

INVITED REVIEW

Impacts of climate change on avian populations

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This review focuses on the impacts of climate change on population dynamics. I introduce the MUP (Measuring, Understanding, and Predicting) approach, which provides a general framework where an enhanced understanding of climate–population processes, along with improved long-term data, are merged into coherent projections of future population responses to climate change. This approach can be applied to any species, but this review illustrates its benefit using birds as examples.

Birds are one of the best-studied groups and a large number of studies have detected climate impacts on vital rates (i.e., life history traits, such as survival, maturation, or breeding, affecting changes in population size and composition) and population abundance. These studies reveal multifaceted effects of climate with direct, indirect, time-lagged, and nonlinear effects. However, few studies integrate these effects into a climate-dependent population model to understand the respective role of climate variables and their components (mean state, variability, extreme) on population dynamics. To quantify how populations cope with climate change impacts, I introduce a new universal variable: the ‘population robustness to climate change.’ The comparison of such robustness, along with prospective and retrospective analysis may help to identify the major climate threats and characteristics of threatened avian species.

Finally, studies projecting avian population responses to future climate change predicted by IPCC-class climate models are rare. Population projections hinge on selecting a multiclimate model ensemble at the appropriate temporal and spatial scales and integrating both radiative forcing and internal variability in climate with fully specified uncertainties in both demographic and climate processes.

Keywords: climatic niche, extinction, extreme events, IPCC, stochastic population projection, uncertainties

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Introduction

Large changes in the Earth's climate are already apparent and changes are expected to continue into the next century (Solomon *et al.*, 2007). There is now ample evidence that individual plants and animals respond to climate change affecting population dynamics and resulting in changes of distribution and species persistence (e.g., reviews Walther *et al.*, 2002; Parmesan, 2006; Hoegh-Guldberg & Bruno, 2010). Birds are one of the most well-studied groups, and have been shown to be very sensitive to climate change at various levels: individual (phenology, life history traits), population, species (distribution and persistence), and community (Møller *et al.*, 2004, 2010; Wormworth & Şekercioğlu, 2011). Changes in phenology such as an advancement of laying date, or poleward and upward shifts in bird ranges have been very well documented, but relatively less documented is the effect of climate change on populations (Crick, 2004).

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Climate change poses a major threat for bird populations (Møller *et al.*, 2004, 2010; Wormworth & Şekercioğlu, 2011). There is a pressing demand for population predictions to future climate conditions to understand the possible impacts of climate change on avian populations and to aid implementation of necessary conservation strategies. Information about actual and potential climate change impacts can be of considerable benefit for managers to refine decisions on species conservation status (e.g., listing, delisting and jeopardy; Intersecretarial Commission on Climate Change, 2007). The criteria for a species to be listed on the Red List of the International Union for the Conservation of Nature (IUCN) now includes projections of future risk to species from climate change (IUCN, 2008). IUCN found that 35% of birds (among 9856 bird species assessed) have traits that render them particularly susceptible to climate change impacts (Foden *et al.*, 2008), with the most vulnerable families being seabirds [e.g., penguins (*spheniscidae*), albatross (*diomedeidae*), *procellariidae* (petrels and shearwater)]; see review of Croxall *et al.*, 2002; Boersma, 2008; Forcada & Trathan, 2009; Ainley *et al.*, 2010;

Barbraud *et al.*, 2012; Sydeaman *et al.*, 2012]. BirdLife International found that extreme climate events account for the largest threat to birds (Wormworth & Şekerçioğlu, 2011), urging for better understanding of such effects on bird populations.

Projecting the impact of future climate change on population persistence hinges on good measurements and thorough understanding of species' susceptibility to climate change, which are critical to both the quality of science and its application to public policy (Berdeaux *et al.*, 2006). The goal of this review is to illustrate a general and comprehensive three-step approach to (i) Measure; (ii) Understand; and (iii) Project the impacts of climate change on populations (MUP approach) using bird studies as examples.

A large number of avian studies have measured the effect of climate on population and life history traits, providing a rich understanding of the multifaceted effect of climate (Step 1). Surprisingly, relatively few studies have integrated these effects into climate-dependent population models to understand the mechanisms underlying these relationships and how climate mean state and variability influence population dynamics by affecting vital rates (i.e., life history traits, such as survival, maturation or breeding, that affect changes in the size and composition of a population) (Step 2). Such understanding of the processes is critical to develop process-oriented models and to advance predictive ecology (Evans, 2012). Only a handful of studies project population responses under future climate change, especially using projections from climate models contributing to the Assessment Report (AR) of the Intergovernmental Panel on Climate Change (IPCC) (Step 3). The difference in the number of publications between these three steps reflects a major gap already identified in the IPCC fourth AR (AR4) (Parry *et al.*, 2007): a lack of studies predicting the ecological impact of future climate change. Ecology needs to become more predictive (Evans *et al.*, 2012), and this review emphasizes important recommendations to project population persistence under future climate change using the three-step MUP framework.

The IPCC defines climate as the 'statistical description in terms of the mean and variability in relevant quantities (i.e., weather variables) over a period of time ranging from months to thousands or millions of years. The classical period is 30 years, as defined by the World Meteorological Organization'. Thus, here, climate refers to long-term interannual variations of weather. Climate change refers to 'a statistically significant variation in either the mean state of the climate or in its variability, persisting for an extended period (typically decades or longer)' (Solomon *et al.*, 2007). These two definitions have two important

consequences: the need to use long-term data (see Step 1: Measuring section) and to consider both the effect of the mean state and variability in climate on bird populations, and their respective roles (see Step 2: Understanding section).

The third step of the MUP approach focuses on projecting population responses (see Step 3: Projection section), which is defined as making a well-informed inference on any future state variable such as population size or persistence based on facts, statistical evidence, or causal relationships with fully specified uncertainties and contingent upon explicit scenarios for climate, land use, human population, technologies, and economic activity (Clark, 2001; Berdeaux *et al.*, 2006). The focus of projecting climate, population size or persistence using various models is not to project whether individual weather events will occur at a particular time or whether a population will go extinct a particular year, which are unpredictable on long time scales, but on the statistics of these state variables in terms of mean, trend, probability of occurrence, or variability over a given time period. The acknowledgement and quantifications of uncertainties and decision risks in any attempt to project the future is vital for informing management decisions and for setting policy. This is important for maintaining public confidence and an increasing number of studies recommend embracing uncertainty to make robust predictions (Beale & Lennon, 2012). Finally, the last section outlines some important challenges and prospects for understanding and predicting avian population responses to climate change.

Step 1: Measuring the effects of climate change on avian populations

Climate impacts size and composition of a population by its effects on vital rates (such as survival, recruitment, or breeding success). Vital rates are influenced by food acquisition and energy allocation processes in response to changes in habitat or food availability driven by climate fluctuations (Fig. 1). Thus, climate influences populations via multiple pathways, involving both direct effects on vital rates and indirect effects mediated through climatic influences on habitat and prey, resulting in complex and lagged responses. Ornithology has an established history of measuring the effects of weather and climate on avian demography (Seavy *et al.*, 2008); partly due to the great efforts by dedicated ornithologists who have collected exceptional long-term data sets over many years (Clutton-Brock & Sheldon, 2010a; Møller & Fiedler, 2010a). Effects of climate change on population abundances and vital rates have been detected for many bird

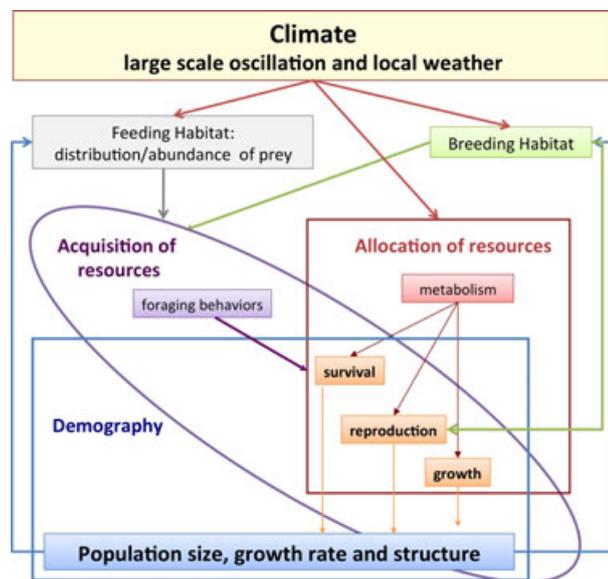


Fig. 1 Description of the processes by which climate affects population. Population size, growth and structure is driven by change in vital rates (e.g., reproduction, growth and survivorship; orange box), as well as immigration and emigration (not shown). Birds' vital rates can be affected by changing climate conditions directly or indirectly through impact on their breeding habitat (green box) or through changes in their food supply/food availability (grey boxes). The amount of food obtained by a bird depends on its foraging behaviors. These acquisition processes are represented in purple and affect the individual's vital rates (orange boxes). Allocation processes (red) describe how the energy is allocated according to tradeoffs between reproduction, growth and survivorship. Finally, population density may affect the food supply/food availability and quality/availability of breeding habitat through intra-specific competition. Among many other factors, these density dependence effects may thus interact with climate impact. Individual heterogeneity in life history traits caused by, e.g., age, sex or experience, is not shown, but also plays an important role in shaping acquisition and allocation processes, hence vital rates and population responses to climate.

species, including passerine birds, waders, seabirds, waterfowl, and raptors (Sæther & Engen, 2010; Wormworth & Şekercioglu, 2011).

Needs for longitudinal data

To measure the effect of climate change on avian populations, long-term data are needed (Clutton-Brock & Sheldon, 2010a,b; Møller & Fiedler, 2010a). Longitudinal censuses provide insights on the effect of climate on avian population size (Lack, 1966; Perrins *et al.*, 1991; Newton, 1998) and a time series analysis is a robust approach to describe population trends and variability in response to climate change (Clutton-Brock & Sheldon, 2010b; Lindström & Forchhammer, 2010).

However, such studies have some limitations in identifying the causes of population fluctuations because it is difficult to disentangle the respective roles of changes in breeding success, survival, emigration, and immigration (Clutton-Brock & Sheldon, 2010b).

Longitudinal individual-based studies enable the measurement and understanding of how climate influences the various vital rates of birds' life history. Individual-based studies over a decade are not rare for birds (especially passerines such as tits and flycatchers), and a handful of studies have even been going on for more than 50 years [e.g., Great Tits (*Parus major*) in the Netherlands: Reed *et al.*, 2013; Visser *et al.*, 2004; seabirds in the Southern Ocean: Barbraud *et al.*, 2012; and Swiss Barn Owls (*Tyto alba*): Altwegg *et al.*, 2006].

Effects of climate change on population abundances

First, numerous studies have shown that avian populations are affected by local climate variables (e.g., temperature, rainfall, and wind) and large-scale atmospheric indices [e.g., North Atlantic Oscillation: NAO; El Niño (EN) tied to the atmospheric phenomenon Southern Oscillation (SO): ENSO; Stenseth *et al.*, 2002, 2003]. For example, species less tolerant to warm climates showed the sharpest declines between 1980 and 2005 among 110 common birds breeding across Europe (Jiguet *et al.*, 2010).

Second, the variability of climate has strong consequence on avian population dynamics. Oscillations in local climate or atmospheric indices may drive population cycles. Jenouvrier *et al.* (2005c) showed that populations and demographic parameters of three Antarctic seabirds fluctuate with a periodicity of 3–5 years that was also detected in sea-ice extent and the SO index.

Extreme weather events are a special case of variability and can have tremendous effects on avian populations. Extreme events are rare and according to the IPCC: 'an extreme weather event would normally be as rare as or rarer than the 10th or 90th percentile'. In an ecological context, extreme events can be characterized by statistical extremity, timing, and abruptness (a function of magnitude over duration) relative to the life cycle of the species affected (Jentsch *et al.*, 2007). Detecting the effects of extreme events on avian populations is extremely difficult due to the lack of long-term data on the appropriate time scale. Most evidence comes from particular events such as hurricane, droughts, and floods. For example, Hurricane Hugo destroyed 70% of the nesting trees of the largest population of the endangered Red-cockaded Woodpecker (*Picoides borealis*) (see review of Moreno & Møller, 2011).

Climate regime shifts, that is, an abrupt change from a stationary climate state to another (Hare & Mantua,

2000) also impact avian populations. Both Arctic species, Thick-billed Murre (*Uria lomvia*) and temperate species, Common Murre (*Uria aalge*) declined during large sea surface temperature (SST) shifts that were linked to two climate regime shifts in 1977 and in 1989 (Irons *et al.*, 2008). The mid-1970s regime shift was the largest recorded in the Northern Hemisphere because both the NAO and the North Pacific Oscillation shifted from a negative to a positive regime.

Third, population responses to climate may vary across season and some bird species may be more sensitive to a particular season. For migrant species, population responses to climate are constrained by different climate conditions during the breeding and nonbreeding season (Small-Lorenz *et al.*, 2013). Species breeding in Europe but wintering in Africa experience larger population declines than those that are more sedentary, suggesting a stronger effect of climate conditions at the wintering grounds for some long-distance migrant bird species (Peach *et al.*, 1991; Thaxter *et al.*, 2010). Studies have also examined the respective effects of climate variations during the breeding season and nonbreeding season on populations in the context of the 'tub-hypothesis' and 'tap-hypothesis' (Lack, 1966; Sæther *et al.*, 2004; Sæther & Engen, 2010). The 'tub-hypothesis' proposes that climate variations during the nonbreeding season influence fluctuations in population size because climate conditions determine the number of birds surviving over winter in combination with density dependence. The 'tap-hypothesis' proposes that climate variations during the breeding season influence fluctuations in population size because climate variations will influence the inflow of new recruits into the population the following year. Although the population fluctuations of altricial birds are most affected by factors occurring during the nonbreeding season ('tap-hypothesis') and nidifugous birds by factors occurring during the reproductive season ('tub' hypothesis) (Sæther *et al.*, 2004), Sæther & Engen (2010) concluded that drawing a general pattern among birds is impossible due to the interplay of climate effects on vital rates, lagged responses, and covariation among vital rates.

Fourth, avian population responses to climate can lag due to climatic, ecological or demographic processes. For example, ecological lags may occur through food web effects such as in polar sea ice ecosystems (Thomas & Dieckmann, 2003; Smetacek & Nicol, 2005). Antarctic Sea ice during winter affects the recruitment of Antarctic Krill (*Euphausia superba*) the following summer (Atkinson *et al.*, 2004), resulting in higher abundance of prey for Antarctic seabirds breeding the next summer (Fraser & Hofmann, 2003; Trivelpiece *et al.*, 2011).

Recruitment processes may also drive lagged effects of climate (Thompson & Ollason, 2001). A general analysis of 29 seabird species suggested that the North

Atlantic Oscillation (NAO) had negative effects on population size through adult survival, but positive effects through lagged effects on offspring recruitment (Sandvik *et al.*, 2012). The NAO effects on populations are stronger through recruitment, and the long time lags involved for long-lived seabirds make their detection difficult, suggesting that its magnitude may still be underestimated (Sandvik *et al.*, 2012).

On the other hand, birds may respond to a predictable climatic event well in advance. For example, populations of Sooty Terns (*Onychoprion fuscatus*) and Common Noddies (*Anous stolidus*) declined when the 20 °C thermocline deepened, which is a signal of an up-coming El Niño event (Devney *et al.*, 2009). During El Niño years, unfavorable warm waters block the nutrient-rich upwelling, disrupting the entire ecosystem from the abundance and distribution of phytoplankton, zooplankton, and fishes to seabirds. The mechanism underpinning this population decline is likely that seabirds skip breeding during El Niño years rather than compromising their survival and future opportunity to reproduce.

Effects of climate change on vital rates

The previous section highlighted several examples of population response to climate. However, it is important to measure climate effects on vital rates to understand the processes that determine population response to climate change (Fig. 1).

First, there are numerous studies documenting strong effects of climate on various vital rates. The majority of studies focus on the effect of local and/or large-scale atmospheric indices on reproduction and/or survival of adult birds. For example, Frederiksen *et al.* (2007) showed a negative effect of SST on the breeding productivity of Black-legged Kittiwake (*Rissa tridactyla*). Grosbois *et al.* (2006) detected effects of local temperature and precipitation as well as a large-scale tropical index (rainfall in the Sahel) on adult survival of Blue Tits (*Parus caeruleus*). The most studied climatic variables are temperature and precipitation, but the choice of variables depends on the environment of the species, its life history and available meteorological measurements. For example, sea ice is an important driver of vital rate variations in polar ecosystems and adult survival of Emperor and Adélie penguins is related to sea ice (Barbraud & Weimerskirch, 2001; Ballerini *et al.*, 2009; Emmerson & Southwell, 2011). Westerly wind in the Southern Ocean is an important driver of breeding success of Wandering Albatross (*Diomedea exulans*) because wind influences their foraging efficiency and in turn their body condition and breeding performance (Weimerskirch *et al.*, 2012).

Several studies have investigated multiple vital rates across the entire life cycle showing the complex interplay between season, climate variables and vital rates. Sillett *et al.* (2000) measured the effect of El Niño Southern Oscillation on the survival, fecundity, and recruitment of Black-throated Blue warblers (*Dendroica caerulescens*). They showed that El Niño Southern Oscillation has a twofold effect on warblers, affecting both their survival in the tropics as well as their reproductive performance in the north.

Although a large number of studies focus on adult survival and fecundity parameters, juvenile survival, recruitment, breeding propensity, and dispersal are equally important to understand population responses to climate, but are less well documented. Juvenile survival and probability of recruitment have been less studied because it is difficult to obtain estimates for long-lived species with delayed maturity when they are not observable on breeding grounds, such as seabirds (Jenouvrier *et al.*, 2008a), and when a large proportion of individuals never return to the study population, such as Lesser Kestrel (*Falco naumanni*) (Mihoub *et al.*, 2010). Interestingly, recruitment and juvenile survival are likely to be more affected by climate variations than adult survival, because adult survival variations are buffered against environmental variations for long-lived species [e.g., Blue-footed Booby (*Sula nebouxii*), Oro *et al.*, 2010]. For seabirds, another critical parameter is the probability of skipping breeding during years when the climate is unfavorable (Jenouvrier *et al.*, 2005b) and Cubaynes *et al.* (2011) found that Red-footed Boobies (*Sula sula*) are more likely to skip breeding in El Niño years. Dispersal remains the most difficult parameter to estimate, and studies detecting an effect of climate change on dispersal are rare. Dugger *et al.* (2010) estimated a low dispersal of breeding Adélie Penguins (<1%) and showed an increase by more than threefold during years of difficult sea ice conditions.

Second, most studies of the effects of climate on vital rates documented indirect effects through availability of habitat or food resources (Fig. 1). For example, breeding performance of the Rhinoceros Auklet (*Cerorhinca monocerata*) declines in warmer spring SST years because recruitment of the Auklet's prey, the sand lance, is temperature-dependent. As spring SSTs increased, the occurrence of sand lance in chicks' diet decreased as well as chicks' growth rate (Hedd *et al.*, 2006).

However, adverse weather conditions and extreme events can also directly impact birds' vital rates. High temperature can cause heat stress and low temperature hypothermia, both of which can reduce birds' breeding success and adult survival. Droughts, storms,

and cyclones can kill birds, while heavy rainfall can flood nests and burrows killing chicks (Bolger *et al.* 2005, Demongin *et al.*, 2010; Chambers *et al.*, 2011; Moreno & Møller, 2011). For example, an extreme large flood of the Lower Mississippi River in 1993 destroyed all eggs, chicks, and fledglings of the least tern (*Sterna antillarum*) (Dugger *et al.*, 2002). More importantly, adverse weather conditions and extreme events can simultaneously affect several vital rates with dramatic consequence for the population. For example, Altwegg *et al.* (2006) showed that two extreme harsh winters simultaneously reduced juvenile and adult survival rates for the Swiss Barn Owl (*Tyto alba*) (Fig. 2). During harsh winters, the snow cover duration is longer, making small mammals unavailable for Barn Owls to hunt.

Third, many studies documented nonlinear relationships between climate and vital rates [e.g.,

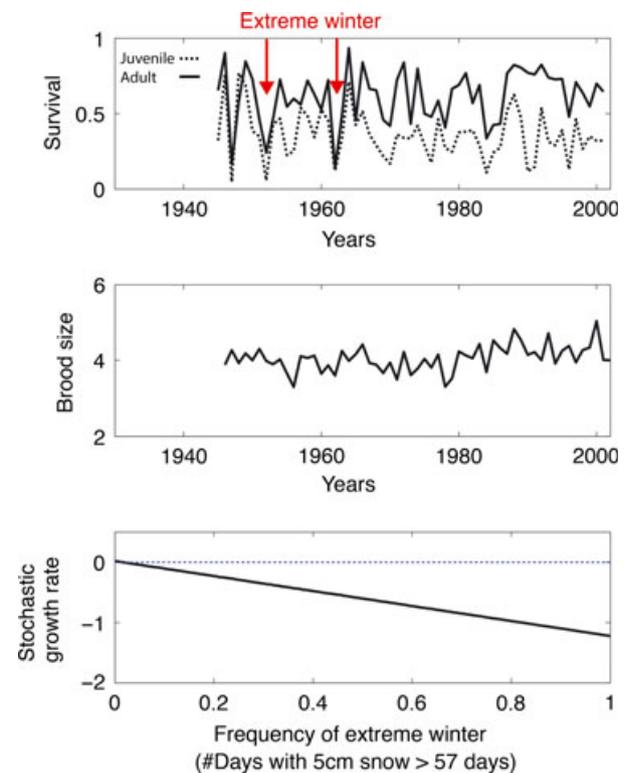


Fig. 2 Impact of extreme harsh winters on the vital rates (survival and brood size) and stochastic population growth rate of the Barn Owl (*Tyto alba*). Survival and brood size time series are from Altwegg *et al.* (2006), and red arrows indicate two extreme winters with the longest snow cover. These extreme events correspond to very rare events (3.5th percentile of the distribution). Appendix S1 describes the population model dependent of extreme harsh winters used to predict the impact of an increase frequency of extreme events on Barn Owl stochastic growth rate.

Cassin's Auklets (*Ptychoramphus aleuticus*): Lee *et al.*, 2007]. Because climate conditions tolerated by a species are limited due to physiological and ecological constraints most studies have detected a bell-shaped relationship [e.g., Adélie Penguin (*Pygoscelis adeliae*): Ballerini *et al.*, 2009; Emmerson & Southwell, 2011; White Stork (*Ciconia ciconia*): Schaub *et al.*, 2005; Nevoux *et al.*, 2008].

Fourth, a climate variable can have opposite effects on different vital rates [e.g., Eurasian Oystercatcher (*Haematopus ostralegus*): van de Pol *et al.*, 2010]. For example, sea ice extent impacts survival and fecundity of Emperor Penguins (*Aptenodytes forsteri*) in opposite ways (Barbraud & Weimerskirch, 2001). During years with extensive winter sea ice, food is likely more abundant the following summer, increasing adult survival. However, foraging trips are longer in extensive sea ice years resulting in fewer hatched eggs.

Finally, the effect of climate varies among seasons and various phases of the life cycle as well as between individuals. Several studies have shown that vital rate responses to climate change may vary between individuals, for example, according to their age (Oro *et al.*, 2010; Pardo *et al.*, 2013), sex (Barbraud & Weimerskirch, 2001; Grosbois & Thompson, 2005), breeding experience (Nevoux *et al.*, 2008), and habitat quality (Dugger *et al.*, 2005; van de Pol *et al.*, 2010). For example, Nevoux *et al.* (2008) showed that the survival and breeding success of inexperienced Black-browed Albatross (*Thalassarche melanophrys*) breeders is affected by climatic conditions, while the survival of experienced breeders is not impacted.

One of the most striking examples of seasonal climate effects over different phases of the annual life cycle is the effect of climate on vital rates of Great Tits breeding in the Netherlands. Vital rates are affected by summer caterpillar abundance and the autumnal beech (*Fagus sylvatica*) crop, both of which are driven by climate fluctuation. Beech crops are an important winter food source affecting the overwinter survival of juvenile and adult Great Tits (Grotan *et al.*, 2009). Caterpillar abundance during summer has an indirect effect on breeding vital rates through a phenological mismatch effect (Visser *et al.*, 1998, 2004). In the Netherlands, advancements in laying dates in response to warmer springs have been insufficient to keep pace with stronger advancements in caterpillar phenology resulting in a population that now breeds much later relative to the seasonal peak in caterpillar abundance (Visser *et al.*, 2003; Visser & Both, 2005). Such a mismatch (i.e., late breeding relative to the caterpillar food peak date) affects Great Tit probability of double-brooding, fledgling success, offspring recruitment, and the number of recruits (Reed *et al.*, 2013).

Summary of step 1

To summarize this first step, there is a huge number of avian studies detecting an effect of climate on populations and vital rates, especially adult survival and reproduction. It reveals multifaceted effects of climate with direct, indirect, lagged, and nonlinear effects. Climate can act in opposite directions on different vital rates, and its effects vary across different seasons and phases of the life cycle, as well as between individuals due to their differences, for example, in age, sex, and experience.

Most of the effects of climate on vital rates are indirect and future effort entails measuring the factors governing these relationships (e.g., determining the impact of food abundance and foraging strategies on vital rates). An increasing effort should also be devoted to measuring the effect of climate on juvenile survival, recruitment, breeding propensity, and dispersal, especially since tremendous improvements in statistical analyses allows for addressing issues of low sample size and detectability (e.g., capture-recapture frequentists or Bayesian approaches with unobservable and multistates models: Williams *et al.*, 2002; Thomson *et al.*, 2009). Further research is critically needed on dispersal processes because they may eventually drive extinctions and colonizations of local populations and species persistence in the face of future climate change.

Each population response to climate effects reflect the unique combination of meaningful climate factors and species life history across different spatial and temporal scales. Several studies have proposed some general biological traits or characteristics inherent to species particularly vulnerable to climate change: those with small populations and range size, specialists, poor dispersers, and migratory species (see Foden *et al.*, 2008), but a quantitative framework is crucially needed. Thoughtful comparison requires the development and application of common dimensionless variables quantifying how populations can cope with climate impacts (e.g., 'population robustness to climate change' see Step 2).

Step 2: Understanding the effect of climate change on avian populations

The next step of the MUP approach is to understand the net effects of a specific change in climate on population dynamics, which are not predicted by simply measuring the effect of individual climate variables on individual vital rates (Ådahl *et al.*, 2006; Zeigler, 2013). This requires to integrate the measured effects of climate on populations and vital rates into a population model. The relationship between the population

growth rate and climate provides critical information on a species' ability to cope with climate change, and here I introduce the concept of 'population robustness to climate change'. Furthermore, comparing the respective role of climate factors and their statistical components (mean vs. variability) may provide thoughtful insight for our understanding of the effects of climate change on population dynamics. Finally, it is important to integrate the effects of climate on vital rates in a population model to better understand the mechanisms. The population growth rate may be relatively insensitive to some vital rates strongly affected by climate variations, or there might be counteracting influences of climate on the population growth rate due to changes in vital rates responding to the same climate variable in opposite directions.

Climate-dependent population models

Understanding the processes by which climate influences avian populations requires developing climate-dependent population models. There are various approaches ranging from nonstructured population models (Lande *et al.*, 2003) and structured population models (Caswell, 2001) to individual-based modeling (Grimm & Railsback, 2005).

First, it is important to consider the assumptions behind climate-dependent population models. Deterministic models assume that population and vital rates follow a determined path, which may or may not be driven by climate time series. Stochastic models integrate random variations caused by demographic stochasticity, environmental stochasticity, or by sampling and uncertainties about parameter estimates (see Step 3). Demographic stochasticity is an individual's chance of surviving or dying, reproducing or not reproducing, whereas environmental stochasticity is temporal variations of the probability to survive and reproduce (Caswell, 2001; Lande *et al.*, 2003; Boyce *et al.*, 2006). Environmental stochasticity can be caused by random climate variations or other environmental factors. Thus, a model could be stochastic by including demographic stochasticity or environmental stochasticity without incorporating random variability in climate itself.

Another important assumption is the stationarity of the environment, that is, the environment fluctuates but its statistical properties (mean, variance, autocorrelation) do not change over time. Most deterministic and stochastic population models assume that the environment is stationary; however, climate is not. To include the nonstationarity of the climate, a time series of the nonstationary environment could be used to project vital rates and population trajectories (e.g., Gotelli & Ellison, 2006).

Second, it is important to include in climate-dependent population models appropriate processes which may interact with climate and influence population dynamics: density dependence, migration, environmental stochasticity generated by processes other than climate, and demographic stochasticity for small populations (Caswell, 2001; Lande *et al.*, 2003; see comprehensive review in Sæther & Engen, 2010). For example, Grotan *et al.* (2009) showed that the population size of Great Tits was strongly affected by the combined effect of the temporal variation in the number of recruits produced locally as well as the number of immigrants, which are both affected by food abundance (beech crop), temperature, density dependence, and environmental stochasticity. Recruitment contributed more to population fluctuation than immigration, and variations in recruitment were more influenced by beech crop and temperature than density-dependence effects.

Last but not least, it is crucial to integrate the effects of climate across the entire life cycle because they can differ among seasons (Altwegg & Anderson, 2009), phase, and stages of the life cycle (Jenouvrier *et al.*, 2010) and can impact vital rates in a variety of ways (van de Pol *et al.*, 2010). Although studies quantifying the effect of individual climate variables on individual vital rates from Step 1 are critical to understand the effect of climate on the species life cycle and are necessary to parametrize population models of Step 2, they do not provide a complete understanding of the population's responses to climate change. Examining only one or few vital rates can lead to erroneous predictions of population responses to climate change (Zeigler, 2013), such as for migratory birds (Small-Lorenz *et al.*, 2013). Ådahl *et al.* (2006) demonstrated that an increase in survival and/or reproduction due to climatically induced increases in the resources do not necessarily lead to an increase in population size owing to the combined effects of demography, density dependence, and behavioral mechanisms filtering the information about the resources (e.g., possible use of environmental cues).

Population growth as function of climate

To understand how a species may cope with climate change and establish comparisons among species, studying the population growth as a function of climate is a powerful approach (Fig. 3). This is very similar to the concept of the 'climatic niche' which represents the climatic conditions that are suitable for species persistence and is driven by species physiological tolerances (e.g., lethal physiological temperatures). The climatic niche breadth has important implications

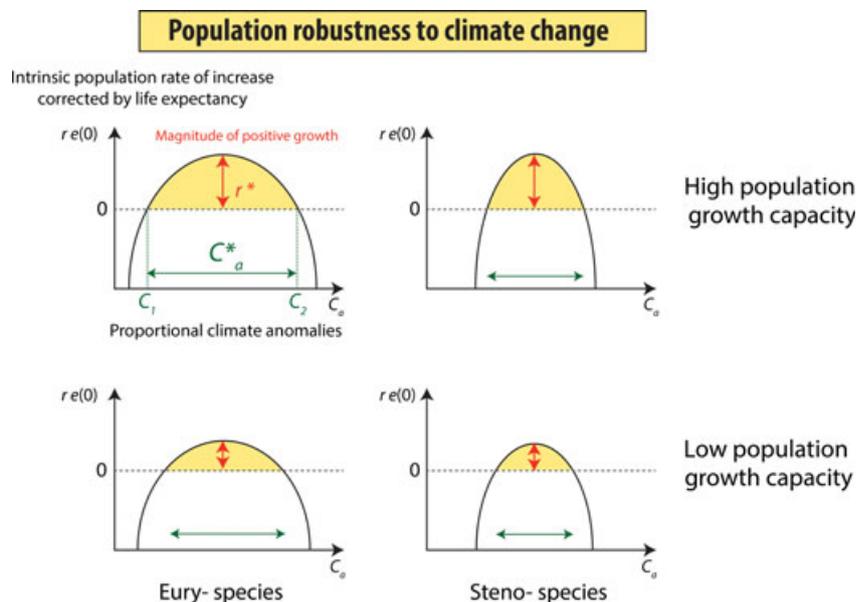


Fig. 3 Description of the ‘population robustness to climate change’. The ‘population robustness to climate change’ is represented by the yellow area. It is a measure combining the range of climatic conditions where the population is capable of increase (i.e., where the intrinsic population rate of increase is positive, noted as C_a^* , green arrow) and the magnitude of how fast a population can grow within C_a^* (e.g., noted r^* , red arrow, for the optimal C_a). Eury- species (wide C_a^* , left panels) may cope better with future climate change than steno- species (narrow C_a^* , right panels) because they may have a greater chance of having a population that may grow under shifting climate conditions. In addition populations with a greater magnitude of positive growth rate for a given climate condition (upper panels) can withstand higher population growth reduction caused by other perturbations (climatic or not) than populations with a limited growth (lower panels).

on species responses to climate change (e.g., Tingley *et al.*, 2009; Monahan & Tingley, 2012). If the relationship between population growth and climate variations is inferred from a single local population, inference at the species level and climatic niche is based on the Janzen hypothesis (Janzen, 1967; Quintero & Wiens, 2013). Janzen assumes that the overall realized climatic niche breadth of a species is set by the temporal variations of climate within-locality and thus spatial variation in climatic conditions is relatively unimportant. This hypothesis has been rarely tested, but Quintero & Wiens (2013) found that within-locality seasonal variation explains most variation in climatic niche breadths among 409 species of frog, lizards and salamanders.

Similar to the climatic niche breadth, the range of climatic conditions, C_a^* , where the population is capable of increase (i.e., where the intrinsic population rate of increase r is positive) can inform the ability of a species to cope with climate change. Eury-species (wide C_a^* , e.g., eurythermal species for temperature) may cope better with future climate change than steno-species (narrow C_a^*) because they may have a greater chance of having a population that may grow under shifting climate conditions. To compare the width range of climatic conditions where the population is growing,

I propose to express the climate covariates C as proportional anomalies (C_a) relative to the mean. Such a dimensionless variable allows for the comparison between various climate variables and species. They can be calculated as follows:

$$C_{at} = \frac{C_t - \bar{C}}{\bar{C}} \quad (1)$$

where C_t is the climate covariate in year t and \bar{C} the mean of C over a specified period of time (usually relative to a present time window of several decades).

In addition to quantifying the climatic range where the population can persist, the relationship between population growth and climate quantifies how fast a population can grow for a specified range of climate conditions r^* . In other words, it measures the population’s ability to withstand or recover from difficult climate conditions and how much extra environmental deterioration a population can tolerate within C_a^* (Fig. 3). To integrate both C_a^* and r^* , I define the ‘population robustness to climate change’ as the area of the region in the $r - C_a$ plane of Figure 3 bounded by the curve $r(C_a)$ and over the interval $C_a^* = [C_1, C_2]$. The ‘population robustness to climate change’, noted R , is computed using integral calculus as:

$$R = \int_{C_1}^{C_2} r(C_a) dC_a \quad (2)$$

To compare 'population robustness to climate change' among short and long-lived species, life expectancy must be considered. Indeed, there is a gradient of life history traits among species resulting in a slow–fast continuum of population growth rates (e.g., in birds: Sæther & Bakke, 2000). Thus, a measure of population growth is given by: $re(0)$; where $e(0)$ is the life expectancy. Under the umbrella of matrix stage structured models, $e(0)$ can easily be calculated (Caswell, 2001 section 5).

Climate mean state, variability, and extreme effects

Climate is changing, both in term of its mean state and its variability (Solomon *et al.*, 2007) and both components affect population dynamics in complex ways (Boyce *et al.*, 2006). In a small songbird population, the dipper (*Cinclus cinclus*), Sæther *et al.* (2000a) showed that half of the environmental stochasticity was explained by variation in mean winter temperature. An increase in mean winter temperature of 2.5 °C increased the expected population size by 58% at carrying capacity and the average population size from 117 to 184 in a nonlinear relationship.

Climate variability can have different impacts on population dynamics than climate mean state; thus, it is important to adopt a stochastic climate approach. Only three avian studies [on Blue Cranes *Anthropoides paradiseus*: Altwegg & Anderson (2009); Eurasian Oystercatchers: van de Pol *et al.*, 2010; Emperor Penguins: Jenouvrier *et al.*, 2012]; have studied the role of climate mean states and variability. van de Pol *et al.* (2010) and Jenouvrier *et al.* (2012) have concluded that the effect of variability is smaller than the effect of the mean states of climate. This is similar to the results found for the effect of temporal variability on vital rates: the sensitivity of population growth rates to standard deviations of vital rates is much lower than the sensitivity to mean vital rates (Morris *et al.*, 2008). Temporal variance in the vital rates is known to reduce the stochastic population growth rate but variations in climate do not necessarily decrease the stochastic growth rate. Indeed, potentially nonlinear relationships between vital rates and climate variables may lead to the opposite pattern: a positive effect of climate variability on the stochastic growth rate (Boyce *et al.*, 2006; Morris *et al.*, 2008; Koons *et al.*, 2009). The effects of an increase in sea ice concentrations (SIC) variance on Emperor Penguin population growth rates can be positive or negative depending on the mean state of SIC (Jenouvrier *et al.*, 2012). Higher rainfall variability during the early breeding season results in a small increase

in Blue Cranes population growth due to the nonlinear relationship between rainfall and reproduction (Altwegg & Anderson, 2009). Finally, an increase in climate variance could increase the strength of covariation between vital rates, which can have a large effect on the population growth rate (Boyce *et al.*, 2006). For example, during extreme events, several vital rates can be affected in the same direction, having a dramatic impact on population size.

The effects of extreme climatic events, however, have been poorly studied despite an increasing awareness of dramatic impacts on wildlife populations (IPCC Special Report on Extreme Events, Easterling *et al.*, 2000). Plus, extreme events are rare, which means there is little data available to make assessments regarding changes in their frequency or intensity. Some bird studies have explored the effect of extreme variability in vital rates on populations, such as the effect of extreme mortality on European Shag (*Phalacrocorax aristotelis*) (Frederiksen *et al.*, 2008) and Barn Owl (Altwegg *et al.*, 2006) populations; and of the extreme massive breeding failures on population recovery of Emperor Penguins (Jenouvrier *et al.*, 2009b). However, those studies did not directly integrate the effect of extreme climatic events on population dynamics (but see van de Pol *et al.*, 2010; Nur *et al.*, 2012) and the effects of extreme events frequency and intensity have yet to be explored. Figure 2 shows the effects of the frequency of extreme harsh winters on a population of Barn Owl using the exceptional long-term data of Altwegg *et al.* (2006). In the absence of harsh winters, the population increases ~2% per year. With the actual frequency of harsh winter (2 events among 58 years = 0.035), the population is projected to decrease by ~2% per year. When the frequency of harsh winters increases, the stochastic population growth rate declines dramatically.

Effects of climate on population dynamics through vital rates

The way climate may drive population dynamics depends on a complex interplay of how the population growth rate (hereafter noted λ) is impacted by changes in vital rates and the amplitude of vital rate fluctuations induced by climate variations. Life-history theory predicts that phenotypic plasticity and selection processes lead to a reduction in the environmentally induced variance of a life history trait having a high impact on λ (Caswell, 1983), which has been called 'environmental canalization theory' (Gaillard & Yoccoz, 2003). Several avian studies have shown that the vital rates to which λ are most sensitive show small temporal variations (Sæther & Bakke, 2000) and are less affected by climate variations (Nevoux *et al.*, 2007, 2010; Oro *et al.*, 2010).

van de Pol *et al.* (2010) found that juvenile survival was more variable in time and more affected by winter temperature than adult survival for the Eurasian Oystercatchers, in agreement with the 'environmental canalization theory.' However, the population dynamic was more affected by change in climate on adult survival (the canalized trait) than juvenile survival, emphasizing the importance of conducting a full demographic analysis with both prospective and retrospective analyses to quantify the potential impact of vital rates and the contribution of their climate-induced variations on λ .

A prospective analysis (known also as perturbation or sensitivity) enables a projection of the consequences of future or hypothetical changes in the vital rates and climate factors on the population growth rate (Caswell, 2000, see supplementary Table S1). For example, Peery *et al.* (2012) detected effects of both temperature and precipitation on vital rates of Mexican Spotted Owl (*Strix occidentalis*). Using a climate-dependent population model and conducting a sensitivity analysis they showed that λ is more sensitive to temperature than precipitation. Thus, a change in temperature will have a greater impact than a change in precipitation on the Spotted Owl population growth rate. Stochastic sensitivity analysis (Tuljapurkar *et al.*, 2003; Caswell, 2005; Haridas & Tuljapurkar, 2005) can disentangle the effect of the mean and variance of individual environmental drivers on the stochastic growth rate and thus is very useful to compare the respective effects of climate mean state and variability.

A retrospective analysis sheds light on how variation in each of the vital rates has contributed to an observed variation in the population growth rate (Caswell, 2000). For example, in long-lived species such as Emperor Penguin, λ is more sensitive to changes in adult survival than breeding success (Jenouvrier *et al.*, 2005a). However, a retrospective analysis shows that adult survival and breeding success variations contribute equally to past population growth variations. During the late 1970s, a dramatic 50% population decrease was caused by a decline in adult survival (especially males) due to an unusually low sea ice extent (Barbraud & Weimerskirch, 2001; Jenouvrier *et al.*, 2010). After the 1980s, it is the increased frequency in massive breeding failure, probably due to years with extensive sea ice extent (Massom *et al.*, 2009), that hinders the population from recovering (Jenouvrier *et al.*, 2009b). To measure variations in λ as a function of (co)variation in the vital rates and climate, life table response experiment (LTRE) methods and other kinds of variance decomposition can be applied, both in deterministic and stochastic environments (Caswell, 2010; 2000; Davison *et al.*, 2010). For stochastic analysis, Caswell (2010) focuses on the

contributions of variation in the environmental components (e.g., autocorrelation) and of population-specific responses of vital rates to these environmental changes. Davison *et al.* (2010) focus on the contributions of differences in the mean and the variance of the vital rates. Thus, deterministic and stochastic LTRE approaches provide useful tools to explore the effects of climate statistical components (mean, variance, extreme, autocorrelation) on population growth rate.

Summary of step 2

To summarize this second step, integrating the measured effects of climate change into a climate-dependent population model permits a thorough understanding of the processes by which climate affects population growth and fluctuations. Modeling tools and information to parametrize models from Step 1 are available, yet there are relatively few studies exploring the respective effects of climate variables, and their components (mean state, variability, extreme) on population dynamics.

Drawing general patterns along the life history gradient, among behavioral traits (migrant vs. resident) or foraging traits (specialists vs. generalists), across taxonomic levels or communities and across climatic zones, may help to identify the major climate threats and threatened avian species. However, such analysis is hampered by the lack of a universal variable quantifying how a population may cope with climate impacts. The 'population robustness to climate change' as well as prospective and retrospective analyses provide such common tools. Prospective and retrospective analyses have proven their powerful application in the context of the 'environmental canalization theory' to infer a general pattern of the effects of vital rate variations on population growth across a life history gradient. Future research entails incorporating the effect of climate mean states and variability; especially since variations in climate do not necessarily translate into similar effects than vital rate variations on the population growth. Finally, process-oriented models including the climate change impacts on vital rates, may help to move forward a predictive ecology (Evans, 2012, see step 3).

Step 3: Prediction of avian population responses to climate change

Although efforts to project population responses to climate change are increasing, this is still a nascent field (Wormworth & Şekercioğlu, 2011; see publication date on Table 1). Climate model simulations included into the assessment reports of the IPCC are a primary means of analyzing climate dynamics and making skillful predictions of future climate change based on state-of-the-art

Table 1 Projections of avian population's responses to climate change using information from IPCC-class models

Species	Climate	Population	Conclusion
Snowy Plover Florida (Aiello-Lammens <i>et al.</i> , 2011)	1 mid-level SRES [†] ; 1 regional model; determinist predictions of sea-level rise	Stochastic predictions of population trajectories, quasi-extinction probability [†] based on habitat availability	Up to 25% quasi-extinction probability; decline of carrying capacity by ~35%
Adélie and Emperor penguins Antarctica (Ainley <i>et al.</i> , 2010)	1 mid-level SRES; selection among 18 AOGCMs; deterministic prediction of sea ice coverage and thickness, wind speeds, precipitation, and air temperatures	Anticipate population trends based on habitat availability	By global average, air temperature reaches 2 °C above preindustrial levels: anticipated decline of colonies north of 70 °S (~50% of Emperor colonies and ~75% of Adélie colonies)
Albatrosses and petrels Southern Ocean (Barbraud <i>et al.</i> , 2010)	Three SRES; selection among 18 AOGCMs; deterministic predictions of sea surface temperature and sea ice extent	Stochastic predictions of population trajectories, quasi-extinction time and probability	Extinction of the Black-browed Albatross population; Increase of Amsterdam Albatross population; snow petrel – 1% change in mean stochastic λ between present and 2075–2100
Four duck species Western boreal forest of North America (Drever <i>et al.</i> , 2011)	1 pessimistic SRES; 8 AOGCMs; stochastic predictions of spring snow cover duration	Stochastic forecasts of mean population size	Median of relative proportional change: increase up to 8.1% for mallard; decline up to –12.4% for american pigeon, –12.9% for scaup, –31% for scoter
Emperor Penguin Antarctica (Jenouvrier <i>et al.</i> , 2009a) (Jenouvrier <i>et al.</i> , 2012)	1 mid-level SRES; selection among 20 AOGCMs; stochastic predictions of years with lower sea ice extent stochastic predictions of sea ice concentration	Stochastic predictions of population trajectories and quasi-extinction probability	The median population size is predicted to decline to 400 (Jenouvrier <i>et al.</i> , 2009) and by 575 breeding pairs (Jenouvrier <i>et al.</i> , 2012)
Tidal Marsh Song Sparrows San Francisco Estuary (Nur <i>et al.</i> , 2012)	1 mid-level SRES; 2 regional models; stochastic forecasts of temperature and precipitation; scenarios of sea-level rise/ extreme tides/nest management	Stochastic predictions of population trajectories and quasi-extinction probability	Quasi-extinction probability vary from 2% for a low sea-level rise scenario up to 60% for high sea-level rise. Occurrence of infrequent extreme tides more than doubled the quasi-extinction probability from 12% to 28% for the medium sea-level rise scenario. Nests management actions can arrest and even reversing these anticipated declines
Spotted Owls Southwestern USA (Peery <i>et al.</i> , 2012)	Three SRES; 4 AOGCMs; stochastic forecasts of temperature and precipitation	Stochastic predictions of population trajectories and quasi-extinction probability	Quasi-extinction probability are up to 99 and 94% for populations at Arizona and New Mexico; no extinction for Southern California population
Eurasian Oystercatcher the Netherlands (van de Pol <i>et al.</i> , 2010)	Four scenarios; 1 regional model; stochastic predictions of temperature	Stochastic predictions of population trajectories and time to extinction	Shift from extinction to stationary fluctuations around a mean population size

Table 1 (continued)

Species	Climate	Population	Conclusion
Cassins Auklet California (Wolf <i>et al.</i> , 2010)	1 mid-level SRES; 1 regional model; deterministic sea surface temperature and upwelling intensity	Stochastic predictions of population trajectories and population growth rate	Up to 0.447 absolute change in mean stochastic population growth rate between 1980–1999 and 2080–2099

*SRES is a Special Report on Emissions Scenarios by the IPCC describing greenhouse gas emissions scenarios making different assumptions for future greenhouse gas pollution, land-use and other driving forces using assumptions about future technological development as well as the future economic development.

†Quasi-extinction probability are defined as a probability of a population decline by $x\%$ or more by 2100; x being defined by each study differently.

λ is the population growth rate.

Anticipating refers to projection based on fact and qualitative expert judgment; forecasting to projection obtained with time series statistical projections and predicting to projection using some level of our understanding of causal mechanisms underlying climate or population processes using mathematical models.

process-oriented climate models. In addition, the IPCC framework permits to include the various sources of uncertainty ranging from future greenhouse gas emission levels to climate modeling. This section describes various approaches to project population responses using climate predictions from IPCC climate models and a handful of avian case studies. The aim is not to criticize the specific approaches chosen in these examples, but instead to reveal the critical challenges of developing an effective and innovative applications of IPCC-class climate models to project population responses to climate change.

Goals of IPCC-class models

It is important that ecologists improve their knowledge of climate models, emissions scenarios, and the capabilities and limitations of climate projections (Seavy *et al.*, 2008). Coupled Atmosphere–Ocean General Circulation Models (AOGCMs) that contributed to the last IPCC Scientific Assessment of Climate Change (2007) incorporate detailed representations of the atmosphere, land surface, oceans, and sea ice. Climate change may be due to natural internal processes or external forcing, or to persistent anthropogenic changes in the composition of the atmosphere or in land use. The Earth's energy balance (i.e., difference between absorbed solar energy and emitted infrared radiation into space) is affected by a 'forced change,' which is a combination of natural (e.g., solar, orbital changes, volcanoes) and anthropogenic forcings (e.g., greenhouse gases, many classes of aerosols). IPCC-class models maintain the global energy balance, and changes in climate can arise due to changes in the 'forced change' or due to internal variations in the climate system, referred as 'natural variability'.

The first goal of climate modeling is to understand the processes that control the most important climate features (such as temperature, precipitation, windiness,

and storminess) and predict the dynamics of these features over long time scales. The focus of climate modeling is not on individual weather events, which are unpredictable on long time scales, but on the statistics of these events in terms of mean and variability over a period of time ranging from months to thousands or millions of years, and on the slow evolution of oceans and ice sheets (Bader *et al.*, 2008).

The second goal of climate modeling is to predict future climate change using various scenarios of future climate forcing and anthropogenic responses to implement mitigation strategies. Impacts of climate change on the environment and society will depend not only on the response of the Earth systems to changes in radiative forcing but also on how human societies respond through changes in technology, economies, lifestyle, and policy. The last IPCC AR4 is based on the Special Report on Emissions Scenarios (SRES, 2000), but the upcoming AR5 is using the new Representative Concentration Pathway (RCP) scenarios (van Vuuren *et al.*, 2011). The RCP are no longer defined by the IPCC but developed by a special group, and differ from SRES by assuming various levels of mitigation. RCP incorporate the complete path from socio-economic → greenhouse gas emissions → long-lived greenhouse gas abundances → forcing of mean climate change. Different climate scenarios should be used to explore the potential ecological consequences of various climate change mitigation strategies (Visser, 2008; Moss *et al.*, 2010), but bird studies that have done so to predict future population responses are rare (but see Barbraud *et al.*, 2010; Peery *et al.*, 2012; Table 1).

Important characteristics of IPCC-class models

There are important characteristics of AOGCM climate simulations and real climate system that should

be considered carefully when attempting to project population persistence under future climate scenarios:

- there are several AOGCMs and a multimodel ensemble is a set of AOGCMs using the same 'forced change' (i.e., scenario);
- the resolution of climate output is larger than the scale at which ecological processes occur;
- models differ in their ability to reproduce the climate and 'Each model tends to simulate some aspects of the climate system well and others not so well, and each model has its own set of strengths and weaknesses.' (Knutti, 2008); and
- both internal variability and radiatively forced changes are important components of the real climate system (Stock *et al.*, 2011).

Thus, projecting population responses to climate change using AOGCM outputs requires (i) using a multimodel ensemble; (ii) extracting the climate output at appropriate temporal and spatial scales; (iii) selecting the appropriate set of models for which the statistical property of the forecasted climate variables agrees well with past observations (known as hindcasting); and (iv) the need to account for both internal variability and radiatively forced changes because climate changes evident at any time and location will be a combination of these two sources.

First, the biologically relevant climate forecasts should be extracted from various IPCC-class models because combining different models exploits the strength of diverse approaches and yields a more appropriate estimate of the uncertainties (Meehl *et al.*, 2007). Although nearly all AOGCMs use the same set of primitive dynamical physical equations, model structural differences arise by different numerical algorithms to solve dynamical physical equations and different approximations, as well as differences in spatial resolutions and configurations of model grids (Bader *et al.*, 2008). Ideally, a set of model simulations from structurally different models using the same forcing but where one or more initial condition ensembles are available from each model should be considered, which is known as multimodel ensembles (Tebaldi & Knutti, 2007). IPCC-class model outputs are freely available from the archive of coupled model output at the Program for Climate Model Diagnosis and Intercomparison (PCMDI, <http://www-pcmdi.llnl.gov/>) (Meehl *et al.*, 2007), with a set of coordinated simulations from more than 20 AOGCMs. Outputs are categorized by variables (e.g., temperature, precipitation), scenario (i.e., climate experiment), and climate models. Each file contains a single output variable (along meta-data) from a single model and a single

simulation (i.e., from a single ensemble member of a single climate experiment) over specified time periods (historical 'control run' or future scenarios) and scales (e.g., month) and specified spatial grid covering the entire surface of the globe. Meta-data contain the coordinate/grid variables, time variables, and variable attributes (names, description, dimensions) and follows the NetCDF Climate and Forecast (CF) Metadata Convention.

Second, the temporal and spatial scales of the variables of interest should be chosen carefully given the resolution of AOGCMs. The temporal and spatial scales at which ecological processes occur are usually finer than the coarse grid of AOGCMs, or the temporal resolution at which climate outputs are saved (due to computational constraints). There are two approaches to address this issue: either using climate covariate at a larger spatial scale than the scale at which the ecological processes occurs assuming it is a good proxy of local climate or downscaling climate projections. Jenouvrier *et al.* (2012) used the first approach, and showed that sea ice concentration at large spatial scale is a good proxy of local sea ice characteristic affecting the life cycle of emperor penguins. Downscaling methods such as statistical downscaling or regional climate models may help to obtain finer-scaled climate data (Bader *et al.*, 2008; Seavy *et al.*, 2008; but see Racherla & Shindell, 2012). For example, Wolf *et al.* (2010) used a regional climate model to forecast changes in the California Current upwelling ecosystem, especially SST and upwelling intensity, to predict the future population growth rate of Cassin's Auklets. Regional climate models are driven by boundary conditions from AOGCM, and several AOGCM(s) should be ideally used (Pierce *et al.*, 2009).

Third, there is no 'best model,' and climate simulations from various state-of-the-science AOGCMs differ. Defining a unique overall figure of merit of a climate model, that is, metric or skill score for its ability to predict future climate change, is extremely difficult and debated (Knutti 2008). Thus, selecting a set of climate models depends on the climate variable of interest, and the ability of climate models to simulate past climate observations gives us some confidence in their ability to simulate the future. AOGCMs forced with observed natural and anthropogenic forcings are able to simulate the observed 20th century global mean temperature well, with typical correlations between models and observations of 95% or better. Other climate variables are still problematic, and for precipitation, the correlation between seasonal means of models and observations is 50% to 60% on scales of a few hundred kilometers (Bader *et al.*, 2008). Therefore, ecologists should compare the statistical properties of the climate

'control run' projection to observations to select the most appropriate multimodel ensembles (Tebaldi & Knutti, 2007; Knutti *et al.*, 2010) at relevant temporal and spatial scales.

Finally, it is important to take into account climate changes generated by both the 'forced change' and natural variability. For example, an average over a set of models may provide climate simulation superior to any individual model and climatologists have used such averaged ensembles to study the 'forced change' signal. However, for assessing the ecological impact of climate change, it is important to integrate the change in natural variability (see Step 2).

To illustrate the importance of considering an ensemble of several selected climate models rather than focusing on a single model, Figure 4a shows the Emperor Penguin population trajectories obtained from sea ice concentrations (SIC) predicted by different climate models. Those five AOGCMs were selected among 20 models for their ability to most accurately reproduce the statistical properties of past sea ice observations (Jenouvrier *et al.*, 2012). If the study had used only the climate model 'ukmo-hadcm3' to predict the Emperor Penguin population persistence by 2100 in Terre Adélie, it would have concluded that Emperor Penguins are not threatened by climate change. On the contrary with 'ccma-cgcm 3-1,' the probability that the population declines by more than 90% by 2100 (noted P_e) is 99%. Including all selected climate models, the conclusion ranges between these two extremes ($P_e=43%$).

Ecological studies often forecast future climate change based on the predicted climate mean state by AOGCMs (e.g., Peery *et al.*, 2012) because these values are very easily accessible in publications (e.g., Solomon *et al.*, 2007). Figure 4b shows the Emperor Penguin population projections obtained using such an approach. Under these assumptions, Emperor Penguins are not threatened by climate change. These contrasting results emphasizes the importance of incorporating the natural variability, the nonstationary and tipping point dynamic predicted by a time series of climate models.

Finally, ecological studies often use the averaged climate ensemble (e.g., Barbraud *et al.*, 2010), ignoring the change in natural climate variability. Figure 4c illustrates how these different assumptions can lead to different outcomes when predicting the population response of Emperor Penguins. Although the effect of climate mean state is greater than the effect of variability on population growth rate (see Step 2), climate variability still plays an important role in population dynamics as shown by the different population trajectories projected using 'forced change' vs. 'forced change + natural variability.'

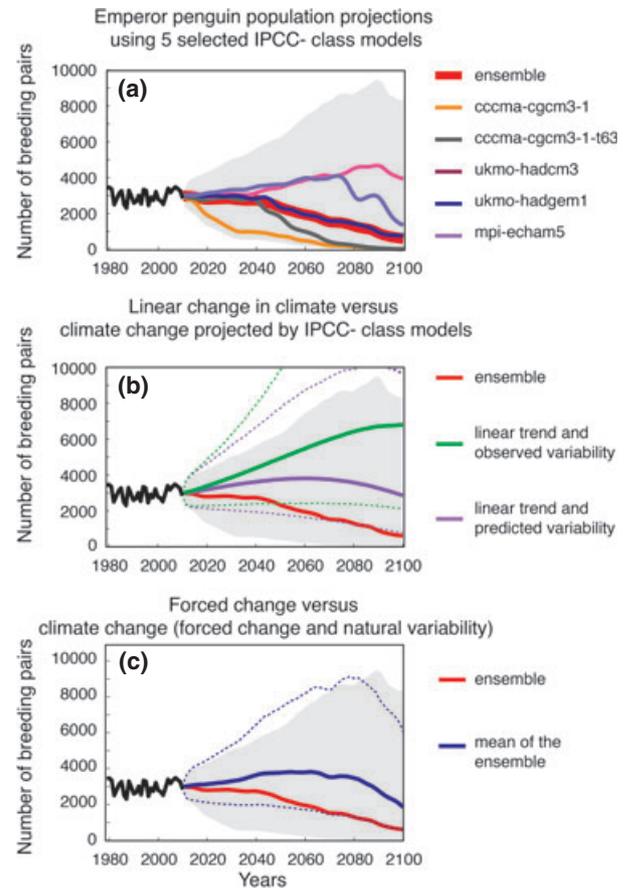


Fig. 4 Projections of the Emperor Penguin population based on sea ice concentration predictions from a multi-model ensemble of five AOGCMs and a mid-level range climate scenario. The black line gives the observed number of breeding pairs from 1979 to 2010. (a) For each AOGCM, the median are shown (thick colored line); the median and 95% envelope (grey area) of the ensemble are shown from the combined 200 000 simulations for the set of five GCMs, which include demographic and climate uncertainties. (b) Comparison of the median and 95% envelope (grey area) for the ensemble and median and 95% envelope (dotted lines) using a linear climate forecast. The linear climate forecast is obtained using the mean SIC predicted by an ensemble of AOGCMs by 2100 (estimates from Lefebvre & Goosse, 2008) and projecting a linear trend from 2010 to 2100. Stochastic SIC forecasts are obtained by sampling at each time t into a normal distribution of mean μ_t and variance σ_t . μ_t is estimated from the linear trend, and σ_t is either the observed variability (calculated from observed data) or the predicted variability (estimates from Lefebvre & Goosse, 2008). (c) Comparison of the median and 95% envelope (grey area) for the ensemble and the median and 95% envelope (dotted lines) from the average of the ensemble. The average of the ensemble, provide better projections of the current forced climate change because this averaging procedure hides the errors from individual models. However, ecologists rarely calculate the variance of the average of the ensemble and thus ignore the full range of natural variability.

Future population responses to climate change: a handful of studies

There are relatively few studies projecting bird populations (Table 1). Among them, two-thirds of the populations are projected to decline if climate changes as predicted by IPCC-class climate models. Ominously, those projected to decline include: Snowy Plover threatened by sea-level rise (Aiello-Lammens *et al.*, 2011); Emperor and Adélie Antarctic Penguins by sea ice decline (Jenouvrier *et al.*, 2009a, 2012; Ainley *et al.*, 2010); Black-Browed Albatross by warmer SSTs (Barbraud *et al.*, 2010); Tidal Marsh Song Sparrows (*Melospiza melodia*) by high sea-level rise and extreme high tide (Nur *et al.*, 2012); Mexican Spotted Owls by wetter and hotter climates in Arizona and New Mexico (Peery *et al.*, 2012) and Cassin's Auklets by warmer SSTs and reduced upwelling intensity of the California upwelling system (Wolf *et al.*, 2010). One may wonder if the predominance of population decline projections results from a publication bias toward 'doom and gloom' scenarios. Evidently, one could also be tempted to conclude that there will be more losers than winners under future climate change. To answer this question, more studies are critically needed.

These studies differ in the approach adopted for projecting population responses to climate using a range of combinations including anticipating, forecasting or predicting climate and populations in the future. Berteaux *et al.* (2006) distinguish anticipation, forecasting and prediction for inferences based, respectively, on facts, statistical evidence, or causal relationships, but acknowledge that projections are often based on mixed approaches. Ainley *et al.* (2010) anticipate that predicted sea ice habitat loss may jeopardize Antarctic penguin colonies north of 70°S, that is, 50% of Emperor colonies (40% of breeding population) and 75% of Adélie colonies (70% of breeding population). Drever *et al.* (2011) forecast the population responses of four duck species to future snow cover duration in the western boreal forest of North America and show that late-nesting duck species will experience the most severe population declines. Wolf *et al.* (2010) predict that the Cassin's Auklet population growth rate will experience an absolute decline of up to 45% if future SST and upwelling intensity change as predicted by a regional model in 2080–2099.

Table 1 illustrates that ecologists are putting great effort into developing population models accounting for demographic processes to predict population trajectories (nine of 10 used structured-matrix population models following Caswell, 2001). They are also including important features of climate models: ~ half used an ensemble of models (averaged or not), three used

different scenarios and four did their own climate model selection. Finally, half of the 10 studies reviewed focused on 'forced change' and ~ half integrated some natural variability, either using the one predicted by climate model or observed variability.

While most of the approaches discussed in Step 2 assume stationary climate conditions, climate change is not stationary, and both the mean state and variability change over time. All studies from Table 1 have acknowledged the nonstationary aspect of climate change, either by using IPCC time series predictions to fully incorporate nonstationary climate processes (e.g., Jenouvrier *et al.*, 2009a, 2012; Barbraud *et al.*, 2010), or by forecasting the trend of climate averages predicted by IPCC-class models (e.g., Nur *et al.*, 2012; Peery *et al.*, 2012), or by focusing on restricted periods where the climate conditions are assumed to be stationary (e.g., a 20-year window for Wolf *et al.*, 2010; a 30-year window for Drever *et al.*, 2011).

Studies directly linking IPCC time series to avian population models are rare (but see Jenouvrier *et al.*, 2009a, 2012; Barbraud *et al.*, 2010). Nonetheless, this approach enables an integration of the pathway of change in mean state and variability in climate, as well as tipping points and extreme event dynamics. Barbraud *et al.* (2010) linked a stochastic population model to deterministic climate projections and showed that future population responses are contrasted among three seabirds breeding in the Southern Ocean. Black-browed Albatross' quasi-extinction is projected by 2100, while the Amsterdam Albatross (*Diomedea amsterdamensis*) population is projected to increase steadily.

It is also important to include some stochasticity in climate when using time series from IPCC-class models, because climate models do not aim to project climate in a particular year, but rather the change in statistical properties, mean state and variances over time. Ideally, this would be obtained from multiple stochastic realizations of each IPCC-class model, but such output are limited from few to a couple of tens runs. For the Emperor Penguin, Jenouvrier *et al.* (2009a) obtained stochastic climate forecasts by discretizing the climate into two states ('warm' and 'regular') and applying a nonparametric binary regression to calculate the forecast frequencies of warm events (see also Hunter *et al.*, 2010 for Polar Bear). For continuous climate variables, Jenouvrier *et al.* (2012) developed a novel approach using smoothed temporal means, variances, and covariances from the predicted climate outputs.

Finally, only one study explored specifically the effect of an increased frequency of extreme climatic events while projecting population responses to future climate conditions (Nur *et al.*, 2012; although Van de Pol *et al.* integrated effect of extreme flooding events in

their analysis of the Oystercatcher). To project population of Tidal Marsh Song Sparrow for the San Francisco Estuary, Nur *et al.* (2012) included the frequency of extreme tides resulting from sea-level rise and/or severe storms in addition to the impact of temperature and precipitation forecasted by a downscaled AOGCM and sea-level rise predicted by a regional climate model (Stralberg *et al.*, 2011). Extreme high tides were the most significant climate factor threatening long-term viability of Song Sparrows due to nest loss from flooding.

Addressing uncertainties

To move forward a predictive ecology, there is a wide range of uncertainties from climate to ecological processes that needs to be addressed through a dialog involving scientists, managers, and policy makers (Clark, 2001; Evans, 2012; Ruete *et al.*, 2012; Sutherland & Freckleton, 2012).

Communicating the degree of uncertainty to the public and policy makers is a critical part of the next AR5. AR5 incorporates two major criteria: the confidence in the validity of a finding and quantified measures of uncertainty or likelihood scale. The first criteria is qualitative and based on the evidence (limited, medium, robust) and agreement statements (low, medium, high). It incorporates the 'type, amount, quality, and consistency of evidence (e.g., mechanistic understanding, theory, data, models, expert judgment) and the degree of agreement' (Mastrandrea *et al.*, 2010; Mastrandrea & Mach, 2011). The second criteria quantifies 'probabilistic estimates of the occurrence of outcomes associated with, unless otherwise noted, high or very high confidence' (Mastrandrea *et al.*, 2010; Mastrandrea & Mach, 2011). It varies from exceptionally unlikely (0–1% probability) to virtually certain (99–100% probability).

Quantified measures of uncertainty in population viability have been addressed by calculating the 'quasi-extinction probability' or the prediction interval for the population size (Lande *et al.*, 2003). The 'quasi-extinction probability' is the probability that the population will decline by more than a specific 'quasi-extinction threshold' over a specific time horizon. Population prediction interval (PPI) is a stochastic interval of population size that includes the unknown population size with a given probability ($1 - \alpha$) over the entire time horizon of interest. PPI avoid the subjective choices of a specific time horizon and quasi-extinction threshold, but not the choice of α . Chatfield (2001) recommended $\alpha = 10\%$, a compromise between lower and higher α -PPIs. Higher α -PPIs are better calibrated for their robustness for outliers and to departures from model assumptions. Lower α -PPIs provide higher confidence than higher α -PPIs but show heavy tails.

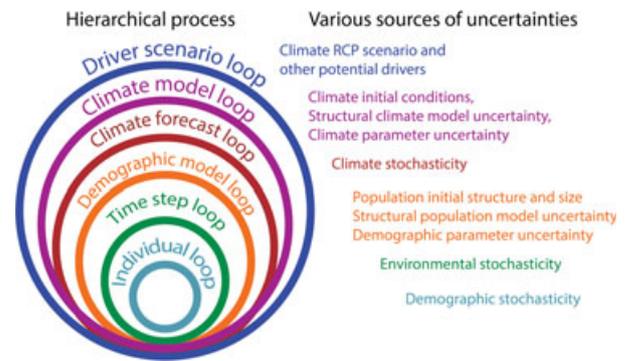


Fig. 5 Description of the various sources of uncertainties, which can be incorporated using a hierarchical process. Colored circles represent the various replication loops of the model. Prediction uncertainty in the climate scenario (or other future driver scenario) is incorporated into the first replication loop. Climate initial conditions, structural model uncertainty and parameter uncertainty are included into a second loop by using a multi-model ensemble of AOGCMs. Climate natural variability using stochastic climate forecast appears in the third loop. Demographic initial conditions, parametric and model structural uncertainties are incorporated into the fourth replication loop, while environmental stochasticity is incorporated into the fifth loop for time steps in the model. Finally, demographic stochasticity simulates the fates of individual organisms within a particular time step and replicate into an inner loop (the individual loop).

They are diverse sources of uncertainties when projecting population responses to climate change ranging from climate to demography (Fig. 5), which can be addressed in a hierarchical process (McGowan *et al.*, 2011). They can be organized in three main categories: data, model, and prediction uncertainties. Climate and demographic data are often observed incompletely with large uncertainty caused by observation and measurement errors. This adds to the temporal variance process some uncertainty in parameter estimates, which is a major component of the second source of uncertainty: model uncertainty. In addition, model uncertainties include structural uncertainties in the model specification and the models' initial and boundary conditions. Structural uncertainty arises from competing scientific theories and simplifications of reality such as inclusion or exclusion of density dependence in population models. The last main source of uncertainty is related to prediction and includes uncertainties on future system drivers and future no-analog climate conditions.

To incorporate uncertainties related to future socio-economic development and emissions/abundance of greenhouse gas, several RCP scenarios should be incorporated. Ecologists may also want to include uncertainty into decision-making frameworks related to other factors than climate (Evans, 2012; Milner-Gulland, 2012). For example, Nur *et al.* (2012) evaluated different

management strategies to improve nest survival of Song Sparrow (by reducing predator populations or access to tidal marsh nesting habitat), which can reverse projected population declines caused by future sea-level rise and extreme high tide events.

Because population projections are contingent on data and model uncertainties in climate, it should be incorporated by using a climate multimodel ensemble and a forecasting approach to build stochastic climate forecasts. Tebaldi & Knutti (2007) argue that integration of all aspects of climate model uncertainty requires using multimodel ensembles, which sample initial condition, parameter as well as structural uncertainties in the model design. It is possible to include uncertainties in the selection of this multimodel ensemble by attributing some weights for each climate model by using the historical relationship between predictions and observations and then sample the number of future stochastic climate forecasts according to these model weights. However, the determination of such weights are still controversial as it is difficult to quantify model skill and derive model weights accordingly (Knutti *et al.*, 2010; Weigel *et al.*, 2010).

Demographic data uncertainty caused by observation and measurement errors may bias estimates of many population parameters or vital rates, which parametrize population models (see review in Morris & Doak, 2002). Many statistical methods are available to quantify such uncertainty in parameter estimations, such as variance decomposition, separating sampling from process variance in temporal variations of vital rates (e.g., Gould & Nichols, 1998) or maximum likelihood statistical methods (e.g., De Valpine & Hastings, 2002) to Bayesian Markov chain Monte Carlo (e.g., Clark & Bjørnstad, 2004; Clark, 2007) in time series analysis. Parameter uncertainty may reduce our ability to precisely predict future population fluctuations (Ellner & Fieberg, 2003; Holmes *et al.*, 2007; Ellner & Holmes, 2008) and several avian studies have highlighted the importance of including parameter uncertainty when making future population projections [e.g., Song Sparrow: Sæther, 2000; Barn Swallow (*Hirundo rustica*): Engen *et al.*, 2001; Piping Plover (*Charadrius melodus*): McGowan *et al.*, 2011]. Including the uncertainties in both demographic parameters and model structure, involve model selection, model averaging, or both (Clark, 2001; Burnham & Anderson, 2002). For example, in the framework of capture-recapture models and maximum likelihood statistical methods, Hunter *et al.* (2010) developed a method to account for both uncertainty in model selection and parameter uncertainty while preserving the covariances among vital rates in population projections. Albeit with quite extensive numerical work in most cases, the Bayesian paradigm

provides powerful new tools which could embrace unknown levels of error, mixture of models, model selection, and averaging (Clark & Gelfand, 2006; Gimenez *et al.*, 2009). These models allow unknown levels of errors to propagate through various submodels (Cressie *et al.*, 2009) as well as integrate multiple stochastic elements (environmental, demographic stochasticity as well as individual heterogeneity) (Clark, 2001, 2005).

There are few studies comparing the different sources of uncertainties. Using data from several passerine species, Sæther *et al.* (2009) studied the effect of different demographic sources of uncertainties on future population projections. They showed that including observation error in the models improves precision in density-independent population predictions and reduces bias for density-dependent population models. In addition, ignoring demographic stochasticity resulted in positively biased population size predictions and imprecise density-independent population predictions. Studies comparing the respective role of the different sources of uncertainties on population projections in response to climate change are rare (but see Ruete *et al.*, 2012). The main source of uncertainties for the Emperor Penguin population (Jenouvrier, unpublished result), as well as in the population of bryophyte (*Buxbaumia viridis*) (Ruete *et al.*, 2012), is the 'AOGCM formulation.' This result emphasizes the importance of using several AOGCMs for predicting future population responses.

Summary of step 3

To summarize this last step, predicting population responses to climate change are now possible thanks to a tremendous advancement in our understanding of the demographic processes, and the availability of climate predictions from IPCC-class models. There are, however, large uncertainties in population and climate predictions. Ecologists sometimes see wide population prediction intervals as indicating 'failure' either to fit the right model or to obtain a usable interval, but prediction intervals could be misleadingly narrow by failing to incorporate the appropriate uncertainty. Uncertainties in data and the model structure could be eventually reduced by improving sampling efforts, our knowledge of the processes and refining models (i.e., by continuous feedback between the three steps of the MUP approach). Situations where uncertainties are large and information content too low to make useful management decisions now could become more informative within a decade by developing new or supporting existing long-term data (Step 1), as well as improving knowledge and refining demographic models (Step 2). Stochasticities and nonlinearities of any ecological system results in uncertainties inherent in predictive ecology, but as Clark (2001) stated: 'Large

inherent uncertainty does not necessarily neutralize efforts to anticipate change.' To address inherent uncertainties, ecologists should incorporate the natural variability and non stationarity of climate processes, which can have a tremendous impact on population dynamics and devote more effort in using multimodel climate ensembles instead of one particular climate model. To provide information to decision-makers and help implement mitigation strategies, several climate scenarios should be incorporated, as well as the inclusion of other drivers than climate change. Indeed, the impact of climate change will interact with other stressors, such as habitat destruction, introduced species, overexploitation, and extinction cascades (chains of extinctions), and effective mitigation conservation strategies may focus on local stressors rather than climate change.

Conclusions: Prospects and challenges

Integrating spatial dynamics

Avian population responses to climate change have often been analyzed in terms of the effect of local climate conditions on temporal population fluctuations at a particular location. However, if negative effects of climate variations on vital rates and populations occur simultaneously over large geographical areas, the consequences for species persistence will be more severe than if they occur only locally (Sæther & Engen, 2010). Climate can induce population synchrony if variations in climate are autocorrelated in space and if populations had the same density-dependent structure known as the 'Moran effect' (Moran, 1953; Royama, 1992). Synchrony is of particular concern for assessing the impact of climate change because species persistence is strongly related to population synchrony. Spatial synchrony has been detected for numerous avian populations, but attributing the 'Moran effect' has been difficult (see review of Sæther & Engen, 2010). Climate can also induce synchrony in vital rate variations and Jenouvrier *et al.* (2008b) have shown that adult survival variations of Cory's shearwater (*Calonectris diomedea*) are synchronized among six populations spread across 4600 km. These synchronous variations are explained by Southern Oscillation Index fluctuations suggesting strong effect of climate at large spatial scales on Cory's shearwater adult survival during the nonbreeding period.

On the other hand, the effect of the same climate variable may show different directions among different populations. Various population responses to climate may result from an interaction between climate and population growth along a latitudinal or environmental gradient (see review Sandvik *et al.*, 2008; Barbraud *et al.*, 2012) or a spatial heterogeneity in the interaction

between climate with other environmental and demographic factors (see review Sæther & Engen, 2010).

Integrating spatial dynamics will also be critically needed to adequately understand and predict how species may cope with climate change because individuals may move permanently to other locations, where climate and associated habitat conditions are more suitable. Temperature isoclines will, in general, move poleward in latitude and upward in altitude, resulting in changes in local population abundance, local extinction and colonization of new habitats, species range shifts (Parmesan, 2006), and species extinctions (Thomas *et al.*, 2004). Birds with high fertility and high dispersal rates may be able to cope with climate change by expanding or contracting their range at the right speed, while birds with lower fertility and limited dispersal rates may not (Schippers *et al.*, 2011). For philopatric species, the colonization of new habitats with favorable climate conditions may occur through the dispersal of pre breeders. At Lancelin Island, five pairs of Common Noddies pioneered a colony in 1991 and the population stabilized around 1200 pairs by 2008 (Wormworth & Şekercioğlu, 2011). Further research should focus on a better understanding of dispersal processes in response to climate change (but see Dugger *et al.*, 2010) and the development of metapopulation models integrating climate impacts or species distribution models including demographic processes (but see Keith *et al.*, 2008; Anderson *et al.*, 2009; Schippers *et al.*, 2011).

Integrating eco-evolution

Species may cope with climate change by adapting to the new local climate conditions (either through microevolution or phenotypic plasticity). Although, there is an increasing agreement that evolutionary processes may play a crucial role for population persistence under future climate change, we know surprisingly little about how changes in climate translate into adaptive phenotypic change (see review of Pelletier *et al.*, 2009; Reed *et al.*, 2010; Gonzalez *et al.*, 2012; Hanski, 2012). Eco-evolutionary approaches are now being developed (e.g., Coulson *et al.*, 2006, 2011; in a climate change context see Baskett *et al.* (2009), Jenouvrier & Visser, 2011). For example, Reed *et al.* (2011) explored how populations of sockeye salmon (*Oncorhynchus nerka*) can persist under scenarios of future river warming and evolutionary changes in migration timing. However, such approaches have yet to be applied to avian populations.

Conclusion

To conclude, the MUP approach provides a general framework within which enhanced understanding of

climate-population processes, along with improved long-term data, are merged into coherent projections of future population responses to climate change. Projecting population responses is not the major endeavor nor a finality in itself; instead, I advocate striving for a richer understanding of the various eco-evolutionary processes in which populations can cope with climate change, through pursuing/establishing new long-term studies, an invaluable source for the MUP approach. Applying the MUP approach using universal quantitative variables (e.g., 'population robustness to climate change') to a broad range of species may provide the foundations to infer general patterns across climatic zones, life history strategies, communities, or ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Impact of extreme harsh winters on the demography of the Barn Owl.

Table S1. Projections of avian population's responses to climate change using information from IPCC- class models.