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Accounting for sources of uncertainty when forecasting population responses to climate change

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Abstract

In Focus: Jaatinen, K., Westerbom, M., Norkko, A., Mustonen, O., & Koons, D. N. (2021). Detrimental impacts of climate change may be exacerbated by density-dependent population regulation in blue mussels. *Journal of Animal Ecology*, *90*, 562–573, https://doi.org/10.1111/1365-2656.13377. Conservation strategies for threatened species are increasingly dependent on forecasts of population responses to climate change. For such forecasts to be accurate, they must account for multiple sources of uncertainty, including those associated with projections of future climate scenarios and those associated with the models used to describe population dynamics. While many population forecasts incorporate parameter uncertainty in abiotic effects and process variance related to unexplained temporal variation, most forecasts overlook the importance of evaluating uncertainty in the structure of the population model itself. By accounting for structural uncertainties in a model of population growth for blue mussels, Jaatinen et al. (2021) demonstrated that density-dependent processes are likely to exacerbate adverse effects of climate change and reduce population viability of this keystone species. These findings highlight the importance of incorporating structural unknowns in population forecasts and the value of approaches that account for multiple sources of climate and model uncertainties. Forecasts that capture a range of possible population trajectories under climate change will help ensure efficient allocation of limited conservation resources.

KEYWORDS

climate projections, density dependence, population forecasts, population growth, uncertainty

Earth's climate is rapidly changing in response to anthropogenic pressures and these climatic changes are expected to continue, and possibly accelerate, over the next century (IPCC, 2014). Understanding how climate change is impacting—and will impact—wildlife species is essential to develop effective conservation strategies. Ecologists increasingly rely on models to forecast (i.e. estimate the future state of) populations in response to potential changes in climate over the near and long term (Dietze, 2017). While the structure and complexity of these models can vary greatly depending on species characteristics and data availability, the accuracy of such predictive models fundamentally depends on two things: (a) the projected values of biologically relevant climate variables at appropriate spatial and temporal scales; and (b) retrospective analyses that characterize the effects of climate (as well as other abiotic and biotic factors) on demographic rates, population abundance and/or rates of population change. Wildlife population forecasts involve numerous sources of uncertainty that are associated with both climate projections and models of population dynamics (Figure 1). Failing to account for these uncertainties can result in biased or misleading forecasts, potentially leading to inefficient allocation of limited conservation resources.

Climate projections can range from relatively simple and deterministic predictions (e.g. percent change in weather variables, such

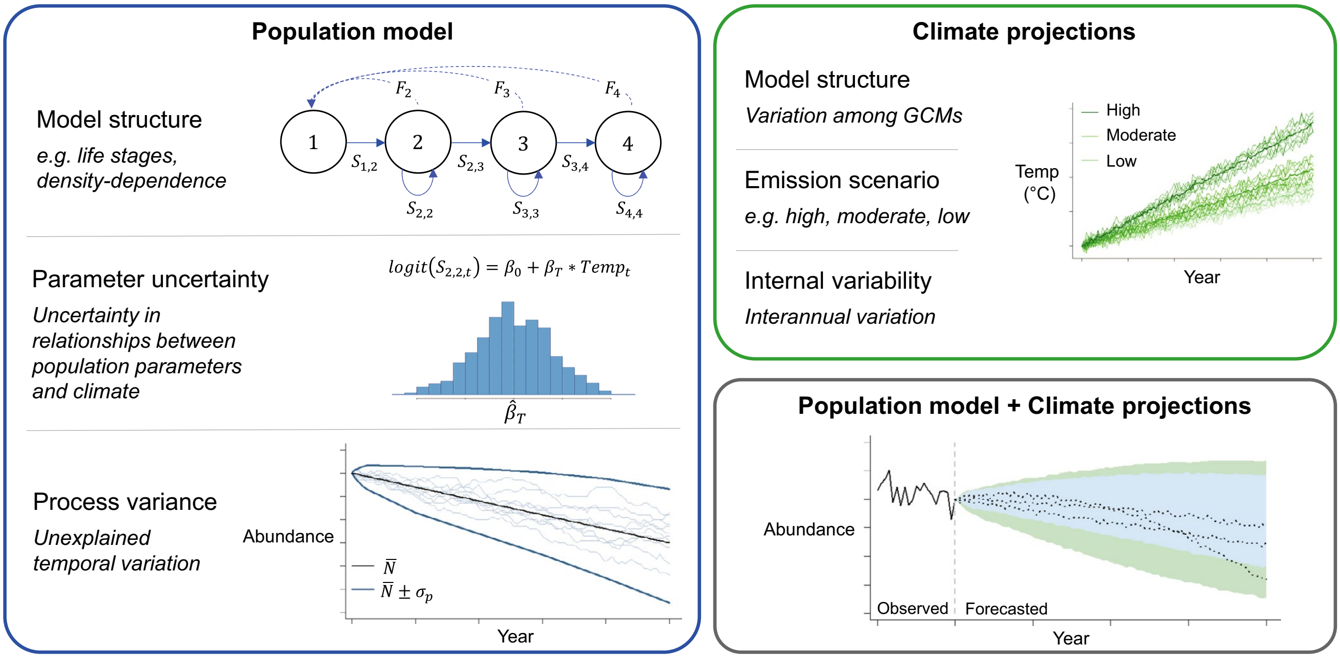

FIGURE 1 Sources of uncertainty in climate-dependent population forecasts. We highlight three sources of uncertainty associated with models used to describe and forecast population trajectories (left): (1) assumptions about population structure and processes driving population change (model structure), (2) uncertainty associated with relationships between population parameters and climate (parameter uncertainty) and (3) temporal variation in population parameters beyond that explained by climate and other factors in the model (process variance). In the left panel, F = stage-specific fecundity; S = stage-specific survival; β_0 = mean survival (on the logit scale); β_T = the effect of temperature (Temp) on survival; N = mean abundance; and σ_p = process variance (unexplained temporal variation in abundance). We also highlight three sources of uncertainty associated with climate projections (top right): (1) variation among global circulation models (model structure), (2) uncertainty about future greenhouse gas emissions (emission scenario) and (3) inter-annual variation in weather (internal variability). Reliable forecasts of wildlife populations rely on methods that can account for these varied sources of uncertainty (bottom right; with blue- and green-shaded areas representing the proportion of total uncertainty associated with population model- and climate-related sources respectively). Failing to account for uncertainties in population forecasts can result in biased inferences and overly confident predictions about how populations are likely to respond to future changes in climate

as temperature or precipitation) to stochastic projections generated from IPCC-class General Circulation Models (GCMs). The availability of fine-scale climate projections has increased considerably with recent advances in climate science, enabling population forecasts to partition climate uncertainty into that associated with structural differences among climate models, future greenhouse gas emission scenarios and inter-annual fluctuations in weather (Figure 1; Hawkins & Sutton, 2009; Knutti & Sedláček, 2013). The relative importance of these sources of uncertainty varies with the spatial and temporal scales of prediction. While inter-annual fluctuations (i.e. internal variability) can be a large source of uncertainty for regional projections of climate over the near term, its importance is overshadowed by uncertainty associated with model structure and emission scenarios over longer time horizons (Gauthier et al., 2016; Hawkins & Sutton, 2009; Iles & Jenouvrier, 2019).

The second factor influencing accuracy and precision of population forecasts is the ability to understand and characterize how abiotic conditions and biotic interactions influence the population dynamics of a target species. Demographic rates, and consequently population abundance, can vary immensely from one year or season to the next. Much of the uncertainty in population forecasts results from an incomplete understanding of the relative importance and interactions among abiotic factors (e.g. climate) and biotic factors (e.g. density dependence; Coulson et al., 2001; Grøtan et al., 2009). Two sources of uncertainty that are frequently included in population forecasts are parameter uncertainty (statistical uncertainty in the relationships between population parameters and abiotic variables) and process variance (unexplained temporal variation in population parameters beyond that explained by variables in the model; Gauthier et al., 2016; Jenouvrier, 2013; Zhao et al., 2019; Figure 1). Jaatinen et al. (2021) accounted for an important, yet often overlooked, source of uncertainty: the structure of the population model.

Population growth models can take a number of forms, depending on a species' life history and the quantity and quality of data available to inform model parameters. For many long-lived vertebrates, ecologists can estimate rates of survival, growth or reproductive output using individual-based measures. Demographic rates can be modelled as a function of climatic variables (as well as other factors), and these climate-dependent measures can be used in stage- or age-based projection models to forecast population abundance or growth rates under different climate change scenarios (e.g. Gamelon et al., 2017; Hansen et al., 2019; Nater et al., 2018). When demographic data are available, forecasts can, and should account for uncertainty about population structure, initial population size, and in a metapopulation context, dispersal among local populations (Iles & Jenouvrier, 2019; Jenouvrier et al., 2020). For other species, like the blue mussels *Mytilus trossulus* described in Jaatinen et al. (2021), it is impossible to track individuals and estimate demographic rates. In these instances, time series of abundance can be used to understand how population density, in addition to abiotic factors, drive changes in population size. Density-dependent processes are known to be important mechanisms driving rates of population change when species depend on one or more limited resources (Turchin, 1995). For many sessile species, such as mussels, competition for both space and food can lead to decreased growth and survival rates (Fréchette et al., 1992; Strayer et al. 2020). Although many retrospective analyses have explored density-dependent processes, few studies have accounted for uncertainty about the strength and form of density dependence in population forecasts (but see Colchero et al., 2009; Reed et al., 2013) or assessed how interactions between population density and climate could affect future population trajectories.

Jaatinen et al. (2021) monitored population densities of blue mussels at six locations off the southern coast of Finland over a 17-year period. They used these data to explore how sea surface temperature and salinity, along with density-dependent processes, affected population dynamics of the keystone species. Both temperature and salinity had strong impacts on mussel populations, but the negative effects of temperature were less severe than expected when population densities were high. Jaatinen et al. (2021) then projected how mussel populations are likely to respond to future increases in temperature and decreases in salinity, exploring a range of values inspired by regional climate projections from an ensemble of GCMs (Meier et al., 2012). The forecasts accounted for many sources of uncertainty: emission scenarios (in a simplified way, with trends in mean salinity and temperature values), parameter uncertainty (using samples from Bayesian posterior distributions) and process variance. They also accounted for uncertainty in the structure of the population model. Specifically, they estimated the probability of population declines under different models of population growth (no density dependence, a density-dependent [Ricker] model with additive climate effects and a density-dependent [Ricker] model that included interactions between population density and climate; Dennis et al. 2006).

This exploration of the different ways in which density-dependent processes could affect population forecasts of blue mussels provided insights that would have been overlooked had analyses simply relied on the best-supported model for population forecasts. Retrospective models had provided evidence that interactions between temperature and density could buffer the population against severe drops in growth rates when densities and temperatures were very high (Jaatinen et al., 2021: Fig. 4). However, comparisons of population forecasts under different density-dependent assumptions demonstrated that when all factors were taken into account, density-dependent mechanisms exacerbated adverse effects of climate change and reduced population viability (Jaatinen et al., 2021: Fig. 6). The extent to which density-dependent processes exacerbate negative effects of climate, as they did in blue mussel populations, or mediate climate change effects via compensatory increases in population growth rates (e.g. as in Nater et al., 2018; Reed et al., 2013) is an emerging field of research. Jaatinen et al.'s (2021) approach could be used in analyses of other species to evaluate the extent to which species traits and/or environmental conditions influence the outcome of interactions between density-dependent processes and climate variables.

The ability to accurately forecast future population states under climate change is rapidly improving as a result of advances in climate science and population modelling, as well as recent surges in the quantity and types of data available on wildlife populations. Population forecasting efforts should aim to infuse mechanism whenever possible. Even when demographic data are not available, population models could account for density-dependent effects (as Jaatinen et al. 2021 did) or use count data to characterize underlying demographic processes (Dail & Madsen, 2011; Zipkin et al., 2014). Yet, increased model complexity may not always improve population forecasts, and could even *decrease* the accuracy of forecasts if responses to abiotic factors are sufficiently variable across time or space (Rollinson et al., 2021). Acknowledging structural uncertainties and potential sources of spatiotemporal variation, however, allows managers and policymakers to make well-informed, data-driven conservation decisions.

Population dynamics are driven by a multitude of biotic and abiotic factors. While we can never identify and describe all the ways in which these factors influence changes in population sizes, it is critical that forecasts account for structural uncertainties in population processes and adequately acknowledge what is less certain and what is unknown. Accounting for multiple sources of uncertainty ensures that population forecasts reflect the full range of possible outcomes under climate change, providing unbiased assessments to inform conservation strategies for imperiled species.

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AUTHORS' CONTRIBUTIONS

E.R.Z. and E.F.Z. co-wrote the article.

DATA AVAILABILITY STATEMENT

There are no data associated with this manuscript.

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