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The abundance of European breeding birds: present and future

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Declaration

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

Christine Howard

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Abstract

Global environmental changes are predicted to have severe consequences for biodiversity and the provisioning of ecosystem services and functions. Historic biodiversity losses have been principally attributed to habitat loss and degradation, and human overexploitation. Today, however, biodiversity is increasingly threatened by anthropogenic climate change. Establishing the relative importance of climate and land use in determining species abundance is important if we are to fully understand the potential impacts of future environmental change. Designating species of conservation concern relies principally on measures of population change, and is inevitably backward- rather than forward-looking. Yet, with projections of substantial future climate change, knowing species that will become imperilled in future is also important for conservation planning. To date, studies of the impacts of future climate change have focussed on projecting range shifts of species, but rarely on projecting species' abundances, which limits their utility for conservation. In this thesis, I investigate the relative importance of climate and land use in determining the recent abundance of breeding birds across Europe, and I assess the potential impacts of future climate change. I use species abundance models, applying novel approaches, to improve the understanding of species-environment relationships. From these, I demonstrate that climate is generally more important than land use in determining recent species abundances at a European scale. Importantly, however, the importance of abiotic factors for determining species abundance varies across Europe, with climate being most important in the north, and land-use in the south. This suggests that northerly distributed species will be particularly susceptible to climate change; unfortunate, given that this is exactly where climate change is projected to be most pronounced. I further demonstrate, for the first time, that the population trends of migratory birds are more closely related to climate on their breeding grounds than climate on their non-breeding grounds. My species' abundance models, using climate and habitat data, estimate national abundances of species well, even when projected into novel parameter space. I then use these models to project the abundance of species under climate change, and demonstrate that substantial changes in both the abundance and distribution of species are highly likely. Furthermore, species responses will be individualistic, leading to significant changes in the distribution of avian communities. In this thesis I have, in part, been able to address some fundamental questions in ecology, including: '*What limits the abundance of migratory species?*' and *'Is climate or habitat the primary determinant of population size in species?'.* The work presented here advances our understanding of the potential future shape of biodiversity, and should inform forward-thinking conservation.

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Chapter 1

General Introduction

1.1 Introduction

Rapid population declines and extinctions of species are occurring at a global scale in response to the widespread destruction of natural habitats (Koh *et al.* 2004). Over 30% of species are predicted to be lost by 2050 (Thomas *et al.* 2004). These unprecedented rates of species extinctions will have significant consequences for the provision of ecosystem functions and maintenance of natural services (Vorosmarty *et al.* 2010; Tittensor *et al.* 2014). The global loss of ecosystem services due to habitat change is estimated to be $US 4.3-20.2 trillion every year, whilst the contribution to human well-being of ecoservices is valued as twice that of global GDP (Costanza *et al.* 2014). Traditionally, the majority of threat to biodiversity has been attributed to local-scale processes, such as habitat loss, degradation, and overexploitation and the impacts of invasive species (Pearce-Higgins & Green 2014). These processes remain significant threats but, arguably, are reducing in importance relative to much larger-scale processes: changes in climate and land use (Bellard *et al.* 2012). Global temperatures have increased on average by 0.85°C since 1880. The global climate is expected to have warmed by an additional 0.3 to 4.8°C by 2100, since 1990 (IPCC 2014). The influence that climatic changes have on the environment is now one of the most widely researched topics in ecology (Zimmermann *et al.* 2010; Cardinale *et al.* 2012). There is already substantial evidence that many species have responded to recent warming (Chen *et al.* 2011), including changes in population trends (Sillett, Holmes & Sherry 2000; Gregory et al. 2009; Saether & Engen 2010), spatial distributions (Parmesan *et al.* 1999; Walther *et al.* 2002; Parmesan & Yohe 2003; Hickling *et al.* 2006; Chen *et al.* 2011; Gottfried *et al.* 2012; Poloczanska *et al.* 2013; Burrows *et al.* 2014), life history parameters (Milner, Elston & Albon 1999; Catchpole *et al.* 2000; Ottersen & Loeng 2000; Coulson *et al.* 2001), phenology (Root *et al.* 2003; Menzel *et al.* 2006b; Both *et al.* 2009; Both *et al.* 2010) and community dynamics (Walther *et al.* 2002; Menéndez *et al.* 2006; Devictor *et al.* 2008; Walther 2010).

There is an urgent need for effective conservation to prevent species extinctions and the projected loss of biodiversity. Such conservation requires the identification of species and communities most at risk from climate change, in order for appropriate action to be taken. Traditionally, using ecological niche theory, studies focussed on predicting how the distribution of species across a landscape will change in response to fluctuations in environmental conditions (Franklin 1995; Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Elith & Leathwick 2009; Zimmermann *et al.* 2010). However, it is population size and trends in population size that determine the conservation status of a species (Mace *et al.* 2008). Furthermore, as abundance is a much more finely resolved characteristic than the occurrence of a species, it is more likely to reflect variations in habitat quality, especially at fine scales (Johnston *et al.* 2013). Although there have been many studies of the responses of individual populations to changes in environmental conditions (Pearce-Higgins *et al.* 2015), the impacts of climate change are thought to operate on species at a much larger scale (Gregory *et al.* 2005; Johnston *et al.* 2013). In addition, causal attribution of biological changes to observed climatic change is complicated given the influence of a range of non-climatic abiotic and biotic factors (Parmesan & Yohe 2003). Currently understanding of what drives changes in the abundance of a species at a national or international scales is limited (with the exception of Renwick *et al.* (2012), Eglington and Pearce-Higgins (2012), and Johnston *et al.* (2013)).

Processes that take place over large temporal and spatial extents, such as climate and land use, are best studied using data collected over the extent at which they operate. Monitoring of various taxa has been very inconsistent over space and time - but one of the best studied taxa is the birds. Some populations of birds, particularly those in Europe, have been intensively monitored for many years, providing spatially diverse, robust long-term data sets (Bart 2005; Bart *et al.* 2007; Gregory & van Strien 2010; Inger *et al.* 2014). This project will focus on European breeding birds, and how their populations vary both spatially and temporally in relation to variations in their environment. In spite of the extensive monitoring that has been carried out on these species, producing robust multi-species population estimates at a supranational scale, understanding of the large-scale drivers of variations in abundance remains limited. In this thesis, I aim to resolve this, disentangling the relative importance of climate, land use and other biotic and abiotic factors in driving large scale variations in the abundances of these species. I will then use this understanding to assess the potential effects of future climate change on the abundance of European birds and the subsequent alterations to avian communities. By considering the large scale abundance patterns of multiple species, these analyses should provide useful predictions of the abundance distributions of European birds, identifying those most susceptible to the threats of future climate change.

In the following section I briefly review a range of impacts that climate change has already been reported to have had on biota, including changes in species' distributions and abundances, and shifts in communities. I then focus on European birds and examine how different environmental factors drive changes in the populations of European birds, the mechanisms by which they may operate and the difficulties associated with understanding the relative importance of these variables in driving abundance. Following this, I provide an overview of the methods that can be used to model the impacts of environmental change on these species, the associated pitfalls of these methods, and the ways in which they can be improved. To better understand the wider implications of the results of this project, I discuss how they may aid the management and conservation of these species. Finally, I summarise the key points of this review and outline the specific aims of this project.

1.2 Climate change and its impacts on biodiversity

Since 1880, global temperatures have increased on average by 0.85°C, with the period between 1983 and 2012 the warmest 30 year period of the last 1400 years in the Northern Hemisphere (IPCC 2014). Temperature increases have been attributed to large increases in the atmospheric concentrations of carbon dioxide (CO_2), driven by anthropogenic greenhouse gas (GHG) emissions since the pre-industrial era (IPCC 2001). Approximately half of anthropogenic CO_2 emissions between 1750 and 2011 have occurred since the 1970’s (IPCC 2014). Emissions of GHGs are driven by population size, economic activities, energy and land use patterns, and climate policy. Future climate will depend on the magnitude of future anthropogenic emissions, natural climate variability and committed warming caused by past emissions (Moss *et al.* 2010). By 2035, global mean surface temperature is projected to be similar across different ranges of future anthropogenic GHG emission scenarios, ranging from 0.3°C to 0.7°C (IPCC 2014). However, by the end of the 21st Century (2081-2100), predicted global mean surface temperature varies significantly across future GHG emission scenarios. Under a scenario of stringent mitigation, temperatures are *unlikely* to exceed 2.0°C. For intermediate and high GHG emission scenarios, warming is *more likely than not* to exceed 2°C (IPCC 2014). The impacts of climate change are strongest and most comprehensive for natural systems (Moss *et al.* 2010). Here I discuss in more detail the observed and potential risks for biodiversity caused by a changing climate.

1.2.1 Range shifts

With the exception of highly mobile and migratory species, which have the capacity to alter the timing or destination of their movements (Walther *et al.* 2002) many species are unable to respond rapidly to the pressures of a fast-changing climate (Parmesan *et al.* 2013). For these more sedentary species, responses to climatic warming should be reflected in slow shifts in their geographic range (Parmesan *et al.* 1999; Thuiller *et al.* 2005) along both latitudinal (Hickling *et al.* 2006) and altitudinal (Wilson *et al.* 2005) clines. These responses are set to occur at the population level rather than the individual, with range shifts resulting from changes in the ratio of extinctions to colonisations of populations at range boundaries (Parmesan *et al.* 1999). Expanding range boundaries occur where there is net colonisation, often at cool, higher altitudinal and latitudinal range margins in conjunction with recent warming. By contrast, retreating range boundaries occur where there is net extinction, often at the warmer, lower latitudinal and altitudinal limits of a species range (Parmesan *et al.* 1999; Hill *et al.* 2002). Given the tangible nature of range shifts, changes in species distributions are now one of the mostly widely researched topics in ecology (Chen *et al.* 2011). A multitude of studies (Parmesan *et al.* 1999; Parmesan & Yohe 2003; Hickling *et al.* 2006; Lenoir & Svenning 2015) have demonstrated consistent trends in range shifts, across species from a variety of taxa, as would be expected from species’ physiological constraints

(Walther *et al.* 2002; Devictor *et al.* 2008; Jiguet *et al.* 2010b), and shown strong links to recent global temperature increases (Chen *et al.* 2011; Gottfried *et al.* 2012; Poloczanska *et al.* 2013; Burrows *et al.* 2014). For example, Chen *et al.* (2011) reported that for multiple taxonomic groups, ranges have recently shifted to higher elevations at an average rate of 11.0 meters per decade, and to higher latitudes at an average rate of 16.9 kilometres per decade. Furthermore, they demonstrated a direct link between temperature change and range shifts, with range shifts greatest in those areas that experienced the highest levels of warming. Despite documented range shifts, there is evidence that species responses to climate change are occurring at a much slower rate than climate change itself (Menéndez *et al.* 2006; Devictor *et al.* 2008). Distributional shifts of birds and butterflies across Europe between 1990 and 2008 caused changes in community composition equating to a 37 km and 114 km northwards shift in communities for the respective taxonomic groups. However, the northward shifts in temperature across Europe for the same period were even faster, equating to 212 km and 135 km lag behind climate for birds and butterflies respectively (Devictor *et al.* 2012). Such time lags occur for three main reasons: limited dispersal which restricts colonisation, long generation times slowing demographic responses, and changes to interspecific biotic interactions (Cahill *et al.* 2013; Pearce-Higgins & Green 2014). This ‘migration lag’ is of particular concern for plant species (Huntley 1991; Corlett & Westcott 2013). Many plants species have few opportunities for dispersal, with the time from seed to first reproduction taking between one and thirty years for the majority of species (Moles *et al.* 2004). Furthermore the majority of species have a limited dispersal range, with recent reviews suggesting that most seeds are dispersed within 10-1500 m of the parent plant, with only species with small wind dispersed seeds routinely exceeding these distances (Clobert *et al.* 2012; Corlett & Westcott 2013). Herptiles (amphibians and reptiles) are another group that may be at particular risk of ‘migration lag’. Known for their poor dispersal abilities and the corresponding high levels of endemism (Williams *et al.* 2000), it has been suggested that many survived the last ice age in glacial refugia (Araújo & Pearson 2005; Baker *et al.* 2015). Limited dispersal and high levels of endemism render these species less able to adapt to environmental changes, and therefore, are at particular risk of future climate change.

1.2.2 Changes in abundance

To date, many studies have focussed on the impacts of climate change on the occurrence of species (Parmesan *et al.* 1999; Parmesan & Yohe 2003; Hickling *et al.* 2006; Chen *et al.* 2011; Lenoir & Svenning 2015), yet climate has also been shown to strongly influence the abundance of a species. Furthermore, as abundance is a more finely resolved variable than occurrence, it can better indicate smaller scale changes in habitat quality (Johnston *et al.* 2013). The impacts of climate on individuals or populations may operate either directly through physiological processes, such as metabolism and reproduction, or indirectly through ecosystem processes and altered species interactions (Stenseth et al. 2002). For instance, it has been shown that through increases to thermoregulatory costs, the mortality rates of Soay sheep (*Ovis aries*) and red deer (*Cervus elaphus*) are positively correlated with precipitation rates across Scotland (Milner, Elston & Albon 1999; Catchpole *et al.* 2000). Warmer temperatures have also been shown to positively affect red deer survival rates, with both survival and body mass being negatively correlated with snow depth (Loison, Langvatn & Solberg 1999). This may be a consequence of reduced thermoregulatory and movement costs but also increased food availability.

Environmental conditions throughout a species' range are not uniform, with individual populations demonstrating local adaptations to environmental conditions (Both et al. 2010). The suitability of an environment for a species is determined by the species' ecological tolerances (Brown, Stevens & Kaufman 1996), which in turn partly determines the local abundance of a species (VanDerWal et al. 2009). Individual fitness, and hence population size, will be greatest in those areas where environmental conditions fall within the optimal range, whilst in areas where environmental conditions are towards the extremes of a species' ecological tolerances individual fitness and local population size will be lower. Populations on the edge of a species' range are often regarded as being less dense, less fit, and less genetically diverse, rendering them more vulnerable to exitnction (Brown, Stevens & Kaufman 1996; Gibson, Van der Marel & Starzomski 2009). Local population dynamics will also be influenced by immigration between spatially separated populations, with source –sink dynamics operating across the entire ecological niche of some species (Pulliam 2000; Grotan et al. 2009). In theory, population growth in a species at equilibrium with the environment should be zero (Brown, Stevens & Kaufman 1996). Climate change has the potential to disrupt this equilibrium, increasing or decreasing local population growth depending on the direction of environmental change in relation to the species' ecological tolerances. This means that climate change can have disparate impacts on populations across a species' range (Jiguet et al. 2010a). For example, in the USA the extinction of some Edith's Checkerspot butterfly *(Euphydryas editha)* populations have been linked with fluctuations in precipitation. The 1975-1977 drought across California led to the extinction of 5 of 21 surveyed populations (Ehrlich *et al.* 1980). Conversely, two further populations went extinct in following winters where precipition was 50-150% greater than average (Dobkin, Olivieri & Ehrlich 1987; Parmesan, Root & Willig 2000). Studies of individual populations can provide more accurate estimates of the local responses to climatic change, than large scale abundance indices. However, localised counts are more susceptible to the influence of variations in local environmental conditions and net emigration and immigration (Lampila *et al.* 2006). Furthermore, it is large scale indices that are of greatest use to practitioners (Gregory *et al.* 2005; Gregory *et al.* 2009; Pearce-Higgins & Green 2014).

1.2.3 Impacts on communities

The species in a community reflect both the relationships between organisms and their environment and the interactions among organisms (Walther *et al.* 2002). With species responding individualistically to climate change, we can expect variation in community composition in future. For example, increases in woody shrubs, local extinctions of common species and increases in the abundance of formerly rare species in the Sonoran desert in south western United States, have all been attributed to recent shifts in regional climate (Brown, Valone & Curtin 1997). Additionally, the range shifts described in section 1.2.1 often result in community level changes. Range expansion at cooler, higher latitude and altitude margins often occurs at a faster rate than range retreat at warmer lower latitudes and altitudes (Thomas *et al.* 2004). Asymmetrical change in distribution may result in increases in community species richness, particularly in cool-temperate regions (Walther *et al.* 2002; Walther 2010). In the early 1990’s, upward colonisation in the European Alps was shown to increase plant species richness by up to 70% on 30 peaks (Pauli, Gottfried & Grabherr 1996). Menéndez *et al.* (2006) reported that despite declines in individual species, the average species richness of British butterfly fauna has increased since 1970-82. They also demonstrated that, due to increases in the distribution of habitat generalist species, there had been a reduction in overall community specialisation. Habitat specialist species, with small, range-restricted populations are regarded as being particularly vulnerable to environmental change (Julliard, Jiguet & Couvet 2004). In contrast, habitat generalists are fairly robust to, and may potentially even benefit from, habitat disturbance (Warren *et al.* 2001). These different responses result in ‘biotic homogenisation‘, a process where ecological communities become increasingly similar (Devictor *et al.* 2008; Le Viol *et al.* 2012). In both Britain (Davey *et al.* 2012) and France (Devictor *et al.* 2008) ‘biotic homogenisation’ of avian communities has been linked to climatic warming.

With changes in community composition come changes in community dynamics. New species interactions may emerge, whilst the balance of existing interactions such as predator-prey and competitive interactions may be affected (Walther *et al.* 2002). These alterations may further enhance the decline and extinction probability of a species, already under pressure to adapt and adjust to climatic change (Stralberg et al. 2009). The strongest evidence for this comes from the marine environment. Long-term fishery data is often related to long-term productivity and survival trends in seabirds. With climate being an important determinant of marine productivity, direct links can be found between temperature and the abundance of seabird prey species (Cushing 1995). Poor breeding success of North Sea Black-legged kittiwakes (*Rissa tridactyla*) has been associated with the negative impact that warm winters have on local Sandeel (*Ammodytes marinus*) recruitment (Frederiksen *et al.* 2004). In addition to changes in prey availability, top-down community pressures may also vary. For some species of Arctic ground-nesting birds, it has been proposed that their low-latitude range margins may be determined by the presence of generalist predators (Pienkowski 1984). With poleward range shifts, we may expect more opportunities for these species to interact, and consequently that the avian prey will be more vulnerable to population decline (Pearce-Higgins & Green 2014). Changes in predator-prey interactions will not be the only source of altered competitive dynamic. There is evidence that increases in the populations of Collared Flycatcher (*Ficedula albicollis*) populations across the Swedish islands of Öland and Gotland are having detrimental effects on co-occurring Pied Flycatcher (*Ficedula hypoleuca*) populations. These sympatric species compete for nesting resources, with male Pied Flycatchers often prohibited from establishing new territories, reducing overall productivity (Sætre, Post & Král 1999).

1.3 Impacts of environmental change on the populations of European birds

Over the past 30 years, populations of the commonest bird species across Europe have declined by 420 million individuals (Inger *et al.* 2014). Whilst some rarer species have seen their populations increase as a result of conservation efforts, for example osprey (*Pandion haliaetus)* (Bretagnolle, Mougeot & Thibault 2008), there have been steep declines in the abundance of more common species. Many of these declines have been attributed to the well documented reductions in farmland birds caused by agricultural intensification (Donald, Green & Heath 2001). Additionally, some widespread species such as House Sparrow (*Passer domesticus*) and Common Starling (*Sturnus vulgaris*) have also experienced dramatic population declines (62% and 53% respectively). Declines in the populations of both rare and widespread species can be linked to deterioration of the quality of the environment at both fine and large scales (Gaston & Fuller 2008).

1.3.1 Climate change

European climate changed considerably over the 20th century, with an increase in average annual surface temperature of 0.8°C (IPCC 2007b). These changes have not been spatially uniform, with the greatest observed temperature increases across the Iberian peninsula, mountainous regions and some parts of Scandinavia (Haylock *et al.* 2008). In addition to temperature changes, precipitation rates have also varied spatially. Over the 20th century, average annual precipitation across Northern Europe increased by between 10 and 40% but decreased by 20% across Southern Europe (IPCC 2007a). Furthermore, these environmental changes are set to increase over the next century, with mean annual temperature across Europe projected to increase by a further 2.5 - 5.5 °C. Mean annual precipitation will also vary, being projected to increase across north and central Europe by up to 20%, but to decrease by up to 45% across southern Europe (IPCC 2007b).

The effects of climatic changes on the distributions of European birds are already being reported (Devictor *et al.* 2008; Jiguet *et al.* 2010b; Le Viol *et al.* 2012). A European wide study showed that species predicted to gain range across Europe during the 21st century have increased, whilst species predicted to experience range reductions have declined (Gregory *et al.* 2009). Significant expansions at northern range limits have been observed for a variety of central European and Arctic species (Brommer, Lehikoinen & Valkama 2012; Virkkala *et al.* 2014). Additionally, range contractions of on average 27% between 1974 and 2010 have been reported for many northern-boreal species, including Brambling *(Fringilla montifringilla)*, Red-necked Phalarope (*Phalaropus lobatus*) and Spotted Redshank (*Tringa erythropus)* (Virkkala et al. 2014; Virkkala & Lehikoinen 2014). Projections of future climate change suggest that species' ranges will continue to track changes in climate and shift polewards. It has been predicted that, by 2050, 71% of species will experience reductions in range size with a median poleward shift of 335 km (Barbet-Massin, Thuiller & Jiguet 2012). Others have projected that, under climate scenarios for 2070-2099, the future breeding ranges of European birds may reduce by 28% and overlap current ranges by 42% (Huntley et al. 2008).

In addition to shifting ranges, other mechanisms by which climate can affect the populations of European birds have been widely reported (Gregory et al. 2009). For instance, the cold winters associated with higher latitudes pose particular challenges for the species that reside in those areas. Long-term studies of the UK population of Great Tits *(Parus major)* reveal that fluctuations in both population size and survival rate are correlated with snow cover, with overwinter juvenile survival rate reduced from 40% to 25% in a snowy winter (Robinson, Baillie & Crick 2007). Wintering Great Tits feed predominantly on beech masts, the abundance of which has been shown to influence overwinter survival (Grotan et al. 2009). With heavy snow cover, these birds have reduced access to these food resources, partially explaining population declines (Robinson, Baillie & Crick 2007). The survival rates of some species of owls have also been correlated with snow cover. Altwegg et al. (2006) reported that the populations of Barn Owls *(Tyto alba)* in Switzerland crashed after harsh winters as deep snow cover reduced access to their small mammal prey. Fluctuations in winter temperature have also been correlated with variations in the populations of waders (Charadrii, (Pearce-Higgins & Green 2014)). When the ground freezes, soil invertebrates become inactive or burrow deeper, which is problematic for species such as Golden Plover and Lapwing *(Vanellus vanellus)* which feed on them (Pearce-Higgins & Yalden 2003). It is not only winter conditions that influence avian populations, but also those during the breeding season. The main food of Song Thrushes *(Turdus philomelos)* during the breeding season is earthworms, the populations of which are strongly determined by soil moisture. When it is dry, the earthworms tend to be inactive or too deep for the thrushes to access and, presumably as a consequence, populations of Song Thrushes have been found to be negatively correlated with drought conditions (Robinson, Baillie & Crick 2007; Pearce-Higgins & Green 2014).

Climate change affects the timing of life history events, with many species demonstrating advancements in their reproductive phenology (Root *et al.* 2003; Menzel *et al.* 2006b; Both *et al.* 2009; Both *et al.* 2010). Parmesan and Yohe (2003) reported that across 677 species from seven taxonomic groups there had been a mean advancement in spring phenological events of 2.3 days per decade over the past four decades. However, these advancements are often species specific and not in synchrony with the phenological changes in other trophic levels (Visser, Both & Lambrechts 2004; Visser & Both 2005; Both *et al.* 2009). In particular, the timing of avian breeding and the peak abundance of food resources during the breeding season may be decoupled (Both & Visser 2005; Pearce-Higgins, Yalden & Whittingham 2005). For example, Golden Plover (*Pluvialis apricaria)* time the hatching of their first clutches to coincide with the emergence of adult tipulids, their main prey (Pearce-Higgins & Yalden 2004). Increases in spring temperature have been shown to correlate with advancements in the timing of Golden Plover first laying dates and of tipulid emergence (Pearce-Higgins, Yalden & Whittingham 2005). However, the predicted magnitude of these changes in response to future climate change were different, with potential advances in Golden Plover first laying dates of 25 days but of only 12 days in tipulid emergence. This mismatch was simulated to reduce the success of Golden Plover breeding attempts. Passerines from temperate regions have also shown variations in their breeding phenology in response to climatic change (Crick & Sparks 1999; Crick 2004). These species have the capacity to ameliorate the effects of climate change on breeding phenology through alterations to clutch size, incubation period and the number of broods raised (Visser *et al.* 2003; Visser, Both & Lambrechts 2004; Visser, Holleman & Gienapp 2006; Both *et al.* 2009). Some insectivorous species, such as some tits (*Parus sp.)* rely on caterpillars in oaks as the main food source for their offspring and therefore must time reproduction so that the maximal needs of their offspring coincides with the timing of peak caterpillar abundance (Visser, Holleman & Gienapp 2006). Both budburst and the peak biomass of herbivorous caterpillars have advanced in response to increasing spring temperatures (0.17 d yr $^{-}$1 and 0.5 d yr^{-1} between 1988 and 2005 respectively) (Both *et al.* 2009). Despite this, not all populations of tits have demonstrated similar advancements in reproductive phenology; some have compensated for reduced productivity by increasing the frequency of second broods (Visser *et al.* 1998; Visser *et al.* 2003).

1.3.2 Land use change

The widespread declines of some species of European birds have been widely linked to changes in habitat management (Donald, Green & Heath 2001; Donald *et al.* 2006; Lemoine *et al.* 2007; Sanderson *et al.* 2015). This is particularly true of agricultural environments, where the large scale declines of farmland birds have been largely attributed to the processes of agricultural intensification (Gregory *et al.* 2005; Donald *et al.* 2006). The process of intensification encompasses a wide range of mechanism including the increased use of pesticides and fertilisers, a greater degree of mechanisation, changes in crop types, the timing of sowing and harvesting of crops, increases in stocking densities, and the spread of monocultures (Vickery *et al.* 2001; Newton 2004b), all of which have resulted in some key changes in agricultural habitats. Homogenisation of the agricultural landscape and the loss of natural and semi-natural habitats has reduced the suitability of these areas for those species that require a variety of habitats for foraging or nesting, including Hoopoe (*Upupa epops*, Barbaro *et al.* 2008), Red-backed Shrike (*Lanius collurio*, Brambilla *et al.* 2010), Common Redstart (*Phoenicurus phoenicurus*, Schaub *et al.* 2010), Lapwing (*Vanellus vanellus*, Galbraith 1988) and Skylark (*Alauda arvensis*, Chamberlain & Gregory 1999). In addition, the intensification of crop management has been shown to have severe effects on some species. For example, the move from spring to winter sown cereals has reduced the availability of both important nesting habitats for Skylarks (Chamberlain *et al.* 1999) and overwinter stubbles, an important food resource for many species during the non-breeding season (Wilson, Taylor & Muirhead 1996). Conversely, in some parts of Europe, the abandonment of farmland habitat has become a key issue. Under the Common Agricultural Policy (CAP) and subsequent drive for increased production, many less productive agricultural systems have become economically unviable, accelerating rates of land abandonment (Van Zanten *et al.* 2014). The resulting re-growth of forest and loss of habitat heterogeneity (Klijn 2004) poses a severe risk for species which favour open breeding habitats (Sirami *et al.* 2008; Vallecillo, Brotons & Thuiller 2009; Nikolov 2010; Zakkak *et al.* 2015). For example, observed population declines in open habitat species such as Tawny Pipit (*Anthus campestris)* and Linnet (*Carduelis cannabina*) have both been associated with land abandonment and vegetation succession (Fonderflick *et al.* 2010).

Changing patterns in woodland management have also been associated with declines in some species of European birds. With reductions in traditional coppicing of broadleaved woodlands, many woodlands across Europe are now subject to little or no management (Hopkins & Kirby 2007). Combined with increased browsing pressures from expanding deer populations, understory vegetation and open habitats are being increasingly lost from many lowland woods and forests (Fuller *et al.* 2007; Holt, Fuller & Dolman 2011). The loss of understory vegetation affects not only the availability of nesting and foraging habitats (Holt, Fuller & Dolman 2011), but also the quality of associated food resources through alterations to invertebrate communities (Stewart 2001).

Wetlands, which contain a large diversity of habitats and are highly productive, provide important breeding and wintering habitat for many species (Paillisson, Reeber & Marion 2002).

However, these habitats are threatened by direct habitat loss, in particular from the drainage for agricultural habitats, deforestation for wood for construction and fuel, and embankment of floodplains for flood protection. In all, it has been estimated that 80% of the original area of European wetlands has been lost, mostly in the past 75 years (EU 2007; Verhoeven 2014), resulting in significant range reductions for globally threatened species such as Great Bittern (*Botaurus stellaris* (Gilbert *et al.* 2005)). Large scale hydrological changes, such as the creation of reservoirs, have immediate effects on some communities of water birds (Faragó & Hangya 2012), whilst water conditions have many direct and indirect impacts on the abundance and composition of water birds (Osiejuk *et al.* 1999; Paillisson, Reeber & Marion 2002). For example, a link has been demonstrated between declines in marshland species such as Great Bittern (*Botaurus stellaris),* Black Tern (*Chlidonias niger),* Sedge Warbler (*Acrocephalus schoenobaenus)* and Great Reed Warbler (*Acrocephalus arundinaceus)* and increases in the level of standing water and eutrophication across The Netherlands (van Turnhout, Hagemeijer & Foppen 2010).

1.3.3 Migration and environmental change

126 species of European birds are regarded as Afro-Palaearctic migrants under the classification strategy outlined by BirdLife (2004). This amounts to approximately 2.1 billion individual birds (Moreau 1972; Wilson & Cresswell 2006; Hahn, Bauer & Liechti 2009). Analyses of long term datasets of the abundance of Afro-Palaearctic migrants have shown that these species have experienced population declines of up to 40%, a rate of change far exceeding any observed in the populations of their resident and short-distance migrant counterparts (Sanderson *et al.* 2006; PECBMS 2009; Vorisek *et al.* 2010; EBCC 2013; Cresswell 2014; Vickery *et al.* 2014). These declines are likely to be a consequence of their complex annual cycles, long migration routes, and dependence on multiple sites, breeding across Europe and over-wintering in sub-Saharan Africa (Newton 2004a; Newton 2008; Newton 2010). Not only are these species susceptible to the pressures of environmental change on their European breeding grounds, as outlined above, they are also exposed to additional pressures on their stop-over and over-wintering sites and during migration.

Away from the breeding grounds, Afro-Palaearctic migrants rely heavily upon wetland, savannah and woodland habitats across the Sahel, where conditions are intimately linked with precipitation rates (Vickery *et al.* 2014). When rainfall in these areas is high, food and habitat resources available to migrants are plentiful (Ockendon, Johnston & Baillie 2014). Yet, despite an apparent increase in rainfall since the 1990's (Fontaine *et al.* 2011), drought conditions have predominated across the Sahel since the 1960's (Nicholson 2000; Fensholt & Rasmussen 2011). The resulting large-scale habitat changes have been widely linked to the declines of Afro-Palaearctic migratory birds (Sanderson *et al.* 2006; Zwarts & van Horssen 2009; Ockendon, Johnston & Baillie 2014). It has been suggested that this operates through impacts on overwinter survival, which has been demonstrated for Hirundidae (Robinson, Balmer & Marchant 2008), Ciconiformes (Nevoux, Barbraud & Barbraud 2008) and Sylviidae (Baillie & Peach 1992; Peach, Hanmer & Oatley 2001). Alternatively, it may operate through carry-over effects on phenology and productivity in the following breeding season (Gordo *et al.* 2005; Zwarts & van Horssen 2009). Drought conditions may also have compounded the effects of other anthropogenically induced habitat changes (Vickery et al. 2014), such as the widespread deforestation of Sahelian woodlands for conversion to agriculture, fuel and grazing (Wilson & Cresswell 2006). Extensive losses of woodland and forest habitats have been documented across sub-Saharan Africa. In Senegal, it is was estimated that 33,000 hectares of woodland and forest were being lost every year (Tappan *et al.* 2004). Forest losses have been shown to have a significant negative effect on the populations of Afro-Palaearctic migrants. For example, an 8% reduction in Nigerian tree density correlated with a 95% decline in the local Subalpine Warbler *(Sylvia cantillans)* population (Cresswell et al. 2007).

There is some evidence that, as for the European breeding ranges, the overall size of species' non-breeding ranges will be reduced as a consequence of spatial shifts in areas of suitable climate (Barbet-Massin *et al.* 2009). However, the consistent directionality in shifts shown in projections of future European ranges is not evident in projections of future African ranges (Doswald *et al.* 2009). This may be a consequence of the less clear environmental drivers of species' distributions in the tropics, with suggestions that precipitation plays a more important role (Gordo *et al.* 2005). Importantly though, the distance between breeding and non-breeding ranges is set to increase under projected future climate change, thus increasing energetic costs and the probability of migration mortality (Alerstam, Hedenström & Åkesson 2003; Doswald *et al.* 2009).

Afro-Palaearctic migrants may also be more vulnerable to the effects of phenological mismatch, with their arrival on the breeding grounds constrained by conditions on the non-breeding grounds and during passage (Both & Visser 2001; Both *et al.* 2006; Both *et al.* 2010). With advancements in spring phenology (outlined above in section 1.3.1), mistimed arrival on the breeding ground may have severe consequences on fitness. Short-distance migrants, those species which spend their non-breeding season in southern Europe instead of sub-Saharan Africa, have advanced their spring migration phenology to a greater extent than have Afro-Palaearctic migrants (Saino *et al.* 2004; Saino *et al.* 2011). Whilst some species of Afro-Palaearctic migrants use endogenous responses to environmental cues, such as photoperiod, to initiate their spring migration (Knudsen *et al.* 2011), these cues will not necessarily reflect conditions on the breeding grounds. The cues used by short-distance migrants may be more closely linked to breeding ground conditions, potentially explaining the reduced ability of Afro-Palaearctic migrants to respond adaptively to climate change (Coppack *et al.* 2003; Coppack *et al.* 2008). Arrival dates may also be affected by conditions during migration. For example, the first arrival dates to the Iberian peninsula of Cuckoos (*Cuculus canorus*), Common Swifts *(Apus apus)*, and Nightingales (*Luscinia megarhynchos*) are linked to temperatures in passage areas (Gordo et al. 2005). The importance of ecological conditions in passage areas is greater for individuals migrating to higher latitudes, with better weather conditions improving refuelling rates and allowing for a faster progression (Ahola *et al.* 2004; Both, Bijlsma & Visser 2005).

1.4 Disentangling the effects of climate and land use change on species' abundances

Climate can have both direct and indirect effects on the productivity, survival and abundance of species. For these reasons, climate is often regarded as the ultimate driver of species' distribution and abundance (Thuiller, Araujo & Lavorel 2004). With this assumption, we would expect the ranges and populations of species to vary in response to climatic change. Yet other abiotic and biotic factors also have a role in influencing species' distribution and abundance, for example land-use, inter- and intra-specific interactions and species specific traits (Boulangeat, Gravel & Thuiller 2012; Wisz *et al.* 2013). When considering the global distribution of suitable climates for a species, suitable habitats can often be found on multiple continents, which only the most widespread of species will have occupied (Pearce-Higgins & Green 2014). Many species are clearly limited not only by abiotic factors, but also their ability to disperse, and the distribution of prey and predators (Boulangeat, Gravel & Thuiller 2012; Wisz *et al.* 2013). Furthermore, those species susceptible to the effects of anthropogenic activities are unlikely to be in equilibrium with climatic conditions, especially given that human activities are only weakly correlated with climate (Thuiller, Araujo & Lavorel 2004). For example, the persecution of birds of prey across Great Britain, has had significant impacts on survival and distribution (Whitfield *et al.* 2004). Some human activities have also increased species' ranges. As a result of substantial increases in the extent and volume of trade and transport over the past century, many species have extended their range beyond what would be physically possible due to human introductions, both intended and accidental (McGeoch *et al.* 2010). If we are to accurately assess the effects of projected climate change on a species, it is important that we understand the relative importance of all of these factors in driving the distribution and abundance of a species.

Disentangling the relative importance of climate, versus other abiotic and biotic factors that cause changes in species' abundance and distribution, is difficult. Although climate is often regarded as the ultimate determinant of species' distribution and abundance, geology, land use, and topography also all operate on species at increasingly finer scales (Franklin 1995; Thuiller, Araujo & Lavorel 2004). Despite the inference from recent studies that the effects of climate change have overtaken land use change (Moller, Rubolini & Lehikoinen 2008; Gregory *et al.* 2009), care needs to be taken when attributing changes in distribution and abundance to climate change. Eglington and Pearce-Higgins (2012) demonstrated that despite the long term abundance of many farmland bird species, including Grey partridges, *(Perdix perdix),* Skylarks (*Alauda arvensis)* and Corn Buntings (*Emberiz calandra),* being closely associated with fluctuations in weather variables, the precipitous population declines of these species are more strongly linked with directional trends in agricultural intensification. Furthermore, species' sensitivity to climate may vary spatially (Finley 2011; Beale, Brewer & Lennon 2014; Jarzyna *et al.* 2014). Habitat differences in species' sensitivity to temperature may confound the detectability of the relative impacts of climate and land-use change, especially for large scale analyses. Despite being of political and scientific interest, the relative importance of these variables in driving both distribution and abundance has rarely been tested (Thuiller, Araujo & Lavorel 2004; Eglington & Pearce-Higgins 2012; Renwick *et al.* 2012), and never at an international scale.

Understanding the drivers of species' distribution and abundance is further complicated for those species that rely upon multiple sites (Sillett & Holmes 2002; Robinson *et al.* 2009; Newton 2010). Migratory species demonstrate complex annual cycles, dependent on multiple sites including both breeding and non-breeding grounds, along with migratory stop-over sites. Susceptibility to environmental change in any one of these multiple habitats renders these species particularly vulnerable to the pressure of anthropogenic induced habitat change (Finch *et al.* 2014; Runge *et al.* 2014). Changes in climate and land use can limit populations of these species, along with other anthropogenic activities such as hunting and persecution (Vickery *et al.* 2014). Disentangling the relative effects of these factors, and understanding which of the residence and staging areas are critically limited, complicates understanding of population change for migratory species (Ockendon *et al.* 2012).

1.5 Modelling species distribution and abundance

Understanding the consequences of climatic change on species could inform their future conservation status and priority for conservation action. Although some impacts of recent climatic change on species have already been observed, the magnitude of future climate change poses an even greater threat. Given the complexity of the relationship between climate and species' distribution and abundance, predicting the impacts of climate for multiple species is difficult. However, by building on the role that climate has in determining a species' distribution (see section 1.2.1), statistical models of the geographic relationship between species' occurrence and abundance and environmental variables can be built. These widely applicable statistical models can then be used to make future projections of species distribution and abundance under various future climate scenarios (Pearce-Higgins & Green 2014).

1.5.1 Species distribution models

Species distribution models (SDMs) or ecological niche models are statistical models of the geographical distribution of species in relation to environmental predictor variables (Guisan & Zimmermann 2000). As a result of both methodological and computational advancements, the application of SDMs in forecasting the potential effects of anthropogenic activity has grown exponentially since the 1990's (Franklin 1995). There are hundreds - if not thousands - of papers detailing their application to a broad set of ecological, evolutionary and conservation questions (Zimmermann *et al.* 2010), and numerous reviews describing their methodology and framework (Franklin 1995; Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Elith & Leathwick 2009; Zimmermann *et al.* 2010). Many papers have focussed on improving the statistical bases of SDMs, including the implementation of new statistical methods. Linear regression models formed the basis of early SDMs, but are often too simplistic for realistic representation (Elith, Leathwick & Hastie 2008). The use of generalised linear regression models (GLM; Mccullagh 1984) and generalised additive models (GAM; Hastie & Tibshirani 1990) allow for both non-linear relationships and data with non-normal error structure to be modelled. More recently, machine learning techniques, such as boosted regression trees (BRT; Elith, Leathwick & Hastie 2008) and random forests (RF; Cutler *et al.* 2007) have been utilised. In contrast to statistical approaches (GLM and GAM), machine learning approaches avoid starting with a data model and instead use an algorithm to learn the relationship between a species distribution and the predictor variables (Breiman 2001b; Elith, Leathwick & Hastie 2008). SDM performance is also dependent upon the data sampling design used for model parameterisation. For example when species are rare, simple random sampling procedures can be highly inefficient, as often sampled sites are unlikely to provide suitable habitat for a species. In these cases random-stratified sampling can be used to ensure a more representative sample (Rushton, Ormerod & Kerby 2004; Guisan *et al.* 2006). Sample size and the prevalence of species across the sampling area can also affect the accuracy of SDMs (Wisz *et al.* 2008). Model quality is clearly influenced by the number of records used in model building (Pearce & Ferrier 2000; Allouche, Tsoar & Kadmon 2006; Guisan *et al.* 2006). For species with a narrow band of thermal tolerances, a small sample size may be sufficient to characterise their distribution in relation to environmental predictors. However, for the majority of species, a large sample size is often required to fully sample the range of environmental conditions in which a species is present (Kadmon, Farber & Danin 2003). Another area of model development concerns dealing with spatial autocorrelation, which is often present in spatial ecological datasets. This occurs where more proximate samples demonstrate a greater degree of similarity in their ecological characteristics than samples more distant from one another (Legendre 1993). Failure to account for this phenomenon when modelling species distributions, leads to the violation of standard assumptions of independence, hence inflating type I errors (Dormann 2007a).

The idea that models trained purely on climatic variables can quantify the impacts of climate change on species has been questioned (Araújo & Luoto 2007; Austin & Van Niel 2011). Many species have already shown range shifts in response to climatic change; however, the rate of these shifts is not as fast as would be expected if climate was the only limiting factor (Menendez *et al.* 2006; Devictor *et al.* 2008). The predictive power of SDMs is subject to the choice and scale of predictor variables, with SDMs producing less reliable predictions when important local or regional factors are missing (Thuiller *et al.* 2003; Thuiller, Araujo & Lavorel 2004). For example, local topography may create important refugia for species, which are not recognised in coarse-scale climate data, whilst differences in light regimes between north- and south- facing aspects in temperate regions produce differences in temperature that can equate to 200 km poleward shift (Austin & Van Niel 2011; Bennie *et al.* 2014; Lawson *et al.* 2014). The inclusion of land use variables is often reported to improve the explanatory power of SDMs, particularly when species' distributions are poorly explained by climate (Thuiller, Araujo & Lavorel 2004; Barbet-Massin, Thuiller & Jiguet 2012). It is clear that both climate and land-use shape species distributions, however, as mentioned above (see section 1.4) the relative importance of these variables is largely unknown (Eglington & Pearce-Higgins 2012; Renwick *et al.* 2012). This is further complicated by the fact that some land use types are strongly determined by climatic factors, for example wetlands (Merot *et al.* 2003) and agricultural lands (Ramankutty *et al.* 2002). Even though the addition of land use variables does not necessarily improve the predictive accuracy of SDMs (Thuiller, Araujo & Lavorel 2004), their inclusion may significantly alter projections of species distributions under future climatic change.

1.5.2 Modelling abundance

Despite many recent advancements in the statistical bases of SDMs (see section 1.5.1), confidence in the predictive capabilities of these models continues to be undermined by conceptual, biotic and algorithmic flaws (Higgins, O'Hara & Römermann 2012). In addition to methodological advancements, it may be that improvements to model performance can be achieved by increasing the quality of data available for model training. Most SDMs use presence only or presence/absence data to characterise the climatic limits of a species' range and to predict how species distributions may change in response to climate change. Studies have compared the relative merits of these two forms of data (Brotons *et al.* 2004; Elith *et al.* 2006; Pearson *et al.* 2006), but few have considered the improvements that could be achieved through the use of abundance data. It may be that the greater information content in abundance data would enable a better assessment of the quality of an environment for a species, in turn allowing for better discrimination of species range boundaries. Furthermore, even though trends in range extent are important for assessing the threat status of a species, it is population size and trends that are the closest correlate of extinction risk (O'Grady *et* *al.* 2004). It has been shown that population declines may occur before any reduction in a species' range is observed (Chamberlain & Fuller 2001), making population size a more sensitive indicator of the effects of future climatic change on a species (Pearce-Higgins & Green 2014). With this in mind, and combined with the fact that it is changes in population that are used for assessing a species' conservation status and priority for action (International Union for Conservation of Nature 2001), directly modelling abundance rather than presence/absence will likely be more informative.

To model a species' abundance distribution, a similar range of techniques can be used to those that model presence/absence data, including both statistical and machine learning approaches, as outlined in section 1.5.1. However, abundance modelling poses some additional problems that need to be accounted for when specifying model structure. In particular, the abundance of a species in any given locality is far more susceptible to the influence of non-climatic factors on environmental quality than occurrence data. For example, a regression of the abundance of 17 breeding seabirds and 45 wintering water birds in Western Europe on local climate variables explained only 1.2% and <0.1% of the variation in fine scale abundance patterns (Johnston *et al.* 2013) . The same model, however, explained 56% of the variation in large scale population trends. Climate may explain large scale population trends, but non-climatic factors and interactions may have greater importance at a site specific level. These non-climatic factors may relate directly to the environment, such as land use, or alternatively result from inter and intra-specific interactions. Birds often demonstrate aggregate or colonial behaviours. Local aggregation as a consequence of behaviour would not be predicted by simple climate-only models (Pearce-Higgins & Green 2014). It is desirable then to include non-climate explanatory variables that may better describe habitat quality or the abundance and distribution of allo- and conspecifics, if we are to forecast the abundance of species under climate projections with certainty (Renwick *et al.* 2012).

1.6 Implications of results for conservation and management

Despite the many advancements in the statistical methods used for modelling the distribution and abundance of species (Franklin 1995; Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Elith & Leathwick 2009; Zimmermann *et al.* 2010), there are still areas for improvement. Cross-species analyses are often used to provide general insights into the susceptibility of species to future environmental change (Bagchi *et al.* 2013; Baker *et al.* 2015). By modelling abundance rather than distribution, both the predictive accuracy of these models and the management application of these approaches may be enhanced. Models of spatial variations in species abundance will allow greater conservation priority to be assigned to those areas where species occur at the highest density both now and in the future. With peripheral populations more likely to become extinct due to natural population fluctuations, there are more risks associated with conserving these populations.

Identifying those areas of a species' future distribution where they will occur at a higher density and most likely to persist, and targeting conservation efforts accordingly, will ensure greater success (Gibson, Van der Marel & Starzomski 2009; McCarthy *et al.* 2011). Furthermore, with population trends being the closest correlate of extinction risk, predictions of abundance are of more use than range predictions in determining the conservation status and priority for action of a species (International Union for Conservation of Nature 2001; O'Grady *et al.* 2004).

Effective conservation measures require understanding of the causal factors driving a species population trends. The best example of this is the application of agri-environment schemes to increase breeding densities of many farmland bird species (Newton 2004b). As explained in section 1.4, the population declines of many species of farmland bird correlate with recent climatic changes, however they have mostly been attributed to agricultural intensification (Donald, Green & Heath 2001; Donald *et al.* 2006). The decline of Grey Partridge (*Perdix perdix)* despite being closely associated with fluctuations in temperature and precipitation (Eglington & Pearce-Higgins 2012), can actually be directly attributed to reductions in field margins. The loss of these less intensively managed areas, results in a scarcity of nesting habitats and increased predation. Furthermore, widespread application of pesticides reduces insect abundance, an important food resource for chicks (Green 1984). With this knowledge, local conservation efforts, for example the non-spraying of field margins, have helped stabilise the national population (Eglington & Pearce-Higgins 2012). Whilst the effectiveness of localised conservation has been enhanced by the application of better informed measures, quantitative multispecies applications to identify priority landscapes at national and international scales are currently lacking (Moilanen *et al.* 2005).

The current reliance of conservation efforts on static protected areas may not avert species losses in the face of climate projections given the poleward and altitudinal shifts in the distributions of species (Parmesan *et al.* 1999; Hickling *et al.* 2006; Brommer, Lehikoinen & Valkama 2012; Virkkala & Lehikoinen 2014). Europe currently has the world's most extensive network of conservation areas, with more than 100,000 sites across 54 countries (Araújo *et al.* 2011; Romao & Reker 2012). Yet these protected areas will not be effective in conserving a large proportion of European plant and terrestrial species under projected climate change. By 2080, 58% of vertebrate and plant species are predicted to lose suitable climate within existing protected areas (Araújo *et al.* 2011). It is widely recognised that to address the challenge of the reduced efficacy of protected areas in the future, new conservation areas will need to be designated (Alagador, Cerdeira & Araújo 2014). The identification and designation of new conservation sites, however, is expensive and conservation budgets are limited (Hannah *et al.* 2007; Wise *et al.* 2012). The combination of improved predictions of species spatial abundance patterns and the identification of core habitats important for species preservation will facilitate more informed spatial conservation planning. Both areas that will remain climatically suitable with time, and those areas that will become increasingly suitable in the future, will be prime candidates for future conservation efforts, can be identified (Vos *et al.* 2008; Alagador, Cerdeira & Araújo 2014). Furthermore, those areas providing important links and corridors between current and future reserves, aiding the movement of species between these sites, can be conserved (Williams *et al.* 2005; Chetkiewicz & Boyce 2009; Saura, Bodin & Fortin 2014).

For species for which connected networks are insufficient for the continued persistence under climatic change, assisted colonisation may provide an alternative solution (McLachlan, Hellmann & Schwartz 2007; Hoegh-Guldberg *et al.* 2008). Species with poor dispersal abilities may be unable to spread into new climatically suitable areas, resulting in reductions in realised niches and increased extinction risk (Warren *et al.* 2001). The idea of moving species to sites where they currently do not occur is often cautioned against. Yet, with a thorough understanding of the habitat requirements of a species conservationists can identify low risk situations where the benefits of ‘assisted colonisation’ are maximised and the risks minimised (Hoegh-Guldberg *et al.* 2008). Willis *et al.* (2009) introduced two species of butterfly into sites beyond their then respective range margins after using SDMs and local expert knowledge to identify potential new suitable habitats. Both introduced populations then proceeded to grow and expand across their new range over the following six years (and continue to prosper). With informed selection of both candidate species and suitable habitat, assisted colonisation can provide an effective mean of enabling species to track climate change. By modelling abundance, we can further enhance our understanding of species habitat requirements, improving the success of future assisted colonisation efforts.

Predictions of abundance are a valuable resource for the implementation of effective management strategies. Knowing which species will become imperilled in future, and where climate change will most impact upon species’ abundance and communities, will be important for conservation planning. However, as I have discussed, the methods required to predict changes in abundance in response to projected climate change are, currently, largely untested. Furthermore, there is only limited understanding of what determines species abundance at a large scale. Establishing the relative importance of climate and land use in determining species abundance is important if we are to fully understand the potential impacts of future environmental change. Here, I present the key aims of this project, and describe how I intend to improve understanding of species abundance modelling, and the potential responses of species’ abundances to large scale environmental change.

1.7 Project Aims

1. **To assess the performance of models of abundance**

   First, I examine the improvements that can be made in models of species distributions, by conditioning them on abundance data rather than occurrence data. As detailed in section 1.5.2, the greater information available from abundance data may significantly improve our understanding of species-environment relationships. I assess whether such models can be used to produce informative spatial predictions of species abundance (Chapter 2).

2. **To understand what drives the abundance of European birds at a large scale**

   Currently, our understanding of the relative importance of climate, land-use and other biotic factors in driving large scale abundance is limited, see section 1.4. Here, I investigate the relative importance of these factors in driving the abundance of European breeding birds. Initially, I focus on the European ranges of these species, and examine how the importance of these variables in determining the abundance of these species varies spatially (Chapter 3). I then extend these analyses to explore the relative importance of conditions on both the breeding and non-breeding ranges of European migratory birds (Chapter 4). With the reported impacts that conditions on non-breeding areas have in driving the populations of migratory species, see section 1.3.3, it is essential that we determine the importance of these factors relative to conditions on the breeding grounds.

3. **Assess the projected impacts of climate change on the abundance of European birds and the consequences for community structure**

   Projections of species abundance are crucial for the effective conservation of species under climate change, see section 1.6. First, I assess the predictive power of spatial models of abundance, and determine their utility for predicting future changes in abundance (Chapter 5). Finally, using these models, I predict the potential effects of climate change on both the abundance of European breeding birds and the subsequent changes in community composition (Chapter 6).

Chapter 2

Improving species distribution models: the value of data on abundance

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2.1 Abstract

Species distribution models (SDMs) are important tools for forecasting the potential impacts of future environmental changes but debate remains over the most robust modelling approaches for making projections. Suggested improvements in SDMs vary from algorithmic development through to more mechanistic modelling approaches. Here, I focus on the improvements that can be gained by conditioning SDMs on more detailed data. Specifically, I use breeding bird data from across Europe to compare the relative performances of SDMs trained on presence-absence data and those trained on abundance data. SDMs trained on presence-absence data, with a poor to slight fit according to Cohen's kappa, show an average improvement in model performance of 0.32 (se ±0.12) when trained on abundance data. Even those species for which models trained on presence-absence data are classified as good to excellent show a mean improvement in Cohen's kappa score of 0.05 (se ±0.01) when corresponding SDMs are trained on abundance data. This improved explanatory power is most pronounced for species of high prevalence. My results illustrate that even by using coarse scale abundance data, large improvements in our ability to predict species distributions can be achieved. Furthermore, predictions from abundance models provide a greater depth of information with regard to population dynamics than their presence-absence model counterparts. Currently, despite the existence of a wide variety of abundance data sets, species distribution modellers continue to rely almost exclusively on presence-absence data to train and test SDMs. Given my findings, I advocate that, where available, abundance data rather than presence-absence data can be used to more accurately predict the ecological consequences of environmental change. Additionally, my findings highlight the importance of informative baseline data sets. I therefore recommend the move towards increased collection of abundance data, even if only coarse numerical scales of recording are possible.

2.2 Introduction

To determine the impacts of future climate and habitat changes on species, ecologists increasingly use species distribution models (SDMs) to quantify species-environment relationships (Guisan & Thuiller 2005). SDMs are now widely used and frequently refined (Guisan & Rahbek 2011; Higgins, O'Hara & Römermann 2012). Nevertheless, confidence in the predictive power of these models continues to be undermined by conceptual, biotic and algorithmic flaws, which include uncertainty regarding variable selection (Austin & Van Niel 2011), unrealistic model assumptions (Schroder & Seppelt 2006; Dormann 2007b), and lack of agreement over the classification of basic concepts (Segurado & Araújo 2004; Araújo & Guisan 2006; Austin 2007). As a result, ongoing debate concerns the strengths and limitations of SDMs and potential areas for their improvement (Araujo & Peterson 2012). Suggested areas of development range from the incorporation of land cover variables and biotic interactions, to accounting for spatial autocorrelation (Guisan & Thuiller 2005; Araújo & Guisan 2006; Dormann 2007a; Bagchi *et al.* 2013) and incorporating biological traits (Higgins, O'Hara & Römermann 2012). Methodological improvements may well increase the predictive performance of SDMs (Araújo & Guisan 2006; Austin 2007). Additionally, we might consider what could be achieved by improving the information available for training data sets. Although the relative value of presence-only and presence-absence data has been widely discussed (Brotons *et al.* 2004; Elith *et al.* 2006; Pearson *et al.* 2006), a third, more detailed form of data is available for many taxa in some regions: abundance data. This may either be an index of abundance, for example based on frequency of reporting rates (Harrison & Cherry 1997), or an estimate of true population size, such as derived from surveys accounting for detectability (Renwick *et al.* 2012). In addition to providing additional information that may be better related to conservation status (Gregory, Noble & Custance 2004; Johnston *et al.* 2013), extinction risk (O'Grady *et al.* 2004) and community structure and function (Davey *et al.* 2012), the greater information content of abundance data could also result in models with a greater ability to discriminate species’ range boundaries, and to produce more accurate models of presence-absence. At present, however, there is no indication of the magnitude of improvements in SDMs that could be gained through using abundance rather than presence-absence data.

Based on the assumption that local abundance is an indicator of habitat quality, SDMs derived from abundance data may reflect the importance of key demographic and environmental factors such as carrying capacity (Pearce & Ferrier 2001). Van Horne (1983) cautioned against the assumption that abundance can be used as an indicator of habitat quality, as some environmental factors and species characteristics, such as detectability, can reduce the probability of a positive correlation between abundance and habitat quality. Nevertheless, by using abundance data and increasing the information available to train SDMs, the ability to predict occurrence may be improved. It is therefore important to understand the extent to which structuring presence-absence data through the use of abundance data improves model performance in cases where land cover and spatial autocorrelation have already been incorporated.

A curvilinear relationship between predictive performance of SDMs and prevalence has been widely reported in the literature (Manel, Williams & Ormerod 2001; McPherson, Jetz & Rogers 2004; Allouche, Tsoar & Kadmon 2006), especially when fit is assessed using the kappa statistic (Santika 2011). A positive relationship between range size and mean abundance has also been reported within many taxonomic groups (Brown 1984). With this in mind, we would expect the mean abundance of low prevalence species to be uniformly low across their range, and therefore abundance values to be little more informative than presence-absence data. The predictive capabilities of models trained on abundance data and models trained using presence-absence data, may therefore be expected to converge at low levels of prevalence.

Here, I use a machine learning technique, random forests, to model the distribution of European breeding-bird atlas data across the scale of the continent. I analyse the relative performance of models trained on abundance data and those trained on presence-absence data. Additionally, I investigate the role of prevalence on the performance of these models to determine if there are limitations to any benefit associated with abundance modelling.

2.3 Methods

2.3.1 Data

Spatial abundance data for 496 species of breeding birds within Europe were obtained from the EBCC (European Bird Census Council) Atlas of European breeding birds (Hagemeijer & Blair 1997). The EBCC atlas provides, for many countries across Europe, a population size estimate for each species in the ca. 50x50 km squares of the Universal Transverse Mercator (UTM) grid. Population size estimates, principally relating to the period 1985 -1988, are based on a 7-point scale (including zero and six logarithmically scaled categories: 1-9, 10-99, 100-999, 1000-9,999, 10,000-99,999, ≥100,000 breeding pairs). For Russia, parts of Belarus, Ukraine, and the Caucasus republics, the data quality of species records was primarily qualitative; therefore, these areas were excluded from the analysis. Likewise, some areas in Western Europe recorded only qualitative presence-absence data, so were excluded from analyses (Figure A1). From the initial 496 species, I excluded introduced species and species which spend a significant proportion of their time at sea (Table A1) because their abundance is unlikely to be strongly linked to terrestrial climate and land use. Due to model-building limitations, particularly when undertaking data-splitting for model validation, those species recorded in fewer than 20 grid cells were also omitted. The remaining 345 species were used for all subsequent analyses in this chapter

2.3.2 Bioclimatic data

Climatic data were derived from the global compilation made by New, Hulme and Jones (1999) for the 30 year interval 1961-1990, the latter part of which corresponds to the period of EBCC bird abundance data collection. Following the formulation of Prentice *et al.* (1992), four bioclimatic variables were calculated for each UTM grid cell: mean temperature of the coldest month (MTCO); mean temperature of the warmest month (MTWA); growing degree days above 5° (GDD5); and the annual ratio of actual to potential evapotranspiration (APET). Through both direct and indirect effects on vegetation, prey, predators, competition or diseases (Gregory *et al.* 2009), these variables can limit species ranges and populations. Previously, these variables have been widely and successfully used in models to describe both the range extents (Thuiller, Araujo & Lavorel 2004; Huntley *et al.* 2007; Oliver *et al.* 2012) and abundance patterns of European birds (Green *et al.* 2008; Gregory *et al.* 2009).

2.3.3 Land use data

Land use data were compiled at the same resolution as the species data. The land use for each cell was derived from an aggregation of the Pan-European Land Cover (PELCOM) 1 km resolution database (Mucher *et al.* 2000); these land use classifications being based on NOAA-AVHRR satellite data. The PELCOM database was chosen over similar finer scale land use datasets due to its complete spatial coverage of the study area, and the homogeneity of the methods used for land-cover classification (Thuiller, Araujo & Lavorel 2004; Araújo *et al.* 2005)**.** Eight land use classifications were used: forest, grassland, urban, arable, wetland, coastal, shrubland, and barren. The percentage coverage of each of these eight classes was calculated for each UTM grid cell.

2.3.4 Statistical modelling

Random forest (RF) models were used to model species distributions from both the abundance and the presence-absence data. This machine learning technique is a bootstrap based classification and regression trees (CART) method (Cutler et al. 2007). Here, to account for a high degree of correlation between climatic covariates (with Pearson's r ranging between 0.61 and 0.9) and the potential for biased variable selection, I use the 'party' package in R, which uses a random forest implementation based on a conditional inference framework (Hothorn, Hornik & Zeileis 2006a; Hothorn, Hornik & Zeileis 2006b; Strobl, Hothorn & Zeileis 2009a; R Development Core Team 2012). As with other classification methods, random forests draw bootstrap samples and a subset of predictors to construct multiple classification trees (Prasad, Iverson & Liaw 2006). The classification trees find optimal binary splits in the selected covariates to partition the sample recursively into increasingly homogeneous areas with respect to the class variable (Cutler *et al.* 2007). Under the conditional inference framework, unbiased variable selection is achieved by using a linear statistic to test the relationship between covariate and response, selecting the covariate with the minimum *P*-value. This linear statistic is also used to optimise the binary split into each homogeneous area (Hothorn, Hornik & Zeileis 2006a; Hothorn, Hornik & Zeileis 2006b; Strobl, Hothorn & Zeileis 2009a). In the case of ordinal response variables, a score vector reflecting the 'distances' between class levels is combined linearly with the linear statistic altering both the selection and binary splitting of variables according to the scale of the ordinal response data (Hothorn, Hornik & Zeileis 2006b).

Random forests make few assumptions about the distribution of variables, are robust to over-fitting, and are widely recognised to produce good predictive models (Breiman 2001a; Liaw & Wiener 2002; Prasad, Iverson & Liaw 2006). These models typically outperform traditional regression based approaches to species distribution modelling and are ideal for modelling categorical and ordinal data (Lawler *et al.* 2006; Magness, Huettmann & Morton 2008; Marmion *et al.* 2009). More established approaches to ordinal data modelling include proportional odds and continuation ratio ordinal regression models (Guisan & Harrell 2000). However these models have limiting assumptions, such as parallelism between classes, and lack the flexibility to identify non-linear, context dependent relationships amongst predictor variables (De'ath & Fabricius 2000; Olden, Lawler & Poff 2008; Strobl, Malley & Tutz 2009).

To account for spatial autocorrelation I included a measure of the surrounding abundance of conspecifics in the first order neighbouring UTM grid cells (Segurado, Araujo & Kunin 2006) as a spatial auto-covariate (SAC). This term accounts for the greater degree of similarity between more proximate samples, that arises through distance-related biological process and spatially structured environmental processes (Dormann *et al.* 2007). I account for potential spatial autocorrelation in my abundance-based models by calculating an indicator of surrounding abundance for each UTM grid cell, using the following equation:

$$\mathrm{L} = \log_{10}\left[\frac{1}{\mathrm{n}}\sum_{\mathrm{i}}^{\mathrm{n}}\frac{1}{2}10^{\mathrm{A_i}}\right] \tag{1}$$

where: L= surrounding local abundance, n= number of adjacent cells, A= categorical abundance, i= abundance category index. The log scaled abundance categories in the adjacent cells are back transformed to the mid-points of the relevant categories; these are averaged and re-transformed to the log scale. For models based on presence-absence data, the spatial autocovariate used the same equation, except that the abundance categories (A_i) were converted to binary (presence-absence) data. Models were fitted using ten-fold cross validation to reduce SAC between training and test data and to minimise over-fitting. I used correlograms to compare autocorrelation in the model residuals with autocorrelation present in the raw data. Correlograms plot a measure of spatial autocorrelation, Moran's I (Moran 1950), between grid cells as a function of the distance between them (Fortin & Dale. 2005; Dormann *et al.* 2007; Kissling & Carl 2008). A value of zero of Moran's I for within model residuals, indicates an absence of spatial autocorrelation. Therefore, a significant deviation from zero suggests that the model is not adequately accounting for spatial autocorrelation (Dormann *et al.* 2007). Here, I note that all of my models showed substantial reductions in residual spatial autocorrelation when compared to that present in the raw data (see Figure 2.1). Species abundance and distribution modelling was carried out using the 'party' package in R (Hothorn, Hornik & Zeileis 2006a; R Development Core Team 2012).

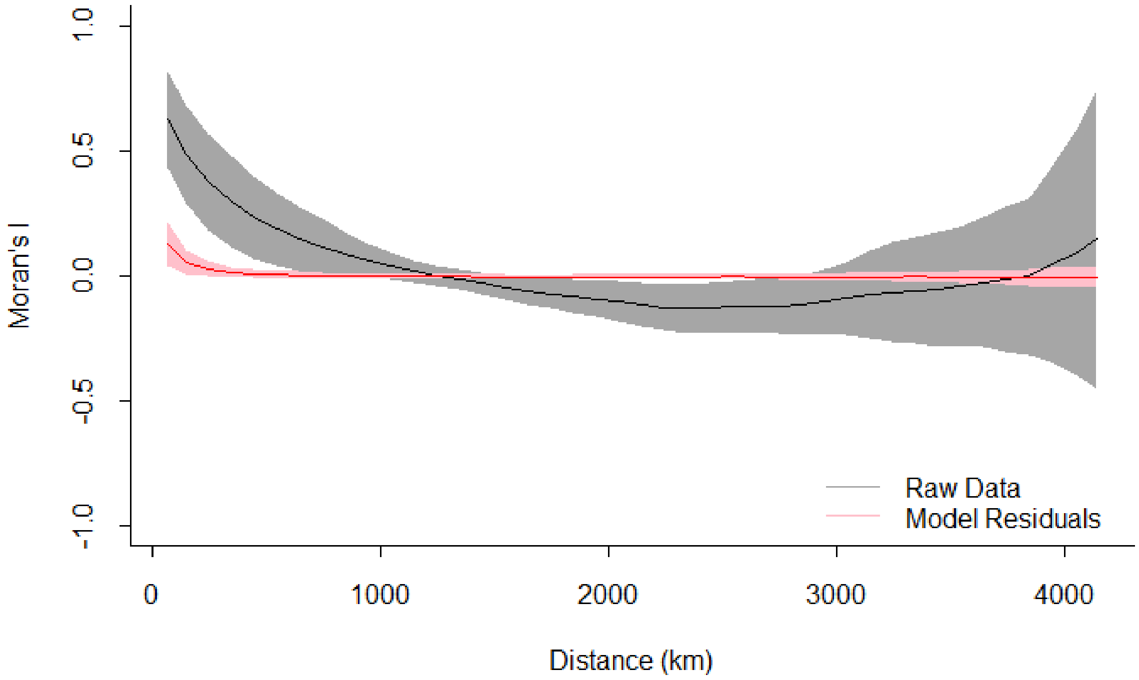

Figure 2.1. Correlogram indicating the mean (shaded areas show standard deviation) of the correlgorams across all 345 species for raw data (black line) and for the residuals after model fitting (red line).

Predictions of the probability of a species occurring at each abundance class were based on the number of votes for each class from the 1000 classifiers that comprised each forest (Robnik-Sikonja 2004). Predicted probability across the abundance classes are summed to give a predicted probability of occurrence, whilst predicted ordinal abundances are based on the class with the majority vote. Ordinal predictions from the distribution model based on abundance data were converted to presence-absence data to enable a direct comparison to recorded presence-absence data.

Model fits of simulated presence-absences derived from the abundance (after conversion to presence-absence data) and presence-absence models to observed presence-absence data were assessed using three methods, which included measures of both model calibration and discrimination. I used two measures of discrimination, which indicate the ability of a model to discriminate between species presence and absence. First, the kappa statistic measures model accuracy whilst correcting for accuracy expected to occur by chance (Cohen 1960); I used this on the simulated occurrences from the cross validated datasets. Kappa is the most widely used measure of discrimination and performance for presence-absence models (Manel, Williams & Ormerod 2001; Pearson, Dawson & Liu 2004; Segurado & Araújo 2004; Allouche, Tsoar & Kadmon 2006) but is criticised for being inherently dependent on prevalence and the often arbitrary choice of threshold value (Allouche, Tsoar & Kadmon 2006; Freeman & Moisen 2008). The second measure of discrimination, therefore, was a threshold independent measure of model performance, the area under the receiver operating characteristic (ROC) curve (AUC) (Manel, Williams & Ormerod 2001; Thuiller 2003; Brotons *et al.* 2004).

As a measure of model calibration, I used calibration curves to assess agreement between the logits of the predicted probabilities and the observed proportions of occurrence in the test data (Zurell *et al.* 2009). The slope and intercept of this regression can provide a measure of model bias and spread (Pearce & Ferrier 2000). Model bias is the systematic over- or under- estimation of the probability of occurrence across the range of a species and results in an upwards or downwards shift of the regression line, causing the intercept to deviate from zero (Reineking & der 2006). The slope of the regression line, fitted to the predicted and observed values on x and y logit axes respectively, indicates the spread of the data. If predicted values lower than 0.5 overestimate the probability of occurrence whilst predicted values greater than 0.5 underestimate the probability of occurrence the slope of the regression line will be greater than one. Conversely a gradient of less than one indicates that predicted values lower than 0.5 are underestimating the probability of occurrence, whilst predicted values greater than 0.5 overestimate the probability of occurrence (Pearce & Ferrier 2000). A perfectly calibrated model will have an intercept of zero and a slope of one (Reineking & der 2006; Zurell *et al.* 2009; Vorpahl *et al.* 2012).

I used a paired t-test on logit-transformed data to assess differences between the predictive performances, according to kappa, of models trained on each data set. The effect of prevalence (the proportion of presences out of 2813 cells) on predictive accuracy was assessed using a GAM, after controlling for species (to account for the paired nature of the data set). The model was fitted with a binomial error structure with a logit link and included species as a random effect, using the ‘mgcv’ package in R (Wood 2011; R Development Core Team 2012).

2.4 Results

Models trained on abundance data, and later converted to presence-absence predictions, were significantly more discriminating than models trained on presence-absence data (Figure 2.2a and b; paired t-tests, kappa $t_{344}=13.23$, $p<0.01$, AUC $t_{344}= 3.72$, $p<0.01$). Measures of model calibration also showed improved performance in the models trained on abundance data, when compared with models trained on presence-absence data. The measures of the intercept of the calibration curve were significantly different between the two models ($t_{344}= 3.88$, $p<0.01$), with 74% of abundance models having an intercept closer to zero than their presence-absence trained counterpart. This significant difference is also true for the slope of the model calibration curves ($t_{344}= 3.33$, $p<0.01$) with the slopes of the calibration curves from 76% of models showing a greater tendency towards one when trained with abundance data rather than presence-absence data. Furthermore, models trained on abundance data generally fitted the observed abundance data well with a mean weighted Cohen’s kappa score (Landis & Koch 1977) of 0.73 (se ± 0.01) (Figure 2.3). The magnitude of the improvement in model performance associated with abundance-trained models varied with the performance of the presence-absence data trained model (Figure 2.4). For presence-absence data trained models with a poor to slight rating kappa score (i.e. less than 0.2) (Landis & Koch 1977), mean kappa improved by 0.32 (se ± 0.12). Unsurprisingly, the magnitude of benefit declined with the fit of the original model, with minimal improvements among presence-absence data trained models that rated as almost perfect (i.e. with a kappa score greater than 0.8).

Improvements in model accuracy resulting from the use of abundance data depended on the metric of model accuracy used. When that metric was kappa, improvements were most marked for models that had performed poorly when presence-absence data were used (Figure 2.4). Poorer performing presence-absence models tended to be those associated with high or low prevalence species (Figure 2.5). Indeed, when kappa was used as the metric of model accuracy, a GAM showed that prevalence had a significant quadratic effect on model accuracy ($z=2.55$, $p=0.01$, $z=1.38$, $p=0.17$), and that the modelling method was also a significant categorical explanator ($z=2.317$, $p=0.02$). There was a marginally significant but weak interaction between prevalence and modelling method ($z=0.18$, $p=0.85$, $z=2.02$, $p=0.04$; Figure 2.5). By contrast, when AUC was used as the metric of model accuracy, improvements owing to the use of abundance data were unrelated to both prevalence and the fit of the equivalent presence-absence model.

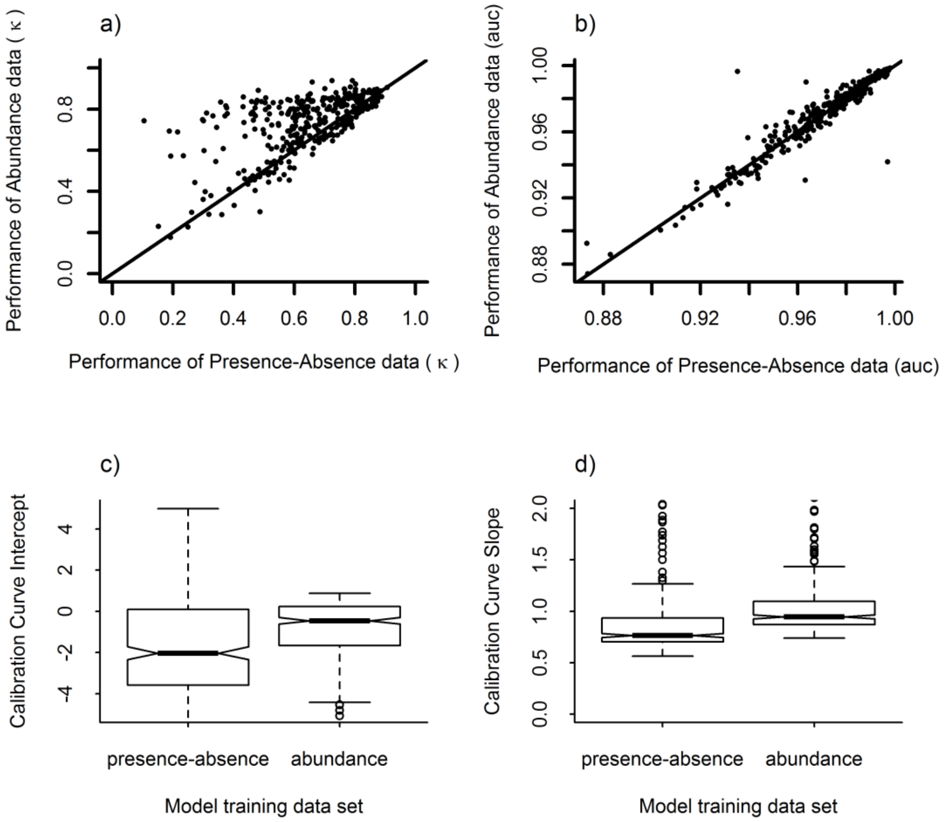

Figure 2.2: Measures of model performance for each form of training data. a) Cohen's kappa, b) AUC, c) Intercept of the model calibration curve and d) slope of the model calibration curve (n=345). Notches indicate the 95% confidence intervals of the median, with a lack of overlap indicating a significant difference at the 5% level.

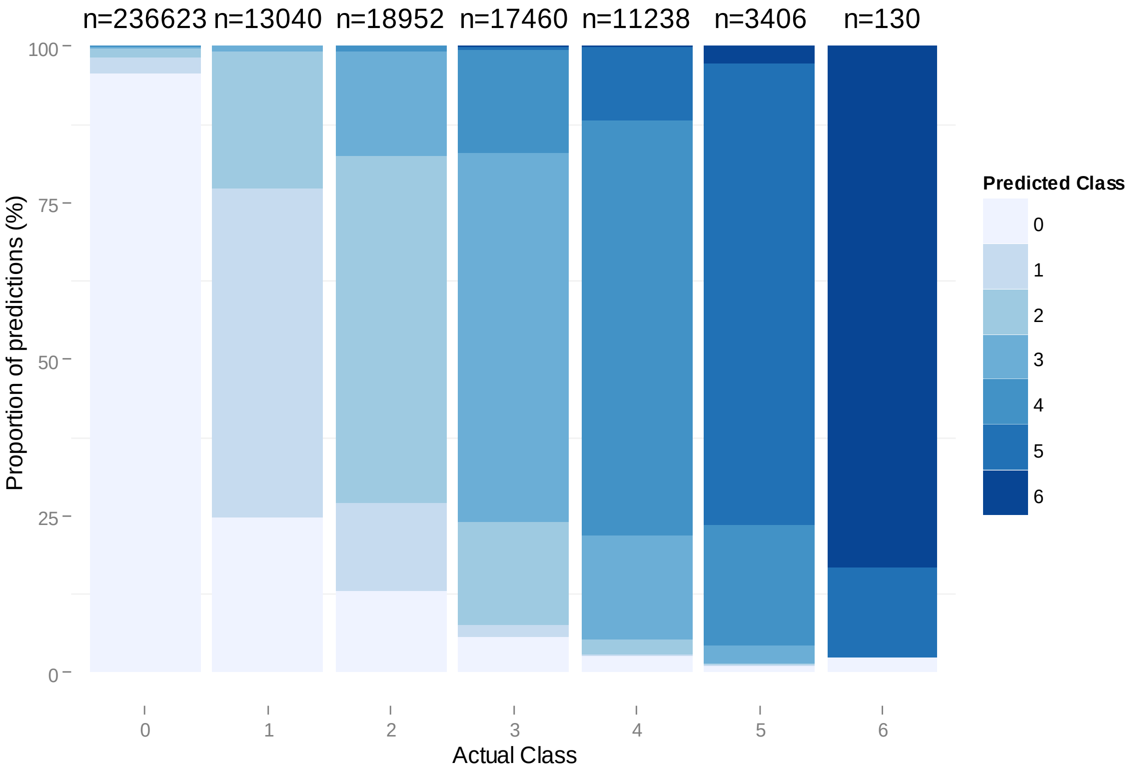

Figure 2.3: Abundance predictions from abundance data trained models. Bars represent the mean proportion of predictions for each abundance class averaged across all species. N values indicate number of observed cells within each abundance class.

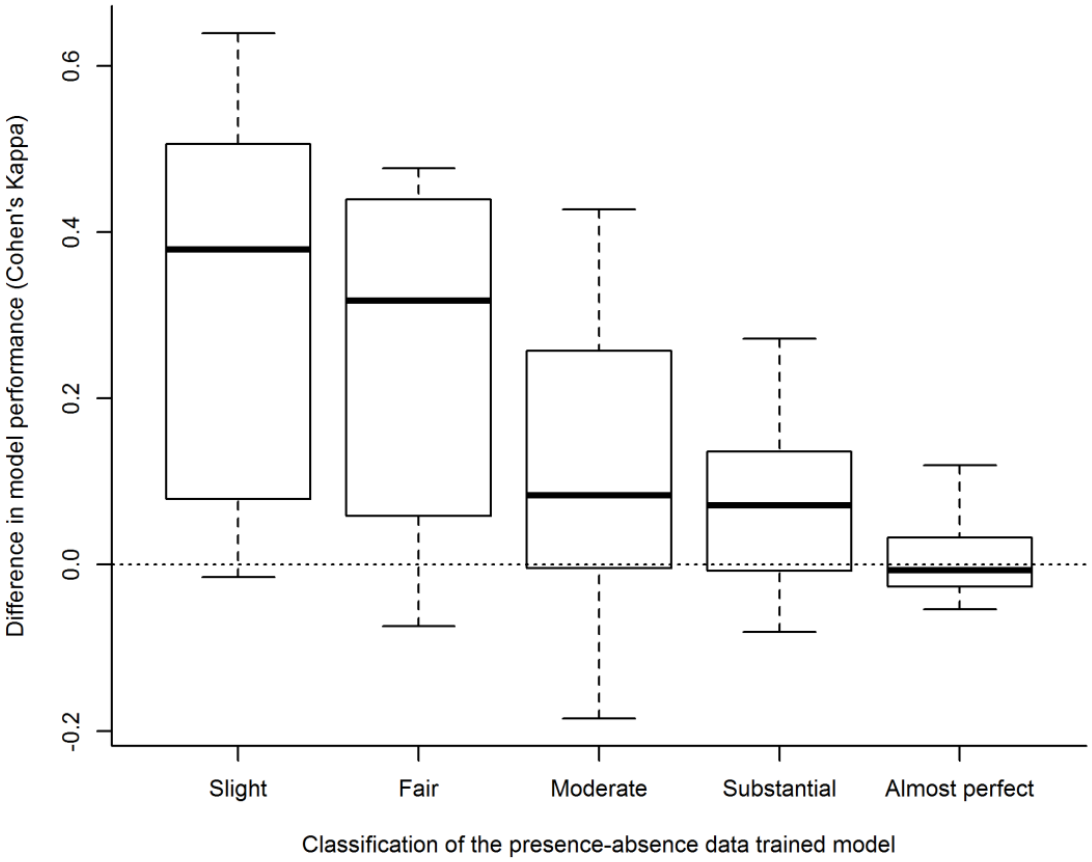

Figure 2.4: Mean difference in Cohen’s kappa scores between abundance data trained and presence absence data trained models, Bins are based on the classification of the presence-absence data trained model according to Landis and Koch (1977). Positive values for differences in kappa score indicate an improvement in model fit, whilst negative values indicate a reduction in model fit.

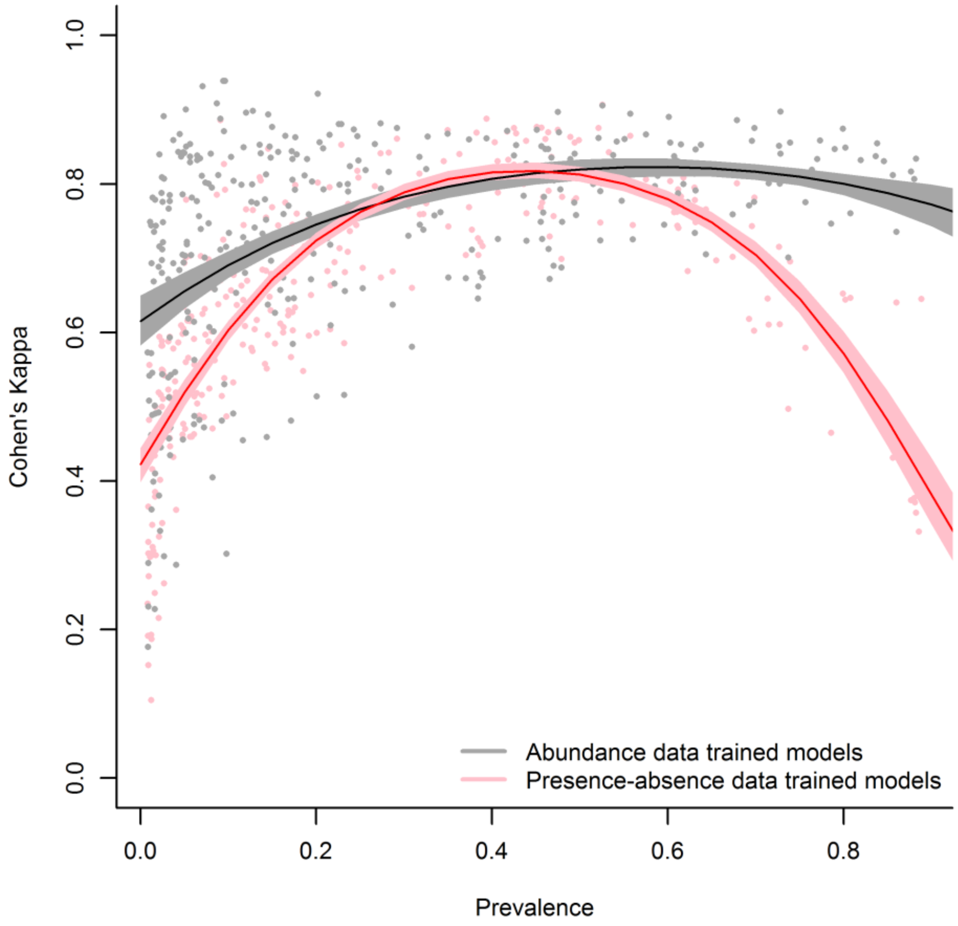

Figure 2.5: Relationship between model accuracies, measured using Cohen's kappa statistic, for models trained on abundance data and those trained on presence-absence data. Shaded areas represent 95% bootstrapped confidence intervals of the mean.

2.5 Discussion

Here I demonstrate the significant improvements in the accuracy of SDMs that can be achieved from using abundance data to train species distribution models. By including measures of abundance I derive a more accurate assessment of the relative suitability of habitats, thereby improving predictive performance. A lack of differentiation between low and high quality habitats may lead to model bias in the presence-absence trained models. For example, occurrences in low quality, wide-ranging habitats will outweigh records from high quality, scarce habitats. Due to the large number of observations, the relative importance of these low quality habitats will be over-weighted in models trained on presence-absence data (Brotons *et al.* 2004).

I also show a hump-shaped relationship between species prevalence and model predictive accuracy. A variety of hypotheses on the causal factor behind this association already exist in the literature (Segurado & Araújo 2004; Allouche, Tsoar & Kadmon 2006; Santika 2011). Here, however, the interacting effects of method and prevalence on model performance are of greater interest. The marginal interaction shows that models built using abundance data generally outperform those built with presence-absence data, particularly for species with low prevalence. This contrasts with expectations based on the positive relationship between range size and local abundance (Brown 1984), which suggest that model performance would converge at low prevalence, owing to the relative lack of differentiation between presence-absence and abundance data (Brotons *et al.* 2004).

These results suggest that models trained on abundance data are better able to identify the relative suitability of habitats than those trained on presence-absence data. The question naturally arises: what biological explanations could underlie this finding? The relationship between environmental suitability and abundance has been widely discussed (Pearce & Ferrier 2001; Nielsen *et al.* 2005). Indeed, VanDerWal *et al.* (2009) demonstrated that spatial patterns of abundance could be predicted using habitat suitability inferred from models based on presence-absence data alone. Using models based on abundance data (rather than presence-absence data), the relative suitability of habitats can be modelled with even greater refinement. This is because information about the suitability of habitats is lost when treating all presences as equal, regardless of the abundance of individuals that the habitat supports. By considering abundance, presences - which are uninformative in presence-absence modelling - gain structure, improving the models' ability to discriminate between fine scale differences in habitat quality. This could be particularly pronounced in situations in which the presence of a species is determined by habitat features that occur at a finer scale than that at which the model is fitted (Brotons *et al.* 2004). For instance, microclimates within a cell may render small patches of that cell suitable for low numbers of individuals, even where the mean climate of the cell is unsuitable; presence-absence data alone would suggest that the mean climate of that cell is as suitable as that of a cell with suitable climate throughout. Additionally this increased level of model refinement and ability to discriminate between finer scale differences in habitat quality may prove beneficial when using the model to project across alternative regions or time periods.

My results suggest that even coarse scale abundance data can deliver large improvements in predicting spatial patterns of occurrence. With this in mind, why are spatial distribution modellers not driving the collection of abundance data? Gibbons *et al.* (2007), suggested that collecting abundance data for bird atlases is no more costly or resource demanding than collecting presence-absence data. Abundance data also provide valuable baselines against which to assess future changes (Cumming 2007). Changes in abundance will be much more rapidly apparent, and hence more rapidly detected, than changes in presence-absence patterns across ranges (which are dependent upon colonisation and extinction events) (Gregory *et al.* 2005). Furthermore, categorical abundance data allow for the use of new and more informative modelling techniques such as density structured models and dynamic range modelling (Keith *et al.* 2008; Zurell *et al.* 2012; Mieszkowska *et al.* 2013). By integrating demographic data with range dynamics, these models aim to reduce bias in future range projections (Pagel & Schurr 2012; Schurr *et al.* 2012). Additionally, existing methods for modelling ordinal data, such as proportional odds models, are being improved by integration with boosting approaches. These algorithms improve prediction accuracy and avoid the overfitting problems associated with a maximum-likelihood approach (Schmid *et al.* 2011; Häring *et al.* 2013). By including population dynamics, dynamic SDMs allow for the temporal aspects of a species' distribution to be investigated, including future abundance trends and species persistence. This in turn allows for a detailed assessment of the long term value of a site for species conservation. It is clear that not only can abundance data trained models predict the distribution of a species with a greater degree of accuracy, but that the information provided by these models is much richer than those predictions provided by distribution modelling.

Currently, many global data sets already contain measures of the local abundance of species (Robertson, Cumming & Erasmus 2010). Aside from periodic atlases, many of these provide annually repeated census data across a broad range of taxa including butterflies (Pollard & Yates 1994), birds (Sauer *et al.* 2012), vascular plants (Preston, Pearman & Dines 2002) ,and plankton (Barnard *et al.* 2004). Despite this array of data, species distribution modellers continue to use presence-absence data to train and test SDMs, choosing to focus on methodological development to enhance model performance (Guisan & Thuiller 2005; Araújo & Guisan 2006; Elith *et al.* 2006; Pearson *et al.* 2006; Higgins, O'Hara & Römermann 2012). To my knowledge, only two papers have attempted to use these abundance data to model species' abundance at a large scale (Renwick *et al.* 2012; Johnston *et al.* 2013), yet here I show that relatively slight increases in the information content of a training data set (the change from binary presence-absence data to a log-scaled set of seven abundance categories) result in significant improvements in model performance. Given this improvement in model accuracy, combined with the creation of better baseline data sets, where existing abundance data are available, I advocate the use of abundance models as tools to predict the ecological consequences of environmental change. Where such data do not exist, I recommend that abundance data be collected alongside presence/absence data because, even if only relatively coarse numerical scales of recording are possible, the benefits are considerable.

Chapter 3

The drivers of avian abundance: patterns in the relative importance of climate and land use

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3.1 Abstract

Climate and land use can have important effects on the local abundances of species but few studies have investigated the relative impacts of these factors. Here, I quantify the relative importance of climate, land use and surrounding population size for determining the abundances of birds across a continent. I used species abundance models to identify the relative importance of different environmental predictors for estimating the local abundances of 342 species of European breeding birds. Models controlling for phylogeny were used to relate species' life history and ecological traits to the ratio of climate to land use importance. The mean of this ratio, across all species occurring in a given area, was mapped to explore spatial variation in the major drivers of abundance. At the scale examined, climate is generally more important than land use for determining species' abundances. However, the abundance of species in neighbouring areas is also a major correlate. Among climate variables, temperature is of greater importance than moisture availability in determining abundances. The relative importance of these variables varies with latitude, with temperature of greatest importance in the north, and moisture availability in the south. Differences in the importance of specific drivers are related to species' ecological traits: climate is of greater importance for determining the abundance of species with larger global ranges or of smaller body mass. Abundances of species occurring in northern Europe, an area predicted to experience climatic changes of high magnitude, are most sensitive to climate, particularly temperature. Given the greater confidence in future projections of temperature than precipitation, this increases confidence in projections of climate change impacts on species in the north, whilst attempts to predict future populations in central and southern Europe may be dependent on less predictable changes in land use and precipitation.

3.2 Introduction

Climate change has been implicated as a major driver of recent variations in the distributions and abundances of birds (Green *et al.* 2008; Gregory *et al.* 2009; Illán *et al.* 2014). However, species' responses to climate change are highly variable in both their magnitude and rate (Walther *et al.* 2002). Understanding the relative effects of climate and concurrent land use changes on the population changes of species is challenging, yet vital to conserving species in future. Regional variations in the extent of recent land use changes are increasingly pronounced (Kaplan, Krumhardt & Zimmermann 2012) with, for example, large differences between eastern and western Europe (Donald, Green & Heath 2001). By contrast, the greatest recent changes in temperature have been observed towards the poles, a trend that is projected to continue through the current century (Stocker, Dahe & Plattner 2013). Regional disparities in expected climate change, and differential species responses to climate change, mean that it is important to understand the extent to which the abundances of species in different areas are driven by climate.

Climate is often regarded as the primary, albeit indirect, driver of avian population dynamics (Thuiller, Araujo & Lavorel 2004). As a result, ecologists frequently use climate projections to predict, through species distribution modelling (SDM), the risks species face under particular climate change scenarios (Elith, Kearney & Phillips 2010). However, species that are affected by human activities are unlikely to be in equilibrium with climatic conditions (Thuiller, Araujo & Lavorel 2004), a pre-requisite for understanding species-climate relationships (Pearson & Dawson 2003). For example, the intensification of agricultural practices across Europe during the last quarter of the 20th century led to widespread changes in the abundance and distribution of many farmland bird populations (Donald, Green & Heath 2001). To account for such confounding issues, land use variables have been incorporated into SDMs and shown to improve their explanatory power significantly (Thuiller, Araujo & Lavorel 2004). However, few studies (but see Eglington and Pearce-Higgins (2012) and Renwick *et al.* (2012)) have directly assessed the relative roles of climate and land use when modelling the abundance, rather than the distribution, of a species, and none has done so at a continental scale. Furthermore, the relative role of climate and land use may vary not only between species but also spatially. Beale, Brewer and Lennon (2014) demonstrated that the influence of climate on the distribution of a species varied across the species' range. To understand the susceptibility of species to climate change, we must first disentangle the relative importance of climate and land use in determining abundance at a scale encompassing a large majority, if not the entirety, of a species' range.

The large-scale declines in the populations of some European birds (Inger *et al.* 2014; Vickery *et al.* 2014) are of growing concern, both in the scientific and political communities. Although specific regional declines (for example, those of farmland bird populations in Britain) have been primarily attributed to agricultural intensification (Chamberlain *et al.* 2000; Donald, Green & Heath 2001), whether climate or land use is the primary driving factor behind large scale variations in populations of European birds is unclear (Thuiller, Araujo & Lavorel 2004; Green *et al.* 2008; Eglington & Pearce-Higgins 2012; Vickery *et al.* 2014). It has been suggested that a hierarchical scheme of environmental controls on species distributions exists, whereby climatic variables operate over the largest scale, with geology and land use determining species' distribution at smaller scales (Thuiller, Araujo & Lavorel 2004). It has also been suggested that, by modelling abundance, we can distinguish finer scale variations in habitat quality that may not have been evident in distribution modelling (Chapter 1, Howard *et al.* 2014); this might enable more accurate assessments of the relative importance of land use and climate for species at a continental scale.

Here, I assess the relative roles of climate and land use in determining the local abundance of breeding-birds across Europe. I examine whether the relative contribution of climate and land use varies among species in relation to ecological traits. My working hypothesis, following previous research (Barbet-Massin, Thuiller & Jiguet 2012; Virkkala & Lehikoinen 2014) on determinants of the ecological niche is that climatic influences will dominate at poleward regions in Europe and that land use will be more important in determining abundance patterns in the more heterogeneous landscapes of central and southern Europe. Specific traits, such as mass and range size (Angert *et al.* 2011; Buckley & Kingsolver 2012) have been linked to the characteristics of species' climatic niches. For example, larger bodied, and wider ranging species occur more frequently in colder climes (Ashton 2002). Based on energy conservatism in endotherms, I might expect large bodied organisms to be less closely tied to climate than would smaller species (due to surface area: volume ratios). Species-specific traits including breeding range size and migratory distance have also been linked to habitat specialisation (Reif *et al.* 2015). Our goal here is to identify those traits that indicate whether a species is most likely to be sensitive to climate change impacts (those whose abundance is most strongly related to climatic variation) or habitat modification (those whose abundance is most strongly related to land use). In addition, I investigate spatial patterns in the role of different drivers of abundance, identifying those areas of Europe in which birds are likely to be more susceptible to climatic or land use change. Given that species' northern range limits are often thought to be determined by their thermal tolerances (Woodward 1987; Addo-Bediako, Chown & Gaston 2000), I might predict that climate will be of greater importance at higher latitudes.

3.3 Methods

3.3.1 Species data

Species data are as indicated in Chapter 2. For these analyses I also excluded three addition species due to model building limitations and model convergence failure. The remaining 342 species were used for all subsequent analyses in this chapter.

3.3.2 Bioclimatic data

Bioclimate data are as indicated in Chapter 2 but in this case only three bioclimatic variables were calculated for each UTM grid cell: mean temperature of the coldest month (MTCO); growing degree days above 5° (GDD5); and the annual ratio of actual to potential evapotranspiration (APET). This was to further reduce the potential of correlated predictor variables to influence the outcome of these results.

3.3.3 Land use data

Land use data are as indicated in Chapter 2.

3.3.4 Surrounding local abundance

Spatial autocorrelation was accounted for in these analyses through the calculation of a spatial autocovariate term, using equation 1, as indicated in Chapter 2. Here, I note that, in those cases where neighbouring cells included marine habitats, the categorical abundance was included in equation 1 as a zero (alternatively, including these cells as missing data had no impact on our findings, Figure A2). I included information only from neighbouring cells immediately adjacent to the focal cell (i.e. first-order neighbours (Dormann *et al.* 2007); higher orders of neighbouring cells were considered, but model fit was best when only first-order neighbours were included (Figure A3).

3.3.5 Statistical analyses

Random forests (RF) were used to model species' abundance and to provide estimates for the relative importance of predictor variables. This machine learning technique is a bootstrap-based classification and regression tree (CART) method (Cutler *et al.* 2007). Robust to over fitting, it is widely recognised to produce good predictive models; hence, it is increasingly applied to species distribution modelling (Cutler *et al.* 2007).

Models were fitted using ten-fold cross validation to reduce SAC between training and test data and to minimise over-fitting. To improve stability, each model was built using 1000 classification trees fitted to a random sample of the observations (approximately 63% of the available data). The remaining ‘out-of-bag’ observations (OOB; a term used with RF models to describe the semi-independent test data not used initially for model fitting) were then cross validated against the resulting trees to estimate model performance (Cutler *et al.* 2007) using a threshold independent measure of model performance, AUC, the area under the receiver operating characteristic (ROC) curve (Manel, Williams & Ormerod 2001). Previous evaluation has shown that these models perform well when assessed using other measures of model discrimination and calibration, in addition to AUC (Chapter 2, Howard *et al.* 2014). These previous analyses also demonstrated that RF models substantially reduced residual SAC relative to that present in the raw data.

Individual variable importance was calculated using a permutation-based measure of the normalised difference in prediction accuracy for the OOB data when the predictor variable is included as originally observed, versus when the predictor variable is randomly permuted. Higher values of AUC indicate a greater degree of association between the variable and response (Cutler *et al.* 2007). To account for potential correlations among predictor variables, a conditional permutation approach, proposed by Strobl *et al.* (2008), was applied using the ‘party’ package in R (Liaw & Wiener 2002; R Development Core Team 2012). Using this approach, the underlying correlation structure is preserved by permuting the predictor variable only within groups of observations. This method provides a fair means of comparison, identifying the relevant predictors and mostly eliminating the preference for correlated variables (Strobl *et al.* 2008). To enable comparisons between species, relative variable importance was calculated by dividing each individual variable importance by the summed importance across all variables for each species. Relative variable importance for each species was aggregated for each of the two broad categories of driver: climate and land use (Ishwaran 2007). The aggregated importance of climate variables was then divided by the aggregated importance of land use variables. This ratio was taken to give a measure of the relative importance of climate and land use for each species (Table A2).

A phylogenetic generalised least squares (PGLS) approach was used to test both for relationships between species-specific traits and the relative importance of climate to land use (hereafter termed ‘relative climate importance’) and for relationships between species-specific traits and the importance of spatial autocorrelation for a species, whilst controlling for phylogenetic non-independence (Freckleton 2009). Species’ traits were taken from BirdLife International (2013) and included mean body mass, generation length, primary habitat association, migratory strategy, and average and maximum natal dispersal distances. Global range size, a measure of the geographic scale over which the drivers of abundance operate, was also included, and was derived from BirdLife International species range polygons (BirdLife International & NatureServe 2012). Prevalence within the study area, which represents the quantity of available data, was calculated as the proportion of UTM squares that were occupied (from Hagemeijer & Blair 1997). Phylogeny was based on a consensus tree built using 5,000 trees sub-sampled from the global phylogeny built by Jetz *et al.* (2012). I compared the AIC corrected for small sample size (AICc) for all subsets of the global model, selecting all models within 6 ΔAICc of the best performing model. To avoid selection of overly complex models, all models with a better-performing simpler nested model were disregarded (Richards 2008). Diagnostic plots were examined for the final model for each analysis to check for heteroscedasticity, non-normal errors and outliers. Phylogenetic analyses were carried out in the 'caper' package in R (Orme *et al.* 2012; R Development Core Team 2012).

Spatial variation in relative variable importance was investigated by calculating the mean ratio of climate and land use importance for all species present within a UTM grid cell. This was applied to all cells where more than 75% of the species present were represented by quantitative data (Figure A1). In total, this accounted for 47.5 % of the UTM grid cells across Europe. As I found little variation in the performance of models for species located in different parts of Europe, these ratios were not corrected for model fit. To test for spatial variation in these ratios, an ordinary least squares regression (OLS) was used to examine the relationship between the mean ratio of climate to land use importance for all species present in a UTM grid cell against the latitude and longitude of the cell. Species richness and heterogeneity of land use (the latter measured using Shannon's diversity index (Forman 1995) within each UTM grid cell were also included in these OLS models and an ANOVA used to identify differences in the explanatory power of variables.

3.4 Results

3.4.1 The relative importance of abundance drivers

Random forest models of the abundance of the 342 species of European breeding bird generally performed well, with a mean AUC score of 0.97 (S.E.± 0.001). An ANOVA comparing the relative importance of the two aggregated variable types (climate and land use) and the spatial autocovariate term across the species models, whilst controlling for species as a random effect, showed an overall significant difference between the three variable-types ($F_{2,1023}=4442$, $p<0.01$, Figure 3.1a). Specifically, despite the models including more land use variables than climate variables and only one SAC term, Tukey's post-hoc analysis revealed that climate was significantly more important than land use ($p=0.05$) in explaining abundance of species. Further, the importance of each of the climate variables in isolation was greater than any of the land use variables. Perhaps unsurprisingly, given the spatial coherence of most species' distributions, the SAC term appeared significantly more important than both climate and land use ($p<0.01$).

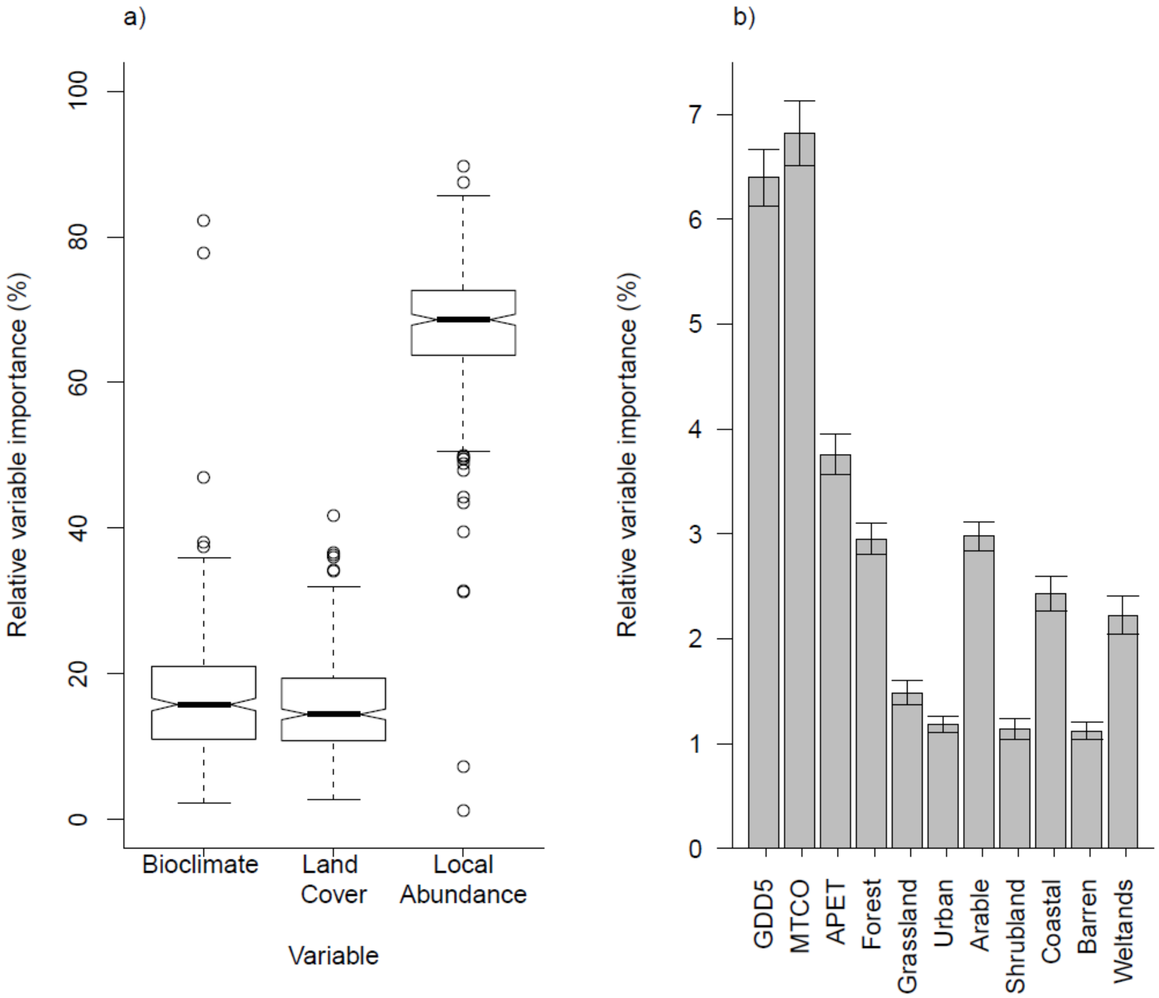


Figure 3.1: Mean relative importance (± se) of climatic and land use variables along with spatial autocorrelation for 342 species in determining species local abundance, for both aggregated variables (A) and individual variables (B). Notches indicate the 95% confidence intervals of the median, with a lack of overlap indicating a significant difference at the 5% level. Circles indicate outliers.

There were also significant differences in the relative importance of individual variables among species ($F_{(11,341)}$= 168.4, p<0.01; Figure 3.1b). In general, within the climatic variables, temperature variables have a much greater impact on species' abundances than moisture availability. Both GDD5 and MTCO were significantly more important than APET (Tukey's post-hoc analysis, p<0.01 for both). The importance of individual land use variables in modelling abundances also differed significantly. In addition, the prevalence of a land use type across Europe was positively correlated with the mean relative importance of that variable (R^2 =0.89) in the models of species abundance. For example forest, arable, coastal and inland wetland land uses were all significantly more related to species' abundances than the grassland, urban, shrubland and barren land uses (Tukey's post-hoc analysis, $p \leq 0.05$ for each comparison). The most important land use variables for a species were those directly related to its primary habitat association (e.g. arable land coverage was the most important variable determining the abundance of farmland species) (Figure A4).

3.4.2 Between species variation in relative variable importance

When testing the relationship between the ratio of the relative importance of climate versus land use variables for species and species-specific traits, a PGLS model retained four variables. These were: a species' primary habitat association, its global range size, its log body mass, and its prevalence across Europe (Table 3.1). This model explained 18% of the observed variance in relative climatic importance. A highly significant positive relationship was found between global range size and the relative climatic importance, whilst body mass and prevalence were significant negative covariates. The relative importance of climate appeared to be unaffected by primary habitat association, with the exception of coastal species, for which climate was less important than for other species (Table 3.1).

A PGLS model testing relationships between the importance of SAC for each species and species-specific traits retained only primary habitat association and log body mass. A highly significant negative relationship was found between body mass and the importance of SAC, whilst SAC was less important for species associated with Mediterranean or tundra and moorland habitats than for species with other primary habitat associations (Table A3).

Table 3.1: Species traits and the relative importance of climate and land use. Estimated coefficients for AIC selected phylogenetically corrected GLS regression models for the ratio of the relative importance of climatic and land use variables in determining the abundance of a species. P-Values significant at the 5% level are shown in bold.

	Effect size	Standard error	t- value	P-value
Intercept (Habitat generalists)	0.66	1.15	0.58	0.57
Primary Habitat association:				
1. Coastal	-0.95	0.31	-3.09	**<0.01**
2. Inland Wetland	-0.22	0.18	-1.22	0.22
3. Tundra, mires and moorland	0.01	0.22	0.06	0.95
4. Boreal and temperate forest	0.32	0.18	1.78	0.08
5. Mediterranean	0.48	0.34	1.41	0.16
6. Agriculture and grassland	-0.06	0.18	-0.33	0.74
7.Montane grasslands	-0.35	0.38	-0.92	0.36
Log (Body mass)	-0.17	0.07	-2.34	**0.02**
Prevalence across Europe	-1.61	0.27	-5.98	**<0.01**
Log (Global range size)	0.23	0.06	3.56	**<0.01**
Lambda: 1				
Residual standard error: 0.509 on 265 degrees of freedom				
Adjusted R-squared: 0.173				

3.4.3 Spatial patterns in the importance of climate and land use

There are clear spatial patterns in relative climatic importance across Europe (Figure 3.2). A regression analysis revealed a significant positive relationship between the mean relative climatic importance for all species present in a UTM grid cell and the latitude of that cell ($F_{1,1716}$=2585, p<0.01); this indicates that the relative importance of climate for determining the abundance of species increases from southern to northern Europe. Significant relationships were also identified between mean relative climatic importance of a UTM grid cell and the longitude, species richness, and land use heterogeneity of that cell. However, the proportion of variance explained by these variables was low (1.20 %, 2.37 %, 0.76 %, respectively), particularly when compared with the proportion of variance explained by latitude (57.50 %, Table A4). Spatial patterning is also evident in the relative importance of individual climatic variables (e.g., see the contrast between a temperature and a moisture related variable; Figure 3.3). There were significant positive relationships between relative importance of both temperature-related variables and latitude (regression of the mean importance of an individual climate variable across all species present in a UTM grid cell against latitude: GDD5, $F_{1,1716}$=7118, p<0.01; and MTCO, $F_{1,1716}$=11353, p<0.01,

Figure 3.3a and b, Table A4). Conversely, the relative importance of APET in explaining abundance declined with latitude (regression [as above]: $F_{1,1716}$=3618, p<0.01, Figure 3.3c, Table A4).

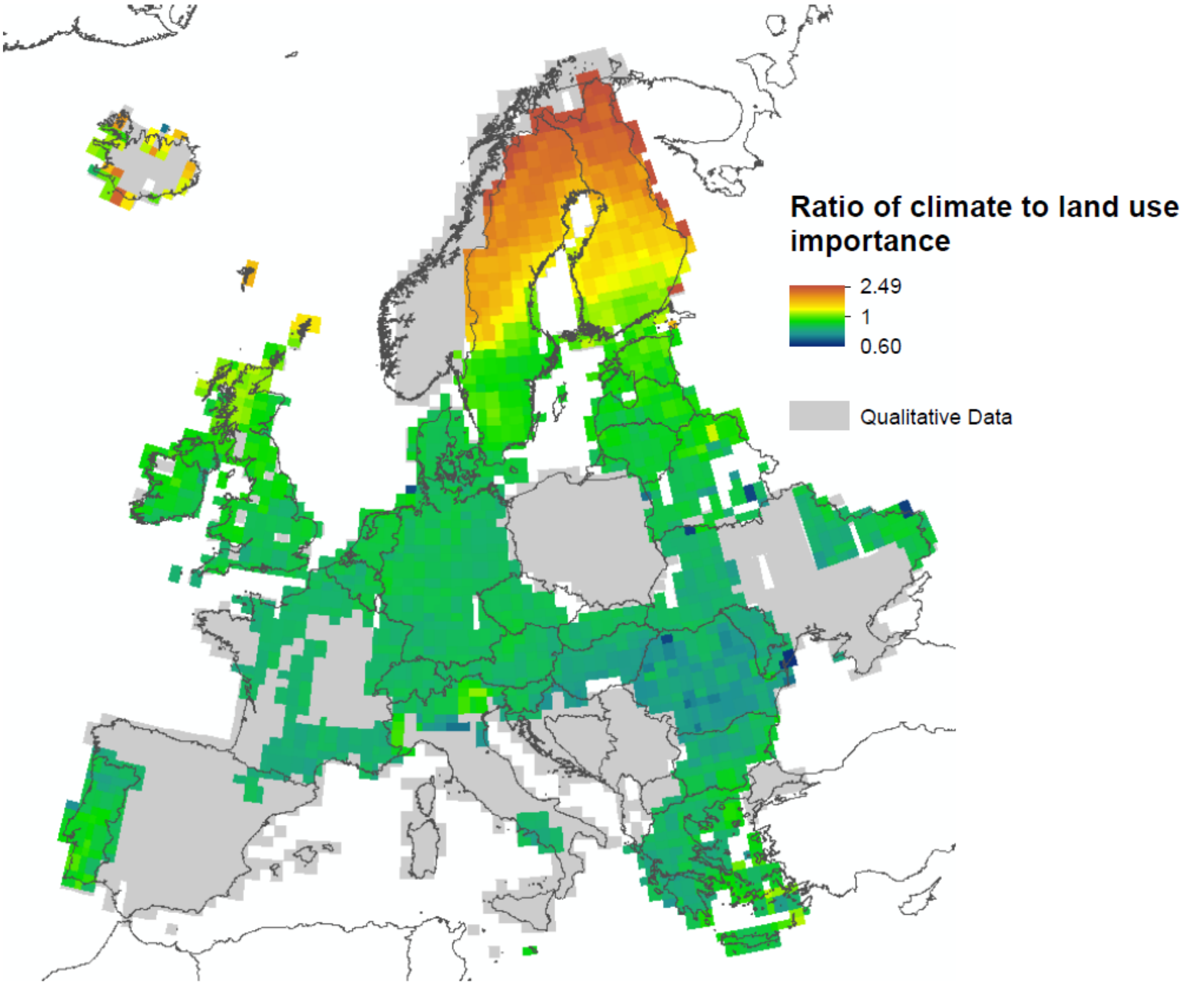


Figure 3.2: Spatial distribution of the ratio of the relative importance of climate to land use for determining the abundance of European bird species present within each UTM grid cell. Grey regions indicate areas omitted from analysis due to paucity of quantitative data – see methods.

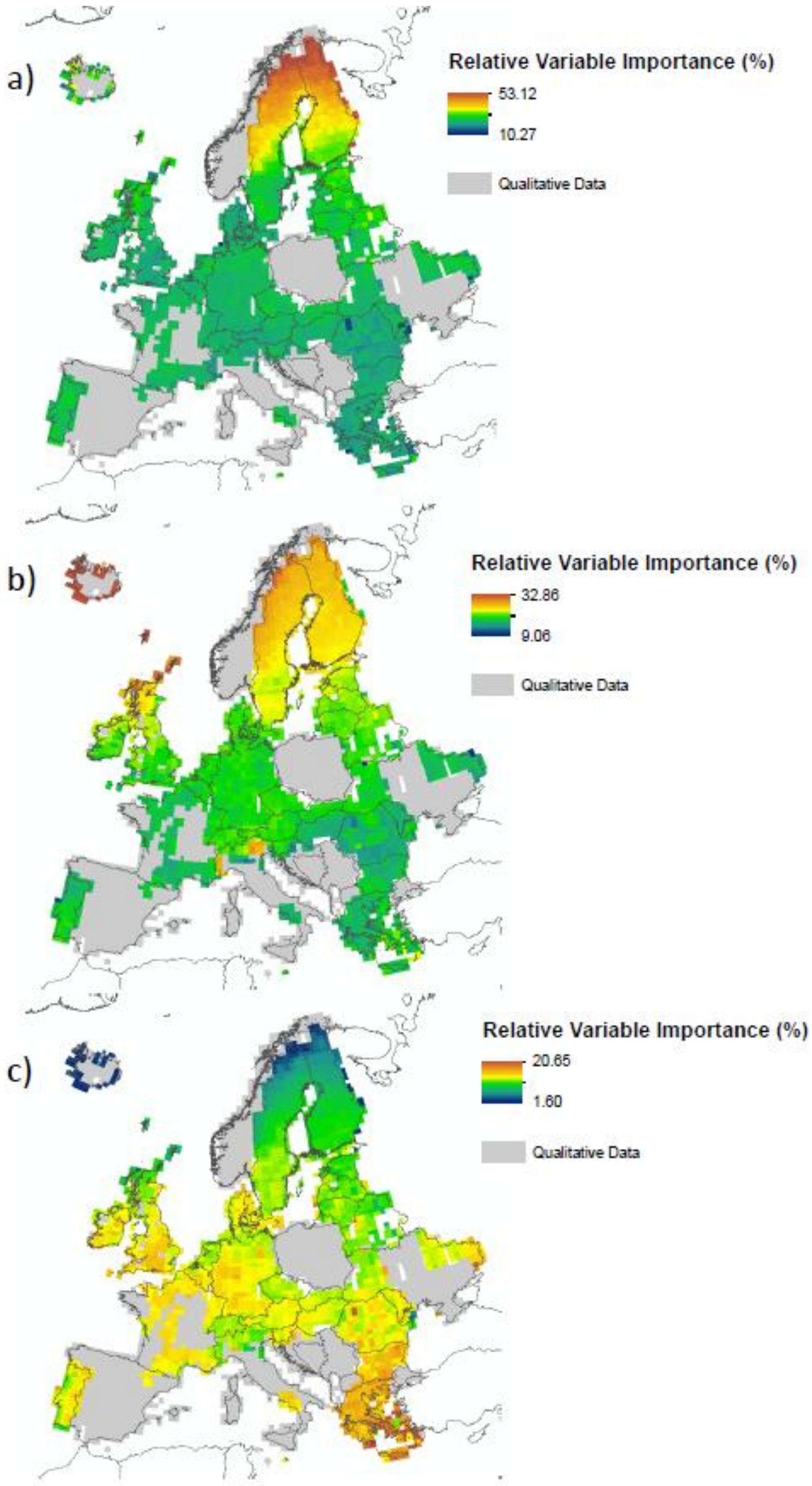


Figure 3.3: Spatial distribution of relative importance for determining the abundance of European birds of measures of: a) Mean temperature of the coldest month (MTCO); b) Growing degree days above 5° (GDD5); and c) Actual to Potential Evapotranspiration Ratio (APET). Grey regions indicate areas omitted from analysis due to paucity of quantitative data – see methods. Note different scales for each plot.

3.5 Discussion

At the spatial scale examined, the abundances of the vast majority of terrestrial European birds are more strongly influenced by climate than by land use. I have demonstrated, for the first time, substantial spatial variation in the relative importance of factors driving local abundance. I now discuss these results in light of three key findings: (1) the substantial differences between land use, climate and neighbouring abundance in their relative importance for determining local species abundance; (2) the strong spatial patterns in variable importance; and (3) the specific traits that predispose a species to the influence of either climate or land use.

3.5.1 Differences in the relative importance of climate, land use and spatial autocorrelation

There is substantial evidence for the individual impacts that changes in both climate and land use have on European bird populations (Lemoine *et al.* 2007; Vickery *et al.* 2014), and conflicting opinions about which is the most important factor affecting avian populations (Thuiller, Araujo & Lavorel 2004; Vickery *et al.* 2014). Here, despite evidence of variation in their importance among species and across space, I have show that climate is usually more influential than land use in driving abundance patterns within a species' range. Previous studies (Thuiller, Araujo & Lavorel 2004) suggested that climate is a better predictor of range extent than land use but here, for the first time, I demonstrate that, within a species' range, climate is also the dominant factor in determining abundance patterns at this larger, landscape scale.

Species' distributions are thought to be determined by a hierarchical scheme of environmental controls, with climatic variables operating over the largest range, and factors such as land use, geology and topography operating at increasingly finer scales (Thuiller, Araujo & Lavorel 2004). This hierarchy may also operate on abundance, favouring a greater importance of climate than land use at a coarse spatial scale. Despite this, I have also shown the importance of land use variables independent of the variability described by climate. Widespread land uses, whose occurrence may not be closely tied to local climate, such as arable land, forestry and inland wetlands, were important determinants of abundance patterns. Surprisingly, I have also identified more localised land use variables, such as shrubland and urban environments, as important predictors of the abundance of some species. This contrasts with previous studies investigating the perceived role of land use variables on range extent (Thuiller, Araujo & Lavorel 2004), where the importance of more localised land use variables was less evident. One explanation for this difference may lie in the difference between presence-absence models (as used by Thuiller et al. 2004) and these abundance models. Specifically, by considering abundance, these models can reflect finer scale differences in habitat quality than can presence-absence models (Howard *et al.* 2014). Abundance models might, thus, expose finer scale species-habitat relationships than those detected by presence-absence modelling. However, this does not mean that climate and/or land use models are sufficient to explain spatial variations in abundance patterns for all species.

By using a conditional inference framework and permutation based approach to assess variable importance, I have also shown that the majority of spatial variation in species' abundance can be related to the abundance of the same species in neighbouring cells. This term partly reflects the degree of the spatial aggregations in climate and land use, as well as in the bird abundance data itself. This could result in estimates of the importance of climate and land use being more conservative than if SAC had not been accounted for. Also incorporated in this term are the effects of unknown spatial processes, such as biotic interactions. The apparent importance of SAC suggests that species' dispersal abilities may be an important factor in determining local abundance, which may in turn indicate potential difficulties in establishing new breeding areas separated from current distributions (Tilman & Kareiva 1997; Dormann *et al.* 2007). My finding that this variable can, in some instances, explain 70% or more of the spatial variation in abundance of a species indicates the importance of accounting for spatial autocorrelation when modelling abundance (Segurado, Araujo & Kunin 2006). Techniques such as hierarchical partitioning can help to understand the extent to which some of the variation in SAC is related to spatial patterning in the other predictor variables but this approach cannot be applied to random forest models.

When climate variables are considered individually, my results indicate that temperature-related variables are of much greater importance than moisture availability in determining abundances across Europe. This is important, as the highest degree of predictive uncertainty for future climates occurs for precipitation forecasting (Theis, Hense & Damrath 2005). With the exception of the Mediterranean region, where precipitation is shown to be an important determinant of abundance, my results suggest that uncertainty around precipitation forecasts may affect future projections of European species range extents to a much lesser extent than currently expected and, thus, that projections of future climate suitability for most species may be more reliable than currently supposed.

3.5.2 Spatial variance in the role of land use and climate in determining abundances

Spatial patterns in the relative importance of climate and land use indicate that the abundances of species that occur in the higher latitudes of Europe are more strongly dictated by climate variables. Despite the correlative nature of the models, their high predictive ability on spatially independent data indicates that our findings are robust. These results, therefore, could have important ramifications with regard to future climate change. Future changes in climate are projected to be greatest in more northerly latitudes of Europe (Virkkala *et al.* 2008; Stocker, Dahe & Plattner 2013), and in a direction unfavourable to most northerly species (Huntley *et al.* 2007). Whilst the past is not necessarily a good predictor of the future, bioclimate models have been shown to have some power in predicting future population changes (Green *et al.* 2008; Gregory *et al.* 2008). The strong dependency on climate of avian abundance in these areas means that constituent species will not only be exposed to some of the strongest climate changes in future but also that their populations are among the most sensitive to such changes. Previous studies have identified that boreal and Arctic species are vulnerable to climate change as a result of projected future declines in range size (Virkkala *et al.* 2008). Given, in addition, that the abundances of these species are particularly strongly related to climatic factors, all other things being equal, populations are likely to be subject to more substantial declines than currently anticipated from considerations of range extent alone.

The relative importance of individual climatic variables also shows spatial patterns, with temperature related variables more important in the north, and moisture availability more important in the south. These findings are in line with the water-energy hypothesis, in which the key factor determining richness variation switches from moisture availability at the equator to energy related variables towards the poles (Hawkins *et al.* 2003; Whittaker, Nogués-Bravo & Araújo 2007), and match latitudinal gradients in the temporal variation in bird populations to both temperature and precipitation (Pearce-Higgins & Green 2014). In those areas where energy inputs are low, such as at higher latitudes, temperature constrains species richness and abundance (Brown & Maurer 1989); by contrast, where temperatures (and hence energy input) are higher, moisture availability constrains richness and abundance (Hawkins *et al.* 2003).

The importance of land use in determining abundance is more evident for species present in the southern regions of Europe. In this context, there are parallels with the apparent climate sensitivity of more northerly species discussed above. Specifically, the future impacts of land use change in Southern Europe may be compounded by the prevalence of land use specialists (as defined by Moreira and Russo (2007)) in these regions. The Mediterranean regions where such species are principally located are also the regions where land use change is likely to be greatest in future (Jetz, Wilcove & Dobson 2007), potentially accelerating rates of population change.

Some countries wholly (Norway and Poland), mostly (Spain), or partly (Italy, France and Iceland), did not provide quantitative spatial estimates of species abundance for the EBCC atlas (Hagemeijer & Blair 1997). This includes some southern regions that are highly heterogeneous in both land use and temperature (Sanderson *et al.* 2002; Barnagaud *et al.* 2012). Whilst it is possible that a paucity of data in these areas may bias the importance of variables towards those regions where data is more fully represented, for example middle and northern Europe, given that we were able to incorporate data from Iberia, southern France, Italy and Greece in the south, and Scotland, Iceland, Sweden and Finland in the north, the full range of variation across both climate and land use is adequately represented in the data. Looking forward, several countries omitted from my analyses have subsequently initiated standardised population monitoring (PECBMS 2009), providing the potential for future analyses to be applied to the entire region. As with all correlative modelling, the predictive ability of these models may not extend to novel regions of parameter space. For example, the introduction of novel land uses to an area could, through a novel combination of climate and land use variables, create a previously unmodelled habitat niche. This is particularly the case for those land uses governed by anthropogenic factors (rather than climatic variables), such as arable or urban land use, which, if introduced to novel regions of northern Europe, could create novel conditions.

3.5.3 Species characteristics and the drivers of abundance

A range of ecological characteristics, such as body mass, range size, and gene frequency have all been linked to the climate sensitivity of species (Buckley & Kingsolver 2012; Parmesan *et al.* 2013). My results provide further evidence for trait-climate relationships. First, my analyses identify a negative relationship between body mass and the importance of climate. This is perhaps unsurprising, given the lower surface area to volume ratio of larger bodied organisms, which renders them less susceptible to climate (Peters 1986). Second, I show a negative relationship between prevalence of a species across Europe and the importance of climate. This is consistent with the idea that an extensive prevalence indicates that a species is adapted to a wide range of climatic conditions (and vice versa) (Addo-Bediako, Chown & Gaston 2000; Ohlemuller *et al.* 2008). Although there are good reasons to expect negative relationships between climatic importance and both body mass and prevalence, attributing causal relationships is vexed in this case. This results from the positive association between body mass and prevalence, as well as the fact that both of these traits are known to increase with increasing latitude (Brown & Maurer 1989).

3.5.4 Conclusions

Here, I present a first comprehensive analysis of the factors determining spatial variation in abundance of a continental avifauna. I compare the relative importance of climate and land use variables in determining the abundance of species, taking into account the importance of spatial autocorrelation. Overall, the importance of climate variables outweighs that of land use in determining species abundances; furthermore, across Europe, the importance of variables related to temperature outweighs those related to moisture, increasing my confidence in projections of the impact of future climate change on European bird species. Spatial variation in relative variable importance shows that climate variables are particularly important for those species present in northern Europe. This knowledge, combined with predictions of high magnitude climatic changes in these areas, indicates that northern bird species in Europe are likely to be amongst those most vulnerable to future climate change impacts on their populations.

Chapter 4

Breeding ground climate drives population trends in migratory birds

4.1 Abstract

Global declines in the populations of migrant species have been attributed to both climate and anthropogenic habitat change. However, the relative contribution of these factors on species' breeding and non-breeding ranges is contentious and has not been satisfactorily addressed. Here, I assess the roles of changes in climate suitability across the breeding and non-breeding ranges, and species' habitat affinities, on the long term population trends of 51 short- and 36 long-distance migratory species of European breeding birds. I demonstrate that the population trends of migratory birds are more closely related to climate on their breeding grounds than climate on their non-breeding grounds. I also show that across both breeding and non-breeding grounds, species with similar habitat preferences underwent similar population trends over the last 31 years. Whilst improvements in climate suitability across the breeding ranges of short-distance migrants led to increases in population trends, the same was not true for long-distance migrants. Overall, the population trends of short-distance migrants can be better explained than those of long-distance migrants, suggesting that additional factors are impacting upon long-distance migrants. Importantly, my results suggest that the combined effects of climate change and habitat-specific drivers on the breeding grounds account for half of the variation in population trend across European migratory species.

4.2 Introduction

Increasingly, climate change is implicated in an emerging global trend whereby migratory species are experiencing more rapid rates of population decline than their resident counterparts (Wilcove & Wikelski 2008; Finch *et al.* 2014). With more than 12% of the world's vertebrates making long-distance movements (Runge *et al.* 2014), the decline of migrant species poses a serious threat to global biodiversity and associated ecosystem services, and is of scientific and political concern (Vickery *et al.* 2014). Understanding the cause of these declines is complicated by the dependence of migrants on a large number of habitats, including their breeding and non-breeding grounds, as well as stop-over sites (Sillett & Holmes 2002; Robinson *et al.* 2009; Newton 2010). Susceptibility to environmental change in any of these habitats renders migrants more vulnerable to the pressures of anthropogenic habitat change than their resident counterparts (Finch *et al.* 2014; Runge *et al.* 2014). Additionally, the need to understand in which of the various staging and residence areas the population is crucially limited, further complicates the elucidation of drivers of population change (Ockendon *et al.* 2012). Both climatic change and anthropogenic induced habitat change have been identified as potentially limiting factors, with increased persecution and hunting also affecting populations (Vickery *et al.* 2014).

Afro-Palaearctic long-distance migratory birds, which breed across Europe and spend the non-breeding season in sub-Saharan Africa, are declining significantly faster than European-breeding resident and short-distance migrant birds (Sanderson *et al.* 2006; Cresswell 2014; Vickery *et al.* 2014) (Figure 4.1). Many of the former species have shown continent-wide patterns of sustained, often severe, decline since *circa* 1970. By contrast, their resident counterparts have generally undergone little or no decline at all during the same period (Sanderson *et al.* 2006; PECBMS 2009; EBCC 2013). The causes of these declines in long-distance migrants are likely to be both population- and species-specific, but with the trend observed across multiple species and multiple breeding populations, changing conditions on the African non-breeding grounds are a putative cause (Sanderson *et al.* 2006; Cresswell 2014). Due to detailed monitoring in temperate Europe (Ockendon *et al.* 2012) there is a clear understanding of how both European climate and anthropogenic land use affect breeding birds (Newton 2004b; Gregory *et al.* 2007; Thaxter *et al.* 2010), and climate trends in Europe have been related to long term variations in population sizes (Green *et al.* 2008; Gregory *et al.* 2009). There is also some understanding of the role of climate on species non-breeding ranges, with both annual fluctuations and long-term trends in migratory bird populations linked to changes in rainfall patterns, for example in the Sahel (Lemoine & Bohning-Gaese 2003; Zwarts & van Horssen 2009; Both *et al.* 2010; Ockendon, Johnston & Baillie 2014; Pearce-Higgins *et al.* 2015). In addition, although the role of land-use change on the breeding grounds has been shown to be an important driver of population change in some species (Donald *et* *al.* 2006; Sanderson *et al.* 2006), little is currently know about the role of land-use impacts on the non-breeding grounds (Wilson & Cresswell 2006; Cresswell *et al.* 2007). The effects of land use, however, are most evident at finer scales, whereas the effects of climate are most apparent across larger areas; climate has been suggested to be the major driver of the distribution and abundance of birds across Europe (Thuiller, Araujo & Lavorel 2004; Chapter 3: Howard *et al.* 2015). Uncertainty remains about the relative role of long-term trends in climatic conditions and habitat on the breeding versus non-breeding grounds on the population trends of European long-distance migrants (Ockendon *et al.* 2012; Vickery *et al.* 2014).

Here, I explore, for the first time, the role of long term trends in climate suitability on both breeding and non-breeding grounds in driving the population sizes of European breeding birds with different migratory strategies and habitat affinities. First, I model the breeding and non-breeding distributions of these birds at a continental scale in relation to long-term mean climate data. I then apply these models to annual climate data to project trends in climate suitability for individual species, across their breeding and non-breeding ranges. In order to determine the extent by which trends in breeding bird population sizes across Europe are directly attributable to climatic change, we analyse the relationship between these climate suitability trends (CST) and long term population trends. Within this analysis, I control for species’ habitat affinities, as different trends between groups may indicate that land use is an important driver of population sizes. Although incorporating measures of land-use change would be preferable to explore the impacts of habitat, these data are not available for both breeding and non-breeding ranges for the time period of interest. I explore how climatic conditions, on both the breeding and non-breeding grounds, and long-term population trends differ among species of different migratory strategies, in order to understand the different drivers of population changes between long- and short-distance migrants.

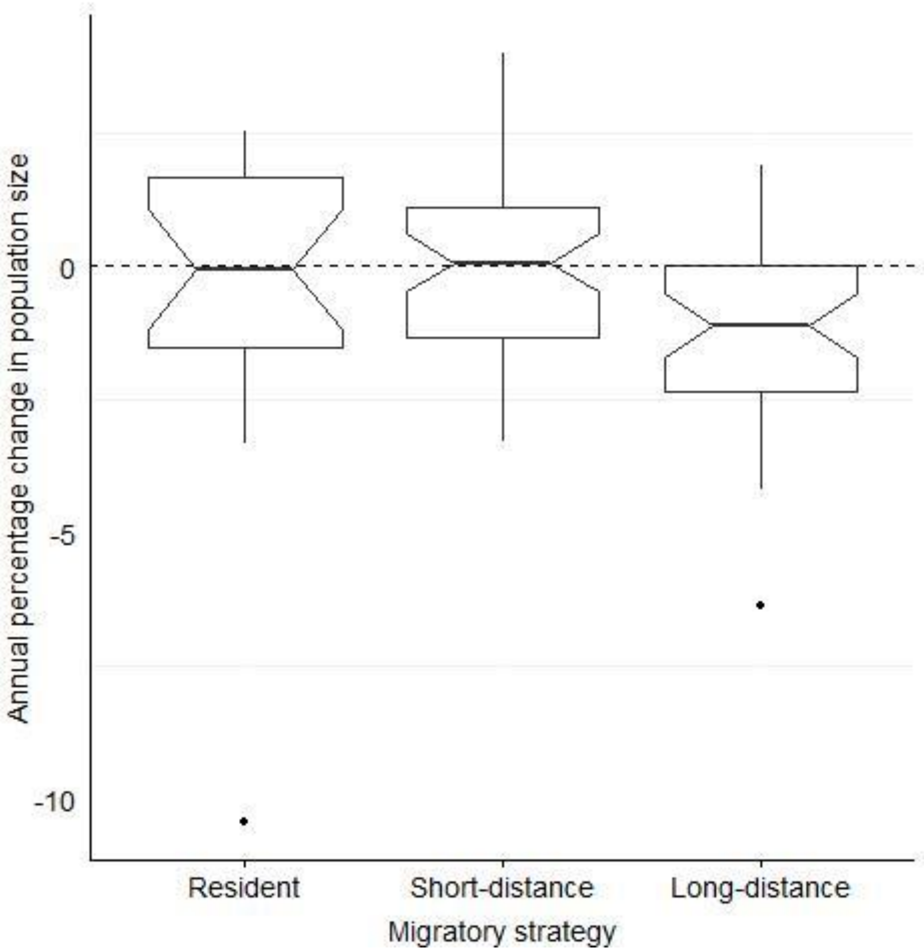


Figure 4.1: Annual percentage change in the population size of 107 common breeding birds across Europe between 1980-2011, separated into resident species (n=20), and short-distance (n=51) and long-distance (or 'Afro-Palaearctic', n=36) migratory species. Notches indicate the 95% confidence intervals of the median, with a lack of overlap indicating a significant difference at the 5% level. Box boundaries show the interquartile range, whilst the line across the box indicates the median. Whiskers identify extreme data points that are no more than 1.5 times the interquartile range on both sides and dots indicate points outlying this range. Population data come from the Pan-European Common Bird Monitoring Scheme (PECBMS, http://www.ebcc.info/pecbm.html).

4.3 Methods

4.3.1 Species data

Population trend data for 93 species of European migratory breeding birds were available from the Pan-European Common Bird Monitoring Scheme (PECBMS, http://www.ebcc.info/pecbm.html) for the period 1980 to 2011. Five of these 93 species were excluded from my analyses as population trend data for these species were only available from 1990. I removed an additional species (*Upupa epops*) from the analysis due to uncertainty regarding the overall direction of the population trend (high standard errors for the PECBMS trend). This left 87 migratory species with long-term population trend data calculated from monitoring data from across 20 European countries (Table A5 and A6). Supranational trends were calculated using log-linear Poisson regression in the software package TRIM (TRends and Indices for Monitoring data) (Pannekoek & van Strien 2001; Gregory *et al.* 2005). Specifically, the regression coefficient obtained by regressing the annual species counts across the 20 countries on calendar year is what I refer to as the population trend. Species were classified into two groups according to their migratory strategy: (1) short-distance migrants, which migrate principally to novel areas of Europe and North Africa in the non-breeding season; (2) and long distance migrants, which spend the non-breeding season entirely in sub-Saharan Africa (see Table A6 for classifications).

Species' range extent data (used to fit species distribution models (SDMs) – see below) were obtained from BirdLife International (BirdLife International & NatureServe 2012) for the 87 species, available as separate breeding and non-breeding ranges for each species. The distribution maps of each species' breeding range were overlaid with a 0.5° x 0.5° grid covering both Europe and the area of Africa north of 20°N. A species was considered present in a 0.5° grid-cell if the cell intersected with the species' breeding distribution. The non-breeding ranges of the 36 species classified as long distance migrants were similarly overlaid with 0.5° grid and converted to presence-absence data, but for an area covering Africa south of 20°N. For the 51 species of short-distance migrants (the non-breeding range for some of which extend into Africa), the non-breeding ranges were gridded for all of Europe and Africa.

Specific trait data for the 87 species of interest were obtained principally from Gregory *et al.* (2009) who had originally derived logged mean mass data from Cramp, Simmons and Perrins (1977-1994) and migratory strategy from Snow *et al.* (1997). Each species' principal breeding range habitat associations were classified as farmland, forest, wetland or 'other', following the classification of PECBMS (http://www.ebcc.info/pecbm.html). Non-breeding range habitat associations were taken from Atkinson *et al.* (2014) and Pearson and Lack (1992), and converted into categories comparable to those from the breeding range (open country, woodland, wetland or other).

4.3.2 Climate data

Data for three climatic variables: mean monthly temperature, precipitation, and percentage cloud cover for 1951 to 2000 (the period during which the majority of data underlying the species' range extent maps were collected), were obtained from the CRU TS 3.2 0.5° dataset (University of East Anglia Climatic Research Unit; Jones 2013). These data were used in conjunction with soil water capacity data and formulations, both from Prentice *et al.* (1992), to calculate four bioclimatic variables at 0.5° resolution for the entire area of interest. The bioclimatic variables were: mean temperature of the coldest month (MTCO), mean temperature of the warmest month (MTWA), the ratio of actual to potential evapotranspiration (APET) and growing degree days above 5° (GDD5). All of these variables have previously been found to be informative in describing both the range extents (Thuiller, Araujo & Lavorel 2004; Huntley *et al.* 2007; Doswald *et al.* 2009) and abundance patterns (Green *et al.* 2008; Gregory *et al.* 2009; Howard *et al.* 2014; Howard *et al.* 2015) of European breeding birds. In addition, annual values for these four bioclimatic variables were calculated, using the same method as above, for the period 1980 to 2011, to match the species' population monitoring period.

4.3.3 Species distribution models

To model the relationship between the mean bioclimate variables from 1951-2000 (the period preceding and including that for which species' range data were relevant) and species distributions, I used an ensemble modelling framework, combining four widely applied techniques. To provide contrast, I used two semi-parametric approaches, Generalised Linear Models (GLMs) and Generalised Additive Models (GAMs), alongside two machine-learning approaches, Generalised Boosting Regression Models (GBM) and Random Forests (RF). These methods have all been shown to produce models that perform well when used in an ensemble SDM approach, and are explained in more detail below (Elith *et al.* 2006; Bagchi *et al.* 2013). Separate SDMs were built for a species' breeding range and its non-breeding range. The bioclimate variables MTCO, APET and GDD5 were used to model the relationship between climate and a species' breeding range distribution. In contrast, when modelling the relationship between climate and species' sub-Saharan non-breeding ranges, MTWA was applied instead of GDD5. This is because MTWA provides a greater degree of discrimination than GDD5 among grid cells in the equatorial regions. GDD5, by contrast, provides greater discrimination at the higher latitudes associated with European migrant breeding ranges. All analyses were performed in R version 3.1.0 (R Core Team 2014).

4.3.4 Spatial autocorrelation

Spatial autocorrelation (SAC) occurs when proximate samples show a greater degree of similarity due to distance-related biological processes and spatially structured environmental processes (Dormann 2007a). Failure to account for SAC within SDMs influences both coefficients and inference in statistical analyses through: (1) the violation of the independence assumption and, (2) auto-correlated residuals and hence inflation of type 1 errors (Legendre 1993). Here, to account for SAC, I utilise a 'blocking' method (Bagchi *et al.* 2013), whereby I split the data into ten sampling blocks based on ecoregions (Olson *et al.* 2001 http://www.worldwildlife.org/science/data; Bagchi *et al.* 2013). Each non-contiguous area of an ecoregion, within the area of study, was classified as a separate sampling unit. These sampling units were then grouped into 10 blocks so that the mean bioclimate was similar across all blocks, but each block covered the full range of bioclimates within the area of study (Moore 2014) (Figure A7).

When fitting a model, nine of the ten blocks were used as the training data set, with model fit assessed using AUC (Manel, Williams & Ormerod 2001; Brotons *et al.* 2004) on the omitted block. As all blocks cover a similar range of bioclimatic data, this method ensures that a similar range of data was used for both testing and training models, whilst also ensuring that the data are spatially segregated. This method has been shown to perform well at a large scale, minimising the influence of SAC whilst allowing models to capture complex spatial processes (Bagchi *et al.* 2013). By sequentially omitting each of the ten blocks, fitting the model to the remaining nine blocks and testing the performance on the omitted block, ten models were fitted for each of the four modelling techniques (outlined below). This resulted in 40 models for both the breeding and non-breeding ranges for all 87 species. To assess model fit, the median AUC calculated for the omitted blocks, was taken across the ten models for each of the four modelling techniques for both the breeding and non-breeding ranges for each of the 87 species.

4.3.5 Generalised Linear Models (GLM)

GLMs (Mccullagh 1984) were used to fit up to, and including, fourth order polynomial relationships between the three relevant bioclimatic variables and individual species occurrence. For each species, after omitting one sampling block for model evaluation, 81 models (3 bioclimate variables ^ 4 polynomial degrees=81 combinations) were fitted to the remaining nine blocks. AUC was then used to assess the model fit using the excluded block of data. This procedure was repeated excluding each of the ten data sampling blocks sequentially. The combination of polynomial terms for each bioclimatic variable that maximised AUC in each of the ten repeated model fittings was then used to fit a final set of 10 models.

4.3.6 Generalised Additive Models (GAM)

Relationships between bioclimate variables and species occurrence were modelled using thin-plate regression splines. Models were fitted to nine blocks of data, after omission of one sampling block for model evaluation using AUC, and the process repeated until each of the ten sampling blocks had been sequentially omitted. These regressions were fitted as a Bernoulli response, using a logit link, and utilised the ‘gam’ function in the ‘mgcv’ R package(Wood 2011; R Development Core Team 2012).

4.3.7 Generalised Boosting Methods (GBM)

Generalised boosting methods, a machine learning technique, builds a large number of simple regression trees, which are then combined to optimise predictive performance (Elith, Leathwick & Hastie 2008). This technique requires the user to set three parameters; learning rate (lr; also known as the shrinkage parameter) determines how much each tree contributes to the final model; tree complexity (tc) controls the number of nodes within a tree; and the number of trees (nt) that are to be retained in the final model. I used a cross validation approach to optimise these parameters for each species. Initially, omitting one block at a time, I fitted a model to the remaining nine blocks using an lr of 0.001, an nt of 5000 whilst allowing tc to vary between 1 and 4. The value of tc that returned the minimum summed error across all blocks from a cross-validation approach was used to fit a final set of 10 models.

4.3.8 Random Forests (RF)

Random forests (Breiman 2001a; Cutler *et al.* 2007), are a classification and regression tree (CART) approach, which draws bootstrap samples and a subset of predictors to construct multiple classification trees (Prasad, Iverson & Liaw 2006). This method requires the user to set two parameters; the number of trees (nt) that will constitute the final model and the number of variables randomly sampled as candidates at each split (mtry). I initially set mtry to vary between one and three and then fitted an RF model with 1000 trees to the data after sequentially omitting one block. I assessed the fit of the model on the omitted block using AUC. I then added 500 trees to the model and reassessed AUC. This process was repeated until any improvement in the value of AUC, as a result of the additional trees, was less than 1%. The values of mtry and nt that maximised mean AUC across the 10 blocks of omitted data were used to fit the final 10 models.

4.3.9 Calculating annual climate suitability and analysis of trends

Applying annual bioclimatic data from Worldclim (Hijmans *et al.* 2005 http://www.worldclim.org/) to the final 40 SDMs for each species (10 block models x 4 modelling techniques), I projected climate suitability for each species for the years 1980 to 2011, for both breeding and non-breeding ranges. I used the mean projected suitability from the 40 SDMs from across all cells within a species' range in any given year as a measure of climate suitability. For the breeding range this mean suitability was evaluated across all of a species' breeding range within the area covered by PECBMS (the region for which we have population trend data; Table A5). Mean suitability for the non-breeding range was calculated across all cells within a species' non-breeding range across Europe and Africa.

After calculating mean annual climate suitabilities for each species, I used a generalised linear regression, with a binomial error structure and a logit link, to regress climate suitability against year. The slope from this regression I term the climate suitability trend (CST) and this indicates, for a species, the overall trend in climate suitability between the years 1980 and 2011. CST was evaluated separately for the breeding and non-breeding grounds for each species.

To assess the relationship between the species' population trend and the CSTs for both the breeding and non-breeding ranges, I fitted a generalised linear regression model. Included within the global model were terms to control for differences in body size (logged mean mass of a species), migratory strategy (either short or long distance) and primary breeding and non-breeding range habitat associations for each species, as detailed above. In the model I also included interactions between CSTs and migratory strategy, as I was interested in the potential for differing contributions of breeding and non-breeding CST for the different migratory groups. Other interactions were not tested for due to the potential for over fitting. I also tested for phylogenetic non-independence following Freckleton, Harvey and Pagel (2002) but found no significant effect, and model performance was not improved by accounting for phylogeny. The most parsimonious models from all biologically sensible subsets of this global model were identified by selecting all models with an AIC value within 6 units of the best performing model but disregarding any models with a better-performing, simpler, nested model (Richards 2008). Additionally, I disregarded any models with greater than 9 degrees of freedom, due to the relatively small sample size (n = 87) (Dahlgren 2010). Model averaging was used across this top candidate model set to produce standardised Akaike model-averaged coefficients and the relative importance of each parameter (Burnham & Anderson 2002).

To investigate further the potential for differing contributions of breeding and non-breeding CST for species with different migratory strategies, I assessed the strength of those interacting terms that were retained in the final averaged model. Species of each migratory strategy were divided into three groups depending upon the relevant CST: species with a CST of less than -0.005 were classed as having been negatively affected by recent climate, positive species were those with a CST greater than 0.005, whilst stable species had a CST in between these values. Due to the relatively small sample size within each CST classification (see Figure 4.4), I tested for statistical significant difference of the median population trend from zero using one-sample Mann-Whitney tests.

4.4 Results

4.4.1 Species distribution models

SDMs fitted to the breeding and non-breeding ranges of all short- (51 spp.) and long-distance (36 spp.) migrants produced useful models for all species using all four SDM approaches. Model fit was very good across the breeding ranges (median AUC = 0.965 (range = 0.820 - 0.994); see Table A7 for individual model technique results)**.** SDMs for species' non-breeding ranges were also good, though median fit was slightly lower than for the breeding range models (median AUC = 0.942 (0.785-0.985); Table A7). The mean annual projections from these models were used to calculate CST values for both the breeding and non-breeding grounds for all 87 species (Table A6).

4.4.2 Predictors of population trends

From the global model set, the candidate model set comprised 6 models with $\Delta AIC_c < 6$ with 9 or fewer degrees of freedom (Table A8). These models were used to calculate model averaged parameter estimates that explained the population trends of the 87 species of migrant bird reasonably well (adjusted R^2=0.48). When considered separately, the population trends of long distance migrants were less well explained by these model averaged parameter estimates than short distance migrant species (R^2=0.18 and R^2=0.58 respectively; Figure 4.2).

Both CST on the breeding grounds and body mass were retained in all candidate models (Table A8), although the effect of CST seemed dependent upon the inclusion of breeding habitat association. 83 % (5) of the top models retained breeding ground habitat, whilst 67 % (4) of the candidate models retained migratory strategy. Non-breeding ground CST and non-breeding ground habitat were retained in only 33 % (2) and 17 % (1) of the top models, respectively. An interaction between breeding ground CST and migratory strategy was also retained in two of the top models, including the best performing model.

Variables associated with the breeding ground were of greater relative importance in the final averaged model, than those variables associated with species' non-breeding grounds (Table A9). In particular, (along with mass [relative importance 1.00]), breeding ground CST and breeding ground habitat were the variables with the greatest relative importance in the final model (1.00, and 0.81 respectively). In contrast, the relative importance of non-breeding ground CST was only 0.14 and non-breeding ground habitat relative importance only 0.19.

Model-averaged parameter estimates indicate a significant positive effect of breeding ground CST on population trend (Figure 4.3, Table A9). By contrast, CST on the non-breeding ground was not significantly related to population trend (Figure 4.3, Table A9). A close to significant interaction between breeding ground CST and migratory strategy was indicated by the model averaged parameter estimates (Figure 4.3, Table A9), suggesting that short distance migrants demonstrate a much stronger positive relationship between breeding ground CST and population trend (and one that differs significantly from zero) than long-distance migrants (Figure 4.4).

Further analysis of the only significant interacting term retained by the model, the interaction between breeding ground CST and migratory strategy, showed that short-distance migrants with a positive CST across their breeding ground had a population trend significantly greater than zero (one-sample Mann-Whitney: V=209, p<0.01, n=21, Figure 4.4, Table A10). The only other category of species to show a difference from zero in their population trends were long-distance migrants with a negative CST across their breeding grounds (trend less than zero; one-sample Mann-Whitney: V= 26, p=0.10, n= 14, Figure 4.4, Table A10).

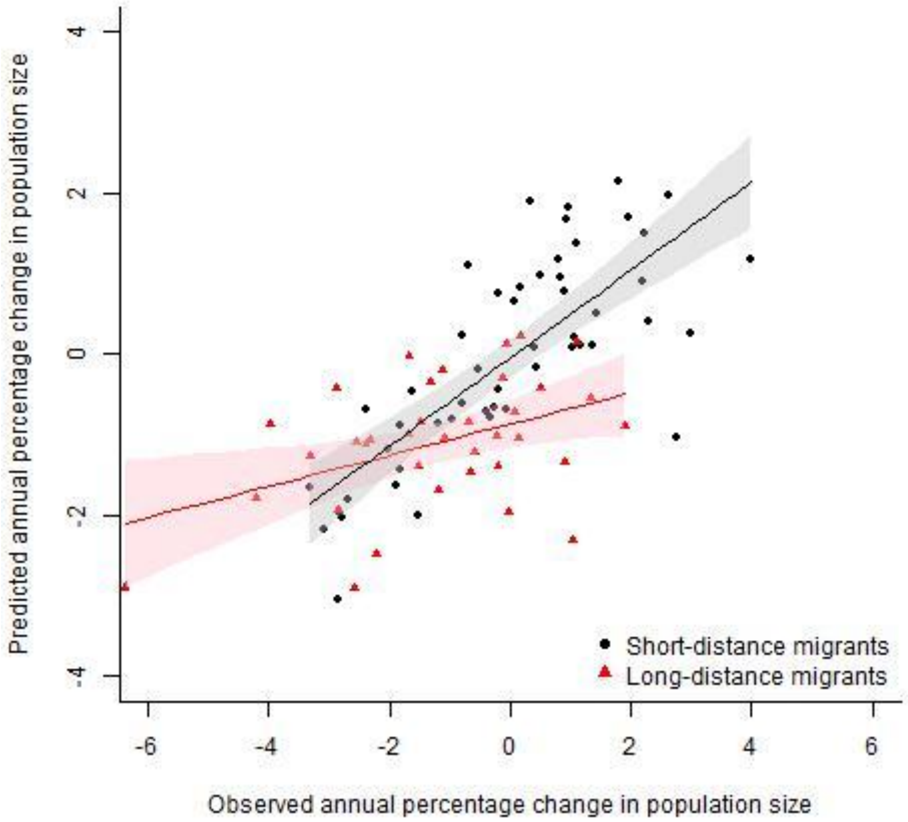


Figure 4.2: Observed against predicted population trends using the standardised model averaged coefficients for 87 species of migratory birds (R^2=0.47). Black indicates short distance migrants (n= 51, R^2=0.58), red indicates long-distance migrants (n=36 R^2= 0.18). Shaded areas represent 95% confidence intervals around the mean

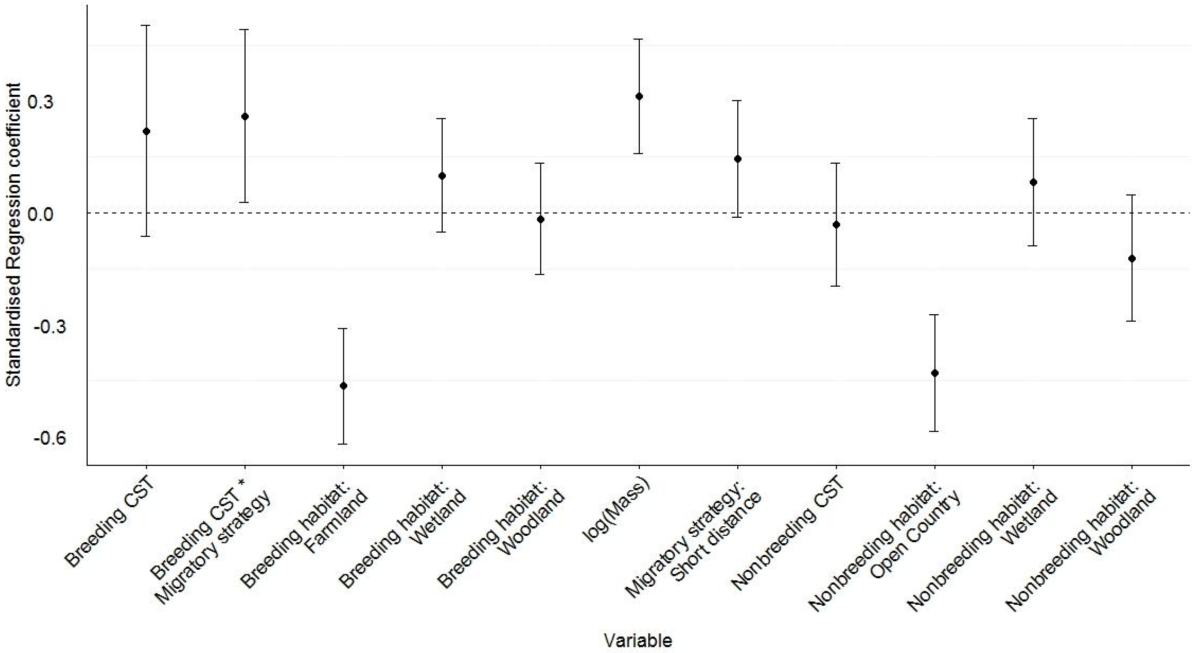


Figure 4.3: Standardised Model-averaged coefficients from OLS regression models of the population trends since 1980, (R2=0.47). Whiskers identify 90% confidence intervals around each coefficient. Intersection of the whiskers with the dashed line at zero indicates that the effect of the parameter is not statistically significant (i.e. $p > 0.10$).

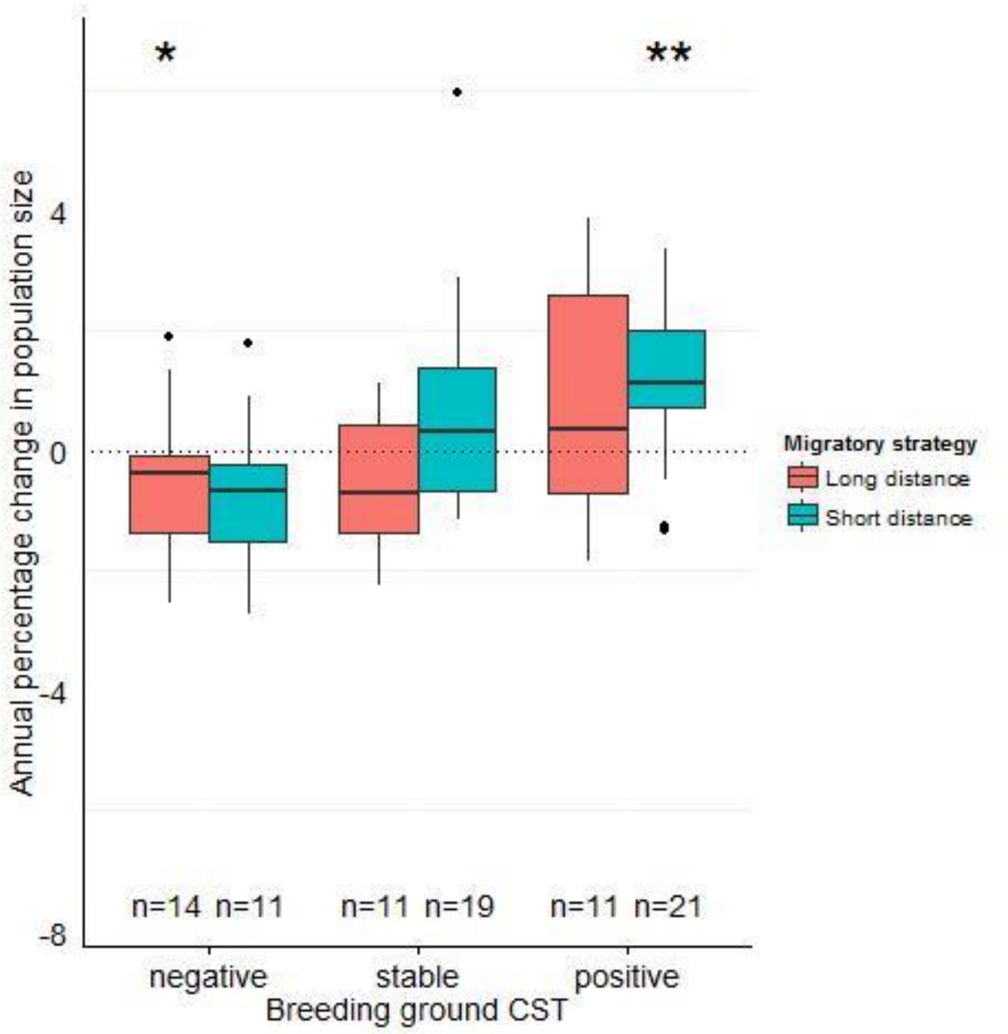


Figure 4.4: Relationship between long term population trends and trend in climate suitability across the breeding ground ranges of 51 short-distance migrant species 36 long-distance migrant species, after controlling for all other variables. The line across each box indicates the median and the box boundaries indicate the interquartile range (IQR).Whiskers identify extreme data points that are non more than 1.5 times the IQR on both sides whilst the dots picture outliers. Statistical significant difference of the median from zero, tested with a one sample Mann-Whitney test, at the 5% level is indicated with ** and at the 10% level with *.

4.5 Discussion

Until now, the relative contribution of climate and habitat on the breeding and non-breeding grounds of European birds, in driving the declines of long-distance migrants (Sanderson *et al.* 2006; Cresswell 2014; Vickery *et al.* 2014) has hitherto been poorly understood. Here I have shown the importance of these variables and how the strength of these relationships varies with a species' migratory strategy. I discuss these results in light of three key findings: 1) long term climate trends and habitat are of greater importance on species' breeding grounds than on their non-breeding grounds; 2) climate trends on the breeding grounds are more important in explaining variation in long term population trends for short- distance migrants than for long-distance migrants; and 3) my ability to explain species' population trends depends on their migratory strategy.

4.5.1 Importance of breeding and non-breeding ground conditions

This is the first large scale direct assessment of the relative importance of climate and habitat, on both the breeding and non-breeding grounds, on populations of migratory birds. I have demonstrated that those variables associated with migratory species' breeding grounds are of relatively greater importance in explaining long-term population trends than those associated with the non-breeding grounds. In particular, these results indicate the importance of climatic conditions on species' breeding grounds, with a positive relationship between population trend and breeding ground CST, even after accounting for migratory strategy, mass and habitat associations. These results corroborate previous research demonstrating that interspecific variation in the recent population trends of European birds is correlated with climatic trends (Green *et al.* 2008; Gregory *et al.* 2009). However, despite the potential for climatic conditions on the non-breeding grounds to impact directly upon population sizes (Bearhop *et al.* 2004; Norris *et al.* 2004; Saino *et al.* 2004; Gordo *et al.* 2005; Studds & Marra 2005; Ockendon, Johnston & Baillie 2014), I found that this effect is weak relative to the effects of breeding ground climate and habitat affinity, when considered across a large number of species at a wide spatial scale. This may be attributable, in part, to the inclusion of some species in this analysis that are considered to be itinerant during the non-breeding season. For example, some sub-Saharan migrants, such as Willow Warblers (*Phylloscopus trochilus)*, move southwards through the non-breeding range over the course of the European winter (Salewski & Jones 2006; Cresswell, Boyd & Stevens 2008; Newton 2008). With non-breeding ranges being used only transiently by some species, long-term climatic conditions in these areas may be less important in driving population trends for these species.

Conditions across the Sahel, a key non-breeding habitat for long-distance migrants, are intricately linked with seasonal precipitation (Ockendon, Johnston & Baillie 2014; Vickery *et al.*

2014). If rainfall in these regions is high, resources available to migrant birds will be plentiful. Since the 1960s, drought conditions have predominated in this area (Nicholson 2000), despite an apparent increase in rainfall across North Africa since the 1990s (Fontaine *et al.* 2011). The resulting habitat changes have been widely linked to the population declines of long-distance migrant birds observed since the 1970s (Sanderson *et al.* 2006). These results show that despite the importance of these long-term climatic trends on the non-breeding grounds for determining the population trends of long-distance migrants, that the population trends of these species are more strongly associated with long-term trends in climate suitability on their breeding ranges.

My analyses, which categorise species according to their habitat preferences, also show systematic differences in population trends between species with different breeding and non-breeding ground habitat affinities. The importance of habitat preferences in explaining variation in population trends, strongly suggests that habitat effects are playing an important role in population trends, with these results indicating that these effects are equally strong on both the breeding and non-breeding grounds (see standardised coefficient values in Figure 4.3, Table A9). This is a well-documented situation in Europe, where the population trends of species have been shown to depend on their breeding ground habitat preferences (Sanderson *et al.* 2006). In particular, these results highlight the population declines exhibited by farmland breeding bird species (Donald, Green & Heath 2001; Donald *et al.* 2006). In a species' non-breeding range, an affinity for open country habitats, a land use type analogous with farmland in Europe, appears to have a negative effect of similar magnitude on species' population trends. Both reduced rainfall (Nicholson 2000) and agricultural intensification have been shown to lead to widespread desertification and habitat degradation in open country habitats across the Sahel (Sanderson *et al.* 2006). Reductions in rainfall and primary productivity will limit available resources in these areas and in turn restrict the populations of migrant birds (Baillie & Peach 1992). This result suggests that systematic changes within broad land-use types in sub-Saharan Africa may be causing changes in populations in suites of species of similar habitats, in a similar way to those observed across Europe.

4.5.2 The role of breeding ground climate suitability in determining long-term population trends

The relationship between trends in climate suitability across species' breeding grounds and their population trends is partially dependent upon migratory strategy. Whilst positive trends in climate suitability across the breeding grounds of short-distance migrants correspond with increasing population trends, this is much less the case for long-distance migrants. The breeding and non-breeding grounds of short-distance migrants are more closely linked than those of long-distance migrants. Increases in climate suitability across the breeding grounds of short distance migrants will not only reflect improvements in breeding conditions but also in over winter survival (Pearce-

Higgins *et al.* 2015). In contrast, improving climate suitability across the breeding grounds of long-distance migrants will have little impact on their overwinter survival. Additionally, long-distance migrants are more exposed to the effects of phenological mismatch (Moller, Rubolini & Lehikoinen 2008; Saether & Engen 2010). Many species rely on a synchrony between the timing of key life history events, such as timing clutch hatching to coincide with key prey availability (Both *et al.* 2006; Both *et al.* 2010). Increases in winter and spring temperatures at high and medium latitudes have led to advancements in spring phenological events, such as leaf unfolding and flowering (Walther *et al.* 2002; Menzel *et al.* 2006a; Schwartz, Ahas & Aasa 2006). To maintain synchrony with the phenology of prey species, it is essential that migratory birds shift the timing of their spring migration to track these advances in phenological events (Saino *et al.* 2011). However, species responses do not all occur at the same rate with many studies reporting a greater advance in the timing of spring migration of short distance migrants that that of long distance migrants (Moller, Rubolini & Lehikoinen 2008; Knudsen *et al.* 2011; Saino *et al.* 2011). Due to the constraints that conditions in their non-breeding grounds and stop-over sites have upon the arrival on the breeding grounds, long-distance migrants are not as adept to adapting the timing of their migration (Both & Visser 2001). This renders them more susceptible to phenological mismatch than their short distance migrant counterparts. Higher spring temperatures, resulting in advancements in tree and insect phenology, have been shown to have negative effects on populations of long-distance migrants (Both & Visser 2001; Pearce-Higgins *et al.* 2015). By modelling mean annual climate, traditional SDMs are unable to capture these phenological shifts in climate. They are, however, able to show that despite beneficial changes in annual climate across the breeding ranges of some long-distance migrants, these species are less able to benefit than their short-distance migrant counterparts.

The demonstration here of the lower ability of breeding ground CST to explain variation in the population trends of long-distance migrant species may also suggest that factors additional to climate on the breeding and non-breeding ground are responsible for the majority of variation in populations of long-distance migrants, which I discuss in more detail below.

4.5.3 Differences between short and long-distance migrants

A large proportion of the variance in the population trends of short distance migrant species was explained by CST and habitat, the latter on both the breeding and non-breeding grounds, as indicated by the performance of the regression models (58% of the variation explained). This was not the case for long distance migrants, where the best models explained a more modest proportion of the variance in long-term population trends (18 % of the variation explained). This is perhaps unsurprising given the high levels of complexity in the annual cycles of long-distance migrant species (Robinson *et al.* 2009), the potential for phenological mismatch outlined above, and that changes in climate suitability at migratory stop-over sites might also be important (Finch *et al.* 2014; Vickery *et al.* 2014). Their use of multiple landscapes through the year also renders long-distance migrants more likely to be exposed to land-use changes during at least part of their annual cycle than are other species (Runge *et al.* 2014). In addition to the pressures experienced by short-distance migrants, long-distance migrants are also susceptible to the effects of mortality during extended migrations. Migration mortality could result from resource depletion and patchy resource availability on passage, as well as direct hunting pressures, an acknowledged cause of mass mortality of Europe-African migrants whilst on migration (Sillett & Holmes 2002; Newton 2010).

4.5.4 Future directions

One area for future development is in improving knowledge of the destinations of birds that migrate out of Europe during the non-breeding season. Recent advancements in tracking and sensing technology are enabling us to fill some of the gaps in our understanding of migration by providing information on the non-breeding ranges of these species (Robinson *et al.* 2010; Renfrew *et al.* 2013; Trierweiler *et al.* 2014; Finch *et al.* 2015). This will ensure that our ability to assess the range and habitat use of these species are equally precise on the non-breeding grounds and the breeding grounds (Vickery *et al.* 2014). Further work should also consider that the causes of migrant declines are likely not only to be species specific but also population specific (Cresswell 2014). Often populations breeding in different parts of Europe over-winter in distinct areas of the non-breeding range (Newton 2010). Currently, our lack of knowledge of the links between the breeding and non-breeding grounds of populations makes evaluating the relative importance of climate on the breeding versus non-breeding range in affecting population trends difficult at a finer, national scale. Future identification of population specific wintering areas, migration routes and stopover locations of different breeding populations will enable a more thorough understanding of the mechanisms driving the declines of long-distance migrants (Ockendon *et al.* 2012).

4.5.5 Conclusions

For the first time I have demonstrated at a continental scale that long-term climate change and habitat associations are of greater importance on breeding grounds rather than non-breeding grounds in determining the population trends of multiple migratory species. I have also shown the effects of both breeding and non-breeding habitat associations on population trends and in particular identified that species that breed on farmland and winter in open country habitats are most likely to have declined. Importantly, I have shown that, in recent decades, long-distance migrants have been less able than short-distance migrants to benefit from improvements in climate suitability across their breeding grounds. Yet, despite these important findings, what drives the population trends of long-distance migrants is still not fully understood. This may be because of the lack of equivalent data from their stop-over locations on migration, when the main mortality may occur (Sillett & Holmes 2002). If this is to be resolved and further declines prevented, population level investigations into the use of non-breeding areas by these species are urgently required.

Chapter 5

Accounting for spatial autocorrelation in predictions of abundance

5.1 Abstract

Assessing the impacts of climate change on species may require the application of species abundance models to projections of future climate. The efficacy of these models to project to novel domains, however, remains untested. A major limitation, that might preclude the use of these models for predicting future patterns of abundance in geographic space, is that they often require information about spatial autocorrelation (SAC). Here, to evaluate the importance of SAC when applying abundance models to novel areas, I compare three methods that are used to predict species abundance: (1) applying models that do not account for SAC, (2) using models that incorporate an SAC adjustment term to form a single round of predictions, and (3) iteratively applying models that incorporate an SAC adjustment term until a stable solution is reached. Here, I utilise Gibbs sampling to estimate abundances whilst concurrently estimating an SAC adjustment term. I evaluate these three approaches in areas with known abundance data. I test the models in two regions: one region is within the model-fitting parameter space, and one is beyond the space used for model-fitting. My study system comprises breeding bird species that are distributed across Europe, and for which I have estimates of abundance in individual 50 km cells across most of Europe. I relate the abundance of these species to climate and habitat variables, and test the ability of the different model types to predict (a) abundance within 50 km cells and (b) larger, national abundance estimates. I show that, when applied within model-fitting parameter-space, methods that did not consider SAC generally predicted abundances in individual cells better than methods that accounted for SAC. However, models that do account for SAC were significantly better at predicting areas of high abundance than models that ignore SAC. In novel regions beyond model-fitting parameter space, the ability to predict abundances in 50 km cells declines markedly across all three methods. In contrast to the individual cell predictive performance, all three approaches were excellent at predicting national bird population estimates when applied within model fitting parameter-space and all had good predictive ability in novel regions. Predictions from a single iteration of SAC were the only ones not to demonstrate significant bias in their deviance. Given that fine scale projections of abundance were universally poor, even when applying the best available approaches to control for SAC, I would caution against making such projections. With accurate large scale projections of abundance, I was able to predict overall changes in populations due to climate change but not advise on management options at smaller spatial scales.

5.2 Introduction

Predicting changes in abundance is key to identifying potential changes in the conservation status of species in response to future climate change (Pereira *et al.* 2010; Dawson *et al.* 2011; Bellard *et al.* 2012; Mair *et al.* 2014). Syntheses of climate change and future impacts on biodiversity rely heavily on species distribution and abundance modelling to define a species' 'ecological niche', and hence to estimate changes under future climate projections (Guisan & Thuiller 2005; Elith, Kearney & Phillips 2010). However, the reliability of species distribution and abundance modelling techniques is subject to several key constraints (Pearson & Dawson 2003; Dormann 2007a; Record *et al.* 2013). Chief among these constraints is the failure of models to account for the non-independence of spatial data, termed spatial autocorrelation (SAC) (Bahn & McGill 2007; Dormann 2007a; Elith, Kearney & Phillips 2010; Bahn & McGill 2013; Record *et al.* 2013). SAC occurs frequently in ecological data and arises because points closer together tend to be more similar in their ecological characteristics, such as species occurrence and abundance, than points that are further apart (Legendre 1993; Record *et al.* 2013). This occurs as a result of either distance-related biological processes, such as dispersal, spatially structured environmental processes, such as soil moisture content, or incorrect model specification (Dormann 2007a). Consequently, SAC can be a serious limitation on the use of species distribution and abundance models for hypothesis testing and prediction. The presence of SAC means that model assumptions of the independence and identical distribution of residuals are violated, which in turn can lead to biased parameter estimates and poor model inference (Legendre 1993; Dormann 2007a). Failure to account for SAC has been shown to result in the misidentification of important driving variables (Lichstein *et al.* 2002; Segurado, Araujo & Kunin 2006; Dormann 2007a; Record *et al.* 2013).

Several methods have been developed to control for the effects of SAC. For example, generalised least squares models (GLS) directly model how the variance around the expected response value at a point co-varies with that of other neighbouring points, by altering the models' variance-covariance matrix (Dormann 2007a; Dormann *et al.* 2007). An alternative method is to subsample the original spatial data in a manner that constrains observations to be spaced sufficiently far apart that they are not subject to correlation (Segurado, Araujo & Kunin 2006). SAC also contains information that one may not wish to 'control' for. Unmeasured ecological factors, for example, population processes such as dispersal, and underlying resources such as soil moisture, may all give rise to a spatially autocorrelated dataset (Dormann 2007a; Dormann *et al.* 2007; Warren *et al.* 2014). Often, species distribution and abundance models incorporate an autocovariate term for SAC in the models as an indirect measure of the importance of these additional processes (Augustin, Mugglestone & Buckland 1996; Keitt *et al.* 2002; Segurado & Araújo 2004; Segurado, Araujo & Kunin 2006; Howard *et al.* 2014). This term not only reflects the extent to which observed abundance is driven by spatial aggregation within the underlying environmental covariates, but also indicates the extent to which these patterns are driven by dynamic ecological processes (Keitt *et al.* 2002). In some cases this term has been shown to explain the majority of variation in species' abundance (Chapter 3, Howard *et al*. 2015).

When utilising species distribution and abundance models for assessing the impact of future climatic change (Thomas *et al.* 2004; Johnston *et al.* 2013; Mair *et al.* 2014), models may be extrapolated to conditions that differ from those used in model calibration, which can result in erroneous predictions (Araújo & Guisan 2006; Heikkinen *et al.* 2006). If correlations between variables change across space (Elith, Kearney & Phillips 2010), or if species-environment relationships are not conserved (Kissling *et al.* 2012; Wisz *et al.* 2013; Snickars *et al.* 2014), projections may not be ecologically meaningful or statistically valid (Record *et al.* 2013). Often, the efficacy of species distribution and abundance models to project into novel domains remains untested (Araújo & Guisan 2006). Furthermore, little is known about the effectiveness of using a model which includes a spatial autocovariate term to project species abundance across an area not included in model fitting and testing. This is, in part, due to the difficulties associated with calculating a spatial autocovariate term across an area without *a priori* abundance data, such as in unsurveyed regions or into the future.

To overcome the problems associated with projecting species abundance across an unsurveyed area, with a model that uses a spatial autocovariate term, here we utilise Gibbs sampling (Geman & Geman 1984). This method iteratively estimates abundance, from which a spatial autocovariate term can be calculated across unsurveyed areas/periods and has been shown to improve the precision of predictions from species distribution models (Augustin, Mugglestone & Buckland 1996; Augustin, Mugglestone & Buckland 1998). The Gibbs sampler is a Markov Chain Monte Carlo (MCMC) method, which allows the estimation of abundances in unsurveyed areas by iteratively building upon initial sample values (Augustin, Mugglestone & Buckland 1996; Augustin, Mugglestone & Buckland 1998).

Here, I test the utility of Gibbs sampling to predict the abundance of European breeding birds across unsurveyed areas whilst taking into account unmeasured ecological factors. I specifically address whether incorporating measures of SAC improves abundance predictions and if these methods produce meaningful abundance predictions in areas beyond model fitting parameter space. I test methods against two datasets for which we include no *a priori* abundance data; (1) a discrete sub-region within model parameter space, and (2) a region beyond model parameter space. These test areas are used as proxies for situations when models are projected into novel areas within or beyond model-fitting parameter space, both of which can arise when predicting changes under future climate change. Model performance is tested by assessing two issues: (1) whether the different models can predict abundance estimates in 50 km UTM grid-cells within the two test regions, and (2) whether models can predict national-scale abundance estimates (from combing grid cell estimates). An ability to estimate the former would give us confidence in using such models to plan fine-scale (i.e. sub-50 km) conservation adaptations actions under climate change. An ability to estimate national populations would suggest such models have most utility in broad-scale conservation planning.

5.3 Methods

5.3.1 Species data

Species abundance data are primarily as described in Chapter 2. However, only species with an independent assessment of national population size from the British Trust for Ornithology's (BTO) New Atlas of Breeding Birds in Britain and Ireland (Gibbons et al. 1993) were included in this analysis. This atlas provides an independent national population size estimates for both Great Britain and Ireland for the period relating to 1988-1991, which corresponds to the period over which the EBCC atlas data were collected. The remaining 181 species were used for all subsequent analyses in this chapter.

5.3.2 Bioclimatic data

Bioclimatic data are as described in Chapter 3.

5.3.3 Land use data

Land use data are as described in Chapter 2.

5.3.4 Model fitting

To model species abundance, I used a machine learning technique, random forests (RF) (Cutler *et al.* 2007). Robust to over-fitting, RF is widely recognised to produce good predictive models; hence, it is increasingly applied to species distribution modelling (Elith *et al.* 2006; Strobl, Malley & Tutz 2009; Elith, Kearney & Phillips 2010; Boulangeat, Gravel & Thuiller 2012). I use RF models in preference to ordinal regression techniques because they make fewer assumptions about the distribution of predictor and response variables (Cutler *et al.* 2007). RF models have been shown to perform well when assessed using several measures of model discrimination and calibration (Chapter 2, Howard *et al.* 2014). I use a conditional inference framework in the R package 'party' to account for potential biased variable selection (Hothorn, Hornik & Zeileis 2006a; Hothorn, Hornik & Zeileis 2006b; Strobl, Hothorn & Zeileis 2009b).

Models were fitted using ten-fold cross validation to reduce SAC between training and test data and to minimise over-fitting. Only data from mainland Europe were used in the process of model fitting. To improve stability, each model was built using 1000 classification trees fitted to a random sample of 70% the observed data from mainland Europe. The remaining 30% of observations from mainland Europe (the semi-independent test data not used initially for model fitting) were used to estimate model performance (Cutler *et al.* 2007) using AUC, a threshold independent measure (Manel, Williams & Ormerod 2001).

To account for SAC in my models a spatial autocovariate term (L) was calculated for each UTM grid cell based on the surrounding abundance (in directly adjacent cells) of conspecifics, based on the EBCC abundance data, using the following equation:

$$L = \log_{10}\left[\frac{1}{n}\sum_{i}^{n}\frac{1}{2}(10^{A_i})\right] \qquad (1)$$

where L is the surrounding local abundance or spatial autocovariate term, n is the number of adjacent cells, A is the categorical abundance scale, and i is the abundance category index. In the formula, the log scaled integer estimates of abundance in the adjacent cells are back transformed and divided by two to give an absolute abundance for each cell relating to the midpoint of the abundance category. The mean of these estimates of surrounding absolute abundances across cells is log transformed to enable direct comparison with the original spatial abundance values on the existing ordinal scale.

For each of the 181 species, two models were fitted to each of the ten cross validation data samples, one that accounts for SAC, and one that does not, with all climate and land use variables remaining the same for both models. This resulted in ten pairs of models for each of the 181 species.

5.3.5 Gibbs sampler

As areas without *a priori* information on abundance have no data with which to calculate a value of the spatial autocovariate term (L) for use in the RF models, initial estimates of abundance using the RF model that does not account for SAC are generated. Then one of the unsurveyed cells is randomly selected and, using the initial estimates of abundance, L is calculated for the focal cell. The abundance estimate is then recalculated for that cell using the RF model that accounts for SAC. This process is repeated for all the unsurveyed cells sequentially and the process repeated iteratively until a final estimate of abundance has been converged upon for each cell. This is explained in full in Table 5.1.

Table 5.1: Gibbs sampling method for predicting abundance, adapted from the method outlined in Augustin, Mugglestone & Buckland (1996)

1. Fit two RF models to surveyed squares using the method outlined
    i. standard RF model
    ii. RF model with spatial autocovariate term
2. Predict abundance across all unsurveyed squares using the standard model.
3. Calculate surrounding local abundance (L) using equation 1 for all unsurveyed squares
4. Using the random forest model with SAC predict abundance for all unsurveyed squares.
5. Recalculate L for all unsurveyed squares using equation 1
6. Perform the Gibbs sampler:
   Do the following T times or until the predictions have converged.
    i. Pick a random square and delete abundance prediction
    ii. Predict abundance using RF model with SAC term
    iii. Recalculate L for square.
    iv. Move onto next square and repeat a. to c. until abundance has been recalculated for all unsurveyed squares
7. Use the sum of the absolute differences of predicted abundance across all squares between each iteration to indicate progress towards convergence. This absolute difference will be zero when the predictions have fully converged.

The number of iterations required (T) depends on how quickly the Gibbs sampler converges. Here, I found that abundance predictions for all cells converged upon (or were stably oscillating around) a final prediction within 20 iterations for 95% of species and within 30 iterations for all 181 species (Figure A8).

The Gibbs sampler produces a prediction of abundance after each iteration, and uses these predictions to generate L. As a result, the predictions from one iteration depend heavily on the predictions from the previous iteration. The predicted abundance for each cell was calculated as the product of the probability of a cell falling within each abundance category, by the log of the midpoint of that abundance category, summed across all abundance categories. This reduced the variation introduced in each iteration and improved convergence rates.

Using the above procedures, three methods with which to predict the spatial abundance of species are produced:

1: Method without SAC- Standard RF model

2: Single iteration SAC- Using RF model that accounts for SAC with L calculated for all cells from a single projection of abundance (stages 1-4 of algorithm in Table 5.1)

3: Gibbs sampling- Using RF model that accounts for SAC, with L calculated by Gibbs sampling

5.3.6 Model Assessment and Comparison

Assessment data sets: The utility of these three methods is assessed on two data sets for which no *a priori* abundance data is included. The first data set is a discrete sub-region from within the model building arena. Due to the computationally intense requirements of Gibbs sampling I limited this area to Germany, Denmark and The Netherlands (hereafter 'DE test data' for brevity). This area is comprehensively covered by quantitative abundance estimates in the EBCC atlas, enabling accurate assessment of model performance. The second data set is from a region beyond model parameter space, which is intended to replicate the type of situation to which species-abundance models conditioned on current distributions might be applied under scenarios of future climate change. For this purpose, the models were applied to a discrete area outside of the model training domain: Great Britain and Ireland (hereafter 'GB test data' for brevity). To ensure that the parameter space occupied by the two test regions were within and beyond model fitting parameter space respectively, a principal components analysis (PCA) was carried out on the three climatic variables (GDD5, MTCO, APET) from across all areas. Using the R package 'ks' (Duong 2007) a multivariate kernel density estimate plot of the first two PCA axes with the data split by three groups (the entire training data set, the assessment region within parameter space and the assessment region beyond parameter space) was produced to assess visually the location of the different parameter spaces. These two test areas are used as proxies for situations when models are projected into novel areas within or beyond model fitting parameter space, both of which can arise when predicting changes under future climate change (Heikkinen *et al.* 2006). To assess model performance, there were, in total, 30 realisations (3 methods x 10 cross-validation data sets) of the spatial abundance for 181 species for both of the test datasets.

Assessment methods: Model performance was tested in two ways. First, I assessed whether the three SAC methods (no SAC, single iteration SAC, Gibbs sampling) could predict abundance estimates in the 50km UTM grid cells for the two test data sets. Cohen's weighted Kappa (Landis & Koch 1977) was used to compare predicted abundances across the 50 km cells against observed abundances for each of the 181 species. Second, by combining these grid cell estimates, I assessed how well the three methods predicted national-scale abundance estimates. Estimates were calculated for each of the 10 realisations of abundance, and for each of the three methods. A mean national abundance estimate was taken across the 10 abundance realisations for each of the three methods for each species. For the DE test data, estimates of combined national abundances from the models were compared with the combined estimates of national abundances from the EBCC atlas data. For the GB test data, the predicted mean national population sizes for the 181 species from the models were compared with estimates of the population sizes from the British Trust for Ornithology's (BTO) New Atlas of Breeding Birds in Britain and Ireland (Gibbons et al. 1993). To check for systematic bias between the recorded and modelled national estimates of abundance for the 181 species, a one-sample two-tailed t-test was used to test for a significant difference between the distribution of the log-transformed deviance and zero. This was repeated separately for each of the three methods and for the two test data sets.

5.4 Results

RF models, both with and without an SAC term, were fitted successfully to spatial abundance data from mainland Europe for 181 species of breeding birds. All models generally performed well with a mean AUC score of 0.96 (standard deviation (S.D.) ± 0.03) when tested on withheld data. However, the models fitted with an SAC term performed significantly better (mean= 0.97, S.D ± 0.03) than those without mean= 0.95, S.D. ± 0.03, Paired t-test: β= 0.02, t_{180} = 21.43, p-value < 0.01; Figure A9).

The first axis of the PCA of all European 50 km cells, based on the three climatic variables (GDD5, MTCO, APET) accounted for 83% of the variability, whilst the second axis accounted for 13% of the variability. The kernel density estimate plot (Figure 5.1) demonstrates that the parameter space occupied by the DE test data was firmly within that of the model training data set, whilst that occupied by the GB test data was significantly different.

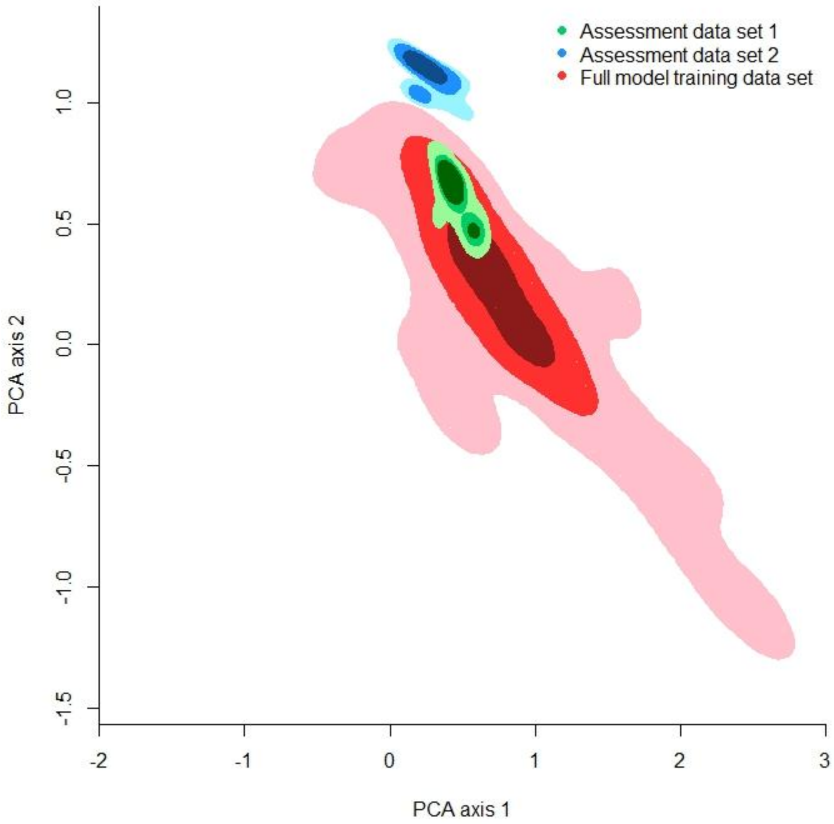


Figure 5.1: Multivariate kernel density plot of the first two axes from a PCA conducted on the three climatic variables (GDD5, MTCO, APET). Areas shaded red indicates points from the entire model training data set. Green shading indicates points from the first assessment data set, Germany, Denmark and the Netherlands, an area within model parameter space. Blue shading indicated points from the second assessment data set, Great Britain and Ireland, an area distinct from model parameter space. The intensity of shading indicates percentage contours, with the lightest shade for each colour showing the 50% contour, the medium shade the 75% contour and the darkest shade the 90% contour.

5.4.1 Comparison of abundance predictions

5.4.1.1 Abundance predictions at the cell level

Predictions of abundance in the 50 km UTM grid cells across the DE test data, were *fair* according to the mean weighted Cohen’s kappa score (Landis & Koch 1977) when calculated across all 181 species. Abundance predictions using the model without SAC, were the most accurate with a mean weighted Cohen’s kappa of 0.63 (S.D.± 0.23, Table 5.2, Figure A10a). Abundance predictions from the single iteration SAC model were significantly worse than the model without SAC (Table

5.2, Figure A10b). The abundance predictions from the Gibbs sampling models were significantly worse than those from both the models without SAC and the single iteration SAC models (Table 5.2, Figure A10c). The relative performance of the three methods in predicting abundance in 50 km cells was not consistent across the observed abundance categories. For the lower abundance categories, the predictions across the DE data set were significantly better using models with no SAC (ANOVA on logit transformed data, with species as an error term: $F_{2,346}= 8.62$, $p<0.01$, Figure 5.2a), whilst at higher abundance categories, abundance predictions were more accurate using single iteration SAC models (ANOVA on logit transformed data with species as an error term: $F_{2,112}= 4.15$, $p=0.02$, Figure 5.2a).

Table 5.2: Model assessment and comparison. Model performance was assessed for each species with Cohen's Weighted Kappa statistic, with a mean across all species and the standard deviation reported here. A repeated measures ANOVA was used to compare the predictive performance of the three methods across all species for each test data set separately**.**

			Method comparisons		
Test data	Method	Cohen's Weighted Kappa (Standard Deviation)	Without SAC	Single SAC iteration	Gibbs Sampling
DE Test Data results					
	Without SAC	0.63 (±0.23)	x	-	-
	Single SAC iteration	0.56 (±0.25)	z=-7.49, p<0.01	x	-
	Gibbs Sampling	0.46 (±0.26)	z=-18.40, p<0.01	z=-10.91, p<0.01	x
GB Test Data results					
	Without SAC	0.21 (±0.20)	x	-	-
	Single SAC iteration	0.22 (±0.22)	z=1.14, p=0.76	x	-
	Gibbs Sampling	0.20 (±0.22)	z=1.26, p=0.62	z=-2.40, p=0.05	x

Abundance predictions in 50 km cells across the GB data set, were slightly worse than those across the DE data set. However, unlike the findings for the DE data set, for the GB data set predictions from models with a single SAC iteration were the most precise (Table 5.2, Figure

A11b). Abundance predictions from the models without SAC, although slightly less precise, were not significantly different from the models with a single SAC iteration (Table 5.2, Figure A11a). The abundance predictions from Gibbs sampling were significantly worse than those from single iteration SAC models but no different from models without SAC (Table 5.2, Figure A11). Again, when tested on the GB data set, the relative performance of the three methods was not consistent across the observed abundance categories. Models with no SAC term produced significantly more accurate abundance predictions than the models including SAC, for the lower abundance categories (Figure 5.2b). For the higher abundance categories, however, models using Gibbs sampling produced the most accurate abundance predictions (Figure 5.2b).

5.4.1.2 National abundance predictions

For the DE data set, predictions of national abundance were most accurate using models with a single SAC iteration (R^2=0.88 for modelled versus recorded populations; Figure 5.3). Predictions using either no SAC or using Gibbs sampling were both, on average, slightly worse than the single iteration predictions (each with an R^2 of 0.86; Figure 5.3). For all three methods a high percentage of the mean predictions of national abundance were within one order of magnitude of the recorded national abundance (method one = 80.11%, method two = 81.03% and method three = 80.66%). All three methods showed significant negative bias in their deviance, although the extent of bias varied between methods. Bias was negative in all methods, with the largest bias in deviance shown by the method without SAC (t_{393}=-5.49, p<0.01, Figure 5.3d), and progressively smaller bias in the single step SAC method (t_{393}=-4.32, p<0.01, Figure 5.3e) and Gibbs sampling (t_{393}=-2.60, p=0.01, Figure 5.3f).

Predictions of national abundance in novel parameter space (the GB dataset) correlated marginally better with the recorded abundances when using no SAC (R^2= 0.48) than with single SAC predictions or Gibbs sampling (R^2= 0.47 and 0.46 respectively). Across all three methods, 56-57% of predicted abundances were within one order of magnitude of the recorded national abundances (57% model without SAC, 56% models with both a single SAC iteration and Gibbs sampling; Figure 5.4). As was the case with cell-based estimates, the degree of bias in deviance between predicted and recorded national abundances varied among methods. The model without SAC displayed significant negative bias in deviance (t_{355}=-2.99, p<0.01, Figure 5.4d), the model with a single SAC iteration had no significant bias (t_{355}=0.90, p=0.36, Figure 5.4e), and the model with Gibbs sampling showed significant positive bias (t_{355}=2.76, p=0.01, Figure 5.4f).

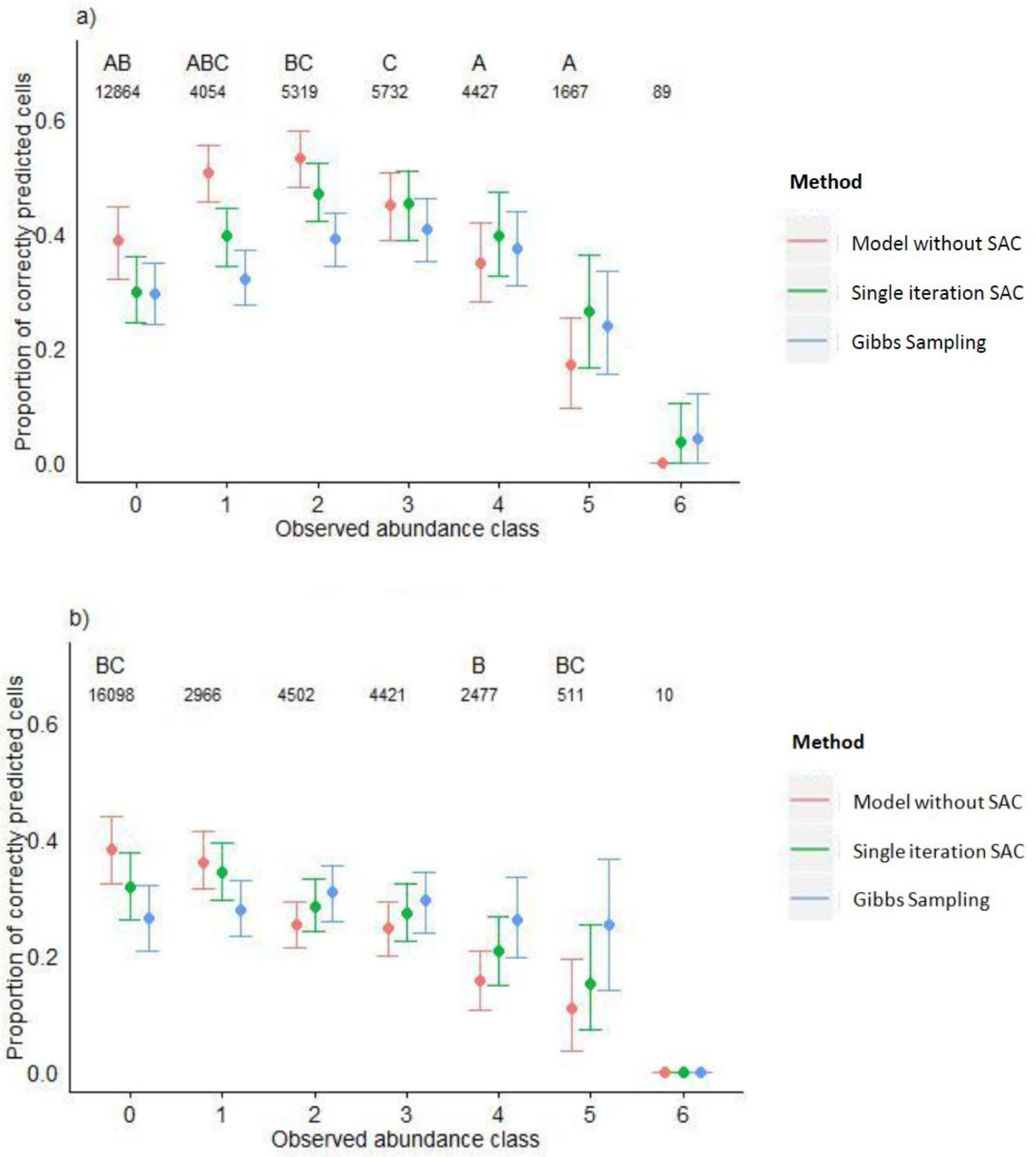


Figure 5.2: Proportion of correctly predicted cells across species between the three different methods, split by each observed abundance category. Part a) shows performance across the first test dataset, an area included within the model building arena, and b) shows performance across the second test dataset, an area beyond the model building arena. Dots represent the mean across all 181 species, whiskers showing the 95% bootstrapped confidence intervals around the means. Letters above the bars denote significant differences in the precision of predictions between methods as indicated by an ANOVA on logit transformed response with species as an error term ($p<0.05$); where A) indicates a significant difference between the precision of models without SAC and single iteration SAC, B), a significant difference between models without SAC and Gibbs sampling and C) a significant difference between single iteration SAC and Gibbs sampling. Numbers below the letters indicate the number of observed cells across all species with that observed abundance class within a data assessment area.

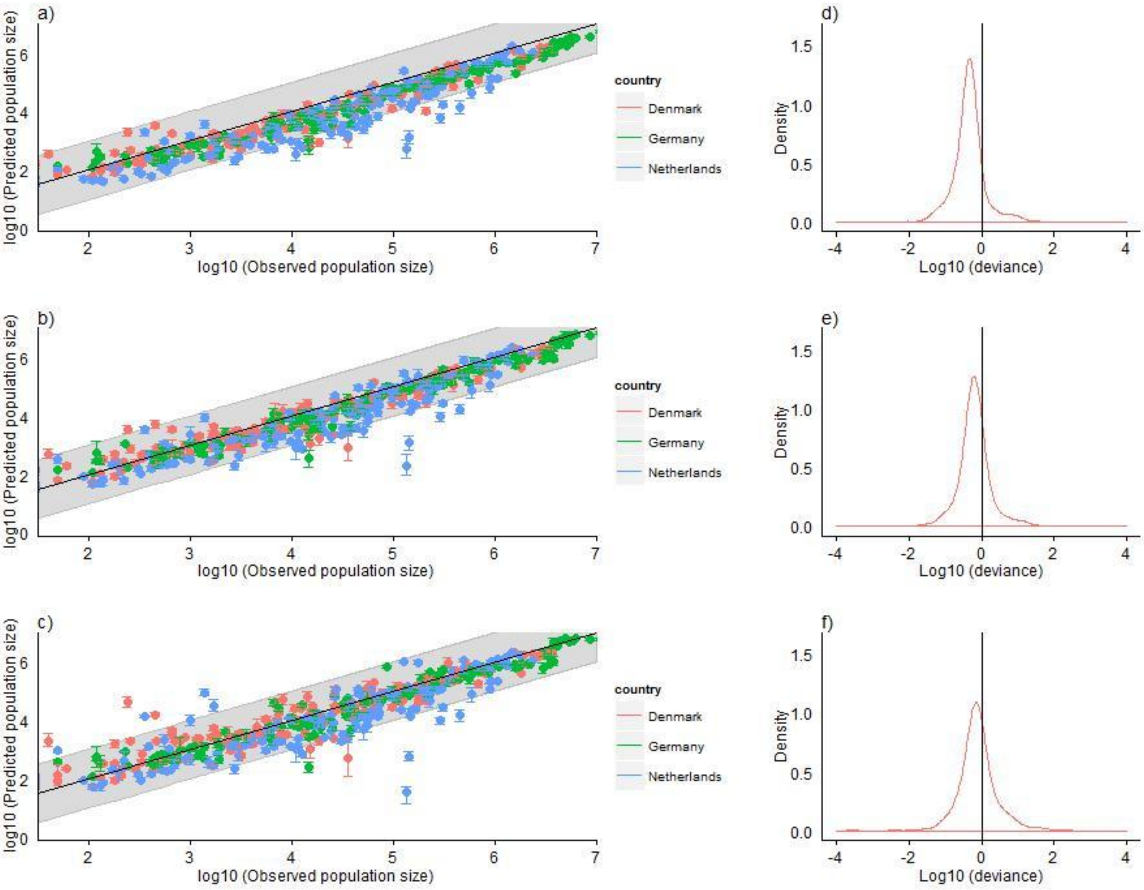


Figure 5.3: Predicted national population sizes for three countries included within the area of model calibration based on spatial abundance predictions from the three methods: a) model without SAC (R^2=0.86), b) single iteration SAC (R^2=0.88) and c) Gibbs sampling (R^2=0.86). Each point represents the mean predicted national population size against the observed national population size for one of the 181 species of interest for either Denmark (coloured red) Germany (coloured green) or The Netherlands (coloured blue). Error bars represent the standard deviations. The black line indicates a one to one relationship, while one order of magnitude from this relationship is indicated by the grey area. The density histograms show the distribution of the log scaled deviance between the observed and predicted total abundance from each of the three methods d) Model without SAC, e) single iteration SAC and f) Gibbs sampling.

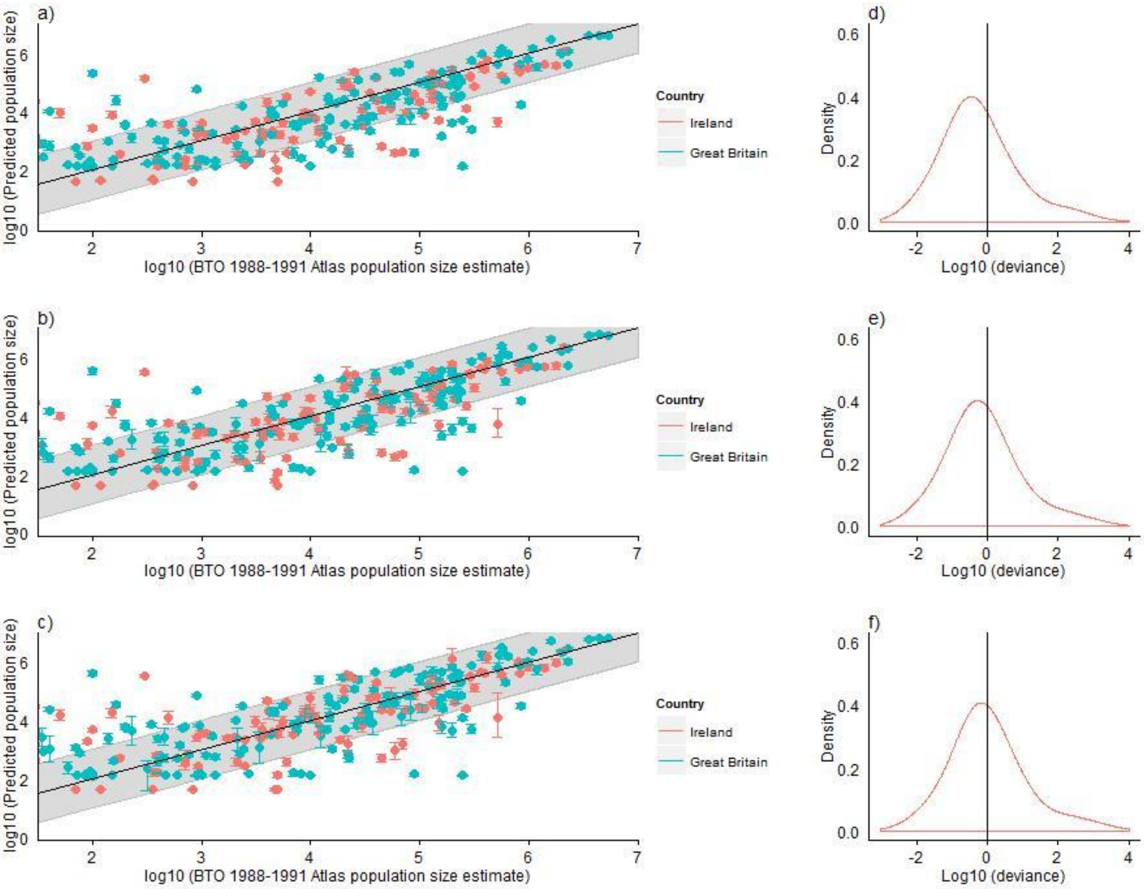


Figure 5.4: Predicted national population sizes for two countries excluded from the area of model calibration based on spatial abundance predictions from the three assessment stages: a) Model without SAC (R^2=0.45), b) Single iteration SAC (R^2=0.47) and c) Gibbs sampling (R^2=0.46). Each point represents the mean predicted national population size against the observed national population size for one of the 181 species of interest for either Ireland (coloured red) or Great Britain (coloured blue). Error bars represent the standard deviations. The black line indicates a one to one relationship, while one order of magnitude from this relationship is indicated by the grey area. The density histograms show the distribution of the log scaled deviance between the observed and predicted total abundance from each of the three methods d) Model without SAC, e) Single iteration SAC, and f) Gibbs sampling.

5.5 Discussion

SAC has been shown to explain much variation in species abundance (Chapter 3, Howard *et al.* 2015) but, until now, methods to incorporate SAC when predicting abundances into novel areas have been lacking. I have shown that, by accounting for unmeasured ecological factors such as dispersal, methods that include SAC terms can predict more precisely where species will be most abundant. In addition, I have shown that these methods can be used to make meaningful predictions of abundance beyond model building parameter space. Here, I discuss these finding in greater detail, and consider the potential for future application of these methods.

I have shown that significant improvements in the predictions of national abundance can be obtained from methods that incorporate SAC. These improvements do not increase precision but do reduce bias. The improvements in performance result from the greater accuracy that SAC-based methods demonstrate when predicting higher order abundance categories at the individual grid-cell level. Clearly, at broad spatial scales, environmental variables can be used to explain patterns in the relative quality of habitats, without necessarily accurately explaining the abundance of a species in a country (Vaz *et al.* 2008). It has been shown that areas where a species is abundant do not always coincide with those areas of highest environmental suitability (VanDerWal *et al.* 2009). This can occur in a number of circumstances. For instance, the buffer effect may result in unexpectedly high abundance in the surrounding areas despite low environmental suitability (Stephens *et al.* 2015). Models that utilise only environmental variables and that do not account for biotic factors such as dispersal could, in such situations, underestimate the abundance in adjacent, less suitable cells (Conlisk *et al.* 2012). Alternatively, species abundance may be dictated by abiotic factors not explicitly modelled, such as microclimate, but the effect of which can be reflected in the SAC term (Dormann 2007a). When environmental suitability is low, a large number of individuals cannot be supported in an area (VanDerWal *et al.* 2009); this is why the inclusion of an SAC term that accounts for the effects of unmeasured biotic factors does not improve the precision of the predictions of lower order abundance classes. It is the core areas of a species' range, where they occur at the highest abundance which are usually of highest priority for conservation (Gibson, Van der Marel & Starzomski 2009). Identifying these high density areas requires both areas of high environmental suitability to be determined and for the role of unmeasured ecological factors for determining the population size to be considered (VanDerWal *et al.* 2009).

Importantly, I have also shown that we can get meaningful predictions of species abundances in areas beyond the parameter space used to train models. The quality of these predictions is dependent upon the scale at which they are considered. Comparisons with an independent estimate indicated that accurate predictions of national scale estimates of abundance in areas beyond the model training parameter space can be made. In particular, estimates from the method using only a single SAC iteration performed well in terms of both precision and lack of bias. Finer scale predictions of abundance at a 50 km resolution from all three methods were less accurate. It is widely acknowledged that model extrapolation is a potential source of error in using species distribution and abundance models for predicting species' responses to future climates (Araújo & Guisan 2006; Heikkinen *et al.* 2006; Mair *et al.* 2014). The importance of a variable in determining the abundance of a species often varies throughout the species' range, a phenomenon referred to as spatial non-stationarity (Finley 2011; Jarzyna *et al.* 2014). By not fully modelling the environmental limits of a species, the complete range in spatial variations in species-environment relationships will not be fully captured (Elith, Kearney & Phillips 2010; Kissling *et al.* 2012; Wisz *et al.* 2013). Given that these models were being applied to conditions distinct from the parameter space of model training, it is unsurprising that they could not fully capture localised species-environment relationships and determine abundance at a fine scale (50 km resolution). Despite these reductions in fine scale predictive accuracy, the broad scale performances of these models, as indicated by their ability to predict national abundances, in conditions different to those of model calibration, are encouraging. Given that it is measures of population's size and trend that are most often used for determining the conservation status of a species (Mace *et al.* 2008), the ability to predict accurately, changes in the abundance of a species at a national scale, will allow those species whose conservation status may alter under projected climate change to be identified. Furthermore, demonstrating that these methods can provide meaningful predictions in a 'novel' region may serve to alleviate some of the concerns regarding model extrapolation. Conclusions drawn from a broad scale can be viewed with greater confidence, but detailed inference at a finer scale may be inappropriate.

When choosing an appropriate modelling technique, it is important to consider the practicality of applying a particular approach (Augustin, Mugglestone & Buckland 1996). Methods that incorporate SAC (the model with a single SAC iteration and the model incorporating Gibbs sampling), provide significantly better predictions both in terms of precision and reduced bias of national estimates of abundance, and hence should be favoured over the method that does not include SAC. However, the process of Gibbs sampling is computationally intensive relative to the other two methods. The method that accounts for SAC as well as the environmental variables not only provides better results than the method that does not account for SAC but also requires less computation than Gibbs sampling.

Here, I have demonstrated that methods that explicitly account for unmeasured ecological factors through the use of an SAC term can be used to predict the abundance of species in areas with no *a priori* information. Furthermore, I have demonstrated that these methods improve the precision of predictions where species occur at high abundance. Identifying those areas where species can occur at high abundance is important for efficient conservation strategies, as it is these populations that are the most likely to persist under climate change (Gibson, Van der Marel & Starzomski 2009). Importantly, by using known abundance distributions I have shown that meaningful predictions of abundance can be obtained outside of the model building arena. This is a significant finding, and should serve to alleviate those concerns regarding the utility of models in cases of model extrapolation (Araújo & Guisan 2006; Elith, Kearney & Phillips 2010; Mair *et al.* 2014) The capacity to quantify, with confidence, variations in a species' national population size in response to future climatic change can enable the timely implementation of conservation measures for those species most at risk from future climate change.

Chapter 6

The future for European birds: changes in abundance and communities

6.1 Abstract

The distributions and abundances of European birds are already responding to climate change but the expected extent and magnitude of these changes under projected climate is unknown. Furthermore, species' responses are highly variable in both their magnitude and rate. Independent species responses to climate change could result in changes in community compositions, competitive interactions and coexistence. Projections of future population sizes and the consequent composition of future communities will inform proactive conservation prioritisation and planning. Here, I predict the abundance distributions of 343 species of European breeding birds under current conditions and under future climate scenarios. I then use a multivariate approach to quantify the potential change in bird communities based on current and future species abundance models. Under future climate scenarios, I project that 55% of species will experience significant reductions in their total abundance within Europe through the present century, but only 7% of species will experience significant increases. Species in the north-east of Europe are projected to experience the greatest declines in abundance within Europe. Furthermore, I project substantial changes in the distribution of avian communities, with sizeable reductions in the distribution of northern and boreal communities and large increases in the area covered by continental and mediterranean communities. These results demonstrate the magnitude and variation in species responses to climate change, illustrating the complexity of assessing the future impacts of environmental change.

6.2 Introduction

It is increasingly important to understand the potential impacts of rapid global climate change for individual species, communities and ecosystems (Wiens et al. 2009; Lurgi, López & Montoya 2012). Species often demonstrate individualistic responses to environmental change due to ecological attributes such as dispersal capabilities, abiotic tolerances, and inter-specific interactions (Guisan & Thuiller 2005; Wisz et al. 2013). This individuality of responses may lead to changes in the structure and composition of the community in an area (Kampichler *et al.* 2012). New combinations of species will result in new species interactions, which may alter community dynamics (Stralberg et al. 2009). Species often have complex antagonistic and mutualistic relationships, with their fates ultimately dependent upon each other (Kissling & Schleuning 2015). Changes in the co-occurrence of species may alter species distributions in ways that cannot be predicted by simple distribution modelling (Stralberg et al. 2009). There is a need to identify sites at which substantial changes in community composition are likely to occur, and species which are most at threat not only from the direct pressures of climatic change, but from the indirect threats resulting from the changes in community composition.

Species distribution models (SDMs) can be used to project future range responses to climatic change (Elith *et al.* 2006). However, determining the conservation status and the priority for action of a species often relies upon assessing population sizes and trends (Gregory et al. 2005). Population trends are the strongest correlate of species' extinction risk (O'Grady *et al.* 2004), and significant reductions in a species' population size often occur prior to reductions in range size (Chamberlain & Fuller 2001). By modelling future abundance, potential changes in the conservation status of a species can be better assessed, enabling the identification of species at greater risk from future climatic change (Pereira *et al.* 2010; Dawson *et al.* 2011; Bellard *et al.* 2012; Renwick *et al.* 2012; Mair *et al.* 2014). Modelling abundance, rather than distribution, provides a more comprehensive understanding of community structure. Species abundances are very variable within and among communities (Gaston & Blackburn 2008), and mathematical evaluations of community types, and community changes, require data on species abundances (Magurran 1988). However, despite the wide application of SDMs and some understanding of the potential changes in species distributions in response to climatic change (Huntley *et al.* 2008; Barbet-Massin, Thuiller & Jiguet 2012), current projections of future species abundance are limited to a few species at local or national scales (Renwick *et al.* 2012; Johnston *et al.* 2013). Information on likely large scale future population changes is useful for conservation planning and prioritisation (Johnston *et al.* 2015). Furthermore, if the multi-species impacts of climate change are to be identified, changes in the abundances of species that co-occur must be considered (Stralberg et al. 2009). Traditionally, studies of the responses of communities to climatic change have investigated change in composition through species turnover metrics (Bakkenes *et al.* 2002; Thuiller *et al.* 2005; Bagchi *et al.* 2013; Baker *et al.* 2015). Yet these measures do not reflect the extent to which the changes in species composition may reflect a broad scale shift in community composition. Under future climate change, an area may be occupied by a entirely different avifaunal community, which, through changes in species interactions, energy transfer and storage may have significant impacts on the wider provision of ecosystem services (Gaston & Fuller 2008; Whelan, Wenny & Marquis 2008; Wenny *et al.* 2011).

Here, I explore how the abundances of a large number of species are projected to change at a continental scale under future climatic change. I investigate to what extent expected changes in spatial patterns of abundance will result in broad scale community shifts across Europe. First, I model and test the abundance distributions of 343 species of breeding birds across Europe using contemporary data. I then use these models to predict the abundance distributions of species under projected future climate change. I also examine the relationship between species ecological traits and projected future changes in abundance, to identify whether there are traits that indicate the susceptibility of species to climatic change. Finally, I classify the current broad scale avian communities present throughout Europe and determine to what extent these will change with future projections of species' abundance distributions. By comparing the present and future distributions of these broad scale communities, we can identify those areas that will experience the greatest changes in species assemblages.

6.3 Methods

6.3.1 Species data

Species data are as described in Chapter 2, however, two additional species were excluded due to model building limitations. The remaining 343 species will be used in all subsequent analyses in this chapter.

6.3.2 Bioclimatic data

Current conditions: Mean monthly temperature and precipitation data were obtained from Worldclim (Hijmans *et al.* 2005, http://www.worldclim.org/) for the period 1950-2000, a period corresponding to that over which the EBCC bird abundance data were collected. Data were obtained at a 2.5' resolution. This fine scale grid was overlaid with the same 50 x 50 km UTM grid for which the species abundance data occurred at. For each UTM grid cell the mean of all included Worldclim grid cells for each climate variable was calculated. These climate data were used to calculate four bioclimate values for each UTM grid cell: mean temperature of the coldest month; growing degree days above 5°; annual precipitation and precipitation seasonality. Through both direct and indirect effects on vegetation, prey, predators, competition or diseases (Gregory *et al.* 2009), these variables can limit species ranges and populations. Previously, these variables have been widely and successfully used in models to describe both the range extents (Beale, Lennon & Gimona 2008; Oliver *et al.* 2012; Bahn & McGill 2013; Barbet-Massin & Jetz 2014) and abundance patterns of European birds (Green *et al.* 2008; Gregory *et al.* 2009; Howard *et al.* 2014).

Future conditions: Predictions of species abundance were made for two time periods (2041-2060 and 2061-2080, hereafter referred to as 2050 and 2070) using data from climate projections from three general circulation models (GCMs) for four representative concentration pathways (RCPs). The four RCPs were developed to represent the full plausible range of anthropogenic greenhouse gas emission scenarios (Stocker, Dahe & Plattner 2013). Global temperatures are simulated to increase the most by the 2100 under the RCP8.5 scenario (3.7°C increase), followed by RCP6.0 (2.2°C increase), RCP4.5 (1.8°C increase) and RCP2.6 (1.0°C). The three GCMs (CCSM4, HADGEM2-ES,MIROC-ESM-CHEM) were selected to represent the range in projected climates in the Fifth IPCC Assessment report (Stocker, Dahe & Plattner 2013) and have all been shown to perform well across Europe (Brands *et al.* 2013; Perez *et al.* 2014). Projections of mean future climate at a 2.5’ resolution were obtained from Worldclim (Hijmans *et al.* 2005, http://www.worldclim.org/) for each of the 24 future climate scenarios: two time periods (2050 and 2070), three GCMs (CCSM4, HADGEM2-ES, MIROC-ESM-CHEM), four RCPs (RCP2.6, RCP4.5, RCP6.0 and RCP8.5). These climate projections were used to calculate values for the four bioclimate values (described above) for each of the UTM grid cells for each of the 24 future scenarios.

6.3.4 Land use data

Current land use data are as described in Chapter 2. Ideally, species abundance predictions would utilise future projections of land use. Such projections, however, are linked not only to forecasts of changing anthropogenic activity but also to projected climate. Such land use data are currently unavailable for the future climate scenarios used here. Furthermore, habitats are expected to change at a much slower rate than climate, with projections rarely showing any spatial trends at a large spatial scale (Barbet-Massin, Thuiller & Jiguet 2012; Martin *et al.* 2013). Therefore, when predicting future species abundances, I assume that coarse-scale land uses will remain unchanged during the current century.

6.3.5 Species abundance modelling

Using the procedure to model and predict spatial abundance using only a single iteration of SAC outlined in Chapter 5, I modelled and predicted the abundance of the 343 species for each UTM grid cell. Predictions of abundance were made for the recent time period (1950-2000) and for each of the 24 combinations of future climate scenarios (two time periods x three GCMs x four RCPs). This provided estimates of both recent and future abundance for all UTM grid cells, including those areas with only qualitative estimates of recent abundance in the EBCC atlas, allowing a full comparison with future predictions. Hereafter, projections made to the recent time period (1950-2000) will be referred to as present data predictions.

Model performance was assessed using both AUC and Cohen's weighted Kappa (Landis & Koch 1977). In contrast to AUC, Cohen's weighted Kappa does not weight all errors equally (Lobo, Jimenez-Valverde & Real 2008) with the greatest weight applied to the most incorrect classification. This provides a fairer assessment of the performance of a model when predicting ordinal data, as is done here (Ben-David 2008). The ability of the models to correctly predict recent abundance was assessed by comparing predicted abundance across the UTM grid cells against recorded quantitative abundance for each of the 343 species (Hagemeijer & Blair 1997).

6.3.6 Assessing effects on individual species

European-wide estimates of total population sizes were calculated for each of the 343 species by combining the median estimate of abundance from across the ten models for each UTM grid cell across Europe. This was done for both recent estimates (for the period 1950-2000) and separately for each of the 12 climate projections for both 2050 and 2070. By comparing the future estimates of total abundance with recent estimates, the proportional effect of future climate change on the total abundance of individual species could be evaluated.

To test for relationships between species' specific traits and the effect of climatic change on their total European abundance, I used a phylogenetic generalised least squares (PGLS) approach (Freckleton, Harvey & Pagel 2002; Freckleton 2009) and model selection. Species traits were taken from BirdLife International and NatureServe (2012) and included mean body mass, generation length, primary habitat association, migratory strategy and mean and maximum natal dispersal distances. European range size, a measure of the geographic scale over which the drivers of abundance operate, was also included, calculated as the proportion of UTM grid cells that were occupied (from Hagemeijer & Blair 1997). The mean latitude and longitude of each species range were also included as range traits. I used a phylogeny based on a consensus tree derived from 5000 trees sub-sampled from the global phylogeny of Jetz *et al.* (2012). For all subsets of the global model, I compared the Akaike information criterion (AIC) corrected for small sample size (AICc), selecting all models within six ΔAICc of the best performing model. To avoid selecting overly complex models, all models with a better-performing simpler nested model were disregarded (Richards 2008). Diagnostic plots were examined for the final model to check for heteroscedasticity, non-normal errors and outliers. Phylogenetic analyses were carried out in the 'caper' package in R (Orme *et al.* 2012; R Development Core Team 2012).

I also investigated spatial variations in the percentage change from the present day to the future in the total number of individuals, of all species, occurring in a cell. For both 2050 and 2070 the median projected number of individuals from across the 12 climate projections (3 GCMs x 4 RCPs) were taken for all species present within a UTM grid cell. I then calculated the percentage change in the total abundance of all species in a cell between present day predictions and the future estimate for both 2050 and 2070. To test for spatial variation in the percentage change in the total abundance of species, an ordinary least squares regression (OLS) was used to examine the relationship between the percentage change in the total abundance of all species in a UTM grid cell between current conditions and both 2050 and 2070, against the latitude and longitude of that cell.

6.3.7 Species turnover

To characterise geographic patterns of changes in community composition, species turnover within each UTM grid cell over time was calculated. For each cell we calculated the Bray-Curtis dissimilarity metric (Bray & Curtis 1957) between the current and all potential future community compositions, based on the predicted abundance for all species simulated to occur within that cell. To test for spatial variation in species turnover, an OLS regression was again used to examine the relationship between the Bray-Curtis dissimilarity metric of a UTM grid cell against the latitude and longitude of that cell.

6.3.8 Community composition analysis

The median current day prediction of species abundance for all 343 species across Europe was used to group cells into communities. For each pair of UTM grid cells the Bray-Curtis dissimilarity metric was calculated based on the current predicted abundance of all species occurring with the cell. Communities were defined using a hierarchical agglomerative cluster analysis, whereby the Bray-Curtis dissimilarity matrix was used to group current cells. Cells were grouped into 10 different communities to represent broad scale species assemblages and ecological sub-regions (Stralberg *et al.* 2009). For each UTM grid cell, for each of the 12 projected climate scenarios (three GCMs x four RCP) for both the 2050 and 2070 projections, I identified the modern day cell with the most similar community according to the Bray-Curtis dissimilarity metric. The community of the future day cell was then classified by the community classification of the most similar present day cell. These community analyses were carried out using the ’vegan’ package in R (R Development Core Team 2012; Oksanen *et al.* 2015).

6.4 Results

6.4.1 Model Evaluation

RF models (with the SAC term) of the abundance of the 343 species of European breeding birds generally performed well: the ten models fitted for each species had a mean AUC across all species of 0.96 (S.D.±0.04). An AUC of >0.9 reflects a model with good discrimination, whilst a model with an AUC of >0.7 has useful discrimination (Franklin 2010). The mean values of Cohen's weighted kappa across the ten models for each species indicated that the models fitted the observed abundance categories for the UTM grid cells well (Landis & Koch 1977): mean weighted Kappa was 0.75 (S.D.±0.15, Figure 6.1). Estimates of the total abundance of species across Europe showed close agreement with estimates based on the observed UTM grid cell abundance (R^2 = 0.92, Figure 6.2).

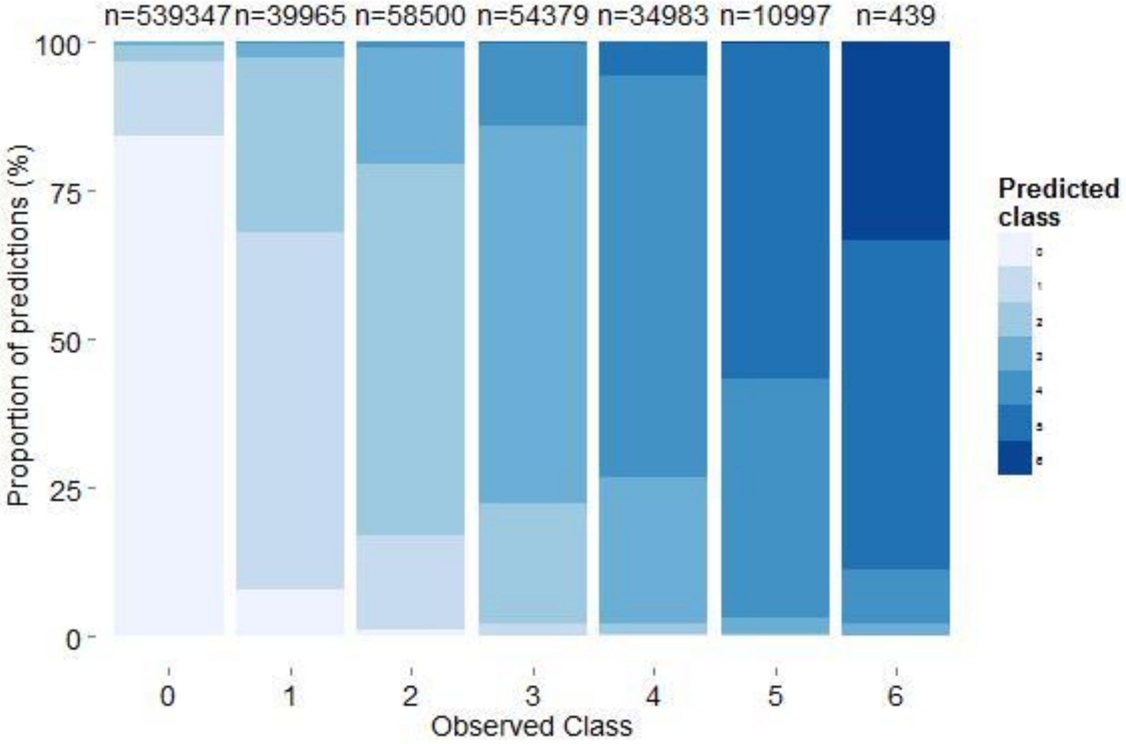


Figure 6.1: Current abundance predictions. Bars represent the mean proportion of predictions for each abundance class averaged across all 343 species. Performance was good with a mean weighted Cohen's Kappa score of 0.75 (S.D.±0.15; (Landis & Koch 1977)). N values indicate number of observed cells within each abundance class..

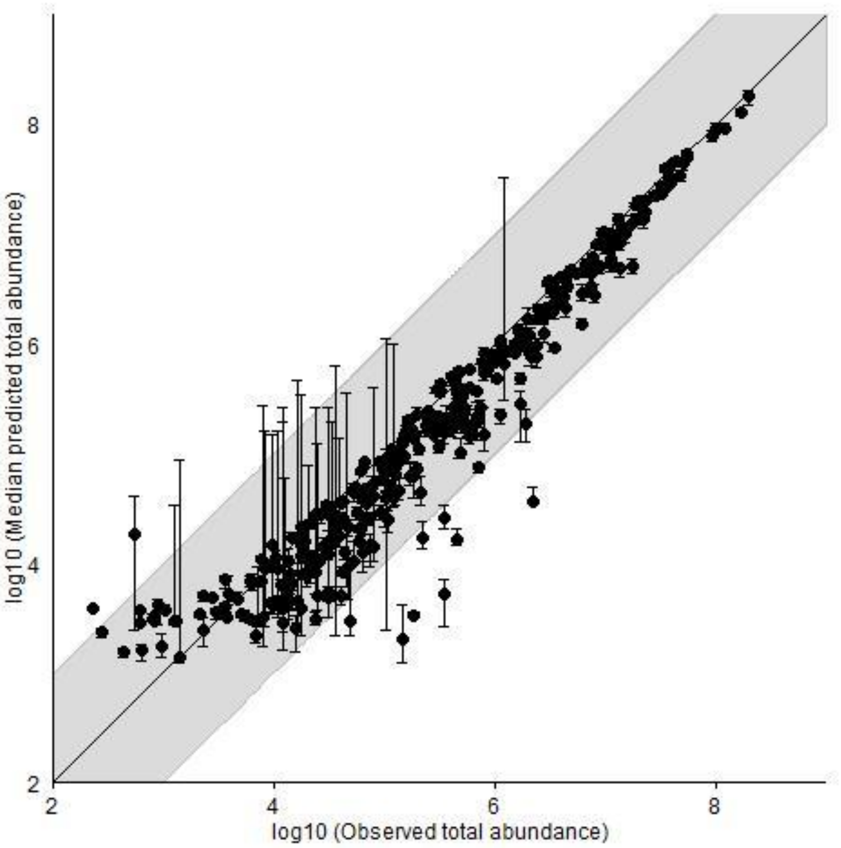


Figure 6.2: Median predictions of observed against predicted total current abundance for 343 species of breeding birds across their entire European range ($R^2 = 0.91$). Each point represents the predicted current median total abundance against the observed total abundance. Error bars represent the 95% quantiles. The black line indicates a one to one relationship, while one order of magnitude from this relationship is indicated by the grey area.

6.4.2 Individual Species

Models indicate that, by 2070, the majority of species (73% of the 343 species analysed) will experience some decline in their total European abundance (i.e. negative percentage growth in median projected abundance across all GCMs, RCPs and model iterations, from the present to 2070). Species' abundances were projected to decrease by 2070 by 32% on average. However, there was a large degree of variation among species, with population changes ranging from a 98% decline to a 118% increase (Figure 6.3). In addition to between species variation, there was also substantial variation for each species in relation to the different GCMs, RCPs and model iterations. Nonetheless, there was directional consensus in the change in total abundance (i.e. the 95% quantiles across all abundance predictions for a species did not overlap 0; filled portions of the bars on Figure 6.3) for 62% of species (212 of 343 spp.). Only 7% of species (25) were consistently projected to increase in abundance by 2070, whilst 55% (187) of species showed a consistent decline in abundance. This should result, on average, in a total decline of 1.08 billion birds by 2050, with a further loss of 320 million birds by 2070. This figure is projected to vary considerably between different RCP scenarios (Table 6.1), with the greatest reductions predicted for the most extreme climate scenario (RCP8.5).

Several species-specific traits are related to the likelihood of a change in abundance in future. The PGLS model of the role of traits on projected abundance changes retained four variables: mean latitude and longitude of the European range, current estimated European population size and a species' primary habitat association (Table 6.2). The model explained 49% of variation in the percentage changes in the total abundance of species. The mean latitude and longitude of a species' European range along with its current European population size were all negatively related to projected abundance change. By contrast, abundance was mostly unaffected by a species' primary habitat association, with the exception of species associated with boreal and temperate forests, for which total abundance declined significantly more than other species. This was true also, but less significantly (p=0.07), for species associated with montane grassland.

A plot of the percentage changes in the median projected total abundance of all species present within a UTM grid cell between both 2050 and 2070 and the present day, showed clear spatial patterns. Areas identified as demonstrating substantial increases in the number of individuals projected to occur within a cell in the future included parts of northern Scandinavia, mountainous regions across central and Eastern Europe and a large part of the Mediterranean (Figure 6.4). The OLS regression analysis of the percentage change in total abundance for a UTM grid cell and the latitude of that cell revealed a significant negative relationship for both 2050 ($F_{2811,1}$= 46.51, p<0.01, Figure 6.4a) and 2070 ($F_{2811,1}$= 195.1, p<0.01, Figure 6.4b). A significant negative relationship was also present between the percentage change in total abundance in a UTM grid cell and the longitude of that cell, for both 2050 and 2070 (2050: $F_{2811,1}$= 69.38, p<0.01, Figure 6.4a; 2070: $F_{2811,1}$=98.3, p<0.01, Figure 6.4b).

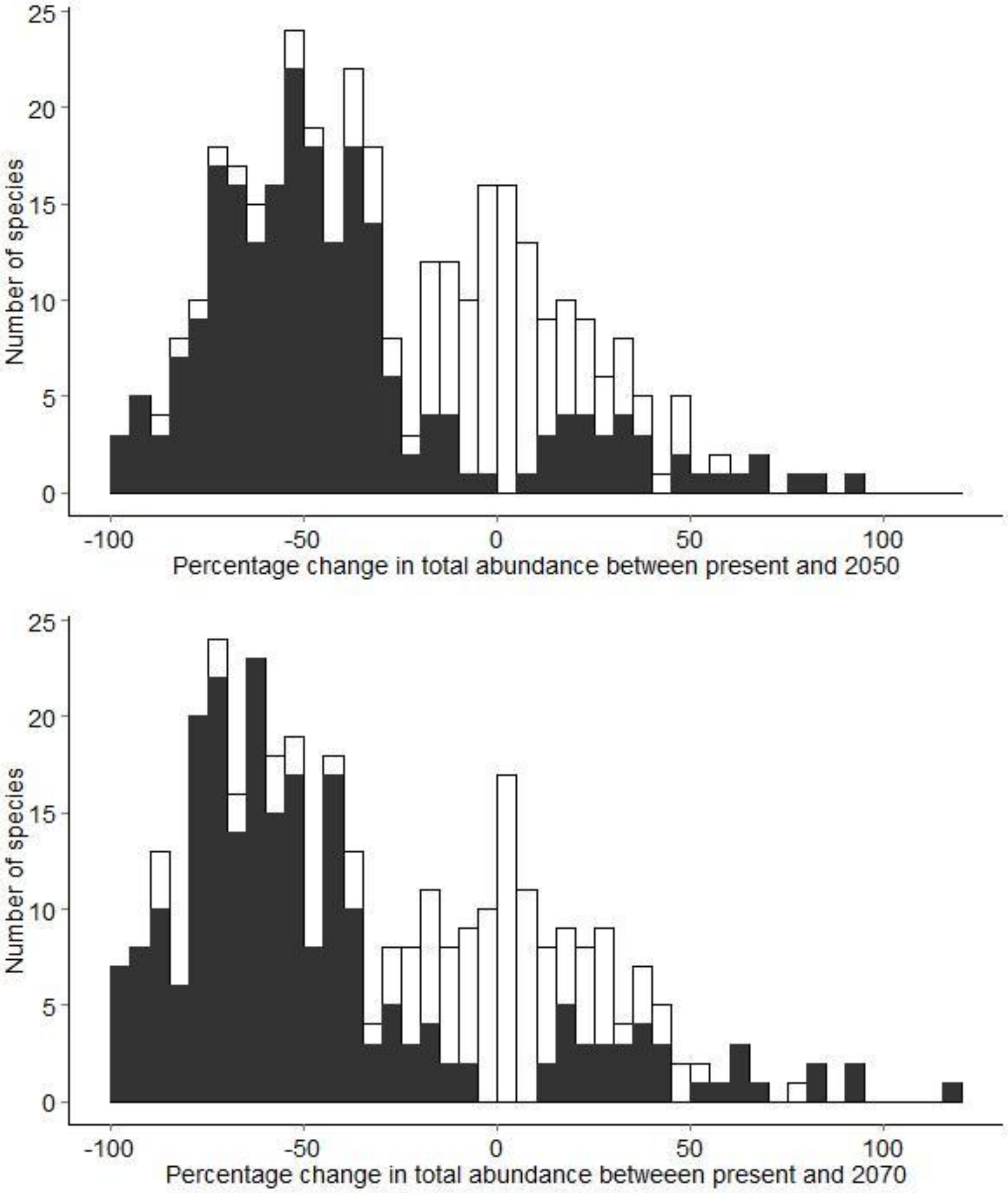


Figure 6.3: Projected impacts of climate change on the total abundance of 343 species of European breeding birds. The histograms represent the distribution of median change across all combinations of GCMs and RCPs in total abundance between current day and A) 2050 and B) 2070. The height of each bar is the number of species that show the percentage change in their total population as indicated by the x-axis. The filled portion of each bar represents the proportion of species that are likely to demonstrate the direction of change indicated (i.e. the 95% quantiles of the abundance projections across the model iterations, GCMs and RCPs did not overlap 0). The open portion of the bars represent those species for which the direction of change indicated was not significant.

Table 6.1: Total estimates of European population size (number of individuals) across all 343 species (with 95% quantiles) for present day, 2050, and 2070

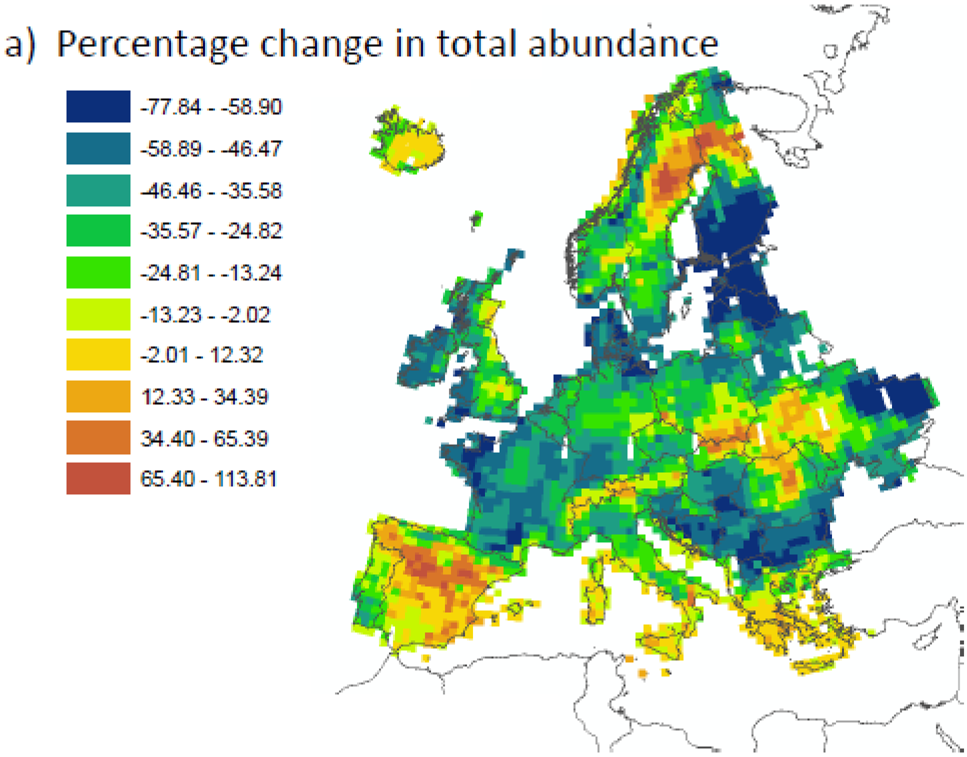
				Absolute change		Proportional change	
	Present	2050	2070	Present - 2050	Present - 2070	Present - 2050	Present - 2070
rcp2.6							
Median	3.16 x 10^9	2.24 x 10^9	2.19 x 10^9	-9.1 x 10^8	-5.10 x 10^7	-0.29	-0.31
Q02.5	2.88 x 10^9	1.50 x 10^9	1.49 x 10^9	-1.4 x 10^9	-8.00 x 10^6	-0.48	-0.48
Q97.5	3.50 x 10^9	3.16 x 10^9	3.18 x 10^9	-3.5 x 10^8	2.00 x 10^7	-0.1	-0.09
rcp4.5							
Median	3.16 x 10^9	2.06 x 10^9	1.91 x 10^9	-1.10 x 10^9	-1.50 x 10^8	-0.35	-0.4
Q02.5	2.88 x 10^9	1.38 x 10^9	1.28 x 10^9	-1.50 x 10^9	-9.90 x 10^7	-0.52	-0.56
Q97.5	3.50 x 10^9	3.03 x 10^9	2.94 x 10^9	-4.8 x 10^8	-8.60 x 10^7	-0.14	-0.16
rcp6.0							
Median	3.16 x 10^9	2.13 x 10^9	1.77 x 10^9	-1.00 x 10^9	-3.60 x 10^8	-0.33	-0.44
Q02.5	2.88 x 10^9	1.41 x 10^9	1.16 x 10^9	-1.50 x 10^9	-2.60 x 10^8	-0.51	-0.6
Q97.5	3.50 x 10^9	3.09 x 10^9	2.91 x 10^9	-4.1+08	-1.80 x 10^8	-0.12	-0.17
rcp8.5							
Median	3.16 x 10^9	1.81 x 10^9	1.42 x 10^9	-1.30 x 10^9	-3.80 x 10^8	-0.43	-0.55
Q02.5	2.88 x 10^9	1.16 x 10^9	8.9 x 10^8	-1.70 x 10^9	-2.70 x 10^8	-0.6	-0.69
Q97.5	3.50 x 10^9	2.82 x 10^9	2.55 x 10^9	-6.8 x 10^8	-2.70 x 10^8	-0.19	-0.27

Table 6.2: Species traits and the abundance responses to future climate change. Estimated coefficients from AIC selected phylogenetically corrected GLS regression models of the proportional change in total abundance between the current day and 2070. P-values significant at the 5% levels are shown in bold.

	Effect size	S.E.	t-value	p
Intercept (habitat generalists)	195.54	27.44	7.13	<0.01
Primary habitat association:				
1. Coastal	-8.69	8.39	-1.04	0.30
2. Inland wetland	-0.06	5.07	-0.01	0.99
3. Tundra, mires and moorland	7.06	7.87	0.90	0.37
4. Boreal and temperate forest	-25.48	5.84	-4.36	**<0.01**
5. Mediterranean	17.75	10.86	1.64	0.10
6. Agriculture and grassland	-0.34	5.20	-0.07	0.95
7. Montane grassland	-23.07	12.51	-1.84	0.07
Mean longitude of European range	-0.90	0.25	-3.62	**<0.01**
Mean latitude of European range	-3.44	0.35	-9.85	**<0.01**
Current European population size	-5.68	2.00	-2.84	**<0.01**

Lambda = 0.98. Residual standard error: 10.92 on 248 degrees of freedom.

Adjusted R-squared = 0.49.



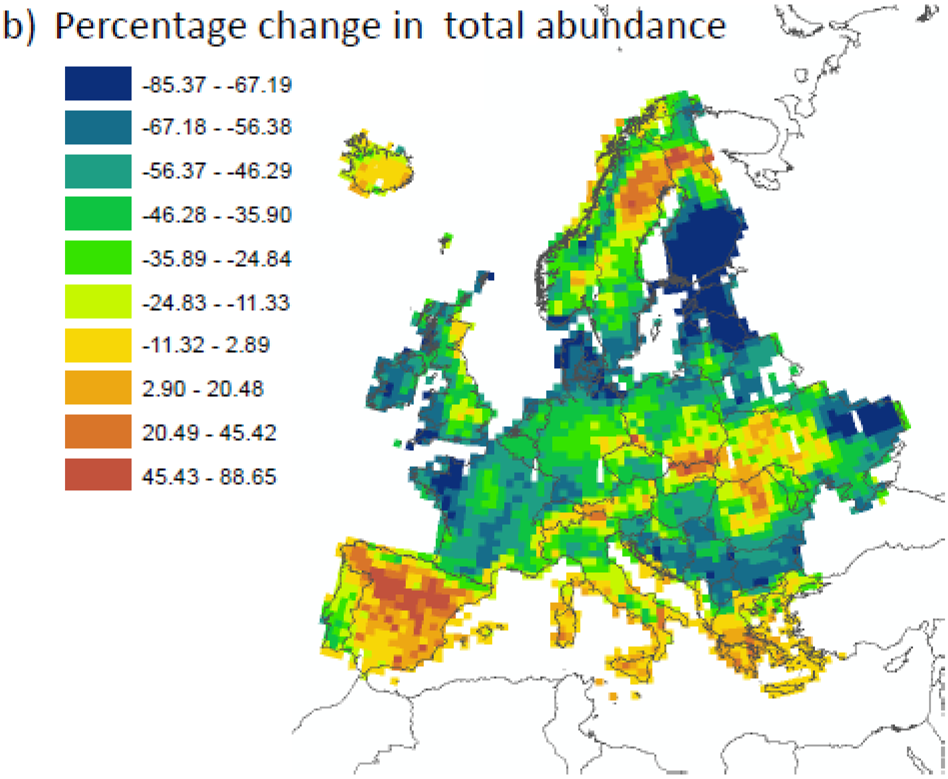


Figure 6.4: Percentage change in the total abundance of all species present in a UTM grid cell between current day abundance estimates and the median projection of abundance across all combinations of GCMs and RCPs for a) 2050 and b) 2070.

6.4.3 Species turnover

The degree of species turnover projected between the present day and 2070 is significantly greater than between 2050 and the present day (t_{2812}=-82.48 p<0.01). Furthermore, there are clear spatial patterns in the degree of species turnover across Europe (Figure 6.5). A regression analysis of the Bray-Curtis dissimilarity metric for a UTM grid cell and the latitude of that cell revealed a significant positive relationship for both 2050 ($F_{2811,1}$= 1085, p<0.01, Figure 6.5a) and 2070 ($F_{2811,1}$= 1587, p<0.01, Figure 6.5b). A significant positive relationship was also present between the Bray-Curtis dissimilarity metric of a UTM grid cell and the longitude of that cell, for dissimilarity to both 2050 and 2070 (2050: $F_{2811,1}$= 283.5, p<0.01, Figure 6.5a; 2070: $F_{2811,1}$= 236.1, p<0.01, Figure 6.5b). This indicates that species turnover will occur at a greater rate in the northern and eastern regions of Europe, with a band of highest turnover running across England, Denmark and the Baltic states (Estonia, Latvia, Lithuania).There is also a clear pattern of reduced turnover projected in regions bordering the northern Atlantic (Ireland, Scotland, Iceland and coastal Norway).

6.4.4 Community composition

Ten community groups were identified from the median present day estimates of species abundance across Europe (Figure 6.6a). The most widely distributed community for present day conditions, occupying 30% of Europe, which I termed sub-continental nemoral, covered most of central Europe and southern England. The next most extensive community was a mediterranean community followed by a boreal-nemoral grouping, occupying 18% and 13% of Europe respectively (Figure 6.6). Substantial changes in the extent of the area covered by these various communities were projected under the different climate scenarios. The results presented are for the HADGEM2-ES GCM and RCP6.0 climate scenario which is considered a “middle of the road scenario”; however, the geographic pattern in these community changes was consistent between the three GCMs and four RCPs. In particular, the area of Europe predicted to be occupied by a continental-nemoral community was predicted to increase in extent by 87% between the present day and 2050 and by 100% between the present day and 2070. The extent of mediterranean communities was also predicted to increase substantially from the present day, with a 35% increase by 2050 and a 78% increase by 2070. Conversely the area covered by some communities was projected to decrease considerably. Northern-boreal communities, for example, were projected to decrease in the amount of Europe that they occupy by 66% and 79% between the present day and 2050 and 2070, respectively. The other notable reduction in the area covered by a community was for boreal-nemoral communities, with reductions in the area occupied between the present day and 2050 and 2070 of 64% and 75% respectively (Figure 6.6).

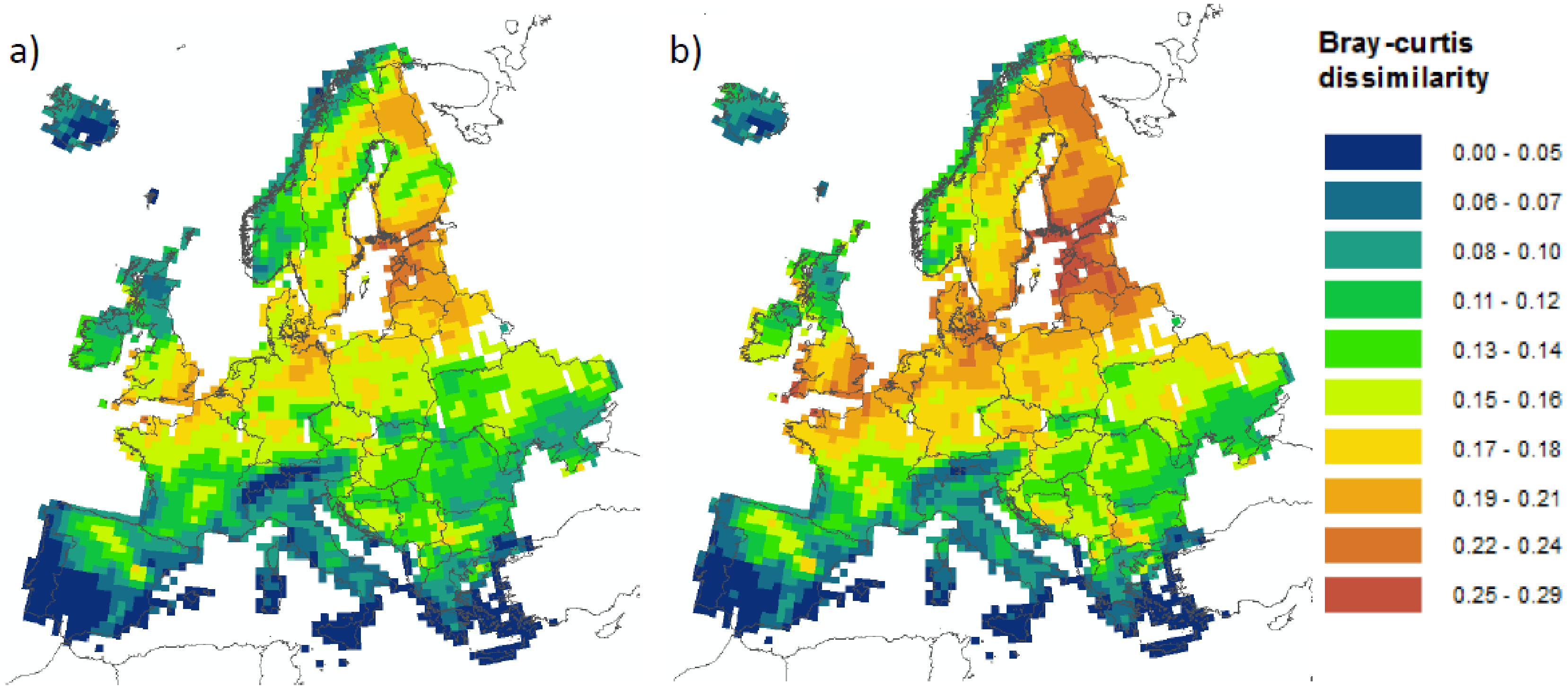


Figure 6.5: Predicted species turnover based on mean predicted species abundance distributions from all climate models. Species turnover was calculated as the Bray-Curtis (BC) dissimilarity between current avian communities and projected bird communities in a) 2050 and b) 2070.

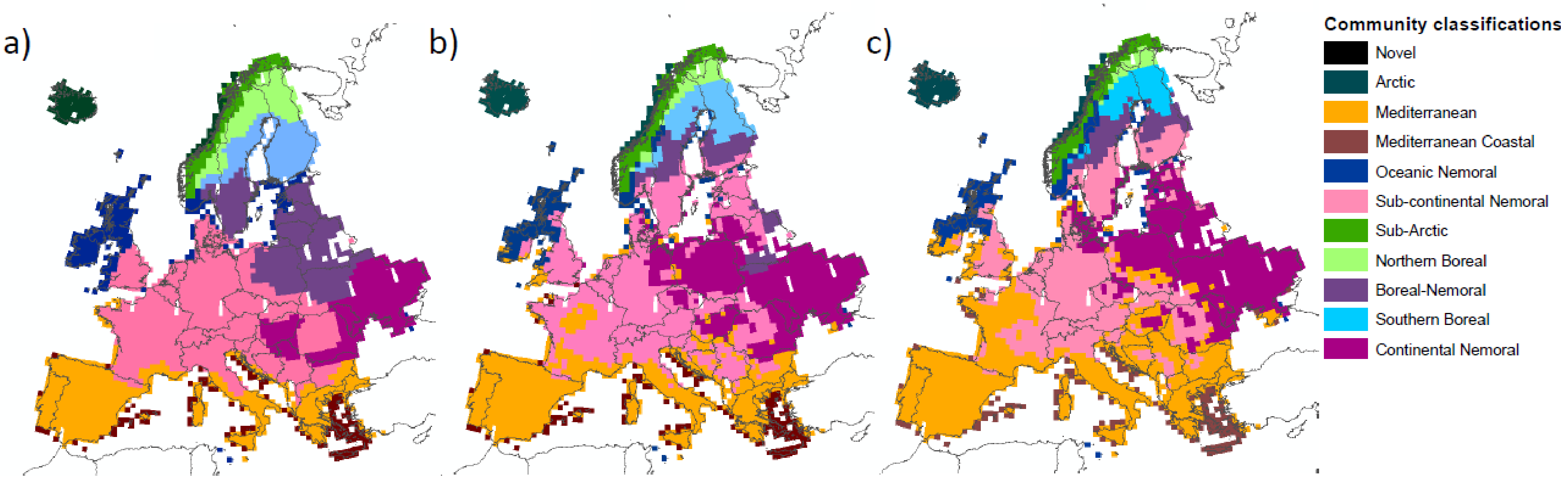


Figure 6.6: Changes in broad scale community classification. a. represents current community classifications, b. community classifications in 2050 and c. community classifications in 2070. Current community classifications are based on those groups identified during the hierarchical clustering analysis for 10 community groups across Europe. Future community classification for each grid cell is based on the classification of the most similar current grid cell according to Bray-Curtis. Predictions of future communities are based on mid-range projections from the HADGEM2-ES GCM and RCP6.0. Classification names for community types are based broadly on the community names used by Huntley *et al.* (2007). However, this naming does not necessarily imply any similarity in terms of either the species composition or diagnostic species (as results are based on abundance data, and a different classification approach, whereas Huntley et al. used only presence-absence data).

6.5 Discussion

The populations of European birds are declining at an alarming rate (Inger *et al.* 2014). However, until now, estimates of the potential impacts of projected climatic change on species abundance have been lacking. Here, and for the first time, I have projected the abundance of a large number of species across Europe. Furthermore, the potential implications of climate change have been quantified for both individual species and for community composition. I have shown that European birds are likely to experience precipitous declines in their populations over the coming century. Worryingly, we estimate that, by 2070, there will be 1.4 billion fewer birds in European, which equates to a 40% reduction in avian abundance. However, we have also shown substantial differences in the potential responses of different species to changes in the climate. Over half the species analysed (55%) are projected to be extremely likely to decline significantly in abundance across Europe by 2070, whilst only 7% of species were extremely likely to show significant increases in abundance over the same period. Here, we discuss how these results compare with previous studies and the potential future impacts of climate change on European birds in light of three key findings: (1) expected impacts of climate change on species; (2) expected spatial variations in species turnover; and (3) expected large scale shifts in community composition.

6.5.1 Expected impacts on individual species

In addition to the estimates of changes in total avian abundance, these projected population trends were linked to a range of ecological characteristics. In particular, those species that are more abundant at present are projected to suffer greater population declines than rare species. This finding is consistent with those of Inger *et al.* (2014). They found that more common species declined at a faster rate than less abundant species between 1980 and 2009, a pattern that according to the results presented here, will not change with future climate change. Inger *et al.* (2014) postulated that the potential cause of this trend is the differences in conservation practices targeted towards rare and common species. As conservation management tends to focus on increasing the numbers of rare species, management often operates at local scales, through the establishment of protected areas. This may have mitigated the impacts of observed climate change on rare species, but has offered little protection for more common species (Hoffmann *et al.* 2010). However, the demonstration that under projected climate change the proportional abundance of more common species will continue to decline to a greater extent than rarer species, suggests that more common species are more vulnerable to the effects of climate change. As more abundant species are typically more widespread, their numbers are linked to habitat quality at a wider landscape scale, rendering them more vulnerable to the effects of widespread climate change (Gaston & Fuller 2008). A substantial body of evidence demonstrates the significance of common birds for the delivery of ecosystem services, such as decomposition, seed dispersal, pollination and pest control (Gaston & Fuller 2008; Whelan, Wenny & Marquis 2008; Wenny *et al.* 2011) . The decline of more common birds may have serious knock-on effects on ecosystem structure and function (Inger *et al.* 2014).

Changes in abundance are also related to a species' primary habitat association. In particular, we project significant declines in the abundances of boreal and montane species, and substantial increases in the abundances of Mediterranean species. The environmental requirements of Mediterranean species reflect conditions towards the warmer end of the temperature gradient across Europe. As temperatures across Europe increase, a greater breadth of potential niches for these species will become available, resulting in population gains. Furthermore, conditions across southern Europe will likely more resemble those of North Africa (IPCC 2014). Given the ranges of many of these Mediterranean species extend into North Africa; climate suitability across southern Europe will likely further improve for these species, increasing their abundance. Conversely, the requirements of boreal and montane species reflect conditions at the colder end of the temperature gradient across Europe. As temperatures increase, the availability and suitability of current habitats for these species will be reduced, and the breadth of potential niches will narrow within Europe (Virkkala *et al.* 2008). Changes in the availability and suitability of potential niches at high and low latitudes may serve to explain the significant negative relationship between latitude and changes in abundance.

Substantial increases are projected in the number of individuals occurring in mountainous regions and some parts of Scandinavia and the Mediterranean. Interestingly, and as reported in the general introduction (section 1.3.1), these are also the areas where observed temperature changes have been greatest (Haylock *et al.* 2008). Furthermore, in comparison to other areas of Europe, these areas are all projected to experience greater than average temperature increases under projected climate change (IPCC 2014). Warming at high latitudes and elevations will increase the suitability of an area for those species previously restricted to lower latitudes and altitudes, aiding colonisation (Walther *et al.* 2002). Altitudinal and latitudinal shifts in species distributions have been widely reported (Hickling *et al.* 2006; Devictor *et al.* 2008; Zuckerberg, Woods & Porter 2009; Chen *et al.* 2011; Virkkala *et al.* 2014), along with increases in species richness in cool-temperate regions (Pauli, Gottfried & Grabherr 1996; Menendez *et al.* 2006; Walther 2010). Yet, this latitudinal gradient in changing abundance has never before been projected for a large number of species at a continental scale. Changes in the total abundance of individuals in an area will likely have impacts on the structure and function of an ecosystem, such as by changing the flux of energy and materials through an ecosystem (Chapin III *et al.* 2000; Inger *et al.* 2014).

6.5.2 Spatial variation in species turnover

Significant spatial variations in species turnover indicate that the extent of change in community composition observed throughout Europe over the next century will be geographically diverse, with the greatest changes in the north. As species track climate changes, previously more southerly species will be increasingly present in more northerly communities. The low level of species turnover across the southern regions of Europe is not what would be expected from some explanations for spatial variations in species turnover (Koleff, Lennon & Gaston 2003). In particular, it has been hypothesised that species turnover should increase at lower latitudes where species tend to have smaller ranges (Gaston *et al.* 2007). Areas of the Mediterranean are increasingly forecast to be colonised by more southerly species, such as those primarily associated with North Africa (Barbet-Massin, Thuiller & Jiguet 2010; Barbet-Massin, Thuiller & Jiguet 2012). These species, however, are not accounted for in this analysis and their encroachment into Europe will not be reflected in these measures of species turnover. This may artificially lower species turnover rates in the Mediterranean regions.

6.5.3 Shifts in broad scale community composition

Frequently, analyses of the impacts of climatic change on species highlight the potential for individualistic species responses to result in variations in community composition and structure (Walther *et al.* 2002; Stralberg *et al.* 2009; Walther 2010). Here, we have demonstrated that these individualistic responses can lead to community-wide changes in the species occupying an area. For instance, across large parts of central Europe and into southern England avian communities are predicted to switch from a sub-continental nemoral community to something more akin to a current mediterranean community. Similarly, large parts of Eastern Europe are predicted to switch from a boreal-nemoral community to a continental or sub-continental community by 2070. The consequences of avifaunal shifts of this magnitude and extent are poorly understood, but will include profound changes in ecosystem functioning and biodiversity (McCarty 2001; Walther 2010). As demonstrated here, the responses of organisms to climate warming are unlikely to be uniform, a trend likely to extend across trophic levels and communities (Voigt *et al.* 2003; Devictor *et al.* 2008). The ensuing mismatch in species interactions could further exacerbate population fluctuations, changing the importance of top-down and bottom-up effects, and modifying trophic cascades (Harrington, Woiwod & Sparks 1999; Lenoir *et al.* 2008; Hoekman 2010; Kratina *et al.* 2012). This, in turn, could result in further community instability and loss of biodiversity (Seifert *et al.* 2014). For example, temperature related community shifts have been observed in local populations of birds, reptiles and amphibians in the highland forests of Costa Rica. With temperature increases reducing the frequency of dry season mist, communities have shifted from ‘cloud forest’ to ‘premontane’ and many associated species including the endemic golden toad

(*Bufo periglenes)* have become locally extinct (Pounds, Fogden & Campbell 1999). Intertidal communities appear to be particularly susceptible to community wide shifts in response to oceanic warming. Invertebrate communities of the rocky intertidal zone show increasing replacement of species with those previously associated with lower latitudes (Barry & Baxter 1995). The associated changes in species abundances and interactions have had a cascade of indirect effects, altering the flow of resources through a system, impacting populations of predators and host species. Interestingly, here we found that coastal communities appear to be the most stable under projected climate change. Previously, we found that the abundances of these species are strongly determined by land use (Chapter 3, Howard *et al.* 2015), so may not be as strongly influenced by climate changes as other communities. Combined with the specific challenges and subsequent adaptations required to inhabit coastal environments (Scholander 1955), we would expect that only a limited number of species have the capacity to colonise these areas, minimising overall community change.

6.5.4 Future directions

The projections of abundance presented here only account for future changes in climate and not other environmental factors, such as land use. Land use changes are known to induce changes in the abundance and distribution of birds (Jiguet *et al.* 2007; Vallecillo, Brotons & Thuiller 2009; Barbet-Massin, Thuiller & Jiguet 2012); therefore, by not accounting for land use change here, these estimates of potential abundance change are likely to be conservative. Current projections of land use change have been shown to make limited impact when assessing large-scale impacts of environmental change (Martin *et al.* 2013). New methods are being developed to improve the spatial resolution and accuracy by which habitat surfaces are calculated (Verburg, Neumann & Nol 2011; Rounsevell *et al.* 2012). With improvements in land use change projections, future studies will be able to refine the projections of abundance presented here and assess the impacts of climate change on these species with a greater degree of accuracy.

Until recently, few studies have explored the impacts of climate change on diversity beyond changes in species richness. Information on changes in the functional (Petchey & Gaston 2002) and phylogenetic diversity (Rolland *et al.* 2012; Winter, Devictor & Schweiger 2013) of a community, may provide greater insight into the resilience and resistance of ecosystems to environmental change. In addition, it is likely that climate change may elicit different responses from different levels within a community, altering species interactions and the transfer of resources through an ecosystem (Devictor *et al.* 2010). Information on the biomass in a community is often preferred by ecologists over information on abundance (Henderson & Magurran 2010). As metabolism scales directly with body mass, biomass is assumed to provide a measure of energy flow and resource use in a system (Brown *et al.* 2004). Therefore, information on biomass and how it is apportioned between the different levels and guilds of a community, can provide very different insights into community structure and how it may alter with climate change, to those indicated by numbers of abundance (Harvey & Godfray 1987; Pagel, Harvey & Godfray 1991; Magurran 2004; Brose *et al.* 2012; Magurran & Henderson 2012).

6.5.5 Conclusions

Here, for the first time, I have projected the abundance of European birds under scenarios of future climate change. Despite significant variations in responses across species and communities, and a promising outlook for species from southern Europe, overall I have predicted substantial declines, especially pronounced for those species currently present in northern Europe. Importantly, I have shown that the most common species across Europe will experience the most severe declines in abundance. This will have severe knock-on effects on ecosystem services and functioning (Inger *et al.* 2014). Yet, the identification of the species and areas projected to experience the greatest changes under climate change will be helpful in developing adaptive management and conservation strategies (Hannah et al. 2007) , hopefully ameliorating projected declines.

Chapter 7

General Discussion

7.1 Synthesis

In this thesis, I investigated the large scale drivers of abundance, and the potential responses of species' abundances to future climate change. To do that, I examined variations in the abundances of European birds in relation to climate, land-use and biotic factors. This work demonstrated that climate is a more important determinant of the abundance of species at a landscape scale than are other abiotic and biotic factors. I showed that this relationship varies spatially, with the importance of climate varying both between species and across species distributions. However, this work also highlighted the importance of considering the role of other biotic and abiotic factors, such as land use and a species' migratory tendencies, in determining species abundance. I demonstrated the large scale impacts that climate change is likely to have on the abundance of species and the subsequent implications for community composition. Importantly, the significant variation in species responses to environmental change that I demonstrated, both between species and spatially, emphasises the complexity of assessing the impacts of future climate change. Alongside these ecological findings, I have provided new methodological insights, particularly into the use and application of abundance modelling techniques.

The main findings in this thesis have both broad implications for future ecological studies and application in planning conservation strategies. I will discuss these in light of three key points:

1) The importance of informative data for ecological studies

2) The benefits and challenges of modelling spatial abundance data,

3) The considerations that need to be addressed when projecting changes under future climate.

7.1.1 The importance of informative data for ecological studies

Throughout this thesis, I have utilised data on species abundances to help improve understanding of what drives variations in population sizes (Chapter Two, Howard *et al.* 2015; Chapter Three) and to assess the potential impacts of future climate change (Chapter Five and Six). I have shown that, by studying variations in abundance, not only can the importance of both abiotic and biotic factors in driving population sizes be better assessed, the fine-scale variations in the quality of a habitat for a species can be better distinguished, something discussed in greater detail below. Despite the improvements in our understanding of species-environment relationships that can be achieved through using abundance data, until recently very few studies attempted to use multi-species abundance datasets (but see Renwick *et al.* 2012; Johnston *et al.* 2013), focussing, instead, on presence absence-data. However, as discussed throughout this thesis, it is population size and trends that are used for assessing the conservation status of a species (International Union for

Conservation of Nature 2001; Mace *et al.* 2008) providing us with a better understanding of a species' susceptibility to climate change. Population size is the strongest correlate of extinction risk (O'Grady *et al.* 2004) and, often, significant declines in abundance may occur before any reduction in range size is observed (Chamberlain & Fuller 2001). Hence, studies of abundance data not only provide a better understanding of ecological relationships than studies of presence-absence data, their output has direct application for conservation planning (Johnston *et al.* 2015).

Given the number of global data sets that already contain measures of species relative abundance, the lack of large scale studies on species abundance is surprising (Robertson, Cumming & Erasmus 2010). In addition to the EBCC atlas of European birds (Hagemeijer & Blair 1997) used throughout this project, abundance data exist for a wide range of taxa. These come in the form of both periodic atlases and annual census data for birds (Sauer et al. 2012; Balmer et al. 2013), butterflies (Pollard & Yates 1994), and plankton (Barnard et al. 2004). Additionally, some less traditional sources of information on the relative abundances of species may be used for studying variations in populations. For example, fishery data have been used to assess spatial and temporal patterns in the abundance of some marine species (Wang et al. 2003; Hedger et al. 2004). Hunting bag data have been used to assess the spatial abundance patterns of many game species including Wild Boar *(Sus scrofa)* (Acevedo *et al.* 2014), Red Deer (*Cervus elaphus)*, Fallow Deer (*Dama dama)* and Roe Deer (*Capreolus capreolus)* (Imperio *et al.* 2010) and Red Grouse *(Lagopus lagopus scotica)* (Thirgood *et al.* 2000; Cattadori *et al.* 2003). Pellet and scat counts have also been shown to provide accurate estimates of relative abundance of Roe Deer (Bouyer *et al.* 2015), Wild Boar (Acevedo *et al.* 2014) and multiple fox species including Pampas Fox *(Pseudalopex gymnocercus)* and San Joaquin Kit Foxes *(Vulpes macrotis mutica)* (García & Kittlein 2005; Smith *et al.* 2006).

The ecological applications of both current and future abundance data are extensive. From a management perspective, forecasts of species abundance, both under environmental change but also across currently unmonitored areas, will be invaluable for conservation planning (Johnston *et al.* 2013; Johnston *et al.* 2015). For effective species level management, it has been suggested that actions should be focussed upon populations large enough to have low extinction risk (McCarthy, Thompson & Possingham 2005; McCarthy, Thompson & Williams 2006; Bottrill *et al.* 2008; McCarthy *et al.* 2011). Spatial predictions of future abundance will enable not only those species most at risk to be identified, but those areas where community change will be greatest. This will allow for the establishment of future protected areas in the most effective locations, and will aid the optimal allocation of resources among current protected areas. From a research perspective, multi-species spatial abundance data can inspire theoretical exploration and investigation. For example, abundance data may allow predictions to be made related to changing composition of food-webs. Abundance data can be used to estimate biomass, which, when paired with known trophic links between species, could be used to estimate fluxes and stocks of energy through a community (Brown & Gillooly 2003). With this understanding, a link may be established between biodiversity theory, the endeavour to understand what determines the number of species that can co-exist in an ecosystem, with metabolic theory, the endeavour to explain the structure of an ecosystem in terms of energy flux. Alternatively, spatial abundance data can be used to better parameterise population models. By combining population models with associated environmental drivers, it is possible to determine the extent to which stochastic fluctuations in the environment can drive growth rates or extinction probabilities of a species (Dennis, Munholland & Scott 1991; García & Kittlein 2005). Furthermore, integrating spatial abundance data with physiological knowledge allows for a more robust understanding of species-environment relationships (Kearney & Porter 2009; Ehrlén & Morris 2015). Mechanistic or process-based models relate the dynamic effects of climatic parameters on abundance and key population parameters, such as fecundity and mortality (Dawson *et al.* 2011). These models can predict the distribution and abundance of a species in response to changes in climate, land use, and biotic processes like competition (McMahon *et al.* 2011; Gillson *et al.* 2013). Given the extensive range of analyses that informative baseline abundance data sets enable, and the greater direct application that knowledge of abundance has for conservation practitioners, it seems intuitive to move towards increased collection of abundance data.

7.1.2 The benefits and challenges of modelling spatial abundance data

Throughout this study I have used random forests, a classification based regression tree analysis, to model species abundance distributions. These models have constantly shown excellent performance, demonstrating both high levels of predictive accuracy and explanatory power. Our results corroborate previous studies on species distributions that show that random forests, along with other classification tree based analyses, consistently outperform more established statistical modelling techniques (Prasad, Iverson & Liaw 2006; Cutler *et al.* 2007; Marmion *et al.* 2009). By modelling species abundance rather than distribution, we have been able to make significant advances in our understanding of species-environment relationships. Initially, I demonstrated significant improvements in predictions of the distribution and abundance of species, through the use of more informative data. Previous attempts to improve species distribution models (SDMs) had focussed primarily on advancing their statistical bases (Araújo & Guisan 2006; Austin 2007; Higgins, O'Hara & Römermann 2012) and, despite investigating the relative value of presence-only and presence-absence data (Brotons et al. 2004; Elith et al. 2006; Pearson et al. 2006), the value of abundance data had not been assessed. Chapter Two (Howard et al. 2014) demonstrated that even by using coarse-scale abundance data, significant improvements in the accuracy of species distribution models can be achieved. By training models on abundance data, instead of presence-absence data, we were better able to identify the relative suitability of a habitat for a species. This may be attributable to the greater statistical power of being able to model changes in abundance throughout the species range and not just at the distributional limits, as is the case when modelling presence-absence data (Johnston *et al.* 2013). Furthermore, with these refinements and the ability to distinguish fine-scale variations in habitat quality, I was able to more accurately assess the relative importance of climate and land use for a species in Chapter Three (Howard *et al.* 2015). This increased level of model refinement and ability to discriminate between fine scale variations in habitat quality, also proved beneficial when using these models to project across alternative regions and time periods, as demonstrated in Chapters Five and Six.

The greater depth of information that can be obtained from using random forests to model abundance is, to some extent, counterbalanced by more practical considerations. Utilising the conditional inference framework to allow models to account for correlations in predictor variables (as done in this thesis) is computationally intensive and often requires parallel computing techniques (Strobl, Malley & Tutz 2009). Furthermore, depending on the sample size and the number of classification trees that the user wishes to fit, random forest models can require large amounts of memory (Gislason, Benediktsson & Sveinsson 2006). This computational intensity became problematic in Chapter Five, preventing large scale assessment of the performance of the Gibbs sampler. The most significant downfall of classification based methods, however, is the lack of clarity regarding the underlying relationships between the dependent and independent variables. Often described as “black-box” type classifiers, random forest models make no assumptions regarding the underlying distribution of the data, allowing for non-linear relationships (Breiman 2001a; Cutler *et al.* 2007). Therefore, obtaining model parameter estimates, which is straightforward for methods such as generalised linear models and generalised additive models, is difficult (Breiman 2001a; Chen, Liaw & Breiman 2004; Magness, Huettmann & Morton 2008). Instead, the method provides measures of variable importance, which was used in Chapter Three (Howard *et al.* 2015). These measures are receiving increased attention throughout ecological studies (Strobl *et al.* 2008; Vincenzi *et al.* 2011; Boulangeat, Gravel & Thuiller 2012) as a means of reliably selecting the most important predictor variables for explaining ecological trends. Even though the unique features and complexity of random forests, raises some practical issues, their predictive performance far exceeds more traditional modelling approaches, and when summarised can provide powerful ecological insights.

7.1.3 Considerations when projecting changes under future climate

Throughout this thesis, I have consistently addressed the need to consider the influence of spatial autocorrelation. In Chapter Two (Howard et al. 2014), I developed a spatial autocovariate term that, by accounting for potential correlation in the environmental covariates of more proximate cells and unmeasured biotic factors such as dispersal, significantly reduced autocorrelation in model residuals. In Chapter Three (Howard *et al.* 2015) I demonstrated that spatial autocorrelation can explain the majority of variance in species abundance distributions in relation to climate and land-use. Despite the apparent importance of this variable in explaining variation in abundance, in Chapter Five I showed that the inclusion of a spatial autocovariate term only improves the predictive performance of these models in very specific cases, such as where species occur at high abundance (i.e., ≥10, 000 breeding pairs in a 50 km UTM grid cell). Given the importance of these high abundance cells in driving the total abundance of a species (Gibson, Van der Marel & Starzomski 2009) and the significance of identifying them for conservation purposes (McCarthy, Thompson & Possingham 2005; McCarthy, Thompson & Williams 2006; McCarthy *et al.* 2011), I included this term when projecting the abundance of species under climate change. This result, however, does raise questions regarding the utility of accounting for spatial autocorrelation when using models of abundance for predictive purposes. With the improvements in our understanding of species-environment relationships gained by modelling abundance rather than presence-absence data, the use of a spatial autocovariate term may not always be necessary.

When projecting species abundance under climate change, we assume that the strength of the relationship between climatic variables and abundance remains constant. Throughout this thesis, I have discussed the potential for spatial non-stationarity in variable importance, and the potential for climate to have varying importance throughout a species range. When utilising species distribution and abundance models to assess the impacts of future climate change, they may be applied to conditions that differ to those used in model calibration (Mair *et al.* 2014). Model extrapolation can result in erroneous predictions (Araújo & Guisan 2006; Heikkinen *et al.* 2006). In Chapter Five, I assessed the performance of species abundance models in novel conditions and demonstrated that these methods can be used to produce informative predictions of abundance in a novel region.

Many of the species considered in this project are migratory, with many spending their non-breeding season in sub-Saharan Africa. In the general introduction (Chapter One), I discussed the potential for conditions across the non-breeding grounds of these species to affect their population sizes (Vickery *et al.* 2014). However, the analyses in Chapter Four, demonstrated that when considered alongside breeding ground conditions, climate and land-use across the African non-breeding grounds were of relatively low importance in driving the populations of migratory species. Therefore, I did not account for conditions away from the breeding grounds when making future predictions of abundance for migratory species. In fact, the results from Chapter Four implied that conditions during migration may be of greater significance for these species. Unfortunately, though, apart from a few recent advancements (Bayly, Rumsey & Clark 2011; Schmaljohann *et al.* 2012; Lemke *et al.* 2013; Saino *et al.* 2015), we only have a vague understanding of the routes and conditions that the majority of species experience during migration

(Vickery *et al.* 2014). Therefore, accounting for the potential impacts of factors outside of the breeding and non-breeding grounds on the abundances of the majority of migratory species is currently not possible. Accounting for the impacts of migratory factors is an important consideration for future analyses, as discussed in more detail below.

7.2 Application for conservation planning

As mentioned throughout this thesis, one of the primary benefits of estimating abundances is the direct application of the estimates for use in conservation planning (Johnston *et al.* 2013; Johnston *et al.* 2015). By monitoring changes in abundance, conservation managers can assess the threat status of a species and prioritise for actions (Mace *et al.* 2008; BirdLife International 2013). Using the projections of future abundance presented in Chapter Six, potential changes in the conservation designation of species under climate change could be identified before they occur, enabling pre-emptive actions. In addition, projections of species spatial abundance can identify areas where the impacts of climate change are projected to be greatest. Information on the abundance of species combined with areas of suitable habitat also has utility for spatial conservation planning. Areas which will remain climatically suitable over time, and areas that will increase in suitability in the future, will be key sites for future conservation efforts; such sites can be identified from projections, such as those presented here (Vos *et al.* 2008; Alagador, Cerdeira & Araújo 2014). Furthermore, the suitability of areas that link current and future protected areas, can be evaluated and incorporated into spatial conservation planning, facilitating the movement of species among these sites (Williams *et al.* 2005; Chetkiewicz & Boyce 2009; Saura, Bodin & Fortin 2014).

Knowledge on the potential abundance responses of species to climate change will allow proactive rather than reactive management strategies. Early evidence suggests that proactive approaches can improve long-term biodiversity conservation outcomes (Cardador *et al.* 2015). For instance, the inclusion of species distribution models into reserve design resulted in more efficient conservation of freshwater biodiversity (Bush *et al.* 2014). Despite the higher initial costs, proactive management can highlight sites that become unsuitable in the future and lead to fewer additional areas being required to meet gaps in protection in the future. Such approaches can also identify protected areas that could be substituted with others that achieve more for conservation (Fuller *et al.* 2010). With the limited resources available to conservation practitioners, robust abundance monitoring, combined with predictive modelling will ensure efficient prioritization and investment into conservation actions that will have the greatest positive impact (Johnston *et al.* 2015).

7.3 Future work

The results presented throughout this thesis, provide the potential for a wide variety of subsequent analyses. In addition to the measures of community compositional change, presented in Chapter Six, these projections of species abundance could also be used to assess changes in functional and phylogenetic diversity. Functional diversity, the variety of biological traits presented by species within an ecosystem, is an important determinant of ecosystem processes (Petchey & Gaston 2002) and has been used to indicate how biodiversity may be affected by environmental stress (Buisson et al. 2013). The kinds of species present within a community strongly influence ecosystem processes, mediating energy and material fluxes either directly or indirectly through alterations to biotic and abiotic conditions (Chapin III et al. 2000). The effects of species extinctions on functional diversity are not always clear, with some species considered functionally identical (Pillar *et al.* 2013). The loss of such functionally 'redundant species' would not have the same impacts on ecosystem processes, as the loss of functionally unique species (Petchey & Gaston 2002). Phylogenetic diversity, the evolutionary distinctiveness of species within a community, has been shown to be a better predictor of ecosystem functioning than species richness (Cadotte, Hamilton & Murray 2009; Cadotte, Albert & Walker 2013). This measure of diversity may act as a proxy for the evolutionary potential of a community and the ability of a system to evolve in response to environmental changes (Thuiller *et al.* 2011). If a community is composed of more closely related species, phylogenetic diversity and hence evolutionary potential will be low. Conversely, if a community is composed of more distantly related species, phylogenetic diversity will be high, and the possibility of having a species with the evolutionary potential to respond to environmental change will increase (Winter, Devictor & Schweiger 2013). Analyses of the potential changes in functional and phylogenetic diversity, in addition to the changes in community composition I presented in Chapter Six, will provide greater insight into the resilience and resistance of ecosystems to environmental change (Chapin III *et al.* 2000).

One of the major gaps in our knowledge, and what currently limits further refinement of the approaches presented here, is the lack of understanding of the use of habitats by trans-Saharan migratory birds outside of their European breeding grounds. For instance, for the majority of species, we know little about their migratory routes, use of stop over sites and movements during their residency across sub-Saharan Africa. Furthermore, it has been suggested that different populations within a species and distinct sub-species may overwinter in different regions of sub-Saharan Africa (Williamson 1955; Morrison *et al.* 2013). This may drive variations in population trends that cannot be explained without comprehensive understanding of the migratory connectivity at both a species and population level (Cresswell 2014). However, recent improvements in tracking technologies are providing useful insight into the large-scale geographical movements and migratory connectivity of avian migrants (Bächler *et al.* 2010). For example, the development of GPS tracking technology to allow greater location accuracy (Guilford et al. 2011), has advanced studies of large bodied birds such as storks (Chevallier et al. 2010) and vultures (García-Ripollés, López-López & Urios 2010). Light-level geolocators provide a suitable alternative to GPS tags, as the latter are currently too large and heavy to be used on smaller bodied species (Bridge et al. 2011). Despite lacking the accuracy of GPS tags, geolocators still provide useful information on the movements of migratory birds, and have revealed the migration routes, stopover sites and wintering grounds of some populations of species including European Hoopoe (*Upupa epops*) (Bächler et al. 2010), Red-backed Shrike (*Lanius collurio)* (Tøttrup et al. 2011) and the Turtle Dove (*Streptopelia turtur*) (Eraud et al. 2013). These tags are currently still too large to use on the smallest of migratory bird species and their widespread application is constrained by the need to recapture individuals to retrieve data (Bowlin *et al.* 2010). We are, however, approaching a period that will revolutionise our understanding of the large-scale movements of migrants. In particular the ICARUS (International Cooperation for Animal Research Using Space; http://icarusinitiative.org/) project will improve knowledge of the global distribution and migratory connectivity of small birds, animals and insects. Data generated by ICARUS and similar big-data animal tracking projects, are expected to provide exciting new insights into the life history and behaviour of migrants. Combining telemetry data with models of species' distributions, abundances and demography could be the next major phase in ecological modelling techniques. If analytical developments can keep pace with technological advancements, real time models that integrate species habitat preferences with movement abilities could be developed. Soon, studies of this nature will do more than inform us about the ecology, evolution and physiology of species; they will use species to inform us about the changing state of our environment (Kays *et al.* 2015).

7.4 Summary

In this thesis, I have demonstrated the overriding importance of climate in determining the abundance of species at a landscape scale. I have also provided insights into the wide range of species potential responses to environmental change. Importantly, I have shown that there are spatial variations in the importance of climate in driving current and potential changes in species' abundance. Future analyses need to consider both these spatial variations but also the importance of other abiotic and biotic factors when assessing the impacts of climate change. I have demonstrated the large scale impacts on species abundance of future climate change. Furthermore, due to the variety of different species responses to climate change, there will also be substantial changes in community composition. The implications of changes in abundance and communities on ecosystem services and functioning are currently unknown, but are a vital area of future research. I have also provided methodological insights in to the use and application of abundance modelling techniques. In particular, this project has demonstrated the benefits of modelling abundance data, both through the potential for direct application of projections of abundance, but also through the improvements in our understanding of species-environment relationships. Integration of these modelling advances into adaptive planning and conservation, should help to conserve current biodiversity and ecosystem functioning, and maintain ecological resilience and evolutionary potential at a landscape scale. In light of these findings, I recommend, that given the improvements to our understanding of species-environment relationships and the benefits for management, conservation organisations should be routinely monitoring abundance, rather than presence-absence.

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Appendices

Table A1: The 154 species excluded from analyses from the 496 species in the EBCC atlas (Hagemeijer & Blair 1997). Reason for a species exclusion from the analyses include primary association with marine habitats, having less than 20 quantitative estimates of abundance across Europe or model convergence failure (indicated below)

Species	Reason	Species	Reason
Fulmarus glacialis	Marine	*Alca torda*	Marine
Pterodro feae	Marine	*Cepphus grylle*	Marine
Pterodro madeira	Marine	*Alle alle*	Marine
Bulweria bulwerii	Marine	*Fratercula arctica*	Marine
Calonect diomedea	Marine	*Anthus petrosus*	Marine
Puffinus puffinus	Marine	*Gavia adamsii*	Small Range
Puffinus yelkouan	Marine	*Pelecanus onocrotalus*	Small Range
Puffinus mauretanicus	Marine	*Pelecanus crispus*	Small Range
Puffinus assimilis	Marine	*Phoenicopterus ruber*	Small Range
Pelagodroma marina	Marine	*Cygnus columbia*	Small Range
Hydrobates pelagicus	Marine	*Anser albifrons*	Small Range
Oceanodroma leucorhoa	Marine	*Anser erythropus*	Small Range
Oceanodroma monorhis	Marine	*Branta leucopsis*	Small Range
Oceanodroma castro	Marine	*Branta bernicla*	Small Range
Phaethon aethereus	Marine	*Marmaronetta angustirostris*	Small Range
Morus bassanus	Marine	*Polysticta stelleri*	Small Range
Phalacrocorax aristotelis	Marine	*Histrionicus histrionicus*	Small Range
Somateria mollissima	Marine	*Bucephala islandica*	Small Range
Somateria spectabilis	Marine	*Oxyura leucocephala*	Small Range
Arenaria interpres	Marine	*Aegypius monachus*	Small Range
Phalaropus fulicarius	Marine	*Circus macrourus*	Small Range
Larus sabini	Marine	*Aquila clanga*	Small Range
Larus genei	Marine	*Aquila nipalensis*	Small Range
Larus audouini	Marine	*Aquila adalberti*	Small Range
Larus glaucoids	Marine	*Tetrao mlokosiewiczi*	Small Range
Larus hyperboreus	Marine	*Tetraogallus caucasicus*	Small Range
Larus marinus	Marine	*Tetraogallus caspius*	Small Range
Rissa tridactyla	Marine	*Alectoris barbara*	Small Range
Pagophila eburnea	Marine	*Francolinus francolinus*	Small Range
Sterna caspia	Marine	*Turnix sylvatica*	Small Range
Sterna bengalensis	Marine	*Porphyrio porphyrio*	Small Range
Sterna sandvicensis	Marine	*Fulica cristata*	Small Range
Sterna elegans	Marine	*Anthropoides virgo*	Small Range
Sterna dougallii	Marine	*Glareola nordmanni*	Small Range
Sterna fuscata	Marine	*Charadrius leschenaultii*	Small Range
Uria aalge	Marine	*Charadrius asiaticus*	Small Range
Uria lomvia	Marine	*Pluvialis fulva*	Small Range

Table A1 continued

Species	Reason	Species	Reason
Pluvialis squatarola	Small Range	*Oenanthe finschii*	Small Range
Hoplopterus spinosus	Small Range	*Oenanthe xanthoprymna*	Small Range
Chettusia gregaria	Small Range	*Oenanthe leucura*	Small Range
Chettusia leucura	Small Range	*Zoothera dauma*	Small Range
Calidris canutus	Small Range	*Turdus ruficollis*	Small Range
Calidris alba	Small Range	*Locustella lanceolata*	Small Range
Calidris minuta	Small Range	*Acrocephalus paludicola*	Small Range
Calidris melanotos	Small Range	*Acrocephalus agricola*	Small Range
Gallinago stenura	Small Range	*Hippolais caligata*	Small Range
Numenius tenuirostris	Small Range	*Hippolais languida*	Small Range
Xenus cinereus	Small Range	*Sylvia sarda*	Small Range
Stercorarius pomarinus	Small Range	*Sylvia conspicillata*	Small Range
Larus ichthyaetus	Small Range	*Sylvia mystacea*	Small Range
Larus armenicus	Small Range	*Sylvia nana*	Small Range
Gelochelidon nilotica	Small Range	*Phylloscopus inornatus*	Small Range
Pterocles orientalis	Small Range	*Phylloscopus lorenzii*	Small Range
Pterocles alchata	Small Range	*Parus cyanus*	Small Range
Columba trocaz	Small Range	*Sitta krueperi*	Small Range
Streptopelia senegalensis	Small Range	*Sitta whiteheadi*	Small Range
Cuculus saturatus	Small Range	*Sitta tephronota*	Small Range
Nyctea scandiaca	Small Range	*Lanius excubitor*	Small Range
Caprimulgus ruficollis	Small Range	*Lanius meridionalis*	Small Range
Apus unicolor	Small Range	*Sturnus roseus*	Small Range
Apus caffer	Small Range	*Carpospiza brachydactyla*	Small Range
Merops superciliosus	Small Range	*Serinus pusillus*	Small Range
Chersophilus duponti	Small Range	*Serinus canaria*	Small Range
Melanocorypha bimaculata	Small Range	*Loxia scotica*	Small Range
Melanocorypha leucoptera	Small Range	*Bucanetes mongolicus*	Small Range
Melanocorypha yeltoniensis	Small Range	*Bucanetes githagineus*	Small Range
Calandrella rufescens	Small Range	*Carpodacus rubicilla*	Small Range
Anthus berthelotii	Small Range	*Pyrrhula murina*	Small Range
Anthus hodgsoni	Small Range	*Emberiza leucceophalos*	Small Range
Anthus spinoletta	Models failed	*Emberiza cineracea*	Small Range
Prunella montanella	Small Range	*Emberiza buchanani*	Small Range
Prunella ocularis	Small Range	*Emberiza aureola*	Small Range
Prunella atrogularis	Small Range	*Emberiza pallasi*	Small Range
Luscinia calliope	Small Range	*Emberiza bruniceps*	Small Range
Tarsiger cyanurus	Small Range		
Irania gutturalis	Small Range		
Phoenicurus erythrogaster	Small Range		
Oenanthe deserti	Small Range		

Table A2: Relative Importance (R.I.) of climate to land use in describing the abundance of the 342 species included for analysis in Chapter 3.

Species	R.I.	Species	R.I	Species	R.I.
Gavia stellata	2.436	*Aythya ferina*	0.694	*Falco columbarius*	2.94
Gavia arctica	2.45	*Aythya nyroca*	0.314	*Falco subbuteo*	0.497
Gavia immer	1.292	*Aythya fuligula*	2.433	*Falco eleonorae*	0.784
Tachybaptus ruficollis	0.767	*Aythya marila*	1.274	*Falco biarmicus*	0.809
Podiceps cristatus	0.517	*Clangula hyemalis*	1.645	*Falco cherrug*	2.847
Podiceps grisegena	0.679	*Melanitta nigra*	2.414	*Falco rusticolus*	0.838
Podiceps auritus	1.891	*Melanitta fusca*	1.247	*Falco peregrinus*	0.613
Podiceps nigricollis	0.361	*Bucephala clangula*	1.783	*Bonasa bonasia*	1.482
Phalacrocorax carbo	1.198	*Mergellus albellus*	2.415	*Lagopus lagopus*	2.781
Phalacrocorax pygmeus	3.705	*Mergus serrator*	2.145	*Lagopus muta*	0.609
Botaurus stellaris	0.247	*Mergus merganser*	3.047	*Tetrao tetrix*	1.121
Ixobrychus minutus	0.536	*Pernis apivorus*	0.635	*Tetrao urogallus*	1.116
Nycticorax nycticorax	0.858	*Elanus caeruleus*	5.058	*Alectoris chukar*	1.675
Ardeola ralloides	0.647	*Milvus migrans*	1.271	*Alectoris graeca*	0.367
Bubulcus ibis	5.501	*Milvus milvus*	0.984	*Alectoris rufa*	1.124
Egretta garzetta	1.619	*Haliaeetus albicilla*	0.525	*Perdix perdix*	0.527
Egretta alba	1.014	*Gypaetus barbatus*	1.299	*Coturnix coturnix*	0.551
Ardea cinerea	0.642	*Neophron percnopterus*	0.869	*Rallus aquaticus*	0.487
Ardea purpurea	1.405	*Gyps fulvus*	1.118	*Porzana porzana*	0.509
Ciconia nigra	0.652	*Circaetus gallicus*	1.647	*Porzana parva*	0.445
Ciconia ciconia	0.522	*Circus aeruginosus*	0.36	*Porzana pusilla*	1.61
Plegadis falcinellus	7.744	*Circus cyaneus*	1.64	*Crex crex*	1.208
Platalea leucorodia	1.448	*Circus pygargus*	0.405	*Gallinula chloropus*	0.648
Cygnus olor	1.379	*Accipiter gentilis*	0.458	*Fulica atra*	0.337
Cygnus cygnus	2.095	*Accipiter nisus*	0.764	*Grus grus*	1.262
Anser fabalis	2.022	*Accipiter brevipes*	1.961	*Tetrax tetrax*	1.261
Anser brachyrhynchus	0.504	*Buteo buteo*	0.429	*Otis tarda*	0.406
Anser anser	1.047	*Buteo rufinus*	1.506	*Haematopus ostralegus*	0.595
Tadorna ferruginea	2.547	*Buteo lagopus*	8.357	*Himantopus himantopus*	0.756
Tadorna tadorna	0.469	*Aquila pomarina*	1.145	*Recurvirostra avosetta*	0.197
Anas penelope	2.312	*Aquila heliaca*	0.522	*Burhinus oedicnemus*	1.779
Anas strepera	0.572	*Aquila chrysaetos*	0.374	*Glareola pratincola*	0.597
Anas crecca	2.922	*Hieraaetus pennatus*	1.08	*Charadrius dubius*	0.51
Anas platyrhynchos	0.912	*Aquila fasciatus*	0.951	*Charadrius hiaticula*	0.917
Anas acuta	2.445	*Pandion haliaetus*	1.524	*Charadrius alexandrinus*	0.282
Anas querquedula	0.698	*Falco naumanni*	0.688	*Eudromias morinellus*	0.784
Anas clypeata	0.744	*Falco tinnunculus*	0.451	*Pluvialis apricaria*	2.418
Netta rufina	0.679	*Falco vespertinus*	0.745	*Vanellus vanellus*	0.845

Table A2 continued

Species	R.I.	Species	R.I.	Species	R.I.
Calidris temminckii	1.86	*Columba oenas*	1.196	*Calandrella brachydactyla*	1.285
Calidris maritima	1.28	*Columba palumbus*	0.961	*Galerida cristata*	1.028
Calidris alpina	0.688	*Streptopelia decaocto*	0.462	*Galerida theklae*	0.763
Limicola falcinellus	1.409	*Streptopelia turtur*	0.892	*Lullula arborea*	0.512
Philomachus pugnax	4.7	*Clamator glandarius*	0.441	*Alauda arvensis*	0.44
Lymnocryptes minimus	2.281	*Cuculus canorus*	0.515	*Eremophila alpestris*	0.545
Gallinago gallinago	2.153	*Tyto alba*	1.688	*Riparia riparia*	0.581
Gallinago media	0.73	*Otus scops*	1.323	*Hirundo rupestris*	0.348
Scolopax rusticola	1.556	*Bubo bubo*	0.559	*Hirundo rustica*	0.513
Limosa limosa	0.37	*Surnia ulula*	4.428	*Hirundo daurica*	0.951
Limosa lapponica	3.144	*Glaucidium passerinum*	1.225	*Delichon urbicum*	0.388
Numenius phaeopus	6.074	*Scolopax rusticola*	1.556	*Anthus campestris*	1.683
Numenius arquata	1.343	*Limosa limosa*	0.37	*Anthus trivialis*	1.542
Tringa erythropus	3.246	*Athene noctua*	1.019	*Anthus pratensis*	1.98
Tringa totanus	0.93	*Strix aluco*	0.64	*Anthus cervinus*	2.531
Tringa stagnatilis	3.013	*Strix uralensis*	1.226	*Motacilla flava*	1.046
Tringa nebularia	2.798	*Strix nebulosa*	2.678	*Athene noctua*	1.019
Tringa ochropus	1.053	*Asio otus*	0.602	*Strix aluco*	0.64
Tringa glareola	2.4	*Asio flammeus*	2.243	*Motacilla citreola*	1.576
Actitis hypoleucos	1.723	*Aegolius funereus*	1.003	*Motacilla cinerea*	1.15
Phalaropus lobatus	4.018	*Caprimulgus europaeus*	0.573	*Motacilla alba*	1.266
Stercorarius parasiticus	0.423	*Apus apus*	0.568	*Bombycilla garrulus*	2.479
Stercorarius longicaudus	2.008	*Apus pallidus*	3.697	*Cinclus cinclus*	0.474
Stercorarius skua	2.57	*Alcedo atthis*	0.702	*Troglodytes troglodytes*	1.574
Larus melanocephalus	0.148	*Merops apiaster*	1.92	*Prunella modularis*	1.638
Larus minutus	1.234	*Coracias garrulus*	1.349	*Prunella collaris*	0.398
Larus ridibundus	0.679	*Upupa epops*	1.308	*Erithacus rubecula*	0.721
Larus canus	2.274	*Jynx torquilla*	0.643	*Luscinia luscinia*	1.923
Larus fuscus	0.533	*Picus canus*	0.43	*Luscinia megarhynchos*	2.051
Larus argentatus	0.717	*Picus viridis*	0.622	*Luscinia svecica*	1.163
Larus cachinnans	0.553	*Dryocopus martius*	0.758	*Phoenicurus ochruros*	0.852
Sterna hirundo	0.989	*Dendrocopos major*	0.419	*Phoenicurus phoenicurus*	1.727
Sterna paradisaea	1.196	*Dendrocopos syriacus*	1.275	*Saxicola rubetra*	1.941
Sterna albifrons	0.316	*Dendrocopos medius*	0.665	*Saxicola torquatus*	1.871
Chlidonias hybrida	0.524	*Dendrocopos leucotos*	0.596	*Oenanthe isabellina*	7.447
Chlidonias niger	0.378	*Dendrocopos minor*	0.806	*Oenanthe oenanthe*	2.38
Chlidonias leucopterus	1.927	*Picoides tridactylus*	1.835	*Oenanthe pleschanka*	6.53
Columba livia	0.573	*Melanocorypha calandra*	1.513	*Oenanthe hispanica*	0.874

Table A2 continued

Species	R.I.	Species	R.I.	Species	R.I.
Monticola saxatilis	0.243	*Phylloscopus trochilus*	2.405	*Sturnus vulgaris*	0.921
Monticola solitarius	2.003	*Regulus regulus*	1.485	*Sturnus unicolor*	0.602
Turdus torquatus	0.806	*Regulus ignicapilla*	1.18	*Passer domesticus*	0.458
Turdus merula	0.593	*Muscicapa striata*	1.285	*Passer X italiae*	0.811
Turdus pilaris	2.92	*Ficedula parva*	1.58	*Passer hispaniolensis*	1.572
Turdus philomelos	1.044	*Ficedula semitorquata*	1.219	*Passer montanus*	0.31
Turdus iliacus	3.366	*Ficedula albicollis*	1.183	*Petronia petronia*	0.885
Turdus viscivorus	0.674	*Ficedula hypoleuca*	1.759	*Montifringilla nivalis*	0.438
Cettia cetti	2.128	*Panurus biarmicus*	0.16	*Fringilla coelebs*	0.401
Cisticola juncidis	1.823	*Aegithalos caudatus*	0.662	*Fringilla montifringilla*	5.719
Locustella naevia	1.16	*Parus palustris*	0.926	*Serinus serinus*	1.066
Locustella fluviatilis	1.235	*Parus lugubris*	1.51	*Carduelis citrinella*	0.54
Locustella luscinioides	0.548	*Parus montanus*	2.04	*Carduelis chloris*	0.475
Acrocephalus melanopogon	0.062	*Parus cinctus*	2.578	*Carduelis carduelis*	0.911
Acrocephalus schoenobaenus	0.881	*Parus cristatus*	0.911	*Carduelis spinus*	1.606
Acrocephalus dumetorum	2.819	*Parus ater*	1.119	*Carduelis cannabina*	0.874
Acrocephalus palustris	0.712	*Parus caeruleus*	0.611	*Carduelis flavirostris*	0.612
Acrocephalus scirpaceus	0.441	*Parus major*	0.454	*Carduelis flammea*	3.886
Acrocephalus arundinaceus	0.391	*Sitta europaea*	0.417	*Carduelis hornemanni*	2.066
Hippolais pallida	1.852	*Sitta neumayer*	0.75	*Loxia leucoptera*	2.845
Hippolais olivetorum	0.905	*Tichodroma muraria*	0.597	*Loxia curvirostra*	1.397
Motacilla citreola	1.576	*Certhia familiaris*	1.777	*Loxia pytyopsittacus*	2.609
Motacilla cinerea	1.15	*Certhia brachydactyla*	1.178	*Carpodacus erythrinus*	1.731
Hippolais icterina	1.491	*Remiz pendulinus*	0.49	*Pinicola enucleator*	1.491
Hippolais polyglotta	2.649	*Oriolus oriolus*	0.528	*Pyrrhula pyrrhula*	1.516
Sylvia undata	1.196	*Lanius collurio*	0.595	*Coccothraustes coccothraustes*	0.635
Sylvia cantillans	1.116	*Lanius minor*	2.018	*Calcarius lapponicus*	2.164
Sylvia melanocephala	1.469	*Lanius senator*	2.094	*Plectrophenax nivalis*	1.103
Sylvia rueppelli	2.245	*Lanius nubicus*	5.468	*Emberiza citrinella*	1.34
Sylvia hortensis	0.91	*Garrulus glandarius*	0.34	*Emberiza cirlus*	1.617
Sylvia nisoria	0.93	*Perisoreus infaustus*	2.814	*Emberiza cia*	0.453
Sylvia curruca	1.56	*Cyanopica cyanus*	2.539	*Emberiza hortulana*	1.281
Sylvia communis	0.642	*Pica pica*	0.42	*Emberiza caesia*	1.4
Sylvia borin	1.532	*Nucifraga caryocatactes*	1.717	*Emberiza rustica*	2.488
Sylvia atricapilla	0.55	*Pyrrhocorax graculus*	0.25	*Emberiza pusilla*	2.285
Phylloscopus trochiloides	1.802	*Pyrrhocorax pyrrhocorax*	0.968	*Emberiza schoeniclus*	1.337
Phylloscopus borealis	2.231	*Corvus monedula*	0.38	*Emberiza melanocephala*	1.334
Phylloscopus bonelli	0.792	*Corvus frugilegus*	0.385	*Miliaria calandra*	1.105
Phylloscopus sibilatrix	1.295	*Corvus corone*	0.668		
Phylloscopus collybita	0.916	*Corvus corax*	0.869		

Table A3: The role of species traits in affecting the importance of spatial autocorrelation in models across all study species. Estimated coefficients are from AIC-selected and phylogenetically corrected GLS regression models of the importance of spatial autocorrelation in determining the abundance of a species. P-values significant at the 5% level are shown in bold.

	Estimated Coefficient	Standard Error	t- value	p-value
Intercept (Habitat generalists)	0.26	0.08	3.18	**<0.01**
Primary Habitat association:				
1. Coastal	-0.05	0.03	-1.89	0.06
2. Inland Wetland	-0.02	0.02	-1.23	0.22
3. Tundra, mires and moorland	-0.11	0.02	-5.35	**<0.01**
4. Boreal and temperate forest	-0.03	0.02	-1.41	0.16
5. Mediterranean	-0.13	0.03	-3.90	**<0.01**
6. Agriculture and grassland	-0.02	0.02	-1.29	0.20
7.Montane grasslands	-0.10	0.04	-2.44	**0.02**
Log (Body mass)	-0.02	0.01	-2.63	**0.01**

Lambda: 0.99
Residual standard error: 0.039 on 267 degrees of freedom
Adjusted R-squared: 0.173

Table A4: Summaries of the results of four analyses of variance (ANOVAs). Four individual ANOVAs were used to assess the drivers of spatial patterns in the relative climatic importance and the importance of APET, MTCO and GDD5 in determining the abundance of species within each UTM grid cell (n=1721). P-Values significant at the 5% level are shown in bold.

Response Variable	Explanatory Variables	Estimated Coefficient	Standard Error	Degrees of freedom	Sum Sq	Mean Sq	F-value	P-value	Explained variance (%)
Relative climate importance	Longitude	0.002	<0.001	1	1.33	1.33	53.81	**<0.01**	1.2
	Latitude	0.024	0.001	1	63.68	63.68	2585.04	**<0.01**	57.5
	Species Richness	-0.001	<0.001	1	2.62	2.62	106.34	**<0.01**	2.37
	Land use heterogeneity	0.072	0.012	1	0.84	0.84	34.26	**<0.01**	0.76
	Residuals	NA	NA	1716	42.27	0.02	NA	NA	38.17
APET	Longitude	-0.001	0.002	1	0.03	0.03	0.02	0.88	0
	Latitude	-0.184	0.004	1	3617.56	3617.56	2699.69	**<0.01**	58.12
	Species Richness	0.012	0.001	1	215.19	215.19	160.59	**<0.01**	3.46
	Land use heterogeneity	-0.753	0.091	1	92.27	92.27	68.86	**<0.01**	1.48
	Residuals	NA	NA	1716	2299.42	1.34	NA	NA	36.94
MTCO	Longitude	0.065	0.005	1	1102.42	1102.42	165.16	**<0.01**	4.48
	Latitude	0.324	0.008	1	11353	11353	1700.91	**<0.01**	46.1
	Species Richness	-0.017	0.002	1	449.45	449.45	67.34	**<0.01**	1.83
	Land use heterogeneity	1.281	0.203	1	266.87	266.87	39.98	**<0.01**	1.08
	Residuals	NA	NA	1716	11453.7	6.67	NA	NA	46.51
GDD5	Longitude	-0.035	0.003	1	312.24	312.24	150.48	**<0.01**	2.75
	Latitude	0.259	0.004	1	7118.14	7118.14	3430.47	**<0.01**	62.69
	Species Richness	-0.014	0.001	1	325.9	325.9	157.06	**<0.01**	2.87
	Land use heterogeneity	0.485	0.113	1	38.18	38.18	18.4	**<0.01**	0.34
	Residuals	NA	NA	1716	3560.66	2.07	NA	NA	31.36

Table A5: Countries providing data for the PECBMS scheme and the period of monitoring used for analysis in each country

Country	Monitoring period
Austria	1998 – 2011
Belgium	1990 – 2011
Czech Republic	1982 – 2011
Denmark	1980 – 2011
Estonia	1983 – 2011
Finland	1983 – 2011
France	1989 – 2011
Germany	1989 – 2011
Hungary	1999 – 2011
Ireland	1998 – 2011
Italy	2000 – 2011
Latvia	1995 – 2011
Netherlands	1990 – 2011
Norway	1995 – 2011
Poland	2000 – 2011
Portugal	2004 – 2011
Spain	1996 – 2011
Sweden	1980 – 2011
Switzerland	1999 – 2011
United Kingdom	1980 – 2011

Table A6: Bird species data. Breeding and non-breeding habitats indicated by the following : FA=farmland,WE= wetland, WO=woodland, O=other. Br= Breeding ground, Nb= Non-breeding ground

Species	Migratory Strategy	Mass	Nb habitat	Br habitat	Br CST	Nb CST	PECBMS trend
Accipiter nisus	Short	5.481	O	O	0.002	0.002	0.998
Acrocephalus arundinaceus	Long	3.303	WE	WE	0.006	0.001	1.011
Acrocephalus palustris	Long	2.477	WE	O	-0.014	-0.001	0.998
Acrocephalus schoenobaenus	Long	2.416	WE	WE	-0.007	0.006	1.001
Acrocephalus scirpaceus	Long	2.51	WE	WE	0.002	0.002	0.999
Actitis hypoleucos	Long	3.945	WE	WE	-0.012	0.006	0.987
Alauda arvensis	Short	3.616	OC	FA	0.01	0.01	0.982
Anas platyrhynchos	Short	6.987	WE	WE	0.001	0.004	1.009
Anthus pratensis	Short	2.912	OC	FA	-0.008	0.007	0.972
Anthus trivialis	Long	3.223	WO	WO	-0.008	0.001	0.975
Apus apus	Long	3.627	O	O	0.014	-0.01	0.999
Ardea cinerea	Short	7.274	WE	WE	0.003	0.004	1.027
Buteo buteo	Short	6.876	O	O	0.005	0	1.023
Carduelis cannabina	Short	2.728	OC	FA	0.011	0.013	0.968
Carduelis carduelis	Short	2.747	O	O	0.018	0.013	1.022
Carduelis chloris	Short	3.325	O	O	0.016	0.011	1.005
Carduelis flammea	Short	2.565	O	O	-0.01	-0.01	0.98
Carduelis spinus	Short	2.674	WO	WO	-0.003	0.009	0.99
Ciconia ciconia	Long	8.153	OC	FA	0.008	0.005	1.013
Circus aeruginosus	Short	6.637	WE	WE	-0.005	0.004	1.041
Coccothraustes coccothraustes	Short	3.989	WO	WO	0.003	0.009	1.012
Columba oenas	Short	5.635	WO	WO	0.004	0.01	1.009
Columba palumbus	Short	6.194	O	O	0.012	0.009	1.02
Corvus frugilegus	Short	6.19	OC	FA	0.002	0.003	1.028
Corvus monedula	Short	5.505	O	O	0.007	0.006	0.993
Cuculus canorus	Long	4.727	WO	O	-0.001	-0.001	0.989
Cygnus olor	Short	9.177	WE	WE	-0.004	0.007	1.018
Emberiza citrinella	Short	3.277	OC	FA	0.004	0.003	0.985
Emberiza hortulana	Long	3.17	OC	FA	-0.004	-0.007	0.938
Emberiza schoeniclus	Short	2.907	WE	WE	-0.01	0.011	0.992
Erithacus rubecula	Short	2.901	O	O	0.008	0.011	1.011
Ficedula hypoleuca	Long	2.451	WO	WO	-0.015	0.011	0.988
Fringilla coelebs	Short	3.04	O	O	0.015	0.011	1.002
Fringilla montifringilla	Short	3.178	O	O	-0.021	0.01	0.974
Fulica atra	Short	6.621	WE	WE	0.004	0.007	1.01
Gallinago gallinago	Short	4.754	O	O	-0.014	0.006	0.976
Gallinula chloropus	Short	5.58	WE	WE	0.01	0.003	1.003

Table A6 continued

Species	Migratory Strategy	Mass	Nb habitat	Br habitat	Br CST	Nb CST	PECBMS trend
Garrulus glandarius	Short	5.081	WO	WO	0.012	0.012	1.008
Hippolais icterina	Long	2.681	WO	O	-0.002	0.002	0.983
Hirundo rustica	Long	2.76	O	FA	0.023	-0.007	0.993
Jynx torquilla	Long	3.512	WO	O	0.004	0.007	0.972
Lanius collurio	Long	3.398	WO	FA	0.008	0	1
Limosa limosa	Long	5.728	OC	FA	-0.004	0.003	0.972
Locustella fluviatilis	Long	2.896	WO	O	-0.006	0.011	0.977
Luscinia luscinia	Long	3.17	WO	O	-0.007	-0.004	0.998
Luscinia megarhynchos	Long	2.907	O	O	0.017	0.009	0.983
Miliaria calandra	Short	4.047	OC	FA	-0.002	-0.002	0.97
Motacilla alba	Short	3.045	O	O	-0.007	0.002	0.997
Motacilla cinerea	Short	2.845	WE	WE	0.007	0.005	1.001
Motacilla flava	Long	2.632	O	FA	-0.009	0.005	0.974
Muscicapa striata	Long	2.681	WO	O	0.001	-0.007	0.985
Numenius phaeopus	Long	6.001	WE	O	-0.022	-0.008	1.005
Oenanthe oenanthe	Long	3.105	WO	O	-0.012	0.008	0.967
Oriolus oriolus	Long	4.369	WO	O	0.012	-0.005	1.002
Parus ater	Short	2.208	WO	WO	0.008	0.005	0.995
Parus caeruleus	Short	2.588	O	O	0.013	0.013	1.014
Parus major	Short	2.944	O	O	0.006	0.006	1.004
Phoenicurus ochruros	Short	2.803	O	O	0.006	0	1.01
Phoenicurus phoenicurus	Long	2.674	WO	WO	-0.008	0.009	1.009
Phylloscopus collybita	Long	2.015	O	WO	0.005	0.003	1.019
Phylloscopus sibilatrix	Long	2.104	O	WO	-0.001	0.007	0.976
Phylloscopus trochilus	Long	2.163	WO	O	-0.007	-0.002	0.985
Pluvialis apricaria	Short	5.366	O	O	-0.014	0.019	0.998
Prunella modularis	Short	2.981	O	O	-0.007	0.009	0.988
Pyrrhula pyrrhula	Short	3.082	WO	WO	-0.001	0.003	0.984
Regulus ignicapilla	Short	1.723	WO	WO	0.004	0.011	0.997
Regulus regulus	Short	1.74	WO	WO	0	0.006	0.982
Saxicola rubetra	Long	2.809	WO	FA	0.001	0.003	0.978
Serinus serinus	Short	2.416	OC	FA	0.008	0.006	0.973
Streptopelia turtur	Long	4.883	WO	FA	0.022	0.01	0.961
Sturnus vulgaris	Short	4.381	OC	FA	0.003	0.014	0.981
Sylvia atricapilla	Short	2.741	O	O	0.009	0.006	1.03
Sylvia borin	Long	2.632	WO	O	0.002	0	0.993
Sylvia communis	Long	2.674	WO	FA	0.007	-0.002	1.011

Table A6 continued

Species	Migratory Strategy	Mass	Nb habitat	Br habitat	Br CST	Nb CST	PECBMS trend
Sylvia curruca	Long	2.313	WO	O	0	0.002	1.001
Sylvia nisoria	Long	3.127	O	FA	0.013	0.004	0.959
Tringa glareola	Long	4.29	OC	O	-0.014	0.001	0.994
Tringa ochropus	Short	4.268	WE	WE	0.004	0.002	1.008
Troglodytes troglodytes	Short	2.186	O	O	0.01	0.01	1.014
Turdus iliacus	Short	4.114	O	O	-0.011	0.014	0.996
Turdus merula	Short	4.727	O	O	0.014	0.013	1.011
Turdus philomelos	Short	4.199	O	O	-0.004	0.007	1.004
Turdus pilaris	Short	4.644	O	O	-0.013	0.007	0.999
Turdus viscivorus	Short	4.745	WO	WO	0.001	0.01	0.992
Vanellus vanellus	Short	5.421	OC	FA	-0.006	0.009	0.972

Table A7: Median AUC results for the 4 distribution modelling techniques for the combined resident and migrant breeding ranges (108 species in total) and the migrant non-breeding ranges (87 species in total). Figures in brackets indicate range of AUC values across all relevant species.

Modelling Technique	Breeding ranges	Non-breeding ranges
GLM	0.962 (0.844-0.995)	0.940 (0.771-0.985)
GAM	0.963 (0.815-0.993)	0.938 (0.794-0.985)
GBM	0.946 (0.792-0.984)	0.947 (0.784-0.993)
RF	0.947 (0.776-0.986)	0.953 (0.763-0.991)

Table A8: Candidate model set derived from global model during model selection and subsequently used for model averaging. Values for model parameters are the model coefficients for continuous values and the presence or absence of factor variables.

Intercept	Breeding ground CST	Breeding habitat association	log(Mass)	Migratory strategy	Non-breeding ground CST	Non-breeding habitat	Breeding CST* Migratory strategy	Degrees of Freedom	Log-likelihood	Δ AICc	Akaike Weight
0.962	0.322	+	0.004	+			+	9	252.64	0.00	0.27
0.962	0.602	+	0.003	+				8	251.12	0.55	0.20
0.962	0.643	+	0.004					7	249.90	0.56	0.20
0.958	-0.045		0.004	+		+	+	9	252.29	0.71	0.19
0.962	0.608	+	0.003	+	-0.195			9	251.36	2.56	0.08
0.962	0.641	+	0.004		0.027			8	249.91	2.98	0.06

Table A9: Standardised Model-averaged coefficients from OLS regression models of the population trends since 1980, including the measure of relative variable importance in the final averaged model. (R^2=0.48)

	Estimate	Adjusted S.E.	z-value	P-value	Relative variable importance
Intercept (Breeding Habitat: other, Non-breeding Habitat: Other, Migratory Description: Long-distance)	0	0	NA	NA	NA
Breeding CST	0.22	0.17	1.28	0.2	1
Breeding Habitat					0.81
Farmland	-0.46	0.09	4.9	<0.01**	
Woodland	-0.02	0.09	0.18	0.86	
Wetland	0.1	0.09	1.08	0.28	
Log(Mass)	0.31	0.09	3.33	<0.01**	1
Migratory description (Short-distance Migrant)	0.14	0.09	1.52	0.13	0.74
Breeding CST* Migratory description (Short-distance Migrant)	0.26	0.14	1.84	0.07*	0.46
Non-breeding habitat:					0.19
Open	-0.43	0.1	4.51	<0.01**	
Woodland	-0.12	0.1	1.18	0.24	
Wetland	0.08	0.1	0.79	0.43	
Non-breeding CST	-0.03	0.1	0.31	0.76	0.14

* = significant at p<0.1, **= significant at p<0.05

Table A10: Summary of one-sample Mann-Whitney tests results

Migratory Strategy	Breeding Ground CST	V-value	p-value
Long-distance	Negative	26	0.10
Long-distance	Positive	48	0.21
Long-distance	Stable	16	0.15
Short-distance	Negative	15	0.12
Short-distance	Positive	209	<0.01
Short-distance	Stable	125	0.24

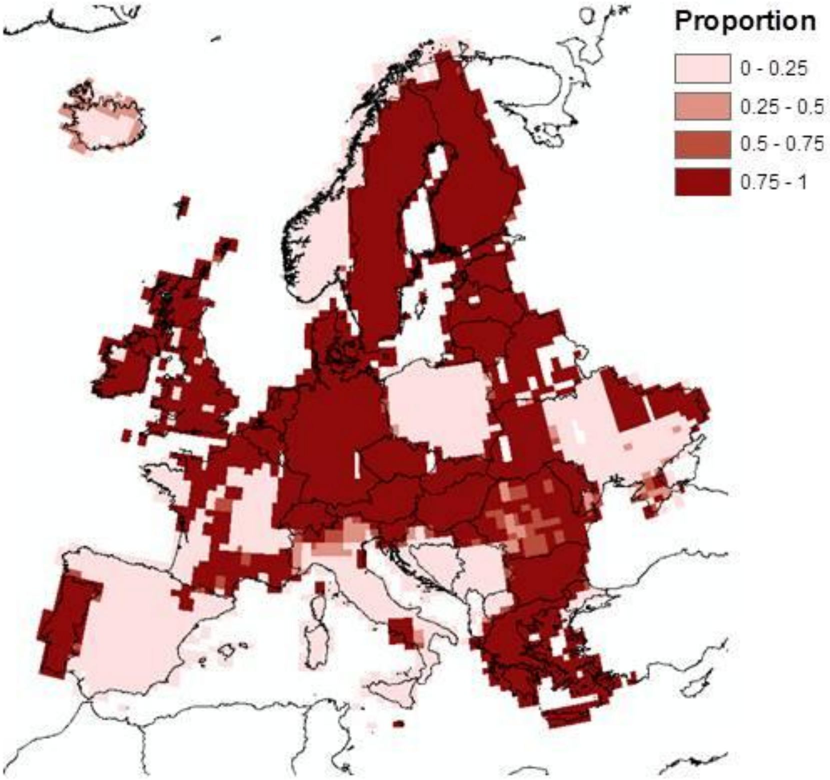

Figure A1: The area of study. Shading represents the proportion of species present within each UTM grid square represented with quantitative ordinal estimates of abundance.

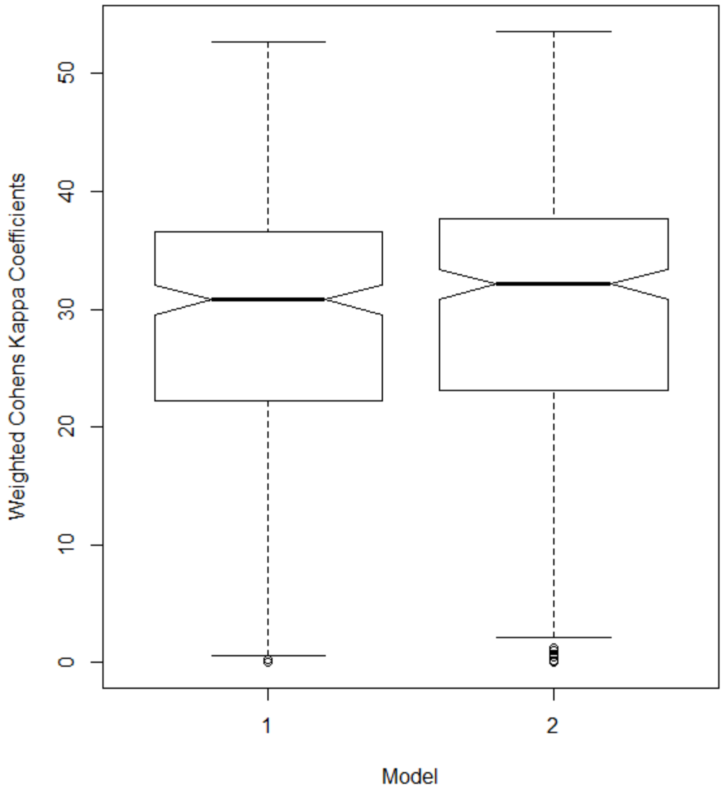

Figure A2: Differing model performance, measured using Cohen's Weighted Kappa Coefficient (Landis & Koch 1977), between models trained including marine cells in the SAC calculation as a zero (1) and those including marine cells in the SAC calculation as missing data (2). A Kruskal-Wallis rank sum test revealed no significant difference (X= 1.7328, p-value = 0.1881), as indicated by notches on box plots.

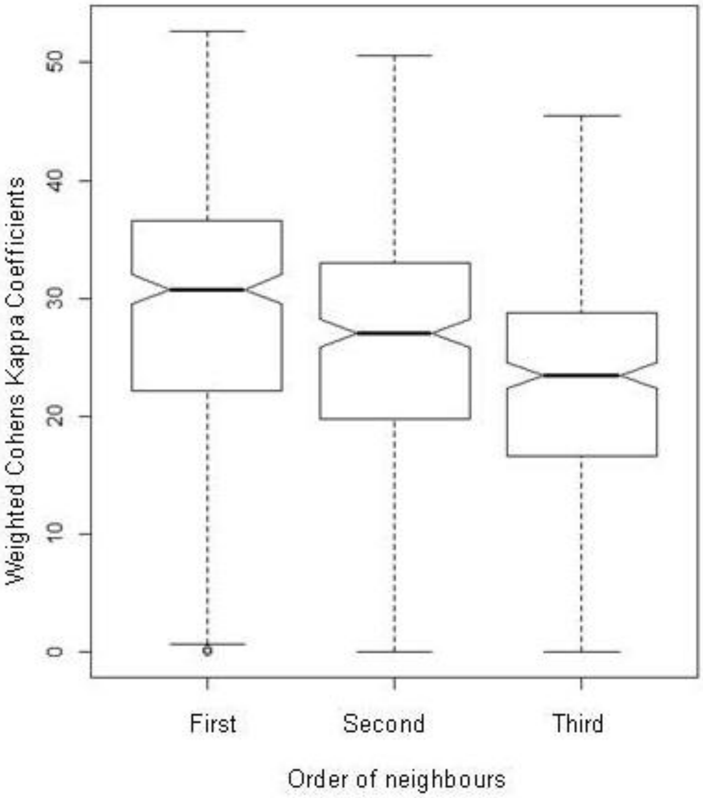

Figure A3: Model performance, measured using Cohen's Weighted Kappa Coefficient (Landis & Koch 1977), for models trained using an increasing number of neighbouring cells, as indicated by the order of neighbours, in the measure of spatial autocorrelation. First order neighbours constitute all cells adjacent to the cell of interest. Second order neighbours, include cells adjacent to first order neighbours when calculating the measure of spatial autocorrelation, along with first order neighbours, and so forth over increasing orders of neighbours.

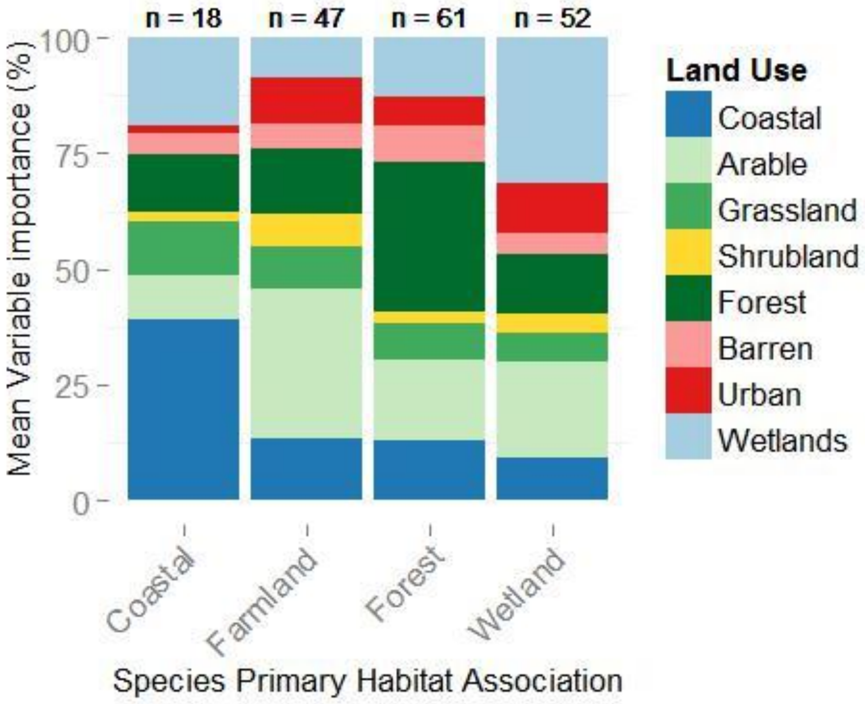

Figure A4: Mean importance of individual land use variables in determining local abundance for species with different primary habitat associations. Here, for the purpose of comparison, the summed importance of individual land use variables for each individual species was scaled to 100 and a mean taken across all species associated with each primary habitat association. N values indicate number of species associated with each primary habitat.

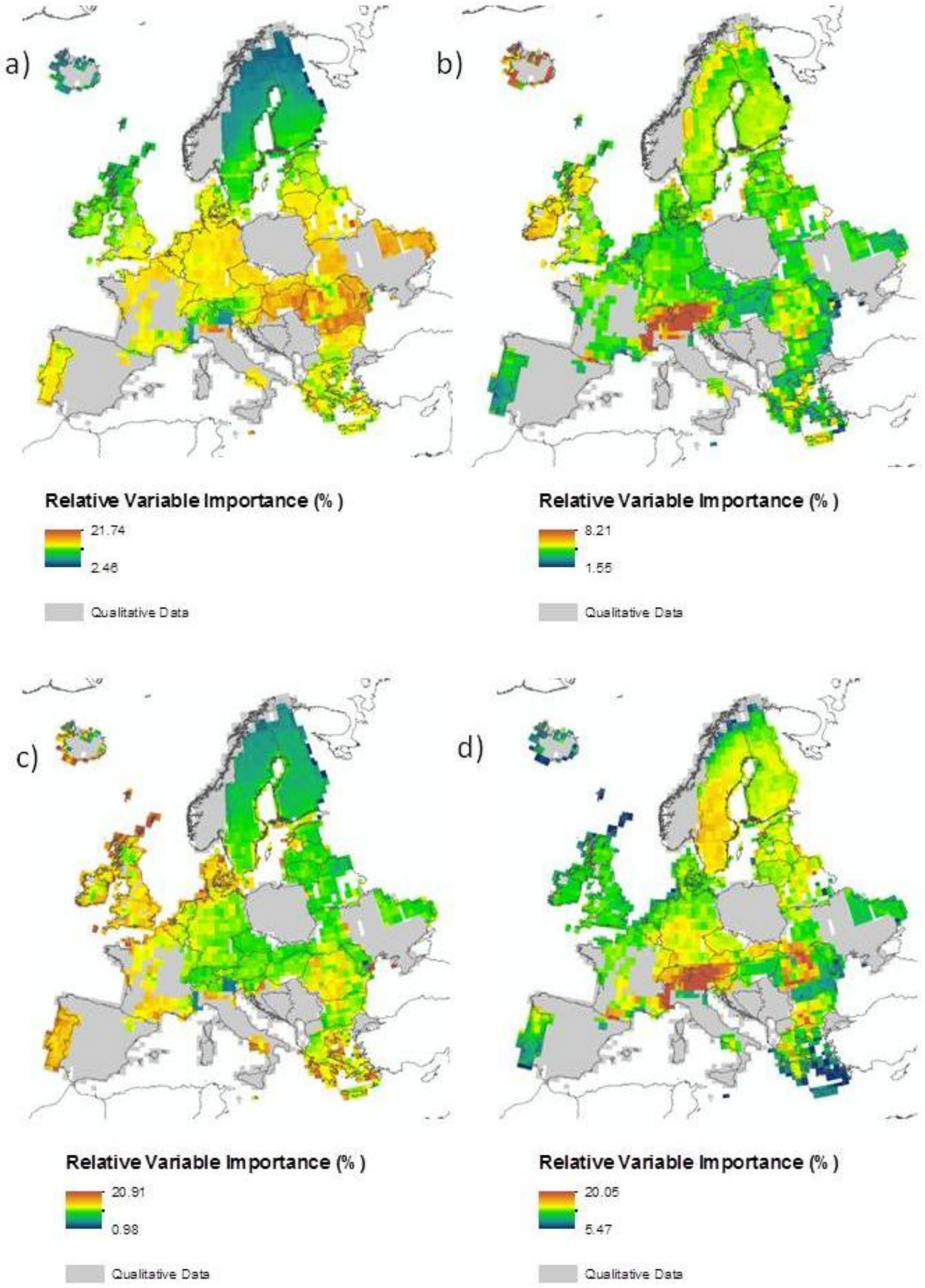

Figure A5: Spatial distribution of the mean relative importance of a variable for determining the abundance of European birds averaged across all species within a UTM grid cell: a) arable b) barren c) coastal, d) forest, e) grassland, f) shrubland, g) urban and h) wetland land use variables. Grey regions indicate areas omitted from analysis due to paucity of quantitative data. Note different scales for each plot. Figures (e) to (h) are overleaf.

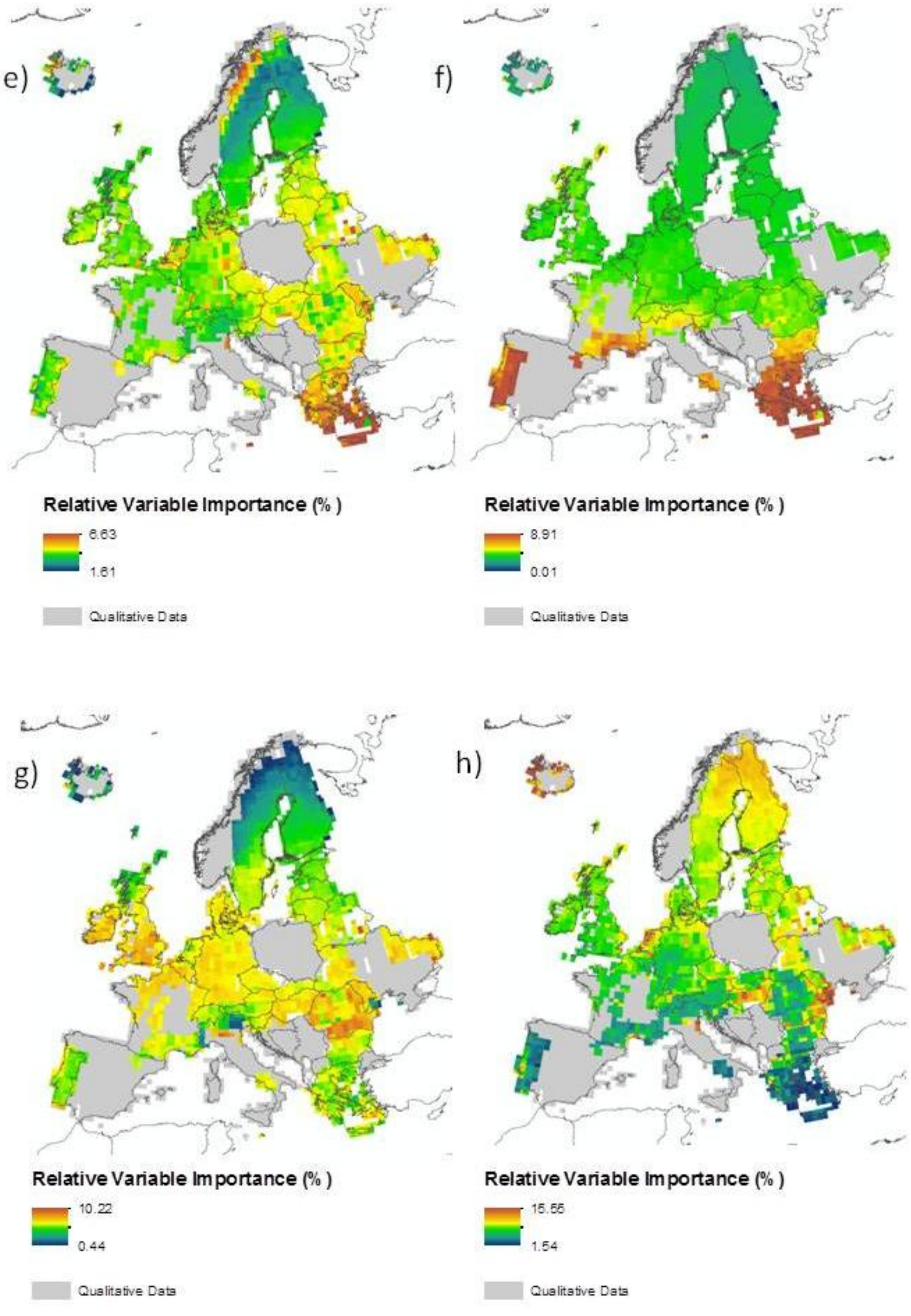

Figure A5: Continued

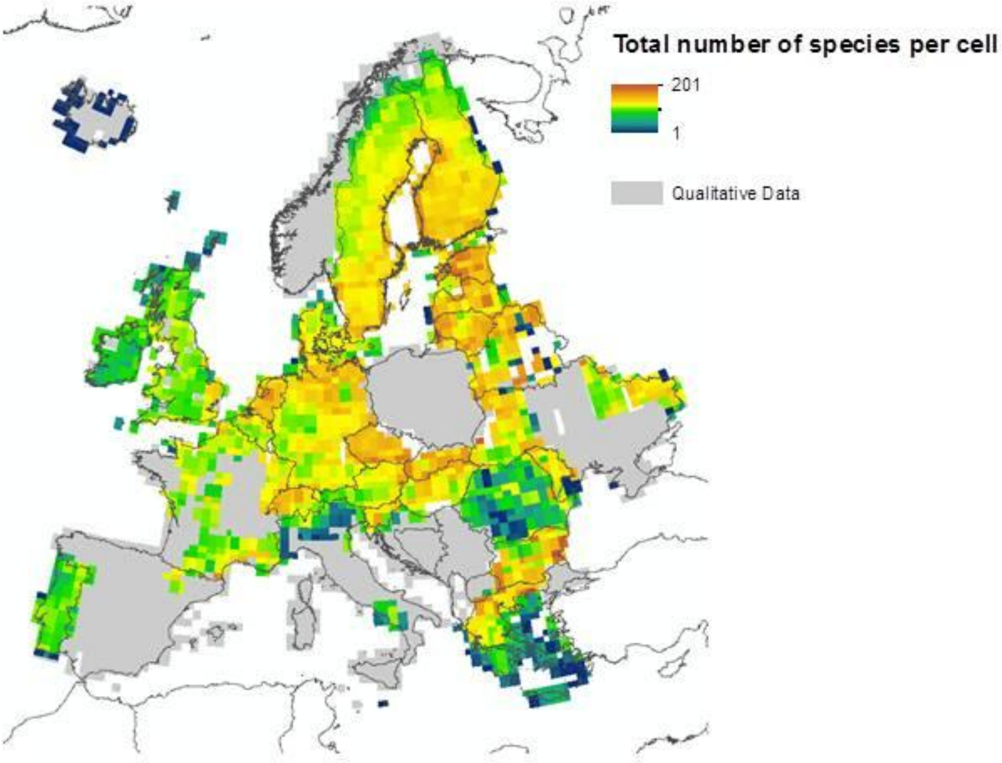

Figure A6: Spatial distribution of species richness across the region used in the study. Colours indicate the total number of species in each grid cell.

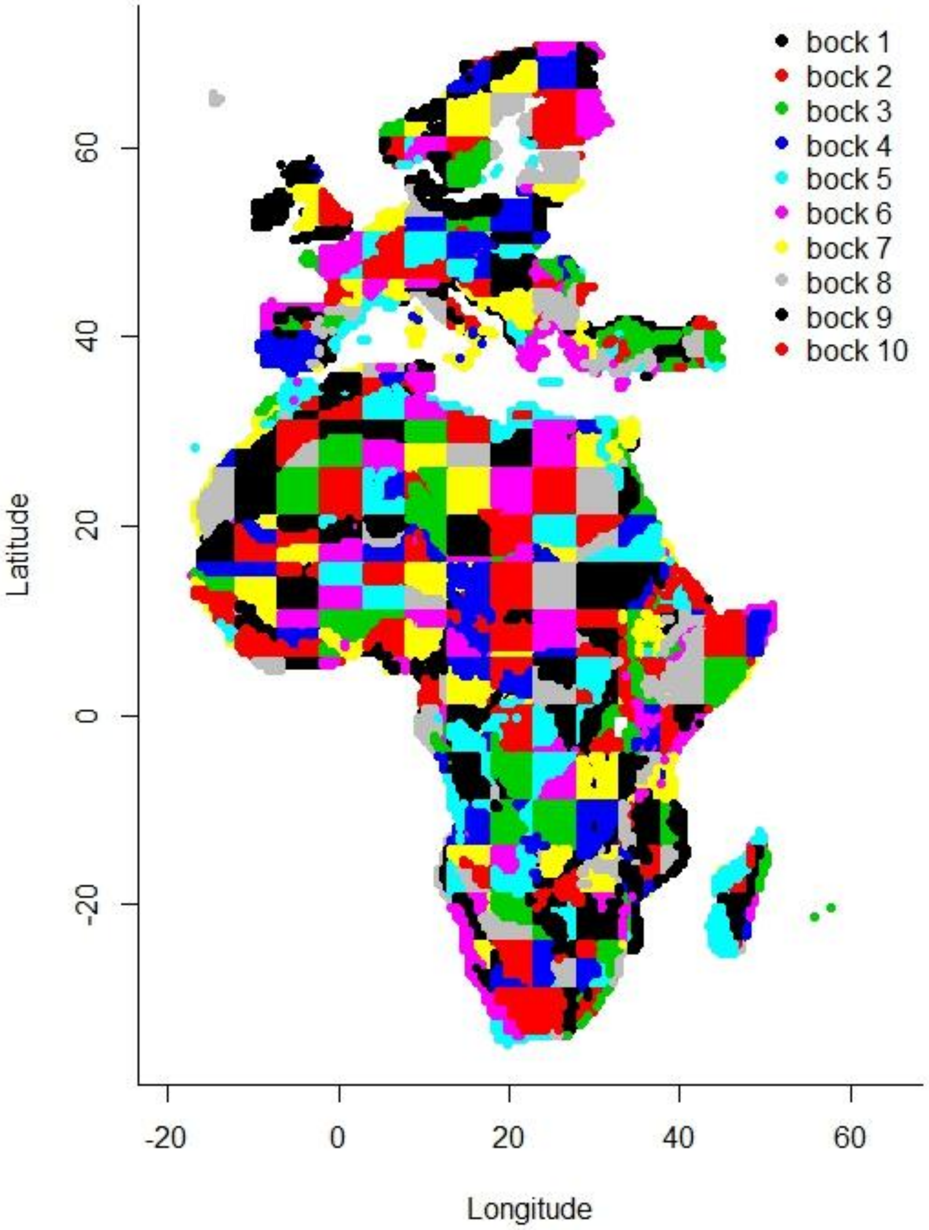

Figure A7: Example of sample blocking used to account for SAC within the SDMs. Here the combined are of Europe and Africa has been divided into 10 sampling blocks according to the ecoregion to which they belong and their bioclimate. This sampling procedure is designed so that mean bioclimate is similar across all blocks but that the full range of bioclimates is covered within each block.

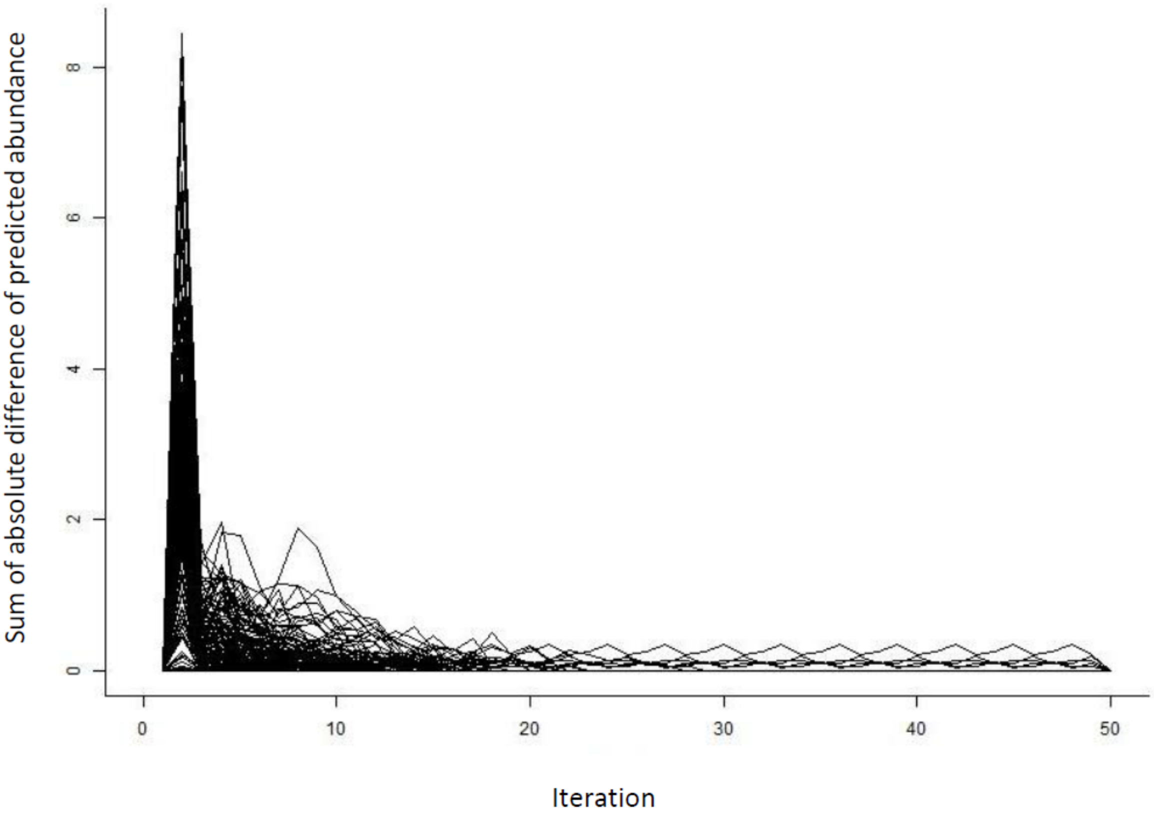

Figure A8: Convergence rates for the Gibbs sampling procedure. Each line represents the mean convergence rate across the ten projections for each of the 181 species.

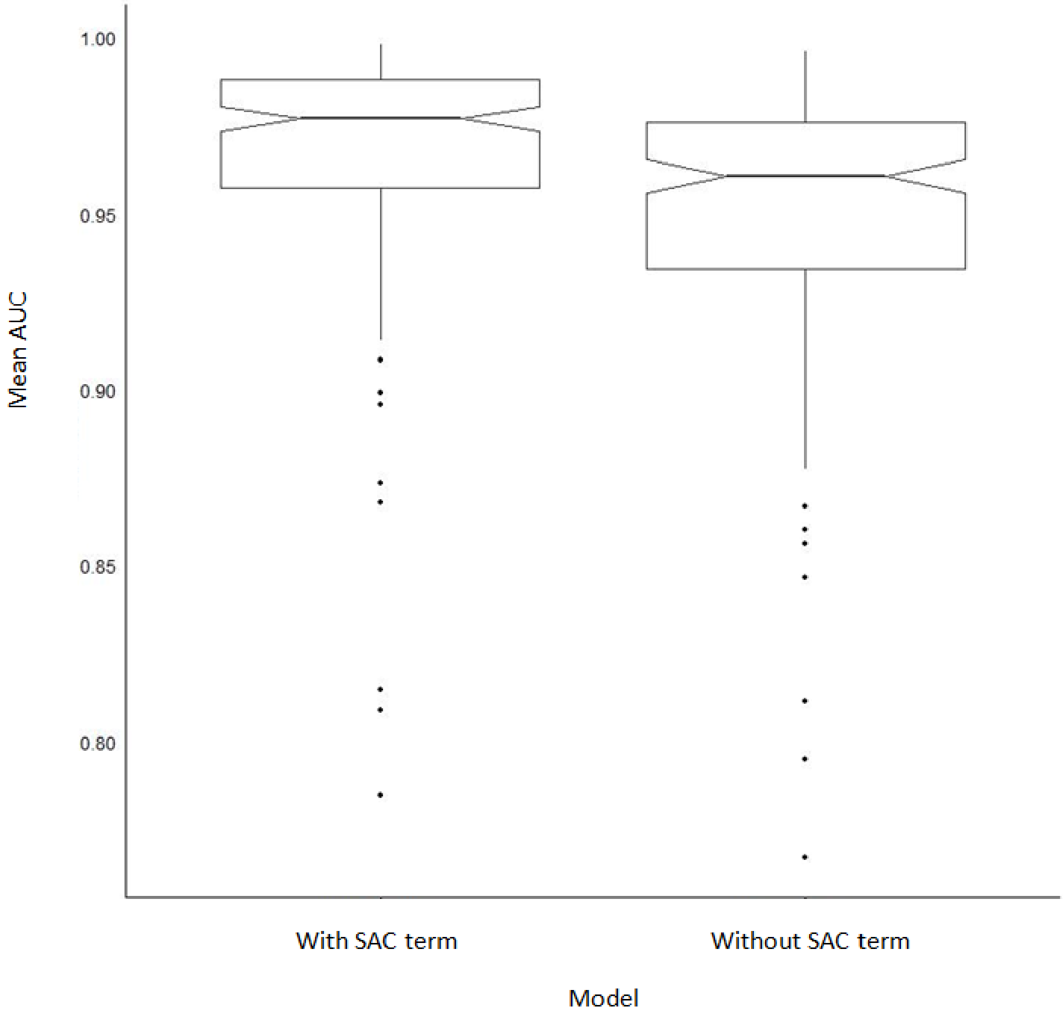

Figure A9: Mean AUC across the 10 models for each species for models both with and without an SAC term (n=181).

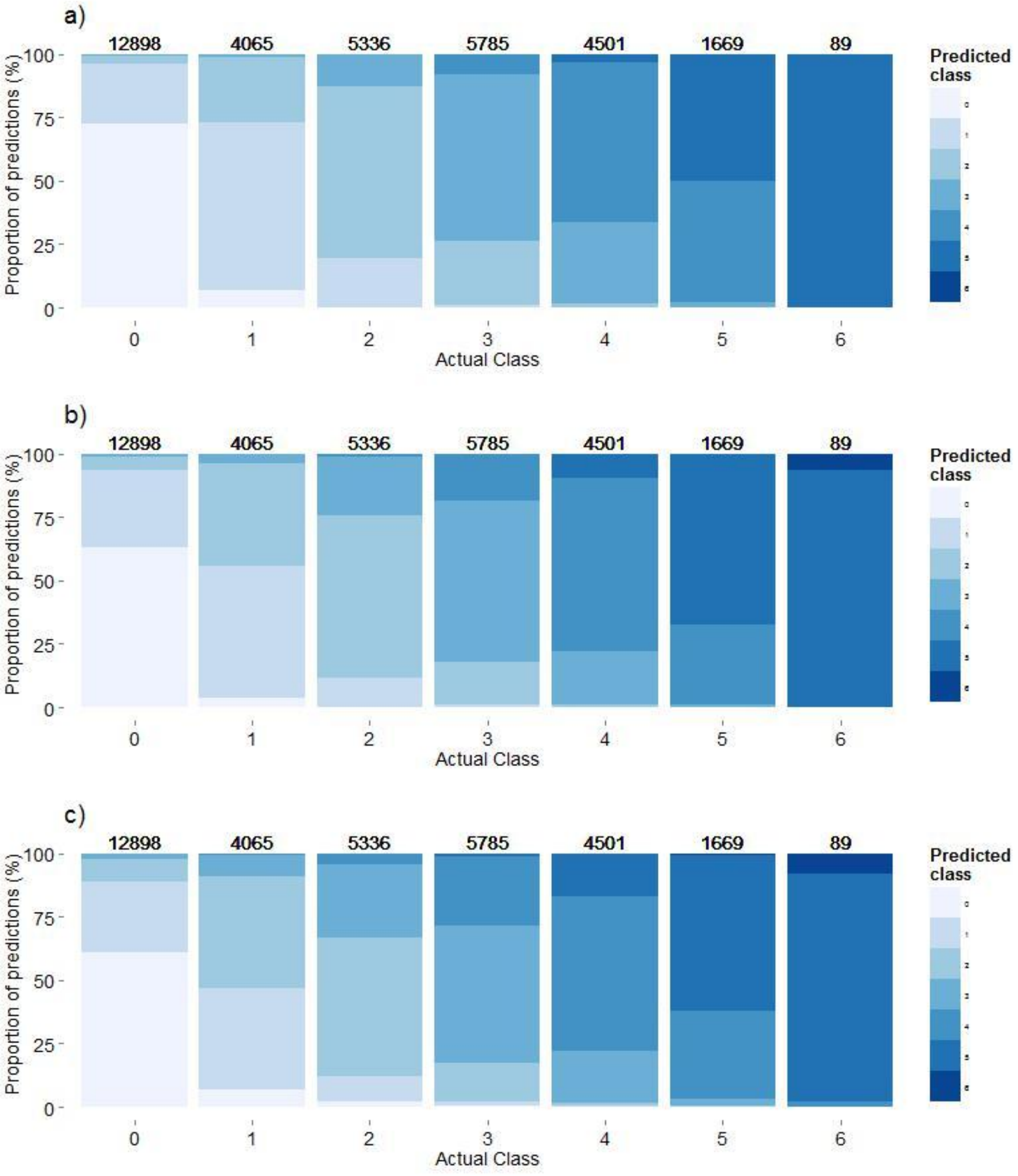

Figure A10: Abundance predictions across an area included in model calibration (Germany, Denmark and The Netherlands) from the three methods: a) abundance predictions from a model without SAC, b) abundance predictions using a single iteration of SAC, and c) after updating the abundance predictions using Gibbs sampling. Bars represent the mean proportion of predictions for each abundance class averaged across all 181 species. The number above each bar indicates number of observed cells within each abundance class.

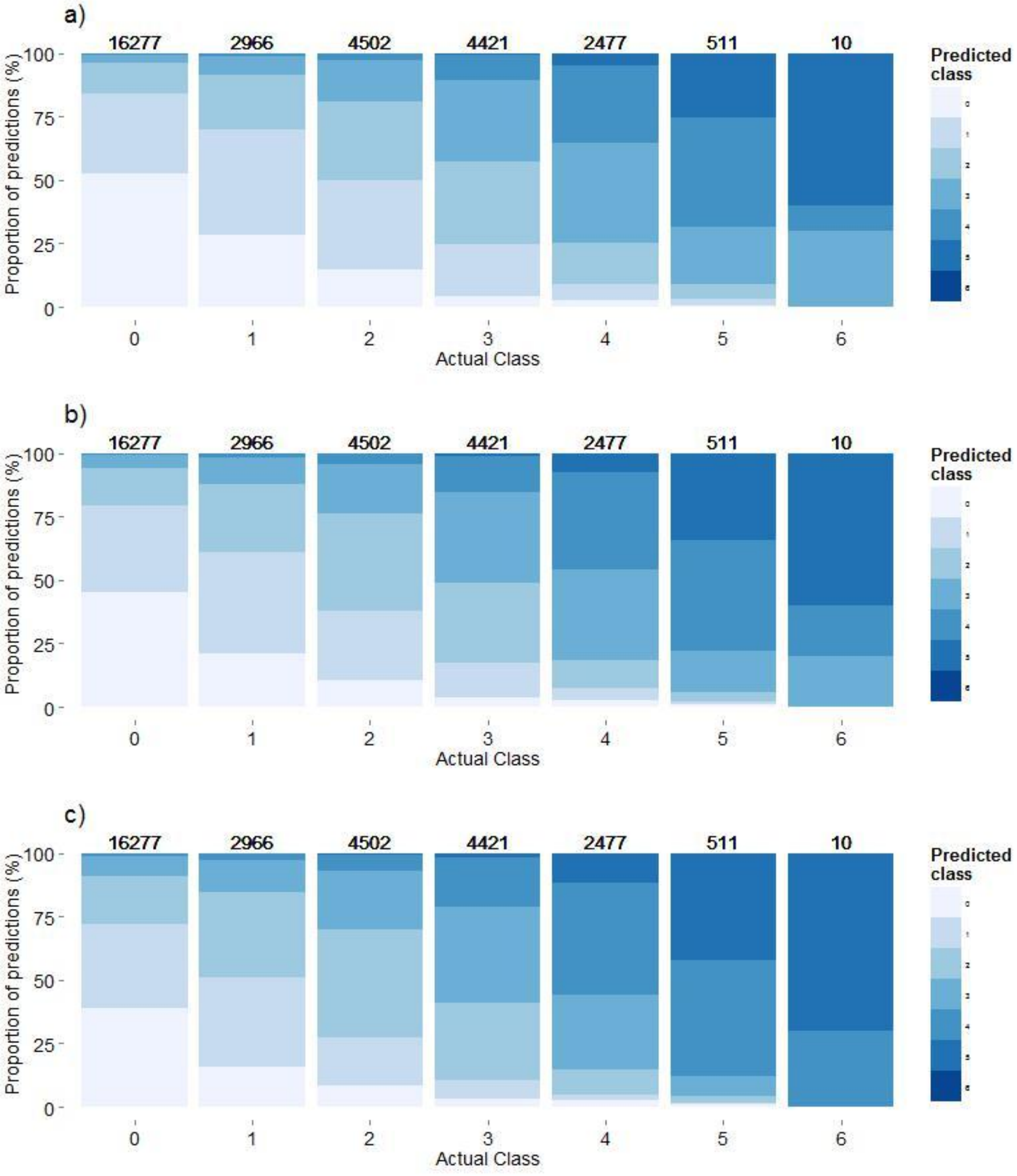

Figure A11: Abundance predictions across an area included in model calibration (Great Britain and Ireland) from the three methods: a) abundance predictions from a model without SAC, b) abundance predictions using a single iteration of SAC, and c) after updating the abundance predictions using Gibbs sampling. Bars represent the mean proportion of predictions for each abundance class averaged across all 181 species. The number above each bar indicates number of observed cells within each abundance class.