# *An Indicator of the Impact of Climate Change on North American Bird Populations*

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# An Indicator of the Impact of Climate Change on North American Bird Populations

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**Abstract:** The value of biodiversity for human welfare is becoming clearer, and for this reason there is increasing interest in monitoring the state of biodiversity and the pressures upon it. A recent study produced a biodiversity indicator showing that the pressure of climate change on bird populations in Europe has increased over the last 20 years (Gregory *et al.*, 2009). In North America, climate change effects on distributions and phenology have been documented for various taxa, especially the Aves. However, evidence of population declines resulting from climate change is comparatively limited. Here, I produce species distribution models based on climate for 380 bird species, all with information available on their population trends across the USA. Following Gregory *et al.*, I make predictions using these models based on past and future climate in the same region. From these I produce two metrics indicating how I expect these species to be affected by climate change. By comparing population indices for those species expected to be positively vs. those expected to be negatively affected by climate change, I derive Climatic Impact Indicators (CIIs) for North American birds. These summarize how the population level impacts of climate change, both positive and negative, have varied over the past 40 years. Much like the indicator for European birds, these indicators show an overall increase in climatic impacts on populations during a period of climatic warming. Furthermore, when indicators are downscaled to the state level around 80% of states exhibit an upwards trend in climatic impacts. I highlight that further work is needed to optimize the method used to produce a CII, and to determine what influences the slope of a CII. Nevertheless, the results presented here are strikingly similar to those seen across Europe, indicating that climatic impacts on populations may have increased across the Northern Hemisphere. **300 words.**

# 1. Introduction

Global climate is changing due to anthropogenic activity (IPCC, 2007), and the consequences of this for wild nature are apparent (Hughes, 2000). It is important to understand the extent of these effects and their underlying mechanisms, especially in light of the value of biodiversity for ecosystem processes (MA, 2005). One approach that has been proposed to assess the community level impacts of climate change is the assembly of climate change indicators for biodiversity (Devictor *et al.*, 2008, Gregory *et al.*, 2009). In particular, by comparing the population trends of species expected to be positively or negatively affected by climate change, Gregory *et al.* (2009) were able to summarize recent changes in climate change impacts on European bird populations. Here I propose to develop a climatic impact indicator (CII) relevant for North American birds in order to quantify the recent impacts of climate change on biodiversity in North America. The indicator will also present a valuable comparison to the impacts observed across Europe. This chapter will:

(i) outline the importance of biodiversity for human welfare, and explore climatic change as a driver of biodiversity decline;
(ii) review the mechanisms by which climate change impacts species at the population level;
(iii) consider biodiversity indicators as a bridge between scientists and policymakers;
(iv) evaluate the utility of species distribution models (SDMs) to explain recent and to project future impacts of climate change;
(v) outline the questions that will be addressed by this work and clarify the aims of the study.

## 1.1. Biodiversity and climate change

Biodiversity describes the variability among living organisms, which includes diversity within species, between species and of ecosystems (CBD, 1992). Almost by definition, biodiversity is coupled with ecological processes at several levels (Mace *et al.*, 2012) and can be considered a measure of the condition of life on earth. Biological systems possess an intrinsic value but are also the platform for a variety of functional processes, for example primary production and nutrient cycling (Cardinale *et al.*, 2012). In turn, these processes provide ecosystem services, such as food and water provision, which are necessary for human welfare (MA, 2005). For this reason, biodiversity conservation strategies might go hand in hand with poverty alleviation efforts (Bullock *et al.*, 2011, Turner *et al.*, 2012).

Experimental evidence has frequently revealed relationships between biodiversity and ecosystem function (Loreau *et al.*, 2001), but the importance of this relationship at a landscape scale has been contested (Schwartz *et al.*, 2000). Long term grassland experiments have demonstrated that even where species richness is high, the impacts of biodiversity loss on functional processes may be substantial (Reich *et al.*, 2012). Recent meta-analyses confirm that biodiversity declines are often associated with a reduction in ecosystem function (Cardinale *et al.*, 2011), and these effects are comparable in magnitude to those caused by other global environmental changes such as nutrient pollution (Hooper *et al.*, 2012). Following this, biodiversity loss either directly influences or is strongly correlated with the state of many ecosystem services (Cardinale *et al.*, 2012). Given the extremely high economic value of these services and their contribution to human well-being, recent biodiversity declines are of great concern (Butchart *et al.*, 2010, Costanza *et al.*, 1997, MA, 2005, Rockstrom *et al.*, 2009).

Recent biodiversity losses are unprecedented; pressures exerted by growing human populations have triggered extinction rates up to 1000 times higher than those prior to modern human existence (Pimm *et al.*, 1995). However, as well as causing species extinctions, drivers of biodiversity decline may also diminish other biodiversity metrics such as species abundance, community structure and the quality and extent of available habitat (Pereira *et al.*, 2010). The main drivers of biodiversity decline in terrestrial systems between 1990 and 2100 have been identified as follows, ranked in order of relative effect size: land use change, climate change, nitrogen deposition and acid rain, biotic exchange, and atmospheric carbon dioxide (Sala *et al.*, 2000). Whilst future trends in land use change and biotic exchange are expected to differ between biomes, pressures such as climate change and nitrogen pollution are predicted to increase universally (MA, 2005). There is also a possibility that extinction drivers may interact synergistically; one driver may amplify the effects of another, and in this case greater rates of biodiversity loss are anticipated (Sala *et al.*, 2000). Acting alone, rapid climatic changes in the Quaternary period gave rise to limited extinctions (Botkin *et al.*, 2007). Nevertheless, climate change is likely to have a greater impact on biodiversity when combined with other modern anthropogenic pressures such as land use change (Brook *et al.*, 2008). Experimental microcosms have revealed a synergistic interaction between habitat fragmentation, harvesting and climate change effects on populations (Mora *et al.*, 2007). In light of this and other evidence, climate change is thought of as a serious threat to biodiversity which is likely to become increasingly prominent in the future (Thuiller, 2007).

Global average temperatures increased by around 0.74°C between 1906 and 2005, and this change has been attributed largely to anthropogenic factors (IPCC, 2007). Biodiversity is expected to respond to many aspects of climate change, including seasonality of rainfall and extreme events such as floods and droughts (Bellard *et al.*, 2012). However, a huge number of biological responses to climate change have already been documented and the majority correspond with changes in temperature (Parmesan, 2006). A recent review has conceptualized the ways in which species can react to changes in climate by considering the movement of their niche along three axes: time (phenological change), space (distributional change) and self (physiological change) (Bellard *et al.*, 2012, Figure 1.1). Theoretically, where populations or species fail to adapt or evolve along one or more of these axes, they will become locally or globally extinct. Whilst local extinctions resulting from climate change have been well documented (Franco *et al.*, 2006, Parmesan *et al.*, 1999, Sinervo *et al.*, 2010), evidence of global extinctions caused by climate change is present but scarce (Pounds *et al.*, 2006). That said, it has been proposed that the process of extinction due to climate change may be time-delayed (Thomas *et al.*, 2006) much like extinctions due to habitat fragmentation (Tilman *et al.*, 1994). An important prerequisite to extinction, though, is population decline (Caughley, 1994).

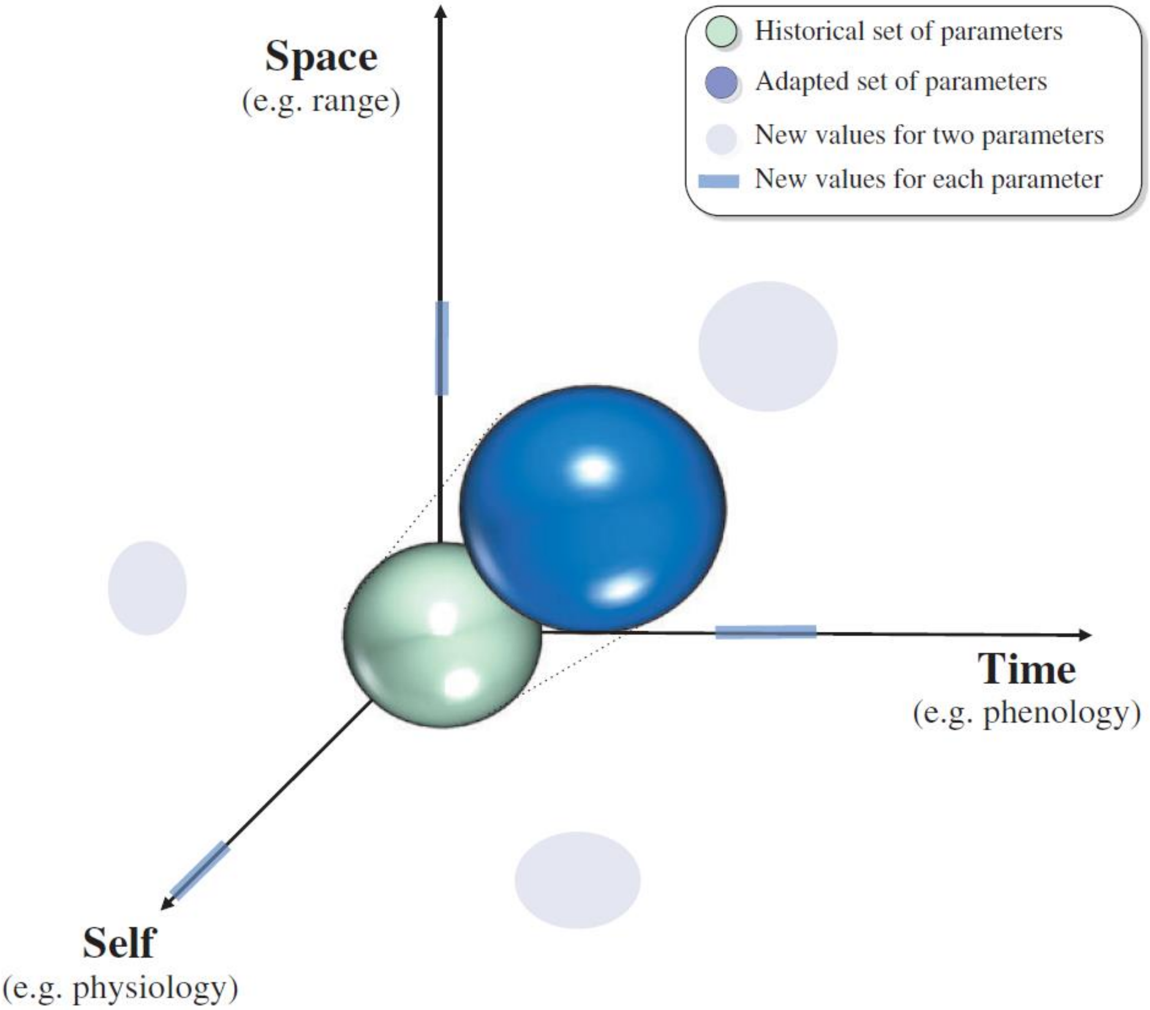

**Figure 1.1.** Conceptual diagram from Bellard *et al.* (2012). Shown are three directions of biological responses to cope with climate change. Axes represent movements in space (e.g. widespread latitudinal range shifts (Hickling *et al.*, 2006)), time (e.g. advanced leafing and flowering dates (Menzel *et al.*, 2006)) and self (e.g. physiological changes in tropical fishes (Johansen & Jones, 2011)).

## 1.2. Mechanisms by which climate change affects populations of species

Large populations of species of conservation concern are more desirable than small populations; one reason for this is that the latter are at a higher risk of extinction due to Allee effects (Brook *et al.*, 2008). Even ignoring extinction risk, population size is an important biodiversity metric with implications for ecosystem services (Mace, 2005). Continued population declines occurring in many biological systems are considered to be economically catastrophic (Balmford *et al.*, 2002) and such changes may take a long time to reverse, with the example of depleted stocks of marine fishes (Hutchings, 2000). Furthermore, population declines in more familiar species can be of great concern to the general public, as illustrated by Britain's relationship with its breeding birds (Greenwood, 2003, in Balmford et al. 2003). Climate change can heavily influence biodiversity at the population level, and this has already happened through a variety of mechanisms. Shifts along the "time" and "space" axes of Bellard et al. (2012) can be and have been responsible for changes in species' abundance. A failure to respond adequately along these axes may also cause population declines, especially where species interactions are altered in the process (Cahill *et al.*, 2013).

The most common reports of biological responses to climate change concern changes in species' phenologies (Parmesan, 2006). Advances in timing of events such as leafing, flowering and fruiting have been widespread, and these are correlated with changes in temperature (Menzel *et al.*, 2006). Phenological responses also occur in animals, as exemplified by earlier egg laying dates of birds in the UK and North America (Crick *et al.*, 1997, Dunn & Winkler, 1999). A large scale study on the pied flycatcher even claimed to establish a causal relationship between climate change and advances in breeding dates (Both *et al.*, 2004). These advances in egg-laying dates have led to population declines; black grouse offspring are exposed to colder conditions with earlier hatching, resulting in increased mortality and population declines (Ludwig *et al.*, 2006). In addition, climate change has led to mismatches in timing between birds breeding and the peak abundance of food for nestlings (Visser & Both, 2005). Some populations of the pied flycatcher have failed to match the advance in timing of the peak abundance of their prey, and this has been linked to population declines of up to 90% (Both *et al.*, 2006). This may be common amongst migratory birds, as European species which have failed to adjust their migration date are generally the same species that are experiencing population declines (Moller *et al.*, 2008). Clearly phenological responses to climate change can strongly impact upon population size.

Climate change responses at the species level materialize not only through changes in timing, but through movements in geographical space. Species' boundaries have largely shifted to higher latitudes and altitudes during recent global warming (Thomas, 2010), demonstrating the importance of the relationship between climate and the broad scale distribution of species (Jiménez-Valverde *et al.*, 2011). Whilst many studies report species' range expansions to higher latitudes (Hickling *et al.*, 2006, Hitch & Leberg, 2007, Thomas & Lennon, 1999), range retractions at the low latitude boundary are detected less frequently (Thomas *et al.*, 2006). This is also the case for altitudinal shifts; cold upper boundaries shifted upwards far more frequently than did warm lower boundaries in tropical studies (Thomas, 2010). Range shifts have been ascribed to local extinction gradients, whereby the ratio of extinctions to colonizations is greater at the warm range margin than at the cool range margin (Franco *et al.*, 2006, Parmesan *et al.*, 1999). Under these conditions, if there is a lack of suitable habitat at the expanding range margin, species' ranges may be prevented from expanding (Hill *et al.*, 1999) and as such might contract overall. Given the established relationship between species' abundance and range size (Brown, 1984), it follows that expansions and contractions will be associated with population increases and declines. Although paleoecological studies reveal that range expansions and contractions have occurred in response to climate for tens of thousands of years, the dispersal ability of species is now heavily limited across habitats fragmented by human activity (Dawson *et al.*, 2011). For this reason, movements of species' ranges could result in expansions, but also retractions and population declines.

A recent meta-analysis found that as well as abiotic changes, changing species interactions are a prominent factor affecting species populations under climate change (Cahill *et al.*, 2013). Direct climate induced impacts on prey or pathogens can be a mechanism for population change, and may be considered distinct from mismatches in species interactions caused by phenological change (Cahill *et al.*, 2013). For example, declines in the golden plover in the UK have been attributed to reduced abundance of their cranefly prey resulting from high summer temperatures (Pearce-Higgins *et al.*, 2010). Conversely, declines in frogs of the genus *Atelopus* were caused by the spread of a fungal pathogen which was facilitated by climate change (Rohr & Raffel, 2010). Where climate change improves species' chances of colonization and establishment in foreign environments, new invasive species could emerge (Hellmann *et al.*, 2008) with possible consequences for native populations (Roy *et al.*, 2012). There are also concerns that existing alien species may increase their invasive potential if climate change enhances their competitive ability (Peterson *et al.*, 2008, Thuiller, 2007). Examples where climate indirectly affects populations through species interactions appear as frequently as those with direct abiotic causes (Cahill *et al.*, 2013).

## 1.3. Biodiversity Indicators for Conservation and Policy

Many governments have pledged through the Convention on Biological Diversity to reduce the rate of biodiversity loss by 2010, and this has signified their acknowledgement of the value of biodiversity for human welfare (Balmford *et al.*, 2005). A variety of biodiversity indicators have been developed to assess progress towards this broad target; these measure pressures on biodiversity (e.g. climate change), the state of biodiversity metrics (e.g. population size), and the degree of political response to biodiversity loss (Mace & Baillie, 2007). A study by Butchart *et al.* (2010) collated a number of indicators to produce a timely evaluation of the achievement of the 2010 target, and found that the rate of biodiversity loss had not significantly decreased. In fact, indicators of biodiversity pressures had actually increased overall (Butchart *et al.*, 2010). This study demonstrated how broad biodiversity indicators can be used to assess conservation efforts, whilst others demonstrate a capacity for indicators to inform policy decisions at a more local scale (Nicholson *et al.*, 2012).

Despite the clear utility of indicators, there are still many aspects of biodiversity conservation which have not been covered by efforts to date (Walpole *et al.*, 2009). Spatial, temporal and taxonomic biases impede the robustness of indicators, and this could be improved in order to assess more specific targets in future (Butchart *et al.*, 2010, Jones *et al.*, 2011, Mace *et al.*, 2010). In addition, many indicators have arisen primarily because of data availability, and not their rigorous methods or biodiversity relevance (Mace & Baillie, 2007). Biodiversity indicators are not greatly informative when presented alone, and should be complimented by a detailed understanding of underlying ecological factors (Gregory *et al.*, 2005). For an indicator to be any use at all, though, it must be designed such that it is suitable for its function.

The gap between scientists and policymakers may have hampered conservation efforts in the past (Mooney & Mace, 2009), and in order to effectively bridge this gap an indicator must be clear and methodologically sound (Mace & Baillie, 2007). In the interests of clarity an indicator should state which attribute of biodiversity it represents, and whether it measures a biodiversity pressure, state, or response (Mace & Baillie, 2007). It is also important to determine the extent to which the indicator is intended to represent biodiversity as a whole (Gregory *et al.*, 2005). Once the purpose of the indicator is clearly defined, appropriate data and methods must be implemented in its design. For example, gaps or biases in the data should be accounted for, and the relationship between the indicator and biodiversity in general should be substantiated (Gregory *et al.*, 2005). Money, time and expertise are always finite, so a more practical indicator is always desirable (Gregory *et al.*, 2005).

Examples of headline indicators of the state of biodiversity that were analyzed by Butchart *et al.* (2010) include a Wild Bird Index, which comprises aggregated population trends for habitat specialist birds across Europe and North America. The Climatic Impact Indicator for European birds developed by Gregory *et al.* (2009) is an example of an indicator of a pressure on biodiversity, because population change is linked to a single driver. An example of an indicator of political response to biodiversity declines is the coverage of protected areas over time (Butchart *et al.*, 2010), which represents the extent of action taken by authorities to prevent further declines. Examples such as these, whilst they are imperfect, are informative at the broadest scale. Indicators represent a conduit through which the most politically relevant information on biodiversity can be presented to and understood by non-scientists.

### 1.3.1. Using Birds to Represent Biodiversity

A large proportion of the information available to assess biodiversity change corresponds to the distributions and populations of avian species. Owing to the continued popularity of birds amongst the general public, these data are also being collected more widely and thoroughly over time (Greenwood, 2007, Gregory *et al.*, 2005). Regional surveys of bird populations are unmatched in scale by surveys on other species groups, and the best examples of these include the North American Breeding

Bird Survey (BBS) (Pereira & David Cooper, 2006). Around 2,500 of over 5,100 roadside survey routes across North America are surveyed each year, providing data for over 420 bird species (Sauer & Link, 2011). Information from the BBS has been useful to understand patterns in bird populations across both space and time, as well as to monitor invasive species (NABCI, 2011, Robbins *et al.*, 1986). Just one example of the usefulness of this huge dataset is the analysis of the causes of declines in the majority of North American grassland birds (Peterjohn & Sauer, 1999). Other examples have involved tracking direct and indirect effects of pathogens on bird populations (LaDeau *et al.*, 2007, Nocera & Koslowsky, 2011). To account for problems such as observer bias that exist in data from the BBS (Link & Sauer, 1998, Sauer *et al.*, 1994), more precise population trend estimates are now being derived using hierarchical models rather than route-regression (Link & Sauer, 2002, Sauer & Link, 2011). Data from large scale bird surveys have had an impact upon policy in the UK (Greenwood, 2003), indicating the importance of such schemes in the context of biodiversity conservation. In addition, population trends have been used to measure the benefits of conservation policy in Europe (Donald *et al.*, 2007) showing that long term BBS data is useful not only to inform conservation policy, but to evaluate it.

Birds are a highly appropriate study taxon when investigating species responses to climate change; this group has shown a marked reaction to changing climates across many species and geographical regions (e.g. Crick, 2004, Hitch & Leberg, 2007, Thomas & Lennon, 1999). There is a relationship between the broad scale distribution of birds and climatic variables (Araújo *et al.*, 2009, Jiménez-Valverde *et al.*, 2011) although the strength of this relationship has been contested (Beale *et al.*, 2008, Beale *et al.*, 2009, but see Peterson *et al.*, 2009). This relationship, as well as the dispersive ability of most birds, may go some way towards explaining the ubiquity of avian distributional responses to climate change. Phenological responses by birds are also widespread (Crick, 2004) as exemplified by advanced egg laying dates in many species (Crick *et al.*, 1997, Dunn & Winkler, 1999). Distributional and phenological changes result in altered species interactions (Cahill *et al.*, 2013), which suggests that climate change responses in birds will affect other taxa and vice versa. It is important to document and understand these signal responses to gauge not only how birds react to climate change, but how other components of biodiversity might do so. Studies projecting avian responses under future climate change are prevalent (Matthews *et al.*, 2004) and often predict that ranges of the majority of species will decrease (Barbet-Massin *et al.*, 2012, Jetz *et al.*, 2007). These predictions may also be alarming for other species groups, although this depends on the extent to which birds can represent biodiversity as a whole.

Recent studies assessing the use of bird species richness to predict the richness of other groups suggest that birds do not always make suitable biodiversity indicators (Eglington *et al.*, 2012). However, as well as testing spatial relationships between diversity of birds and of other taxa, it is important to consider whether temporal change in assemblages of birds reflects changes in other groups (Favreau *et al.*, 2006). Birds tend to be near the top of the food chain, and as a result it is thought that they are highly responsive to changes in their biotic environment (Gregory *et al.*, 2005). This might explain the evidence that links population trends in birds with trends in other taxa; many studies have shown declines of farmland birds in parallel with declines in other groups, especially invertebrates, resulting from agricultural intensification (Benton *et al.*, 2002, in Gregory *et al.*, 2005, Robinson & Sutherland, 2002). In light of such evidence, Gregory *et al.* (2005) argue that their farmland bird population index might hold some value as a biodiversity indicator. However, it is not uncommon for some species groups to respond negatively to a driver of biodiversity change whilst others respond positively, so there is always a need for caution when using one species group to represent many others. Whilst birds may not always be able to represent biodiversity as a whole, they are important in their own right owing to their role in ecosystem services such as pest control and seed dispersal (Whelan *et al.*, 2008). Indicators of population trends in bird species are important for conservation policy even if they are not representative of trends in other taxa.

## 1.4. Species distribution modeling in the context of climate change

The applications of Species Distribution Models (SDMs) are extremely diverse, ranging from spatial conservation planning to discovery of new populations of species (Araújo & Peterson, 2012). One of the most popular uses of SDMs is to predict future effects of climate change on biodiversity (e.g. Thomas *et al.* 2004). Thomas *et al.* (2004) used

SDMs to predict the change in range size of a variety of taxa under climate change with two extreme dispersal scenarios and predicted that 15-37% of taxa within the study area would be committed to extinction by 2050. Whilst such studies have been criticized in light of the variability between different modeling processes (Thuiller *et al.*, 2004) and possible misrepresentation of results through sensationalist media (Ladle *et al.*, 2004), they highlight the utility of SDMs to speculate future impacts of climate change on biodiversity. SDMs rarely take into consideration biotic interactions, species dispersal or evolutionary change (Pearson & Dawson, 2003). In light of this, whilst models may be useful for asking 'what if' questions, it is important not to place too much faith in their projections as reliable predictions for the future (Araújo *et al.*, 2005).

When analyzing species distributions with regard to climate change, SDMs often focus on establishing the 'bioclimate envelope' of a species (Pearson & Dawson, 2003). The bioclimate envelope may be determined in two main ways: by correlating a species' current distribution with climate variables (the correlative approach), or by understanding a species' physiological responses to changes in climate (the mechanistic approach) (Hijmans & Graham, 2006). A variety of model classes are commonly used to calculate the bioclimate envelope, amongst them Generalized Linear Models (GLM), Generalized Additive Models (GAM), Classification Tree Analyses (CTA) and Artificial Neural Networks (ANN) (Thuiller, 2004). In fact, recently adopted modeling methods such as machine learning have been shown to outperform older ones (Elith *et al.*, 2006). Once the climate envelope of a species has been determined, resultant models may be applied to future climate scenarios to project the potential future distribution of that species (e.g. Huntley *et al.*, 1995). However, there is a high level of variability between the broad range of common modeling techniques (Pearson *et al.*, 2006, Thuiller, 2003, Thuiller, 2004) and climate change scenarios (Thomas *et al.*, 2004).

To account for such uncertainty, a process termed 'ensemble forecasting' has been proposed; this involves making projections using a range of different models and scenarios to produce more robust forecasts (Araújo & New, 2007). A suggested platform for this process is BIOMOD (Thuiller *et al.*, 2009), a package implemented in the statistical analysis program R (R Development Core Team, 2012). BIOMOD offers a convenient and accessible means to project species distributions, as it has options to include a variety of model classes, validation methods and climate scenarios (Thuiller *et* *al.*, 2009). However, even when using ensemble forecasting, projections are dependent on both the species analyzed and the classes of model used (Thuiller, 2003, Thuiller, 2004). This necessitates validation of SDMs before reaching any sound conclusions from them.

Validation of SDMs may be carried out using three main methods: resubstitution, data partitioning and using independent data. Resubstitution is the process whereby models are validated using the same data which was used to calibrate them (Araújo *et al.*, 2005). Resubstitution has the fault that if a model overfits to the calibration data, validating it against the same data may misrepresent the model's accuracy when predicting independent data (Araújo *et al.*, 2005). Partitioning of the data to emulate an independent data set (often splitting data 70:30, e.g. Thuiller, 2003, Thuiller, 2004) assumes that random samples from the original data constitute independent samples (Araújo *et al.*, 2005). This is not true; both resubstitution and data partitioning fail to account for spatial autocorrelation or temporal correlation in species distributions and climate variables (Araújo *et al.*, 2005). It has been shown that validating models using non-independent data (i.e. resubstitution or data partitioning) produces over optimistic estimates of model accuracy when compared to validation using independent data (Araújo *et al.*, 2005). Whilst rarely available, independent data is desirable when validating SDMs. One way to obtain such data is from known distributions of the study species in different regions (Peterson, 2003). Whilst models can still be useful without truly independent data to validate them, this is contingent on their appropriate use and acknowledgement of their assumptions and limitations (Araújo & Peterson, 2012).

SDMs often use presence-absence data for the distributions of species (Thuiller *et al.*, 2009), but models derived from these data can be used to make inferences with regard to spatial patterns in species abundance (VanDerWal *et al.*, 2009). There exists a central tendency of species' abundance in space, and it is thought that this is associated with gradients in environmental suitability (Brown, 1984). SDMs allow an index of environmental suitability to be derived by correlating present distributions of a species with environmental variables, and this index can be used to predict species abundance (Van Couwenberghe *et al.*, 2012). Similar approaches have related modeled temporal changes in climatic suitability for bird species to their recent population trends, offering a form of validation for the use of SDMs in future projections (Green *et al.*, 2008). In this way, SDMs can be used not only to predict changes in biodiversity due to climate change, but to retrodict them. Gregory *et al.* (2009) took this a step further and used the relationship between trends in populations and climate suitability to produce a simple climatic impact indicator for European bird populations from 1980-2005. However, another study demonstrates that climate suitability is less able to predict population stability, which is an important factor for long term population persistence (Oliver *et al.*, 2012). SDMs can be used to offer an indication of some population-level impacts of recent climate change, but not all (Gregory *et al.*, 2009).

## 1.5. Aims

In this project I will make use of two freely available and independent datasets relevant to North American birds. Species distributions will be obtained from the BirdLife International database (BirdLife International, 2013) and population trends will be obtained from the North American Breeding Bird Survey (BBS) (Sauer *et al.*, 2012).

Using the distribution dataset, I will produce species distribution models (SDMs) relating the distributions of 384 avian species to bioclimate across North America. These SDMs will then be used to derive two metrics of the relationship between a given species and climate change: CST, which represents the slope of climatic suitability for a species between 1968 and 2011, and CLIM, which represents whether a species' range is likely to increase or decrease by the end of the century under projected climate change. Using these metrics, I will separate species into two groups – those expected to benefit from climate change, and those expected to lose.

Using the population trends dataset, I will summarize overall population change for each species between 1968 and 2011. Species level population trends will then be merged based on the two groups produced using SDMs. If climate change has affected avian populations since 1968, then species expected to benefit from climate change might increase in abundance, whilst others decline. It is on this basis that climatic impact indicators (CIIs) will be produced; these will compare population trends for the two groups of species, such that an increase in a CII over time will mean that "climate winners" have shown greater overall population increases than "climate losers" (Figure

1.2). The data used to produce SDMs and those used to produce population trends are independent, and so this result would be consistent with a strong impact of climate change on avian populations over the past half-century (Gregory *et al.,* 2009). Two CIIs will be produced for avian populations across mainland USA – one using CST to group species and one using CLIM.

Following this, state-level CIIs will be produced in order to deconstruct the USA CII and better understand climatic impacts on populations at more local scales. State-level CIIs will then be merged, however, producing a novel "composite" USA CII. This will offer a collective interpretation of climatic impacts on populations of avian species across the USA whilst retaining the resolution of the state-level approach.

During the production of CIIs, I will explore how the model class used to relate a species' distribution to bioclimate affects the outcome of a CII. I will also determine the outcome of using two different methods to classify species into those expected to be positively or negatively affected by climate change. The spatial and temporal scale of the study (first across the entire mainland USA, then at the state level, annually between 1968 and 2011) is often dictated by the availability of data on distributions and population trends.

The indicators produced will fill an important geographical gap amongst indicators on the pressure of recent climate change on biodiversity. This study will use similar methods to Gregory *et al.* (2009) on a separate region covering a comparable range of latitudes. This will bridge a significant geographical gap in current understanding of population level climate change impacts, and establish whether the trends observed across Europe are also occurring elsewhere. Using a novel method, I will also assemble CIIs at the state level and combine them to produce a composite USA CII. In doing so, I will optimize the production of simple CIIs that will ultimately be useful to monitor our progress towards broad biodiversity targets (Mace & Baillie, 2007). This will help to narrow the gap between scientists and policy makers in future (Mooney & Mace, 2009).

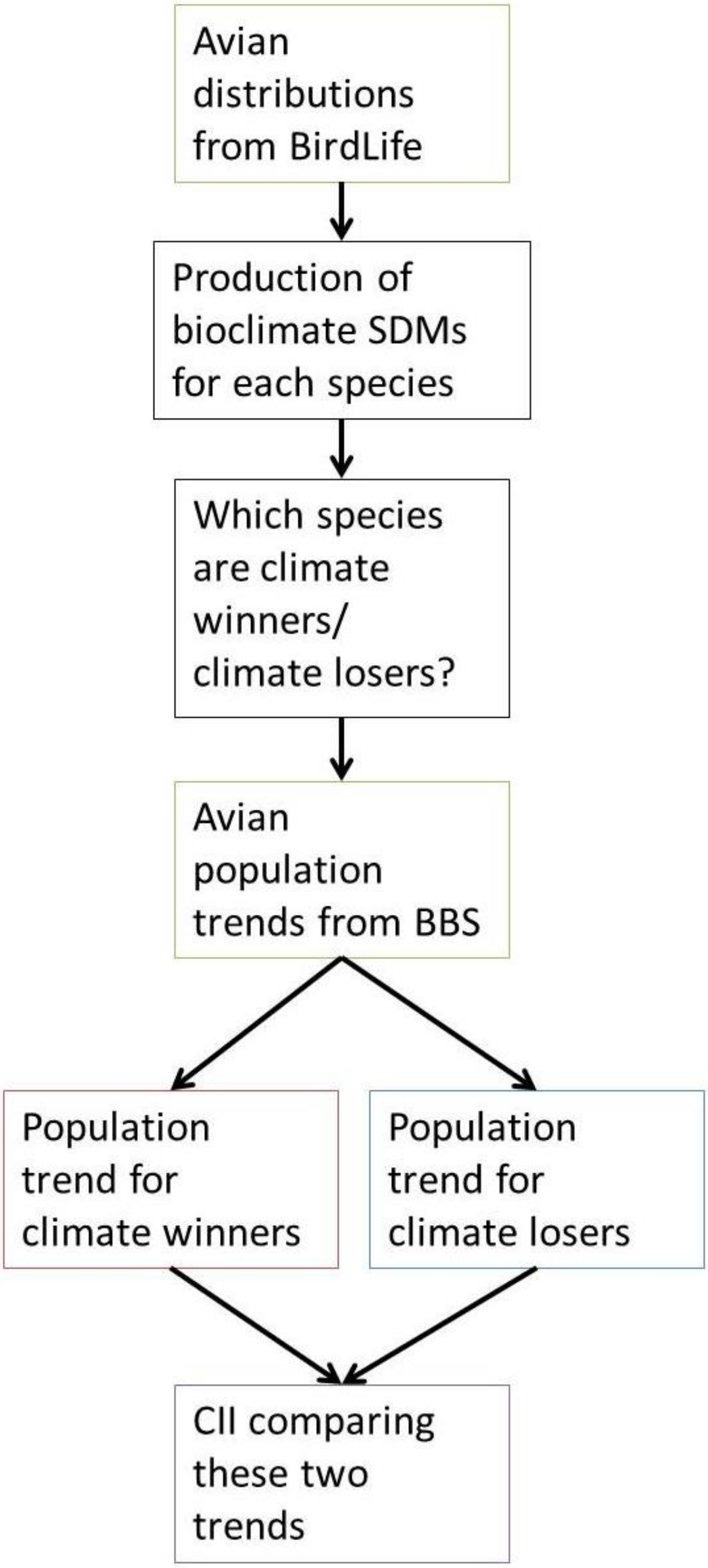

**Figure 1.2.** Flow diagram outlining the core stages of the production of a climatic impact indicator (CII).

# 2. Modeling Distributions of North American Bird Species Using Bioclimatic Variables

## 2.1. Introduction

Global average temperatures have been rising rapidly over the past 50 years (IPCC, 2007) and as a consequence species distributions have shifted uphill and towards the poles (Hickling *et al.*, 2006, Thomas, 2010). This response has been widespread across many taxa, demonstrating the significance of the broad scale association between climate and species' distributions (Jiménez-Valverde *et al.*, 2011). Species distribution models (SDMs) can make use of this relationship by correlating a species' occurrence with the climate found across its range (Pearson & Dawson, 2003). They may then be used to predict that species' distribution based on climate variables in a different time or place. For this reason SDMs have a variety of applications, ranging from predicting future effects of climate change on biodiversity (e.g. Thomas *et al.*, 2004) to retrodicting changes in population size based on climate suitability (Green *et al.*, 2008). Gregory *et al.* (2009) used SDMs to determine which European bird species were expected to be positively or negatively affected by recent climate change. This allowed a comparison of the population trends for these two groups, indicating how strongly recent climate change has affected populations of European bird species.

In order to make inferences from SDM predictions, it is important that they are adequately validated (Araújo *et al.*, 2005). Wherever possible SDMs should be evaluated using data that are independent of those used to calibrate them, but such data are rarely available. As a compromise, individual SDMs can be validated in the absence of independent data using the following methods:

> *Resubstitution:* SDMs are validated using the same data that were used to calibrate them. Predicted distributions based on the full calibration dataset are compared with observed distributions. However, if a model overfits to the calibration data, testing the model on the same data will misrepresent the model's accuracy (Araújo *et al.*, 2005).
>
> *Data partitioning:* The data are partitioned randomly to emulate an independent dataset (often splitting data 70:30, e.g. Thuiller, 2003, Thuiller, 2004). A model

built with the calibration data (70%) is used to predict the remaining test data (30%) in order to assess its performance. Whilst this approach is preferred to resubstitution, it assumes that random samples from the original data constitute independent samples (Araújo *et al.*, 2005).

Both data partitioning and resubstitution fail to account for spatial autocorrelation or temporal correlation in species distributions and climate variables (Araújo *et al.*, 2005). Although these methods are imperfect, they offer an indication of how an individual model performs in the absence of independent data. Other methods exist to evaluate individual model performance, for example spatial segregation of data through *k*-fold partitioning (Bagchi *et al.*, 2013). Alternatively, it is possible to use SDMs to predict changes in abundance over time (Green *et al.*, 2008), and this approach will be considered in later chapters.

SDMs are useful not only to predict individual species' distributions according to climate, but to predict community properties such as species richness (Ferrier & Guisan, 2006) and composition (Benito *et al.*, 2013). This can be done by aggregating SDM predictions for different species in the same region, creating what has been termed stacked-species distribution models (S-SDMs, Guisan & Rahbek, 2011). Performance of S-SDMs must be evaluated based on their ability to predict community properties in the present; Benito *et al.* (2013) have suggested directly comparing observed and predicted species richness in a given location, and using similarity indices such as the Sorensen's index to compare observed and predicted species composition (see Koleff *et al.*, 2003). By building and evaluating S-SDMs as well as SDMs, it is possible to determine not only how well individual models perform, but how well a large number of such models perform at the community level.

In this project, SDMs will be used to separate North American birds into groups of species expected to be positively or negatively affected by climate change. By comparing the multispecies population trends of these two groups, it will be possible to produce a climatic impact indicator (CII) much like the European indicator produced by Gregory *et al.* (2009). To this end, in this chapter I develop three classes of SDMs for 384 North American bird species (listed in Appendix 1). Prior to making predictions from these SDMs, it must be confirmed that they can adequately predict existing distributions. I test this by validating my models in two ways: Firstly, SDMs are validated individually by data partitioning. Recent climate is used to predict a species' current distribution in a random subset of grid cells, and this is compared with the observed distribution to give an indication of each model's predictive power. Secondly, I evaluate the combined predictive power of these models by producing three S-SDMs, one for each model class, and assessing the ability of each to predict species richness and community composition. I will compare the performance of different model classes throughout the evaluation process to determine which of the model classes, if any, are most suitable to make predictions in further analyses.

## 2.2. Methods

### 2.2.1. Study Species, Study Area and Climate Variables

The main incentive to produce SDMs in this chapter was to later derive a CII using population trends from the North American Breeding Bird Survey (BBS). For this reason, only those 425 species considered by the BBS to have reliable survey-wide trends were originally considered for modeling (Sauer *et al.*, 2012). Models were calibrated based on terrestrial climate data, so species listed as seabirds on the BirdLife International database were excluded from these analyses (BirdLife International, 2013). Preliminary work demonstrated that SDMs produced for seabirds performed significantly worse than those produced for terrestrial species. Furthermore, 12 introduced species were excluded on the basis that their distributions would be determined largely by historical factors such as residence time, and not by climate (Wilson *et al.*, 2007). Two other species were excluded as their composite population trends were unavailable. Preliminary work revealed no difference between predictive performance of SDMs produced for migrants and those produced for non-migrants, so both groups were included in the final analysis. Following the selection process, 384 (90%) of 425 species remained. Breeding distribution maps for these species were obtained from BirdLife International (2013) and overlaid with a 30' latitude × longitude grid (roughly 50 × 50 km). A species was considered present in all cells that intersected its distribution according to BirdLife, following Bagchi *et al.* (2013).

The study area used to develop the SDMs comprised the vast majority of the primary land mass of North America, extending from Canada, through the United States and Mexico, as far south as Costa Rica (Figure 2.1). This range of latitudes and longitudes (10° - 80° N, 170° - 50° W) was selected to encompass the northern and southern range margins of the vast majority of the 384 North American breeding species to be modeled, including the entirety of mainland Canada, USA and Mexico for which BBS data exist. Whilst the majority of the breeding distributions of these species fall within continental North America, the breeding distribution of some birds will fall only partly within the study area (Figure 2.1). Nonetheless, the selected region represents the single most suitable area in which to produce generic SDMs for all 384 species. Only mainland North and central America was considered during modeling as offshore islands are likely to contain very different avian communities which are not recorded under the BBS. Greenland and other islands surrounding continental North America were excluded from the study area using the 'raster' package (Hijmans & van Etten, 2012) in R (R Development Core Team, 2012). In addition, grid cells with percentage land cover of 10% or lower were excluded, as were 47 cells (<0.5% of total area) whose land-mass was predominantly inter-tidal. The final study area comprised 11,216 grid cells.

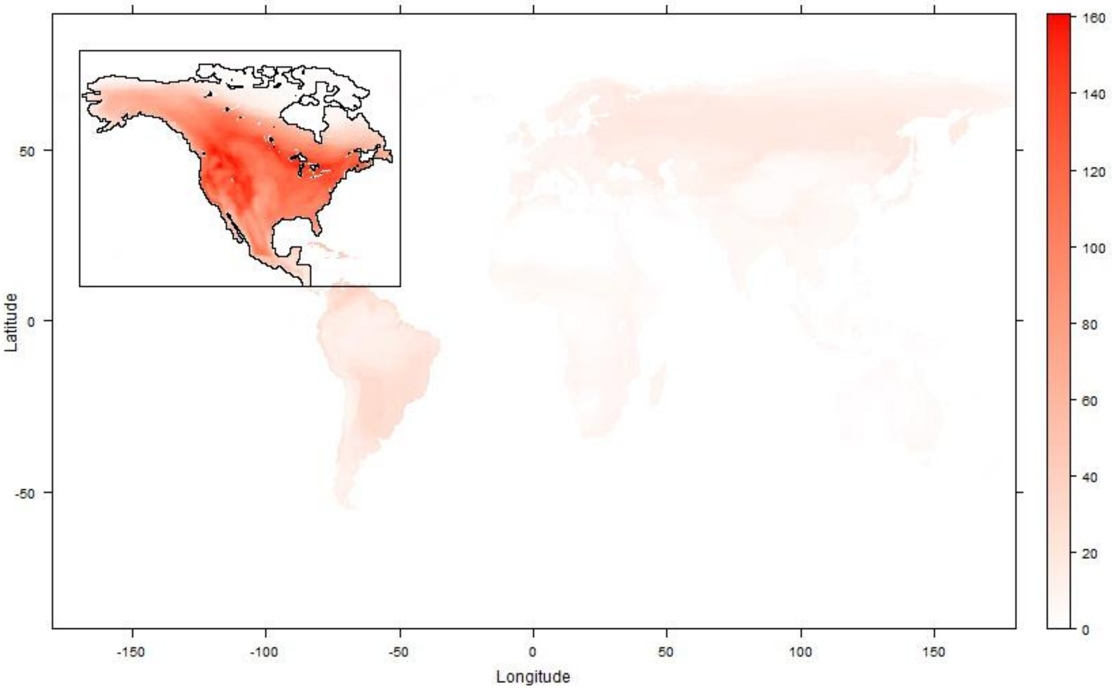

**Figure 2.1.** Global species richness of the 384 study species. The vast majority of the distributions of these species fall within North America. The box surrounding North America indicates the initial selection of latitudes and longitudes (10° N, 80° N, 170° W, 50° W), whilst the outline inside this box represents the final study area after selecting the largest unbroken terrestrial area within that box.

The BirdLife range extent maps corresponded to the occurrence of species from 1951-2000 (Stuart Butchart, Pers. Comm., October 2012). As such, mean monthly temperature, precipitation and percentage sunshine data were obtained for this period from WorldClim (Hijmans *et al.*, 2005, http://www.worldclim.org/) and the CRU TS2.1 database (Mitchell & Jones, 2005, http://www.ipcc-data.org/obs/cru_ts2_1.html) following Bagchi *et al.* (2013). Soil water capacity data were obtained from Prentice *et al.* (1992). 1951-2000 averages of three bioclimatic variables were calculated to represent the principal climatic limits on temperate species (Huntley *et al.*, 1995), using the methods of Prentice *et al.* (1992). These variables were mean temperature of the coldest month (MTCO), the annual ratio of actual to potential evapotranspiration (APET, representing moisture), and annual temperature sum above 5°C (GDD5). These variables have been used to accurately model bird distributions at a broad scale (Araújo *et al.*, 2011, Huntley *et al.*, 2006), but have also been used successfully to predict population trends of European bird species (Green *et al.*, 2008, Gregory *et al.*, 2009). These variables may limit species' population dynamics and distributions directly, or they may have indirect impacts by affecting interacting species such as predators, prey or pathogens.

### 2.2.2. SDM Calibration and Evaluation

Three widely used modeling techniques were used to relate the 384 species' distributions to bioclimatic variables: Generalized Additive Models (GAMs, Hastie & Tibshirani, 1990), Generalized Linear Models (GLMs, MacCullagh & Nelder, 1989) and Random Forests for Classification and Regression (RFs, Breiman, 2001). These three model classes are useful to relate species' distributions to bioclimatic variables, but can differ considerably in their predictive performance depending on the predictor variables used and the species considered (Benito *et al.*, 2013, Elith *et al.*, 2006, Pearson *et al.*, 2006). GAMs and GLMs represented two well used semi-parametric methods, whilst RFs provide an alternative machine learning approach. The R package 'BIOMOD' (Thuiller *et al.*, 2009) was used to calibrate these three model types for each species, with methods as follows:

*Generalized Additive Models:* GAMs were fitted using cubic spline smoothers to relate species distributions to bioclimate. For each species, the response variable (presence) was considered as a function of each bioclimatic predictor. For each predictor the data were divided evenly into 4 neighbourhoods along the x-axis, and a 3rd degree polynomial curve was fitted to each neighbourhood. After joining the curves for each neighbourhood, the resulting smoothed relationships for each variable were combined additively. BIOMOD uses an automated bidirectional stepwise process to select the most significant variables for each species.

*Generalized Linear Models:* GLMs were used to fit polynomial relationships between species distributions and bioclimate. Using AIC as a selection criteria, BIOMOD uses an automated bidirectional stepwise process to select the most parsimonious model.

*Random Forests:* 500 classification trees were built for each species. If N is the number of cases in the training dataset, each tree sampled N cases with replacement from this data. At each node in a classification tree, a random subset of predictors was used to split the dataset. Each tree is grown to the largest extent possible, with no pruning. The final model predictions are averaged across component trees.

GAMs, GLMs and RFs were evaluated individually by data partitioning. For each species and model class combination, a model was calibrated using 70% of cells selected at random. This model was then used to predict the species' occurrence in the remaining 30% of cells (hereafter 'test cells'). Two measures of agreement between predicted and observed distributions of the test cells were calculated: The area under the curve (AUC) of a receiver operating characteristic (ROC) plot and Cohen's Kappa (*K*) goodness-of-fit statistic (see Fielding & Bell, 1997, Peterson *et al.*, 2011). The data partitioning process was carried out ten times for each species and model class combination, and the mean of each of the two agreement statistics was calculated. Neither AUC nor Cohen's *K* of the three model classes were normally distributed. In addition, the test scores of species between model classes were not independent. For these reasons, test statistics were compared between model classes using non-parametric Wilcoxon's matched-pairs tests, following Eskildsen *et al.* (2013). To improve inferences made from multiple comparisons, a Bonferroni corrected threshold for significance was implemented (Rice, 1989).

The importance of each variable for a species in each model class was determined using the following procedure. Firstly a prediction was made for that species and model class based on the calibration dataset. Following this, one of the predictor variables was randomised and a second prediction was made. To see what effect randomising this variable had on a model's prediction, a correlation was performed between the initial predicted probability of occurrence in each cell and probability of occurrence after randomisation. The importance of the randomised variable was calculated as '1 – correlation score', with a value of 1 indicating high importance and 0 indicating very low importance. As some correlations were negative, importance values were at times higher than 1. This was taken to indicate even higher importance of the randomised variable (Thuiller *et al.*, 2009). This importance measure was calculated for each variable in each species and model class combination.

### 2.2.3. S-SDM Calibration and Evaluation

For each species, each model class was used to predict probability of occurrence in each cell based on the same climate data that was used in model calibration (i.e. by resubstituition, see Araújo *et al.*, 2005). Three S-SDMs were then built, one for each model class, by aggregating the predicted probability of occurrence of each of the 384 species in each cell. To provide a comparison with observed data, the observed distributions of all species were also aggregated.

For each S-SDM, two summary statistics were produced. The ability of each S-SDM to predict species richness was assessed by performing a Pearson's correlation between observed and predicted species richness across grid cells. This correlation was taken to represent the ability of each model class to predict the correct number of species in each cell, and will be referred to as *Rpp* (Richness predictive performance). The second summary statistic represented the ability of each S-SDM to predict the correct species composition of each cell. This was calculated by converting probabilities of occurrence for each species in each cell to binary format in BIOMOD. This was done for a given prediction using the threshold that maximized the Cohen's $K$ goodness-of-fit statistic between observed and predicted distributions during data partitioning (see 2.2.2.). A community confusion matrix was then produced for each cell of that S-SDM (Table 2.1). From this, the predicted community of species was compared with the observed community by calculating Jaccard's index of similarity in each cell ($J$) as

$$J = a / (a + b + c) \qquad \textbf{Eq.1}$$

where $a$ is the number of species correctly predicted to be present, $b$ is the number of species incorrectly predicted to be present and $c$ is the number of species incorrectly predicted to be absent (Table 2.1). $J$ can range between 0 and 1, with a value of 0 indicating that no species were predicted correctly in a cell, and a value of 1 indicating that all species were predicted correctly in a cell. For each S-SDM, *Cpp* (Composition predictive performance) was taken to be the mean of $J$ across all cells.

**Table 2.1.** A community confusion matrix used to determine the success rate ($J$) when predicting the community in each cell, substituting *a, b* & *c* into equation 1.

| | | **Observed Species Status** | |
|---|---|---|---|
| | | Present | Absent |
| **Predicted Species Status** | Present | *a* | *b* |
| | Absent | *c* | *d* |

## 2.3. Results

The three types of SDM were fitted successfully to the distributions of all 384 species. AUC values of 0.5 indicate that a model performed no better than a random classifier, whilst AUC values of 1 indicate perfect discrimination by an SDM (Swets, 1988). In general, AUC values between 0.7 and 0.9 indicate reasonable predictions (Peterson *et al.*, 2011), and AUC for each species in each model class did not fall below 0.7 in this study. However, the median AUC across species was consistently above 0.95, indicating very good predictive ability for the vast majority of models of each class (Table 2.2, Figure 2.2a). Cohen's $K$ for the majority of models exceeded 0.7, which demonstrates substantial agreement between observed and predicted distributions under data partitioning (Landis and Koch (1977), Table 2.3, Figure 2.2b). However, a small proportion of models performed poorly according to the Kappa statistic, with two scoring below 0.2 indicating only slight agreement (Landis & Koch, 1977). Wilcoxon's matched-pairs tests revealed that AUC differed consistently among the three model classes; in all three comparisons one model class significantly outperformed the other at the Bonferroni corrected threshold for significance ($P < 0.008\dot{3}$). The same was true when comparing Cohen's $K$ between model classes. RFs outperformed GAMs according to both AUC ($V = 8595$, $P < 0.001$, Table 2.2) and Cohen's $K$ ($V = 1615$, $P < 0.001$, Table 2.3). RFs also outperformed GLMs according to both AUC ($V = 6260.5$, $P < 0.001$, Table 2.2) and Cohen's $K$ ($V = 1181.5$, $P < 0.001$, Table 2.3). Lastly, GAMs outperformed GLMs according to both AUC ($V = 54152.5$, $P < 0.001$, Table 2.2) and Cohen's $K$ ($V = 64332$, $P < 0.001$, Table 2.3). Across all model classes, GDD5 was the most important bioclimatic variable on average (Figure 2.3), closely followed by MTCO, whilst APET was consistently of low importance.

In S-SDM evaluation, all model classes predicted species richness patterns effectively. All correlation scores between observed and predicted richness of cells (Rpp) exceeded 0.9 (Figure 2.4). When taking the mean species richness across the three model classes, it is clear that geographical patterns in predicted richness approximately match patterns in observed richness (Figure 2.5). Individually, though, RFs clearly outperformed the other models (Figure 2.4). When predicting community composition, GAMs and GLMs achieved similar *Cpp* scores (<0.7, Figure 2.6), which indicated that on average, fewer than 7 in 10 species were correctly predicted to occur in a given cell. RFs, however, had a *Cpp* score very close to 1 (Figure 2.6), which indicates nearly complete agreement between observed and predicted composition in each cell. Figure 2.6 shows that whilst Jaccard's similarity index varied in space for GAMs and GLMs, for RFs this value was uniformly close to or exactly 1. For GAMs and GLMs, S-SDMs predicted community composition most effectively in the eastern USA, but failed to capture communities in higher altitude areas in western USA, such as the Rocky Mountains. Performance for these two model classes is also especially poor in Alaska and much of Canada, but did not drop below ~0.4 in the USA.

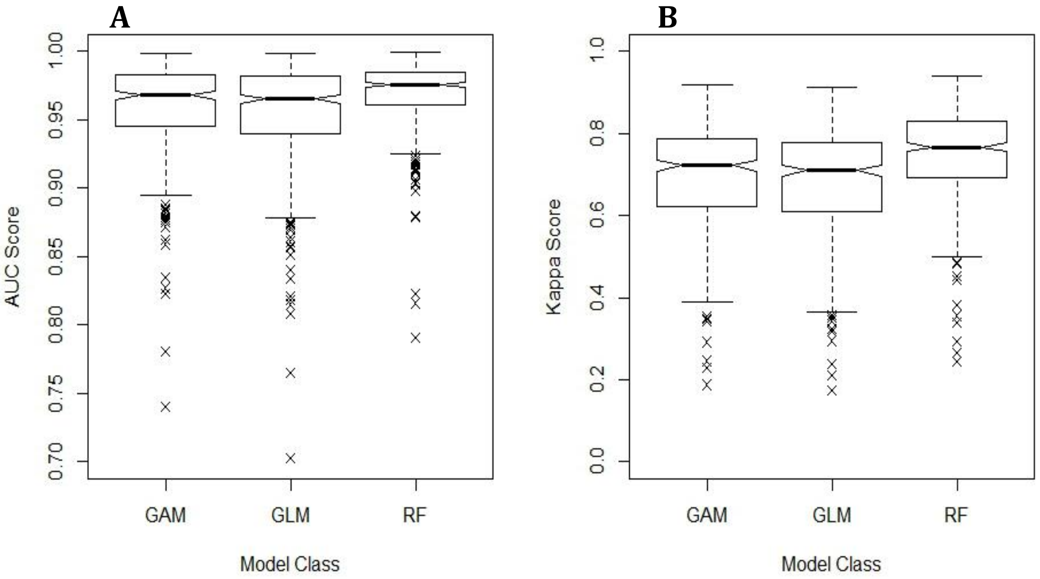

**Figure 2.2.** Box and whisker plots of **(A)** AUC scores and **(B)** Cohen's *K* scores across species for each model class. Higher AUC/*K* indicates improved predictive performance of a model. Boxes represent the inter-quartile range (IQR) of scores across species, whilst whiskers extend to 1.5 times the IQR with points outside these considered outliers. Notches represent 95% confidence intervals around the median. Where the notches of two plots do not overlap, it is considered strong evidence that the two medians differ significantly (Chambers *et al.*, 1983).

**Table 2.2.** Median area under the curve of a receiver operating characteristic plot (AUC) and frequency of improvement in AUC over other model classes are displayed for Generalized Additive Models (GAMs), Generalized Linear Models (GLMs) and Random Forests (RFs). BIOMOD reports AUC to 3dp, so there was not always a detectable difference in AUC between any two models. For example, under data partitioning RFs demonstrated improved AUC over GAMs for 80% of species. Wilcoxon's matched-pairs comparisons of AUC between model classes were always significant at the Bonferroni corrected threshold ($P < 0.008\dot{3}$).

| Model Class | Median AUC | Frequency of Improvement of AUC (%) | | |
|---|---|---|---|---|
| | | GAM | GLM | RF |
| GAM | 0.968 | | 84% | 16% |
| GLM | 0.965 | 2% | | 13% |
| RF | 0.976 | 80% | 84% | |

**Table 2.3.** Median Cohen's *K* and frequency of improvement in *K* over other model classes are displayed for Generalized Additive Models (GAMs), Generalized Linear Models (GLMs) and Random Forests (RFs). BIOMOD reports *K* to 3dp, so there was not always a detectable difference in *K* between any two models. For example, under data partitioning RFs demonstrated improved *K* over GAMs in 94% of species. Wilcoxon's matched-pairs comparisons of *K* between model classes were always significant at the Bonferroni corrected threshold ($P < 0.008\dot{3}$).

| Model Class | Median *K* | Frequency of Improvement of *K* (%) | | |
|---|---|---|---|---|
| | | GAM | GLM | RF |
| GAM | 0.722 | | 84% | 6% |
| GLM | 0.710 | 13% | | 5% |
| RF | 0.767 | 94% | 95% | |

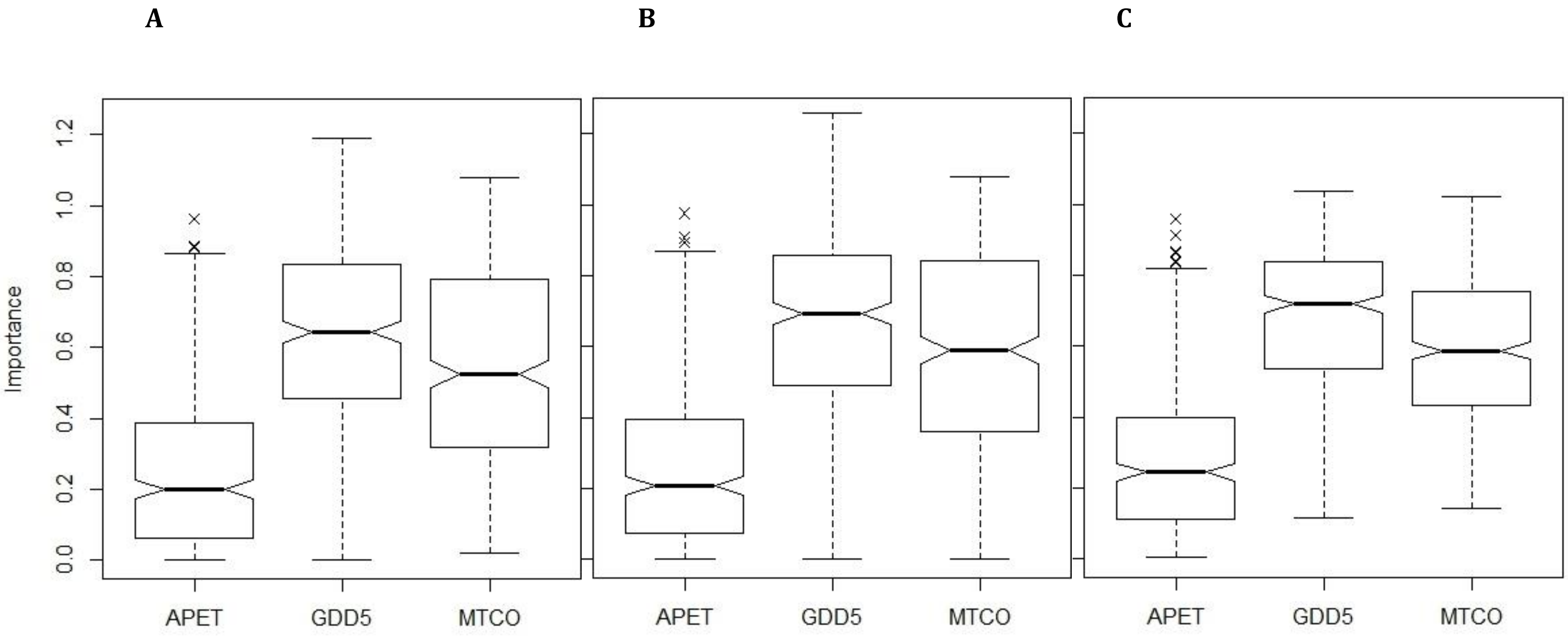

**Figure 2.3.** Box and whisker plots displaying importance of each variable across species in **(A)** GAMs **(B)** GLMs and **(C)** RFs. Notches roughly represent 95% confidence intervals. Higher values of importance indicate that the variable had a strong influence on predictions made by a model. Where the notches of two plots do not overlap, it is considered strong evidence that the two medians differ (Chambers *et al.*, 1983). Importance was calculated using the methods outlined in 2.2.2.

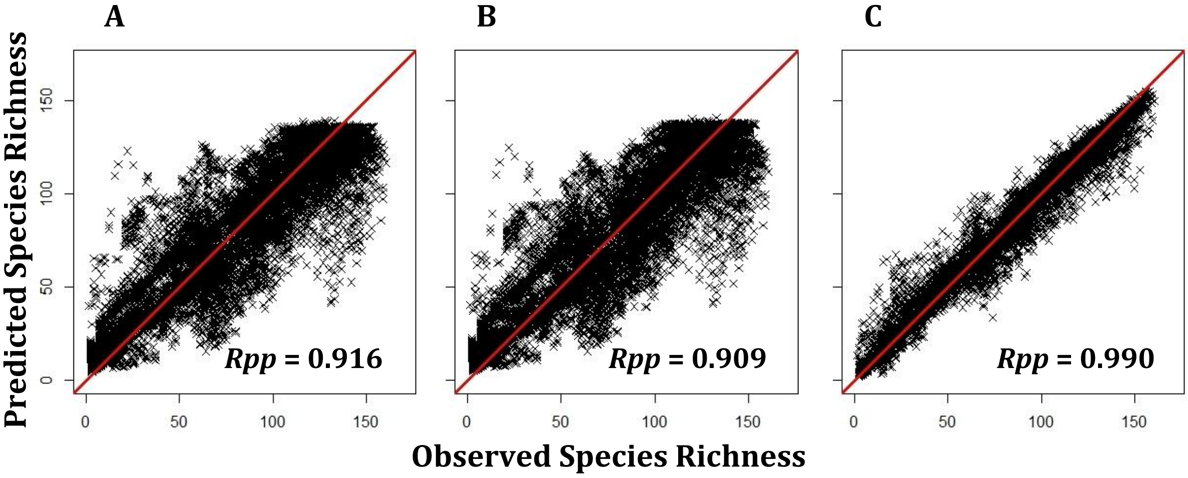

**Figure 2.4.** Scatter plots showing the relationship between observed and predicted study species richness across cells according to **(A)** GAMs **(B)** GLMs and **(C)** RFs. 1:1 lines are displayed in red to represent equality. The Pearson's correlation score of this relationship (*Rpp*) is also displayed for each model class.

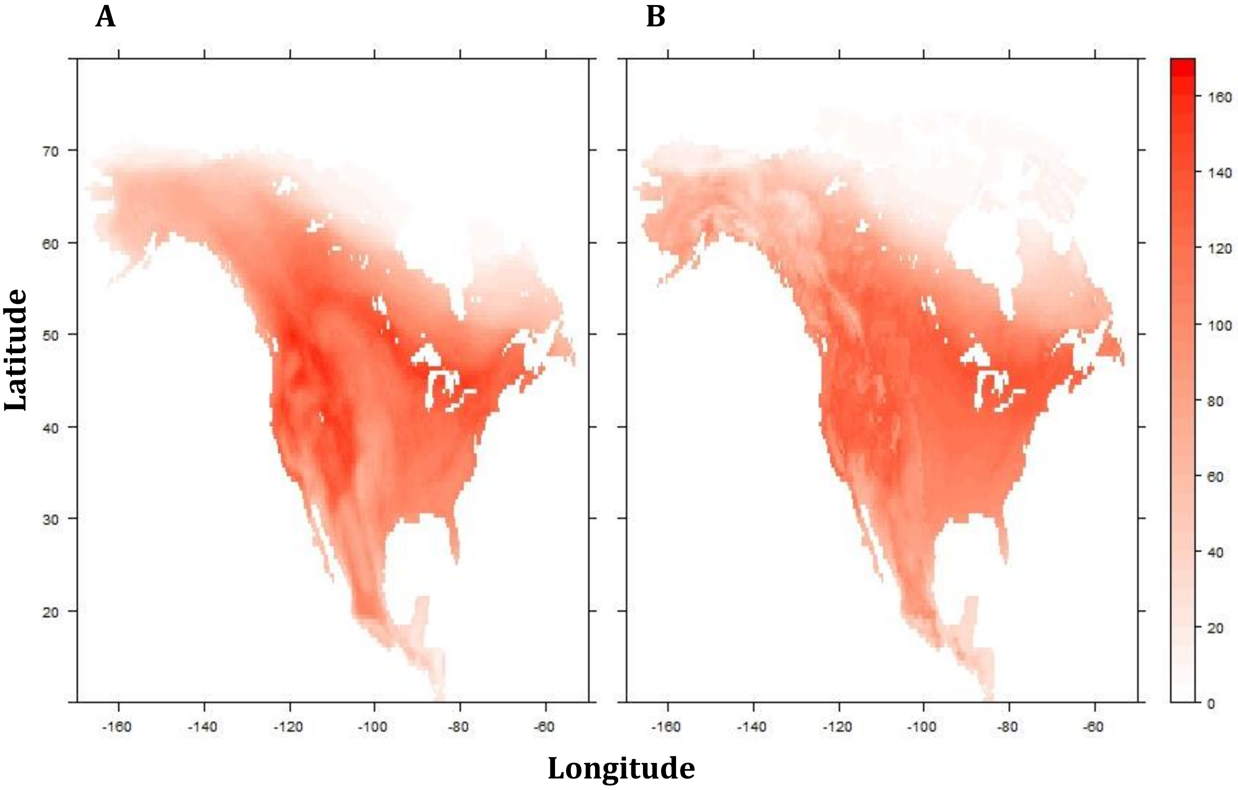

**Figure 2.5.** **(A)** Observed study species richness and **(B)** species richness according to predictions from three classes of SDMs. Darker cells exhibited higher species richness than lighter cells. Predicted species richness in each cell is represented by the mean of predictions from GAMs, GLMs and RFs.

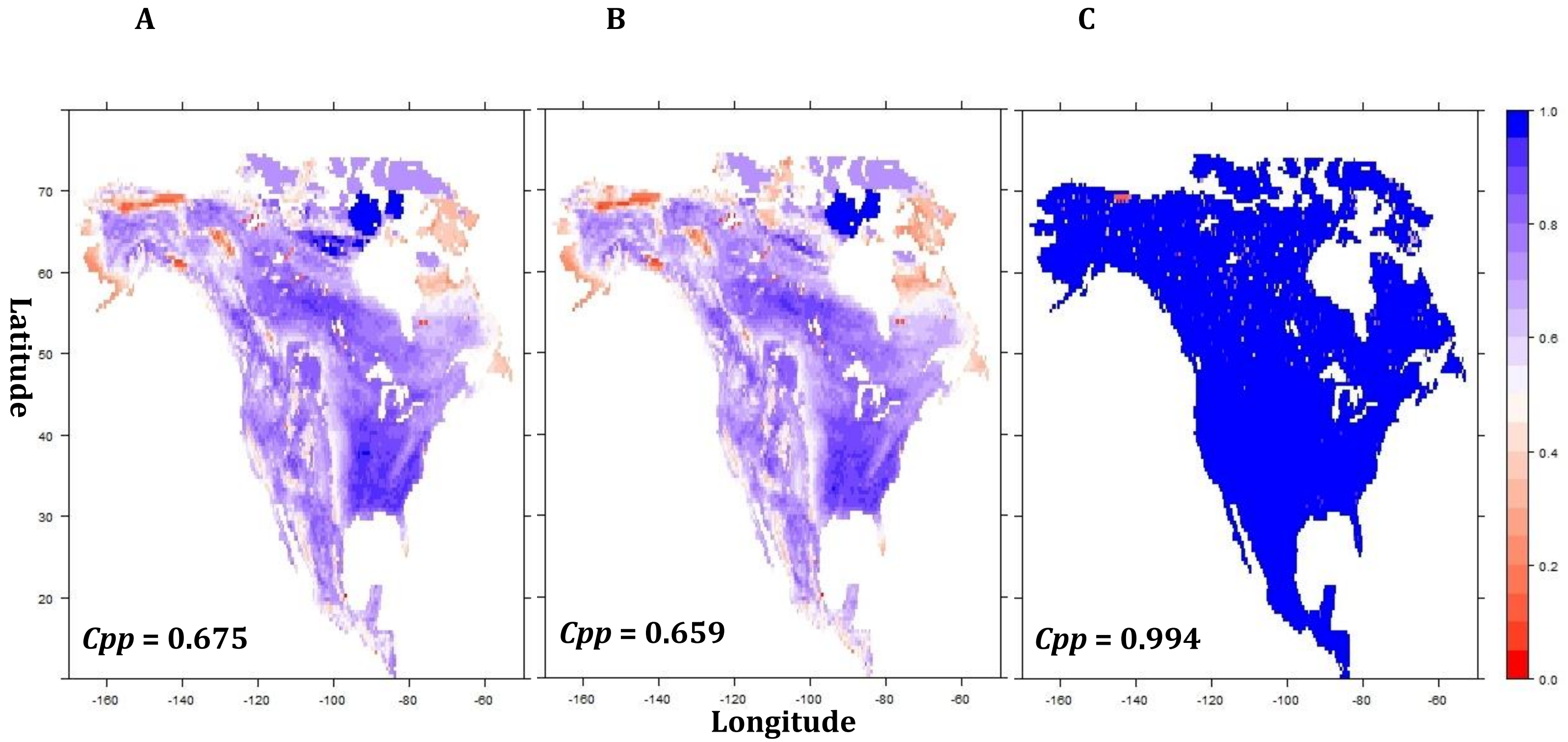

**Figure 2.6.** Jaccard's similarity index (*J*) between the observed community and that predicted under resubstitution across grid cells for **(A)** GAMs **(B)** GLMs and **(C)** RFs. Red cells scored low in similarity tests, white cells were intermediate, and blue cells scored highly. The mean of *J* across cells (*Cpp*) is also displayed for each model class.

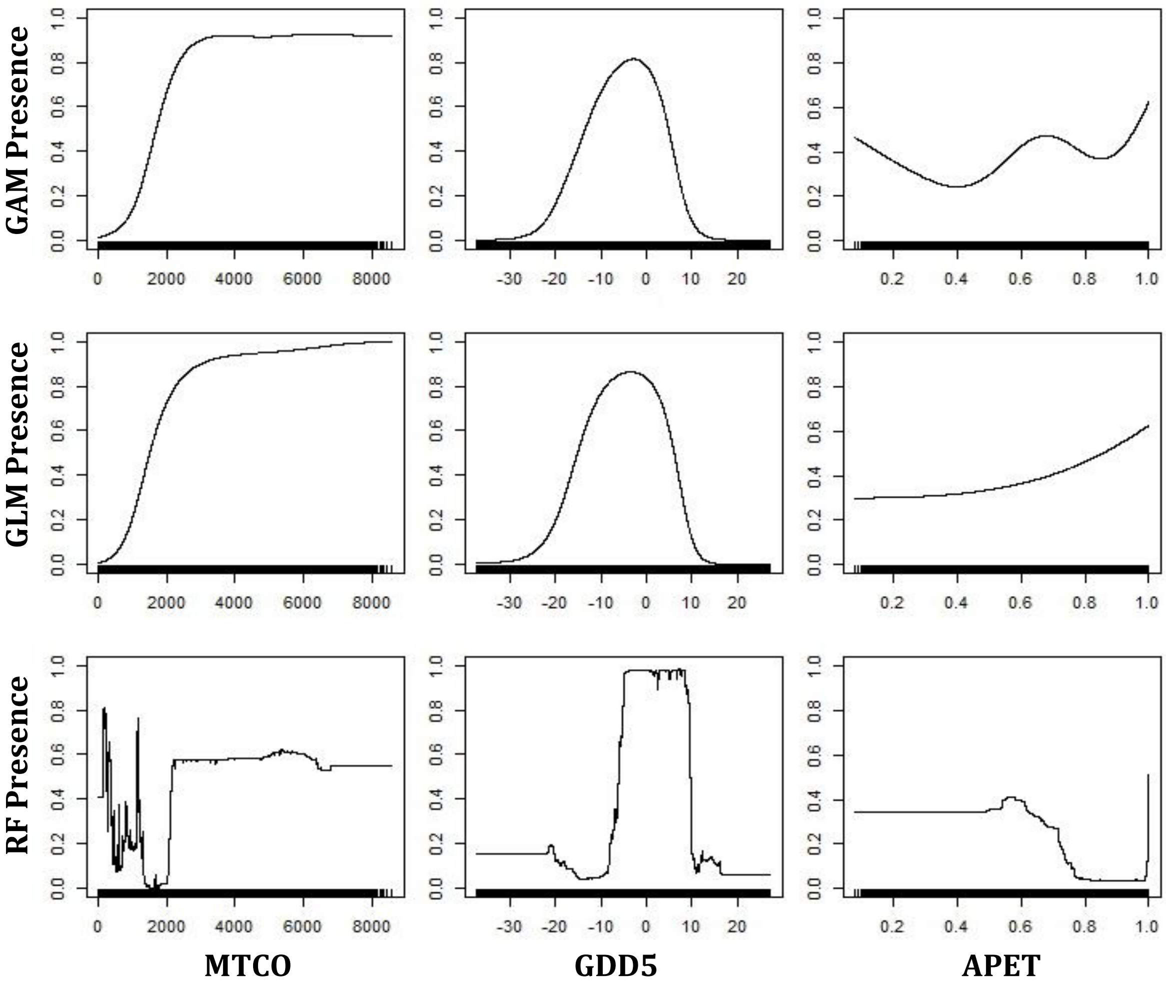

**Figure 2.7.** Example response curves displaying the relationship between each bioclimatic variable and predicted probability of occurrence of Cooper's Hawk (*Accipiter cooperii*) as captured by the three model classes.

## 2.4. Discussion

SDM evaluation by data partitioning revealed that model performance was very good according to AUC in the vast majority of cases (94%, Peterson *et al.*, 2011), or substantial according to Cohen's *K* in most cases (61%, Landis & Koch, 1977). Whilst this is encouraging, interpreting these evaluation measures using generic categories is not especially useful because they are subjective and contingent on the nature of the response variable (Peterson *et al.*, 2011, Vaughan & Ormerod, 2005). For example, Swets (1988) found that the degree of confidence to be had in AUC varied when it was applied to models of different systems.

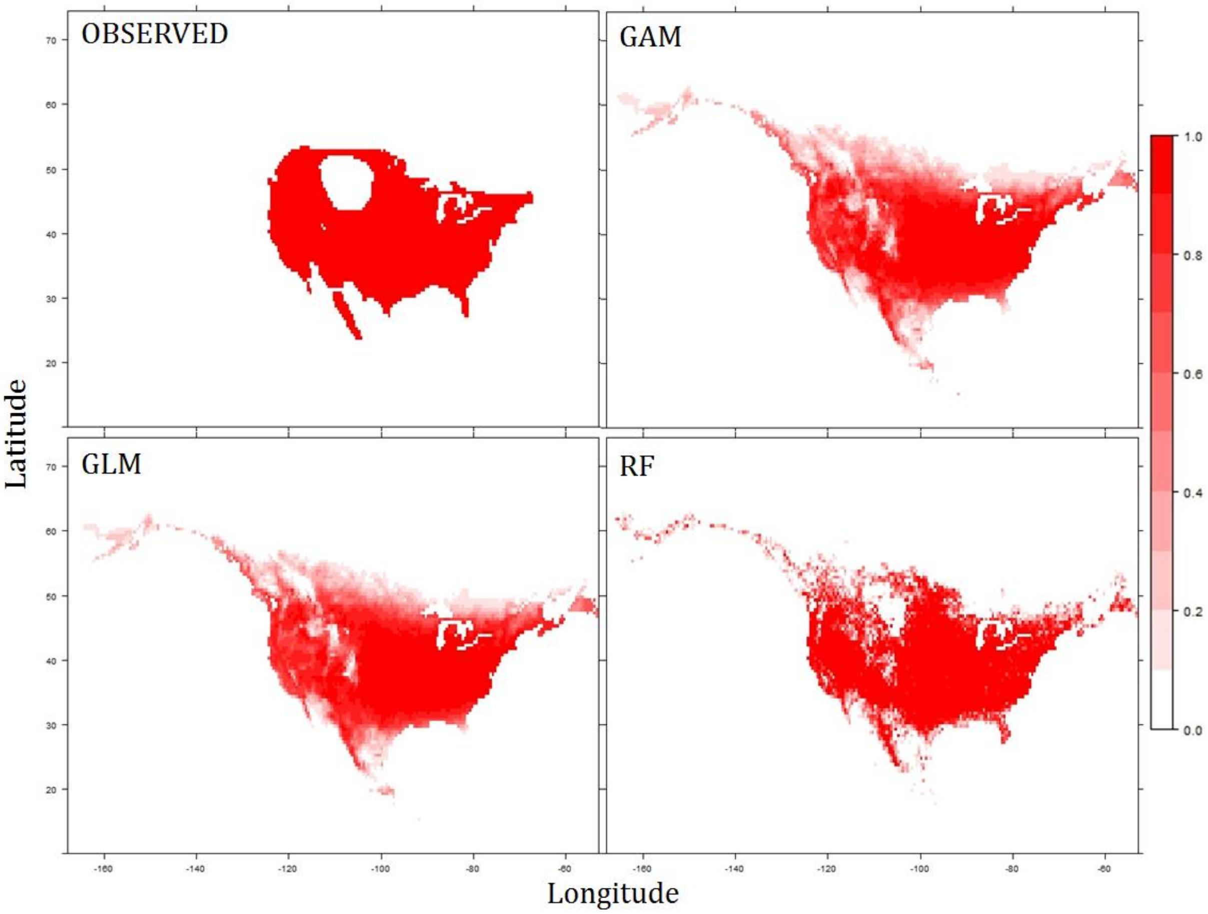

**Figure 2.8.** Visualisation of the performance of SDMs in predicting the occurrence of Cooper's Hawk *Accipiter cooperii* based on the calibration dataset (resubstitution). The top left panel shows observed occurrence of *Accipiter cooperii* across North America according to BirdLife (2013). The top right, bottom left and bottom right panels present predicted probability of occurrence according to GAM, GLM and RF model classes respectively. Deeper red colouration indicates a higher predicted probability of occurrence.

Unlike the majority of previous studies evaluating SDMs, S-SDMs for each model type were also assessed here based on their ability to predict at the community level. In general, observed and predicted species richness was highly correlated across grid cells (Figure 2.4). However, it is important for S-SDMs to predict not only the correct number of species in each cell, but also the correct species composition. On average just under 7 in 10 species were correctly allocated in each cell by GAMs and GLMs, whilst RFs predicted species composition almost perfectly (Figure 2.6). In addition, in the case of GAMs and GLMs there was clear spatial variation in ability to predict community composition (Figure 2.6). Especially low values of *J* occurred in GAM and GLM predictions throughout Alaska and most of Canada. In general, this was due to models predicting species to be absent where they are, in fact, present. Despite this, community simulations produced using all model types appear to be reasonably accurate.

Two methods were used to compare model performance in this study: Data partitioning in individual model evaluation, and resubstitution in evaluation of S-SDMs. The more robust of these is data partitioning; random samples from the original dataset are more independent than using the full calibration dataset to test models through resubstitution (Araújo *et al.*, 2005). According to both AUC and *K*, RFs outperformed GAMs and GLMs in the vast majority of cases (Table 2.2, Table 2.3). RFs have been demonstrated to outperform other SDMs in the past, both under individual evaluation (Cutler *et al.*, 2007, Marmion *et al.*, 2009) and through S-SDMs (Benito *et al.*, 2013). The use of resubstitution to build S-SDMs here means it is difficult to confidently reach conclusions from S-SDMs alone. Figure 2.6 should therefore be interpreted with caution; there was a very dramatic improvement of RFs over GAMs and GLMs when they were tested by resubstitution in S-SDMs (Figure 2.6), but RFs did not perform anywhere near as well under data partitioning (Figure 2.2a & 2.2b). Given this distinction, as well as the nature of the response curves for RFs when compared with those from GAMs and GLMs (e.g. Figure 2.7), it appears that RFs are over-fitting to the calibration dataset in this study. This might be attributable to the lack of pruning of RFs in BIOMOD. As such, whilst RFs performed well in interpolative evaluation (here, data partitioning) this may not be representative of their potential during extrapolation (Heikkinen *et al.*, 2012). Since this study will use SDMs to make predictions based on climate in different time periods, it is important to remember that the models which perform well based on the above evaluation methods may not in fact be the most transferrable.

Whilst the individual model classes in this study have their shortcomings, the use of SDMs in general has its limitations. Whilst climate does have a broad scale impact on avian species distributions (Jiménez-Valverde *et al.*, 2011), there are also a range of other factors influencing them. The models in this study do not directly consider the impact of biotic interactions (e.g. competition, predation or food availability) on distributions. However, this study aims to use SDMs to predict climatic suitability for each species, thus it was appropriate to only consider bioclimatic predictors. The three bioclimatic variables used in this study proved adequate to simulate the range extent for almost all of the 384 species. It may have been possible to refine model fits for some species with variables chosen to reflect known species-specific limitations. However, as the aim of this modeling is to produce a climate indicator based on species-climate relationships across many species, using the same climate variables across all candidate species makes the indicator more transparent and comparable to similar studies. The importance of MTCO and GDD5 across species makes sense in light of metabolic limits of temperature on avian distributions (Root, 1988). However, APET is of low importance across the majority of models, indicating that moisture was not so strong a limiting factor for most species here (Figure 2.3).

Accounting for spatial autocorrelation could have improved model evaluation in this study, as this is a major concern when making inferences from SDMs (Beale *et al.*, 2008). To do so, test data can be spatially segregated through *k*-fold partitioning (Bagchi *et al.*, 2013). Unfortunately, this is not possible within BIOMOD, highlighting a trade-off between accessibility and flexibility when using this platform to produce SDMs. However, in chapter 3 I validate these SDMs using independent abundance data, which is a robust and independent test of these species-climate relationships (Green *et al.*, 2008). Evidence is presented in Figure 2.6c that random forests are over-fitting to the calibration dataset, so later chapters will test whether use of this model class affects the overall conclusion of the climatic impact indicator (CII) that is produced. Otherwise, the evidence outlined in this chapter suggests that models of all three classes are of an acceptable standard to make predictions of climate suitability for individual species. As a result, in the following chapters I use these SDMs to simulate how each species has been affected by climate change over recent decades and relate changing abundances to climate.

# 3. An Indicator of the Impact of Climate Change on Populations of Bird Species in the USA

## 3.1. Introduction

Climate change has been identified as a major driver of recent biodiversity change, and its effects on biodiversity are likely to become more pronounced in the future (MA, 2005, Sala *et al.*, 2000, Thuiller, 2007). Climate driven changes to species' distributions and phenology in recent years may result in population declines and extinctions, especially where species interactions are altered (Cahill *et al.*, 2013, Parmesan, 2006).

Future climate change, leading to a significant reduction in biodiversity (Thomas *et al.*, 2004), is likely to have negative consequences for ecosystem services and human welfare (MA, 2005).

Through the Convention on Biological Diversity (CBD, 1992), many governments pledged to reduce the rate of biodiversity loss by 2010 (Balmford *et al.*, 2005). To assess progress towards meeting such broad conservation targets, detailed biodiversity data must often be condensed to produce indicators summarizing progress or change. Such indicators can describe the state of biodiversity (e.g. population size), the pressures upon it (e.g. climate change), or even the degree of political response to alleviate biodiversity declines (Mace &  Baillie, 2007). By collating 31 such indicators, Butchart *et al.* (2010) were able to demonstrate convincingly that the 2010 CBD target had not been met. Whilst indicators are necessary to track progress toward achieving conservation targets, spatial, temporal and taxonomic biases exist amongst the indicators currently available (Jones *et al.*, 2011, Mace *et al.*, 2010, Walpole *et al.*, 2009).

Gregory *et al.* (2009) developed a novel indicator to summarize the pressure of climate change on bird populations across Europe, and this was one of the indicators used to assess whether the 2010 biodiversity target had been met (Butchart *et al.*, 2010). Following Brown (1984), Gregory *et al.* (2009) assumed that distributions and densities of species would change in parallel under climate change, and used simulated distributional change according to species distribution models (SDMs) to categorize species as likely to be either positively or negatively affected by ongoing climate change. To determine the expected effect of climate change on a species between 2000 and 2100 (CLIM) the simulated current range extent for a species was compared with that predicted under climatic scenarios for the late 21st century. CLIM represented the log of the ratio of the projected future range extent to the recent simulated range extent, so a positive value would indicate that a species is expected to gain range under future climate change. To justify using this metric, Gregory *et al.* (2009) found that expected future distributional change and recent observed population change were positively correlated across species. Given this relationship they then compared the multispecies population trends for two species groups: Those expected to experience improved climate suitability under climate change, and those expected to experience declining climate suitability. As predicted, they found that the multispecies population trend for species expected to be adversely affected by climate change decreased relative to the trend for those expected to be favourably affected. Considered together these trends demonstrated an increase in climate change impacts on bird populations across Europe since 1980, coinciding with a period of climatic warming.

Gregory *et al.* (2009) also quantified the expected effect of climate change on a given species using an alternative approach. They used SDMs to simulate climate suitability across Europe for a species in each year from 1980-2002, based on observed climate data. They then calculated a climate suitability trend (CST), which was represented by the slope of mean climate suitability across Europe over time. As such, if the predicted climate suitability of a species increased overall between 1980 and 2002, the CST value for that species would be positive. They found that recent population trends of European birds were more strongly associated with long term predicted climate change effects (CLIM) than they were with climate change effects over recent decades (CST). They attributed this to increased variability of CST, where climate trends are summarized over a shorter time period. The use of climate projections (CLIM) as opposed to observed climate (CST) to assess impacts of climate change on species is less intuitive and introduces other sources of uncertainty, in the form of predictions of General Circulation Models (GCMs) and emissions scenarios. However, Gregory *et al.* (2009) found that CLIM performed better than CST when retrodicting the population trends of their study species, and thus used CLIM to develop their climatic impact indicator (CII).

Biodiversity indicators are most useful when the ecological factors driving them are well understood (Gregory *et al.*, 2005), and climate change may affect populations of bird species in North America in many ways. Climate change effects on both the phenology and distributions of North American birds have been documented (Dunn & Winkler, 1999, Hitch & Leberg, 2007). If a mismatch between the timing of the emergence of a species and its food occurs, phenological change may act as a mechanism for population declines (Both *et al.*, 2006, Visser & Both, 2005). A relationship exists between species density and range size (Brown, 1984) so where a species' distribution expands or contracts due to climate change, population increases or declines are likely to follow. Changes in species interactions under climate change will also affect populations (Cahill *et al.*, 2013). For example, population declines of the

Golden Plover *Pluvialis apricaria* have been explained by reduced abundance of its cranefly prey caused by warm summer temperatures (Pearce-Higgins *et al.*, 2010). Through mechanisms such as the above it is anticipated that climatic impacts on bird populations across the USA are likely to have increased in recent years, mirroring the trend seen in Europe (Gregory *et al.*, 2009).

Here, I use the SDMs calibrated in the previous chapter to derive both CST and CLIM for 380 bird species that breed across mainland USA, where high quality population trends are available (Sauer *et al.*, 2012). To assess the performance of SDMs when predicting changes in abundance, I relate CST and CLIM to the population trend of each species. Applying the same methods used on European breeding birds to another well-monitored region (Robbins *et al.*, 1986) on a different continent will bridge a significant geographical gap amongst climate change indicators. It will also help to establish whether the trends observed across Europe are likely to be part of a larger scale trend of population changes due to recent climate change.

## 3.2. Methods

### 3.2.1. Study Area, Study Species and Quantifying the Expected Effect of Climate Change

Although models had been calibrated across the majority of the continent of North America, it was unsuitable to produce CIIs including Canada and Mexico. This was because neither was sufficiently covered under the BBS to have confidence that the collated data reflected regional trends (Figure 3.1). In addition, chapter 2 demonstrated poor performance of GAMs and GLMs across much of Alaska and Canada, so producing predictions for these areas seems unlikely to give accurate estimates of climatic suitability for a species. Accordingly, this chapter focuses on mainland USA (excluding Alaska) to develop a broad scale CII. After removing Alaska, Canada and Mexico from the study site, 4 of the 384 species for which SDMs were calibrated no longer occurred within this area. This left 380 species that were used to create CIIs for mainland USA.

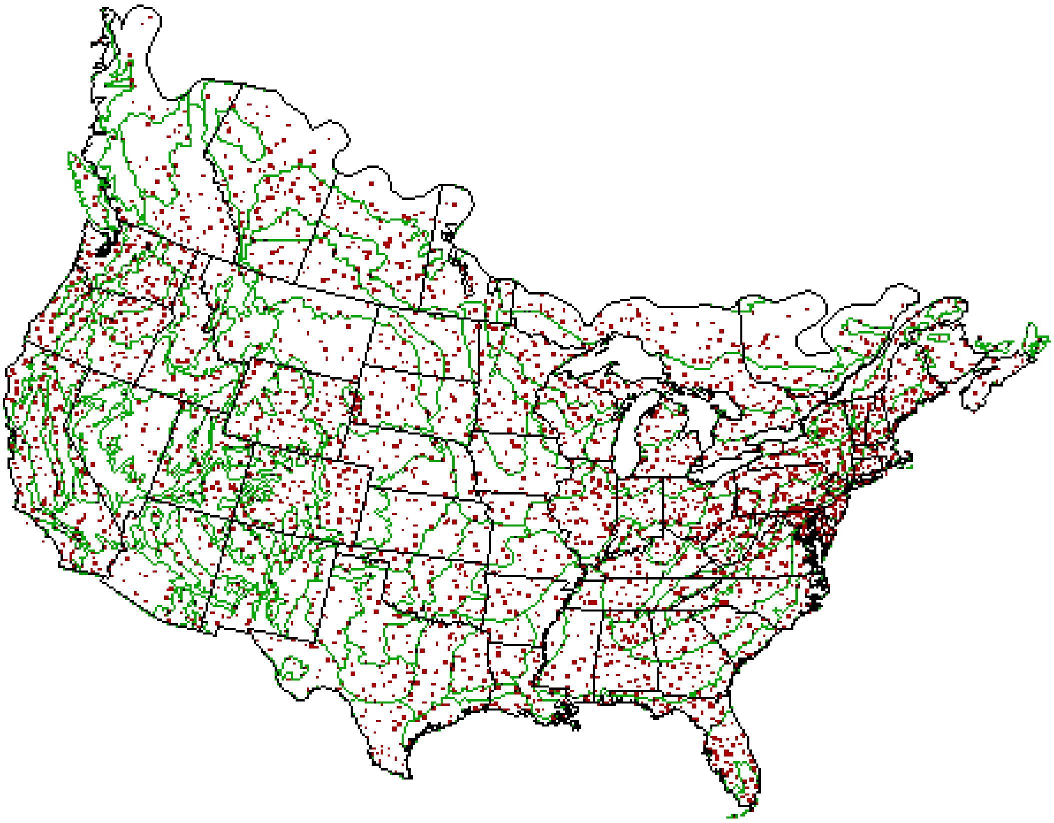

**Figure 3.1.** Map of North America showing locations of North American Breeding Bird Survey routes (shown in red) from Sauer *et al.* (2012). State and provincial boundaries (black lines) are also displayed.

All analyses were carried out using R (R Development Core Team, 2012). Generalized Additive Models (GAMs), Generalized Linear Models (GLMs) and Random Forests (RFs) were produced for the North American distributions of the 380 species as in chapter 2. For each species, CST was calculated using predictions from SDMs based on annual values of MTCO, GDD5 and APET from 1968-2011. These bioclimatic variables were calculated as in chapter 2, but with mean monthly temperature, precipitation and percentage sunshine data obtained for this period from the CRU TS3.2 database (Harris *et al.*, 2013). Predictions for the occurrence of each species in each year from 1968-2011 were produced according to each model class individually. Then an ensemble prediction was made using the "bounding box" method outlined in Araújo and New (2007), taking the median probability of occurrence of a species from predictions made using each of the three model classes. In this way, species occurrence in each cell was essentially determined based on a majority vote between model classes. From the predictions from each individual model class, as well as the ensemble prediction for each species, the mean probability of occurrence across all cells was taken in each year from 1968-2011. CST was then calculated according to ensemble predictions for each species as the slope of the regression of the logit annual mean probability of occurrence on year (Figure 3.2). In the same way, CST was also calculated according to predictions from individual model classes. This was done in order to later compare CST CIIs derived using different model classes.

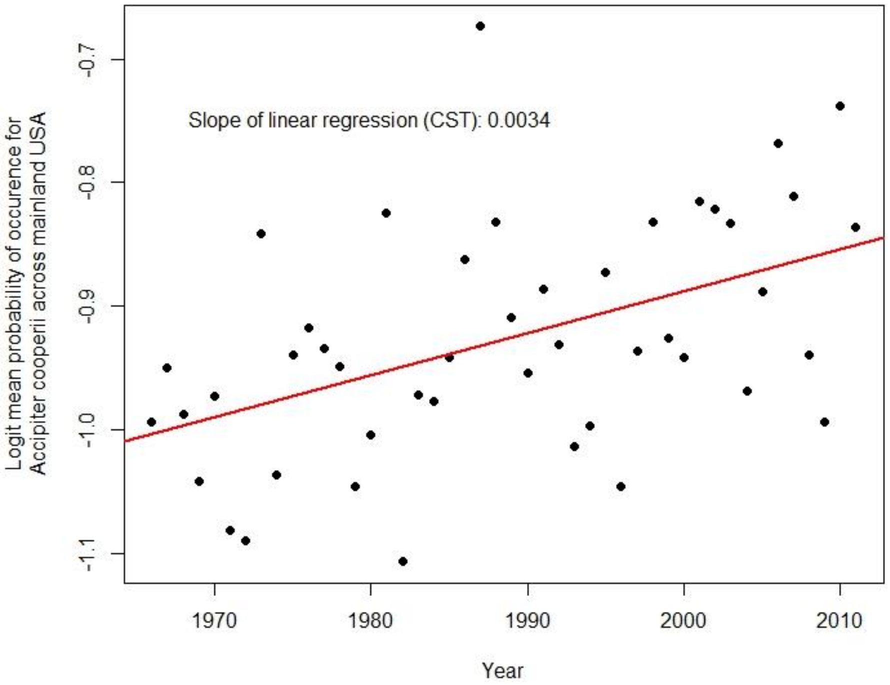

**Figure 3.2.** Illustration of how CST is calculated for a given species. Shown is logit climatic suitability for Cooper's Hawk *Accipiter cooperii* from 1966-2011. Climatic suitability is calculated as the mean probability of occurrence across mainland USA according to an ensemble prediction from three classes of SDMs. CST is the slope of the regression of logit climatic suitability on year (red line). This species has a positive CST value of 0.0034, suggesting that SDMs predict that this species will have responded positively to recent climate change.

In order to calculate CLIM, projections of MTCO, GDD5 and APET from 2071-2100 were obtained based on all combinations of four General Circulation Models (GCMs) and three Special Report on Emissions Scenarios (SRES, Nakicenovic *et al*., 2000) scenarios. SRES scenarios represent the demographic, economic and technological drivers that may affect future emissions (IPCC, 2007). Following Bagchi *et al.* (2013) a variety of GCMs (HadCM3, MPI-ECHAM5, GFDL-2.1 and NCARCCSM3) and SRES scenarios (A2, A1B and B1) were selected, covering a range of projections of climate and emissions. Following this, a prediction was made for each species using each model class based on climate data from each GCM and SRES combination. In this way, 36 projections (3 model classes × 4 GCMs × 3 SRES scenarios) were produced for each species. In order to calculate CLIM an estimate of the recent simulated range was also required for each species. This was calculated for each species according to each model class by making predictions based on the baseline climate data which was used to calibrate the models (1950-2000, see Chapter 2).

An ensemble CLIM value was calculated for each species as follows: The future potential range extent for each of the 36 future projections was calculated by summing probability of occurrence across all cells in a given projection. In the same way the recent simulated range extent was calculated 3 times for each species, once for each model class. A CLIM value was calculated as the log of the ratio of the extent of a future potential range to that of a recent simulated range (Figure 3.3). 36 values of CLIM were calculated for each species, comparing each future range extent with the recent simulated range calculated according to the same model class. For example, the CLIM value for the projection from a GAM under a given GCM and SRES scenario was compared with the recent simulated range according to a GAM as well. The final ensemble value of CLIM for a species was represented by the mean of these 36 CLIM values, following Gregory *et al.* (2009).

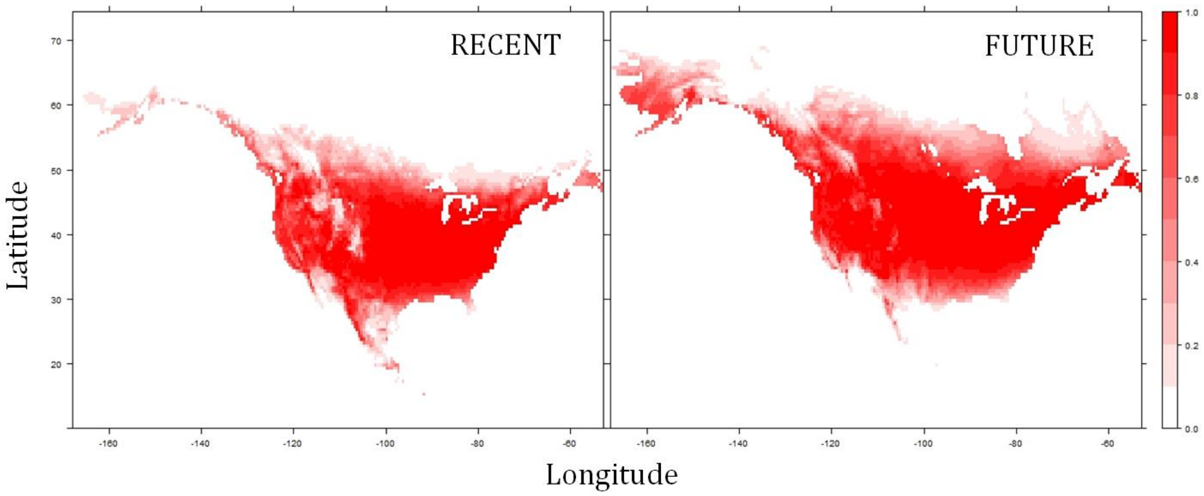

**Figure 3.3.** Illustration of how CLIM is calculated for a given species and climate projection. Predicted probability of occurrence of Cooper's Hawk *Accipiter cooperii* is shown according to a GAM based on recent climate (left panel) and future climate (right panel). Recent climate was approximated using the same data used to calibrate the GAM, whilst future climate was derived from a combination of a GCM (MPI-ECHAM5) and an SRES (A1B) scenario. Whilst climatic suitability is expected to increase across North America for *Accipiter cooperii*, an overall northwards shift means that this species is expected to lose climatic suitability in mainland USA. Summed climatic suitability in mainland USA approximates to 2960 for the prediction under recent climate, but falls to 2866 for the prediction under future climate. A CLIM value is calculated as the log of the ratio of the extent of the future potential range to that of the recent simulated range. Following this, CLIM for *Accipiter cooperii* under this GCM and SRES scenario equates to -0.032, indicating that this species is expected to be slightly negatively affected by future climate change. The ensemble value for CLIM, however, was calculated for each species as the mean of 36 such values that were produced using different model classes and climate projections.

Annual population indices for the 380 study species in the USA between 1968 and 2011 were obtained from the North American BBS (Sauer *et al.*, 2012). The overall USA population trend from 1968-2011 was then calculated for each species as the regression coefficient of annual indices on calendar year from a log-linear Poisson regression model (Gregory *et al.*, 2009). To evaluate the ability of SDMs to predict population trends for each species, a linear regression was performed using first CST and then CLIM to predict observed population trend across species. Further to this, to determine whether climatic suitability changes over the past 40 years have been in the same direction as projected changes in species' ranges for 2100, the CLIM value for each species was regressed on their CST value.

### 3.2.2. Producing a CII for the USA using CST and CLIM

Using all the reliable population trend data available from the North American BBS for bird species in the USA, multispecies population indices were produced to summarize the trends of those species expected to be positively affected by climate change and those expected to be negatively affected. These groups were defined as those species with positive values of CST (CST+) and those with negative values (CST-). Species were also sorted into these two groups according to positive and negative values of CLIM (CLIM+/CLIM-). Composite multispecies population indices for these four groups were then calculated following Gregory *et al.* (2009):

1. For each species in the group, a complete time series of population indices were available from 1968-2011 (for an explanation of these indices see Link & Sauer, 2002). Trends were standardized across species by dividing the index value for each year by the value for 1968, so that the starting value for all species was the same.
2. The time series of indices for the *i*th species, with a length of 44 years, was converted to 43 log change values of $X_{i,j} = \log(I_{i,j+1} / I_{i,j})$. $I_{i,j}$ is the population index value in year $j$ and $I_{i,j+1}$ is the value for the following year.
3. Whilst species had already been sorted into CST+ and CST- groups, it is anticipated that species with larger absolute values of CST will have population trends that are more greatly affected by climate change. In light of this, the

weight for the contribution of each species to a multispecies index was calculated for the $i$th species in the $j$th year as

$$w_{i,j} = \frac{|CST_i|}{\sum_{s=1}^{v} |CST_s|}$$

where $v$ is the number of species with a viable value of $X_{i,j}$ in the year $j$ (here, 380 every year). *CST* is interchanged with *CLIM* for the CLIM+ and CLIM- indices. In this way, the bearing of the index was determined more by those species expected to be strongly affected by climate change than those not expected to be affected at all.

4. Then, the sum of $w_{i,j} \cdot X_{i,j}$ was calculated across species for the $j$th year. This represented the log of the proportional change in the multispecies index for a group between year $j$ and year $j$+1. After setting the initial value of the index to 100 in 1968, these change values were used to calculate values of the multispecies index up to 2011.

The CIIs produced here assume that CST+/CLIM+ species and CST-/CLIM- species are similarly susceptible to non-climatic environmental changes. If this is true, it would be expected that the multispecies indices for these two groups would show similar trajectories if there was no effect of climate change. However, if recent climate change has affected populations of these species, it would be expected that the CST-/CLIM- index would decline relative to the CST+/CLIM+ index. As such, by taking the ratio of the CST+/CLIM+ index to the CST-/CLIM- index in each year, we can summarize the magnitude of both positive and negative impacts of climate change on bird populations over time. By doing so, a CST CII and a CLIM CII were developed.

Following the above methodology, multispecies population indices were then developed for three more pairs of species groups; those species with positive and negative CST values according to each of the three model classes (CST+ and CST- according to GAMs, GLMs and RFs). From these three pairs of indices, three more CST CIIs were produced. In order to determine agreement between the CIIs produced by different model classes, the trajectories of these three CST CIIs were compared with one another and with that produced according to ensemble predictions. For both ensemble CLIM and CST CIIs, as well as the CST CIIs produced using individual model classes, 90% confidence intervals were produced based on 200 bootstrap replicates. Each bootstrap resampled the 380 study species with replacement, and then built a CII from this sample.

## 3.3. Results

131 (34%) species were expected to be positively affected by climate change according to CLIM, and 197 (52%) were expected to be positively affected according to CST. There was 75% agreement between CST and CLIM when classifying species into these two groups. 179 (47%) of species had positive observed population trends between 1968 and 2011. No significant relationship was found between observed population trend and CST across species ($F(1,378)=1.21$, $p=0.272$). However, a significant positive relationship was established between observed population trend and CLIM ($R^2=0.01$, $F(1,378)=4.452$, $p=0.036$) and between CST and CLIM ($R^2=0.45$, $F(1,378)=310.5$, $p<0.001$).

Both CST+ and CLIM+ multispecies indices were fairly similar to their counterparts (CST- and CLIM-) for the first five years, after which they diverged (Figures 3.4a & 3.5a). According to both CST and CLIM, this divergence has occurred with the index for species expected to be positively affected by climate change increasing relative to the index for species expected to be negatively affected. This is expected if the impact of recent climate change on populations has increased, resulting in two CIIs with positive trajectories (Figures 3.4b & 3.5b). However, the divergence between the two multispecies population indices was greater and more consistent over time according to CLIM than according to CST (Figures 3.4a & 3.5a). As such, the CII derived using CLIM has an upwards trend of a greater magnitude than that derived using CST (note the difference in scale of the Y-axis between Figures 3.4 & 3.5). Additionally, the bootstrap confidence intervals for the CST CII narrowly overlap 100 in 2011, demonstrating reduced certainty in the overall direction of this indicator. The CST CIIs constructed according to predictions by GAMs, GLMs and RFs individually did not differ strongly from the ensemble CST CII (Figure 3.6). Furthermore, comparing the three CIIs from individual model classes reveals that they constitute almost identical indicators with practically no differences in their shape, and very minor differences in their trajectories.

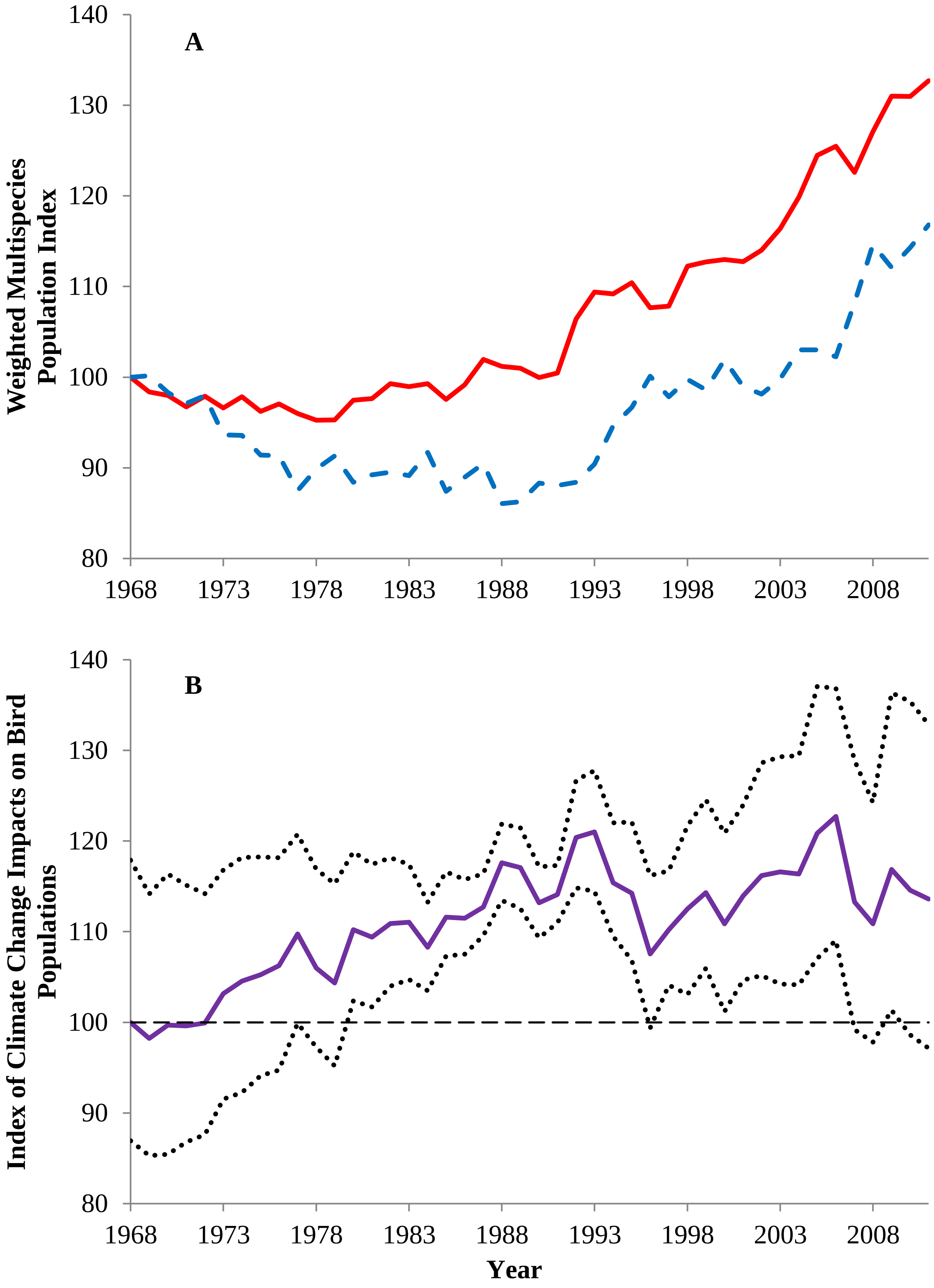

**Figure 3.4. (A)** Weighted multispecies population indices for two groups of North American terrestrial birds from 1968 to 2011 in the USA. The solid red line represents species that are expected to have experienced increased climatic suitability under recent climate change (1968-2011) according to ensemble predictions from species distribution models (CST+). The dashed blue line represents species expected to have experienced decreased climatic suitability under recent climate change (CST-). **(B)** The climatic impact indicator (CII) for the USA based on CST. The purple line represents the ratio of the population index for CST+ species to that for CST- species. The dotted lines show 90% bootstrap confidence intervals for annual values from 200 bootstrap replicates. Both the multispecies population indices and the CII are set to 100 in 1968.

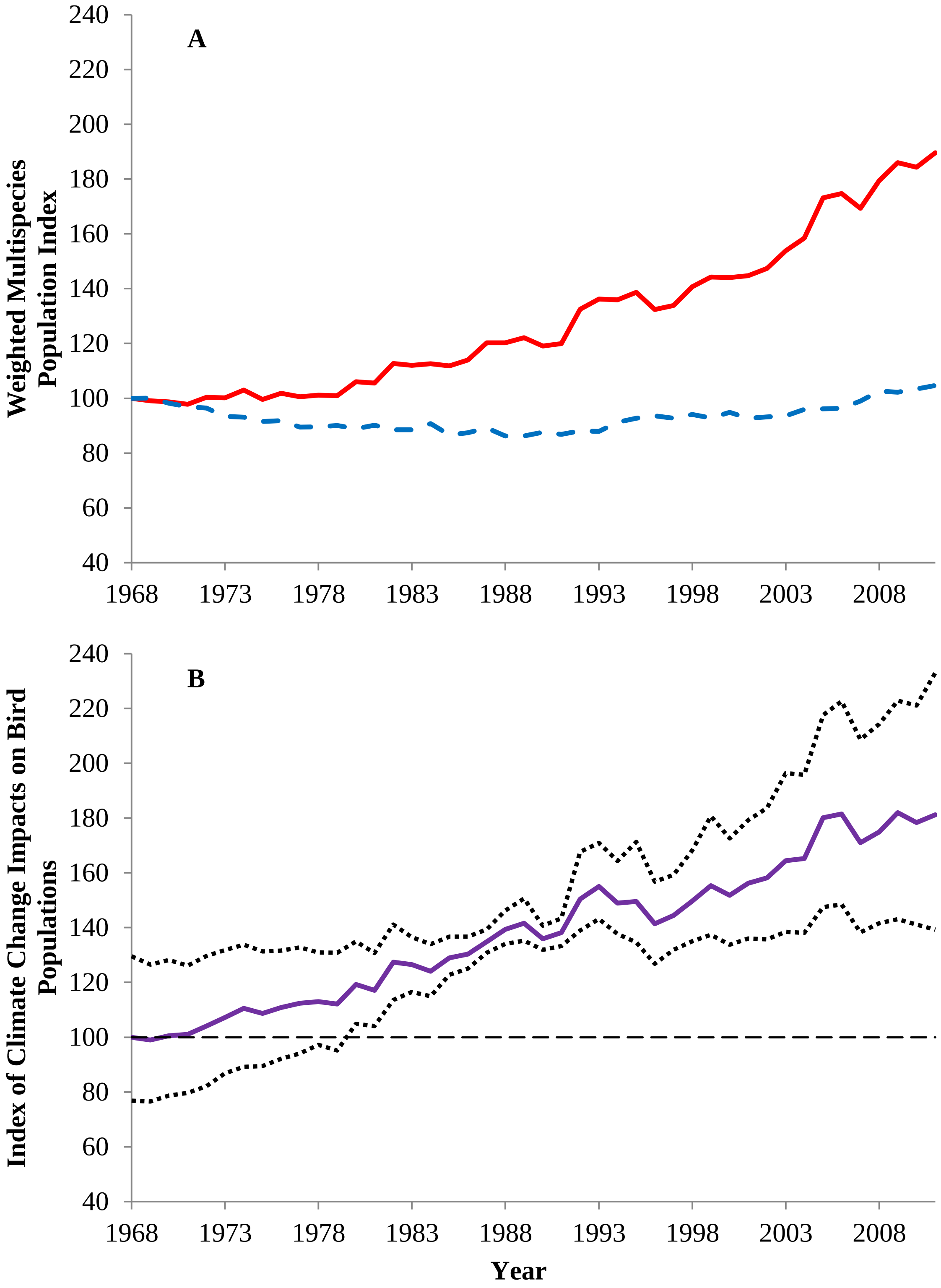

**Figure 3.5. (A)** Weighted multispecies population indices for two groups of North American terrestrial birds from 1968 to 2011 in the USA. The solid red line represents species expected to expand their range under future climate change according to an ensemble prediction from species distribution models (CLIM+). The dashed blue line represents species expected to contract their range under future climate change (CLIM-). **(B)** The climatic impact indicator (CII) for the USA according to CLIM. The purple line represents the ratio of the population index for CLIM+ species to that for CLIM- species. The dotted lines show 90% bootstrap confidence intervals for annual values from 200 bootstrap replicates. Both the multispecies population indices and the CII are set to 100 in 1968.

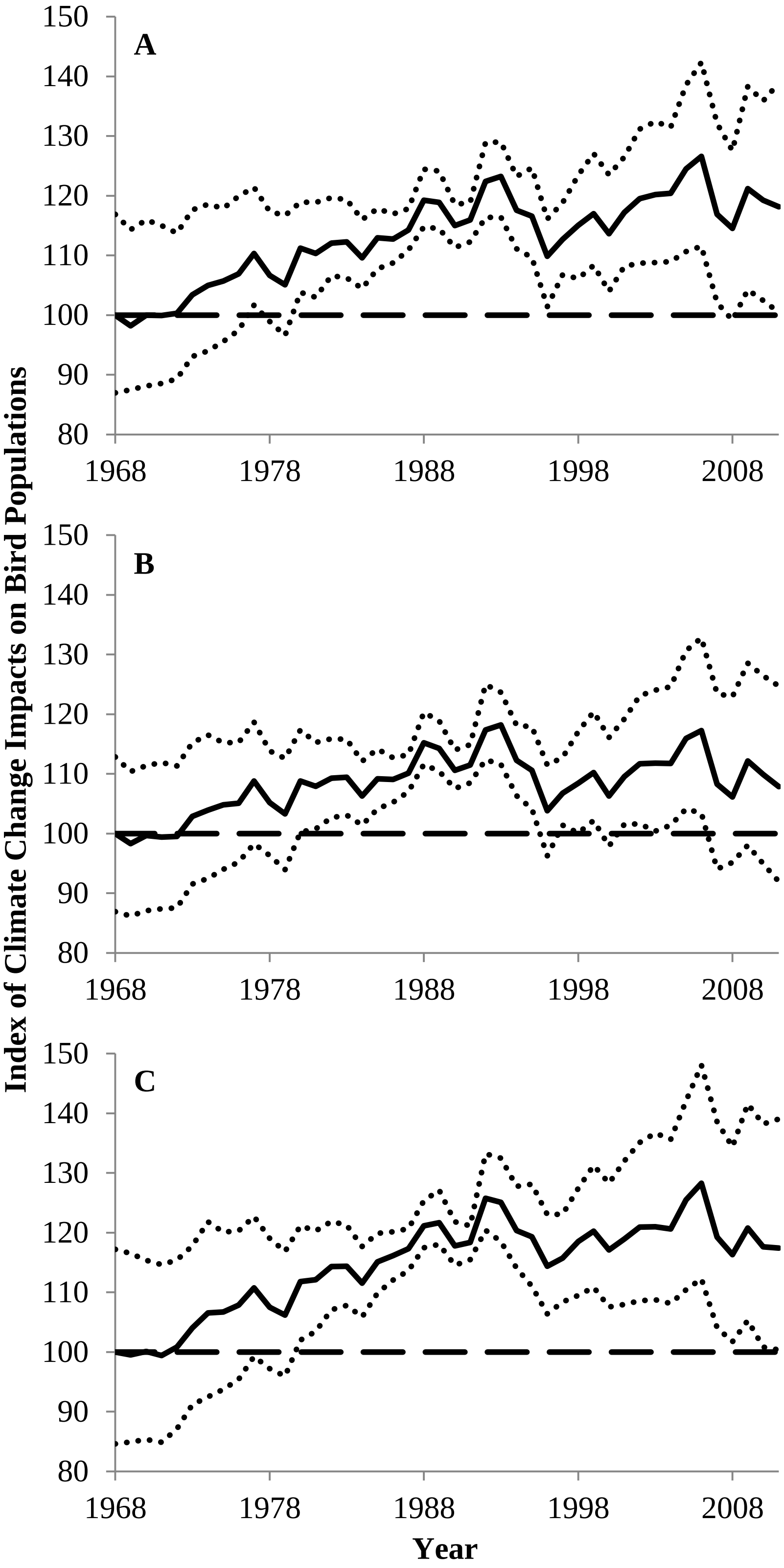

**Figure 3.6.** Three CIIs representing the ratio of the weighted population index for species expected to be positively affected by climate change (CST+) to that for species expected to be negatively affected by climate change (CST-). CST was calculated using predictions based on climate variables from 1968-2011 using **(A)** generalized additive models (GAMs), **(B)** generalized linear models (GLMs) and **(C)** random forests (RFs). The dotted lines show 90% bootstrap confidence intervals for annual values from 200 bootstrap replicates. The CIIs are set to 100 in 1968.

## 3.4. Discussion

According to the SDMs used in this study, 48% of species were expected to be adversely affected by recent climate change (CST<0), whilst 66% were projected to be negatively impacted by changes in climate up to 2100 (CLIM<0). In light of documented polewards shifts in species distributions under recent climate change (Hickling *et al.*, 2006), it seems likely that these expected range contractions within the USA will be caused by species shifting North into Canada. Whilst other studies predict that avian ranges will generally contract under future climate change (Barbet-Massin *et al.*, 2012, Jetz *et al.*, 2007), a smaller majority would be likely to show this effect if predicted distributions in Canada were considered. Gregory *et al.* (2009) found a slightly greater proportion of species expected to decline in extent across Europe; 75% of species in Europe had a future potential range that was smaller than the recent simulated range (CLIM<0). One explanation for this might be that whilst the USA clearly widens in the north, this is not true for Europe (Chapter 1, Figure 1.1). Thus, during a northwards shift, the distribution of an American species might on average be less likely to contract than the distribution of a European species, simply as a result of available land area.

The significant relationship between observed population trend and CLIM across species provides a form of independent validation of the SDMs produced in this study, and suggests that they are useful to predict species abundance. However, no significant relationship was found between observed population trend and CST across species, such as that found for rare birds in the UK (Green *et al.*, 2008). A relationship also existed between population trends and CLIM, but not CST, across common bird species in Europe (Gregory *et al.*, 2009). This suggests that CLIM might generally be a better predictor of observed population trends than CST. However, the biological significance of this relationship between CLIM and population trends might be contested here, given such a small value for $R^2$. Gregory *et al.* (2009) argued that CST is sensitive to annual extremes in bioclimatic variables, and for this reason it is less able to retrodict changes in abundance. CST is still an appropriate way to quantify expected effects of climate change on species' distributions because, unlike CLIM, it does not depend on future projections of climate change. In addition, when considering population level impacts of climate change between 1968 and 2011, it is more intuitive to capture a species' relationship with climate changes in the same time period. The use of CLIM to produce a

CII in this study assumes that recent climate change has progressed in the same direction as projected future climate change according to GCMs. CST and CLIM were highly correlated in this study, as they were in Gregory *et al.* (2009), offering some confirmation that this is the case.

Both CST+ and CLIM+ multispecies indices increased between 1968 and 2011 (Figure 3.4a & Figure 3.5a), but the increase was greater for the CLIM+ index. Furthermore, whilst the CST- index showed a marginal increase after 1990, the CLIM- index remained relatively stable. For these reasons the CLIM CII (Figure 3.5a) exhibits a stronger, more defined upwards trend than does the CST CII (Figure 3.4a). Clearly the two methods used to quantify the expected effect of climate change on species lead to considerably different CIIs. This is true despite 75% agreement between the two methods when sorting species into those expected to be positively or negatively affected by climate change. The method used to determine expected climate change effects on species should be carefully considered before finalizing the CII for a given region. However, there was very little divergence between CIIs derived using CST according to the 3 different model classes (Figure 3.6). This was also seen to be true for CLIM CIIs in preliminary work. This is encouraging, because different methods can be used to relate a species' distribution to climate whilst still reaching the same conclusion as to climatic impacts on populations. Still, the selection of bioclimatic predictors used in SDMs could be tailored to individual species to improve CST and CLIM calculations in future.

Despite the differences in CST and CLIM multispecies indices, according to both methods the trend for species expected to be positively affected by climate change consistently increased relative to its counterpart (Figure 3.4a & Figure 3.5a). As such, the overall trend for both CIIs is positive, although this is less clear under CST than under CLIM (Figure 3.4b & Figure 3.5b). Both methods show a detectable increase in the impact of climate change on populations of bird species in the USA, a result that is very similar to, if not stronger than, that reported by Gregory *et al.* (2009) for Europe.

Whilst the European indicator showed evidence of both positive and negative effects of climate change, the indicators here are driven by increases in the CST/CLIM+ indices rather than decreases in CST/CLIM- indices. This accords with evidence of range expansions in response to recent climate change, but comparatively few reports of range contractions and extinctions (Thomas *et al.*, 2006). This result contrasts with that for Europe, where divergence between CLIM+ and CLIM- indices occurred in both directions, with the CLIM- index decreasing reasonably consistently (Gregory *et al.*, 2009). However, the European study also comprised fewer than half the species in this study over a time period that was approximately half as long, so the multispecies population indices were bound to be more variable than those presented here.

It must be taken into account that land use dynamics may change in parallel with climate (Clavero *et al.*, 2011), and this may have affected the outcome of the indicators produced in this study. For example, in the latter half of the 21st century the eastern USA lost more agricultural land and underwent higher rates of urbanization than did the western USA (Brown *et al.*, 2005). Such processes are likely to affect avian populations, and where these changes are correlated with climatic impacts the indicator presented here might over- or underestimate the impacts of climate change.

It is important to remember that the strong upwards signal in these CIIs does not apply to the whole North American continent, but to mainland USA (excluding Alaska). Even within the USA, information on bird populations is biased as survey routes are situated more densely in the East (Figure 3.1). Preliminary work including Canada and Mexico in analyses demonstrated that an extremely high proportion (>95%) of species were expected to be positively affected by climate change across North America. Even if bird populations were adequately surveyed in Canada and Mexico, according to these SDMs a very small group of species would be expected to be negatively affected by climate change across the entire North American continent (5%). For this reason the resulting CII would have extremely large confidence intervals.

In order to make use of all available information in this study, all 380 species with adequate USA population indices were included in CIIs. It is expected that species with populations strongly affected by other factors such as habitat loss or persecution will fall evenly into the CST/CLIM+ and CST/CLIM- groups, so that population changes which are not related to climate will balance each other out in the CII. However, Gregory *et al.* (2009) excluded two species of raptors with distributions and populations strongly influenced by pesticide poisoning and persecution. In a similar vein, in future work it might be apt to exclude from USA indicators persecuted species and species such as the American Crow *Corvus brachyrhynchos,* whose population has changed recently due to West Nile virus (LaDeau *et al.*, 2007).

Using readily available information on bird distributions and populations, the CIIs developed in this chapter provide a robust indication that climatic impacts on bird populations in the USA have steadily increased over the last 40 years. This has filled a large geographical gap amongst the climate change indicators currently available, and revealed results that are strikingly similar to those seen across Europe. These indicators might stand alongside that of Gregory *et al.* (2009) as indicators of the pressure of climate change on biodiversity over time (Mace & Baillie, 2007). In this way it may contribute to future assessments of biodiversity loss (e.g. Butchart *et al.*, 2010) and help to bridge the gap between scientists and policymakers (Mooney & Mace, 2009). These USA indicators can be easily updated as new information becomes available on bird populations in future and as the North American BBS expands to Canada and Mexico (Ziolkowski *et al.*, 2010). In addition, an exciting prospect would be to combine indicators for Europe and the USA to work towards assembling a CII for the northern hemisphere.

A CII for the entire USA is liable to underestimate changes in climatic impacts over time for the following reason: Whilst a given species may be expected to experience increased climatic suitability under climate change in some areas in the USA, it may be expected to experience reduced suitability in others. When considering this species across the entire USA, it may appear that climatic suitability is expected to remain constant over time. Thus, a species which may in fact be strongly affected by climate change will not appear this way according to CST or CLIM across the entire USA. To address this issue, future work will involve downscaling CIIs to the state level, making it possible to detect finer scale climatic impacts which were not previously accounted for.

# 4. Downscaling USA Climatic Impact Indicators to the State-Level

## 4.1. Introduction

Recent climate change has affected species distributions, phenology and abundance (Cahill *et al.*, 2013, Parmesan, 2006) and is likely to be a threat to global biodiversity in future (Thuiller, 2007). Biodiversity is important for human welfare (MA, 2005), so there is an urgent need to monitor the state of biodiversity and the pressures upon it (Mace & Baillie, 2007). This can be done using biodiversity indicators, which present a large amount of information on aspects of biodiversity in an intuitive way (Gregory *et al.*, 2005). Many indicators produced to date have proven fit for the purpose of monitoring long term changes in biodiversity (Butchart *et al.*, 2010). However, biodiversity indicators generally arise where data is available, so spatial and taxonomic biases exist amongst them (Mace & Baillie, 2007, Walpole *et al.*, 2009). Given that the production of biodiversity indicators is data-limited, it is important to ensure that the methods used to summarize these data are optimized and suitable for the indicator's function (Gregory *et al.*, 2005).

By comparing population trends of avian species expected to be positively or negatively affected by climate change, Gregory *et al.* (2009) produced an indicator summarizing the pressure of climate change on European bird populations. This indicator was useful in an exploration of recent biodiversity declines (Butchart *et al.*, 2010), but there are potential ways in which the methodology of this indicator could be improved. For example, during the process of determining how species are expected to be affected by climate change, Gregory *et al.* (2009) quantified the change in climatic suitability for a species under future climate change using species distribution models (SDMs). A single metric named 'CLIM' was calculated for each species, representing the ratio of the future potential range extent to the recent simulated range extent across Europe. Many species' have responded to climate change by shifting their distributions uphill and towards the poles (Hickling *et al.*, 2006, Thomas, 2010). Following this, if a species' suitable climate shifts without expanding or contracting at the continental scale, then this species would have a neutral value of CLIM despite a clear expected impact of climate change upon it. For this reason it might be useful to produce climatic impact indicators (CIIs) at a smaller geographical scale to capture these previously overlooked impacts (Figure 4.1).

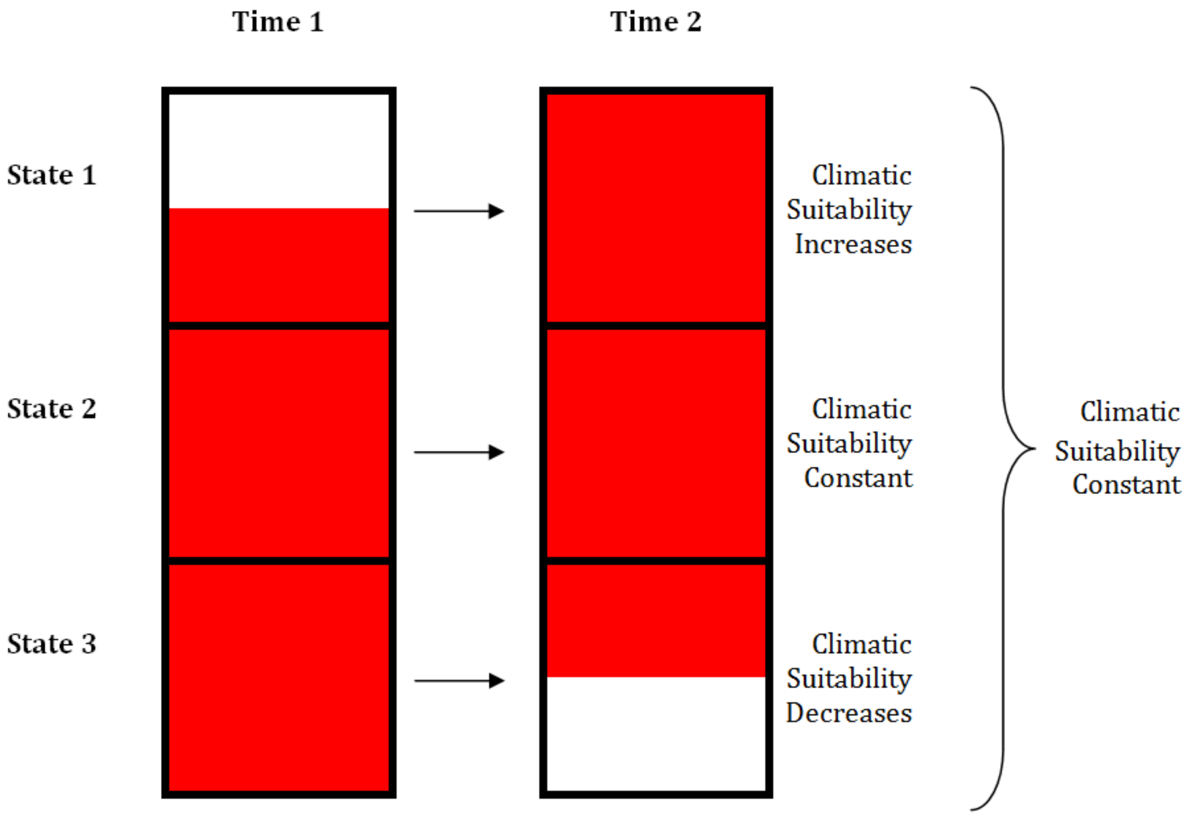

**Figure 4.1.** Conceptual diagram showing the movement of climate suitability for a species (shaded red) through three geographical regions (here, states). Mean climatic suitability appears constant when considering the three states as a whole across two time periods. However, when considered individually, two of the three states demonstrate a clear change in mean climate suitability for this species.

In the previous chapter, I aimed to address a geographical bias in climate change indicators by producing a USA CII similar to that produced by Gregory *et al.* (2009) for European birds. In this chapter, I apply a novel approach to produce a USA CII designed to include climatic impacts on populations that were not detected by the indicators in Chapter 3. To do so, I will produce state-level CIIs using climate suitability trends (CST, see Chapter 3) to determine how species are expected to be affected by climate change in individual states. By merging these state-level CIIs, I will then produce a USA CII which captures climatic impacts at a finer scale. In addition, having produced close to fifty separate indicators, I will be able to explore the effects of latitude and size of a state on the trajectory of its indicator. This study will trial a CII method which has been developed by Durham University and RSPB, and which has just been accepted as an updated indicator of climate change impacts on bird populations by the European

Environment Agency (S. Willis, pers. comm., December 2013). This method will contribute to the optimization of an indicator of climatic impacts on bird populations in the USA. The results will be highly applicable when considering how best to derive a CII for the Northern Hemisphere in future work.

## 4.2. Methods

### 4.2.1. Predicting the Expected Effect of Climate Change

CST CIIs were produced for all 48 states in mainland USA, with state boundary information obtained from the ESRI ArcGIS web site (ESRI, 2013). For each species in each state, CST was calculated using ensemble predictions from SDMs based on annual values of MTCO, GDD5 and APET from 1968-2011. This was done following methods identical to those presented in chapter 3.2.1. CST for each species in each state was then calculated as the slope of the regression of the logit annual mean probability of occurrence on year.

### 4.2.2. Producing State-Level CIIs using CST

Annual population indices for the 380 species considered in USA CIIs in chapter 3 were obtained for each state between 1968 and 2011 from the North American BBS (Sauer *et al.*, 2012). 6,956 such population indices were available across the 48 states, representing a mean of 145 species per state. These population trends were standardized across species and states by dividing the index value for each year by the value in the first recorded year, so that the starting value was the same for each trend. A subset of the 380 species was included in a state CII, based on availability and quality of population trends for that state. At the state level, population indices for some species behaved erratically and were removed according to the following criteria:

To determine whether the population trend for the $i$th species in the $j$th state was erratic, due to e.g. the species being irruptive in its movement between states or due to some other factor, the time series of indices of length $n$ was converted to $n$-1 values of

$\mathrm{X}_{i,j,k} = I_{i,j,k+1} / I_{i,j,k}$.

Where $I_{i,j,k}$ is the population index value in year $k$ and $I_{i,j,k+1}$ is the value for the following year. As such, $X_{i,j,k}$ represents the proportional change between the year $k$ and the year $k+1$.

If any of these proportional change values were below 0.1 or above 10, representing a change of an order of magnitude between two years, then that species was excluded from the CII for that state. Of the available population indices across the 48 states, 6,767 (97%) remained after removal of trends suggesting either irruptive species or erratic inter-year trend behavior (perhaps due to low or changed recording effort).

Multispecies population indices were produced for each of the 48 states to summarize the trends of those species expected to be positively affected by climate change, and those expected to be negatively affected. Species were sorted into these two groups according to CST, and the multispecies population indices were calculated for each state following Gregory *et al.* (2009) similarly to chapter 3.2.2:

1. The time series of indices for the *i*th species, with a length of *n* years, was converted to *n*-1 log change values of $X_{i,j} = \log(I_{i,j+1} / I_{i,j})$. $I_{i,j}$ is the population index value in year *j* and $I_{i,j+1}$ is the value for the following year.
2. Whilst species had already been sorted into CST+ and CST- groups, it is anticipated that species with larger absolute values of CST will have population trends that are more greatly affected by climate change. In light of this, the weight for the contribution of each species to a multispecies index was calculated for the *i*th species in the *j*th year as

   $$w_{i,j} = \frac{|CST_i|}{\sum_{s=1}^{v} |CST_s|}$$

   where *v* is the number of species with a viable value of $X_{i,j}$ in the year *j*. In this way, the bearing of the index was determined more by those species expected to be strongly affected by climate change than those not expected to be affected at all.
3. Then, the sum of $w_{i,j} \cdot X_{i,j}$ was calculated across species for the *j*th year. This represented the log of the proportional change in the multispecies index for a group between year *j* and year *j*+1. After setting the initial value of the index to 100 in 1968, these change values were used to calculate values of the multispecies index up to 2011.

4. Using this methodology, two composite multispecies indices were developed for each state. These described those species expected to be positively affected by climate change according to CST (CST+) and those expected to be negatively affected (CST-).

Under the premises outlined in chapter 3.2.2, a CST CII was derived for each state by taking the ratio of the CST+ index to the CST- index in each year. 90% bootstrap confidence intervals were also calculated for each state following chapter 3.2.2. In order to produce a USA CII accounting for climatic impacts on bird populations at the state-level, the CIIs for individual states were combined by taking the geometric mean of the index in each year across the 48 states. As such, each state was given an equal weighting in the context of the resultant USA CII, regardless of its size or avian population density.

To explore the impact of other potentially influential variables on the CII for a given state, we related the slope of a least squares regression of the common logarithm of that CII on calendar year to potential covariates. The size of a state was calculated as the number of grid cells (approximately 50×50km each) within a state, whilst the latitude of a state was taken as the mean latitude across those cells. The relationship of the slope of CIIs across states with state size (Size), state latitude (Lat), the proportion of species expected to be positively affected by recent climate change in a state (CST+) and the number of species included in a CII (Sp) was explored using a generalized linear model (GLM, MacCullagh & Nelder, 1989). Models were built using all combinations of the four predictors, and model selection was then carried out using the Akaike Information Criterion (AIC, Akaike, 1973) following Richards (2008). Models including both Size and Sp as predictors were not considered as these predictors were highly correlated (Pearson's correlation of 0.72). Models including both Lat and CST+ were ignored for the same reason (Pearson's correlation of 0.66).

## 4.3. Results

CST was successfully derived for all 6,767 species-state combinations for which population indices were available. In 31 of 48 states (65%) the majority of species had CST values which were negative, suggesting that at the state level climate suitability has generally decreased under recent climate change according to SDMs. Figure 4.2 suggests that a smaller proportion of species expressed positive CST values in the southern and eastern states.

Of the 48 CIIs produced, 38 (79%) had a positive slope according to a least squares regression. Figure 4.3 displays a selection of indicators representing states with varying proportions of species expected to be positively affected by recent climate change (CST+). Florida and Maryland were the two states with the lowest proportion of CST+ species, and were also those two states with CIIs that increased the most rapidly (Figure 4.3a & 4.3b). Approximately half of species in South Dakota and New Jersey were expected to be positively affected by recent climate change. Whilst South Dakota demonstrated reduced climatic impacts over time, the CII for New Jersey showed a clear increase after 1985 (Figure 4.3c & 4.3d). North Dakota and Minnesota were the two states with the greatest proportion of CST+ species, and both CIIs displayed strong downwards trends (Figure 4.3e & 4.3f). Figure 4.4 presents CIIs for states of a spectrum of sizes. Rhode Island and Delaware were the two smallest states which also had the first and fifth lowest study species richness. Both CIIs have strong upwards trends, but both were highly variable in the bootstrapping process (Figure 4.4a & 4.4b). New York and Arkansas were both of the median size, and these CIIs demonstrated upwards trends (Figure 4.4c & 4.4d). Texas and Montana were the largest states, with the first and third highest richness of study species respectively, and both CIIs showed a strong upwards trend (Figure 4.4e & 4.4f). By taking the geometric mean of all indices across states, a composite USA CII was developed (Figure 4.5). This indicator exhibited a consistent upwards trend since 1968, as expected given that the vast majority of its component states also demonstrated upward trends.

The most parsimonious model to predict the slope of the CII in a given state according to ΔAIC was that including significant negative effects of the latitude (Lat, $\beta$ = $-6.6 \times 10^{-4}$, $t(45) = -2.19$, $p = 0.034$) and the size of a state (Size, $\beta = -7.3 \times 10^{-5}$, $t(45) = -2.61$, $p = 0.012$). However, the model selection process revealed six models with a ΔAIC value of ≤6 and lower than all simpler nested versions (Table 4.1, see Richards (2008)) containing combinations of negative effects from all four predictors. This indicates that the proportion of species expected to be positively affected by climate change (CST+) and the number of species included in a CII (Sp) were also related to the slope of an indicator. However, the top three models (ΔAIC ≤2) did not include Sp as a predictor. Figure 4.6 depicts geographic variation in CII slope among states.

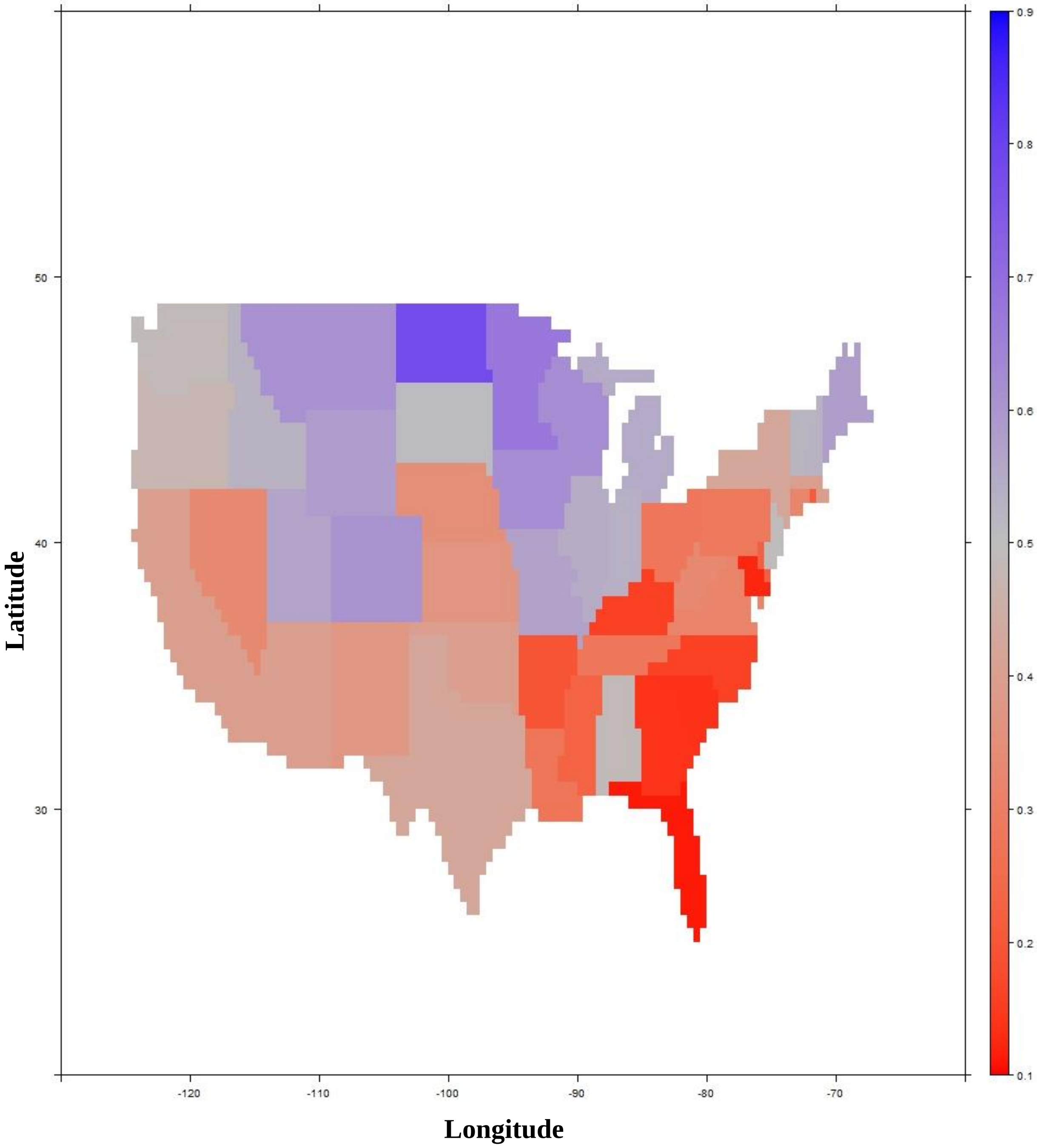

**Figure 4.2.** The proportion of species expected to be positively affected by climate change across 48 states in mainland USA. States with a lower proportion of species expected to be positively affected are shaded red, whilst states with a higher proportion of such species are shaded in blue. States with a more even proportions of species expected to be positively or negatively affected by climate change are shaded grey. The expected effect of climate change on a species was quantified by using SDMs to predict climate suitability for each species in each state from 1968-2011, and recording the direction of change in climate suitability over time.

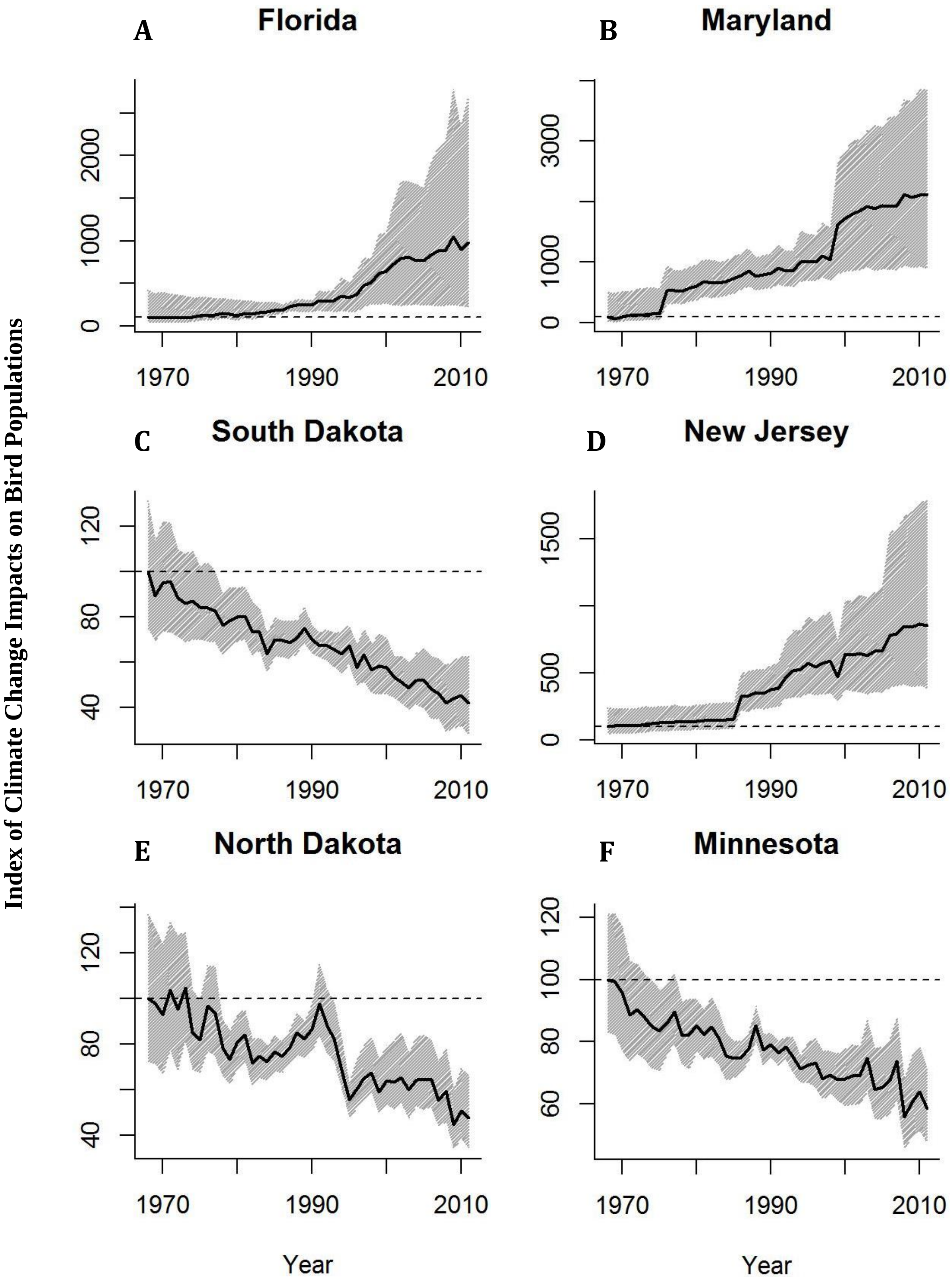

**Figure 4.3.** CIIs for those states in the USA with the highest (A & B) median (C&D) and lowest (E&F) proportions of species expected to be negatively affected by climate change. The name of the state to which a CII corresponds is displayed above it. The solid line on each graph represents the ratio of the population index for species expected to be positively affected by recent climate change (CST+) to that for those expected to be negatively affected (CST-). The shaded area indicates 90% bootstrap confidence intervals for annual values from 200 bootstrap replicates. All CIIs were set to 100 in 1968.

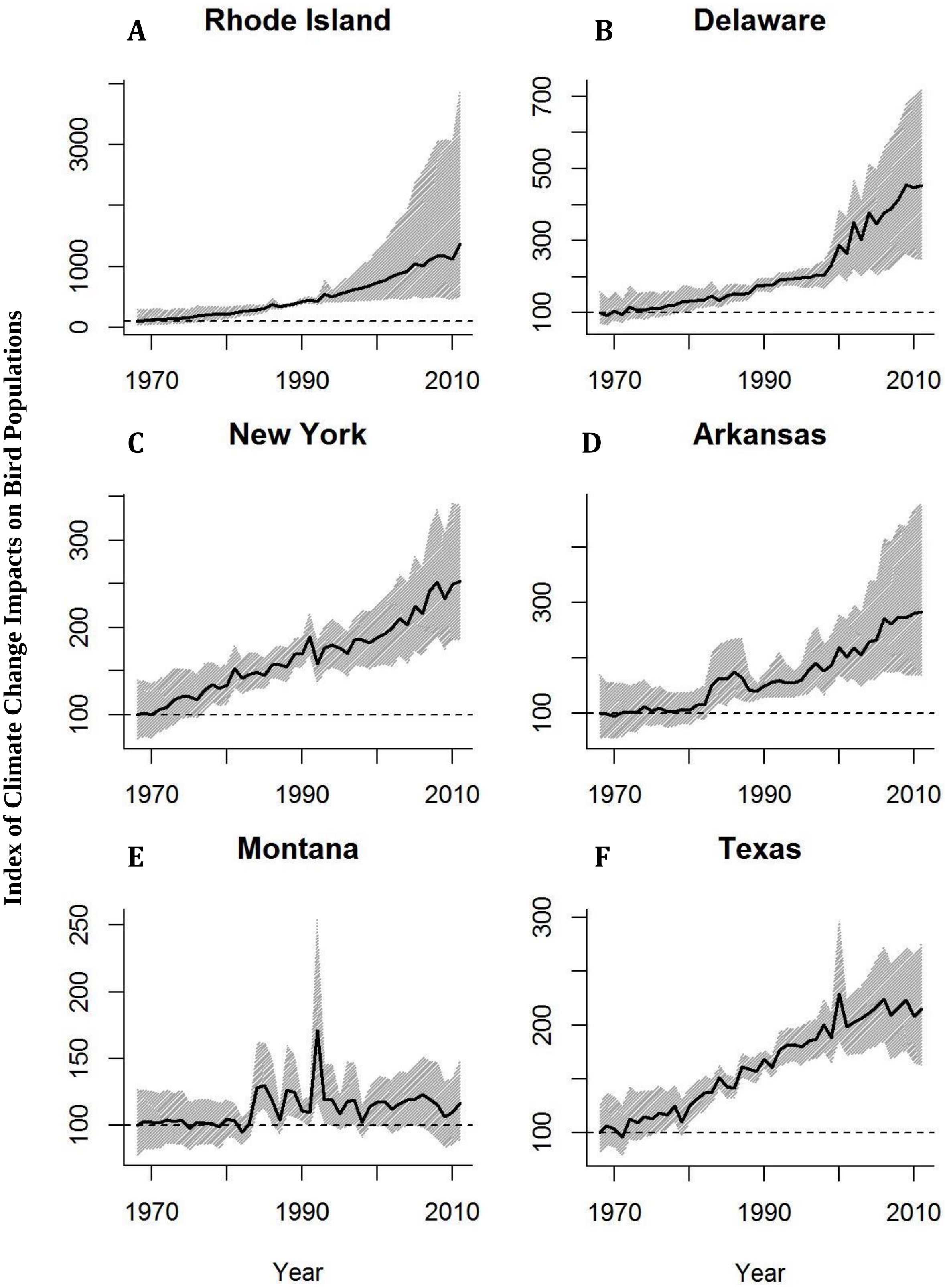

**Figure 4.4.** CIIs for the smallest (A & B) median sized (C&D) and largest (E&F) states in the USA. The name of the state to which a CII corresponds is displayed above it. The solid line on each graph represents the ratio of the population index for species expected to be positively affected by recent climate change (CST+) to that for those expected to be negatively affected (CST-). The shaded area indicates 90% bootstrap confidence intervals for annual values from 200 bootstrap replicates. All CIIs were set to 100 in 1968.

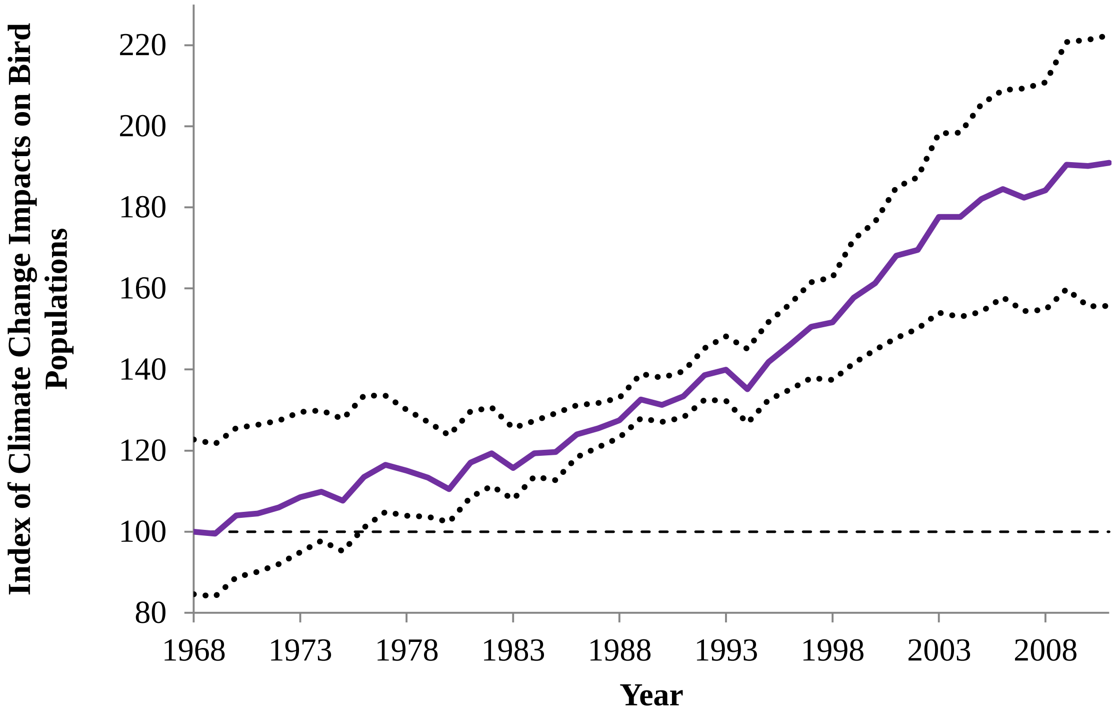

**Figure 4.5.** A composite CII for the USA, taken as the geometric mean of 48 CST CIIs derived independently for the mainland states. The purple line represents the CII, whilst the dotted lines indicate 90% bootstrap confidence intervals for annual values from 200 bootstrap replicates. The CIIs was set to 100 in 1968.

**Table 4.1.** Model selection results from GLMs relating the slope of the CII for a given state to different combinations of predictors. These predictors are mean latitude of a state (Lat), proportion of species expected to be positively affected by recent climate change (CST+), the size of a state (Size) and the number of species included in the CII for that state (Sp). Coefficients are displayed for each predictor in the models in which it was included. For each model, log-likelihood (LL) and ΔAIC values are displayed. Only the most parsimonious models (those with a ΔAIC value that is ≤6 and lower than all simpler nested versions (see Richards (2008)) and the null model (model 7) are displayed.

| Model | Lat | CST+ | Size | Sp | LL | ΔAIC |
|---|---|---|---|---|---|---|
| **1** | $-6.6 \times 10^{-4}$ | | $-7.3 \times 10^{-5}$ | | 156.19 | 0.00 |
| **2** | | $-1.9 \times 10^{-2}$ | $-5.1 \times 10^{-5}$ | | 155.97 | 0.44 |
| **3** | | $-2.3 \times 10^{-2}$ | | | 154.47 | 1.05 |
| **4** | | | $-7.1 \times 10^{-5}$ | | 153.77 | 2.46 |
| **5** | | | | $-1.2 \times 10^{-4}$ | 153.74 | 2.51 |
| **6** | $-6.3 \times 10^{-4}$ | | | | 152.80 | 4.40 |
| **7** | | | | | 150.82 | 6.07 |

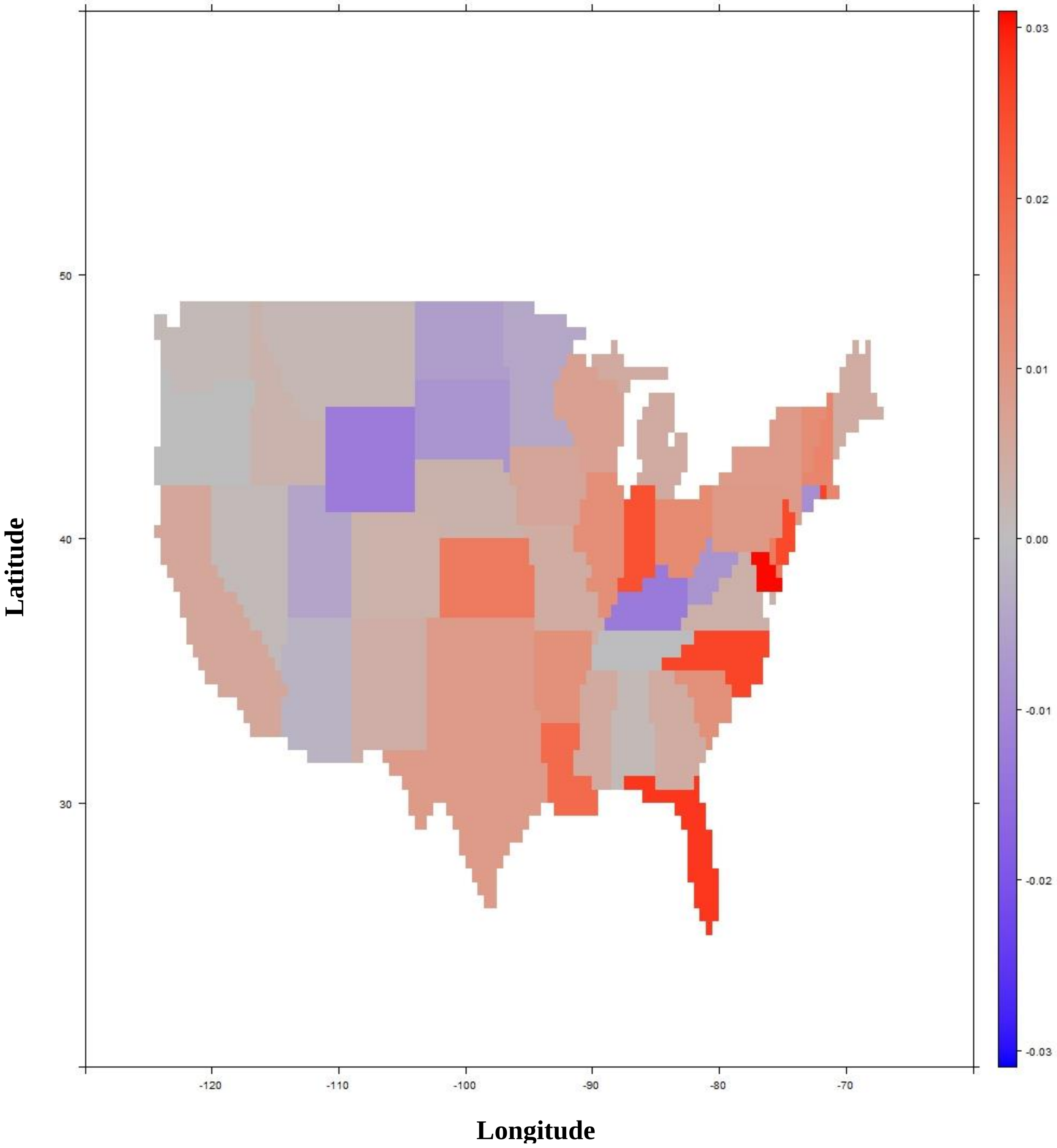

**Figure 4.6.** The slope of climatic impact indicators (CIIs) produced for 48 states in mainland USA. States with bird populations which have experienced the greatest increase in climatic impacts between 1968 and 2011 are shaded red, whilst those which have experienced the greatest decrease in climatic impacts are shaded in blue. States with relatively stable climatic impacts are shaded grey. CIIs were derived for each state by comparing the multispecies population indices for bird species expected to be positively and negatively affected by climate change.

## 4.4. Discussion

Deriving CST at the state level yielded different results from those found across the USA; in chapter 3 just 48% of species were seen to experience reduced climatic suitability according to SDMs across mainland USA. In contrast, the majority of species were expected to be negatively affected by climate change in 65% of individual states, with almost 90% of species in some states having negative CST values (Figure 4.2). These expected climatic effects were overlooked in USA-wide analyses, as some species would appear to have constant climate suitability across the USA when in fact they have experienced reduced suitability in some states and increased suitability in others (Figure 4.1). For this reason, calculating expected climatic effects at a smaller scale and building indicators for each state determines the extent of climatic impacts on populations more comprehensively. Climatic suitability decreased for a greater proportion of species in the eastern and southern states (Figure 4.2). This might be explained by suitable climate shifting northwards for most species in this study, in line with evidence of polewards shifts in the distributions of a variety of taxa under climate change (Hickling *et al.*, 2006, Thomas, 2010) including North American birds (Hitch & Leberg, 2007). The western USA constitutes a more altitudinally heterogeneous landscape than the eastern USA (Gesch, 2002). For this reason climatic suitability might shift uphill and be retained within the western states, but shift northwards out of the eastern states resulting in decreased CST values.

The vast majority of the CIIs constructed for the 48 mainland states (79%) had a positive slope, indicating that increases in climatic impacts on bird populations across the USA are widespread but not universal. This reinforces the result found in chapter 3, whereby climatic impacts appear to be increasing across the USA as a whole. However, some of the CIIs developed for individual states express much steeper increases than the USA CII produced with the same method (Figure 4.3a & 4.3b compared with Figure 4.2 in Chapter 4.3). The CIIs displayed for Florida, Maryland, Rhode Island and Delaware show sharp increases, with index values in 2011 of up to 20 times the index value in 1968. Occasionally extreme increases in state level indicators might be attributed to a smaller number of species inducing variability in an indicator, as made evident through the bootstrap confidence intervals for these states (e.g. Figure 4.3a & 4.3b). Alternatively, these extreme results might be driven by greater relative changes in climatic suitability for species at the state level (Figure 4.1) or relative population changes which are more pronounced at the state level (Sauer *et al.*, 2012).

The vast majority of states demonstrated increases in climatic impacts over time, as expected given unprecedented recent temperature increases (IPCC, 2007). Some states did demonstrate decreased climatic impacts on bird populations over time, however (e.g. Figure 4.3c, e and f). This could represent a failure of SDMs to adequately predict climate suitability for species within a state, or confounding effects of other drivers of population change such as changes in land use. It is possible that the above is also true for some of the states with increasing CIIs; landscape gradients may often be correlated with climate change impacts (Clavero *et al.*, 2011). Nevertheless the majority of indicators increase over time during a period of warming, thus it is likely that the CIIs produced here are largely driven by climate. Furthermore, when the 48 state level indicators were combined to form a composite indicator of climatic impacts on bird populations in the USA, a stable upwards trend was evident. This not only consolidates the overall conclusion that climatic impacts on bird populations have increased in the USA under recent climate change, but suggests that by downscaling CIIs to state level and recombining them it is possible to detect climatic impacts which were previously not accounted for (Figure 4.5). A comparison of this composite CST CII (Figure 4.5) with the CST CII presented for the entire USA (Figure 3.2 in Chapter 3) reveals that despite using the same method to quantify expected effect of climate change on a species (CST), the composite indicator captures a far greater increase in climatic impacts on bird populations over the same time period. This is a result which has also recently been seen when producing CII for Europe based on combining individual country CIIs (Stephen Willis, Pers. Comm., 26 September 2013).

During model selection, the proportion of species expected to be positively affected by climate change (CST+) and the latitude (Lat) of a state were negatively related to the slope of the CII for that state (Table 4.1). Mean temperature increases have not been greater at lower latitudes within the USA (IPCC, 2007), so it is unclear what might be causing states at lower latitudes to be experiencing greater increases in climatic impacts. Also displaying a negative relationship with the slope of a state CII were the size (Size) and study species richness (Sp) of a state (Table 4.1). This might be because indicators for smaller states detect climatic impacts that those for the larger states cannot, for reasons similar to those described in Figure 4.1. For example, a species' suitable climate might shift within a larger state but not increase or decrease, resulting in a CST approximating zero. However, such a shift in a smaller state is more likely to correspond with a significant gain or loss of suitable climate for that species, so small states are likely to exhibit more extreme values for CST. However, it must be taken into account that CIIs including fewer species will exhibit greater variability, so those CIIs with the steepest increases in climatic impacts are likely to also be the most variable in the bootstrapping process. Whilst the models produced here to predict the slope of the CII within a state were useful, there are a number of other parameters which would have been likely to improve them. For example, including changes in e.g. mean temperature since 1968 for each state within the GLM analyses may indicate that bird trends changed most where greatest temperature changes have been recorded.

The use of the state as a unit to downscale the indicator presented in chapter 3 is subject to criticism. State boundaries do not divide the USA based on biologically relevant factors such as climate, so it is difficult to reach conclusions about the ecological mechanisms that might cause state-level indicators to differ from one another. However, state boundaries represent political divisions, which is appropriate given that the intention of a CII is to communicate biodiversity information to policymakers (Mace & Baillie, 2007). Furthermore, population trends for North American birds are already available for each species in each state, making the state-level approach the most straightforward to downscale population indices. The method used to construct the composite CST CII for the USA (Figure 4.5) crudely combines the 48 state level indicators, with all states contributing equally to the indicator. It may have been more appropriate to weight each state's contribution to the composite CII according to its species richness or relative abundance of avian species, or maybe even by the balance of CST+ and CST- species (down-weighted states where there is poor representation in one group). However, at this stage it was unclear what the most appropriate weighting method would be. Further work could usefully focus on this issue.

The indicators presented in this chapter consolidate the main finding of chapter 3; climatic impacts on populations of bird species in the USA have shown a detectable increase during a period of climatic warming (IPCC, 2007). This represents an important addition to evidence of climate change effects on the phenology and distribution of North American bird species (Dunn & Winkler, 1999, Hitch & Leberg, 2007). In addition, by exploring an alternative method by which to construct a more detailed climatic impact indicator, this chapter offers an improvement on the methods of Gregory *et al.* (2009). By summarizing complex information on the pressure of climate change on biodiversity, this composite CII for the USA (Figure 4.5) will be useful to review progress toward conservation targets in future. This method could be applied to Europe, and eventually contribute to the development of a CII for those areas in the northern hemisphere where data are available. Beyond this, the production of state-level indicators has given a valuable insight into what drives the trajectory of a CII, as well as demonstrating just how variable CIIs might be across space (Figure 4.6). It is recommended that future work strives to better understand the drivers of the slope of a CII by considering more factors than were included here.

# 5. Conclusions

This study set out primarily to determine whether the impacts of climate change on populations of bird species has increased across North America, as they have in Europe (Gregory *et al.*, 2009). In order to do so a number of climatic impact indicators (CIIs) were developed, depicting the changing pressure of climate change on avian populations over time. With caution, these might be considered indicators of the pressure of climate change on biodiversity across North America, depending on the extent to which population trends in birds are mirrored by those in other taxa (Gregory *et al.*, 2005). The threat of climate change to biodiversity is anticipated to increase greatly in future (Thuiller, 2007). In light of the consequences of this for ecosystem services and human welfare, the use of new and existing methods to better understand the recent impacts of climate change was timely and relevant. In the process of reaching conclusions about climatic impacts on biodiversity in North America, some insights were also gained with regard to production and interpretation of SDMs.

In order to quantify the expected impact of climate change on populations of each species, SDMs of three classes (GAMs, GLMs and RFs, see chapter 2.2.1) were fitted to the recent distributions of 384 North American bird species based on three bioclimatic variables (MTCO, MTWM and APET, see chapter 2.2.2). Of these variables, MTCO was the most important predictor across species, followed by GDD5 and then APET, which makes sense in light of expected abiotic limits on avian distributions (Root, 1988). Both data partitioning and resubstitution were used to assess the fit of these models individually and in S-SDMs respectively (see chapter 2.3). According to both methods RFs surpassed GAMs, which surpassed GLMs, when predicting the baseline distribution of each species. Benito *et al.* (2013) presented a comparison of 19 SDM methods when predicting distributions of 1224 tree species in Mesoamerica, and within this selection the ranking of GAMs, GLMs and RFs was the same as that presented in Chapter 2. This could suggest that the characteristics of these models that cause them to perform better or worse are conserved even when predicting very different groups of species. Model fit for the three model classes across species was deemed adequate for the purposes of quantifying climate suitability trends across species.

Using predictions from ensemble SDMs, recent climate suitability trend (CST) and expected change in range extent under future climate change (CLIM) were calculated for 380 avian species with distributions in the USA. According to CST just over half of these species (52%) were expected to be positively affected by climate change, whilst according to CLIM the proportion was much lower (34%). In Europe, just 25% of species were expected to be positively affected by climate change according to CLIM (Gregory *et al.*, 2009). A number of studies have predicted contractions in avian distributions under future climate change (Barbet-Massin *et al.*, 2012, Jetz *et al.*, 2007), and CLIM predicted that a greater proportion of species would be negatively affected by climate change. This makes sense as CLIM quantified expected climate change impacts based on climate change over a longer period. Using first CLIM, and then CST, species were sorted into two groups: those expected to be positively, and those expected to be negatively affected by climate change. For each of these groups under each of the two methods, a multispecies population index was produced using information from the North American Breeding Bird Survey (BBS, Sauer *et al.*, 2012). CIIs were derived by taking the ratio of the positive index to the negative index, and both the CST and CLIM CIIs demonstrated a clear increase in climatic impacts on bird populations over the past 40 years (see chapter 3.3, Figures 3.2 & 3.3). The trend was stronger according to CLIM than CST, and population trend was positively correlated with CLIM across species. The CLIM metric produced by Gregory *et al.* (2009) was also correlated with population trends of European bird species, and the corresponding CII also demonstrated an overall upwards trend.

The CIIs presented in chapter 3 give strong evidence that climatic impacts on populations of bird species in North America have increased under recent climate change, as they have across Europe. Population changes could have been driven by climate change directly, for example as a result of phenological change (Both *et al.*, 2004) or indirectly, through interspecific interactions (Pearce-Higgins *et al.*, 2010). However, it must also be considered that these two indicators still only cover a small subset of the earth's terrestrial surface. Furthermore, both indicators mainly summarize information derived from temperate biomes in the northern hemisphere. Population trends for avian species are unavailable in other geographical regions, and thus these indicators represent a biased sample of climate change impacts worldwide.

The impact of climate change on the distribution of each species was calculated across mainland USA such that if a species' range shifted within the USA, but did not expand or contract, the species would be considered unaffected by climate change (see Chapter 4.1, Figure 4.1). To account for this, CST indicators were downscaled to the state level to capture climatic impacts on species at a finer scale. CIIs were produced for each of 48 mainland states in the USA, of which 38 (79%) demonstrated a positive slope based on a least squares regression of the indicator value on calendar year. These state level indicators were combined to produce a composite CII for the USA, and this indicator increased more steeply than CIIs developed in chapter 3 for the entire USA (chapter 4.3, Figure 4.5). As predicted, considering changes in climate suitability for a species at the state level has produced an indicator which detects climatic impacts that were previously overlooked. As indicators were produced for 48 states, a model was produced to test for an effect of various attributes of a state on the slope of that state's CII. In the most parsimonious model, significant negative effects were detected of the size and latitude of a state on the slope of its indicator. The reasons for greater climatic impacts at lower latitudes is unknown, as mean temperature changes over recent decades were not greater in the Southern USA than in Northern USA (IPCC, 2007). However, it is possible that climate suitability trends in smaller states might reflect finer scale changes in climate suitability for a species, resulting in steeper indicators. Above all, the findings of chapter 4 consolidate the conclusion from chapter 3; that climatic impacts on populations of avian species have increased across the USA over the last 40 years.

Whilst this project has gone some way toward quantifying climatic impacts on bird populations in the USA, there are several shortcomings to the methods used. Just three classes of SDM were used, which was a small subset of those available (Benito *et al.*, 2013). A greater variety of model classes might be used in future work, as this might produce a better consensus of the expected effect of climate change on each species' distribution. In addition, the model evaluation methods used here were not able to account for spatial autocorrelation. The use of resubstitution whilst evaluating SDMs should generally be avoided, as this method will give an overly optimistic view of predictive performance when a model over-fits to the distribution of a species (Araújo *et al.*, 2005). Future work should account for spatial autocorrelation during model validation, perhaps through *k*-fold partitioning of the data (Bagchi *et al.*, 2013). The possibility also exists that the indicators presented here partially reflect changes in populations caused by pressures other than climate change. This will be true where other pressures, such as land use change, occur in parallel with climate change (Clavero *et al.*, 2011). To assess this, future work might use available datasets on agricultural intensity across states to see if this is related to the slope of a state's CII (Mineau & Whiteside, 2013). When constructing a composite CII for the USA from the 48 state-level CIIs, all states were weighted equally regardless of size or species richness. This may have biased the composite indicator by giving small states a large contribution relative to their size, and future work should find ways to improve on this.

Previous work has revealed impacts of climate change upon avian distributions (Hitch & Leberg, 2007) and phenology (Van Buskirk *et al.*, 2009) in the USA. Evidence is presented here that the impact of climate change on bird populations in the USA has increased during a period of climatic warming (IPCC, 2007). These changes mirror those detected across Europe (Gregory *et al.*, 2009). In addition, the CIIs produced in chapters 3 and 4 are biodiversity indicators that summarize large quantities of information in a form that is easy for policy-makers to interpret. Representing "pressure" indicators in the pressure-state-response framework of Mace and Baillie (2007), these CIIs can be updated as new information becomes available on climate change and bird populations in the USA. It is anticipated that these indicators, or future generations thereof, might be of use when performing assessments of progress towards biodiversity targets (Butchart *et al.*, 2010). However, a priority for future work in producing CIIs should be to expand the breadth of coverage to exploit all available data on avian population trends. A target for the near future might be to produce a CII for the Northern hemisphere, for example. In addition, population trends are available for many vertebrate taxa other than birds (Collen *et al.*, 2009), and the inclusion of these data would make CIIs more representative of biodiversity in general. Unfortunately, it was beyond the scope of this study to divide avian species in North America into functional or taxonomic groups and investigate how they differ in their population level responses to climate change. Future work should incorporate this into analyses to shed light on the processes underlying the 'broad sense' trends which are summarized in a CII.

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# Appendix 1

**Table A1.** Listed below are the 384 species for which SDMs were produced in Chapter 2. Species names follow those listed on the BirdLife web site (BirdLife International, 2013). Approximate range size was calculated by taking the number of cells occupied by that species in the data later used to calibrate SDMs. This number was then multiplied by 2500km$^2$, the approximate area of one cell.

| Species Name (Genus species) | Approximate Range Size in North America (km$^2$) |
|---|---:|
| Accipiter cooperii | 8,495,000 |
| Accipiter gentilis | 14,245,000 |
| Accipiter striatus | 14,450,000 |
| Actitis macularius | 18,172,500 |
| Aechmophorus clarkii/occidentalis | 5,675,000 |
| Aeronautes saxatalis | 4,030,000 |
| Agelaius phoeniceus | 15,855,000 |
| Aimophila ruficeps | 1,097,500 |
| Aix sponsa | 6,657,500 |
| Ammodramus bairdii | 1,015,000 |
| Ammodramus caudacutus/nelsoni | 1,845,000 |
| Ammodramus henslowii | 1,305,000 |
| Ammodramus leconteii | 3,862,500 |
| Ammodramus maritimus | 142,500 |
| Ammodramus savannarum | 5,485,000 |
| Amphispiza belli | 1,152,500 |
| Amphispiza bilineata | 2,357,500 |
| Anas acuta | 14,282,500 |
| Anas americana | 12,772,500 |
| Anas clypeata | 11,647,500 |
| Anas cyanoptera | 4,155,000 |
| Anas discors | 10,352,500 |
| Anas fulvigula | 182,500 |
| Anas platyrhynchos | 16,965,000 |
| Anas rubripes | 5,207,500 |
| Anas strepera | 5,160,000 |
| Anhinga anhinga | 1,322,500 |
| Anthus spragueii | 1,302,500 |
| Aphelocoma californica | 2,300,000 |
| Aquila chrysaetos | 16,732,500 |
| Archilochus alexandri | 2,420,000 |
| Archilochus colubris | 5,407,500 |
| Ardea herodias | 14,400,000 |
| Arremonops rufivirgatus | 422,500 |
| Asio flammeus | 17,645,000 |
| Athene cunicularia | 5,690,000 |
| Auriparus flaviceps | 1,647,500 |
| Aythya affinis | 7,490,000 |
| Aythya americana | 6,185,000 |
| Aythya collaris | 6,377,500 |
| Aythya valisineria | 5,482,500 |
| Baeolophus bicolor | 2,997,500 |

| | |
|---|---|
| Baeolophus inornatus | 182,500 |
| Baeolophus ridgwayi | 1,082,500 |
| Bartramia longicauda | 4,092,500 |
| Bombycilla cedrorum | 9,070,000 |
| Bonasa umbellus | 10,830,000 |
| Botaurus lentiginosus | 10,755,000 |
| Branta canadensis | 16,507,500 |
| Bubo virginianus | 21,005,000 |
| Bubulcus ibis | 10,655,000 |
| Bucephala albeola | 7,067,500 |
| Buteo jamaicensis | 17,782,500 |
| Buteo lineatus | 3,635,000 |
| Buteo platypterus | 5,280,000 |
| Buteo regalis | 3,082,500 |
| Buteo swainsoni | 9,177,500 |
| Butorides virescens | 6,860,000 |
| Calamospiza melanocorys | 1,855,000 |
| Calcarius ornatus | 977,500 |
| Callipepla californica | 1,165,000 |
| Callipepla gambelii | 530,000 |
| Callipepla squamata | 1,340,000 |
| Calypte anna | 497,500 |
| Calypte costae | 540,000 |
| Campylorhynchus brunneicapillus | 1,737,500 |
| Caprimulgus arizonae/vociferus | 4,637,500 |
| Caprimulgus carolinensis | 1,745,000 |
| Caracara cheriway | 1,437,500 |
| Cardinalis cardinalis | 5,835,000 |
| Cardinalis sinuatus | 1,410,000 |
| Carduelis lawrencei | 137,500 |
| Carduelis pinus | 9,947,500 |
| Carduelis psaltria | 3,492,500 |
| Carduelis tristis | 8,852,500 |
| Carpodacus cassinii | 1,660,000 |
| Carpodacus mexicanus | 7,637,500 |
| Carpodacus purpureus | 5,825,000 |
| Casmerodius albus | 7,947,500 |
| Cathartes aura | 10,792,500 |
| Catharus fuscescens | 4,375,000 |
| Catharus guttatus | 10,945,000 |
| Catharus ustulatus | 10,622,500 |
| Catherpes mexicanus | 4,295,000 |
| Catoptrophorus semipalmatus | 2,610,000 |
| Centrocercus minimus/urophasianus | 1,465,000 |
| Certhia americana | 7,752,500 |
| Chaetura pelagica | 6,277,500 |
| Chaetura vauxi | 2,282,500 |
| Chamaea fasciata | 250,000 |
| Charadrius montanus | 825,000 |

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| Charadrius vociferus | 16,242,500 |
| Chondestes grammacus | 5,847,500 |
| Chordeiles acutipennis | 1,897,500 |
| Chordeiles minor | 15,065,000 |
| Cinclus mexicanus | 6,827,500 |
| Circus cyaneus | 16,670,000 |
| Cistothorus palustris | 5,532,500 |
| Cistothorus platensis | 2,385,000 |
| Coccothraustes vespertinus | 4,742,500 |
| Coccyzus americanus | 5,117,500 |
| Coccyzus erythropthalmus | 5,507,500 |
| Colaptes chrysoides | 360,000 |
| Colinus virginianus | 4,342,500 |
| Columbina inca | 2,530,000 |
| Columbina passerina | 2,162,500 |
| Contopus cooperi | 12,810,000 |
| Contopus sordidulus | 8,255,000 |
| Contopus virens | 4,347,500 |
| Coragyps atratus | 3,775,000 |
| Corvus brachyrhynchos | 13,615,000 |
| Corvus caurinus | 572,500 |
| Corvus corax | 21,462,500 |
| Corvus cryptoleucus | 1,107,500 |
| Corvus ossifragus | 925,000 |
| Crotophaga sulcirostris | 1,365,000 |
| Cyanocitta cristata | 7,395,000 |
| Cyanocitta stelleri | 3,812,500 |
| Cyanocorax yncas | 490,000 |
| Cypseloides niger | 1,067,500 |
| Dendragapus obscurus | 2,202,500 |
| Dendrocygna autumnalis | 960,000 |
| Dendrocygna bicolor | 542,500 |
| Dendroica caerulescens | 1,317,500 |
| Dendroica castanea | 3,537,500 |
| Dendroica cerulea | 777,500 |
| Dendroica coronata | 13,660,000 |
| Dendroica discolor | 1,542,500 |
| Dendroica dominica | 1,905,000 |
| Dendroica fusca | 2,422,500 |
| Dendroica graciae | 1,030,000 |
| Dendroica magnolia | 4,855,000 |
| Dendroica nigrescens | 1,897,500 |
| Dendroica occidentalis | 352,500 |
| Dendroica palmarum | 4,565,000 |
| Dendroica pensylvanica | 2,917,500 |
| Dendroica petechia | 19,872,500 |
| Dendroica pinus | 2,092,500 |
| Dendroica striata | 9,922,500 |
| Dendroica tigrina | 3,407,500 |

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| Dendroica townsendi | 2,015,000 |
| Dendroica virens | 4,107,500 |
| Dolichonyx oryzivorus | 4,475,000 |
| Dryocopus pileatus | 6,910,000 |
| Dumetella carolinensis | 7,522,500 |
| Egretta caerulea | 1,197,500 |
| Egretta thula | 5,115,000 |
| Egretta tricolor | 582,500 |
| Elanoides forficatus | 577,500 |
| Elanus leucurus | 1,462,500 |
| Empidonax alnorum/traillii | 16,537,500 |
| Empidonax difficilis/occidentalis | 3,225,000 |
| Empidonax flaviventris | 7,152,500 |
| Empidonax hammondii | 3,632,500 |
| Empidonax minimus | 7,517,500 |
| Empidonax oberholseri | 3,047,500 |
| Empidonax virescens | 3,045,000 |
| Empidonax wrightii | 1,205,000 |
| Eremophila alpestris | 21,462,500 |
| Eudocimus albus | 500,000 |
| Euphagus carolinus | 11,010,000 |
| Euphagus cyanocephalus | 6,290,000 |
| Falco columbarius | 14,740,000 |
| Falco mexicanus | 4,252,500 |
| Falco peregrinus | 14,107,500 |
| Falco sparverius | 17,312,500 |
| Fulica americana | 11,692,500 |
| Gallinago gallinago | 16,802,500 |
| Gallinula chloropus | 5,207,500 |
| Geococcyx californianus | 2,865,000 |
| Geothlypis trichas | 14,815,000 |
| Glaucidium gnoma | 1,640,000 |
| Grus canadensis | 13,455,000 |
| Gymnorhinus cyanocephalus | 1,305,000 |
| Haliaeetus leucocephalus | 13,830,000 |
| Helmitheros vermivorum | 1,767,500 |
| Himantopus mexicanus | 2,375,000 |
| Hirundo rustica | 15,037,500 |
| Hylocichla mustelina | 3,702,500 |
| Icteria virens | 6,430,000 |
| Icterus bullockii | 3,775,000 |
| Icterus cucullatus | 1,117,500 |
| Icterus galbula | 9,277,500 |
| Icterus parisorum | 1,627,500 |
| Icterus spurius | 4,895,000 |
| Ictinia mississippiensis | 770,000 |
| Ixobrychus exilis | 3,685,000 |
| Junco hyemalis | 14,055,000 |
| Lanius ludovicianus | 9,202,500 |

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| Limnothlypis swainsonii | 1,102,500 |
| Limosa fedoa | 1,417,500 |
| Lophodytes cucullatus | 6,230,000 |
| Loxia curvirostra | 8,435,000 |
| Loxia leucoptera | 11,877,500 |
| Megaceryle alcyon | 17,877,500 |
| Megascops asio | 5,135,000 |
| Megascops kennicottii | 3,787,500 |
| Melanerpes aurifrons | 1,237,500 |
| Melanerpes carolinus | 3,030,000 |
| Melanerpes erythrocephalus | 5,815,000 |
| Melanerpes formicivorus | 1,290,000 |
| Melanerpes lewis | 2,297,500 |
| Melanerpes uropygialis | 545,000 |
| Meleagris gallopavo | 7,487,500 |
| Melospiza georgiana | 7,900,000 |
| Melospiza lincolnii | 10,510,000 |
| Melospiza melodia | 12,587,500 |
| Melozone aberti | 167,500 |
| Melozone crissalis | 335,000 |
| Melozone fuscus | 1,530,000 |
| Mimus polyglottos | 10,310,000 |
| Mniotilta varia | 6,580,000 |
| Molothrus aeneus | 2,085,000 |
| Molothrus ater | 12,355,000 |
| Myadestes townsendi | 4,650,000 |
| Mycteria americana | 177,500 |
| Myiarchus cinerascens | 3,432,500 |
| Myiarchus crinitus | 5,527,500 |
| Myiarchus tyrannulus | 1,252,500 |
| Nucifraga columbiana | 2,535,000 |
| Numenius americanus | 2,395,000 |
| Nyctanassa violacea | 2,352,500 |
| Nycticorax nycticorax | 8,807,500 |
| Oporornis agilis | 1,507,500 |
| Oporornis formosus | 1,992,500 |
| Oporornis philadelphia | 3,420,000 |
| Oporornis tolmiei | 3,225,000 |
| Oreortyx pictus | 357,500 |
| Oreoscoptes montanus | 2,202,500 |
| Oxyura jamaicensis | 7,365,000 |
| Pandion haliaetus | 12,982,500 |
| Parabuteo unicinctus | 1,730,000 |
| Parkesia motacilla | 2,485,000 |
| Parkesia noveboracensis | 10,932,500 |
| Parula americana | 3,535,000 |
| Parus atricapillus | 11,147,500 |
| Parus carolinensis | 2,282,500 |
| Parus gambeli | 3,077,500 |

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| Parus hudsonicus | 10,690,000 |
| Parus rufescens | 1,222,500 |
| Passerculus sandwichensis | 19,350,000 |
| Passerella iliaca | 11,415,000 |
| Passerina amoena | 3,132,500 |
| Passerina caerulea | 5,140,000 |
| Passerina ciris | 1,342,500 |
| Passerina cyanea | 6,150,000 |
| Patagioenas fasciata | 2,410,000 |
| Pelecanus erythrorhynchos | 1,505,000 |
| Perisoreus canadensis | 10,592,500 |
| Petrochelidon fulva | 717,500 |
| Petrochelidon pyrrhonota | 14,465,000 |
| Peucaea aestivalis | 720,000 |
| Peucaea cassinii | 1,952,500 |
| Phainopepla nitens | 1,180,000 |
| Phalaenoptilus nuttallii | 4,517,500 |
| Pheucticus ludovicianus | 4,505,000 |
| Pheucticus melanocephalus | 4,777,500 |
| Pica nuttalli | 95,000 |
| Picoides albolarvatus | 552,500 |
| Picoides arcticus | 9,462,500 |
| Picoides borealis | 580,000 |
| Picoides dorsalis | 11,652,500 |
| Picoides nuttallii | 192,500 |
| Picoides pubescens | 15,757,500 |
| Picoides scalaris | 2,590,000 |
| Picoides villosus | 16,370,000 |
| Pinicola enucleator | 10,315,000 |
| Pipilo chlorurus | 1,832,500 |
| Pipilo erythrophthalmus | 7,252,500 |
| Pipilo maculatus | 3,955,000 |
| Piranga flava | 1,122,500 |
| Piranga ludoviciana | 4,557,500 |
| Piranga olivacea | 2,820,000 |
| Piranga rubra | 3,195,000 |
| Platalea ajaja | 82,500 |
| Plegadis chihi | 1,512,500 |
| Plegadis falcinellus | 272,500 |
| Podilymbus podiceps | 14,427,500 |
| Polioptila caerulea | 6,450,000 |
| Polioptila melanura | 1,037,500 |
| Pooecetes gramineus | 7,417,500 |
| Porphyrio martinicus | 1,445,000 |
| Porzana carolina | 12,070,000 |
| Progne subis | 6,005,000 |
| Protonotaria citrea | 2,187,500 |
| Psaltriparus minimus | 2,677,500 |
| Pyrocephalus rubinus | 2,277,500 |

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| Quiscalus major | 170,000 |
| Quiscalus mexicanus | 4,622,500 |
| Quiscalus quiscula | 9,462,500 |
| Rallus elegans | 3,280,000 |
| Rallus limicola | 6,262,500 |
| Rallus longirostris | 97,500 |
| Recurvirostra americana | 2,725,000 |
| Regulus calendula | 12,975,000 |
| Regulus satrapa | 8,035,000 |
| Rhynchophanes mccownii | 822,500 |
| Riparia riparia | 13,815,000 |
| Rynchops niger | 155,000 |
| Salpinctes obsoletus | 5,602,500 |
| Sayornis nigricans | 1,897,500 |
| Sayornis phoebe | 7,507,500 |
| Sayornis saya | 9,557,500 |
| Scolopax minor | 4,600,000 |
| Seiurus aurocapilla | 6,265,000 |
| Selasphorus platycercus | 622,500 |
| Selasphorus rufus | 1,977,500 |
| Selasphorus sasin | 17,500 |
| Setophaga ruticilla | 8,110,000 |
| Sialia currucoides | 5,567,500 |
| Sialia mexicana | 1,777,500 |
| Sialia sialis | 5,657,500 |
| Sitta canadensis | 9,045,000 |
| Sitta carolinensis | 9,235,000 |
| Sitta pusilla | 892,500 |
| Sitta pygmaea | 2,007,500 |
| Sphyrapicus nuchalis | 2,300,000 |
| Sphyrapicus ruber | 1,285,000 |
| Sphyrapicus thyroideus | 690,000 |
| Sphyrapicus varius | 6,002,500 |
| Spiza americana | 3,672,500 |
| Spizella atrogularis | 730,000 |
| Spizella breweri | 3,767,500 |
| Spizella pallida | 4,202,500 |
| Spizella passerina | 15,787,500 |
| Spizella pusilla | 4,185,000 |
| Steganopus tricolor | 4,695,000 |
| Stelgidopteryx serripennis | 10,560,000 |
| Stellula calliope | 1,417,500 |
| Strix varia | 7,465,000 |
| Sturnella magna | 5,032,500 |
| Sturnella neglecta | 7,455,000 |
| Tachycineta bicolor | 15,667,500 |
| Tachycineta thalassina | 7,327,500 |
| Thryomanes bewickii | 3,207,500 |
| Thryothorus ludovicianus | 3,165,000 |

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| Toxostoma bendirei | 812,500 |
| Toxostoma crissale | 942,500 |
| Toxostoma curvirostre | 1,887,500 |
| Toxostoma lecontei | 235,000 |
| Toxostoma longirostre | 272,500 |
| Toxostoma redivivum | 162,500 |
| Toxostoma rufum | 6,185,000 |
| Tringa flavipes | 7,605,000 |
| Tringa melanoleuca | 6,290,000 |
| Tringa solitaria | 8,477,500 |
| Troglodytes aedon | 8,557,500 |
| Troglodytes troglodytes | 6,595,000 |
| Turdus migratorius | 21,375,000 |
| Tympanuchus cupido | 420,000 |
| Tympanuchus phasianellus | 8,782,500 |
| Tyrannus couchii | 482,500 |
| Tyrannus forficatus | 1,412,500 |
| Tyrannus tyrannus | 10,667,500 |
| Tyrannus verticalis | 5,457,500 |
| Tyrannus vociferans | 1,342,500 |
| Tyto alba | 8,400,000 |
| Vermivora celata | 10,637,500 |
| Vermivora chrysoptera | 1,530,000 |
| Vermivora cyanoptera | 1,882,500 |
| Vermivora luciae | 370,000 |
| Vermivora peregrina | 6,650,000 |
| Vermivora ruficapilla | 3,332,500 |
| Vermivora virginiae | 225,000 |
| Vireo bellii | 2,595,000 |
| Vireo cassinii | 1,075,000 |
| Vireo flavifrons | 3,305,000 |
| Vireo gilvus | 10,080,000 |
| Vireo griseus | 3,002,500 |
| Vireo huttoni | 1,172,500 |
| Vireo olivaceus | 10,207,500 |
| Vireo philadelphicus | 3,615,000 |
| Vireo plumbeus | 1,260,000 |
| Vireo solitarius | 4,315,000 |
| Vireo vicinior | 467,500 |
| Wilsonia canadensis | 3,455,000 |
| Wilsonia citrina | 2,010,000 |
| Wilsonia pusilla | 11,830,000 |
| Xanthocephalus xanthocephalus | 5,567,500 |
| Zenaida asiatica | 2,472,500 |
| Zenaida macroura | 11,625,000 |
| Zonotrichia albicollis | 7,735,000 |
| Zonotrichia leucophrys | 11,527,500 |
| Zoothera naevia | 5,337,500 |