

CHAPTER 12

Projected population consequences of climate change

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12.1 Introduction

Many atmospheric and oceanic climate processes will change in the coming century (IPCC 2013). These processes affect vital rates of individuals (such as survival, growth, reproduction, and dispersal) that govern the dynamics of natural populations (Chapter 7). Appropriate decision-making and wildlife policy requires anticipating the future state of populations in a changing climate and a rigorous accounting of uncertainty in those future states (Clark et al. 2001; Dietze 2017a).

Population forecasts estimate the future state of populations (Dietze 2017a) and can range from local to global in spatial extent, and from days to centuries in time. Population predictions are forecasts that are based solely on current knowledge of a system and are typically focused on the near term (Dietze et al. 2018). At longer timescales, processes such as technological innovation, socioeconomic change, and policy development cannot be fully anticipated but may have strong effects on the overall behaviour of the system. Yet, it is at these longer timescales that the effects of climate change will be most pronounced (Hawkins and Sutton 2009). Longer-term population forecasts that are contingent on particular scenarios of future change are called projections.

Projecting avian population dynamics in response to climate change requires several integrated steps (reviewed in Jenouvrier 2013). The first step is

measuring the effect of climate on the complete life cycle of the studied species, thereby accounting for multiple seasonal and carry-over effects of climate. At this step, variation in vital rates is partitioned into components owing to measured climate variables along with vital rate variation owing to unexplained (i.e., unmeasured) factors, while removing spurious variation owing to imperfect detection or other observation error (Kéry and Schaub 2012). This first step has been the focus of hundreds of studies (see Chapters 5 and 7).

The second step is examining the demographic pathways through which climate influences overall population dynamics. This step requires integrating the statistical relationships between climate and vital rates (found in step one) into population models. At this step, population models become climate-dependent. Climate can be modelled as deterministic or stochastic, while vital rates can be entirely driven by climate or include additional ‘unexplained’ variation. Resulting models can then be used to evaluate the short- or long-term dynamics resulting from different climate scenarios. For example, they can be used to project population dynamics resulting from climate that is 2 °C warmer on average (even if climate is modelled deterministically; Dybala et al. 2013), or to project the respective role of a change in climate average versus variability, including extreme events (Jenouvrier et al. 2012; Pardo et al. 2017). Simultaneously, perturbation analyses can provide insights to the relative influence of climate properties, channelled through

different demographic pathways, and the potential for trade-offs among life cycle components (Caswell 2001; McLean et al. 2016; Jenouvrier et al. 2018b).

The final step is fusing climate-dependent population models with projections of future climate from IPCC-class atmospheric–oceanic global circulation models (AOGCMs). AOGCMs project (often nonlinear) changes in climate over time, and critically, provide quantitative estimates of uncertainty in future climate change for multiple climate variables (Hawkins and Sutton 2009). AOGCMs thereby provide a means for uncertainty in future climate to be fully propagated to population forecasts.

Here, we focus on this third step of projecting avian population responses to climate change by linking climate-dependent population models with projections of future climate from IPCC-class AOGCMs; Chapter 7 discusses the related issue of estimating climate effects on vital rates and incorporating them into population models (step 2 in our approach), along with several aspects of forecasting. We first discuss biological considerations of this approach: characterizing the full life cycle (section 12.2) and considering spatial heterogeneity and dispersal processes (section 12.3). We then highlight important methodological challenges: matching the scale of ecological processes with the scale of climate projections (section 12.4) and fully propagating climate and demographic uncertainty to population forecasts (section 12.5). Throughout, we use examples from a long-term study of emperor penguins (*Aptenodytes forsteri*) at Terre Adélie to illustrate key points. Finally, we conduct a literature search to compile a list of studies that have linked IPCC-class climate projections with avian population models (section 12.6). We conclude by discussing commonalities and differences among these studies, along with future prospects and challenges associated with forecasting avian population dynamics under climate change.

12.2 Biological considerations

12.2.1 Consideration of the full life cycle and relevant dimensions of population structure

Climate change will affect birds across their entire life cycle (Carey 2009; Jenouvrier 2013). Failure to

account for effects on multiple life cycle stages can severely misrepresent the effect of climate on population dynamics (Ådahl et al. 2006). Climate effects on vital rates can be contrasted and/or delayed between various states of the life cycle, while evolutionary pressures, trade-offs, and physiological constraints can cause vital rates to respond differently to the same climate variables. For example, sea ice conditions impact survival and fecundity of emperor penguins in opposite ways (Barbraud and 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 these extensive sea ice years resulting in fewer hatched eggs.

Population models must therefore account for relevant dimensions of population structure, such as differences in vital rates across age, stage, or size classes (Caswell 2001), and sex differences (Jenouvrier et al. 2010). Avian life histories vary considerably (Sæther and Bakke 2000; Sibly et al. 2012), ranging from fast-paced life histories such as house sparrows (*Passer domesticus*) that mature in a single year and produce up to four broods per season, to those with a slow pace of life such as wandering albatross (*Diomedea exulans*) that require up to 11 years to reach reproductive maturity and only produce one egg every two years. All bird populations consist of overlapping generations, but a slower pace of life generates a higher degree of population (st)age structure, which in turn, can strongly mediate the population consequences of climate change. Below, we discuss several key dimensions of population structure that affect avian responses to climate.

Climate often affects younger birds differently than older birds. For example, Oro et al. (2010) found that survival of young blue-footed boobies (*Sula nebouxii*) responded negatively to winter sea surface temperature (SST), while survival of older individuals showed no response. In a black-browed albatross (*Thalassarche melanophris*) population, Pardo et al. (2017) detected strongly nonlinear effects of SST on young and old individuals, but only a weak linear effect on prime-aged individuals. Simultaneously, reproductive success responded differently to SST across age classes. As a result, extreme climate events altered the stage structure of the population with a predicted increase in the proportion of

juveniles in the population in a warmer climate with more frequent extreme events.

Body size is a key correlate of vital rates in birds and other animals (Stearns 1992). Body size influences energetic requirements, thermal tolerances, and predation pressure, and is often a reliable indicator of individual quality (Blanckenhorn 2000). For instance, wing length influences the survival and reproduction of black-browed albatross by likely reducing energetic costs incurred during flight. Accordingly, larger-winged individuals have higher fitness and are better able to cope with sub-optimal sea surface temperatures (Jenouvrier et al. 2018b). However, because body size both influences environmental sensitivity (e.g., Lindström, 1999) and simultaneously responds plastically to environmental conditions (Cooch et al. 1991a, b), it is difficult to predict general relationships between avian body size and environmental sensitivity. Accordingly, studies have reported increasing, decreasing, or equivocal responses of avian body size to climate warming (Gardner et al. 2011; Sheridan and Bickford 2011). Reported effects are hypothesized to occur through a variety of pathways, including direct effects on physiology, changes in food availability, and shifts in predation pressure, among others. In cases where body size influences climate sensitivity, a consideration of population size structure may be required to reliably forecast population dynamics.

Breeding structure of the population can also strongly influence population dynamics. This is especially the case for long-lived species that often have extensive pre-breeding and non-breeding components of the population that occupy different habitats, are subjected to different climate, and experience different energetic constraints than breeders. In southern fulmar (*Fulmarus glacialisoides*), approximately 40 per cent may skip breeding, and this proportion varies in response to climate fluctuations (Jenouvrier et al. 2005a).

Finally, sex structure (i.e., the ratio of males to females in a population) is relevant to population forecasting when (1) skewed sex ratios cause population growth to be limited by an inability of females to find mates, and (2) the vital rates of each sex differ or respond to climate differently. Both have been observed in birds. Bird populations often exhibit

skewed sex ratios, caused by sex differences in multiple life cycle processes. For example, in wandering albatross, older mothers produce more female hatchlings, while higher quality mothers (those that have higher breeding success) tend to produce more male hatchlings (Weimerskirch et al. 2005). Subsequently, mortality risk in many bird species is greater for juvenile males than females, owing to larger body sizes and higher energetic constraints (Clutton-Brock 1986). Yet, mortality risk for adult breeders is highest for the sex that incubates eggs (i.e., females in most species). This leads to male-skewed sex ratios in most bird species (Donald 2007), and females are thus rarely limited by lack of suitable mates. Emperor penguins offer a striking counter-example in which males incubate eggs during the Antarctic winter. As a result, adult males experience higher energetic demands, have lower survival, and are more sensitive to climate (particularly winter sea ice extent) than females (Jenouvrier et al. 2005b). The increased sensitivity of males to winter sea ice was responsible for a large decline in the Terre Adélie population of emperor penguins during a climate regime shift in the 1970s. In this case, a two-sex population model provides better descriptions of overall population dynamics by accounting for breeding limitation when operational sex ratios are uneven (Jenouvrier et al. 2010).

Population structure (owing to age, stage, sex, or other dimensions) generates transient dynamics, such that short-term population growth rates and long-term population abundances depend on the initial structure of the population (Stott et al. 2011). Transient dynamics can also interact with other population processes (e.g., demographic stochasticity) to influence extinction risk (Iles et al. 2016). Thus, even with perfect knowledge of the initial abundance of the population, uncertainty in initial stage structure can yield uncertain forecasts (also see section 12.4.2).

12.2.2 Consideration of spatial heterogeneity and dispersal

Projected changes in climate vary across the globe (see Chapter 2). Simultaneously, uncertainty in the amount of future climate change varies strongly across regions (see section 12.3.2). Populations separated

in space will therefore experience different levels of climate change in the future, relative to their respective baselines, affecting the level of spatial heterogeneity in the environment. For example, in Antarctica, AOGCMs project marked regional and seasonal patterns of sea ice change by the end of the century (see Figure 5 in supplementary information of Jenouvrier et al. 2014). This has important consequences for emperor penguins, which breed in colonies scattered around the Antarctic continent. A species-level threat assessment study (Jenouvrier et al. 2014) projected that the most threatened colonies are located in Dronning Maud and Enderby Lands, where projected sea ice concentration (SIC) declines are largest and conditions are most variable. Conversely, colonies in the Ross Sea will experience the least loss of sea ice and are projected to increase relative to their present size by 2100. Overall, at least two-thirds of the colonies are projected to become endangered by sea ice decline by 2100, and the global population is projected to decline by at least 19 per cent (Figure 12.1).

Climate change may also alter the spatial distribution of other factors such as disease prevalence, with concomitant effects on population growth.

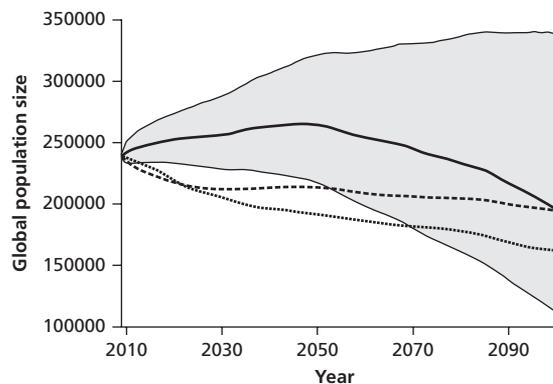


Figure 12.1 Forecast for global population size of emperor penguins using three different climate model selection criteria. Solid black line is median forecast (and associated 90% confidence intervals) resulting from selection of climate models that best reproduce local conditions at each emperor penguin colony. Thus, each colony is forecast using a different ensemble of climate models. Thin hashed grey line is median forecast based on four climate models that are known to accurately reproduce Pan-Antarctic sea ice conditions, but may not reproduce historical climate well for some individual emperor penguin colonies. Thick hashed grey line is median forecast using all AOGCMs.

Liao et al. (2015) projected the dynamics of three Hawaiian honeycreepers under future climate change, while simultaneously modelling the future prevalence of mosquito-borne malaria. Their forecasts indicated that malaria transmission to native birds would increase strongly under mid and high emissions scenarios, with accompanying declines in bird populations. Furthermore, while high elevation habitats historically provided refuge from malaria, their models indicated that climate change would drastically increase malaria transmission in these areas.

Accounting for spatial heterogeneity in avian population forecasts is particularly challenging for at two reasons: 1) demographic responses to climate can differ across space (e.g., owing to local adaptation or species interactions), and 2) dispersal rates can be difficult to estimate but can strongly influence population responses to climate change. We discuss these challenges below.

First, vital rates and their responses to climate can differ across space (Drever et al. 2012; Peery et al. 2012; Zhao et al. 2016), introducing spatial variation in population parameters and their uncertainty (we discuss parameter uncertainty more fully in section 12.3.2). For example, Peery et al. (2012) found that mean reproductive output of spotted owls (*Strix occidentalis*) was negatively correlated with nesting season temperature for a population in Arizona, but positively correlated for a population in southern California. Interestingly, these divergent responses occurred across the same range of climate variation. Differences in population sensitivity to the same climate variation can be driven by multiple processes. First, different populations can be adapted to local conditions, generating different reaction norms to the same environmental drivers. For example, a common garden experiment revealed that blue tits (*Parus caeruleus*) from two populations experienced large differences in the onset of laying date, owing to different adaptive responses to photoperiod (Lambrechts et al. 1997). Second, the strongest effects of climate are often indirect, channelled through effects on species interactions (Ockendon et al. 2014). Demographic responses to climate will therefore often depend on the larger ecological community, which varies across space. For example, in lesser snow geese (*Anser caerulescens caerulescens*),

reproductive success was much more responsive to seasonal temperature in breeding habitats that contained higher plant diversity (Iles et al. 2018). Simultaneously, unexplained process variation in reproductive success was three to five times higher in those habitats, suggesting that plant diversity also affected snow goose sensitivity to unmeasured climate variables.

Second, projecting population responses to climate change requires full consideration of the ability of species to disperse (Travis et al. 2012; Ehrlén and Morris 2015), especially when the population decline is driven by climate changes that exceed the tolerance of a species or when acclimation and adaptation are insufficient to allow species persistence (Visser 2008). For example, the Southern Ocean Oscillation Index was a strong predictor of local demography for a population of Scopoli's shearwater (*Calonectris diomedea*), but immigration from other populations almost completely counterbalanced the net effects on population growth (Tavecchia et al. 2016). For emperor penguins, dispersal behaviours can either offset or accelerate climate-driven global population declines relative to a scenario without dispersal (Jenouvrier et al. 2017). Specifically, dispersal may increase the global population by up to 31 per cent or decrease it by 65 per cent, depending on the rate of emigration and distance individuals disperse. Thus, in some cases dispersal can act as an 'ecological rescue' mechanism to offset the global population decline of species endangered by climate change.

12.3 Methodological challenges

12.3.1 Match between scale of ecological process and climate projection

Climate models simulate historical and future climate on a three-dimensional lattice around the globe, typically at resolutions between 1 and 5 degrees latitude and longitude. In contrast, ecological studies commonly focus on the effects of local weather on populations, given that the local environment is the proximate cause of demographic variation (van de Pol et al. 2013). Thus, climate projections are made at coarse spatial scales relative to those at which the factors affecting population processes are typically measured. This disparity introduces

several complications for using AOGCM outputs in population forecasts.

First, the effects of local-scale climate on populations can differ from the coarse-scale climate outputs that are available from AOGCM simulations. To deal with this problem, studies can estimate the effect of coarse-scale (rather than local-scale) climate on populations (Hallett et al. 2004). However, this approach may obscure the proximate causes of population fluctuations and exaggerate spatial differences in population sensitivity to climate (van de Pol et al. 2013). Alternatively, climate model outputs can be downscaled using statistical relationships between local-scale weather and coarse-scale climate, or dynamically by linking global AOGCMs with finer-resolution regional climate models (Snover et al. 2013). For example, Wolf et al. (2010) generated downscaled projections of coastal upwelling based on regional AOGCM projections of wind along the California coast to forecast the population dynamics of Cassin's auklets (*Ptychoramphus aleuticus*).

The second complication for using AOGCM outputs in population forecasts is that grid resolutions vary among AOGCMs (Figure 12.2a), and in many cases, the entire study area may be subsumed within a single AOGCM pixel. Individual AOGCM pixels are subject to high forecast uncertainty and bias (Hawkins and Sutton 2009; also see section 12.3.2). To ameliorate this issue, AOGCM outputs should be averaged over multiple pixels. Correlation maps can be used to evaluate the spatial resolution over which climate can be safely aggregated without losing fidelity to demographic responses to local climate. For emperor penguins, Jenouvrier et al. (2012, 2014) used sea ice concentration averaged across several pixels of an AOGCMs grid (Figure 12.2b) to improve the accuracy of sea ice forecasts. This large sector includes the foraging area of emperor penguins, defined by the maximum foraging distances from the colony, of about 100 km during the breeding season and at least 650 km during the non-breeding season. Figure 12.2b illustrates that sea ice concentrations for many pixels in this large spatial sector are strongly correlated to the local sea ice concentration within the foraging area, and can be aggregated to reduce uncertainty in sea ice forecasts while maintaining strong correlations with local dynamics.

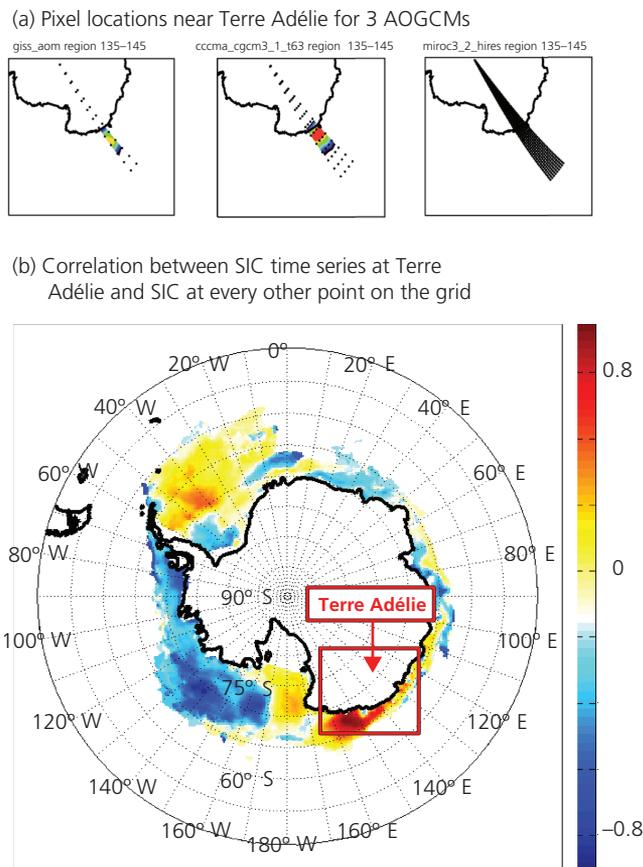


Figure 12.2 AOGCM output for the area surrounding Terre Adélie, Antarctica. (a) AOGCMs differ in their spatial resolution, and thus in the number of pixels encompassing the study area (grid for CMIP3). (b) Jenouvrier et al. (2012, 2014) used a correlation map to estimate the correlation between a time series for sea ice at the location of the local population and at other areas around Antarctica. From this, they determined that local sea ice was correlated with conditions across a much larger area. This provided justification for averaging AOGCM predictions of sea ice across larger spatial extents, reducing forecast uncertainty.

12.3.2 Uncertainties must be fully propagated to population forecasts

Uncertainty is central to population forecasting and enters in every step, from climate modelling (e.g., uncertainty in current climate conditions and future climate change) to demographic modelling (e.g., uncertainty in the responses of vital rates to climate parameters, residual vital rate covariation, etc.) to population modelling (e.g., uncertainty in population abundance and stage structure). Depending on their origin, uncertainties propagate to forecasts differently (Dietze 2017b). Accordingly, forecast uncertainty is dominated by different processes across

various spatial and temporal horizons. For example, in climate models, uncertainty in local-scale, short-term forecasts is dominated by uncertainty in initial conditions. Yet, uncertainty in large-scale, 100-year forecasts is dominated by structural uncertainties among climate models and emissions scenarios (Hawkins and Sutton 2009). Similarly, the magnitude of various sources of uncertainty in avian population forecasts depends on a variety of factors, including the spatial and temporal scale of forecasts, sample size, model complexity, and life history of the species. Forecasts that fail to include these key sources of uncertainty will be falsely overconfident, eroding trust in ecological science and

hindering ecological understanding (Dietze 2017a). Forecasting therefore requires a quantification of uncertainty in each model component, and importantly, full propagation of these uncertainties to forecasts. Below, we highlight the key sources of uncertainty in avian population forecasts.

Uncertainty in simulations of future climate arises from three sources (Figure 12.3; Hawkins and Sutton 2009): (1) imperfect knowledge of initial climate conditions, (2) structural differences among climate models, and (3) uncertainty in future climate emissions. Climate models and their associated uncertainties are also discussed in Chapter 2. Here, we briefly review these uncertainties with respect to their relevance for avian population forecasts.

Weather dynamics are chaotic. Thus, even infinitesimal uncertainty in the initial state of climate simulations will ultimately grow over time until it approximates the long-term statistical distribution of each climate variable. This component of climate

forecasting is called ‘internal variability’ and typically dominates uncertainty in short-term to medium-term forecasts, especially at small spatial scales (Hawkins and Sutton 2009). However, uncertainty due to internal climate variability reaches an eventual asymptote, usually by 10 years into the future (Figure 12.3a and d; identical uncertainty at 15 and 80 years). Thus, other sources of uncertainty eventually dominate longer forecasts. To measure uncertainty due to internal variability, the same climate model must be simulated many times with initial conditions on each run drawn from probability distributions describing the observation error for climate variables. Alternatively, uncertainty due to internal climate variability can be approximated by using a post hoc approach to estimate the statistical properties of climate variables from a single run. For example, Jenouvrier et al. (2012, 2014) estimated a smoothed mean and variance from a single run of each climate model, and used these estimated

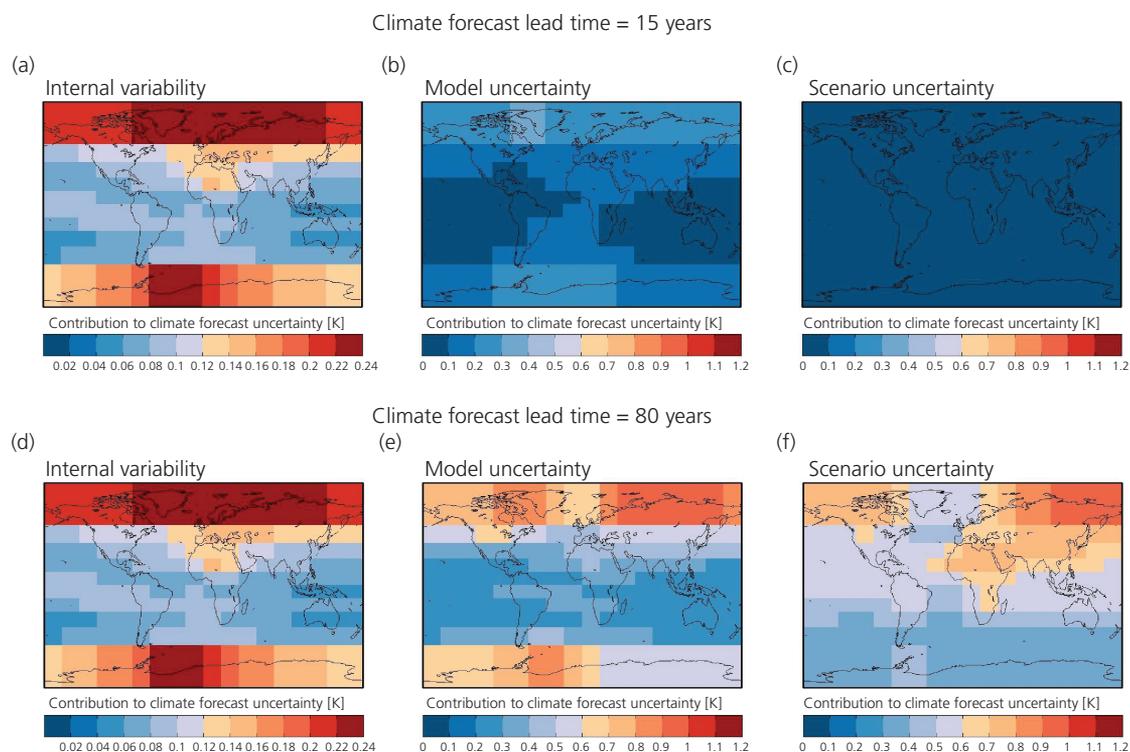


Figure 12.3 Relative sources of uncertainty in forecasts of surface temperature for 15 years into the future (a–c) and 80 years into the future (d–f). Figure is reproduced with permission from the interactive climate uncertainty visualization tool (available at <http://ncas-climate.nerc.ac.uk/research/uncertainty>), as described in Hawkins and Sutton (2009).

parameters to generate repeated stochastic simulations of climate for each model.

Climate models contributing to IPCC projections are produced by over 20 different research groups from institutions across the world. There is no ‘best’ climate model; rather, models produced by each group differ slightly in their biases, inclusion of particular physical processes, and numerical approximations (Knutti et al. 2013). Differences between these models give rise to ‘model uncertainty’ in climate projections. This source of uncertainty can be substantial for both short- and long-term climate projections (Hawkins and Sutton 2009). Quantification of model uncertainty requires simulating future climate using multiple models. Furthermore, models differ in their ability to recreate particular aspects of historical climate. Thus, it is often prudent to select a subset of models that are known to reproduce the climate variables of interest (Jenouvrier 2013; Snover et al. 2013) or perform various model selection methods (Jenouvrier et al. 2017). Notably, selection of climate models can strongly influence population forecasts (Figure 12.1), and formal methods for climate model selection for ecological forecasting remains an active area of research.

Uncertainty in future greenhouse gas concentrations are encapsulated by four representative concentration pathway (RCP) scenarios in the fifth IPCC report (van Vuuren et al. 2011). Each scenario represents a different ‘plausible future’, depending on socioeconomic change, technological innovation, land use modification, and carbon emissions. This source of uncertainty is negligible in short-term climate forecasts because near-term emissions are similar under any plausible future. Yet, scenario uncertainty (along with model uncertainty) dominates long-term climate forecasts (Hawkins and Sutton 2009). Scenario uncertainty can be quantified by comparing forecasts from multiple RCPs or earlier equivalents, such as the A1, A2, B1, and B2 scenarios from the Special Report on Emissions Scenarios used in the fourth IPCC report.

Population models rely on (often noisy and biased) data to derive statistical relationships between vital rates and climate variables. Sampling variation and imperfect detection of individuals can introduce substantial bias and noise into raw data, which must be corrected statistically. The goal of demographic

analysis is to remove these sources of spurious error and generate estimates of true population parameters, such as numbers of individuals, current structure of the population, parameters describing vital rate distributions, relationships between vital rates and environmental variables (e.g., climate effects and density-dependence), and unexplained ‘residual’ variation in (and covariation among) vital rates. As with uncertainty in climate forecasts, each source of demographic uncertainty contributes differently to population forecasts (Figure 12.4).

In general, the effect of initial condition uncertainty, owing to imperfect knowledge of population sizes or structure, will depend on the details of the population model. For example, the effect of uncertainty in initial population abundance (Figure 12.4b) will depend on population growth rates (uncertainty in abundance will compound faster when population growth rates are high), whether population dynamics are density dependent (and how fast carrying capacity is reached), and whether population dynamics are chaotic or internally stable. Similarly, uncertainty in initial population structure will generate higher forecast uncertainty if populations are capable of more extreme transient dynamics. However, the effect of uncertainty in initial population structure may only manifest after a certain amount of time, depending on the nature of transient dynamics (Figure 12.4c).

Uncertainty in estimates of vital rate parameters, their relationships with environmental variables (e.g., climate, habitat, other species, etc.), or the effect of density dependence upon them is grouped under parameter uncertainty. Parameter uncertainty compounds over time (Figure 12.4d) and often dominates uncertainty in long-term demographic forecasts. For example, Gauthier et al. (2016) forecasted the abundance of greater snow geese under future climate change. At 40 years in the future, almost 90 per cent of prediction variance was due to parameter uncertainty. Fortunately, this source of uncertainty can be reduced by collecting more data, which in turn, can generate more precise parameter estimates.

Process variance (sometimes called process error) is the residual (co)variance in vital rates that is not explained by explicit variables. Vital rate (co) variation generates stochastic population dynamics (Figure 12.4e), which have been the subject of much

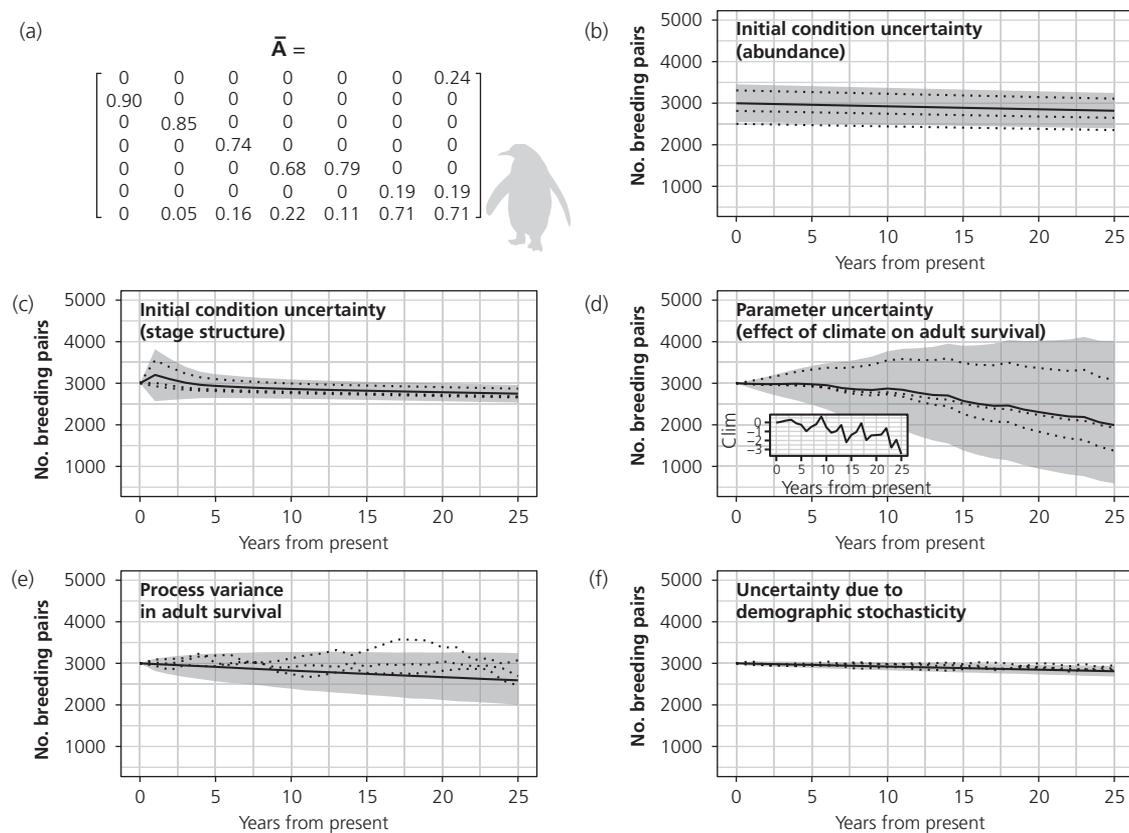


Figure 12.4 Sources of demographic uncertainty and resulting patterns of error propagation for a hypothetical emperor penguin population forecast. (a) Matrix model and mean vital rates were adapted from Jenouvrier et al. (2005a). (b) to (f) illustrate the uncertainty in population forecasts resulting from different sources of uncertainty in the model, but perfect knowledge of all other parameters, including initial population structure. (c) Uncertainty in initial population structure, but perfect knowledge of initial total abundance. (d) Uncertainty in the linear relationship between adult survival and a climate variable, but assuming perfect knowledge of future climate. (e) Process variance in adult survival, modelled as a logit-normal process with no temporal autocorrelation. (f) Demographic stochasticity; treating survival and breeding probability as binomial processes, and fertility as a Poisson process. Black line depicts median estimate, grey ribbons depict 95% credible envelope. Dotted lines depict three separate realizations of the population model.

theoretical study (Lande 1993; Doak et al. 2005). It is now well appreciated that process (co)variance in vital rates can strongly influence population growth. Like parameter uncertainty, process variance compounds over time. However, unlike parameter uncertainty, process variance does not decline with larger sample sizes; rather, process variance can only be reduced by including better explanatory covariates for vital rates. Che-Castaldo et al. (2017) detected extremely high process variance in local population growth rates of Adélie penguins, precluding accurate short-term forecasts. Yet, this source of uncertainty could be ameliorated by aggregating abundance

over larger spatial extents (i.e., across multiple sub-populations).

Demographic stochasticity introduces uncertainty into forecasts by applying probabilistic vital rates to discrete numbers of individuals; ultimately, this represents a biological consequence of sampling variation in vital rates. When populations are large, uncertainty due to demographic stochasticity is negligible (Figure 12.4f). However, demographic stochasticity can exert an overwhelming influence on small populations, leading to ‘chance extinctions’ in otherwise viable populations (Lande 1993; Lande et al. 2003; Iles et al. 2016).

12.4 Current state of science and roadmap for the future

12.4.1 Literature search for IPCC-dependent avian population forecasts

We conducted a literature search to compile a list of studies that have made avian population projections by coupling demographic models with IPCC projections. Using the Web of Science search engine, we searched for all papers with topics: (*bird** OR *avian*) AND (*population** OR *abundan** OR *demograph** OR *vital rate**) AND (*ensemble** OR *climat** OR *GCM** OR *IPCC* OR *climate chang** OR *AR5* OR *AR4* OR *RCP** OR *SRES*) AND (*project** OR *forecast**). We included several other relevant studies we knew of that were not returned by this search. We also searched all papers that had cited any of the suitable studies we located. We only included studies that estimated explicit relationships between vital rates and climate variables, fused these with IPCC-class projections of future climate change, and projected population abundance (step 3; Jenouvrier 2013). We omitted studies that used population models to project long-run dynamics under a hypothetical stationary future climate (van de Pol et al. 2010; Dybala et al. 2013; Pardo et al. 2017), though such studies are extremely useful for understanding the pathways through which climate affects overall population dynamics (step 2, Jenouvrier 2013; Jenouvrier et al. 2018b).

In total, we found 18 studies that met our criteria for inclusion (Table 12.1). These studies projected the future abundance of 24 avian species. Of these, only three species were projected to increase in abundance under future climate change: Amsterdam albatross (*Diomedea amsterdamensis*; though this population is increasing under current climate conditions), greater snow goose (though forecasts were highly uncertain by 2050), and white-throated dipper (*Cinclus cinclus*). Conversely, declines in abundance were projected for at least 15 species under mid- to high-emissions scenarios. For the remaining species, populations are projected to remain approximately stable (e.g., American wigeon, *Mareca americana*; greater and lesser scaup *Aythya marila* and *A. affinis*, respectively) or forecasts are equivocal

owing to different projections among studies (e.g., mallard, *Anas platyrhynchos*) or high forecast uncertainty (wood thrush, *Hylocichla mustelina*).

12.4.2 Roadmap for future research

We focus the remainder of this chapter on the strengths and commonalities among existing avian population projections, while highlighting ongoing challenges and future opportunities. Our goal is not to criticize previous studies, but rather to contextualize existing forecasts and provide a roadmap for future work. Forecasting is an inherently iterative process, benefiting from continuous model assessment and refinement (Dietze et al. 2018).

Age-structure and breeding stage was commonly accounted for in population forecasts (14/18 studies), often by using matrix modelling approaches (Caswell 2001). This reflects the strong body of age- and stage-structured demographic information in ornithology. Spatial structure was considered in eight studies, either by allowing for spatial differences in the amount of future climate change (Jenouvrier et al. 2014), explicitly incorporating dispersal among sub-populations or habitats (Aiello-Lammens et al. 2011; Harris et al. 2012; Bonnot et al. 2017; Jenouvrier et al. 2017), or less frequently, by estimating spatial differences in population responses to climate (Drever et al. 2012; Peery et al. 2012; Zhao et al. 2016). Future research will benefit from examining the effects of individual heterogeneity on climate sensitivity (e.g., owing to differences in body size, individual behaviours, or latent factors). In particular, one promising avenue is the use of finite mixture models to account for unobserved individual heterogeneity in vital rates (Hamel et al. 2017; Jenouvrier et al. 2018a), and to capture latent spatial variation among individuals (Guéry et al. 2017).

Studies varied widely in the sources of climate forecast uncertainty they included (Table 12.1; Figure 12.5), indicating a need for increased consistency in future studies. Internal variability in climate models was rarely incorporated, either by initiating the same climate models with multiple initial conditions, or by generating stochastic climate forecasts from statistical summaries of a single climate model. Conversely,

Table 12.1 List of studies that forecasted avian responses to climate change by explicitly coupling IPCC-class climate simulations with population models. Study species correspond to AOU codes (where applicable). Lead time describes time horizon of forecast. Uncertainty abbreviations are: internal climate variability (CIn), climate model uncertainty (CMo), climate scenario uncertainty (CSc), demographic parameter uncertainty (DPar), demographic process variance (DProc), uncertainty in initial population abundance (PAb), uncertainty in initial population stage structure (PSt), and uncertainty due to demographic stochasticity (DSto). **Bold/underline** indicates source of uncertainty was explicitly included in model.

| Study | Species | Lead time | Spatial extent | Climate variables | Population structure | Uncertainties included | Projected effect of climate change |
|------------------------------|-------------------------------------|------------------|-------------------------------------|--------------------------------------|--------------------------------------|--|---|
| 1 Aiello-Lammens et al. 2011 | SNPL | 2010–2100 | Florida, USA | Sea Level | Stage, Sex, Spatial (with dispersal) | CIn, CMo, CSc , DPar, DProc , PAb, PSt, DSto | Increased risk of population decline and quasi-extinction under 2 m sea level rise |
| 2 Ballerini et al. 2015 | ADPE | 2010–2100 | Ross Sea, Antarctica | Sea Ice Extent | Stage | CIn , CMo , CSc , DPar, DProc , PAb, PSt, DSto | Declines and likely local extinction by 2050 in the absence of immigration, under mid-range emissions scenario (A1B) and other scenarios of increased frequency of extreme events |
| 3 Barbraud et al. 2011 | BBAL, AMAL, SNPE | 2007–2057 | Indian Ocean, Australia, Antarctica | Sea Surface Temp, Sea Ice Extent | Stage | CIn, CMo , CSc , DPar, DProc , PAb, PSt, DSto | Likely extinction of BBAL. Likely increase of AMAL. Declines of SNPE, depending on scenario of climate change |
| 4 Bonnot et al. 2017 | WOTH, PRAW | 2000–2100 | Central USA | Temp, Precip, Wind Speed | Stage Spatial (with dispersal) | CIn, CMo, CSc , DPar , DProc , PAb, PSt, DSto | Slight declines for wood thrush. Severe declines for prairie warbler |
| 5 Drever et al. 2012 | MALL, AMWI, Scaup spp., Scoter spp. | 2020, 2050, 2080 | Boreal forest, North America | Snow cover (spring) | Spatial | CIn , CMo, CSc, DPar, DProc, PAb, PSt, DSto | Possible increase in MALL abundance. Possible decrease in AMWI and scaup abundance. Likely decrease in scoter abundance |
| 6 Gamelon et al. 2017 | White-throated dipper | 2013–2050 | Southern Norway | Temp (winter) | Age Stage | CIn , CMo, CSc, DPar , DProc , PAb, PSt, DSto | Probable increase in abundance |
| 7 Gauthier et al. 2016 | GSGO | 2012–2050 | North America (species range) | Temp (spring and summer) | Age Stage | CIn , CMo , CSc , DPar , DProc , PAb, PSt, DSto | Probable increases under future warming, but low signal-to-noise ratio |
| 8 Harris et al. 2012 | Black-backed cockatoo | 2000–2100 | Kangaroo Island, Australia | Temp (Jan and July), Precip (annual) | Age Stage Spatial (with dispersal) | CIn, CMo , CSc , DPar, DProc , PAb, PSt, DSto | Population increase under current climate. Severe population declines under high emissions |
| 9 Jenouvrier et al. 2009 | EMPE | 1960–2100 | Terre Adélie (Antarctica) | Sea Ice Extent | Age Stage | CIn , CMo , CSc, DPar , DProc, PAb, PSt, DSto | Decline in abundance, high risk of quasi-extinction by 2100 |
| 10 Jenouvrier et al. 2012 | EMPE | 2010–2100 | Terre Adélie (Antarctica) | Sea Ice Conc | Age Stage Sex | CIn , CMo , CSc, DPar , DProc , PAb, PSt, DSto | High probability of decline in abundance by 2100 under mid-range emissions scenario |

Continued

Table 12.1 Continued

| Study | Species | Lead time | Spatial extent | Climate variables | Population structure | Uncertainties included | Projected effect of climate change |
|---------------------------|------------------------|-----------|---------------------------------------|--|--------------------------------------|---|--|
| 11 Jenouvrier et al. 2014 | EMPE | 2010–2100 | All known emperor penguin colonies | Sea Ice Conc | Age Stage Sex | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | Declining population trends for all populations by 2100 under mid-range emissions scenario |
| 12 Jenouvrier et al. 2017 | EMPE | 2010–2100 | All known emperor penguin colonies | Sea Ice Conc | Spatial (dispersal) | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | All populations declining by 2100, regardless of dispersal scenario |
| 13 Liao et al. 2015 | Amakihi, Apapane, Iiwi | 2010–2100 | Hawaiian islands | Temp, Precip | Spatial, Disease-structure | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | Increased warmth and reduced rainfall caused malaria infection of birds, especially at high elevation, leading to decreased population abundance |
| 14 Nur et al. 2012 | SOSP | 2010–2060 | California, USA | Temp, Precip, Sea level, Tide height | Stage | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | Increasing abundance if sea level rise is low-med. Decreasing abundance if sea level rise is high |
| 15 Peery et al. 2012 | SPOW | 2000–2100 | Southwest USA | Temp, Precip | Age Stage Spatial (with immigration) | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | Severe declines in Arizona and New Mexico populations due to climate change |
| 16 Thomson et al. 2015 | SHAL | 2100 | Tasmanian islands | Daily Max Temp, Sea Surface Height, Rainfall | Age Stage Sex | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | Decrease in population abundance under climate warming, especially under hotter A2 scenario |
| 17 Wolf et al. 2010 | CAAU | 2100 | California, USA | Sea Surface Temp, Upwelling | Stage | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | Declines in population growth, owing to negative relationship between SST and breeding/survival, and projected increases in SST (and potential decreases in upwelling) |
| 18 Zhao et al. 2016 | MALL | 2100 | Prairie pothole region, North America | Temp, Precip, Pond Density | Spatial | <u>CIn</u> , <u>CMo</u> , <u>CSc</u> , <u>DPar</u> , <u>DProc</u> , <u>PAb</u> , <u>PSt</u> , <u>DSto</u> | Declines in Mallard density under future warming (4°C) |

climate model uncertainty was commonly considered in forecasts, either by using model-averaged climate projections, or less commonly, by conducting population forecasts using multiple climate models (though only the latter approach provides a stochastic climate-dependent projection and allows for uncertainty due to internal climate variability to be fully propagated to forecasts). Scenario uncertainty was considered in about half the studies, by evaluating population responses under multiple emissions scenarios. When not included, studies invariably chose a mid-range emissions scenario for climate projection. We urge ecologists to take advantage of the free availability of climate forecasts supervised by the Coupled Model Intercomparison Project (<https://www.wcrp-climate.org/wgcm-cmip/wgcm-cmip6>), allowing a full integration of all three sources of climate forecast uncertainty. The most recently completed phase of the project (CMIP5) includes more climate models and output variables than previous phases, and importantly, includes several runs of the same AOGCMs and experiment. This allows for uncertainty due to internal variability in climate models to be more fully incorporated into ecological projections.

Studies also varied widely in the sources of demographic uncertainty they included (Table 12.1; Figure 12.5). Uncertainty in demographic parameters (including vital rate responses to climate) was

explicitly propagated to forecasts in less than half of the studies. We flag this as an important area of improvement for future research. Parameter uncertainty compounds over time in forecasts and is often the dominant source of forecast uncertainty at long timescales (Gauthier et al. 2016; Dietze 2017b). Failure to account for this source of uncertainty results in highly overconfident end-of-century forecasts. It is therefore likely that many of the forecasted population declines in our literature search are less certain than reported.

Demographic process variation (i.e., residual variation in vital rates not explained by climate) was included in almost all studies, likely because vital rate (co)variation and its consequences have a rich tradition in the study of wildlife population ecology (Tuljapurkar 1990; Caswell 2001; Doak et al. 2005). Demographic stochasticity was only included in five studies; most forecasted populations were large enough that the effects of demographic stochasticity are negligible and were thus explicitly omitted (Jenouvrier et al. 2009, 2012, 2014; Barbraud et al. 2011; Gauthier et al. 2016). Yet, the role of demographic stochasticity increases as population abundance declines, which could compound the negative effects of climate change documented by several studies. The inclusion of demographic stochasticity in forecasts may, therefore,

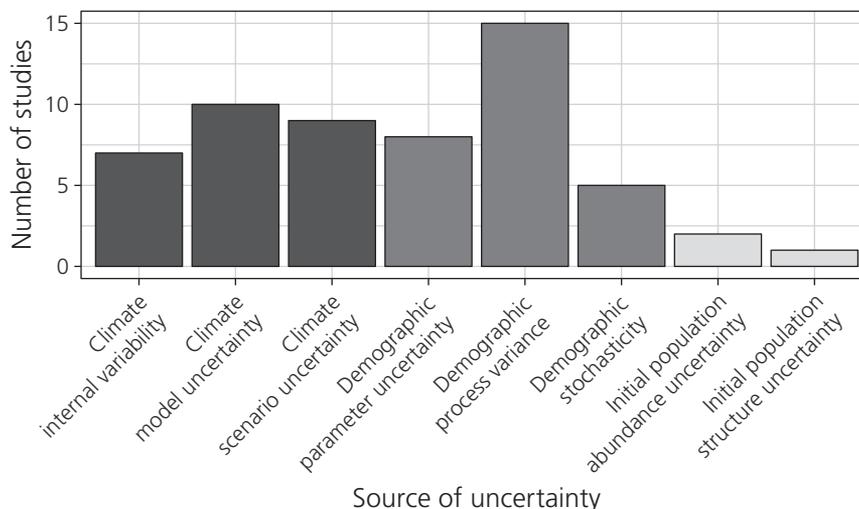


Figure 12.5 Sources of forecast uncertainty explicitly included in climate-dependent avian population forecasts (based on Table 12.1).

be especially important for populations that experience strongly negative effects of projected climate change.

The effect of uncertainty in initial population size was only considered in two studies (Harris et al. 2012; Gamelon et al. 2017), and uncertainty in initial (st)age structure was considered in one (Gamelon et al. 2017). Uncertainty in the initial sex or spatial structure of populations was not considered in any forecasts. Instead, forecasts were often initiated at the long-term stable (st)age distribution. For end-of-century forecasts, these sources of uncertainty are likely negligible relative to climate and parameter uncertainty. However, initial condition uncertainty (in both climate and population state) dominate near-term forecast uncertainty. Near-term forecasting is emerging as an important paradigm with high relevance to dynamic management and decision support (Harris et al. 2018; Humphries et al. 2017; Dietze et al. 2018). While all of the studies in our literature search focused on long-term responses to climate change (i.e., by 2100), we expect that near-term forecasts will become increasingly common over the next decade.

Methods to fully incorporate and partition forecast uncertainties are more accessible than ever (Dietze 2017a, b). Comparative studies will be invaluable for elucidating the dominant sources of uncertainty in population forecasts and how these vary across spatial and temporal scales, among life histories, and between study systems. Accordingly, comparative uncertainty analysis will be critical for guiding management and prioritizing monitoring efforts under climate change.

Other challenges also remain. Many species and populations are considered too data-deficient to assign IUCN Red List status, indicating a critical lack of basic knowledge about population size, trends, and distribution (Butchart and Bird 2010). For a larger number of species, a better understanding of the full life cycle and how it is affected by climate is needed. Well-studied populations will primarily benefit from work aimed at identifying better predictors of population responses that are matched with the scale of climate projections. In parallel, the spatial resolution of climate models is unlikely to improve substantially in the near term. Improved methods for downscaling coarse-grained

climate projections may thus be important for generating local-scale predictions of climate, especially in cases where climate at larger spatial scales is not ecologically relevant (Snober et al. 2013).

Finally, eco-evolutionary processes (Chapters 7 and 11) and species interactions (Chapter 15) are critical determinants of future population responses to climate change, though including these processes in population forecasts remains a substantial challenge. Recent studies have identified considerable latent differences among individuals within a population (i.e., unobserved individual heterogeneity), both in terms of life history traits (Jenouvrier et al. 2015; Jenouvrier et al. 2018a) and responses to climate (Guéry et al. 2017). If these differences are genetically determined, individual heterogeneity forms the basis for evolutionary change. Yet, pedigrees are poorly resolved or non-existent in most populations, resulting in large uncertainties in trait heritability. Species interactions can also strongly modify demographic responses to climate (e.g., Ockendon et al. 2014; Liao et al. 2015; Iles et al. 2018). Multi-species population forecasts, especially across trophic levels, are thus an important area of continued research.

12.5 Conclusions

Population forecasting is a nascent discipline compared to the large body of literature on avian natural history, climate impacts, and demography. Despite the large body of literature on the impact of climate on vital rates, there are surprisingly few studies that have developed climate-dependent population models, and even fewer studies linking these population models to climate forecasts from IPCC-class models (to date, only 17 studies to our knowledge). Yet, the increasing sophistication and number of climate models (Chapter 2) and numerous studies of climate impacts on bird demography (Chapters 7 and 11) now allow for building population forecasts under climate change with uncertainties fully specified. Because forecasting is a process that requires iterative model building, performance assessment, and model correction (Dietze et al. 2018), we strongly encourage ecologists to take advantage of the tools and data currently available for this task.

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