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The impacts of climate change on long-distance migratory birds

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Submitted for the degree of Doctor of Philosophy

Department of Biosciences

Durham University

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Table of Contents

Author’s Declaration

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

Chapter 2 has been published as:

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Kieran Lawrence

June 2023

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This thesis has been the product of four years of exceptionally hard work but, whilst I am incredibly proud of myself for its production, this would not have been possible without the guidance and support of many outstanding people.

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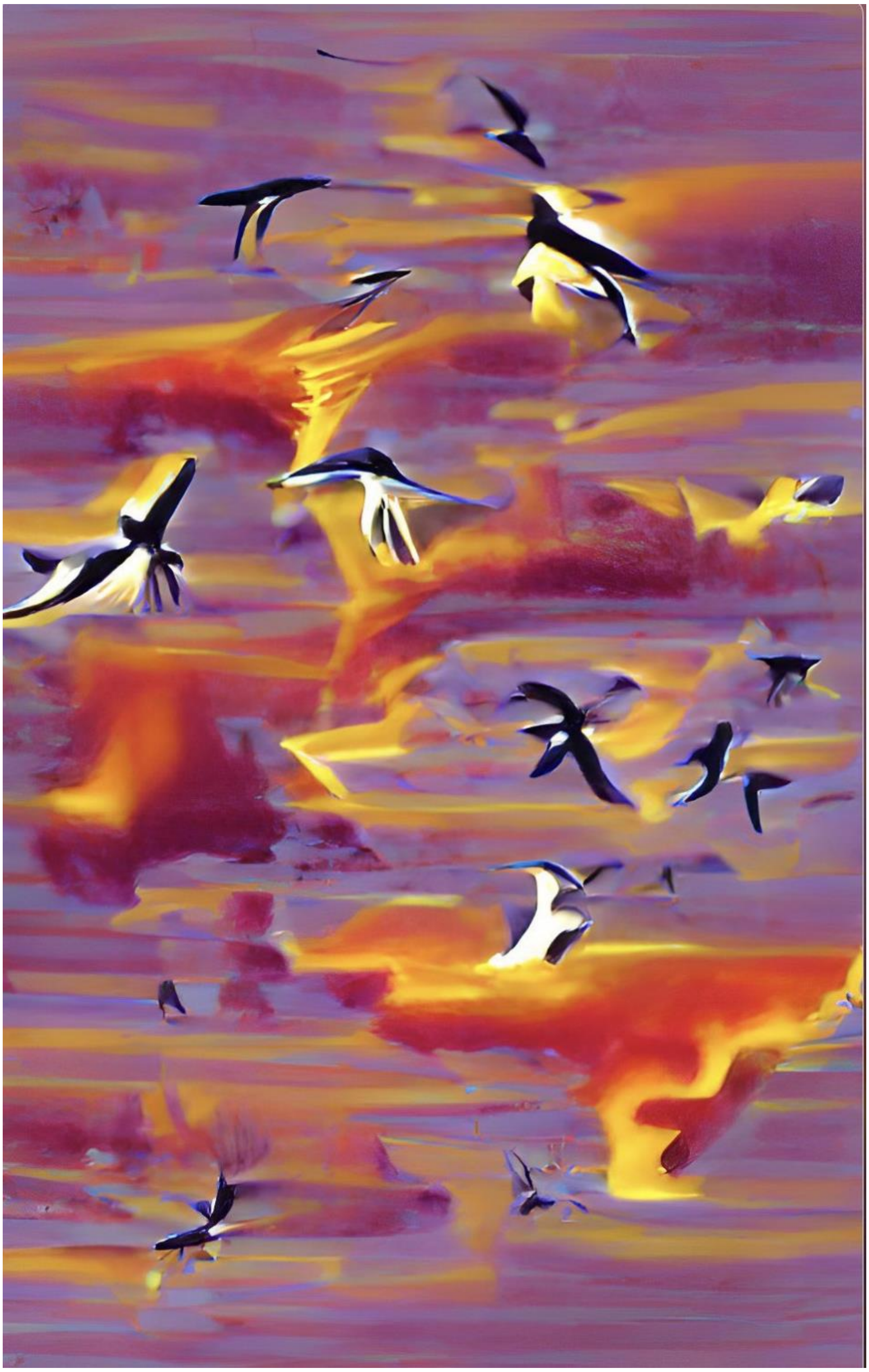
Finally, and most importantly, this thesis must be dedicated to my wife, Hebe. Despite the stress of a self-funded PhD and a global pandemic, the last few years have been the happiest and quickest of my life and I genuinely could not have achieved this without her.

Abstract

Biodiversity is declining globally, and, increasingly, these declines are attributed to the impacts of climate change. Migratory species are particularly vulnerable to these impacts due to an increased likelihood of encountering environmental change. Potentially as a result, migrants have experienced rapid, recent population declines, with long-distance migratory birds having declined at faster rates than both residents and even their short-distance migratory counterparts. Given the prevalence of long-distance migratory behaviour across birds, such declines are likely to have contributed significantly to the overall loss of biodiversity and its associated ecosystem services. However, our understanding of the past, present, and future impacts of climate change on these species and, therefore, our ability to implement measures to prevent further declines remains limited. In this thesis, I use of a variety of datasets and statistical techniques to fill in a number of these knowledge gaps, identifying the impacts of climate change on long-distance migratory birds in three main areas: (1) migratory phenology, (2) population trends, and (3) migratory journeys. First, I make use of citizen science and bird observatory records to show that pre-breeding departure from the non-breeding grounds has advanced over the last 60 years, whilst post-breeding migration has been delayed. I highlight the real possibility that continuation of these trends could result in long-distance migrants "short-stopping" and adopting a short-distance migratory strategy. Next, I demonstrate, for the first time, that trends in and the drivers of the population trends of migratory birds are similar across species breeding in North America and Europe. On the breeding grounds, climate appears to be more important than land-use, whereas the converse is true on the non-breeding grounds. I then show that the climate-driven poleward shifts in species' ranges that are predicted for the end of the century would see the breeding and non-breeding ranges of the world's long-distance, but not short-distance, migratory birds shift in opposite directions. As a result, individuals will be required to migrate further, making additional stopovers to refuel and, therefore, spending longer on migration overall. Finally, I use reconstructions of pre-historic climate to demonstrate that, whilst migration distances were likely to have previously been significantly shorter, long-distance migration was as prevalent a phenomenon at the last glacial maximum as it is today. Together, my results show that, whilst species show some adaptive capacity to climate change, long-distance migrants are unlikely to be able to cope with further changes in climate and, without help, will suffer further declines. Furthermore, we still lack vital data for the study of migratory birds, which precludes a complete understanding of their population trends. However, given the spatial consistency of my findings, future conservation planning that accounts for the increased vulnerability of migratory species can likely be implemented in spatially disparate locations with similar success.

Chapter 1

General Introduction



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1.1 The global biodiversity crisis

The current rate at which our world is losing biodiversity has reached a crisis state. The vast majority of global ecosystem and biodiversity indicators are displaying rapid declines (IPBES, 2019). 75% of the world's land surface has been significantly altered, flying insect biomass has decline by over 75% in the last 30 years, and vertebrate populations have declined by 68% since 1970 (Hallmann et al., 2017; IPBES, 2019; WWF, 2020). Extinction rates are currently hundreds of times higher than background rates, with 25% of plant and animal species (totalling over a million species) that have been assessed currently threatened by extinction (IPBES, 2019; Pimm et al., 1995). It would require only these threatened species to go extinct for the globe to have entered its sixth mass extinction event (Barnosky et al., 2011).

An immeasurable moral and ethical argument for the reversal of such declines in biodiversity exists, largely centred around the intrinsic value and "right-to-life" of the millions of species with which we share the planet (Ehrlich & Wilson, 1991; Hambler, 2004; Rolston, 1988). Beyond these, declines in biodiversity present an increasingly unignorable threat to the economic opportunities and services that healthy, intact, and diverse ecosystems provide. These range from direct uses, such as food, energy, and medicine provision, to the indirect benefits of ecosystem services, e.g. nutrient cycling, carbon sequestration, and pollination (Balvanera et al., 2006; Cardinale, 2012; Emmett Duffy et al., 2017; Stachowicz et al., 2007). Biodiverse ecosystems also provide important ecotourism opportunities, as well as a variety of cultural and mental health benefits (Balmford et al., 2015; Fuller et al., 2007; IPBES, 2019). Placing a monetary value on biodiversity may be seen as a dangerous and difficult prospect, however estimates suggest that these services are worth over $140 trillion, annually (Costanza et al., 2014), highlighting their worth along many axes of 'value'.

1.1.1 Reversing the decline

Clearly, the decline of the world's biodiversity must be stemmed. Over the past 30 years, numerous international strategies have been adopted to this end, with the UN Convention on Biological Diversity's "Strategic Plan for Biodiversity 2011-2020" being the most recent of these (CBD, 2011). This plan outlined 20 "Aichi Biodiversity Targets", which placed responsibility on individual countries to stop biodiversity loss at the national level. However, even with the recognition of the scale of threat that biodiversity loss poses, we have fallen almost entirely short of these targets (Buchanan et al., 2020; Butchart et al., 2019; IPBES, 2019). Much of this shortfall has been attributed to a lack of clarity and feasibility of the aims of these strategies, as well as an inability to assess progress towards them (Butchart et al., 2016; Green et al., 2019). Biodiversity plans, and their targets, must become more tangible and directed if we are to reverse these declines.

The post-2020 global biodiversity framework is a step in the right direction for conservation targets and planning (CBD, 2022). New goals include protecting 30% of the world's surface by 2030 and reducing the extinction risk of all species tenfold by 2050. However, targets such as the latter will require the identification of declining populations, in addition to those threatened with future decline. Furthermore, stemming, or entirely preventing, such declines will require a detailed understanding of the major drivers of decline and the mechanisms by which they act. With a limited pool of funding for conservation, as well as a shift to a more global conservation perspective, projects should maximise the number of species and populations protected for every unit of investment. Therefore, although there are likely to be nuances in the extent of population declines and their drivers, it should be a priority to identify not only declining populations, but also broad taxonomic and geographic patterns of decline.

1.1.2 Migratory species

Likely due to their overt visibility and widespread nature, the movements of animals have fascinated humans for millennia (Runge et al., 2015). From the blacking out of the sun by over two billion Passenger Pigeons *Ectopistes migratorius* (Fuller, 2014) to herds of two million ungulates tracking rains across the plains of East Africa (Pennycuick, 1975) or the utterly mind-boggling trans-Pacific flights of the Bar-tailed Godwit *Limosa lapponica* (Battley et al., 2012), migration presents some of the greatest spectacles and physical feats the natural world has to offer. Migration has been observed in a variety of taxa, including fish, insects, reptiles, birds, and mammals, and enables species to exploit the richness of world's resource (Somveille et al., 2015; Wilcove & Wikelski, 2008). Potentially the earliest recording of "tracked" migration comes from *Pfeilstorch* (german for "arrow stork"), a White Stork *Ciconia ciconia* found in Germany in 1822 with an arrow of central African hardwood stuck through its neck. The essence of this event has been retained in modern studies of migratory animals, with individuals fitted with unique markers and, more recently, electronic tags, enabling them to be tracked across the globe (Bridge et al., 2011). Such studies have uncovered the huge variety of migratory destinations, timings, and routes that exist across taxa around the globe.

Unfortunately, detailed study has also revealed that the populations of migratory species are declining (Wilcove & Wikelski, 2008). These declines are occurring at a faster rate than those of resident species and are more rapid in long-distance migrants than their short-distance counterparts (Holt, 2000; Sanderson et al., 2006). The abundance, global distribution and detailed monitoring of birds makes them a useful taxon with which to study declines and their drivers. Furthermore, with around 16% of all birds performing “true” migrations, i.e. not including nomadic or altitudinal migrants, declines in these populations present a major threat to global biodiversity and its associated ecosystem services (Kirby et al., 2008).

Hunting and persecution of individuals on migration and the impacts of land-use change at breeding, non-breeding and stopover sites have all been identified as important drivers of decline in the populations of long-distance migratory birds (Kirby et al., 2008; Studds et al., 2017; Vickery et al., 2014). However, as with many taxa, climate-change has become increasingly implicated in these declines. Moreover, climate change is predicted to continue to impact migrants in the future, exacerbating the impacts of other existing current and projected future threats (Both et al., 2006; Howard et al., 2020; Ockendon et al., 2014; Peach et al., 1991; Sanderson et al., 2006). Land surface temperatures rose by 1.59^{o}C between 1850 and 2020, and are likely to rise by at least a further 1.5^{o} by the end of the 21st century (IPCC, 2021). These changes have impacted, and will continue to impact, the phenology, distributions, interactions and, ultimately, demography of migratory species (Both et al., 2006; Finch et al., 2014; Huntley et al., 2008; Lemoine & Bohning-Gaese, 2003). Long-distance migrants are particularly susceptible to the effects of climate-change, as impacts may occur at any one of the numerous sites they utilise through their annual cycle, including breeding and non-breeding areas, migratory stopover sites, and the airspaces through which they migrate.

Recent study has improved our understanding of the past, present, and potential future impacts of climate-change on long-distance migratory birds (discussed in section 1.3). However, gaps in our knowledge remain, ultimately limiting our ability to prevent or reverse declines in these populations. In this thesis, I aim to identify and fill in some of these gaps, providing a more detailed understanding of the likely impacts of climate change on migrant species and a base to implement more effective conservation measures in relation to identified threats. In the following section, I summarise the declines that have occurred in long-distance migratory birds across the globe. I then discuss the major drivers of these population declines, before focusing specifically on the impacts of climate change on the long-distance migrants. After identifying the major knowledge gaps, I describe the main methods that can be used to answer those remaining questions. I conclude by describing the main aims of the thesis.

1.2 Declines in the populations of long-distance migratory birds

Migratory species are declining globally (Wilcove & Wikelski, 2008). Declines in migratory species are particularly well documented in birds, likely due to a combination of their global abundance, relative ease of recording, and prevalence of migration across taxa (Kirby et al., 2008). Over half of all migratory birds have suffered population declines since the 1980s (Runge et al., 2015) and, crucially, these declines have occurred more rapidly and across a greater proportion of species than those experienced by their resident counterparts (Heldbjerg & Fox, 2008; Robbins et al., 1989; Thaxter et al., 2010; Vickery et al., 2014). Further distinction can be made between migratory species, as populations of long-distance migrants, typically classified as those that migrate from temperate breeding areas to tropical non-breeding sites, are declining at faster rates than those of short-distance migratory species, which are typically classified as those that remain within temperate areas year-round (Holt, 2000; Sanderson et al., 2006).

Declines in populations of long-distance migratory birds are not spatially isolated, but have occurred in all three of the major migration flyways across the globe (Kirby et al., 2008). Studies have considered a variety of areas and species, but in the Americas up to 71% of Nearctic-Neotropical migratory species have suffered decline since 1950 (Holt, 2000; Robbins et al., 1989). 40% of trans-Saharan migrants exhibited substantial population decline between 1970 and 2000 (Sanderson et al., 2006). A lack of detailed monitoring in the Australasian flyway has precluded broad-scale analyses of population trends, however migratory shorebirds in this flyway showed population declines of 73% between 1983 and 2006 and, over a similar timescale, long-distance migratory land birds decline more rapidly than other species in Japan and South Korea (Amano & Yamaura, 2007; Kim et al., 2021; Nebel et al., 2008).

Around 1,500 bird species are truly migratory and declines in these populations have contributed and will continue to contribute heavily to the overall loss of global biodiversity and ecosystem services (Kirby et al., 2008). Migratory species are particularly important in terms of ecosystem services, providing these in pulses, in a number of locations, at different times of year, and linking otherwise disparate areas (Bauer & Hoye, 2014; Willson & Halupka, 1995). As individuals move, foraging and being preyed upon, they transport nutrients and energy, control pests, disperse seeds, facilitate the dispersal of parasites and pathogens. Many species provide ecotourism opportunities and even cultural services - swallows heralding the return of spring and the tradition of The Times newspapers letters on the first cuckoo of the year, for example. Migrants, especially those that travel long distances, therefore impact a greater number of communities, ecosystems, and landscapes than sedentary species. As such, in addition to declines in long-distance migratory populations occurring more rapidly than in their resident or short-distance migratory counterparts, they are also likely to have a disproportionate impact on global ecosystem provisioning.

1.2.1 Drivers of populations declines of long-distance migratory birds

Migratory birds rely on multiple, spatially segregated sites throughout their annual cycle: for the breeding and non-breeding periods, and stopover sites used for resting/refuelling between these (Newton, 2008). Whilst this reliance has not intrinsically led to decline in migratory populations, it increases their susceptibility to any threats (Finch et al., 2014; Runge et al., 2014). For every additional location utilised, the likelihood that individuals will encounter a process that reduces their fitness increases. Furthermore, migration is the period of highest mortality throughout the annual cycle and any disruption to these journeys is likely to have major impacts on populations (Rushing et al., 2017; Sillett & Holmes, 2002). Taken together, these factors may help to explain why long-distance migrants are declining more rapidly than either their short-distance counterparts or resident species. Long-distance migrations take longer and require the use of a greater number of stopover sites, thereby increasing the risk of reduced fitness.

Unfortunately, the reliance of migratory species on numerous sites also complicates the identification of the causes of population declines (Vickery et al., 2023; Zurell et al., 2018). With a lack of information on demographic rates and changes to habitats/environments throughout these annual cycles, it is difficult to identify the stage at which populations are becoming limited and, therefore, why these declines are occurring. This is especially true for long-distance migrants, whose non-breeding and stopover sites are typically found in the tropics and subtropics, where there is a particular paucity of data (Vickery et al., 2023). Nevertheless, through detailed monitoring, particularly in Europe and North America, links between several anthropogenic threats and population declines of long-distance migratory birds have been made. Below, I first summarise the impacts of three major factors that threaten migrants: land-use change, hunting, and collision with artificial structures. In addition, disease, disturbance, and pollution may also impact long-distance migratory birds, however their pervasiveness is less well-documented, so they are not covered in detail.

Land-use change has been the most frequently cited driver of declines in the populations of long-distance migratory birds, not least as land-use changes are occurring globally (Kirby et al., 2008). As human populations have grown, and demand for space and resources has increased, habitat loss and degradation have occurred across most ecosystems (IPBES, 2019). For birds, this has resulted in a loss of a variety of resources, including nesting and roosting locations, but potentially most importantly, food availability (Vickery et al., 2014). Food limitations can increase competition among migratory individuals, particularly at stopover sites where resources are often limited (Kirby et al., 2008). Consequently, the body condition of individuals may decline, ultimately resulting in reduced productivity and increased mortality. For example, species associated with farmland habitats in Europe and North America have declined rapidly since 1950 (Donald et al., 2006; Gregory et al., 2019; Sutherland et al., 2012), a pattern that has extended to migratory species (Howard et al., 2020). These declines have been attributed to the intensification of farming practices, increased use of pesticides, drainage of land and overgrazing, all of which are likely to lead to reduced habitat quality. Such processes, in addition to woodcutting and burning, have also occurred in sub-Saharan Africa, resulting in the decline of migrant species associated with open, dryland habitats in the non-breeding season (Atkinson et al., 2014; Sanderson et al., 2006). Moreover, the rapid global expansion of agriculture has resulted in the loss of other habitats and, therefore, those species associated with them.

Deforestation across all three of the major migratory flyways has been linked with declines in the populations of long-distance migrants (Newton, 2008). For example, on the Thai-Malay peninsula, it is estimated that 80% of lowland inland forest and 90% of mangroves, both of which are important non-breeding habitats for migratory birds, have been lost (Kirby et al., 2008). In addition to the direct impacts of habitat loss, forest fragmentation may also result in increased nest predation and parasitism, which may in turn reduce productivity levels (Robbins et al., 1989). Many wetland habitats have also been lost due to agricultural expansion, as they are drained for conversion to cropland or dammed for irrigation, practices which have been particularly prevalent in Europe and Africa (Newton, 2004; Vickery et al., 2014). In Asia, however, the major threat comes from industrial development on mudflats and wetlands. In East and south-east Asia, 80% of these habitats have been lost in this way, whereas in China and South Korea, mudflats are being lost at over 1% per year (Amano et al., 2010; Ma et al., 2014). Migratory waders which rely on the Yellow Sea as a migratory staging site have declined rapidly as a result (Studds et al., 2017; Sutherland et al., 2012).

Hunting and trapping on migration and on the non-breeding grounds are also likely to have contributed to the decline of long-distance migratory birds, particularly of species migrating between Europe and Africa (Vickery et al., 2023). Mediterranean and Middle Eastern countries are well-known hotspots for hunting, both legal and illegal, of species on passage in spring and autumn. It is estimated that 10-40 million birds of over 400 bird species are killed or taken in these regions each year (Brochet et al., 2016, 2019). Hunting also poses a threat, particularly to migratory shorebirds on passage, in North America and Asia (Gallo-Cajiao et al., 2020). In the latter, migratory land birds may be mainly threatened by trapping for the pet trade (Yong et al., 2021). 66-84 million songbirds are estimated to be kept in Java alone, although the extent to which migratory species are involved is unknown (Marshall et al., 2020). Whilst it is difficult to identify population-level impacts of such threats, due to a lack of data on the numbers of each species taken and the migratory routes of breeding populations, hunting of long-distance migratory species such as the European Turtle Dove *Streptopelia turtur*, Ortolan Bunting *Emberiza hortulana* and Yellow-Breasted Bunting *Emberiza aureola* has been shown to be unsustainable (Jiguet et al., 2019; Kamp et al., 2015; Lormée et al., 2020). At the extreme, hunting played a large part in the extinction of migratory species such as the Passenger Pigeon *Ectopistes migratorius*, Eskimo Curlew *Numenius borealis* and Slender-billed Curlew *Numenius tenuirostris* (Gallo-Cajiao et al., 2020). Hunting and trapping can clearly have a large impact on the populations of long-distance migratory birds, particularly those which migrate through bottlenecks and, therefore, a large proportion of the population are targeted.

Increasingly, collision with man-made structures whilst individuals are migrating is cited as a threat to long-distance migratory populations (Newton, 2007). Buildings, towers, and masts act as obstacles for birds to navigate, and collision can be fatal. Long-distance migrants are at particular risk, as many species migrating from the tropics to temperate areas do so nocturnally (Kirby et al., 2008). In North America, as many as 1 billion birds may die annually through collision with artificial structures (Loss et al., 2014). Wind turbines and power lines also present a threat and, whilst numbers of fatalities are likely much lower than that of building strikes (thousands per year, rather than millions), poorly planned siting can lead to large numbers of collisions (Kirby et al., 2008). For example, wind-farms or power-lines located at migration bottlenecks or near major staging sites, such as wetlands, pose a substantial threat, particularly to larger and/or soaring species (Gauld et al., 2022). However, few direct links between collision threat and declines in long-distance migratory populations have been made.

1.3 The impacts of climate change on long-distance migratory birds

The Intergovernmental Panel on Climate Change's (IPCC) sixth assessment report (2021) highlighted that global land surface temperatures between 2011 and 2020 were 1.59^{o}C higher than 1850-1900. Each of the last four decades have been successively warmer than that which preceded it, as well as any decade since 1850. Temperatures have increased faster in the last 50 years than any other 50-year period in the last 2000 years and were last as high as they are currently 125,000 years ago. Global precipitation patterns have also changed, with average precipitation over land and the frequency and intensity of heavy precipitation events increasing since the 1950s. These changes can be attributed almost entirely to anthropogenic greenhouse gas (GHG) emissions. Carbon dioxide concentrations have reached 410 ppm, higher than any point in the last two million years. Methane and nitrogen dioxide are also at their highest concentrations for

800,000 years. Due to these rises in GHGs, global warming and variation in precipitation patterns will continue to the end of the century. Temperatures will rise by at least 1.5°C by 2100, unless significant reductions in GHGs are achieved, although further rises of up to 5.7°C are not out of the question under high emission scenarios.

As a result of the magnitude and rate of these changes, climate change has rapidly become one of the leading drivers of global biodiversity loss, both through its own direct impacts and the exacerbation of other threats, such as land-use and overexploitation (IPBES, 2019). Furthermore, many of the impacts felt by species will continue or worsen by the end of the century, whilst others may not yet be fully recognised. The declines of long-distance migratory birds are no exception to this and are increasingly attributed to climate change (Runge et al., 2015; Wilcove & Wikelski, 2008). Whilst many of the impacts of climate change on long-distance migrants are the same as those felt by resident and short-distance migratory species, long-distance migratory birds may be more severely affected - the “additional effect” hypothesis (Sanderson et al., 2006). Furthermore, because of the fundamental life-history differences between these sets of species, long-distance migrants face several threats from climate change that do not impact their resident or short-distance migratory counterparts - the “unique cause” hypothesis (Sanderson et al., 2006).

Current knowledge of the impacts of climate change on long-distance migratory birds can be grouped into three main areas, changes in: phenology, abundance, and geographic distribution. Below, I discuss these impacts in turn, and identify gaps in the existing literature that may preclude our understanding of the declines of long-distance migrants.

1.3.1 Phenology

Behavioural adaptations are often the first responses to climate change, as they occur at the level of the individual and, comparative to other responses, require few generations to spread through the population (Huntley et al., 2010). Many species have responded to changes in climate by altering the timings of their annual cycle, and advancements in reproductive phenology are well documented (Parmesan et al., 2003; Root et al., 2003; Thackeray et al., 2016). The timings in breeding grounds of plant leaf-out, insect emergence and egg laying in birds have advanced in many areas in response to warmer spring temperatures (Burgess et al., 2018; Post et al., 2018). However, the magnitude of these advances is not consistent across trophic levels, as higher levels have typically responded slower, leading to mismatch in the timings of previously aligned events (Both et al., 2009; Visser et al., 2004). For breeding birds, this has resulted in the peak food demand of chicks often occurring after the peak in food abundance, which can lead to reduced productivity (Burgess et al., 2018; Jones & Cresswell, 2010). As such, the least flexible species, in terms of egg-laying date, have declined most rapidly, along with those populations in areas with the shortest or earliest peak of food (Both et al., 2006; Both & Visser, 2001).

Whilst advancements in breeding dates have occurred, the reproductive phenologies of long-distance migratory birds and their breeding habitats show a greater degree of mismatch than that of their resident and short-distance migratory counterparts (Møller et al., 2008). This may have contributed to the rapid population declines of long-distance migrants through reduced productivity and survival. These differences between migratory strategies are likely due to existing mismatch being exacerbated by the need of long-distance migrants to judge breeding conditions from another continent, or hemisphere. Species are likely to have developed endogenous, circannual rhythms, which trigger departure from the non-breeding grounds in response to day-length, leading to later arrival, in phenological terms, on the breeding grounds each year (Helm et al., 2009; Taylor et al., 2016). Furthermore, many long-distance migrants rely on multiple stopover sites along their migratory routes for refuelling (Howard et al., 2018). Any mismatch in the time of arrival and resource availability at these sites is likely to slow down journey times as individuals take longer to refuel, leading to yet later breeding ground arrival and further mismatch (Finch et al., 2014). In contrast, the phenology of residents and short-distance migrants is likely more closely tied to the phenology of the breeding grounds, whilst migratory journeys are also shorter and less susceptible to disruption, enabling species to more accurately coordinate breeding phenology (Møller et al., 2008).

To compensate for comparatively late arrival on the breeding grounds, long-distance migratory individuals have reduced the time between arrival and laying date. However, some species are likely to have already reached their physiological limit, as laying date is now constrained by arrival date (Both & Visser, 2001; Newton, 2008). Many long-distance migrants have advanced the timing of their arrival on the breeding grounds and, as a result, have declined less than species that have not (Gill et al., 2013; Jonzén et al., 2006; Møller et al., 2008; Newson et al., 2016). As such, the ability of species to adapt to further increases in temperature and advances in the phenology of breeding habitats is likely to be determined by their ability to advance arrival dates. The extent to which this will be possible will depend on the mechanisms by which earlier breeding ground arrival is achieved, i.e., earlier departure from non-breeding grounds or faster migration speed, and the cues utilised to inform these decisions. Study of pre-breeding arrival on the breeding grounds, or at stopover sites along the way, has shown that long-distance migrants are arriving earlier at intermediate stopover sites each year and have increased migration speed following these stopovers (Jonzén et al., 2006; Tøttrup et al., 2008).

Furthermore, species appear to able to utilise multiple environmental cues, including rainfall, temperature and the North Atlantic Oscillation index, to anticipate conditions on the breeding grounds (Gordo & Sanz, 2008; Hüppop & Hüppop, 2003; Saino et al., 2007). However, due to paucity of data, analyses of trends in, and drivers of, the phenology of long-distance migration from the non-breeding grounds is lacking. Therefore, it remains unclear whether these earlier arrivals are driven by earlier departure or faster migration. This is an important distinction, as the ability to further advance breeding ground arrival differs between the two. Departure dates may be limited by the speed of pre-migratory fattening and the level of correlation between departure cues and breeding ground conditions, whereas the speed of migration has physiological limits (Studds & Marra, 2011).

Whilst warmer temperatures have advanced the timing of spring, they have also delayed the onset of autumn, thereby increasing the length of the growing season (Menzel & Fabian, 1999). This may enable all birds, including long-distance migrants, to extend the breeding season, raise additional broods, and boost productivity (Walther et al., 2002). Equally, however, there may exist pressure to arrive on the non-breeding grounds before the onset of the tropical dry season, when resource availability drops off markedly (Jenni & Kéry, 2003). A consensus trend in the timing of post-breeding migration does not exist, which likely reflects inter-specific variation in the determinants of post-breeding migration, i.e., physiological constraints on brood number, moult strategy and the location of non-breeding sites (Bitterlin & Van Buskirk, 2014; Jenni & Kéry, 2003; Van Buskirk et al., 2009). However, for species that have delayed post-breeding and advanced pre-breeding migration, significant changes to the temporal partitioning of their annual cycle are likely to have occurred and will continue to occur. Unfortunately, such trends have yet to be assessed from breeding or non-breeding locations.

1.3.2 Abundance

Changes in climate have occurred so rapidly that behavioural adaptations have been insufficient to enable individuals to remain within their climatic niche (Parmesan et al., 2013). As a result, climate has also influenced the abundance of long-distance migratory populations (Gregory et al., 2009; Howard et al., 2015). This may occur directly through physiological processes, as the climate of a species existing range becomes more or less suitable, or shifts beyond the environmental tolerances of locally adapted populations (Stenseth et al., 2002). Alternatively, climate may act indirectly, increasing or decreasing habitat quality within a species distribution, or impacting the populations of other species, altering the strength of species interactions, all of which can impact survival, productivity and, therefore, population levels.

Weather conditions also impact breeding success, as cold and wet conditions are typically associated with smaller clutch sizes and reduced chick survival (Finch et al., 2014). However, the fledging success of some species is positively correlated with spring rainfall, potentially due to increased food availability (Robinson, 2005). Similarly, whilst warmer conditions typically lead to higher productivity, droughts in North America were associated with declines in neotropical migrants (Newton, 2004). Species distribution modelling approaches have shown that the climates of both North America and Europe have influenced the population trends of species breeding on those continents since 1980, as species predicted to benefit from changes in climate have fared better than those predicted to be negatively impacted (Mason et al., 2019; Stephens et al., 2016). Relationships are likely to depend on the specific combinations of temperature and precipitation, as well as the species. However, overall, breeding climate clearly has an impact on the demography of long-distance migratory birds.

Climate, particularly precipitation, on the non-breeding grounds of long-distance migrants has also been identified as a potential driver of population trends (Ockendon et al., 2014; Sanderson et al., 2006; Vickery et al., 2014). Drought conditions in the Sahel during the 1980s resulted in the decline in extent of wetland habitats, but also the decline in quality of terrestrial habitats, which are dominated by shallow-rooted vegetation and were already declining due to anthropogenic habitat destruction (Atkinson et al., 2014; Newton, 2004; Thaxter et al., 2010). Long-distance migrants associated with these habitats declined more rapidly than other species during this period (Atkinson et al., 2014; Sanderson et al., 2006). Such changes to habitat quality and extent led to reduced survival over the non-breeding period, due to lower food availability. However, they may also lead to carry-over effects on breeding success, as pre-breeding condition is affected by non-breeding food availability (Finch et al., 2014; Gordo et al., 2005). Lower habitat quality and food availability results in poorer body condition on arrival at the breeding grounds, which may lead to reduced productivity. Phenological mismatch on the breeding grounds may also be exacerbated by these effects, as pre-migratory moult and fattening are delayed by reduced food availability, both for individuals spending the non-breeding period in these areas, or those using them as a refuelling stopover site. At the extreme, mortality on migration may have increased due to starvation, but also may continue to increase as the frequency of extreme weather events increases (Kirby et al., 2008).

It has been suggested that the magnitude of the effects of climate change on species abundances is weaker for long-distance migrants than their short-distance counterparts (Howard et al., 2020). Moreover, when assessed holistically with other drivers, climate on the non-breeding grounds appears relatively unimportant for long-distance migrants.

This discrepancy between species of differing migratory strategies may be attributed to the impacts of phenological mismatch, which are less severe for short-distance migrants (Møller et al., 2008). Furthermore, milder winters in temperate regions may increase over-winter survival of resident and short-distance migrants that remain in these areas year-round (Forchhammer et al., 2002; Lemoine & Bohning-Gaese, 2003; Sanderson et al., 2006). This increases competition for resources such as food and nesting locations, which could reduce the survival and productivity of long-distance migrants, which are already at a handicap due to their comparatively late arrival on the breeding grounds. It is important to note, however, that there is a paucity of holistic, full-annual cycle studies of the relative impacts of the various potential drivers of decline. To my knowledge, there are none that analyse the population trends of long-distance migratory birds outside of the Afro-Palearctic flyway.

1.3.3 Geographic distribution

Declines in abundance are likely to occur most rapidly in populations at the edge of species' ranges, where conditions are assumed to be less optimal than at the centre of the range and, consequently, individuals are less fit (Brown et al., 1996; Gibson et al., 2009). Declines in climate suitability at range margins may, therefore, lead to localised extinctions and reductions in overall range size. Conversely, if climatic suitability increases adjacent to a range margin, local populations may be able to newly colonise those areas, increasing range size, provided there is suitable habitat. The occurrence of both processes simultaneously can lead to shifts in species' ranges, which are now well documented across a range of taxa (Chen et al., 2011). Given the rate and magnitude of climate change, range shifts are predicted to continue until the end of the century, at an even greater extent to those already observed (Barbet-Massin et al., 2009, 2012).

The distributions of species across temperate realms, including the breeding ranges of long-distance migratory birds, have typically experienced contractions at equatorward edges of range margins and expansions at poleward ones (Gillings et al., 2015; Parmesan et al., 1999; Zuckerberg et al., 2009). This has occurred as species track their climatic range into cooler regions, resulting in a general poleward shift by 16.9 kilometres per decade, averaged across a multitude of taxonomic groups, largely across North America and Europe (Chen et al., 2011). However, poleward margin expansions do not always occur to the same extent as equatorward margin contraction, resulting in declines in species' range extents. Furthermore, these changes in range size have impacts on population size, as numbers of individuals of species predicted to gain range since 1980 have increased, whereas those predicted to lose range have declined in number (Gregory et al., 2009). Huntley et al. (2007) projected that 71% of European breeding birds would suffer range contractions by 2050, with ranges 28% smaller and overlapping previous ranges by just 42%, on average. This problem is particularly prevalent for species breeding at high latitudes that have very limited space available for colonisation. It is possible that several species may go extinct as their ranges are compressed to the poleward limits of the landmass (Kirby et al., 2008).

The non-breeding ranges of long-distance migratory birds are also predicted to shift by the end of the century, accompanied by overall losses in range extent, though the projected direction of movement is less uniform between species (Barbet-Massin et al., 2009; La Sorte & Thompson, 2007). Poleward shifts are forecast for species non-breeding ranges at mid-to-high latitudes, following temperature changes. However, bird distributions across the tropics, including those non-breeding ranges of long-distance migrants, may be more closely linked to precipitation than temperature (Hawkins et al., 2003; Howard et al., 2015). As forecasts for precipitation are less clear and more spatially variable than temperature predictions, responses are likely to be more variable, potentially with stronger longitudinal influences (e.g. Vanderwal et al., 2013). Nonetheless, given the breeding and non-breeding distributions of long-distance migrants largely occur in separate biogeographic realms, on different continents and occasionally in separate hemispheres, predicted shifts in the two ranges could move them in different directions (Doswald et al., 2009). Hence, the migratory distances of long-distance migratory birds in the Afro-Palearctic flyway are predicted to increase significantly by the end of the century (Howard et al., 2018). Given the need for additional energy to fly longer distances, these future migratory journeys are predicted to require more refuelling stopovers. As migration is the period of highest mortality for birds, due to an unknown distribution of resources and predators, any increases to these journeys are likely to have negative impacts on survival and population trends (Rushing et al., 2017; Sillett & Holmes, 2002). Zurell et al. (2018) concluded that the threats of breeding range loss, non-breeding range loss and increase in migration distance occur independently, and a failure to account for changes to migratory journeys could lead to the underestimation of threat level for 50% of global long-distance migratory species. Longer migrations for Europe-African migrants, requiring more stopovers, are projected to take 2.4 days longer, on average, in future (Howard et al., 2018). Whilst this may seem a small change given existing intra-specific variation in migratory timings; this has the potential to exacerbate existing phenological mismatch. However, comprehensive studies of the impacts of future climate change on long-distance migratory birds beyond the Europe-Africa flyway are currently lacking.

Despite these potential impacts, long-distance migratory birds may be less susceptible to the negative effects of range shifts than resident species, given their inherent ability to move considerable distances. Residents are often more sedentary and may struggle to keep pace with the range shifts necessary to remain within their climatic niche (Pearce-Higgins & Green, 2012). In contrast, long-distance migrants show considerable plasticity in their movements and can alter both the timing and destination of migrations within relatively short timescales (Bearhop et al., 2005; Berthold, 2001). This plasticity has allowed some species, including the Eurasian Blackcap *Sylvia atricapilla,* Common Chiffchaff *Phylloscopus collybita*, Pacific Golden Plover *Pluvialis fulva* and Bar-headed Goose *Anser indicus*, to begin a process known as "short-stopping" (Berthold et al., 1992; Elmberg et al., 2014). Rather than migrating to the tropics during the non-breeding season, some populations remain within temperate regions, made possible by less harsh, warmer winters. In essence, some populations become short-distance migrants, which would likely benefit from increased survival due to shorter migrations and, as individuals are closer to the breeding grounds and more able to judge conditions on them, reduce the degree of reproductive phenological mismatch. However, the possibility of this occurring for a wide range of species is yet to be explored.

Insight into the ability of long-distance migrants to further increase the length of their migratory journeys may also be gained by considering previous changes and the origin of migration. Currently, long-distance migratory behaviour enables species to exploit ephemeral resource peaks with reduced competition at high latitudes, whilst avoiding the harsh winters there (Somveille et al., 2015, 2018). However during glacial periods, many currently temperate regions are likely to have been uninhabitable year-round (Hewitt, 2000; Lovette, 2005; Taberlet et al., 1998). Breeding distributions may have been located significantly closer to the distributions of the non-breeding season, requiring shorter migrations than today, and maybe even permitting residency. If species have previously responded to a warming globe by increasing migration distances, they may be able to do so again in future. The extent of long-distance migratory behaviour at the last glacial maximum is debated, though the limited evidence points towards persistence of migration in the Afro-Palearctic flyway but possible adoption of more sedentary behaviour in North America (Malpica & Ornelas, 2014; Milá et al., 2006; Ponti et al., 2020b; Thorup et al., 2021; Zink & Gardner, 2017). However, to date, a global simulation of the potential for persistence of long-distance migratory behaviour back to the last glacial maximum has not been performed. Therefore, the comparability of changes to migratory behaviour between the two flyways, as well as their extrapolation to the Australasian flyway, is limited.

1.4 Methods to study the broad-scale impacts of climate change on long-distance migratory birds

Due to their complex annual cycles, identifying the impacts of climate change on phenology, abundance and distribution is more difficult for long-distance migratory birds than their resident and short-distance migratory counterparts (Vickery et al., 2023; Zurell et al., 2018). To do so requires data from breeding, non-breeding, and passage areas, which are often located thousands of kilometres apart. Moreover, to identify causal links between conditions in one area and demography in another, data on individual movements may be required, as explanatory power may otherwise be lost due to intra-specific variation in phenology and demography, as well as low migratory connectivity, i.e. the mixing of multiple breeding populations on the non-breeding grounds (Finch et al., 2017).

Tracking of individuals, such as by bird ringing/tagging or using various tagging technologies (from geolocators to GPS tracking devices), has provided valuable insight into the impacts of variation in contemporary climate on several long-distance migratory species (Ambrosini et al., 2011; Cheng et al., 2019; Fraser et al., 2019; Gill et al., 2013; Ouwehand et al., 2016; van Wijk et al., 2012; Wellbrock et al., 2017). However, to identify broad-scale spatial and taxonomic patterns of the impacts of climate change, tens or hundreds of species must be studied simultaneously, and over an extended period. Therefore, a significant issue with the use of individual tracking to address these questions is the feasibility of acquiring data from a sufficiently large sample of individuals to be representative of the populations of a species, and across many species.

Bird ringing, or banding, is a relatively inexpensive method of individual tracking, but only provides information from the points of capture and recapture. The latter is particularly troublesome, as rates of recapture for many migratory birds are low and incredibly high re-trapping effort would be required across the non-breeding ranges to provide useful data (Bächler et al., 2010). Moreover, across flyways, ecological data is often more difficult to collect across the non-breeding range, for a multitude of reasons (Cayuela et al., 2009; Magurran, 2017). Technological advances have led to the development of tags that may be fitted to birds to record date, time, and location, continuously (e.g., Åkesson et al., 2012; Thorup et al., 2017). However, GPS and satellite tags, which provide the most accurate location data, remain too large for deployment on the smallest of migratory birds, particularly those tags that actively relay information and require a large battery source (Vickery et al., 2023). Of those that store data and can, therefore, be fitted to small birds, i.e., geolocators and archival GPS tags, a sufficient sample size of individuals is often precluded by, as with ringing studies, the need to recapture individuals for the retrieval of tracking data (Bridge et al., 2011). Assessment of the impacts of climate change on a wide suite of long-distance migratory species using tracking technologies is currently unfeasible, at least until further improvements in tag performance are achieved. Instead of using such tracking methods to focus on individuals, most studies have taken a population-wide approach.

In many cases, reproductive and migratory phenology has been quantified from observations or trapping records from bird observatories (Both et al., 2006; Burgess et al., 2018; Jonzén et al., 2006; Tøttrup et al., 2008). However, citizen science observations, through projects such as eBird and EuroBirdPortal (Sullivan et al., 2009; eurobirdportal.org), are becoming increasingly valuable, as spatial and temporal effort can be increased (Mayor et al., 2017; Mondain-Monval et al., 2021; Newson et al., 2016; Studds et al., 2017). To assess changes in the demography of migratory species, studies have typically made use of long-term abundance data collated through standardised recording schemes such as the North American Breeding Bird Survey and Pan-European Common Bird Monitoring Scheme, which provide population trends for many species back to as early as the mid-1960s (Sauer et al., 2020; https://pecbms.info/). Furthermore, such data can also be used to analyse contemporary changes in geographical distribution (Chen et al., 2011). Use of such population wide datasets has enabled the identification of broad-scale changes in phenology, abundance, and distribution, as well as relating these to changes in climatic and environmental variables, such as temperature, rainfall, and habitat condition (via, for example, NDVI, the normalized difference vegetation index; Balbontín et al., 2009; Finch et al., 2014; Newton, 2004; Saino et al., 2007). However, in many cases, it can be more informative to relate changes in abundance and distribution to changes in the suitability of climate that are relevant to the focal species' climatic niche. Furthermore, contemporary observational data do not allow for the prediction of abundance or distribution to future or prehistoric climates. Instead, species distribution modelling has become a widely utilised tool for these purposes (Zimmermann et al., 2010).

1.4.1 Species distribution modelling

The term species distribution modelling (SDM), or niche envelope modelling, encompasses a variety of statistical and machine learning techniques that relate a species' geographic distribution to environmental variables. By applying these models to observed, projected, or reconstructed climate data, they enable the assessment of changes in climate on the suitability of an area for a species, which can even be used to generate binary presence/absence predictions. As such, they can, and have been, used to assess the extent to which species abundances and distributions have changed in response to contemporary climate change (Gregory et al., 2009; Howard et al., 2020; Mason et al., 2019; Stephens et al., 2016). Furthermore, they may be used to predict the impacts of further climate change on species (Doswald et al., 2009; Howard et al., 2018; Huntley et al., 2007) or understand species' prehistoric distributions (Thorup et al., 2021; Zink & Gardner, 2017). Due to computational and methodological advancements, these models have become one of the most widely utilised techniques in macroecology (Franklin, 1995).

SDMs can be applied to any species for which distributions are known and the relevant climate data are available. Distributions for most of the world's vertebrates are now available from a variety of sources, such as presence-only data from the Global Biodiversity Information Facility (GBIF, 2023) or presence-absence data in the form of range polygons from the International Union for Conservation of Nature (IUCN, 2018). Breeding and non-breeding distribution polygons for the world's birds are available from Birdlife International and NatureServe (2016). Reconstructed prehistoric, observed contemporary and projected future climate data are also published regularly (Beyer et al., 2020; Harris et al., 2014; Hijmans et al., 2005). One of the major benefits of SDMs is, therefore, the ability to build an SDM for any species, including both the breeding and non-breeding distributions of migratory species, and project their distribution to several periods, irrespective of species-specific localities of distribution, habitat association or trophic level.

Despite their clear utility, SDMs have several shortcomings that should be considered during their use and interpretation, or studies risk making erroneous predictions (Pearson & Dawson, 2003). Firstly, the ability of models to accurately project observed distributions is improved with a larger sample size, so rare, range-restricted species can seldom be modelled accurately (Guisan et al., 2006). Furthermore, projected distributions represent just that, projections. As they are based entirely on the correlation between climate and species' distributions, they do not account for the mechanisms by which changes in distribution are achieved (Araújo & Peterson, 2012). For studies interested in the climatic suitability of an area, this is unlikely to present an issue, as presence/absence predictions are not required. However, where the goal is to gain present/absence predictions, "realised" distributions will be restricted compared to projections by the ability of species to disperse, habitat availability in the climatically suitable area and species interactions (Jetz et al., 2007; Urban et al., 2016). By contrast, simulated extinctions may not be realised if substantial extinction debts, i.e. the lag between a location becoming climatically unsuitable and a species disappearing from that area, exist (Howard et al., in press.; Rumpf et al., 2019). The issue of dispersal may be less consequential for projections of the distributions of long-distance migratory species, as individuals travel thousands of kilometres every year, potentially enabling more frequent, stochastic, long-distance dispersal (Nathan, 2006). However, migratory journeys tend to occur in within defined flyways, so dispersal outside of these may be unlikely (BirdLife International, 2010). Furthermore, many long-distance migrants are very site faithful and, whilst natal dispersal distances are likely to be higher in migrants than resident species, range shifts could still become limited by these (Catry et al., 2004; Paradis et al., 1998). Habitat availability and species interactions are sometimes assumed to be modelled implicitly by environmental variables in SDMs, as sympatric species are likely to show similar environmental tolerances to the focal species. Although, in the face of land-use change and general biodiversity loss, whereby habitats and species that may be predicted to occur based on climate alone are anthropogenically removed, these assumptions can clearly be violated. However, it is often hypothesised that, as SDMs are typically built at a coarse scale, climate is likely to be a more important determinant of distributions than the effects of e.g. habitat and species interactions, which would operate at finer spatial scales (Howard et al., 2015). Finally, models projected to different time periods assume that climatic niches are conserved through time and that little, if any, adaptive micro-evolution takes place (Urban et al., 2016). Despite these caveats and assumptions, SDMs have been shown to accurately predict changes in abundance and distribution when applied properly, with adequate consideration of their limitations (Araújo et al., 2005; Gregory et al., 2009; Mason et al., 2019; Piirainen et al., 2023; Stephens et al., 2016).

1.5 Thesis aims and outline

In this thesis, I aim to further our knowledge of the existing and likely future impacts of climate change on long-distance migratory birds, focusing on three main areas: phenology of migration, abundance, and migratory journeys. By filling the knowledge gaps outlined above (see section 1.3), I hope to improve our understanding of the drivers of declines experienced by this group of species and identify potential sources of further decline. This should provide a greater base of knowledge on which to implement conservation practice and policy. Below, I identify three specific aims of my thesis and provide an outline of my four data chapters.

1. **Identify whether phenological trends in long-distance migration on the non-breeding grounds mirror those on the breeding grounds.**

   In Chapter 2, I use observation and trapping records of a suite of trans-Saharan migratory birds from two non-breeding locations along the East-Atlantic flyway, one in sub-Saharan Africa and one in southern Europe. I use these to analyse changes in the timing of pre- and post-breeding migration and identify the environmental cues, drivers and limiting factors of these trends. By combing pre- and post-breeding migration dates, I also analyse trends in the time spent on the breeding and non-breeding grounds each year.

2. **Assess the impacts of climate change on the population trends of long-distance migratory birds across multiple flyways.**

   In Chapter 3, I use annual population data for species covered by the North American Breeding Bird Survey and Pan-European Common Bird Monitoring Scheme. By standardising a definition of short- and long-distance migrants across multiple flyways, something which has not occurred to date, I first assess whether trends in the populations of these two groups are consistent across the Americas and Afro-Palearctic. I then use SDMs and species-specific habitat preferences, alongside relevant climate- and land-use data, to analyse the relative influence of climate and land-use change on the breeding and non-breeding grounds on the population trends of migratory birds in both flyways.

3. **Assess the potential global impacts of climate change on long-distance migratory journeys.**

   In Chapter 4, I build SDMs for the world's long-distance migratory birds and use climate projections to project species distributions at the start and end of the 21st century. Alongside estimates of species-specific, maximum potential flight ranges, I use these projections to simulate migratory journeys in each period. I then assess how migration distance, number of refuelling stopovers, and overall migratory duration are likely to be affected by climate change and compare these changes between the three major migratory flyways across the globe. Then, in Chapter 5, I assess how pre-historic changes in climate may have affected long-distance migratory journeys across the globe. I use SDMs, alongside climate reconstructions, to project the distributions of the world's long-distance migratory birds in every 1000-year period, back to the last-glacial maximum, 22,000 years ago. I analyse how seasonal species richness patterns, range sizes, range overlaps and migration distances are likely to have changed through the current interglacial period.

Chapter 2

Phenological trends in the pre- and post-breeding migration of long-distance migratory birds

The Common Chiffchaff *Phylloscopus collybita* – a European breeding species which previously spent the non-breeding period exclusively in and to the south of the Mediterranean but, due to milder winter, has now begun to overwinter in the UK.
Photo credit: Jack Bucknall

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2.1 Abstract

Phenological mismatch is often cited as a putative driver of population declines in long-distance migratory birds. The mechanisms and cues utilised to advance breeding ground arrival will impact the adaptability of species to further warming. Furthermore, timing of post-breeding migration potentially faces diverging selective pressures, with earlier onset of tropical dry seasons favouring migration advancement, whilst longer growing seasons in temperate areas could facilitate delayed departures. Despite this, few studies exist of migration phenology on the non-breeding grounds or on post-breeding passage. Here, I use first-arrival and last-departure dates of 20 species of trans-Saharan migratory birds from tropical non-breeding grounds (The Gambia), between 1964 and 2019. Additionally, I use first-arrival and last-departure dates, as well as median arrival and departure dates, at an entry/departure site to/from Europe (Gibraltar), between 1991 and 2018. I assess phenological trends in pre- and post-breeding migration, as well as individual species' durations of stay in breeding and non-breeding areas. Furthermore, I assess the extent to which inter-annual variation in these timings may be explained by meteorological and ecological variables. I find significant advances in pre-breeding migration at both locations, whilst post-breeding migration is delayed. At Gibraltar, these trends do not differ between first/last and median dates of migration. The combination of these trends suggests substantial changes in the temporal usage of the two continents by migratory birds. Duration of stay (of species, not individuals) within Europe increased by 16 days, on average, over the 27-year monitoring period. By contrast, duration of species' stays on the non-breeding range declined by 63 days, on average, over the 56-year monitoring period. Taken together these changes suggest substantial, previously unreported alterations to annual routines in Afro-Palearctic migrants.

2.2 Introduction

Long-distance migratory birds have evolved to take advantage of spatially-segregated, ephemeral resource peaks (Newton, 2008; Somveille et al., 2018). This typically involves a pre-breeding migration from non-breeding locations at lower-latitude areas to mid- to high-latitude areas to breed. To time departure from the non-breeding grounds to coincide with resource peaks required for breeding, migrants must anticipate conditions on the breeding grounds, often from a different continent, or even hemisphere. It is likely that over long periods of selection, species have developed finely-tuned, endogenous circannual rhythms, triggering pre-breeding migration in response to increasing day-length (Helm et al., 2009; Marra et al., 2005). This may leave long-distance migrants vulnerable to uncoupling of day-length triggers on the non-breeding grounds and conditions on the breeding grounds.

Advancement in phenology is one of the most frequently documented biological responses to recent climate change, with events such as leaf bud-burst, insect emergence and bird breeding now occurring significantly earlier in the year in temperate regions than they did at the end of the last century (Burgess et al., 2018; Post et al., 2018). These advances exhibit significant spatial variation, due to the relationship between latitude and extent of warming and, therefore, the phenology of mid- to high-latitude areas has advanced more rapidly than those of the tropics (Post et al., 2018). The use of day-length as a departure cue should result in migratory populations arriving on breeding grounds at approximately the same time each year but substantially later than previously in phenological terms, leading to phenological mismatch (Saino et al., 2011; Taylor et al., 2016). Behavioural plasticity may, in some situations, permit a reduction in the time between arrival and breeding, enabling advances in laying date despite no change in arrival date (Newton, 2008). However, the severity of recent phenological shifts may have pushed some species to their physiological limits, with breeding date now constrained by the timing of arrival (Both & Visser, 2001). Perhaps as a consequence, advancements in breeding ground arrival are now well documented, as species attempt to adjust to these environmental changes (Gill et al., 2013; Jonzén et al., 2006; Newson et al., 2016). However, these advances in arrival may remain insufficient to track phenological shifts in, for example, prey availability on the breeding grounds, as evidence for phenological mismatch between migrants and their breeding habitats is plentiful (Burgess et al., 2018; Mayor et al., 2017; Møller et al., 2008; Saino et al., 2011).

The inability to track phenological advances on the breeding grounds has been frequently proposed as a putative cause of population declines of long-distance migrants (e.g. Jones & Cresswell, 2010). Mismatches are likely to lead to reduced food availability during the peak demand by chicks, ultimately leading to reduced productivity (Burgess et al., 2018). Additionally, migrants may be outcompeted by resident species that fill similar breeding niches, due to the residents' ability to better judge the onset of the breeding season (Wittwer et al., 2015). Such effects could impact long-distance migrants more than their short-distance counterparts, which winter closer to the breeding grounds and, therefore, may be more capable of anticipating breeding ground conditions (Møller et al., 2008). Given the certainty in further warming of mid- and high-latitudes, it is likely that the phenology of breeding habitats will continue to advance (Burgess et al., 2018). Thus, migrants will be required to continue to advance breeding ground arrival and breeding date if they are to avoid further population declines.

The extent to which long-distance migratory species are capable of responding to phenological advances on the breeding ground will depend on the mechanisms by which they adjust breeding ground arrival date. Coppack and Both (2002) suggest adjustments to pre-breeding migration schedules, i.e., advancement of non-breeding ground departure or increased migration speed, as potential mechanisms. Perhaps the most parsimonious explanation for these adjustments is through selection for individuals that either utilise departure cues that are matched with advanced breeding ground phenology or which migrate more rapidly. These individuals would, therefore, migrate inherently earlier or faster than others within the population, though this relies on sufficient variation in endogenous migratory timing existing within migrant populations (Gill et al., 2013). Alternatively, individual plasticity may allow for year-to-year variation in migratory strategy. As such, migrants may make use of environmental cues, in addition to day length, to predict conditions on the breeding grounds (Saino et al., 2007; Saino & Ambrosini, 2008). If so, the ability of long-distance migrants to further advance breeding ground arrival date will be constrained by the level of correlation between these cues and the phenological state of the breeding grounds, which may be low given the high level of spatial heterogeneity expected in future climatic changes (Post et al., 2018).

The availability and extent of phenological data from Europe and North America mean that, to date, the vast majority of studies on migration and migration phenology are based on these regions. These studies have provided further insight into the pre-breeding migratory timings of Holarctic migrants, e.g. earlier stopover site arrival (Jonzén et al., 2006; Stervander et al., 2005) and increased migration speed following these stopovers (Marra et al., 2005; Tøttrup et al., 2008). However, this geographic bias of data has hitherto limited the study of similar trends in tropical and sub-tropical non-breeding areas and, as such, it remains unclear whether advances in breeding ground arrival are mirrored by advanced departures from the non-breeding grounds or by altered migration speed (though see Altwegg *et al.* (2012) and Bussière *et al.* (2015), which suggest advanced pre-breeding departure of a limited suite of migrants from South Africa). Many studies have found correlations between breeding ground/stopover site arrival date and non-breeding ground conditions. Such correlated conditions have included: rainfall (Gordo & Sanz, 2008; Saino et al., 2007), the normalized difference vegetation index (NDVI; Saino *et al.*, 2004; Gordo and Sanz, 2008; Balbontín *et al.*, 2009), temperature (Cotton, 2003; Gordo et al., 2005; Saino et al., 2007) and the North Atlantic Oscillation (NAO) index; the latter representing the difference between the normalised sea-level pressures at the Azores and Iceland, over the period December-March (Forchhammer et al., 2002; Hüppop & Hüppop, 2003; Jonzén et al., 2006). Together these studies suggest that migrants do make use of multiple environmental cues to anticipate conditions on the breeding grounds. Species tend to arrive on their breeding grounds earlier in years of high rainfall and higher NDVI on non-breeding grounds, potentially due to increased food availability enabling earlier and/or more rapid pre-migratory fattening and hence migration onset. Higher winter NAO index values, which tend to correlate with earlier, more productive springs in western Europe, were similarly associated with earlier breeding ground arrival, whereas responses to higher pre-departure temperatures on the non-breeding grounds are more varied (e.g. Gordo et al., 2005 cf. Saino et al., 2007). Whilst temperature could act as a direct cue to advance departure, it could also act via modulating food availability. However, whilst these variables appear to modulate breeding ground arrival, given that none of the studies mentioned above consider departure dates from non-breeding sites, it is unclear which aspect of pre-breeding migration they affect. In the Americas, increased tropical rainfall has been related to advanced departure of migrants from non-breeding areas, acting through increased food availability (Studds & Marra, 2011). This suggests that the ability to advance departure could be limited by the ability to advance fat-loading prior to leaving non-breeding areas. However, this evidence is limited to a single species in one area. Further studies incorporating timing of pre-breeding departures from non-breeding sites are necessary to better understand the mechanisms of advanced breeding ground arrival.

Whilst the study of pre-breeding departures from non-breeding grounds has received little attention, post-breeding departure timing is similarly neglected relative to breeding ground arrival phenology, even across Europe and North America. This may be due to less obvious and consistent phenological patterns during this period, potentially a result of less stringent time constraints on departure when compared to pre-breeding migration (Haest et al., 2019; La Sorte et al., 2015). In areas such as the Sahel in Africa, deteriorating conditions (in terms of NDVI and potentially food availability) over the north temperate late-summer to autumn period may place pressure on species to maintain current post-breeding migration phenology. In contrast, a lengthening growing season across mid- to high-latitudes over the last century, due to increased autumn temperatures, could permit long-distance migrants to extend their stay on the breeding grounds, perhaps even extending the breeding season (Menzel & Fabian, 1999; Walther et al., 2002). Those studies that have considered post-breeding migration of long-distance migrants have reflected this variation in potential selective pressures, with advancement (Jenni & Kéry, 2003), delay (Bitterlin & Van Buskirk, 2014; Kovács et al., 2011) and no trend (Van Buskirk et al., 2009) in departure from breeding grounds all reported. However, there are few studies of arrival phenology in non-breeding areas. Therefore, despite a lack of consensus in trends of post-breeding departures, migratory strategies of long-distance migrants away from these areas could have changed significantly. For example, species may increase migration speed to avoid hostile conditions on their migratory journey or utilise less-direct routes to take advantage of additional resources. Such factors, combined with the advance of pre-breeding migration, could result in substantial changes to the temporal partitioning of the annual cycle of long-distance migrants. Hence, there is a clear need to analyse trends in the timing of, not only pre-breeding, but also post-breeding migration to and from the non-breeding grounds.

Here, I use a novel dataset of departure and arrival dates of European-breeding migratory species to their African non-breeding range, and through a passage site on the boundary between Europe and Africa. I use these data, in combination with meteorological and ecological variables, to assess trends in departure and arrival dates at sites away from the breeding range, over a 28-56 year period. By studying phenology at these non-breeding localities, I aim to infer whether: (1) pre-breeding migration on the non-breeding grounds and/or at an intermediate migratory site has advanced, in line with those phenological changes observed on the breeding grounds, (2) the phenology of post-breeding migration has undergone any significant change at either site and (3) species are spending longer on European breeding grounds as a result of longer growing seasons and hence either altering the amount of time on the non-breeding range, or the speed of their migration to the non-breeding range.

2.3 Materials and methods

2.3.1 Study sites and species data

I extracted annual first-arrival and last-departure dates of trans-Saharan migratory bird species from two datasets, one from the northern edge of the sub-Saharan African non-breeding range and the other on the migratory route, on the Europe/Africa border. The first consisted of observations of 20 migratory passerine bird species (Appendix Table S1) recorded year-round by local ornithologists in The Gambia (**Fig. 1**), monitored between 1964 and 2019 (though discontinuously in some periods). I excluded observations of migrants remaining in The Gambia in June and July (the northern European breeding season), as these were likely to represent individuals that were unlikely to have migrated due to, for example, poor condition or injury. The second dataset consisted of daily bird ringing totals for 14 migratory passerine bird species from Gibraltar Bird Observatory (**Fig. 1**). Standardised ringing occurred daily at this site in spring and autumn, between 1991 and 2018. Exact start and end dates of ringing efforts varied between years (Appendix Table S2), due to the suitability of weather for ringing, but typically covered the periods February-May and August-November and, therefore, should encompass the earliest pre-breeding and latest post-breeding migration dates for all the migrant species I consider. The first record of a trapped individual of a species in the spring, and the last trapping record in autumn were extracted as the first and last observation for each year, respectively. Two migrant species (Eurasian Blackcap *Sylvia atricapilla* and Common Chiffchaff *Phylloscopus collybita*) for which I had arrival/departure dates in The Gambia were present year-round at Gibraltar (i.e. they had a small resident/overwintering population), so extracting first and last migration dates for these species at Gibraltar was not possible. A further four species (Northern Wheatear *Oenanthe oenanthe*, Western Olivaceous Warbler *Iduna opaca*, White Wagtail *Motacilla alba* and Yellow Wagtail *Motacilla flava*) that occurred in The Gambia were trapped very infrequently at Gibraltar, so were removed from the dataset (Appendix Table S1).

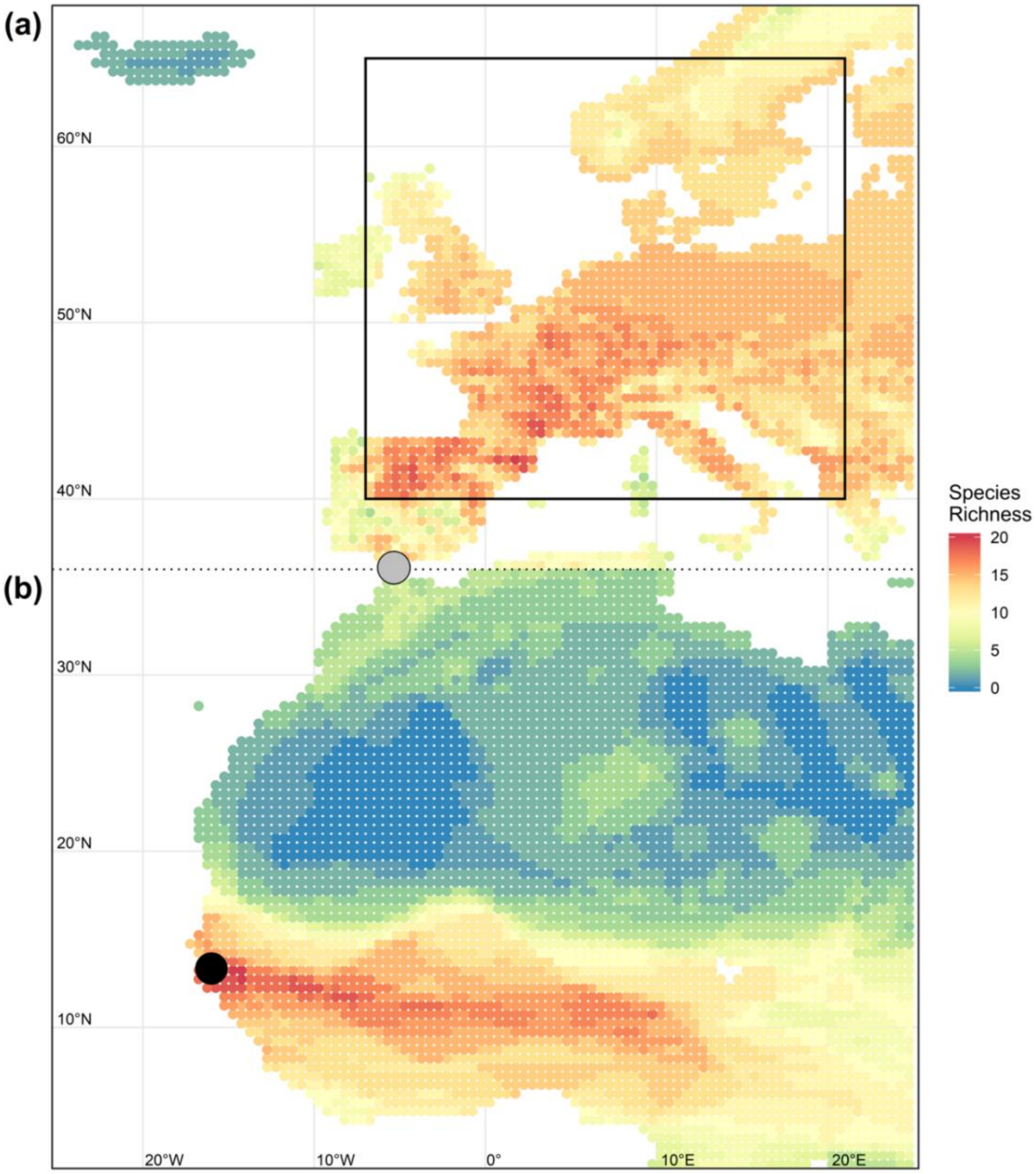

Figure 1. *Map of Africa and Europe, showing the study areas in The Gambia (black circle) and Gibraltar (grey circle). The box highlights the area defined as representing the core Western Europe breeding area for the study species, used when extracting meteorological variables. Shading represents, for the 20 study species: (a) breeding species richness across Europe and (b) non-breeding species richness across North-West Africa (dotted line differentiates (a) and (b)). Gibraltar and The Gambia represent, in Europe and sub-Saharan Africa respectively, major first arrival and last departure locations for trans-Saharan migrants on the east-Atlantic flyway.*

Migrants departing from The Gambia in Palearctic spring are likely to follow the east-Atlantic flyway (Appendix Fig. S1) into Europe and many may, therefore, be expected to utilise Gibraltar, situated at the narrowest passageway between Europe and Africa on this flyway, as a site to rest/refuel (BirdLife International, 2010). Therefore, when combined, these two datasets allow an analysis of long-term trends in timing of pre-breeding and post-breeding migration for a suite of common trans-Saharan migrants. Additionally, for years in which successive first arrival and last departure dates were available, I calculated durations of stay for individual species within Europe and in sub-Saharan Africa. It should be noted that duration of stay, as defined here, represents the time spent within a region by a species, i.e. from the first individual arriving to the last individual departing, and not the mean duration of individuals. Further, I assume that spring arrival and autumn departure dates from Gibraltar reflect the approximate duration of stay of the East Atlantic flyway populations of a species in Europe. Similarly, I assume that first post-breeding arrival and last pre-breeding departure from The Gambia reflects the approximate duration of stay of these populations within sub-Saharan Africa. This enabled an analysis of trends in duration of stay to assess whether the temporal partitioning of the annual cycle of migrants has changed over time.

The use of first and last dates to assess changes in phenology are susceptible to bias through changing observer effort and underlying population trends (Sparks et al., 2001; Tryjanowski & Sparks, 2001). For example, increasing observer effort could result in earlier arrival dates and later departure dates from a site. By contrast, declining populations could result in later apparent arrival and earlier apparent departure dates, a consequence of the reduced likelihood of detecting individuals from a smaller population. Observer effort remained similar throughout the study period in both locations, minimising the risk of the former situation. By contrast, populations of several long-distance migrants have declined in recent decades. Hence, if I observed delayed arrival and advanced departures from my study sites, I could struggle to differentiate phenological change from recording bias. In fact, the results from Gibraltar demonstrated trends in migratory timings in the opposite direction to that which would be expected given recorded population declines, giving confidence that I detected real phenological changes, albeit perhaps slightly conservative give the declines of some species. Furthermore, whilst overall trends in migratory timings from The Gambia occurred in the directions that may be predicted through population changes, there was no correlation between individual species' migratory and population trends (Appendix Fig. S2). An additional consideration when using first and last recording dates is the tendency for first arriving individuals to advance their migration more rapidly than the bulk of the population (Lehikoinen et al., 2019; Sparks et al., 2007; Tøttrup et al., 2006). Therefore, trends observed in first and last individuals have the potential to be more extreme than that shown by the remainder of the population. The best available data for The Gambia do not permit extraction of median population phenological responses in the Sahelian non-breeding areas, though data for Gibraltar do permit median passage estimations. Hence, for Gibraltar, in addition to first arrival and last departure dates, I also extracted and analysed (see below) median passage dates for both pre- and post-breeding migration. I used daily ringing totals from Gibraltar for a species across a passage period to estimate the median passage date of all individuals. I extracted medians, rather than mean migration dates, as trapping effort was consistent throughout the ringing periods and not biased to, for example, weekends. I also estimated, for Europe, durations of stay for species in each year, based on these median passage dates. I could then assess whether trends in, and drivers of, migratory timing differed between first/last and median passage at Gibraltar, a point part way through the migratory journey.

2.3.2 Meteorological and environmental data

Fortnightly NDVI values were obtained for the period 1982-2012 (the maximum period for which annual data were complete), for four areas on the east-Atlantic flyway: the Sahel, North Africa, Gibraltar, and Western Europe (**Figs. 1 & 2**). Data were downloaded from the Global Inventory Modelling and Mapping studies group (GIMMS; Tucker *et al.*, 2005). The Sahel was defined as the area 18°W-10°E and 14°-18°N immediately to the north of The Gambia, and North Africa as the area encompassing 10°-2°W and 30°-36°N (**Fig. 2**); NDVI data were extracted for both regions. Both areas exhibit high NDVI seasonality (**Fig. 2**), where ephemeral resource peaks produce useful refuelling sites for migrants prior to/following the crossing of the Sahara. The eastern boundary of the Sahel was set at 10°E as I expect that individuals migrating further east than this would be less likely to follow the east-Atlantic flyway to/from western Europe. The southern and eastern boundaries of the North African region were selected to encompass the region of highest NDVI seasonality beyond Europe. Sahelian NDVI was highly correlated with Gambian NVDI (r_s>0.7). As I considered Sahelian NDVI as better representing overall sub-Saharan conditions, I used these data in models in preference to Gambian NDVI. In addition, species could utilise this wider Sahelian region as a final stopover site prior to crossing the Sahara, which could impact Gambian departure dates. I extracted site-specific NDVI data separately for Gibraltar given the possibility that migrants might decide whether to stop at this restricted passage site based on NDVI in the local area, which was not strongly correlated with North African NDVI. I calculated Gibraltarian NDVI for the area 5.37°-5.34°W, and 36.1°-31.16°N. Finally, I calculated NDVI for Western Europe using the area 7°W-21°E, and 40°N-65°N. This area encompassed the highest breeding richness and the majority of range extents for populations of the 20 focal study species that were likely to use the East Atlantic migration flyway through Gibraltar (**Fig. 1**). The eastern boundary of the Western European region was set as I expect that individuals breeding further east would be less likely to migrate along the East-Atlantic flyway through both Gibraltar and The Gambia (BirdLife International, 2010).

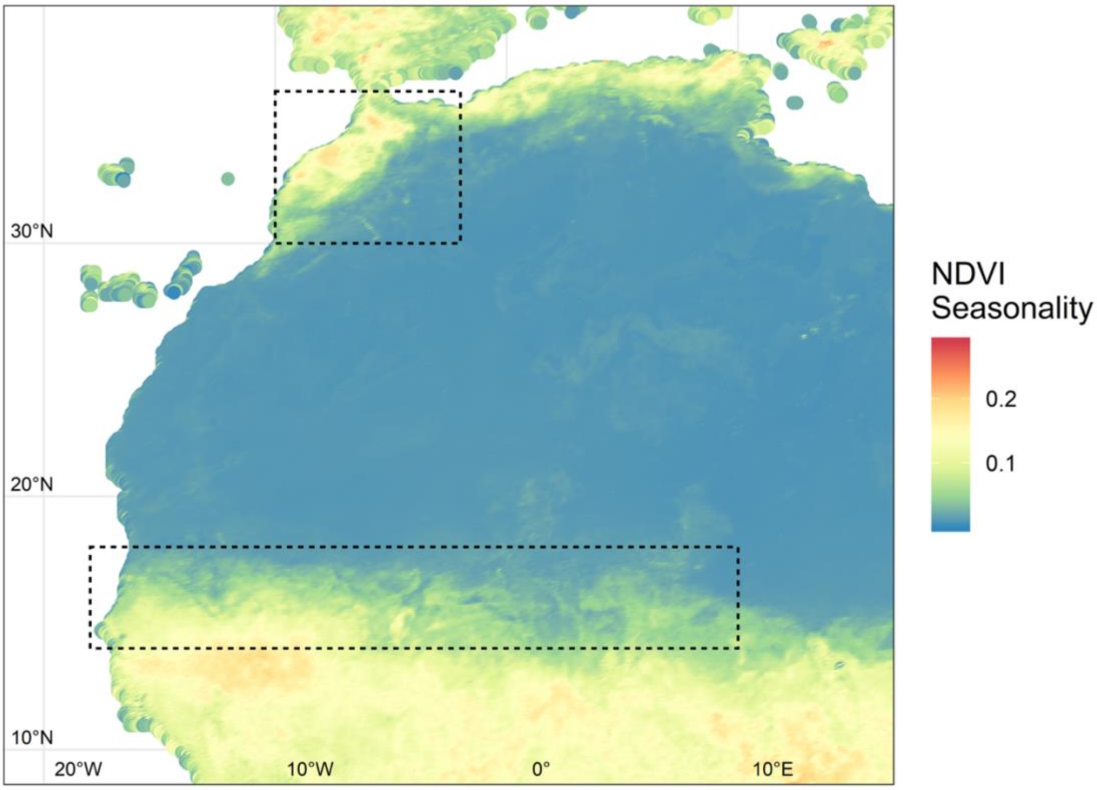

Figure 2. *NDVI seasonality (expressed as the mean standard deviation of annual NDVI over the period 1982-2012, derived from fortnightly records) of north-west Africa. The box highlights the area defined as North Africa (top) and the Sahel (bottom), used when extracting meteorological variables.*

For the Sahel, North Africa, and Gibraltar regions, I calculated annual mean NDVI values separately for individual species, dependent upon their mean phenology. Mean NDVI was estimated for each species over the two months prior to mean departure and arrival dates (i.e. the mean date across all years of monitoring) in both The Gambia and Gibraltar. I hypothesise that NDVI will alter food availability, in turn impacting upon departure decisions and/or migration speed. For example, when exploring potential drivers of pre-breeding departure dates from The Gambia, mean Sahelian NDVI for the two months prior to species-specific mean departure date over the whole study period from The Gambia was calculated. Whereas, when exploring drivers of pre-breeding arrival dates at Gibraltar, mean Sahelian NDVI for the two months prior to species-specific mean arrival date over the whole study period in Gibraltar was calculated. As large inter-specific variation in the timing of migration schedules exists, the mean arrival/departure dates and, therefore, NDVI values were calculated on a species-specific basis. For each species, I calculated the mean date of first/last recorded individual, across all years for which data were available, of all four migratory events: Gambian pre-breeding departure, Gibraltar pre-breeding arrival, Gibraltar post-breeding departure and Gambian post-breeding arrival (Appendix Table S3). Additionally, I calculated the mean dates of median arrival and departure at Gibraltar. The mean NDVI of the two months prior to these mean arrival/departure dates were then calculated for each species, for each year for The Sahel, North Africa, and Gibraltar regions. This method ensured that the NDVI calculation period was fixed for each species enabling comparisons across years, whilst avoiding bias that might occur if its estimation window was altered each year in relation to a species annual phenology. Additionally, I calculated mean NDVI for August and September for each year across the western European region. The latter aimed to reflect post-breeding vegetation productivity in breeding areas, which could influence post-breeding departure dates through altered food availability. I did not calculate the mean NDVI of Europe in spring, as I included yearly winter NAO index values (see below), which correlates with productivity levels in Europe (Forchhammer et al., 2002).

NDVI was also used to identify the timing of the end of Sahelian growing season each year. To do so, I fitted a smoothed function to fortnightly NDVI data over an annual cycle between March to February, following the methods of Mason *et al.* (2014). The period March to February was chosen to capture the start and end of the annual Sahelian NDVI cycle (Appendix Fig. S3). I calculated the maximum second derivative following an annual NDVI peak. This represented the point at which NDVI was declining most rapidly back to its dry season minima.

Monthly temperature data for the period 1960-2015 were downloaded from the Climatic Research Unit (CRU; Harris *et al.*, 2014), for the same four areas for which NDVI data were acquired, as well as for The Gambia. Unlike NDVI data, temperature data for The Gambia and the Sahel were not highly correlated ($r_s<0.7$). Mean temperature data were calculated in much the same way as NDVI. For The Gambia, the Sahel, North Africa and Gibraltar, I calculated yearly species-specific mean temperatures over the two months prior to their mean departure and arrival dates over the whole study period in both The Gambia and Gibraltar. For Western Europe, I calculated mean annual temperature across the August – September period.

Finally, monthly values of the North Atlantic Oscillation index for the period 1963-2019 were downloaded from CRU (Jones et al., 1997), representing the difference in normalised sea level pressure over the Azores and south-west Iceland. Yearly winter NAO index values were extracted from these data, taken as the cumulative NAO index over the months December to March, prior to pre-breeding migration (Hüppop & Hüppop, 2003).

2.3.3 Analyses of migration phenology

As migratory timings can be considered as species traits and, therefore, not phylogenetically independent, I used phylogenetic linear mixed models (PLMMs) to analyse both trends and drivers of inter-annual variation in migratory timings, at both The Gambia and Gibraltar. I fitted PLMMs with pre-breeding or post-breeding migration dates or durations of stay as a continuous response variable, depending on the specific analysis, using the R package “MCMCglmm” (Hadfield, 2010). The species ID and the phylogeny were included as random effects, the former to account for variability in the data caused by species-specific migration schedules. The phylogeny was built as a 50% majority-rule consensus tree (O’Reilly & Donoghue, 2018; Rubolini et al., 2015), using 1000 samples of the posterior distribution produced by Jetz et al. (2012). I used an uninformative, inverse Wishart distribution as a prior for both the random effects and residual variance. To fit the model, I ran an MCMC chain for at least 200,000 generations, recording model results every 1000 generations and ignoring the first 2000 generations as burn-in. I fitted each model four times and merged the four chains after verifying convergence using Gelman-Rubin diagnostics in the R package “coda” (Plummer et al., 2006). I also visually inspected trace plots for each model to verify model convergence. I assessed the performance of each model by calculating conditional R^2 following the methods of Nakagawa & Schielzeth (2013). This multi-species approach was undertaken as I anticipated that individual species trends might be weak due to the paucity of data and the inherent variability likely in such data. This was confirmed in an exploratory data analysis, using linear models on individual species data (Appendix Figs. S4-6).

I first analysed trends in pre-breeding migration, post-breeding migration and duration of stay, fitting PLMMs, as previously described, with year as the sole continuous predictor variable in the models. Then, to identify drivers of inter-annual variation in pre-breeding and post-breeding migration timing, more complex models were fitted containing plausible combinations of potentially important meteorological and environmental predictors. Year was retained as a predictor variable in these models to minimise the likelihood of finding spurious relationships with climatic variables which were themselves correlated with year (Iler et al., 2017). For Gibraltar, I conducted these analyses twice, first on the dates from first/last individuals and second using median passage dates.

The combinations of meteorological/environmental variables included in models differed between analyses (**Table 1**), as the drivers of migration are likely to differ both spatially and temporally. To facilitate parameter exploration, I scaled each continuous predictor variable using *z*-transformations. Species with fewer than six years of data available for any individual analysis were removed from that analysis (Appendix Table

S4). Sample sizes for models of the drivers of inter-annual variation in migratory timing were reduced in comparison to that of phenological trends in migration, as meteorological data were not available for the entire study period (**Table 2**).

Table 1. Candidate meteorological variables included in the models to predict the timing of pre-breeding and post-breeding migration in The Gambia and Gibraltar.

Location	Model	Meteorological variable
The Gambia	Pre-breeding departure	NAO Index
		Gambian temperature
		Sahelian NDVI
	Post-breeding arrival	European temperature
		European NDVI
		North African temperature
		North African NDVI
		Onset of Sahelian dry season
Gibraltar	Pre-breeding arrival	NAO Index
		Sahelian temperature
		Sahelian NDVI
		North African temperature
		North African NDVI
	Post-breeding departure	European temperature
		European NDVI
		Gibraltar temperature
		Gibraltar NDVI
		Onset of Sahelian dry season

Table 2. Summary of datasets used to analyse trends in the timings of pre-breeding migration, post-breeding migration and duration of stay, as well as the drivers of inter-annual variation in the timings of pre-breeding and post-breeding migration. Datasets for first/last and median individuals at Gibraltar are identical, so are only included once here.

Analysis	**Location**	**Event**	**Start Date**	**End Date**	**Nº of species**	**Total observation years**
Trend models	The Gambia	Pre-breeding departure	1965	2019	19	314
		Post-breeding arrival	1964	2018	19	333
		Duration of stay	1964	2018	13	150
	Gibraltar	Pre-breeding arrival	1992	2018	14	319
		Post-breeding departure	1991	2018	14	312
		Duration of stay	1992	2018	13	258
Drivers models	The Gambia	Pre-breeding departure	1988	2012	18	208
		Post-breeding arrival	1987	2012	16	197
	Gibraltar	Pre-breeding arrival	1992	2012	13	237
		Post-breeding departure	1991	2012	14	245

2.4 Results

2.4.1 Trends in migratory timings

PLMMs were fitted separately to assess trends in first arrival and last departure dates of trans-Saharan migrants, at both The Gambia and Gibraltar. Models explained the trends in the timings of pre-breeding and post-breeding migration less well in The Gambia ($R^2 = 0.49$; $R^2 = 0.63$, respectively) than in Gibraltar ($R^2 = 0.84$; $R^2 = 0.82$, respectively), but performed well overall. Furthermore, I found significant trends in the timing of both events, at both locations (Appendix Table S5). Pre-breeding migration showed significant advancements at both locations, at rates of 0.44 days per year in The Gambia and 0.28 days per year in Gibraltar, between 1965-2019 and 1992-2018, respectively (**Fig. 3**). In contrast, post-breeding migration was significantly delayed at both locations, though at reduced rates compared to pre-breeding migration. Between 1964-2018 and 1991-2018, post-breeding migration was delayed by 0.24 days per year in The Gambia and 0.19 days per year in Gibraltar, respectively. Although both trends appear more pronounced in The Gambia, significant overlap of confidence intervals occurs with the Gibraltar model estimates (Appendix Table S5). PLMMs fitted to assess trends in median arrival and departure dates at Gibraltar also performed well ($R^2 = 0.7$; $R^2 = 0.68$ respectively), though slightly less well than the models of first arriving spring individuals and last departing autumn individuals. The temporal trends were again significant and had very similar slopes to those seen when analysing first arrivals and departures (**Fig. 3**) but with different intercepts, the latter as would be expected. Median pre-breeding migration date advanced by 0.27 days per year (cf. 0.28 days in first arrivals), whilst post-breeding migration was delayed by 0.22 days per year (cf. 0.19 days in last departures). Hence, overall, the advance in pre-breeding migration and the delay in post-breeding migration at Gibraltar were robust to whether I considered either the first arriving or last departing individuals versus the median passage in spring/autumn.

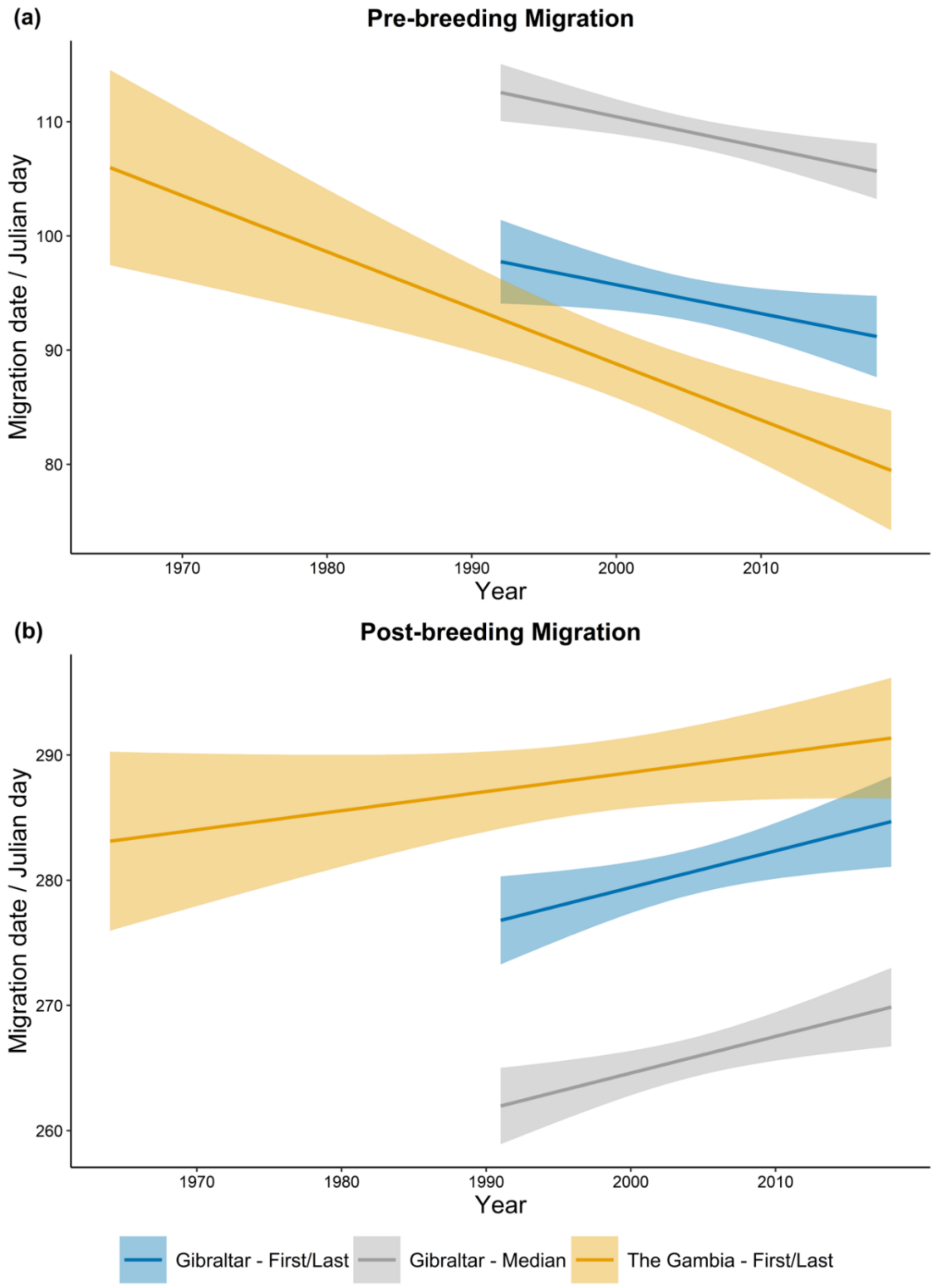

Figure 3. *Phenological trends in* ***(a)*** *pre-breeding and* ***(b)*** *post-breeding migration date at The Gambia and Gibraltar. Lines show the mean migration date across species, predicted by a linear model, with shaded regions displaying the 95% confidence intervals.*

PLMMs were also fitted to assess trends in duration of stay within sub-Saharan Africa and Europe, based on first arriving and last departing individuals. Whilst models performed similarly well in The Gambia and Gibraltar ($R^2 = 0.76$ and $R^2 = 0.79$, respectively), the trends in duration of stay differed markedly (**Fig. 4**). Due to delayed post-breeding arrival and advanced pre-breeding departure, trans-Saharan migrants following the east-Atlantic flyway spend significantly less time in sub-Saharan Africa now than in 1964. Over this period, duration of stay decreased by 1.15 days per year, equating to a total reduction in stay length of over 63 days. Whereas, in Europe, advancements in pre-breeding arrival of the first individuals and delays to post-breeding departure of the last individuals led to a significant increase in the duration of stay of migrant species (Appendix Table S5). Between 1992 and 2018, duration of stay in Europe increased by 0.59 days per year (i.e., an opposite change to that in sub-Saharan Africa but changing at half the rate *cf.* sub-Saharan Africa), a total increase of over 16 days in just 27 years. Duration of stay within Europe was very similar when median passage times (as opposed to first/last individuals) were used (though model fit was slightly weaker: $R^2 = 0.67$; **Fig. 4**), with the median duration of stay increasing by 0.54 days per year. No significant difference existed in the rate of change of duration of stay in Europe between those calculated based on first/last dates through Gibraltar and those based upon median passage dates (Appendix Tables S5 & 6).

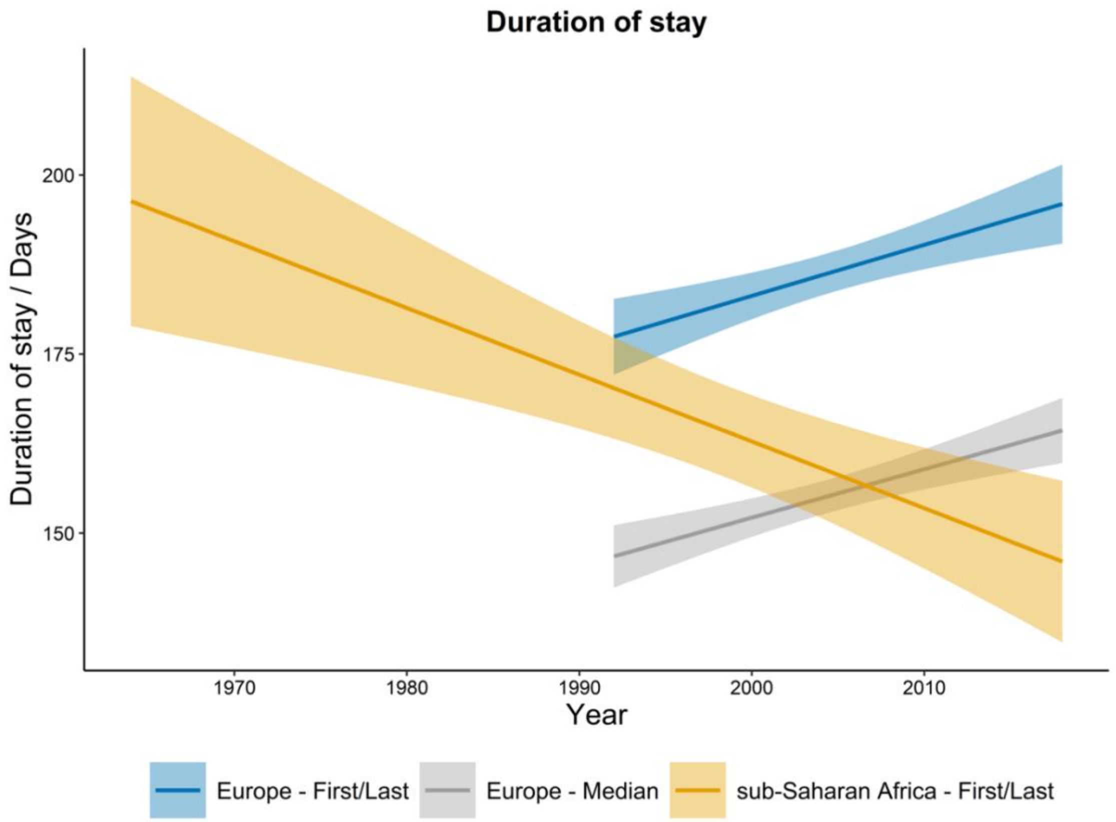

Figure 4. *Phenological trends in durations of stay within Europe and sub-Saharan Africa. Lines show the mean duration of stay across species, predicted by a linear model, with shaded regions displaying the 95% confidence intervals. Europe – First/Last trends are based on those individuals arriving first and departing last at Gibraltar. Whereas Europe – Median trends represents duration of stay based on median passage dates. Duration of stay in sub-Saharan Africa is based on first arrival and last departure dates in The Gambia.*

2.4.2 Drivers of arrival and departure trends

PLMMs were fitted separately to identify drivers of inter-annual variation in the timing of pre-breeding and post-breeding migration of trans-Saharan migrants, at both The Gambia and Gibraltar. For The Gambia, where data collection ran from 1964, the dataset to which these models were fitted was truncated in comparison the previous analyses (**Table 2**), as NDVI data were available only from 1982. As ringing data for Gibraltar were only available from 1991, there was no need to truncate this dataset. Potentially as a result of this reduced sample size, models explained variation in the timing of both pre-breeding and post-breeding migration of first/last individuals better for Gibraltar (R^2=0.79 and R^2=0.81, respectively) than for The Gambia (R^2=0.12 and R^2=0.5, respectively).

I found significant effects of meteorological variables on the timing of first/last pre-breeding migration dates at both The Gambia and Gibraltar, though the exact drivers differed between locations (**Fig. 5a & b**; Appendix Tables S7 & 8). Dates of last pre-breeding departure from The Gambia showed a significant negative relationship with pre-departure NDVI of the Sahel, with higher NDVI values resulting in earlier observed departure. Additionally, I found a positive relationship, which bordered on significance, between pre-breeding departure dates and pre-departure temperatures of The Gambia. By contrast, dates of first pre-breeding arrivals at Gibraltar showed a significant positive relationship with the winter NAO index. I also found a positive relationship approaching significance between pre-breeding Gibraltarian arrival dates and North African NDVI. Negative relationships between year and pre-breeding migration were found at both locations.

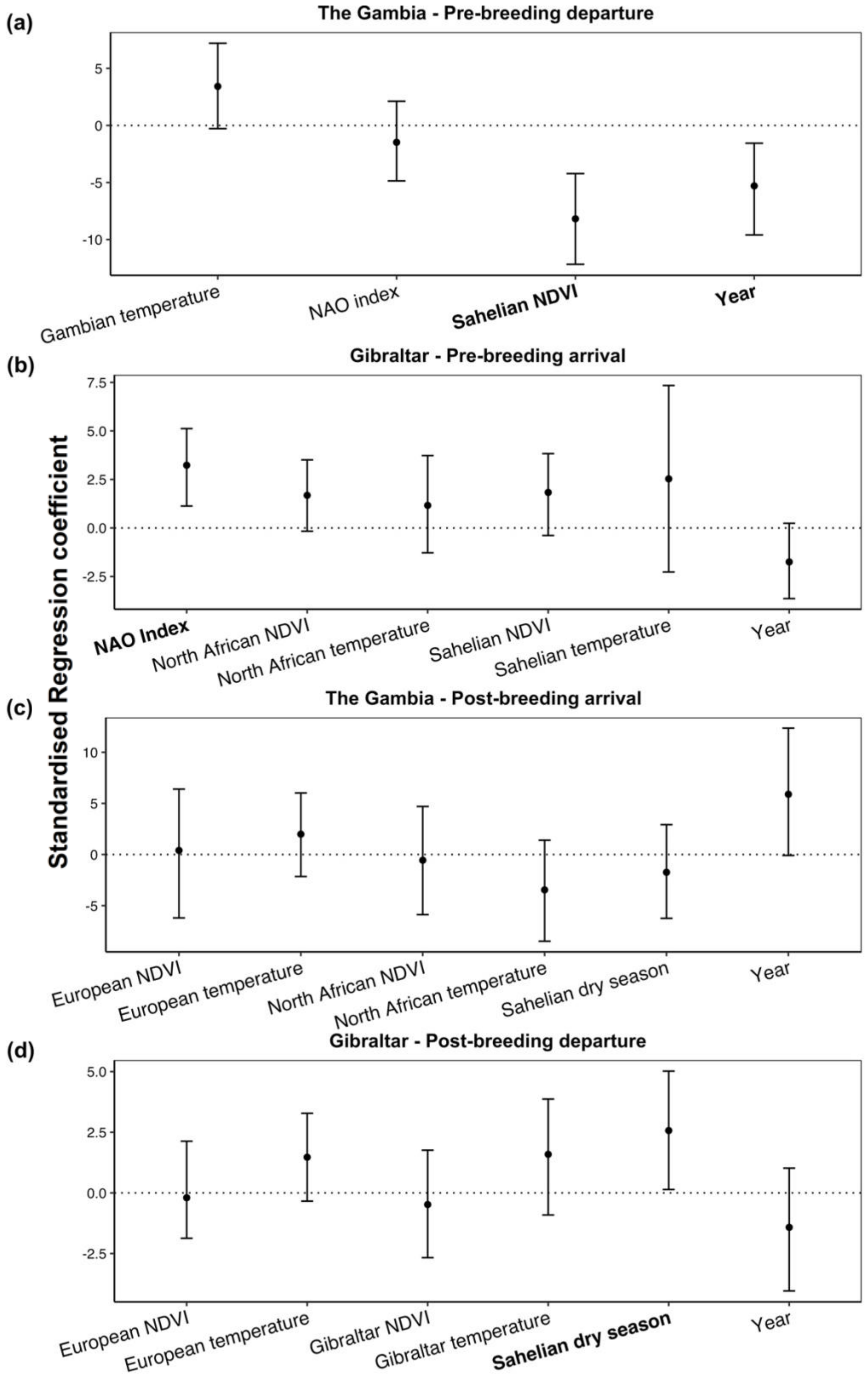

Figure 5. *Parameter coefficients from phylogenetic linear mixed models, used to assess the drivers of first and last pre-* ***(a, b)*** *and post-breeding* ***(c, d)*** *migration dates, in both The Gambia* ***(a, c)*** *and Gibraltar* ***(b, d)****. Error bars display 95% confidence intervals (CIs) around coefficients. Those CIs that overlap zero (dashed line) indicate non-significant effects, where p>0.05. Variables deemed significant using this approach are displayed in bold on the x-axes.*

Much like the models predicting pre-breeding migration, the relationships between the meteorological variables and first/last post-breeding migration dates varied between locations (**Fig. 5c & d**). I found no significant relationships between meteorological/ecological variables and dates of post-breeding arrival in The Gambia, although there was a weak negative relationship with pre-arrival NDVI of North Africa (Appendix Table S9). In contrast, dates of post-breeding departure from Gibraltar showed a significant positive relationship with the start date of the Sahelian dry season (which typically occurs in October), i.e., in years of earlier dry season onset, departure from Gibraltar was earlier. Additionally, although not significant at the p=0.05 level, dates of post-breeding departure from Gibraltar also showed a positive relationship with European autumn temperatures (Appendix Table S10).

The drivers of median migration dates at Gibraltar differed slightly from those of first/last dates (Appendix Fig. S7). Median dates of pre-breeding arrival at Gibraltar showed a significant negative relationship with pre-arrival North African NDVI, in addition to a significant positive relationship with pre-arrival temperatures of the Sahel. Median post-breeding departure dates from Gibraltar were significantly negatively correlated with European autumn NDVI and pre-departure Gibraltarian NDVI. Additionally, year was retained as a significant driver in both models, showing a strong negative relationship with arrival dates and a strong positive relationship with departure date (Tables S11 & 12).

2.5 Discussion

Here, I have demonstrated advancements in the timing of pre-breeding migration of trans-Saharan migratory birds at both a tropical non-breeding area and an intermediate passage site. Additionally, I found delays to the timing of post-breeding migration of these same migrants at both locations. As a result of these contrasting trends, I observed substantial alterations to the temporal partitioning of the annual cycles of these species, at least in terms of when the first and last individuals of species arrive and depart from the regions. I also found that, at Gibraltar, the intermediate passage site, the trends of changing passage date over time did not differ significantly between first/last individuals and the median passage date, though clearly median passage dates differed from first and last arrival/departure dates. Here, I discuss these results, as well as the exploration of the factors identified as potential drivers of the observed trends. I go on to discuss the implications of these findings in relation to the potential impacts of continued climate change on the phenology and population trends of long-distance migrants.

Overall, I found that pre-breeding migration had advanced significantly, both in terms of departure from The Gambia and on passage at Gibraltar, the latter for both first and median dates of arrival. These findings are in line with phenological changes observed on the breeding grounds, with rates of advancement at Gibraltar most similar (0.28 days/year at Gibraltar cf. e.g. 0.26 days/year on the breeding grounds; Tøttrup et al., 2006). Additionally, despite being of greater mean magnitude, advancements in departure dates from The Gambia over time (0.44 days/year) overlapped significantly with those at Gibraltar, so could also be considered comparable to those on the breeding grounds. The similarity in rates of phenological change at the two study sites during pre-breeding migration are consistent with unaltered migratory speeds over time, though, without tracking individual birds, this cannot be proven. Hence, advances in arrival at Gibraltar are likely to have been driven, at least partially, by concurrent advances in departure from The Gambia (Ouwehand & Both, 2017), and it may even be the case that departures from Gambia have advanced more than at the intermediate passage site and on the breeding grounds.

The last departure of individuals of species from The Gambia, heading for the breeding grounds, occurred earlier in years of high pre-departure Sahelian NDVI, when resources were assumed to be more plentiful there. This is similar to findings in the Americas, which showed that departure from tropical non-breeding areas is facilitated by increased food availability (Studds & Marra, 2011). Thus, individuals are probably able to gain mass more rapidly and, therefore, depart at an earlier date. The median arrival of individuals at Gibraltar tended to occur later in years of high pre-arrival temperatures across the Sahel. These conditions are correlated with colder and, therefore, later

European springs in which it may be costly to arrive early (Saino & Ambrosini, 2008). Alternatively, higher Sahelian temperatures may lead to more rapid declines in resources. This may limit pre-departure fattening rates, resulting in delayed departure from the Sahel and, therefore, arrival at Gibraltar. The median passage occurred earlier in years of higher North African NDVI, again potentially due to greater resource availability on refuelling stopovers. In contrast, timing of the first pre-breeding arrivals at Gibraltar was positively related to the winter NAO index, rather than temperature or NDVI variables. Hence, and in contrast to studies from the breeding grounds (Forchhammer et al., 2002; Hüppop & Hüppop, 2003; Jonzén et al., 2006), the earliest migrating individuals tended to arrive at Gibraltar later in years of strongly positive NAO, despite this correlating with typically wet and warm European springs. In such conditions, earlier arrival might have been expected to be advantageous. However, the more arid conditions across north-western Africa associated with these positive NAO conditions may limit food availability, forcing individuals to increase the length of resource replenishing stopovers (Jones et al., 2003). In fact, the NAO index showed a strong negative correlation with NDVI of the North African region prior to arrival (R_s = -0.61), which may explain why the drivers of first and median arrivals appear to differ. Additionally, local weather patterns across Africa resulting from these positive NAO conditions, e.g. stronger trade winds and more frequent Atlantic storms, could serve to “hold up” early migrating individuals across north-western Africa (George & Saunders, 2001; Jones et al., 2003). In order to account for these delays, migration speed may be increased following such pre-breeding stopovers, as has been observed in North America (Marra et al., 2005).

Year was a significant predictor of the latest pre-breeding migration departures in The Gambia and of subsequent median arrival dates at Gibraltar and approached significance for the first arriving individuals at Gibraltar (p=0.08), with both pre-breeding Gambian departure and Gibraltarian arrival dates becoming earlier in recent years. The retention of year, in addition to environmental variables in the models, suggests that an additional driver of these trends may have been excluded from the models. Perhaps more simply, there may be increasing selection over time for individuals that migrate earlier. It has been suggested that advances in the breeding ground arrival dates of long-distance migratory birds are driven not by plasticity in individual arrival date but rather by advanced arrival dates of progressive generations of new recruits (Gill et al., 2013). As development and miniaturization of tracking technology continues, testing such hypotheses for small passerine species may well become viable.

The ability to advance pre-breeding migration from their non-breeding grounds may render migrants more resilient to phenological advancements on the breeding grounds than previously thought, as individuals are not solely reliant on the ability to increase migration speed, which itself is likely to have morphological and physiological limits. However, notwithstanding uncertainty in future climatic predictions, declines in rainfall are forecast for some tropical regions, including the western Sahel (Biasutti, 2019). This may result in reduced productivity and, hence, fewer resources for refuelling in these areas. This could result in migrating birds needing longer to gain resources for migration, potentially constraining early departures from the non-breeding grounds (Marra et al., 2005). Alternatively, the changing distribution of resources could result in poleward shifts in non-breeding distributions, leading to shorter migrations for some species (La Sorte & Thompson, 2007). Such reduced migratory tendencies, and consequent fitness benefits have been observed recently in species such as White Stork in Europe (Cheng et al., 2019). However, for long-distance migrants whose breeding and non-breeding ranges are largely in different hemispheres, this could result in increased migration distances and, therefore, longer migratory durations (Howard et al., 2018).

In contrast to pre-breeding migration, I found that post-breeding migration occurred progressively later at both locations over time and for both median and last departure dates at Gibraltar. None of the meteorological or ecological variables included in models were related to Gambian post-breeding arrival dates. However, last autumn departure from Gibraltar was positively correlated with the onset of the Sahelian dry season. Thus, individuals departed from southern Europe earlier in years when the Sahelian dry season occurred earlier. I hypothesise that this occurred as individuals attempted to reach sub-Saharan Africa before Sahelian resources declined, to reduce the risk of starvation on arrival (Jenni & Kéry, 2003). However, the mechanisms that could lead to such a response are unknown. It may be possible that individuals are able to use environmental cues within Europe, such as temperature, precipitation, or pressure patterns, that are correlated with conditions in the Sahel, to anticipate the latest feasible departure period.

Median departure dates from Gibraltar showed a negative relationship with European autumn NDVI and, more locally, Gibraltarian NDVI. Higher NDVI values prior to departure may enable more rapid fat-loading, enabling earlier departure. This could suggest that drivers of post-breeding migration differ between individuals of the population on different migratory schedules. The latest migrating individuals, potentially from the most northerly parts of the breeding range, typically departed from Europe in October (Appendix Table S3). Therefore, the measure of European NDVI, which was calculated over August and September, may have little relevance to the timing of their departure. Instead, the senescence of resources in the Sahel, which typically begins in September and becomes more severe as the year progresses, may place a greater pressure on the migratory timing of these individuals (Jenni & Kéry, 2003). In contrast, median post-breeding departure typically occurred in September and individuals may be more able to take advantage of increased resources across Europe during this period, to depart more rapidly from the breeding grounds. These individuals, which may be from more centrally or southerly distributed breeding populations (and hence, start and finish breeding earlier), potentially migrate sufficiently early that the decline of resources in the Sahel is unlikely to impact their survival. Interestingly, year was retained as a significant predictor of median but not last departure dates at Gibraltar.

Due to the opposing trends in timing of pre- and post-breeding migration, population-level durations of stay of trans-Saharan migratory species changed significantly in both Europe and sub-Saharan Africa. Models indicated that, on average, duration of stay (i.e. presence of any individuals of a species) within Europe, for populations passing Gibraltar, increased by over two weeks, across 27 years, whilst sub-Saharan Africa stay durations declined by over two months over the 55-year study period; the change in duration of stay at Gibraltar being consistent for both median passage and the timing of first arriving (spring) and last departing (autumn) individuals. Due to the population-level nature of the data utilised in this study, I was unable to assess changes in the time individuals spent in the North African region between Gambia and Gibraltar. Notwithstanding the fact that these results represent population-wide changes in phenology, they represent substantial, and previously undocumented, changes to the temporal-partitioning of the annual cycle of these long-distance migrants. These findings and their potential impacts, discussed below, highlight the need for increased focus on recording the phenology of post-breeding migration, as well as pre-breeding migration away from the breeding grounds.

Due to the inevitability of further rises in global temperatures, continued advancement of the spring phenologies of temperate ecosystems are likely (Vitasse et al., 2011). As such, pre-breeding migration is likely to continue to advance, unless individuals become limited by, for example, food availability. Furthermore, and counter to the suggestion of Jenni & Kéry (2003), I found that the timing of the Sahelian dry season has shown significant delays in recent times (Appendix Fig. S8). Currently, predictions of future rainfall across the Sahel vary among climatic models (Biasutti, 2019). However, if the recently observed delays to dry season onset continue, this could further reduce the necessity for some populations to depart from breeding grounds rapidly post-breeding. As a result, it is possible that species will further extend their annual duration of stay within Europe, at the expense of that within sub-Saharan Africa. This could result in the evolution of short-distance migratory strategies for some populations of these migrants, as has been observed in the Eurasian Blackcap *Sylvia* *atricapilla*, and predicted in selection experiments (Berthold et al., 1992a; Pulido & Berthold, 2010). This is particularly interesting when considering the forecasts of increased migratory distance for long-distance Afro-Palearctic migrants, which are yet to account for the potential development of "short-stopping" (Doswald et al., 2009; Elmberg et al., 2014; Howard et al., 2018).

If it were to become climatically viable, shorter-distance (e.g. within the western Palearctic) migration would likely confer numerous benefits to populations that formerly undertook long-distance migrations. Firstly, shorter migration distances should result in reductions in both stopover number and migratory duration (Howard et al., 2018). Periods of migratory flight and stopover are both times of particularly high mortality, due to factors such as increased predation risk and unknown resource availability (Newton, 2008). Therefore, a reduction in migration distance should positively affect individual survival (Cheng et al., 2019). Additionally, shorter-distance migratory populations may be better able to anticipate breeding ground phenology, utilising better linked cues for timely pre-breeding departure (Both et al., 2010; Jonzén et al., 2006). Alongside reduced duration of pre-breeding migration, such populations should become less phenologically mismatched than long-distance migratory populations of the same species (Bearhop et al., 2005). However, such changes in migratory strategy would also have knock-on effects on temperate and tropical ecosystems. For example, an increase in avian richness in the Western Palearctic over the non-breeding period may increase competition for resources, with potential deleterious impacts upon resident and short-distance migratory species that spend the non-breeding season in this region. Conversely, through competitive release, a reduction in non-breeding species richness in tropical regions could benefit other species using the former non-breeding areas of migrants. However, as migrants are typically itinerant during the non-breeding season, due to the ephemeral nature of the resources they utilise, resident African species may be less capable of benefitting from any excess resource.

In conclusion, these findings provide new insight into the changing annual cycles of long-distance migrants under a period of recent rapid climate change. Long-distance migrants advanced pre-breeding departure from tropical non-breeding grounds aiding adaptation to rapid phenological advancement on breeding grounds. However, potential declines in productivity in these tropical areas may limit species' abilities to continue these advancements, due to the inability to further advance fat-loading prior to pre-breeding departure. An opposing trend in post-breeding migration meant that, at a population level, long-distance migrants now spend a markedly shorter period of time on the non-breeding grounds than they did in the latter part of the last century. Through continuation in these trends and selection for reduced migratory activity, we may see adoption of new migratory strategies in populations of these long-distance migratory species.

Chapter 3

Consistency in the drivers of the population trends of migratory birds in the Americas and Afro-Palearctic flyways

The Eurasian Wigeon *Mareca penelope* (left), a European breeding migrant, alongside its North American breeding counterpart, the American Wigeon *Mareca americana* (right). *Photo credit: Jack Bucknall*

3.1 Abstract

Migratory species have complicated annual cycles, which makes the identification of drivers of population change difficult. Declines have typically been attributed to environmental change, to which migratory species, given their use of multiple disparate areas annually, are particularly susceptible. Previous work has suggested that the primary drivers of population trends are climatic in origin on the breeding grounds but non-climatic on the non-breeding grounds. However, to date, an assessment of the relative impacts of climate- and land-use change across multiple migration flyways has not occurred. Such information is vital to understand widespread drivers of migrant population changes and, consequently, to inform their conservation. Here, I use population data from the North American Breeding Bird Survey and the Pan-European Common Bird Monitoring Scheme to calculate population trends for long- and short-distance migrants across North America and Europe. Using species-distribution models and species-specific habitat requirements, I produce trends in species-specific suitability of climate and land cover on their breeding and non-breeding ranges. Controlling for species' habitat preference, migratory strategy, migratory dispersion, body mass, and phylogeny, I assess the relative importance of climate and land cover suitability in explaining the population trends of migratory birds. I find that the drivers of population trends of migratory birds are consistent across the two continents. Specifically, climate on the breeding grounds and land cover on the non-breeding grounds are the dominant drivers of population change. The consistency of these signals among long-distance migrants across two continents is strongly suggestive that future actions to reverse widespread population declines should focus principally on habitat improvement on the non-breeding ranges and climate adaptation on their breeding grounds.

3.2 Introduction

Halting the loss of the world's biodiversity has rapidly become a global priority, though with limited success to date (BirdLife International, 2022; Butchart et al., 2010; Ceballos et al., 2015; Tittensor et al., 2014). Targeting future conservation action will require the identification of populations undergoing decline, with both the severity and impacts of decline a potential metric for priority setting (IUCN Standards and Petitions Committee, 2022). Once those declining populations have been identified, the drivers of those declines must also be elucidated if they are to be addressed.

Migratory birds represent a group that has undergone severe population declines, particularly over the last 60 years (Kirby et al., 2008; Wilcove & Wikelski, 2008). Moreover, these declines have occurred more rapidly than in their resident counterparts (Bairlein, 2016; Robbins et al., 1989; Sanderson et al., 2006). Given between 15 and 20% of the world's ~10,000 bird species undertake yearly migrations (Kirby et al., 2008; Somveille et al., 2018), population declines in migratory species are likely to have contributed significantly to the global loss of biodiversity, and to have profoundly affected ecosystem functioning in many areas.

Identifying the drivers of population declines in migratory birds is complicated by their use of multiple spatially segregated areas for the breeding, migratory and non-breeding periods, making it difficult to identify the critical stage(s) driving changes. However, climate- and land-use change have been cited with increasing frequency in relation to these losses (Both et al., 2006; Kirby et al., 2008; Møller et al., 2008; Sanderson et al., 2006). Migratory populations are more susceptible to environmental change than residents as they utilise more than one site during their annual cycle, which increases the likelihood that individuals are exposed to these threats (Runge et al., 2014; Vickery et al., 2023). This may help to explain why long-distance migrants are declining at a faster rate than their short-distance migrant and resident counterparts (Sanderson et al., 2006; Vickery et al., 2014). Long-distance migrants spend longer in their migratory phase than other forms of migrant and, given that migration is typically the period of highest mortality for such species, might naturally be expected to have lower rates of population growth than other species, increasing their risk of declines (Rushing et al., 2017; Sillett & Holmes, 2002). Moreover, with some long-distance migrants having breeding and non-breeding ranges in different hemispheres, there is a risk future climate change will lead to greater migration distances in future, via diverging poleward range shifts, further exacerbating mortality risk (Howard et al., 2018; Zurell et al., 2018). Identifying how such threats have impacted migratory populations in recent decades may enable action to reverse these negative trends and plan for future threats (Pacifici et al., 2015).

Monitoring of birds across the globe, but particularly in Europe and North America, has identified the impacts of land-use change on the population trends of migratory species (Howard et al., 2020; Sullivan et al., 2015; Thaxter et al., 2010). Globally, land-use change has led to the loss and degradation of many habitats (Newbold et al., 2015). Much of this has occurred in the form of increasing extent and intensity of agriculture, including increases in pesticide use, drainage, woodcutting, and overgrazing (IPBES, 2019; Kirby et al., 2008). For example, the widespread decline of European farmland species has largely been attributed to such processes operating within Europe (Donald et al., 2006; Gregory et al., 2019), but also in the open habitats of sub-Saharan Africa where many long-distance migrants spend the non-breeding period (Atkinson et al., 2014; Beresford et al., 2019; Sanderson et al., 2006). In America, Europe and Asia, deforestation and reclamation of wetlands have been identified as important drivers of the global decline in migratory birds (Kirby et al., 2008). Beyond the direct effects of habitat loss, fragmentation of forests has led to increased nest predation and parasitism (Newton, 2008; Robbins et al., 1989). Drainage and development on wetlands may be particularly important at migratory stopover sites, as surrounding terrestrial habitats are entirely unsuitable for wetland species (Ma et al., 2014; Studds et al., 2017).

Understanding of the impacts of climate-change on migratory birds has also recently increased. Species favoured by recent changes in climate within Europe and North America have fared better than those predicted to be negatively impacted (Mason et al., 2019; Stephens et al., 2016), whilst climate, particularly rainfall, in sub-Saharan Africa has been linked to the overwinter survival, pre-breeding condition, breeding success and overall population trends of trans-Saharan migrants (Atkinson et al., 2014; Ockendon et al., 2014; Peach et al., 1991; Sanderson et al., 2006). Increased temperatures in temperate areas have enhanced productivity and over-winter survival of some residents and short-distance migrants (Meller et al., 2018; Pearce-Higgins et al., 2015). In contrast, these conditions have led to decline in populations of long-distance migrants, possibly through increased intraspecific competition with those species that have benefitted (Pearce-Higgins et al., 2015). Furthermore, asynchronous responses to warmer temperatures may lead to reduced productivity, through mismatches in the phenology of species' breeding attempts and their associated habitats in temperate regions. This has been shown especially to be true for long-distance migrants that must anticipate breeding conditions from different continents (Both et al., 2009; Visser et al., 1998; Visser & Both, 2005).

Whilst those studies of land-use and climate change have provided an insight into the potential impacts of environmental change on bird populations, very few consider the impacts of both processes on migratory species during multiple stages of the annual cycle. As the drivers of population trends differ between migratory strategies, the impacts of environmental change on resident species may not apply directly to migrants (Howard et al., 2020). Furthermore, analysing impacts of climate and land-use change separately makes it difficult to assess their relative importance. Similarly, many studies focus on the impacts of environmental change on only one part of the annual cycle, i.e., the breeding or non-breeding seasons or the two migratory periods between these locations. This does not enable the identification of the critical period during which migratory populations are limited. Therefore, the extent to which we can utilise these studies to identify the main priorities for further research, or action to reverse these trends, is limited. A holistic study by Howard et al. (2020) suggested that climate change is the most important driver of recent population trends of short- but not long-distance migratory birds on European breeding grounds. On the non-breeding grounds, land-use change had a significant impact on populations trends of all migratory species. This research provided a solid foundation for further research and practical conservation within this flyway but likely cannot be generalised to impacts on migrants across other flyways. Study of these relationships is needed across a wide suite of migratory species in multiple flyways to assess the importance of, and spatial variation in, drivers of the trends in migratory populations. The is especially important considering the diverging fates of bird populations in different flyways, which may highlight spatially heterogenous drivers of decline (Stephens et al., 2016).

Here, I use annual population indices from the North American Breeding Bird Survey (NABBS) and the Pan-European Common Bird Monitoring Scheme (PECBMS) to analyse population trends for 311 species of consistently monitored migratory bird across the two continents over the period 1980 to 2017. I produce composite population indices over the same period for long- and short-distance migrants, separately, in both locations. I use species distribution models (SDMs) and species-specific habitat preferences to produce climate and land-cover suitability trends for each species' breeding and non-breeding range. I use these, along with species traits, such as migratory strategy, migratory dispersion, habitat preference and body mass, to analyse the relationship between species' environmental suitability trends and their population trends in the Afro-Palearctic and Americas flyways. From this, I explore whether: (1) the rates of population decline in long- and short-distance migrants are consistent in Europe and North America and (2) the relative impacts of climate- and land-use change on the population trends of migratory birds differ between the two flyways.

3.3 Materials and methods

3.3.1 Species data

For North America, annual population indices were acquired for all 548 species monitored by NABBS (Sauer et al., 2020), covering the period 1966 to 2019, over the 48 contiguous states of the USA. For Europe, annual population indices were acquired for all 168 species monitored by PECBMS (https://pecbms.info/), covering the period 1980 to 2017, over the 28 countries covered by the scheme. Within Europe, some species were not monitored for the entirety of the study period, owing to the varying timescales of separate national recording schemes. Therefore, I excluded any species for which monitoring commenced post-1998 (thereby recorded for fewer than 20 years) or for which there was a period of limited geographical coverage, leaving 131 PECBMS species. I further excluded any species that primarily utilise marine habitats during the breeding or non-breeding season, as my methods of assessing trends in climate and land-use suitability (described below) are not informative for such species. Using these criteria, I removed 17 'marine' species from the NABBS dataset and one species from the PECBMS dataset. I removed one species, Turtle Dove *Streptopelia turtur*, from the European dataset, as populations of this species are recognised to have been heavily impacted by hunting pressure and, as such, recent trends are unlikely to be explained by changes in climate or land-use (Vickery et al., 2014; Zwarts et al., 2015). This left 531 NABBS species and 129 PECBMS species.

Breeding and non-breeding range polygons for all PECBMS and all possible NABBS species were obtained from BirdLife International (Birdlife International and NatureServe, 2016). NABBS and BirdLife taxonomies differ and, therefore, distribution polygons were only available for 408 species in the NABBS dataset. Breeding ranges were intersected with a 0.5^{o} x 0.5^{o} grid covering the "temperate" realms (defined as the amalgamation of the Nearctic, Palearctic, Saharo-Arabian, and Sino-Japanese realms from Holt et al. (2013); Appendix Fig. S9), as the area for which I possessed population data for my study species falls entirely within these realms. Non-breeding ranges were intersected with a 0.5^{o} x 0.5^{o} grid covering the whole world, as non-breeding ranges of my study species spans both temperate and tropical realms. Species were classed as present in a grid cell if a range polygon overlapped more than 10% of any cell.

Although some species (48 NABBS and 86 PECBMS) have ranges that extend beyond the focal flyways of this study, I excluded these areas of range in my modelling framework as I had no trend data for such populations. To do so, I identified the longitudinal boundaries of the Americas, Afro-Palearctic and Australasian flyways, as these are the three coarsest global flyways that retain relevance to the available population data. I clipped NABBS species distributions to the Americas flyway and

PECBMS species to the Afro-Palearctic flyway. To define the modelling arenas for these separate flyway populations, I plotted the breeding richness of all non-soaring, land birds classified as a “full migrant” by Birdlife International and NatureServe (2016) that spend the non-breeding period solely within the regions that a flyway encompasses (i.e., N, C and S Americas for the Americas flyway, Europe and Africa for the Afro-Palearctic flyway, and Asia, Oceania and Australia for the Australasian flyway). I then did this in reverse, i.e., plotting the non-breeding richness of all species that spend the breeding period solely within those regions. This approach enabled the identification of the main areas over which species that utilised each flyway were distributed, and hence the most parsimonious longitudinal boundaries for each flyway (**Table 1**, Appendix Figs. S10 & 11). Reassuringly, my boundaries fall broadly in line with previously suggested flyway boundaries (Mondain-Monval et al., 2019; Newton, 2008).

Table 1. Longitudinal boundaries of the three main migration flyways and the numbers of migrants classified as long- and short-distance migrants from the North American Breeding Bird Survey (Americas) and Pan-European Common Bird Monitoring Scheme (Afro-Palearctic) dataset.

Flyway	**Longitudinal Boundary**		**Long-distance migrants**	**Short-distance migrants**
	West	**East**		
Americas	170°W	30°W	68	162
Afro-Palearctic	30°W	65°E	36	45
Australasian	65°E	170°W	NA	NA

As I only wished to consider migratory species, I first removed any species for which the breeding and non-breeding distributions overlap entirely (151 NABBS and 37 PECBMS species), defining these as residents. The remaining 257 NABBS and 92 PECBMS species were then classified as either long- or short-distance migrants, using criteria described below, with a further subset (utilising mixed migratory strategies) being excluded. To date, there is not a clear global definition of long- vs. short-distance migrants. This presents an issue for comparability among studies, and across different flyways. The general trend, however, is to define migratory syndromes based on the location of species’ breeding and non-breeding distributions, rather than by the distance over which species migrate. Species which breed within the temperate realms, i.e. the Holarctic, and spend the non-breeding period in the tropics are typically defined as “long-distance” migrants (Holmes & Sherry, 2001; Holt, 2000; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014). Species that breed within the temperate realms and for which most of the population spends the non-breeding period within the temperate realms are typically defined as “short-distance” migrants. Consequently, I followed these generally accepted definitions but formalised their application to allow us to systematically apply definitions across both the Americas and Afro-Palearctic flyways. Those species for which 100% of the non-breeding range occurs in the “tropical” realms (defined as the amalgamation of the Panamanian, Neotropical, Afrotropical, Madagascan, Oriental, Oceanian, and Australian realms from Holt et al. (2013); Appendix Fig. S9) were defined as long-distance migrants (34 NABBS and 24 PECBMS species). I classified as long-distance migrants a further subset of species that satisfied the following two criteria: (1) more than 80% of the non-breeding range occurs in the tropical realms and (2) the area of the overlapping region of the breeding and non-breeding ranges within the temperate realms accounts for less than 20% of the overall breeding range within the temperate realms (34 NABBS and 12 PECBMS species). This enabled the inclusion of species that are largely long-distance migrants (e.g., Subalpine Warbler *Sylvia cantillans*), whilst avoiding the inclusion of species with a large resident range that extends across the tropics, but which are migratory within the temperate realms (e.g., Cattle Egret *Bubulcus ibis*). Short-distance migrants were defined as those species for which less than 50% of the non-breeding range occurs in the tropical realms and are, therefore, predominantly migratory within the temperate realms (162 NABBS and 45 PECBMS species). I excluded the remaining species (i.e., those with more than 50% of their non-breeding range in the tropical realms but not qualifying as a long-distance migrant; 27 NABBS and 11 PECBMS species), many of which have large resident populations in the tropics, which would reduce the relevance of climate suitability projections to European or North American populations. Using these definitions, I identified 68 long-distance and 162 short-distance migrants in the Americas and 36 long-distance and 45 short-distance migrants in the Afro-Palearctic.

I calculated population trends for each species as the coefficient of a log-linear Poisson regression of annual population index against year, with the index value of the initial year set to 100. To ensure comparability across the datasets, NABBS data were truncated to the same period as that for PECBMS, i.e., 1980 to 2017. Additionally, to deal with potential issues relating to the impact of sampling error in the calculation of species population trends on later analyses, I calculated the standard error of each regression coefficient (following Howard et al., 2020).

In addition to calculating trends in the extent of available land cover for each species (details below), all species were assigned a primary breeding and non-breeding habitat preference, based on various literature sources (Appendix Tables S13 & 14). Trends in land cover availability account for changes in the overall extent of suitable habitat, whereas identification of similar population trends across species with shared habitat affinities should also enable the identification of the effects of changes in habitat quality. To allow for comparability between the Americas and Afro-Palearctic, I simplified habitat preferences from Howard et al. (2020) and Mason et al. (2019) to four broad categories. These categories were as follows: (1) *farmland*, comprising farmland, grassland, and savanna (latter widely used for grazing in the subtropics and tropics), and other arable land type; (2) *forest*, comprising forest, shrubland, and woodland; (3) *inland wetland*, i.e., any non-marine waterbody, and (4) *other*, i.e., urban environments.

Species which disperse throughout a larger range during the non-breeding season may be more resilient to environmental change, as individuals have a larger choice of areas to spend the non-breeding period and, therefore, are less impacted by the loss of small areas of habitat (Gilroy et al., 2016; Koleček et al., 2018). Therefore, I calculated a continuous measure of migratory dispersion, i.e., the size of a species breeding range compared to that of the non-breeding range, following the methods of Gilroy et al. (2016).

I used the individual species yearly population indices to calculate multi-species population indices for long- and short-distance migrants separately, in both North America and Europe. To do so, I calculated the geometric mean and standard deviation of the annual indices for each group in each location, giving each species an equal weighting in the calculation (following Gregory et al., 2005; Howard et al., 2020).

3.3.2 Climate data and suitability trends

Global, monthly temperature and precipitation data spanning the period 1950 to 2017 were downloaded from CRU TS v 3.26 at 0.5^o resolution (Harris et al., 2014). I used these data to calculate, for each year, five bioclimatic variables that have previously been shown to accurately explain the distributions and abundances of migratory birds (Howard et al., 2020). To ensure that climate variables were as relevant to species distributions as possible, mean temperature of the warmest period (MTWA), mean temperature of the coldest period (MTCO) and total precipitation (TP) were calculated separately for the breeding and non-breeding seasons, so that they coincided with the general timeframe that migrants would be present in these areas (Ponti et al., 2020a). For the breeding range, these variables were calculated over the period March to September, whereas for the non-breeding range these were calculated over the period August to February (Howard et al. 2020). Additionally, I calculated the seasonality of both temperature (TS) and precipitation (PS) over the entire year, to account for the ephemeral productivity of areas utilised by migrants during certain periods, which are otherwise unproductive.

I modelled the relationship between each species' distribution within the relevant flyway and the mean values of the five bioclimatic variables (MTWA, MTCO, TP, TS, and PS) over the period 1950 to 2000, when most of the data underlying the BirdLife distribution polygons was collected. Models were built separately for breeding and non-breeding distributions, using the seasonally relevant values for MTWA, MTCO and TP. I used an ensemble modelling framework, combining four high-performing and widely-applied modelling techniques: Generalized Additive Models (GAMs), Generalized Linear Models (GLMs), Generalized Boosted Regression Models (GBMs) and Random Forests (RFs; Bagchi et al., 2013). To provide the models with meaningful absence data, I excluded climatic data from any biogeographic realm (Holt et al., 2013) in which the species for which I was building the model did not occur.

Spatial autocorrelation occurs when samples located next to one another show similar values – presence or absence values in this instance. This phenomenon can be driven by factors other than relationships between climate and occurrence. Therefore, failure to account for spatial autocorrelation in SDMs may violate the independence assumption of many models (Dormann, 2007). This can lead to inaccurate, biased estimation of coefficients, an increase in type 1 errors and, therefore, influence spatial inference and prediction. To deal with issues associated with spatial autocorrelation in my SDMs I used the "blocking" method of Bagchi et al. (2013), splitting presence/absence data into ten separate sampling blocks based on ecoregions (Olson et al., 2001); doing this separately for American and Afro-Palearctic datasets. Each non-contiguous portion of an ecoregion was used as a sampling unit. Sampling units were combined to form ten blocks, such that the area and mean bioclimate data were approximately equal for each block, whilst also covering the full range of bioclimates. Models were fitted to nine of the blocks and model fit tested on the omitted block. This was repeated ten times, sequentially omitting each of the sampling blocks, which resulted in 40 models for each species' breeding and non-breeding range (4 techniques x 10 blocks). Model performance was assessed on the omitted block using the area under the curve (AUC) of the receiver operator characteristic curve (Manel et al., 2001).

GAMs were used to model the relationship between species presence and absence using thin-plate regression splines. Models were fitted with a binomial response, using a logit link function, in the R package "mgvc" (Wood, 2017). GLMs were used to fit up to, and including, third order polynomial relationships between the five bioclimatic variables and each species presence and absence values. 243 models (3 polynomial degrees ^ 5 bioclimatic variables = 243 combinations) were fitted to nine of the sampling blocks and model fit assessed using AUC from the prediction to the omitted sampling block. This was repeated, omitting each of the sampling blocks in turn. The combination of polynomial terms that maximised model AUC across the ten blocks was used to fit the final ten models. GBMs were fitted using the R package “gbm” (Ridgeway, 2019). I used a cross validation approach to optimise tree complexity, omitting one sampling block, fitting to the remaining nine and assessing error on the omitted block. This was repeated, omitting each of the sampling blocks in turn. The learning rate (shrinkage parameter) was set at 0.001, the tree complexity allowed to vary between one and four and 5000 trees retained in the final model. The tree complexity that resulted in the lowest error, summed across the testing blocks, was used to fit the final ten models. RFs were fitted using the R package “randomForest” (Breiman, 2001). The number of trees in the final model was initially set to 100 and the number of variables randomly sampled at each split (mtry) allowed to vary between one and three. I used a similar cross validation method as for GBMs, omitting one sampling block, fitting to the remaining nine and assessing AUC on the omitted block. After assessing AUC on the omitted block, 500 trees were added, and the fit was reassessed. This procedure was repeated until the resulting improvement in AUC was less than 1%. The number of tree and value of mtry that maximised the mean AUC across the ten blocks was used to fit the final ten models.

For both breeding and non-breeding ranges, I used these models in combination with the yearly bioclimatic data to predict the yearly probability of occurrence of each species in each 0.5^o x 0.5^o cell in the relevant flyway, over the period 1980 to 2017. I then calculated the median suitability across the 40 models for each cell in each year. This was followed by an overall median suitability across all cells in which a species is currently distributed, for the breeding and non-breeding ranges, separately. This enabled the calculation of a “climate suitability trend” (CST) for each species. To do so I fitted a binomial generalised linear model, with a logit link, to regress annual climate suitability against year, over the same period for which each species’ population data were available. I did this separately for breeding and non-breeding ranges and took the regression coefficient from each model as the CST for each range. To ensure I only considered trends in climate that directly impact the populations studied here, I calculated overall median breeding suitability only over the cells of a species breeding range that were within the area covered by NABBS or PECBMS.

3.3.3 Land cover data and suitability trends

Global, annual land cover data were downloaded from the European Space Agency Climate Change Initiative (2017; ESA CCI: https://www.esa-landcover-cci.org/?q=node/164). These data are available over the period 1992 to 2015 at a 300-metre spatial resolution and assign each unit to one of 22 possible land cover types. I used these data to quantify the annual proportion of suitable land cover in each species breeding and non-breeding range. To do so, I aggregated the ESA land cover types to nine broad habitat categories (shrubland, grassland, cropland, broadleaved forest, needle-leaved forest, wetlands and water bodies, urban, bare areas and sparsely vegetated), following the methods of Howard et al. (2020). The suitability of these nine habitat categories was then evaluated for each species in both the breeding and non-breeding season (Appendix Tables S15-18). Where possible, I extracted suitability classifications for European species from Howard et al. (2020). For European species for which such data were not available, and for all North American species, I used breeding and non-breeding habitat descriptions from Billerman et al. (2022) to assess the suitability of each of the nine habitat categories. I then calculated the proportion of each species' breeding and non-breeding range that contained suitable habitat in each year over the period 1992 to 2015. As when calculating climate suitability, for the breeding range, I calculated this proportion only over the cells of a species breeding range that are within the area covered by PECBMS or NABBS.

After calculating the proportion of suitable land cover across each species' breeding and non-breeding ranges in each year, I calculated a "land cover suitability trend" (LCST) for each species using the same method as for the CSTs. I built a binomial generalised linear model, with a logit link, to regress annual proportion of suitable land cover against year. I only included data over years for which each species' population data were available, to ensure that LCSTs were relevant to the associated population trends. I calculated LCSTs separately for breeding and non-breeding ranges and took the regression coefficient from each model as the LCST for each range.

3.3.4 Modelling drivers of population trends

I used phylogenetic linear mixed models (PLMMs) to analyse which factors are the most important in driving the population trends of North American and European migrants. PLMMs were used to account for the non-independence of population trends between species with shared ancestry. Models were fitted separately for North America and Europe, with species' population trends as a continuous response variable, using the R package "MCMCglmm" (Hadfield, 2010). In each model, I included a phylogeny of the relevant species, as well as the standard error of the populations trends as random effects (the latter to account for the influence of sampling error in their calculation). CST and LCST for both the breeding and non-breeding breeding season were included as fixed effects, alongside species' migratory strategy and dispersion. I found that species' breeding and non-breeding primary habitat preferences were significantly correlated for both North American ($X^2_9 = 252.1$, $p < 0.001$) and European ($X^2_9 = 78.6$, $p < 0.001$) species. Therefore, I included only breeding habitat preference as a fixed effect. Finally, I included the logged mean body mass of each species, extracted from Dunning (2007), as a fixed effect, as this has previously been shown to influence the species' population trends (Howard et al., 2020). To facilitate parameter comparison, I scaled each continuous predictor variable using *z*-transformations.

I used an uninformative, inverse Wishart distribution as a prior for both the random effects and residual variance. To fit the model, I ran an MCMC chain for at least 220,000 generations, recording model results every 20 generations and ignoring the first 20,000 generations as burn-in, generating around 1,000 independent samples for each model. I verified convergence using trace plots and Gelman-Rubin diagnostics in the R-package “coda” (Plummer et al., 2006). To enable comparability with other studies and account for phylogenetic uncertainty, rather than fitting one model with a consensus tree, I fitted 100 separate models using 100 different, randomly-selected samples of the posterior distribution produced by Jetz et al. (2012). Posterior outputs of each model were then combined and means, standard deviations and 95% credible intervals were calculated for each fixed effect. I also calculated the percentage of variance explained by each fixed effect and assessed the performance of each model by calculating marginal R^2 following the methods of Nakagawa & Schielzeth (2013).

To analyse trends in environmental variables found to significantly affect the population trends of migratory birds, I fitted PLMMs to regress the annual breeding climate suitability index and annual non-breeding land cover suitability index against year, in North America and Europe, separately. For breeding climate suitability, these models were fitted to data for long-distance and short-distance migrants combined, as their breeding ranges occur on the same continent, so are impacted by similar trends in climate. For non-breeding land cover suitability, however, these models were fitted separately for long-distance and short-distance migrants, as the non-breeding ranges of the former are distributed across the tropics, whereas that of the latter mostly across the temperate realms. Therefore, species of different migratory strategies are likely to be affected by different degrees of land-use change. Fitting of PLMMs was as above, though each model was fitted four times and the four chains merged after verifying convergence. The phylogeny was built as a maximum clade credibility tree, using 1000 samples of the posterior distribution produced by Jetz et al. (2012).

3.4 Results

3.4.1 Population trends of migratory birds

Populations of long-distance migrants have, on average, declined since 1980, in both North America and Europe (**Fig. 1**). Declines in North America were consistent throughout the study period. In contrast, an initial rapid decline during the 1980s in Europe was followed by a slight recovery at the end of the decade, and then a steady decline thereafter. Overall, the magnitude of the declines of long-distance migrants were similar between North America and Europe.

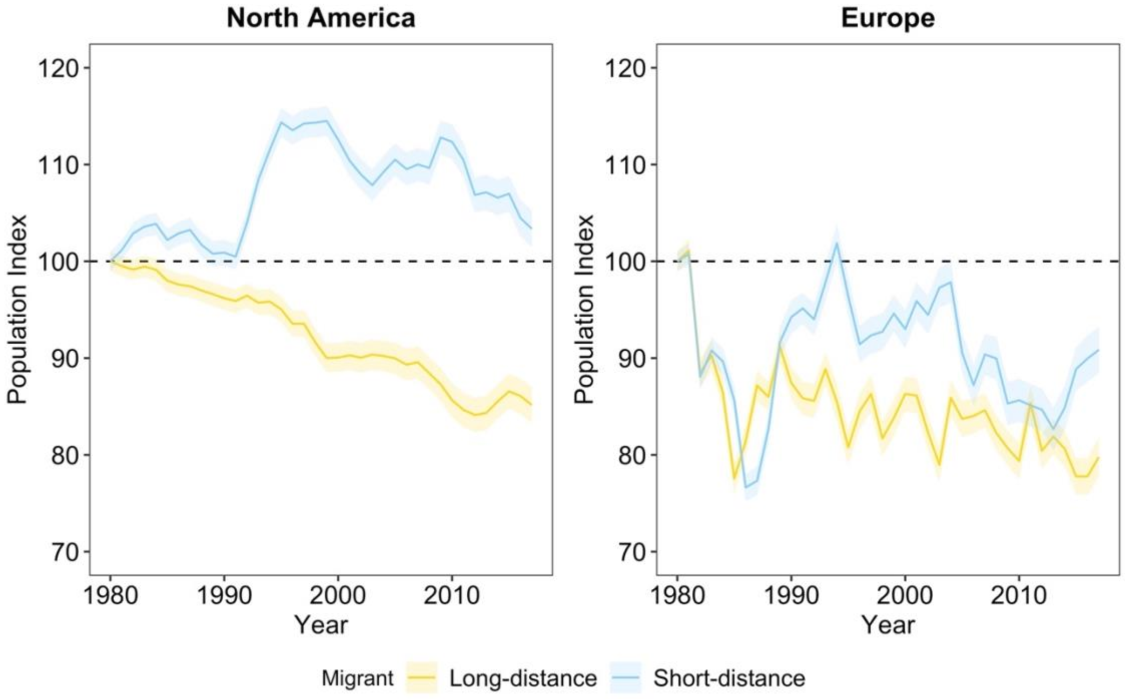

Figure 1. *Composite population indices for long- (LD) and short-distance (SD) migrants, monitored by the North American Breeding Bird Survey (North America;* $n_{LD} = 68$*,* $n_{SD} = 162$*) and the Pan-European Common Bird Monitoring Scheme (Europe;* $n_{LD} = 36$*,* $n_{SD} = 45$*), between 1980 and 2017. Solid line represents the geometric mean taken across all species, whilst the shaded area around this line represents the geometric standard deviation. 1980 index is set arbitrarily to 100.*

On average, over the study period short-distance migrants declined across Europe but increased slightly across North America (**Fig. 1**). The European short-distance migrant declines were less severe than that of long-distance migrants on the same continent, and the trend showed more inter-annual variation. Their populations declined at a similar rate to long-distance migrants during the 1980s, but by 1995 had recovered to their 1980 levels. This was followed by a period of variable, but overall decline to 2017. Population trends of short-distance migrants in North America were also variable over the study period. Population levels were stable between 1980 and 1990, before increasing in the 1990s. Between 2000 and 2017, populations then declined but remained at higher levels than in 1980.

3.4.2 Species distribution models

Species distribution models for both the 230 North American and 81 European species performed well when fitted to both breeding (North American mean AUC: 0.97 ±0.02; European mean AUC: 0.97 ±0.02) and non-breeding distributions (North American mean AUC: 0.98 ±0.03; European mean AUC: 0.95 ±0.04).

3.4.3 Drivers of population trends

PLMMs explained the population trends of migratory birds on both continents reasonably well, although the model for European species (marginal R^2 = 0.53 ±0.01) performed considerably better than that of North America (marginal R^2 = 0.20 ±0.01).

In North America, breeding CST, non-breeding LCST and an association with wetland habitats were all positively related to migrant population trends (**Fig. 2a**). The effect of wetland habitats, with which 53 species were associated, was particularly strong and explained the largest percentage of the overall variance explained by fixed effects (31.2% ±17.3; **Fig. 2b**). By contrast, there were no significant relationships between migrant population trends and any of the other variables: non-breeding CST, breeding LCST, forest/woodland or farmland/grassland habitats, migratory strategy or dispersion, and body mass. Whilst having a non-significant positive relationship with population trends, body mass explained the second highest proportion of the overall variance (21.7% ±17.6; **Fig. 2b**).

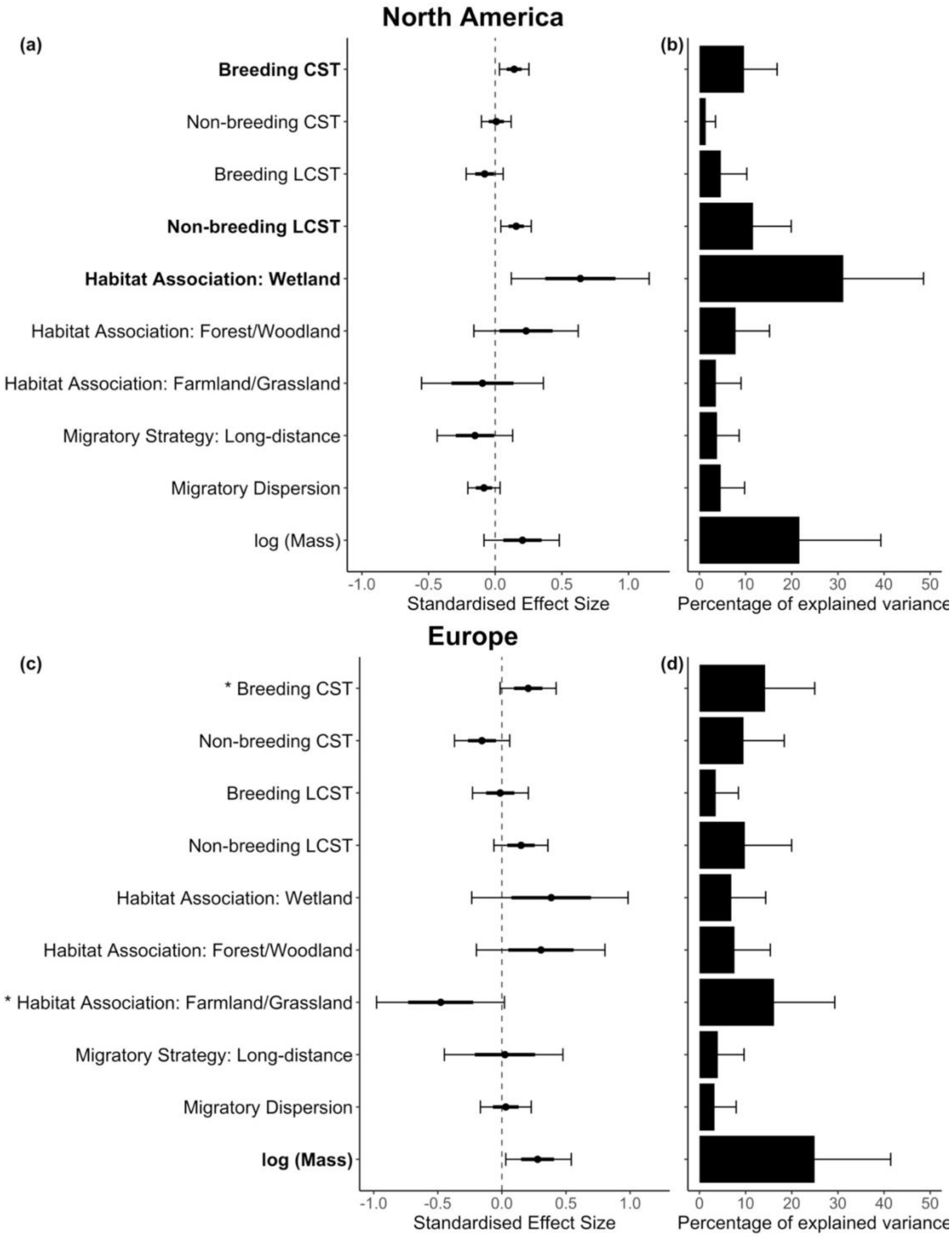

Figure 2. *(a) & (c) Standardised effect sizes and (b) & (d) percentage of variance explained by each variable in PLMMs of population trends of (a) & (b) North American and (c) & (d) European migratory birds. In (a) & (c), points represent the mean effect size, averaged over the 100 separate PLMMS. Thin bars represent 95% credible intervals around these means and thick bars represent the standard deviation. Variables displayed in bold showed a significant relationship with population trends, i.e. credible intervals did not overlap 0. Variables marked with an asterisk (*) are significant at the 10% level. In (b) & (d), bars display the mean percentage of variance explained by each*

variable, averaged over the 100 separate PLMMs. Bars represent the standard deviations of these means. Reference values for habitat association and migratory strategy were "other" and "short-distance", respectively.

In Europe, the only significant effect was a positive relationship between body mass and migrant population trend (**Fig. 2c**), which also explained the highest percentage (25.0% ±16.5) of the overall variance of any fixed effect (**Fig. 2d**). At the 10% significance level, an association with farmland/grassland habitats, displayed by 23 species, had a significant negative effect on species' population trends (**Fig. 2c**). Additionally, as for American migrants, breeding CST showed a positive relationship with species' population trends. These variables explained the second and third highest percentage of the overall explained variance (16.2% ±13.1 and 14.2% ±10.8, respectively; **Fig. 2d**). Of the non-significant predictor variables, non-breeding LCST, which was positively related to species' population trends (as in American species), explained the next highest percentage of the overall variance (9.8% ±10.1; **Fig. 2d).**

On average, the mean climatic suitability of the cells within the breeding distributions of migratory species appeared to decline between 1980 and 2017 in North America and Europe (**Fig. 4**), though a significant decline was found only in the latter (Appendix Table S19). These trends showed high inter-annual variability on both continents, though this variability was larger in North America than in Europe. Mean climate suitability indices in North America ranged between 65.3 to 111.4, compared to 82.9 to 102.7 in Europe.

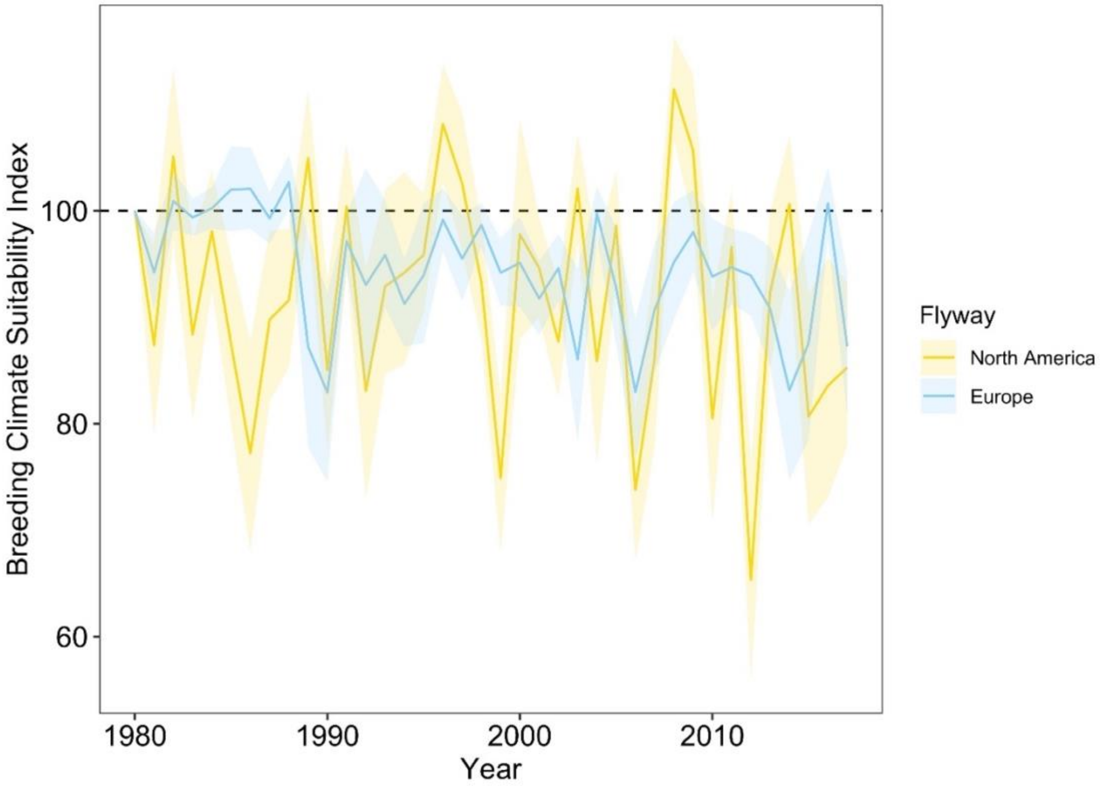

Figure 4. *Composite indices of breeding ground climate suitability for migrants monitored by the North American Breeding Bird Survey (North America; n = 230) and the Pan-European Common Bird Monitoring Scheme (Europe; n = 81), between 1980 and 2017. Solid line represents the geometric mean taken across all species, whilst the shaded area represents the 95% confidence intervals around this mean. 1980 index is set arbitrarily to 100.*

Non-breeding land cover suitability declined significantly, and at similar rates, for both long- and short-distance migrants in North America between 1992 and 2015 (**Fig. 5**; Appendix Table S20). However, interspecific variation was much higher for long-distance migrants than their short-distance counterparts. In Europe, land cover suitability declined significantly for long-distance migrants but increased significantly for short-distance migrants over the study period, with similarly high variability in these trends among species (**Fig. 5**; Appendix Table S20). Notably, however, the magnitude of changes in the land-cover suitability was far lesser than that of climate – around 2% for LCST compared to up to 40% for CST.

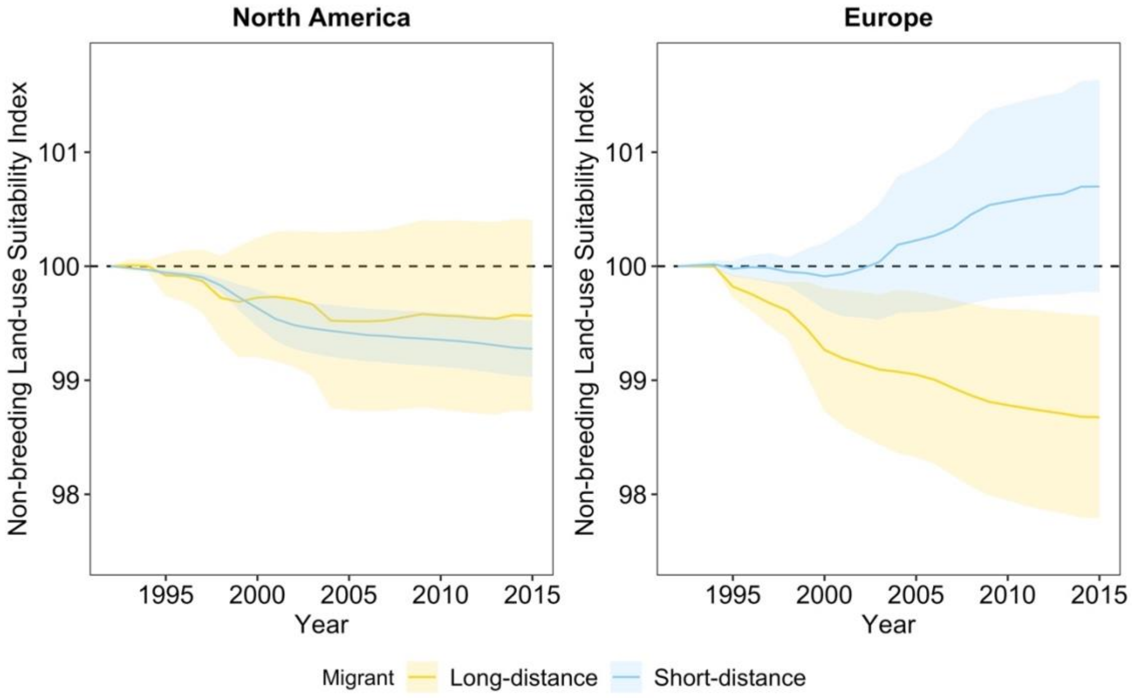

Figure 5. *Composite indices of non-breeding ground land-use suitability for long- (LD) and short-distance (SD) migrants, monitored by the North American Breeding Bird Survey (North America;* $n_{LD} = 68$*,* $n_{SD} = 162$*) and the Pan-European Common Bird Monitoring Scheme (Europe;* $n_{LD} = 36$*,* $n_{SD} = 45$*), between 1992 and 2015. Solid line represents the geometric mean taken across all species, whilst the shaded area represents the 95% confidence intervals around this mean. 1980 index is set arbitrarily to 100.*

3.5 Discussion

I have conducted, to my knowledge, the first multi-flyway, analysis of the simultaneous effects of climate- and land-use change on the breeding and non-breeding ranges of migratory birds. My main finding is that the drivers of these population trends are consistent across two of the major global flyways for migratory birds (the Americas and the Afro-Palearctic). By standardising the differentiation of long- and short-distance migrants, I have also shown that the magnitude of declines in the populations of long-distance migrants is similar in North America and Europe. However, whereas the populations of short-distance migrants have also declined in Europe, they have increased in North America. Here, I discuss the role of key drivers of the population trends of migratory birds and the novelty of the finding that these drivers are similar across spatially segregated global migration flyways.

In North America, breeding CST and non-breeding LCST showed significant positive relationships with the populations of migratory birds after for other potentially confounding factors. In Europe, the positive relationship between population trends and breeding CST was significant only at the 10% level, and that of non-breeding LCST not even at this level. This is perhaps unsurprising given the smaller sample of species in Europe (n = 81) than in North America (n = 230) and, therefore, the reduced ability to detect significant effects amongst other potentially confounding variables. Despite this, these two variables explained a relatively large proportion of the European model's variance (breeding CST: 14.2% and non-breeding LCST: 9.8%). Howard et al. (2020), who used similar data and species to explore trends in European migratory birds, found significant positive effects of both breeding CST and non-breeding LCST on population trends at the 5% level, which is suggestive that the reduced sample size for Europe affected my ability to detect influential variables. I included only 81 species compared to the 100 species in their study, due to my standardised definition of migratory behaviour across two characteristically different flyways (the Americas flyway lack a natural barrier to migration for the separation of long- and short-distance migrants, such as the Sahara Desert in the Afro-Palearctic system). Considered in combination with the study of Howard et al. (2020), my results reveal the importance of climate on the breeding grounds and land cover on the non-breeding grounds for migratory birds in North America and Europe.

The impacts of changes in breeding climate suitability and non-breeding land cover on migratory North American and European bird populations are not novel concepts (Atkinson et al., 2014; Cresswell et al., 2009; Howard et al., 2020; Kirby et al., 2008; Mason et al., 2019; Stephens et al., 2016). However, I have, for the first time, conducted a parallel analysis to highlight similarities in the key drivers of migrant population changes on the breeding and non-breeding grounds over the two flyways. As such, these are important findings for the understanding of the drivers of the global decline in migratory bird populations and the stages of the annual cycle at which populations are being limited.

On average, breeding CST appeared to decline on both continents between 1980 and 2017, though this trend was non-significant in North America, likely due to the high level of inter-annual variation. Declines in breeding CST may explain the observed declines in both sets of migrants in Europe and long-distance migrants in North America. Non-breeding LCST over the study period declined for all migrants in North America and long-distance migrants in Europe but increased for short-distance migrants in Europe. Whilst this, again, helps to explain the population trends of long-distance migrants, these trends occur in the opposite direction to those one might expect for short-distance migrants, which are increasing in North America and declining in Europe. This is possibly due to land-use change in both North America and Europe (where short-distance migrants principally spend the non-breeding period) occurring along management intensity gradients (e.g., removal of hedgerows/shrubs, pesticide use, overgrazing, lowering/raising of water levels, loss of woodland understorey or forest fragmentation; Kuemmerle et al., 2016; Rounsevell et al., 2012; Sleeter et al., 2013). Therefore, habitats across these continents may have changed in quality, rather than in extent; the former being something my LCST cannot assess. In contrast, large-scale conversion of tropical forests and savannah to agriculture in the Americas and Africa, which are utilised by long-distance migrants, are more likely to be represented within my LCST variable and potentially why I detected effects of non-breeding LCST on migrant population trends.

Habitat association was important in explaining the population trends of migratory birds on both continents. Wetland species in North America showed more positive population trends than species associated with other habitats. Waterfowl and waterbirds are known to have recovered in North America due to the success of conservation initiatives (North American Bird Conservation Initiative, 2022). In fact, the increase in North American short-distance migratory populations (of which 45/162 show wetland association c.f. 8/68 in long-distance migrants) observed in the early 1990s coincides with the implementation of the North American Wetlands Conservation Act in 1989. In Europe, I found that farmland/grassland species have declined more rapidly than others. This is a well-documented trend, attributed to the intensification of agricultural practices in Europe and Africa (Beresford et al., 2019; Donald et al., 2006; Gregory et al., 2019; Sanderson et al., 2006). Given that 13 of the 46 European short-distance migrants in this study are associated with this habitat, this may help to explain the overall decline of this species group. Overall, habitat association may function as a better proxy for the impacts of land-use change in North America and Europe than LCST.

I found no evidence for the impacts of breeding LCST or non-breeding CST on the populations of migratory birds on either continent. This has previously been reported for European species (Howard et al., 2020), but may still be surprising considering the wealth of evidence for the impacts of breeding land cover and non-breeding climate when studied alone. Agricultural intensification, deforestation/afforestation and loss/gain of wetlands in North America and Europe have all been linked to changes in bird populations in both locations, as have changes to rainfall patterns in species' non-breeding grounds (Donald et al., 2006; Kirby et al., 2008; Ockendon et al., 2014; Peach et al., 1991; Robbins et al., 1989; Sutherland et al., 2012; Vickery et al., 2014). It is possible that species' habitat associations accounted for much of the variation that might be expected to have been explained by breeding LCST on both continents. Additionally, we lack detailed information on the migratory connectivity of country/state-level populations (i.e., the extent to which one breeding population mixes with others during the non-breeding season; Finch et al., 2017). Therefore, I was forced to consider population trends and calculate environmental variables at the continental level. As land cover changes occur heterogeneously across both continents, the effects of changes in land cover extent are likely to have been diluted in my models and, hence, reduced in apparent importance (Kuemmerle et al., 2016; Sleeter et al., 2013).

The lack of information on species' migratory connectivity may also help explain the apparent lack of importance of climate on the non-breeding grounds. Non-breeding CST was calculated over the area that, to the best of my knowledge, was used by the majority of the breeding populations during non-breeding period. However, migratory connectivity is typically low in long-distance migrants in both North America and Europe, meaning that the populations I consider here are likely to mix with different migratory or even tropical resident populations of the same species (Finch et al., 2017). As such, CST values may be less relevant to the focal breeding populations of this study. More generally, our understanding of non-breeding ranges at a fine scale is much less detailed than that of breeding ranges (Howard et al., 2020). As I calculated CST values at a relatively coarse scale, they should still be relevant for most species. However, some long-distance migratory species on both continents are itinerant during the non-breeding season, tracking resource peaks between spatially segregated areas, and, therefore, do not occupy the full extent of the mapped non-breeding range for the full season (Cresswell et al., 2009; Renfrew et al., 2013; Thorup et al., 2017). Therefore, the area over which CST are calculated, may not reflect the areas utilised by these species well.

I found that models performed notably better in Europe (53%) than in North America (20%). The explanation for this is not immediately apparent but may be due to the area over which population trends were analysed. The area covered by PECBMS is around 4.5Mkm^2, compared to 8Mkm^2 for NABBS. As such, there is greater potential for spatial variation in the drivers of population trends across North America, compared to Europe, again highlighting the need to consider populations at the sub-continental level.

Further work is required to determine species' fine-scale distributions away from the breeding grounds (Cresswell, 2014), the connectivity of different breeding populations (Finch et al., 2017) and detailed species' specific habitat requirements (Vickery et al., 2023). Increasing our knowledge of these preferences, alongside data on individual demography and migratory routes, will enable us to further understand the declines of migrant species. Advances in tracking technology have recently been made, including the development of the ICARUS and Motus projects (Taylor et al., 2017; https://www.icarus.mpg.de/en). Reductions in the cost and size of tags, the latter permitting their use on smaller birds, present one avenue to increase our knowledge of non-breeding distributions and migratory connectivity, as well as gain individual-level data (Finch et al., 2017; Jacobsen et al., 2017; Renfrew et al., 2013). The development of genoscapes, whereby breeding and non-breeding populations may be linked using genetic data, may also provide insights into connectivity, although this also requires sampling from across large portions of species' non-breeding ranges (Ruegg et al., 2020).This additional information could be used to increase our fine scale understanding of the impacts of environmental change on migratory birds and, therefore, inform the implementation of conservation measures to reverse the declines of migratory species. Given my findings, that similar processes drive population trends on both continents, similar conservation policy and action could be adopted in both flyways. This is likely to focus around climate adaptation on the breeding grounds, such as the protection of sites forecast to experience the least impacts from climate change and the identification of sites of microclimate refugia. On the non-breeding grounds, habitat must be protected from degradation, though the exact strategies for achieving this must also be explored further.

In conclusion, I have demonstrated that the populations of long-distance migratory birds across North America and Europe have declined at similar rates since 1980, whereas short-distance migrants have increase in North America and decreased in Europe. Most importantly, alongside habitat association, climatic change on the breeding grounds and land-use changes on the non-breeding grounds are important drivers of these trends on both continents. This is a major step towards understanding the global decline of migratory species and may provide a basis to implement similar conservation strategies on both continents. However, our understanding of the annual cycles of migratory species away from the breeding grounds remains limited and detailed research from these areas, in addition to information on habitat suitability for species in such areas, is needed.

Chapter 4

A global assessment of the potential impacts of climate change on bird migrations: changes to distance, stopover number and duration of journeys

The Barn Swallow *Hirundo rustica* - one of the most widely distributed migratory birds around the globe. Long-distance migratory populations of the Barn Swallow can be found in each of the Americas, Afro-Palearctic and Australasian flyways.

Photo credit: Jack Bucknall

4.1 Abstract

For long-distance migratory birds, whose breeding and non-breeding ranges are frequently in separate hemispheres, climate-change driven poleward shifts in species' ranges have been predicted to result in longer migratory journeys, necessitating more stopovers on migration and longer duration migrations. By contrast, breeding and non-breeding ranges of short-distance migrants are typically projected to shift in the same direction, resulting in only moderate changes to migratory distances and durations. However, to date a global assessment of the impacts of climate change on long-distance migratory journeys is lacking. Here, I address this omission, combining projections of species' range shifts with species-specific, maximum potential flight range data to simulate changes to migratory journeys over the 21st century for 298 species of long-distance migratory bird and 176 species of short-distance migratory bird, which are distributed across the globe. After validating simulated journeys against tracked journeys from published studies, I assess whether migration distance, stopover number, and overall journey duration are projected to change significantly over the century, comparing projected changes to migration for long- and short-distance migrants. I then compare the magnitude of such changes to migratory journeys across the three major migration flyways (Americas, Afro-Palearctic, and Australasian) and across three major taxonomic groups (passerines, shorebirds, and waterfowl), to assess which species groups are most at risk to these threats. I find that, globally, migration distances of long-distance, but not short-distance, migrants are predicted to increase significantly by the end of the century, with concurrent increases in the number of stopovers required on migration and the overall duration of the journey. These changes are predicted to be of the greatest magnitude in the Americas flyway, whilst passerines are predicted to see the largest increase in the number of stopovers. Such increases to the length of migratory journeys are likely to compound the current declines experienced by long-distance migratory birds, both through increases in mortality on migration and the exacerbation of phenological mismatch. My results highlight the additional threat posed by climate-change to long-distance migrants, compared to their resident and short-distance migratory counterparts, which will need to be incorporated into future conservation planning and research, if further declines in biodiversity are to be avoided.

4.2 Introduction

Climate change is now considered one of the leading drivers of recent biodiversity loss (IPBES, 2019). Range shift/loss and phenological mismatch are just two of the many climate change-driven impacts that have already led to population declines (Howard et al., 2020; Møller et al., 2008; Saino et al., 2011). Given global temperatures are set to rise by at least 1°C by the end of the century, assessment of the potential for further impacts on populations is needed (IPCC, 2021). This is especially important to enable the identification of taxa at greatest risk from these impacts and, consequently, to direct conservation efforts more effectively.

One group of species likely to be particularly impacted by climate change are long-distance migrants, which make annual movements between separate, usually very distant, breeding, and non-breeding areas. Their reliance on multiple, spatially segregated areas renders migratory species more vulnerable to environmental change than residents, due to the increased number of locations over which these threats may be encountered, and the need for resources to be available across connecting sites at the correct time of the migratory journey (Howard et al., 2018; Robinson et al., 2009). This increased general risk to migratory species is reflected in the population trends of long-distance migratory birds. Species that migrate from the Holarctic to the sub-tropics and tropics (i.e., inter-biogeographic realm migrants, but hereafter referred to as long-distance migrants) have declined more rapidly than both residents and species which migrate within the Holarctic (i.e., intra-biogeographic realm migrants, but hereafter referred to as short-distance migrants; Holt, 2000; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014). If these patterns are replicated globally, this has major implications on both global biodiversity and ecosystem service provisioning, given the significant number of the world's vertebrates that undertake annual long-distance migrations (Bairlein, 2016; Howard et al., 2020; Kirby et al., 2008; Wilcove & Wikelski, 2008), and that these species provide invaluable services (e.g. pest control, cultural services) across continents (Bauer & Hoye, 2014).

The distributions of numerous taxa have shifted poleward in response to climate change as species attempt to track their climatic niche (Chen et al., 2011; La Sorte & Thompson, 2007). Furthermore, the distributions of many bird species are predicted to continue to shift towards the poles due to further warming (Barbet-Massin et al., 2009, 2012). Whilst such changes impact all species, including resident and short-distance migratory birds, they bring additional threats to long-distance migrants. With their breeding and non-breeding distributions usually in different biogeographic realms, often on different continents, and not infrequently on different hemispheres, differing range shifts of breeding and non-breeding ranges could result in increased migration distances for long-distance migrants. This would be especially true for species with breeding and non-breeding range in different hemispheres, with their respective poleward range shifts in each area potentially shifting in opposite directions. Migration distances are likely to increase even for long-distance migrants whose ranges occur in the same hemisphere, as their breeding ranges occur at higher latitudes and such areas have experienced, and are projected to experience, more rapid warming than lower latitude areas (IPCC, 2021). This could result in range shifts of greater relative magnitude for breeding versus non-breeding ranges. This likely poses less threat to short-distance migrants, as both their breeding and non-breeding ranges are more closely co-located and, hence, are more likely to experience similar climatic, and consequently range changes.

In birds, longer migrations require additional fuel for flight, which may necessitate additional stopovers for refuelling. Therefore, the overall duration of journeys may increase due to any extra days spent at stopover sites to rest and refuel, but also through the increase in time required to fly between more separated breeding and non-breeding grounds. Mortality during migratory journeys is reportedly higher than at any other stage of the annual cycle of migratory species and, as such, any increase in duration is likely to have negative consequences for populations (Rushing et al., 2017; Sillett & Holmes, 2002). Furthermore, unless the timing of departure from non-breeding areas is advanced, longer durations of migration will result in delayed arrival on the breeding grounds. This may exacerbate phenological mismatch of breeding, which is already more severe in long-distance migrants than their resident and short-distance migratory counterparts, and could further impact the productivity of migrant populations (Both et al., 2010).

Existing projections of potential changes to migratory journeys have focused almost solely on the Afro-Palearctic flyway (Doswald et al., 2009; Howard et al., 2018; Visser et al., 2009). Generally, these projections have supported the hypothesis that trans-Saharan, i.e., long-distance, migrants are likely to face increased migration distances in future. However, despite an equal, if not greater, richness of long-distance migratory bird species in the Americas and Australasian flyways (Somveille et al., 2013), there have been few projections of climate change impacts on migratory journeys in these parts of the globe, or in other taxa. The only global study to my knowledge (Zurell et al., 2018) projected no consistent change to the migration distances of long-distance migrants of a variety of taxa across the Holarctic by 2041-60. However, the definition of a long-distance migrant used by this study (a minimum 10° latitudinal difference between breeding and non-breeding range centroids) would include intra-biogeographic realm migrants – species that would typically be classified as short-distance migrants. Therefore, the lack of a consistent change to migration distances could be the result of the amalgamation of changes to both long- and short-distance migrants. As such, the global pervasiveness of potential changes to the migratory journeys of long-distance migrants remains unclear. Clearly defining and separating these groups prior to projecting migratory journeys may reveal more obvious and significant trends.

Previous studies have also tended to focus solely on passerines, despite the prevalence of migration in other taxonomic groups, such as waders, waterfowl, and near-passerines. Furthermore, changes to migratory journeys may vary substantially between such groups, especially in terms of stopover number and duration of migration, as fat loading capabilities vary across taxa, enabling some species to fly for longer periods of time and distances without refuelling (Newton, 2010). This may allow such species to complete longer migrations without the need to take extra refuelling stopovers. Therefore, a lack of consideration of these additional species may lead to predictions that are not representative of all long-distance migrants.

Here, I assess the potential impact of climate change on the migratory journeys of 464 species of migratory bird, from 14 taxonomic orders. These species are globally distributed and consist of 322 flyway-specific populations (defined below) of long-distance migrant, those species that migrate between the temperate and tropical realms, and 270 flyway-specific populations of short-distance migrant, those species that migrate within the temperate realms. This represents the vast majority the world’s “fully” migratory birds, i.e., those with spatially distinct breeding and non-breeding grounds. I build species distribution models for each species’ breeding and non-breeding range separately and project these to mean climate data for recent (1950-2000) and future (2060-2080) periods. I estimate species-specific flight ranges using species’ physiological and morphological traits in flight range equations. Combining this information with projections of breeding and non-breeding ranges, I simulate migratory journeys for individuals of each migratory population during the recent and future time periods. These migration simulations are validated using data from published tracking studies. I explore changes in migratory distance, stopover number and overall duration of journeys between the two time periods, for long- and short-distance migrants, to produce a first global synthesis of current and future migrations of birds across the three major terrestrial migration flyways and three major taxonomic groups (passerines, shorebirds, and waterfowl).

4.3 Materials and methods

4.3.1 Species data and migratory status

Breeding and non-breeding distribution range data were derived from range polygons for 1,675 terrestrial bird species that are classified as a "full migrant" by Birdlife International and NatureServe (2016). These are species for which "a substantial proportion of the global or regional population makes regular or seasonal cyclical movements beyond the breeding range, with predictable timing and destinations", i.e., excluding altitudinal migrants, nomadic and irruptive species. Of these, species that utilise soaring flight for a significant portion of their migratory journey (storks, raptors etc.) were excluded, due to issues with estimating the energetic requirements for such flight styles, leaving 1,151 species. Breeding and non-breeding polygons for all the latter species were intersected with a 0.5^o x 0.5^o grid and were classed as present if the polygon overlapped with 10% or more of a cell.

Some species occur across the globe but, within the species, different populations typically migrate within specific flyways, i.e., specific routes between breeding and non-breeding locations shared by multiple species. Without separating these distinct populations, I risked simulating unrealistic migrations (e.g., a Barn Swallow *Hirundo rustica* migrating from Europe to South America, rather than the actual European-African migration undertaken by the European breeding populations) and would also be unable to compare changes to migratory journeys between flyways. Therefore, I divided species' ranges into separate populations following the Americas, Afro-Palearctic and Australasian flyway definitions of Chapter 3 (**Table 1**, Appendix Figs. S10 & 11).

There were four possible ways to define the migratory populations of a species using this system of flyway delineations. (1) Single-flyway species (n = 858) – e.g., Marsh Warbler *Acrocephalus palustris* – whose breeding and non-breeding ranges occur exclusively in the same flyway and the species migrates entirely within this flyway. (2) Multi-flyway species (n = 190) – e.g., Barn Swallow *H. rustica* – whose breeding and non-breeding ranges occur in the same two or all three flyways. For such species, I linked the breeding and non-breeding ranges for each 'population' using a distinct flyway. (3) Trans-flyway species (n = 103) – e.g., Northern Wheatear *Oenanthe oenanthe* – whose breeding range occurs exclusively in one flyway but with at least part of the non-breeding range in a different flyway, or vice versa. In both scenarios, I linked the entirety of the breeding and non-breeding ranges as one population but (as described below) excluded such species from analyses comparing the three flyways. (4) Multi-trans-flyway species (n = 5) – e.g., Bar-tailed Godwit *Limosa lapponica* – whose breeding and non-breeding ranges span multiple flyways but whose 'populations' do not follow discrete flyways connecting breeding and non-breeding ranges, e.g., the breeding range of the Bar-tailed Godwit *L. lapponica* spans all three flyways, but the non-breeding range occurs only in the Afro-Palearctic and Australasian flyways. Multi-trans-flyway species, of which there were only five, were excluded from the study, as were unable to differentiate migratory populations and, therefore, could not accurately simulate migratory journeys.

Table 1. *Longitudinal boundaries of the three main migration flyways and, following my definitions of migratory status, the numbers of migrants classified as long- and short-distance migrants in each of the four flyway categories. Numbers in brackets represent the number of migrants in each category for which the breeding and non-breeding ranges are entirely separate.*

Flyway	**Longitudinal Boundary**		**Long-distance migrants**	**Short-distance migrants**
	West	**East**		
Americas	170ºW	30ºW	71 (64)	96 (52)
Afro-Palearctic	30ºW	65ºE	48 (40)	36 (18)
Australasian	65ºE	170ºW	140 (96)	55 (36)
Trans-flyway	NA	NA	64 (54)	13 (8)

I excluded any species' population for which the area of the overlapping region of the breeding and non-breeding ranges accounted for more than 20% of either range. This was to reduce the likelihood of simulating unrealistic migrations within these "resident" portions of the species' range and exclude any "partial" migrants, i.e., species that consist of some migratory and some non-migratory populations. This threshold of 20% was set as many species that have small portions of overlapping ranges are still regularly considered as long- or short-distance migrants (e.g. see species lists of Robbins et al. (1989) and Sanderson et al. (2006)) and, therefore, merit inclusion in these projections. To assess the impact of including species with some overlapping breeding and non-breeding range, I also created a further refined species list which included only species for which the breeding and non-breeding ranges did not overlap at all (**Table 1**). I undertook all further analyses on both datasets. However, as there were no substantial differences between the results, I include only analyses for the fuller species list here (for analyses using the restricted species list, see Appendix Tables S35-40 and Fig. S18).

Different studies have typically used different definitions of long-distance migration in birds. However, a global study, such as being conducted here, requires a definition that is robust across regions. Modelling migration for species that migrate within the tropical continents (i.e., South America, Africa, Australasia and Oceania) is difficult, due to their less inter-annually predictable distributions and itinerant or nomadic migratory behaviours (Barshep et al., 2017; Faaborg et al., 2010; Jahn et al., 2020). Therefore, I excluded any species for which less than 80% of their breeding range was within the Holarctic (defined as the amalgamation of the Nearctic, Palearctic, Saharo-Arabian, and Sino-Japanese realms from Holt et al. (2013); Appendix Fig. S9). For the remaining species, i.e. those that breed within temperate areas, whilst there is a lack of an agreed upon definition for “long-distance” migrants, most studies refer to those species that spend the non-breeding period in the tropics (Holmes & Sherry, 2001; Holt, 2000; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014). In contrast, “short-distance” migrants are those that remain within the Holarctic during this period. Therefore, I defined long-distance migrants as those with at least 80% of their non-breeding range within the tropics (defined as the amalgamation of the Panamanian, Neotropical, Afrotropical, Madagascan, Oriental, Oceanian, and Australian realms from Holt et al. (2013); Appendix Fig. S9). Short-distance migrants were then defined as those species with less than 50% of their non-breeding range in the tropics, i.e., most of this range is found within the Holarctic. I excluded the remaining species (with between 50 and 80% of the non-breeding range in the tropics), as they likely consist of populations with numerous migratory strategies and such species are often classified as both long- and short-distance migrants in different studies (J. P. Holt, 2000; Robbins et al., 1989; Sanderson et al., 2006; Vickery et al., 2014).

As species may have long-distance migratory populations in one flyway but short-distance migratory populations in others, I calculated the degree to which the breeding and non-breeding ranges overlapped separately for each flyway population. I did the same to estimate the extent to which each of these flyway-specific distributions overlapped with the Holarctic/tropics. Using these criteria, 298 species, consisting of 323 flyway populations, were classified as long-distance migrants and 176 species, consisting of 200 flyway populations, were identified as short-distance migrants (**Table 1**).

4.3.2 Species distribution projections

I modelled the relationship between each species’ global distribution and five bioclimatic variables. Models were built separately for breeding and non-breeding distributions, with the bioclimatic variables used to model these distributions downloaded from WorldClim (Hijmans et al., 2005). These were average values over the period 1950-2000 (hereafter referred to as “2000”), at a 2.5’ resolution. I intersected the data with the same 0.5^{o} x 0.5^{o} grid that was intersected with species distributions and applied bilinear interpolation using the “resample” function in the “raster” package in R to assign values to cells (Hijmans et al., 2014).

Selection of the specific bioclimatic variables used to model species distributions followed the methods of Titley et al. (2021). I first generated all possible combination of eight bioclimatic variables which have previously been found to predict the distributions of species well (bioclimatic variables 1, 4, 5, 6, 12, 13, 14 and 15). Any combinations containing less than three variables overall or that did not contain at least one temperature and one rainfall variable were removed. I then removed any combinations in which two variables were highly correlated ($r > 0.7$), leaving 38 candidate combinations. Each of the remaining combinations were used to build a Generalized Additive Model (GAM), using the same methodology as in Chapter 3, for all 464 of my study species. Model sets for each species were then ranked by Akaike Information Criterion and the best combination, and that which was used to fit species distribution models (SDMs), was identified as that which occurred in the top quartile of ranked combinations most often – this being mean annual temperature, temperature seasonality, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality. Appendix Tables S21 and 22 show the number of times each combination occurred in the top quartile of species' model sets, for the breeding and non-breeding ranges.

I utilized the same ensemble modelling framework as in Chapter 3, combining GAMs, Generalized Linear Models (GLMs), Generalized Boosted Regression Models (GBMs) and Random Forests (RFs; Bagchi et al., 2013). To provide the models with meaningful absence data, I excluded climatic data from any biogeographic realm in which the modelled species did not occur (following the definitions of Holt et al., 2013). To deal with issues associated with spatial autocorrelation I used the "blocking" and model performance assessment methods of Chapter 3 (Bagchi et al., 2013).

Future projections of the five bioclimate variables used to model species distribution were downloaded from WorldClim (Hijmans et al., 2005). These were average values over the period 2061-2080 (hereafter referred to as 2070), at a 2.5' resolution. Projections covered three general circulation models (GCMs; CCSM4, HADGEM2-ES and MIROC-ESM-CHEM) and four representative concentration pathways (RCPs; 8.5, 6.0, 4.5 and 2.6), together making up 12 climate scenarios. I intersected the data with the same 0.5^o x 0.5^o grid that was intersected with current climate data and applied bilinear interpolation using the "resample" function in the "raster" package in R to assign values to cells (Hijmans et al., 2014).

For each species, I used the SDMs to predict the probability of occurrence of the species in each 0.5^o x 0.5^o cell for the year 2000 climate, as well as for the 12 climatic scenarios (3 general circulation models x 4 representative concentration pathways) for 2070. For each cell, the median suitability across the 40 models was calculated for 2000, and across the 40 models and 12 climatic scenarios for 2070. A threshold was then applied to these median suitability values, to convert them to presence/absences, giving a predicted distribution for 2000 and 2070. This threshold was set to maximise agreement between observed and predicted presence/absence values, based on maximum kappa (Freeman & Moisen, 2008). Thresholds were calculated separately for breeding and non-breeding distributions.

As similar climates may occur on opposite sides of the equator, species distributions may be projected to occur in areas of the opposite hemisphere to that in which the species spends the breeding (or non-breeding) season. This mirrored climate effect is equally like to occur in present day (2000) or future (2070) projections. To deal with this, projections were restricted to the biogeographic realms in which the species currently occurs and those immediately adjacent, thus still enabling species ranges to expand in a biologically realistic manner (Holt et al., 2013).

I analysed whether breeding and non-breeding ranges were predicted to shift in different directions, separately for each of the three major flyways, and for long- and short-distance migrants. I calculated range centroids for current and future distribution, as well as the bearing and geodesic distance between the two, for each species using the R package "geosphere" (Hijmans, 2015). I used a circular ANOVA, using the R package "circular" (Lund et al., 2022), to compare the directions of predicted shifts in the centroids of breeding and non-breeding ranges between 2000 and 2070. Additionally, for long- and short-distance migrants in each flyway, I calculated the mean shift in latitude and longitude of breeding and non-breeding range centroids across all species in each group and, from this, calculated the bearing and geodesic distance of the mean shift.

4.3.3 Flight range estimations

I estimated the potential flight ranges of each species, using the program Flight 1.25 (https://booksite.elsevier.com/9780123742995/; Pennycuick, 2008). Flight range calculations were based on species-specific measures of wingspan, wing area, fat-free body mass and levels of fat reserves. I estimated the maximum distance and time that an individual could fly in still air conditions at an altitude of 500m, a commonly cited migration altitude (Howard et al., 2018; Newton, 2008, 2010), before depleting 95% of a given starting fat reserve.

Where possible, wingspan and wing area measurements were extracted from various literature sources (Appendix Table S23). For species for which wingspan measurements could not be sourced in the literature (83 species, 18%), I estimated values using phylogenetic multiple imputation, through the R package "Rphylopars" (Ellington et al., 2015; Goolsby et al., 2017; Penone et al., 2014). In addition to the wingspan data of all migratory land birds for which I was able to source published data (706 species; Appendix Table S23), I included the Kipp's distance and wing chord (Appendix Table S23; Tobias et al., 2022), body mass and migration distance for each species, to improve the accuracy of the imputation. Migration distance was included as species which migrate further typically have longer and thinner wings (Bowlin & Wikelski, 2008) and was calculated as the geodesic distance between the breeding and nonbreeding range centroids, using the R package "geosphere" (Hijmans, 2015). For species that had populations in multiple flyways, I calculated this distance in all flyways and used the mean of these values. For each species, I imputed the wingspan 1000 times, utilising a different sample of the posterior distribution produced by Jetz et al. (2012) each time, and calculated the mean wingspan value. To assess the accuracy of this procedure, I replicated it on species for which I had wingspan data. I first randomly removed wingspan estimates for 18% of species, in line with the percentage missing from the actual dataset, and then ran the imputation. I found that this method produced accurate estimates of wingspan (least squares regression: $R^2 = 0.97$, $n = 127$; Appendix Fig. S12).

For species for which I could not find published wing area measurements (378 species, 81%), I utilised the formula developed by Howard et al. (2018), which can accurately predict wing area from wingspan, wing chord and Kipp's distance measurements (Fig. S13; Appendix Table S23). First, carpal length (Figure S13) was estimated as:

$$\text{Carpal length} = \frac{\text{wingspan} - (2 * \text{primary wing chord})}{2}$$

Wing area was then estimated using:

$$\text{Wing area} = 2 * \left[(\text{carpal length} * \text{secondary length}) + \left(\frac{\text{primary wing chord} * \text{secondary length}}{2}\right)\right]$$

Body mass for all species were obtained from Dunning (2007; Appendix Table S23). As post-stopover fat loads are likely to differ from the fat loads at the very start of migration for many species, I estimated two separate maximum potential flight ranges for each species – an initial departure flight range and a post-stopover flight range. To do so, I extracted typical pre-departure fat loads, daily refuelling rates and stopover lengths from various literature sources (Appendix Table S23). Post-stopover fat loads were then calculated by multiplying daily refuelling rates and stopover lengths for each species. Such data are not readily available for many species, so values were assigned based on broad taxonomic groupings (orders or, where finer separation was deemed appropriate, families). Nevertheless, for some species, all large non-passerines, data from a close relative were not available. For these species, I assigned a pre-departure fat load of 20% of fat-free body mass and refuelling rate of 2% of fat-free body mass per day, as these represent average fat loading figures for larger non-passerines (Newton, 2010).

4.3.4 Simulating migratory journeys

To simulate migration for each species (or flyway-specific population for species using more than one flyway), I first selected a migration destination site (breeding range) and a migration initiation site non-breeding range, within the respective flyway. Selection of these sites (cells) was weighted by the probability of a species occurrence across all cells within their respective breeding or non-breeding range, with probability derived from the predictions of cell suitability from SDMs. I calculated the migration distance as the geodesic distance between these two points, using the R package "geosphere" (Hijmans, 2015). This 'straight-line' migration may be likened to pre-breeding migration, during which it is assumed that individuals make the fewest deviations from a straight path, to arrive on the breeding grounds as early as possible (Horton et al., 2016). I repeated this process 1000 times for each flyway-specific population.

Using the species-specific flight range data, each migration was divided into a journey consisting of an initial departure flight, any necessary refuelling stopovers, and associated post-stopover flights. For each individual simulation, the number of stopovers taken to complete the migration was recorded. As each leg of the migratory journey has an associated duration (based on flight speed of the individual species), I was able to calculate the total time in flight. I also calculated the number of days required to complete the in-flight portions of a complete migration by dividing the total flight hours by the number of hours a species could migrate each day. From the literature, species were classified as migrating nocturnally, diurnally, or showing no preference (Appendix Table 23). Where I could not find a classification within the literature (14/464 species), I assigned species to the category to which most species in the same family (6 spp.) or order (8 spp. for which there were no other species in the same family with circadian migratory data) were classified. Nocturnal migrants were assigned to migrate for 9 hours per day, whereas diurnal species, as well as those showing no preference, could migrate for 15 hours per day – these figures representing approximate day and night lengths during spring migration (Howard et al., 2018). Finally, combining these flight days with the number of days spent on refuelling stopovers (calculated by multiplying the number of stopovers by the species-specific stopover lengths) gave the total duration of the migratory journey.

Where possible, I validated simulations of migration using published tracking studies that provided details on tracked migration distance, estimated stopover number and overall duration of migration. I used Mann–Whitney U tests to compare empirical migration distances, stopover numbers and overall durations for individual species with a random sample of equal size from the 1000 migration simulations of each flyway population of those same species. I repeated this comparison procedure 1000 times for each flyway population and the mean test statistics were calculated and are reported here. I used published tracking data only from studies of pre-breeding migratory journeys (i.e., in the boreal spring), as these are likely to be most similar to straight-line simulations. I also only included species in validation tests for which published data were available for at least 6 journeys. Published tracking data that satisfied these criteria were available for 27 species (see Appendix Table S24).

4.3.5 Analyses to changes in migratory journeys

To analyse whether migratory journeys are predicted to change globally by the end of the century, I first tested for changes in migration distance, stopover number and duration between 2000 and 2070, for each species (or flyway-specific population), using unpaired t-tests on the 1000 migration simulations for the population in each period. Additionally, to assess whether these metrics had changed on average across the globe, I utilised phylogenetic linear mixed models (PLMMs) to explore changes among populations over time. I used PLMMs as migratory traits might not be phylogenetically independent. I fitted PLMMs with either (1) mean migration distances, (2) stopover numbers or (3) migratory durations, for all populations, as a continuous response variable and the time periods, 2000 and 2070, as a categorical predictor variable, using the R package “MCMCglmm” (Hadfield, 2010). In all PLMMs, the species ID and the phylogeny were included as random effects, the former to ensure these were paired analyses. The phylogeny was the same as used to impute species wingspan data. I used an uninformative, inverse Wishart distribution as a prior for both the random effects and residual variance. To fit the model, I ran an MCMC chain for at least 200,000 generations, recording model results every 1000 generations and ignoring the first 2000 generations as burn-in. I fitted each model four times and merged the four chains after verifying convergence using Gelman-Rubin diagnostics in the R package “coda” (Plummer et al., 2006). I also visually inspected trace plots for each model to verify model convergence.

I tested for differences in changes to migration distance, stopover number and duration between the three major flyways (Americas, Afro-Palearctic and Australasian) in both long- and short-distance migrants but excluded trans-flyway species that utilise multiple flyways within one migration. I also compared changes to migration distance, stopover number and duration across the major taxonomic orders, including orders that contained more than 30 species to enable to the use of PLMMs. As a result, for long-distance migrants I compared changes to the migratory strategies of Passeriformes (passerines) and Charadriiformes (shorebirds), and for short-distance migrants I compare Passeriformes and Anseriformes (waterfowl). To test for differences in changes to migratory journeys between flyways or taxonomic groups, I fitted zero-intercept PLMMs with either mean changes in migration distance, stopover number, or duration as the response variable and either flyway or taxa as the predictor variable, depending on the specific analysis. I analysed flyway and taxonomic groups separately to enable identification of the broadest groups most at risk to the impacts of climate change on migratory journeys. By doing so, I risked identifying spurious differences if taxa and flyway were correlated. To test for this, I performed chi-squared tests and found that for both long-distance ($X^2 = 2.63$, df = 2, $p = 0.27$) and short-distance migrants ($X^2 = 5.13$, df = 2, $p = 0.08$) there was no significant association between the flyways and taxonomic groups. I assessed the performance of each model by calculating conditional R^2 following the methods of Nakagawa & Schielzeth (2013).

I calculated the change in mean migration distance between 2000 and 2070 for each population in the three major flyways, i.e., not including trans-flyway migrants, and used this to calculate the mean change in migration distance across all species currently occurring in each 0.5^o cell across the globe. Values for the mean change in migration distance in each cell were then clustered using the Jenks natural breaks method in the R package “classInt” (Bivand et al., 2023). I plotted these values for all cells (though excluded cells with fewer than 3 species simulated).

4.4 Results

4.4.1 Species distribution models and projections

Projections indicated that, based on climatic factors alone, 13 species will be committed to losing the entirety of at least one of their climatically suitable breeding or non-breeding ranges across the globe, and therefore go extinct, by 2070. Using the median projection across all 2070 climate scenarios, I found that 12 populations of long-distance migrant and 6 populations of short-distance migrant were projected to lose the entirety of either the breeding or non-breeding range, within their respective flyway (**Table 2**). All populations, except the Long-toed Stint *Calidris subminuta*, are either distributed north of 64°N, so likely have no landmass to the north available for future colonisation, or have small existing ranges (less than 330,000km^2), for which the limited combinations of climatic variables are not predicted to occur in 2070. *C. subminuta* is patchily distributed across Asia, so despite having a slightly larger overall range, the species is made up of ~10 populations for which range extent is much smaller.

Table 2. *Long- and short-distance migratory populations which are projected to lose the entirety of at least one of their breeding or non-breeding range by 2070, in each of the major flyways. Bold species names indicate species which lose range in all flyways in which they are present and, therefore, projected to go globally extinct. Also presented are the latitudinal centroids and overall size of the seasonal range projected to disappear.*

Species	**Flyway**	**Migratory status**	**Seasonal range lost**	**Centroid latitude**	**Range size (km^2)**
Allen's Hummingbird *Selasphorus sasin*	Americas	Short-distance	Non-breeding	9°S	82,000
Black Turnstone *Arenaria melanocephala*	Americas	Short-distance	Breeding	66°N	365,000
Golden-cheeked Warbler *Setophaga chrysoparia*	Americas	Long-distance	Breeding	31 °N	54,000
Kirtland's Warbler *Setophaga kirtlandii*	Americas	Long-distance	Breeding	45 °N	38,000
Aquatic Warbler *Acrocephalus paludicola*	Afro-Palearctic	Long-distance	Breeding	52 °N	330,000

Greater White-fronted Goose *Anser albifrons*	Afro-Palearctic	Short-distance	Breeding	70 °N	698,000
Little Stint *Calidris minuta*	Afro-Palearctic	Long-distance	Breeding	69 °N	613,000
Pink-footed Goose *Anser brachyrhynchus*	Afro-Palearctic	Short-distance	Non-breeding	54 °N	190,000
Chinese Leaf-warbler *Phylloscopus yunnanensis*	Australasia	Long-distance	Non-breeding	19 °N	228,000
Emperor Goose *Anser canagicus*	Australasia	Short-distance	Non-breeding	54 °N	123,000
Little Curlew *Numenius minutus*	Australasia	Long-distance	Breeding	68 °N	1,279,000
Red Knot *Calidris canutus*	Australasia	Long-distance	Breeding	74 °N	1,098,000
Sanderling *Calidris alba*	Australasia	Long-distance	Breeding	76 °N	690,000
Sharp-tailed Sandpiper *Calidris acuminata*	Australasia	Long-distance	Breeding	71 °N	684,000
Silver Oriole *Oriolus mellianus*	Australasia	Long-distance	Breeding	27 °N	97,000
Long-toed Stint *Calidris subminuta*	Trans-flyway	Long-distance	Breeding	57 °N	603,000
Bristle-thighed Curlew *Numenius tahitiensis*	Trans-flyway	Long-distance	Breeding	64 °N	104,000
McKay's Bunting *Plectrophenax hyperboreus*	Trans-flyway	Short-distance	Breeding	55 °N	36,000

Species distribution models for the 464 species of migratory bird performed well when fitted to both breeding (mean AUC: 0.96 ±0.032) and non-breeding distributions (mean AUC: 0.94 ±0.048).

4.4.2 Predicted range shifts

In all three flyways, the average breeding range shift of long-distance migrants was projected to shift in a north or north-westerly direction, whereas, on average, non-breeding ranges shifted to the south-east (**Fig. 1a, c & e**). This pattern appears stronger in the Americas and Afro-Palearctic flyways than in the Australasian, where the non-breeding ranges of many species are also projected to shift in a north/north-westerly direction. However, in general, I found a significant difference between the mean direction of projected shifts in the breeding and non-breeding range centroids of long-distance migrants in all three flyways: Americas (circular ANOVA: $F_{1,136} = 206$, $p < 0.001$), Afro-Palearctic (circular ANOVA: $F_{1,90} = 100.2$, $p < 0.001$) and Australasian (circular ANOVA: $F_{1,266} = 26.8$, $p < 0.001$).

Projected average breeding and non-breeding range shifts of short-distance migrants occurred broadly in the same direction (**Fig. 1b, d & f**), although the non-breeding ranges of a small subset of species in the Americas flyway are projected to shift to the south-east, as opposed to the general north/north-easterly shift of the breeding ranges. However, the mean direction of projected centroid shifts for short-distance migrants did not significantly differ between the breeding and non-breeding ranges, in all three flyways: Americas (circular ANOVA: $F_{1,186} = 0.37$, $p = 0.54$), Afro-Palearctic (circular ANOVA: $F_{1,66} = 0.02$, $p = 0.88$) and Australasian (circular ANOVA: $F_{1,106} = 1.01$, $p = 0.32$).

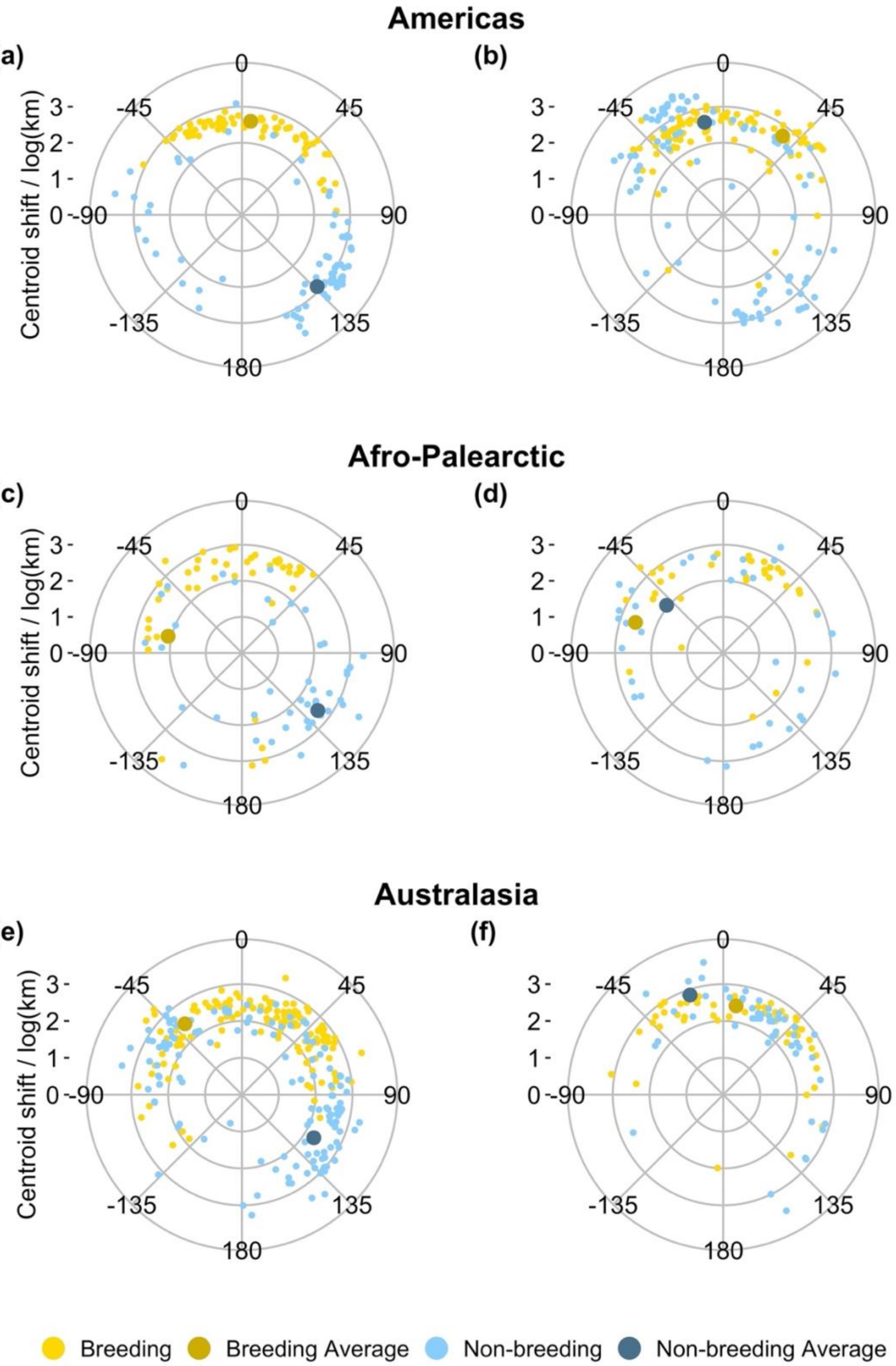

Figure 1. *Projected direction and distance of breeding (yellow) and non-breeding (blue) range centroid shifts between 2000 and 2070, for* ***(a, c & e)*** *long- and* ***(b, d & f)*** *short-distance migrants in each of the Americas (n = 69 and 94, respectively), Afro-Palearctic (n = 46 and 34, respectively) and Australasian (n = 134 and 54, respectively) flyways. Each point represents the 2070 range centroid of an individual flyway population, with the centre of the plot representing the 2000 range centroid. The larger and darker points*

show the mean breeding and non-breeding shifts, calculated as the bearing and geodesic distance of the mean change in centroid latitude and longitude across all long- or short-distance migrants in each flyway.

4.4.3 Validation of migratory journey simulations

Estimates of migration distance did not differ significantly from those from tracking studies for 75% (9/12 published examples) of populations for which I had data were found. I overestimated the mean migration distances of two populations and underestimated that of one population (Appendix Table S25, Fig. S14). I predicted the number of stopovers on migration slightly less well, with estimates from 64% (7/11 published examples) of populations accurate when compared with stopover numbers from tracking data. Stopover number was significantly overestimated for one population and underestimated for three (Appendix Table S26, Fig. S15). Overall durations of migration from tracked studies did not differ significantly from my estimates for 70% (14/20) of populations. The migratory durations of two populations were overpredicted and underpredicted for four populations (Appendix Table S27, Fig. S16).

4.4.4 Potential impacts on global migratory journeys

I predict that the mean migration distance of the 311 populations of long-distance migratory birds across the globe will increase by 336km, on average, between 2000 and 2070 (**Figure 2a**; PLMM: $L_{95} = 203.2$, $U_{95} = 473.5$, $R^2 = 0.87$). Specifically, t-tests on the 1000 migration replicates for each population indicated that, under my distribution projections, migration distance will increase significantly for 64% of these populations (Appendix Table S28). In contrast, I found no significant difference between the mean predicted migration distance in 2000 and 2070 for the 194 populations of short-distance migrants (PLMM: $\beta = -191.3$, $L_{95} = -402.7$, $U_{95} = 25.1$, $R^2 = 0.7$). I found that migration distances are predicted to increase significantly for 46% of these populations and to decrease significantly for 42% (Appendix Table 28).

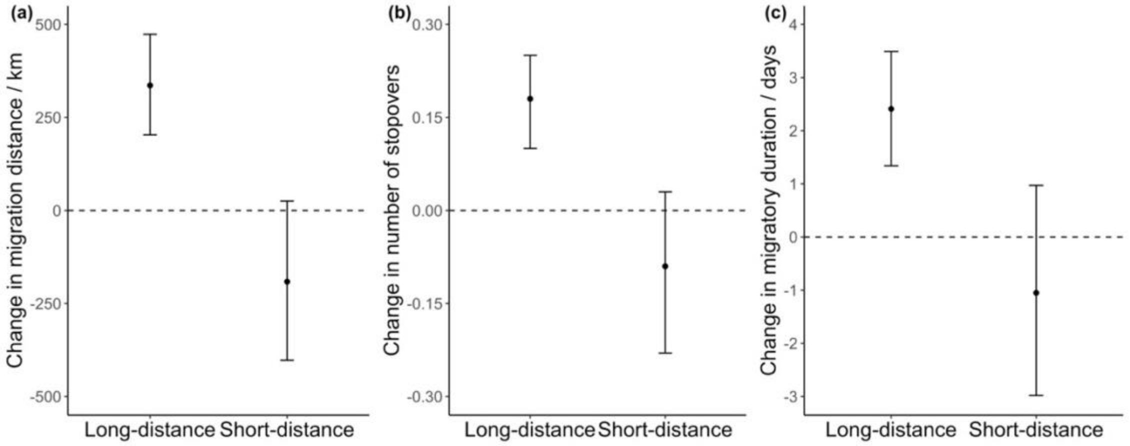

Figure 2. *Effect sizes from PLMMs, representing changes in mean predicted* ***(a)*** *migration distance,* ***(b)*** *stopover number and* ***(c)*** *migratory duration between 2000 and 2070 for long- (n = 311) and short-distance (n = 194) migratory birds. Error bars represent the upper and lower 95% confidence intervals.*

In line with increases in migration distance, the mean number of stopovers that long-distance migrants are required to make on migration is also predicted to increase significantly by 2070 (**Figure 2b**; PLMM: $\beta = 0.18$, $L_{95} = 0.1$, $U_{95} = 0.25$, $R^2 = 0.87$), with 62% of populations stopping over more regularly in migration simulations at the end of the century than in those at the start of it (Appendix Table S29). T-tests on the 1000 migration replicates for each population indicated that the average journey would require at least one whole additional refuelling stopover for 7% of long-distance migratory populations in 2070, compared to 2000. Furthermore, the mean duration of long-distance migratory journeys is predicted to increase significantly between 2000 and 2070 and I predict that, on average, long-distance migratory journeys will take 2.41 days longer by the end of the century across the globe (**Figure 2c**; PLMM: $L_{95} = 1.34$, $U_{95} = 3.49$, $R^2 = 0.87$).

In contrast, I predict that the mean stopover number (PLMM: $\beta = -0.09$, $L_{95} = -0.23$, $U_{95} = 0.03$, $R^2 = 0.8$) and overall duration (PLMM: $\beta = -1.05$, $L_{95} = -2.98$, $U_{95} = 0.97$, $R^2 = 0.8$) of short-distance migratory journeys will not change significantly over the same period. Significant rises in stopover number are predicted for 41% short-distance migratory populations however significant falls are predicted for 42% of populations (Appendix Table S29). Similarly, I predict that migratory duration for 45% of these same populations will increase significantly but decrease significantly for 41% (Appendix Table S30).

4.4.5 Comparing changes across flyways & taxa

I predict that mean migration distances of long-distance migratory populations will increase significantly in all three of the major global flyways between 2000 and 2070 (Table S31). These predicted increases are significantly greater in the Americas than those in either the Afro-Palearctic or Australasian flyways (**Fig. 3a**), with a mean increase of 1001km compared to 447km and 309km, respectively.

Figure 4 shows the mean change in migration distance between 2000 and 2070 in each 0.5^o cell across the globe. Whilst increases in mean migration distance are predicted for species occurring in most cells globally, these are greatest for species breeding in central North America and/or spending the non-breeding period in central America or southern South America. Additionally, the migration distances of species breeding in a small area of southern China/northern Indochina and/or moving to eastern Australia for the non-breeding period are also predicted to increase greatly. In contrast, I found the smallest mean increases in species that breed in the northern Palearctic and/or spend the non-breeding period in the western Palearctic. Species spending the non-breeding period in and around equatorial Africa and Asia are also predicted to see comparatively little change to their migration distances.

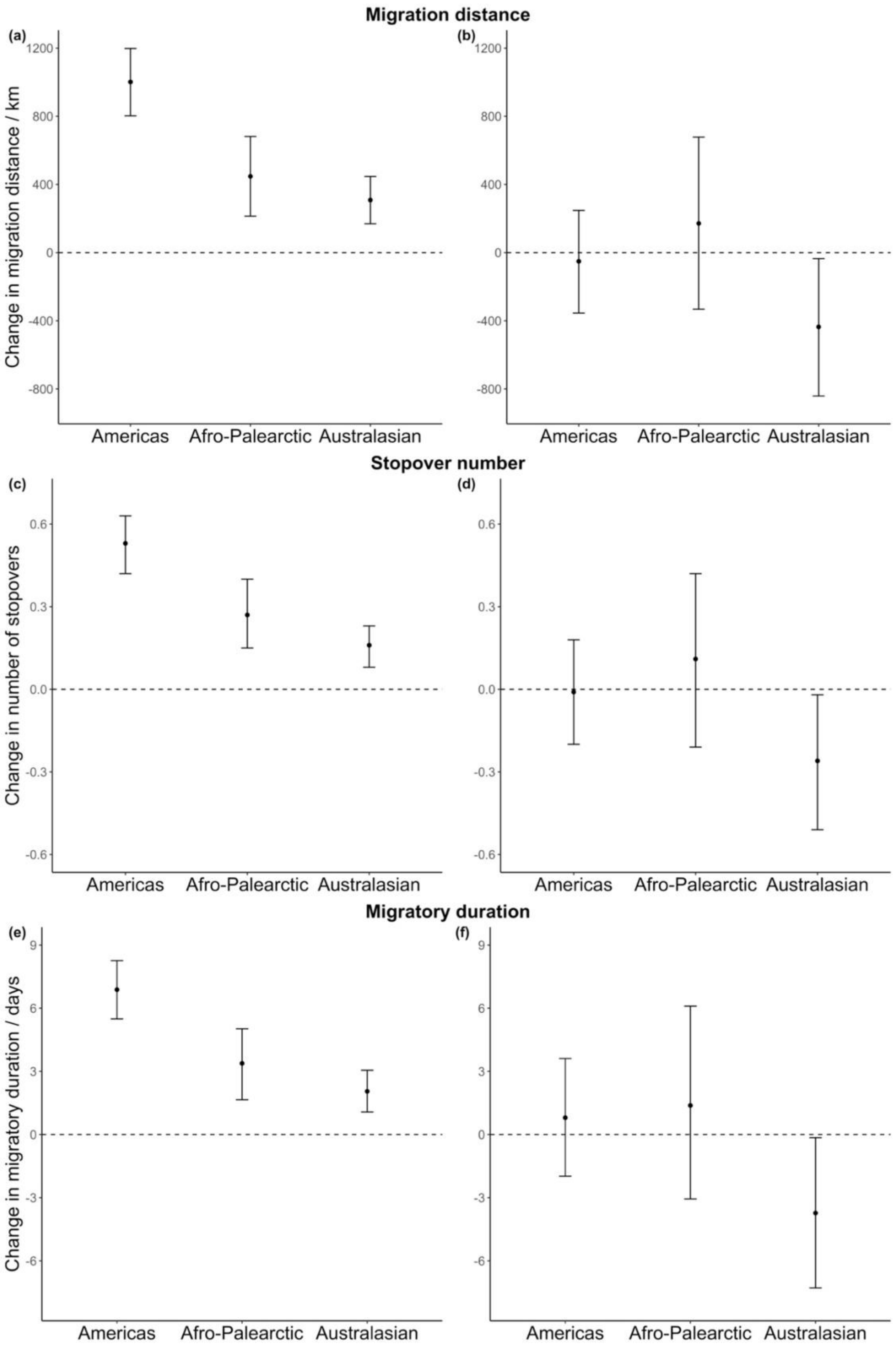

Figure 3. *Effect sizes from PLMMs, representing changes in mean predicted* ***(a & b)*** *migration distance,* ***(c & d)*** *stopover number and* ***(e & f)*** *migratory duration between 2000 and 2070. These are presented for long-* ***(a, c & e)*** *and short-distance* ***(b, d & f)*** *migratory birds in each of the Americas (n = 69 and 94, respectively), Afro-Palearctic (n = 46 and*

34, respectively) and Australasian (n = 134 and 54, respectively) flyways, separately. Error bars represent the upper and lower 95% confidence intervals.

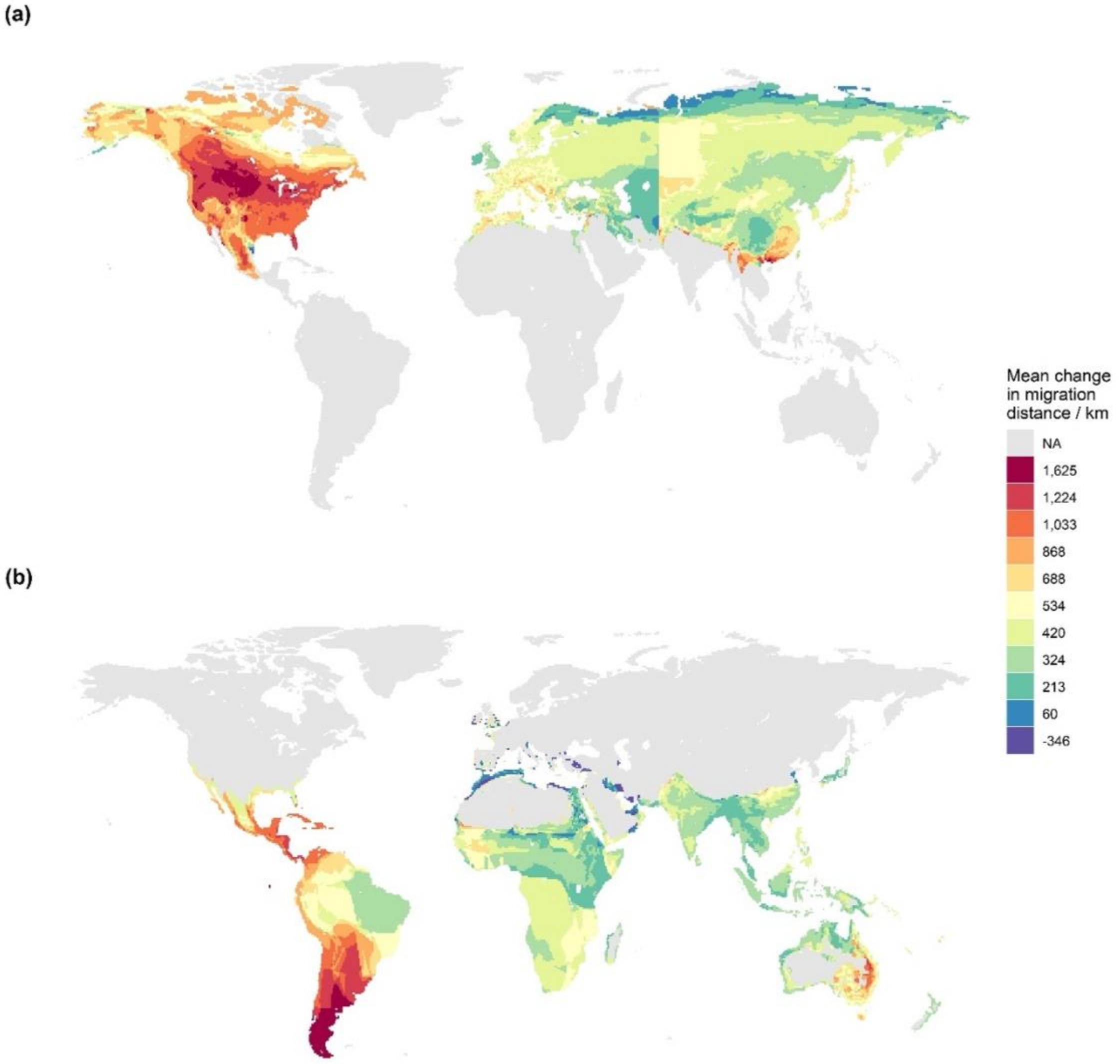

Figure 4. *Global mean changes in the migration distance of long-distance migrants. Colours represent the mean difference in simulated migration distance between 2000 and 2070, averaged across all species (excluding trans-flyway migrants) present in a grid cell during the* ***(a)*** *breeding and* ***(b)*** *non-breeding seasons at the present day. Values are grouped using Jenks natural breaks and the value associated with each colour represents the maximum value of each grouping, with the minimum value -1206km. NA represents cells with less three species present.*

Mean stopover number and migratory duration of long-distance migrants are also predicted to increase significantly in all three flyways by the end of the century (Appendix Table S31). As with migration distance, predicted increases in stopover number are significantly greater in the Americas than in either the Afro-Palearctic or Australasian flyways (**Fig. 3c**). 87% of populations in the Americas are predicted to, on average, require a significantly greater number of stopovers in 2070 than in 2000, compared to 72% and 62% in the Afro-Palearctic and Australasian flyways, respectively. Increases in overall migratory duration within the Americas (6.9 days) were significantly greater than those within the Afro-Palearctic (3.4 days) and Australasian flyways (2.1 days; **Fig. 3e**).

The mean predicted migration distance, stopover number and migratory duration of short-distance migrants are not predicted to change significantly between 2000 and 2070 within the Americas or Afro-Palearctic flyways (Appendix Table S32). However, I predict significant decreases in all three of these migration metrics for short-distance migrants following the Australasian flyway (**Fig. 3**). On average, these migratory journeys will be 436km shorter and take 3.7 days less. Furthermore, significantly fewer numbers of stopovers will be required to complete such migratory journeys for 44% of these species.

The mean migration distance, stopover number and overall duration of long-distance migratory journeys undertaken by both shorebirds and passerines are predicted to increase significantly between 2000 and 2070 (Appendix Table S33). The magnitude of these increases in migration distance and duration did not differ significantly between the two taxa, however predicted increases in the number of stopovers were significantly greater for passerines than shorebirds (Appendix Fig. S17). I found no significant changes to predicted mean migration distance, stopover number or migratory duration of short-distance migratory passerines or waterfowl (Appendix Table S34).

4.5 Discussion

Predictions of increased migration distance under climate change are not restricted to species following the Afro-Palearctic flyway but a global threat facing long- but not short-distance migratory birds. These changes are the result of shifts in the breeding and non-breeding ranges of these species. Whilst the two ranges are projected to shift in broadly the same direction in short-distance migrants, due to largely being in the same hemisphere, they diverge in long-distance migrants, shifting towards opposite poles. To meet the greater demands for rest and fuel driven by these longer migration distances, long-distance migrants will be required to take more frequent stopovers on migration, which, alongside a greater amount of time spent in migratory flight, is predicted to lead to greater migratory durations.

Migration is a period of extremely high mortality for birds, due to both the high energetic demands of migratory flight and the unknown distribution of resources and predators at stopover sites (Newton, 2008; Sillett & Holmes, 2002). These predicted increases in migration distance and stopover numbers are likely to lead to higher rates of mortality for long-distance migrants and, therefore, exacerbate the current divergence in population trends between long- and short-distance migratory birds, whereby the former are declining at a much faster rate than the latter (Sanderson et al., 2006; Vickery et al., 2014). Furthermore, the predicted increase in duration of migration would see individuals of long-distance migratory populations arrive markedly later (up to 8 days in some species) at the breeding grounds, unless departure from the non-breeding grounds is advanced significantly. This is likely to increase the severity of phenological mismatch currently experienced by long-distance migrants, potentially reducing productivity and increasing competition with both residents and short-distance migrants, which would both have longer to establish territories prior to the return of long-distance migrants (Both et al., 2010; Burgess et al., 2018; Møller et al., 2008; Wittwer et al., 2015).

Long-distance migrants possess the ability to advance their departure from the non-breeding grounds and arrival at breeding sites, however, this is already necessitated by the advancing phenology of temperate ecosystems, caused by warmer global temperatures (Gill et al., 2013; Lawrence et al., 2021; Newson et al., 2016). Moreover, these advancements in departure may be insufficient even for this purpose alone, due to being limited by food availability prior to departure (Lawrence et al., 2021; Studds & Marra, 2011). Therefore, the requirement for even further advancement of pre-breeding migration may be outside of the physiological capabilities of many, if not all, long-distance migrants and delayed breeding ground arrival may further contribute to population declines.

Whilst these threats will be posed to long-distance migrants in all three major flyways, they are predicted to be most severe for species migrating within the Americas. Thus, long-distance migrants in this flyway may experience the greatest rise in mortality and the sharpest declines in populations. The smallest increases/largest decreases in predicted migration distance occurred for species with a portion of their non-breeding distribution in Europe, North Africa, and the Middle East. Therefore, at least part of the non-breeding ranges of these species are likely to shift in the same direction as their breeding ranges, resulting in little change to the migratory journey. Additionally, increases in migration distance were relatively small (200-300km) for species spending the non-breeding period in equatorial Africa and Asia. In contrast, the migration distances of species spending the non-breeding season in Central America are predicted to increase by around 1000km. Moisture availability appears to be a more important driver of species richness and abundances in equatorial regions than temperature (Hawkins et al., 2003; Howard et al., 2015). Therefore, the non-breeding ranges of these species are less likely to show a poleward shift and, instead, be driven by more complicated changes in precipitation patterns. As such, species in Central America may have to move south into the Amazon basin to track their climatic niche, whereas shifts of such magnitude may not be necessary for species in Africa and Asia.

More land can be found at a greater range of latitudes in the Americas than either the Afro-Palearctic or Australasian. The magnitude of warming is predicted to be larger at higher compared to lower latitudes (IPCC, 2021). As a result, species spending the non-breeding period at high latitudes in South America will be exposed to greater temperature rises than those in Africa or Australasia and, therefore, are likely to be required to shift the furthest to track their climatic niche. Additionally, breeding ranges are likely to become constricted against the edge of the landmass in the Palearctic, but not the Nearctic, due to a greater extent of landmass available for poleward colonisation in the latter. Presenting a similar scenario to the south, the limit of African landmass occurs at 35^{o}S, compared with 55^{o}S in South America. Whilst landmass in Australasia does extend further than in Africa (45^{o}S), this consists of relatively small islands (the Malay Archipelago) and Australia, the latter being largely made up of desert and likely unsuitable for colonisation. Therefore, whilst species in the Americas have a large amount of land available for colonisation to the north of their breeding and south of their non-breeding ranges, respectively, there is a much stricter limit on the extent to which species in the Afro-Palearctic or Australasian flyways can shift. Therefore, whilst species following the Afro-Palearctic and Australasian flyways may not be required to lengthen their migratory journeys quite as severely, they may face an increased risk of range loss.

Longer migratory journeys with more stopovers, which will take longer overall, are predicted for both long-distance migratory passerines and shorebirds. However, as predicted, the number of extra stopovers required varied between the two taxa. Increases in the predicted number of stopovers were significantly greater for passerines than for shorebirds. This is likely due to the greater fat loading capabilities of the latter, enabling them to fly further before having to stop to refuel (Newton, 2010). As such, it could be deemed that populations of passerines are most at risk to the threat of increased mortality on migration. However, shorebirds are highly reliant on specific, patchily distributed stopover sites (mudflats) and decline rapidly when these are lost (Catry et al., 2004; Studds et al., 2017). In contrast, passerines are less tied to precise locations, likely due to more widespread suitable habitat. Therefore, whilst a greater number of additional stopovers are predicted to be required for passerines, they may be more capable of carrying these out than shorebirds.

The importance of these findings and their implications highlight a clear need for further development of techniques to model migratory journeys. Whilst my models allow for short-stopping, i.e., individuals remaining within the temperate realms for the non-breeding season due to milder winters (Elmberg et al., 2014), they do not account for the potential fitness benefits of doing so. Mortality is expected to decrease as individuals spend less time on migration, whilst productivity may increase as populations spending the non-breeding period closer to the breeding grounds are better able to judge the onset of the breeding season and thus reducing the severity of phenological mismatch (Lawrence et al., 2021). Adoption of this strategy by long-distance migratory populations would see a reversal in the changes I predict here, with migratory journeys becoming shorter rather than longer. Additionally, my models accurately simulated the migratory journeys of most, but not all, species for which tracking data exists. This is likely due to the simplicity of the straight-line migration simulations. Individuals of many species are likely to diverge from a straight line so that they can stop to refuel in areas with sufficient resources, utilise the prevailing wind direction to maximise flight distance whilst minimising energy expenditure or avoid extensive ecological or geographical barriers (Howard et al., 2018). Therefore, both dynamics should be incorporated into future migration simulations to increase their biological realism.

Finally, accurate distribution data underpin species distribution models and inaccurate data will lead to inaccurate distribution projections and, therefore, migration simulation. However, our knowledge of the tropical distributions of migratory species is limited and available distributional data are both spatially and temporally coarse (Howard et al., 2020). Furthermore, relatively little is known about the migratory connectivity of species' populations (Finch et al., 2017). Understanding how breeding populations are spatially segregated and where each spends the non-breeding season is fundamental for the simulation of migration. This is especially pertinent when considering the impact that differing migration patterns (i.e. leapfrog migration, whereby more northerly breeding populations spend the nonbreeding period in more southerly locations, or chain migration, where more northerly breeding populations spend the nonbreeding period in more northerly locations; Newton, 2008) may have on the exposure of different long-distance migratory populations to the impacts of climate change on migration. Given the latitudinal variation in those predicted changes to migratory journeys in all three flyways, there is likely to be intraspecific variation in those impacts, rather than simply those species-wide effects I have predicted here. Moreover, the impact of leapfrog vs. chain migration is unlikely to show consistent patterns across species, but rather vary depending on each species specific distributions. Therefore, specific consideration of these factors when simulating migratory journeys would improve the accuracy of predictions and increase their utility for understanding the potential effects of climate change on migration. However, due to the paucity of data on the patterns adopted by each species, I was unable to do so here. Increasing our understanding of the movements of migratory populations away from the breeding grounds should be a priority for future work.

In conclusion, my findings demonstrate, for the first time, that increases in migration distance, stopover number and overall migratory duration are likely to threaten long-distance migratory birds across the globe by the end of the century. These changes are likely to exacerbate the current declines of such species, underlining the need for conservation focus on long-distance migrants. Furthermore, the severity of these impacts is predicted to be spatially and taxonomically heterogenous, which may necessitate even more finely focussed conservation efforts. The differences in magnitude of change between flyways highlights the complexity of interacting factors that determine species responses to climate change and the need to consider multiple risks when assessing the level to which species are threatened. Mechanistic migration modelling and better understanding of species' migratory connectivity and tropical ranges represent areas of research that would contribute significantly to our prediction of existing and predicted threats to migratory species.

Chapter 5

Changes to long-distance avian migration through the interglacial period

A tundra landscape in Svalbard – the breeding grounds of a variety of high arctic breeding long-distance migrants, such as the Sanderling *Calidris alba* and Red Knot *Calidrid canutus*. *Photo credit: Billy Lindblom (CC BY SA 2.0)*

5.1 Abstract

The current global climate enables long-distance migratory birds to exploit ephemeral resource peaks for breeding, typically at high latitudes, and avoid harsh conditions during the non-breeding period, typically by migrating to lower latitudes. However, during glacial periods, high latitudes are likely to have been uninhabitable and breeding ranges may have been distributed significantly closer to the non-breeding grounds, potentially leading to sedentary behaviour in current migrants. There are conflicting opinions regarding changes to migratory schedules through the interglacial period, and a global study of such events is lacking. Here, I use species distribution models alongside paleoclimate data to retrospectively project the millennial distributions and migration distances of all northern hemisphere temperate-to-tropical migrants from present day to the last glacial maximum (LGM), 22,000 years ago. I simulate species breeding ranges to have been markedly smaller and constrained to southern glacial refugia towards the LGM, with non-breeding ranges projected to have been concentrated around the equator. Nevertheless, I project that long-distance migration persisted globally as a strategy at the LGM, albeit at typically reduced distances. This highlights potential flexibility in migratory journeys but also that the migratory journeys predicted for the end of the current century far exceed any that are likely to have occurred since the LGM.

5.2 Introduction

Migratory birds make bi-annual journeys between spatially segregated breeding and non-breeding sites. For many long-distance migrants, this typically involves migration from temperate to tropical regions and back. These journeys are energetically costly, resulting in higher mortality than at any other period of the annual cycle (Sillett & Holmes, 2002). However, they enable individuals to take advantage of ephemeral resources across space and time. By breeding in temperate regions and spending the non-breeding period in the tropics, long-distance migrants can: (1) exploit a surplus of resources for breeding and avoid high levels of competition from resident species, increasing productivity and (2) avoid harsh temperate winters, reducing mortality during the non-breeding season (Somveille et al., 2015). However, long-distance migratory birds are currently declining more rapidly than resident and short-distance migratory species (Robbins et al., 1989; Sanderson et al., 2006). Given that around 15% of the world's ~10,000 bird species are migratory, this poses a serious threat to global biodiversity and its associated services (Kirby et al., 2008; Somveille et al., 2018).

Variability in the population trends of species utilising different migratory strategies are increasingly attributed to the impacts of climate change on survival and productivity (Runge et al., 2014; Wilcove & Wikelski, 2008), although changing conditions away from breeding grounds could also be important (Howard et al., 2020). As further climatic changes are predicted globally in future, long-distance migratory birds are likely to continue to decline. Moreover, novel potential impacts of these changes are beginning to be identified. For example, the migration distances, and associated number of stopovers and overall durations, of the world's long-distance migratory birds are predicted to increase significantly by the end of the century, as their breeding and non-breeding distributions move further apart (Howard et al., 2018; Zurell et al., 2018). As mortality during migration is the highest at any period of the annual cycle, increases in the length of migratory journeys may further exacerbate current population declines of long-distance migratory birds.

The seasonal distributions of migratory birds are well explained by global climate, to the extent that migratory species maintain a more consistent year-round climatic niche than do residents (Eyres et al., 2020; Somveille et al., 2015). However, climatic conditions have not been consistent through the earth's history. During glacial periods, including the last glacial maximum (LGM, circa 22,000 years ago), temperate regions are likely to have lacked the seasonality experienced today and many would have been entirely uninhabitable due to the presence of ice sheets across the Holarctic (Hewitt, 2000; Lovette, 2005; Taberlet et al., 1998; **Fig. 1**). Assuming climatic niches persist through time, the ranges of species currently distributed in temperate regions are likely to have been located further from the poles than at present (Thorup et al., 2017; Zink & Gardner, 2017). For long-distance migrants, this could result in breeding and non-breeding ranges being closer together than they are currently. Given the adaptive plasticity of migratory behaviour, migrations may, therefore, have been significantly shorter at the LGM (Bearhop et al., 2005; Berthold et al., 1992; Berthold, 2001). Subsequently, as temperatures increased and ice sheets retreated, migration distances are hypothesised to have increased as species tracked suitable breeding climates to higher latitudes (Newton, 2008). The extent to which migration distances of long-distance migratory birds changed between the LGM and the present day could provide insight into the adaptability of these species to predicted future changes to migratory journeys.

Figure 1. Extent of ice sheets (blue) over global terrestrial habitats (grey) at the peak of the last glacial maximum (22,000 years ago). Data used to produce figure from Beyer et al. (2020)

The capacity for fossil evidence to answer questions about migration is limited, due to both the low preservation of bird bones and, even when present, the inability to infer migratory connectivity (Ruegg et al., 2006; Somveille et al., 2020; although see Ponti et al. (2020) for fossil evidence from Africa of migratory behaviour in sandpiper species at the LGM). Instead, studies have generally used phylogeographic or species distribution modelling (SDM) approaches to assess the persistence of long-distance migration at the LGM, which has led to competing hypotheses. SDM studies have suggested that long-distance migrants currently distributed across the western Palearctic are thought to have retained their migratory behaviours during the last glacial period, as southern Europe and North Africa are considered to have remained suitable for breeding, whilst the persistence of the Sahara Desert maintained the separation of breeding and non-breeding ranges (Ponti et al., 2020b; Thorup et al., 2021). By contrast, a combination of SDM and phylogeographic work has led to the conclusion that long-distance migrants in the Nearctic are considered to have been previously sedentary in Central/South America, when the majority of North America was covered by the Laurentide ice sheet (Malpica & Ornelas, 2014; Milá et al., 2006; Zink & Gardner, 2017). However, it has been suggested that this was inconsistent among species (Zink & Gardner, 2017) with, for some species, North America remaining suitable for breeding (e.g. Ruegg et al., 2006). The only global assessment, to date, of change to migratory routes during the post-glacial (Somveille et al., 2020) predicted that migratory strategies persisted across all three of the major migratory flyways (i.e., Americas, Afro-Palearctic and Australasian; BirdLife International, 2010) at the LGM, despite a reduction in Nearctic migration distances. This study used a "seasonally-explicit distributions simulator" (SEDS), saturating the world with virtual bird species. As such, predictions did not differentiate between long- and short-distance migrants, and indeed were unable to project real species' responses (i.e., changes in migration distances or transitions to sedentary behaviour). By contrast, a species-specific SDM approach to simulating changing ranges throughout the inter-glacial period, whilst still being unable to account for inter-specific competition, should enable the analysis of coarse scale geographic and taxonomic patterns of change to global long-distance migrants.

Here, I build SDMs for the contemporary breeding and non-breeding distributions of 331 species of long-distance migrants, representing all obligate northern hemisphere temperate-to-tropical migrants across the globe. I use these models to hindcast species' distributions every 1000 years, back to the LGM, 22,000 years ago. Using these retrospective projections, I analyse changes in global richness patterns of long-distance migratory birds, as well as changes to range size and migration distance for individual species, and the overlap of breeding and nonbreeding ranges. By analysing such changes, I aim to infer the extent to which long-distance migration persisted as a life-history strategy at the LGM, and to gain insights into the likely flexibility of past migrations, which could inform future flexibility.

5.3 Materials and methods

5.3.1 Species data

Breeding and non-breeding distribution polygons were obtained from BirdLife International, for all land birds classified as a "full migrant" (Birdlife International and NatureServe, 2016), comprising 1675 species. Breeding and non-breeding polygons for all species were intersected with a 0.5° x 0.5° grid and were classed as present if the polygon overlapped more than 10% of any cell.

Many long-distance migratory birds have breeding and non-breeding distributions that span continents. However, these ranges are typically made up of discrete populations, which migrate along different flyways, with little overlap. Therefore, to ensure I accurately simulate migrations, I first separated populations that utilise different flyways. To do so, I used the longitudinal boundaries of the Americas, Afro-Palearctic and Australasian flyways from Chapter 3 (**Table 1**) and followed the definition of single-flyway, multi-flyway, trans-flyway, and multi-trans-flyway species from Chapter 4 to differentiate discrete migratory populations whose individuals follow different flyways. Multi-trans-flyway species, of which there were only four, were removed, due to an inability to distinguish between migratory populations.

Table 1. Longitudinal boundaries of the three migration flyways and the numbers of long-distance migrants in each of the four flyway categories.

Flyway	**Longitudinal Boundary**		**Long-distance migrants**
	West	**East**	
Americas	170°W	30°W	75
Afro-Palearctic	30°W	65°E	62
Australasian	65°E	170°W	163
Trans-flyway	NA	NA	65

To separate long-distance migratory populations, I utilised the methods of Chapter 4. Populations were classified as long-distance migrants if at least 80% of the current breeding range occurs in the 'temperate' realms (Nearctic, Palearctic, Saharo-Arabian and Sino-Japanese) and at least 80% of the non-breeding range occurs in the 'tropical' realms (Panamanian, Neotropical, Afrotropical, Madagascan, Oriental, Oceanian, and Australian; Holt et al., 2013). Using this method, I identified 331 species of long-distance migratory bird, consisting of 365 separate populations (**Table 1**). The remaining species were excluded from the study, on the basis that they were not currently obligate long-distance migrants.

5.3.2 Species distribution projections

I used data from Beyer et al. (2020) [at 0.5º resolution] for 19 bioclimatic variables at 1000-year intervals, spanning from the present-day to 22,000 years ago (the time of the LGM). To ensure consistency in spatial scale, I intersected the climate data with the same 0.5º x 0.5º grid that was intersected with current species distributions, applying bilinear interpolation using the “resample” function in the “raster” package in R to assign bioclimatic values to grid cells (Hijmans et al., 2014).

I modelled the relationship between each species’ current global distribution and five of the 19 available bioclimatic variables, using data for the same contemporary time period. The bioclimatic variables used to model, and subsequently project, distributions were selected following the methods of Chapter 4 (Titley et al., 2021). Temperature seasonality, minimum annual temperature, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality were identified as the best explanatory bioclimatic variables for both current breeding and non-breeding distributions (Appendix Tables S41 & 42). Using this approach, models were built separately for the breeding and non-breeding distributions of each species.

I utilized the same ensemble modelling framework as in Chapter 3, combining Generalized Additive Models (GAMs), Generalized Linear Models (GLMs), Generalized Boosted Regression Models (GBMs) and Random Forests (RFs). To provide the models with meaningful absence data, I excluded climatic data from any biogeographic realm in which the modelled species did not occur (Holt et al., 2013). To deal with issues associated with spatial autocorrelation I used the “blocking” and model performance assessment methods of Chapter 3 (Bagchi et al., 2013).

For each species, I used these models to predict the probability of occurrence of the species in each 0.5º x 0.5º cell at 1000-year time steps, starting at the present day and going back to 22,000 years ago. For each cell, the median suitability across the 40 models was calculated for each 1000-year period. I applied the thresholding technique of Chapter 4 to convert suitability values to presence/absences, giving a predicted distribution for each species in each period.

5.3.3 Assessing changes to migratory behaviour

I calculated the directions in which breeding and non-breeding ranges have shifted since the LGM separately for each of the flyways. To do so, I calculated the bearing and geodesic distance between the centroids of each population’s current range and that at the LGM, using the R package “geosphere” (Hijmans, 2015). I used a circular ANOVA, using the R package “circular” (Lund et al., 2022), to compare the directions of predicted shifts in the centroids of breeding and non-breeding ranges between 22,000 years ago and the present-day. Additionally, for each flyway, I calculated the mean shift in latitude and longitude of breeding and non-breeding range centroids across all species in each group and, from this, calculated the bearing and geodesic distance of the mean shift.

To explore changes in richness of these present-day long-distance migrants across the globe, I calculated the difference in projected richness between the LGM and present day for each 0.5^o cell. Values for the change in species richness in each cell were then grouped using the Jenks natural breaks method in the R package “classInt” (Bivand et al., 2023).

For each population in each thousand-year period, I calculated the change in breeding and non-breeding range size compared to that of the present-day, using the R package “raster” (Hijmans et al., 2014). To analyse how range sizes in each flyway have changed over time, I fitted phylogenetic linear mixed models (PLMMs), as range size may be phylogenetically correlated. For each flyway, I fitted a PLMM with change in range size since the LGM, from all populations, as a continuous response variable and time after LGM as a categorical predictor variable, using the R package “MCMCglmm” (Hadfield, 2010). I used the methods of Chapter 2 to fit all PLMMs and assessed the performance of each model by calculating conditional R^2 following the methods of Nakagawa & Schielzeth (2013).

To calculate the migration distance of each population in each 1000-year period, I used the methods of Chapter 4. This method incorporates intra-specific variation in migratory journeys, as well as likelihood of occurrence, so should simulate migration distances more realistically than distances between breeding and non-breeding range centroids. To analyse trends in migration distances over time, for each flyway, I fitted a PLMM with mean simulated migration distance, from all populations, as a continuous response variable and time after LGM as a categorical predictor variable.

Resident species, by definition, have overlapping breeding and non-breeding distributions. Therefore, to assess the potential for individuals to switch to a non-migratory strategy at the LGM, I calculated the degree of overlap of the breeding and non-breeding distributions in each 1000-year period. For the breeding distribution, this was calculated, as the percentage of the range that overlaps with the non-breeding range – and vice-versa for the non-breeding range. I then analysed trends in range overlap over time, for each flyway, by fitting a PLMM with percentage overlap, from all populations, as a continuous response variable and time after LGM as a categorical predictor variable. This was performed for breeding and non-breeding ranges, separately.

5.4 Results

5.4.1 Species distribution models and individual species projections

Species distribution models for the 331 species of long-distance migratory bird performed well when fitted to both breeding (mean AUC: 0.97 ±0.03) and non-breeding distributions (mean AUC: 0.94 ±0.04).

Figures 2-4 show examples of projected breeding and non-breeding distributions at six separate 1000-year time steps between the present-day and the LGM for a long-distance migrant in each of the Americas (Swainson's Thrush *Catharus swainsoni*), Afro-Palearctic (Collared Flycatcher *Ficedula albicollis*) and Australasian flyways (Pallas's Grasshopper Warbler *Locustella certhiola*). In all three examples, breeding ranges were distributed further south at the LGM than they are currently. Furthermore, these breeding ranges were smaller than at the present-day, especially for the Swainson's Thrush and Collared Flycatcher, for which the LGM ranges were just 30% and 3% of their current size, respectively. These changes were less exaggerated for the Pallas's Grasshopper Warbler in the Australasian flyway, which retained 96% of its current range, likely due to a much smaller ice sheet extent than in the North America and Europe (**Figure 1**). The non-breeding ranges of all three species showed a shift towards or concentration around the equator. For the Pallas's Grasshopper Warbler, this was accompanied by a decrease in range size, with the LGM range 41% of the size of the current range. In contrast, the sizes of the Swainson's Thrush's and Collared Flycatcher's ranges were 46% and 31% larger than at present, respectively. This is likely due to the availability of less landmass around the equator in Asia than in South America and Africa.

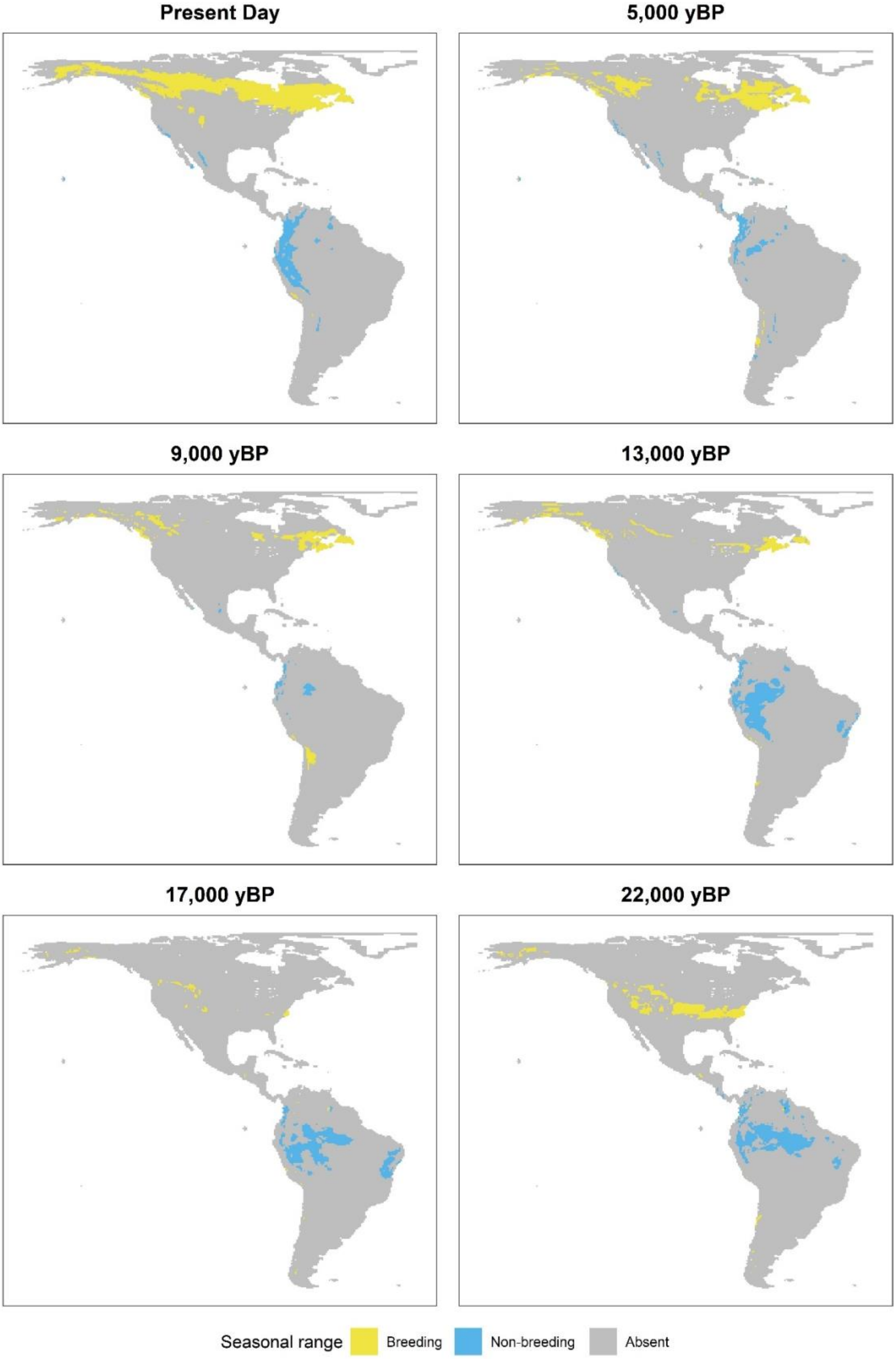

Figure 2. Projected breeding and non-breeding distributions of Swainson's Thrush *Catharus swainsoni*, a long-distance migratory bird in the Americas flyway, during six separate thousand-year time windows between the present day and the last glacial maximum (22,000 years ago; yBP = years before present).

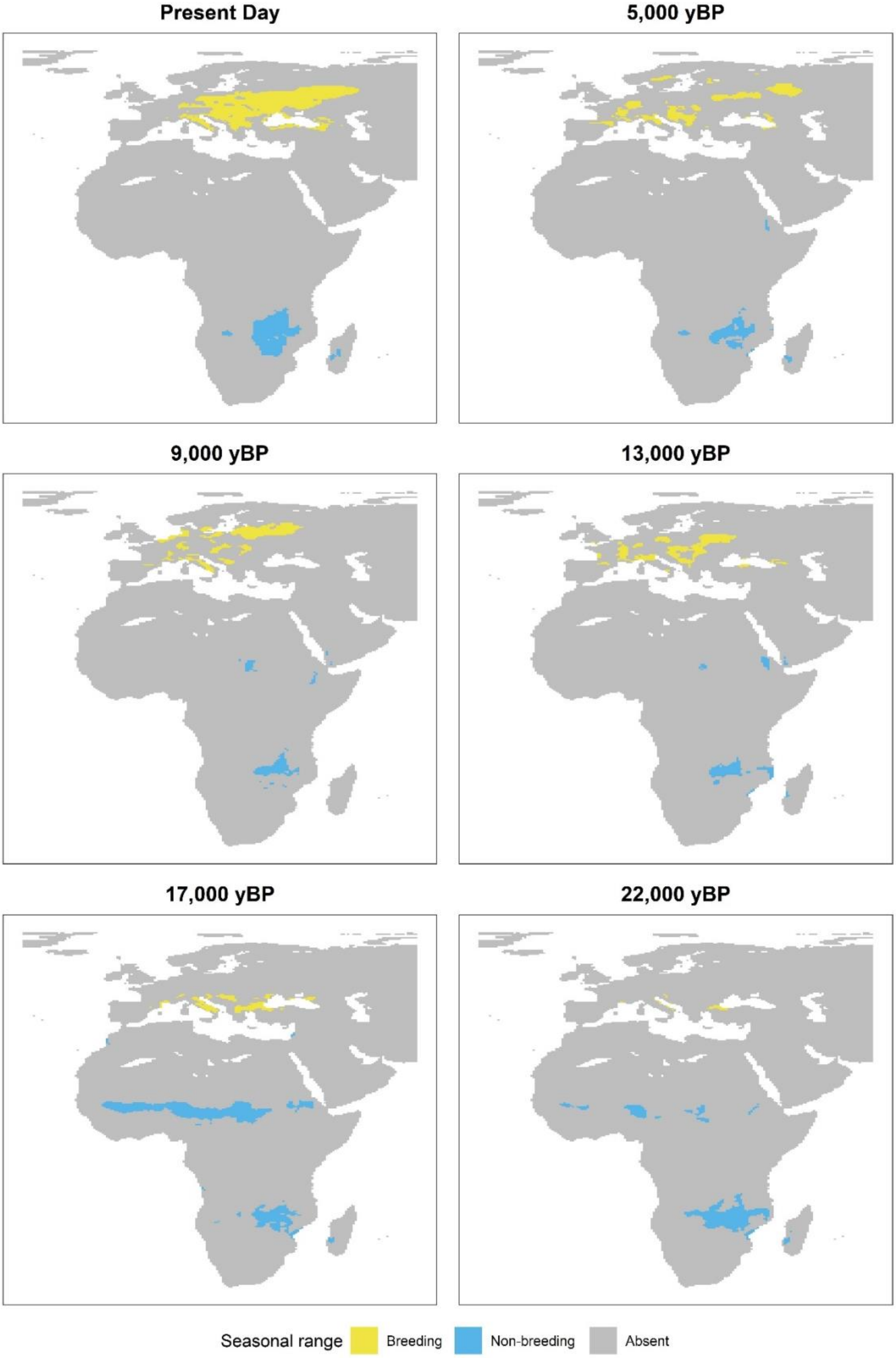

Figure 3. Projected breeding and non-breeding distributions of Collared Flycatcher *Ficedula albicollis*, a long-distance migratory bird in the Afro-Palearctic flyway, during six separate thousand-year time windows between the present day and the last glacial maximum (22,000 years ago; yBP = years before present).

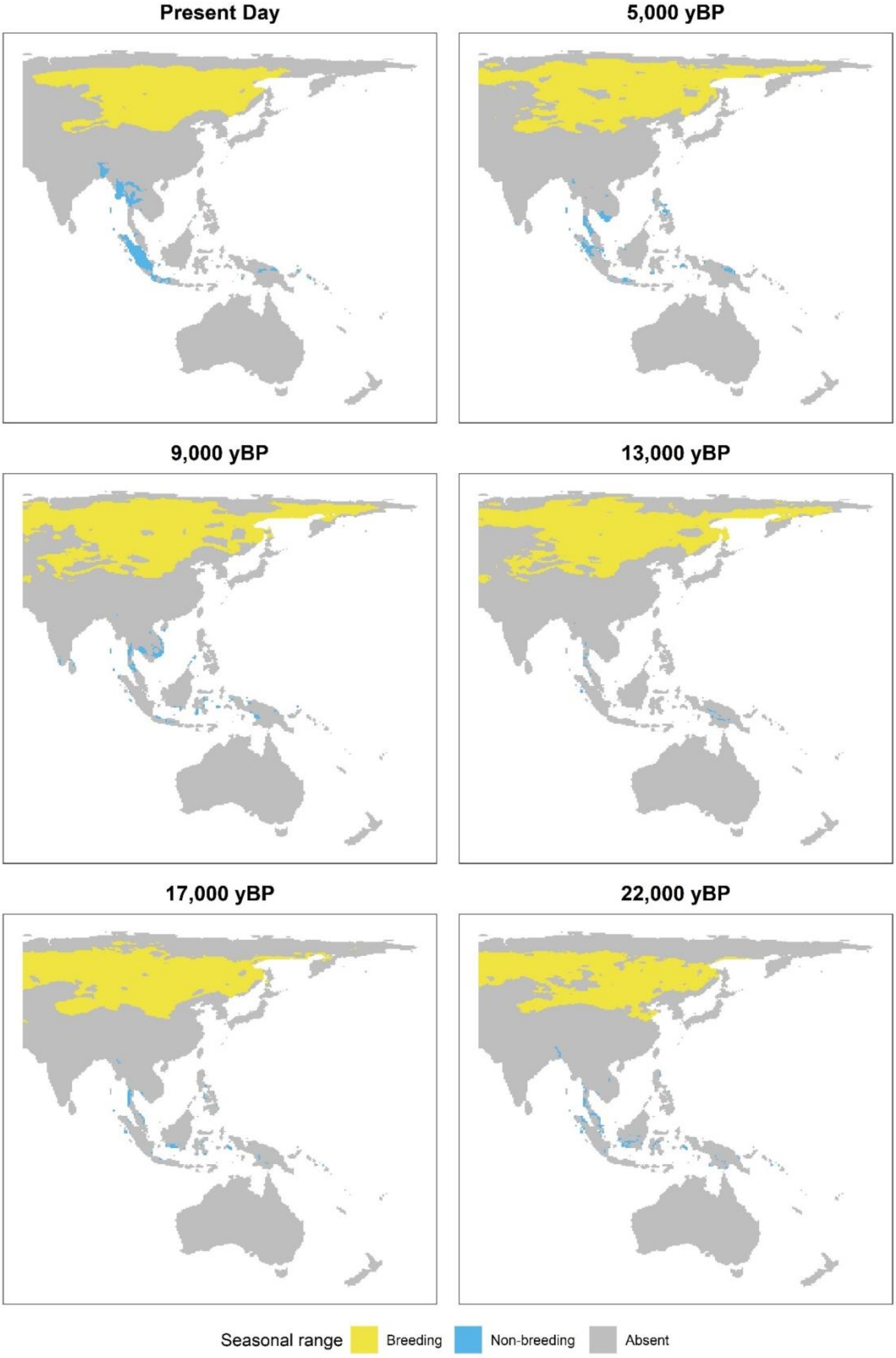

Figure 4. Projected breeding and non-breeding distributions of Pallas's Grasshopper Warbler *Locustella certhiola*, a long-distance migratory bird in the Australasian flyway, during six separate thousand-year time windows between the present day and the last glacial maximum (22,000 years ago; yBP = years before present).

Using unpaired t-tests to compare the 1000 estimates of migration distance in each period, I found that the migrations of Pallas's Grasshopper Warbler were significantly longer at the LGM than they are currently ($\bar{x}_{current} = 5294$km, $\bar{x}_{LGM} = 5727$km, $t = -6.9$, $df = 1997$, $p < 0.001$). In contrast, the migration distances of the Swainson's Thrush ($\bar{x}_{current} = 6424$km, $\bar{x}_{LGM} = 5867$km, $t = 7.4$, $df = 1961$, $p < 0.001$) and Collared Flycatcher ($\bar{x}_{current} = 7174$km, $\bar{x}_{LGM} = 5841$km, $t = 31.2$, $df = 1409$, $p < 0.001$) were significantly shorter at the LGM than at present, due to southward contractions of their breeding ranges. Despite this, all three species appeared to remain as long-distance migrants at the LGM, with migrations distances more than 5000km and non-overlapping breeding and non-breeding ranges.

5.4.2 Species richness and range changes

Projections indicated that, at the time of the LGM, species' breeding ranges were distributed, on average, around 1000km further south than they are currently (**Fig. 5**). On average, non-breeding ranges in the Americas and Australasian were distributed to the south-east of their current ranges (**Fig. 5**). In contrast, in the Afro-Palearctic flyway, LGM non-breeding ranges were distributed to the north-west of their current ranges. However, in all three flyways, directions of non-breeding range shift appear bimodal, with one group shifting to the north-west and the other to south-east (**Fig. 5**). Nonetheless, between the LGM and the present day, species' non-breeding ranges shifted in significantly different directions to their breeding ranges in all three of the Americas (circular ANOVA: F1,146 = 105.9, $p < 0.001$), Afro-Palearctic (circular ANOVA: F1,96 = 43.1, $p < 0.001$) and Australasian (circular ANOVA: $F_{1,292} = 62.9$, $p < 0.001$) flyways.

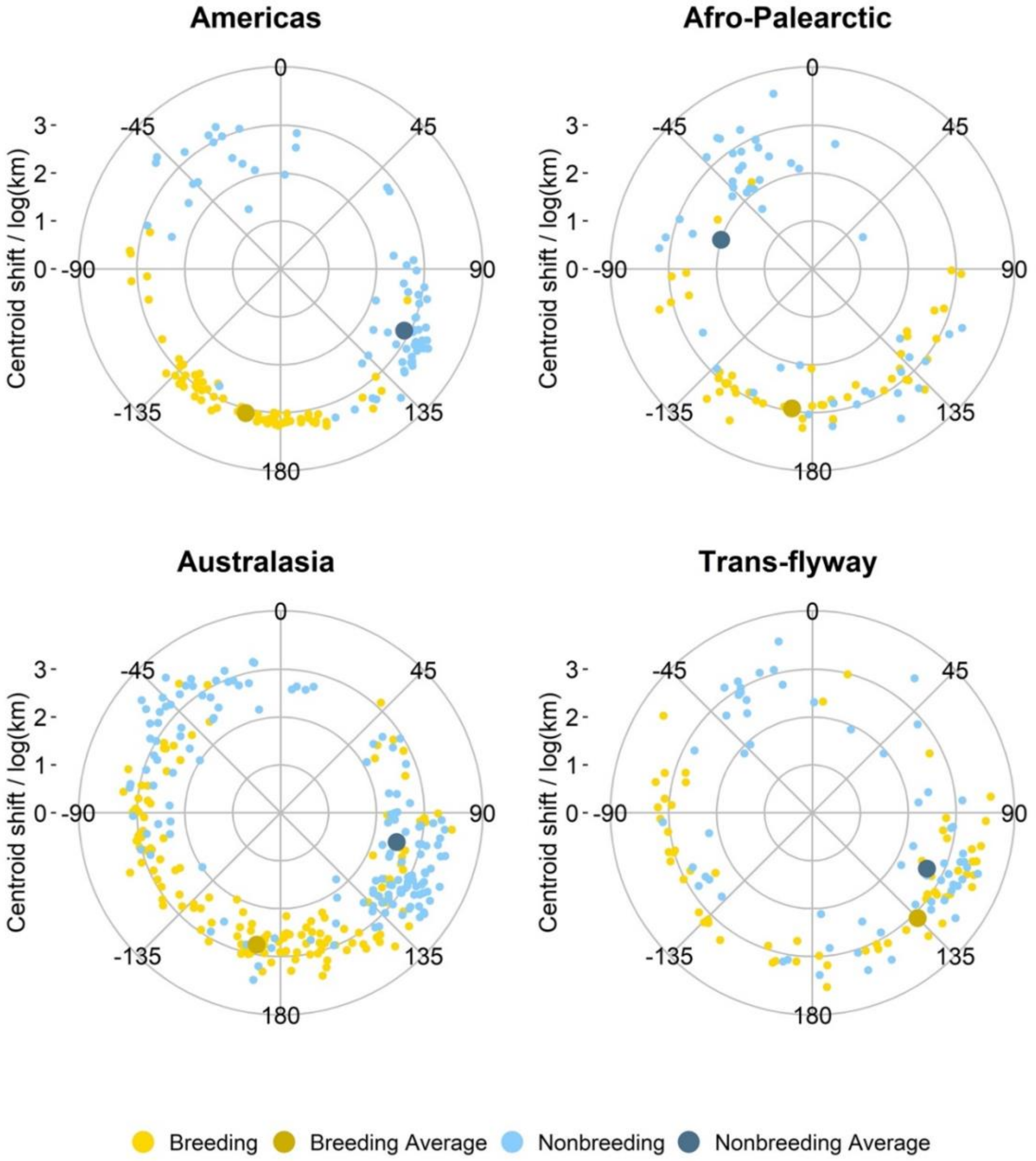

Figure 5. *Projected differences in the centroids of breeding (yellow) and non-breeding (blue) ranges between the present day and 22,000 years ago, for American (n = 69), Afro-Palearctic (n = 49), Australasian (n = 147) and trans-flyway (n = 63) long-distance migratory birds. Each point represents the range centroid of an individual flyway population 22,000 years ago, with the centre of the plot representing the present-day range centroid. The larger and darker points show the mean breeding and non-breeding differences, calculated as the bearing and geodesic distance of the mean difference in centroid latitude and longitude across all long-distance migrants in each flyway.*

In line with observed shifts in species' ranges, projections showed that, globally, the breeding richness of long-distance migratory birds north of ~35^{o}N at the LGM was poorer than that of the present day. This is particularly true for eastern North America, the Western Palearctic and parts of eastern Russia (**Fig. 6**). Additionally, the breeding species richness of the southern United States and parts of North Africa, the Middle East, and Central/East Asia was projected to have been greater at the LGM compared to today. Similarly, species non-breeding distributions are projected to have been more concentrated around the equator at the LGM (although see richness increase in north-west Africa and Iberia; **Fig. 7**). This may help to explain the bimodal distribution of range shifts shown in **Figure 1**, as species non-breeding distributions have shifted both north and south away from the equator.

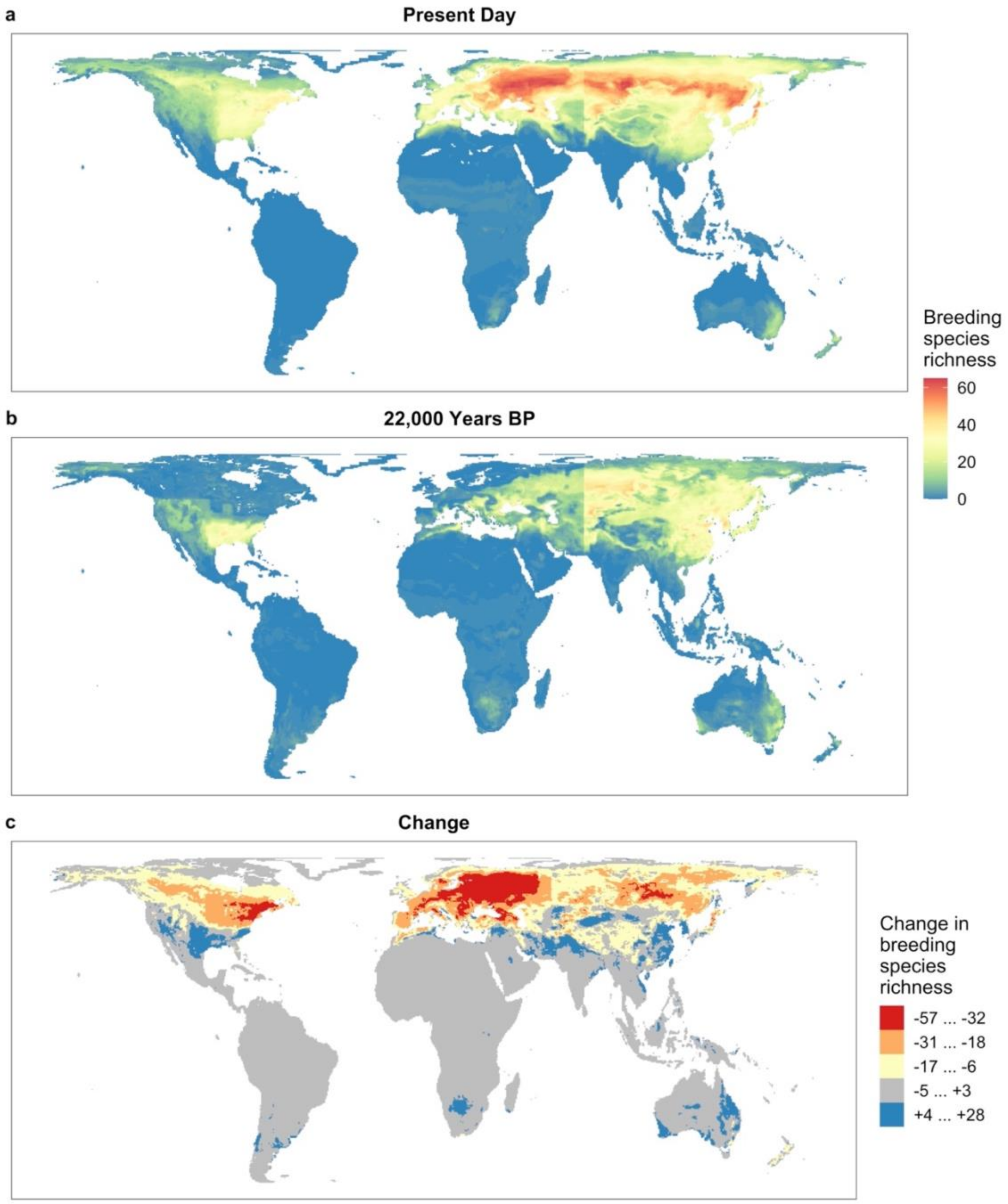

Figure 6. *Species richness of long-distance migratory birds during the breeding season at both* ***(a)*** *the present day and* ***(b)*** *the last glacial maximum (22,000 years ago).* ***(c)*** *shows the different in richness between the two periods. For* ***(c)****, values are grouped using Jenks natural breaks. Red colours represent fewer species at the last glacial maximum, blue colours represent more.*

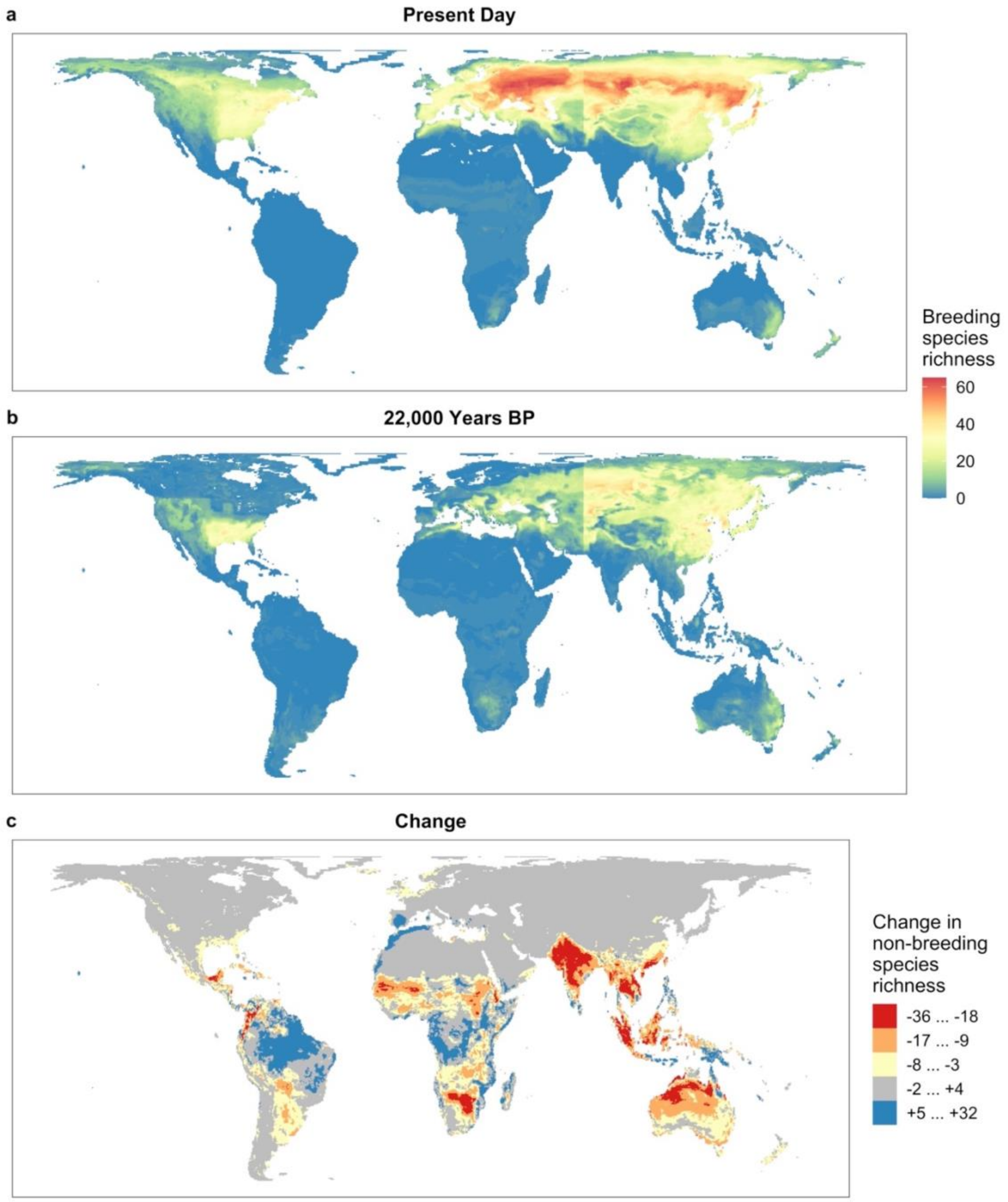

Figure 7. *Species richness of long-distance migratory birds during the non-breeding season at both* ***(a)*** *the present day and* ***(b)*** *the last glacial maximum (22,000 years ago).* ***(c)*** *shows the different in richness between the two periods. For* ***(c)****, values are grouped using Jenks natural breaks. Red colours represent fewer species at the last glacial maximum, blue colours represent more.*

Notably, gains in breeding species richness at the LGM appear much smaller in extent than losses (**Fig. 6c**). This may be due to species' breeding ranges contracting to the south, rather than shifts of the entire range towards the equator (**Fig. 6b**; and see example **Figs 2-4**). I found that, over the last 22,000 years, the size of species' projected breeding ranges increased significantly in all flyways (**Fig. 8**; **Table 2**). On average, breeding ranges have grown by 2.7Mkm^2 (million km^2) in the Americas, 2.4Mkm^2 in the Afro-Palearctic, 1Mkm^2 in Australasia and 3.6Mkm^2 for trans-flyway migrants. In relative terms, breeding ranges at the LGM were 62% smaller in the Americas, 69% smaller in the Afro-Palearctic, 24% smaller in Australasia and 38% smaller for trans-flyway migrants compared to the present day. The non-breeding ranges of Australasian migrants grew by a similar extent to their breeding ranges (1Mkm^2; **Fig. 8**; **Table 2**). Non-breeding ranges of Afro-Palearctic (0.7Mkm^2) and trans-flyway (0.6Mkm^2) migrants also increased in size, but by significantly less than their breeding ranges. The non-breeding ranges of species in America declined by 0.3Mkm^2 between the LGM and present day.

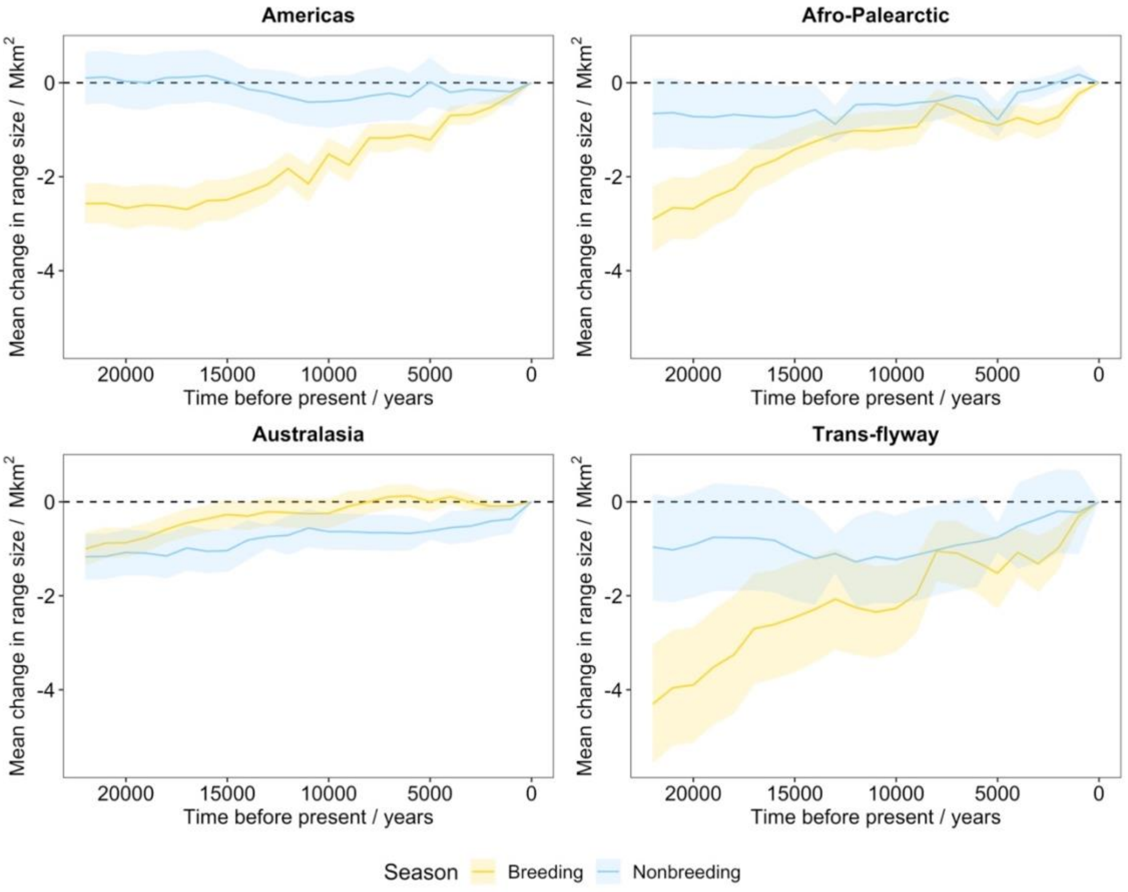

Figure 8. *Changes in the extent of breeding and non-breeding ranges of American (n = 69), Afro-Palearctic (n = 49), Australasian (n = 147) and trans-flyway (n = 63) long-distance migratory birds, between the last glacial maximum (22,000 years ago) and the present day. Solid line represents the mean change relative to the current range size, taken across all species, whilst the shaded area represents the 95% confidence intervals around this mean.*

Table 2. *Coefficients from phylogenetic linear mixed models, assessing trends in the size of species' projected range size between the last glacial maximum (22,000 years ago) and the present day, for American (n = 75), Afro-Palearctic (n = 62) and Australasian (n = 163) and trans-flyway (n = 65) long-distance migratory birds. Estimates represent change in square kilometres per year. Lower and upper are the 95% confidence intervals around estimates.*

Range	Flyway	Estimate	Lower	Upper	R^2
Breeding	Americas	121.8	115.4	128	0.96
	Afro-Palearctic	111.1	102.4	119.6	0.97
	Australasian	44.4	39.2	49.6	0.97
	Trans-flyway	161.8	147.1	176.3	0.97
Non-breeding	Americas	-15.5	-23.9	-7.1	0.96
	Afro-Palearctic	31.7	16.7	46.9	0.96
	Australasian	43.9	39.0	48.9	0.96
	Trans-flyway	29.3	16.4	42.6	0.92

5.4.3 Changes to migratory journeys

Projections for 51 of the 365 long-distance migratory populations indicated that suitable climate for at least one of the breeding or non-breeding distributions was entirely lacking in at least one of the thousand-year periods between the LGM and the present day. I removed these populations from the following analyses of migratory behaviour, to avoid issues with incomplete time series data.

Migration distances of less than 1000km were projected for just two of the 314 populations of long-distance migrant in any of the 1,000-year periods back to the LGM, one of which was already projected to perform sub-1000km migrations during the present day. I found that, on average, mean migration distances increased significantly in each of the three major flyways between the LGM and the present day (**Table 3**). However, these trends were relatively weak in magnitude, meaning that migration distances were just 462km less in the Americas, 638km less in the Afro-Palearctic and 176km less in Australasia at the LGM compared to the present day. Moreover, these represent increases of just 21km, 29km and 8km every thousand years, respectively, since the LGM. Migration distances in these flyways were projected to increase between 22,000 and 13,000 years ago, before levelling out, or even declining slightly (**Fig. 9**). In contrast, mean migration distances of trans-flyway migrants have declined steadily over the last

22,000 years, resulting in an average overall decrease of 286km since the LGM. Furthermore, I found little evidence for increasing levels of overlap between the breeding and non-breeding ranges of long-distance migrants between the LGM and the present day (**Table 4**; **Fig. 10**). Projected breeding and non-breeding distributions in any of the 1,000-year periods overlapped by more than 20% for just 31 populations, of which such an overlap was already projected at the present-day for nine of those populations. Together, these trends in migration distance and distributional overlaps indicate that the vast majority of species performed long-distance migrations throughout the current interglacial period.

Table 3. *Coefficients from phylogenetic linear mixed models, assessing trends in the mean migration distance between the last glacial maximum (22,000 years ago) and the present day, for American (n = 68), Afro-Palearctic (n = 48) and Australasian (n = 138) and trans-flyway (n = 62) long-distance migratory birds. Estimates represent change in kilometres per year. Lower and upper are the 95% confidence intervals around estimates.*

Flyway	**Estimate**	**Lower**	**Upper**	**R^2**
Americas	0.021	0.015	0.026	0.81
Afro-Palearctic	0.029	0.025	0.033	0.84
Australasian	0.008	0.005	0.012	0.88
Trans-flyway	-0.013	-0.019	-0.007	0.78

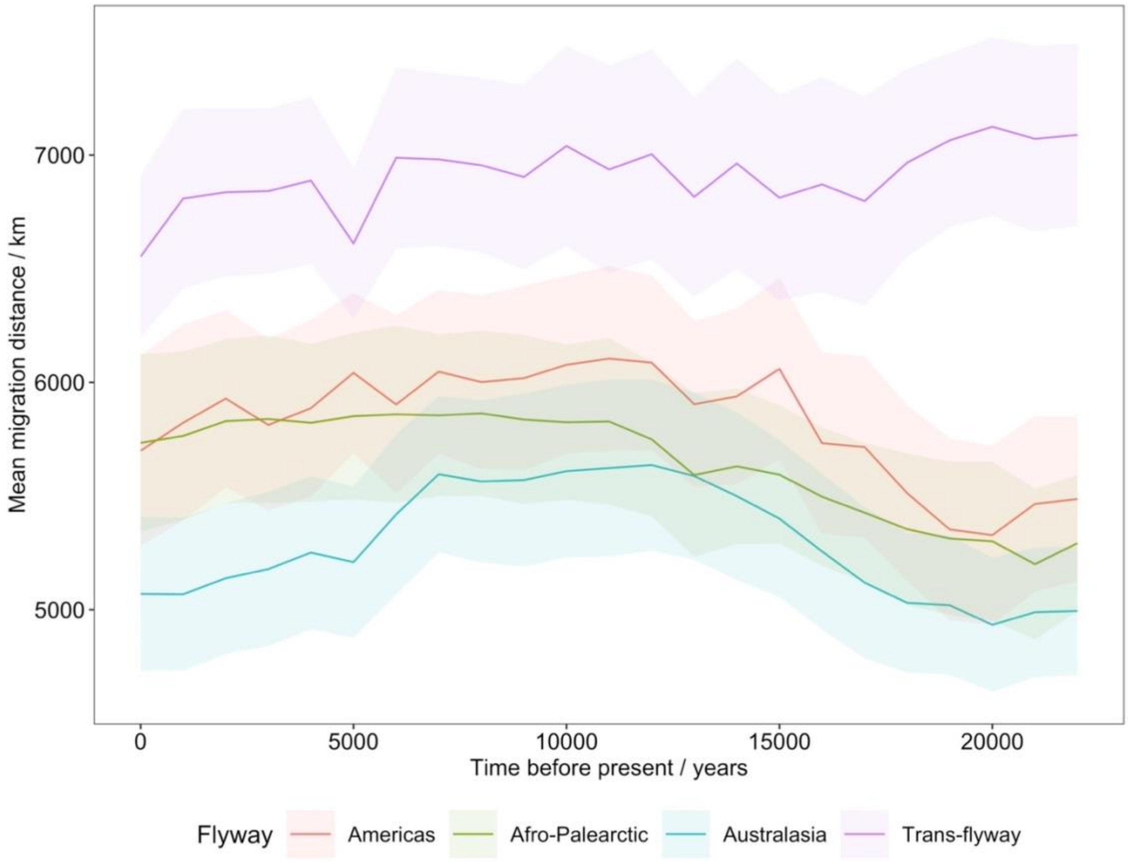

Figure 9. *Changes in mean migration distances of American (n = 68), Afro-Palearctic (n = 48) and Australasian (n = 138) and trans-flyway (n = 62) long-distance migratory birds, between the last glacial maximum (22,000 years ago) and the present day. Solid line represents the mean taken across all species in that flyway, whilst the shaded area represents the 95% confidence intervals around this mean.*

Table 4. *Coefficients from phylogenetic linear mixed models, assessing trends in the extent of overlap between species' projected breeding and non-breeding ranges between the last glacial maximum (22,000 years ago) and the present day, for American (n = 68), Afro-Palearctic (n = 48) and Australasian (n = 138) and trans-flyway (n = 62) long-distance migratory birds. Estimates represent change in overlap, as a percentage of the overall range size, per year. Lower and upper are the 95% confidence intervals around estimates.*

Range	**Flyway**	**Estimate**	**Lower**	**Upper**	**R^2**
Breeding	Americas	$-4.5x10^{-8}$	$-1.7x10^{-7}$	$8.3x10^{-8}$	0.98
	Afro-Palearctic	$4.0x10^{-7}$	$1.4x10^{-7}$	$6.5x10^{-7}$	0.83
	Australasian	$-3.8x10^{-7}$	$-6.1x10^{-7}$	$-1.5x10^{-7}$	0.86
	Trans-flyway	$2.9x10^{-7}$	$-2.2x10^{-9}$	$5.8x10^{-7}$	0.36
Non-breeding	Americas	$2.9x10^{-7}$	$1.9x10^{-8}$	$3.8x10^{-7}$	0.8
	Afro-Palearctic	$6.9x10^{-7}$	$3.5x10^{-7}$	$1.0x10^{-6}$	0.92
	Australasian	$-2.2x10^{-7}$	$-3.4x10^{-7}$	$-9.9x10^{-8}$	0.8
	Trans-flyway	$2.2x10^{-7}$	$7.6x10^{-8}$	$3.5x10^{-7}$	0.78

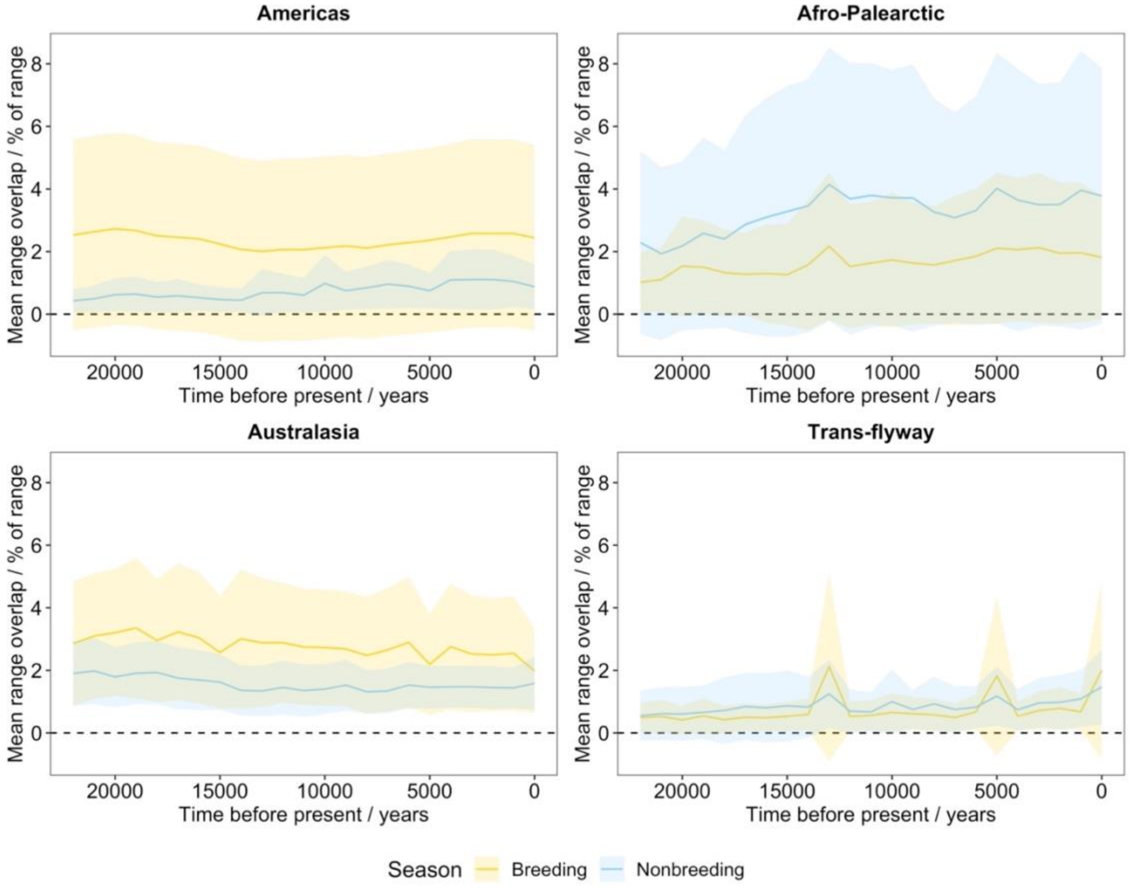

Figure 10. *Changes in the extent of overlap between projected breeding and non-breeding ranges of American (n = 69), Afro-Palearctic (n = 49), Australasian (n = 147) and trans-flyway (n = 63) long-distance migratory birds, between the last glacial maximum (22,000 years ago) and the present day. Solid line represents the mean overlap as a percentage of the overall range size taken across all species, whilst the shaded area represents the 95% confidence intervals around this mean.*

5.5 Discussion

My findings indicate that, at the time of the LGM, long-distance migration was as prevalent a global phenomenon as it is today. The breeding ranges of long-distance migrants were constrained to climate refugia in the south and migration distances were likely shorter than at present, but not to the extent that species' breeding and non-breeding ranges overlapped significantly and they became sedentary. These conclusions are similar to those of Somveille et al. (2020), despite their inclusion of short-distance migratory birds and utilisation of a SEDS, rather than a species-specific SDM approach. Below, I discuss my findings in more detail, considering their implications for long-distance migratory birds facing changes to their migratory journeys and identify challenges for the improvement of our understanding of palaeodistributions.

I found that, at the LGM, the centroids of breeding ranges were located around one thousand kilometres further south than at the present-day. However, rather than this representing a shift in the entire range to equatorial regions, species distributions appear to have been largely restricted to the southern margins of the present-day temperate realms. The subsequent increases in breeding range size since the LGM are consistent with findings that populations underwent rapid expansion from significantly smaller sizes during glacial periods (Malpica & Ornelas, 2014; Milá et al., 2006). Declines in breeding species richness and breeding range size were most prevalent in North America and the Western Palearctic. Again, these trends align well with the findings of Somveille et al. (2020) and can be explained by the extent of ice sheets at the last glacial maximum. Of the two main northern hemisphere ice sheets, the Laurentide sheet extended furthest south, rendering most of North America uninhabitable, whilst the Eurasian ice sheet covered most of northern Europe, but very little of Asia (**Fig. 1**).

In contrast to breeding ranges, non-breeding distributions appear to have shifted in two opposite directions over the last 22,000 years, with one group of species shifting to the north-west and the other to the south-east. This appears to have occurred as species dispersed from a concentration around the equator. This high non-breeding species richness around the equator likely explains the smaller non-breeding range sizes of Australasian species at the LGM, as the extent of landmass around the equator is significantly smaller than in the Americas or Afro-Palearctic flyways.

As species' breeding ranges were previously closer to their non-breeding ranges, migration distances in the three major global flyways were, on average, significantly shorter at the LGM than the present-day. However, as breeding ranges did not show substantial shifts into the tropics, mean migration distances remained around 5000km at the LGM. Furthermore, migration distances of trans-flyway migrants were previously significantly longer, and have shortened over the last 22,000 years, potentially as ice sheets have retreated and allowed individuals to breed closer to non-breeding locations. Additionally, I found little change to the levels of overlap between breeding and non-breeding ranges. Previously high levels of overlap would indicate that species were able to survive in one location, year-round and, therefore, adopt a sedentary strategy. Taken together, these results indicate that most species remained as long-distance migrants at the LGM and extensive changes to migratory routes have not occurred through this inter-glacial period.

Long-distance migration is likely to have evolved deeper in the avian lineage and, therefore, significantly earlier in time. Long-distance migrations have seemingly not undergone large increases to migratory distance, at least at the scale or rate of changes predicted by the end of the current century (Howard et al., 2018; Zurell et al., 2018; Chapter 4). Furthermore, climate change over the last 22,000 years has enabled the expansion of breeding ranges and increases in population size (Malpica & Ornelas, 2014; Milá et al., 2006). During this century, expansions of species' breeding distributions at northern range margins are projected to be mirrored by contractions at southern margins (Chen et al., 2011; Huntley et al., 2008). Furthermore, it is likely that many species' breeding ranges at high latitudes will become squeezed against the edge of landmasses, with no further space to retreat into. Therefore, despite long-distance migrants having adjusted to previous increases in global temperatures, contemporary climate change is likely to bring about novel impacts, which are likely to have negative consequences for populations.

For several species, projections indicated that in at least one 1000-year period over the last 22,000 years, no suitable climate during either the breeding or non-breeding period existed. Given that these species are extant today, suitable climate must have existed in these periods. Zink & Gardner (2017) interpreted this as species becoming sedentary in the non-breeding range. This would indicate that, over a relatively long period, species were able to adapt to new climates to exploit areas with better resources for breeding. However, for some species, suitable climate on the non-breeding grounds was also lost. It is possible that both species' breeding and non-breeding climatic tolerances have evolved throughout the current interglacial period and, therefore, the assumption of a static climatic niche through time are violated. Alternatively, species may have persisted at smaller spatial scales than the coarse one I modelled at here, particularly on the breeding grounds, where species are acknowledged to have survived in glacial refugia (Taberlet et al., 1998). To further our understanding of the origins of long-distance migration, as well as its persistence through glacial periods, future research should aim to improve our understanding of palaeodistributions and the likelihood that micro-evolution of climatic niches occurred over the timescales.

Furthermore, I could not utilise the same definition of a long-migrant to assess the migratory strategy of each species in each 1000-year period as I did for my initial identification of long-distance migrants for inclusion in the study. This is because biomes and, therefore, the biogeographic realms used in this definition are likely to have shifted significantly over the last 22,000 years, in response to the retreat of glaciers (Beyer et al., 2020). Use of the current distribution of these realms could lead to the erroneous identification of shifts to a short-distance migratory strategy, despite species remaining as long-distance migrants but shifting their breeding distribution equatorward in line with shifts in the temperate realms. Future work could aim to reconstruct these biogeographic realms at the time of the LGM and enable a consistent assessment of migratory strategy in different periods. Additionally, my results provide an understanding of species-specific responses of long-distance distance migrants to glacial-interglacial cycles. However, I was unable to account for the local-scale effects of interspecific competition, which are known to drive the seasonal distributions of migratory birds (Somveille et al., 2018). As highlighted by Somveille et al. (2020), there is potential to combine my SDM approach with their spatially explicit distribution simulation and assess differences between SDM projected and SEDS predicted communities.

In conclusion, I have demonstrated that long-distance migration persisted globally at the point of the last glacial maximum. Breeding ranges were confined to glacial refugia to the south of their current distributions, but not significantly closer to their non-breeding ranges, which were concentrated around the equator. As such, long-distance migrants are unlikely to have recently undergone changes to their migratory journeys of a similar scale or rate of to those predicted by the end of the 21st century. However, potential changes to species' climatic niches and the influence of inter-specific competition should be incorporated into future predictions of palaeodistributions.

Chapter 6

General Discussion

A Motus receiving station at Spurn Bird Observatory, part of the wider Motus Wildlife Tracking System – a potential future avenue for the year-round tracking of even the world's smallest long-distance migratory birds. *Photo credit: Jonnie Fisk*

6.1 Summary

Climate change has rapidly become a major global driver of biodiversity loss (IPBES, 2019). In this thesis, I investigated the impacts of climate change on long-distance migratory birds, which represent a rapidly declining and particularly susceptible group of species, the latter due to their complicated annual cycles (Robbins et al., 1989; Runge, Watson, et al., 2015; Sanderson et al., 2006). More specifically, I examined the impacts of changes in climate on migrants under three general subject areas: (1) the phenology of migration, (2) population trends, and (3) migratory journeys. In all three cases, I worked with large-scale multi-species and multi-region datasets to provide consensus on patterns and drivers of change and contribute to our understanding of migratory species and their population and range changes. This approach contrasts with many other studies that focus on either individual or small numbers of species, and which typically explore impacts on only one component or areas of a migrant's annual cycle. To date, most studies of migrants have occurred in Europe and North America and typically focused on changes on the breeding range (though increasingly, with satellite-tagging advances, migratory journeys are being explored). Consequently, our understanding of the past, present, and potential future threats and changes to long-distance migrants has been limited. This has ultimately restricted our ability to reverse or, more preferably, prevent the widely documented declines of recent decades. By utilising a variety of datasets and statistical/analytical techniques, I have filled some clear knowledge gaps and, in doing so, have improved the holistic understanding of the impacts of changes in climate on these species. In this chapter, I summarise and synthesise my main findings and their implications for the understanding of changes to long-distance migratory populations, before identifying avenues for potential further study.

6.1.1 The phenology of migration

By studying the phenology of long-distance migration away from the breeding grounds in Chapter 2 (Lawrence et al., 2021), I identified that species are able to advance the timing of departure from their tropical non-breeding grounds prior to breeding, in response to phenological changes on the breeding grounds. This finding highlights that advancement in the arrival of individuals on the breeding grounds, and therefore breeding dates, is not entirely driven by increased migration speeds as individuals approach the breeding grounds and can cue into the phenology of these habitats (Altwegg et al., 2012; Gill et al., 2013; Newson et al., 2016; Post et al., 2018). Instead, populations are adapting their departure to breeding habitats even when on another continent, either through selection for earlier migration individuals or individual plasticity in response to environmental cues correlated with conditions on the breeding grounds

(Emmenegger et al., 2014). This may provide species with some adaptive capacity to respond to further changes in climate and avoid further disruption of phenological trophic relationships on the breeding grounds and, consequent population declines. However, these advances have been suggested to be limited to some extent by food availability prior to departure and by weather conditions encountered on migration (Pulido, 2007; Studds & Marra, 2011; Chapter 2). Due to the ongoing deterioration and desertification of tropical habitats, attributed to both climate- and land-use change, in addition to the increasing frequency of storms, species may be limited in their ability to continue to advance the timing of their pre-breeding migration and, therefore, arrival on the breeding grounds (Biasutti, 2019; IPCC, 2021; Marra et al., 2005; Newton, 2004). As a result, the reproductive phenologies of long-distance migrants may become further mismatched with that of their breeding habitats, leading to declines in breeding productivity and, therefore, populations.

In Chapter 2 I also found that longer temperate growing seasons and later senescence of tropical resources have enabled species to delay the timing of their post-breeding migration, both in terms of arrival at tropical non-breeding and passage through temperate stopover sites. Together, these trends have resulted in long-distance migratory birds now spending significantly more of the year within their breeding ranges and, therefore, less of the year on the non-breeding grounds than they did 60 years ago – a previously unreported phenomenon. Continuation of these trends could eventually result in populations of some long-distance migrants remaining within the temperate realms year-round, essentially becoming short-distance migrants, as has happened in recent decades with mixed strategy migrants, such as the Eurasian Blackcap *Sylvia atricapilla* in the UK and White Storks *Ciconia ciconia* within Europe (Berthold et al., 1992a; Cheng et al., 2019). Given short-distance migratory populations have typically performed better than those of long-distance migrants, this could result in a more positive outlook for the latter (Robbins et al., 1989; Sanderson et al., 2006). By spending the non-breeding period closer to the breeding grounds, populations are likely to benefit from: (1) a better ability to judge conditions on the breeding grounds and reduce their level of reproductive phenological mismatch and (2) reduced mortality associated with shorter migration distances (Lemoine & Bohning-Gaese, 2003; Møller et al., 2008; Sillett & Holmes, 2002). Again, however, the ability of many species to adopt this strategy is unknown and the actual outcome is likely to be species-specific, depending on their climatic tolerances and the determinants of current migration schedules. Further study of the timings of pre- and post-breeding migration and their drivers is required from non-breeding and passage areas. First, to assess the consistency of these trends in other species and locations within the Afro-Palearctic flyway, in addition to the Americas and

Australasia, but also to identify those species that are likely capable of adopting this “short-stopping” strategy.

6.1.2 Population trends

By using population data from the NABBS (Sauer et al., 2020) and the PECBMS (https://pecbms.info/) in Chapter 3, I found that, over the last 40 years, long-distance migrants have declined more rapidly than their short-distance counterparts in both Europe and North America. Taking a holistic approach, I then identified that the drivers of these trends also seem to be consistent across the two continents. Climate on the breeding grounds is an important driver of migrant population trends, more so than land cover (Howard et al., 2020; Mason et al., 2019; Stephens et al., 2016). This is despite a wealth of evidence suggesting that land cover modifications, such as those resulting from the intensification of agriculture, have driven major declines of some species (Donald et al., 2006; Gregory et al., 2019). On the non-breeding grounds, the converse is true, and climate did not appear to contribute significantly to the state of breeding populations (Howard et al., 2020; Vickery et al., 2014). Again, this contrasts with well-documented impacts of rainfall on the non-breeding grounds impacting survival and subsequent productivity (Atkinson et al., 2014; Sanderson et al., 2006).

It is apparent that changes in climate, as well land-use, have contributed to the declines of long-distance migrants, with the rate and magnitude of change seemingly too rapid for species to adapt in-situ. Given that the climate will continue to change globally, and the growing human population will continue to increase demand for resources, long-distance migrants face continued declines (IPBES, 2019; IPCC, 2021). These findings are informative, not only for our understanding of the declines of migratory birds, but for the implementation of conservation action and policy. With knowledge of the major threats, species most at risk could be identified and conserved. Governments, conservation non-governmental organisations (NGOs), and protected area managers must collaborate to identify the best practices to do so. On the breeding grounds, protected area design should consider the need for suitable climate in future, identifying and protecting those areas in which species may persist unthreatened from climate change. The ability of microclimate refugia to preserve species, in situ, on a smaller scale also needs to be explored. Potentially most importantly, stakeholders, and particularly NGOs, need to proactively explore the possibilities for habitat protection in tropical non-breeding areas. In contrast to the breeding grounds, focus on intensive protection of a few sites is likely to be unsuccessful, given the high migratory dispersion and low connectivity exhibited by long-distance migrants. Instead, it has been suggested that widespread, shallow “land-sharing” strategies may be more effective (Vickery et al., 2023). However, the practicalities and cost-effectiveness of implementing these measures must be investigated.

6.1.3 Migratory journeys

Looking to the future, in Chapter 4 I showed that predicted increases in migration distance, stopover number and the overall duration of migratory journeys by the end of the century will threaten not only long-distance migratory birds in the Afro-Palearctic flyway, but those in all three major migratory flyways across the globe (Howard et al., 2018). In contrast, the migratory journeys of short-distance migrants were predicted not to change. These changes are likely to have significant negative impacts for populations of long-distance migrants. Longer migrations would likely lead to greater mortality, as migration represents the period of lowest survival through the annual cycle (Rushing et al., 2017; Sillett & Holmes, 2002). Furthermore, longer migrations are likely to exacerbate the likelihood of phenological mismatch, as breeding- and non-breeding ranges move further apart, which could result in declines in productivity (Both et al., 2006; Møller et al., 2008). The identification of these trends before they have occurred could enable proactive conservation, in addition to simple recognition of the threat. For example, protection of important areas along migratory routes may help species to complete these longer migrations, providing habitats of better quality with more resources for refuelling.

Looking into the past, I found that long-distance migration is likely to have persisted as a global phenomenon back to the last glacial maximum (LGM) and continued through the current inter-glacial, as has been previously suggested (Somveille et al., 2020). This is despite major reductions in the size of breeding ranges compared to today, as species were restricted to southern glacial refugia. Since the LGM, breeding ranges have expanded poleward, and migration distances have increased as a result. Moreover, these increases in migration distance between the LGM and the present day were predicted to have been greater than those projected to occur between the present day and the end of the current century for the world's long-distance migrants. Thus, given past changes to the scale and (in all likelihood) routes of migration, long-distance migrants may display some adaptive capacity to future changes to migratory journeys. However, it is important to note that those past increases in migration distance occurred at a much slower rate than will be required in future. Furthermore, they occurred due the colonisation of newly available habitat, which saw species increase their range size and expand their populations (Miller et al., 2021). In contrast, predicted future changes would be the result of a rapid, forced range shifts, with many species' breeding ranges contracting (Howard et al., 2018; Huntley et al., 2007). Therefore, the level of adaptation to these further changes is likely to be limited.

6.2 Synthesis

Climate change has impacted and will likely continue to impact populations of long-distance migratory birds in a myriad of ways. Whilst species display some adaptive capacity to these changes through behavioural and distributional responses, these may remain insufficient for the rate and magnitude of change. Such responses may be limited by external pressures, including the effects of land-use change, or themselves bring about further negative impacts, i.e. range shifts leading to longer migratory journeys. This highlights the inequality in the level of threat posed to long-distance migrants by climate change, compared to their resident and short-distance migratory counterparts – a trend which is also likely to apply to taxa other than birds.

Short-stopping represents a feasible adaptation strategy that would likely enable long-distance migrants to alleviate/avoid many of the negative impacts of climate change. By adopting short-distance migratory strategies and spending the non-breeding period closer to the breeding grounds, populations are likely to be more in tune with the phenology of breeding habitats and are likely to suffer lower mortality on migration. As mentioned throughout this thesis, migratory behaviour is an inherently plastic trait, with its initial evolution enabling species to exploit year-round optimal conditions (Somveille et al., 2018). Migration has continued to evolve through history, changing dependent on environmental conditions (Somveille et al., 2020). Species have moved freely along the resident to long-distance migrant continuum, with populations taking on partial and short-distance strategies along the way. At the height of the last glacial maximum, migratory journeys are likely to have been significantly shorter, as areas suitable for breeding were located closer to the equator (Chapter 5). In this century, it is areas suitable during the non-breeding season that may be shifting. Warmer climates and increased food availability have enabled previously obligate long-distance migratory species to adopt partial migratory strategies, with positive fitness consequences (P. Berthold et al., 1992; Cheng et al., 2019; Soriano-Redondo et al., 2023). Considering this known plasticity alongside observed trends in occupancy of the breeding and non-breeding areas (Chapter 2), it is not out of the realms of possibility that many more species will begin to "short-stop". However, given the lack of evidence of demographic impacts of such behavioural changes, future conservation planning must account for the increased vulnerability of long-distance migrants, or we are likely to witness the continued rapid decline of migratory species, with major impacts on global biodiversity and its associated ecosystem services.

One small positive to take is that consistency in the drivers of decline across flyways may, at least, enable collaboration between researchers and practitioners to conserve these species using similar measures in otherwise disparate locations.

Moreover, these measures may be implemented proactively, rather than reactively, stopping declines before they have begun.

Despite the progress made in this thesis towards understanding the impacts of climate change on long-distance migratory birds, several questions remain. Many revolve around limitations in the currently available data used to explore such impacts. Over the last 30 years, our understanding of the annual cycles of these species, and the impacts of climate change on them, has increased rapidly through greater access to data related to individual movements, population trends/distributions, and remotely sensed environmental variables. However, we must now increase our understanding of the impacts of climate change at smaller scales, particularly at the individual or sub-continental population level. Such study would alleviate the effects of intra-specific variation in phenology and demography, as well as low migratory connectivity, which might otherwise lead to an apparent decoupling of climate change and its impacts (Finch et al., 2017; Howard et al., 2020). Unfortunately, due to such intra-specific variation, this level of study requires a wealth of spatially and temporally fine-scale species data, which is currently limited. If we are to further our understanding of population declines and address them, we must first expand the data available for study.

6.2.1 The need for additional data

Currently, the lives of long-distance migrants away from the breeding grounds are likely to present the most basic gap in our knowledge. This paucity is not limited to just one trait but includes species' phenologies, habitat requirements, and even distributions (Howard et al., 2020; Lawrence et al., 2021; Vickery et al., 2014, 2023). Whilst some study has occurred in tropical regions, their sheer vastness and lack of recording means sizeable knowledge gaps still exist. Non-breeding distributions represent an area where our knowledge is particularly lacking and an area where additional data might improve our understanding of the impacts of climate change. Currently, the best available presence/absence distributional data for the world's long-distance migratory birds, required for modelling studies like those of Chapters 3, 4, and 5, is only available to the level of the entire season, i.e., breeding or non-breeding (Birdlife International and NatureServe, 2016). However, during the non-breeding season long-distance migrants are itinerant, tracking resource peaks. This may result in them only occupying a small proportion of the overall distribution at any one time (Cresswell et al., 2009; Renfrew et al., 2013; Thorup et al., 2017). As such, whilst SDMs built on such seasonal distribution data may appear to predict the distributions of species well, they likely lose much of the nuance of the relationship between species' distributions and environmental variables (Runge et al., 2015). Therefore, simulated values of climatic suitability of areas that are built from SDMs using the entire non-breeding polygons (i.e., assuming all cells are continually occupied during the non-breeding season and across years), as in Chapter 3, are likely to be less closely tied to the population trends than models based on the real usage of such areas. Rigorously collected data on intra-seasonal distributions on the non-breeding range are currently lacking for most species, though the rapid expansion of citizen science recording schemes, such as eBird (Sullivan et al., 2009), may well provide such data soon. A better understanding of intra-seasonal movements would likely improve models and hence aid in diagnosing the impacts of non-breeding ground climate on migrant populations.

Another key factor in better understanding population changes is the connectivity of breeding and non-breeding populations; that is, the extent to which separate breeding populations overlap and intermix during the non-breeding season (Finch et al., 2017; Lemke et al., 2013). Again, such data is lacking for most species and, therefore, despite possessing sub-continental level population data from North America and Europe, we remain unable to link these breeding sub-populations to specific non-breeding areas. Given that changes in abundance are non-uniform across the breeding range (Brlík et al., 2021; Sauer et al., 2020), utilisation of continent-level population data (Chapter 3) in analyses is likely to dilute the signals of climate change and land-cover trends on population trends, as these changes are averaged out over a wider area. This lack of data also presents challenges for the accurate simulation of migration. For example, to link specific breeding and non-breeding populations in Chapters 4 and 5, I identified the longitudinal boundaries of the three major global migratory flyways: the Americas, Afro-Palearctic and Australasian flyways (BirdLife International, 2010). Whilst this may accurately represent the migratory pathways for most species, there are likely to be some situations where this is not the case, especially at the boundaries of these flyways. In these cases, the length of migratory journeys may be less accurately estimated, especially when considering pre-historic or future climatic scenarios. Models built on species' global or broad flyway distributions can identify the loss or gain of suitable climate for that entire species or flyway population. However, if migratory populations function at smaller scales, i.e., the sub-continent level, individuals of different populations are likely adapted to localised climates and will, therefore, respond differently to climate change (Both et al., 2010). By projecting distributions at the level of the three flyways, changes in range size and migratory journeys for specific populations may be overlooked.

Knowledge of the degree of linkage between breeding, non-breeding and intermediate stopover sites has also likely limited the assessment of the environmental cues, drivers and limiting factors of migratory journeys, population changes and phenological changes. Studies typically relate the timing of migration to environmental factors measured over wide areas, as I did in Chapter 2 (Balbontín et al., 2009; Gordo & Sanz, 2008; Saino et al., 2007). As with continental population data, phenology-covariate relationships are likely to be diluted using such coarse scale data. Knowing the likely non-breeding sites and stopover locations of migrants arriving at specific breeding sites, or vice versa, would enable the calculation of environmental variables most relevant to the phenology of that population.

There is a paucity of information of all types from across the non-breeding and stopover locations, and on the connectivity of populations among sites. However, even on the breeding grounds data are lacking. This is particularly true in relation to the Australasian flyway (Allcock et al., 2022). This has precluded the assessment of recent population trends of migrants in this flyway and of the potential drivers of any changes, at least on the scale possible in Europe and North America (Kirby et al., 2008). Furthermore, until very recently, migratory phenology had received little to no attention in the Australasian flyway, owing to the lack of long-term data (Allcock et al., 2022). Many species of long-distance migrant in the Australasian flyway are declining, and land-use change and the illegal taking of birds are often cited as causal factors (Amano et al., 2010; Sutherland et al., 2012; Yong et al., 2021). However, the spatial and taxonomic extent of these declines, their severity compared to those of residents and short distance migrants, and the involvement of climate change is relatively unknown. To further assess the consistency of trends observed in Europe and North America, detailed study of long-distance migratory populations in the Australasian flyway is needed.

Overall, there are multiple gaps in the data available to help understand migratory processes. Filling these gaps will lead to additional insight and improved understanding of the impacts of climate change and of other drivers on bird populations. In the following section, I highlight some areas of data needs for migrant birds and the additional insights such information could provide.

6.3 Future work

Advancements in technology continue to present opportunities to further the fields of ecology and conservation, with automated recording of environmental and species data increasing the potential scope and scale of research. Technologies used to track individual birds, specifically, are providing data from long-distance migratory birds that was, until very recently, unattainable (Robinson et al., 2010; Vickery et al., 2023). PTT and GPS tags can provide instantaneous data (accurate down to a few metres for the latter) due to their communication with satellites. However, such real time access requires considerable battery power and, therefore, a sizeable battery, which precludes their use on the smallest species (Vickery et al., 2023). Non-archival GPS tags and geolocators weigh considerably less, some down to less than half a gram (Bridge et al., 2011). However, access to data requires the retrieval of tags, which can often prove challenging. From a practical standpoint, many of these tags also remain expensive, making it unfeasible for any one project to track large numbers of individuals. Therefore, at current, a balance of weight, cost and recovery rates preclude the tracking of a sufficient numbers of individuals to provide population-representative data, especially of the smallest passerines (Vickery et al., 2014). However, they still can, and have, provided invaluable data on the timing and locations of many species' movements (e.g. Fraser et al., 2017; Hewson et al., 2016; Renfrew et al., 2013; Thorup et al., 2021). Moreover, it is anticipated that further miniaturization of many of these tags and the expansion of projects such as ICARUS and Motus will enable their use on an even broader range of species, therefore presenting an exciting prospect for further research (Taylor et al., 2017; Vickery et al., 2023; https://www.icarus.mpg.de/en). In fact, the previously identified need for intra-seasonal and population-specific non-breeding distributions are likely only identifiable through such technology. Genoscape analyses, i.e., the linkage of breeding and non-breeding populations using genetic data, also present a viable option to assess migratory connectivity, without restriction to large species or the need to recapture individuals (Bay et al., 2021; Ruegg et al., 2020). Although, such analyses would still require the capture of large numbers of individuals during the non-breeding period.

Tracking technologies also provide the opportunity for more detailed study of the phenology of migration. Migration data from individuals can be used to assess changes in migration speed (Briedis et al., 2018; McKinnon et al., 2016; Ouwehand & Both, 2017), something which is not feasible using population-wide data. Tracking could also permit more accurate assessment of, for example, time spent on breeding and non-breeding grounds and the location of refuelling stopovers on migration. Moreover, repeated tracking of individuals over multiple years would provide information on individual inter-annual plasticity in departure dates and migration speeds, and whether trends in migration advancement/delay are likely due to selection for certain migration schedules (Gill et al., 2013). Such changes could be related to the environmental conditions encountered by individuals. Analyses at this fine scale are likely to retain the nuance of the relationships between climate and migratory phenology (Bauer et al., 2008; Thorup et al., 2017), as the influence of temporal and spatial variation in conditions/timings is avoided. At its most holistic, individual data could be combined with nest records to assess the impacts of climate across the whole annual cycle, including productivity, to more clearly identify the mechanism behind population changes. Such mechanisms might include carry-over effects from the non-breeding grounds or migratory period on productivity versus the impacts of changing resource availability on the breeding grounds.

At present, even the most advanced models of bird migration under climate change that have been widely applied assume linear migration, i.e. they consider the great circle distance between two points in the breeding and non-breeding ranges (Howard et al., 2018; Zurell et al., 2018). Yet many long-distance migrants make large deviations from the shortest migratory path and follow different routes in spring and summer (Jacobsen et al., 2017; Schmaljohann et al., 2012). Prevailing winds, resource availability, and barrier avoidance are suggested to influence these migratory strategies, though these impacts have seldom been quantified (Newton, 2008). Tracking of species-specific migratory routes and stopover locations could be used to analyse such relationships, which in turn could be used to inform migration simulation. Mechanistic models, another technique growing in utilisation due to computational advancements, could provide the means to implement such variables into simulations (Bauer & Klaassen, 2013). This would likely require the collection of additional data from several locations for model development, such as the rate of pre-migratory fattening, and more detail on variation migratory paths and refuelling stopovers, in combination with remote-sensed earth observation data. Such data might permit the development and testing of more biologically realistic simulations of past and recent migratory journeys, which in turn could inform realistic future migration simulations. Such models could be used to provide far more informative simulations than the straight-line routes currently used. For example, whilst the simulations of migration presented in Chapter 4 indicate that species could adopt short-stopping strategies in future, this was based purely on the climatic suitability of regions and did not account for the feasibility of the necessary migratory journeys to move between locations. Given the predicted future changes to climate and land-use it is highly likely that the current localities of potential refuelling sites for long-distance migrants will alter in future. Mechanistic models of migration, built to maximise the fitness of individuals, could account for this, and assess the likelihood of adopting altered strategies by the end of the century. Furthermore, such models would provide the opportunity to identify whether future changes to migratory journeys would increase the passage of species through areas of high hunting or persecution pressure or those proposed for development of infrastructure with which migrating birds could collide. They could also be used to identify current and future important stopover locations and assess their current level of overlap with protected areas.

Finally, future assessments and predictions of the impacts of climate change on long-distance migratory species should also consider the increasingly interacting threat of land-use change (Mantyka-Pringle et al., 2012). The IPBES identified this as the main global threat to biodiversity and an ever-growing human population is only likely to contribute further to this (IPBES, 2019). In Chapter 3, land-use was shown to be potentially a more important driver of population trends than climate in non-breeding areas in both the Americas and Afro-Palearctic flyways. This finding is reinforced by a wealth of studies highlighting the impacts of habitat loss on long-distance migratory birds (Atkinson et al., 2014; Sanderson et al., 2006). Such considerations are likely to require further study of species' habitat requirements, particularly how similar land cover types of different quality affect their suitability for species. For example, the decline of many populations has been attributed to the expansion of agriculture. However, much habitat degradation now appears to be occurring along management intensity gradients, through processes such as drainage, woodcutting, grazing and pesticide use, rather than overt losses (Kuemmerle et al., 2016; Rounsevell et al., 2012; Sleeter et al., 2013). Therefore, despite much land being categorised as agricultural, the quality for species can vary greatly. Without detailed knowledge of such relationships, we are unable to assess the true impacts of land-use change on species population trends.

6.4 Conclusions

In this thesis, I have contributed valuable information for the understanding of the impacts of climate change on the phenology, abundance, and migratory journeys of long-distance migratory birds. I demonstrated that species possess some adaptive capacity to these changes, though the extent to which these will enable species to avoid further population declines requires further research. Nonetheless, without appropriate conservation intervention, long-distance migrants are likely to continue to decline. Reversal of the global declines in biodiversity will require a concerted effort to conserve migratory species across a variety of taxa. Whilst this should be possible in theory, the knowledge base required to do so is still not complete, and largely limited by a lack of information on species away from their breeding grounds. However, I have identified clear pathways to increase our understanding of the annual cycles of long-distance migrants and, therefore, the impacts of climate change on their population trends at a finer scale. Such understanding should enable more tangible efforts to conserve long-distance migratory species across the globe, especially through the increased collaboration of researchers, practitioners, and policymakers.

Appendices

Table S1: Species list for which observation data were collected in The Gambia, additionally highlighting their inclusion (Y) or exclusion (N) from the Gibraltar dataset.

Species	**Common Name**	**Included in Gibraltar data?**
Acrocephalus scirpaceus	Eurasian Reed Warbler	Y
Anthus trivialis	Tree Pipit	Y
Ficedula hypoleuca	Pied Flycatcher	Y
Hippolais polyglotta	Melodious Warbler	Y
Iduna opaca	Western Olivaceous Warbler	N
Lanius senator	Woodchat Shrike	Y
Luscinia megarhynchos	Common Nightingale	Y
Motacilla alba	White Wagtail	N
Motacilla flava	Western Yellow Wagtail	N
Muscicapa striata	Spotted Flycatcher	Y
Oenanthe oenanthe	Northern Wheatear	N
Phoenicurus phoenicurus	Common Redstart	Y
Phylloscopus bonelli	Western Bonelli’s Warbler	Y
Phylloscopus collybita	Common Chiffchaff	N
Phylloscopus trochilus	Willow Warbler	Y
Saxicola rubetra	Whinchat	Y
Sylvia atricapilla	Eurasian Blackcap	N
Sylvia borin	Garden Warbler	Y
Sylvia cantillans	Western Subalpine Warbler	Y
Sylvia communis	Common Whitethroat	Y

Table S2: Yearly start and end dates to standardised spring and autumn bird ringing at Gibraltar bird observatory.

Year	**Spring**		**Autumn**	
	Start	**End**	**Start**	**End**
1991	-	-	04-September	25-November
1992	02-January	18-May	10-July	08-November
1993	17-January	25-May	24-July	19-December
1994	29-January	23-June	28-July	26-December
1995	08-January	22-May	23-July	28-October
1996	19-February	27-April	03-August	27-October
1997	08-March	23-May	06-July	06-December
1998	19-February	22-April	13-July	18-December
1999	16-February	26-May	08-July	26-November
2000	03-January	15-May	27-July	19-December
2001	23-March	27-April	21-July	08-December
2002	21-January	15-May	28-July	08-November
2003	03-February	01-May	27-June	25-November
2004	31-January	01-May	29-August	27-November
2005	01-February	08-June	23-August	19-November
2006	19-January	07-June	24-August	30-November
2007	18-January	09-June	19-September	27-November
2008	24-January	23-April	02-October	07-December
2009	27-January	05-May	20-September	02-November
2010	24-January	07-May	02-October	13-November
2011	19-January	11-May	14-July	26-October
2012	04-January	03-May	15-September	15-November
2013	03-February	02-May	01-August	10-November
2014	26-January	01-May	25-September	20-November

2015	07-February	28-April	18-September	20-November
2016	28-January	13-May	14-September	05-November
2017	12-February	03-May	27-September	02-November
2018	13-February	11-May	14-September	24-November

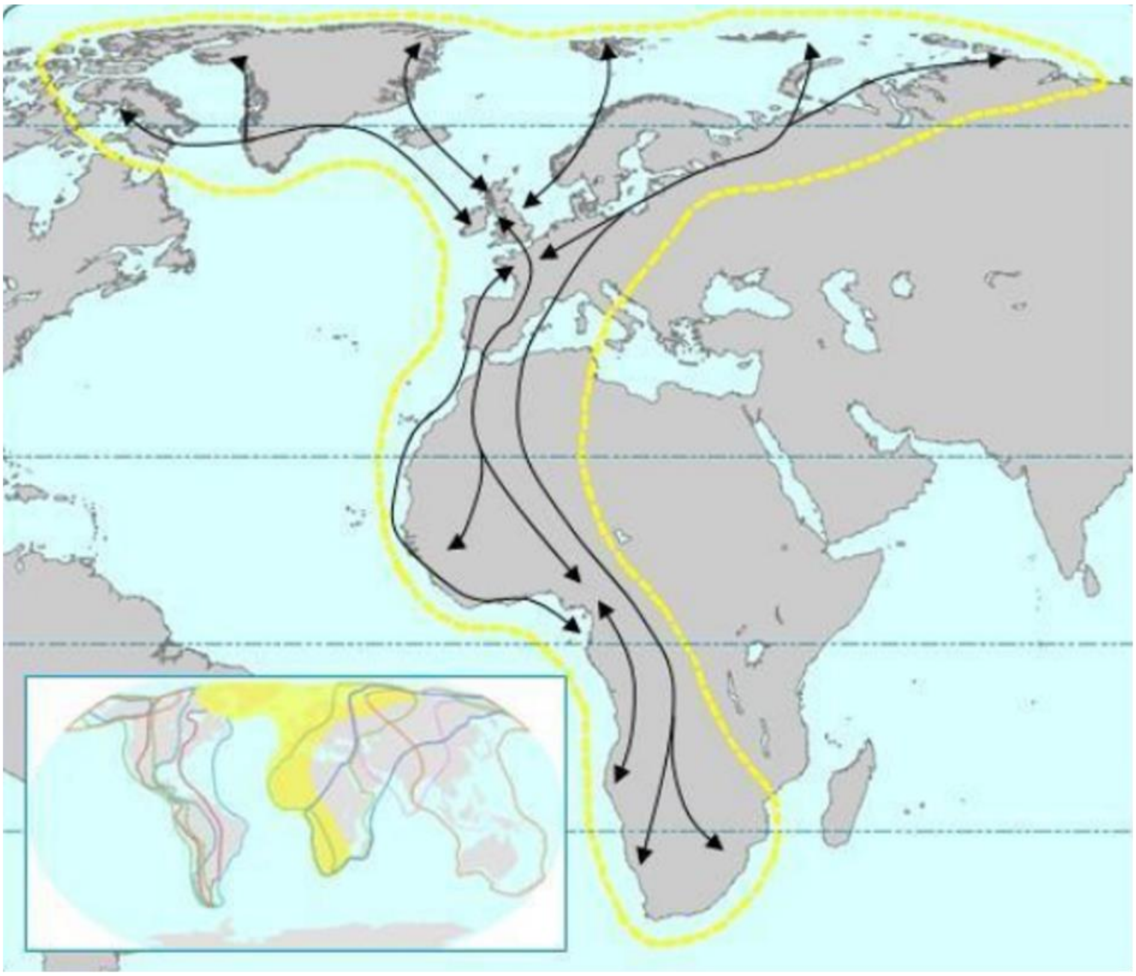

Figure S1. The east-Atlantic flyway (surrounded by dashed yellow line). Inset shows position (highlighted) relative to seven other main flyways (from BirdLife International, 2010).

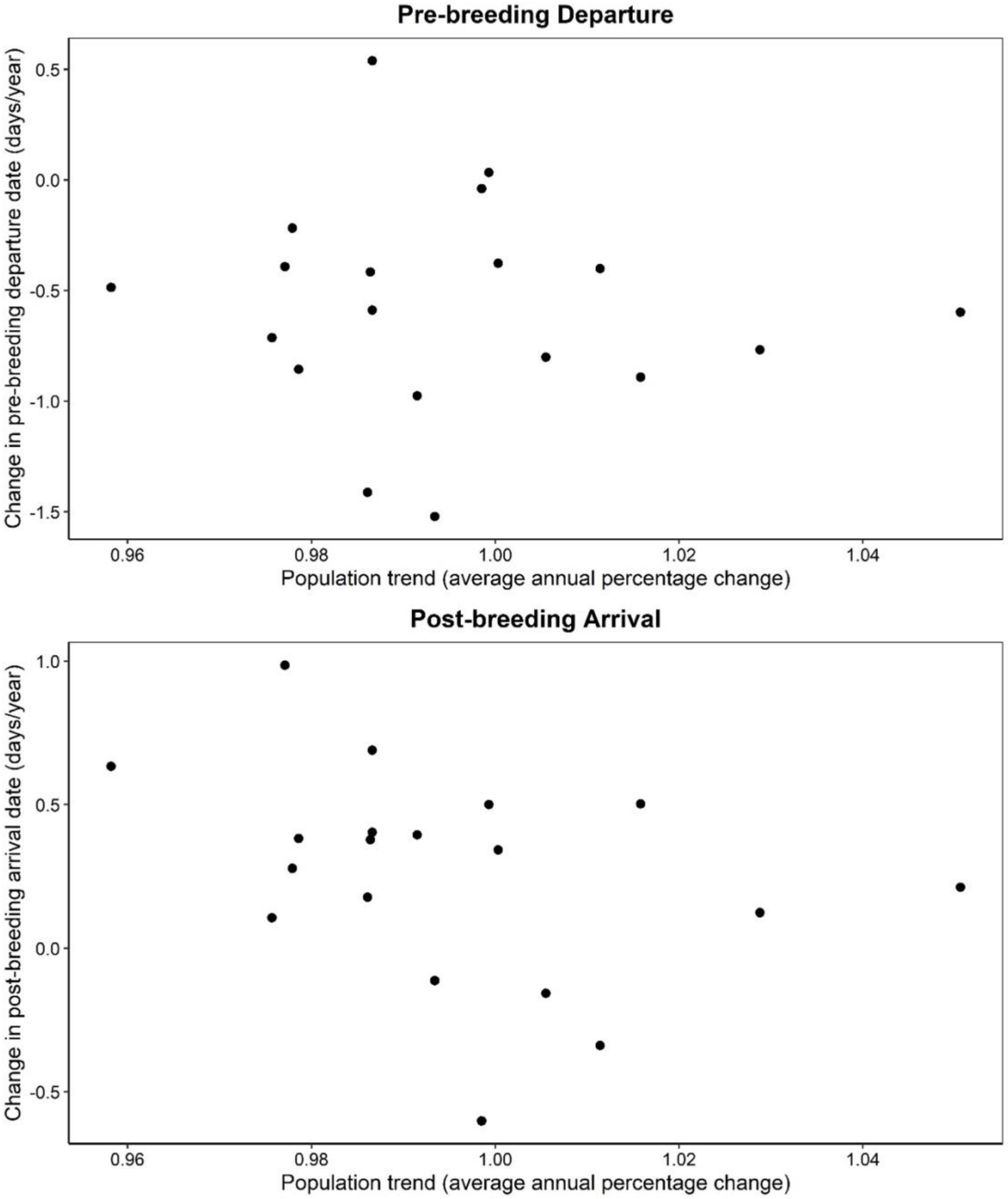

Figure S2: Relationships between migration date and population trends, for pre-breeding departure (B = -1.74, p = 0.76) and post-breeding arrival (B = -6.11, p = 0.15) in The Gambia. Western Olivaceous Warbler was not included in this analysis as population trends were not available.

Table S3: Mean months of arrival and departure at The Gambia and Gibraltar. For the latter, mean months for first, last and median dates are given. A and B denote the first and second half of each month, respectively, which were required due to the fortnightly nature of the NDVI data.

Species	Gambia		Gibraltar			
	Last Departure	**First Arrival**	**First Arrival**	**Median Arrival**	**Median Departure**	**Last Departure**
Eurasian Reed Warbler	March B	October B	April B	May A	September B	October A
Tree Pipit	March B	October B	April A	April A	October A	October A
Pied Flycatcher	April B	September B	April A	April B	September B	October A
Melodious Warbler	April A	October A	April B	April B	September A	September B
Western Olivaceous Warbler	April A	September B	N/A	N/A	N/A	N/A
Woodchat Shrike	March B	November B	April A	April A	August B	September A
Common Nightingale	March A	October B	March B	April A	September B	October A
White Wagtail	March B	October B	N/A	N/A	N/A	N/A
Western Yellow Wagtail	April A	October B	N/A	N/A	N/A	N/A
Spotted Flycatcher	May A	October A	April B	May A	September B	October A
Northern Wheatear	March A	October B	N/A	N/A	N/A	N/A
Common Redstart	March B	October B	April A	April B	October A	October B
Western Bonelli’s Warbler	March A	November A	March B	April B	September A	September B

Common Chiffchaff	March B	October B	N/A	N/A	N/A	N/A
Willow Warbler	April B	September B	March B	April A	September B	October B
Whinchat	March B	October A	April B	April B	September B	October A
Eurasian Blackcap	April A	November A	N/A	N/A	N/A	N/A
Garden Warbler	April B	October A	April A	April B	September B	October B
Western Subalpine Warbler	March A	October A	March A	April A	September B	October A
Common Whitethroat	March B	October B	April A	April B	September B	October A

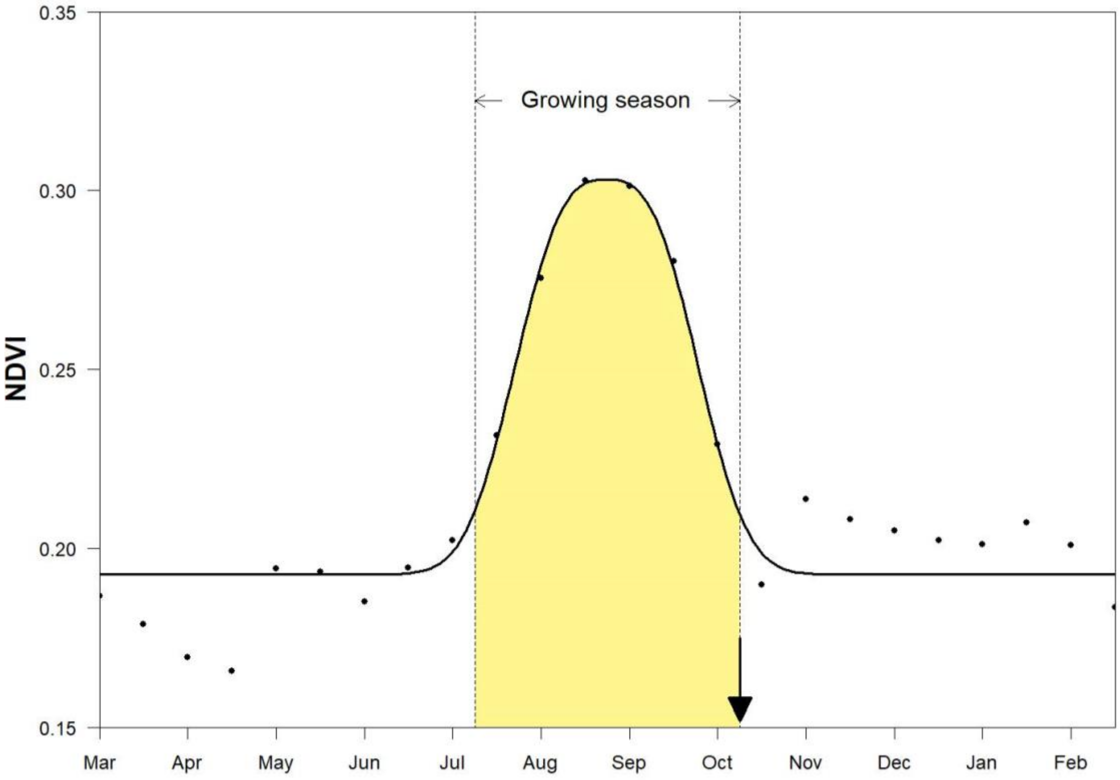

Figure S3: Example of smoothed function fitted to bi-monthly Sahelian NDVI data, from March 2000 to February 2001. The growing season (highlighted) is delineated by the two maximum second derivates (MSD) of the function, one prior to and one following the peak NDVI value. The date at which the second MSD occurred (bold arrow) was taken as the end of the Sahelian growing season.

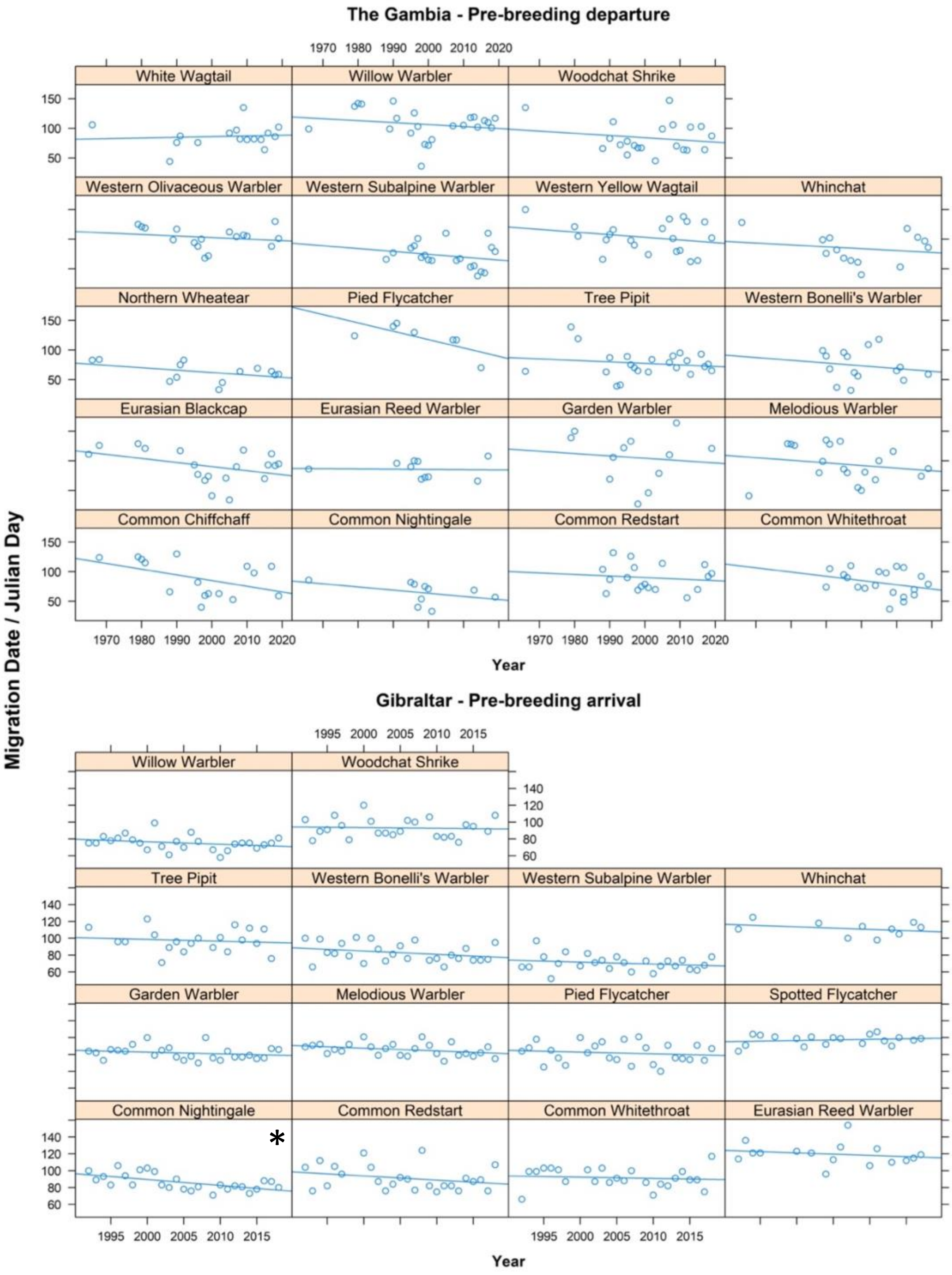

Figure S4: Individual species trends in yearly last pre-breeding departure dates at The Gambia and yearly first pre-breeding arrival dates at Gibraltar. Significant trends, i.e. $p<0.05$, are marked with an asterisk.

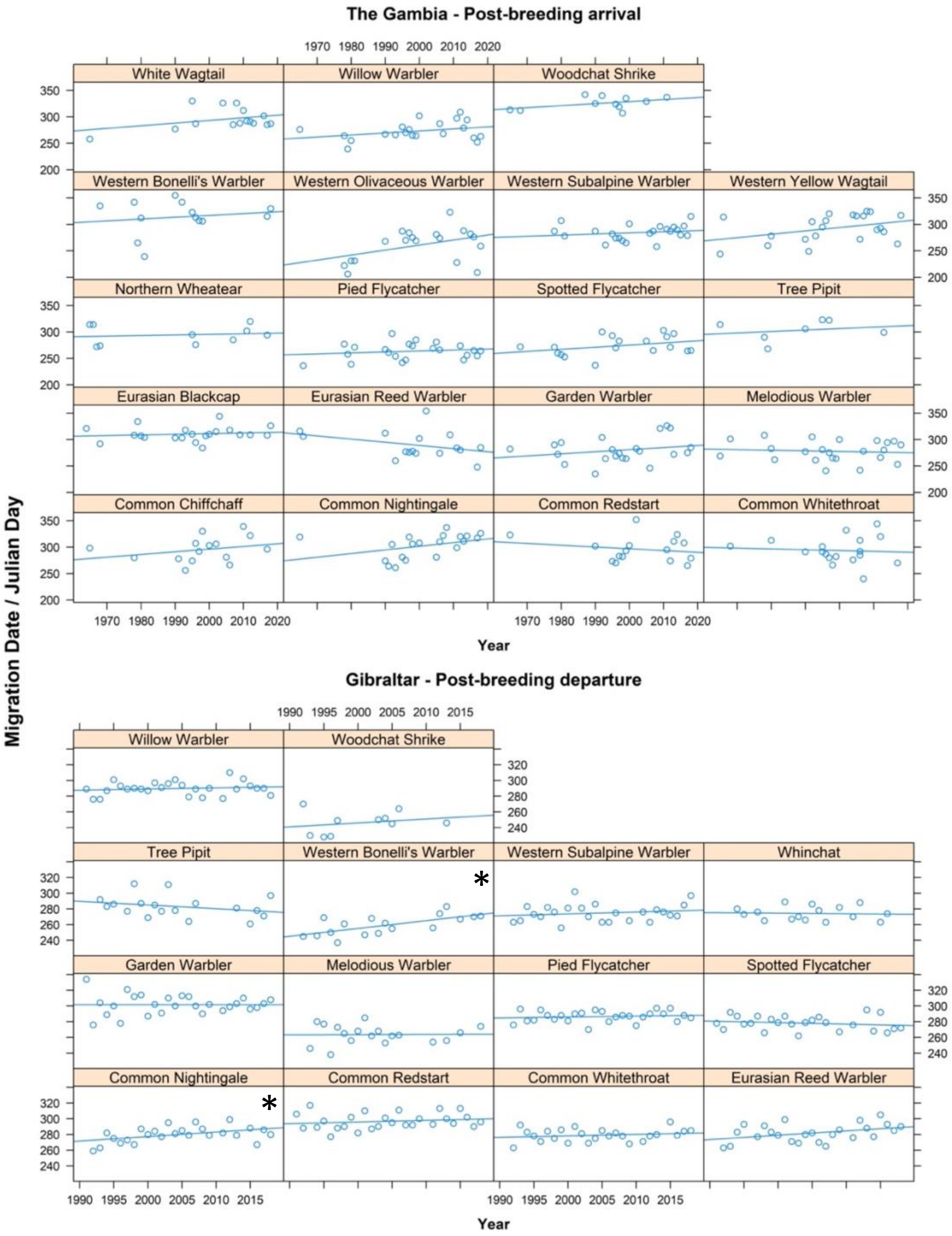

Figure S5: Individual species trends in yearly first post-breeding arrival dates at The Gambia and yearly last post-breeding departure dates at Gibraltar. Significant trends, i.e. $p<0.05$, are marked with an asterisk.

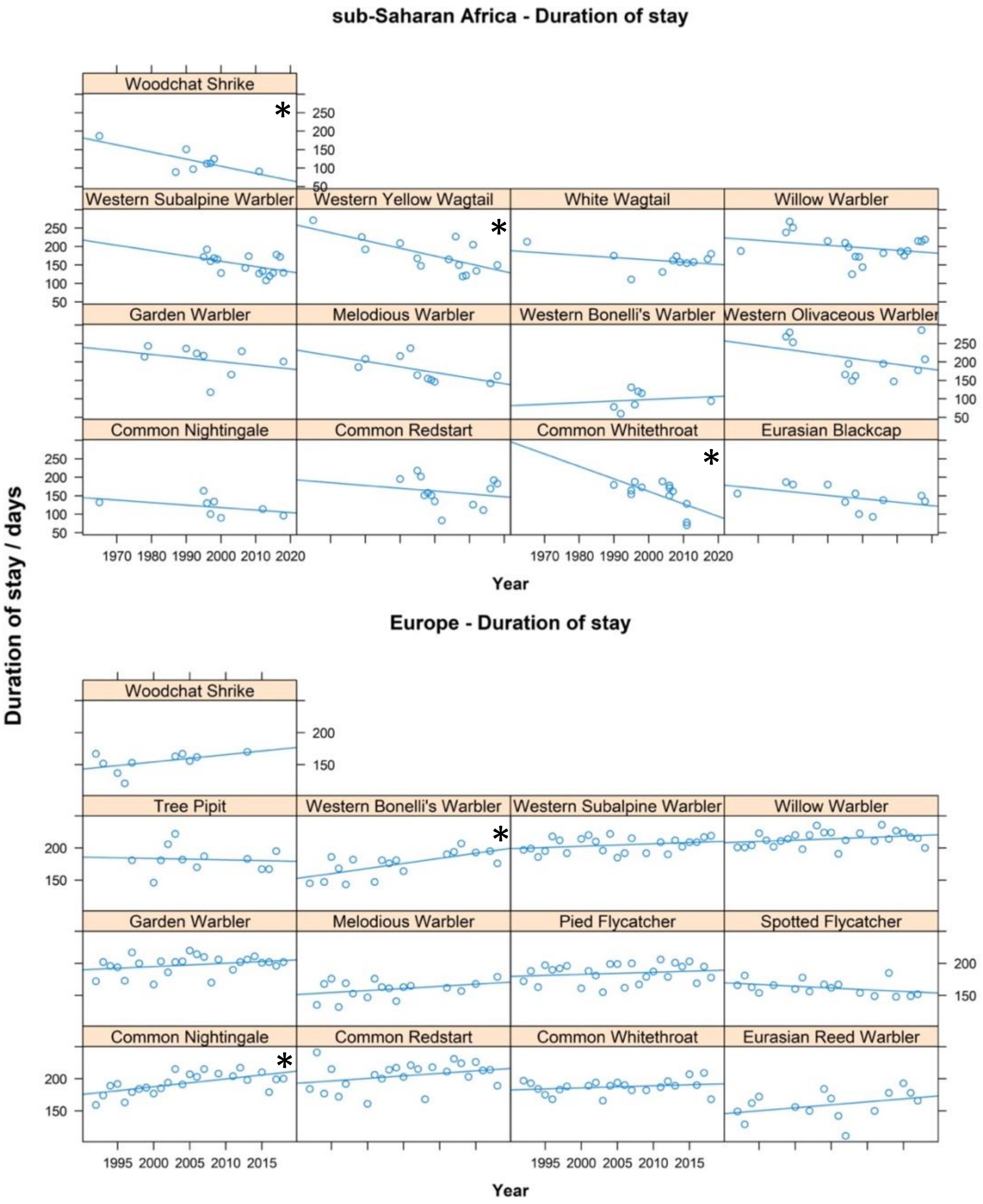

Figure S6: Individual species trends in yearly duration of stay in both sub-Saharan Africa and Europe, derived as the duration between first arrival and last departure in The Gambia and Gibraltar, respectively. Significant trends, i.e. $p<0.05$, are marked with an asterisk.

Table S4: List of species excluded from specific analyses, as a result of having less than six years of data in that analysis.

Analysis	**Location**	**Event**	**Excluded species**
Trend models	The Gambia	Pre-breeding departure	Spotted Flycatcher
		Post-breeding arrival	Whinchat
		Duration of stay	Common Reed Warbler Common Chiffchaff Northern Wheatear Pied Flycatcher Spotted Flycatcher Tree Pipit Whinchat
	Gibraltar	Pre-breeding arrival	N/A
		Post-breeding departure	N/A
		Duration of stay	Whinchat
Drivers models	The Gambia	Pre-breeding departure	Pied Flycatcher Spotted Flycatcher
		Post-breeding arrival	Tree Pipit Western Bonelli's Warbler Northern Wheatear Whinchat
	Gibraltar	Pre-breeding arrival	N/A
		Post-breeding departure	N/A

Table S5: Regression coefficients from phylogenetic linear mixed models, assessing trends in pre-breeding migration, post-breeding migration and duration of stay of migrants in The Gambia (1964-2019) and Gibraltar (1991-2018), using first arrival and last departure dates. Estimates represent change of timing in days per year. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

		Estimate	**Confidence Intervals**		**P-Value**	**λ**
			Lower	**Upper**		
PRBM	Gambia	-0.44	-0.63	-0.21	<0.001	0.45 (0.22, 0.68)
	Gibraltar	-0.28	-0.42	-0.14	<0.001	0.82 (0.68, 0.92)
POBM	Gambia	0.24	0.08	0.4	0.006	0.6 (0.41, 0.77)
	Gibraltar	0.19	0.05	0.34	0.02	0.8 (0.68, 0.92)
DoS	Gambia	-1.15	-1.59	-0.74	<0.001	0.71 (0.54, 0.90)
	Gibraltar	0.59	0.35	0.81	<0.001	0.77 (0.61, 0.9)

Table S6: Regression coefficients from phylogenetic linear mixed models, assessing trends in pre-breeding migration, post-breeding migration and duration of stay of migrants in Gibraltar (1991-2018), using median arrival and departure dates. Estimates represent change of timing in days per year. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

	Estimate	**Confidence Intervals**		**P-Value**	**λ**
		Lower	**Upper**		
PRBM	-0.27	-0.39	-0.15	<0.001	0.67 (0.49, 0.85)
POBM	0.22	0.08	0.37	0.006	0.65 (0.47, 0.84)
DoS	0.54	0.31	0.75	<0.001	0.62 (0.41, 0.83)

Table S7: Regression coefficients from phylogenetic linear mixed-models used to assess relationship between last pre-breeding departure dates in The Gambia and several meteorological variables. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

λ = 0.01 (0.00, 0.07)	**Estimate**	**95% Confidence Limits**		**P-Value**
		Lower	**Upper**	
Gambian Temperature	3.42	-0.28	7.2	0.06
NAO Index	-1.48	-4.86	2.12	0.37
Sahelian NDVI	-8.18	-12.17	-4.22	<0.001
Year	-5.3	-9.6	-1.56	0.01

Table S8: Regression coefficients from phylogenetic linear mixed-models used to assess relationship between first pre-breeding arrival dates in Gibraltar and several meteorological variables. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

λ = 0.74 (0.55, 0.92)	**Estimate**	**95% Confidence Limits**		**P-Value**
		Lower	**Upper**	
NAO Index	3.23	1.13	5.12	<0.001
North African NDVI	1.68	-0.17	3.51	0.08
North African temperature	1.16	-1.28	3.73	0.36
Sahelian NDVI	1.83	-0.39	3.83	0.1
Sahelian temperature	2.53	-2.27	7.34	0.31
Year	-1.75	-3.64	0.24	0.08

Table S9: Regression coefficients from phylogenetic linear mixed-models used to assess relationship between first post-breeding arrival dates in The Gambia and several meteorological variables. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

λ = 0.44 (0.16, 0.68)	**Estimate**	**95% Confidence Limits**		**P-Value**
		Lower	**Upper**	
European NDVI	0.4	-6.2	6.4	0.86
European temperature	1.99	-2.15	6.02	0.37
North African NDVI	-0.56	-5.88	4.7	0.8
North African temperature	-3.46	-8.48	1.4	0.16
Sahelian dry season	-1.74	-6.24	2.92	0.45
Year	5.89	-0.09	12.36	0.07

Table S10: Regression coefficients from phylogenetic linear mixed-models used to assess relationship between last post-breeding departure dates in Gibraltar and several meteorological variables. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

λ = 0.78 (0.64, 0.93)	**Estimate**	**95% Confidence Limits**		**P-Value**
		Lower	**Upper**	
European NDVI	-0.2	-1.87	2.13	0.89
European temperature	1.47	-0.34	3.28	0.09
Gibraltar NDVI	-0.48	-2.67	1.76	0.7
Gibraltar temperature	1.59	-0.91	3.87	0.19
Sahelian dry season	2.57	0.14	5.02	0.04
Year	-1.42	-4.04	1.02	0.27

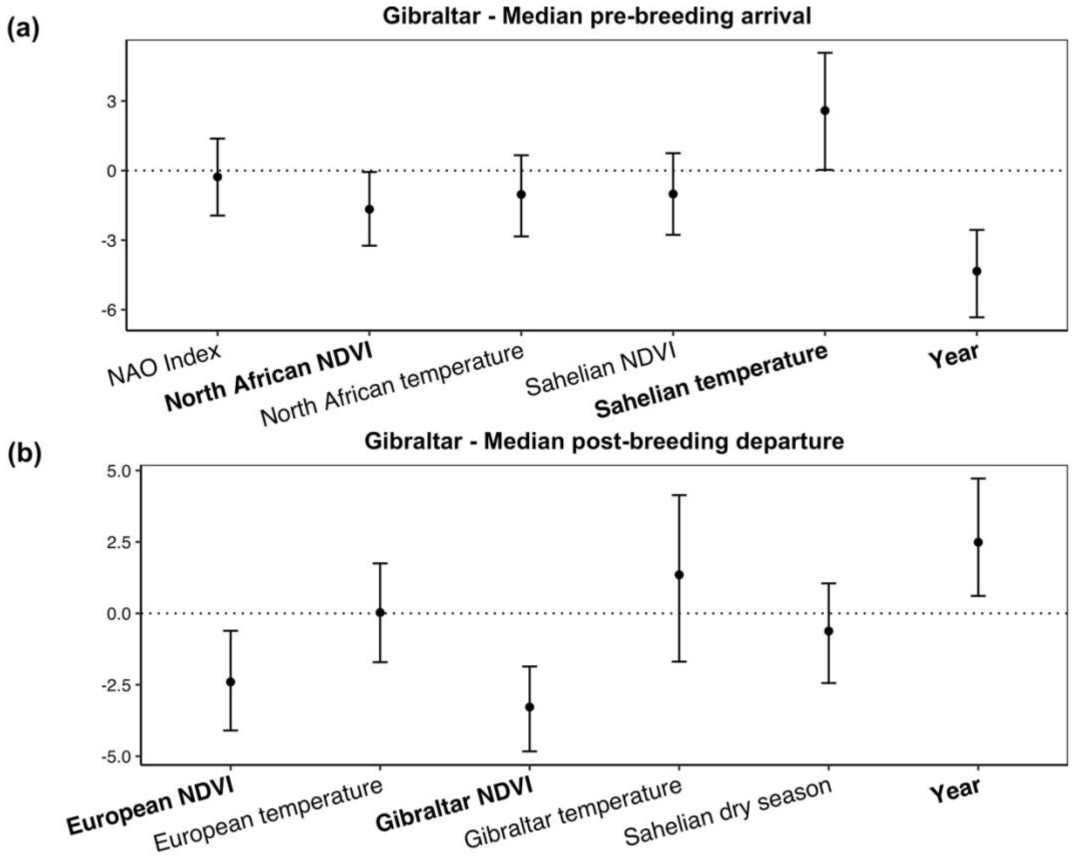

Figure S7: Parameter coefficients from phylogenetic linear mixed models, used to assess the drivers of median pre- and post-breeding migration dates in Gibraltar. Error bars display 95% confidence intervals (CIs) around coefficients. Those CIs that overlap zero (dashed line) indicate non-significant effects, where p>0.05. Variables deemed significant using this approach are displayed in bold on the x-axes.

Table S11: Regression coefficients from phylogenetic linear mixed-models used to assess relationship between median pre-breeding arrival dates in Gibraltar and several meteorological variables. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

	Estimate	**95% Confidence Limits**		**P-Value**
λ = 0.62 (0.4, 0.82)		**Lower**	**Upper**	
NAO Index	-0.27	-1.94	1.38	0.77
North African NDVI	-1.67	-3.24	-0.06	0.04
North African temperature	-1.03	-2.84	0.66	0.24
Sahelian NDVI	-1.01	-2.77	0.75	0.25
Sahelian temperature	2.59	0.03	5.08	0.04
Year	-4.34	-6.33	-2.56	<0.001

Table S12: Regression coefficients from phylogenetic linear mixed-models used to assess relationship between median post-breeding departure dates in Gibraltar and several meteorological variables. Phylogenetic signals (λ) are displayed with their confidence intervals (lower, upper).

	Estimate	**95% Confidence Limits**		**P-Value**
λ = 0.68 (0.5, 0.86)		**Lower**	**Upper**	
European NDVI	-2.4	-4.1	-0.61	0.009
European temperature	0.03	-1.71	1.75	0.97
Gibraltar NDVI	-3.28	-4.83	-1.86	<0.001
Gibraltar temperature	1.35	-1.69	4.14	0.37
Sahelian dry season	-0.62	-2.44	1.05	0.48
Year	2.49	0.61	4.72	0.02

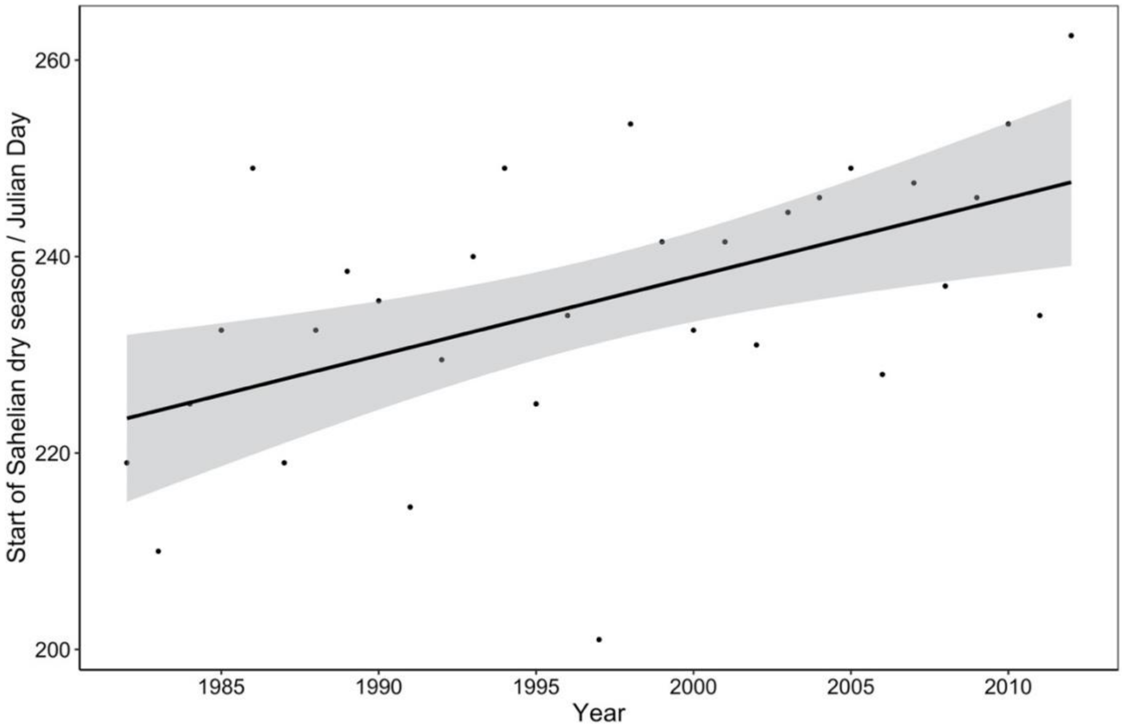

Figure S8: The annual timing of Sahelian dry season onset, measured as the point at which NDVI was declining most rapidly back to its dry season minima, showed a significant positive trend (B = 0.8, p = 0.002, R^2 = 0.28) between 1982 and 2012.

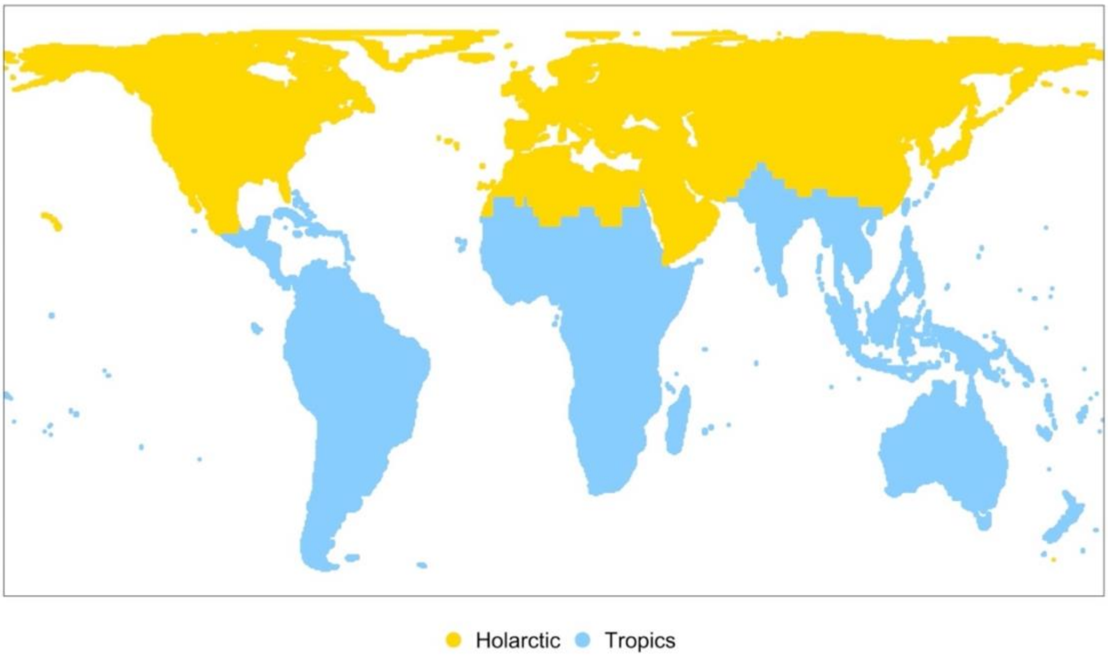

Figure S9. Global map showing the boundaries of the Holarctic and tropical realms used to define long- and short-distance migrants, adapted from Holt et al.'s (2013) zoogeographic regions. The Holarctic realm is a combination of the Nearctic, Palearctic, Saharo-Arabian, and Sino-Japanese realms, whereas the tropics combines the Panamanian, Neotropical, Afrotropical, Madagascan, Oriental, Oceanian, and Australian realms.

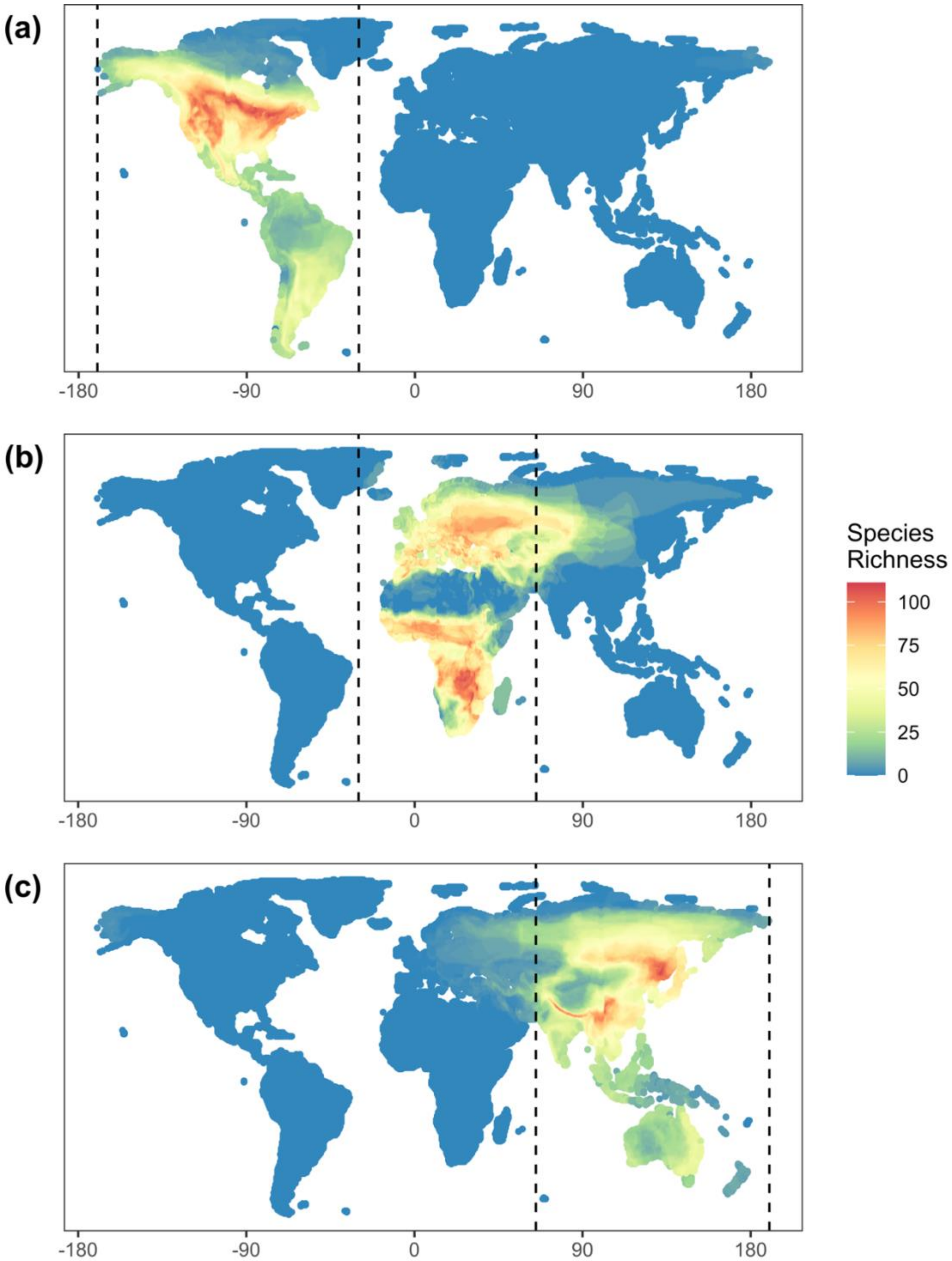

Figure S10. The breeding species richness of all non-soaring, “full migrants” (as defined by Birdlife International and NatureServe (2016)), which spend the nonbreeding period solely within one of **(a)** the Americas, **(b)** Europe and Africa or **(c)** Asia, Oceania and Australia. Dotted lines represent the longitudinal boundaries of each flyway.

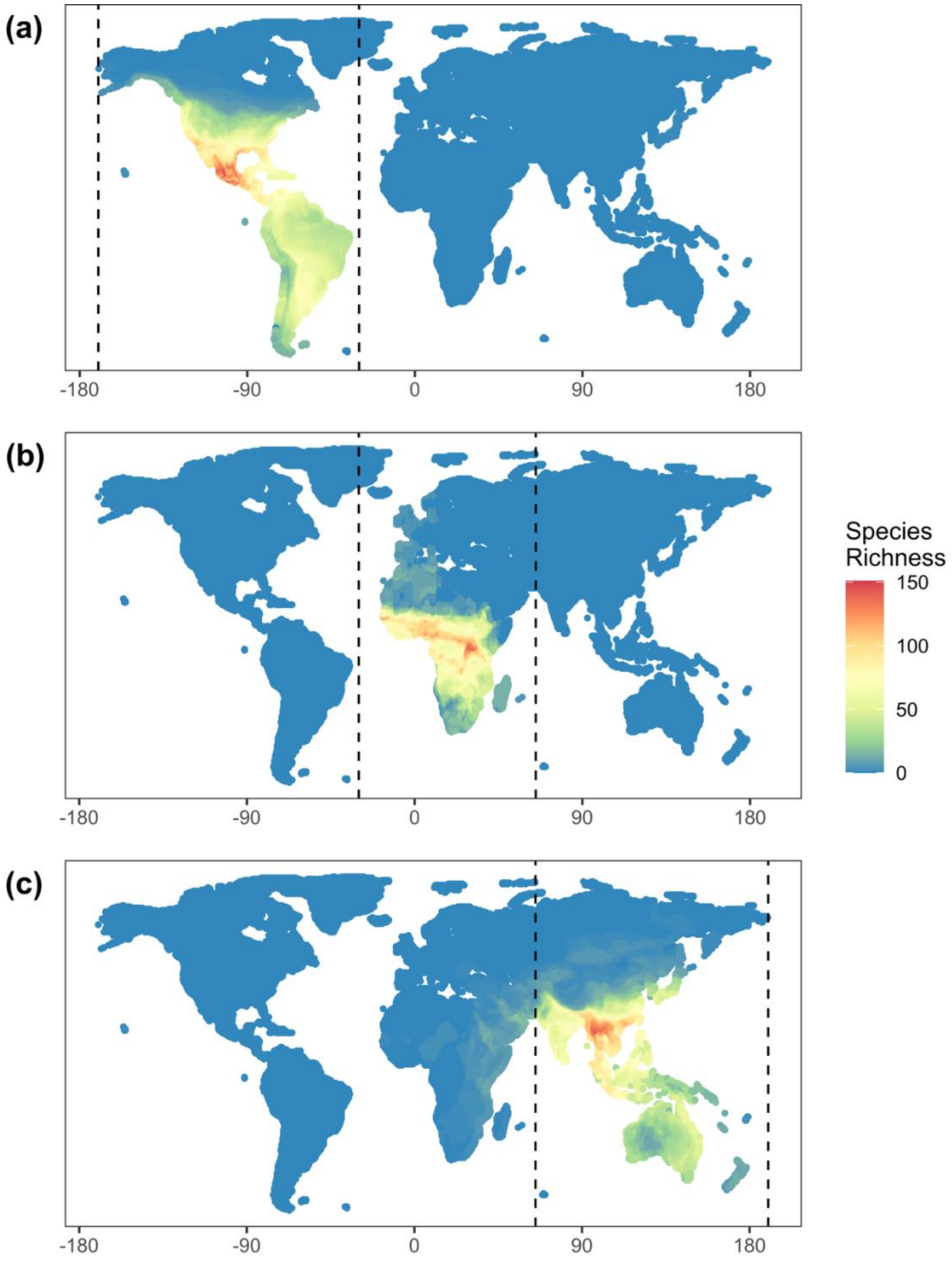

Figure S11. The nonbreeding species richness of all non-soaring, “full migrants” (as defined by Birdlife International and NatureServe (2016)), which spend the breeding period solely within one of **(a)** the Americas, **(b)** Europe and Africa or **(c)** Asia, Oceania and Australia. Dotted lines represent the longitudinal boundaries of each flyway.

Table S13. Breeding and non-breeding habitat preferences of 230 North American migratory bird species. Available in supporting excel file.

Table S14. Breeding and non-breeding habitat preferences of 82 European migratory bird species. Available in supporting excel file.

Table S15. The suitability of nine land cover categories for 230 North American migratory bird species during the breeding season. The nine categories were associated with land cover classes from the ESA CCI-LC maps (shown in brackets). Species preferences were based on descriptions from Billerman et al. (2022). 1 indicates suitability, 0 indicates not suitable. Available in supporting excel file.

Table S16. The suitability of nine land cover categories for 230 North American migratory bird species during the non-breeding season. The nine categories were associated with land cover classes from the ESA ESA CCI-LC maps (shown in brackets). Species preferences were based on descriptions from Billerman et al. (2022). 1 indicates suitability, 0 indicates not suitable. Available in supporting excel file.

Table S17. The suitability of nine land cover categories for 82 European migratory bird species during the breeding season. The nine categories were associated with land cover classes from the ESA ESA CCI-LC maps (shown in brackets). Species preferences were principally taken from Howard et al. (2020), then for species for which data was not available, were based on descriptions from Billerman et al. (2022). 1 indicates suitability, 0 indicates not suitable. Available in supporting excel file.

Table S18. The suitability of nine land cover categories for 82 European migratory bird species during the non-breeding season. The nine categories were associated with land cover classes from the ESA ESA CCI-LC maps (shown in brackets). Species preferences were principally taken from Howard et al. (2020), then for species for which data was not available, were based on descriptions from Billerman et al. (2022). 1 indicates suitability, 0 indicates not suitable. Available in supporting excel file.

Table S19. Regression coefficients from phylogenetic linear mixed-models used to assess trends in breeding climate suitability between 1980 and 2017 in North America and Europe.

		95% Confidence Limits		
Flyway	**Estimate**	**Lower**	**Upper**	**P-Value**
North America	0.02	-0.07	0.10	0.70
Europe	-0.1	-0.15	-0.6	<0.001

Table S20. Regression coefficients from phylogenetic linear mixed-models used to assess trends in non-breeding land cover suitability between 1992 and 2015, in North America and Europe, for long- and short-distance migrants.

Flyway	Migratory status	Estimate	95% Confidence Limits		P-Value
			Lower	Upper	
North America	Long-distance	-0.018	-0.027	-0.009	<0.001
	Short-distance	-0.035	-0.038	-0.032	<0.001
Europe	Long-distance	-0.074	-0.084	-0.063	<0.001
	Short-distance	0.038	0.028	0.049	<0.001

Table S21. Number of times each combination of bioclimatic variables occurred in the top quartile of each species' model sets, assessed using Akaike Information Criterion of GAMs built to model species' breeding distributions.

Variable combination	Number of occurrences in top quartile
bio1.bio4.bio13.bio14.bio15	455
bio4.bio5.bio13.bio14.bio15	447
bio1.bio4.bio13.bio15	383
bio1.bio4.bio12.bio15	375
bio4.bio5.bio12.bio15	368
bio4.bio5.bio13.bio15	367
bio1.bio4.bio13.bio14	354
bio4.bio5.bio13.bio14	337
bio1.bio4.bio14.bio15	303
bio4.bio5.bio14.bio15	262
bio1.bio13.bio14.bio15	111
bio1.bio4.bio12	87
bio1.bio4.bio13	72
bio1.bio4.bio14	67
bio5.bio13.bio14.bio15	61
bio4.bio13.bio14.bio15	60
bio6.bio13.bio14.bio15	60
bio4.bio5.bio15	59

bio4.bio5.bio14	56
bio1.bio4.bio15	51
bio4.bio5.bio12	51
bio4.bio5.bio13	46
bio1.bio13.bio15	33
bio1.bio13.bio14	29
bio1.bio12.bio15	27
bio5.bio12.bio15	20
bio5.bio13.bio15	19
bio5.bio13.bio14	15
bio4.bio12.bio15	9
bio6.bio12.bio15	8
bio1.bio14.bio15	7
bio4.bio13.bio14	7
bio5.bio14.bio15	7
bio4.bio13.bio15	5
bio6.bio13.bio14	4
bio4.bio14.bio15	3
bio6.bio13.bio15	3
bio6.bio14.bio15	2

Table S22. Number of times each combination of bioclimatic variables occurred in the top quartile of each species’ model sets, assessed using Akaike Information Criterion of GAMs built to model species’ non-breeding distributions.

Variable combination	Number of occurrences in top quartile
bio1.bio4.bio13.bio14.bio15	457
bio4.bio5.bio13.bio14.bio15	442
bio1.bio4.bio12.bio15	397
bio1.bio4.bio13.bio15	382
bio4.bio5.bio12.bio15	349
bio4.bio5.bio13.bio15	335
bio1.bio4.bio13.bio14	300
bio4.bio5.bio13.bio14	263
bio1.bio4.bio14.bio15	232
bio4.bio5.bio14.bio15	199
bio4.bio13.bio14.bio15	167
bio6.bio13.bio14.bio15	140
bio1.bio4.bio12	105
bio1.bio4.bio13	80
bio4.bio5.bio12	73
bio1.bio13.bio14.bio15	69
bio4.bio5.bio13	64
bio1.bio4.bio14	63
bio1.bio4.bio15	62
bio4.bio12.bio15	58
bio6.bio12.bio15	55
bio6.bio13.bio15	49
bio4.bio5.bio15	45
bio5.bio13.bio14.bio15	44

bio4.bio13.bio15	35
bio4.bio5.bio14	34
bio1.bio12.bio15	22
bio6.bio13.bio14	18
bio4.bio14.bio15	16
bio6.bio14.bio15	16
bio1.bio13.bio15	13
bio5.bio12.bio15	12
bio4.bio13.bio14	11
bio1.bio13.bio14	8
bio5.bio13.bio15	8
bio1.bio14.bio15	4
bio5.bio14.bio15	2
bio5.bio13.bio14	1

Table S23. Species data used to derive species' wing area, estimate flight ranges and simulate migratory journeys. Sources for data are given where they were not given in the main text. Available in supporting excel file.

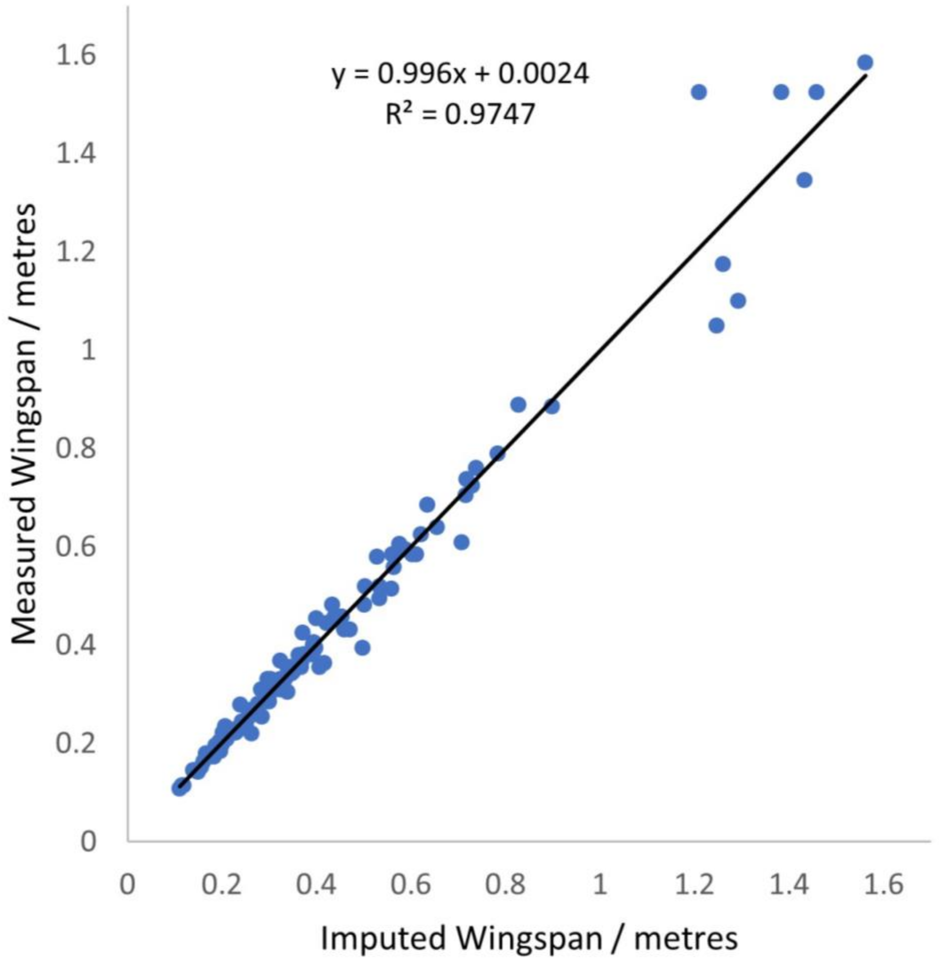

Figure S12. Wingspan estimates from phylogenetic multiple imputation in relation to measured wingspans for 127 species of migratory bird.

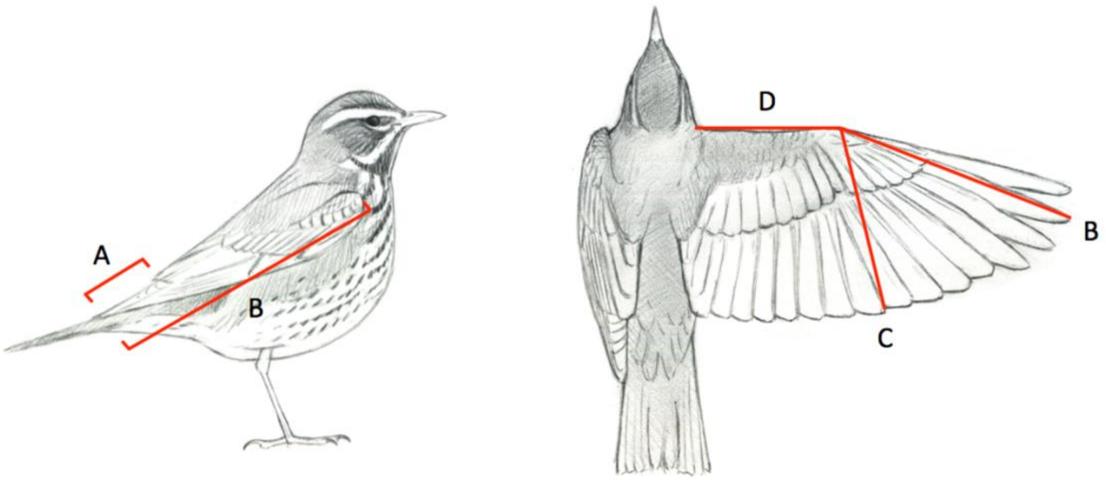

Figure S13. Wing morphology of a migratory bird species (Redwing, Turdus iliacus) from Howard et al. (2018). Lines indicate biometric variables related to dispersal ability and used in this study to calculate wing area: A, primary extension (Kipp's distance); B, primary wing chord; C, secondary length; D, carpal length. The wingspan is the total distance between the tips of the two open wings.

Table S24. Migration distance, stopover number and overall duration data for 27 species from published tracking studies and the flyway within which the tracking studies took place. Available in supporting excel file.

Table S25. Mean test statistics from 1000 Mann-Whitney U tests used to compare empirical migration distances from published tracking studies with a random sample of equal size from the 1000 migration simulations of each flyway population. Distances of *Plectrophenax nivalis* and *Anas crecca* were overestimated, whereas that of *Ficedula semitorquata* was underestimated (Appendix Fig. S14).

Flyway	**Species**	**n**	**Mean U-statistic**	**U-Statistic SD**	**Mean p-value**	**p-value SD**
Americas	*Catharus ustulatus*	29	258.1	59.9	0.06	0.14
	Hirundo rustica	17	198.4	17.7	0.12	0.14
	Hylocichla mustelina	34	438.3	82.9	0.2	0.25
	Plectrophenax nivalis	18	52.8	23.7	0.01	0.03
	Tyrannus tyrannus	8	19.6	9.8	0.31	0.31
Afro-Palearctic	*Anas crecca*	17	68.3	21.2	0.04	0.08
	Ficedula semitorquata	11	104.8	8.9	0.01	0.04
Australasian	*Anser albifrons*	12	110.1	15.8	0.11	0.19
	Numenius phaeopus	7	34.6	7	0.31	0.29
	Tringa totanus	12	85.9	18.6	0.41	0.32
Trans-flyway	*Calidris tenuirostris*	8	18.2	9.9	0.28	0.31
	Charadrius hiaticula	9	34.4	9.3	0.53	0.3

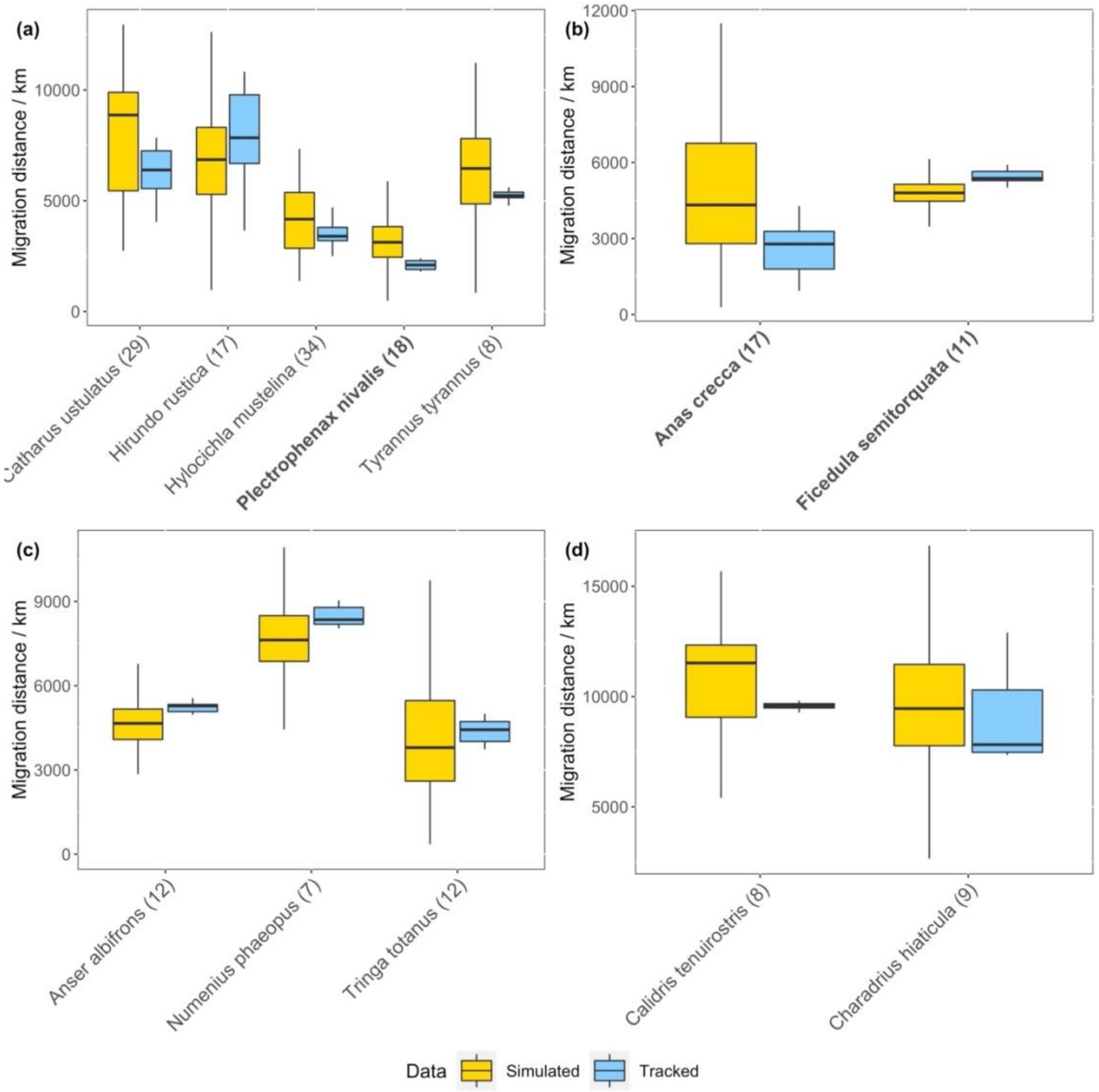

Figure S14. Comparison of simulated and tracked migration distances for migrants in the **(a)** Americas, **(b)** Afro-Palearctic and **(c)** Australasian flyways, as well as for **(d)** trans-flyway migrants. Simulated data are from the 1000 migration replications, using species distribution projections and flight range calculations. Tracked data are from published studies (Appendix S2.2). The number after each species name represents the number of individual migratory journeys available for that species. Species names are presented in bold where a significant difference was found between simulated and tracked journeys, following Mann-Whitney U testing.

Table S26. Mean test statistics from 1000 Mann-Whitney U tests used to compare empirical migratory stopover numbers from published tracking studies with a random sample of equal size from the 1000 migration simulations of each flyway population. Stopover numbers of *Anser albifrons, Caprimulgus europaeus* and *Charadrius hiaticula* were underestimated, whereas that of *Phoenicurus phoenicurus* was overestimated (Appendix Fig. S15).

Flyway	**Species**	**n**	**Mean U-statistic**	**U-Statistic SD**	**Mean p-value**	**p-value SD**
Americas	*Aythya valisineria*	10	42.3	12.5	0.48	0.31
Afro-Palearctic	*Actitis hypoleucos*	9	36.3	9	0.55	0.29
	Anas crecca	17	208.4	22.2	0.08	0.14
Australasian	*Anser albifrons*	12	136.5	3.3	<0.001	<0.001
	Numenius phaeopus	7	37.9	4	0.12	0.15
	Tringa totanus	12	106.8	7.8	0.05	0.09
Trans-flyway	*Apus apus*	11	38.6	6.6	0.17	0.15
	Calidris tenuirostris	8	32.4	6.8	0.61	0.27
	Caprimulgus europaeus	15	216	4.5	<0.001	<0.001
	Charadrius hiaticula	9	69.6	5.1	0.02	0.03
	Phoenicurus phoenicurus	7	6.5	4.6	0.04	0.09

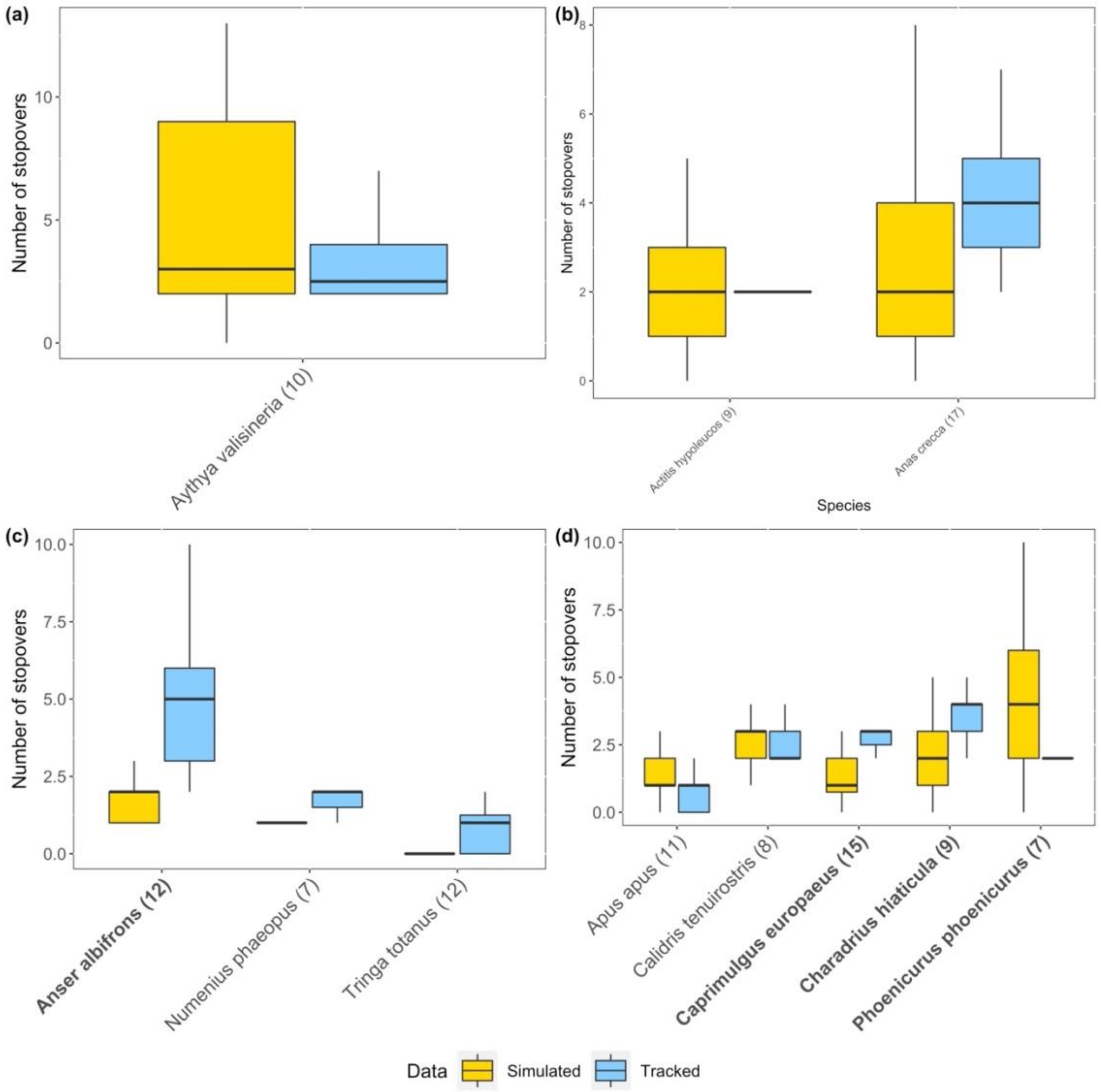

Figure S15. Comparison of simulated and tracked stopover numbers for migrants in the **(a)** Americas, **(b)** Afro-Palearctic and **(c)** Australasian flyways, as well as for **(d)** trans-flyway migrants. Simulated data are from the 1000 migration replications, using species distribution projections and flight range calculations. Tracked data are from published studies (Appendix S2.2). The number after each species name represents the number of individual migratory journeys available for that species. Species names are presented in bold where a significant difference was found between simulated and tracked journeys, following Mann-Whitney U testing.

Table S27. Mean test statistics from 1000 Mann-Whitney U tests used to compare empirical migration durations from published tracking studies with a random sample of equal size from the 1000 migration simulations of each flyway population. Migration durations of *Catharus ustulatus, Plectrophenax nivalis, Ficedula semitorquata* and *Anser albifrons* were underestimated, whereas those of *Actitis hypoleucos* and *Ficedula hypoleuca* were overestimated (Appendix Fig. S16).

Flyway	**Species**	**n**	**Mean U-statistic**	**U-Statistic SD**	**Mean p-value**	**p-value SD**
Americas	*Catharus guttatus*	10	64.4	13.9	0.34	0.3
	Catharus ustulatus	29	614.1	39.4	0.01	0.02
	Hirundo rustica	7	19.4	6.4	0.49	0.3
	Hylocichla mustelina	32	584	47.6	0.39	0.27
	Plectrophenax nivalis	18	282.9	20.4	0.002	0.01
	Tyrannus tyrannus	8	21.2	7.4	0.35	0.3
Afro-Palearctic	*Actitis hypoleucos*	9	4.3	5.9	0.008	0.03
	Anas crecca	17	164.6	26.7	0.44	0.3
	Ficedula semitorquata	10	99.5	0.7	<0.001	<0.001
	Hirundo rustica	9	40.9	7.5	0.65	0.25
Australasia	*Anser albifrons*	12	135	8.1	0.001	0.005
	Numenius phaeopus	7	38.8	7.6	0.17	0.23
	Tringa totanus	12	87.2	9.8	0.43	0.26
Trans-flyway	*Apus apus*	17	96.8	19.6	0.18	0.2
	Calidris tenuirostris	8	14.4	6.9	0.14	0.19
	Charadrius hiaticula	8	15.5	7.8	0.19	0.24

	Ficedula hypoleuca	37	20.2	15.6	<0.001	<0.001
	Lanius collurio	13	94.9	20.5	0.46	0.31
	Luscinia megarhynchos	9	18.4	10.1	0.15	0.22
	Oenanthe oenanthe	44	689.9	85.5	0.06	0.1

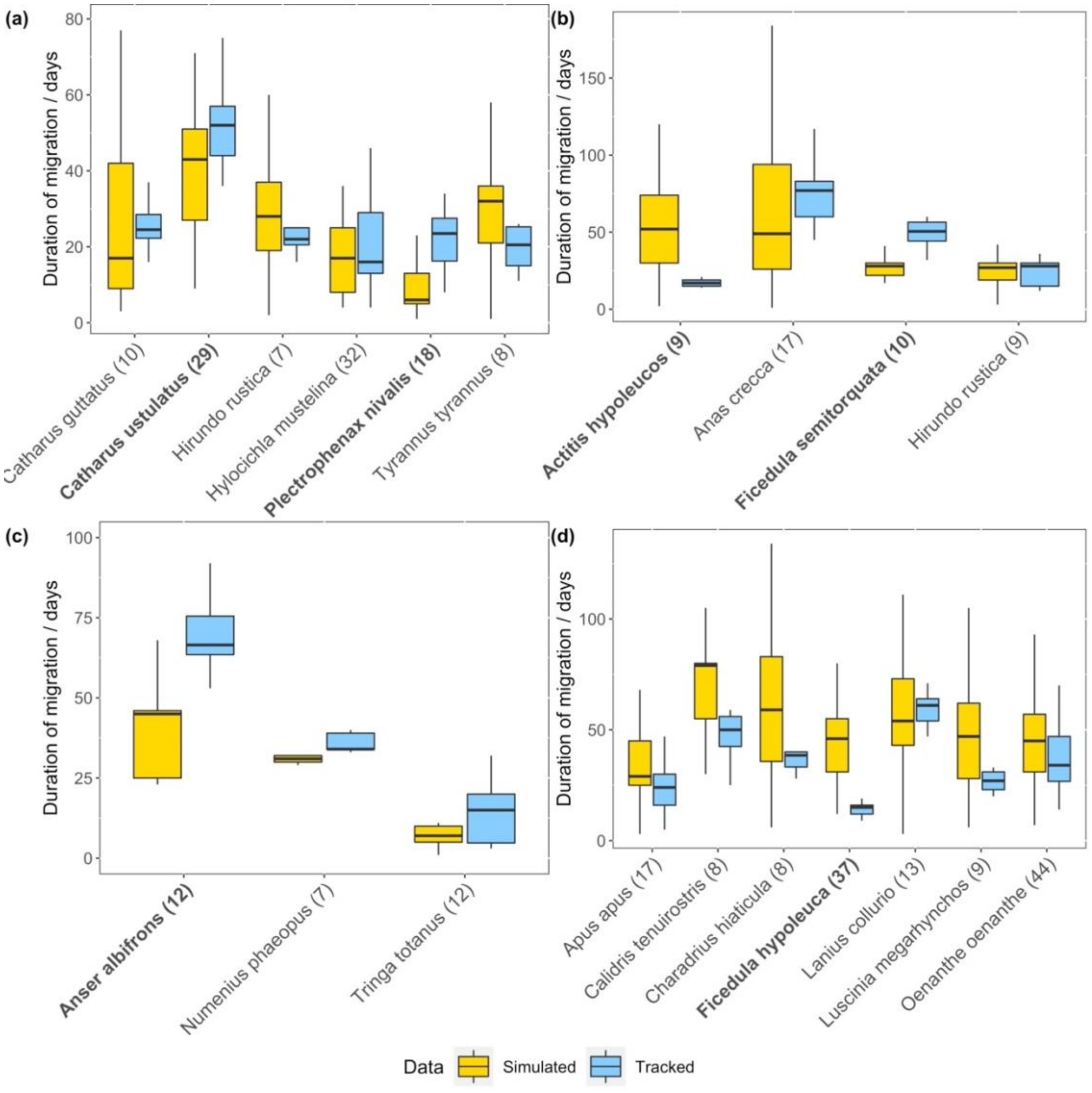

Figure S16. Comparison of simulated and tracked migratory durations for migrants in the **(a)** Americas, **(b)** Afro-Palearctic and **(c)** Australasian flyways, as well as for **(d)** trans-flyway migrants. Simulated data are from the 1000 migration replications, using species distribution projections and flight range calculations. Tracked data are from published studies (Appendix S2.2). The number after each species name represents the number of individual migratory journeys available for that species. Species names are presented in bold where a significant difference was found between simulated and tracked journeys, following Mann-Whitney U testing.

Table S28. Results of unpaired t-tests on the 1000 migration replicates to test for change in migration distance between 2000 and 2070 for all 464 populations of long- and short-distanced migrant. Available in supporting excel file.

Table S29. Results of unpaired t-tests on the 1000 migration replicates to test for change in stopover number between 2000 and 2070 for all 464 populations of long- and short-distance migrants. Available in supporting excel file.

Table S30. Results of unpaired t-tests on the 1000 migration replicates to test for change in migration duration between 2000 and 2070 for all 464 populations of long- and short-distance migrants. Available in supporting excel file.

Table S31. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of long-distance migrants between 2000 and 2070 in each of the Americas (n = 69), Afro-Palearctic (n = 46) and Australasian (n = 134) flyways. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Flyway**	**Estimate**	**Lower**	**Upper**	**p**
Distance $R^2 = 0.5$	Americas	1001.3	802.6	1198.2	<0.001
	Afro-Palearctic	447.4	213.7	681.3	0.001
	Australasian	308.5	169.1	446.7	<0.001
Stopover $R^2 = 0.51$	Americas	0.53	0.42	0.63	<0.001
	Afro-Palearctic	0.27	0.15	0.4	<0.001
	Australasian	0.16	0.08	0.23	<0.001
Duration $R^2 = 0.55$	Americas	6.88	5.49	8.26	<0.001
	Afro-Palearctic	3.38	1.65	5.02	<0.001
	Australasian	2.05	1.07	3.05	<0.001

Table S32. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of short-distance migrants between 2000 and 2070 in each of the Americas (n = 94), Afro-Palearctic (n = 34) and Australasian (n = 54) flyways. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Flyway**	**Estimate**	**Lower**	**Upper**	**p**
Distance	Americas	-51.1	-354.6	247.7	0.74
$R^2 = 0.33$	Afro-Palearctic	171.4	-332	677.7	0.5
	Australasian	-436	-841.6	-354	0.03
Stopover	Americas	-0.01	-0.2	0.18	0.88
$R^2 = 0.36$	Afro-Palearctic	0.11	-0.21	0.42	0.49
	Australasian	-0.26	-0.51	-0.02	0.03
Duration	Americas	0.8	-1.98	3.61	0.54
$R^2 = 0.36$	Afro-Palearctic	1.38	-3.06	6.1	0.53
	Australasian	-3.73	-7.29	-0.15	0.046

Table S33. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of long-distance migratory charadriiformes (n = 68) and passeriformes (n = 211) between 2000 and 2070. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Taxa**	**Estimate**	**Lower**	**Upper**	**p**
Distance	Passeriformes	571.3	436.1	707	<0.001
$R^2 = 0.65$	Charadriiformes	412.2	181.2	631.7	0.001
Stopover	Passeriformes	0.35	0.28	0.42	<0.001
$R^2 = 0.42$	Charadriiformes	0.14	0.02	0.26	0.02
Duration	Passeriformes	3.65	2.68	4.64	<0.001
$R^2 = 0.42$	Charadriiformes	3.65	2	5.31	<0.001

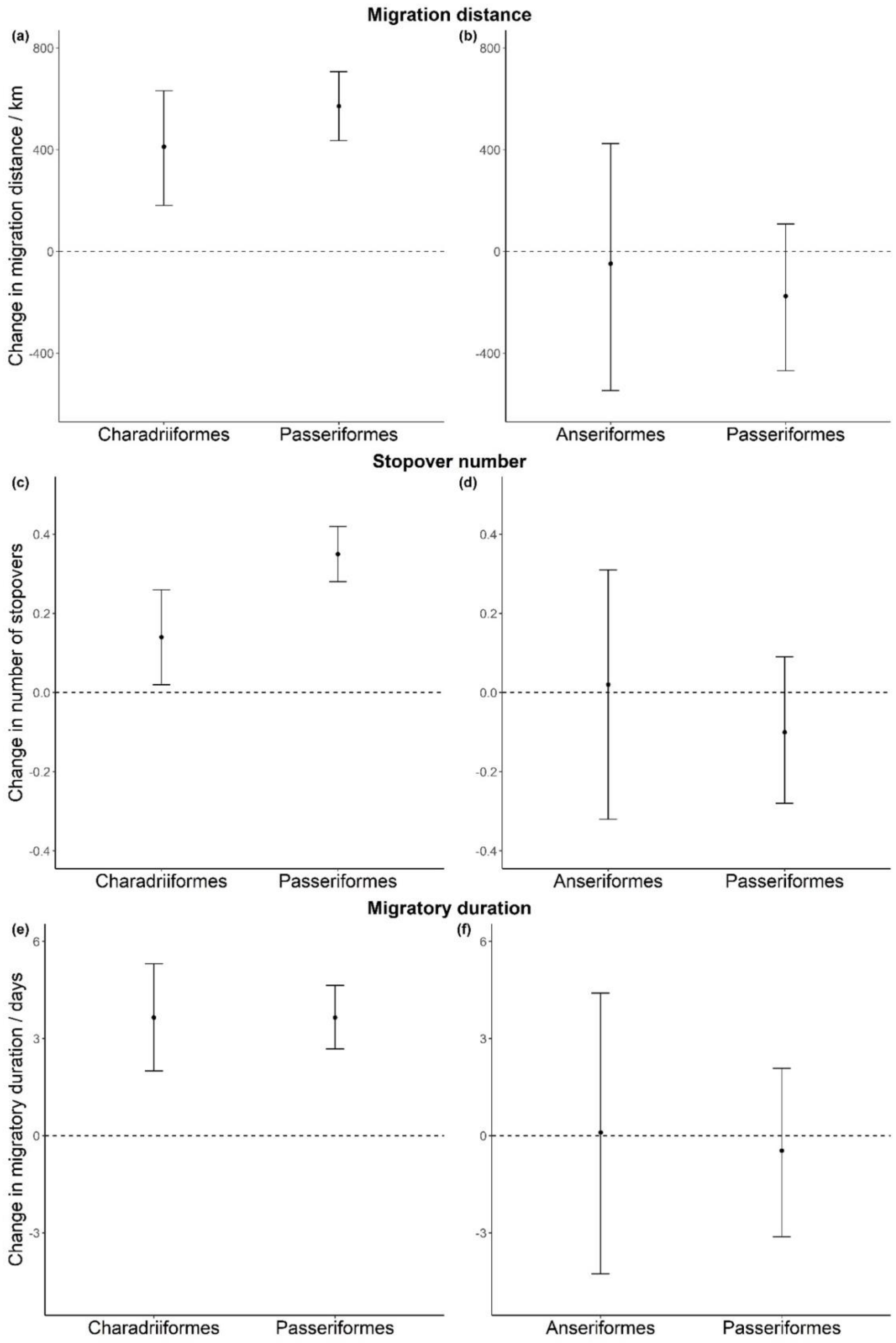

Figure S17. Effect sizes from PLMMs, representing changes in mean predicted **(a & b)** migration distance, **(c & d)** stopover number and **(e & f)** migratory duration between 2000 and 2070 for **(a, c & e)** long-distance migratory charadriiformes (n = 68) and passeriformes (n = 211) and **(b, d & f)** short-distance migratory anseriformes (n = 41) and passeriformes (n = 118). Error bars represent the upper and lower 95% confidence intervals.

Table S34. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of short-distance migratory anseriformes (n = 41) and passeriformes (n = 118) between 2000 and 2070. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Taxa**	**Estimate**	**Lower**	**Upper**	**p**
Distance $R^2 = 0.58$	Passeriformes	-175.3	-468.9	108	0.21
	Anseriformes	-47.7	-547.4	423.9	0.84
Stopover $R^2 = 0.42$	Passeriformes	-0.1	-0.28	0.09	0.3
	Anseriformes	0.02	-0.32	0.31	0.91
Duration $R^2 = 0.4$	Passeriformes	-0.46	-3.12	2.08	0.71
	Anseriformes	0.1	-4.27	4.4	0.95

Table S35. Results of multiple circular ANOVA tests used to test for differences in the mean direction of shifts of the breeding and non-breeding ranges of long- and short-distance migrants in the three major flyways.

Migratory Status	**Flyway**	**n**	**df**	**F**	**p**
Long-distance	Americas	64	1,122	179.3	<0.001
	Afro-Palearctic	40	1,74	72.2	<0.001
	Australasian	96	1,178	14.6	<0.001
Short-distance	Americas	52	1,100	1	0.33
	Afro-Palearctic	18	1,30	7.1	0.01
	Australasian	36	1,68	0.5	0.48

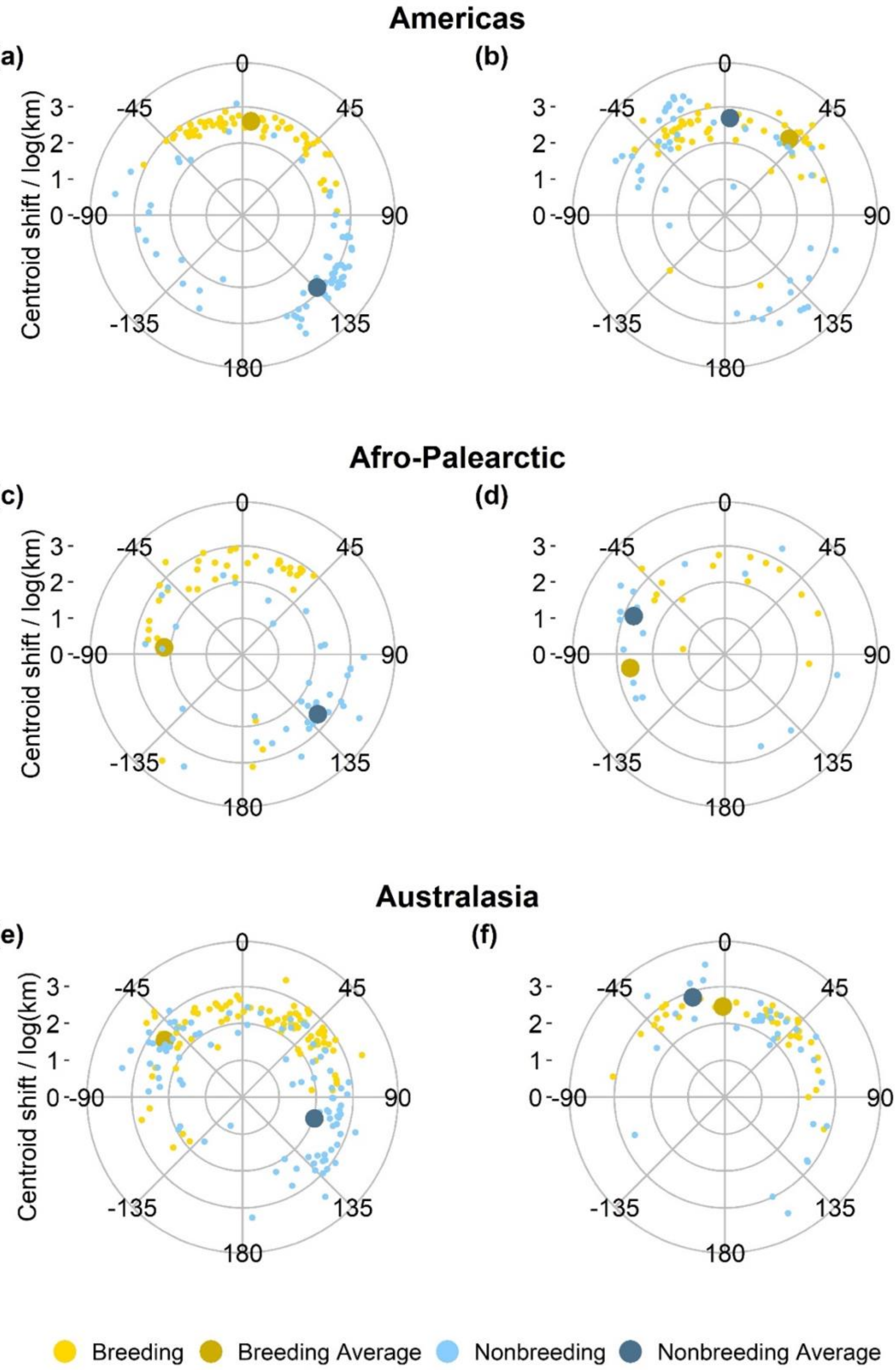

Figure S18. Projected direction and distance of breeding (yellow) and non-breeding (blue) range centroid shifts between 2000 and 2070, for **(a, c & e)** long- and **(b, d & f)** short-distance migrants in each of the Americas (n = 64 and 52, respectively), Afro-Palearctic (n = 40 and 18, respectively) and Australasian (n = 96 and 36, respectively) flyways. Each point represents the 2070 range centroid of an individual flyway population, with the centre of the plot representing the 2000 range centroid. The larger and darker points show the mean breeding and non-breeding shifts, calculated as the bearing and geodesic distance of the mean change in centroid latitude and longitude across all long- or short-distance migrants in each flyway.

Table S36. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of all long- (n = 242) and short-distance (n = 109) migrants across the globe between 2000 and 2070. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Migratory status**	**Estimate**	**Lower**	**Upper**	**R^2**	**p**
Distance	Long-distance	304.8	144.5	463.8	0.85	<0.001
	Short-distance	-195.4	-477.3	89.5	0.72	0.2
Stopover	Long-distance	0.16	0.08	0.25	0.86	<0.001
	Short-distance	-0.13	-0.3	0.04	0.7	0.14
Duration	Long-distance	2.31	0.98	3.63	0.86	0.001
	Short-distance	-2.17	-4.85	0.54	0.74	0.12

Table S37. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of long-distance migrants between 2000 and 2070 in each of the Americas (n = 64), Afro-Palearctic (n = 40) and Australasian (n = 96) flyways. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Flyway**	**Estimate**	**Lower**	**Upper**	**p**
Distance	Americas	1000	805.2	1197.7	<0.001
$R^2 = 0.54$	Afro-Palearctic	478.5	237.3	730.5	<0.001
	Australasian	258.5	94.4	424.6	0.004
Stopover	Americas	0.53	0.43	0.62	<0.001
$R^2 = 0.53$	Afro-Palearctic	0.31	0.19	0.44	<0.001
	Australasian	0.14	0.06	0.22	0.001
Duration	Americas	6.99	5.56	8.46	<0.001
$R^2 = 0.55$	Afro-Palearctic	3.69	1.9	5.53	<0.001
	Australasian	1.78	0.57	2.96	0.005

Table S38. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of short-distance migrants between 2000 and 2070 in each of the Americas (n = 52), Afro-Palearctic (n = 18) and Australasian (n = 36) flyways. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Flyway**	**Estimate**	**Lower**	**Upper**	**p**
Distance $R^2 = 0.23$	Americas	-122.3	-547.5	306.5	0.56
	Afro-Palearctic	229.1	-537.6	1001.1	0.57
	Australasian	-366.1	-887.8	147.8	0.17
Stopover $R^2 = 0.43$	Americas	-0.1	-0.37	0.16	0.42
	Afro-Palearctic	0.14	-0.33	0.61	0.54
	Australasian	-0.23	-0.55	0.08	0.15
Duration $R^2 = 0.51$	Americas	-0.88	-4.74	3.04	0.63
	Afro-Palearctic	0.85	-6.19	7.62	0.84
	Australasian	-4.24	-8.91	0.52	0.06

Table S39. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of long-distance migratory charadriiformes (n = 58) and passeriformes (n = 164) between 2000 and 2070. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	**Taxa**	**Estimate**	**Lower**	**Upper**	**p**
Distance $R^2 = 0.86$	Passeriformes	295.4	98.2	495.1	0.002
	Charadriiformes	326.4	-4.53	661.8	0.06
Stopover $R^2 = 0.4$	Passeriformes	0.35	0.28	0.42	<0.001
	Charadriiformes	0.14	0.02	0.26	0.02
Duration $R^2 = 0.66$	Passeriformes	3.65	2.68	4.64	<0.001
	Charadriiformes	3.65	2	5.31	<0.001

Table S40. Coefficients from phylogenetic linear mixed models, assessing differences in the predicted migration distance, stopover number and migratory duration of short-distance migratory anseriformes (n = 26) and passeriformes (n = 64) between 2000 and 2070. Estimates represent change in kilometres, number of stopovers and days, respectively. Lower and upper are the 95% confidence intervals around estimates.

Analysis	Taxa	Estimate	Lower	Upper	p
Distance	Passeriformes	-123	-500.7	256	0.53
$R^2 = 0.6$	Anseriformes	-492.4	-1076.4	97.9	0.09
Stopover	Passeriformes	-0.07	-0.31	0.17	0.57
$R^2 = 0.35$	Anseriformes	-0.34	-0.72	0.04	0.08
Duration	Passeriformes	-0.25	-3.59	3.07	0.92
$R^2 = 0.47$	Anseriformes	-7.18	-12.49	-1.94	0.01

Table S41. Number of times each combination of bioclimatic variables occurred in the top quartile of each species' model sets, assessed using Akaike Information Criterion of GAMs built to model species' breeding distributions.

Variable combination	Number of occurrences in top quartile
bio4.bio5.bio13.bio14.bio15	329
bio4.bio5.bio12.bio15	309
bio4.bio5.bio13.bio15	302
bio4.bio5.bio13.bio14	292
bio4.bio5.bio14.bio15	213
bio1.bio13.bio14.bio15	118
bio4.bio5.bio12	90
bio4.bio13.bio14.bio15	84
bio4.bio5.bio14	76
bio4.bio5.bio15	71
bio6.bio13.bio14.bio15	66
bio4.bio5.bio13	65
bio5.bio13.bio14.bio15	53
bio1.bio12.bio15	36
bio1.bio13.bio15	33

bio1.bio13.bio14	31
bio4.bio13.bio15	30
bio4.bio12.bio15	27
bio6.bio12.bio15	16
bio1.bio14.bio15	14
bio4.bio13.bio14	12
bio6.bio13.bio15	12
bio5.bio13.bio14	11
bio5.bio13.bio15	9
bio6.bio14.bio15	4
bio5.bio12.bio15	3
bio6.bio13.bio14	3
bio4.bio14.bio15	1
bio5.bio14.bio15	0

Table S42. Number of times each combination of bioclimatic variables occurred in the top quartile of each species' model sets, assessed using Akaike Information Criterion of GAMs built to model species' breeding distributions.

Variable combination	**Number of occurrences in top quartile**
bio4.bio5.bio13.bio14.bio15	328
bio4.bio5.bio13.bio15	300
bio4.bio5.bio12.bio15	296
bio4.bio5.bio13.bio14	235
bio4.bio13.bio14.bio15	173
bio4.bio5.bio14.bio15	160
bio6.bio13.bio14.bio15	119
bio4.bio5.bio12	94
bio4.bio12.bio15	86
bio1.bio13.bio14.bio15	75
bio4.bio5.bio13	71
bio5.bio13.bio14.bio15	56
bio6.bio12.bio15	54

bio4.bio5.bio15	52
bio4.bio13.bio15	47
bio6.bio13.bio15	28
bio4.bio5.bio14	27
bio1.bio12.bio15	26
bio4.bio13.bio14	18
bio1.bio13.bio15	15
bio6.bio13.bio14	12
bio5.bio12.bio15	10
bio5.bio13.bio15	10
bio4.bio14.bio15	8
bio6.bio14.bio15	6
bio1.bio13.bio14	4
bio1.bio14.bio15	3
bio5.bio14.bio15	3
bio5.bio13.bio14	1

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