












## SYNTHESIS OPEN ACCESS

# Linking Climate and Demography to Predict Population Dynamics and Persistence Under Global Change

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## ABSTRACT

Predicting the effects of climate change on plant and animal populations is an urgent challenge for understanding the fate of biodiversity under global change. At the surface, quantifying how climate drives the vital rates that underlie population dynamics appears simple, yet many decisions are required to connect climate to demographic data. Competing approaches have emerged in the literature with little consensus around best practices. Here we provide a practical guide for how to best link vital rates to climate for the purposes of inference and projection of population dynamics. We first describe the sources of demographic and climate data underlying population models. We then focus on best practices to model the relationships between vital rates and climate, highlighting what we can learn from mechanistic and phenomenological models. Finally, we discuss the challenges of prediction and forecasting in the face of uncertainty about climate-demographic relationships as well as future climate. We conclude by suggesting ways forward to build this field of research into one that makes robust forecasts of population persistence, with opportunities for synthesis across species.

## 1 | Introduction

Climate is a key limiting factor of the distribution and abundance of species. With unprecedented and rapid changes to

climate, the challenge of predicting species' responses to climate change is ever more urgent. Ecologists are increasingly called upon to predict the fates of local populations and entire species—are they likely to go extinct if they are currently rare,

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become rare if they are currently common, or become more challenging management problems if they are pests? Meeting this challenge requires the ability to project changes in abundance and distribution in response to changes in key climate drivers. Such changes ultimately reflect how climate drivers, through their direct and indirect effects, influence rates of births, individual growth and deaths. Thus, population biology provides a robust framework and tools for predicting the impacts of climate change on biodiversity.

In principle, characterising population-level responses to climate appears straightforward. When there is information on how individual-level vital rates (e.g., survival, growth, reproduction, also called ‘demographic rates’) are influenced by climate, we can build environment-dependent demographic models that explicitly incorporate hypothesised climate drivers. For example, matrix or integral projection models can use seasonal temperature or snow melt date as predictors of vital rates, leading to inference of how climate affects population growth and viability. Climate-explicit demographic models are thus multiple models in one: the process model of population dynamics that describes how individuals move through their life cycle via recruitment, survival, growth and reproduction, and the empirical sub-models that describe how these vital rates depend on climate drivers, with the latter often in the form of statistical regressions. With such models, we can project how population dynamics will change in the face of forecasted climate change (Fordham et al. 2013; Williams et al. 2015; Iler et al. 2019; Ozgul et al. 2023; Félix-Burrue et al. 2025; Anderson et al. 2025). In practice, however, numerous factors related both to the processes being modelled and methodological choices turn this seemingly straightforward approach into a more complex series of decisions. Here, we explore these decisions and their implications, and offer practical guidance. We argue that, even amid emerging challenges, identifying the climate drivers of demography is tractable, and building forecasts based on these inferences is necessary and worthwhile.

Environment-dependent demographic models have a long history in ecology, though until recently, environmental drivers have typically been modelled implicitly. For example, classic theory for population dynamics in variable environments describes how a distribution of environmental states affects vital rates and fitness (Lewontin and Cohen 1969; Tuljapurkar 1989). This classic theory has led to approaches that provide a useful way to understand population viability when vital rates fluctuate, without assigning the cause of fluctuations (Crone et al. 2011; Fowler et al. 2024). However, while environment-implicit approaches may be useful to describe population dynamics in a variable but stationary environment, they are limited in their ability to forecast responses to directional environmental change (Ehrlén and Morris 2015). Achieving the latter requires a transition from implicit to explicit treatment of environmental drivers, where the causal effect of climate variables is articulated through statistical modelling.

Over the last two decades, researchers have started to more explicitly model environmental drivers of vital rates (Coulson et al. 2001; Adler and HilleRisLambers 2008; Williams et al. 2015), a departure from earlier approaches that sought to decipher climate signals from time series of abundance data

(reviewed in Turchin 2013). Explicit consideration of vital rates, which have a more direct physiological connection to environmental conditions than abundance, allows one to examine the demographic mechanisms through which climate variation affects populations, and to identify how climate differentially affects vital rates. Doing so is particularly important given that covariance between vital rates may buffer or exacerbate the impact of environmental variation (Doak et al. 2005). Yet even among studies that employ a bottom-up demographic approach linking climate to vital rates, competing methods have emerged in the literature with little consensus around best practices.

Therefore, our aim is to provide a practical guide for forecasting population dynamics under climate change through environment-explicit demographic modelling. We first consider how empiricists generate or derive data for the underlying components of these models: demographic data and hypothesised climate drivers. We then present an overview of how vital rates can be linked to climate, highlighting what we can learn about responses to past, present and future climate from a spectrum of models ranging from mechanistic to phenomenological. We also discuss how these models can be used to understand and to make predictions with respect to climate variation across time and space. Finally, we dive into the challenges of prediction and forecasting in the face of uncertainty about current climate-demography relationships as well as future climate change, and provide recommendations for ways forward.

## 2 | What Goes Into a Climate-Explicit Demographic Model?

### 2.1 | Demographic Data

Any climate-demography relationship must be defined using data that captures variation in demographic performance in parallel with variation in one or more climate variables that are known or hypothesised to be drivers of demography. Demographic performance is often measured through direct observation of individual-level survival, growth, reproduction and recruitment. For sessile organisms, these data are typically collected by tagging individuals and following them through time or, for mobile organisms, through mark-recapture methods. Vital rates can also be estimated through inverse modelling from changes in population abundance and structure (Félix-Burrue et al. 2021; Paniw et al. 2023; Malchow et al. 2023), or from biogenic time series such as those captured in annual rings of trees, bivalve shells and fish otoliths (Morrongiello et al. 2012; Evans et al. 2021). Through any means, demographic data are time- and labour-intensive to collect. As a consequence, there is abundant demographic data for relatively few species, usually only over a few years and in relatively localised areas, and mostly in temperate zones (Estes et al. 2018; Römer et al. 2024).

A full demographic model accounting for all components of the life cycle is essential for understanding and then predicting population dynamics, and maximises insights gained from how individual vital rates respond to climate drivers. This is because individual vital rates, as well as the same vital rate at different life stages or ages, can make different contributions to population growth and fitness (quantified by sensitivities or elasticities).

Individual vital rates may also covary positively or negatively across environmental gradients due to intrinsic physiological trade-offs or unique responses to exogenous drivers (Knops et al. 2007; Compagnoni et al. 2016). For example, negative effects of warming on survival and recruitment of alpine plants were compensated for by positive effects on growth (i.e., ‘demographic compensation’), buffering the decline in fitness across geographic variation in temperature (Doak and Morris 2010). For these reasons, the effects of climate on single vital rates may paint an incomplete and possibly misleading picture about how changes in climate affect population viability (Iler et al. 2019). There may be contexts in which it is valuable to focus on the climate drivers of only one vital rate when vital rate data are not available for the entire life cycle. For example, long time series of tree ring widths provide rich insight into climate drivers of tree growth (Fritts 1976; Clark et al. 2021), but they are typically not accompanied by information on survival, reproduction and recruitment, unless sampled in a forest plot-based monitoring context (Heilman et al. 2022).

## 2.2 | Climate Data

The climate data that can be linked to vital rates take many forms, but will generally relate to or derive from temperature and precipitation. We use ‘climate’ to refer to long-term properties of temperature and precipitation distributions, such as means, variances and auto-correlation, as being distinct from ‘weather’, the short-term realisation of climate. Climate-demography relationships are typically estimated from weather data during the approximate times and places of demographic observations. For most ecological applications, weather data are directly recorded by instrumentation such as nearby weather stations or on-site sensors, or interpolated via climate model ‘downscaling’ to generate inferred weather histories at high spatial and temporal resolution. Through the availability of data products like PRISM, ClimateNA (Wang et al. 2016), CHELSA (Karger et al. 2017) and WorldClim (Fick and Hijmans 2017), downscaled weather data are now available for much of the terrestrial biosphere dating back decades or centuries—an innovation from climate science that is transforming ecology. Downscaled data capture regional trends in weather station data, usually located at 2 m height (Wang et al. 2016). However, plants and other sessile organisms respond directly to the climate they experience near the ground, which can differ from data collected above 2 m due to buffering from other organisms and differences in wind due to surface roughness (Scherrer and Körner 2010; Christiansen et al. 2024). Choosing the spatial scale of weather data relative to demographic observations is an important step, as fine-scale microsite conditions may be strongly predictive of demography but difficult to forecast, while regional conditions may have robust forecasts but correspond only loosely to the realised environment of the focal organism; this choice is therefore best informed by the aims of the study.

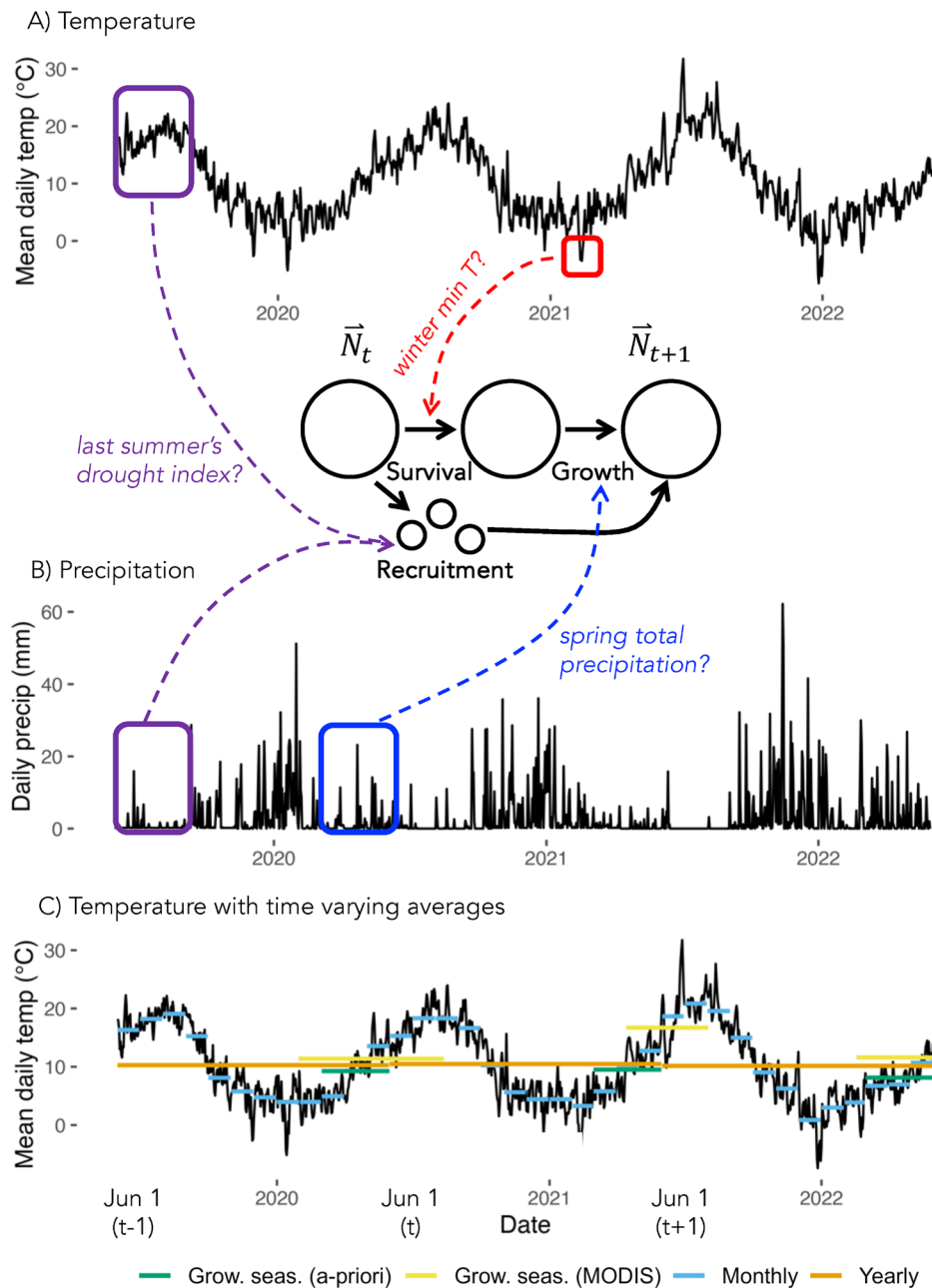
Whether downscaled or measured locally, weather data typically come in the form of time series of temperature and precipitation that may have a temporal resolution as fine as minutes, hours, days or months, depending on the source. Demographic data are usually collected at coarser temporal resolutions, typically annually (but see Shriver 2016). This mismatch of

temporal scale therefore requires decisions about whether and how to collapse or aggregate the weather time series to match the temporal resolution of demographic responses (Figure 1). Direct summaries include taking the mean, variance or minimum/maximum of temperature or precipitation, which can be applied annually or seasonally (Figure 1), in addition to using the duration of time that conditions were below or above certain climate thresholds (e.g., growing degree days or freezing degree days). Alternatively, multivariate approaches such as principal components analysis (PCA) can be used to integrate multiple climate variables, or the same variable across different time periods, into fewer axes of variation. When the ultimate goal is to make future projections, considering what forecasted climate data are available is essential to choosing which climate variables to consider. This will be particularly true for demographic models driven by PCA climate axes when covariance among historical climate variables differs from covariance among future climate variables (Louthan et al. 2021).

While temperature and precipitation are at the core of most climate-demography relationships, other, related variables may be used in climate-demography modelling as potentially more meaningful indicators of how the focal organisms experience climate. Derived climate variables such as drought indices, including the Palmer Drought Severity Index (PDSI) and Standardised Precipitation Evapotranspiration Index (SPEI) (Palmer 1965; Vicente-Serrano et al. 2010), or growing or freezing degree days, combine several climate variables in ways that may be ecologically relevant. Some studies focus on environmental ‘indicator variables’ that are driven by temperature and/or precipitation but more directly capture their impacts on the focal organism. Examples include sea ice extent (Jenouvrier et al. 2009), sea surface temperature (Pardo et al. 2017), soil moisture content (Matlaga et al. 2024), salinity (Lee et al. 2022), snow depth (Mignatti et al. 2012) and snowmelt date (Iler et al. 2019). Using composite or indicator variables may more realistically or directly capture climate effects (compared to direct measurements of raw climate variables), even as some composite variables rely on models that introduce additional assumptions or uncertainty.

## 2.3 | Capturing Climate Variation With Demographic Data

Possible approaches for quantifying or generating climate variation in tandem with demographic data are numerous (Table 1). In the demography literature, climate variation is most commonly captured through observational studies replicated across space and/or time, where each location and/or time period offers a unique climate sample. As with any observational approach, confounding variables could complicate inference of the causal role of climate. In addition or alternatively to observational data, variation in climate can be generated experimentally in the lab or field. For example, the abundant literature on thermal performance curves is built on largely laboratory-based manipulations of temperature, where it is possible to subject organisms to temperatures more extreme than those they would experience in the field (Angilletta 2009; Sunday et al. 2012). In the context of predicting climate change effects on population persistence, lab experiments that measure effects on multiple vital rates have



**FIGURE 1** | Linking multidimensional climate data to model a hypothetical population with an annual demographic census. (A) Mean daily temperature (°C) and (B) Total daily precipitation (mm) across 3 years (June 1, 2019—May 31, 2022, Cowichan Garry Oak Preserve, near Duncan, BC, Canada), with annual demographic census from 1 year ( $N_t$ ) to the next ( $N_{t+1}$ ). Adults (large circles) can grow and survive and new individuals (small circles) can be added to the population. Climate variables that drive vital rates might include a short time window (e.g., daily lowest minimum winter temperature, shown in red), a seasonal window (e.g., spring precipitation, shown in blue) or a proxy or indicator variable derived from multiple climate drivers (e.g., last summer's drought index combines precipitation and temperature, shown in purple). (C) Averages for temperature across varying intervals shown by horizontal lines: Yearly, monthly or growing season (designated using knowledge of the system or MODIS data) to show different ways a daily temperature profile might be summarised.

the most utility compared to those that focus only on one vital rate (Wada et al. 2024). Lab experiments necessarily trade off rigorous control of abiotic conditions with the realism gained from experiments manipulating conditions in the field, where other biotic and abiotic drivers of population dynamics are present (Anderson and Wadgymar 2020).

In the field, experiments can provide insight into expected future conditions, including those not represented in long-term data,

and allow for direct manipulation of climate (Table 1). Common experimental manipulations of climate include warming chambers (Elmendorf et al. 2012; Compagnoni and Adler 2014), snow removal (Griffith and Loik 2010; Anderson et al. 2025) and rainfall manipulation (Levine et al. 2011; Smith et al. 2024). The best of both worlds, and perhaps the gold standard, would combine experimental and observational approaches to expand coverage of abiotic environmental variation and infer causality through randomised experiments, while using observational data to



TABLE 1 | Study types and data sources for linking climate and demography.

Study type	Examples and references	Advantages	Disadvantages
Experimental—lab	Thermal performance curves generated in temperature chambers (Gremer et al. 2020; Wada et al. 2024)	Isolates causal effect of driver in a controlled environment	Lab environment missing realism of field conditions
Experimental—field manipulation	Snowmelt manipulations (Compagnoni and Adler 2014; Iler et al. 2019; Anderson et al. 2025); rainout shelters (Reed et al. 2021; Loesberg and Williams 2025), open top chambers (OTCs) (Oldfather et al. 2021)	Isolates causal effect of driver	Logistics may constrain sample size, temporal duration, size structure coverage and study taxon
Experimental—field common garden	Common garden experiments across climate gradients (Schwinning et al. 2022), corresponding to elevation (Anderson et al. 2025), latitude/longitude (Moutouama et al. 2025)	Advantage over natural populations is controlling genotype effects and detecting genotype by environment interactions	Relies on ambient climate, so causal effects of specific drivers may still be hard to disentangle
Observational—biogenic	Tree rings (Perret et al. 2024; Evans et al. 2024), fish otoliths (Morrongiello et al. 2012), whale ear wax (Trumble et al. 2013)	Often very long time series, and unique ability to track individual differences	Usually only one vital rate
Observational—time	Long-term demography, often one or few populations (Coulson et al. 2001; Campbell 2019; Lindell et al. 2022; Saracco et al. 2022; Cooper et al. 2024)	Captures the true distribution of climate variation that the population experiences through time	Many things change from year to year, may be hard to isolate causal effects of climate driver
Observational—space	Short-term studies with broad spatial extents (DeMarche et al. 2021; Félix-Burrue et al. 2025); forest inventories (García-Callejas et al. 2017; Schultz et al. 2022; Yang et al. 2022; Guyennon et al. 2023)	Captures the true distribution of climate variation that the species experiences across its distribution	May require assumption of space-for-time substitution in forecasting/projection, which can be misleading (see Table 3)
Observational—time and space	Tree rings from many sites (Perret et al. 2024; Evans et al. 2024); bird counting surveys (Oedekoven et al. 2017; Viana and Chase 2022); long-term demography studies at many sites (Angert 2009; Dávila-Hernández et al. 2025)	Great way to capture lots of realistic climate variation, ability to decompose and compare spatial and temporal effects of climate variables	Conducting long-term studies at many sites is challenging, spatial and temporal climate drivers may differ
Experimental + observational	Experiments (rainfall manipulation, OTCs, transplants) coupled with observational data from many sites (Merow et al. 2017; DeMarche et al. 2018; Anderson et al. 2025)	Isolates causal drivers and examines their influence alongside other sources of demographic variation	Most expensive and time-consuming

bolster sample sizes and capture natural patterns of variation. For example, Iler et al. (2019) combined 15 years of observational snowmelt data with snow removal experiments to build a model of demographic responses to advancing snowmelt in a Rocky Mountain perennial plant. Despite the difficulty of this combined approach, and recognising the potential for other drivers of population dynamics to muddle or modulate the climate driver–vital rate relationships, experimental elements can bolster causal inference.

Variation in vital rates observed across space can be driven by genetic rather than, or in addition to, environmental differences. Experiments provide the opportunity to decompose contributions from genetic and environmental factors, although they may be practical only for sessile or low mobility organisms. Specifically, common garden, transplant and provenance experiments can reveal how local adaptation modulates demographic responses to climate factors across species' ranges (Anderson and Wadgymar 2020; Souther et al. 2022; Anderson et al. 2025). For example, the universal response function approach (Chakraborty et al. 2019) estimates how climate affects the performance of genotypes sourced from different average climates, although these analyses almost always focus on a single performance metric taken at a single time point (e.g., tree height or stem basal area 20 years after trial start). In a recent example, using a series of common gardens across an elevational gradient coupled with demographic models, Anderson et al. (2025) found evidence for strong local adaptation, supported by stochastic population models, but that most genotypes were adapted to cooler climates than the ones they currently experience. Ultimately, even without the ability to conduct such experiments, it is important to recognise the potential for genetic factors, and local adaptation in particular, to influence the conclusions drawn from purely spatial observational data.

### 3 | Linking Climate and Demography

Before building statistical models that link climate and vital rates, it is helpful to identify hypotheses of when in the life cycle and demographic census interval climate drivers might influence vital rates (Figure 1). Such hypotheses narrow the many possible links between candidate climate drivers and demographic responses. A useful starting point is to draw a life cycle diagram with vital rates clearly identified (e.g., as in Rees et al. 2014). Then, with knowledge of the natural history of the species or related species, the climate of the ecosystem or ecoregion, and common performance-limiting factors for the type of organism (e.g., herbaceous plant, endothermic animal), consider which climate drivers may be most important and where in the life cycle their influence may be most acute (Figure 1). Doing so requires consideration of how to collapse the multi-dimensional nature of most climate data (multiple variables at high temporal resolution) and the timing of when climate drivers influence vital rates. We first consider the selection of climate drivers, highlighting the distinction between mechanistic and phenomenological models, and then consider approaches that can be used to determine the appropriate timing of climate drivers (see Table 2 for a range of statistical approaches, with examples, and Table 3 for possible challenges that may emerge during data collection and model-building, with suggested solutions).

When one or a few climate drivers are known to be at the core of the physiological mechanisms influencing vital rates, this knowledge can be used in a highly mechanistic way, where the parameters that relate vital rates to climate drivers derive from physiological processes. For example, thermal performance curves, a cornerstone of thermal ecology, have a characteristic intermediate optimum, often with left skew—shallow increase in performance with increasing temperature below the optimum and sharp decrease above (Angilletta 2009), but can also skew right (e.g., in soil moisture-limited plants (Evans et al. 2025)). Thermal performance curves are often estimated for one or few vital rates, which can inform how vital rates may change under future climate change (Nespolo et al. 2024), recognising that the shape and optimum can evolve with climate change (Stark et al. 2025). A few studies have gone further and assembled thermal performance curves for multiple vital rates into full population models (Armitage and Jones 2019; Richard et al. 2023; Johnson et al. 2023; Wada et al. 2024) or for population growth rates directly (Deutsch et al. 2008).

Where one climate driver is hypothesised or known to have tight links to vital rates, the hypothesised driver can be incorporated into purely statistical vital rate models that capture the influence in a phenomenological way (i.e., not derived from physiological mechanisms). Climate-demography studies have used regression models to capture effects of known or hypothesised driver variables such as snowmelt date on alpine plants (Iler et al. 2019; Campbell 2019), sea ice melt date on seabirds (Jenouvrier et al. 2009, 2020), El Niño Southern Oscillation index (ENSO) on desert plants (Félix-Burrue et al. 2021, 2025), and water availability index and growing degree day on temperate forests (Kunstler et al. 2011, 2021). Estimated regression coefficients may not have a well-established physiological interpretation. Yet, whether intended or not, every statistical model implicitly corresponds to a biological hypothesis or assumption through the functional form of the model, which is why even 'phenomenological' models include elements of mechanism. For example, including a climate driver as a simple first-order regression covariate assumes the response is strictly linearly increasing or decreasing with respect to the climate driver, which may not be physiologically sensible, depending on the range of measurement and projection. In the context of linear models, incorporating climate drivers with second-order terms accommodates the possibility of non-monotonic responses, when sufficient data are available. For example, demographic response to variation in temperature or precipitation is commonly modelled as a second-order polynomial (Miller and Compagnoni 2022; Malchow et al. 2023), allowing for intermediate optima that mirror a first-principles physiological expectation (e.g., thermal performance curve). Alternatively, generalised additive models using spline basis functions or various machine learning methods may allow the data to guide the specific form of climate dependence without requiring a priori assumptions (Teller et al. 2016; Tenhumberg et al. 2018; Hindle et al. 2019; Pichler and Hartig 2023). Ultimately, the choice of statistical model (Table 2) requires consideration of the study goals (e.g., understanding or forecasting), and not only sufficient data, but also care in determining whether the functional form is biologically sensible, particularly when the goal is forecasting beyond the range of observations and into future climate conditions (Figure 3).

Where several climate drivers are thought to be candidates, statistics can help guide selection among a suite of candidate

TABLE 2 | Statistical/quantitative approaches for fitting climate-demographic rate relationships.

	Modelling framework	Description	Examples	Advantages	Disadvantages
Phenomenological/ Statistical approaches	Linear models (LM), Generalised linear models (GLM), Linear mixed models (LMM), Generalised linear mixed models (GLMM)	Traditional statistical regression; must specify climate covariate(s) and functional form (e.g., polynomial); model selection may help with both	Dalgleish et al. (2011); Morrongiello and Thresher (2015); Williams et al. (2015); Csörgő et al. (2017); Iler et al. (2019); Oldfather and Ackerly (2019); Campbell (2019); Ozgul et al. (2023)	Simple and accessible without specialised statistical training; flexible in modelling different types of response variables	Requires aggregation of weather histories into simple covariates; limited options for shape of climate sensitivity (linear, polynomial)
	Generalised additive models (GAM), Generalised additive mixed models (GAMM)	Must specify climate covariate(s) but the data can guide functional form (e.g., non-monotonic) depending on basis number or complexity penalty	Dahlgren et al. (2016); Teller et al. (2016); Hefley et al. (2017); van Moorsel et al. (2023)	Naturally accommodates complex nonlinearity between climate and demographic response variables	Risk of over-fitting climate sensitivity with poor extrapolation performance; sensitive to small sample size, especially at extreme climate values
	Sliding window (ClimWin)	Specific application of linear or additive modelling that uses model selection for identifying time windows of covariate influence preceding the response observation	van de Pol et al. (2016); Evers et al. (2021); Lv et al. (2023)	Allows use of climate time series without requiring aggregation; requires little prior knowledge of the system, can detect long lags and critical windows of climate influence	Inherently exploratory; some risk in selecting windows without ecological understanding; difficult to account for model uncertainty
	Stochastic antecedent modelling (SAM)	Specific application of linear or additive modelling in which climate covariate(s) are time-integrated according to a weights estimated from data	Ogle et al. (2015); Elston et al. (2017); Peltier et al. (2018)	Allows use of climate time series without requiring aggregation; compared to sliding windows, allows for variation in weighting intensity	Challenging to implement (Bayesian approaches may be needed). Potentially hard to formulate a scientific explanation of results. Users still need to choose climatic predictors a priori
	Functional linear models (FLM)	Specific application of linear or additive modelling in which time series of climate covariate(s) is fit as a smooth function	Teller et al. (2016); Tenhumberg et al. (2018); Kerr et al. (2021); Hindle et al. (2023)	Allows for use of climate time series without requiring aggregation. Compared to SAM, temporal weighting of weather history achieved by smooth function of time.	Risk of overfitting complex climate sensitivity

(Continues)

TABLE 2 | (Continued)

Modelling framework		Description	Examples	Advantages	Disadvantages
Mechanistic/ Physiological Approaches	Machine learning/ random forest	Non-parametric machine-learning approach that makes few assumptions about linearity or distributions	Teller et al. (2016)	Useful for estimating nonlinear relationships and high-order interactions	Results can be difficult to interpret, and difficult to propagate uncertainty from vital rates to population model
	Regularisation and sparse modelling/ ridge regression	Reduces model variance by shrinking coefficients (ridge) or setting less-supported coefficients to zero (sparse approaches); does variable selection at the same time as fitting model	Lazaridis et al. (2011); Grames and Forister (2024)	May help identify best-supported climate covariates; reduces model variance and reduces degree of overfitting	Shrinks coefficients toward zero; more conservative
	Dynamic energy budget	Demography explicitly tied to energetic constraints	van der Meer (2006); Smallegange et al. (2017)	Good for mechanistic prediction; uses information at different scales (e.g., individual, population, food web)	Requires detailed data and physiological understanding
	Thermal performance curves	Demographic response to temperature guided by physiology	Amarasekare and Johnson (2017); Buckley and Kingsolver (2021); Johnson et al. (2023); Nespolo et al. (2024)	Climate sensitivity based on metabolic principles	Difficult to estimate for all vital rates that comprise population growth rate
	Physiology—other	<i>Ad hoc</i> models that incorporate physiological processes and constraints: simple plant growth models (e.g., 3-PG model), critical threshold models	Almeida et al. (2004); Nespolo et al. (2024)	Strongly mechanistic, with clear causal links between climate drivers and demographic response	Requires specialised knowledge not commonly held by demographers; may be difficult to assemble into population model



**TABLE 3** | Tips and tricks for getting started with climate-demography modelling. Challenges are ordered in the table from system and climate data to running and interpreting models.

Challenge	Potential solutions with example(s) and resources
Sites and years have a lot of background variation that isn't climate driven, as far as I can tell.	With enough replication, random effects can isolate site or year variation due to climate versus background spatial or temporal heterogeneity. If not, climate coefficient estimates will have a lot of error, and that may be okay as long as that uncertainty is propagated forward
I don't have climate data for my site(s). Should I use a downscaled climate product or a local weather station? For the latter, how far is too far?	First consider the study goal. For inference, proximity to a weather station is most important in topographically complex landscapes and microclimate data can improve inference (Christiansen et al. 2024). Downscaled climate data will also work fine. For prediction, ensure that climate projection data are downscaled in the same way.
Too many available climate variables, and many are highly correlated	Identify those that are more supported by the literature as drivers of vital rates and population dynamics (use a priori/natural history knowledge (Lindell et al. 2022)), and/or identify groups of interchangeable climate variables (due to collinearity) and choose a representative variable from each group. Alternatively, use a PCA to create a synthetic driver or two, with the caution that it's harder to forecast to future climates
Interpreting lagged and dormant season contributions of climate variables	Include lagged and dormant season climate in model selection (Tenhumberg et al. 2018; Evers et al. 2021, 2023; Anderson 2023). When interpreting, consider: do contributions make sense? Have a biological explanation? Are there potential indirect effects?
What if I only have good vital rate data for some life stages?	This is a common challenge for building demographic models, particularly for cryptic life stages, and not unique to making connections to climate. Possible solutions include trying a range of sensible values (Metcalf et al. 2008), using estimates from congeners (Moutouama et al. 2025) or using inverse estimation (González et al. 2016).
Is it okay for me to use space for time substitution? I have really limited temporal data, but I have some spatial replication.	Be aware that climate-demography relationships estimated across space can be the opposite of climate-demography relationships across time (Perret et al. 2024; Evans et al. 2024). Think carefully about the assumptions of space for time substitution (Lovell et al. 2023, SFTS; Kharouba and Williams 2024) and consider whether climate-demography relationships should be aligned across space vs. time in your study species or group (same in sign, allowing SFTS) versus not. Go forward with caution!
I suspect my population is subject to density dependence.	Fit density-dependent models using the best data you have (e.g., total population numbers; spatially explicit individual locations) (Dahlgren et al. 2016; Chu et al. 2016), include density $\times$ climate interactions where possible (Ehrlén and Morris 2015).
Models don't converge because climate variables are measured on vastly different scales (e.g., mean seasonal temp and total seasonal precipitation)	Standardise your variables (Schielzeth 2010) and if needed, investigate other solutions for model convergence (Harrison et al. 2018). Alternatively, use composite variables (e.g., drought indices) or PCA, with the caution that it is harder to forecast to future climates
Computing power demands for geographic forecasts with IPMs are very high	Not insurmountable, but worth considering in advance how to overcome, could include making code more efficient, working on a super computer/cluster (parallelisation, e.g., R package 'parallel'), and/or decreasing granularity of geographic space (larger pixels) or the IPM (lower-dimension matrix).
Interactions: among climate variables and/or between climate variables and size/stage	For interactions between climate variables, could instead use PCA to collapse climate variables or an index that collapses them (e.g., drought index). For climate $\times$ size interactions, ask whether they are statistically supported and do the interactions make sense (Tredennick et al. 2018). Cautionary note: may need a lot of data to find statistical support for interactions (Gelman et al. 2020).

drivers. For example, Dalglish et al. (2011) constrained their set of climate predictors of vital rates in grassland perennial plants to climate variables from the current or previous growing season that were significantly correlated with random effects of year derived from mixed effects models, and then used AIC model selection on this subset of climate predictors to choose the best-supported model. The choice of model selection criteria may

be best guided by the aims of the study, as out-of-sample performance metrics such as root mean square error (RMSE) may be more relevant than AIC for forecasting applications (Félix-Burrue et al. 2025). In another example, Özgül et al. (2023) constrained their analyses for modelling the effects of climate change on grey mouse lemurs in Madagascar to six seasonal climate variables, for example, choosing maximum temperature

instead of mean temperature, because the maximum has changed far more than the mean in the past 25 years. This example highlights an alternative way to select climate drivers: rather than focusing on biological responses, starting with historical or projected climate change may point to dimensions of climate that are changing most rapidly, and would therefore be a natural focus for forecasting. On the other hand, the strongest aspects of climate change may not be the most important climate drivers of demography (Czachura and Miller 2020).

After choosing a set of candidate climate drivers, one must consider the time window over which each might be most important, both in terms of the duration (e.g., month vs. season vs. year) and whether the time window coincides with or lags the window of demographic observation. For duration, a climate driver might be important over a very short time window, such as a critical winter low temperature below which an organism cannot survive (Tanner et al. 2017; Lancaster and Humphreys 2020; Kang et al. 2025) versus integrated over an entire season or census interval. A vital rate might be influenced by a climate driver in the current census interval, or the effect of the climate drivers might be lagged. For example, growth from time  $t$  to  $t+1$  (i.e., 1 year later) might be influenced by precipitation and/or temperature in  $t-1$ ; such lagged effects have been documented across a range of plant and animal species (Iler et al. 2019; Chen et al. 2020; Evers et al. 2021; Karunarathna et al. 2024). For organisms that alternate between growing and dormant seasons (e.g., perennial herbaceous plants going dormant in winter or hibernating mammals), evidence supports that climate during the dormant season can be an important contributor to vital rates (Paniw et al. 2019; Evers et al. 2021; Ogilvie and CaraDonna 2022; Nespolo et al. 2024), even if the precise mechanism is not known.

Rigorously modelling the influence of climate drivers may require consideration of more nuanced aspects of timing, beyond the presence or absence of lags. Given that climate data are typically available on a finer time scale than demographic data (Figure 1), a candidate climate driver can be represented as a time series leading up to the demographic census (e.g., daily, weekly or monthly precipitation over the year preceding flowering or breeding). The question then becomes: when during this history did the climate driver most strongly influence demographic outcomes? This question can be answered through temporal weighting of weather history, which assigns greater weights to periods of high influence. Weights may be defined 'by hand' if expert knowledge or insights from a climate-demography life cycle diagram (Figure 1) pinpoint the critical periods of influence (Hindle et al. 2019). More commonly, weights will need to be 'learned' from data through statistical inference.

Several approaches have been recently developed for inferring the temporal weighting of weather history from data (Table 2). Sliding window approaches such as ClimWin (van de Pol et al. 2016) use model selection criteria to compete many candidate models that differ in the timing and duration of temperature and precipitation effects on demographic responses. For example, using this approach, Lv et al. (2023) identified cold temperatures over a two-week period in the non-breeding season of a passerine bird as the main driver of decreased survival. Stochastic antecedent modelling (SAM), typically implemented

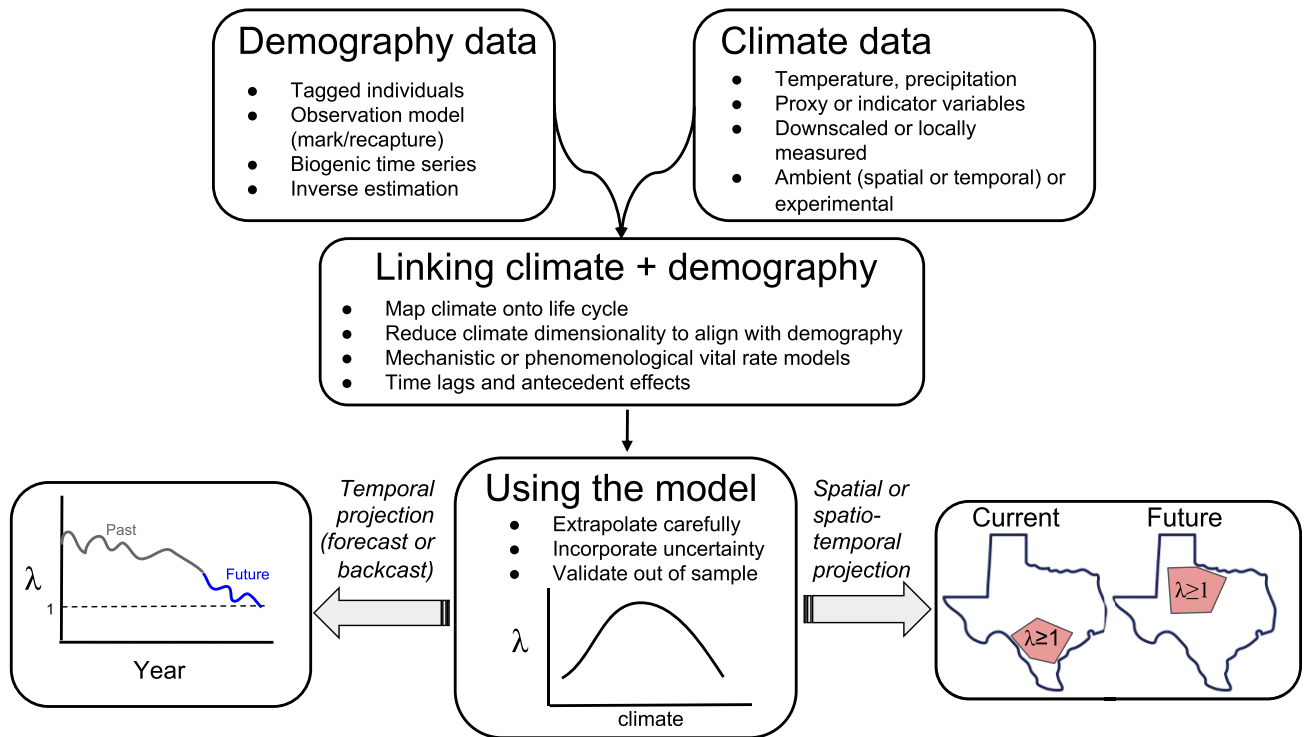
in a Bayesian framework, estimates weights associated with each climate window preceding the observed response, thus explicitly incorporating lags and quantifying ecological 'memory' as part of model fitting (Ogle et al. 2015, Compagnoni et al. 2024). Unlike sliding windows, in which the influence of the climate covariate is turned 'on' (within the window) or 'off' (outside the window), SAM allows the weight of each time window to vary continuously and can therefore detect greater subtleties in climate influences. Peltier et al. (2018) used SAM to model climate drivers of tree growth (annual ring width), showing that temporal weights of climate covariates were concentrated during the year immediately preceding ring formation, with a weaker signal of drought conditions 2–4 years prior. Finally, functional linear modelling (FLM) is conceptually similar to SAM but temporal weighting is derived from a smooth spline function that treats time continuously rather than as discrete windows (Teller et al. 2016; Tenhumberg et al. 2018). Hindle et al. (2019) found that FLM had better predictive performance for Soay sheep demography than choosing critical windows of climate influence a priori, but was no better than a simple, seasonally aggregated composite variable (winter North Atlantic Oscillation). Yet another approach to explore climate effects within census intervals is a model that accommodates demographic and climate data at different temporal resolutions, such as a Cox proportional hazards model (also known as survival analysis), which can estimate the impact of daily weather on annual plant survival (Tomasek et al. 2019) or multi-year tree survival as a function of annual weather (Fortin et al. 2025).

These competing approaches for the timing of climate driver effects have distinct advantages and disadvantages (Table 2). Proportional hazard models are useful for weather events that occur between census intervals, but are less suited to accounting for long lags. Sliding windows are easy to implement and highly flexible for exploring all sorts of timing and lags, but the results may be difficult to interpret and sensitive to spurious correlations. SAM and FLM may be a useful intermediate, capable of detecting subtle features of timing and less likely to return hard-to-interpret time windows of climate sensitivity.

#### 4 | Using a Climate-Demography Model

Once climate-demography relationships have been statistically defined at the level of vital rate sub-models, the next step is using a population model to make inferences about how climate drivers influence population viability under observed conditions (i.e., understanding), or to make forecasts for population- or species-level effects of climate change (i.e., predicting). What it means to 'use the model' will vary widely across applications. For the purposes of studying population viability in the context of climate change, key outputs will commonly include—but are not limited to—the asymptotic population growth rate  $\lambda$  or, when temporal variability is incorporated (due to climate variability and/or 'background' fluctuations), the stochastic growth rate  $\lambda_s$ . Here we discuss key considerations related to validation, inference and prediction for the different types of model outputs.

Just as climate-demography relationships are typically inferred from spatial or temporal environmental variation, a



**FIGURE 2** | Visual summary of steps to link climate to demography from collecting the data to using the model.

fully parameterised climate-explicit demographic model can be projected across space and/or through time (Figure 2). Temporal projection can go in both directions, informing how population viability has responded to historical environmental change ('back-casting', e.g., Smith et al. 2005; Czachura and Miller 2020) or will respond to future change (classic forecasting, e.g., Jenouvrier et al. 2009). Spatial projections can inform suitable niche space across a geographic range ( $\lambda$  or  $\lambda_s \geq 1$ ) (Merow et al. 2017; Pagel et al. 2020; Schultz et al. 2022; Şen et al. 2024) and can be combined with temporal dynamics to backcast or forecast geographic shifts in suitable niche space (Malchow et al. 2023; Moutouama et al. 2025). Moutouama et al. (2025) used climate-demography relationships derived from geographically distributed common garden experiments to forecast likely poleward range shifts of Texas grasses. In the spatial and spatiotemporal dimensions, climate-explicit demographic models can function as a more mechanistic alternative to species distribution models (Merow et al. 2017), quantifying potential for range shifts under future climate conditions based on lower-level mechanisms of vital rate responses to the environment and without requiring assumptions about range equilibria (Evans et al. 2016; Briscoe et al. 2019). However, it is important to recognise the assumptions required to scale up models intended for local population dynamics to predict the dynamics across entire species' ranges, particularly regarding genetic variation and landscape-scale processes such as disturbance, dispersal and connectivity (Adler et al. 2020).

Ecologists have long relied on the assumed interchangeability of spatial and temporal environmental variation (i.e., space-for-time substitution, (Lovell et al. 2023)). This would imply, for example, that climate-demography relationships derived from long-term data from one population could predict spatial

demographic variation across the species' geographic range, and vice versa. Recent work highlights that this assumption of substitutability can be strongly misleading in practice (Perret et al. 2024; Evans et al. 2024; Kharouba and Williams 2024). Central among the reasons for this is local adaptation, which may alter the climate optima or tolerance breadth of different populations and make inference from spatial sampling a poor proxy for local response to climate change through time, and vice versa (Perret et al. 2024). Other biotic lags ('slow' processes like colonisation and extinction) can similarly cause inferences derived from spatial and temporal data to diverge (Adler et al. 2020; Stemkovski et al. 2025). Climate-demography modelling will generally be on firmer ground when the dimension of model projection (spatial or temporal) aligns with the dimension of climate variation over which the model is parameterised. Where demographers have spatiotemporal data to infer climate responses, a useful diagnostic is to check whether purely spatial (e.g., among populations in a single year) versus purely temporal (e.g., among years within a single population) climate responses are similar in magnitude and direction. In some cases, such diagnostics may indicate that spatial and temporal estimates are effectively substitutable, such as for emperor penguins, where both spatial and temporal variation shared the same climate driver of underlying vital rates with matching magnitude and direction (Şen et al. 2025). More research is needed to better understand and anticipate the species and settings in which the effects of spatial and temporal climate variation on demography can versus cannot be treated as substitutable.

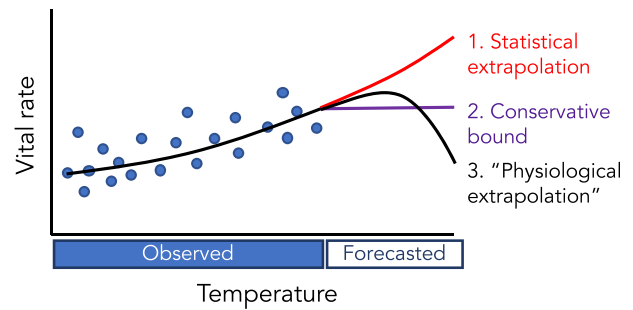
Even when model parameterisation and projection are aligned in space or time, the domain of projection will often include environmental conditions that are poorly represented or entirely

unrepresented in the parameterisation data. This is especially true for predicting responses to future climate, which for many regions will likely include conditions with no present-day analogue (Feng et al. 2024). In such cases there are several ways in which vital rate models could be extrapolated beyond the bounds of observed conditions (Figure 3). First, naive extrapolation beyond observed limits of a climate variable is one option, but it is important to visualise the extrapolated predictions to ensure they are biologically sensible (Owens et al. 2013; Conn et al. 2015). Linear models with log-link functions or higher-order polynomial terms, for example, can lead to wildly unrealistic predictions just beyond the limits of observed conditions. A more conservative approach would place upper and/or lower limits on vital rate functions, analogous to ‘clamping’ in species distribution models (Anderson 2013; Beck et al. 2023), so they cannot exceed the response at the most extreme observed values of the climate driver (Louthan et al. 2022). Alternatively, physiological principles may dictate how vital rates will respond beyond observed conditions. For example, a vital rate may increase monotonically with increasing temperature over some observed range but physiological principles tell us that the effects of increasing temperature must eventually become negative (Figure 3A).

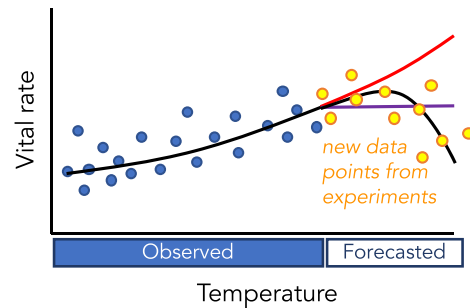
Experiments provide opportunities to create no-analogue combinations of climate variables as a way to bridge the gap between current and future climate (figure 3B; Stevens and Latimer 2015; Kieckbusch et al. 2024), or to examine changes in climate variability along with changes in mean climate (Rudgers et al. 2023). Finally, some of the most ecologically important types of climate change involve changes in the frequency of extreme events, such as droughts or hurricanes, rather than shifts in the mean or range of climate values. Through biased re-sampling of observed conditions, it is possible to model changes in the frequency of extreme states such as drought years (Williams et al. 2015) or low sea ice years (Hunter et al. 2010), even without a mechanistic understanding of the effects of extreme conditions on vital rates (Morris and Doak 2002; Fowler et al. 2024). Re-sampling observed years has the advantages of entirely avoiding extrapolation while preserving correlations between vital rates without having to model them explicitly (Metcalf et al. 2015), which can be challenging (Compagnoni et al. 2016).

Given the central aim of predicting responses to climate change, it is important to validate climate-explicit models to gain confidence that they make reasonable predictions. Model ‘validation’ takes on a double meaning for climate-explicit demographic models, because both the population model and the sub-models describing how vital rates depend on climate require validation. The vital rate sub-models (Table 2) should be evaluated for their predictive accuracy, ideally both in and out of sample, when possible (Tredennick et al. 2017; Harris et al. 2018). Fitted statistical models are generative, and can and should be used to simulate data for comparison with real data; this is a standard in-sample diagnostic step of a Bayesian workflow (i.e., ‘posterior predictive checks’) but is not limited to Bayesian analysis (Miller and Ellner 2025). At the level of the population model, predictions like the one-time-step-ahead growth rate given recent weather conditions or climate

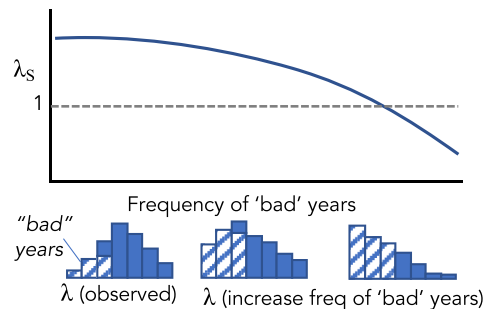
#### A) Experiments not possible



#### B) Option 1: simulate forecasted conditions with experiments combined with observations



#### C) Option 2: biased re-sampling of observed conditions



**FIGURE 3** | Making predictions for demographic and population growth rate(s) under future climate change scenarios. Generic vital rate shown as a function of temperature. (A) Where experiments are not possible, extrapolation to forecasted temperature can take several forms: statistical extrapolation, which follows the functional form of the statistical model; conservative bound—a threshold set based on some a priori knowledge; a physiological extrapolation based on expected responses to climate extreme. (B) Experimental manipulations can be combined with ambient climate variation from spatial or temporal sampling to bridge the gap between observed and forecasted conditions. (C) Biased re-sampling of observed conditions can examine the consequences of changing frequency of environmental extremes, even if climate and physiological mechanisms of ‘bad’ years are not known.

niche suitability across geographic space could be evaluated against independent observations to assess model adequacy. For example, Moutouama et al. (2025) found that model predictions of climate niche suitability (where  $\lambda \geq 1$ ) compared favourably to independent occurrence records. However, other studies have found that demographic responses to climate are poor predictors of species’ occurrence (Lee-Yaw et al. 2022; Schultz et al. 2022; Şen et al. 2024). Diagnosing the causes



of poor validation metrics—for example, whether mismatches between predicted and observed occurrence reflect a statistical issue (model mis-specification) or a biologically interesting process (non-equilibrium dynamics, other influences on species' occurrence such as biotic interactions or disturbance) may itself be a substantial undertaking. The recurring, longitudinal nature of much demographic research lends itself to iterative near-term forecasting (Dietze et al. 2018), providing an opportunity to train and improve vital rate and population models against an ever-changing backdrop of climate drivers.

Successful validation can bolster confidence in meaningful prediction but, to keep expectations realistic, it is worth considering which predictive targets might be more appropriate and achievable than others.  $\lambda$  and  $\lambda_s$  are 'asymptotic' metrics (predicting the long-term behaviour of a population assuming environmental conditions are stationary), and may be useful indicators of directional responses to environmental change (Lindell et al. 2022) or the potential for population viability ( $\lambda \geq 1$ ) under a given set of conditions (Diez et al. 2014). The overall sensitivity of  $\lambda$  (or  $\lambda_s$ ) to a climate driver reflects the combined sensitivities of  $\lambda$  (or  $\lambda_s$ ) to the vital rates and the sensitivities of the vital rates to the climate driver (McLean et al. 2016). Decomposing these sensitivities through Life Table Response Experiments (Caswell 2001) can nevertheless provide rich insight into how and why population viability responds to environmental drivers, at least over observed conditions (Maldonado-Chaparro et al. 2018; Iler et al. 2019; Schultz et al. 2022). Doing so also illustrates the importance of integrating climate effects across the life cycle, as vital rates with high sensitivity to climate may contribute weakly to population growth, or vice versa. Beyond asymptotic metrics, near-term measures, such as transient growth rates and sensitivities (Maldonado-Chaparro et al. 2018) or population size or extinction risk over some forecast horizon (Félix-Burrueal et al. 2025), could be more meaningful and tractable targets for prediction, as climate change is creating non-stationary environmental variation (shifts in mean and/or variance) for many populations and species. Historically, population projection models do not have a stellar record of predictive accuracy (Crone et al. 2013); as climate-demography case studies accumulate, it will be interesting to see if the inclusion of important climate drivers helps to increase model skill and predictive accuracy.

As is always the case in ecological forecasting, accounting for uncertainty is an important part of prediction and should be standard practice in climate-demography forecasts. Uncertainty arises from model uncertainty, parameter estimation and background 'process error' (e.g., year-to-year and site-to-site differences that are not explained by climate), among other sources (Dietze 2017). Even with high confidence in parameter estimates for climate-demography relationships, process error can contribute substantial uncertainty to ecological forecasts (Czachura and Miller 2020). Bayesian analysis is a common way to incorporate uncertainty in climate-demography contexts: because a function of a random variable is itself a random variable, posterior probability distributions of vital rates can be naturally propagated into posterior distributions of quantities derived from the vital rates, such as population growth rate or extinction risk (Elder and Miller 2016; Iler et al. 2019). Bootstrapping

is a non-Bayesian alternative that can similarly quantify uncertainty (Larios et al. 2020). Finally, uncertainty about the future derives not only from climate-demography models, but also (and perhaps mainly!) from the climate change forecast itself. Few studies have incorporated uncertainty in the climate forecast alongside uncertainty in demographic responses to climate drivers (Gauthier et al. 2016; Heilman et al. 2022; Jenouvrier et al. 2025). Some of those studies suggest that the variability among the Global Climate Models (GCMs) in climate forecasts dwarfs the uncertainty associated with population responses to climate (Louthan et al. 2022).

## 5 | Where Do We Go From Here?

Despite the myriad decisions and potential challenges described above, we encourage researchers to forge ahead as we urgently need better projections for the effects of climate change on biodiversity. This includes working with the demographic and climate data currently in hand, while considering how to supplement with experiments, and starting studies with new species of concern. Here we offer some general guidance for climate-demography modelling, as well as a few cautionary notes, then conclude with recommendations for ways to move the field forward.

1. **Best practices for identifying hypothesised climate drivers that link to demography.** Overall, the particular climate variables to use will depend on the goal of the study (see Table 3 for more tips for getting started). For studies with the aim of forecasting, selecting climate variables that are used in Global Circulation Models for future climate will be valuable. For studies aimed at understanding climate drivers of local populations, microclimate or local weather data should provide the strongest inference. To quantify how anomalous a climate driver is across years for a particular study system, climate drivers can be scaled by a historical mean and standard deviation for each study location. Doing so serves two purposes. First, it is good practice to put climate drivers on the same scale in their interactions with vital rates (Schielzeth 2010). Second, we see an opportunity to compare, with caution, coefficients of climate sensitivities for different vital rates across climate drivers as well as across studies to ask questions across taxa about how the sensitivities of vital rates to climate vary in time and space. Caution is necessary because, depending on the research question, absolute climate sensitivities may be more meaningful; for example, when comparing responses of plants to drought across sites that vary dramatically in baseline precipitation, scaled climate drivers may be less informative. Finally, when possible, validating models, ideally with out-of-sample data, allows for estimating how well predictions perform, thus increasing the robustness of conclusions, particularly when decision making hinges on the results (Yates et al. 2023).
2. **Climate drivers can interact with other drivers of demography.** While here we have argued for the utility and urgency of determining the demographic effects of climate drivers, climate can of course interact with other

drivers, including but not limited to biotic interactions and disturbances (Suttle et al. 2007; Chu et al. 2016; Louthan et al. 2022). Since such interactions can modify the effects of climate on demography, knowing the natural history of a system and quantifying the effects of other drivers where possible is important. At the same time, when it is not possible to quantify non-climatic drivers, researchers can proceed, while taking caution when interpreting results. Even when the overall current trends, for example, population dynamics, are well described, the underlying mechanisms that led to a statistically supported link between climate and vital rates may be incorrectly identified, which would limit our ability to predict future population dynamics when relationships with non-climatic drivers change.

3. **Check for physiological sensibility.** All model builders need to consider whether the models they are fitting for vital rates are physiologically sensible. This consideration is critical regardless of how much data or prior knowledge one might have for the link between physiology and climate. This link is explicitly built in for more mechanistic models, but lacking for purely statistical approaches, which can include climate responses that are overly simplistic (e.g., unbounded linear functions from univariate regressions) or overly complicated (e.g., step functions from machine learning algorithms). When more phenomenological models are used for forecasting, this will mean considering, for example, what happens when the model extrapolates to more extreme conditions and using data and common sense to determine if the extrapolation is sensible (Figure 3A).
4. **Avoid fishing expeditions while staying open to unexpected results.** For many researchers, the steps of choosing candidate climate driver(s) and how they are integrated across which seasons and with which lags could be daunting. Despite the challenges, we caution researchers to avoid 'fishing expeditions', such as comparing all possible models (which could number in the hundreds or thousands) with a model selection approach. On the flip side, we encourage researchers to wield their prior knowledge with humility; that is to allow themselves to be surprised by unanticipated connections, thus opening up new hypotheses to evaluate. One way to balance these considerations is to use the climate—life cycle diagram approach (Figure 1) to guide the exploration of biologically reasonable possibilities.

Among all the idiosyncrasies in how populations and species respond to climate and in how ecologists construct models that link climate to population dynamics, we urge researchers to seize the opportunities to make this field more synthetic and comparative. One initial way forward is to build vital rate models with standardised climate variables, and then in population models, compare sensitivities of vital rates to changes in climate, and finally to compare sensitivities to climate across taxa. Effects of climate change are predicted to be larger when climate sensitivities align with the vital rates that are most strongly driving population dynamics (McLean et al. 2016), such as survival and growth of long-lived species and those on the slow end of the life history continuum. We can evaluate this prediction (and the converse, that species with fast life histories should respond more strongly to climate change when climate drivers have the

largest effects on reproduction) drawing on data from across taxa. Comparative demography is already a well-developed field (Franco and Silvertown 2004; Salguero-Gómez et al. 2016); we see an opportunity to extend the success of comparative demography to comparative climate-demography.

A next step is to ask questions about tipping points at which populations will become critically and negatively affected by climate change, for example, temperatures where  $\lambda_s \leq 1$  (Doak and Morris 2010). Tipping points can be identified from phenomenological or mechanistic models, and may result from a nonlinear relationship between one vital rate and a climate variable, or where demographic compensation among vital rates is insufficient to maintain  $\lambda \geq 1$ . Next questions include: How common are tipping points and at what level of climate anomaly do they occur? Are tipping points stronger with respect to temperature versus precipitation and how does that vary by biome? Are certain vital rates more likely to be involved in tipping points and/or demographic compensation? Do certain vital rates tend to be impacted 'first' (with less extreme climates) than others, and does that relate to life history? Due to selection, vital rates with low variability tend to have the largest eigenvalue elasticities (Pfister 1998), suggesting that those vital rates should be first to respond, but as historical conditions are left behind, does this relationship hold? Although we may not yet have the data, and recognise that identifying tipping points may sometimes be elusive (Hillebrand et al. 2020), we can work toward answers to these questions that will inform our predictions not only for well-studied species, but also for populations and species for which we have sparse to no data.

Another way forward for synthesis studies is with a focus on linking physiology to demography to population models, a realm where we lack theory beyond that surrounding thermal performance curves. We need to know how and whether physiological expectations for vital rate responses to environmental indicator variables (e.g., thermal performance curves, growing degree days based on microclimatic measurements) perform better than predictors such as temperature and precipitation for making forecasts. Even within a population, individuals may have different thermal performance curves (Stark et al. 2025), leading to the question and drawing on the literature of individual heterogeneity in demography (Kendall et al. 2011; Vindenes and Langangen 2015), do individuals within the same population have different responses to climate? And if so, how much does that affect population and species-level responses to changes in climate? Clearly, genetic variation is one source of individual heterogeneity, which sets the stage for evolutionary rescue to result in different outcomes than might be predicted by a purely ecological forecast (Olazcuaga et al. 2023). Finally, although we are beginning to accumulate studies demonstrating that microsite conditions can be important drivers of population dynamics (Oldfather and Ackerly 2019; Ray et al. 2023), in general, we do not yet know how site and microsite conditions might mediate or exacerbate the effects of climatic anomalies (Nicolè et al. 2011).

In sum, we see a new synthetic field just beginning to develop that will identify where to expect strong links between climate drivers of populations and species, and thus where to expect strong effects of the rapidly changing climate. As this field develops,

we encourage researchers to make predictions for how climate change will affect species of concern. The most robust predictions will come from models that are validated and quantify sources of uncertainty. We remain optimistic that collectively these contributions will lead to not only better understanding and prediction, but more effective management strategies to mitigate the effects of climate change on biodiversity.

### Author Contributions

All authors are members of a working group that developed the content of this article over a 2-day meeting. J.L.W. and T.E.X.M. organised the working group and drafted the manuscript. All authors contributed edits in preparation for manuscript submission.

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### Data Availability Statement

The climate data and code used to generate Figure 1 are openly available on Zenodo: <https://zenodo.org/records/17407813>.

### Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70283>.

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