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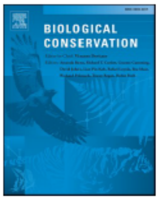

# Optimizing demographic analysis in the face of missing data years to improve conservation of threatened species

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## ABSTRACT

Quantification of population dynamics and predictions of species viability rely on estimates of vital rates and an understanding of the ecological drivers of these rates. Most standard methods for assessing impacts of drivers, such as climate, on vital rates require annual demographic data for many individuals over multiple years. However, many real studies have either planned or unplanned data gaps. Vital rates are usually estimated over annual transitions, therefore one year of missing data results in two missing estimates. Additionally, relating annual climate variation to changes in vital rates is challenging if studies do not collect data annually. To avoid this loss of information due to missing data, we developed and then tested a Bayesian modeling approach for a dataset with missing years. Using an 18-year study of the rare plant *Eriogonum brandegeei* we estimate vital rates, their relationship to annual climate, and stochastic population growth. By comparing model performance across data subsets, as well as in tests using simulated data, we find that the approach works well with missing years of demographic data and removes the need to ignore information from multi-year transitions. This generalizable approach increases the useability of available data to study species dynamics despite patchy demographic data.

## 1. Introduction

Assessing the viability of populations or the impacts of climate and other stressors ideally uses the quantification of demographic, or vital, rates and how environmental drivers determine these rates. The typical approach for estimating effects of multiple drivers on vital rates requires detailed demographic data for multiple individuals every year for considerable periods of time (Morris and Doak, 2002). Such data allow straightforward statistical modeling of how vital rates vary in time and space (Coutts et al., 2021) and are influenced by climate, ecological interactions and management actions using standard statistical models (Gross et al., 1998; Bakker et al., 2009). However, collecting individual demographic data is time and labor intensive, which commonly results in either limited sample sizes or missing years of data (Doak et al., 2005). These data gaps sometimes arise due to unforeseen logistical challenges (e.g., COVID-19 in the summer of 2020 prevented planned data collection in many studies around the world), as well as from planned lapses in data collection due to budget constraints. In addition, concerns of impact from disturbances caused by monitoring activities (e.g., trampling) can also limit sampling visits to only some years. In most cases, researchers simply do not use the data spanning the missing year(s), but this involves a serious loss of information. Since predictions of population growth and most vital rates are made for annual *transitions*, one missing year of data results in two missing transitions in what are often already limited datasets (Kindsvater et al., 2018). In addition, it is difficult to directly tie annual climate variation to vital rate changes if demographic data collection does not occur each year.

To address this common problem, we develop and then apply a flexible analysis approach for the estimation of vital rates and their dependence on annual climate variables in the face of missing data. We use a Bayesian modeling approach to estimate vital rates and their dependence on climate drivers, and incorporate parameter uncertainty in these estimates into downstream analyses. Using Bayesian modeling with demographic data is not new (Ellison, 2004, Dorazio, 2016, Elderd and Miller, 2016, de la Horra et al., 2017). Our general strategy is similar to that of many 'hidden process' models (e.g. Clark et al., 2005; Shriver, 2016). Such models treat unobserved states of an individual as parameters that can be estimated, linking together observations that can occur across multiple transitions or that have significant observation errors (De Valpine, 2012). This general approach is the basis of mark-resight analyses as well as multiple other population models that feature uncertain or missing observations (Shefferson et al., 2001, Thomson et al.,

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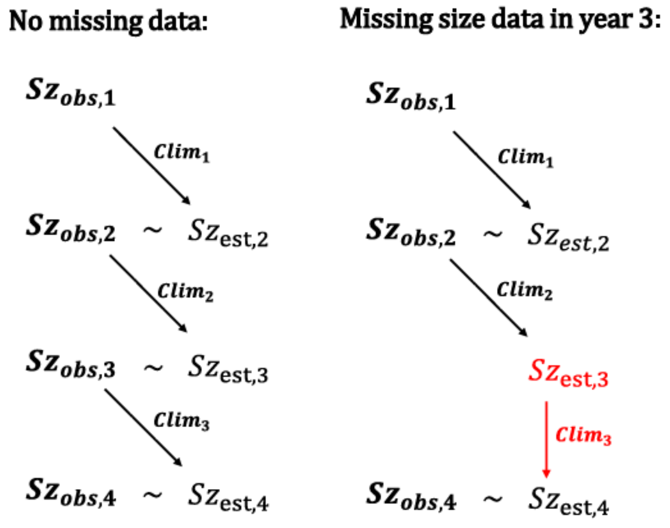

**Fig. 1.** Illustration of our approach for handling missing data to model demographic rates. This figure shows a simplified schematic just for plant size data. The left side of the figure shows the approach used in normal fitting routines, and in our approach without missing data. After the first year, estimated plant size in each year, $Sz_{est,t+1}$, is based on observed size the year before, $Sz_{obs,t}$. These estimates are used to predict the observed size in year t+1, with the comparisons then used to estimate the best parameters of the model. Note that the estimated growth in each year is also influenced by annual changes in environmental conditions, indicated by $clim_t$, the climate conditions from year t to t+1. On the right we indicate how we deal with missing plant size data (year 3 in this example; red): the prediction for size in year t is in this case based on at least one and possibly more years of estimated sizes, rather than coming directly from an observed size the prior year. In the real model, predictions also include those for survival and reproductive rates.

2008, Sandercock, 2010, Rose et al., 2021), and include both Bayesian and non-Bayesian methods (Kéry and Royle, 2020). However, our approach of using Bayesian methods to address the problem of missing data is not commonly used or understood in demographic analysis. Nor has it been assessed for accuracy in the context of sampling that skips entire years of data collection, as opposed to the vagaries of finding and observing individuals within observation periods. We apply this method to an 18-year study of the rare perennial plant *Eriogonum brandegeei*, estimating all required vital rates and then using these to predict stochastic growth rates.

## 2. Methods

*Study species and datasets: Eriogonum brandegeei* Rydberg (Polygonaceae; Brandegee's buckwheat) is a mat-forming iteroparous perennial herb endemic to Colorado, U.S.A. (Reveal, 1969). From 2004 to 2022, twelve transects were monitored at two nearby locations on Bureau of Land Management land in Fremont County, CO. Annual demographic censuses were performed from 2004 to 2013 during August. To decrease potential negative impacts from trampling, no data were collected from 2014 to 2015. Starting in 2016, censuses were performed every other year with the intent of detecting long-term trends while minimizing impact. Size of a plant is based on the number of vegetative rosettes; further details of the monitoring and size classification are given in Appendix A.

We obtained total monthly precipitation and mean monthly daily mean temperature data from the PRISM Climate Group (Oregon State University, http://prism.oregonstate.edu) for 1991–2022. Since seasonal climate measures are likely to be more meaningful for plant performance than annual values, we aggregated monthly climate variables (mean daily temperature and total precipitation) into seasonal values for fall (August–November), winter (December–March), and summer (April–July). For each demographic transition, corresponding climate data was from the 12 months preceding the ending census (e.g., climate data for 2004 is August–November 2003 [fall], December 2003–March 2004 [winter], and April–July 2004 [summer]). Climate in the study years was representative of the variation seen in longer term climate records (Fig. A.1).

*Statistical analysis:* All analyses of demographic and climate data were done using R version 4.3.1 (R Core Team, 2023). We first determined the functional form for size effects and the support for different climate drivers using GLMM models and AIC for model selection with the annual data from 2004 to 2013 that did not include any missing years of field data (see Appendix A for detailed description). We used GLMM model selection instead of Bayesian model selection due to constraints on computational time for the latter. While ideally model selection would also be done using the same approach as the final parameter estimation, we suspect that many other researchers will face the same constraints, necessitating use of a faster approach to run the many analyses needed for model selection.

We then refit the best supported model form with all or subsets of the data, including the use of transitions that contained missing information. To allow model fitting when datasets had missing years, we adopted a Bayesian framework which allowed estimation of size, survival, and reproduction and their dependence on climate variables in years where a plant was not observed. Specifically, Markov Chain Monte Carlo (MCMC) chains with a Gibbs sampler were used to estimate the distributions of all vital rate model parameters, using JAGS ver. 4.3.0 (Plummer, 2017) called from the R package runjags (Denwood, 2016).

Fig. 1 illustrates our modeling approach and an example of how it handles missing years. Across years without missing observations, the vital rate models for survival and growth correspond to typical generalized linear mixed models (GLMMs), with survival and size (if surviving) in year t+1 a function of size in year t and climate variables during the transition, as well as random effects of transect. Similarly, probability of reproduction and inflorescence number (if reproducing) in year t are functions of size and climate in that same year. For years without field data, the model creates estimates of size, survival, and other vital rate outcomes, which are then the basis for estimated growth and survival into the subsequent year, as well as reproduction in the current year (Fig. 1). Note that survival probability after a multi-year transition is estimated as the product of the estimated annual survival probabilities, just as size at the end of a multiyear transition is estimated from growth over each transition. This procedure allows us to estimate annual climate effects even when missing some years of demographic data. It also allows us to estimate total inflorescence production in transects, and therefore to fit estimates of new plants arising per inflorescence, even when a year of reproduction data is missing. Note that in making these reproductive output estimates, we use the estimated probability that each plant was alive in a year, multiplied by the size-specific estimate of probability of reproducing and the inflorescences produced if reproducing, summed across all plants. If a plant was observed to still be alive at the first census following one or more missed years, it was then known to be alive during those preceding periods and treated accordingly in the models. Because estimated survival and growth influence reproduction and recruitment, all vital rates and their dependence on climate are fit simultaneously. Additional modeling details are in Appendix A and code to run these models is provided at github.com/DenverBotanicGardens/ErBr_Goebl_etal.

We ran all MCMC models with uninformative normal and uniform priors (Table A.3). The posterior sampling was based on 30,000 iterations after 10,000 steps of burn-in, 3 chains, and thinning to every 10 samples. Convergence and parameter correlation were checked for all models (Figs. A.2–A.7).

To assess how well the MCMC model performed with missing years of data as well as with different amounts of data, we compared model outputs from datasets containing missing years versus no missing years (consecutive year data). In addition to the full dataset of 1771 plant

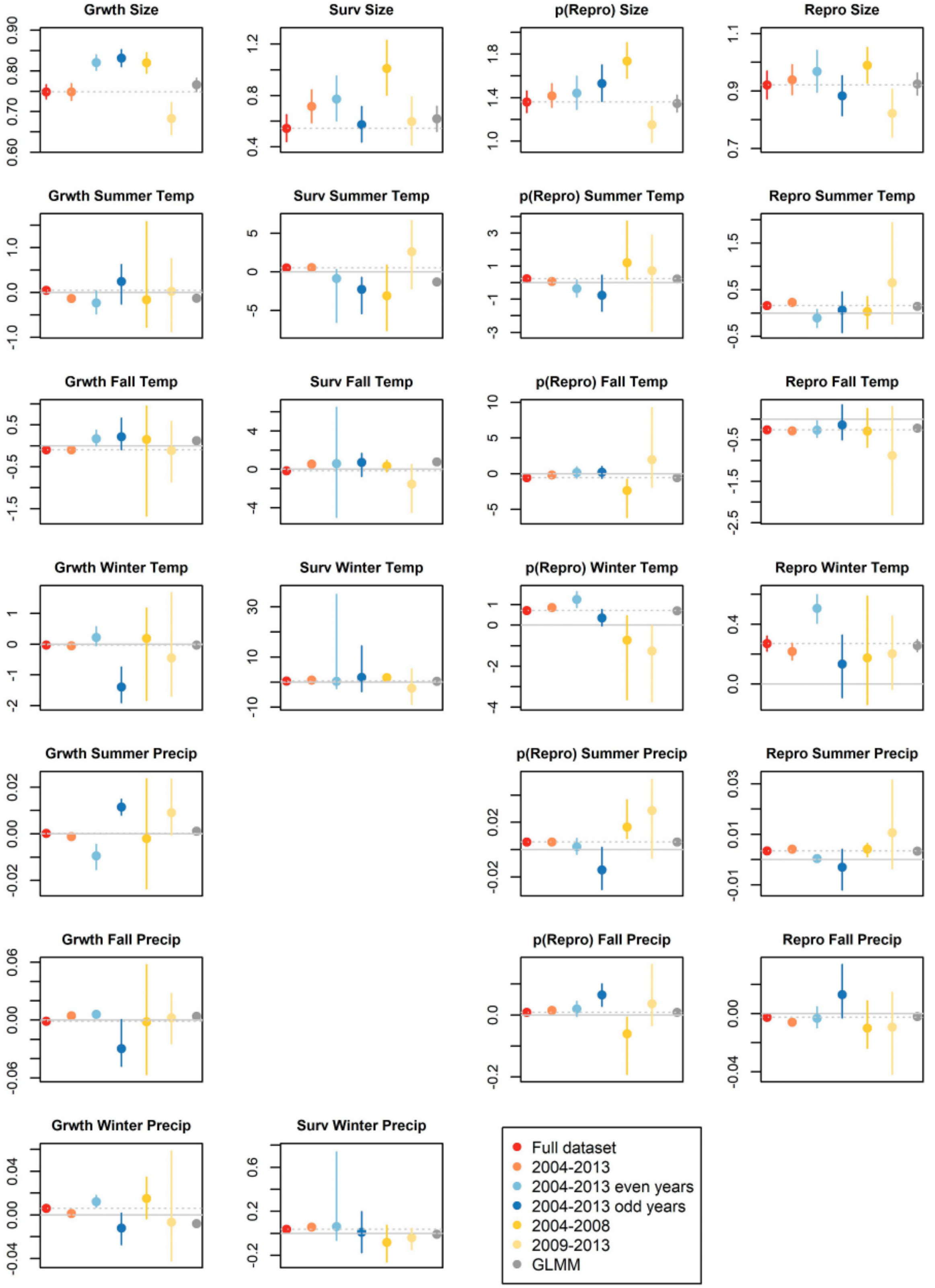

**Fig. 2.** Median parameter estimates from MCMC posterior distribution sampling for each variable (rows) in all vital rate models (columns) when using datasets with missing years (full & pruned datasets) and consecutive year only data (2004–2013, 2004–2008, 2009–2013). Mean parameter estimates are also shown for GLMM versions of each vital rate model (grey points). Error bars show 10th and 90th quantiles for posteriori parameter distributions (MCMC models) or +/-1 standard error (GLMM models). Grwth = growth, Surv = survival, p(Repro) = probability of reproducing, Repro = amount of reproduction, Temp = temperature, Precip = precipitation. Horizontal solid lines are at zero to help visualize the magnitude and direction of effects. Horizontal dotted lines indicate the median estimate from the full dataset for reference.

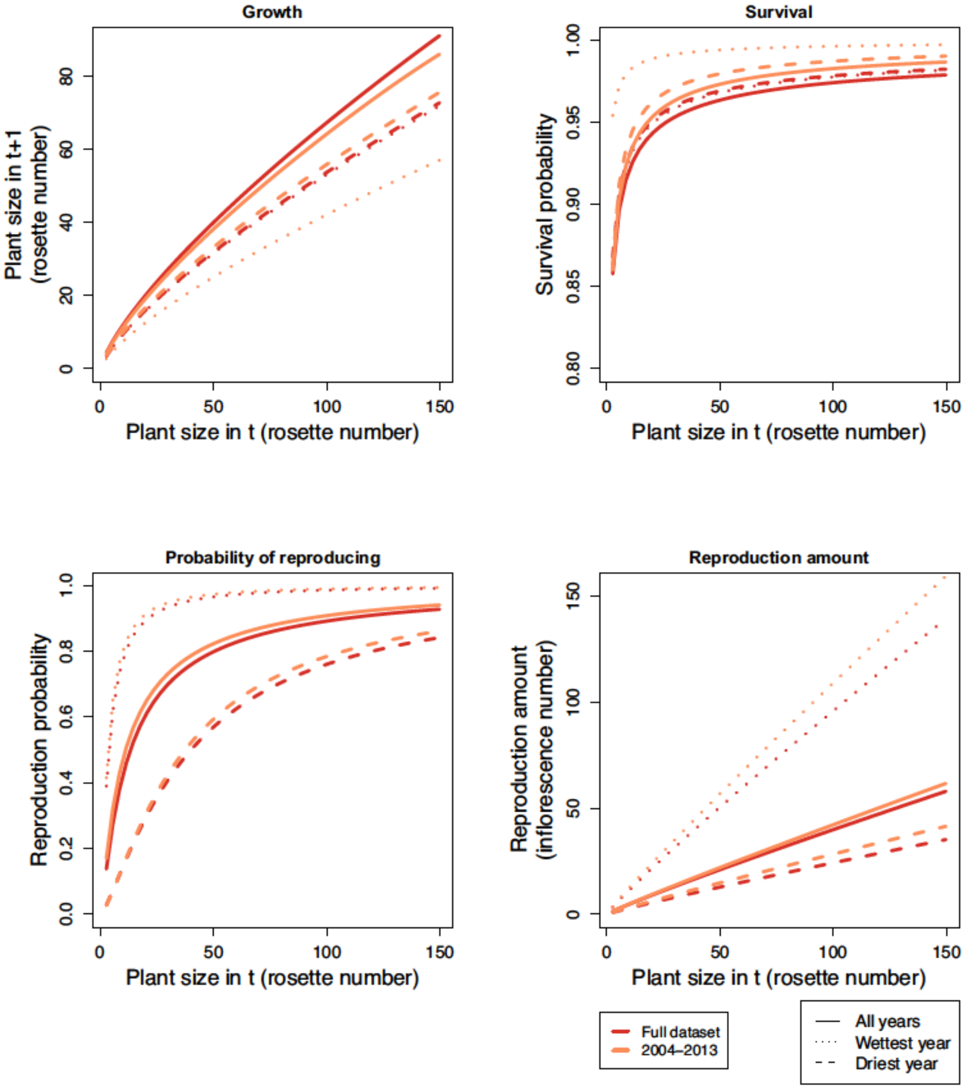

**Fig. 3.** Modelled vital rates for growth, survival, reproduction probability, and reproduction amount averaged across transects and parameter values in relation to plant size. Vital rate models were parameterized with either the full dataset (2004–2022 with gaps; red), or consecutive year data from 2004 to 2013 (orange). Solid, dotted, and dashed lines represent mean vital rate values across all years (2004–2022), the wettest (2015), and driest (2011) years of the data collection period, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

observation years (consecutive year data from 2004 to 2013, followed by data only in years 2016, 2018, 2020, and 2022), we also fit models to just the longest stretch of consecutive years (2004–2013; 1519 plant observation years), and 2004–2013 data after pruning to include only odd or even years, and to shorter consecutive year data (2004–2008 and 2009–2013; 821 and 698 plant observation years, respectively). These different datasets include cases with and without missing data that also span different total years of demographic observations. We then compared results between datasets for annual vital rate parameter estimates and the effect of climate on the vital rate to plant size relationship.

We also generated simulated data with known vital rate parameters for three different life history patterns to test model performance with missing data. One life history uses the growth and survival rate parameters estimated for *E. brandegeii*, while the other two have increased growth rates and either moderate or highly reduced survival for larger plants (Fig. A.8), which we hypothesized would make parameter estimation with missing years of data more challenging. For each life history, we generated 10 replicate simulations of individual plant fates over 20 years. For the observed life history (that of *E. brandegeii*) we also generated longer datasets representing 40 years. To test the effects of missing data on model performance, and similar to our real data, the simulated datasets contained 10 consecutive years of demographic data, plus an additional 10 or 30 years with missing data every other year. In these simulations, we maintained sample sizes of approximately 50 to 300 individuals per year by adding seedlings to the sample in each year. For each simulated dataset, we then used either our MCMC model or a GLMM (fit using all data, with no missing information) to estimate growth and survival parameters. We compared the resulting parameter estimates to each other and to the input parameters used to generate the simulated data. Further details of these simulations are provided in Appendix A.

To gauge the downstream effects of our estimation method on *E. brandegeei* population inference, we used the estimated annual vital rates to construct size-structured demographic models (SSDMs) and used them to predict population numbers over the course of the study period as well as short-term stochastic population growth rates ($\lambda_{SS}$). SSDMs, which can be viewed as either matrix models of high dimension or as integral projection models (Doak et al., 2021), use discrete time intervals for analyzing discretized vital rates that are continuous functions of a state variable, usually size. Details of model construction and analysis are given in Appendix A.

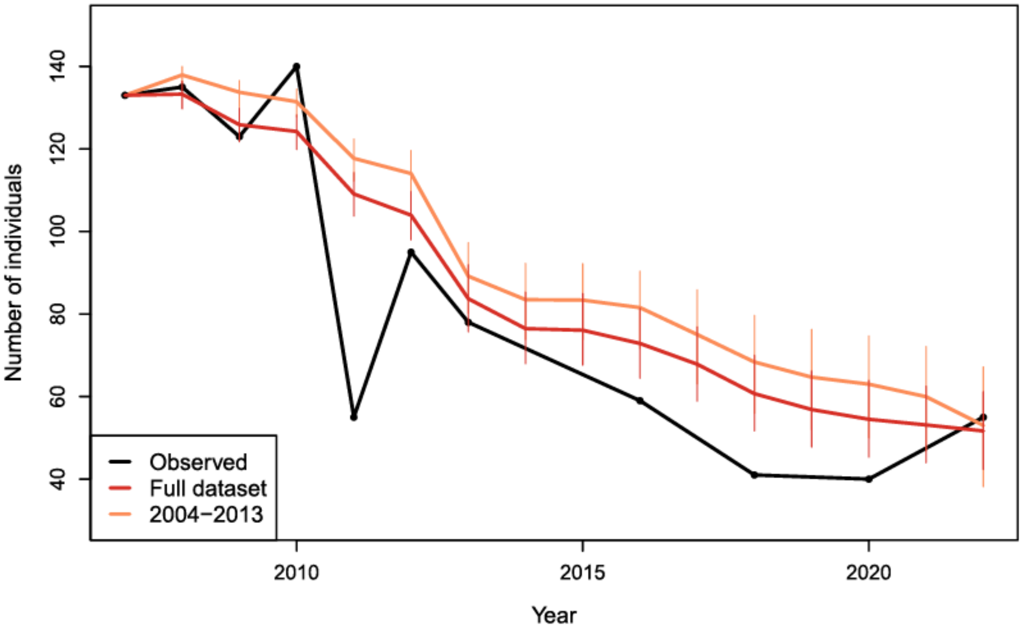

**Fig. 4.** Observed (black) and predicted (colors) number of individual plants over the study period. We present values starting in 2007, as the number of observed individuals between 2004 and 2007 changed substantially due to additional (mostly large) plants being added to the study. Only plants larger than 5 rosettes are included. Predicted population sizes are based on a demographic projection model using vital rate models parameterized with either the full dataset (2004–2022 with gaps; red), or consecutive year data from 2004 to 2013 (orange). The observed population size in 2007 of 133 individuals was set as the starting point for predictions to allow comparison. Error bars show 5th and 95th quantiles to reflect parameter uncertainty ($n = 1000$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 3. Results

In analyses of *E. brandegeei* data, we found satisfactory convergence within- and between chains and low autocorrelation from our MCMC model for all vital rate parameters (Table A.5, Figs. A.2–A.7). The a posteriori parameter distributions of most vital rates were similar between datasets with missing (full or pruned datasets) and no-missing data (2004–2013, 2004–2008, or 2009–2013) and between the GLMM and MCMC model fits (Fig. 2). In particular, GLMM parameter estimates and MCMC parameter estimates using the full and long consecutive year (2004–2013) datasets were very similar. We found that use of the shortest sets of data (pruned, 2004–2008, and 2009–2013) led to the widest posterior distributions and also resulted in some model convergence issues (Fig. 2; Tables A.7–A.10). In general, these short datasets (pruned and consecutive) produced less consistent estimates.

Predicted size-dependent vital rate curves, and their dependence on rainfall, were similar for models fit with the full and long consecutive year data (Fig. 3). We saw the largest deviations between these two datasets in size-dependent growth and survival curves in the wettest year. This is presumably since the wettest year, 2015, was not in the consecutive year data and therefore this model is less reliable for making predictions for climate years that are more extreme than those in the dataset. Following from the higher deviations in parameter estimates, vital rate curves for the shorter datasets (pruned and consecutive) were less consistent (results not shown).

Models fit to our simulated datasets showed that our MCMC approach returns parameter values for growth and survival models that are as accurate as those from GLMMs that use data without missing years. For all three life histories, there is no qualitative difference in the accuracy of these two methods, even though the MCMC approach is dealing with alternate year missing data (Figs. A.9–A.11). In addition, our comparison of results from MCMC fits with and without missing data show little difference in accuracy (Fig. A.12). The longer, 40-year datasets show only slightly improved accuracy in parameter estimation over the 20-year datasets (Fig. A.13). We also note that the parameters for annual climate effects are estimated well, in addition to size coefficients (Figs. A.9–A.13). Translating parameter estimates into size- and climate-specific vital rates also indicate that the MCMC fits are as accurate as the GLMM estimates that model data without missing years (Figs. A.14–A.16). Both GLMM and MCMC models tended to perform somewhat less well with life histories with lower survival rates. In both cases, size parameters were systematically under-estimated for these life histories (Figs. A.10–A.11). This is probably due to both the 'regression to the mean' effect and also due to the capping of low numbers of particularly large predicted sizes, which, though rare, have high leverage.

Returning to the *E. brandegeii* data, we used the posterior distributions of parameter estimates from the full and long consecutive year datasets to predict the changing numbers of individuals in each year of the study period and compared these estimates to the actual recorded number of individuals over the same timeframe (Fig. 4). While predicted numbers from both model fits were similar to the observed numbers, both slightly overestimated population size in most years; this overestimation was less pronounced when using the full compared to the consecutive year dataset (Fig. 4).

Finally, we used the vital rate fits to predict $\lambda_{SS}$ from year to year, using the structured population models and the observed sequence of climate years over this period (Fig. 5). We find that the full and long consecutive year datasets produce similar distributions of $\lambda_{SS}$ estimates that center around 0.96. Results based on the shorter datasets all have wide, often multi-modal, distributions that largely overlap $\lambda_{SS} = 1$.

## 4. Discussion

We developed a modeling approach to estimate population viability of a rare species from a dataset with multiple years entirely lacking data. Our modeling approach allows better use of datasets with missing years of demographic data by negating the need to throw away information over multi-year transitions. Thereby this approach increases the power of available datasets to study the dynamics of populations for which only patchy demographic data often exists. Importantly, the modeling approach allows estimation of not only the mean and variance of vital

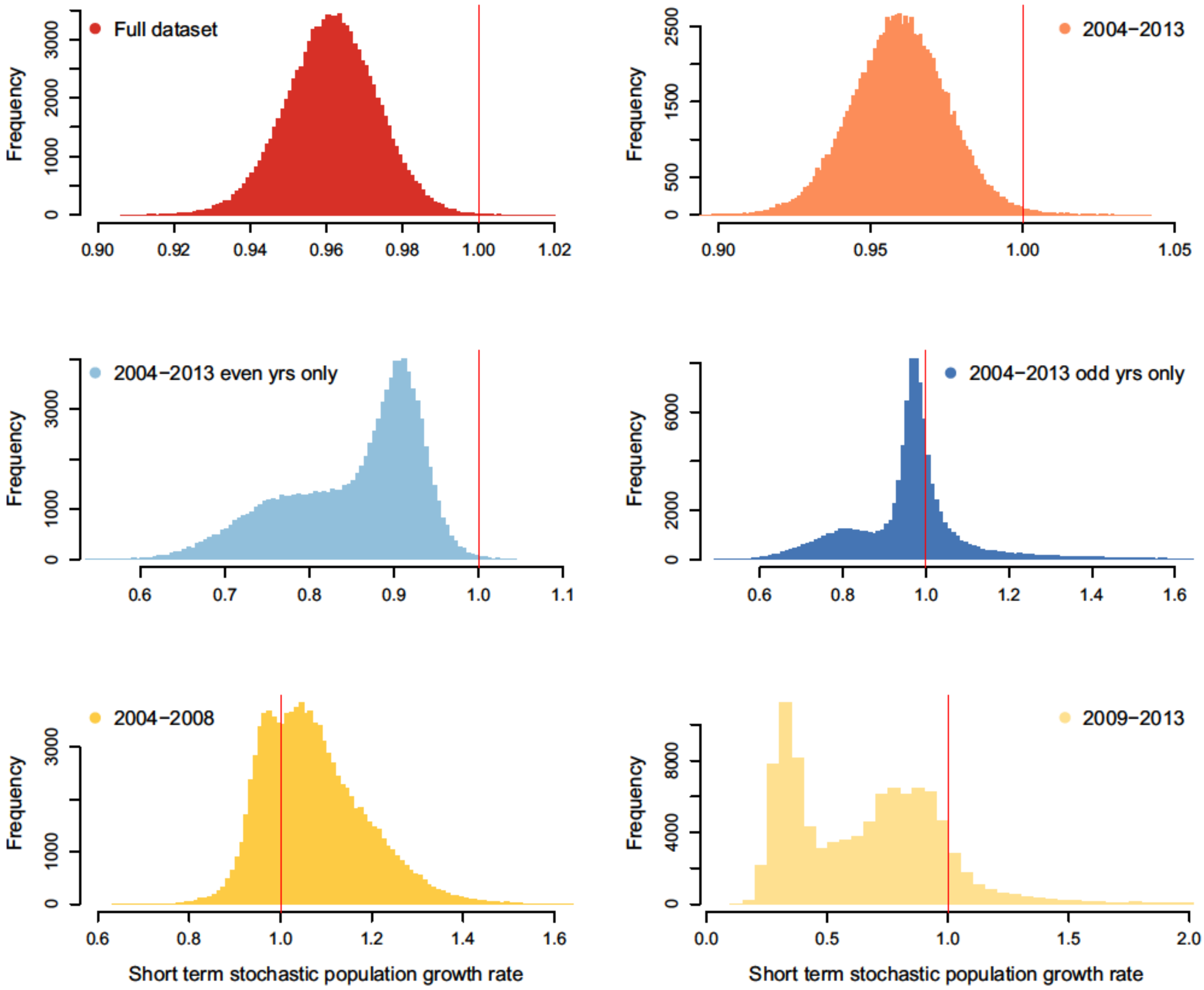

**Fig. 5.** Short-term stochastic population growth rate ($\lambda_{SS}$) estimates from climate-driven projection models run for 100-year simulations. Each iteration of the simulation consisted of randomly selecting climate conditions from climate data of the recent past (2002–2021). Different colors represent different datasets. Variation in estimates is due to parameter uncertainty ($n = 1000$) as well as environmental stochasticity ($n = 100$). The red vertical lines indicate a $\lambda_{SS}$ value of 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rates, but also their dependence on environmental drivers, a critical part of population analysis in the age of climate change. This approach is designed to be applicable to any demographic study, regardless of taxa. In particular, our simulation results indicate that the approach will work for shorter-lived species as well as medium to long lived ones, such as *E. brandegeii*. Having high survival over multiyear transitions is therefore not a prerequisite for results that are as accurate as those coming from complete datasets of the same duration.

While this approach works well for the presented 18-year dataset, there are limitations to obtaining robust results driven by dataset length and quality. Our results suggest that if every other year data collection had been used for the entirety of this study, the data may have been insufficient to generate robust vital rate models. This conclusion is based on the high uncertainty in results based on models parameterized with the short, pruned data. These pruned datasets were at most half as large as the long consecutive year and full datasets, so convergence issues are likely to arise as much from small datasets as missing year data per se. This is corroborated by the results of the short consecutive year datasets, which also show high uncertainty in parameter and downstream estimates. For the short datasets, estimates of a given parameter varied substantially when using even versus odd years between 2004 and 2013, or when using the consecutive years 2004–2008 versus 2009–2013 (Fig. 2). This demonstrates model sensitivity to inputs when datasets are small, particularly in systems with high interannual climate variability (Fig. A.17). But the results do not suggest that missing annual data per se was an issue.

Similarly, we find that use of 40- rather than 20-years of simulated data resulted in more consistent parameter estimates (Fig. A.13), although this improvement was surprisingly small. Future work to test a wider range of missing data patterns (such as irregular gaps) and sample sizes, including both monitored individuals and number of years, will be needed to fully confirm how robust the method is. As well as if having some consecutive years of data collection will always be important to improve model parameterization. This will likely depend on the individual growth patterns of the focal species (Che-Castaldo and Inouye, 2011), the level of year-to-year observation error, and how strongly vital rates depend on annually varying drivers. An added complication arises from a particular type of observation error: the ability to consistently define individuals when clonal or spreading growth patterns are common, which can add substantial error in both survival and growth estimates (DePrenger-Levin, 2024). Beyond observation error, species with large decreases or increases in size from year to year may also make growth estimation more challenging over years of missing data, because there is greater variance in true outcomes and hence much greater variance in potential size changes over multiple transitions that would still result in the same ending sizes (Doak and Morris, 1999).

Beyond the analysis of existing data, our modeling approach could also be used to plan future data collection. In particular, to quantify the statistical costs of skipping some years of data collection versus the benefits of reduced monitoring time and expense. As we suggested above, this tradeoff is likely to differ with life history, responsiveness to climate or other annual environmental variation, as well as with aspects of monitoring method that influence observation errors. Other studies have concluded that having higher quality, longer-term, but less frequent data collection can be preferable for inferring temporal changes in population size using abundance data, given that demographic rates have already been established (Humbert et al., 2009). And some authors have argued sparse temporal data for many populations can produce robust estimates of species demographic distributions using integral projection models (Merow et al., 2014).

The approach used here suggests that for continued monitoring of *E. brandegeei*, maintaining every other year sampling shows no obvious downsides and should be sufficient for capturing population dynamics. Predicted changes in population size over the study period were close to those observed (Fig. 4). It should be noted, however, that the models consistently overestimated population size. This is mostly due to an overestimation of small plants, which were disproportionately overestimated compared to any other size class (Fig. A.18). We found improvement in predicted numbers when small plants (<5 rosettes) were excluded. This is likely due to poor estimation of seedling recruitment and the difficulty in finding small plants, leading to misestimation of their vital rates. This is likely to be a challenge for many species with low recruitment and many small, difficult to spot individuals. Which emphasizes the need to expand field efforts devoted to seedling (or offspring more generally) data collection, when possible, to improve model performance. Another notable difference between observed and predicted values was in 2011 when there was a sharp decline in population size that largely rebounded the following year. This decline was due to some plant mortality following a particularly dry year (Fig. A.17) but most of the decline was likely due to detection issues of plants that appeared dead above-ground but that resumed growth the following year. The models captured a slight decline in 2011, likely explained by drought-driven mortality, but the majority of the decline was not captured well.

Our results can help guide future monitoring efforts for rare species, specifically in developing strategies to obtain robust vital rates in early stages of monitoring that can then allow for reduced sampling efforts in future years. A main application of our modeling approach is for determining population dynamics of rare or threatened species. Our estimates of short-term stochastic lambda for *E. brandegeii* were below 1, indicating population decline. Future analyses will use our vital rate modeling approach in combination with population models driven by climate change predictions to assess dynamics of this rare species and predictions of extinction risk with increasing climate alterations. Investigations of this kind, in general, can facilitate an understanding of how populations may respond to climate change and allow for appropriate conservation actions that can increase the likelihood of persistence (Wan et al., 2022, Hindle et al., 2023).

## CRediT authorship contribution statement

**April M. Goebl:** Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation. **Michelle DePrenger-Levin:** Writing – review & editing, Validation, Resources, Investigation, Data curation. **Rebecca A. Hufft:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition. **Daniel F. Doak:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

## Declaration of competing interest

All authors have seen and approved the current version of the manuscript. The article is the original work of the authors and has not been submitted elsewhere for publication consideration.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110855.

## Data availability

Demographic data and R scripts used for modeling and data analysis are publicly available on GitHub at https://github.com/DenverBotanicGardens/ErBr_Goebl_etal

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