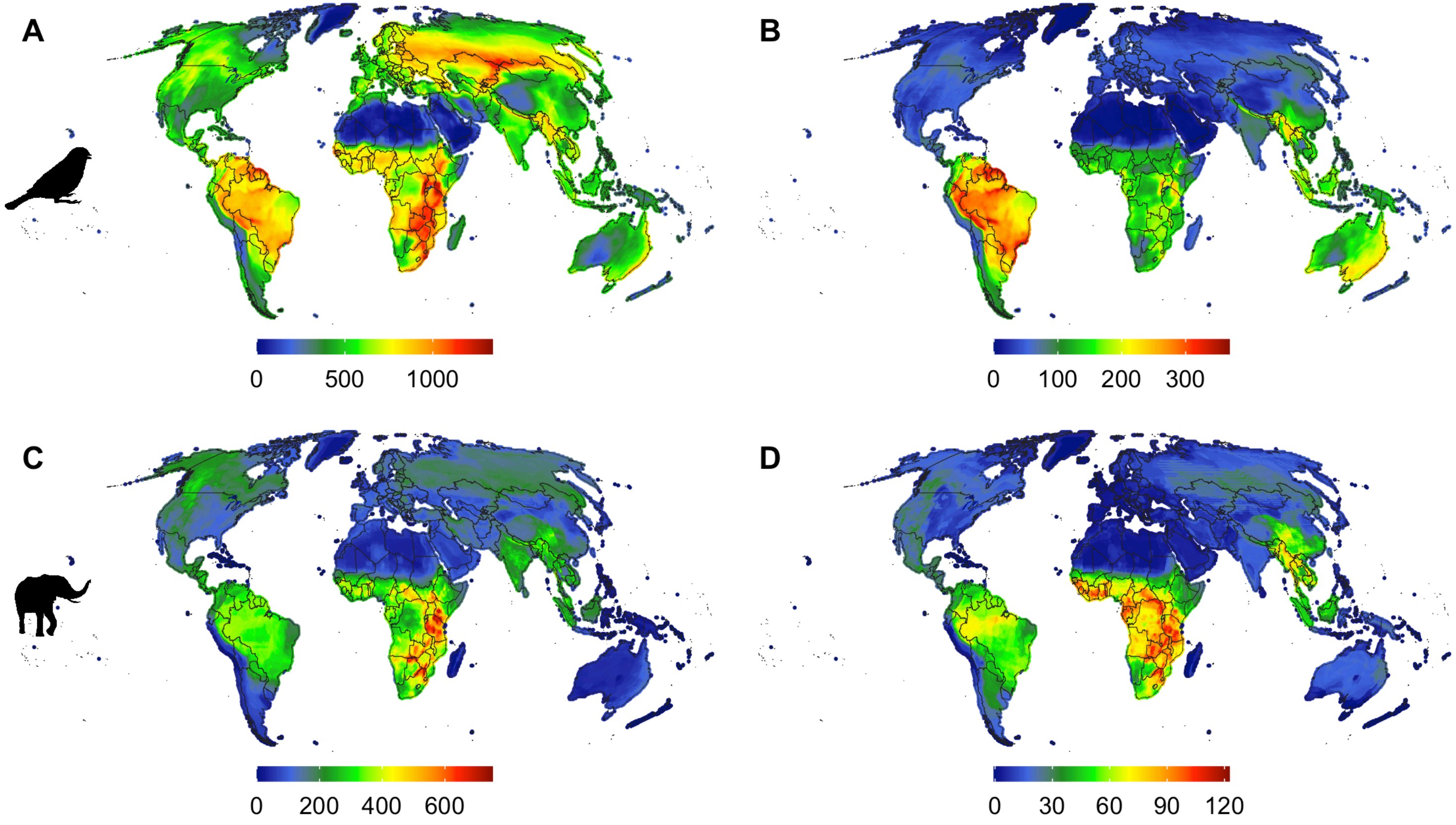

Figure 2.2: Geographic variation in the *attractiveness* of birds and non-volant terrestrial mammals. The maps show cumulative predicted *attractiveness* (**A** & **C**) and cumulative positive residuals, calculated by subtracting the actual number of guides citing a species from the predicted number (a possible metric of under-utilised wildlife tourism potential) (**B** & **D**). Model predictions were derived from both the probability of a non-zero response according to the binary components of 500 zero-altered Markov Chain Monte Carlo GLMMs, and the posterior means of the Poisson distributions. **B** & **D** are based on birds (n = 3,601) and mammals (n = 663) with positive residuals. Scales differ between **A**-**D** to aid comparison between plots.

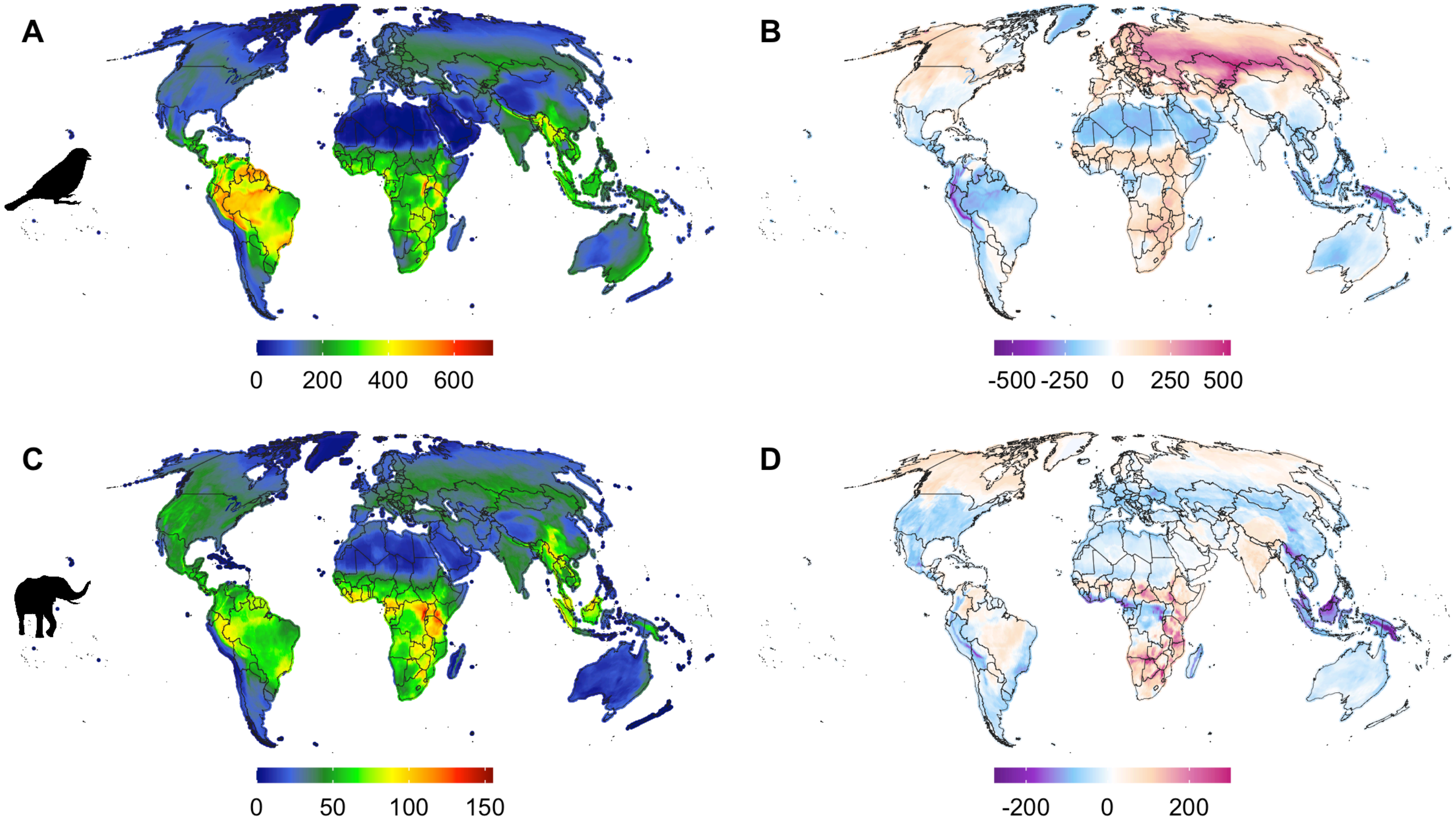

Figure 2.3: Geographic variation in richness of birds and non-volant terrestrial mammals and differences in species *attractiveness* after accounting for species richness. The maps show species richness (**A** & **C**), and residuals from linear models in which the cumulative predicted *attractiveness* of species occurring in terrestrial grid cells was explained by species richness (**B** & **D**), where positive residuals reflect higher *attractiveness* than expected based on species richness, and negative residuals indicating the opposite.

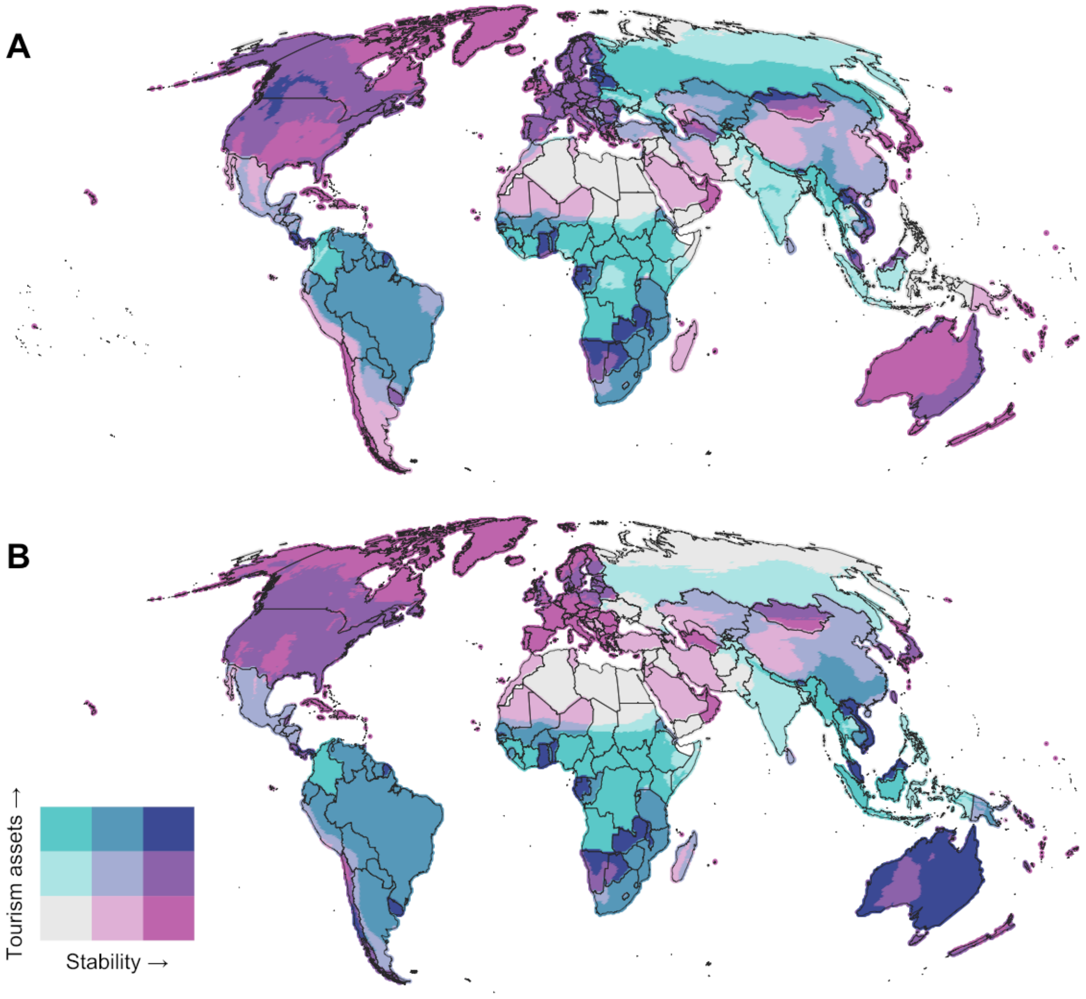

Figure 2.4: The suitability of countries for wildlife tourism development, based on political stability and wildlife tourism assets. Wildlife tourism assets were measured as **A** cumulative predicted *attractiveness* of all birds and mammals and **B** cumulative residual values for all birds and mammals with positive residuals (a measure of overlooked tourism potential). Colours diverge at the $\frac{1}{3}$ quantiles of wildlife tourism assets (from grey: low wildlife tourism assets, to turquoise: high wildlife tourism assets) and political stability (from grey: low stability to pink: high stability). Political stability data were obtained from the World Bank Group (2018). No estimates exist for Western Sahara and Somaliland (shown in white).

2.5. DISCUSSION

2.5.1. Determinants of species *attractiveness*

The results of this study provide the first insights into which species tourists find *attractive* and the key factors that determine species *attractiveness* globally. The major determinants of the birds and mammals that comprise the subset of wildlife tourism attractions selected by guides were body mass, range size, time partitioning, remoteness, political stability, extinction risk, evolutionary distinctiveness, habitat associations, and, among birds, migratory behaviour. The same traits were almost equally good at predicting *attractiveness* among the subset of those selected by guides (i.e., how many guides they were mentioned in).

Body mass appeared especially influential in determining species *attractiveness*. The attractiveness of large-bodied species is already widely recognized and capitalized on by conservation organisations, retailers, and tour companies alike (Clucas et al., 2008; Di Minin et al., 2012; Maciejewski and Kerley, 2014b; Okello et al., 2008). For tourism purposes, large-bodied species are likely attractive because they are both aesthetically appealing and more visible (Reynolds and Braithwaite, 2001). Sociality was particularly important for mammal *attractiveness* as well, and coloniality also influenced bird *attractiveness*, confirming findings of other studies that tourists are drawn to groups of animals (Di Minin et al., 2012; Okello et al., 2008). The attractiveness of social species may reflect their greater numbers and higher visibility, as well as increased viewing opportunities of interesting behaviours such as mating, fighting and grooming (Czajkowski et al., 2014; Dolata, 2006; Okello et al., 2008). This likely applies especially to species that aggregate in large numbers for animal rituals, such as migrations, as indicated by my results, which offer the first empirical evidence that migratory birds are more *attractive* to wildlife tourists than resident species.

Previous studies have found a preference among tourists for endemic and endangered species (Di Minin et al., 2012; Veríssimo, Fraser, et al., 2009). In this study, I found a relatively strong positive effect of range size on the likelihood a species was selected as an attraction by guides. However, range size interacted with remoteness such that, among species selected by guides, wide-ranging species were more *attractive* if they were accessible to tourists and range-restricted species were more *attractive* if they occurred in remote sites. There was also an interaction between range size and extinction risk in birds, with those at greater risk of extinction being more *attractive* if they were range-restricted, and those at lower risk being more *attractive* if they were widespread. No interaction was found between range size and extinction risk among mammals, but endangered mammals were more likely to be selected by guides as attractions. The interactions described here are complex, but I speculate that they indicate two converging types of tourism attractions: widespread, common, and accessible species and range-restricted, endangered, and remote species. The former may be attractive to tourists because they are more familiar and easier to observe in the wild (Macdonald, Burnham, et al., 2015), while preferences for the latter may be attributable to their rarity and/or because they are less likely to have been seen by tourists at other sites or at home (Di Minin et al., 2012;

Veríssimo, Fraser, et al., 2009). The effect of remoteness suggests that tourists are more likely to invest the extra time and money required to reach remote sites that contain range-restricted species. At the same time, those restricted to remote regions, such as rainforests, mountain ranges and islands, may be particularly alluring because of their wild and exotic nature.

The *attractiveness* of species to wildlife tourists was expected to be influenced by the habitat in which species occur (Cumming and Maciejewski, 2017). Landscape features, such as mountain ranges, water bodies, and vegetation are important tourism attractions for many well-known and popular PAs (Goodwin and Leader-Williams, 2000; Lindsey, Alexander, et al., 2007; Packer et al., 2014; Turpie and Joubert, 2001). Because dense vegetation could reduce the visibility of wildlife, it has been suggested that open grasslands are optimal for wildlife viewing (Gray and Bond, 2013; Kiss, 2004). I found some evidence to support this, as mammals occurring in open habitats were more likely to be selected by guides than those occurring in bare, shrubland, forested and mosaic habitats. In line with the importance of visibility, my results also confirm that diurnal species, which were more likely to be selected by guides, make the best tourism attractions (Okello et al., 2008; Reynolds and Braithwaite, 2001). However, the effects of habitat types were not consistent across taxa, with birds associated with aquatic habitats being more *attractive* to tourists than those that live in open vegetation. The attractiveness of aquatic birds might reflect some aspect of people's affinity to oceans, wetlands, and rivers, greater opportunities for viewing feeding, breeding and nesting behaviours, and/or greater concentrations of animals that congregate at such features as lakes or cliffs (Beerens et al., 2017; Gatto et al., 2008). Similar attractions to geological formations such as mountain peaks and cliffs might explain why birds in bare habitats were also found to be more *attractive* (Powell, Brownlee, et al., 2012). The contrasting effect of bare habitats, which may also be considered relatively open, on bird and mammal *attractiveness*, may reflect a combination of the ephemerality of resources in habitats such as deserts, and species dispersal abilities. That is, birds may be able to take advantage of seasonal or periodic gluts in resources in such habitats, during which time they may be relatively abundant, and therefore easy to observe, disappearing when resources decline (e.g., nomadic birds). In contrast, mammals, which tend to be resident and have lower dispersal ability, probably occur at very low densities in bare habitats.

Political stability has been proposed as reasons for the poor performance of some wildlife tourism destinations such as Kenya (Akama and Kieti, 2003). This study provides the first empirical evidence that safety concerns, as well as perhaps the less well developed infrastructure in unstable countries, influences species *attractiveness* for wildlife tourism (Akama and Kieti, 2003; Willemen et al., 2015). Continued unrest likely contributed to the low predicted *attractiveness*, compared with species richness, in places such as the Congo (BBC, 2021).

Previous studies have identified preferences for species uniqueness among birders, in terms of behavioural or ecological characteristics (Veríssimo, Fraser, et al., 2009), but mine is the first study to demonstrate the *attractiveness* of evolutionary distinct birds and mammals to wildlife tourists. These unique species are likely attractive to tourists partly due to their rarity – it is less likely that tourists will have seen similar species elsewhere – and because of this their appearance and behaviour may be perceived as particularly interesting. The platypus *Ornithorhynchus anatinus*, for example, the sole living representative of its family, is an 'unusual' egg-laying, duck-billed, and venom-producing mammal that can only be seen in eastern Australia.

There are a number of additional traits that likely influence species attractiveness which were not included in this study, but are worth bearing in mind for future research. For instance, people are thought to prefer 'cute' or 'cuddly' species with human-like attributes such as forward-facing eyes (Lorimer, 2007; Macdonald, Burnham, et al., 2015). Colouration has been identified as a particularly important trait for birdwatchers (Veríssimo, Fraser, et al., 2009). A recent study also highlighted the role of birdsong in enhancing peoples' experience with nature (Ferraro et al., 2020). The appeal of birdsong is also reflected in the proliferation of birdsong 'radio' (e.g., the 'Let Nature Sing campaign' by the UK's Royal Society for the Protection of Birds). I explore the role of some physical traits at a smaller scale in the United Kingdom in Chapter 5, but, due to a lack of data, I was unable to explore their role at this larger scale.

I assign species with a fixed *attractiveness* index, but it is also worth noting that attractiveness may vary within species, depending on factors such as species composition, abundances and local rarity (Bandara and Tisdell, 2005). For example, the waterbuck *Kobus ellipsiprymnus* and giraffe *Giraffa camelopardalis* are uncommon species to see in Amboseli National Park, Kenya, where they may be of greater interest to tourists than elsewhere because they are not often seen in the park (Okello et al., 2008). At a global level, incorporating such information, especially abundances, is challenging, and new monitoring programs must fill in critical data gaps in global population abundance data, but measures of local rarity could feasibly be estimated in future studies by calculating range sizes within regions, countries or PAs (Arbieu, Grünewald, Martín-López, et al., 2018; Proença et al., 2017).

2.5.2. Potential wildlife tourism hotspots

Beyond revealing the influence of key species traits on *attractiveness*, my results provide novel insights into the spatial distribution of wildlife tourism potential throughout the terrestrial world, representing an important step in prioritisation of tourism investment. Wildlife tourism is a global industry spanning much of the Earth's habitable land mass. I identified hotspots where wildlife tourism potential is greatest, based on *attractive* bird and mammal assemblages, which include some of the best-known wildlife tourism destinations e.g., East Africa, the Amazon, and the Pantanal. The geographic distribution of these hotspots indicates significant, and often untapped, financial opportunities available to countries in sub-Saharan Africa, South America and South East Asia that protect, market, and develop their natural assets in the right way for wildlife tourism.

Unfortunately, one of the problems of producing metrics on tourism potential is that it is hard to discuss the validity of the results in terms of actual tourism levels (WTTC, 2016). It is likely that for some hotspots, high tourism potential will not correlate with high tourist numbers/revenue. Although they may share many of the same *attractive* species as more stable, neighbouring countries, instability, violence and terrorism in some African countries, particularly Central and West Africa, Colombia, and countries of Southern and South East Asia, may limit tourism development. Amazonian countries, as well as parts of East and Southern Africa, have more favourable political systems, suggesting there may be more scope for tourism growth. However, relative long-term political stability, coupled with abundant wildlife assets, in some West and Southern African e.g., Botswana and South East Asian countries e.g., Singapore, as well as Australia, French Guiana, Uruguay, and Chile, suggest they are best positioned for wildlife tourism development. It has also likely contributed to the success of popular destinations in Europe and North America (Balmford, Green, et al., 2015), reflected in this study in relatively high species *attractiveness* but low residuals. Improved political stability and security may offer significant opportunities for other countries in the future. Building a strong domestic tourism industry could also help reduce a country's susceptibility to low numbers of international arrivals resulting from, sometimes misinformed, perceptions of instability (Muhoho-Minni and Lubbe, 2017), but internal security issues for domestic tourists must be addressed.

Several sites that are recognized as prime wildlife tourism destinations were not highlighted as such in this study, pointing to some limitations in my methodology. Madagascar and Papua New Guinea, internationally renowned for their unique and interesting wildlife, are good examples, predicted to have much lower *attractiveness* than expected based on species richness. Failure to pick up the tourism potential of these islands could be attributed to the fact that some of their most popular inhabitants i.e., lemurs and birds-of-paradise, were often grouped together in the tourism literature, which would have had the effect of under-estimating the *attractiveness* of individual species. The inclusion of a greater range of more detailed resources (e.g., brochures or guides directed towards more specialist or experienced tourists, for whom specificity may be more important) may better reflect *attractiveness* of individual species. Other well-known tourism localities owe their appeal more so to a handful of iconic or flagship species and/or wildlife spectacles than the entire species assemblages (e.g., pandas *Ailuropoda melanoleuca* in China, tigers *Panthera tigris* in India, wildebeest *Connochaetes taurinus* migrations in the Serengeti), and such places may have been been overlooked in this research. However, my *attractiveness* index could help managers identify whether they posses attractive species that could serve as flagships, and towards which marketing and promotional material could draw attention.

Target audiences for the guides were mostly tourists from Western, English-speaking countries, which in many destinations represent the average, international tourist. Although they represent an important subset of tourists (Goodwin, Kent, et al., 1997; Guimarães et al., 2015), focussing on this group may have introduced additional biases into my results. Surveys have found that more specialised and/or domestic tourists have more diverse preferences, as well as greater preferences for less high-profile species (Di Minin et al., 2012). Experienced or domestic tourists may also be less deterred by issues such as remoteness or political stability. The above examples of Madagascar and Papua New Guinea could, in part, reflect the long-distance flights and large travel budgets required to reach these remote islands from Western source countries, compared with destinations such as Costa Rica or South Africa. Extending my work by collating data from tourism promotional material directed towards different subsets of tourists may flag wildlife tourism hotspots that were missed by this study. The rising higher-income classes of emerging economies, such as India, where there is growing demand for wildlife tourism (Balmford, Beresford, et al., 2009; Karanth and DeFries, 2011), should be considered priority markets for future research.

2.5.3. Implications for conservation

The species *attractiveness* index developed in this study can inform PA management at large spatial scales, including informing marketing and/or conservation strategies. There is clear economic justification for preserving attractive species – abundant and diverse wildlife tourism attractions can attract more visitor who provide funds from entry and activity fees, and may allow PAs to charge higher admissions costs, leading to greater tourism revenue. There are also conservation reasons to focus attention on these species. Threatened and range-restricted species were among the most *attractive* to tourists, and many iconic and charismatic species are under real threat of extinction (Courchamp, Jaric, et al., 2018). Tapping into the high tourism potential of these species could be an effective way of maximising conservation outcomes for species that are of high conservation concern globally. Furthermore, tourists appear to be particularly interested in evolutionary distinct species, such that tourism could play a pivotal role in preserving unique evolutionary history and phylogenetic diversity, a growing component of conservation (Isaac et al., 2007; Jetz, Thomas, Joy, Redding, et al., 2014).

Amid debate around the conservation benefits of wildlife tourism, several case studies have demonstrated that increased tourist numbers/prices can lead to increased investment and support towards conservation efforts (Buckley, 2009). These include tourism operations focussed on flagship species, such as mountain gorillas *Gorilla beringei beringei* in Rwanda (Nielsen and Spenceley, 2011), sub-nosed monkeys *Rhinopithecus roxellana* in China (Xiang et al., 2011), and tigers *P. tigirs* in India (Macdonald, Gallagher, et al., 2017). McGowan et al. (2020) determined that a flagship approach can help achieve place-based conservation objectives, including the conservation of broader biodiversity, not just the focal species. In this study, I found substantial overlap between hotspots of *attractive* species and sites identified as targets for biodiversity conservation, including the Andes, the Brazilian Atlantic forest, montane Africa, the central Asian mountains, the Himalayas, the Amazonia, and the Guinean forests of West Africa (Allan et al., 2019; Brooks, Mittermeier, et al., 2006; Mittermeier et al., 2003; Sanderson et al., 2002; Scheffers et al., 2019). Tourism focussed on flagship species in these regions could therefore facilitate cost-effective conservation action that could help ensure the survival of vulnerable and important species and habitats.

The diversity of *attractive* species provides flexible options from which managers can choose the most appropriate flagships that best align with the local ecological and cultural context (Bowen-Jones and Entwistle, 2002). An important question remains: what is causing the poor performance of some species, as reflected by positive residuals? One possible explanation is that species *attractiveness* is determined not only by a species' attributes, but also by its reputation, media exposure, and familiarity. For example, the spotted hyena *Crocuta crocuta* emerged as one of the top species (#12 among mammals) whose modelled *attractiveness* was higher than observed *attractiveness*, which could be attributed to the negative publicity that this species has traditionally received in the media. In contrast, frequent targets of conservation campaigns and the media, e.g., the tiger *Panethera tigris* (Netflix's Tiger King), giant panda *A. melanoleuca* (WWF), and chimpanzee *Pan troglodytes* (Jane Goodall Institute), were often selected more times by guides than predicted based on their traits.

This link between media attention and attractiveness suggests that public awareness and marketing campaigns might be an effective way of improving people's attitudes towards under-rated species i.e., those identified in this study as having high residuals (Kerley et al., 2003). In doing so, managers may be able to raise the profile of under-utilized sites, while reducing pressure on the more heavily sought-after species and sites (Goodwin and Leader-Williams, 2000). This is already being done at some sites, such as Addo Elephant National Park, South Africa, where information brochures and road signs drawing attention to the threatened status and intriguing behaviour of the flightless dung-beetle *Circellum bacchus* have succeeded in turning the species into 'charismatic microfauna' (Kerley et al., 2003). The effect of 'flagship fatigue', whereby over-exposure reduces the effectiveness of a flagship species, could facilitate greater interest in new, less high-profile charismatic species.

Expanding the current scope of wildlife tourism by promoting under-rated or overlooked species could help strengthen the role of wildlife tourism in biodiversity conservation. However, increasing tourism numbers/prices does not guarantee that the extra revenue will be re-invested towards environmental objectives. More research is needed into whether increased tourism revenue is, in reality, being directed towards improving conservation efforts, as well as supporting local communities (Karanth and DeFries, 2011). International tourism and travel also raise important worries regarding effects on local people and CO_2 emissions (Job and Paesler, 2013; Mbaiwa, 2003; Muñoz et al., 2019; Sebele, 2010). Addressing these concerns is beyond the scope of my research, but they highlight the importance of ethical, effective, and sustainable management of wildlife tourism. Another issue that has received substantial attention in the scientific literature is the effect of tourism activities on the focal species of interest, especially when these species are already endangered, which needs to be managed when increasing visitor numbers to PAs (Sekercioglu, 2002; Steven, Pickering, et al., 2011). Flash photography, stocking of charismatic species, and feeding animals are just a number of tourism activities that can have negative impacts on focal (and even non-focal) species, including injury, stress or death of animals, and disruption of crucial behaviours such as feeding or breeding (Castley et al., 2001; Macdonald, Gallagher, et al., 2017; Maciejewski and Kerley, 2014a,b). By highlighting which species are of interest to tourists, my global index of *attractiveness* could help managers find the middle ground between keeping a species 'out of sight out of mind', which can result in lack of conservation attention, and 'loving a species to death' (Newsome, Moore, et al., 2013), whereby pressure from tourism activities puts species at risk, which may require limiting access towards priority species or sites during breeding seasons e.g., fences (Cassini et al., 2004) or installing infrastructure to minimize disturbance e.g., bird hides (Ikuta and Blumstein, 2003).

2.6. CONCLUSION

I used wildlife tourism literature to advance our understanding of wildlife tourists' preferences, identifying hotspots of bird and mammal assemblages that are most attractive to the global, Western or English-speaking tourist and locating potentially missed opportunities for conservation funding, as well as local development. The spatial framework I presented could be used to help guide conservation action, PA management, tourism investment, and development planning from national to sub-national scales. Countries striving to meet the ambitious targets laid out by the United Nations SDGs and the Aichi Targets should prioritise investment of limited budgets towards localities with high wildlife tourism potential, thereby maximising the potential for wildlife tourism to contribute towards multiple goals simultaneously. My study encapsulates preferences of a major subset of wildlife tourists, but the development of this work to include the wider community could reveal additional wildlife tourism hotspots. In Chapter 3, I will explore how different attributes of the tourism experience, including wildlife *attractiveness*, relate to the popularity of PAs for wildlife tourism. Together, this information could 1) contribute to the identification and management of novel wildlife tourism destinations; 2) make wildlife tourism potential visible to decision-makers; and 3) help to orient investments and incentives to those sites with high wildlife tourism potential. In Chapter 4, I will use this information to forecast future wildlife tourism potential under different climate change scenarios. In light of the financial challenges associated with protecting biodiversity, establishing wildlife tourism operations at priority hotspots could open up and secure a sustainable source of revenue for biodiversity conservation, both inside and outside of PAs, as well as provide revenue for local development in rural areas.

Chapter 3

Determinants of Protected Area Popularity for Global Wildlife Tourism

3.1. ABSTRACT

Protected areas (PAs) are major wildlife tourism destinations worldwide. Managing and marketing PAs to optimize the benefits of wildlife tourism can contribute to biodiversity conservation and sustainable development through generation of revenue and employment. This requires an understanding of what makes PAs popular for wildlife tourism. Statistics on PA visitation by wildlife tourists, to date, remain scarce. Using wildlife tourism literature, I develop a proxy of PA *popularity* based on citation frequency by guidebooks, brochures, and websites. In a series of generalised linear mixed models, I show that, on the whole, PAs that are cited most frequently as destinations in wildlife tourism literature are larger, older, relatively accessible, have stricter management categories, a lower density of tourism amenities, and aesthetic landscape features e.g., higher elevational range and water bodies. I also provide the first evidence that PAs with more attractive, rarer species communities are cited more often than those with less attractive, more common species assemblages. PAs in East and Southern Africa, Southern Asia (particularly India), the western United States, Costa Rica, the Peruvian Amazon, the Iberian Peninsula, and Eastern Europe were predicted to be the most *popular* for wildlife tourism globally. Tourism investment and management should be prioritised towards these regions to encourage PA visitation (while ensuring PAs are not over-visited), thereby harnessing the potential benefits for biodiversity conservation and local people. PA popularity, as derived from wildlife tourism literature, was significantly correlated with annual visitor numbers, suggesting that these resources offer a novel data source for human use of PAs.

3.2. INTRODUCTION

In the face of continuing biodiversity loss (Tittensor et al., 2014), safeguarding important biodiversity sites through protected areas (PAs) is a key component of global conservation strategies (CBD, 2010). However, around the world, financial resources and political support for PAs are limited, leading to the proliferation of paper parks, where management is ineffective and biodiversity continues to decline (Wilkie, Carpenter, and Zhang, 2001). Inadequate investment in conservation can be attributed, in part, to the high and inequitable costs of setting aside land for protection, which often fall disproportionately on local communities and governments of lower income countries. Coupled with this is a failure to recognize the benefits of biodiversity and well-functioning ecosystems, which, in an extrinsic sense, seldom outweigh the competitive monetary incentives for land development over protection. Given the need for further investment in PAs if they are to be successful conservation tools, alternative sources of revenue are needed, both to cover important management costs and offset the costs incurred by gateway communities living alongside them (Wilkie and Carpenter, 1999).

PAs have come under greater pressure to ‘pay their way’, and an increasingly important goal of PAs has been the supply of ecosystem services (ES). PAs provide opportunities to experience, enjoy and learn about nature through tourism, a cultural ES that contributes to human well-being and environmental awareness (Buckley, Brough, et al., 2019; Powell and Ham, 2008). The abundance and diversity of wildlife within PAs, which is often higher than on non-protected land (Gray, Hill, et al., 2016), represents a major natural attraction, with many tourists visiting PAs to view free-roaming animals in their natural habitat. This non-consumptive form of wildlife tourism can benefit biodiversity conservation, as well as people, in a number of ways, including through the generation of sustainable revenue and employment opportunities (UNWTO, 2018; WTTC, 2016). Effectively managing wildlife tourism activities in PAs is crucial to optimise these co-benefits, which requires allocating resources towards priority PAs with high tourism potential and designing, managing, and marketing PAs in line with tourist preferences and activities (Heagney et al., 2018; Kim et al., 2019). Wildlife tourism is also known to sometimes have negative effects on biodiversity through increasing disturbance to species, or through harmful effects on the environment e.g., pollution and habitat loss (Buckley, 2011). The demand for nature-related tourism is on the rise worldwide (Balmford, Beresford, et al., 2009), and a better understanding of patterns of PA popularity could prove vital for informing management decisions relating to minimising adverse environmental effects through control of visitor behaviour (Steven, Castley, et al., 2013).

Numerous studies have begun to provide important insights into the factors that influence PA visitation. These include the presence of charismatic species as well as broader biodiversity (e.g., species richness, threatened species, habitat diversity) and aesthetic landscapes (e.g., vegetation, water bodies, elevation) (Arbieu, Grünewald, Schleuning, et al., 2017; Chung et al., 2018; de Castro et al., 2015; Hausmann, Toivonen, Fink, et al., 2019; Hausmann, Toivonen, Slotow, et al., 2017; Loureiro et al., 2012; Naidoo and Adamowicz, 2005a; Schägner, Brander, et al., 2016; Siikamäki et al., 2015). In general, older, larger PAs, with stricter protection have been found to be more heavily visited than smaller, more recently designated PAs with weaker protection (Balmford, Green, et al., 2015; Chung et al., 2018; Neuvonen et al., 2010; Xiao, Aultman-Hall, et al., 2018). PAs that are more accessible and with more and better quality tourism amenities (e.g., hotels) have also been found to be more heavily visited. The socio-economic and political conditions of a country or a site have been found to influence visitation as well, with PAs in richer countries and with larger local human populations receiving more visitors (Balmford, Green, et al., 2015; Chung et al., 2018; Hausmann, Toivonen, Fink, et al., 2019; Schägner, Brander, et al., 2016). Finally, PAs with higher temperatures and lower rainfall have been found to be more heavily visited, demonstrating the importance of climatic factors (Chung et al., 2018; Richardson and Loomis, 2004).

Thus far, studies assessing the factors affecting PA visitation patterns have depended mostly on information on visitor numbers. Yet visitation data is often patchy, due to difficulties associated with collating such data (see Buckley, 2009). Moreover, visitor numbers do not contain information on the motivations of tourists e.g., hiking vs. wildlife watching, and the factors driving tourists to PAs will depend on the reasons behind their visit. Consequently, empirical evidence regarding the drivers of wildlife tourism, specifically, across the global PA network, remains limited. Furthermore, the role of biodiversity itself in attracting visitors is not well understood, creating potential conflicts between PA management goals. I develop a new approach to fill in this gap in our knowledge. I use widely available data collated from wildlife tourism 'guides' to derive a proxy for PA popularity. As resources such as guidebooks and brochures become ubiquitous in tourists' decision-making, they serve as a growing source of information on the PAs being considered by tourists for wildlife watching. Puhakka et al. (2011) adopted a similar approach that utilised wildlife tourism literature, extracting information from the itineraries of national tour operators to identify areas that are most popular for birdwatching in Peru, and found that sites identified by tour operators as top wildlife watching destinations overlapped with those identified in interviews with birdwatchers and key informants.

I use the number of guides a PA is mentioned in, as a wildlife tourism site, as a proxy for PA *popularity*. The terms *popularity* and *popular* are italicised throughout this thesis when referring to this proxy. I then quantify the importance of a suite of factors, previously shown (or suspected) to influence tourists' decision-making, in driving spatial variation in PA *popularity* at a global scale, using generalised linear mixed models (GLMMs). I assess the influence of these factors at the continental level to establish how their effects vary geographically. I validate these models using PA visitation data to determine whether they can be used to predict the number of visitors (i.e., not just wildlife tourists) to PAs worldwide. The main objectives of this study are to:

1. examine the key characteristics that influence the citation frequency of PAs in the wildlife tourism literature,
2. identify the most *popular* PAs where wildlife tourism represents a potential sustainable source of revenue for biodiversity conservation and local communities,
3. determine whether data from wildlife tourism literature can be used to build a robust, predictive model of PA visitation.

3.3. METHODS

I obtained a comprehensive dataset on PAs by aggregating data from international institutions, national statistical agencies, online datasets and peer-reviewed literature. The primary data source for this study was the World Database of Protected Areas (WDPA, 2018), which contains information on 235,489 PAs. I concentrated on terrestrial and coastal PAs with polygon data and a management category between "II" and "VI", excluding Antarctic PAs, as well as category "I" PAs, where tourism and recreation activities are mostly prohibited (Balmford, Green, et al., 2015). I removed those covering $< 1\text{km}^2$ of land, which some estimates suggest is the minimum area needed to support intact communities of vertebrate species (Gurd et al., 2001).

I recorded PAs promoted as tourism destinations to see birds and/or mammals in the 42 wildlife tourism resources listed in Chapter 1 Table 1.1. The total number of guides in which a PA was cited as a destination was used as the PA's index or proxy of relative *popularity*. PAs not mentioned in any guide were assigned a *popularity* index of zero. I derived 21 predictor variables (Table 3.1), which were expected to influence the *popularity* of PAs as destinations for wildlife viewing, including 1) mammal *attractiveness*; 2) bird *attractiveness*; 3) mammal community rarity; 4) bird community rarity; 5) proportion of grassland cover; 6) proportion of forest cover; 7) proportion of land occupied by water; 8) habitat diversity; 9) altitudinal range; 10) mean annual temperature; 11) mean annual rainfall; 12) PA size; 13) PA age; 14) management category; 15) international designation; 16) national park designation; 17) local human population density; 18) remoteness; 19) density of tourism amenities, 20) Human Development Index (HDI); and 21) political stability.

3.3.1. PA attribute data

PA species lists were predicted by overlaying PA polygons, obtained from the WDPA (2018), with digitized geographical range maps, downloaded from the International Union for Conservation of Nature (IUCN, 2016) and BirdLife International and Handbook of the Birds of the World (2016) (see Appendix Section B.1 for further details). At first, species with even small amounts of overlap with a PA were considered present. I then used information on species' habitat suitability and altitudinal limits from the IUCN (Brooks, Pimm, et al., 2019; Rondinini, Di Marco, et al., 2011) to remove species from PAs that did not contain suitable habitat or did not lie within the species' altitudinal range. I obtained species data using data from the R package 'rredlist' (Chamberlain et al., 2020). I extracted the altitudinal range of PAs using the Global Multi-resolution Terrain Elevation Data (GMTED) (U.S. Geological Survey, 2010). I categorized the habitats present in each PA using Climate Change Initiative land cover data from the European Space Agency (ESA CCI, 2018), matching this to the habitats listed in level 2 of the IUCN Habitat Classification Scheme, following the crosswalk displayed in Appendix Table C.1 and published by Santini, Butchart, et al. (2019). Given the difficulties of inventorying rodents and other small mammals ($<$ 1kg) and because they are rarely promoted as wildlife attractions (Lindsey, Alexander, et al., 2007; Tobler et al., 2008; Voss and Emmons, 1996), these species were removed from PA species lists.

I conducted an extensive search for species inventories (or checklists) for validation purposes, by entering combinations of the search terms "species", "birds", "mammals", "list", "inventory", "checklist", and "protected area" into major search engines. PA checklists were available from technical reports, environmental assessments, official PA websites, biodiversity databases, conservation agencies, citizen science databases e.g., `www.GBIF.org` and other secondary sources. I obtained checklists for a subset of 1,022 PAs from 103 nations (see Appendix Fig. C.1), which are available at `https://github.com/mairekirkland/thesis_datasets`.

Table 3.1: Explanatory variables of PA *popularity* worldwide used in the GLMMs.

Variable	Description	Time period	Mean (±SD)	Source	Link
Mammal *attractiveness*	Cumulative *attractiveness* of all terrestrial mammals occurring in the PA	2016	105.17 (86.92)	Chapter 2	—
Bird *attractiveness*	Cumulative *attractiveness* of all birds occurring in the PA	2016	508.17 (211.23)	Chapter 2	—
Mammal community rarity	The continental or global rarity of the PA's terrestrial mammal community	2016	—	—	—
Bird community rarity	The continental or global rarity of the PA's bird community	2016	—	—	—
Sqrt grassland cover	Proportion of cells with grassland cover (∼300m resolution)	2018	0.16 (0.26)	ESA CCI (2018)	https://www.esa-landcover-cci.org/
Forest cover	Proportion of cells with forest cover (∼300m resolution)	2018	0.54 (0.39)	ESA CCI (2018)	https://www.esa-landcover-cci.org/
Sqrt water bodies	Proportion of cells with water bodies (∼300m resolution)	2018	0.12 (0.24)	ESA CCI (2018)	https://www.esa-landcover-cci.org/
Habitat diversity	Shannon's diversity of land cover types	2018	0.74 (0.50)	ESA CCI (2018)	https://www.esa-landcover-cci.org/
Sqrt elevational range	Difference between highest and lowest altitudinal point, in metres	2010	13.63 (10.22)	U.S. Geological Survey (2010)	https://www.usgs.gov/centers/eros/science/
Mean temperature	Mean monthly temperature in °C (∼1km resolution)	1970-2000	10.75 (6.68)	*WorldClim 2.0 Beta version 1* (2016)	https://www.worldclim.org/
Mean rainfall	Mean monthly precipitation in mm (∼1km resolution)	1970-2000	84.50 (48.59)	*WorldClim 2.0 Beta version 1* (2016)	https://www.worldclim.org/
Log_{10} size	Area of PA in km^2	2018	0.98 (0.84)	WDPA (2018)	https://www.protectedplanet.net/
Age	Years since PA was established from 2020	2018	30.40 (18.95)	WDPA (2018)	https://www.protectedplanet.net/
IUCN management category	"II" – 1, "III" – 2, "IV" – 3, "V" – 4, "VI" – 5	2018	—	WDPA (2018) & Holness, S. (02 May 2019) pers. comm. (SANparks)	https://www.protectedplanet.net/
International designation	Yes/No statement indicating whether PA covered by Ramsar or UNESCO designations	2018	—	WDPA (2018)	https://www.protectedplanet.net/
National park designation	Yes/No statement indicating whether PA is designated a national park	2018	—	WDPA (2018)	https://www.protectedplanet.net/
Sqrt local population density	Mean annual population density, measured as the number of persons/km^2, within the PA itself and a 100km buffer around the PA (∼1km resolution)	2000-2015	7.36 (5.88)	CIESIN (2017)	https://sedac.ciesin.columbia.edu/
Sqrt remoteness	Mean travel time, in hours, to high-density urban centres (>1,500 people) (∼1km resolution)	2015	9.84 (7.79)	Weiss et al. (2018)	https://malariaatlas.org/
Sqrt tourism facilities	Density of tourism facilities, within the PA itself and a 100km buffer around the PA	2020	0.30 (0.32)	*OpenStreetMap* (2020)	https://planet.openstreetmap.org/
HDI	Mean HDI of the host country	1991-2015	0.82 (0.10)	World Bank Group, 2018	https://databank.worldbank.org/databases
Political stability	Mean political stability of the host country	1996-2015	0.54 (0.71)	World Bank Group, 2018	https://databank.worldbank.org/databases

Jaccard's index, often used to compare species communities of different sites (Yue and Clayton, 2005), was used to assess similarity between the two sets of species lists (i.e., predicted lists from intersected range maps vs. species inventories obtained from the literature), which was calculated as:

$$J = \frac{M_{11}}{M_{10} + M_{01} + M_{11}}$$

where M_{11} represents the total number of species listed as present in both lists, and M_{10} and M_{01} represents the total number of species recorded in one list but not the other. Kendall's tau-b (τb) correlation coefficient was then used to explore the relationship between Jaccard's similarity and PA attributes. I also explored correlations between summed species *attractiveness* within PAs derived from both sets of lists, to determine whether my putative species lists could accurately predict species *attractiveness*.

I assigned PAs a separate measure of bird and mammal *attractiveness* by summing predicted species *attractiveness* scores, obtained from Chapter 2, of all species predicted to occur in the PA (i.e., based on intersected range maps). The rarity of predicted mammal and bird communities within PAs was calculated using k-means clustering, where PAs with similar communities were grouped together (Bholowalia and Kumar, 2014). The number of clusters was chosen using the 'elbow method', whereby the optimal number is that at which the improvement of the within-cluster sum of squares begins to decline as another cluster is added, which was ~50 for mammals and ~60 for birds (Fig. 3.1). The rarity of each community was then calculated according to the following:

$$R_i = 1 - \frac{F_i - 1}{F_{max}}$$

where F_i is the frequency of community i and F_{max} is the frequency of the most common community. Higher values of R refer to greater rarity, and vice versa. PAs with no birds or mammals present were assigned a rarity index of zero. I calculated a rarity index for communities at a global scale, as well as within continents, to be used in the global and continental models, respectively.

I used ESA CCI (2018) data, which comprise 35 different land cover types, to determine the proportion of different habitats and the diversity of habitats within each PA. I calculated Shannon's diversity of habitats, excluding land cover types 10 to 40 and 190, which correspond to cultivated land and urban areas, respectively (see Appendix Table C.1). Although some charismatic species can be seen in artificial landscapes e.g., jaguars *Panthera onca* in cattle ranches (Tortato and Izzo, 2017), the habitats themselves were not expected to contribute to

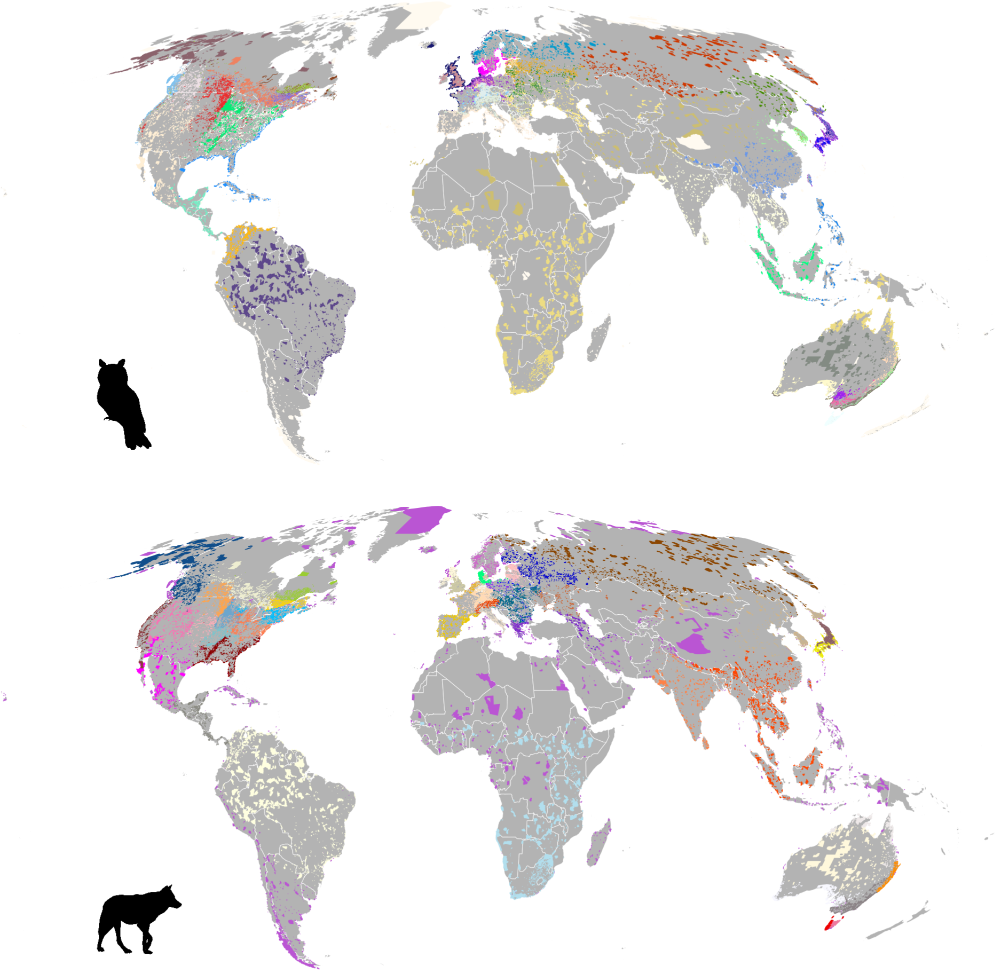

Figure 3.1: PAs grouped into clusters with similar bird (top) and mammal (bottom) communities. k-means clustering was used to group PA bird and mammal assemblages into 60 and 50 clusters, respectively. Colours represent different community clusters. Note that to minimize the within-cluster sum of squares, the k-means algorithm gives more 'weight' to larger clusters. That means k-means allows smaller clusters to exist far away from the center of that cluster, while using that center to split up a much larger cluster. This may account for the higher number of clusters observed in the north temperate regions, where there are a higher number of PAs. While this method may capture the rarity of species' communities in the tropics due to the lower number of PAs in the former, the k-means algorithm may underestimate their rarity because of the above limitation.

the appeal of the natural scenery. Shannon's index, widely used to calculate species diversity at a site (Peng et al., 2018), is denoted as:

$$Shannon's\ H = -\sum_{i=1}^{L} p_i \ ln \ p_i$$

where, in this case, L is the total number of land cover types in the PA and p_i is the proportion of grid cells within the PA containing the ith land cover type. I calculated elevational range within PAs using the GMTED (U.S. Geological Survey, 2010) and mean monthly temperature and rainfall using data from *WorldClim 2.0 Beta version 1* (2016) (Fick and Hijmans, 2017). The WDPA provided data on PA size, which for coastal PAs was calculated based on the area of the terrestrial portion of the PA, to align with the focus of this study on land-based tourism activities. The WDPA also contained information on the IUCN management category of PAs, and PA age. The latter was treated as a nuisance variable to control for the fact that younger PAs were likely to be mentioned by less guides because some were published before their designation. I estimated the mean annual human population density within a PA and a 100km buffer around its perimeter, using the Gridded Population of the World (2000-2015) data from the Center for International Earth Science Information Network (CIESIN, 2017). PA remoteness was calculated as the mean travel time to the nearest high-density urban centre by overlaying PA polygons onto the global accessibility map developed by Weiss et al. (2018).

I extracted marked Points of Interest (POIs) relating to 19 types of buildings, amenities, and paths (see Appendix Table C.2) that provide facilities for wildlife tourism activities. I obtained the latest information about geolocated marked points from *OpenStreetMap* (2020). OpenStreetMap, a crowd-sourced geographic database, provides freely accessible data on tourism facilities available globally (Barrington-Leigh and Millard-Ball, 2017; Jokar Arsanjani et al., 2015). POIs were intersected with buffered PA polygons to determine the density of amenities in and around each PA. I assigned PAs the mean political stability and HDI value of the country in which they reside, using data published by the World Bank Group (2018) across a twenty-year period. HDI is a composite index of life expectancy, education, and per capita income, used to rank countries by levels of human development, where higher values indicate longer lifespan, higher education level, and higher national income, and vice versa. I intersected polygons, as well as point data from the WDPA, to identify PAs designated under national legislation, that were also, at least partially, covered by international legislation (i.e., the United Nations Educational, Scientific and Cultural Organization (UNESCO) World Heritage Convention, the UNESCO Man and the Biosphere Programme and the Ramsar Convention).

Less than 1% ($n = 272$) of PAs, which were missing data for one or more of the above potential explanatory variables, were removed from the dataset used for analysis (Appendix Fig. C.3). I also removed spatially overlapping PAs to reduce pseudo-replication, keeping the PA with the lowest management category because, for conservation purposes, it is important that PAs are managed under their strictest designation (Deguignet et al., 2017). The resulting dataset contained 41,766 PAs. Raster data had a spatial resolution of 30 arc second ($\sim$1km at the equator), apart from the ESA CCI data and GMTED, which had a 10 arc second ($\sim$300m) and 7.5 arc second ($\sim$225m) resolution, respectively. Spatial analyses were conducted using

Robinson's projection in QGIS with the 'Zonal Statistics' and 'Zonal Histogram' tools (QGIS Development Team, 2019) and the 'rgdal', 'rgeos', 'raster', 'sf', and 'vegan' packages of R Version 3.6.0 (Bivand, Keitt, et al., 2020; Bivand, Rundel, et al., 2020; Hijmans, Etten, et al., 2020; Oksanen et al., 2019; Pebesma et al., 2020; R Development Core Team, 2018).

3.3.2. Data analysis

I performed a square-root transformation on some predictors prior to analysis (Table 3.1), either because they showed a relatively skewed distribution or to account for non-linear relationships. I converted IUCN management category to a continuous scale ("II" = 1, "VI" = 5), where a lower number means stricter protection. Initially, connectivity between PAs, calculated as the total area of neighbouring PAs (excluding proposed and category "I" PAs) that lie within a buffered PA, was considered as a potential predictor variable. However, Kendall's τb revealed a strong correlation between PA connectivity and size ($\tau b = 0.996$, $P < 0.0001$, Appendix Fig. C.2). I chose to retain PA size over connectivity based on *a priori* assumptions regarding the most important factors that influence visitation (Balmford, Green, et al., 2015). Only weak correlations were found between the response variable and the species *attractiveness* variables, despite being derived from the same data source ($\tau b \leq 0.10$), indicating sufficient independence of data. Covariates were centred and standardised to a mean of zero and a standard deviation of one to improve model convergence and aid interpretation of model parameters. I grouped North and South America together and also combined Asia and Oceania for the continental models to ensure adequate sample sizes for model fitting.

I used Variance Inflation Factors (VIFs) to estimate multicollinearity (O'brien, 2007) between predictor variables. VIFs were < 10, the threshold used to indicate strong collinearity (Quinn and Keough, 2002). I explored quadratic effects of temperature and rainfall, assuming that both would have an optimal medium value or range for attracting tourists. The majority of models indicated no significant quadratic effects, so these terms were dropped from subsequent analysis (all $P \geq 0.12$), apart from the quadratic term for temperature in the Africa model, which was retained.

The response variable was a count variable with a high degree of zero responses, so I ran a series of GLMMs using Poisson and negative binomial distributions with and without accounting for zero-inflation. I used the 'glmmTMB' package in R (Brooks, Kristensen, et al., 2017a,b) to run models on both the global dataset as well as at a continental scale. I used likelihood ratio tests to compare alternative models and found significant zero-inflation and over-dispersion (all $P < 0.0001$). I inspected model residuals and performed goodness-of-fit tests using the DHARMa package (Hartig, 2020), which uses a simulation-based approach to create readily interpretable scaled residuals from fitted GLMMs. Based on the results of these tests, I continued with hurdle GLMMs (Brooks, Kristensen, et al., 2017a,b) in which a zero-truncated negative binomial model with a log link, where the variance increases quadratically, was used to model the number of guides a PA was mentioned in (i.e., a PA's *popularity* index), using only those PAs appearing in at least one guide (hereafter 'frequency model'). I used a logistic model with a log link to model the probability of a non-zero response (i.e., the probability of a PA being selected by the guides, hereafter 'binomial model') using all PAs.

I included the region (see Appendix Table C.3) and country in which PAs are located as random effects to account for the hierarchical structure of the data, but due to convergence issues and low variances, the random effect of 'region' was removed from the America model. I tested the residuals for spatial autocorrelation, using global Moran's I, where -1 indicates perfect clustering of dissimilar values, one indicates clustering of similar values, and zero indicates perfect randomness of values (i.e., no autocorrelation). I found no problems of spatial autocorrelation ($P > 0.05$) in all regions other than the Americas ($I = -0.11$, $SD = 0.02$, $P = 0.031$) and Africa ($I = -0.07$ $SD = 0.09$, $P = 0.043$), where there was evidence of slight negative autocorrelation. However, DHARMa is known to often show slight patterns in the residuals, even if the model is specified correctly, because of biases in random effect estimates, and at large sample sizes, such as I have in my datasets, these differences can emerge as significant (Hartig, 2020). This, coupled with the low values for Moran's I, led me to conclude that spatial autocorrelation was unlikely to be an issue in my models.

I used the continental models to predict the *popularity* of PAs worldwide. These predictions were aggregated at the continental and national levels by summing predicted *popularity* of PAs from each region to estimate the wildlife tourism potential provided by a country's PA network.

Preliminary data exploration revealed strong correlations between mammal *attractiveness* and mammal richness ($\tau b = 0.942$, $P < 0.0001$), as well as bird *attractiveness* and bird richness ($\tau b = 0.784$, $P < 0.0001$), within PAs (Appendix Fig. C.2). Given my interest in exploring the role of biodiversity in PA *popularity*, I ran the same models again, but swapped *attractiveness* for richness variables, to determine whether species *attractiveness* explained more variation in PA *popularity* than richness. I used a pseudo-R^2 measure, calculated as the squared correlation between the response and the predicted values, to compare the relative fit of competing models

(Graham, 2003; Street et al., 2017; Zheng and Agresti, 2000). Statistical analyses for this chapter were performed using R Version 3.6.0 (R Development Core Team, 2018).

3.3.3. Model validation

I explored the relationship between mean annual PA visitation rates, and both observed and predicted *popularity*, in order to validate my models and establish whether they could be used to estimate PA visitation worldwide. I produced a database of PA visitor records, using data from Balmford, Green, et al. (2015) and a range of other sources (available at `https://github.com/mairekirkland/thesis_datasets`). I conducted an extensive systematic search for visitor data by inputting the terms "visitor numbers" or "visitation" combined with "protected area", "national park" or "reserve" into general search engines. Where visitor data were referred to but not available online, I contacted relevant stakeholders from governmental and non-governmental agencies, as well as researchers and managers of PA administrations across the world, to request available visitation data. PA visitation data published in the grey literature are often published in national languages, so I searched for data in both English and Spanish, and occasionally had publications translated from other languages, including French, German, and Romanian. Relevant conference proceedings on PA visitation were examined, with a large amount of data originating from the International Conference on Monitoring and Management of Visitor Flows. The wide search method was adopted to minimize publication and language bias.

I collated available visitor data for the period of 1996-2019. Where multiple sources provided different estimates of visitor numbers within the same year, I assessed the quality and accuracy of the estimates (e.g., using information on how they were collected, favouring a peer-reviewed source over the grey literature, identifying obvious outliers/anomalies) and/or identified the exact geographic area for which the estimates were derived and selected the most relevant or reliable estimate. In most cases, however, this was not possible, so an average for that year was calculated instead. I aggregated repeated annual visitor numbers at each PA across all years into a single value of average annual visitation. In total, I obtained visitor numbers for 991 of the PAs in my dataset, from 67 countries/territories (Fig. 3.2).

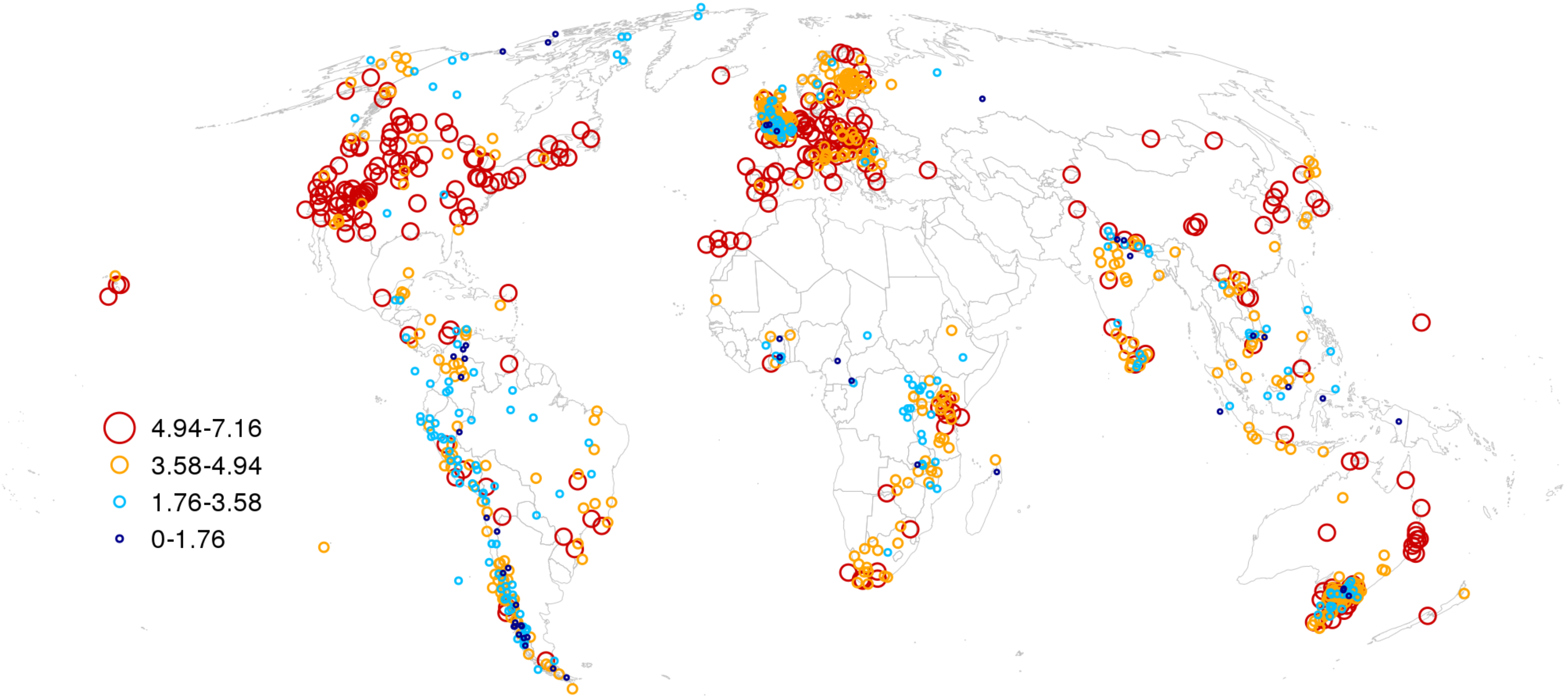

Figure 3.2: Log$_{10}$ annual visitation rates for 991 terrestrial and coastal PAs, obtained from published literature, governmental and non-governmental agencies, researchers, and PA managers. PAs are displayed as circles, the size and colour of which reflect visitation rates. Jenks natural breaks were used to determine break points for the colour and size scale. Jittering was applied to points to aid visualisation.

I then fit linear models using ordinary least squares, in which annual visitation (both visitor numbers and density) was regressed against observed and predicted PA *popularity*, separately. I included an interaction term with the continent in which a PA is located to account for geographic variation in the relationship between the *popularity* indices and visitation statistics. Prior to analysis, each numeric variable was $\log_{10}$-transformed to obtain a normal distribution in the residuals. Likelihood ratio tests on spatial and non-spatial models, in which PA centroid coordinates were used to define different correlation structures, using the ‘nlme’ package in R (Pinheiro et al., 2020), revealed no significant spatial autocorrelation (P = 1).

3.4. RESULTS

3.4.1. Similarity between species lists

PA inventories obtained from online resources were the source of 182,561 bird and 11,735 mammal occurrence records, while range map predictions (i.e., species occurrences predicted by intersecting PA polygons with species range maps) produced 249,387 bird and 14,283 mammal occurrence records for the same subset of PAs. Fifty four percent (n = 134,204) of range map predictions for birds had matching records from PA inventories, and 63% (n = 8,986) of predictions for mammals were confirmed by inventory records. These numbers reflected 74% of bird inventory records and 77% of mammal inventory records falling within the boundaries of range map predictions (see Fig. 3.3 for a visual representation of matching and non-matching occurrence records).

The majority of birds (65%, n = 5,838) and mammals (74%, n = 528) had most of their range map predicted occurrences (> 50%) confirmed by online inventories (Fig. 3.4). However, only 17% (n = 1,490) of birds and 23% (n = 167) of mammals had all of these predictions confirmed by inventories, while 11% (n = 999) of birds and 9% (n = 66) of mammals had no matching inventory records. Most birds (86%, n = 7,723) and mammals (78%, n = 556) also had over half of their inventory records contained within range map predictions, and ∼30% (n = 2,736 birds and 210 mammals) of species had all of these inventory records within range map predictions. Four percent (n = 389) of birds and 9% (n = 65) of mammals had inventory records that fell entirely outside of range map predictions (Fig. 3.4).

Jaccard’s index indicated reasonable similarity between the range map-derived species lists and available species inventories for each inventoried PA, with slightly greater similarity among mammal (J = 0.52, n = 698) than bird (J = 0.45, n = 913) lists. Jaccard’s index was

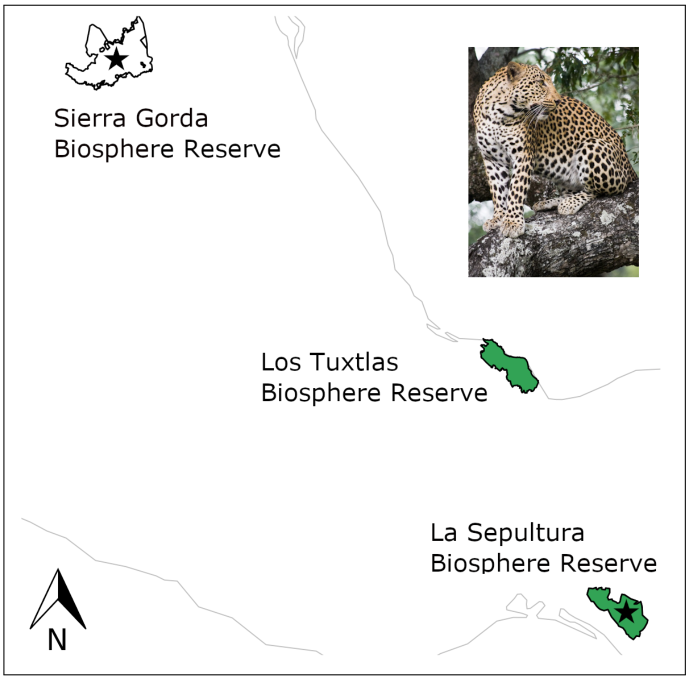

Figure 3.3: A subset of occurrence records for the jaguar *Panthera onca* in large ($>$ 1,000km^2) PAs within part of southern Mexico. PAs coloured in green are those that intersected with species range maps and encompassed suitable habitat and elevation ranges, such that the jaguar *P. onca* was predicted to occur within the PA. Stars represent known occurrence records based on PA inventories. PAs where the jaguar *P. onca* does not occur based on both range map predictions and PA inventories are not shown.

positively correlated with PA size, HDI and political stability, and negatively correlated with local human population density (see Appendix Table C.4).

There was a moderate to high correlation between species *attractiveness* estimates obtained from the two sets of species lists for birds (τb = 0.277, P $<$ 0.0001) and mammals (τb = 0.689, P $<$ 0.0001), respectively (Appendix Fig. C.4). For a large proportion of PAs, predicted *attractiveness* of bird (50%, n = 453) and mammal (47%, n = 329) assemblages was substantially greater than observed *attractiveness* (i.e., *attractiveness* predicted by species range maps was at least 10% greater than *attractiveness* calculated from observed checklists). In contrast, predicted *attractiveness* was substantially lower ($\geq$ 10%) than inventory-derived observed *attractiveness* for 30-35% of PAs (n = 322 birds and 204 mammals). Less than 10% difference in *attractiveness* estimates was considered within normal levels of expected variation.

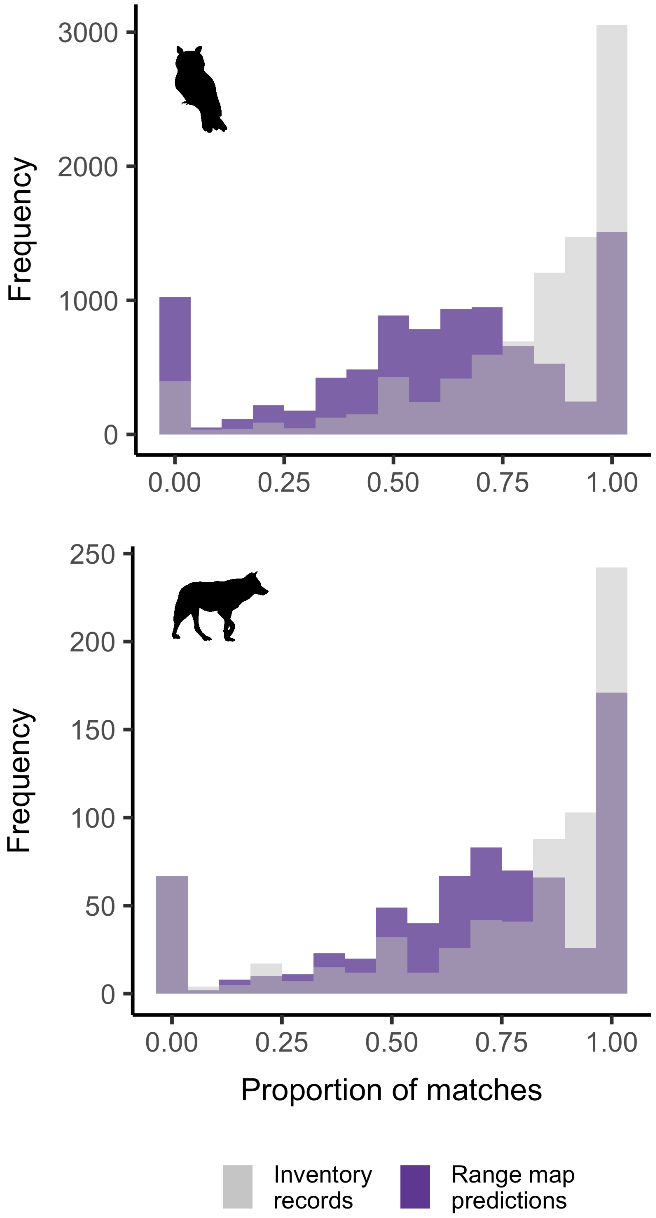

Figure 3.4: Overlap between online inventory and predicted IUCN/BirdLife range map occurrence records, shown as histograms of the proportion of inventory records that fall, for each species, within expert range map predicted boundaries (grey) and the proportion of predicted records based on expert range maps that, for each species, match inventory records (dark purple). The results are shown separately for birds (n = 9,001) and mammals (n = 713).

3.4.2. Raw guidebook data

Sixty-three percent (n = 1,919) of sites mentioned in guides were of PAs listed in the WDPA dataset. Almost half of these (46%, n = 888) were excluded from analysis because they did not meet the requirements discussed in the Methods section. The remaining 1,090 of PAs make up ∼3% of the PAs in the final PA dataset (Fig. 3.5). The mean number of guides a PA was mentioned in (i.e., mean observed PA *popularity*) of those mentioned was 2.54 (SD = 2.86), while 56% (n = 611) of those were only mentioned by one guide. The majority of PAs mentioned in the wildlife tourism literature were from Asia and Africa. Bwindi Impenetrable Forest in Uganda was cited most often by guides, while other African PAs, such as Serengeti National Park in Tanzania, Kruger National Park in South Africa, Etosha National Park in Namibia, and Masai Mara National Parks in Kenya were also *popular*, based on guide citations. *Popular* Asian PAs included Yala National Park in Sri Lanka and the tiger reserves of India. The United States and Costa Rica also had some of the most *popular* PAs, including Yellowstone National Park in the former, and Arenal National Park in the latter. Manu National Park in Peru, Kakadu National Park in Australia, and Doñana National Park in Spain, were among the most *popular* PAs (Fig. 3.5).

3.4.3. Global drivers of PA *popularity*

Twelve predictors in the global binomial model had significant effects on whether the PA was selected by guides or not, and six predictors in the global frequency model showed significant relationships with the number of guides a PA was cited in (Fig. 3.6). The relationships between the variables and PA *popularity* were as follows: PA age, size, national park and international designation, and the proportion of water bodies within a PA all had positive effects on both the probability of a PA being selected by guides and the number of guides a PA was cited in, while IUCN management category, had a negative effect, such that PAs with stricter protection were more *popular* than those with less protection. The variable that exerted the strongest influence in the binomial model (i.e., on whether a PA was selected by the guides or not) was national park designation, and in the frequency model (i.e., the number of guides a PA was mentioned in) it was PA size. Although not influential in the frequency model, the density of tourism amenities and PA remoteness had negative effects on the likelihood of a PA being selected by guides, while political stability had the opposite effect. Likewise, bird *attractiveness* and community rarity had positive effects in the binomial model (Fig. 3.6), but were not influential in the frequency model, whereas mammal *attractiveness* had a relatively strong effect in the frequency model, positively influencing the number of guides a PA was cited in, but not in the binomial model.

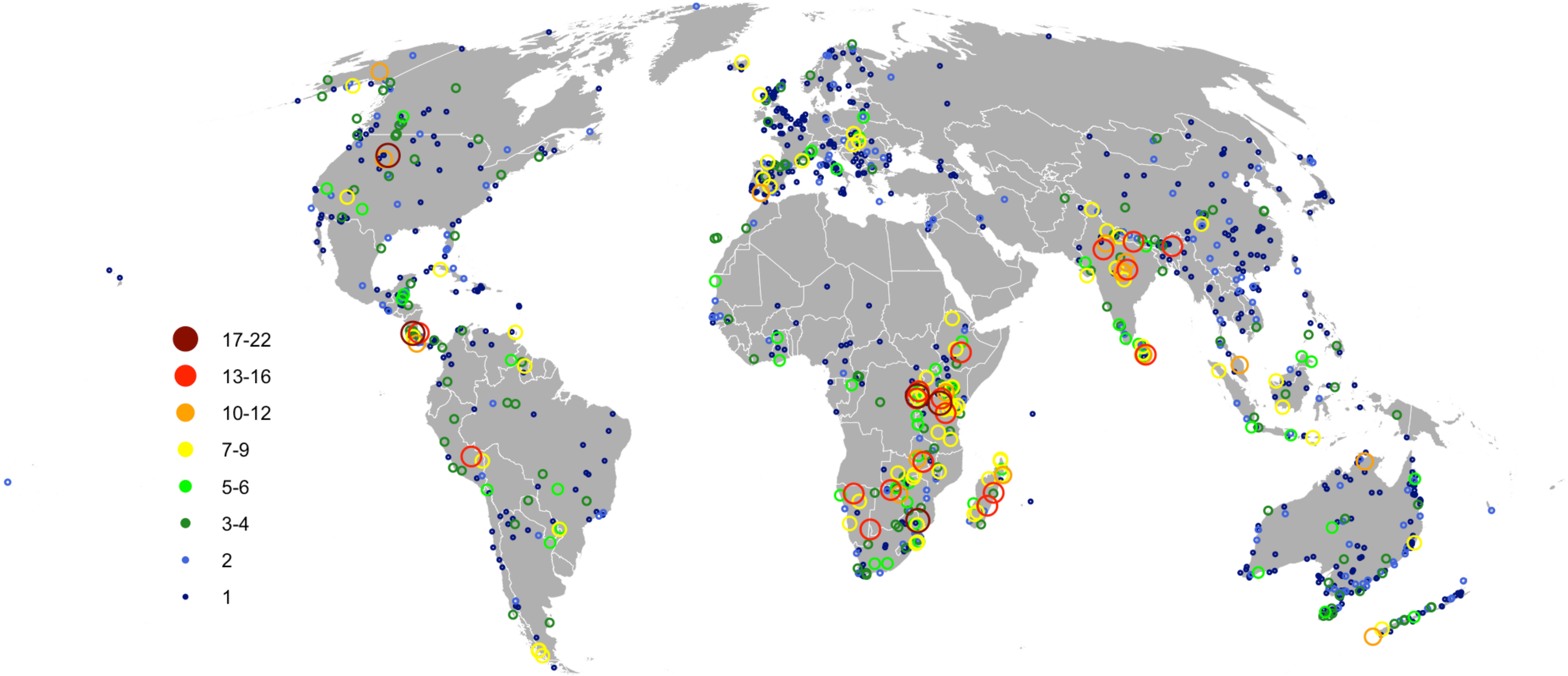

Figure 3.5: The observed *popularity* of PAs, measured as the number of guides a PA was cited in, showing only those PAs mentioned at least once by guides (n = 1,090). PAs are displayed as points to add visualisation, the colour and size of which reflect observed *popularity*. Jenks natural breaks were used to determine break points for the colour and size scale.

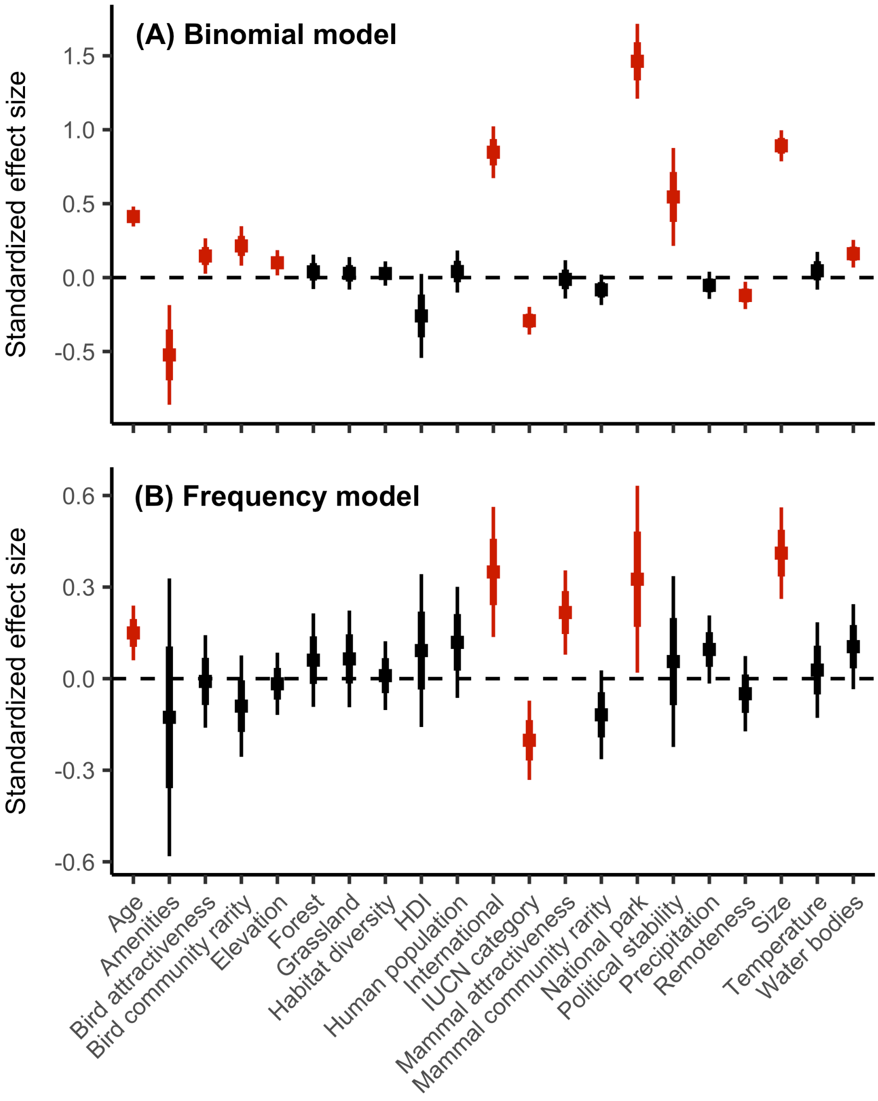

Figure 3.6: Coefficient plot of variables influencing the *popularity* of PAs globally, showing **A** the variables that influence whether a PA is mentioned by a wildlife tourism guide or not (binomial model) and **B** the variables that influence the number of guides a PA is mentioned in (frequency model). Significant variables are shown in red. The centre points denote the coefficient values, the thick bar denotes the standard errors, and the thin bars denote the 95% lower and upper confidence intervals. Coefficient descriptions can be found in Appendix Table. C.5.

3.4.4. Spatial variation in the drivers of PA *popularity*

The binomial models identified relatively consistent effects, across continents, of PA attributes on the probability that a PA was selected by guides (Fig. 3.7A). Their influence at the continental level largely reflected their effects at the global scale, though some variation existed. PA age, size, international and national park designation had positive effects, with the latter having a particularly strong effect, on whether a PA was mentioned or not by guides, reflecting global patterns. IUCN management category had a negative effect on the likelihood of a PA being mentioned by the guides everywhere but in Asia and Oceania. The density of amenities had a negative in the European binomial model, mirroring the negative effect in the global model, but contrasting with the positive effect in the European frequency model (Fig. 3.7B), as well as the positive effect in the American binomial model (Fig. 3.7A). The positive effect of bird *attractiveness* on whether a PA was selected by guides, indicated by the global binomial model, was also present in Africa, Asia and Oceania. The positive effect of global bird community rarity was mirrored by a positive effect at the continental level in the Americas and Africa, while mammal community rarity had a positive effect on whether a PA was selected by guides in the Americas and Europe. The positive effect of the proportion of water bodies on the probability a PA was mentioned by guides, evident at the global scale, was present in Europe, where habitat diversity and grassland cover also had positive effects. In the Americas, grassland cover had a negative effect, as did forest cover. Political stability had a universally positive (though not always significant) effect on the likelihood of a PA being selected by guides, reflecting the relationship identified in the global model. PA remoteness and elevation, though significantly influential in the global binomial model, were not found to be significant in the binomial models of any continent. In contrast, HDI which was not significant in the global binomial model, had a negative effect on whether PAs in the Americas were mentioned by guides. Temperature and precipitation had positive and negative effects on the likelihood of a guide selecting a PA from Asia and Oceania as a wildlife tourism destination, respectively (Fig. 3.7A).

Most of the important variable effects in the global frequency model were reflected in the individual continental frequency models, apart from mammal attractiveness, which had no effect on the number of guides a PA was mentioned in in any continent (Fig. 3.7B). PA size had the strongest and most widespread effect on a PA's *popularity* index, positively influencing the number of guides a PA was mentioned in across all continents, except Europe. IUCN management category had a relatively strong negative effect in Africa, Asia, and Oceania. The only variable, apart from size, to have a significant effect on the number of guides PAs were mentioned in in the Americas was national park designation, which had a strong, positive effect on popularity. PA age had a positive effect in Africa and Europe. The designation of a PA under international legislation had positive effects in Asia and Oceania, where, despite no global effect of these variables, local human population density and proportion of land covered by water also had positive effects on PA *popularity* indices. The rarity of bird communities also had a strong negative effect in this region. By contrast, mammal community rarity had a positive effect in Africa, which was very close to the cut-off for statistical significance (P

= 0.050). Temperature and the density of amenities had positive effects on the number of guides citing PAs in Europe (Fig. 3.7B). The quadratic term for temperature in the Africa model showed that PAs with intermediate temperatures were mentioned by more guides than those at temperature extremes (see Appendix Fig. C.5).

3.4.5. The contribution of species *attractiveness* vs. species richness to PA *popularity*

The global and continental models that contained species *attractiveness*, as opposed to species richness variables, explained more variation in PA *popularity*, reflected in higher pseudo-R^2 values. The increase in fit from using *attractiveness* over richness was marginal in the global model, and more substantial in the continent models. Although explaining less variation in PA *popularity* than *attractiveness*, models including species richness as predictor variables had greater explanatory power than those excluding both variables, apart from in Africa, where models without richness variables had greater explanatory power (Appendix Table C.7).

3.4.6. Geographic patterns of predicted PA *popularity*

Africa had the highest summed PA *popularity* as predicted by the continental models (Fig. 3.8), despite hosting only 4% of PAs in my dataset. Sub-Saharan Africa was identified as a major global hotspot of high *popularity*, particularly East and Southern Africa (Fig. 3.9). Aberdare and Masai Mara National Parks in Kenya, Zahamena and Andringitra National Parks in Madagascar, Serengeti National Park and Selous Game Reserve in Tanzania, Hwange National Park in Zimbabwe, Kafue National Park in Zambia, and Kruger National Park in South Africa are some examples of the PAs contributing to this *popularity* (Appendix Fig. C.6).

Southern and South East Asia also emerged as major hotspots with high predicted PA *popularity* globally (Fig. 3.9). India hosts a particularly large number of highly *popular* PAs (Fig. 3.8), including the Sundarbans and Bandipur National Parks (Appendix Fig. C.7). Nepal, Sri Lanka, Indonesia, and Malaysia were also predicted to have high PA *popularity*, with Chitwan, Ujung Kulon, and Wilpattu National Parks predicted to be among the most *popular* PAs globally. Several PAs in the Middle East, particularly Kirthar and Urumieh Lake National Parks in Pakistan and Iran, respectively, received relatively high predicted *popularity* scores (Appendix Figs. C.7 & C.8). PAs in Oceania, individually, had relatively low *popularity* (Fig. 3.9). Fiordland National Park in New Zealand was an exception, receiving one of the

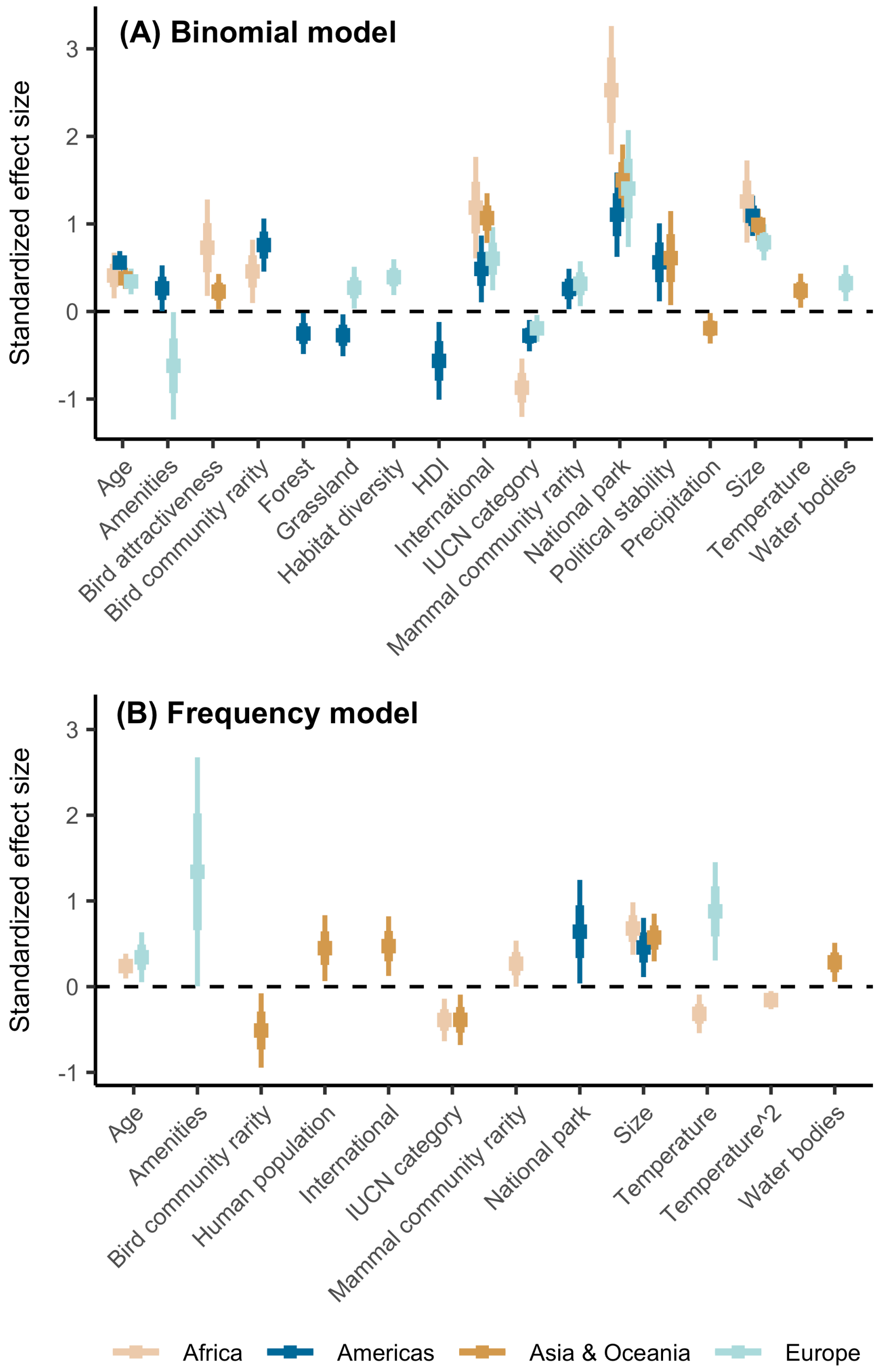

Figure 3.7: Coefficient plots of significant variables (i.e., using P $\leq$ 0.050 as the cut-off) influencing the *popularity* of PAs across continents, shown separately for Africa (n = 1,871), the Americas (n = 11,925), Asia and Oceania (n = 10,637), and Europe (n = 17,333). **A** shows their effects on the likelihood of a PA being selected by at least one guide (binomial model) and **B** shows their effects on the number of guides a PA was cited in (frequency model). The centre points denote the coefficient values, the thick bar denotes the standard errors, and the thin bars denote the 95% lower and upper confidence intervals. Coefficient descriptions, including for non-significant variables, can be found in Appendix Table C.6.

highest predicted *popularity* scores (Appendix Fig. C.8). The large number of relatively *popular* PAs in Australia also contributed to high summed *popularity* at the national level (Fig. 3.8).

Manu National Park was predicted to be one of the most *popular* PAs globally (Fig. 3.9), along with other PAs in the Peruvian Amazon, such as Bahuaja-Sonene and Alto Purú National Parks (Appendix Fig. C.9). Patagonian PAs, such as Bernardo O'Higgins National Park in Chile and Nahuel Huapi National Park in Argentina, also emerged as having high predicted *popularity* (Appendix Fig. C.9). Some of the more *popular* PAs globally were located in the United States and Costa Rica, including, again, Yellowstone, as well as Glacier Bay and Denali National Parks, located in the former, and Braulio Carrillo and Tortuguero National Parks and La Amistad International Park, located in the latter (Appendix Fig. C.10).

Spain emerged as having high summed predicted PA *popularity* globally (Fig. 3.8), hosting a number of *popular* PAs located in the Canary Islands, as well as the highly *popular* Doñana National Park (Appendix Fig. C.11). France and Italy also host relatively *popular* PAs, including the Pyrenees National Park, located in the former, and Gargano National Park, in the latter. PAs in Eastern Europe, such as Hortobágy and Kiskunsági National Parks in Hungary and Tatransky National Park in Slovakia, received relatively high predicted *popularity* across Europe, as did those in Scandinavia, such as Øvre Anárjohka National Park in Norway (Appendix Fig. C.11).

3.4.7. Validating tourism literature data

Of the PAs for which I sourced visitor data, 46% (n = 452) had only one estimate of annual visitor numbers since 1996. A total of 5,940 annual visitor observations were obtained, equating to ∼267 million visits a year. On average, each PA received 270,112 (SD = 871,896) visitors annually, but visitor numbers differed widely between PAs. The most heavily visited PA in the dataset was Golden Gate National Recreation Area, US, with an estimated ∼14 million visitors a year. Twenty four PAs apparently received no visitors in the years monitored: 16 in Chile, two in Colombia, two in Cameroon, one in Peru, one in the United Kingdom, one in Russia, and one in Zambia. Thirty three percent (n = 326) of PAs with visitor data were selected by at least one of the reviewed guides, and were therefore assigned an observed *popularity* index greater than zero.

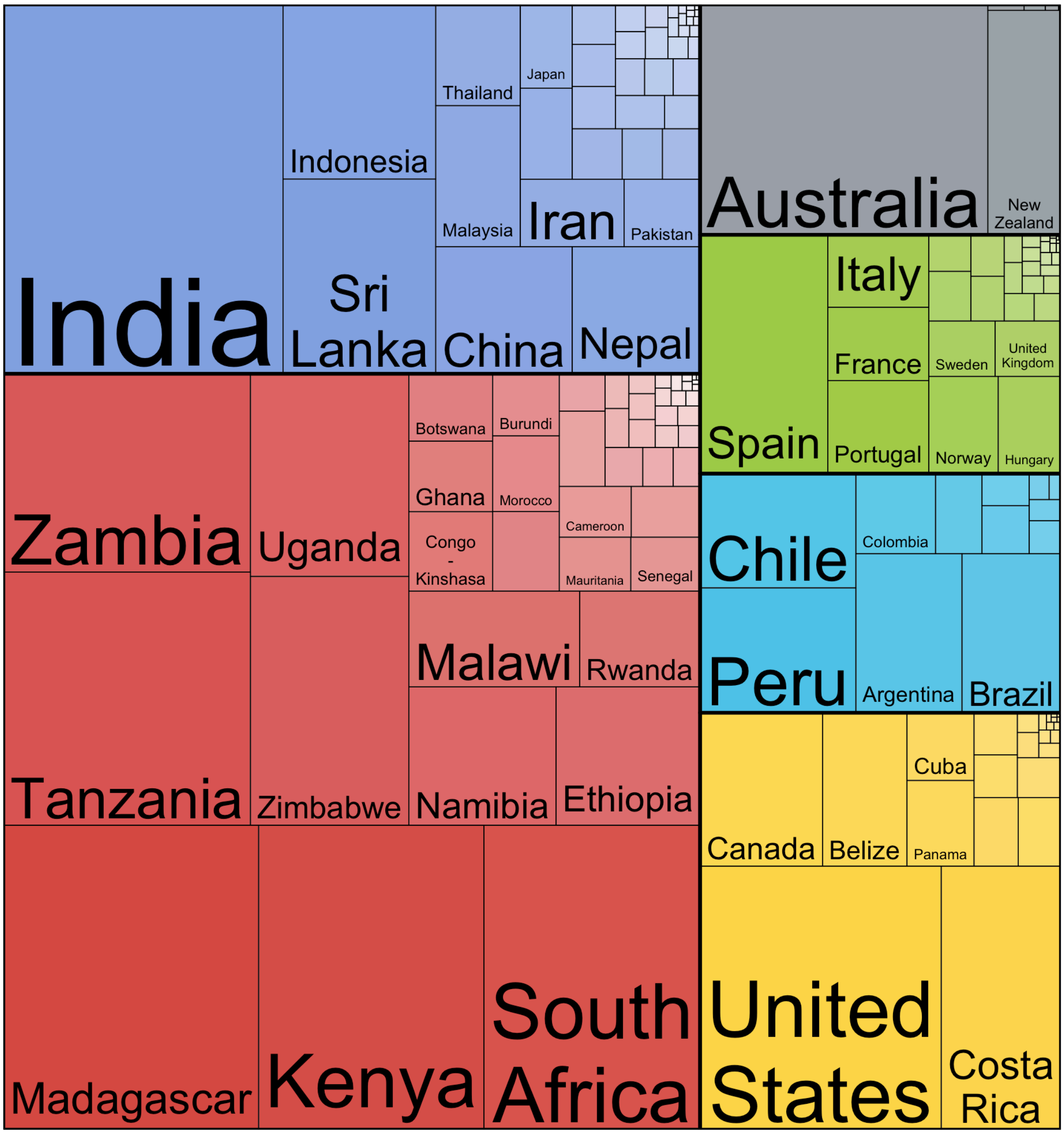

Figure 3.8: Summed PA *popularity*, calculated by predicting the *popularity* (i.e., citation frequency in wildlife tourism guides) of all PAs using continental hurdle GLMMs, and then aggregating *popularity* by countries and continents. The size of each section is proportional to the ranked predicted *popularity* of all PAs within each country and continent.

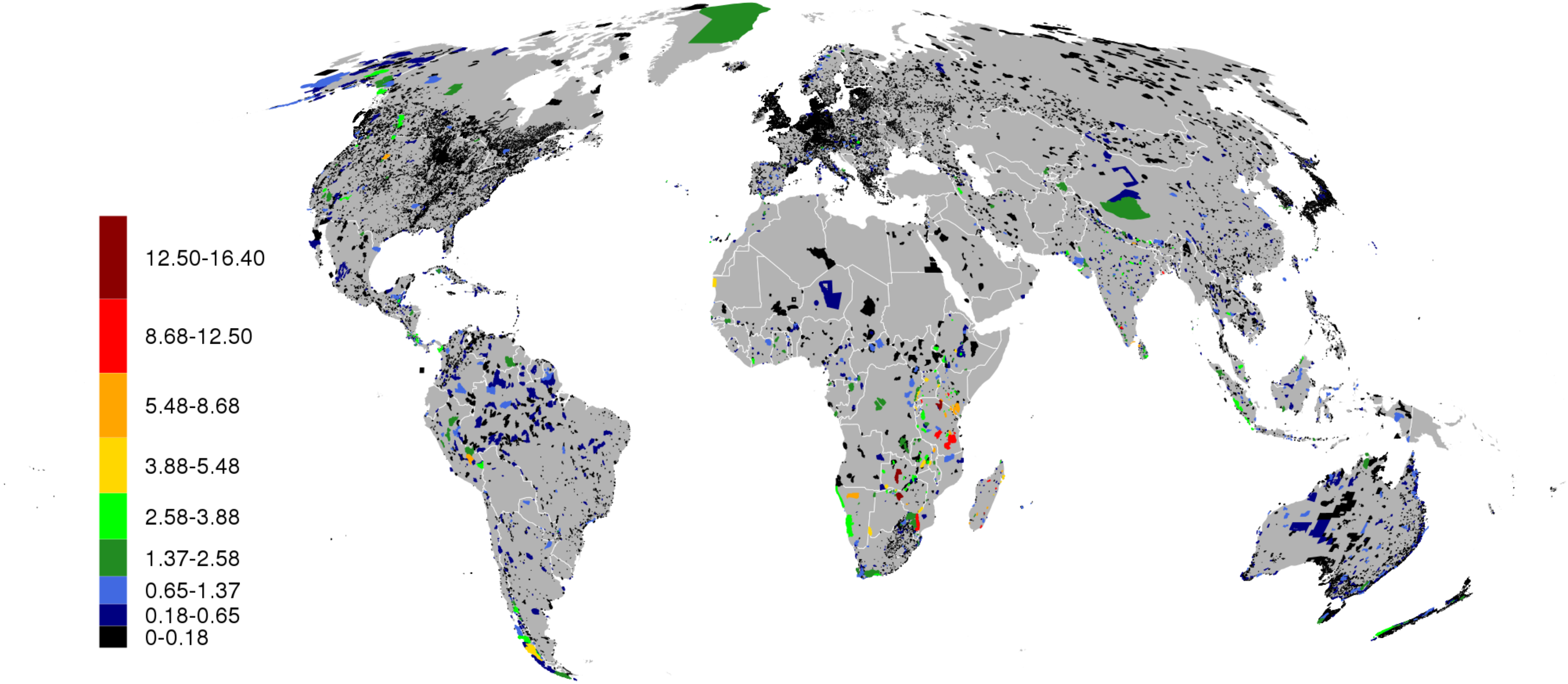

Figure 3.9: The predicted *popularity* of PAs globally. PA *popularity*, as determined by citation frequency by wildlife tourism guides, was predicted separately for each continent/region (Africa, Asia and Oceania, Europe, the Americas) using hurdle GLMMs. Jenks natural breaks were used to determine break points for the colour scale. Zoomed in views of different regions are shown in Appendix Figs. C.6-C.11.

Examination of visitor data using linear models revealed significant positive relationships between visitation rates and both observed ($\beta = 1.60$, 95% CI = 1.0-2.19, P < 0.001, Fig. 3.10A) and predicted PA *popularity* ($\beta = 0.56$, 95% CI = 0.23-0.88, P = 0.001, Fig. 3.10B) globally. Overall, visitation rates tended to be higher in the Europe, Oceania, and North America (Fig. 3.10). The relationship between observed PA *popularity* and visitation rates was strongest in South America, followed by Europe and Africa, where relationships were significantly stronger than in North America (Tukey's-adjusted P ≤ 0.021, Appendix Fig. C.12). Africa exhibited the strongest relationship between predicted *popularity* and visitation rates, followed by Oceania, North America, and Europe, and a weak to no relationship was observed in Asia, but the differences in these relationships between continents were not significant (Tukey-adjusted P ≥ 0.177, Appendix Fig. C.12). The models explaining visitation as a product of either observed or predicted PA *popularity* and the continent in which a PA occurred had moderate explanatory power, with an R^2 of 0.25 each. There was no significant relationship between PA *popularity* and visitor density, calculated as the number of visitors divided by the area of land covered by the PA (P ≥ 0.078).

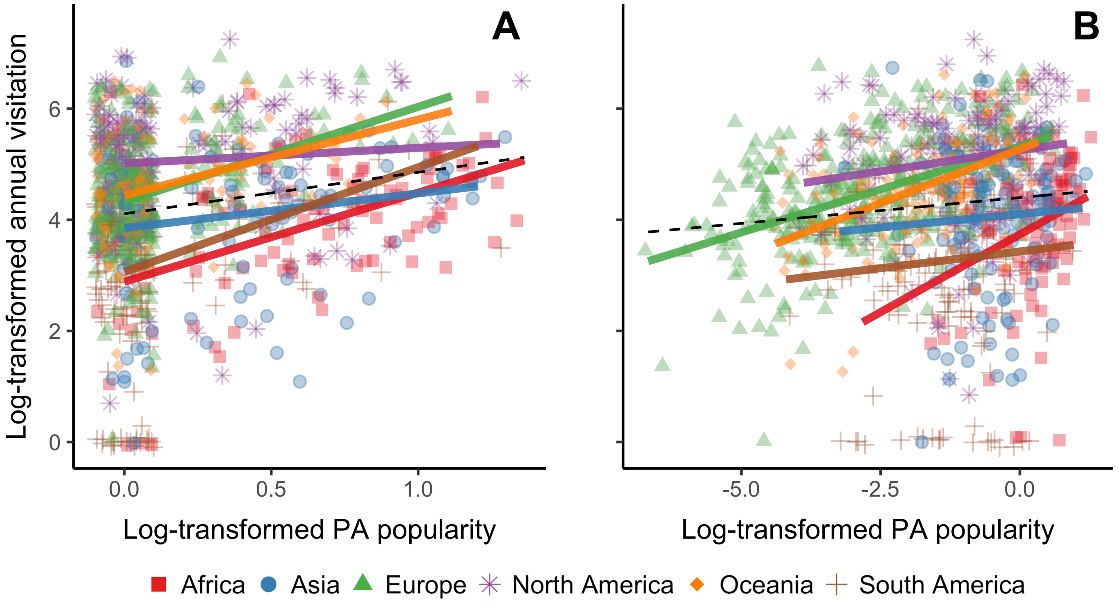

Figure 3.10: Log$_{10}$-transformed PA *popularity* and mean annual visitation rates (n = 991), showing **A** observed *popularity* as determined by raw guidebook data and **B** predicted *popularity* based on continental models. Points are jittered along the x-axis and show individual PAs, the colour and shape of which reflect the continent in which they are located. The black dashed line depicts the regression slope from linear models across all PAs globally and the coloured lines reflect trends within each continent

3.5. DISCUSSION

As the demand for nature-related tourism in PAs grows worldwide (Balmford, Beresford, et al., 2009), understanding patterns of popularity and causes of variation (and potential vulnerability to tourism) is crucial to inform management and marketing strategies. To date, PA visitation and survey data regarding human use of PAs, particularly with respect to wildlife tourism, is limited, unreliable, and/or patchy (Balmford, Green, et al., 2015). I proposed and applied a novel modelling approach that uses wildlife tourism literature to derive a proxy for PA *popularity*, focussing on larger ($> 1\text{km}^2$) terrestrial and coastal PAs. I found that data from wildlife tourism literature represents a novel global information source on the likely popularity of PAs. The positive relationship between my PA *popularity* index and visitation data suggests that wildlife tourism literature provides a robust proxy for assessing direct use values, in this case the value of wildlife tourism, associated with PAs at a global scale.

3.5.1. The role of biodiversity in wildlife tourism

Amid growing debate regarding the role of tourism in conservation (Krüger, 2005; Lindsey, Alexander, et al., 2007), my results demonstrate that biodiversity is a central – though not exclusive – element of wildlife tourism in PAs. Crucially, while previous studies have found contrasting evidence for the role of biodiversity in influencing visitation (Chung et al., 2018; Hausmann, Toivonen, Fink, et al., 2019; Siikamäki et al., 2015; Winterbach et al., 2015), my study is the first to demonstrate that species *attractiveness* underpins wildlife tourism across the global network of terrestrial and coastal PAs. Marginal differences in model fit at the global level suggest that *attractiveness* may be most relevant in determining wildlife tourism patterns at the continental scale. However, competing models found that in Africa and Asia (see Appendix Table C.7), species richness may be strongly associated with wildlife tourism patterns, indicating that broader biodiversity, including less charismatic species, may also be important (Hausmann, Toivonen, Slotow, et al., 2017). Mine is also the first study to show that tourists are more interested in seeing wildlife communities that are regionally and/or globally rare. The results indicate that management strategy matters as well – PAs managed under stricter protection, which are associated with higher biodiversity (Gray, Hill, et al., 2016), were more *popular* than those managed under less strict protection. At least in Europe, habitat-level diversity seems also to be important. The observed connections between different components of biodiversity values and PA *popularity* confirms the direct linkage between conservation and the provisioning of ES such as wildlife tourism and suggests that managing PAs for both biodiversity and wildlife tourism simultaneously is possible (as long as appropriate conservation strategies are employed) (Balmford, Green, et al., 2015).

The paucity of species inventories means that range maps currently provide the best method for deriving species lists at a global scale. Nevertheless, the attributes derived from my putative species lists will likely contain some inaccuracies and biases that are worth keeping in mind. I attempted to improve predictions from range maps using information on species' habitat and altitudinal requirements, but predicted species lists were still only $\sim$50% similar to observed species checklists. PA species lists were most similar in larger PAs in less densely populated and more politically stable areas. This may be because i) larger PAs encompass more of a species' suitable habitat; ii) PAs and species in more stable regions are better studied; and iii) PAs in less densely populated regions may be at lower threat from hunting and invasive species, such that range maps may be less likely to falsely predict the presence of a species (Cantú-Salazar and Gaston, 2013). The *OpenStreetMap* (2020) data, used to calculate the density of amenities in PAs, may suffer from similar biases, potentially being more accurate in more accessible, wealthier regions, but testing this explicitly was beyond the scope of my study (Bright et al., 2018).

There may also have been inconsistencies in the alignment and coverage of some geographical range maps and the coastlines of the base land maps, which could account for inaccuracies in the species lists of island and coastal PAs (Ridgely et al., 2007). Additional errors in PA species lists may have originated from the use of coarse land cover data, which are unlikely to reflect the nuanced habitat requirements of specialist species (Bellamy et al., 2020). I was also unable to consider factors such as the minimum home range requirements for species or the requirements of a sustainable viable population in a PA, such that PAs may have been too small to support some species (Santini, Boitani, et al., 2016). In line with the notion that range maps contain a relatively high degree of false presences and would therefore over-estimate species richness (Jetz, McGeoch, et al., 2019), range map derived lists more often over-estimated the *attractiveness* of PAs' species assemblages.

Despite these issues, significant correlations between species *attractiveness* derived from range maps and species inventories suggest that my predicted species lists can be used to derive reliable proxies of species diversity measures. Moreover, discrepancies between species lists may also have arisen from the incomplete nature of many checklists (Sorte and Somveille, 2019). Alongside the continuous update and improvement of species range maps (Ficetola et al., 2014), greater investment is needed to obtain up-to-date and complete PA checklists, including through the use of citizen science (e.g., `www.eBird.org` and `www.GBIF.com`).

3.5.2. PA attributes driving variation in *popularity*

The results of this study show that the PAs that are the most frequently cited destinations in the wildlife tourism literature are those that have more *attractive* and rare species assemblages, a wider elevational range and higher availability of water sources. They are also older, larger, more accessible, managed under stricter IUCN categories, have been designated national parks, protected under international legislation, have lower densities of amenities (e.g., accommodation, transport), and are located in more politically stable countries. Although age was treated as a nuisance variable, it is worth mentioning that its positive effect on PA citations could partially reflect the greater popularity of older PAs uncovered by other researchers (Balmford, Green, et al., 2015; Chung et al., 2018). While the above findings are generally consistent with our current understanding of what factors influence wildlife tourists' decision-making, certain variables had unexpected effects on PA *popularity*, and are therefore discussed in more detail below.

Contrasting the findings of other studies that human use of PAs is greater in those with greater amenities (Hausmann, Toivonen, Fink, et al., 2019; Schägner, Brander, et al., 2016), my models identified a negative effect of tourism amenities on the likelihood a PA was selected by guides as a wildlife tourism destination, both at the global level and in Europe. The unexpected result from my study could reflect the fact that PAs in less developed areas, especially in Europe, conjure up greater perceptions of nature and ´wildness', and therefore may be higher up on people's destination 'wishlist' for wildlife watching. Little is known about the effect of 'sense of place' (i.e., sense of connection with nature) (Hausmann, Slotow, Burns, et al., 2016) on visitor numbers, but it can be assumed that human-made structures may reduce the attractiveness of a PA to tourists interested in experiencing nature and viewing wildlife (Tverijonaite et al., 2019). Yet among European PAs selected by guides, those with greater densities of amenities were mentioned in more guides. Interpreted together, these findings could suggest that PAs with greater amenities are less likely to be selected as destinations for wildlife watching, perhaps because of a degraded 'wilderness' experience, but of those that are selected, PAs with more amenities may be more heavily visited because they can support more visitors and/or enhance wildlife viewing activities (e.g., bird hides). Unlike in Europe, in the Americas, PAs with greater amenities were more likely to be selected by guides. This could perhaps reflect the importance of amenities and infrastructure in the relatively difficult to access tropical forests of South America, where dense vegetation also reduces visibility for wildlife watching, and where destinations, even those with some level of tourism development, may still be perceived as ‘wild’, compared to places such as Europe.

Other effects observed in the Americas contradict past findings (Chung et al., 2018; Hausmann, Toivonen, Fink, et al., 2019). Firstly, PAs in less developed regions were less likely to be selected by wildlife tourism guides. Again, differences between studies could have arisen because, whereas the majority have looked at PA visitation, in terms of actual footfall, I explored *popularity* within a global ‘bucket-list’ of places people would like to visit to watch wildlife. PAs in richer countries, like the United States, may therefore be more heavily visited due to a larger local human population that can afford to travel and recreate (Balmford, Green, et al., 2015; Chung et al., 2018; Heagney et al., 2018), but those in the ‘exotic’, megadiverse, but relatively under-developed, countries of Latin American, may be higher up on people’s ‘travel wishlist’. Secondly, PAs with lower grassland and forest cover less likely to be selected by guides than those with greater cover. PAs with lower forest cover, where wildlife is likely easier to observe, were expected to be more popular, but grassland cover was expected to increase PA popularity for the same reason (Arbieu, Grünewald, Schleuning, et al., 2017). My finding might reflect the appeal of mountainous or coastal PAs, such as Los Glaciares National Park in Argentina and Kenai Fjords National Park in the United States, where vegetation cover is low, offering good visibility of wildlife, as well as aesthetic views and recreational opportunities such as hiking and mountaineering (Pearce, Strickland-Munro, et al., 2016). Or, it could reflect tourists’ preferences for habitat types not included in this study. For instance, Emas National Park, located in the Pantanal region of Brazil, one of the prime wildlife tourism destinations in South America, is predominantly covered by shrubland, which may represent an optimal habitat for wildlife watching, whereby too little vegetation may be seen as less aesthetically appealing, but too much may impede wildlife watching (Arbieu, Grünewald, Schleuning, et al., 2017).

The last unanticipated finding was that bird community rarity across Asia and Oceania had a negative effect on PA popularity, contradicting patterns observed elsewhere. The underlying reasons are unclear, but spatial patterns of rarity in this part of the world suggest that PAs with rare bird communities may be less accessible and/or occur in less stable areas, such as the Australian outback, the New Guinea Highlands, and Kamchatka in Russia, than those with more common communities (see Appendix Fig. C.13).

The different effects of temperature on PA *popularity* are also worth discussing in more detail.

In Eurasia and Oceania, temperature had a positive effect on PA *popularity*, but in Africa, it had a quadratic effect, whereby medium values of 15-16°C were found to be optimal. This may have to do with consistently high temperatures in Africa, where annual temperatures across PAs are on average of $\sim$20°C, so medium temperatures may be perceived as more comfortable for tourism activities in this continent. Lower average temperatures of 8-13°C in Eurasia and Oceania probably means that relatively warm temperatures are perceived as more pleasant.

3.5.3. Spatial patterns in PA *popularity* and visitation

East and Southern Africa, Southern and South East Asia (particularly India), the western United States, Costa Rica, the Peruvian Amazon, Patagonia, the Iberian Peninsula, and Eastern Europe are home to many of the most *popular* PAs globally. Despite biases in the geographic distribution of the visitation data, PA *popularity* determined using wildlife tourism literature corresponds well with the available empirical information about where people go, and some of the most *popular* PAs highlighted in this study are already well-known and *popular* wildlife tourism destinations receiving many visitors. Tanzania, for example, has a rapidly growing tourism industry, with international arrivals increasing from $\sim$500,000 in 2000 to $>$ 1.5 million in 2018 (Melubo, 2019), which can be largely attributed to a few of its most renowned PAs, including those of the Serengeti-Ngorongoro ecosystem, which generates over US\$100 million a year from e.g., park entrance fees, hunting licences, lodge fees, overnight fees (Hopcraft et al., 2015). The tiger reserves of India are also highly regarded destinations for wildlife tourism, with visitation growing from 1.7 million in 2004-2005 to 4.6 million in 2014-2015 (171% growth) and tourism now contributing as much as $\sim$US\$3.2 million in Ranthambore National Park (Karanth, Jain, et al., 2017; Karanth and DeFries, 2011). However, such numbers pale in comparison to the value of the US National Park System, where visitation reached $>$ 300 million visits in 2019 (U.S. NPS, 2019). Yellowstone National Park is among the most heavily visited, with four million visitors spending an estimated \$507 million in gateway regions and communities.

The discrepancies between visitor numbers and *popularity*, particularly where visitation appears to be falling short, point to an important finding of this research, which is that some PAs may be under-performing as wildlife tourism destinations. Mount Elgon National Park, in Uganda, is a good example of this, receiving only $\sim$2,000 visitors annually, but highlighted as one of the top PAs with the highest predicted *popularity* globally (ranking at #37). The relatively low visitation in Africa, South America, and Asia could reflect the significant scope for tourism growth in these regions. Their remoteness from the major source countries of international tourists i.e., Australia, Europe, United States, and Canada (UNWTO, 2019), whereby long-haul flights and large travel budgets are required to reach them, could be a particularly important factor contributing to low visitation rates.

Of course, discrepancies between PA *popularity* measures and visitation will have arisen from focus of this study on wildlife tourism – many tourists will visit PAs for non-wildlife related attractions, such as landscape attractiveness, archaeological sites, national monuments, hiking or climbing opportunities. For example, the Lake District in the UK, and the Golden Gate National Recreation Area in the US, which were only mentioned in one guide, were among the most heavily-visited PAs, which indicates that large numbers of people may be visiting the sites for their landscape and cultural attractions.

The weaker correlation between PA visitation and *popularity* in some regions, such as Asia and North America, could reflect the biases in the wildlife tourism resources used in this study, which as discussed in Chapter 2, were directed mostly towards source markets in Western or English-speaking countries. Tourists originating from elsewhere, including emerging countries such as China, which make up a significant portion of domestic wildlife tourists, as well as international wildlife tourists visiting e.g., the US, may have different preferences and motivations to those captured in this study (Cong et al., 2017; Thomsen and Tenney, 2019). The inclusion of additional resources, particularly those aimed at emerging economies, would provide information on the preferences of a wider subset of tourists and could improve the predictive accuracy the methodology adopted in this study.

3.5.4. PA management and policy implications

The global maps of PA *popularity* produced in this study could contribute to the achievement of the Aichi Target 2, which aims at "*reflecting the values of biodiversity in spatial planning and resource management exercises, including through the mapping of biodiversity and related ecosystem services*" (CBD, 2018). In doing so, these maps could be part of an efficient resource allocation process whereby governments and investors are better informed to prioritize PAs with high tourism potential, thereby preserving and capitalising on this important cultural ES.

The findings regarding those features that influence PA *popularity* can inform the designation, design, and marketing of PAs to enhance their appeal or publicity to tourists. For instance, the importance of *attractive* species assemblages suggests that managers could encourage visitation to PAs by conserving and promoting key species that are *attractive* to tourists. Visitation might also be increased by expanding or designating larger PAs, simultaneously contributing to the achievement of Aichi Target 11, which sets out goals for "*expanding protected area networks and other effective area based conservation measures*" (CBD, 2018). Improving the accessibility of hard-to-reach ecosystems/species could also attract more visitors. Governments worldwide should promote stability and peace, which would address important safety concerns among tourists, but managers could reduce the susceptibility of tourism localities to *perceived* political unrest by encouraging domestic tourism. The results of the continental models indicate that management actions may need to be tailored to different regions: increasing tourism facilities, such as accommodation or wildlife viewing structures, as is already occurring through the development of e.g., rainforest canopy walkways, may draw tourists to PAs in the Americas, and managers in Europe may be able to increase visitation by conserving habitat diversity and water sources. The results can be used to tailor tourism marketing and promote wildlife tourism in sites that lack the traditional charismatic species, originally considered to have limited wildlife tourism potential, by focusing on other characteristics that attract tourists (Lindsey, Alexander, et al., 2007). Alongside management efforts, foreign visitors, who may be less familiar with PAs than domestic visitors, may benefit from new or increased information dissemination.

Success within the competitive tourism market comes with its own challenges. The funnelling of visitors towards a few of the best-known PAs, such as Yellowstone in the United States, means that over-crowding is becoming a pervasive problem that is causing environmental degradation and disturbance, including erosion, pollution, and congestion (Timmons, 2019). Furthermore, some of the management implications of this study, like developing amenities and improving access to PAs, could generate negative environmental impacts, including via congestion and over-crowding and increased encroachment by poachers, at the same time damaging the natural beauty and perceptions of wildness (Kanwal et al., 2020), and could take money away from conservation. The most popular PAs should be a priority for management and monitoring actions aimed at minimizing human pressure (Buckley, 2002; Klanjšček et al., 2018). De-marketing may be required to reduce demand and control visitation if visitor numbers become unsustainable (Armstrong and Kern, 2011), deflecting tourism pressure towards under-utilised sites, or encouraging visitation by more specialist tourists, who are thought to be more environmentally friendly (Buckley, 2013; Hausmann, Toivonen, Slotow, et al., 2017). Infrastructure development, although potentially exacerbating pressure on the environment, could help manage visitor flows. Visitor centres or kiosks, restrictions, including advance booking systems, timed entry systems, entry quotas, permits, and limits on group size, can be put in place to limit the number of people entering (or equally lifted to encourage visitation) (Leung et al., 2018).

The above examples highlight concerns over using ‘conservation for tourism’ and not ‘tourism to support conservation’ (Hausmann, Slotow, Burns, et al., 2016). The link between vegetation and *popularity* also raises such concerns. There was some evidence that open or low vegetation cover may be preferred by tourists visiting PAs, which may optimise tourists’ chances of spotting wildlife (Arbieu, Grünewald, Schleuning, et al., 2017). However, managing for such habitats, where the natural habitat consists of more dense vegetation, will likely lead to the degradation of the habitat. Natural vegetation is also considered an important part of the PA’s scenery (Grünewald et al., 2016), such that creating artificially open habitats may not be advisable for tourism purposes either.

3.6. CONCLUSION

I provide new insights into global patterns of wildlife tourism across the world’s larger terrestrial and coastal PAs by quantifying *popularity* among generalist, Western and/or English-speaking tourists, based on information obtained from wildlife tourism literature. My models predicted visitor numbers with reasonable accuracy, suggesting that wildlife tourism literature can serve as a proxy for human use of PAs, which could supplement technological advancements such as remote sensing and social media data in helping to assess global PA visitation (Hausmann, Toivonen, Fink, et al., 2019; Hausmann, Toivonen, Slotow, et al., 2017). The results of this study can inform the prioritisation of investment and management efforts aimed at promoting opportunities to support biodiversity conservation and poverty alleviation through wildlife tourism. I found that PAs with high biodiversity value, and in less developed regions, were *popular* for wildlife tourism, which may provide necessary funding for conservation, bring jobs to local communities, generate government revenues, and create new markets for goods and services in regions where they are arguably most needed. PAs in East and Southern Africa, Southern and South East Asia, Costa Rica, the Peruvian Amazon, Patagonia, the Iberian Peninsula, Eastern Europe, and the western United States were predicted to be the most *popular* globally. However, any management action (e.g., land acquisition, infrastructure development) designed to encourage visitation may be limited by funding (Jackson and Gaston, 2008; Khadaroo and Seetanah, 2008), and may also produce unwanted negative environmental effects (Buckley, 2011). Wildlife tourism enterprises must therefore strike a balance between satisfying tourist demand and minimising the stress and disturbance caused to the environment.

The supply of recreational services is not the main purpose of PAs, but should instead be considered a co-benefit that can provide economic justification for PA creation and conservation through tourism expenditure and investment.

Chapter 4

Climate Change Impacts on Global Wildlife Tourism

4.1. ABSTRACT

The past two decades have seen substantial research into climate change impacts on tourism. Yet research has been focussed largely on the direct impacts of changing temperatures. Little attention has been paid to how changes in species' ranges, as species attempt to stay within climatically favourable conditions, will influence destination attractiveness for wildlife tourism. Here, I highlight areas around the world where wildlife tourism operations may be most at risk from climate-induced species range shifts, and therefore most in need of urgent intervention, as well as areas that may potentially benefit from these range shifts. I use ensemble species distribution models to assess the potential impact of climate change on the ranges of the world's birds (n = 8,275) and non-volant terrestrial mammals (n = 2,869), taking into account uncertainty in climate models and species dispersal. Combining these models with the data from wildlife tourism literature collated for Chapter 2, I explore changes in range extent for those species most frequently cited as tourism attractions, and summarize predicted changes in the *attractiveness* of species assemblages across the Earth's land mass. The main wildlife tourism hotspots where summed predicted *attractiveness* is projected to decline include East Africa and the tropical forests of South America. The high dependence of these regions on wildlife tourism, coupled with a lowered adaptive capacity, makes them particularly vulnerable to climate-induced species range shifts. In contrast, the tropical Andes, the Himalayas, the Pampas region of South America, the montane regions of Africa, and the Central Asian mountains were projected to increase in summed species *attractiveness*. Managers and local communities need to anticipate and plan for negative climate change impacts on wildlife tourism, and may be able to exploit novel opportunities, created by the emergence or loss of attractive species.

4.2. INTRODUCTION

Tourism, especially that which relies on natural attractions, is inherently dependent on climatic conditions, and is therefore considered to be highly sensitive to the impacts of anthropogenic climate change. These impacts can be direct (e.g., more variable or extreme weather, 'better' weather, flooding, snow cover change) or indirect, through effects on natural and human resources (e.g., changing species' distributions/abundances, reduced landscape aesthetics, damage to tourism infrastructure). They can influence the seasonality of tourism, tourists' selection of destinations, available tourist activities and attractions, and/or the overall satisfaction of a vacation. Given that wildlife is a key tourism asset (Lindsey, Alexander, et al., 2007; Okello et al., 2008; Willemen et al., 2015), and a primary response of species to climate change is to shift their ranges to track preferred climatic conditions (Pecl et al., 2017), climate change is likely to greatly alter the relative attractiveness of species assemblages for wildlife tourism localities, and hence long-term viability of wildlife tourism businesses. The redistribution of species around the world, as with other climate change impacts, will likely create 'winners' and 'losers', with sites becoming more or less attractive to tourists due to the emergence or loss of attractive species. The capacity for wildlife tourism to help countries meet internationally agreed conservation and sustainable development targets requires that the sector adapts to the negative impacts of climate change and exploits any novel opportunities that arise. In order to anticipate, plan for, and proactively influence visitation, a thorough understanding of the potential changes in tourism potential based on projected species range shifts is crucial.

Over recent decades, a growing body of research has revealed important insights into the relationship between the climate and tourism, and how climate change might impact future visitation patterns. For instance, Fisichelli et al. (2015) explored visitation to US national parks by relating historical visitor data to temperature, and found that warming temperatures would lead to increased visitation for most parks. Pröbstl-Haider et al. (2015) explored summer tourism in the Alps using questionnaires to investigate possible behavioural changes of tourists, and found that more comfortable temperatures and more days of sunshine would increase tourist numbers. Richardson and Loomis (2004) used visitor surveys to predict changes in visitation to Rocky Mountain National Park, US, and discovered that increasing temperatures could lead to an increase in visitation, while changes to elk *Cervus elaphus* populations would have no effect. Scott, Jones, et al. (2007) adopted a combined approach, and concluded that in the short-term, warming temperatures and a lengthening of the warm-weather season would increase visitation to Waterton Lakes National Park, Canada. In the longer-term, they predicted that the indirect effects of climate change on the natural resources, including mammal populations and glacial retreat, would ultimately lead to a decrease in visitation (Scott, Jones, et al., 2007). Meanwhile, Uyarra et al. (2005) found that tourists were unwilling to return to Bonaire and Barbados for the same holiday price in the event of coral bleaching and loss of beach area, respectively.

The majority of studies conducted so far have focussed on the direct role of a few climatic variables, predominantly temperature, on tourism patterns, while few studies have considered the indirect impacts on wildlife resources. The analysis of Chapter 2 revealed that some species are more *attractive* for wildlife tourism than others, as indicated by the frequency of citations of species in wildlife tourism guides, due to factors that relate to their aesthetic appeal, as well as their visibility and accessibility, and perhaps familiarity. Thus, predicted shifts in species' ranges represent a significant concern for tourism business that are highly dependent on the predictable occurrence of attractive species. The loss of attractive species from a site could reduce and eventually eliminate a key tourist attraction, potentially reducing tourist satisfaction and eventually tourist numbers, as people switch to more attractive destinations, leading to significant financial losses. Uncertainty in wildlife tourism as an economic venture poses a threat to the many protected areas (PAs) and gateway communities living alongside them that depend on this industry (Buckley, 2012; Karanth and DeFries, 2011; Mearns, 2012; Morrison et al., 2012; Steven, Castley, et al., 2013). In contrast, some existing (and potential) wildlife tourism localities stand to benefit from climate change – a growth in visitor numbers precipitated by the colonisation of a site by attractive species could increase tourism revenue. For some high-visitation sites though, more visitors could put greater pressure on natural resources and place additional stress on existing infrastructure that could lead to increased annual maintenance and investment costs.

Already, climate-induced range shifts have had observable impacts on tourism and recreation economies, including negative financial repercussions (Pecl et al., 2017). Jellyfish *Cotylorhiza tuberculata* build up from warmer temperatures in a Mediterranean lagoon has had a negative effect on local tourism economies (Ruiz et al., 2012), whereas in southeast Australia, a range-extending sea urchin *Centrostephanus rodgersii* has overgrazed macroalgae, resulting in the loss of up to 150 associated taxa and contributing to reduced catches for popular recreational fisheries species dependent on large seaweed (Ling et al., 2009). There are also examples of climate change benefiting tourism or recreation through species range shifts. For example, highly prized fish recently emerging in southeastern Australia has benefited recreational fishing industries (Gledhill et al., 2015). Alaskan whale-watching businesses are reportedly benefiting from changes to the timing of whale migrations, with whales arriving earlier in the season and remaining for longer (Pagnan, 2003).

As well as being a highly climate-sensitive sector, tourism is also a growing contributor to climate change, accounting for roughly $\sim$5% (with a high estimate of 12.5%) of CO_2 emissions, and it is also known to exacerbate water scarcity, land use change, and the spread of diseases (Gössling, 2005). The latter may particularly problematic for nature-based tourism, which often occurs in remote areas where tourists may be exposed to a larger variety of species and pathogens. Low-carbon and other forms of sustainable tourism are therefore vital to decouple future tourism growth from negative environmental change. Identifying sites that are likely to increase in visitation may be a key precursor for implementing these.

The current limited understanding of how global species redistributions will affect tourism visitation patterns remains a major obstacle in our ability to adapt to and mitigate climate change. There are also major regional biases in empirical research into climate change impacts on tourism generally, with a notable lack of research in regions with typically lower adaptive capacity e.g., Africa, where financial, institutional, and technological limitations reduce the ability to respond successfully to climate variability and change (Hoogendoorn and Fitchett, 2018). In this study, I explore how climate change might influence the *attractiveness* of species assemblages for wildlife watching worldwide. I do not predict changes in tourist behaviour or visitor numbers, but instead explore changes in destination attractiveness by linking the number of guides citing species as tourism attractions to tourism potential. I combine the data collated from wildlife tourism guides, outlined in Chapter 2, with species distribution models (SDMs) to explore how the migration of birds and mammals across the terrestrial world, as they track changes in the climate, might alter spatial patterns of wildlife tourism. I identify areas of high risk, where a loss of attractive species could lead to a decline in visitation, potentially reducing the tourism revenue available for conservation and local people. I also identify areas that may benefit from colonising attractive species, which could lead to increased visitation and associated financial rewards, but where attention on reducing negative impacts of over-crowding may need to be focussed.

4.3. METHODS

4.3.1. Species distribution data

I used the ensemble SDMs (also known as bioclimatic envelope or niche modelling) developed by Mark Titley (unpublished data) from the Conservation Ecology Group at Durham University, which built upon the methods of Bagchi et al. (2013), to model species responses to climate change. This method depends on statistical associations between current species distributions and environmental variables, such that projected changes in environmental variables (due to e.g., climate change) can then be used to infer changes in the distributions of species' ranges. Current species distribution data were obtained for 10,930 species of bird from BirdLife International and Handbook of the Birds of the World (2016) and for 5,381 species of terrestrial mammal from the International Union for Conservation of Nature (IUCN, 2016). The polygons were filtered to keep only native breeding or resident ranges where the species is extant. They were then rasterized to a global grid of 48.25 x 48.25 km cells ($\sim$0.5° at 30° North/South) and transformed to a cylindrical equal-area projection (Behrmann projection) to avoid biasing the models by oversampling high latitudinal regions (Budic et al., 2016). Species whose polygons overlapped by $\geq$ 10% with the underlying grid cell were considered present in that cell. For each species, 1,000 pseudo-absence points were randomly sampled from the same zoogeographic realm(s) in which the species was found (Holt et al., 2013).

4.3.2. Bioclimatic variables

M. Titley adopted a systematic approach to select a set of bioclimatic predictor variables that are broadly ecologically relevant, non-collinear, and that produce high-performing models when tested on a random subset of species. Eight bioclimatic variables were selected from the *WorldClim 2.0 Beta version 1* (2016) dataset (Fick and Hijmans, 2017; Hijmans, Cameron, et al., 2005) that have been widely used in niche modelling and have been used to accurately model species distributions under changing climate conditions (Stephens et al., 2016). They were: 1) annual mean temperature; 2) temperature seasonality; 3) maximum temperature of the warmest month; 4) minimum temperature of the coolest month; 5) annual precipitation; 6) precipitation of the wettest month; 7) precipitation of the driest month; and 8) precipitation seasonality. There were 219 possible combinations of the eight variables, in sets of three up to eight, of which 10 sets were discarded because they did not contain both temperature and precipitation variables. The remaining 209 sets of combinations were then tested for collinearity and sets with Pearson's pairwise correlations between variables of r $\geq$ 0.7 were discarded (Dormann et al., 2013). This resulted in a final selection of 38 candidate combinations of predictor variables that are biologically relevant at a coarse scale and sufficiently uncorrelated to avoid producing unstable models.

In order to identify the best set of predictor variables for projecting species distributions, the 38 candidate combinations were used to build generalised additive models, using the R package 'mcgv' (Wood, 2017), for a random subset of 200 bird and 200 mammal species. The models were then ranked according to model performance, using the Akaike information criterion, and the number of times that a predictor variable appeared in the top quartile of candidate sets was tallied. The final set of predictor variables included 1) annual mean temperature; 2) temperature seasonality; 3) precipitation of the wettest month; 4) precipitation of the driest month; and 5) precipitation seasonality. This combination was in the highest performing quartile of candidate variable combinations for > 90% of mammal and bird species.

4.3.3. Species distribution modelling

Downscaled data from the global climate models (GCMs) of the Coupled Model Intercomparison Project Phase 5 (Hijmans, Cameron, et al., 2005) were used to project future climate variables. Outputs from three different GCMs (HadGEM2-ES, CCSM4, and MIROC-ESM-CHEM) and four greenhouse gas concentration trajectories - Representative Concentration Pathways (RCPs) - were used to take into account variation in climate projections. I focus primarily on two RCP scenarios – RCP 2.6 and RCP 6.0, the latter predicting greater concentrations of atmospheric greenhouse gases and greater increases in average global temperatures.

Following the blocking approach by Bagchi et al. (2013), the data were split into ten spatially disaggregated blocks to account for the spatial dependence in the models. Non-contiguous portions of the world's terrestrial ecoregions were used as the sampling units to divide the data; these units were then grouped into 10 blocks using the 'blockTools' package in R (Moore and Schnakenberg, 2016), such that the total area and mean bioclimate was approximately equal in each block, and each block contained the full range of bioclimates (Bagchi et al., 2013). Ten-fold cross-validation was then used to assess model performance, whereby each block was left out in turn to be used as a testing dataset, and models were trained on the remaining 90% of data. An ensemble of four different model types was used to project species' climatic niches, which has been demonstrated to reduce overfitting and improve predictive performance, especially for rare species (Breiner et al., 2015; Lomba et al., 2010). These were generalised linear models; generalised additive models; random forests; and boosted regression trees. The models were then used to project current and future climatic niches (for the year 2070, based on the average between 2061 and 2080). One hundred and twenty projections of future ranges were produced per species (10 blocks x 4 model types x 3 GCMs) for each RCP scenario.

The projected ranges were limited to the surrounding or adjacent zoogeographic realms in which each species occurs (Holt et al., 2013), since realms are often defined by biogeographical barriers that define a species' range limits. They were then clipped to a species' buffered range polygon, determined by a species' theoretical dispersal distance, to exclude suitable climates far away from their current range. Natal dispersal estimates for birds were obtained from BirdLife International (2017b) and for mammals were based on home range size and the models produced by Santini, Marco, et al. (2013). These estimates were then multiplied by the projection time period (2016 to 2070) and divided by species' generation length to determine the distance each species could feasibly disperse from its current range edge within the projected time period.

The projected probability of occurrence obtained from each model was converted into a binary presence-absence value using a threshold that maximised sensitivity plus specificity (Liu, Berry, et al., 2005). The final projected niche distribution was determined by taking the mean presence/absence value from all models for each grid cell, weighted by the area under the receiver operator characteristic curve, to give greater influence to better performing models, which was then rounded up/down to once again produce a binary value. Eighteen per cent (n = 1,866) of birds and 29% (n = 1,144) of mammals (or 21% of species across both groups) were excluded from the SDMs either because they had very restricted ranges (less than five grid cells) or their ranges could not be split up in the 'blocking' method to two or more blocks (McPherson et al., 2004; Stockwell and Peterson, 2002).

4.3.4. Climate-induced impacts on wildlife tourism potential

I combined projected species distributions, produced by M. Titley, with the predicted number of guides a species was cited in (i.e., predicted species *attractiveness*), calculated in Chapter 2. I explored climate change impacts on top attractor species, defined as the upper quartile of all species ranked by predicted citations, by calculating projected changes in species' range sizes between the years 2016 and 2070. I identified climate-threatened species as those expected to decrease in range size by $\geq 10\%$, a threshold chosen to eliminate species expected to experience minimal change in range size. I identified hotspots of threatened species by calculating the richness of attractor species projected to decrease in range size by $\geq 50\%$ occurring in each equal-area terrestrial grid cell. I identified hotspots of 'prospering' species by mapping the ranges of attractor species whose ranges were projected to increase by $\geq 10\%$. I calculated changes in the summed predicted *attractiveness* of species occurring in each grid cell and identified hotspots where these changes are projected to be most severe. I did this separately for birds and mammals. Because the range sizes of many species are expected to change as the climate changes, and range size was found in Chapter 2 to be a predictor of guide citation frequency, I conducted a sensitivity analysis to explore the sensitivity of my climate change projections to species range size. To do this, I predicted the future *attractiveness* of each species using their projected range sizes according to the two RCP scenarios, and explored how this influenced projected patterns of summed species *attractiveness*.

Focussing on sub-Saharan Africa, a major hotspot for wildlife tourism (see the Results section of Chapter 2), I calculated changes in cumulative predicted *attractiveness* of species averaged across grid cells falling within the boundaries of PAs (n = 888), downloaded from the World Database on Protected Areas (WDPA, 2018), and explored the implications of this for the wildlife tourism potential of PAs. I used Tanzania's Serengeti National Park, one of the most popular PAs worldwide (see Chapter 3), as a case study, to explore the changes in the composition of its mammal assemblage that might be driving these changes.

4.4. RESULTS

4.4.1. Changes in range extent of top attractor species

The ranges of 33% of birds (n = 760) and 40% of mammals (n = 319) within the top quartile of species for each taxon, when ranked by predicted citations in wildlife tourism guides, were projected to decline by $\geq 10\%$ by 2070 under RCP 2.4. Numbers increased to 48% of birds (n = 1,110) and 53% of mammals (n = 421) under RCP 6.0. Among these was the mammal predicted to be cited as an attraction by the most guides, the African elephant *Loxodonta africana*, which was projected to lose up to 26% of its current range under RCP 6.0 (Table 4.1, Fig. 4.1). One hundred and one attractor species were predicted to decline in extent by $\geq 50\%$ (51 birds and 50 mammals) under RCP 2.6 and 284 (n = 165 birds and 119 mammals) under RCP 6.0. Five species (three birds and two mammals) under RCP 2.6 and up to 16 (eight birds and eight mammals) under RCP 6.0 were predicted to have no remaining climatically suitable areas within dispersal distance in the year 2070 (Table 4.2). On average, bird and mammal species within the top quartile of most predicted citations were projected to experience larger contractions in range size than the remaining 75% of species, with greater losses predicted for RCP 6.0 (Fig. 4.2).

Based on current species climatic niches, richness of top attractor species is highest in sub-Saharan Africa, particularly East Africa, with high richness of *attractive* birds also projected throughout much of the Amazon basin, the Guianan Shield, and the Brazilian Atlantic coastal forests, as well across Europe stretching into central Asia (Fig. 4.3). The Himalayan region and mainland South East Asia also have a relatively high richness of attractor species (Fig. 4.3). Most of the attractor species predicted to experience significant range losses ($\geq$ 50%) occur in the tropical forests of South America, with the Amazon basin containing a particularly high number of such species (Fig. 4.4), including species predicted to lose all of their range (e.g., Spix's red-handed howler monkeys *Alouatta discolor* and red-bellied titi monkeys *Callicebus molochi*, see Table 4.2). The Albertine Rift Valley, and sub-Saharan Africa more generally, is home to many species projected to contract in range size under RCP 6.0, as are South East Asia and the northern portion of Oceania, though numbers here were slightly lower than in the aforementioned regions (Fig. 4.4). The Canadian and Eurasian Arctic and sub-Arctic regions also host numerous *attractive* birds, though not mammals, projected to lose over half of their range, with greater losses projected under RCP 6.0 (Fig. 4.4).

Contrasting the projected declines in range extent for some of the most frequently cited attractor species, under RCP 2.6, 10% (n = 232) of birds and 8% (n = 53) of mammals within the top quartile of species, when ranked by predicted citation frequency, were predicted to experience an expansion in range size of $>$ 10%. Under RCP 6.0, the number of birds with projected expansions was slightly higher, at 11% (n = 257). The species with the largest predicted expansion was the Mongalla gazelle *Eudorcas albonotata* – up to 472% under RCP 6.0 (Fig. 4.1). The Guinean Forests of West Africa and the western United States host relatively high numbers of attractor species whose ranges were predicted to expand by $>$ 10% (Fig. 4.5). Eastern Europe through to Western Asia, as well as the Orinoco plains of Venezuela and Colombia, the coastal lowlands of the Guianas, the Caribbean and the Gran Chaco and Pampas regions of South America, were also highlighted as potential 'refugia' for birds, hosting *attractive* birds predicted to increase in range size (Fig. 4.5).

Table 4.1: Current and future range extents, calculated as the number of equal-area grid cells, of the top 20 birds and mammals with the highest predicted citation frequency by wildlife tourism guides. Future ranges are projected for the year 2070 under RCP 2.6 and RCP 6.0

Rank	Scientific name	Common name	Current range extent	Future range extent		Proportion of current range		Overlap with current range (%)	
				RCP 2.6	RCP 6.0	RCP 2.6	RCP 6.0	RCP 2.6	RCP 6.0
	Birds								
1	*Pandion haliaetus*	Osprey	20145	19025	18501	0.94	0.92	84.7	77.2
2	*Morus bassanus*	Northern gannet	5368	5176	4782	0.96	0.89	84.4	75.1
3	*Vultur gryphus*	Andean condor	1856	1750	1672	0.94	0.90	93.5	89.6
4	*Struthio camelus*	Ostrich	5721	5514	5555	0.96	0.97	90.4	90.4
5	*Sula sula*	Red-footed booby	9100	10429	10980	1.15	1.21	98.9	99.0
6	*Spheniscus magellanicus*	Magellanic penguin	356	336	319	0.94	0.90	94.4	89.6
7	*Aquila chrysaetos*	Golden eagle	25990	25941	25150	1.00	0.97	93.6	89.6
8	*Phoenicopterus roseus*	Greater flamingo	7030	5938	4591	0.84	0.65	81.4	63.1
9	*Haliaeetus albicilla*	White-tailed eagle	10329	9882	9340	0.96	0.90	89.6	84.1
10	*Grus grus*	Common crane	8906	8263	7937	0.93	0.89	82.2	74.0
11	*Jabiru mycteria*	Jabiru	6780	7372	7555	1.09	1.11	98.7	98.3
12	*Sagittarius serpentarius*	Secretarybird	8691	8526	8294	0.98	0.95	92.1	89.9
13	*Haliaeetus leucocephalus*	Bald eagle	7672	7238	6223	0.94	0.81	83.5	67.9
14	*Falco peregrinus*	Peregrine falcon	29453	27201	25962	0.92	0.88	86.3	81.4
15	*Uria aalge*	Common guillemot	3015	2417	2083	0.80	0.69	63.4	53.4
16	*Pelecanus crispus*	Dalmatian pelican	4947	4967	5145	1.00	1.04	88.1	88.2
17	*Ciconia nigra*	Black stork	13956	13405	13045	0.96	0.93	83.7	78.1
18	*Uria lomvia*	Brünnich's guillemot	3542	3344	2927	0.94	0.83	70.3	59.6
19	*Antigone canadensis*	Sandhill crane	7047	6077	5121	0.86	0.74	79.4	65.0

Rank	Scientific name	Common name	Current range extent	Future range extent		Proportion of current range		Overlap with current range (%)	
				RCP 2.6	RCP 6.0	RCP 2.6	RCP 6.0	RCP 2.6	RCP 6.0
20	*Neophron percnopterus*	Egyptian vulture	15066	15680	16114	1.04	1.07	96.7	97.2
	Mammals								
1	*Loxodonta africana*	African elephant	5229	4198	3864	0.80	0.74	82.7	71.2
2	*Ursus arctos*	Brown bear	24376	22258	20915	0.91	0.86	86.6	80.5
3	*Hippopotamus amphibius*	Hippopotamus	5865	6049	6155	1.03	1.05	92.5	92.1
4	*Ceratotherium simum*	White rhinoceros	6366	5482	4597	0.86	0.72	84.6	71.3
5	*Panthera leo*	Lion	4921	3873	2994	0.78	0.61	75.3	57.5
6	*Ursus maritimus*	Polar bear	7115	4686	3797	0.66	0.53	63.9	52.6
7	*Puma concolor*	Puma	12505	12638	12587	1.01	1.01	98.8	98.4
8	*Elephas maximus*	Asian elephant	1897	1634	1355	0.86	0.71	83.5	68.3
9	*Ursus americanus*	American black bear	8117	8397	7732	1.03	0.95	91.2	81.4
10	*Diceros bicornis*	Black rhinoceros	4242	3385	2746	0.80	0.65	79.8	64.7
11	*Panthera onca*	Jaguar	7678	8088	8234	1.05	1.07	100.0	100.0
12	*Syncerus caffer*	African buffalo	6168	6351	6377	1.03	1.03	93.3	91.8
13	*Crocuta crocuta*	Spotted hyena	8472	8619	8585	1.03	1.01	96.9	95.8
14	*Alces alces*	Moose	10808	10382	9934	0.96	0.92	97.5	68.6
15	*Tragelaphus oryx*	Common eland	4110	3258	2517	0.79	0.61	78.7	61.1
16	*Canis lupus*	Wolf	29181	26834	26150	0.92	0.90	90.9	88.1
17	*Acinonyx jubatus*	Cheetah	10622	8185	7404	0.77	0.70	67.0	57.4
18	*Kobus ellipsiprymnus*	Waterbuck	5927	5742	5136	0.97	0.87	90.2	80.3
19	*Orycteropus afer*	Aardark	11932	11882	11621	1.00	0.97	96.4	94.5
20	*Myrmecophaga tridactyla*	Giant anteater	7313	7110	6291	0.97	0.86	93.8	81.8

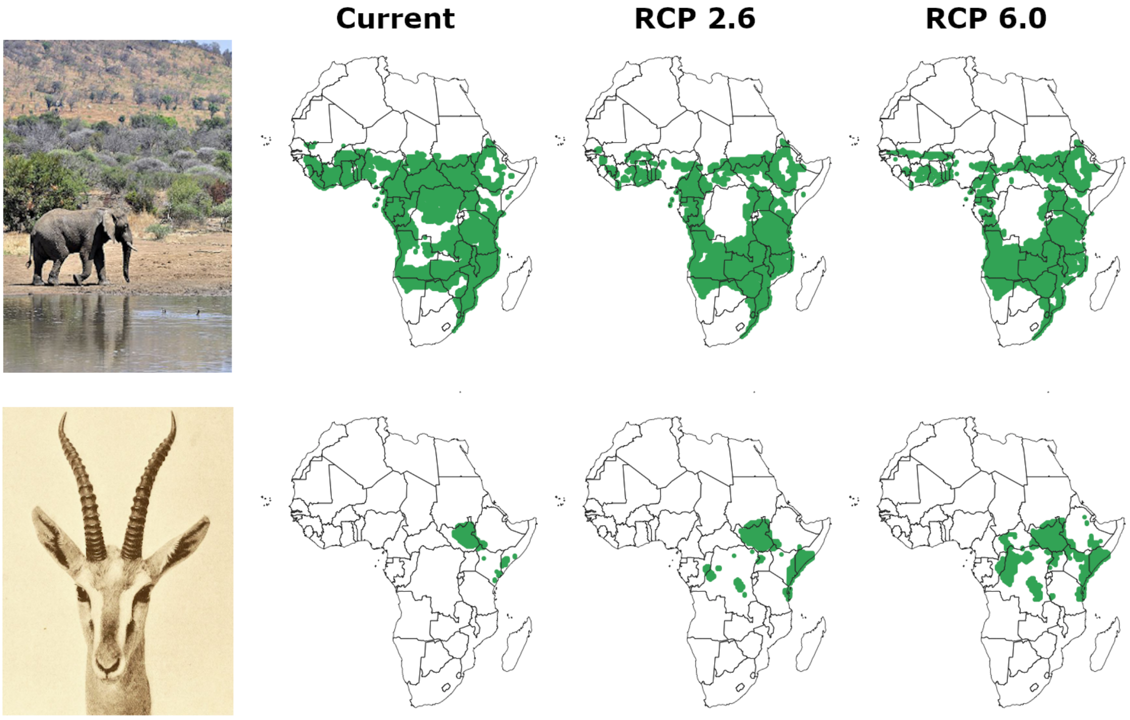

Figure 4.1: Projected breeding range of the African elephant *Loxodonta africana* (top) and the Mongalla gazelle *Eudorcas albonotata* (bottom) under current and future climatic conditions. Projections of future ranges are for the year 2070 and are based on two greenhouse gas concentration pathways (RCP 2.6 and RCP 6.0), and averaged across four model types and three different GCMs.

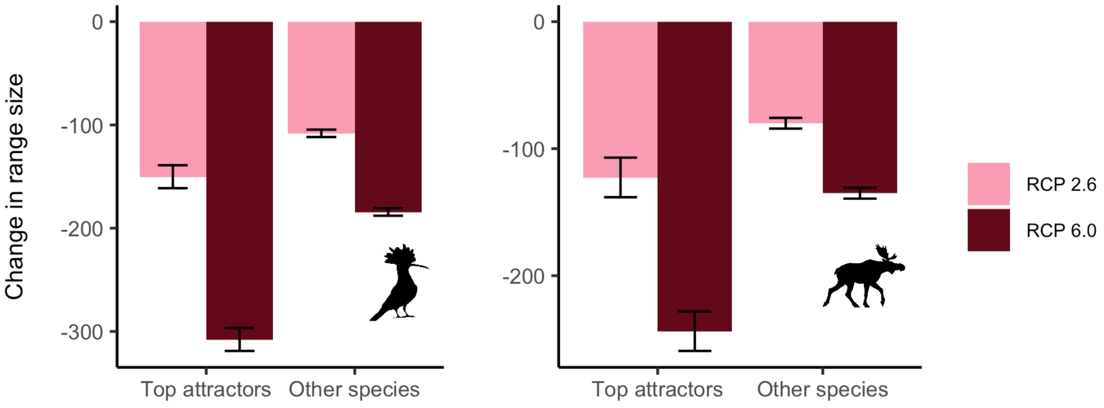

Figure 4.2: The average change in range size for top attractors (based on citation frequency by wildlife tourism guide) vs. the remaining 75% of species. Changes in range size were calculated as the differences in the number of occupied equal-area grid cells between the years 2016 and 2070. Results are shown for RCP 2.6, shown in light pink, and RCP 6.0, in dark red. The error bars show the standard error of the mean.

Table 4.2: Current and future range extents of top attractors projected to go extinct by 2070 (i.e., lose all of their current range within dispersal distance) under RCP 2.6 and/or RCP 6.0. Range extents were calculated as the number of equal-area grid cells and top attractors are those bird and mammal species within the top quartile of species ranked by decreasing predicted citation frequency by wildlife tourism guides

Rank	Scientific name	Common name	Current range extent	Future range extent		Proportion of current range	
				RCP 2.6	RCP 6.0	RCP 2.6	RCP 6.0
	Birds						
445	*Calidris acuminata*	Sharp-tailed sandpiper	669	0	0	0.000	0.000
140	*Leucogeranus leucogeranus*	Siberian crane	244	0	0	0.000	0.000
1314	*Numenius tenuirostris*	Slender-billed curlew	77	0	0	0.000	0.000
2291	*Setophaga kirtlandii*	Kirtland's warbler	27	1	0	0.037	0.000
2445	*Todus multicolor*	Cuban tody	74	3	0	0.041	0.000
1621	*Priotelus temnurus*	Cuban trogon	78	6	0	0.077	0.000
1222	*Podiceps gallardoi*	Hooded grebe	64	8	0	0.125	0.000
2806	*Acrocephalus paludicola*	Aquatic warbler	401	46	0	0.114	0.000
	Mammals						
298	*Alouatta discolor*	Spix's red-handed howler	271	0	0	0.000	0.000
949	*Callicebus moloch*	Red-bellied titi	506	0	0	0.000	0.000
589	*Ateles marginatus*	White-cheeked spider monkey	447	1	0	0.002	0.000
945	*Saguinus mystax*	Moustached tamarin	425	9	0	0.021	0.000
504	*Phaner furcifer*	Masoala fork-marked lemur	28	1	0	0.036	0.000
751	*Allocebus trichotis*	Hairy-eared dwarf lemur	45	2	0	0.044	0.000
660	*Petrogale purpureicollis*	Purple-necked rock-wallaby	94	9	0	0.096	0.000
772	*Setonix brachyurus*	Quokka	20	8	0	0.400	0.000

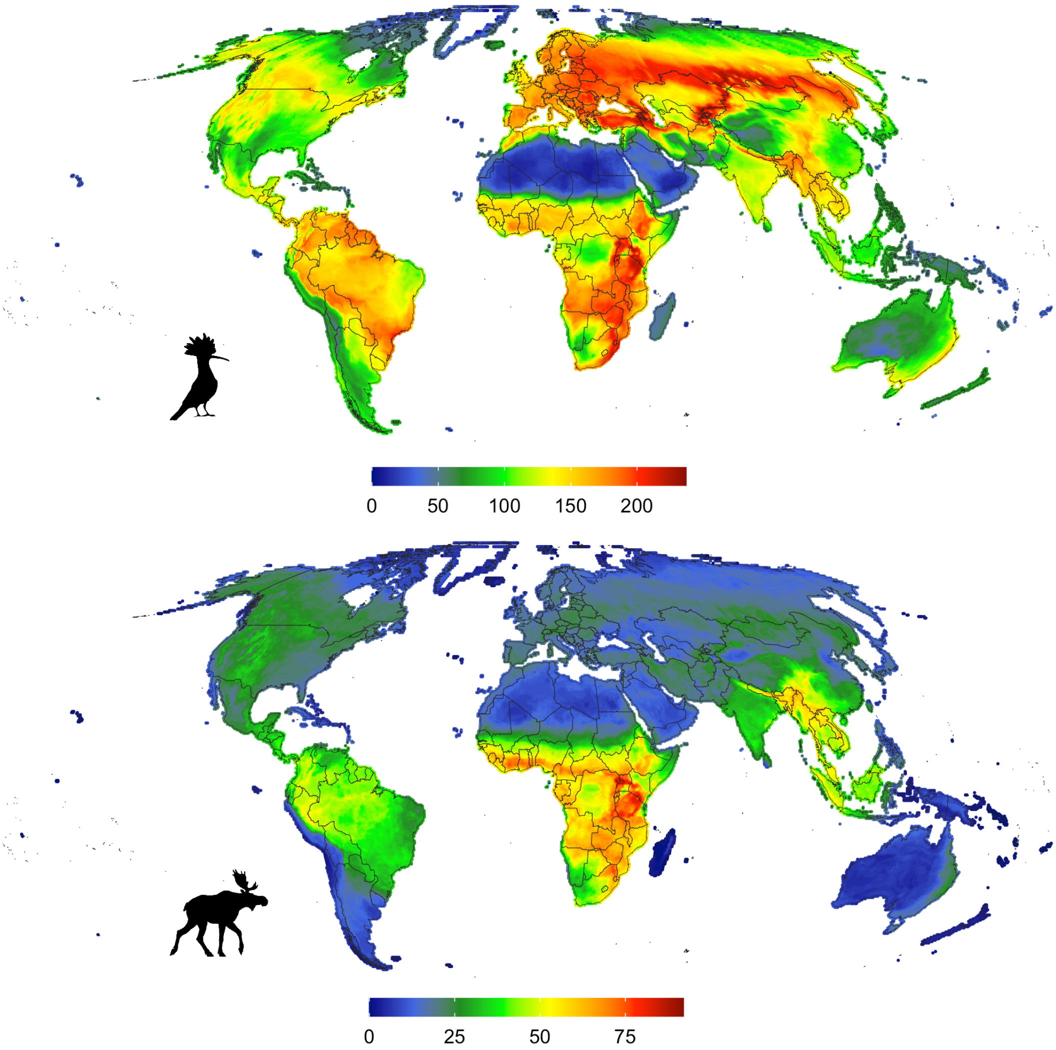

Figure 4.3: Current richness of top attractor species, based on citation frequency of birds (n = 2,530) and terrestrial mammals (n = 850) by wildlife tourism guides. Note that richness was calculated based on projected climatic niches, not realised species distributions.

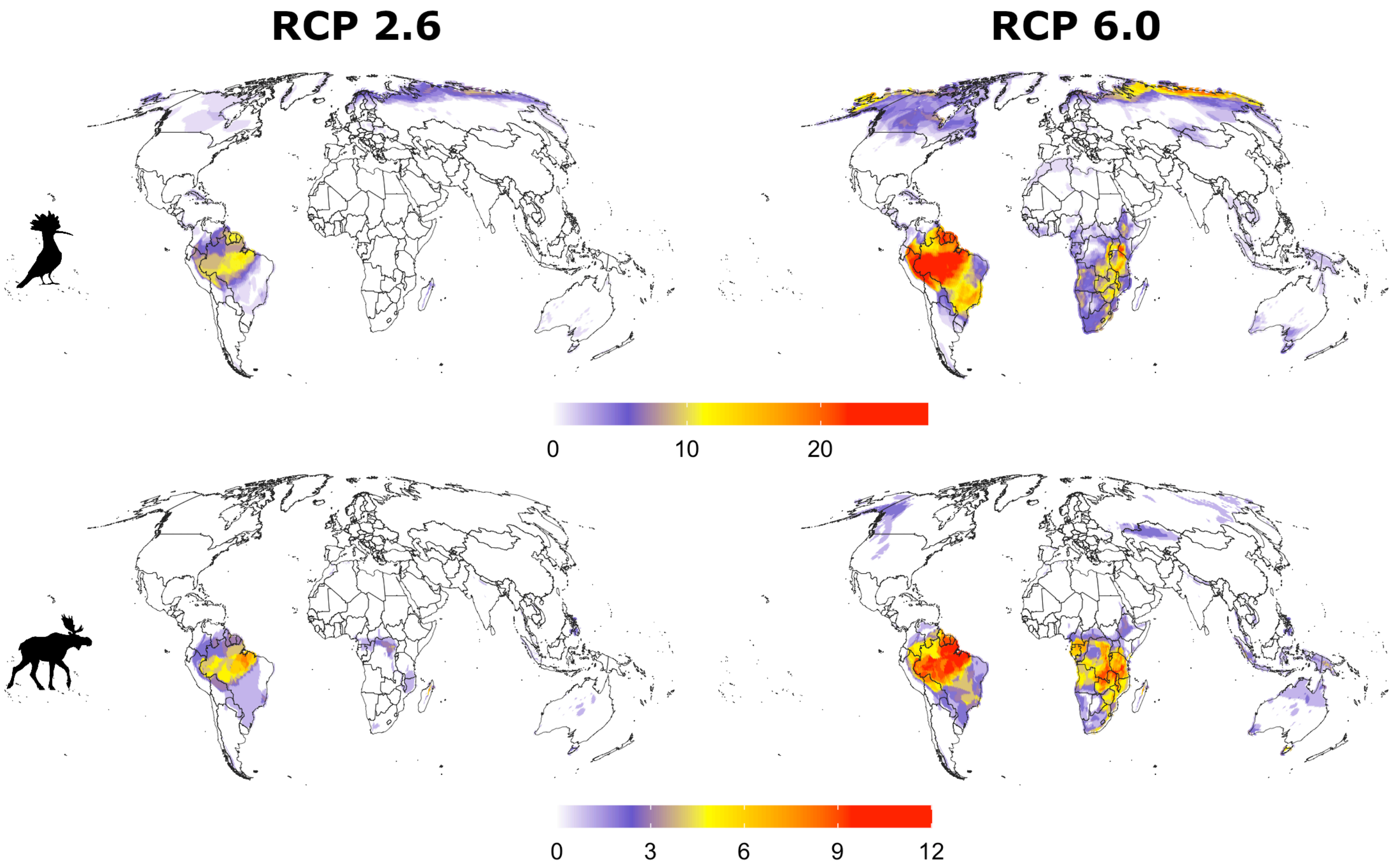

Figure 4.4: Current richness of top attractor species, based on citation frequency by wildlife tourism guides, predicted to lose $\geq$ 50% of their current range extent by 2070, based on an ensemble across four SDMs types and three different GCMs.

4.4.2. Geographical patterns of projected changes in species attractiveness

Simulated patterns of current predicted *attractiveness* (i.e., number of guides a species was cited in as a tourism attraction) of birds and mammals based on climatic niche projections (Fig. 4.6) matched well with observed patterns produced by species range polygons (Chapter 2 Fig. 2.2). They were also similar to future patterns of *attractiveness* (Fig. 4.6). However, *attractiveness* over much of the world's land mass was projected to decline by the year 2070 (Fig. 4.7), with total cumulative *attractiveness* declining by 4.4% and 8.6% under RCP 2.6 and RCP 6.0, respectively. The impacts of climate change on *attractiveness* were more pronounced for birds than mammals. RCP 6.0, which predicts greater increases in average global temperatures, also showed more pronounced changes in species *attractiveness* than RCP 2.6, but, with few exceptions, relative patterns of projected change were similar between the two RCP scenarios (Fig. 4.7). If changes in species ranges' as a result of climate change are taken into account, predicted *attractiveness* for up to 39% (n = 2,540) of birds and 62% (n = 1,614) of mammals declined, resulting in the total predicted species *attractiveness* across the world's terrestrial land mass may decline by 11.6% of the under RCP 6.0.

Changes in species *attractiveness* followed a latitudinal trend (Fig. 4.8), closely matching patterns of species richness (Fig. 4.9). The Arctic regions of North America and Eurasia were predicted to increase in *attractiveness* for both taxa (Fig. 4.7), despite attractors projected to substantially decline in range extent in these regions (Fig. 4.4). In contrast, lower latitudes were predicted to decrease in *attractiveness* (Fig. 4.8), including the boreal forests of Alaska and Canada (though Russia's boreal forests were projected to increase in *attractiveness*), the temperate regions of North America and Europe, and the Euro-Mediterranean region (Fig. 4.7). Large areas of sub-Saharan Africa, particularly across Central and East Africa, and the Amazon basin and the Guianan Shield in South America, were also projected to decline substantially in species *attractiveness*. Some sites at lower latitudes were projected to increase in *attractiveness*, often corresponding to montane or desert regions. The Central Asian mountains, the Himalayas, the southern Arabian Peninsula, and to a lesser degree, the Black Sea region of Turkey, emerged as isolated sites of increasing *attractiveness* in Eurasia. The Mesoamerican biodiversity hotspot of Central America, the tropical Andes, the Atlantic forest of Brazil and particularly the Pampas region of South America were also projected to increase in *attractiveness*. In Africa, increased species *attractiveness* was projected for the Horn of Africa, the Eastern branch of the Rift Valley, the Sahel, and Southern Africa (Fig. 4.7).

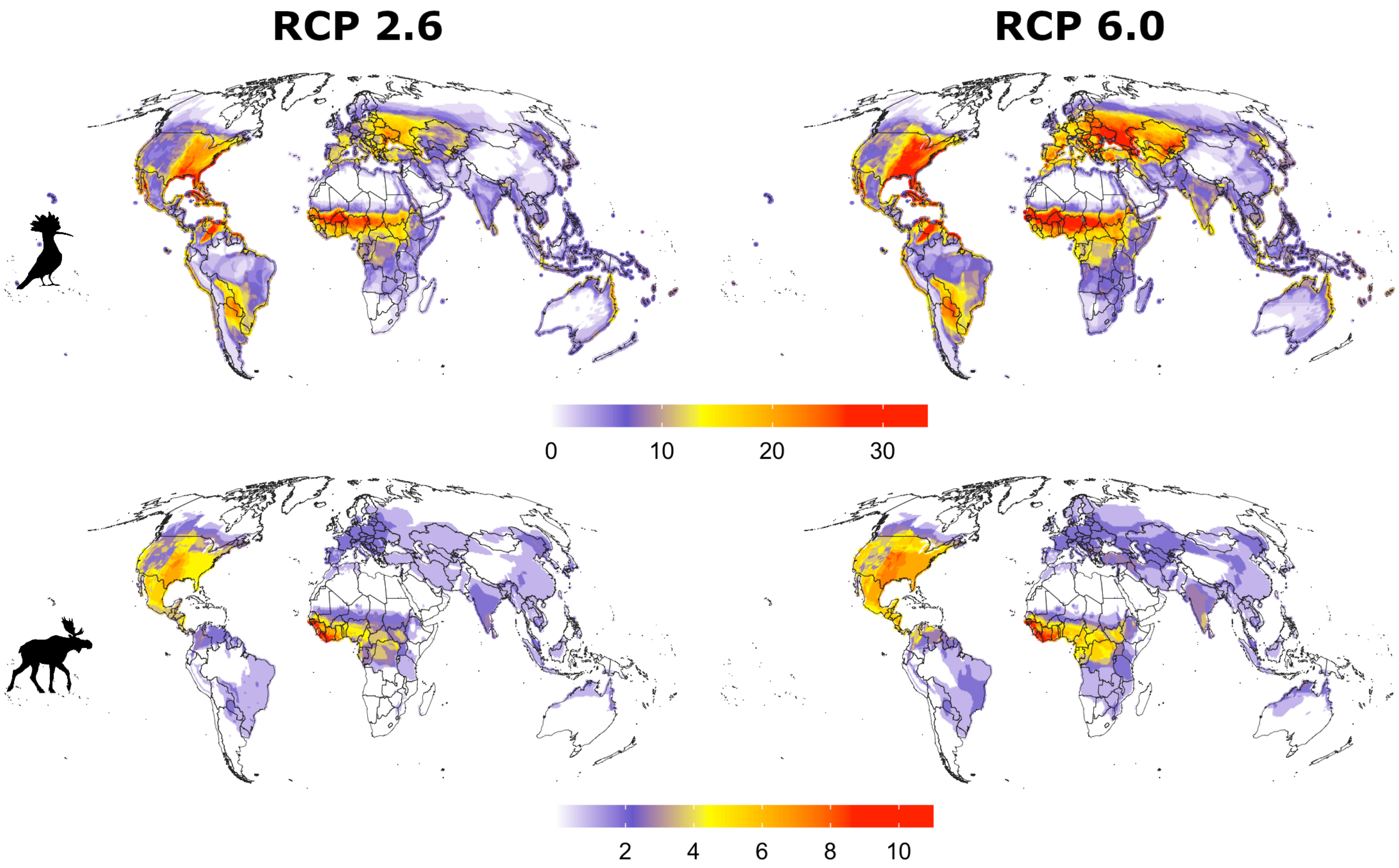

Figure 4.5: The current richness of top attractors, based on citation frequency by wildlife tourism guides, whose current range extent was predicted to expand by $>$ 10% by 2070, based on an ensemble across four SDMs and three different GCMs.

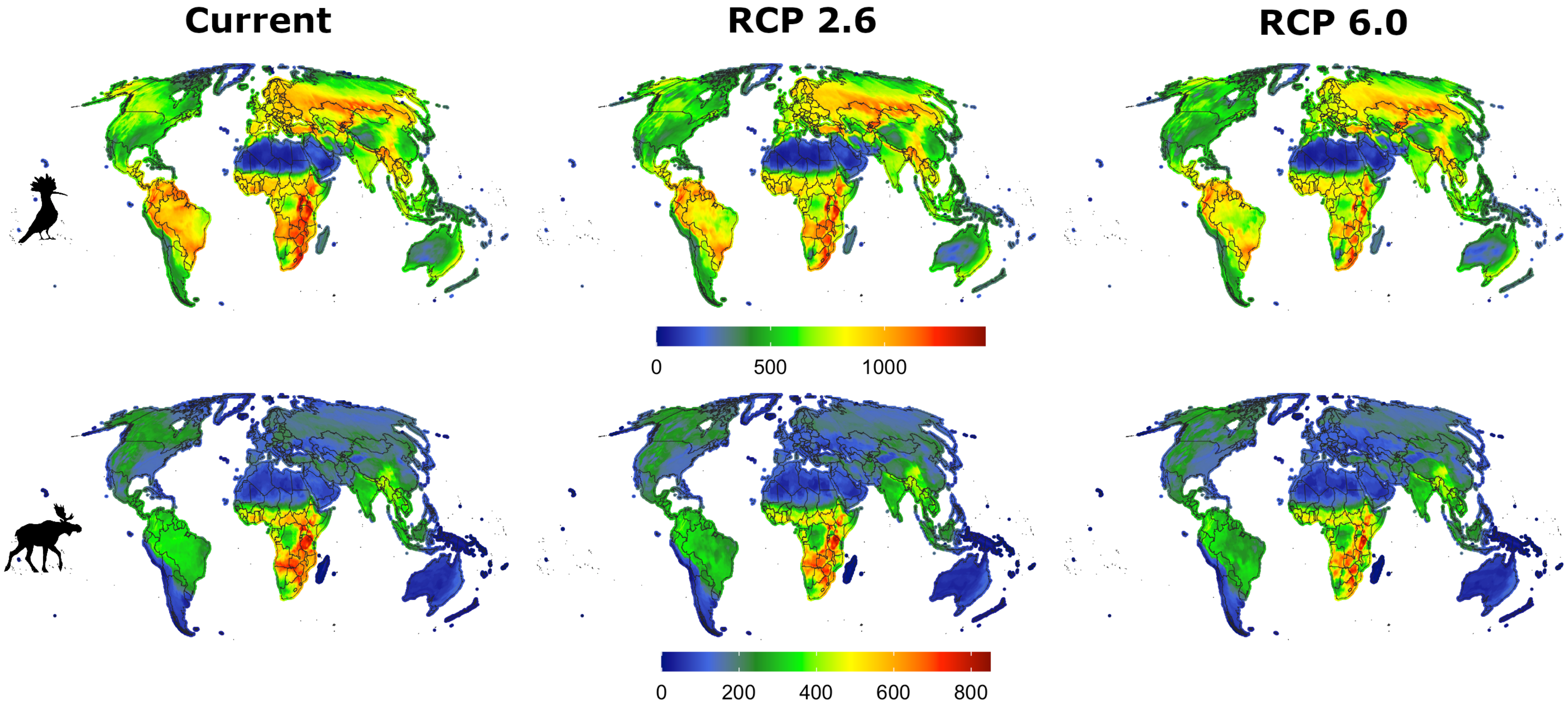

Figure 4.6: Predicted cumulative species *attractiveness* of modelled birds (n = 8,275) and mammals (n = 2,869) for the years 2016 and 2070, the latter projected to two different greenhouse gas concentration trajectories (RCP 2.6 and RCP 6.0), based on an ensemble across four SDMs and three different GCMs.

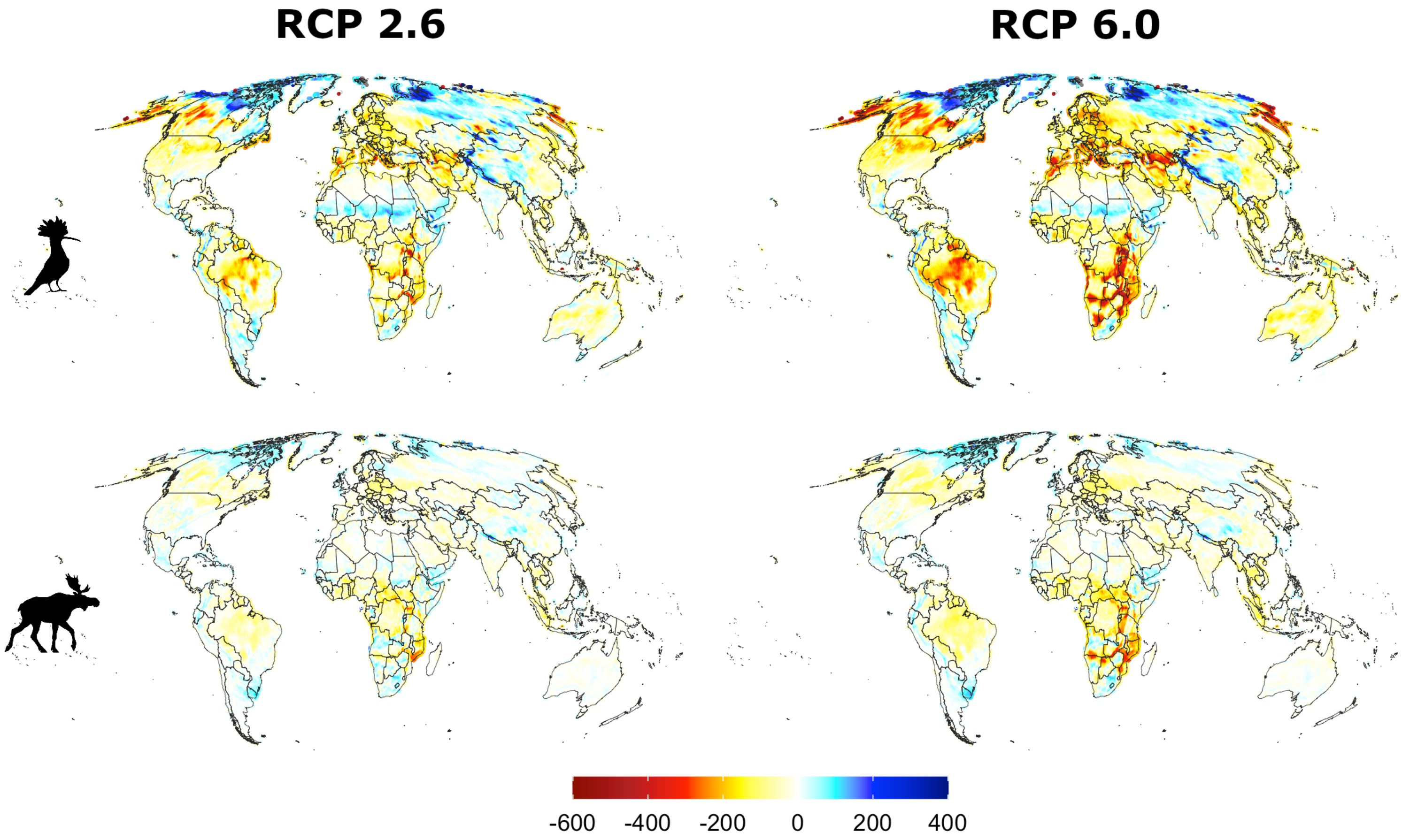

Figure 4.7: Geographical patterns of climate-induced changes in wildlife tourism potential, showing the difference in cumulative *attractiveness* indices for the year 2070 compared with 2016. Results are shown individually for birds (n = 8,275) and mammals (n = 2,869) and RCP 2.6 and 6.0. Changes in cumulative species *attractiveness* were calculated as the difference in the stacked probability of occurrence obtained from climate-based SDMs for each species and averaged across four model types and three different GCMs, multiplied by the species' *attractiveness* index, calculated in Chapter 2.

4.4.3. Projected changes in sub-Saharan African PAs

Ninety-one per cent (n = 807) and 88% (n = 761) of PAs in sub-Saharan Africa, mostly located along East and Southern Africa, were projected to decrease in mean cumulative bird and mammal *attractiveness* by 2070, respectively. PAs with some of the greatest projected declines in species *attractiveness* included the Zambezi Delta and Gorongosa National Park in Mozambique, Lake Kariba in Zimbabwe, Moremi Game Reserve and the Okavango Delta (particularly for birds) in Botswana, Serengeti National Park and Selous Game Reserve in Tanzania, Toro-Semliki Wildlife Reserve in Uganda, and Meru National Park in Kenya (Fig. 4.10). A small number of PAs were predicted to increase in species *attractiveness*, most notably Golden Gate Highlands National Park in South Africa, where the greatest increase in bird *attractiveness* was projected. Bale Mountains National Park in Ethiopia and Odzala-Kokoua National Park in the Republic of Congo are other examples of the more well-known PAs projected to increase in *attractiveness*. Ngorongoro National Park in Tanzania, projected to decline in bird *attractiveness*, was among the PAs with the largest projected increase in mammal *attractiveness*. The large Termit and Ennedi Massifs in Niger and Chad, respectively, were projected to increase greatly in bird *attractiveness*, but not mammal *attractiveness* (Fig. 4.10).

In Tanzania's Serengeti National Park, declining species *attractiveness* was associated with a contraction in range size of 16% of its most *attractive* mammals (i.e., those within the top quartile of mammals most frequently cited in wildlife tourism guides globally). On average, range sizes of *attractive* mammals within the park were projected to decline by 48% (SD = 24.5) by 2070, under RCP 4.5 (Fig. 4.11). The white rhinoceros *Ceratotherium simum*, the common eland *Taurotragus oryx*, the giraffe *Giraffa camelopardalis*, and the black rhinoceros *Diceros bicornis* were some of the most *attractive* species projected to shrink in range size within the park. Five of these species were projected to go locally extinct, including the particularly *attractive* roan antelope *Hippotragus equinus*. Twelve species were projected to go locally extinct within the park under RCP 6.0, including the highly *attractive* giraffe *G. camelopardalis*. Only 11 species were projected to increase in range extent across Serengeti National Park under RCP 4.5 (Fig. 4.11). The average increase in range size was 166% (SD = 129.8). The most *attractive* mammal identified in Chapter 2, the African elephant *L. africana*, which was projected to decrease in range size across the continent, was projected to increase by 150% in the Serengeti National Park (Fig. 4.1). Three mammals that are among the most *attractive* species globally, but are currently absent from Serengeti National Park, were projected to colonise the park as the climate becomes more suitable: the Congo clawless

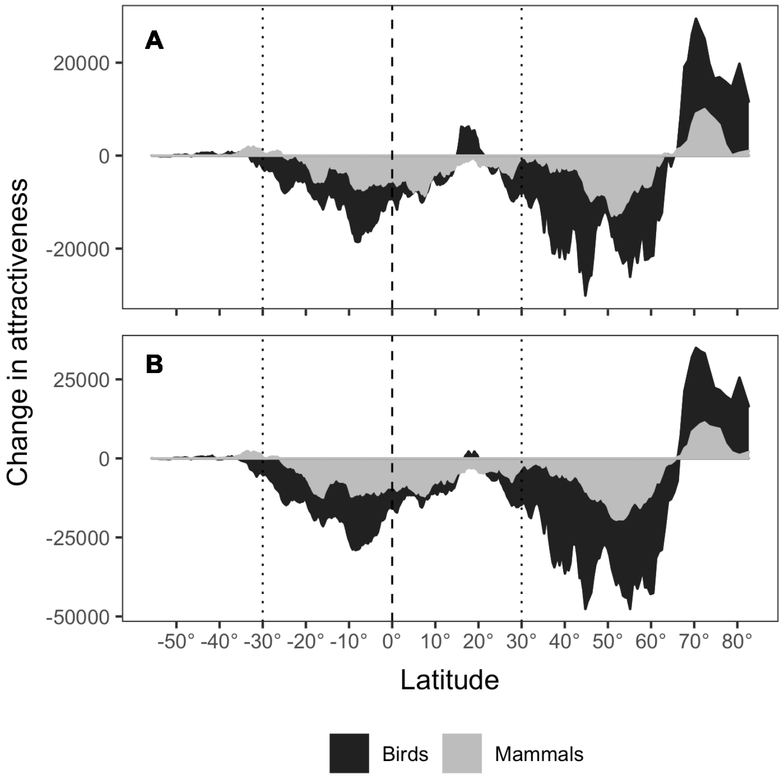

Figure 4.8: Changes in species *attractiveness* across the world's land mass for birds and mammals between 2016 and 2070 by 0.5° latitudinal band, under **A** RCP 2.6 and **B** RCP 6.0.

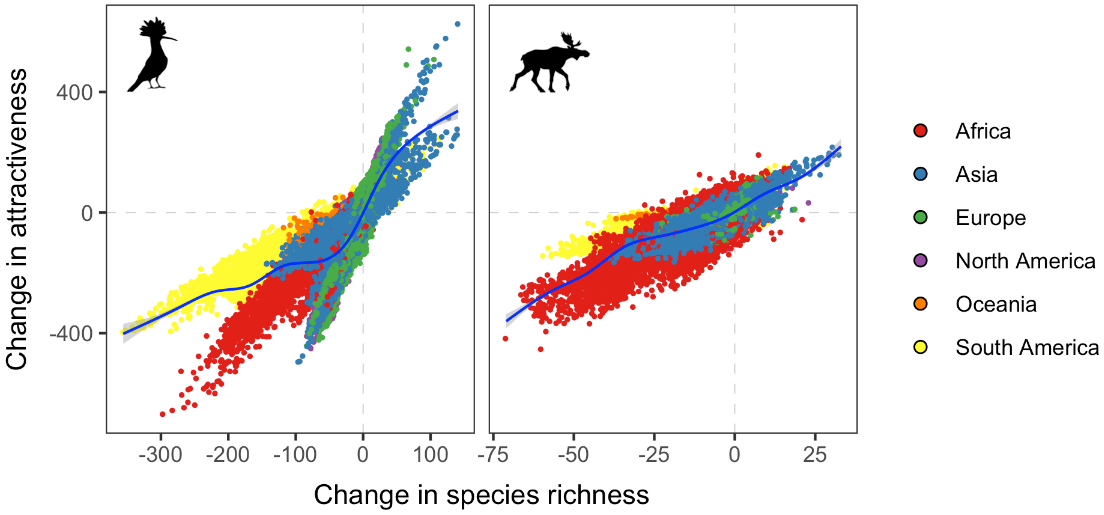

Figure 4.9: The relationship between changes in species richness and species *attractiveness* for birds and mammals between 2016 and 2070. The points represent global equal-area terrestrial grid cells and are coloured by the continent in which they are located. The blue line indicates locally estimated scatterplot smoothing fits. Results for different RCP scenarios were quantitatively similar and so those of an intermediate scenario (RCP 4.5) are shown.

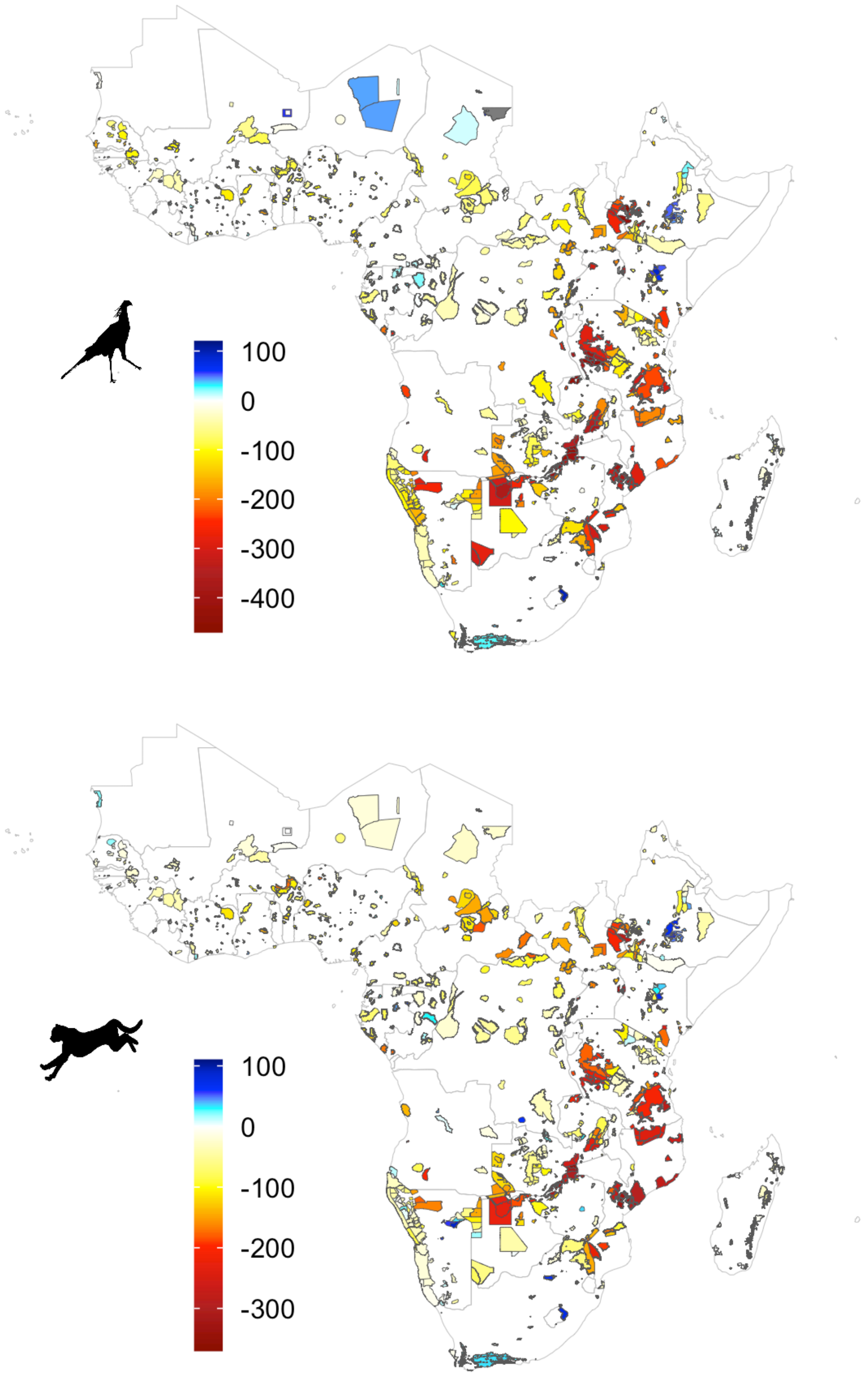

Figure 4.10: Projected mean change in cumulative *attractiveness* of birds and mammals between 2016 and 2070 in PAs (n = 888) of sub-Saharan Africa, under RCP 4.5.

otter *Aonyx congicus* (ranked as #138 most *attractive* mammal globally), the red river hog *Potamochoerus porcus* (#154), and the common reedbuck *Redunca arundinum* (#105).

4.5. DISCUSSION

4.5.1. Climate change impacts on wildlife tourism

The global maps of climate change impacts produced in this study are an important first step in the prioritization of adaptation efforts for wildlife tourism. The results suggest that large proportions of bird and terrestrial mammal distributions are likely to be negatively impacted by climate change, reflected in a decrease in the availability of climatically suitable areas towards the end of the 21st century. Combining projected changes in species ranges with species *attractiveness* indices developed in Chapter 2, I found that attractor species may be disproportionately impacted, with large projected declines in range extents compared with less *attractive* species, supporting the notion that our most charismatic species are at high risk of extinction (Courchamp, Jaric, et al., 2018). Accordingly, most of the terrestrial land mass was projected to decrease in *attractiveness* for wildlife tourism, in terms of their bird and mammal assemblages. Changes were more pronounced in some regions than others, however, and in some cases species *attractiveness* was projected to increase. The findings of this study largely indicate a shift in *attractiveness* away from lower latitudinal and lowland areas towards higher latitudes and montane regions, coinciding with changing patterns of species richness (Hof et al., 2018). Greater changes in species *attractiveness* were projected under RCP 6.0, which projects larger increases in global average temperatures, but regions with a substantial loss or gain of attractor species emerge even under RCP 2.6.

The main hotspots of declining species *attractiveness*, to a large extent, overlap with hotspots of threatened attractors (i.e., species within the top quartile of predicted *attractiveness* projected to contract in range size by $\geq$ 50%). They also correlate with current and potential wildlife tourism hotspots identified in Chapter 2. The popular wildlife tourism localities of sub-Saharan African, particularly East Africa, were predicted to lose much of their attractiveness by 2070, potentially placing financial pressure on the region's many iconic PAs that depend on wildlife tourism revenue. The Amazon basin, the Guianas, and the Brazilian Atlantic forests were highlighted as South American impacted hotspots, where a loss of attractor species could jeopardize the viability of wildlife tourism operations. Other sites, including some well-known wildlife tourism destinations, were predicted to become even more

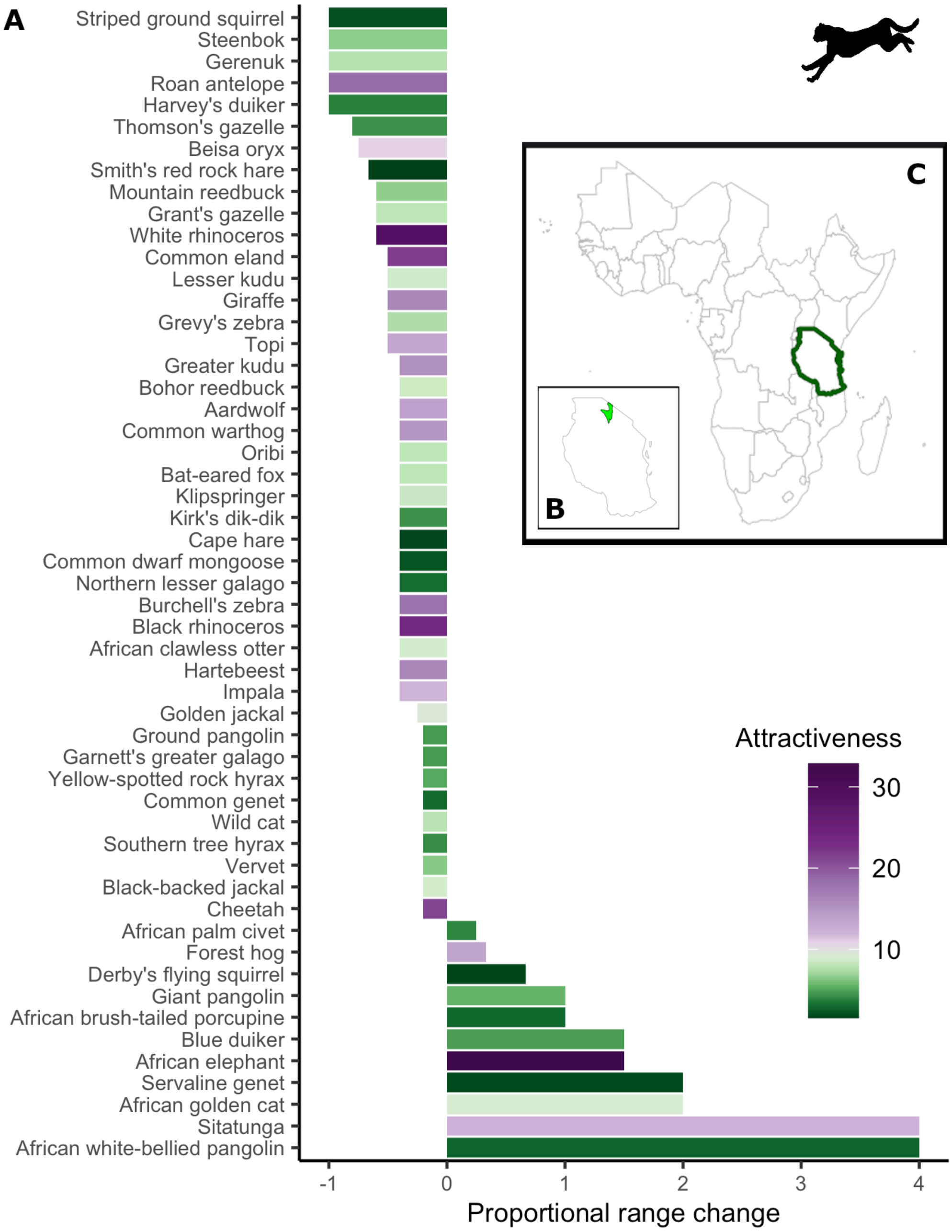

Figure 4.11: The impacts of climate change on *attractive* mammals (n = 56) (i.e., those within the top quartile of most *attractive* mammals globally) in Serengeti National Park, showing **A** changes in range size of each species as a proportion of their current range size, the **B** the location of Serengeti National Park within Tanzania, and **C** the location of Tanzania within sub-Saharan Africa. Results are shown for RCP 4.5. Species with no projected change (n = 213) in range extent are not shown. Bars are coloured by predicted *attractiveness* scores of each species, modelled in Chapter 2.

attractive, and may gain competitive advantage in the future. These include the Pampas region of South America, the montane regions of Africa, the Central Asian mountains, the Himalayas, and the tropical Andes (though decreases in *attractiveness* were projected for the surrounding foothills). Russia's Taiga forest was highlighted as an area of high tourism potential based on *attractive* species assemblages, with increases projected for the future. Currently, this region is not highly-visited by tourists (Naturetrek, 2020a), perhaps due to non-wildlife related factors known to influence visitation, such as accessibility or political stability (see Chapter 3). The impacts of climate change on wildlife tourism may therefore be less pronounced in Russia.

The areas with the highest projected impacts of climate change on species *attractiveness* correspond with areas highlighted by various studies as being at high risk from climate change. For example, Pacifici et al. (2018) predicted high numbers of climate-vulnerable mammals to occur in the Amazon basin and East Africa, while Hof et al. (2018) projected climate-driven declines in bird richness to be particularly high in South America. The substantial decrease in species *attractiveness* in the tropics, resulting from climate change alone, is concerning, given that habitat loss e.g., via deforestation is also known to be a major driver of range reduction and extinction for tropical birds and mammals (Sodhi et al., 2011; Symes et al., 2018). The impacts of habitat loss and fragmentation may exacerbate those of climate change, compromising a species' capacity for rapid dispersal or refugial retreat (Brook et al., 2008; Opdam and Wascher, 2004) and/or hindering a species' ability to track shifts in suitable environmental conditions or access suitable habitat (Cushman, 2006). I did not incorporate land-use in this study due to uncertainties, poor data availability, and the coarse scale of global land cover and land-use change projections, but some of the at-risk regions flagged by my study have been projected to be impacted by both climate and land-use change (see Hof et al., 2018). These include the Atlantic forests of Brazil and parts of West and East Africa, where the risks to wildlife tourism operations predicted by this study may be conservative. Furthermore, some areas predicted to increase in species *attractiveness* have been highlighted as being threatened by land-use change, including the Pampas region of South America and Mesoamerica, potentially preventing these regions from receiving the projected benefits for wildlife tourism (Naylor et al., 2005). By omitting factors such as land cover, which also influence species distributions, it is important to note that the SDMs produced by M. Titley reflect the potential future distribution of climatic niches, not the realised distributions of the species themselves.

The importance of land cover in determining species distributions highlights an additional, important point, which is that it is possible that species could tolerate climates outside those encompassed by their current range. For species with highly restricted ranges, human land-uses may be an important determinant of species absences from areas with suitable climate (although most such highly range-restricted species were not included in my analysis, as discussed in the Methods). Species may also have some adaptive potential and may be able to tolerate climate change or evolve in response to it, and therefore may be more resilient to climate change than niche modelling might suggest. However, the rapidity of climate change relative to the generation length of birds and mammals means evolutionary responses are unlikely to be important in these taxa on the timescales I have explored, and most evidence suggests that spatial responses tend to be the most common response to changing climatic conditions, albeit with substantial lags in some systems (Pecl et al., 2017).

The more climate vulnerable areas may be at risk from multiple climate change threats, which are unlikely to occur in isolation (Fitchett et al., 2016). A site that is projected to decrease in species attractiveness, for example, could also face challenges associated with increased incidence of storms, which may further deter tourists (Dube and Nhamo, 2020), but which is difficult to project. Moreover, climate change is expected to influence species' behaviours in myriad ways, which may have opposite effects on the wildlife tourism experience. In areas of reduced rainfall, wildlife may become easier to locate and observe as greater concentrations of animals gather around fewer water sources, potentially enhancing visitor satisfaction, even if that area loses some of its attractor species (Dube and Nhamo, 2020), but again, this is hard to project. Alternatively, in this global system, changes at one site may have repercussions for competitors, so that a negative impact, such as the loss of attractor species, at one site may have a knock-on positive effect elsewhere, creating an opportunity for a competitive site to attract these tourists (Scott, Gössling, et al., 2012).

The still limited understanding of tourists' preferences and behaviours is an important conceptual barrier for climate change impact and adaptation studies to overcome. This is especially true of 'future' tourists. The preferences of today's tourists have been influenced by the era that tourists are living in, and whether tourists travelling in the 2070s will be deterred from visiting a site that has declined in attractiveness, if they have never experienced the wildlife assemblages that today's visitors use to define and measure the quality of a wildlife watching experience, remains unclear. Linked with this is the idea that species threatened by climate change may become more attractive as they become rarer, such that places predicted to lose attractiveness may retain or even experience an increase in their appeal as wildlife tourism destinations if they represent one of the last strongholds for endangered species. 'Last chance' tourism, in which tourists visit disappearing destinations or seek an encounter with disappearing species, is becoming increasingly common. Climate change is a major motivation for this form of tourism and some of the most popular destinations are those at greatest risk from climate change, where attractor species are predicted to experience significant decreases in range size, such as the Arctic (Groulx et al., 2016).

4.5.2. Implications for management

The results of this study illustrate spatial patterns in climate change impacts on attractiveness for wildlife tourism using species range maps to make projections. However, the appropriate spatial resolution for macro-ecological analyses based on range map data is a matter of debate (Hurlbert and Jetz, 2007). In this study, species distributions were projected at relatively coarse scale, with cell sizes $> 2{,}300$ km^2. Because species are unlikely to be present throughout the whole area outlined by their range maps, even at this coarse scale, the area of occupancy of individual species (i.e., where the species is present) is likely to be over-estimated for all but the most common species, leading to uncertainty in the exact species composition of hotspots. Consequently, I outline the broad management implications of my study, but these are not intended to guide local conservation or management.

Tourists themselves have the greatest capacity to adapt to climate change (depending on finances, time and knowledge), with the relative flexibility and freedom to avoid destinations negatively impacted by climate change, and instead visit those that become more attractive as the climate changes. In contrast, low or disjunct awareness of climate change risks from tourism operators, and/or little evidence of long-term strategic planning in anticipation of future climatic changes, indicates relatively little adaptive capacity (Hoogendoorn, Grant, et al., 2016; Marshall et al., 2011; Mkiramweni et al., 2016; Wolfsegger et al., 2008). Governmental climate change policies of many countries also tend to be in the early stages, with those for the tourism sector lagging behind sectors such as agriculture, energy and water (Hambira and Saarinen, 2015). Low adaptive capacities in low income counties, where large changes in species *attractiveness* are projected (Hambira and Saarinen, 2015; Rogerson, 2016; Scott, Hall, et al., 2019), puts them at higher risk from climate-induced threats, and may limit their ability to adapt to positive changes for wildlife tourism. Immediate action in priority areas that involves raising awareness of climate threats, and robust, proactive adaptation is needed to help managers and local communities anticipate, adapt to and/or capitalise on changes in species assemblages, and ensure wildlife tourism remains an effective means of financing conservation efforts and sustainable development (Hannah et al., 2007).

Revising current conservation policy and biodiversity management plans will be an essential component of climate change adaptation. Expanding PA coverage and connectivity, as called for in the Aichi Targets (CBD, 2010), will be vital to create more permeable landscapes and facilitate the dispersal and survival of species across their future ranges. In conjunction with this, improved management, both inside and outside of PAs, will be needed to preserve crucial habitat and natural resources for endangered species, particularly in climate-vulnerable regions where human land-use is also threat. These activities might include such diverse strategies as drilling for water to ensure water sources for wildlife persist during periods of drought (Saarinen, Hambira, et al., 2012; Tervo-Kankare et al., 2018). Assisted colonisations, whereby species are introduced into novel areas to track changes in climate, could feasibly be informed by species attractiveness to tourists to maximise economic returns and overcome financial barriers (Willis et al., 2009). The diversification of tourism offerings will be a critical part of adaptation, and is already being implemented in various destinations (Hambira and Saarinen, 2015). For example, hot air balloon safaris and mobile camping have been introduced to the Serengeti to match changing wildlife migration patterns (Kilungu, Leemans, et al., 2017), whereas, in the Egyptian Red Sea, dive operators are diversifying their offerings to include birdwatching, and lessons on astronomy and Indigenous foods, culture, and music (Marshall et al., 2011). The economic development of emerging countries and increased international travel may provide a new customer base that will facilitate diversification (Scheyvens, 2007). Where an increase in destination attractiveness leads to unsustainable visitor numbers or over-crowding, managers may need to control numbers and tourism activities, through e.g., infrastructure such as kiosks, hides, and fences, to minimise negative tourism impacts (Cassini et al., 2004; Ikuta and Blumstein, 2003).

There are numerous obstacles and issues associated with potential adaptation strategies that may prevent or impede effective adaptation to climate change (Hoogendoorn and Fitchett, 2018; Kaján, 2014). Responses to rising temperatures or droughts may include creating shaded areas or drilling for water, all of which could place additional stress on already limited natural resources (Hambira, Saarinen, et al., 2013; Saarinen, Hambira, et al., 2012). Adaptation strategies must therefore be balanced with the often conflicting objectives of mitigation initiatives (Kupika and Nhamo, 2016). The greening of accommodation establishments and attempts towards carbon-neutral tourist destinations will be important in reversing the trend of growing greenhouse gas emissions from tourism (Gössling and Schumacher, 2010). Targeting tourism products towards domestic tourists could also be an effective way of limiting emissions from long-haul flights, while simultaneously minimising the negative social impacts often associated with international tourism (see Stelios and Melisidou, 2007). Wherever adaptation leads to added conservation and management costs, tourism fees, such as PA entrance costs, must be reviewed and increased accordingly to ensure the burden does not fall entirely on the national population (Dube and Nhamo, 2020).

4.6. CONCLUSION

The salient findings of this study stand regardless of the RCP scenario – climate change will drastically alter the species assemblages of important wildlife tourism sites around the world. The coming decades are likely to see changes in visitor use patterns as a result. This study emphasizes the urgency of adaptation efforts needed in wildlife tourism localities worldwide to adapt to changing species distributions and provides a framework for prioritising areas where urgent intervention is needed. Managers and local communities in sub-Saharan Africa, South America and Central and Southern Asia need to anticipate and adapt to potential negative impacts brought about by either too low visitor numbers to support tourism businesses or too many visitors, reducing recreation enjoyment or increasing pressure on natural resources, and should to be ready to exploit beneficial opportunities that arise. The tourism sector itself is a powerful driver of climate change, and with economic growth in the middle classes and increased demand for tourism experiences, the issue of mitigation will become increasingly prominent. However, by helping to conserve biodiversity, sustainable and low carbon wildlife tourism may also play a key role in mitigating climate change impacts, as more-diverse systems could be more resilient.

Chapter 5

Attractiveness of Birds and Terrestrial Mammals for British Wildlife Tourism

5.1. ABSTRACT

Wildlife watching is a popular component of the British tourism industry, providing substantial benefits to local economies. Attracting tourists and achieving tourist satisfaction has become an increasingly important goal in the management of many protected areas (PAs) in order to maximise tourism revenue. Yet not much is known about the types of species that are most sought-after by wildlife tourists, and the United Kingdom represents a particularly under-researched area in this regard. In light of this, I adopt the same approach to that of Chapter 2 and use wildlife tourism literature to assess the attractiveness of birds and mammals for British wildlife tourism. Combining an *attractiveness* index that I derive from citation frequency within a series of guides, with species trait data, I explore the drivers of species *attractiveness* in the United Kingdom. Mirroring the results from Chapter 2, *attractiveness* was influenced by body mass, range size, extinction risk/conservation status, and coloniality. Time partitioning also influenced species *attractiveness* in the United Kingdom. The differences in the effects of particular traits globally, compared with in the United Kingdom, indicate that wildlife tourist preferences are diverse and depend on the type of tourist e.g., domestic British tourists vs. international, globe-trotting tourists. I use data on influential traits and occurrence data to map British wildlife tourism hotspots. I overlay these data with PA boundaries to identify sites with *attractive* species assemblages and/or where key species occur. The findings of this chapter demonstrate the substantial potential for wildlife tourism to generate significant revenue for conservation and local economies across much of the United Kingdom. By using a novel data source that provides a broader insight into wildlife tourist preferences than traditional surveys, my results can inform marketing and management of wildlife tourism sites across the country, helping managers capitalise on this important cultural ecosystem service.

5.2. INTRODUCTION

The desire to see wildlife is becoming an important motivator for tourism in the United Kingdom (Curtin, 2013; Curtin and Wilkes, 2005). Rising memberships of British environmental organisations, such as the Royal Society for the Protection of Birds, with $>$ 1.2 million members (RSPB, 2019), The Wildlife Trusts (2020), with $>$ 850,000 members, and the Woodland Trust (2020), with 500,000 members, reflect growing interest in wildlife and wildlife-oriented recreational activities, such as visiting protected areas (PAs) and photographing animals. These activities form important components of wildlife tourism. Especially in remote regions with few employment alternatives, wildlife tourism contributes significantly to local economies throughout the United Kingdom by creating jobs and generating revenue (Shiel et al., 2002), conveying benefits to local communities, supporting conservation efforts, and providing economic incentives for pro-environmental behaviours. Increasingly, wildlife tourism is also seen as a potential economic justification for wildlife reintroductions, whereby individuals of a species are returned to sites where they were historically resident (Auster et al., 2020; Seddon et al., 2007), which may be particularly relevant in the United Kingdom, where many large, charismatic species have been extirpated. Understanding which species attract tourists and where these species occur could help enhance and expand the United Kingdom's tourism products by informing marketing and management strategies to accommodate tourist preferences, thereby maximising its conservation and societal benefits (Dickie et al., 2006).

Major national datasets on tourism and outdoor recreation in the United Kingdom exist, which indicate that the natural environment contributed an estimated £12 billion to this industry in 2019 (Office of National Statistics, 2021). The People and Nature surveys revealed that, among adults participating in outdoor recreation, 13% and 10% of adults visited nature and wildlife reserves in England and Scotland, respectively (Natural England, 2020; Stewart and Eccleston, 2020). According to the RSPB, £11.8 million is spent annually by reserve visitors, primarily through spending on accommodation, food, and fuel (Dickie et al., 2006; Shiel et al., 2002). Scotland is arguably the United Kingdom's premier wildlife tourism destination, where the net economic impact of wildlife tourism (excluding hunting and fishing) is estimated at £65 million (Tourism and Hospitality Research, 2010). Certain species have significant value as flagships for British wildlife tourism. The Galloway Kite Trail, launched following the reintroduction of the red kite *Milvus milvus*, brought £2.63 million of additional tourist spending into the county of Dumfries and Galloway between 2004 and 2009 (Molloy and Rollie, 2010). On the Isle of Mull, tourism associated with the white-tailed eagle *Haliaeetus albicilla* generates £5 million annually (Molloy, 2011), and ~290,000 people visit reserves across the United Kingdom to see ospreys *Pandion haliaetus*, generating £3.5 million for the local economy (Dickie et al., 2006).

Although it is widely accepted that some species, such as the flagship species mentioned above, are preferred by tourists, quantitative information regarding the attractiveness of wildlife for tourism, and with it, spatial patterns of wildlife tourism potential, is lacking. In Chapter 2, I reviewed the scientific literature on the drivers of species attractiveness for wildlife tourism and added to a growing body of research by exploring how species' traits and range attributes, which relate to a species' aesthetic appeal, visibility, and accessibility, predispose species to being more successful attractions in the global wildlife tourism industry. Here, I apply that global analyses to the smaller, national scale within the United Kingdom, identifying which species are most *attractive* for British wildlife tourism and exploring how the factors influencing species *attractiveness* in the United Kingdom might differ from those that drive *attractiveness* at the global scale.

To do this, I explore the species cited in wildlife tourism literature with reference to British sites. Most wildlife tourism guides from which data were extracted for this study were published in the United Kingdom, and therefore the information provided on British sites is likely targeted towards domestic tourists. Since wildlife tourist preferences are known to be diverse (Di Minin et al., 2012; Lindsey, Alexander, et al., 2007), those of domestic wildlife tourists from the British Isles are expected to differ from the globe-trotting, international wildlife tourist visiting far-away destinations. Again, where the term *attractive*, and its derivatives, are italicised, this refers specifically to my index of *attractiveness*, based on citation frequency by guides. This index serves as a measure of a species' potential to attract tourists, as opposed to other uses of the term to refer to physical or aesthetic appeal (Reynolds and Braithwaite, 2001; Veríssimo, Fraser, et al., 2009). The main aims of this study are to:

1. determine the traits that drive species *attractiveness* to tourists wildlife watching in the United Kingdom,
2. model the most *attractive* bird and mammals in the United Kingdom and test this against citation data, and
3. identify sites of high wildlife tourism potential within the United Kingdom based on *attractive* species assemblages.

Following the presentation of the results from this analysis, I compare them to those of Chapter

2, and discover what the wider implications are for tourism management and conservation projects in the United Kingdom.

5.3. METHODS

5.3.1. Data compilation

I obtained a comprehensive list of 621 bird species that have occurred in the United Kingdom from the Checklist of the Birds of Britain (McInerny et al., 2018) and aligned this with the avian taxonomies of BirdLife International (2017a). From this initial list, I collated data on a subset of 286 bird species that regularly occur across the United Kingdom and are classified by the Red List for Birds (Eaton et al., 2015). For analysis, I excluded passage visitors, vagrants, and winter migrants, using information from the British Birds Rarities Committee (BBRC, 2020) and the British Trust for Ornithology (BTO, 2020), as well as species with breeding ranges of $<$ 10 10km x 10km grid cells, due to issues regarding data quality. I recognize that such birds are known to be of interest to tourists, and many bird-watchers will purposefully visit areas to see rare and vagrant species (Booth et al., 2011). In this study, however, I focus more on general wildlife tourism, not the more specialised birdwatching or 'twitcher' element, in which vagrants are likely more important. I also removed breeding birds that have largely originated from individuals escaped from captivity, such as the snow goose *Anser caerulescens*, and introduced birds that are being subjected to eradication programmes in the United Kingdom, such as the ruddy duck *Oxyura jamaicensis*. I focussed my analysis on the remaining 174 species that are classified as resident breeders and have established, self-sustaining populations in the United Kingdom.

I obtained a list of 70 terrestrial mammal species from the UK Mammal List (The Mammal Society, 2019). I examined a subset of 38 mammals, excluding species of the order Chiroptera, the European mole *Talpa europaea*, and rats, all of which rarely attract tourists, due to negative perceptions, nocturnal behaviour, and/or subterranean habits (Knight, 2008). Domesticated cattle and feral sheep were also excluded. British Red List status was unavailable for 13 non-native mammals, and the wild boar *Sus scrofa* was classed as 'Data Deficient'. However, apart from the raccoon *Procyon lotor*, which is not yet established in the United Kingdom, these mammals were retained for analyses, both in order to increase sample sizes for mammals, and because non-native mammals are often cited as tourism attractions in the United Kingdom e.g., the red-necked wallaby *Macropus rufogriseus* and reindeer *Rangifer tarandus*. The greater white-toothed shrew *Crocidura russula* and lesser white-toothed shrew *Crocidura suaveolens*, which are not found on the mainland of the United Kingdom, were also removed from analyses.

Nine wildlife tourism guides published since 1984 were used to extract data on key wildlife watching sites, and the species of note at these sites, by MRes student Holly Appleby and BSc student Matilda Taylor of the Durham University Conservation Ecology Group (Table 5.1). These guides were chosen due their focus on the United Kingdom, their popularity as wildlife tourism guidebooks (determined by their being top hits returned by search engines and their winning of awards e.g., Travel Guide Book of the Year), and their comprehensive overview of British wildlife tourism. These data were supplemented with data from British sites mentioned in the broader global guides used in Chapter 2 (see Chapter 1 Table 1.1 for the full list). The British guides, like the global guides, were largely targeted towards generalist wildlife enthusiasts (one guide was targeted towards more specialist tourists interested primarily in dragonflies, but it also mentioned mammals and birds of interest). I explored species *attractiveness* using the total number of guides a species was mentioned in (with reference to a British site) across all guides, using the same procedure outlined in the Chapter 2 Methods.

Table 5.1: List of the British wildlife tourism guides from which species mentions were recorded.

British wildlife tourism guides
Dudley, S., Dudley, C. and Mackay, A. (2007) *Watching British Dragonflies*. Shrewsbury, UK: Subuteo Natural History Books.
Hywel-Davies, J. and Thom, V. (1984) *The Macmillan Guide to Britain's Nature Reserves*. London, UK: Macmillan.
Lowen, J. (2016) *A Summer of British Wildlife*. Chalfont St Peter, UK: Bradt Travel Guides.
Ordanance Survey (1989) *Nature Atlas of Great Britain, Ireland and the Channel Isles*. London, UK: Duncan Petersen Publishing.
Regan, P. (2009) *Where to go wild in Britain, A month-by-month guide to the UK's best wildlife experiences*. London, UK: Dorling Kindersley.
Somerville, C. (2013) *Where to See Wildlife in Britain and Ireland*. London, UK: HarperCollins.
Taylor, M. (2009) *RSPB Where to Discover Nature*. London, UK: Helm.
Tipling, D. (1996) *Top Birding Spots in Britain and Ireland*. London, UK: HarperCollins.
Walters, M. and Gibbons, B. (2003) *Britain: Travellers' Nature Guide*. Oxford, UK: Oxford University Press.

For all species of interest, various traits and range attributes, outlined in Chapter 2, were collated, including 1) body mass; 2) extinction risk; 3) evolutionary distinctiveness; 4) habitat association; 5) trophic level; 6) time partitioning; 6) sociality in mammals; 7) coloniality among birds; and 8) migration tendency among birds. For a description of how these data were obtained, see the Methods section of Chapter 2. Gaps in body mass information on three bird species in the global dataset – the common kingfisher *Alcedo atthis*, common firecrest *Regulus ignicapilla*, and Egyptian goose *Alopochen aegyptiaca* – were filled in using data from Cramp and Perrins (1978-1994).

In addition to these attributes, the smaller scale of this study enabled me to include a number of other traits expected to influence species *attractiveness*, including 9) colour richness; 10) bright or iridescent colouration in birds; the presence of 11) unusual appendages; 12) adornments; and 13) distinct patterning; 14) range size within the United Kingdom; 15) British status (i.e., whether the species is native or introduced); 16) conservation status within the United Kingdom; and 17) UK Biodiversity Action Plan (BAP) status (i.e., whether the species is listed as a conservation priority).

The physical attribute data for birds and mammals were extracted from illustrations from del Hoyo and Collar (2014-2016) and the Handbook of the Mammals of the World series (Wilson, Mittermeier, et al., 2009-2019) by H. Appleby (birds) and Laidlaw Scholar Edward Hart (mammals), both from the Durham University Conservation Ecology Group. The attributes were chosen to reflect aesthetic features known e.g., colouration and patterning (Frynta et al., 2010; Lišková and Frynta, 2013; Macdonald, Gallagher, et al., 2017; Prokop and Fančovičová, 2013; Stokes, 2007), or suspected e.g., unusual or distinctive adornments and appendages (Macdonald, Burnham, et al., 2015), to influence species attractiveness or charisma. Male illustrations of each species were used to derive physical attribute data, because, with very few exceptions e.g., the dotterel *Eudromias morinellus*, they tend to be the most brightly coloured, ornately patterned, and ornamented of the sexes.

The number of distinct colours on a species was recorded, including colouration on fur, bare skin, or other features, as a measure of colour richness. The World Bank's Poverty Gap Index (Haughton and Khandker, 2009) was modified into a Bright Colour Index (BCI) for each bird species, to capture the effect of bright and iridescent colouration (Macdonald, Burnham, et al., 2015). BCI was calculated using the following formula:

$$BCI = \frac{1}{N}\sum_{j=1}^{q}\frac{4-y_j}{4}$$

where N is the sum of colour values expressed by a species, ranging on an intensity scale from dark (1), dull (2), pale (3), medium (4), bright (5), to iridescent (6), q is the total number of colours above the medium intensity value of 4, and y_j is the value of the colour j that is above the medium intensity value of 4. The BCI therefore considers how far plumage colouration exceeds a threshold level of brightness or iridescence. BCI was not calculated for mammals, which generally do not exhibit bright colours or iridescence. Appendix Fig. D.1 provides examples of two bird species with high and low BCI values.

The presence of one or more of the following features was used to identify distinct patterning: prominent patches, head patterning, vermiculation (i.e., surface pattern of dense but irregular lines), spots, stripes, streaks, and speckles. The presence of unusual appendages was determined by one or more of the following features: large bill (approximately body length, excluding the tail and neck, or longer) for birds; large eyes (25% of the length between the muzzle tip and the base of the pinna i.e., the outer part of the ear) and large ears (length $>$ 50% of the surface area of half of the face) for mammals (see Appendix Figs. D.2 & D.3); and long legs, neck, or tail (approximately body length or longer) for both birds and mammals. Unusual adornments were identified on the basis of one or more of the following features: crest, ornamental bill, ornamental feathers, wattle (i.e., external fleshy growth), hackles (i.e., long neck feathers), frontal shield (i.e., rounded knob on forehead extending above bill), and gular pouch (i.e., bare skin connecting the beak to the neck, forming a pouch) among birds; and horns, antlers, and an elongated proboscis, among mammals.

British range size was calculated as the number of 10km x 10km grid cells that each bird and mammal species occupied, using data from the Bird Atlas 2007–2011 (BA2010 and WA2010; Balmer et al., 2013) and the National Biodiversity Network Atlas (NBN, 2020), respectively. I used mammal occurrence data from 2007 onwards, to coincide with the most recent bird surveys. The national extinction risk of British species was obtained from the Birds of Conservation Concern dataset (Eaton et al., 2015), which categorises species' levels of risk ranging on a continuous scale from 'Green' (1), to 'Amber' (2), to 'Red' (3), and from the UK Mammal List, which categorises species from 'Least Concern' (1) to 'Critically Endangered' (5). I assigned an extinction risk value of zero to non-native mammals with no relevant British extinction risk. I used the global extinction risk, based on the International Union for Conservation of Nature (IUCN) Red List, to fill in the gap for the wild boar *S. scrofa*, which is classed as 'Data Deficient' within the United Kingdom (i.e., its status is unknown). I recorded whether species were native to the United Kingdom or introduced, using information from the BTO (2020) and The Mammal Society (2019). Species listed as UK BAP priorities were obtained from the Joint Nature Conservation Committee (JNCC, 2019). These variables were included to explore suggestions that locally rare or threatened species are more attractive to tourists (Grünewald et al., 2016; Maciejewski and Kerley, 2014b; Okello et al., 2008).

5.3.2. Data analysis

Log_{10}-transformations were applied to body mass and range size prior to analysis to adjust for non-linear relationships and reduce the leverage of a relatively small number of large, wide-ranging species. I did not include British status in the bird model; only seven species were classed as 'introduced'. I included a metric that reflects both temporal and spatial availability of viewing opportunities in the bird model, by dividing range sizes into breeding and wintering ranges, and multiplying each measure by the length of each season, hereafter referred to as 'spatio-temporal availability'. Mammals do not exhibit the same degree of seasonality (apart from the hedgehog *Erinaceus europaeus* and dormouse *Muscardinus avellanarius*, which hibernate during the winter), so I simply included range size as a predictor variable in the mammal model. I included quadratic terms for these range attributes, but in the case of mammals, this term was non-significant ($P = 0.38$), so was removed from analyses. I excluded primary habitat and global extinction risk from the mammal model, because of the large number of possible predictor variables relative to the mammal sample size and a lack of variability among these traits; 76%, ($n = 29$) of mammal species were associated with forest habitats and 90% ($n = 34$) were classified as 'Least Concern'. Covariates were centred and standardised to a mean of zero and a standard deviation of one to improve the interpretability of parameter estimates. I assessed collinearity between predictors using Variance Inflation Factors (VIFs) in the 'car' package in R (Fox et al., 2020). No analysis reported VIFs greater than seven, suggesting multicollinearity was not a concern (Zuur et al., 2010).

To explore the relationship between the number of guides a species was mentioned in (i.e., observed *attractiveness* scores) and potential explanatory variables, I fit generalised linear models (GLMs) to the bird and mammal datasets in R Version 3.6.0 (R Development Core Team, 2018). After aligning taxonomies to the bird taxonomy used by Jetz, Thomas, Joy, Hartmann, et al. (2012) and the mammal taxonomy of Wilson and Reeder (2005), model residuals were tested for phylogenetic signal using the R package 'phytools' (Revell, 2020). The results indicated that data points were independent of each other, despite relatedness between species ($P \geq 0.58$). There was no evidence of over-dispersion ($P = 1$) (Cameron and Trivedi, 1990), or zero-inflation (all species were mentioned at least once by a guide).

Sample sizes of the British datasets were relatively small compared with the global datasets analysed in Chapter 2. I therefore used the 'MuMIn' package (Bartoń, 2020) to explore all possible combinations of explanatory variables and produce a set of parsimonious candidate models that achieve good predictive power with as few predictor variables, thereby minimizing the risk of overfitting models. I used a cut-off of $\Delta_i \leq 2$ to select the 'top-performing' models (Richards, 2008; Richards, Whittingham, et al., 2011), where Δ_i is the difference in the corrected Akaike information criterion (AICc) between model i and the top ranked model (i.e., AICc$_i$ -AICc$_{top}$). For each predictor, full model-averaged parameter estimates were estimated to account for model selection uncertainty (Lukas and Clutton-Brock, 2009). Because of possible biases in relying on model-averaged estimates for inference (Richards, 2008; Richards, Whittingham, et al., 2011), I also report parameter estimates for the predictors in the full (i.e. the model with all variables included) and top (i.e., $\Delta_i = 0$) models. I considered only combinations of mammal models with less than six model parameters to avoid overfitting. For birds, I only retained models that included the quadratic term of spatio-temporal availability if its linear term was present. I calculated Nagelkerke's R^2, using the package 'rcompanion' (Mangiafico, 2020), as a measure of goodness-of-fit. This pseudo-R^2 is used to estimate the proportion of variance in the response variable that is explained by the predictor variables for GLMs, with larger R^2 values indicating better model fit, and a maximum value of one (Nagelkerke, 1991).

I predicted the *attractiveness* of species using the model-averaged parameters i.e., I made predictions using each model in the subset of top-performing models (all models of $\Delta_i \leq 2$) and multiplied these by the models' Akaike weights (Cade, 2015; Harrison et al., 2018). I explored spatial patterns of bird and mammal *attractiveness* by combining predicted *attractiveness* with species distribution data from Balmer et al. (2013) and the NBN (2020), respectively. I highlighted hotspots for wildlife tourism by mapping summed predicted *attractiveness* scores of all species present in each 10km^2 grid cell across Great Britain. I also explored spatial patterns of the *attractiveness* of a subset of rarer species (see Appendix Table D.1), defined as those with range sizes of $\leq$ 1,000 equal-area grid cells, to identify hotspots that might be masked by the distributions of widespread species. Northern Ireland and the Channel Islands were excluded from these maps because of limited ecological data availability and comparability on species occurrences, resulting from different data collection methods and scales (Christie, 2011; Jackson and Gaston, 2008).

I explored how the distribution of *attractive* species might influence the wildlife tourism potential of British terrestrial and coastal PAs by extracting the mean cumulative *attractiveness* of grid cells located within the PA boundaries using the ‘raster’ package in R (Hijmans, Etten, et al., 2020); summed cumulative *attractiveness* was expected to create a bias towards larger PAs covering a larger number of grid cells. I extracted PAs from the World Database of Protected Areas (WDPA, 2018) that had been officially designated, were $> 1\text{km}^2$, and had management categories between II and VI. I also calculated the maximum *attractiveness* of species occurring within PAs to identify those where tourists may be drawn to key species, regardless of the *attractiveness* of the entire species assemblage. I did this separately for all species and a smaller subset of rare species (i.e., breeding range sizes $\leq$ 1,000 grid cells), assuming that the *attractiveness* of rarer species may be more important in tourists’ decision-making than the *attractiveness* of the entire species assemblage. I compared my measures of species *attractiveness* within PAs to visitation statistics for 188 PAs to explore the role of different aspects of biodiversity in British PA visitation. PA visitation data were collated using data from Balmford, Green, et al. (2015) and a range of other sources, obtained through extensive systematic searches using general search engines and by contacting relevant stakeholders from governmental bodies and charity organisations e.g., the RSPB and Natural England (see Chapter 3 Methods for more details on how these data were obtained).

5.4. RESULTS

5.4.1. Predictors of species *attractiveness*

There was considerable model selection uncertainty when comparing candidate models predicting bird *attractiveness*, with substantial support for 53 models. These models included 14 of the 17 variables from the full model (Fig. 5.1) and the same four significant variables, though only five (trophic level, coloniality, British Red List status, spatio-temporal availability and its quadratic term) appeared in all top-performing models, with colour richness also appearing in almost all models (Table 5.2). Models that did not include colour richness all, instead, included body mass.

Five competing models were identified that best explained variation in mammal *attractiveness* and included six of the 13 variables included in the full model and two of the same significant variables – BAP priority status and range size – which were the only variables to appear in all models (Fig. 5.1, Table 5.2). The parameter estimates were relatively consistent across models, with all models indicating strong, positive effects of BAP priority status and range size on mammal *attractiveness* (Table 5.2). However, the presence of unusual appendages, which the full model found to have a significant negative effect, did not appear in any of the top-performing models. In contrast, body mass and British status (i.e., whether the species was native), which was not significant in the full model, emerged as significant, positive predictors of mammal *attractiveness* in the top model, but not after model-averaging. Time partitioning (i.e., nocturnality vs. diurnality) and unusual adornments were the only other variables to be retained after model selection, but their effects were non-significant. Nagelkerke's R^2 values for the mammal models were larger than those of the bird models, indicating greater explanatory power (Table 5.2).

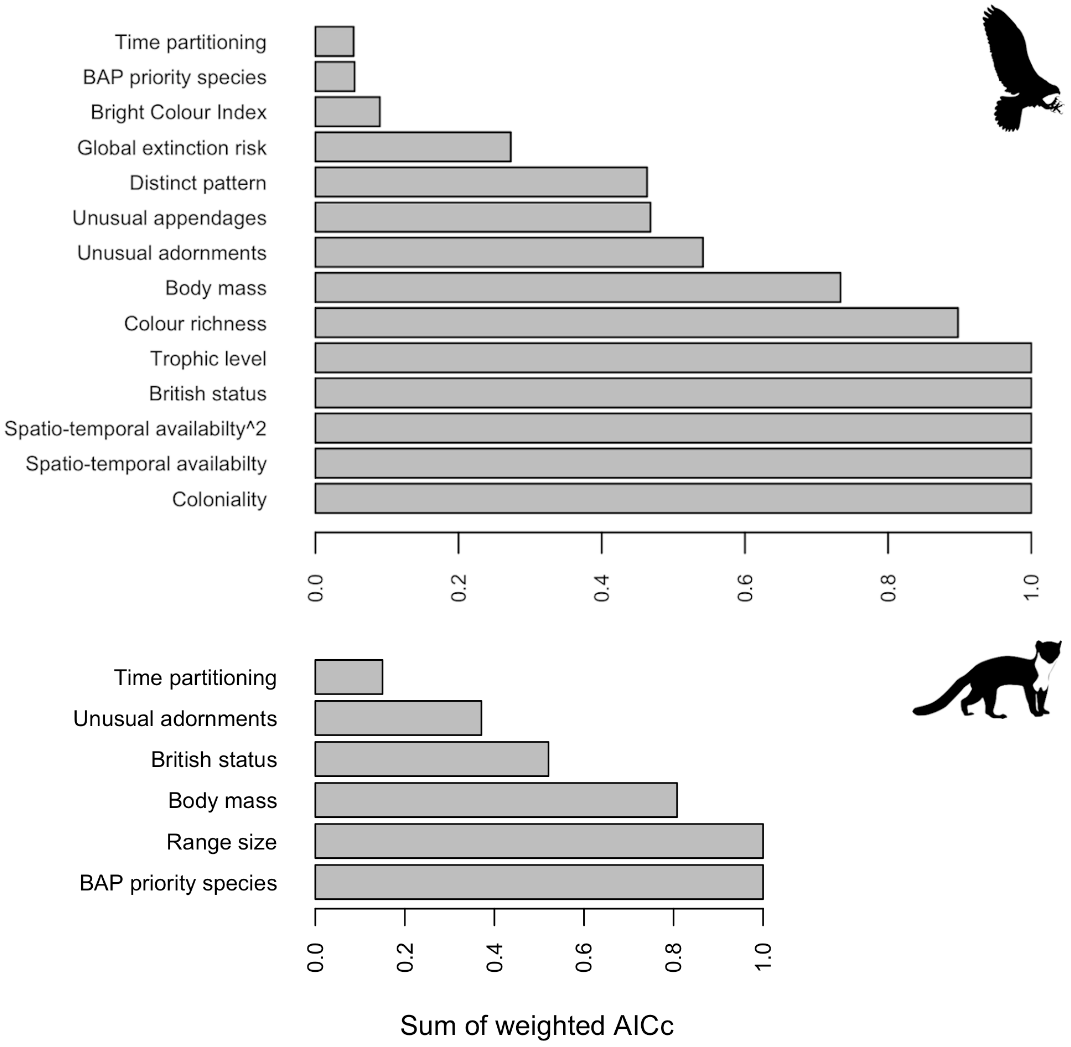

Figure 5.1: The relative importance of each predictor of bird (top) and mammal (bottom) *attractiveness* for British wildlife tourism, as indicated by the sum of model Akaike weights for each predictor variable across top-performing models within $\Delta_i \leq 2$ of the best model. Variables not selected by any of the top models are not shown.

5.4.2. Key species for British wildlife tourism

There were 29,743 mentions of bird species across all guides. The mean *attractiveness* of birds (i.e., the mean number of guides a species was mentioned in) was 8.30 (SD = 3.60). On the whole, mammals appeared in guides less often than birds, with only 2,244 site-specific mentions and a mean *attractiveness* of 6.74 (SD = 3.76). Seabirds such as the Atlantic puffin *Fratercula arctica*, waders, waterfowl, and the white-tailed sea-eagle *H. albillica*, were predicted to be most *attractive* among birds (Table 5.3). The Eurasian otter *Lutra lutra* was predicted to be the most *attractive* mammal, while other carnivore species and deer, such as red deer *Cervus elaphus*, also scored highly (Table 5.3). Comparisons of observed and predicted *attractiveness* scores revealed notable discrepancies between species' rankings (Fig. 5.2). The iconic golden eagle *Aquila chrysaetos*, for example, which was mentioned frequently in the guides, had relatively low predicted *attractiveness*. In contrast, the Eurasian magpie *Pica pica*, the European hedgehog *E. europaeus*, and the wild boar *S. scrofa* had some of the highest predicted *attractiveness* relative to their observed *attractiveness* scores (Fig. 5.2).

5.4.3. Spatial patterns in species *attractiveness*

British coastal regions, along with inland parts of eastern England, had the highest summed predicted *attractiveness* of birds (Fig. 5.3A). The coast of southern and eastern England emerged as a major hotspot with high predicted *attractiveness* of the most range-restricted bird species (Fig. 5.3B). Aside from northwest Scotland, much of Great Britain had high cumulative predicted *attractiveness* of mammals (Fig. 5.3C), reflecting the widespread distribution of some of the most *attractive* species e.g., the otter *L. lutra*, though high *attractiveness* was concentrated in Norfolk and Suffolk. When focussing on mammals with more restricted ranges, finer-scale hotspots of *attractiveness* emerge, including the Highlands, and the county of Dumfries and Galloway, in Scotland, the Forest of Dean, Norfolk and Suffolk in the south of England, and much of Wales (Fig. 5.3D). Spatial patterns of cumulative species *attractiveness* largely reflect patterns in species richness (Pearson's correlation test, $r \geq 0.92$, $P \leq 0.001$).

Table 5.2: Coefficients for predictor variables explaining the *attractiveness* of breeding birds (n = 174) and non-volant terrestrial mammals (n = 38) in the United Kingdom, from the full GLMs, and the final models, based on the best model and a subset of top-performing models within ΔAICc $\leq$ 2 of the best model. Standardized β coefficients, standard errors, and P values for each variable are shown. AICc, Nagelkerke's R^2, and the number of variables (k) for each model are also shown.

Variable	Full model		Top model		Model-averaging	
	β coefficient (±SE)	P	β coefficient (±SE)	P	β coefficient (±SE)	P
Birds						
Migratory behaviour (1-4)	-0.00 (0.03)	0.879	–	–	–	–
BAP species	-0.06 (0.08)	0.442	–	–	0.00 (0.02)	0.885
Global extinction risk (1-5)	0.04 (0.04)	0.222	–	–	0.01 (0.03)	0.660
Spatio-temporal availability	0.06 (0.06)	0.277	0.06 (0.05)	0.301	0.05 (0.05)	0.337
Spatio-temporal availability^2	-0.16 (0.06)	**0.005**	-0.18 (0.05)	**0.001**	-0.18 (0.05)	**0.001**
Evolutionary distinctiveness	-0.00 (0.02)	0.861	–	–	–	–
Log$_{10}$ body mass (g)	0.03 (0.03)	0.349	0.06 (0.03)	**0.034**	0.04 (0.04)	0.256
British Red List (1-3)	0.07 (0.03)	**0.018**	0.07 (0.03)	**0.008**	0.07 (0.03)	**0.011**
BCI	-0.03 (0.03)	0.359	–	–	0.00 (0.01)	0.836
Colour richness	-0.06 (0.03)	0.067	–0.06 (0.03)	0.052	-0.06 (0.03)	0.105
Distinct pattern	0.15 (0.11)	0.145	0.16 (0.10)	0.118	0.07 (0.10)	0.505
Unusual appendages	-0.16 (0.10)	0.098	–	–	-0.06 (0.09)	0.495
Unusual adornments	0.15 (0.09)	0.101	–	–	0.08 (0.10)	0.420
Colonial	0.17 (0.06)	**0.005**	0.16 (0.05)	**0.003**	0.16 (0.06)	**0.005**
Diurnal	-0.09 (0.12)	0.473	–	–	-0.01 (0.04)	0.883
Omnivore	0.19 (0.10)	0.050	0.19 (0.09)	**0.034**	0.18 (0.09)	0.052
Carnivore	0.28 (0.08)	**0.001**	0.29 (0.07)	**<0.001**	0.28 (0.08)	**<0.001**
Bare habitat	-0.18 (0.14)	0.192	–	–	–	–
Forest	-0.13 (0.10)	0.219	–	–	–	–
Shrubland	-0.18 (0.13)	0.180	–	–	–	–

Variable	Full model		Top model		Model-averaging	
	β coefficient ($\pm$SE)	P	β coefficient ($\pm$SE)	P	β coefficient ($\pm$SE)	P
Artificial habitat	-0.25 (0.13)	0.065	–	–	–	–
Aquatic habitat	-0.09 (0.10)	0.348	–	–	–	–
AICc	862.57		853.45		–	
Nagelkerke's R^2	0.45		0.41		–	
k	17		7		14	
Mammals						
BAP species	0.52 (0.22)	**0.020**	0.32 (0.13)	**0.012**	0.42 (0.16)	**0.010**
Native	0.34 (0.21)	0.086	0.29 (0.14)	**0.043**	0.17 (0.20)	0.3940
Log_{10} range size (# grid cells)	0.25 (0.10)	**0.016**	0.30 (0.08)	**<0.001**	0.30 (0.09)	**0.001**
Evolutionary distinctiveness	0.09 (0.08)	0.263	–	–	–	–
Log_{10} body mass (kg)	0.28 (0.16)	0.081	0.35 (0.07)	**<0.001**	0.26 (0.15)	0.082
British Red List (1-5)	0.03 (0.10)	0.757	–	–	–	–
Colour richness	0.20 (0.11)	0.072	–	–	–	–
Distinct pattern	-0.19 (0.19)	0.320	–	–	–	–
Unusual appendages	-0.38 (0.17)	**0.022**	–	–	–	–
Unusual adornments	0.23 (0.34)	0.493	–	–	0.23 (0.36)	0.521
Group living	0.26 (0.25)	0.305	–	–	–	–
Diurnal	0.45 (0.26)	0.080	–	–	0.03 (0.09)	0.729
Omnivore	0.22 (0.25)	0.377	–	–	–	–
Carnivore	0.37 (0.28)	0.181	–	–	–	–
AICc	193.36		188.19		–	
Nagelkerke's R^2	0.82		0.73		–	
k	13		4		6	

Table 5.3: The observed and predicted *attractiveness* scores of the top 15 most *attractive* breeding birds and non-volant terrestrial mammals in the United Kingdom based on predicted number of wildlife tourism guides citing species as attractions.

Common name	Scientific name	Order	*Attractiveness* score	
			Observed	Predicted
Birds				
Atlantic puffin	*Fratercula arctica*	Charadriiformes	23	16.41
European shag	*Phalacrocorax aristotelis*	Suliformes	15	16.16
Northern gannet	*Morus bassanus*	Suliformes	21	15.65
Arctic jaeger	*Stercorarius parasiticus*	Charadriiformes	16	14.52
Razorbill	*Alca torda*	Charadriiformes	19	14.48
Common murre	*Uria aalge*	Charadriiformes	21	14.25
White-tailed sea-eagle	*Haliaeetus albicilla*	Accipitriformes	11	14.05
Common eider	*Somateria mollissima*	Anseriformes	13	14.03
Common tern	*Sterna hirundo*	Charadriiformes	11	13.40
Sandwich tern	*Thalasseus sandvicensis*	Charadriiformes	11	13.40
Arctic tern	*Sterna paradisaea*	Charadriiformes	16	13.39
Pied avocet	*Recurvirostra avosetta*	Charadriiformes	12	13.32
Black-tailed godwit	*Limosa limosa*	Charadriiformes	10	13.31
Black-necked grebe	*Podiceps nigricollis*	Podicipediformes	7	13.24
Northern fulmar	*Fulmarus glacialis*	Procellariiformes	19	13.21
Mammals				
Eurasian otter	*Lutra lutra*	Carnivora	14	14.03
Red deer	*Cervus elaphus*	Cetartiodactyla	17	13.74
Roe deer	*Capreolus capreolus*	Cetartiodactyla	13	12.27
European hedgehog	*Erinaceus europaeus*	Eulipotyphla	5	10.85
Brown hare	*Lepus europaeus*	Lagomorpha	7	10.62
Red squirrel	*Sciurus vulgaris*	Rodentia	15	10.36
Mountain hare	*Lepus timidus*	Lagomorpha	12	10.23
Fallow deer	*Dama dama*	Cetartiodactyla	10	9.96
European polecat	*Mustela putorius*	Carnivora	7	9.54
Pine marten	*Martes martes*	Carnivora	14	9.53
Wild cat	*Felis silvestris*	Carnivora	10	9.42
European badger	*Meles meles*	Carnivora	12	9.16
Water vole	*Arvicola amphibius*	Rodentia	6	9.10
Reeves' muntjac	*Muntiacus reevesi*	Cetartiodactyla	8	8.73
Sika deer	*Cervus nippon*	Cetartiodactyla	9	8.60

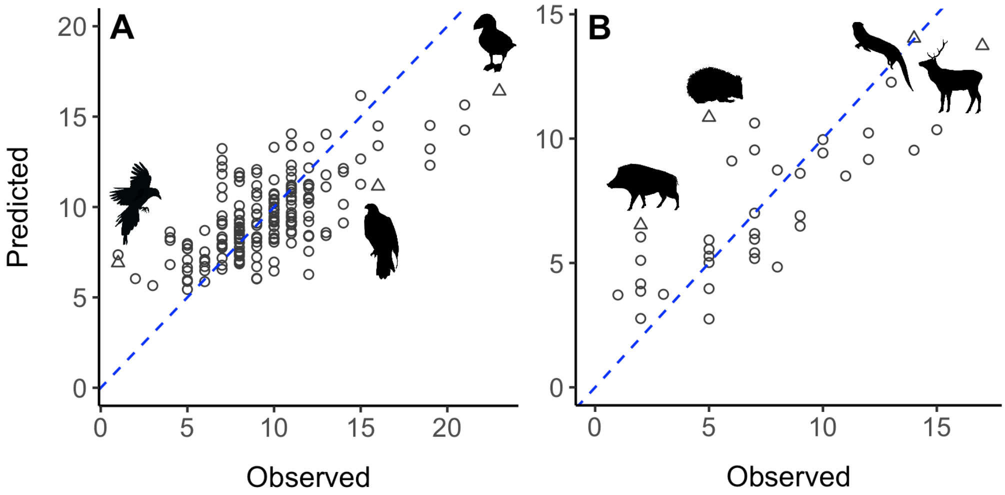

Figure 5.2: The observed and predicted *attractiveness* scores of A **breeding birds and** B **non-volant terrestrial mammals within the United Kingdom**, as determined by the number of wildlife tourism guides a species was mentioned in. The blue dashed line represents a 1:1 relationship between observed and predicted *attractiveness*. Silhouettes are shown for a select few notable species discussed in the text and shown in the plots as triangles, including **A** the Eurasian magpie *Pica pica*; the golden eagle *Aquila chrysaetos*; and the Atlantic puffin *Fratercula arctica*; as well as **B** the red deer *Cervus elaphus*; European otter *Lutra lutra*, the European hedgehog *Erinaceus europaeus*; and the wild boar *Sus scrofa*.

5.4.4. The *attractiveness* of British PAs

The mean *attractiveness* of a PA's entire species assemblages was strongly correlated with that of rare species (Appendix Fig. D.6), particularly for birds. PAs across Southern England scored highly in mean *attractiveness*, with highest scores in PAs in Norfolk and Suffolk (Fig. 5.4), particularly in coastal PAs, such as the RSPB's renowned Minsmere Nature Reserve on the Norfolk Coast. PAs in Wales, and along the Welsh-England border, as well as in the Scottish Highlands, particularly around the Cairngorms, also scored particularly highly for mammals. The widespread nature of some of the most *attractive* species e.g., the otter *L. lutra* resulted in many PAs having similarly high maximum *attractiveness* of all species. For visual purposes, Fig. 5.4B & 5.4D therefore display maximum *attractiveness* values of rare species ($\leq$ 1,000 grid cells). PAs of the Scottish Highlands and islands had high maximum *attractiveness* values, particularly for mammals. The Peak District National Park and Forest of Bowland Area of Natural Outstanding Beauty, in Central England, also scored highly in maximum *attractiveness* of mammals. PAs along the entire coast of Great Britain had the highest maximum *attractiveness* of birds.

The mean *attractiveness* of species occurring within a PA was not correlated with visitation

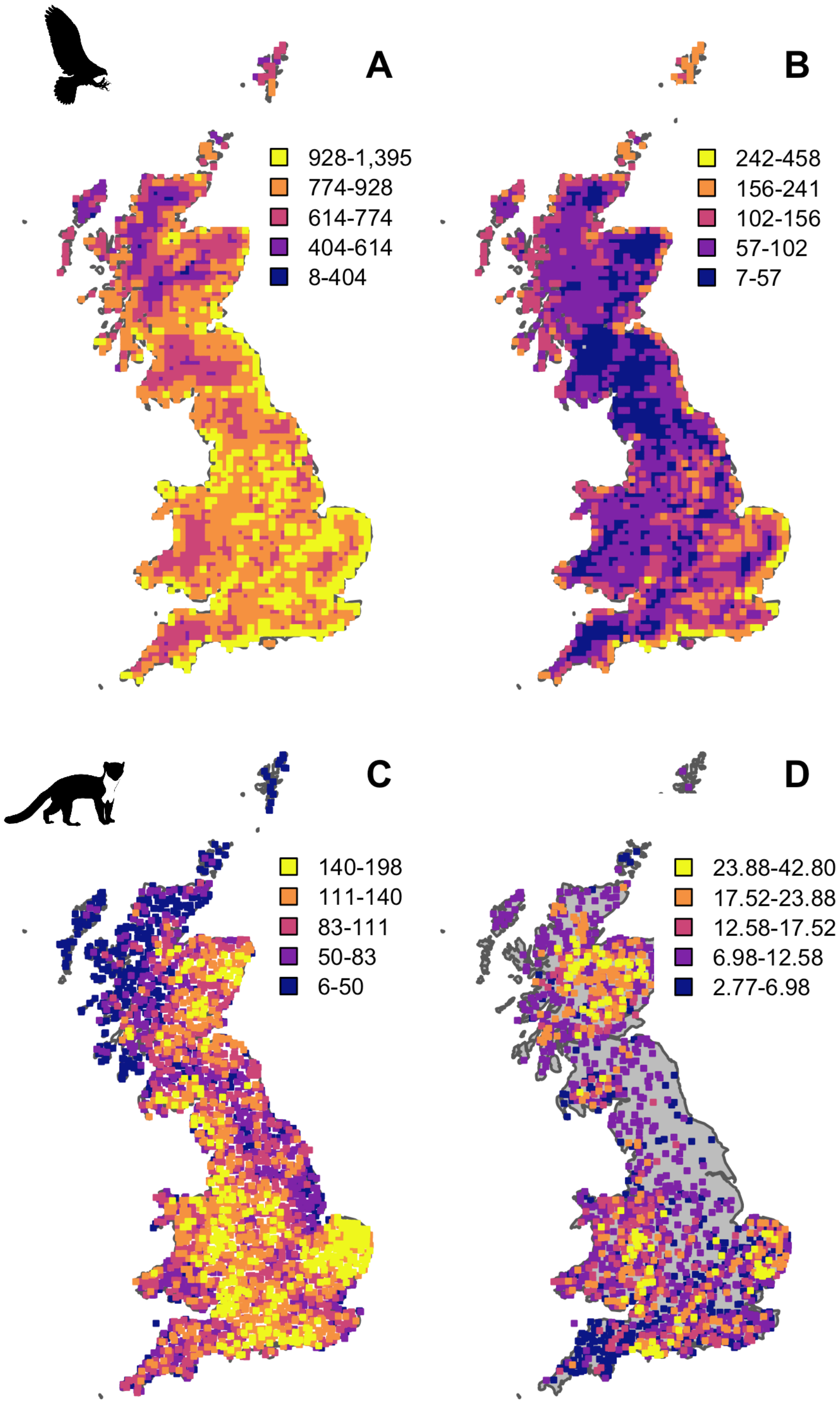

Figure 5.3: Spatial patterns of species *attractiveness* in Great Britain, showing cumulative *attractiveness* of all **A** breeding birds (n = 182) and **C** non-volant terrestrial mammals (n = 38) in each 10km^2 grid cell, and rare **B** birds (n = 84) and **D** mammals (n = 16), defined as those present in $\leq$ 1,000 equal-area grid cells, listed in Appendix Table D.1. Species *attractiveness* was predicted using the top GLMs within ΔAICc $\leq$ 2 of the best model. Jenks natural breaks were used to determine break points for the colour scale. Grey areas in **D** represent areas with no rare species.

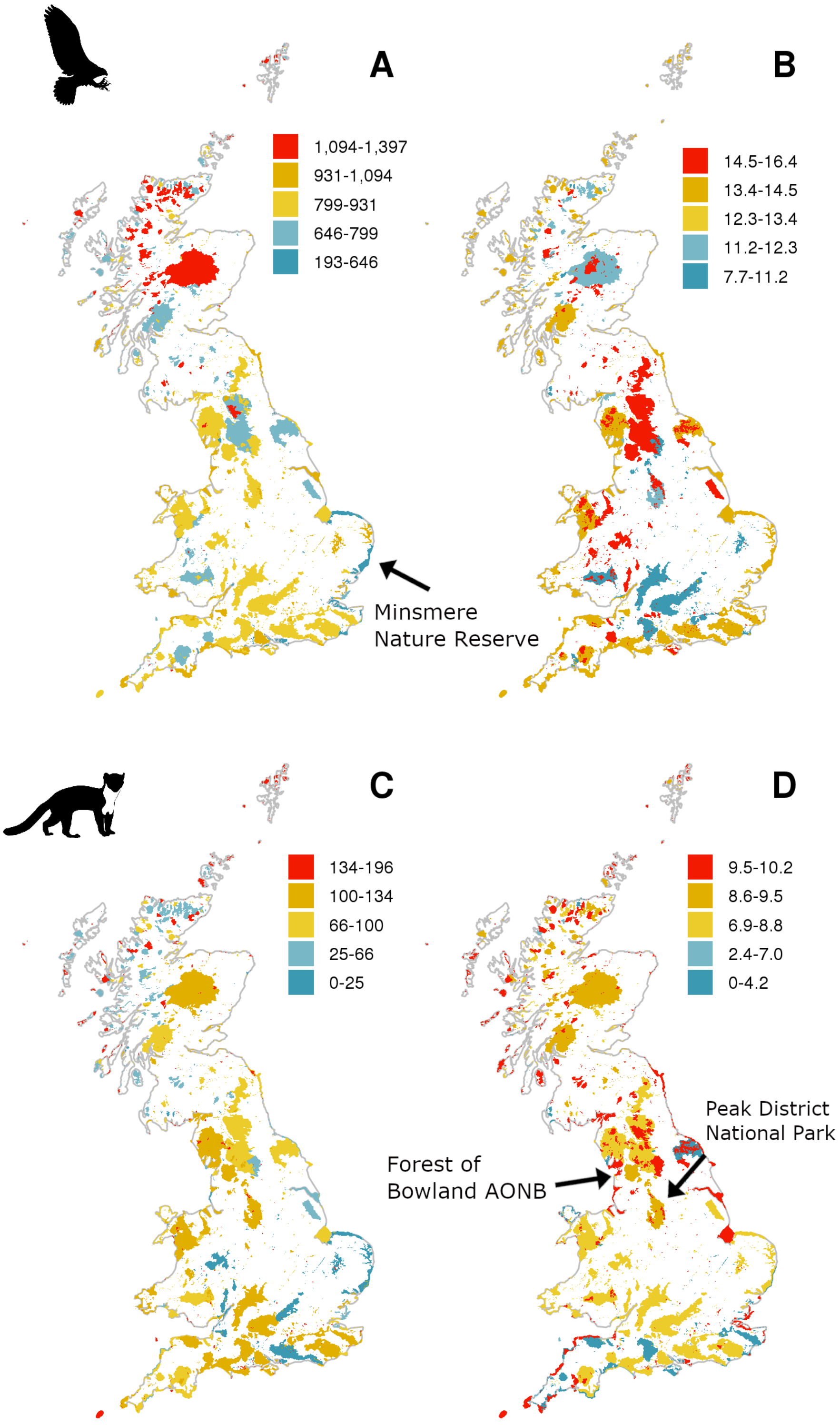

Figure 5.4: Bird and mammal *attractiveness* within British terrestrial and coastal PAs (n = 2,137), calculated as the **A** & **C** mean cumulative *attractiveness* of all species and **B** & **D** maximum *attractiveness* of rare species occurring within equal-area grid cells located within or intersecting the boundaries of the PAs. PAs discussed in the text are labelled: Minsmere Nature Reserve, Peak District National Park, and Forest of Bowland Area of Outstanding Natural Beauty.

($P \geq 0.065$), except when measuring *attractiveness* of rare mammals, which revealed a slight negative correlation (τb = -0.11, $P = 0.036$) (Appendix D.6). However, the latter may more be an artefact of size; PAs with greater *attractiveness* of rare species tended to be smaller (τb = -0.18, $P \leq 0.001$) and size was positively correlated with visitation (τb = 0.32, $P \leq 0.001$). There was no significant correlation between the maximum *attractiveness* scores of mammals and PA visitor numbers ($P \geq 0.103$), but maximum *attractiveness* values of birds occurring in a PA were significantly correlated with visitation, both when including all birds (τb = 1.64, $P = 0.002$) and only rarer birds (τb = 1.31, $P = 0.011$) (Appendix D.6).

5.5. DISCUSSION

5.5.1. Determinants of species *attractiveness*

The results from this study provide novel insights into the characteristics of British wildlife that influence their *attractiveness* to tourists, supplementing those, from Chapter 2, of the global drivers of wildlife tourism. In general, people visiting the United Kingdom seemed to prefer colonial, predatory birds of conservation concern, with medium viewing availability (i.e., not too rare, not too common). In contrast, large-bodied, wide-ranging, native mammals of conservation priority tended to be most *attractive* to tourists.

The most influential factor in determining bird *attractiveness* was trophic level, with carnivorous (and perhaps omnivorous) birds being substantially more *attractive* than herbivores. The attractiveness of carnivores has been attributed to the excitement or appeal of watching predatory animals engaging in interesting behaviours, such as hunting or diving for fish (Lišková and Frynta, 2013; Tremblay, 2002). Energetics of trophic level transfers also means that carnivores tend to be less common than herbivores, and therefore their rarity may make them even more attractive to tourists. No effect of trophic level was found in the global analysis (see Results in Chapter 2), suggesting that a preference for carnivorous birds is not universal. The lack of an effect of trophic level on mammal *attractiveness* in the United Kingdom might have to do with many carnivores being small and/or nocturnal species e.g., shrews, as well as stoats and weasels *Mustela* spp., and an absence of our formerly native large, charismatic carnivores e.g., Eurasian lynx *Lynx lynx* and wolves *Canius lupus*.

Indeed, the top-ranking model for each taxon, which excluded potentially confounding variables (e.g., trophic level for mammals and unusual adornments for birds), revealed body mass to have a strong, positive influence on *attractiveness*, adding to the growing body of evidence that large animals are attractive to tourists (Clucas et al., 2008; Di Minin et al., 2012; Maciejewski and Kerley, 2014a; Okello et al., 2008). In contrast, while nocturnal habits may have limited the *attractiveness* of carnivorous mammals, it did not directly detract from the *attractiveness* of either taxon in the United Kingdom (i.e., nocturnal species were no less *attractive* than diurnal species), contradicting global patterns. This could reflect the attractiveness of nocturnal species in the United Kingdom like the hedgehog *E. europaeus*, which was voted the United Kingdom's 'national wildlife emblem', the European badger *Meles meles* (the runner up) (Nuwer, 2013), as well as the few nocturnal birds e.g., owls.

Coloniality had a relatively strong, positive effect on bird *attractiveness*. This is consistent with global patterns identified in Chapter 2. Less than 5% of citations were obtained from global guides (n = 1,199), suggesting that the overwhelming *attractiveness* of seabirds was not an artefact of the inclusion of these guides, which might have been expected given the international reputation for the UK's seabird colonies (RSPB, 2021a). Contrasting the strong effect at the global level, social grouping had no effect on mammal *attractiveness* in the United Kingdom. This might reflect the rarity of large congregations of mammals in the United Kingdom, compared to those of birds, which nest in colonies of thousands of individuals, and also compared to the large aggregations of mammals seen in places such as the African savanna, where thousands of ungulates come together for annual migrations. Thus, while deer may be a popular attraction in the United Kingdom, the small herds they form, of up to ~40 individuals, may not be contributing to their *attractiveness* (The Mammal Society, 2020).

The physical appearance and colouration of an animal has been suggested to contribute to its aesthetic appeal (Frynta et al., 2010; Lorimer, 2006, 2007; Macdonald, Burnham, et al., 2015; Veríssimo, Fraser, et al., 2009; Veríssimo, Vaughan, et al., 2017). The lack of data available for most of the world's birds and mammals meant that I was unable to explore the role of many physical attributes on species *attractiveness* globally. In this chapter, contrary to expectations, I found no clear evidence that physical attributes or colouration influenced species *attractiveness*. Although the full mammal model (i.e., before model selection) indicated a negative effect of unusual appendages, it was removed from the top-performing models, suggesting it did not strongly influence *attractiveness*. Instead, it may reflect the prevalence of such features in rodents e.g., mice, which rarely attract tourists due to their small size and nocturnal behaviour. Other factors not explored in this study may be more important e.g., forward-facing eyes or 'cuteness' (Macdonald, Burnham, et al., 2015).

There was some evidence from Chapter 2 that supports the notion that range-restricted species (such as endemics) are of great interest to tourists (Veríssimo, Fraser, et al., 2009). In the United Kingdom, however, widespread mammals appeared to be more *attractive*. The *attractiveness* of widespread mammals may have been artificially inflated by my methodology, in which widespread species may have been mentioned by more guides simply because they are present at a greater number of sites. Nevertheless, it is possible that range-restricted mammals may be less *attractive* to tourists in the United Kingdom because many of those with the smallest ranges are non-native to the United Kingdom e.g., the reindeer *R. tarandus*, which my results indicated could make them less *attractive* to tourists. The *attractiveness* of wide-ranging species could also be put down to the ease of observing them in the wild, relative to more range-restricted species. For instance, the Scottish wildcat *Felis silvestris*, restricted to a few locations in Scotland, is notoriously difficult to see (despite this, it was in the top 15 most *attractive* British mammals, see Table 5.3). Furthermore, range size data for British species may not necessarily reflect rarity (Booth et al., 2011). For example, the otter *L. lutra*, which is now geographically widespread across the United Kingdom, is considered a BAP priority species due to low population densities and fragmented populations, and also perhaps because of its restricted historical distribution. The attributes more indicative of rarity or threat status within the United Kingdom, such as British Red List, BAP status, and global extinction risk, were found to positively influence the *attractiveness* of birds and/or mammals.

I did not find any evidence that migrants were more *attractive* than resident species in the United Kingdom. Some resident birds, such as the black grouse *Lyrurus tetrix*, are well-known to be favoured among tourists, but the removal of rare, passage migrants or wintering species may have led my models to under-estimate the *attractiveness* of bird migrations, considered one of the UK's most impressive natural events (RSPB, 2021b). I also found no effect of evolutionary distinctiveness on the *attractiveness* of British birds and mammals. I suspect that this might reflect a lack of public knowledge about evolutionary unique British species; the Zoological Society of London's EDGE of existence programme is a global conservation initiative that highlights unique focal species around the world and those that are most often used as flagships by the organisation e.g., the shoebill *Balaeniceps rex* and echidnas *Zaglossus* spp., do not occur in the United Kingdom.

Exploration of species residuals (i.e., predicted – observed *attractiveness*) brought about unexpected results, and many British species with the highest residuals, used as a measure of possible overlooked tourism potential in Chapter 2, were deemed unlikely to be very attractive to tourists. Issues associated with using wildlife tourism literature to develop a proxy for species *attractiveness* were discussed in Chapter 2, but I suspect high residuals in this chapter to be indicative of missing predictor variables, that may be more important at the national scale, as opposed to overlooked tourism potential. Of particular note was that species with the highest residuals included those that can often be seen in gardens and cities e.g., the Eurasian magpie *P. pica*. The primary habitat association of each species was included as a predictor in the bird models, but many species often seen in urban areas were not associated with artificial habitats in the BirdLife dataset. The abundance and ease of viewing these species in cities and/or at home means they are probably unlikely to be of great interest to tourists, particularly those visiting rural and natural areas (Baker and Harris, 2007; Cannon et al., 2005), even if they possess traits that otherwise would make them attractive to tourists (e.g., the magpie *P. pica* is relatively large, colourful, and has a long tail). Supplementing the habitat data to incorporate information on which birds can be seen in gardens or urban areas could control for this, and doing so could help shed light on the role of physical attributes in determining species *attractiveness*.

This analysis also did not account for people's perceptions of some species as pests and/or dangerous e.g., the magpie *P. pica* and wild boar *S. scrofa* (Cannon et al., 2005; Chiron and Julliard, 2013; The Mammal Society, 2015). This might have partly contributed to the lower predicted *attractiveness* of range-restricted species, which may have been persecuted in the past, and may still be viewed negatively by some of the general public due to e.g., perceived impacts on people and/or other native wildlife. To some degree, this might indicate overlooked tourism potential, as marketing and educating the public, as well as minimising any negative impacts on local people and/or wildlife, could be an effective way of improving attitudes towards these less popular species (Conejero et al., 2019; Curtin and Papworth, 2018). In the case of the wild boar *S. scrofa*, discrepancies may have arisen from the lack of knowledge regarding its status and distribution within the UK.

Negative residuals indicated relatively low predicted *attractiveness* for species known to be 'iconic' or of great interest for tourists, most notably the golden eagle *A. chrysaetos*. Not incorporating mythological and cultural depictions in the models could partly explain is – the golden eagle *A. chrysaetos* may be particularly well-known and interesting to tourists in the United Kingdom because of its prevalence as a symbol in Western cultures. In addition, as discussed in Chapter 2, the focus of tourism and conservation marketing of select species (e.g., RSPB's 'Project Puffin' and Scotland's 'Big Five', which include the otter *L. lutra*, red deer *C. elaphus*, red squirrel *Sciurus vulgaris* and golden eagle *A. chrysaetos*), and the media in general, could be inflating their *attractiveness* above that which would be expected based on their traits alone.

5.5.2. British wildlife tourism hotspots

The maps produced for this study indicate that large expanses of Great Britain have high wildlife tourism potential based on the presence of *attractive* birds and mammals. These maps were able to flag up sites, including PAs, that are renowned for wildlife watching in the British Isles, including the Cairngorms and Norfolk and Suffolk (Naturetrek, 2020b). The Highlands and islands in Scotland, much of Wales, the southern and eastern coast of England, as well as inland parts of Norfolk and Suffolk, emerged as hotspots of *attractive* species with more restricted-ranges, potentially raising their competitive advantage, if their wildlife viewing opportunities are considered rare and/or unique. Scotland and the entire coast of Great Britain also emerged as having high maximum mammal and bird *attractiveness*, respectively, indicating the presence of key *attractive* species that could be used as tourism flagships. Thus, tourism operators in the Scottish Highlands could (and already do) attract visitors by capitalising on the presence of 'must-see' (or at least 'hope-to-see') species such as the wildcat *F. silvestris*, which cannot be seen elsewhere (DiscoverWildife, 2021).

Previous studies conducted in the UK and Ireland have found that biodiversity can have positive impacts on wildlife tourism, by attracting tourists and encouraging longer visits (Loureiro et al., 2012; White et al., 2017). In this study, visitation to PAs was not correlated with cumulative species *attractiveness*, but it was linked to maximum *attractiveness* scores of bird species occurring within the PA. This might suggests that PA visitor patterns are driven more so by the presence of a few flagship birds than the entire diversity of species. This is consistent with high tourist numbers recorded at strongholds for key *attractive* species, such as the Isle of Mull, home to the white-tailed sea eagle *H. albicilla*. Dyfi National Nature Reserve in Wales, a popular site for viewing the osprey *P. halieatus*, which ranked at #19 in *attractiveness* of British birds, has also recorded high visitor numbers, receiving > 2.5 thousand visitors annually. In contrast, mammal *attractiveness* was not correlated with visitation.

The lack of, or relatively weak correlations, between species *attractiveness* measures and visitation could be reflective of a large proportion of PA visitors who are non-wildlife tourists, visiting PAs for reasons other than to watch wildlife. Indeed, some of the UK's most well-known parks, such as the Peak District and Lake District National Parks, are highly regarded, and even managed, primarily for their landscapes, cultural heritage, and recreational activities, rather than for wildlife (Brown, 2013; Suckall et al., 2009). Factors unrelated to wildlife or nature, such as those explored in Chapter 3, may also influence visitation more strongly. For instance, accessible, densely populated regions of the United Kingdom will have a larger pool of potential local tourists than more remote, sparsely populated regions (Mancini et al., 2019). The size of the PA will also be important, as indicated in Chapter 3, and by correlations in this chapter (see Appendix D.6). Climate is known to be important, with many visitors probably avoiding some of the colder regions in the winter, particularly in Scotland, and biting insects (e.g., midges in Scotland during the warmest periods of the year) are known to be an issue for British tourism (Aylen et al., 2014).

5.5.3. Conservation management implications

PA managers in regions possessing *attractive* species assemblages, or even a few potential flagship species, should incorporate information on species *attractiveness* into general decision-making. Targeted conservation and marketing campaigns based on said information would allow managers to preserve and promote important wildlife tourism assets, encouraging visitation by wildlife tourists (and potentially allowing for higher admission costs), thereby maximising available funds from wildlife tourism for conservation. The growing interest in wildlife from the general public could facilitate the expansion (and redistribution) of wildlife tourism in British PAs (potentially taking pressure off some of the more heavily-visited sites). However, protecting attractive species for tourism is not the sole focus of PAs, and it is vital that other objectives are met, including the protection of less attractive species that are of high conservation value and the preservation of broader biodiversity. A healthy balance should be met to ensure that PAs thrive in the future, not only as tourism destinations, but also as valuable conservation resources.

The results of this study help make an economic argument for wildlife reintroductions by highlighting reintroduced species that have large potential to attract wildlife tourists to sites across the United Kingdom e.g., the white-tailed sea eagle *H. albicilla*, as well as the pine marten *Martes martes* and red squirrel *S. vulgaris* (Seddon et al., 2007). Prospects for reintroductions may be particularly favourable in the United Kingdom, where many large, charismatic species have been extirpated or persecuted in the past (Yalden, 1999). Several reintroduced species, such as the Eurasian beaver *Castor fiber* and the sea eagle *H. albicilla*, are already helping to ‘pay their way’ by boosting tourist footfall at reintroduction sites and bringing about economic benefits for local economies (Auster et al., 2020; Gaywood, 2018; Molloy, 2011).

I was unable to explore the *attractiveness* of former species that are now extinct in the United Kingdom, which could have substantial tourism potential if reintroduced. Furthermore, some species that have only recently been reintroduced to the United Kingdom may have been under-represented in guides; three of the guides focussing on British wildlife tourism were published over 20 years ago and could be considered ‘out of date’ (Cohen et al., 2014). For example, the beaver *C. fiber* was first reintroduced in 2009 (Gaywood, 2018; UK Government, 2020), so the number of guides a beaver could be cited in, and therefore its *attractiveness* index, was limited by the fact that some of the British guides were published before reintroductions took place. The golden eagle *A. chrysaetos*, common crane *Grus grus*, osprey *P. haliaetus*, great bustard *Otis tarda*, lynx *L. lynx*, wolf *C. lupus*, wild boar *S. scrofa* and beaver *C. fiber* are all either subjects of past reintroduction projects or contenders for future reintroductions to the United Kingdom (Rae and Wright, 2020; Taylor, 2015). According to predicted *attractiveness* scores from Chapter 2, these species fall within the top 100 most *attractive* birds and 100 most *attractive* mammals globally.

Of course, as indicated by my research, differences exist between the types of species that are *attractive* at the global and national scale. There is the possibility that these species, at least at the outset, may be even more *attractive* if returned to the United Kingdom, than in countries where they have remained or persisted for longer, if their novelty and rarity adds to their *attractiveness* (Auster et al., 2020). The tourism benefits from reintroduced species may therefore be reduced over time, as the species becomes more widespread. Tourism businesses may be able to plan for this and maintain benefits in the longer term through management and marketing. On the Isle of Mull, white-tailed sea eagles *H. albicilla* are an increasingly important motivation for visiting the area, suggesting their attractiveness has, in fact, grown since their initial reintroduction in 1975 (Molloy, 2011). Further research into the attitudes of tourists visiting the United Kingdom towards candidates for reintroductions, as well as into realised post-reintroduction impacts, is required.

5.6. CONCLUSION

The results of this study indicate that many of the factors identified in Chapter 2 that drive *attractiveness* of birds and mammals for wildlife tourism globally also have an important role in determining the popularity of species in the United Kingdom. However, some differences exist, supporting the notion that tourists preferences are heterogeneous and depend on the type of tourist e.g., international tourists visiting other continents vs. British domestic tourists (Di Minin et al., 2012; Lindsey, Alexander, et al., 2007). I was able to explore the role of physical appearance e.g., colouration and adornments in determining *attractiveness*, thanks to the smaller scale of this study, though I found no evidence that species *attractiveness* was significantly influenced by these traits (Veríssimo, Fraser, et al., 2009). I identified bird and mammal assemblages across the United Kingdom that are most *attractive* to wildlife tourists, helping to inform management and marketing initiatives aimed at maximising the benefits of wildlife tourism and redistributing tourism visitation nationally. The more nuanced factors that might be more influential in domestic tourism, compared with global, international wildlife tourism, such as the ability to see particular species at home, should be explored in greater detail.

Chapter 6

General Discussion

6.1. SYNTHESIS

Mirroring growing demand from today's society, wildlife tourism has been the focus of many recent studies. Collectively, these studies have drawn attention to the wildlife tourist typology (Curtin and Wilkes, 2005; Hvenegaard, 2002); the economic and conservation potential of wildlife tourism development (Di Minin et al., 2013; Lindsey, Alexander, et al., 2007; Puhakka et al., 2011); and wildlife tourist preferences (Guimarães et al., 2015; Hausmann, Toivonen, Slotow, et al., 2017; Maciejewski and Kerley, 2014b). However, notwithstanding this research, there has been little examination of the drivers of wildlife tourism globally.

In this thesis, I use wildlife tourism literature as a novel data source to identify important species that are *attractive* to tourists globally, and at the national scale across the United Kingdom, based on citation frequency by wildlife tourism guides. I also use information from these resources to explore how a range of features of the wildlife tourism experience, including the presence of *attractive* species, influence the *popularity* of protected areas (PAs) for watching wildlife. I emphasize the importance of understanding climate-induced species range shifts and predict their impacts on wildlife tourism. I summarize and discuss the major findings of this thesis and the implications they have for applied conservation and management below. Specifically, I discuss my results in relation to:

1. the traits that make species *attractive* to tourists, defined by the number of wildlife tourism guides citing species as attractions, focussing on birds and non-volant terrestrial mammals,
2. the factors that influence PA *popularity* for wildlife tourism, again defined by guide citation frequency, and
3. the top sites highlighted for their high wildlife tourism potential

I go on to discuss the implications of this research and the potential of wildlife tourism within the context of a changing world, specifically with respect to climatic change. Finally, I outline the application of these results to biodiversity conservation, and to future ecological studies.

6.1.1. What traits make species *attractive* to tourists?

The identification of the factors that influence species attractiveness or charisma is critical for identifying potentially important species and the sites at which they occur, thereby informing the development of marketing and management plans for attracting visitors and ensuring tourist satisfaction (Grünewald et al., 2016; Veríssimo, MacMillan, et al., 2011; Willemen et al., 2015). Moreover, such information could help managers minimize negative ecological impacts, by deflecting pressure away from species and sites that are most heavily sought-after, towards those that are currently overlooked or under-utilised (Okello et al., 2008). Part of a growing body of research, the findings from Chapter 2 add to our current understanding of the birds and mammals that attract tourists, and why. To date, most studies into wildlife tourism preferences have been carried out on a small scale and focus on a subset of species – typically the well-known, large-bodied, charismatic species. Calls have therefore been made for research that explores tourists' interests in a wider range of species (Buckley, 2013). To my knowledge, this is the first such study to be conducted at such a large scale, providing comprehensive analyses of species *attractiveness* to, predominantly, generalist tourists from Western and/or English-speaking countries, that incorporates all bird and non-volant terrestrial mammals worldwide.

From this analysis, I found that body mass was the most influential trait in determining species *attractiveness*, confirming well-documented interest in large-bodied species (Clucas et al., 2008; Di Minin et al., 2012; Maciejewski and Kerley, 2014b; Okello et al., 2008). Species living in social and colonial groups were also found to be more *attractive* than solitary species, particularly in the case of mammals. I found evidence to support the idea that dense vegetation and nocturnality may be an impediment for wildlife viewing (Arbieu, Grünewald, Schleuning, et al., 2017; Grünewald et al., 2016; Reynolds and Braithwaite, 2001; Winterbach et al., 2015). I also found birds occurring in aquatic or bare habitats to be most *attractive*, which could reflect a human affinity towards water or geological formations. I identified complex interactions between the effects of range size, remoteness, and extinction risk on species *attractiveness*, which I propose are indicative of two different types of attractive species: well-known, common, accessible species vs. unfamiliar, rare, and remote species. I also provide the first empirical evidence of the *attractiveness* of evolutionary distinct species and migratory birds for wildlife tourism, as well as the role of politically stability, across the species range, in determining *attractiveness* for wildlife tourism.

In Chapter 5, I conducted similar analyses on a smaller scale, focussing on British wildlife tourism, and it is informative to contrast the species characteristics that are attractive to tourists at the global and national scale. Several factors that were identified as influential in the global analyses had comparable effects on species *attractiveness* for British wildlife tourism, such as coloniality in birds, body mass in mammals, and extinction risk/conservation status.

One notable difference was the apparent *attractiveness* of carnivorous birds in the United Kingdom, which can be attributed partly to the thrill of observing predatory species hunting or fishing (Lišková and Frynta, 2013; Tremblay, 2002). The lack of evidence of this effect at the global scale, or in mammals, suggests that this effect may not be present everywhere. A preference for predatory birds may have been exacerbated in the United Kingdom by the fact that we have eradicated all of our former large mammal carnivores (e.g., wolf *Canis lupus*, bear *Ursus arctos*, lynx *Lynx lynx*), leaving predatory birds as the main remaining large, diurnal predators. Owing to the smaller scale of the British study, I was also able to explore the role of a wider range of physical attributes in species *attractiveness*, but found no clear evidence for their effects.

6.1.2. What factors influence PA *popularity* for wildlife tourism?

The majority of sites (63%) mentioned in wildlife tourism literature are PAs, reflecting their popularity as destinations for wildlife watching. In Chapter 3, I explored the factors that determine which PAs are most *popular*, including the *attractiveness* of species assemblages using predicted *attractiveness* scores from Chapter 2, along with other potentially influential variables identified or implicated by past studies. The subsequent findings provide insight into which destinations have high wildlife tourism potential and therefore should be the focus of tourism investment and management. Overall, *popular* PAs were identified as those with more *attractive* and rarer species assemblages, a wider elevational range and higher availability of water sources, and lower densities of tourism amenities. They also tended to be larger, more accessible, managed under stricter management categories, designated national parks, internationally protected, and located in more politically stable parts of the world. My measures of PA *popularity* explained 25% of the variation in recorded visitor numbers, suggesting that wildlife tourism literature (in this case aimed largely at Western, English-speaking tourists) offers valuable information on PA visitation, serving as an alternative to time-consuming and costly methods of collecting visitor data, particularly when being applied to PAs across large spatial scales.

The results of this chapter have important and novel implications for wildlife tourism management. First, while studies have explored the relationship between species richness (or richness of threatened species) and visitor numbers, my results demonstrate that the *attractiveness* of species assemblages often matters more than simply species numbers. The strong links between PA *popularity* and different components of biodiversity (i.e., species *attractiveness*, species richness, community rarity, and habitat diversity) and management strategies reinforces the economic case for biodiversity conservation and suggests that wildlife tourism and biodiversity conservation can be achieved simultaneously. Second, my models demonstrate that the features influencing tourists' decisions to visit PAs vary geographically, implying that management for tourism purposes may need to be context specific. PA managers and conservation stakeholders could use the information provided in this thesis to tailor tourism marketing and management strategies to maximise wildlife tourist interest, in order to promote and ensure the sustainability of wildlife tourism, including by attracting tourists to sites that lack well-known iconic species.

6.1.3. Priority sites for wildlife tourism

The geographic distribution of *attractive* species worldwide indicates significant and untapped financial opportunities available to countries in sub-Saharan Africa, South America and South East Asia that protect, market, and develop their wildlife assets in the right way. Substantial overlap exists between some of hotspots identified for having high richness of *attractive* species and priority sites identified as targets for biodiversity conservation (Allan et al., 2019; Brooks, Mittermeier, et al., 2006; Mittermeier et al., 2003; Sanderson et al., 2002; Scheffers et al., 2019). These species could serve as flagships for these places, facilitating broad and cost-effective conservation action that could help ensure the survival of vulnerable and important species and habitats. Despite criticism of the flagship approach, a recent paper by McGowan et al. (2020) suggests that such an approach can work, whereby important sites for biodiversity can be prioritised while simultaneously capitalising on the fundraising potential of flagship species.

After taking into account myriad factors that were expected to influence tourists' decisions to visit PAs, including the presence of *attractive* wildlife, as well as safety concerns, remoteness, amenities etc., my results suggest that those located in India and East and Southern Africa, the Peruvian Amazon, and Patagonia, are most suitable for wildlife tourism. The Iberian Peninsula and the western portions of the United States, where species *attractiveness* was slightly lower, were also flagged for their popular PAs. These regions should be prioritised for wildlife tourism investment, as well as management efforts to reduce the risk of over-visitation, in order to capitalise on wildlife tourism opportunities and the benefits they offer for biodiversity conservation and local people.

Unfortunately, with the increasing threat of climate change, some of these priority sites may be at risk of losing their competitive advantage in the tourism market. The main hotspots where species range shifts may cause severe declines in visitation, placing financial strain on tourism economies, include East Africa, the Amazon basin, and the Guianas. By contrast some sites, including montane regions in Africa, South America, and Asia, and the Pampas region of South America, may benefit from climate change due to colonisation by *attractive* species, but environmental impacts of increased visitation may need to be addressed. Sites considered the last 'stronghold' of some species with declining populations, such as the Arctic, may also see increased visitation.

6.2. APPLICATIONS FOR MANAGEMENT

Understanding wildlife tourists' decision-making processes is critical for managing tourism sustainably and responsibly and ensuring it remains a viable economic venture (Eagles and McCool, 2002). The results of my research provide broad insights into the processes influencing wildlife tourism patterns globally, and, together with more fine-scale and reliable data on PA visitor numbers, can help manage visitor behaviour and secure tourism revenue under future climate change, and also minimise the negative impacts of tourism activities.

The results of Chapter 3 suggest that the quality of the wildlife viewing experience at PA could be enhanced by increasing the availability or visibility of preferred species through conservation efforts aimed at protecting or increasing abundances of these species, which may include reintroductions and the preservation of habitats for key species e.g., coastal regions for migratory shorebirds (Amano et al., 2010; Murray et al., 2014; Yang et al., 2017), and also through the creation of viewpoints, hides or nest cameras to increase viewing opportunities of such species. This might lead critics of wildlife tourism to argue that narrow viewing preferences, particularly among less experienced tourists, limits the wildlife tourism potential of PAs that lack preferred species (e.g., charismatic megafauna) (Leader-Williams and Dublin, 2000a). The trait-based analysis of species *attractiveness* from Chapter 2 raises two key points: (1) a wider range of species may attract tourists than originally thought, and (2) some of these species with high tourism potential may currently be under-valued. The major implication of my findings is that it is possible to expand the current list of species that are used to attract a more generalist, less experienced tourist to particular destinations. In doing so, managers could raise the tourism potential of currently under-utilized sites that host overlooked species, but which lack the more high-profile charismatic megafauna, thereby broadening the context in which wildlife tourism represents a viable economic venture that can contribute to biodiversity conservation and local development.

The considerable *attractiveness* of endangered, endemic, and evolutionary distinct species suggests that wildlife tourism may provide valuable funding and economic incentive to help conserve the most vulnerable species. As mentioned, *attractive* species could also serve as tourism flagships, and some may serve as umbrella species (e.g., large, wide-ranging species) potentially promoting the conservation of wider, less-charismatic biodiversity. (Andelman and Fagan, 2000; Li and Pimm, 2016). However, it is important that the risks to vulnerable species and sites from tourism activities are mitigated. Management for wildlife tourism must strike a balance between increasing tourism activity and revenue and ensuring ethical and sustainable tourism activities. The results obtained from Chapter 2 can help managers reduce environmental impacts of tourism by identifying species that will be most heavily sought-after. There is also the concern that rare species that become more common through effective conservation may become less attractive (e.g., white rhinos *Ceratotherium simum* in South Africa, bitterns *Botaurus stellaris* in the UK), potentially diluting tourist income to former refugia for rare species. The finding that more common (and accessible) species represent a potentially different kind of tourism attraction suggests that tourism business may be able to plan for this to maintain benefits in the longer term, through effective management and marketing.

Chapter 2 also provides important implications for tourism marketing. Although there was a strong correlation between observed and predicted species *attractiveness*, the *attractiveness* of a sizeable number of species was under-predicted by my models, suggesting that other factors not explored in this study may also influence *attractiveness*. The identities of some of those species whose *attractiveness* was over- or under-predicted suggests that successful tourism attractions are, to some extent, created or upheld by media exposure, reputation, and familiarity. The species that are often represented by conservation campaigns (Leader-Williams and Dublin, 2000a; Veríssimo, MacMillan, et al., 2011), on commercial products (Macdonald, Burnham, et al., 2015; Smith et al., 2012), or have broad presence across social media and fiction (Di Minin et al., 2013; Macdonald, Burnham, et al., 2015; Veríssimo, Vaughan, et al., 2017) were often mentioned in more guides than would be predicted based on their traits. In contrast, species that have received negative publicity, such as the spotted hyena *Crocuta crocuta*, were among those with high over-estimated *attractiveness*.

The link between media attention, familiarity, and *attractiveness* suggests that public awareness campaigns, targeted advertising, and visitor education might be an effective way of improving people's attitudes towards currently under-rated species, and may be essential to exploit the full suite of potential tourism flagship species (Kerley et al., 2003; Veríssimo, Vaughan, et al., 2017). The creation of new markets for overlooked species would enable managers to open up wildlife tourism opportunities and raise the profile of under-utilized sites, capitalising on under-exploited opportunities and generating greater financial support for conservation, as well as gateway communities. At the same, pressure could be reduced on the more heavily sought-after species and sites (Goodwin and Leader-Williams, 2000). The over-exposure of flagship species can lead to 'flagship fatigue', facilitating shifts in public interest to new, under-appreciated species (Bowen-Jones and Entwistle, 2002), so-called 'Cinderella' species (Smith et al., 2012), simultaneously supporting conservation initiatives and educating the public by raising awareness of wider biodiversity (Goodwin and Leader-Williams, 2000).

Emerging economies, such as those in Asia and South America, whose residents are increasingly visiting conservation areas in their own countries and abroad, could be the targets of marketing campaigns to raise awareness of wider biodiversity and help support alternative markets, expanding the international tourist base beyond the traditional Western target audiences (Balmford, Beresford, et al., 2009). It is also important to start educating the next generation of visitors about broader aspects of biodiversity (Di Minin et al., 2013). Children's perceptions and assumptions about the natural world may be influenced by repeated exposure to media sources, such as Disney films like the Lion King, which may persist into the future, potentially significantly contributing to the negative perception that Western people have today of certain species like spotted hyenas *C. crocuta* (Glickman, 1995).

The management of wildlife for tourism requires an appreciation for local attitudes. Akin to conservation flagship campaigns, focussing tourism initiatives on some species may be locally inappropriate (Bowen-Jones and Entwistle, 2002; Di Minin et al., 2013; Mamo, 2015). For example, tourism based on potentially dangerous species *Panthera tigirs* may be unappealing to local stakeholders and may lead to reduced support for conservation initiatives. Besides changing local attitudes towards such species, the diversity of *attractive* species identified by my research provide flexible options from which managers can choose the most appropriate flagships, that best align with the local ecological and cultural context, to link with conservation initiatives (Bowen-Jones and Entwistle, 2002). Furthermore, ensuring that the economic benefits of tourism reach local people may compensate for wildlife-related impacts, as well as contributing to sustainable development in rural areas. Previous research has demonstrated that rarely are these benefits shared with local stakeholders (see Chapter 1 Section 1.5 for more details) (He et al., 2008; Mbaiwa, 2003; Mbaiwa and Stronza, 2010). Moving beyond strict control of PA budgets by central governments towards new public-private-community partnerships could help channel an important part of the revenue generated from tourism directly to local people living in or around PAs and improve local attitudes towards conservation (Jorge et al., 2013).

Besides the presence of *attractive* wildlife, findings from Chapter 3 revealed other factors that influence tourists' decisions that can inform effective management of PAs globally, so that wildlife tourism benefits can be realised. Protecting larger areas of habitat to sustain a higher diversity of attractive species (and general biodiversity) could be an effective way of both increasing a PA's *popularity* among tourists, and also progressing towards the Aichi PA coverage targets (CBD, 2018). Improving accessibility would also likely increase PA visitation. Promoting peace, coupled with positive coverage in the media, could help create perceptions of formerly unsafe countries as secure destinations, likely leading to increased visitation (Muhoho-Minni and Lubbe, 2017) e.g., as occurred in Rwanda (Maekawa et al., 2013). Some of the implications for PA management are specific to particular continents/regions, but care needs to be taken when considering these. PA managers in the Americas, for example, may be able to attract more tourists by maintaining relatively open landscapes with low vegetation cover, but findings that tourists favour natural landscapes and their associated habitats (Grünewald et al., 2016) suggest that creating or managing artificially open habitats for optimal wildlife viewing, where the natural habitat consists of more dense vegetation, may not be advisable. There was some evidence that, in Europe, managers may be able to increase *popularity* among tourists through developing and improving infrastructure and services, such as accommodation, transport links, wildlife viewing structures e.g., bird hides, but they may need to be careful not to degrade perceptions of ´wildness'.

Any development or management initiative aimed at maximising visitation may be limited by funding (Jackson and Gaston, 2008; Khadaroo and Seetanah, 2008), and could generate a negative environmental impact, including congestion and over-crowding, simultaneously damaging the natural beauty and perceptions of wildness, and also potentially taking money away from conservation (Kanwal et al., 2020). Managers must therefore ensure that development for tourism is done in a sustainable manner. De-marketing (i.e., the use of advertising to decrease demand for a product) may be a useful way of controlling visitors to PAs with excess tourism demand (Armstrong and Kern, 2011), and deflecting tourism pressure towards under-utilised sites (Lindsey, Alexander, et al., 2007). This could involve reducing/changing focal species in marketing; adding to the time and expense necessary for tourists to reach a site; introducing or increasing prices at the site; reducing the level of information in marketing. These approaches could discourage visitation, directing visitor pressure away from an over-crowded site or a vulnerable species. Shifting attention to less well-known, but equally, if not more, attractive species could encourage visitation by specialist or experienced tourists, who are thought to be more environmentally friendly (Buckley, 2013; Di Minin et al., 2013; Hausmann, Toivonen, Slotow, et al., 2017). Infrastructure development may also help manage visitor flows; when tourists are required to enter a PA through e.g., a visitor centre or kiosk, restrictions can be put in place to limit the number of people entering, or lifted to encourage visitation (Leung et al., 2018). A well-known example of such an approach being implemented is in Volcanoes National Park, Rwanda, where visiting mountain gorillas *Gorilla beringei beringei* is strictly controlled and prices have increased over the years. The ethical conundrum is that visitation may be restricted to wealthy tourists, limiting opportunities for less wealthy people to connect with and learn about nature, which may in turn have negative implications for conservation (Bentz et al., 2016; Schuhmann et al., 2016; Skibins et al., 2013).

The dependence of wildlife tourism on nature means that is it particularly vulnerable to the impacts of climate change. Stakeholders in wildlife tourism must therefore adapt to climate-induced changes in species assemblages, ensuring wildlife tourism remains an effective means of financing conservation efforts and sustainable development of local communities (Hannah et al., 2007). Revising current conservation policy and biodiversity management plans will be an essential component of climate change adaptation, which may including enlarging PA coverage and improving connectivity to facilitate migrations; improving management both inside and outside of PAs e.g., drilling for water (Saarinen, Hambira, et al., 2012; Tervo-Kankare et al., 2018); assisted colonisation of species (Willis et al., 2009); and diversifying tourism offerings e.g., hot air balloon safaris and mobile camping to match changing wildlife migration patterns, including offering and promoting non-nature related activities and attractions e.g., astronomy, food, and music (Marshall et al., 2011). Adaptation strategies must be balanced with the often conflicting objectives of mitigation initiatives (Kupika and Nhamo, 2016), which should include greening of accommodation establishments, attempts to reach carbon-neutral tourist destinations, and marketing products towards domestic tourists (see Stelios and Melisidou, 2007).

6.3. FUTURE WORK

6.3.1. Heterogeneous tourist preferences

The majority of guides selected for this study were targeted towards generalist wildlife tourists, predominantly from Western, English-speaking countries. This group represents an unknown, but undoubtedly large, proportion of the global wildlife tourism market (Goodwin, Kent, et al., 1997; Guimarães et al., 2015). However, tourist preferences are known to be diverse and vary between different types of tourists (Di Minin et al., 2013; Hausmann, Toivonen, Slotow, et al., 2017; Lindsey, Alexander, et al., 2007; Okello et al., 2008). More experienced, domestic tourists have been found to be more interested in less charismatic biodiversity than more generalist, international tourists (Di Minin et al., 2012). The inclusion of additional resources (e.g., in-country tour operators of destination countries, Chinese language guidebooks) into subsequent research may help address limitations in the availability of research on non-Western tourists and improve the coverage of under-represented tourism source markets (Cong et al., 2017; Stone and Nyaupane, 2018). The rising middle classes of the world's emerging economies (e.g. China, India, South America and Africa) make up an increasingly important proportion of tourists visiting PAs and should be considered priority markets for research (Karanth and DeFries, 2011; Scholes and Biggs, 2004; Thomsen and Tenney, 2019). Tourist preferences for wildlife experiences are also thought to change over time (Kilungu, Munishi, et al., 2014), suggesting an adaptive approach should be adopted, whereby newly published and up-to-date guides are consulted, to explore tourist preferences over time.

6.3.2. Additional traits and taxa

Additional traits not considered by this study, but which may influence the tourism potential of birds and terrestrial mammal species e.g., familiarity, physical traits, and birdsong (Macdonald, Burnham, et al., 2015), which have been discussed in Chapters 2 & 5, should be incorporated into future research. The attractiveness of other taxa for wildlife tourism should also be considered. The *attractiveness* of some well-known wildlife tourism sites may not have been captured fully by this study because of its focus on birds and terrestrial mammals. Indeed, part of the draw of places like Madagascar, South Africa and Australia, highly regarded for their wildlife watching opportunities, is down to their marine life e.g., whales, dolphins, and sharks. Marine wildlife is also an important component of the United Kingdom's wildlife tourism industry (O'Connor et al., 2009). In other regions, other terrestrial taxa such as reptiles are important components of wildlife tourism (e.g., chameleons in Madagascar, tortoises on the Galapagos Islands, Komodo dragons *Varanus komodoensi* in Indonesia).

6.3.3. Incorporating land-use

The projected species distributions illustrated in Chapter 4 reflect the impacts of climate change on species distributions, irrespective of changes in land-use. Yet land-use change is a major threat to biodiversity (Newbold et al., 2015; Vitousek et al., 1997), which can amplify or exacerbate climate change impacts (Oliver and Morecroft, 2014), and in areas such as the tropics, it may outweigh the threat of climate change for species (Jetz, Wilcove, et al., 2007). The lack of available land-use data matching the global climate models from the Fifth Assessment report, at the time that the climate change projections in this thesis were conducted, precluded the consideration of land-use in species distributions, but land cover and land-use change should ideally be used to refine species distribution projections.

6.3.4. PA visitor monitoring

Chapter 3 involved a comprehensive review of available visitor data for PAs worldwide, which was found to be patchy and inconsistent across regions, reinforcing requests for more consistent visitor monitoring techniques. Visitor numbers, as well as information on carrying capacities, are a crucial piece of information needed for assessing the value, importance, and sustainability of different natural areas for recreation, predicting the impacts of tourists, and assessing the economic contribution of tourism. The lack of accurate PA visitor data is therefore a major obstacle for tourism management and research (Eagles, 2014; Hill and Courtney, 2006). Advancements in automated visitor counting technologies e.g., trail cameras, drones, high resolution satellite imaginary, social media data, mobile phone traffic, and smart phone apps may allow for more accurate and precise visitor estimates at lower costs (Schägner, Maes, et al., 2017).

6.4. WILDLIFE TOURISM DURING A PANDEMIC

There are pressing reasons to invest in communities and conservation areas that protect nature through wildlife tourism – nature loss and unsustainable wildlife consumption are at the root of zoonotic infectious diseases, such as the novel coronavirus, Ebola and HIV/AIDS. The natural world underpins people's survival, well-being and sustainable development, providing clean air, water, food, and jobs, and serving as a 'natural medicine'. Wildlife tourism can provide an economic incentive to preserve large intact areas for conservation, providing an alternative to other human land-use, such as agriculture and bushmeat hunting, which increase contact between people and wildlife and facilitate the spread of zoonotic diseases. Necessary protocols and procedures must be adopted to ensure that wildlife tourism activities do not lead to unsafe interactions with wildlife that can similarly lead to disease outbreaks (e.g., as occurs when viewing primates such as gorillas *Gorilla* spp. and orangutans *Pongo* spp.), which becomes of particular concern when wildlife tourism involves handling animals or animal performances.

The current COVID-19 pandemic also highlights the importance of having long-term financing for conservation and socio-economic development that is not solely dependent on tourism revenue. The World Travel & Tourism Council (Paxton, 2020) estimates that up to 75 million jobs are at risk from the virus, including community game guards, conservancy staff, and those providing goods and services, and anticipates an economic loss of up to US$2.1 trillion. PAs, including those already impacted by e.g., poaching, are being put in greater danger because of job losses in tourism and a reduction in resources for management, threatening local wildlife and communities whose livelihoods depend on tourism (Lindsey, Allan, et al., 2020).

Millions of Indigenous and rural people around the world have long conserved biodiversity not for economic gains, but through cultural values, traditions, and locally rooted livelihoods. For instance, in the East African savannas, wildlife outside of PAs live alongside livestock on land managed and conserved through pastoral grazing systems (Western et al., 2020). These community initiatives are inherently less dependent on tourism revenue, and can actually promote and facilitate tourism operations by protecting biodiversity and maintaining ecosystem functioning, creating a more resilient and efficient form of stewardship. The strength of wildlife tourism should therefore be considered its contribution to a resilient and lasting approach to conservation and to diversify economies, not in being a panacea for conservation and poverty alleviation everywhere.

6.5. CONCLUSIONS

This thesis has contributed to the growing body of research on wildlife tourism and its related activities at the global scale, addressing important gaps identified in the literature. The research I conducted has demonstrated the usefulness and advantages of using wildlife tourism literature to answer questions related to the drivers of wildlife tourism and its implications for conservation and sustainable development, providing information at a wider spatial scale than is feasible using traditional techniques. The key findings include assessing the attributes of bird and mammal species that are *attractive* tourists; the factors that make PAs *popular* wildlife watching destinations and how these vary across continents; priority sites with high wildlife tourism potential; and the potential impacts of climate change on spatial patterns of wildlife tourism. Opportunities exist to enhance the role of wildlife tourism in biodiversity conservation through improved marketing and management. The largely positive relationship between wildlife tourism and different levels or components of biodiversity ensures that prospects for wildlife tourism to contribute to international conservation goals are promising. Next steps should involve research into the values and preferences of a wider range of audiences and greater investment in PA visitor monitoring. Refining climate change projections by including land-use change should provide more accurate insights into wildlife tourism potential in a changing world.

Appendices

Appendix A

Chapter 1

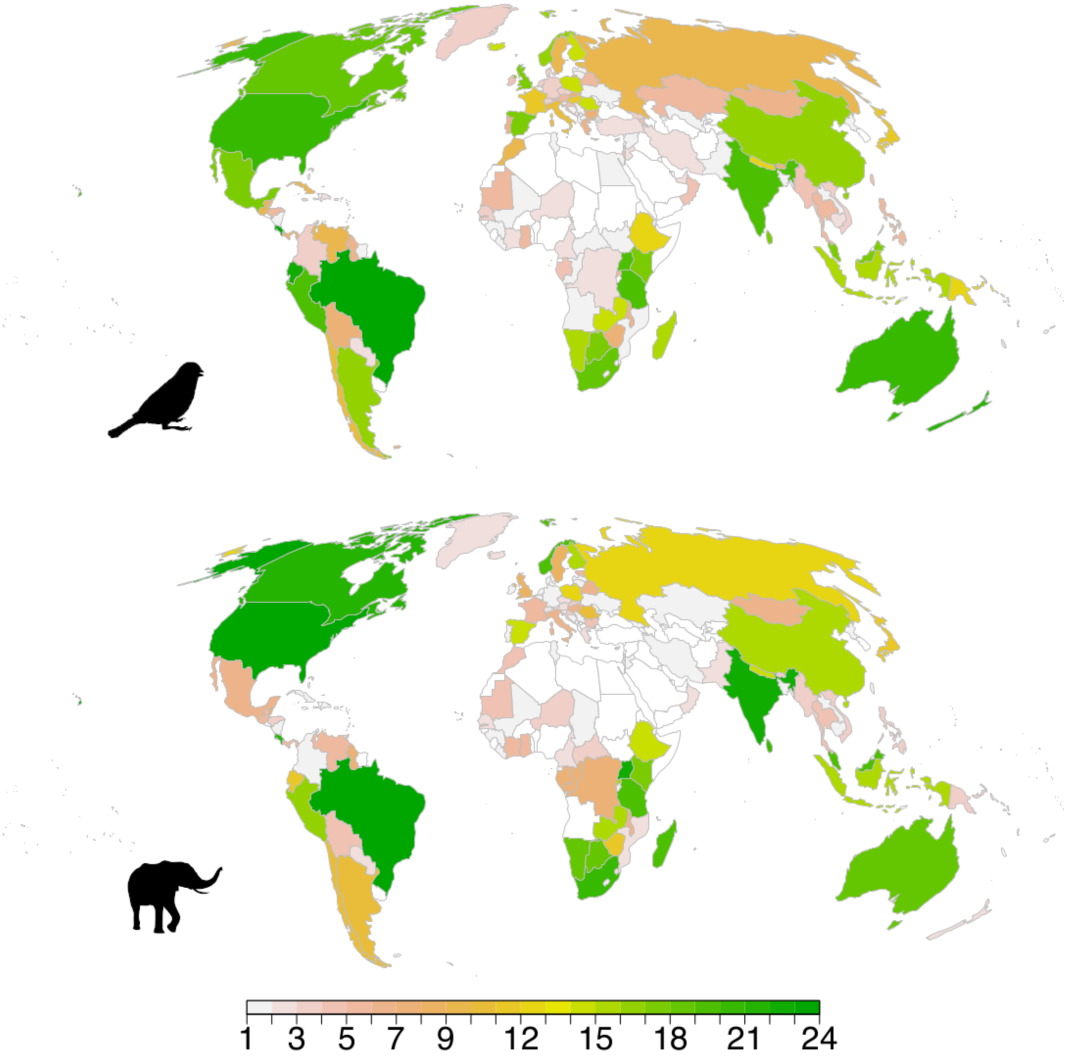

Figure A.1: Geographic coverage of wildlife tourism guides included in the analyses. Countries are coloured by the total number of guides in which they are mentioned with reference to birds (top) and/or mammals (bottom).

Appendix B

Chapter 2

Table B.1: Habitat types used by BirdLife International (2017b) and the categories in which I grouped them for my analysis.

Birdlife habitat	Category used in my analysis
Grassland	Open vegetation
Savanna	Open vegetation
Desert	Bare
Forest	Forest
Shrubland	Shrubland
Artificial/Aquatic & Marine	Artificial
Artificial/Terrestrial	Artificial
Marine Coastal/Supratidal	Aquatic
Marine Intertidal	Aquatic
Marine Neritic	Aquatic
Marine Oceanic	Aquatic
Wetlands (inland)	Aquatic
Rocky areas (e.g., inland cliffs, mountain peaks)	Bare
Caves and Subterranean Habitats (non-aquatic)	Other
Other	Other

Table B.2: Habitat types used by the Global Mammal Assessment programme (2017) and the categories in which I grouped them for my analysis.

Global legend	Category used in my analysis
Cultivated and Managed areas	Artificial
Post-flooding or irrigated croplands (or aquatic)	Artificial
Post-flooding or irrigated shrub or tree crops	Artificial
Post-flooding or irrigated herbaceous crops	Artificial
Rainfed croplands	Artificial
Rainfed herbaceous crops	Artificial
Rainfed shrub or tree crops (cashcrops, vineyards, olive tree, orchards,...)	Artificial
Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)	Mosaic
Mosaic cropland (50-70%) / grassland or shrubland (20-50%)	Mosaic
Mosaic cropland (50-70%) / forest (20-50%)	Mosaic
Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)	Mosaic
Mosaic grassland or shrubland (50-70%) / cropland (20-50%)	Mosaic
Mosaic forest (50-70%) / cropland (20-50%)	Mosaic
Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)	Forest
Closed (>40%) broadleaved evergreen and/or semi-deciduous forest	Forest
Open (15-40%) broadleaved semi-deciduous and/or evergreen forest with emergents	Forest
Closed (>40%) broadleaved deciduous forest (>5m)	Forest
Open (15-40%) broadleaved deciduous forest/woodland (>5m)	Forest
Closed (>40%) needle-leaved evergreen forest (>5m)	Forest
Closed (>40%) needle-leaved deciduous forest (>5m)	Forest
Open (15-40%) needle-leaved deciduous or evergreen forest (>5m)	Forest
Open (15-40%) needle-leaved deciduous forest (>5m)	Forest
Open (15-40%) needle-leaved evergreen forest (>5m)	Forest
Closed to open (>15%) mixed broadleaved and needleaved forest	Forest
Closed (>40%) mixed broadleaved and needleaved forest	Forest
Open (15-40%) mixed broadleaved and needleaved forest	Forest
Mosaic forest or shrubland (50-70%) and grassland (20-50%)	Mosaic
Mosaic grassland (50-70%) and forest or shrubland (20-50%)	Mosaic
Closed to open (>15%) (broadleaved or needle-leaved, evergreen or deciduous) shrubland (<5m)	Shrubland
Closed to open (>15%) broadleaved or needle-leaved evergreen shrubland (<5m)	Shrubland
Closed to open (>15%) broadleaved evergreen shrubland (<5m)	Shrubland
Closed to open (>15%) needle-leaved evergreen shrubland (<5m)	Shrubland
Closed to open (>15%) broadleaved deciduous shrubland (<5m)	Shrubland
Closed (>40%) broadleaved deciduous shrubland (<5m)	Shrubland
Open (15-40%) broadleaved deciduous shrubland (<5m)	Shrubland
Closed to open (>15%) herbaceous vgt (grassland, savannas or Lichens/Mosses)	Open vegetation
Closed (>40%) grassland	Open vegetation
Closed (>40%) grassland with sparse (<15%) trees or shrubs	Open vegetation
Open (15-40%) grassland	Open vegetation
Open (15-40%) grassland with sparse (<15%) trees or shrubs	Open vegetation
Lichens or Mosses	Open vegetation
Sparse (<15%) vegetation	Open vegetation
Sparse (<15%) grassland	Open vegetation
Sparse (<15%) shrubland	Open vegetation
Sparse (<15%) trees	Open vegetation
Artificial surfaces and associated areas (Urban areas >50%)	Artificial
Bare areas	Bare
Consolidated bare areas (hardpands, gravels, bare rock, stones, boulders)	Bare
Non-consolidated bare areas (sandy desert)	Bare
Salt hardpands	Bare
Permanent Snow and Ice	Snow ice

Table B.3: Summary statistics of the observed and imputed data for incomplete variables, calculated using pooled data over 25 imputations. % = (number of species with trait data/number of species) x 100, N = number of species with trait data, SD = standard deviation, Min = minimum, Max = maximum.

Trait	%	Observed					Imputed				
		N	Mean	SD	Min	Max	N	Mean	SD	Min	Max
Birds											
Log$_{10}$ body mass	84.5	8418	1.71	0.69	0.28	5.05	1550	1.70	0.68	0.28	4.64
Log$_{10}$ range size	99.9	9965	5.47	1.26	-0.53	8.32	3	5	1.74	0.47	7.65
Extinction risk	99.4	9918	-	-	-	-	50	-	-	-	-
Political stability	99.9	9963	-0.14	0.46	-2.58	1.37	5	-0.17	0.56	-1.26	1.32
Coloniality	99.9	9956	-	-	-	-	12	-	-	-	-
Mammals											
Log$_{10}$ body mass	81.7	3117	-0.50	1.11	-3.03	3.58	697	-0.50	0.57	-2.64	1.91
Log$_{10}$ range size	99.3	3788	5.13	1.25	0.28	7.96	26	4.66	0.90	1.95	6.75
Evolutionary distinctiveness	99.5	3795	9.77	6.54	2.09	88.83	19	10.79	5.38	4.65	29.16
Extinction risk	89.6	3419	-	-	-	-	395	-	-	-	-
Political stability	99.5	3795	-0.14	0.44	-2.58	1.12	19	-0.25	0.14	-0.51	0.23
Remoteness	99.3	3786	173.99	302.77	0	2159.92	28	181.93	153.04	-474.50	740.94
Trophic level	99.6	3798	-	-	-	-	16	-	-	-	-
Time partitioning	81.8	3121	-	-	-	-	693	-	-	-	-
Sociality	59.6	2274	-	-	-	-	1540	-	-	-	-
Habitat	99.4	3791	-	-	-	-	23	-	-	-	-

Table B.4: The phylogenetic signal, measured as mean best-fitting λ, and standard errors (SE) for traits with missing data.

Trait	Birds		Mammals	
	λ	SE	λ	SE
Body mass	0.97	0.001	0.98	0.001
Extinction risk	0.50	0.013	0.77	0.006
Range size	0.68	0.002	0.34	0.005
Evolutionary distinctiveness	-	-	1.00	0.000
Time partitioning	-	-	0.96	0.001
Political stability	0.66	0.008	0.68	0.005
Remoteness	-	-	0.72	0.003
Trophic level	-	-	0.98	0.000
Habitat	-	-	0.85	0.006
Sociality	0.91	0.002	0.97	0.001

Table B.5: Results of the accuracy tests for the phylogenetic imputation procedure, showing the normalized root mean squared prediction (NRMSE) for continuous traits and the percentage of misclassified categorical traits. Imputation was carried out on five bird and five mammal datasets with randomly inserted missing data (40%) using five phylogenetic trees, resulting in 25 imputed datasets for each taxon.

Trait	Birds	Mammals
	NRMSE	
Body mass	0.000	0.001
Range size	0.007	0.013
Evolutionary distinctiveness	-	0.008
Extinction risk	0.012	0.018
Remoteness	-	0.071
Political stability	0.002	0.003
	Incorrect classifications (%)	
Time partitioning	-	37.87
Trophic level	-	22.25
Habitat	-	57.12
Sociality	7.08	11.41

Table B.6: Coefficients from the full Markov Chain Monte Carlo generalised linear mixed models (GLMMs) explaining the *attractiveness* of birds (n = 9,968) and non-volant terrestrial mammals (n = 3,814), showing the results from the binomial model (predicting the probability of a species being selected by wildlife tourism guides) and the frequency model (i.e., truncated Poisson model predicting the number of guides a species was cited in).

Variable	β coefficient	Standard deviation	Lower 95% credibility limits	Upper 95% credibility limits
BIRDS				
Binomial				
Log_{10} body mass (g)	0.20	0.07	0.06	0.35
Evolutionary distinctiveness	0.17	0.05	0.08	0.26
Political stability	0.30	0.03	0.24	0.37
Log_{10} range size (km^2)	0.05	0.04	-0.04	0.14
Remoteness (km)	0.06	0.05	-0.03	0.16
Extinction risk (1-5)	0.03	0.04	-0.06	0.11
Omnivore	0.07	0.10	-0.12	0.26
Carnivore	0.11	0.11	-0.10	0.32
Diurnal	0.33	0.34	-0.34	1.01
Colonial	0.22	0.13	-0.03	0.48
Bare habitat	0.27	0.20	-0.12	0.67
Forest	-0.07	0.09	-0.25	0.12
Shrubland	0.01	0.11	-0.22	0.23
Artificial	0.06	0.14	-0.21	0.34
Aquatic	0.00	0.14	-0.27	0.27
Other habitat	-0.07	0.59	-1.22	1.09
Migratory behaviour (1-4)	0.09	0.03	0.03	0.16
Range size x remoteness	0.11	0.03	0.06	0.16
Range size x extinction risk	-0.04	0.02	-0.09	0.00
Frequency				
Log_{10} body mass (g)	0.41	0.03	0.34	0.47
Evolutionary distinctiveness	0.10	0.02	0.06	0.13
Political stability	0.06	0.02	0.02	0.10
Log_{10} range size (km^2)	0.31	0.02	0.26	0.35
Remoteness (km)	0.01	0.03	-0.04	0.06
Extinction risk	0.00	0.02	-0.04	0.03
Omnivore	-0.05	0.05	-0.15	0.04
Carnivore	-0.07	0.05	-0.17	0.04
Diurnal	0.37	0.13	0.12	0.62
Colonial	0.13	0.05	0.03	0.23
Bare habitat	0.29	0.08	0.13	0.44
Forest	0.03	0.05	-0.06	0.12
Shrubland	0.11	0.06	0.00	0.22
Artificial	0.05	0.07	-0.08	0.17
Aquatic	0.20	0.06	0.09	0.31
Other habitat	0.40	0.25	-0.11	0.89
Migratory behaviour (1-4)	0.17	0.01	0.14	0.20
Range size x remoteness	-0.05	0.01	-0.07	-0.02
Range size x extinction risk	-0.04	0.01	-0.06	-0.02

Variable	β coefficient	Standard deviation	Lower 95% credibility limits	Upper 95% credibility limits
MAMMALS				
Binomial model				
Log_{10} body mass (kg)	0.64	0.17	0.30	0.98
Evolutionary distinctiveness	0.33	0.09	0.15	0.52
Political stability	0.41	0.10	0.22	0.60
Log_{10} range size (km^2)	0.53	0.11	0.31	0.75
Remoteness (km)	-0.16	0.10	-0.36	0.03
Extinction risk (1-5)	0.21	0.10	0.02	0.40
Omnivore	0.25	0.20	-0.14	0.65
Carnivore	0.32	0.34	-0.34	0.99
Cathemeral	0.09	0.30	-0.50	0.68
Crepuscular	-0.42	0.41	-1.25	0.34
Diurnal	-0.12	0.25	-0.61	0.38
Group living	0.09	0.24	-0.37	0.57
Bare habitat	-1.14	0.39	-1.91	-0.39
Forest	-0.77	0.26	-1.29	-0.25
Shrubland	-0.82	0.36	-1.53	-0.12
Mosaic	-0.75	0.29	-1.33	-0.18
Artificial	-0.69	0.39	-1.46	0.06
Range size x remoteness	-0.08	0.08	-0.23	0.07
Frequency model				
Log_{10} body mass (kg)	0.75	0.05	0.64	0.85
Evolutionary distinctiveness	0.12	0.03	0.06	0.17
Political stability	0.11	0.05	0.01	0.21
Log_{10} range size (km^2)	0.37	0.05	0.28	0.46
Remoteness (km)	-0.06	0.04	-0.15	0.02
Extinction risk (1-5)	-0.01	0.03	-0.08	0.05
Omnivore	0.14	0.08	-0.02	0.30
Carnivore	0.22	0.12	-0.01	0.46
Cathemeral	0.13	0.10	-0.07	0.33
Crepuscular	0.15	0.12	-0.09	0.38
Diurnal	0.23	0.07	0.08	0.37
Group living	0.35	0.07	0.21	0.50
Bare habitat	-0.29	0.14	-0.57	-0.02
Forest	-0.03	0.09	-0.21	0.15
Shrubland	0.06	0.14	-0.22	0.34
Mosaic	-0.10	0.11	-0.31	0.11
Artificial	0.25	0.13	-0.01	0.51
Range size x remoteness	-0.17	0.03	-0.23	-0.10

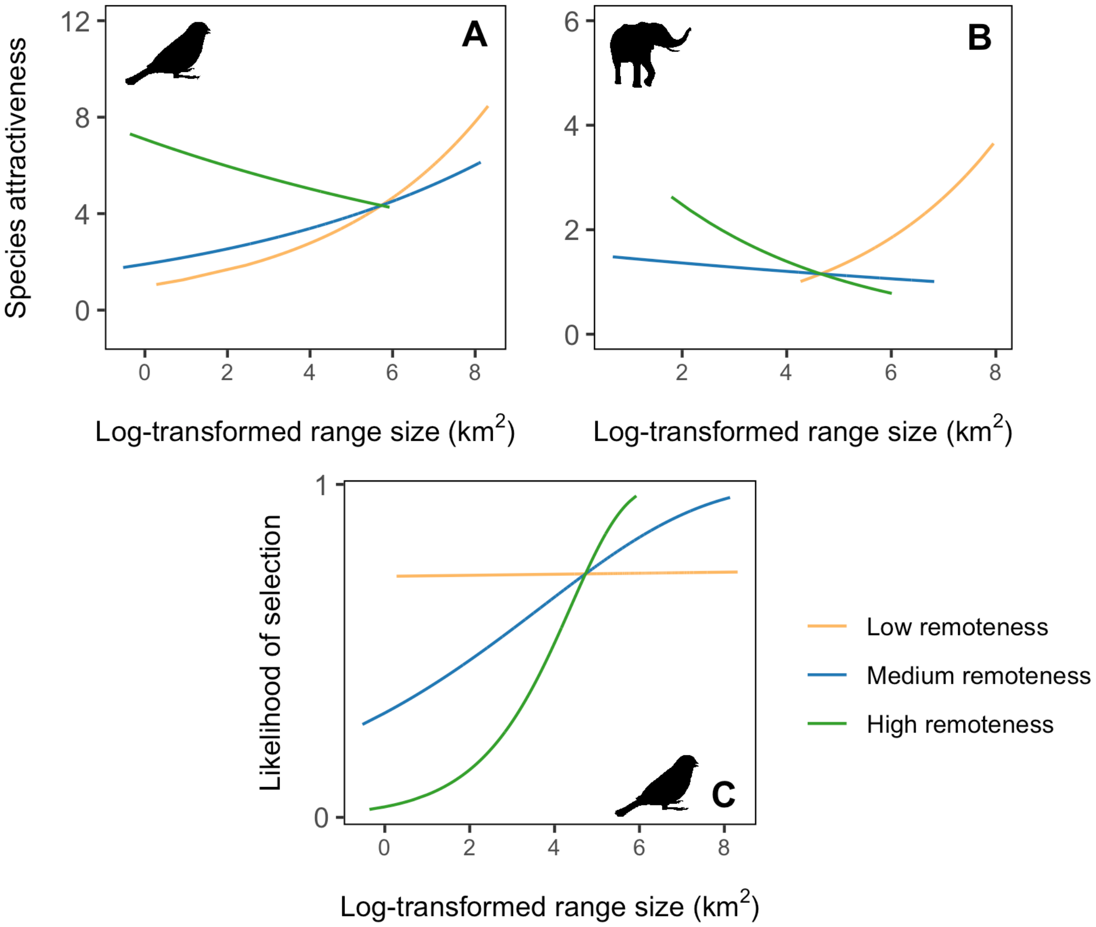

Figure B.1: The effects of range size and remoteness on the *attractiveness* of birds and mammals for wildlife tourism, showing the regression slopes from 500 hurdle phylogenetic Markov Chain Monte Carlo GLMMs. **A**-**B** show their effects in the frequency part of the models, which explored the number of guides a species was mentioned in as a tourism attraction, and **C** shows their effects in the binomial part, exploring the likelihood a species was selected by guides. Remoteness, measured as the shortest straight-line distance between a species' range margin and the closest large airport, was converted from a continuous variable to a three-category variable for graphical purposes and used to colour regression lines.

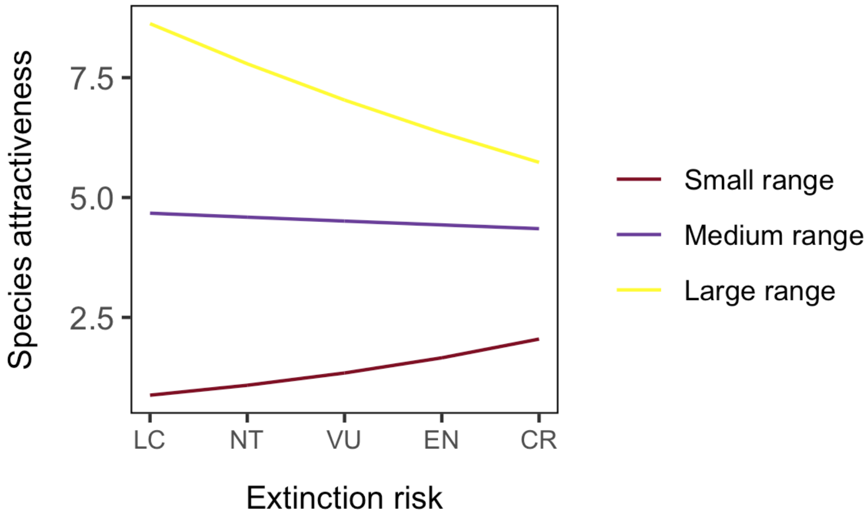

Figure B.2: The effects of range size and extinction risk on the *attractiveness* of birds for wildlife tourism, showing regression slopes from the frequency part of 500 hurdle Markov Chain Monte Carlo GLMMs. Species *attractiveness* was measured as the number of guides citing a species as a tourism attraction. Species' range size was converted from a continuous variable to a three-category variable for graphical purposes and used to colour regression lines. LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

Appendix C

Chapter 3

C.1. Compiling PA species lists

Because most PAs do not have comprehensive species lists, I predicted species lists by overlaying PA polygons with digitized geographical range maps, downloaded from IUCN (2016) and BirdLife International (2017a). I included only those species coded in the databases as 'extant' and 'probably extant'. I excluded 'introduced' species, but 'vagrant' species were retained since they are known to attract tourists (Booth et al., 2011; Callaghan et al., 2018). I also removed rodents, bats, and other small mammals (< 1kg), which are rarely promoted as wildlife attractions and are difficult to record in the wild (Lindsey, Alexander, et al., 2007; Tobler et al., 2008; Voss and Emmons, 1996). Marine mammals were also removed due to the focus of this study on the terrestrial world. I used the WDPA (2018) to extract the digitized boundaries of coastal and terrestrial PAs. I then intersected PA boundaries with species range maps to predict species lists for each PA i.e., a list of species expected to occur in each PA. However, rather than reflecting a species' true distribution, species range maps simply outline the known limits to species' geographic ranges, across which species may not be uniformly distributed e.g., if some habitats are unsuitable or some areas are geographically isolated (Rondinini, Wilson, et al., 2006). Thus, expert range maps may contain inaccuracies, particularly false presences, where maps cover areas of unsuitable habitat or terrain, and may over-estimate species richness within PAs (Jetz, McGeoch, et al., 2019). I refined species lists using information on species' habitat suitability and altitudinal limits, obtained from the IUCN Red List (Brooks, Pimm, et al., 2019; Rondinini, Di Marco, et al., 2011), removing species from a list if the PA did not contain suitable habitat or did not encompass the species' altitudinal range.

I extracted the altitudinal range of PAs using the U.S. Geological Survey (2010) data and categorized the habitats present in each PA using ESA CCI (2018) land cover data, matching this to the IUCN Habitat Classification Scheme in level 2 using the crosswalk published by Santini, Butchart, et al. (2019), displayed in Appendix Table C.1. I regarded habitats that were only 'marginally' suitable, where species occur in the habitat only irregularly or infrequently, or only a small proportion of individuals are found in the habitat, as unsuitable, but retained habitats where the suitability is unknown, to avoid removing possibly suitable habitats. Less than 1% (n = 28) of birds and 3% (n = 161) of mammals did not have any suitable habitat that matched the ESA land cover types. Forty nine percent (n = 2,350) of mammals did not have estimates of both upper and lower altitudinal limits, whereas only 14% (n = 1,432) of birds were missing such information. Less than 1% (n = 1,331) of PAs were missing habitat data that corresponded with any IUCN classes, and even fewer (n = 97) were missing both altitudinal limits. In cases where species could not be removed because of missing data, a conservative approach was taken, and these species were retained. Inevitably, after refining these lists, many species records (22% of birds, 11% of mammals) were dropped.

I validated species lists using checklists or inventories (i.e., observed species presences) from the peer-reviewed and grey literature, management plans, technical reports, environmental assessments, official PA websites, biodiversity databases, conservation agencies, citizen science databases, and other secondary resources. I verified that species lists from PAs with the same or similar names corresponded to the correct polygon provided by the WDPA (2018). I assessed if species lists were considered 'essentially complete' by searching for keywords in the accompanying text (i.e., 'complete', 'comprehensive', 'incomplete', and 'exhaustive'). I obtained species inventories for a subset of 1,022 of my PAs. I obtained more inventories for birds (n = 913) than for mammals (n = 699), but only 20% (n = 187) and 25% (n = 178) of bird and mammal checklists, respectively, were considered, at least essentially, complete. I aligned species names with the taxonomies used by BirdLife International (2017a) and the IUCN (2016), so that I could match species nomenclature used in inventories to species lists predicted by expert range maps. I removed subspecies, undetermined species (e.g., listed at the genus level or no match in the geographic range dataset), and where possible, introduced species from checklists. There were large spatial biases in the availability of species checklists, particularly those considered complete. One hundred and one and 77 countries were covered by bird and mammal lists, respectively, collectively covering 103 countries, with lists originating mostly from the Americas, Europe, Eastern Australia, the Indian subcontinent, and East Africa (Appendix Fig. 3.2).

Table C.1: Cross-walk between IUCN Habitat classification scheme at level 2 and ESA CCI (2018) categories, published by Santini, Butchart, et al. (2019)

IUCN code	IUCN habitat description	ESA CCI code	ESA CCI habitat description
1	Forest - Boreal	60	Tree cover, broadleaved, deciduous, closed to open (>15%)
1.1	Forest - Boreal	61	Tree cover, broadleaved, deciduous, closed (>40%)
1.1	Forest - Boreal	62	Tree cover, broadleaved, deciduous, open (15-40%)
1.1	Forest - Boreal	70	Tree cover, needleleaved, evergreen, closed to open (>15%)
1.1	Forest - Boreal	71	Tree cover, needleleaved, evergreen, closed (>40%)
1.1	Forest - Boreal	72	Tree cover, needleleaved, evergreen, open (15-40%)
1.1	Forest - Boreal	80	Tree cover, needleleaved, deciduous, closed to open (>15%)
1.1	Forest - Boreal	81	Tree cover, needleleaved, deciduous, closed (>40%)
1.1	Forest - Boreal	82	Tree cover, needleleaved, deciduous, open (15-40%)
1.1	Forest - Boreal	90	Tree cover, mixed leaf type (broadleaved and needleleaved)
1.2	Forest - Subarctic	60	Tree cover, broadleaved, deciduous, closed to open (>15%)
1.2	Forest - Subarctic	62	Tree cover, broadleaved, deciduous, open (15-40%)
1.2	Forest - Subarctic	70	Tree cover, needleleaved, evergreen, closed to open (>15%)
1.2	Forest - Subarctic	72	Tree cover, needleleaved, evergreen, open (15-40%)
1.2	Forest - Subarctic	80	Tree cover, needleleaved, deciduous, closed to open (>15%)
1.2	Forest - Subarctic	82	Tree cover, needleleaved, deciduous, open (15-40%)
1.3	Forest - Subantarctic	60	Tree cover, broadleaved, deciduous, closed to open (>15%)
1.3	Forest - Subantarctic	62	Tree cover, broadleaved, deciduous, open (15-40%)
1.3	Forest - Subantarctic	70	Tree cover, needleleaved, evergreen, closed to open (>15%)
1.3	Forest - Subantarctic	72	Tree cover, needleleaved, evergreen, open (15-40%)
1.3	Forest - Subantarctic	80	Tree cover, needleleaved, deciduous, closed to open (>15%)
1.3	Forest - Subantarctic	82	Tree cover, needleleaved, deciduous, open (15-40%)
1.4	Forest - Temperate	50	Tree cover, broadleaved, evergreen, closed to open (>15%)
1.4	Forest - Temperate	60	Tree cover, broadleaved, deciduous, closed to open (>15%)
1.4	Forest - Temperate	61	Tree cover, broadleaved, deciduous, closed (>40%)
1.4	Forest - Temperate	62	Tree cover, broadleaved, deciduous, open (15-40%)

IUCN code	IUCN habitat description	ESA CCI code	ESA CCI habitat description
1.4	Forest - Temperate	70	Tree cover, needleleaved, evergreen, closed to open (>15%)
1.4	Forest - Temperate	71	Tree cover, needleleaved, evergreen, closed (>40%)
1.4	Forest - Temperate	72	Tree cover, needleleaved, evergreen, open (15-40%)
1.4	Forest - Temperate	80	Tree cover, needleleaved, deciduous, closed to open (>15%)
1.4	Forest - Temperate	81	Tree cover, needleleaved, deciduous, closed (>40%)
1.4	Forest - Temperate	82	Tree cover, needleleaved, deciduous, open (15-40%)
1.4	Forest - Temperate	90	Tree cover, mixed leaf type (broadleaved and needleleaved)
1.5	Forest - Subtropical/Tropical Dry	60	Tree cover, broadleaved, deciduous, closed to open (>15%)
1.5	Forest - Subtropical/Tropical Dry	62	Tree cover, broadleaved, deciduous, open (15-40%)
1.5	Forest - Subtropical/Tropical Dry	70	Tree cover, needleleaved, evergreen, closed to open (>15%)
1.5	Forest - Subtropical/Tropical Dry	72	Tree cover, needleleaved, evergreen, open (15-40%)
1.6	Forest - Subtropical/Tropical Moist Lowland	50	Tree cover, broadleaved, evergreen, closed to open (>15%)
1.6	Forest - Subtropical/Tropical Moist Lowland	60	Tree cover, broadleaved, deciduous, closed to open (>15%)
1.6	Forest - Subtropical/Tropical Moist Lowland	61	Tree cover, broadleaved, deciduous, closed (>40%)
1.7	Forest - Subtropical/Tropical Mangrove Vegetation Above High Tide Level	170	Tree cover, flooded, saline water
1.7	Forest - Subtropical/Tropical Mangrove Vegetation Above High Tide Level	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
1.8	Forest - Subtropical/Tropical Swamp	160	Tree cover, flooded, fresh or brakish water
1.9	Forest - Subtropical/Tropical Moist Montane	50	Tree cover, broadleaved, evergreen, closed to open (>15%)
1.9	Forest - Subtropical/Tropical Moist Montane	71	Tree cover, needleleaved, evergreen, closed (>40%)
1.9	Forest - Subtropical/Tropical Moist Montane	90	Tree cover, mixed leaf type (broadleaved and needleleaved)
2.1	Savanna - Dry	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)
2.1	Savanna - Dry	120	Shrubland
2.1	Savanna - Dry	122	Deciduous shrubland
2.1	Savanna - Dry	130	Grassland
2.2	Savanna - Moist	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
2.2	Savanna - Moist	100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)
2.2	Savanna - Moist	110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)
3.1	Shrubland - Subarctic	120	Shrubland
3.1	Shrubland - Subarctic	121	Evergreen shrubland
3.1	Shrubland - Subarctic	122	Deciduous shrubland

IUCN code	IUCN habitat description	ESA CCI code	ESA CCI habitat description
3.2	Shrubland - Subantarctic	120	Shrubland
3.2	Shrubland - Subantarctic	121	Evergreen shrubland
3.2	Shrubland - Subantarctic	122	Deciduous shrubland
3.3	Shrubland - Boreal	120	Shrubland
3.3	Shrubland - Boreal	121	Evergreen shrubland
3.3	Shrubland - Boreal	122	Deciduous shrubland
3.4	Shrubland - Temperate	120	Shrubland
3.4	Shrubland - Temperate	121	Evergreen shrubland
3.4	Shrubland - Temperate	122	Deciduous shrubland
3.5	Shrubland - Subtropical/Tropical Dry	120	Shrubland
3.5	Shrubland - Subtropical/Tropical Dry	121	Evergreen shrubland
3.5	Shrubland - Subtropical/Tropical Dry	122	Deciduous shrubland
3.6	Shrubland - Subtropical/Tropical Moist	120	Shrubland
3.6	Shrubland - Subtropical/Tropical Moist	121	Evergreen shrubland
3.7	Shrubland - Subtropical/Tropical High Altitude	120	Shrubland
3.7	Shrubland - Subtropical/Tropical High Altitude	121	Evergreen shrubland
3.7	Shrubland - Subtropical/Tropical High Altitude	122	Deciduous shrubland
3.8	Shrubland - Mediterranean-type Shrubby Vegetation	120	Shrubland
3.8	Shrubland - Mediterranean-type Shrubby Vegetation	121	Evergreen shrubland
3.8	Shrubland - Mediterranean-type Shrubby Vegetation	122	Deciduous shrubland
4.1	Grassland - Tundra	130	Grassland
4.1	Grassland - Tundra	140	Lichens and mosses
4.1	Grassland - Tundra	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
4.1	Grassland - Tundra	152	Sparse shrub (<15%)
4.1	Grassland - Tundra	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
4.2	Grassland - Subarctic	130	Grassland
4.2	Grassland - Subarctic	140	Lichens and mosses
4.2	Grassland - Subarctic	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
4.2	Grassland - Subarctic	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
4.3	Grassland - Subantarctic	130	Grassland
4.4	Grassland - Temperate	130	Grassland
4.5	Grassland - Subtropical/Tropical Dry	130	Grassland
4.6	Grassland - Subtropical/Tropical Seasonally Wet/Flooded	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
4.7	Grassland - Subtropical/Tropical High Altitude	130	Grassland
5.1	Wetlands (inland) - Permanent Rivers/Streams/Creeks (includes waterfalls)	210	Water bodies

IUCN code	IUCN habitat description	ESA CCI code	ESA CCI habitat description
5.1	Wetlands (inland) - Tundra Wetlands (incl. pools and temporary waters from snowmelt)	210	Water bodies
5.11	Wetlands (inland) - Alpine Wetlands (includes temporary waters from snowmelt)	210	Water bodies
5.12	Wetlands (inland) - Geothermal Wetlands	210	Water bodies
5.13	Wetlands (inland) - Permanent Inland Deltas	210	Water bodies
5.14	Wetlands (inland) - Permanent Saline, Brackish or Alkaline Lakes	210	Water bodies
5.15	Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Lakes and Flats	210	Water bodies
5.16	Wetlands (inland) - Permanent Saline, Brackish or Alkaline Marshes/Pools	210	Water bodies
5.17	Wetlands (inland) - Seasonal/Intermittent Saline, Brackish or Alkaline Marshes/Pools	210	Water bodies
5.18	Wetlands (inland) - Karst and Other Subterranean Hydrological Systems (inland)	NA	NA
5.2	Wetlands (inland) - Seasonal/Intermittent/Irregular Rivers/Streams/Creeks	210	Water bodies
5.3	Wetlands (inland) - Shrub Dominated Wetlands	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
5.4	Wetlands (inland) - Bogs, Marshes, Swamps, Fens, Peatlands	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
5.5	Wetlands (inland) - Permanent Freshwater Lakes (over 8ha)	210	Water bodies
5.6	Wetlands (inland) - Seasonal/Intermittent Freshwater Lakes (over 8ha)	210	Water bodies
5.7	Wetlands (inland) - Permanent Freshwater Marshes/Pools (under 8ha)	210	Water bodies
5.8	Wetlands (inland) - Seasonal/Intermittent Freshwater Marshes/Pools (under 8ha)	210	Water bodies
5.9	Wetlands (inland) - Freshwater Springs and Oases	210	Water bodies
6	Rocky areas (eg. inland cliffs, mountain peaks)	200	Bare areas
6	Rocky areas (eg. inland cliffs, mountain peaks)	201	Consolidated bare areas
7.1	Caves and Subterranean Habitats (non-aquatic) - Caves	NA	NA
7.2	Caves and Subterranean Habitats (non-aquatic) - Other Subterranean Habitats	NA	NA
8.1	Desert - Hot	200	Bare areas
8.1	Desert - Hot	201	Consolidated bare areas
8.1	Desert - Hot	202	Unconsolidated bare areas

IUCN code	IUCN habitat description	ESA CCI code	ESA CCI habitat description
8.1	Desert - Hot	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
8.1	Desert - Hot	153	Sparse herbaceous cover (<15%)
8.2	Desert - Temperate	200	Bare areas
8.2	Desert - Temperate	201	Consolidated bare areas
8.2	Desert - Temperate	202	Unconsolidated bare areas
8.2	Desert - Temperate	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
8.2	Desert - Temperate	153	Sparse herbaceous cover (<15%)
8.3	Desert - Cold	201	Consolidated bare areas
8.3	Desert - Cold	202	Unconsolidated bare areas
8.3	Desert - Cold	150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)
8.3	Desert - Cold	140	Lichens and mosses
9.1	Marine Neritic - Estuaries	210	Water bodies
9.1	Marine Neritic - Pelagic	210	Water bodies
9.2	Marine Neritic - Subtidal Rock and Rocky Reefs	210	Water bodies
9.3	Marine Neritic - Subtidal Loose Rock/pebble/gravel	210	Water bodies
9.4	Marine Neritic - Subtidal Sandy	210	Water bodies
9.5	Marine Neritic - Subtidal Sandy-Mud	210	Water bodies
9.6	Marine Neritic - Subtidal Muddy	210	Water bodies
9.7	Marine Neritic - Macroalgal/Kelp	210	Water bodies
9.9	Marine Neritic - Seagrass (Submerged)	210	Water bodies
10.1	Marine Oceanic - Epipelagic (0-200m)	210	Water bodies
10.2	Marine Oceanic - Mesopelagic (200-1000m)	210	Water bodies
10.3	Marine Oceanic - Bathypelagic (1000-4000m)	210	Water bodies
12.1	Marine Intertidal - Rocky Shoreline	201	Consolidated bare areas
12.2	Marine Intertidal - Sandy Shoreline and/or Beaches, Sand Bars, Spits, Etc	202	Unconsolidated bare areas
12.3	Marine Intertidal - Shingle and/or Pebble Shoreline and/or Beaches	202	Unconsolidated bare areas
12.4	Marine Intertidal - Mud Flats and Salt Flats	202	Unconsolidated bare areas
12.5	Marine Intertidal - Salt Marshes (Emergent Grasses)	180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water
12.6	Marine Intertidal - Tidepools	210	Water bodies
12.7	Marine Intertidal - Mangrove Submerged Roots	210	Water bodies
13.1	Marine Coastal/Supratidal - Sea Cliffs and Rocky Offshore Islands	201	Consolidated bare areas
13.2	Marine Coastal/supratidal - Coastal Caves/Karst	201	Consolidated bare areas
13.3	Marine Coastal/Supratidal - Coastal Sand Dunes	202	Unconsolidated bare areas
13.4	Marine Coastal/Supratidal - Coastal Brackish/Saline Lagoons/Marine Lakes	201	Consolidated bare areas

IUCN code	IUCN habitat description	ESA CCI code	ESA CCI habitat description
13.5	Marine Coastal/Supratidal - Coastal Freshwater Lakes	201	Consolidated bare areas
14.1	Artificial/Terrestrial - Arable Land	10	Cropland, rainfed
14.1	Artificial/Terrestrial - Arable Land	11	Cropland, rainfed, Herbaceous cover
14.1	Artificial/Terrestrial - Arable Land	12	Cropland, rainfed, Tree or shrub cover
14.1	Artificial/Terrestrial - Arable Land	20	Cropland, irrigated or post-flooding
14.2	Artificial/Terrestrial - Pastureland	130	Grassland
14.3	Artificial/Terrestrial - Plantations	12	Cropland, rainfed, Tree or shrub cover
14.4	Artificial/Terrestrial - Rural Gardens	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
14.4	Artificial/Terrestrial - Rural Gardens	40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)
14.5	Artificial/Terrestrial - Urban Areas	190	Urban areas
14.6	Artificial/Terrestrial - Subtropical/Tropical Heavily Degraded Former Forest	30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)
15.1	Artificial/Aquatic - Water Storage Areas (over 8ha)	210	Water bodies
15.1	Artificial/Aquatic - Karst and Other Subterranean Hydrological Systems (human-made)	NA	NA
15.2	Artificial/Aquatic - Ponds (below 8ha)	210	Water bodies
15.3	Artificial/Aquatic - Aquaculture Ponds	210	Water bodies
15.4	Artificial/Aquatic - Salt Exploitation Sites	202	Unconsolidated bare areas
15.5	Artificial/Aquatic - Excavations (open)	202	Unconsolidated bare areas
15.6	Artificial/Aquatic - Wastewater Treatment Areas	190	Urban areas
15.7	Artificial/Aquatic - Irrigated Land (includes irrigation channels)	20	Cropland, irrigated or post-flooding
15.8	Artificial/Aquatic - Seasonally Flooded Agricultural Land	20	Cropland, irrigated or post-flooding
15.9	Artificial/Aquatic - Canals and Drainage Channels, Ditches	210	Water bodies
16	Introduced vegetation	NA	NA
17	Other	NA	NA
18	Unknown	NA	NA
9.8.1	Outer Reef Channel	210	Water bodies
9.8.3	Foreslope (Outer Reef Slope)	210	Water bodies
9.8.4	Lagoon	210	Water bodies
9.8.5	Inter-Reef Soft Substrate	210	Water bodies
9.8.6	Inter-Reef Rubble Substrate	210	Water bodies

Table C.2: List of Points of Interesting (POIs) used in the analysis. POIs were tourist services marked in *OpenStreetMap* (2020)

Type	Service
Amenity	Parking
Building	Train station
	Transportation
Leisure	Bird hide
Railway	Station
Tourism	Alpine hut
	Apartment
	Camp pitch
	Camp site
	Caravan site
	Chalet
	Guest house
	Hostel
	Hotel
	Information
	Motel
	Picnic site
	Viewpoint
	Wilderness hut

Table C.3: List of the 23 geographic regions used as random effects in the analyses of PA *popularity*.

Region
South America
Central America
Caribbean
Southern Europe
Middle Africa
Australia and New Zealand
Western Africa
Eastern Europe
Northern America
Eastern Africa
Northern Europe
Western Europe
Southern Asia
Western Asia
Eastern Asia
South-Eastern Asia
Southern Africa
Northern Africa
Central Asia
Polynesia
Melanesia
Northern Asia
Micronesia

Table C.4: Kendall's tau-b (τb) correlation coefficient between Jaccard's similarity of bird (n = 962) and mammal (n = 739) lists and PA features.

PA feature	Birds		Mammals	
	τb	P	τb	P
HDI	0.102	**<0.001**	0.053	**0.044**
Political stability	0.176	**<0.001**	0.071	**0.008**
Area	0.137	**<0.001**	0.155	**<0.001**
Local population	-0.137	**<0.001**	-0.113	**<0.001**
Remoteness	0.030	0.169	0.048	0.061
Age	0.034	0.122	0.020	0.429

Table C.5: Coefficients from the global hurdle GLMM predicting PA *popularity*, showing the results from the binomial model (predicting the probability of a PA being selected by guides as a wildlife tourism destination) and the frequency model (i.e., truncated negative binomial model predicting the number of guides a PA was cited in).

	β coefficient	Standard error	Lower 95% confidence interval	Upper 95% confidence interval	P
Binomial model					
Water bodies	-0.16	0.05	-0.25	0.07	**0.001**
Temperature	-0.05	0.07	-0.17	0.08	0.480
Size	-0.89	0.05	-1.00	0.79	<**0.001**
Remoteness	0.12	0.05	0.03	0.21	**0.010**
Precipitation	0.05	0.05	-0.04	0.14	0.264
Political stability	-0.55	0.17	-0.88	0.21	**0.001**
National park	-1.46	0.13	-1.72	1.21	<**0.001**
Mammal community rarity	0.08	0.05	-0.02	0.19	0.115
Mammal attractiveness	0.01	0.07	-0.12	0.14	0.853
IUCN category	0.29	0.05	0.20	0.39	<**0.001**
International	-0.85	0.09	-1.02	0.67	<**0.001**
Human population	-0.04	0.07	-0.18	0.10	0.574
HDI	0.26	0.15	-0.02	0.54	0.074
Habitat diversity	-0.03	0.04	-0.11	0.05	0.514
Grassland	-0.03	0.06	-0.14	0.08	0.610
Forest	-0.04	0.06	-0.16	0.08	0.513
Elevation	-0.10	0.04	-0.19	0.01	**0.021**
Bird community rarity	-0.21	0.07	-0.35	0.08	**0.002**
Bird attractiveness	-0.15	0.06	-0.27	0.03	**0.017**
Amenities	0.52	0.17	0.19	0.86	**0.002**
Age	-0.41	0.03	-0.48	0.35	<**0.001**
Frequency model					
Water bodies	0.10	0.07	-0.03	0.24	0.141
Temperature	0.03	0.08	-0.13	0.19	0.726
Size	0.41	0.08	0.26	0.56	<**0.001**
Remoteness	-0.05	0.06	-0.17	0.07	0.433
Precipitation	0.10	0.06	-0.13	0.18	0.094
Political stability	0.06	0.14	-0.22	0.34	0.695
National park	0.33	0.16	0.02	0.63	**0.037**
Mammal community rarity	-0.12	0.07	-0.26	0.03	0.111
Mammal attractiveness	0.22	0.07	0.08	0.35	**0.002**
IUCN category	-0.20	0.07	-0.33	0.07	**0.002**
International	0.35	0.11	0.14	0.56	**0.001**
Human population	0.12	0.09	-0.06	0.30	0.200
HDI	0.09	0.13	-0.16	0.34	0.471
Habitat diversity	0.01	0.06	-0.10	0.12	0.863
Grassland	0.06	0.08	-0.09	0.22	0.423
Forest	0.06	0.08	-0.09	0.21	0.438
Elevation	-0.02	0.05	-0.12	0.09	0.746
Bird community rarity	-0.09	0.08	-0.26	0.08	0.288
Bird attractiveness	-0.01	0.08	-0.16	0.14	0.906
Amenities	-0.13	0.23	-0.58	0.33	0.585
Age	0.15	0.05	0.06	0.24	**0.001**

Table C.6: Coefficients from the continental hurdle GLMMs predicting PA *popularity*, showing the results from the binomial models (predicting the probability of a PA being selected by guides as a wildlife tourism destination) and the frequency models (i.e., truncated negative binomial model predicting the number of guides a PA was mentioned in) for each continent.

	β coefficient	Standard error	Lower 95% confidence interval	Upper 95% confidence interval	P
AFRICA					
Binomial model					
Water bodies	-0.14	0.14	0.15	-0.42	0.342
Temperature	0.11	0.12	0.35	-0.13	0.356
Temperature^2	-0.11	0.23	0.34	-0.56	0.637
Size	1.26	0.24	1.72	0.79	<**0.001**
Remoteness	-0.09	0.17	0.25	-0.43	0.596
Precipitation	0.13	0.19	0.50	-0.24	0.493
Political stability	0.41	0.38	1.15	-0.32	0.273
National park	2.53	0.37	3.26	1.79	<**0.001**
Mammal community rarity	0.32	0.21	0.73	-0.09	0.123
Mammal attractiveness	-0.08	0.25	0.41	-0.57	0.740
IUCN category	-0.87	0.17	-0.54	-1.20	<**0.001**
International	1.19	0.30	1.77	0.61	<**0.001**
Human population	-0.16	0.25	0.33	-0.65	0.530
HDI	-0.47	0.55	0.61	-1.56	0.395
Habitat diversity	-0.27	0.16	0.04	-0.57	0.088
Grassland	-0.02	0.19	0.36	-0.39	0.936
Forest	0.23	0.17	0.57	-0.11	0.185
Elevation	-0.28	0.17	0.05	-0.61	0.097
Bird community rarity	0.46	0.18	0.82	0.10	**0.013**
Bird attractiveness	0.73	0.28	1.28	0.18	**0.009**
Amenities	0.39	0.25	0.89	-0.11	0.126
Age	0.41	0.13	0.67	0.15	**0.002**
Frequency model					
Water bodies	0.007	0.092	-0.17	0.19	0.935
Temperature	-0.157	0.054	-0.26	-0.05	**0.004**
Temperature^2	-0.317	0.115	-0.54	-0.09	**0.006**
Size	0.678	0.156	0.37	0.98	<**0.001**
Remoteness	-0.139	0.113	-0.36	0.08	0.217
Precipitation	0.113	0.092	-0.07	0.29	0.216
Political stability	0.081	0.089	-0.09	0.26	0.363
National park	0.071	0.198	-0.32	0.46	0.720
Mammal community rarity	0.268	0.137	0.00	0.54	**0.050**
Mammal attractiveness	0.187	0.143	-0.09	0.47	0.190
IUCN category	-0.389	0.127	-0.64	-0.14	**0.002**
International	0.080	0.160	-0.23	0.39	0.616
Human population	-0.198	0.167	-0.52	0.13	0.236
HDI	-0.042	0.199	-0.43	0.35	0.835
Habitat diversity	0.149	0.102	-0.05	0.35	0.144
Grassland	-0.227	0.153	-0.53	0.07	0.137
Forest	-0.029	0.102	-0.23	0.17	0.775
Elevation	-0.131	0.093	-0.31	0.05	0.158
Bird community rarity	0.049	0.115	-0.18	0.28	0.669
Bird attractiveness	-0.096	0.163	-0.42	0.22	0.554
Amenities	0.292	0.189	-0.08	0.66	0.122

	β coefficient	Standard error	Lower 95% confidence interval	Upper 95% confidence interval	P
Age	0.240	0.074	0.10	0.38	**0.001**
AMERICAS					
Binomial model					
Water bodies	0.01	0.09	0.20	-0.17	0.877
Temperature	0.24	0.15	0.54	-0.05	0.102
Size	1.09	0.12	1.32	0.86	**<0.001**
Remoteness	-0.15	0.09	0.03	-0.33	0.109
Precipitation	-0.03	0.09	0.15	-0.21	0.760
Political stability	0.56	0.23	1.01	0.12	**0.014**
National park	1.11	0.25	1.59	0.62	**<0.001**
Mammal community rarity	0.26	0.12	0.49	0.03	**0.029**
Mammal attractiveness	-0.02	0.11	0.20	-0.24	0.867
IUCN category	-0.28	0.09	-0.10	-0.46	**0.003**
International	0.49	0.19	0.87	0.10	**0.012**
Human population	-0.02	0.12	0.21	-0.24	0.890
HDI	-0.56	0.23	-0.12	-1.01	**0.013**
Habitat diversity	-0.01	0.08	0.15	-0.18	0.869
Grassland	-0.27	0.12	-0.03	-0.51	**0.026**
Forest	-0.25	0.12	-0.02	-0.49	**0.035**
Elevation	0.09	0.08	0.24	-0.06	0.253
Bird community rarity	0.76	0.15	1.06	0.45	**<0.001**
Bird attractiveness	0.00	0.11	0.22	-0.22	0.992
Amenities	0.26	0.13	0.53	0.00	**0.048**
Age	0.56	0.07	0.69	0.43	**<0.001**
Frequency model					
Water bodies	-0.06	0.14	-0.33	0.21	0.663
Temperature	-0.09	0.20	-0.49	0.31	0.654
Size	0.46	0.18	0.11	0.80	**0.010**
Remoteness	-0.13	0.12	-0.37	0.12	0.299
Precipitation	0.22	0.11	0.00	0.44	0.052
Political stability	0.31	0.28	-0.23	0.86	0.260
National park	0.64	0.31	0.04	1.25	**0.037**
Mammal community rarity	-0.17	0.15	-0.47	0.13	0.266
Mammal attractiveness	0.06	0.13	-0.21	0.32	0.681
IUCN category	0.09	0.13	-0.16	0.34	0.478
International	0.20	0.25	-0.30	0.69	0.438
Human population	-0.27	0.17	-0.60	0.07	0.116
HDI	-0.20	0.28	-0.76	0.35	0.472
Habitat diversity	0.01	0.12	-0.22	0.24	0.946
Grassland	0.02	0.18	-0.33	0.37	0.909
Forest	-0.04	0.17	-0.37	0.30	0.827
Elevation	-0.02	0.10	-0.21	0.17	0.840
Bird community rarity	-0.08	0.21	-0.49	0.33	0.711
Bird attractiveness	0.20	0.15	-0.10	0.50	0.193
Amenities	0.18	0.17	-0.16	0.51	0.310
Age	0.11	0.10	-0.09	0.31	0.268
ASIA & OCEANIA					
Binomial model					
Water bodies	0.13	0.08	0.28	-0.02	0.095
Temperature	0.24	0.10	0.43	0.04	**0.017**

	β coefficient	Standard error	Lower 95% confidence interval	Upper 95% confidence interval	P
Size	0.99	0.09	1.17	0.81	**<0.001**
Remoteness	-0.14	0.10	0.05	-0.33	0.159
Precipitation	-0.19	0.09	-0.02	-0.37	**0.031**
Political stability	0.61	0.27	1.15	0.07	**0.026**
National park	1.50	0.21	1.91	1.09	**<0.001**
Mammal community rarity	-0.01	0.09	0.17	-0.19	0.902
Mammal attractiveness	-0.02	0.09	0.16	-0.20	0.833
IUCN category	-0.15	0.08	0.01	-0.31	0.075
International	1.07	0.15	1.35	0.78	**<0.001**
Human population	-0.04	0.15	0.26	-0.35	0.773
HDI	-0.50	0.26	0.01	-1.01	0.056
Habitat diversity	-0.10	0.07	0.04	-0.24	0.150
Grassland	0.13	0.08	0.29	-0.03	0.114
Forest	0.17	0.10	0.36	-0.03	0.097
Elevation	0.09	0.08	0.24	-0.07	0.275
Bird community rarity	0.08	0.16	0.38	-0.23	0.618
Bird attractiveness	0.23	0.10	0.43	0.02	**0.028**
Amenities	0.06	0.19	0.44	-0.31	0.737
Age	0.38	0.06	0.50	0.26	**<0.001**
Frequency model					
Water bodies	0.28	0.12	0.06	0.51	**0.015**
Temperature	0.18	0.13	-0.08	0.44	0.182
Size	0.57	0.14	0.30	0.85	**<0.001**
Remoteness	-0.27	0.14	-0.55	0.01	0.057
Precipitation	-0.16	0.11	-0.38	0.05	0.138
Political stability	-0.26	0.27	-0.79	0.28	0.347
National park	0.21	0.32	-0.42	0.84	0.513
Mammal community rarity	0.21	0.13	-0.05	0.47	0.108
Mammal attractiveness	0.21	0.11	0.00	0.42	0.052
IUCN category	-0.39	0.15	-0.68	-0.09	**0.010**
International	0.47	0.18	0.13	0.82	**0.008**
Human population	0.45	0.20	0.06	0.83	**0.022**
HDI	0.28	0.28	-0.27	0.83	0.318
Habitat diversity	0.04	0.10	-0.15	0.23	0.651
Grassland	0.20	0.13	-0.04	0.45	0.106
Forest	0.14	0.15	-0.14	0.43	0.331
Elevation	0.09	0.10	-0.11	0.28	0.401
Bird community rarity	-0.51	0.22	-0.95	-0.08	**0.021**
Bird attractiveness	-0.17	0.15	-0.45	0.12	0.258
Amenities	-0.21	0.27	-0.73	0.31	0.425
Age	0.01	0.09	-0.18	0.19	0.953
EUROPE					
Binomial model					
Water bodies	0.32	0.10	0.53	0.12	**0.002**
Temperature	-0.05	0.15	0.24	-0.34	0.756
Size	0.79	0.11	1.00	0.58	**<0.001**
Remoteness	0.08	0.09	0.25	-0.09	0.358
Precipitation	-0.17	0.09	0.01	-0.35	0.065
Political stability	0.71	0.40	1.49	-0.06	0.072
National park	1.40	0.34	2.07	0.74	**<0.001**
Mammal community rarity	0.32	0.13	0.57	0.06	**0.015**
Mammal attractiveness	-0.03	0.12	0.21	-0.26	0.832

	β coefficient	Standard error	Lower 95% confidence interval	Upper 95% confidence interval	P
IUCN category	-0.19	0.08	-0.04	-0.35	**0.014**
International	0.60	0.18	0.96	0.24	**0.001**
Human population	-0.31	0.17	0.03	-0.65	0.072
HDI	-0.21	0.36	0.49	-0.92	0.556
Habitat diversity	0.39	0.10	0.60	0.19	$<$**0.001**
Grassland	0.27	0.12	0.51	0.03	**0.026**
Forest	0.12	0.14	0.39	-0.16	0.407
Elevation	-0.06	0.11	0.16	-0.29	0.589
Bird community rarity	0.11	0.10	0.31	-0.09	0.273
Bird attractiveness	0.07	0.12	0.31	-0.17	0.561
Amenities	-0.62	0.31	-0.01	-1.23	**0.047**
Age	0.34	0.07	0.49	0.20	$<$**0.001**
Frequency model					
Water bodies	0.33	0.28	-0.22	0.89	0.238
Temperature	0.88	0.29	0.31	1.45	**0.003**
Size	0.08	0.29	-0.48	0.64	0.789
Remoteness	0.52	0.30	-0.07	1.11	0.083
Precipitation	-0.39	0.29	-0.96	0.19	0.186
Political stability	-0.29	0.54	-1.34	0.77	0.596
National park	-0.53	0.73	-1.95	0.90	0.468
Mammal community rarity	-0.16	0.39	-0.93	0.61	0.685
Mammal attractiveness	0.35	0.28	-0.20	0.91	0.212
IUCN category	-0.24	0.19	-0.61	0.13	0.197
International	0.80	0.43	-0.04	1.64	0.060
Human population	-0.90	0.53	-1.94	0.15	0.092
HDI	1.44	0.74	-0.01	2.89	0.052
Habitat diversity	0.04	0.27	-0.48	0.57	0.873
Grassland	0.54	0.29	-0.03	1.11	0.063
Forest	0.63	0.38	-0.11	1.37	0.095
Elevation	0.43	0.25	-0.05	0.91	0.080
Bird community rarity	0.25	0.29	-0.31	0.82	0.380
Bird attractiveness	0.17	0.32	-0.47	0.80	0.604
Amenities	1.34	0.68	0.00	2.68	**0.049**
Age	0.34	0.15	0.05	0.63	**0.021**

Table C.7: Results of separate models of PA *popularity*, fitted with (1) mammal and bird *attractiveness*, (2) mammal and bird richness, and (3) neither *attractiveness* nor richness as predictor variables. The performance of each model (pseudo-R^2) is shown, and standardized regression coefficients (β), standard deviations (SD), P values from each model are shown for variables of interest. All other variables (see Table 3.1) are present in all models.

	Binomial		Frequency		
	β (±SD)	P	β (±SD)	P	R^2
Global					
Mammal *attractiveness*	-0.012 (0.066)	0.853	0.217 (0.070)	**0.002**	0.396
Bird *attractiveness*	0.146 (0.061)	**0.017**	-0.009 (0.077)	0.906	
Mammal richness	0.043 (0.066)	0.569	0.143 (0.083)	0.086	0.395
Bird richness	0.004 (0.067)	0.953	0.104 (0.078)	0.182	
None	—	—	—	—	0.376
Africa					
Mammal *attractiveness*	-0.083 (0.250)	0.740	0.187 (0.143)	0.190	0.512
Bird *attractiveness*	0.728 (0.281)	**0.009**	-0.096 (0.163)	0.554	
Mammal richness	-0.088 (0.315)	0.779	-0.146 (0.170)	0.389	0.498
Bird richness	0.651 (0.333)	0.051	0.334 (0.179)	0.063	
None	—	—	—	—	0.503
Asia and Oceania					
Mammal *attractiveness*	-0.019 (0.092)	0.833	0.210 (0.108)	0.052	0.260
Bird *attractiveness*	0.227 (0.103)	**0.028**	-0.166 (0.146)	0.258	
Mammal richness	-0.044 (0.096)	0.648	0.248 (0.118)	**0.035**	0.245
Bird richness	0.155 (0.116)	0.181	-0.155 (0.161)	0.334	
None	—	—	—	—	0.238
Americas					
Mammal *attractiveness*	-0.019 (0.113)	0.867	0.055 (0.134)	0.681	0.383
Bird *attractiveness*	0.001 (0.114)	0.992	0.199 (0.153)	0.193	
Mammal richness	-0.122 (0.141)	0.388	-0.093 (0.175)	0.597	0.368
Bird richness	0.005 (0.144)	0.971	0.329 (0.185)	0.076	
None	—	—	—	—	0.341
Europe					
Mammal *attractiveness*	-0.026 (0.121)	0.832	0.353 (0.283)	0.212	0.180
Bird *attractiveness*	0.070 (0.121)	0.561	0.168 (0.324)	0.604	
Mammal richness	-0.031 (0.112)	0.779	0.100 (0.324)	0.758	0.140
Bird richness	0.054 (0.125)	0.667	0.125 (0.378)	0.742	
None	—	—	—	—	0.091

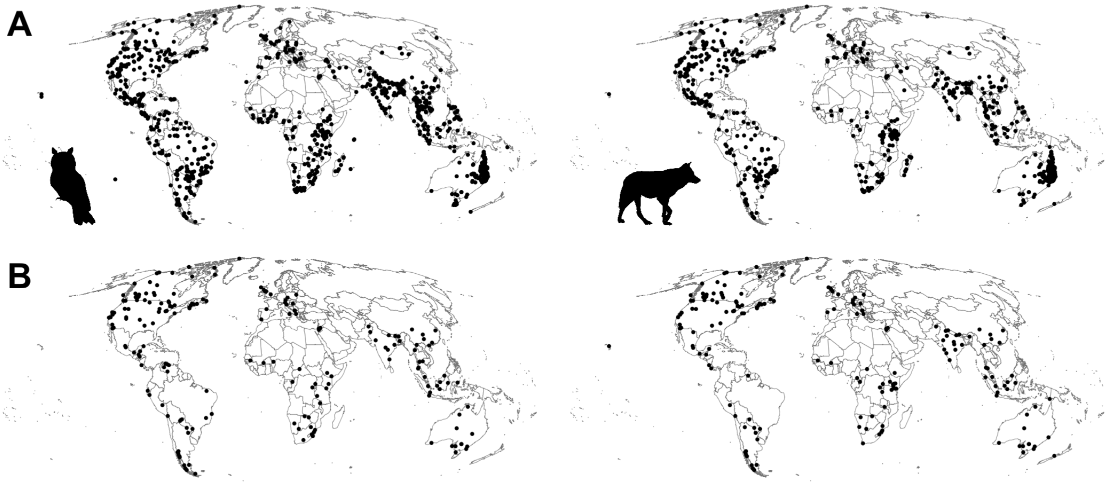

Figure C.1: Locations of PAs with available species inventories, shown separately for birds and mammals. The maps show **A** all PAs with inventories of birds (n = 913) and mammals (n = 699), and **B** PAs with bird (n = 187) and mammal (n = 178) inventories considered complete or comprehensive, based on the accompanying text descriptions. PA inventories were obtained from peer-reviewed articles, grey literature, management plans, technical reports, official PA websites, biodiversity databases, conservation agencies, citizen science databases, and other resources.

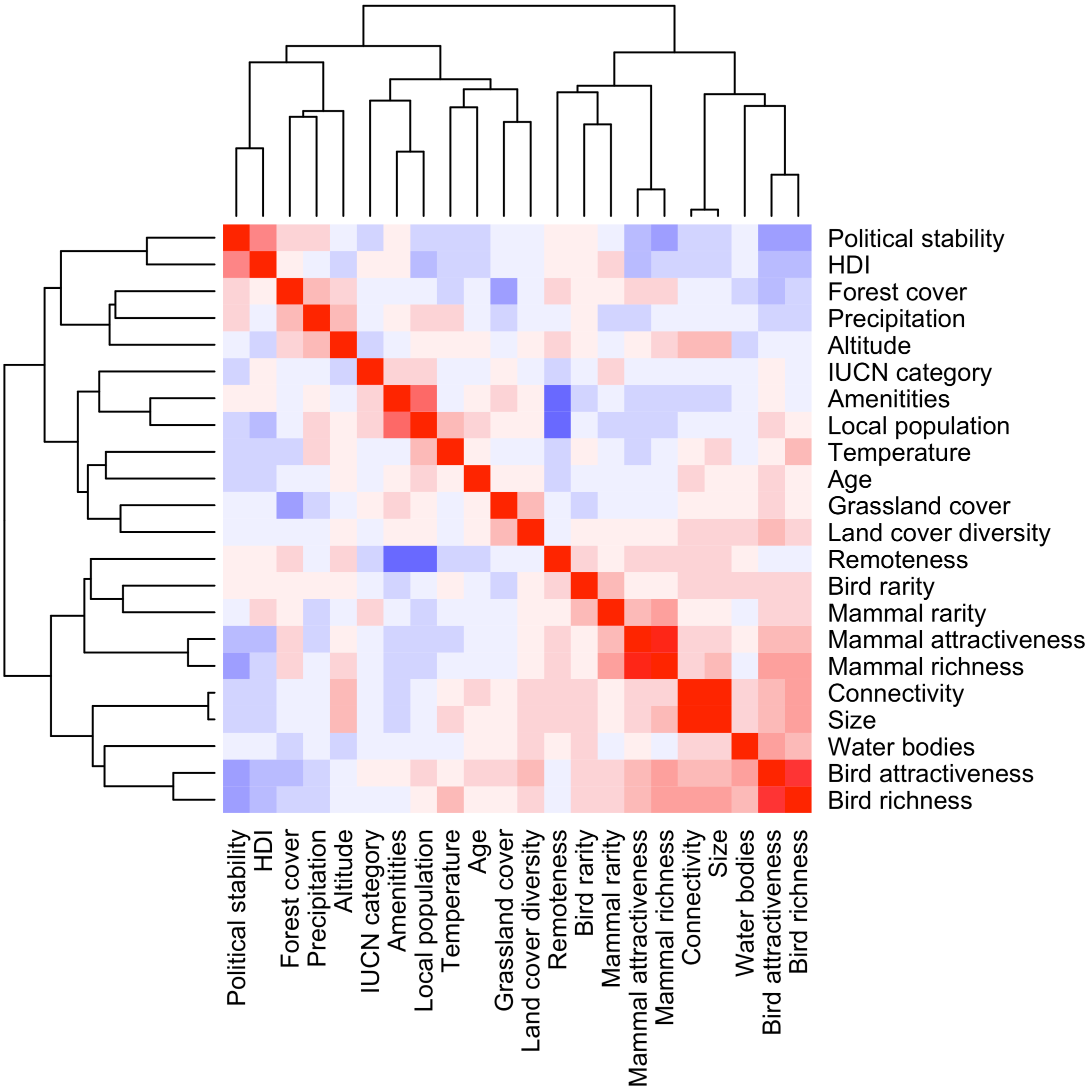

Figure C.2: Kendall's tau-b (τb) correlation between potential explanatory variables of PA *popularity*. Red indicates a positive correlation for a given pair, and blue indicates a negative correlation. The darker the colour, the stronger the correlation. The length of the dendrogram branches represents the distance between variables or clusters of variables calculated from bivariate Kendall's τb correlations.

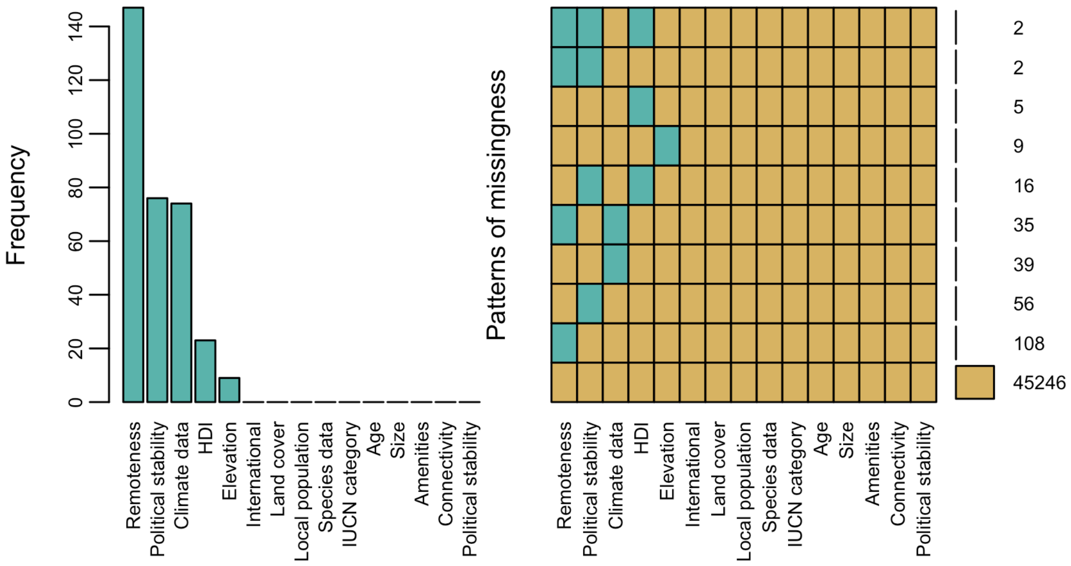

Figure C.3: Patterns of missing data for PAs (n = 45,518), showing the proportion of missing data (shown in teal) for each variable and the proportion of different combinations of missing data. The numbers on the right-hand side represent the number of PAs with each combination i.e., 45,246 PAs had data for all attributes. Land cover data includes land cover diversity and proportions of grassland, forest, and water bodies. Species data includes mammal and bird *attractiveness*, richness, and community rarity.

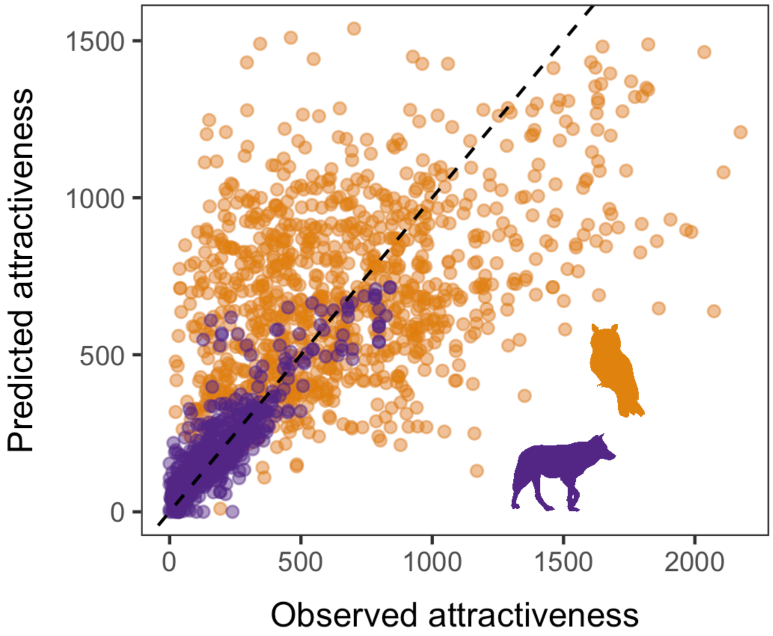

Figure C.4: The relationship between observed and predicted total *attractiveness* scores of mammals (n = 699) and birds (n = 913) for PAs, using species lists from inventories and expert range maps, respectively.

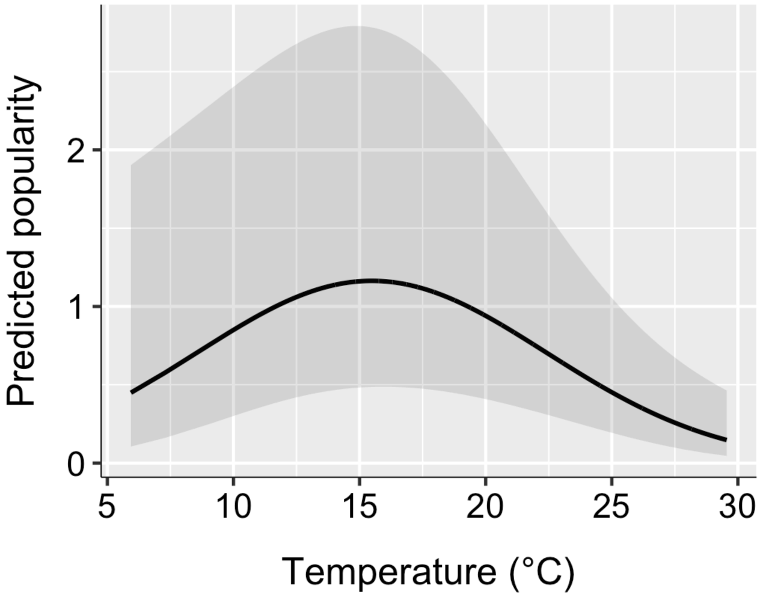

Figure C.5: The effect of temperature (°C) on PA *popularity* in Africa, indicated by a significant quadratic term in the frequency (i.e., zero-truncated negative binomal) part of the hurdle GLMM.

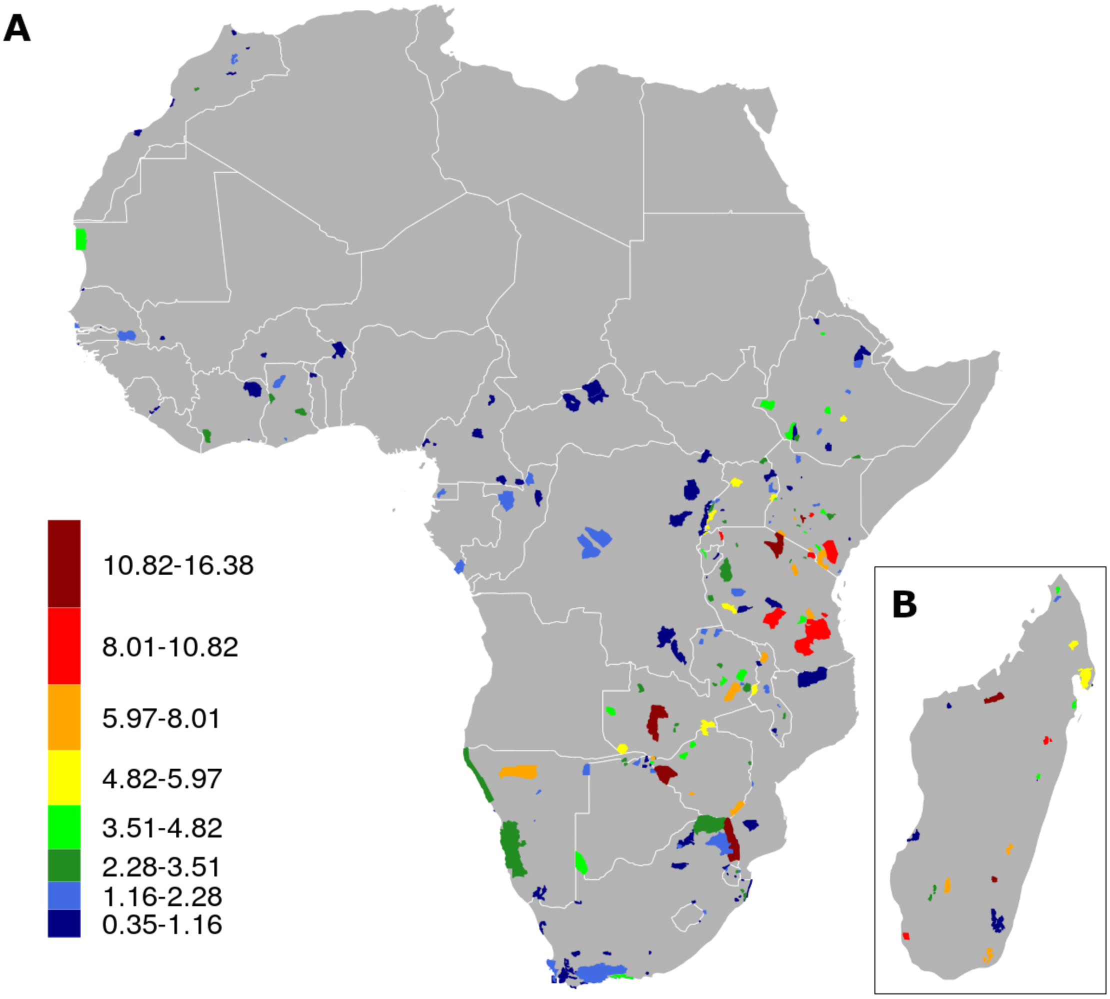

Figure C.6: PA *popularity* in Africa, based on predictions from the negative binomial hurdle GLMM for Africa. Jenks natural breaks were used to determine break points for colour scale. PAs below the lowest break i.e., < 0.35 are not shown to aid in the visualising of more *popular* PA. **A** shows PA *popularity* across the mainland Africa, while **B** shows a close up of PA *popularity* in Madagascar.

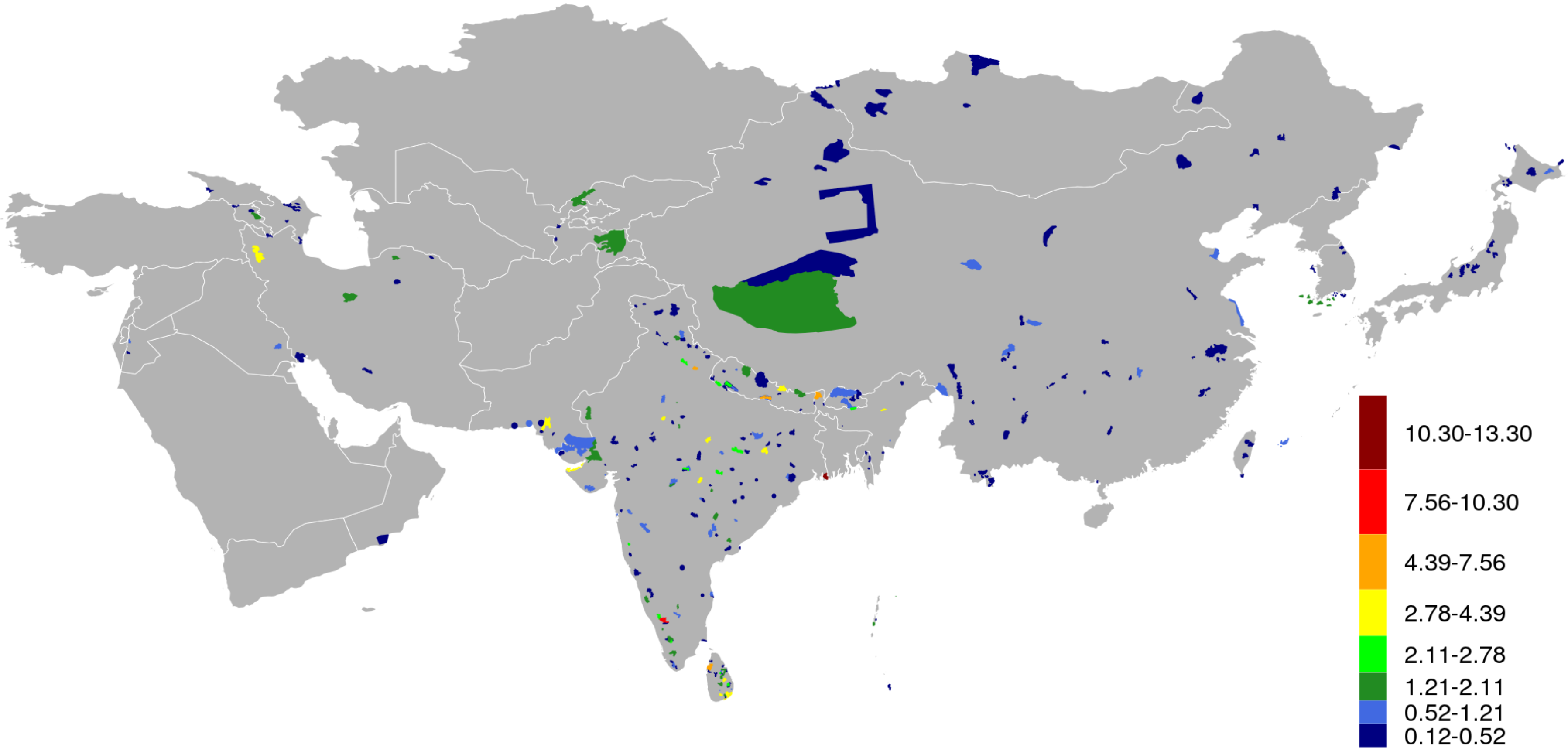

Figure C.7: PA *popularity* in Asia (excluding South East Asia), based on predictions from the negative binomial hurdle GLMM for Asia and Oceania. Jenks natural breaks were used to determine break points for colour scale. PAs below the lowest break i.e., < 0.12 are not shown to aid in the visualising of more *popular* PA. Russia is also not shown as it had no PAs that fell above the lowest break.

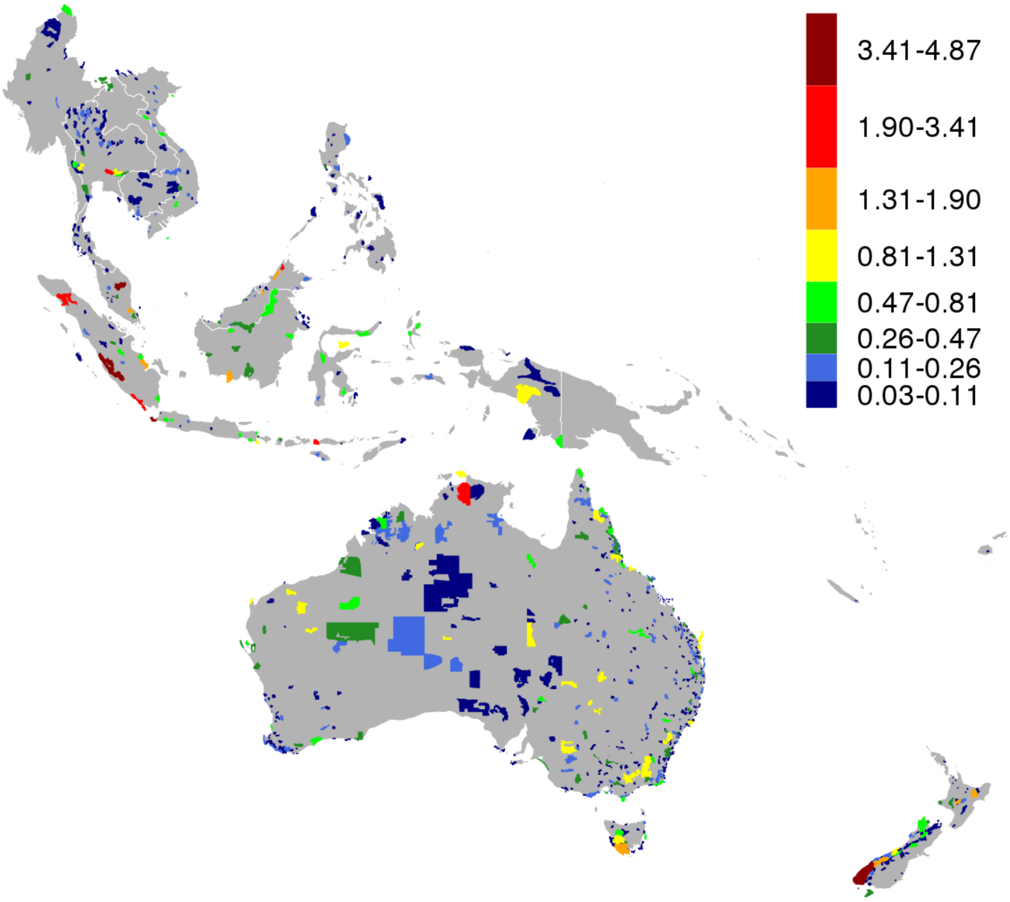

Figure C.8: PA *popularity* in South East Asia and Oceania, based on predictions from the negative binomial hurdle GLMM for Asia and Oceania. Jenks natural breaks were used to determine break points for colour scale. PAs below the lowest break i.e., < 0.03 are not shown to aid in the visualising of more *popular* PAs.

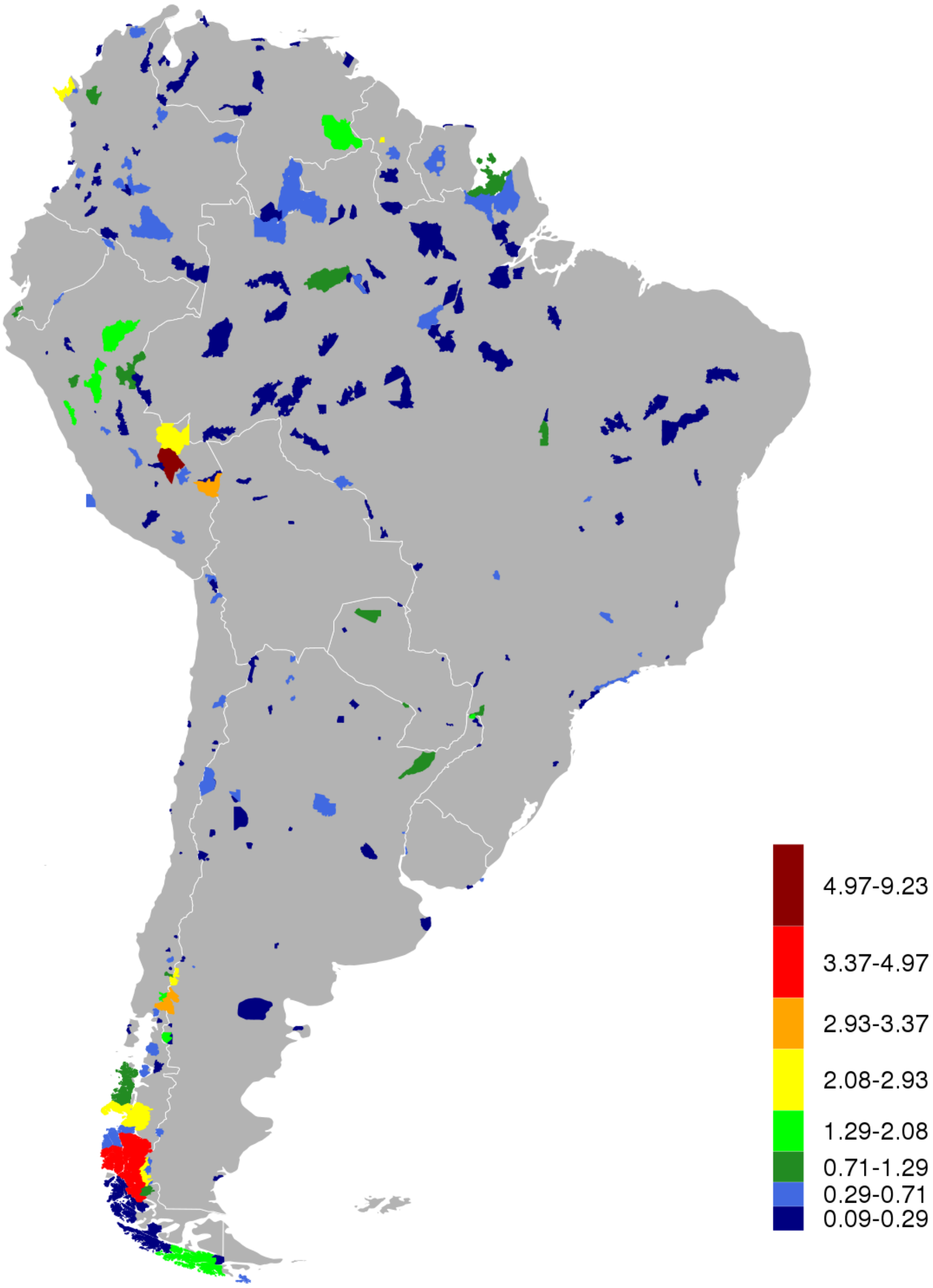

Figure C.9: PA *popularity* in South America, based on predictions from the negative binomial hurdle GLMM for the Americas. Jenks natural breaks were used to determine break points for colour scale. PAs below the lowest break i.e., < 0.09 are not shown to aid in the visualising of more *popular* PAs.

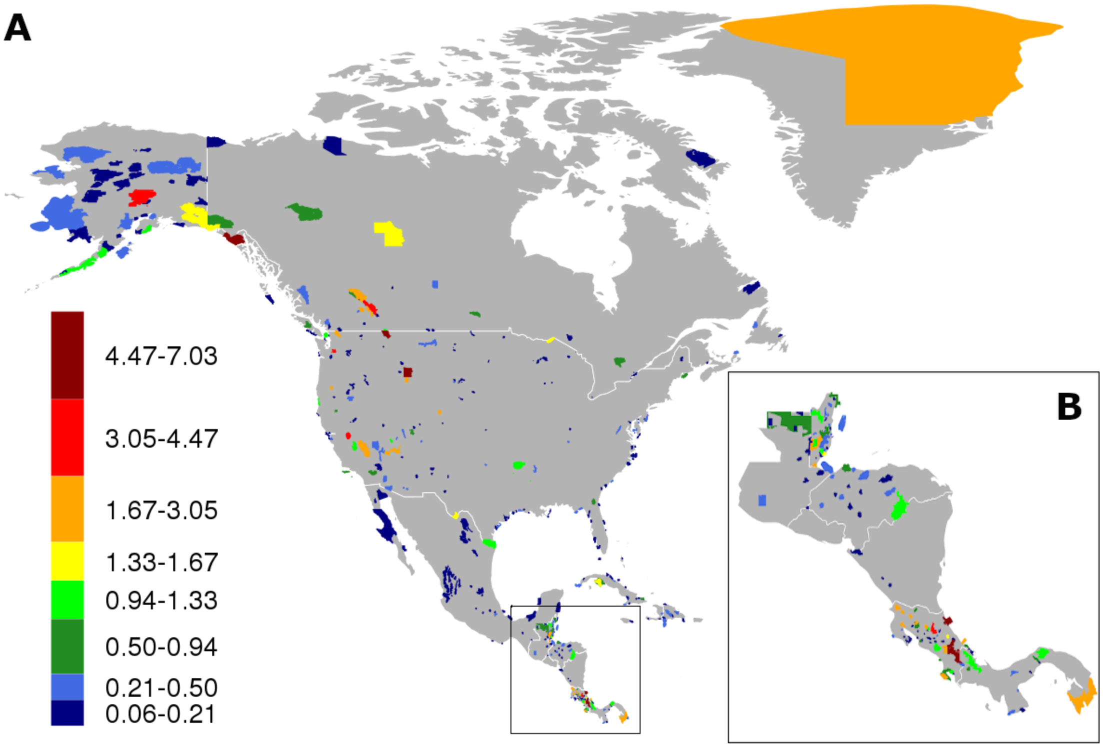

Figure C.10: PA *popularity* in North America, based on predictions from the negative binomial hurdle GLMM for the Americas. Jenks natural breaks were used to determine break points for colour scale. PAs below the lowest break i.e., < 0.06 are not shown to aid in the visualising of more *popular* PAs. **A** shows PA *popularity* across the whole of the continent, while **B** shows a close up of PA *popularity* in Central America (excluding Mexico).

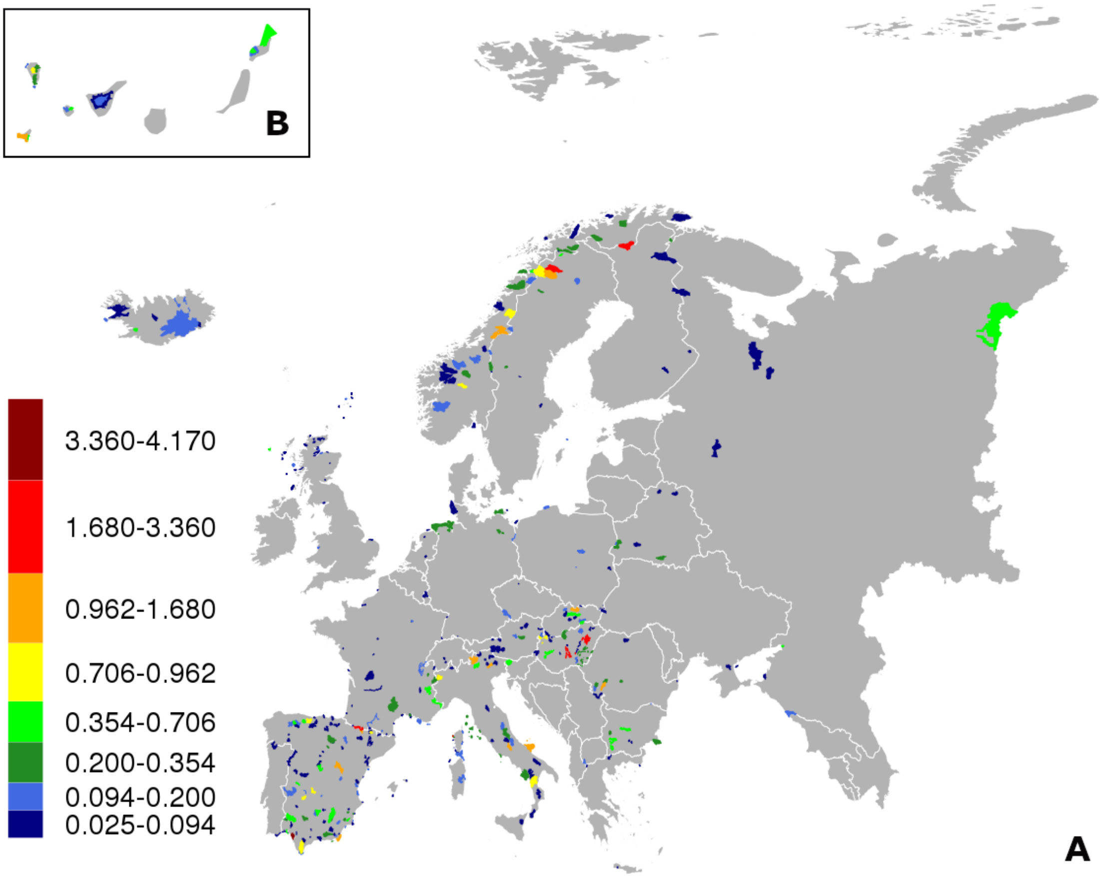

Figure C.11: PA *popularity* in Europe, based on predictions from the negative binomial hurdle GLMM for Europe. Jenks natural breaks were used to determine break points for colour scale. PAs below the lowest break i.e., < 0.025 are not shown to aid in the visualising of more *popular* PAs. **A** shows PA *popularity* across the whole of continent, while **B** shows a close up of PA *popularity* in the Canary Islands.

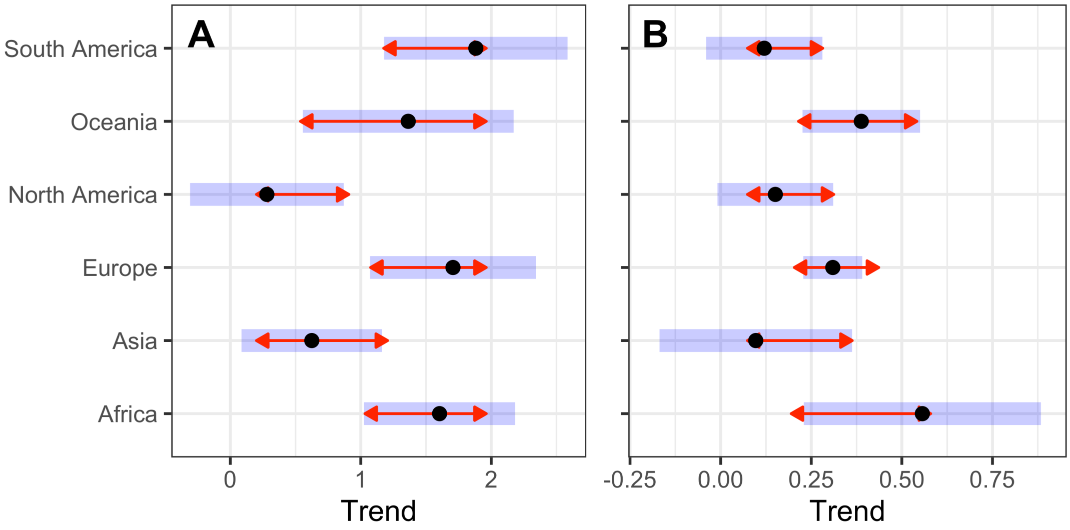

Figure C.12: Linear trend within each continent between PA *popularity* and annual visitation (n = 991), showing the trend with **A** observed *popularity* (i.e., number of guides citing each PA) and **B** predicted *popularity*. The central mark denotes the estimated trend, and the blue bars denote the 95% confidence intervals. The red arrows are used for comparisons among trends, such that if they overlap, the differences between trends are not significant (Lenth, 2020).

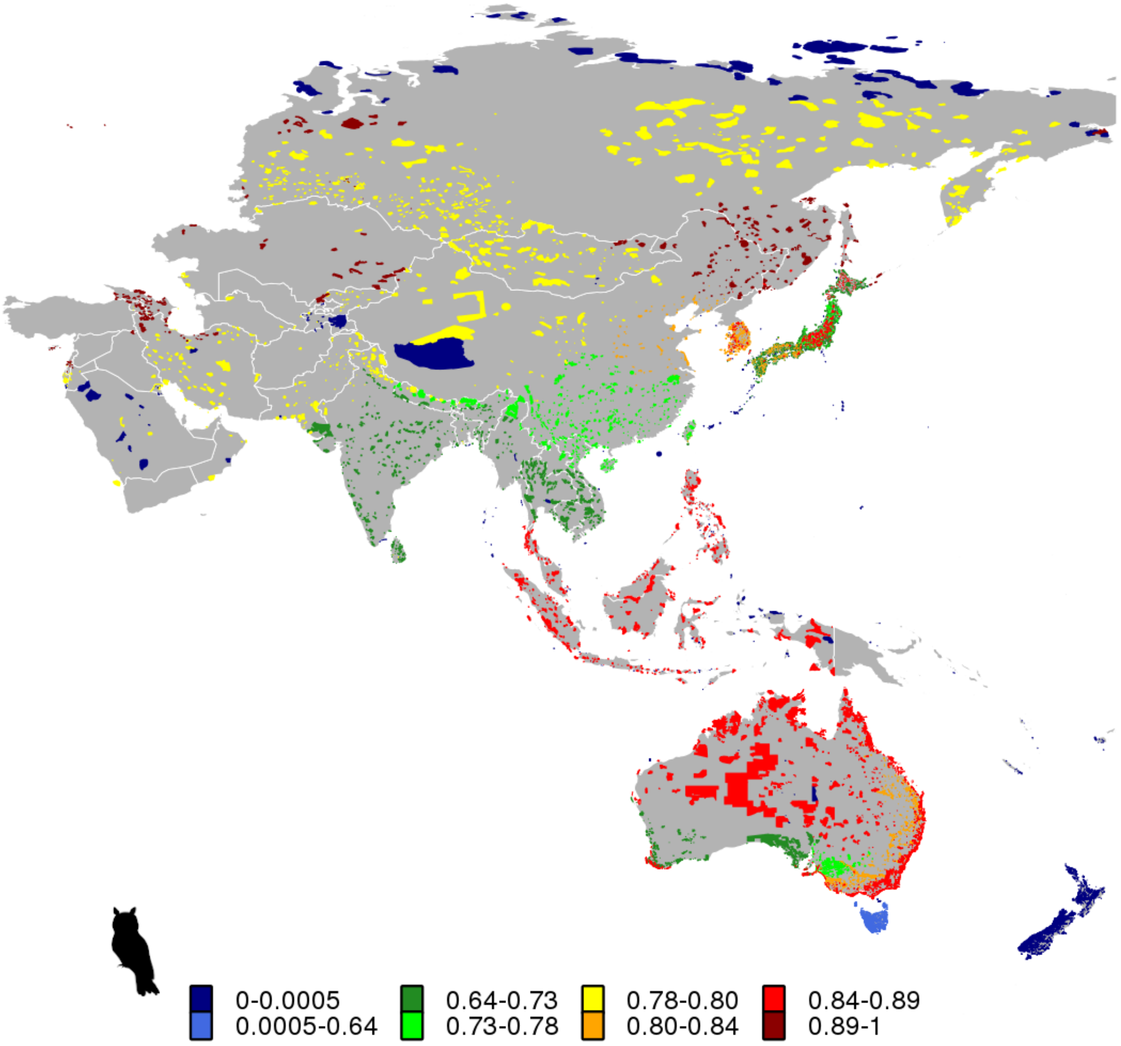

Figure C.13: Rarity of bird assemblages within PAs of Asia and Oceania. k-means clustering was used to group bird assemblages into distinct clusters with similar bird compositions (n = 35). Rarity was calculated as $R_i = 1\text{-}((F_i\text{-}1)/\max(F))$, where F_i is the frequency of cluster i and max(F) is the frequency of the most common cluster. Higher values refer to greater rarity and lower numbers refer to lower rarity. PAs where birds are absent were assigned a value of zero. Jenks natural breaks were used to determine break points for colour scale.

Appendix D

Chapter 5

Table D.1: List of rare birds (n = 83) and terrestrial mammals (n = 16) in the United Kingdom, defined as those with a breeding range size of ≤ 1,000 10km grid cells, in order of increasing range size.

Common name	Scientific name	Range size
Birds		
Red-necked phalarope	*Phalaropus lobatus*	16
Horned grebe	*Podiceps auritus*	16
Roseate tern	*Sterna dougallii*	18
Redpoll	*Acanthis flammea*	21
Common crane	*Grus grus*	21
Golden pheasant	*Chrysolophus pictus*	26
Cirl bunting	*Emberiza cirlus*	28
Northern gannet	*Morus bassanus*	33
Montagu's harrier	*Circus pygargus*	36
Black-tailed godwit	*Limosa limosa*	41
Whimbrel	*Numenius phaeopus*	42
Manx shearwater	*Puffinus puffinus*	42
Western capercaillie	*Tetrao urogallus*	51
Common goldeneye	*Bucephala clangula*	53
Eurasian thick-knee	*Burhinus oedicnemus*	54
Black-necked grebe	*Podiceps nigricollis*	54
Crested tit	*Lophophanes cristatus*	59
European storm-petrel	*Hydrobates pelagicus*	60
European honey-buzzard	*Pernis apivorus*	81
Eurasian bittern	*Botaurus stellaris*	82
Bearded tit	*Panurus biarmicus*	84
Sandwich tern	*Thalasseus sandvicensis*	95
White-tailed sea-eagle	*Haliaeetus albicilla*	99
Hawfinch	*Coccothraustes coccothraustes*	113
Arctic jaeger	*Stercorarius parasiticus*	119
Little tern	*Sternula albifrons*	124
Black redstart	*Phoenicurus ochruros*	135
Pied avocet	*Recurvirostra avosetta*	141
Dartford warbler	*Sylvia undata*	149
Woodlark	*Lullula arborea*	155
Rock ptarmigan	*Lagopus muta*	175
Atlantic puffin	*Fratercula arctica*	181
Garganey	*Spatula querquedula*	212
Arctic loon	*Gavia arctica*	218
Common firecrest	*Regulus ignicapilla*	218
Egyptian goose	*Alopochen aegyptiaca*	232
Western marsh-harrier	*Circus aeruginosus*	251
Corncrake	*Crex crex*	261
Red-billed chough	*Pyrrhocorax pyrrhocorax*	282
Osprey	*Pandion haliaetus*	286
Common murre	*Uria aalge*	290
Razorbill	*Alca torda*	301
Black-legged kittiwake	*Rissa tridactyla*	317
European nightjar	*Caprimulgus europaeus*	328

Common name	Scientific name	Range size
Arctic tern	*Sterna paradisaea*	347
Red-throated loon	*Gavia stellata*	353
Common nightingale	*Luscinia megarhynchos*	367
Eurasian wigeon	*Mareca penelope*	382
Golden eagle	*Aquila chrysaetos*	413
Cetti's warbler	*Cettia cetti*	421
Short-eared owl	*Asio flammeus*	426
Black grouse	*Lyrurus tetrix*	433
Ring ouzel	*Turdus torquatus*	439
Mandarin duck	*Aix galericulata*	502
Common eider	*Somateria mollissima*	531
Northern goshawk	*Accipiter gentilis*	533
European pied flycatcher	*Ficedula hypoleuca*	534
Black guillemot	*Cepphus grylle*	537
Lesser spotted woodpecker	*Dryobates minor*	560
Twite	*Linaria flavirostris*	562
Corn bunting	*Emberiza calandra*	596
Little ringed plover	*Charadrius dubius*	600
European turtle-dove	*Streptopelia turtur*	624
European shag	*Phalacrocorax aristotelis*	647
Hen harrier	*Circus cyaneus*	659
Red-breasted merganser	*Mergus serrator*	661
Great cormorant	*Phalacrocorax carbo*	711
Northern fulmar	*Fulmarus glacialis*	715
Eurasian golden plover	*Pluvialis apricaria*	715
Red kite	*Milvus milvus*	735
Common tern	*Sterna hirundo*	756
Gadwall	*Mareca strepera*	768
Western yellow wagtail	*Motacilla flava*	785
Merlin	*Falco columbarius*	811
Wood warbler	*Phylloscopus sibilatrix*	820
Great black-backed gull	*Larus marinus*	845
Goosander	*Mergus merganser*	874
Common quail	*Coturnix coturnix*	890
Northern long-eared owl	*Asio otus*	901
Western water rail	*Rallus aquaticus*	917
Common gull	*Larus canus*	924
Whinchat	*Saxicola rubetra*	925
Eurasian woodcock	*Scolopax rusticola*	992
Mammals		
Reindeer	*Rangifer tarandus*	4
Fat dormouse	*Glis glis*	20
Red-necked wallaby	*Macropus rufogriseus*	28
Common vole	*Microtus arvalis*	33
Beaver	*Castor fiber*	57
Wild boar	*Sus scrofa*	122
Chinese water deer	*Hydropotes inermis*	142
House mouse	*Mus musculus*	264
Wildcat	*Felis silvestris*	412

Common name	Scientific name	Range size
Yellow-necked mouse	*Apodemus flavicollis*	413
Sika deer	*Cervus nippon*	506
Mountain hare	*Lepus timidus*	659
Hazel dormouse	*Muscardinus avellanarius*	677
Pine marten	*Martes martes*	804
Harvest mouse	*Micromys minutus*	875
Polecat	*Mustela putorius*	926

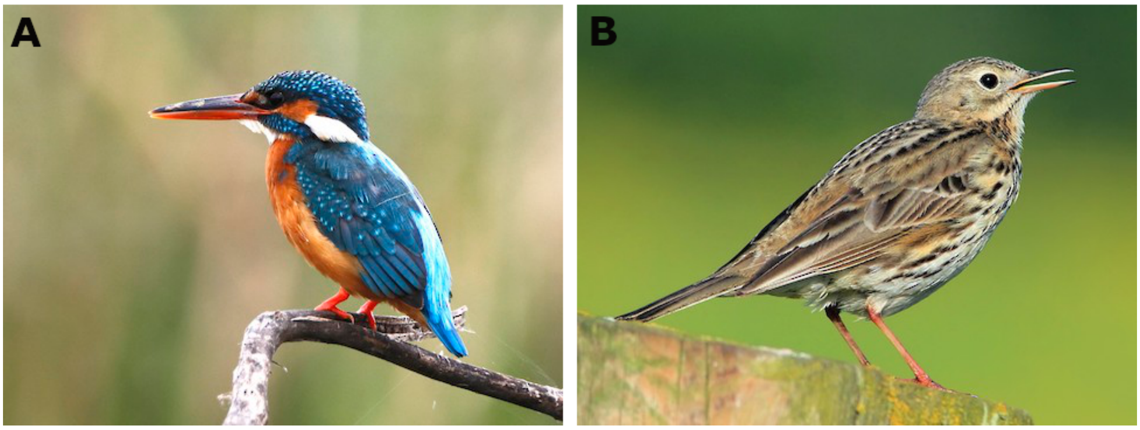

Figure D.1: Examples of species with a high and low BCI, showing **A**, the common kingfisher *Alcedo atthis*, with bright and iridescent blue feathers and **B** the meadow pipit *Anthus pratensis* , with no iridescent or bright colouration. Photographs by M. S. Novelkumar and Anne Carrington-Cotton, respectively, downloaded from https://birdsoftheworld.org/bow/.

Figure D.2: A visual demonstration of how the size of the ears of British species was measured, using the Scottish wild cat *Felis silvestris* as an example. The ear for this species was categorized as large when its surface area, circled in yellow, was $>$ 50% the surface area of half the face, the latter measured from the end of muzzle to the start of the ear.

Figure D.3: A visual demonstration of how the size of the eyes of British species was measured, using the red squirrel *Sciurus vulgaris* as an example. The eye was categorized as large when the diameter of the eye, represented by the white line, was $>$ 25% the length between the end of muzzle and the start of ear, represented by the green line.

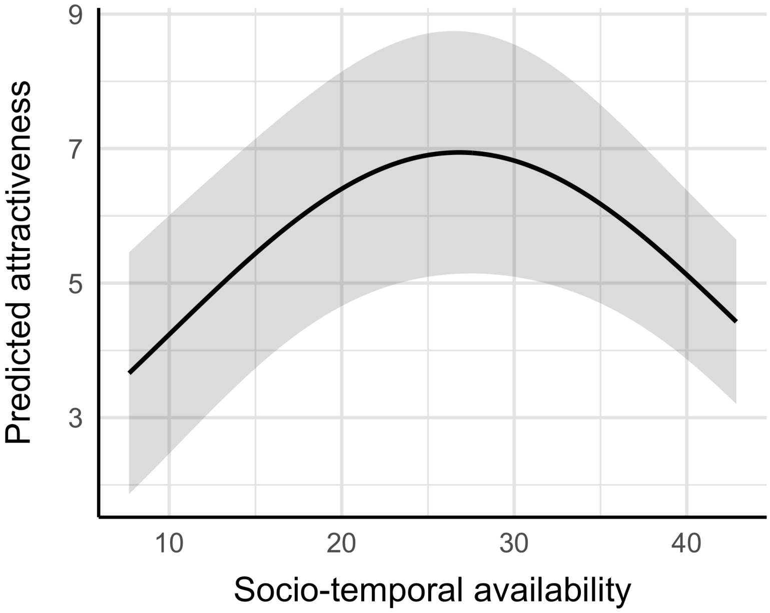

Figure D.4: The effect of spatio-temporal availability on bird *attractiveness* in the United Kingdom, indicated by a significant quadratic term in the GLM. This measure of spatial and temporal viewing availability was calculated by dividing bird range sizes into breeding and wintering ranges, and multiplying each by the length of each season.

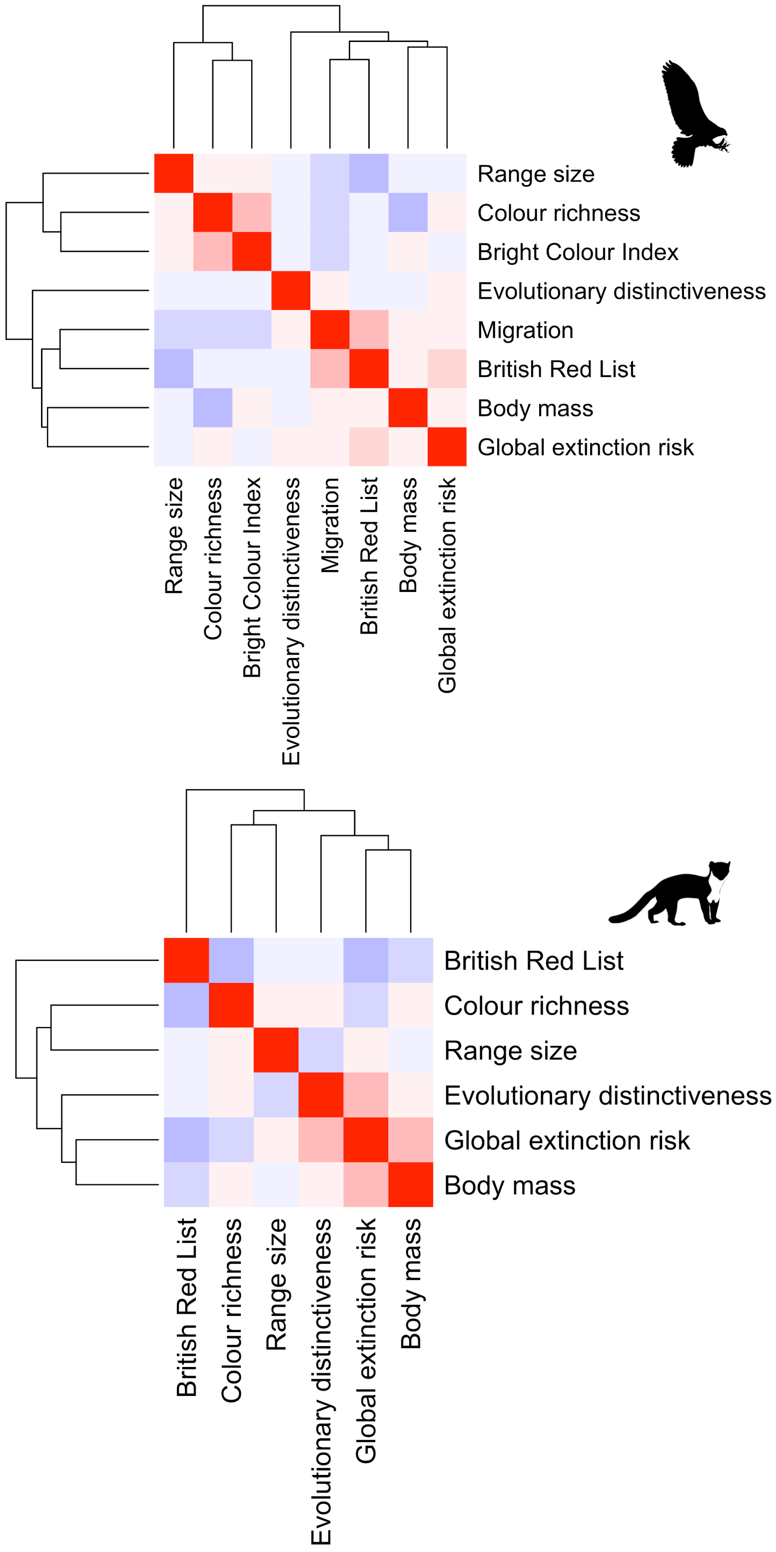

Figure D.5: Kendall's tau-b (τb) correlation between potential explanatory variables of bird and mammal *attractiveness*. Red indicates a positive correlation for a given pair, and blue indicates a negative correlation. The darker the colour, the stronger the correlation. The length of the dendrogram branches represents the distance between variables or clusters of variables calculated from bivariate Kendall's τb correlations.

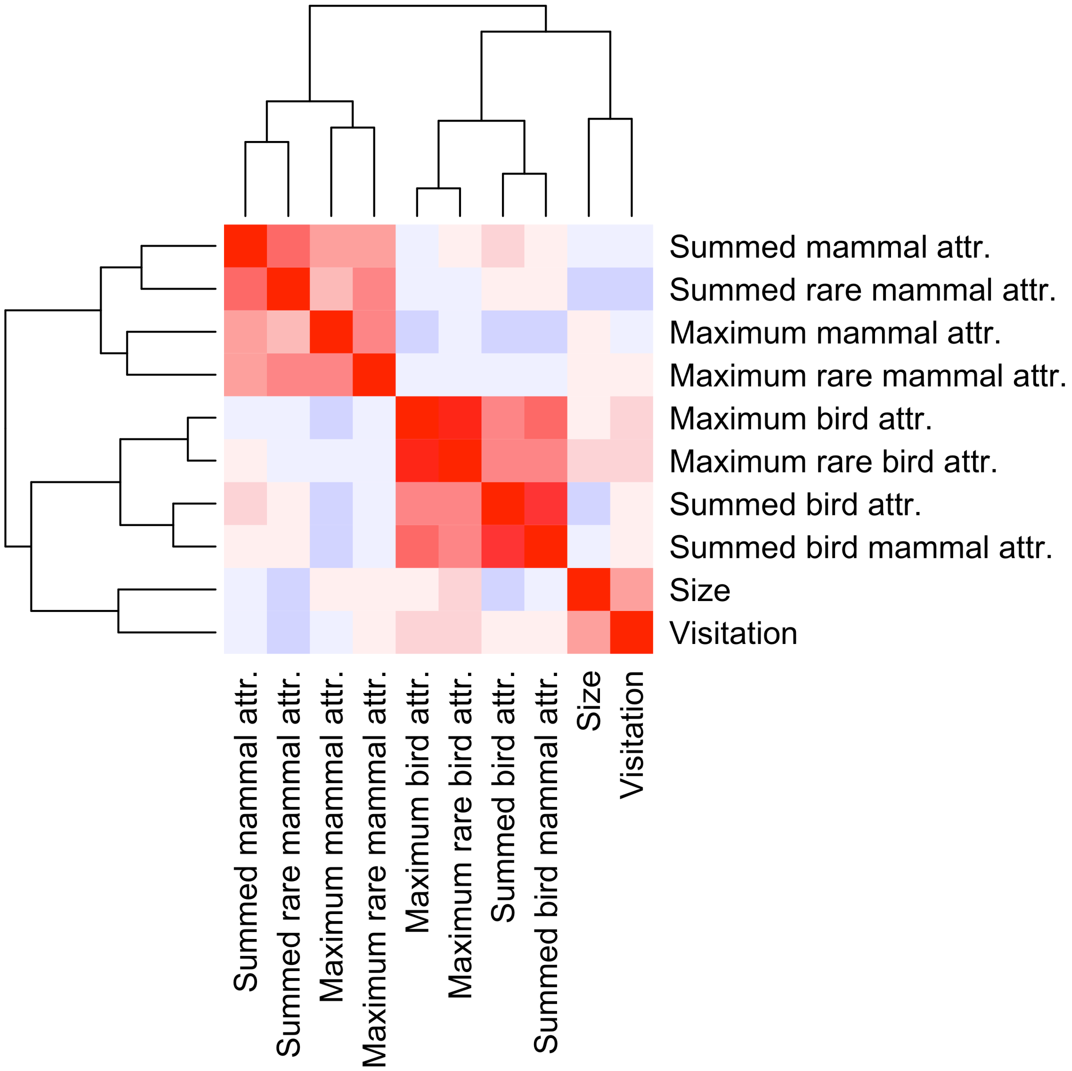

Figure D.6: Kendall's tau-b (τb) correlation between *attractiveness* measures, size, and visitation of British coastal and terrestrial PAs. Red indicates a positive correlation for a given pair, and blue indicates a negative correlation. The darker the colour, the stronger the correlation. The length of the dendrogram branches represents the distance between variables or clusters of variables calculated from bivariate Kendall's τb correlations.

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