



Ability of Matrix Models to Explain the Past and Predict the Future of Plant Populations

ELIZABETH E. CRONE,* MARTHA M. ELLIS,† WILLIAM F. MORRIS,‡ AMANDA STANLEY,§
TIMOTHY BELL,** PAULETTE BIERZYCHUDEK,†† JOHAN EHRLÉN,‡‡ THOMAS N. KAYE,§
TIFFANY M. KNIGHT,§§ PETER LESICA,*** GERARD OOSTERMEIJER,†††
PEDRO F. QUINTANA-ASCENCIO,‡‡‡ TAMARA TICKTIN,§§§ TERESA VALVERDE,****
JENNIFER L. WILLIAMS,†††† DANIEL F. DOAK,‡‡‡‡ RENGAIAN GANESAN,§§§§
KATHYRN MCEACHERN,***** ANDREA S. THORPE,§ AND ERIC S. MENGES†††††

*Harvard Forest, Harvard University, 324 N Main Street, Petersham, MA 01366, U.S.A. email ecrone@fas.harvard.edu

†Wildlife Biology Program, University of Montana, Missoula, MT 59812, U.S.A.

‡Biology Department, Duke University, Box 90338, Durham, NC 27708-0338, U.S.A.

§Institute for Applied Ecology, P.O. Box 2855, Corvallis, OR 97339-2855, U.S.A.

**Chicago State University, 9502 South King Drive, Chicago, IL 60628, U.S.A.

††Lewis & Clark College, 0615 S.W. Palatine Hill Rd., Portland, OR 97219, U.S.A.

‡‡Department of Botany, Stockholm University, Lilla Frescativägen 5, SE 10691, Stockholm, Sweden

§§Department of Biology, Washington University in St. Louis, St. Louis, MO 63130, U.S.A.

***Division of Biological Sciences, University of Montana, Missoula, MT 59812, U.S.A.

†††Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH, Amsterdam, The Netherlands

‡‡‡Department of Biology, University of Central Florida, Orlando, FL 32816-2368, U.S.A.

§§§Botany Department, University of Hawai'i at Manoa, Honolulu, HI 96822, U.S.A.

****Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, México, D.F. 04510, México

††††National Center for Ecological Analysis and Synthesis, 735 State Street Suite 300, Santa Barbara, CA 93101, U.S.A.

‡‡‡‡Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, U.S.A.

§§§§Suri Sehgal Centre for Biodiversity and Conservation, Ashoka Trust for Research in Ecology and the Environment (ATREE), Royal Enclave, Srirampura, Jakkur, PO Bangalore- 560064, India

*****U. S. Geological Survey, WERC, Channel Islands Field Station, 1901 Spinnaker Drive, Ventura, CA 93001, U.S.A.

†††††Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33862, U.S.A.

Abstract: *Uncertainty associated with ecological forecasts has long been recognized, but forecast accuracy is rarely quantified. We evaluated how well data on 82 populations of 20 species of plants spanning 3 continents explained and predicted plant population dynamics. We parameterized stage-based matrix models with demographic data from individually marked plants and determined how well these models forecast population sizes observed at least 5 years into the future. Simple demographic models forecasted population dynamics poorly; only 40% of observed population sizes fell within our forecasts' 95% confidence limits. However, these models explained population dynamics during the years in which data were collected; observed changes in population size during the data-collection period were strongly positively correlated with population growth rate. Thus, these models are at least a sound way to quantify population status. Poor forecasts were not associated with the number of individual plants or years of data. We tested whether vital rates were density dependent and found both positive and negative density dependence. However, density dependence was not associated with forecast error. Forecast error was significantly associated with environmental differences between the data collection and forecast periods. To forecast population fates, more detailed models, such as those that project how environments are likely to change and how these changes will affect population*

dynamics, may be needed. Such detailed models are not always feasible. Thus, it may be wiser to make risk-averse decisions than to expect precise forecasts from models.

Keywords: density dependence, ecological forecasting, environmental change, matrix projection models, plant population dynamics, population viability analysis, precipitation, temperature

Habilidad de los Modelos Matriciales para Explicar el Pasado y Predecir el Futuro de las Poblaciones de Plantas

Resumen: *La incertidumbre asociada con el pronóstico ecológico ha sido reconocida durante un largo tiempo pero rara vez se cuantifica su seguridad. Evaluamos que tan bien la información de 82 poblaciones de 20 especies de plantas a lo largo de 3 continentes explica y predice la dinámica de población de las plantas. Realizamos parámetros con modelos matriciales con base en estadios con datos demográficos a partir de plantas marcadas individualmente y determinamos que tan bien estos modelos pronostican el tamaño de las poblaciones al menos 5 años en el futuro. Los modelos demográficos simples pronosticaron pobremente las dinámicas de población; solamente el 40% de las poblaciones observadas cayó dentro de los límites de confianza de 85% de nuestros pronósticos. Estos modelos sin embargo explicaron la dinámica de población a lo largo de los años en los que se colectaron datos; los cambios observados en el tamaño de la población durante el periodo de colecta de datos estuvieron positivamente correlacionados con la tasa de crecimiento de la población. Así, estos modelos son por lo menos una manera segura de cuantificar el estado de la población. Los pronósticos débiles no estuvieron asociados con el número de plantas individuales o con los años de datos. Probamos si las tasas vitales dependían de la densidad y encontramos que existe dependencia hacia la densidad tanto positiva como negativa, sin embargo la dependencia de densidad no se asoció con el error de pronóstico. El error de pronóstico estuvo significativamente asociado con diferencias ambientales entre la recolección de datos y los periodos de pronóstico. Para predecir el destino de las poblaciones se necesitan modelos más detallados, como aquellos que proyectan los cambios probables en el ambiente y como estos cambios afectarán a la dinámica de las poblaciones. Tales modelos tan detallados no siempre son factibles. Por ello puede ser mejor tomar decisiones aversas a riesgos que esperar pronósticos precisos de los modelos.*

Palabras Clave: análisis de viabilidad poblacional, dependencia de la densidad, dinámica poblacional de plantas, modelos de proyección matricial, precipitación, pronóstico ecológico, temperatura

Introduction

Ecologists are increasingly asked to forecast how populations will respond to anthropogenic environmental changes such as habitat loss or climate change or to management actions such as control of invasive species. Matrix projection models are the primary models used to study plant and animal population dynamics (Morris & Doak 2002; Crone et al. 2011). Part of the appeal of matrix models is that their relative transparency and ease of use makes them widely accessible. These models combine age- or stage-specific vital rates (birth, death, and growth rates) to project population change through time. Model projections are used in 2 distinct ways (roughly analogous to projection versus prediction [sensu Caswell 2001]). First, they integrate multiple vital rates into a single metric, the population growth rate. This integration is useful when management affects some vital rates positively and others negatively (e.g., Lennartsson & Oostermeijer 2001; Crone et al. 2009a; Farrington et al. 2009) or when some vital rates have much larger effects than others on population growth rate (e.g., Crouse et al. 1987; Biek et al. 2002; Adams et al. 2005). Second, model projections can be interpreted as forecasts of populations' future fates, for example, in population viability analysis for endangered species (Brook et al. 2000; Menges 2000).

Matrix models are more often used to integrate vital rates than to make forecasts (Beissinger & Westphal 1998; Caswell 2001; Crone et al. 2011), and modelers have cautioned for decades against interpreting projections as forecasts (cf. Caswell 1989). Nonetheless, about one-third of published studies present matrix model results as literal forecasts of population fates (Crone et al. 2011), and growing demand for ecological forecasts (Clark et al. 2001; Carpenter 2002) has led to interest in using such models to predict population dynamics (Brook et al. 2000; Coulson et al. 2001; Ellner & Holmes 2008). Similarly, listing and recovery decisions for endangered species that include quantitative population projections from matrix models have been presented as a standard of excellence (Schemske et al. 1994; Morris et al. 2002; Neel et al. 2012).

Because of their relative simplicity, matrix models have been criticized as possibly not realistic enough to make meaningful projections or forecasts (Beissinger & Westphal 1998; Bierzychudek 1999; Coulson et al. 2001). Numerous researchers have proposed more realistic extensions to these models (e.g., Rees & Ellner 2009; Tuljapurkar et al. 2009; Ezard et al. 2010). An additional concern is that most matrix models are density independent, whereas many populations have density-dependent vital rates (Beissinger & Westphal 1998; Bierzychudek 1999). Finally, a widely cited caution against interpreting

model projections as forecasts is that predictions only apply to the environmental conditions that occurred during data collection for model parameterization (Caswell 2001; Coulson et al. 2001).

We explicitly tested the utility of matrix models for understanding and predicting plant population dynamics by comparing model predictions to observed population changes. We know of only one other broad test of demographic model predictions. Brook et al. (2000) evaluated population viability forecasts for 21 vertebrate populations and concluded that population models accurately forecast population fates. However, their conclusions have been criticized on several levels, including the fact that they were based only on species with unusually extensive demographic data. We know of 5 tests of population model forecasts for individual plant species (Kephart & Paladino 1997; Bierzychudek 1999; Lindborg & Ehrlén 2002; Van Mantgem & Stephenson 2005; Schodelbauerova et al. 2010). Model predictions were accurate in at most 3 of these (Kephart & Paladino 1997; Van Mantgem & Stephenson 2005; Schodelbauerova et al. 2010). Relative to these past studies, our analyses provide a more comprehensive test of models fit to typical plant population data. We also evaluated whether matrix models explain population dynamics during the study period and forecast future dynamics (i.e., testing utility for projection and prediction). Although it may seem obvious that models should reproduce population dynamics during the data-collection period, there are several reasons why they might not. For example, calculated growth rates would not match observed population dynamics if demographic parameters were poorly estimated, if population age or stage structure were not at equilibrium (e.g., Ezard et al. 2010), if vital-rate variation was not incorporated into the model appropriately (e.g., confounding estimation error or differences among individuals with environmental stochasticity) (Kendall & Fox 2002), or if parameters were averaged inappropriately (Tuljapurkar et al. 2003).

If forecasts fail to predict what populations actually do, then to identify methods to produce better forecasts, one must pinpoint the causes of that failure. We explored 3 possible causes: sample sizes are too small or forecast periods too long relative to the data-collection period; density-independent models fail to account for important density-dependent processes; and environmental changes produce vital-rate changes between the data-collection and forecast periods.

Methods

Demographic Data and Matrix Construction

In our analyses, we used data from 82 populations of 20 plant species. All data were collected by one or more

coauthors of this paper. We included only populations for which stochastic population models with independent, identically distributed variation seemed to us ecologically appropriate. For example, we excluded populations affected by disturbances such as mowing or fire. Our study-specific methods, transition matrices, and population vectors are available through the Ecological Society of America's Ecological Archives (Ellis et al. 2012).

The study sites for most species (13) were in the United States; others were in Mexico, India, or Sweden (Supporting Information). The number of populations per species varied from 1 to 10. Plant vital rates are typically estimated from plot-based monitoring and annual surveys (Lesica 1987). All our studies used plot-based methods, included 3 or more annual matrices, and were followed by a population survey conducted at least 5 years after the last year of demographic data collection (see Ellis et al. [2012] for details). For cases in which demographic data were collected continuously up to the final survey, we deleted the final 5 or more years of demographic data to create a forecast period. For these data sets, we used the population structure of the last year as the final survey.

For each population, we defined stages appropriate to the species' biology and the sampling effort and created stage-based annual matrices from demographic data on individually marked plants. The number of matrices per population varied from 3 to 12 (median = 5) (Ellis et al. 2012). We calculated stage-based vital rates (stasis, growth, and regression) directly from observed individual fates with our own code and functions from the *popbio* package in R (Stubben & Milligan 2007). Small sample sizes occasionally required us to calculate some vital rates from data pooled across years or estimated from other sources (Ellis et al. 2012). Methods for estimating fecundity parameters varied by study but generally followed published models for each species and were usually calculated either from ratios of new recruits to numbers of reproductive plants in the previous year or from annual seed counts combined with germination and seed-bank studies (Ellis et al. 2012). Vital rates for cryptic stages (e.g., seeds in the seed bank or dormant plants) were estimated with diverse methods, typically relying on data from additional experiments (e.g., buried seed bags [Ellis et al. 2012]).

We calculated metrics related to total population size (N), both observed and predicted, only for visible stages. We did not include dormant individuals, those in seed banks, and some other stages (depending on the species) (Ellis et al. 2012).

Testing Model Predictions

First, we tested whether models were a meaningful way to integrate vital rates within a study period. We compared asymptotic measures of population change (deterministic and stochastic population growth rates, λ and λ_S ,

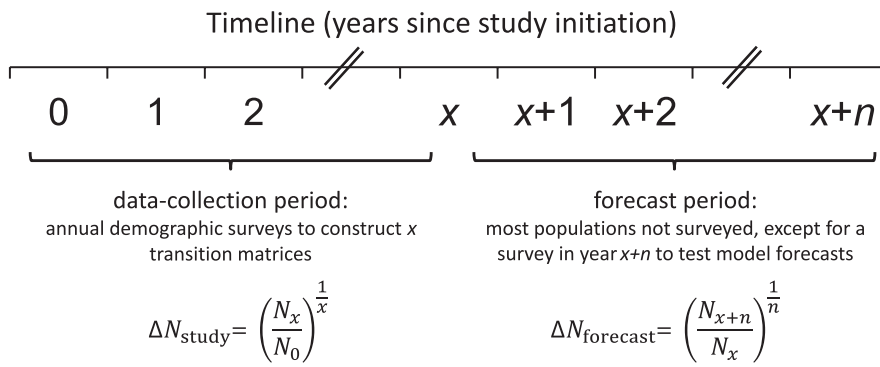


Figure 1. Timeline of data collection relative to observed population growth rates, ΔN_{study} and $\Delta N_{\text{forecast}}$.

respectively) with observed changes in population size during the years when data were collected for model parameterization (hereafter, data-collection period) (Fig. 1). To calculate λ , we used the leading eigenvalue of the mean of the matrices. We calculated λ_S with Tuljapurkar's (1982) approximation for realized population growth in the presence of independently and identically distributed environmental fluctuations. We calculated observed changes in abundance as annual per capita population growth rates, ΔN_{study} , defined as $(N_x/N_0)^{1/x}$, where x is the length of the data-collection period and N_0 and N_x are population sizes (i.e., the sum of the stage distribution vector) in the first and last years of this period, respectively. We evaluated several kinds of population growth rates, some calculated with matrix models and others calculated from population size observations. Although all are per capita growth rates, we used $\Delta N_{\text{subscript}}$ to represent growth rates calculated from ratios of observed total population sizes in different years and $\lambda_{\text{subscript}}$ to represent growth rates calculated from models (Table 1).

Second, we tested the ability of models to forecast future population fates. We did this by comparing model predictions to population sizes in the final survey (hereafter, forecast period) (Fig. 1 & Table 1). As above, we compared λ and λ_S with observed annual per capita

growth rates ($\Delta N_{\text{forecast}}$, defined as $[N_{x+n}/N_x]^{1/n}$, where n is the length of the forecast period).

In addition, we evaluated predictions of transient population dynamics during the forecast period (see Ezard et al. [2010] for discussion of transient versus asymptotic forecasts). To make transient forecasts, we projected populations forward from the last observed stage vector in the data-collection period. For stochastic simulations, we used matrix selection (sensu Kaye & Pyke 2003) (i.e., sampling with replacement from the available matrices with equal probability). Matrix selection is the most typical way in which plant ecologists incorporate environmental stochasticity into demographic projections (Crone et al. 2011). We estimated transient population growth rates, $\lambda_{\text{trans}} = (\tilde{N}_{x+n}/N_x)^{1/n}$, where \tilde{N}_{x+n} is the median predicted population size from 1000 stochastic simulations. We also tabulated the number of observed population sizes at the end of the forecast period (N_{x+n} in Table 1) that fell within the 95% confidence limits (i.e., between the 2.5th and 97.5th percentile) of simulated values of the final population sizes. As additional tests of model forecasts, we repeated the asymptotic analyses twice. First, we weighted the stage vector by the reproductive values of each stage class. Second, we used only the stage class with the largest reproductive value.

Table 1. Definitions of symbols used in analyses of projections and forecasts from matrix population models.

Metric	Description
Variables calculated from observed number of individuals	
N_x	total population size at start of forecast period, observed (noncryptic) stages only
N_{x+n}	total population size at end of forecast period, observed (noncryptic) stages only
ΔN_{study}	observed population growth rate over the data-collection period: $(N_x/N_0)^{(1/x)}$
$\Delta N_{\text{forecast}}$	observed population growth rate over the forecast period: $(N_{x+n}/N_x)^{(1/n)}$
Variables calculated from matrices and simulations	
λ	deterministic population growth rate from the mean matrix
λ_S	stochastic population growth rate computed from Tuljapurkar's (1982) approximation
\tilde{N}_{x+n}	median total projected population size at the end of the forecast period (observed stages only)
λ_{trans}	transient population growth rate $(\tilde{N}_{x+n}/N_x)^{(1/x)}$
Covariates of forecast error, calculated from the data	
x	number of annual transition matrices (i.e., number of annual population surveys during the study period minus 1)
n	forecast period: number of years between the end of the original study and the end of the forecast period
SS	mean sample size (weighted by elasticities)
CTLs	conditional total lifespan (computed with Cochran and Ellner's [1992] method)

Table 2. Results of analyses signed and absolute (unsigned) prediction error as functions of covariates calculated from the demographic data.*

Analysis type	Sample size (SS)		No. of matrices (x)		Years in forecast period (n)		Conditional total lifespan (CTLS)	
	t	p	t	p	t	p	t	p
Signed prediction error, $\Delta N_{\text{forecast}} - \lambda_{\text{trans}}$								
fixed, multivariate	-1.28	0.203	2.01	0.048	0.26	0.792	1.11	0.273
fixed, univariate	-1.30	0.199	1.92	0.058	-0.46	0.643	0.58	0.565
mixed, multivariate	-1.44	0.141	2.11	0.044	-0.40	0.367	0.53	0.345
mixed, univariate	-1.43	0.143	2.23	0.035	-0.99	0.243	0.19	0.390
Absolute prediction error, $ \Delta N_{\text{forecast}} - \lambda_{\text{trans}} $								
fixed, multivariate	0.06	0.956	-0.43	0.668	-0.44	0.660	-1.56	0.124
fixed, univariate	-0.07	0.984	-0.00	0.996	-0.25	0.804	-1.59	0.135
mixed, multivariate	0.47	0.356	-0.79	0.290	-0.05	0.397	-0.99	0.242
mixed, univariate	0.37	0.371	-0.68	0.315	0.24	0.368	-1.02	0.236

*Abbreviations are as in Table 2.

The reproductive-value-weighted vector is insensitive to transient dynamics (Engen et al. 2009), and both response variables are less sensitive than λ or λ_S to fluctuations in stage classes with low reproductive value (e.g., seedling pulses followed by seedling mortality). The reproductive-value-weighted analyses did not reveal stronger correlations between observed and forecasted changes in population size and are not discussed further.

We calculated both Pearson correlations and Kendall's rank correlations between observed (ΔN_{study} or $\Delta N_{\text{forecast}}$) and modeled (λ , λ_S , or λ_{trans}) population growth rates with all populations and with arithmetic mean values for each species. For species with 3 or more populations, we calculated Pearson and rank correlations among populations. We evaluated the significance of analyses of multiple populations within species on the basis of a single p value for combined probabilities from independent tests (Sokal & Rohlf 1995). In addition, we calculated the ratio of observed to modeled population growth rates from zero-intercept regressions of observed versus modeled population growth rates. If estimated population growth rates are unbiased, the slope of this line should be one.

Causes of Forecast Error

We evaluated possible causes of forecast error with 3 separate analyses. First, we conducted exploratory analyses of metrics that could be calculated directly from the demographic data and were likely to be associated with forecast error. Second, we estimated the strength of density dependence in each population and then tested whether density dependence was associated with forecast error. Third, we related changes in temperature and precipitation between the data-collection and forecast periods to forecast error.

We selected 4 covariates that could be straightforwardly calculated from demographic data and that we thought would most likely affect forecast error: number

of matrices used to parameterize models (x in Tables 1 and 2); length of the forecast period (n in Tables 1 and 2); sample size (mean number of individuals per stage per year, weighted by the matrix-column-wise sum of each stage's elasticity); and conditional total lifespan (Cochran & Ellner 1992). We expected predictions of population size to improve with a longer data-collection period (more matrices), shorter forecast period, larger sample size, and longer lifespan (because a larger fraction of the plants from the data-collection period would still be alive in the test year).

We conducted multiple regressions to relate both signed and unsigned prediction error to these 4 covariates. We modeled signed prediction error, which was approximately normal, with linear regression. We modeled absolute (unsigned) prediction error, which was skewed and (by definition) bounded at zero with gamma-family generalized linear regressions. For our first analysis, we treated populations as independent observations. To ensure that our analyses were not omitting key explanatory covariates, we also analyzed prediction error with univariate regressions for each covariate and used mixed models with species included as a random effect. These results were not statistically significant and are not discussed further.

Density dependence, often cited as a reason why matrix models may not explain past or predict future population dynamics (e.g., Bierzychudek 1999), generates specific expectations about forecast error. If vital rates are negatively density dependent, forecasts of population size should be too high for populations that grew during the data-collection period and too low for populations that declined. Positive density dependence (i.e., Allee effects) produces the opposite pattern (see Supporting Information).

To quantify density dependence, we estimated the leading eigenvalue for each annual transition matrix for each year t of the study, λ_t , and the total population size each year, N_t , defined as the sum of all plants over all

observed (noncryptic) stages. We estimated density dependence from a linear mixed model of λ_t versus N_t , with species and population nested within species as random effects. The leading eigenvalue for each annual transition matrix for each year t of the study is an integrated measure of the asymptotic effect of density N_t on all vital rates. If population growth declines as density increases (i.e., a negative slope), this linear function can be reparameterized as the discrete logistic model of population growth. A positive slope indicates an Allee effect over the range of densities observed in the study years. To compare density dependence across taxa and populations, we standardized both λ_t and N_t to have a mean of zero and a standard deviation of one for each population. This rescaling allowed us to compare the effects of density across species with disparate growth forms.

The expected association between density dependence (slope of λ_t vs. N_t , hereafter β) and prediction error depends on the population growth rate during the data-collection period. From first principles, we expected a positive correlation between signed prediction error ($\Delta N_{\text{forecast}} - \lambda_{\text{trans}}$) and the product of ($\Delta N_{\text{study}} - 1$) and β (Supporting Information). However, in our data, λ_{trans} and ΔN_{study} were strongly positively correlated, and β was usually negative (see Results), which would also produce a positive correlation. Therefore, we evaluated the statistical significance of this association relative to a null distribution. To obtain the null distribution, we created bootstrapped data sets in which observed values of β were combined with random pairs of values for prediction error and λ_{trans} (selected by sampling with replacement from the full set of pairs). We also explored correlations between β and signed and unsigned prediction error to look for possible alternative associations.

We obtained climate data for populations in the continental United States (59 populations of 13 species) from Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al. 2010). For each population, we calculated 4 metrics, the mean and the among-year variance for both annual precipitation (μ_{precip} and σ^2_{precip}) and mean daily maximum temperature ($\mu_{t\text{max}}$ and $\sigma^2_{t\text{max}}$). We compared values of these 4 variables between the data-collection period plus 2 prior years (to account for the potential effects of prior conditions on demographic rates) and the forecast period.

We used the standard deviation of annual precipitation and mean daily maximum temperature from 1960 to 2009 to calculate the expected differences in each response variable between the 2 periods. If a variable is approximately normally distributed, the expected standard error of the mean, \bar{X} , and the variance, S^2 , for a sample of i years are

$$SE_{\bar{X}} = \sqrt{\frac{\sigma^2}{i}}$$

and

$$SE_{S^2} = \sqrt{\sigma^2 \left(\frac{2}{i-1} \right)}.$$

The variance of the difference of each variable (between the 2 periods) is the sum of the squared standard errors for each period (calculated by substituting x and n for i in the equations above). The expected difference is the 50th percentile of the distribution defined by this variance.

To test whether values of each variable differed significantly between the data-collection and forecast periods, we analyzed the absolute value of the observed minus expected difference with one-sample t tests. To test whether change in these variables were associated with poor forecast ability, we calculated a multiple regression between the absolute value of the prediction error and the absolute value of the difference in each variable with gamma-family generalized linear regressions.

Results

Matrix population models successfully integrated vital rates of individual plants. The ΔN_{study} variable was strongly positively correlated with both λ and λ_S ($r = 0.65$ and $r = 0.77$, respectively) (Figs. 2a & b). Other patterns also matched expectation from general theory. The stronger correlation of ΔN_{study} with λ_S than with λ is consistent with the expectation that stochastic population models are more realistic than deterministic ones. Lambda tended to predict population sizes that were slightly too large (slope of zero-intercept regression of ΔN_{study} vs. λ , 0.976 [SE 0.015]), whereas λ_S was an unbiased predictor (slope of zero-intercept regression of ΔN_{study} vs. $\lambda_S = 1.017$ [SE 0.010]) (Figs. 2a & b), which is consistent with the assumption that environmental stochasticity generally results in lower population growth rates than predicted by deterministic models.

Matrix models did not successfully forecast future fates of the populations we studied. Neither λ nor λ_S was correlated with $\Delta N_{\text{forecast}}$ (Figs. 2c & d) ($r = 0.01$, $p = 0.91$; $r = 0.01$, $p = 0.95$, respectively). Furthermore, model predictions were biased; final population sizes tended to be smaller than predicted by either λ or λ_S (Figs. 2c & d) (ratio of $\Delta N_{\text{forecast}}$ to λ and λ_S , from zero-intercept regressions: 0.855 [SE 0.027] and 0.893 [SE 0.025], respectively). These errors were not caused by transient population dynamics. Observed and simulated transient population growth rates were not significantly correlated (among all populations: $r = 0.04$, $p = 0.76$; among species means: $r = -0.02$, $p = 0.94$, and among populations within species: $\bar{r} = 0.04$, $p > 0.99$), and only 40% of observed population sizes fell within the 95% limits of transient model forecasts, although these limits were usually very wide (Fig. 3).

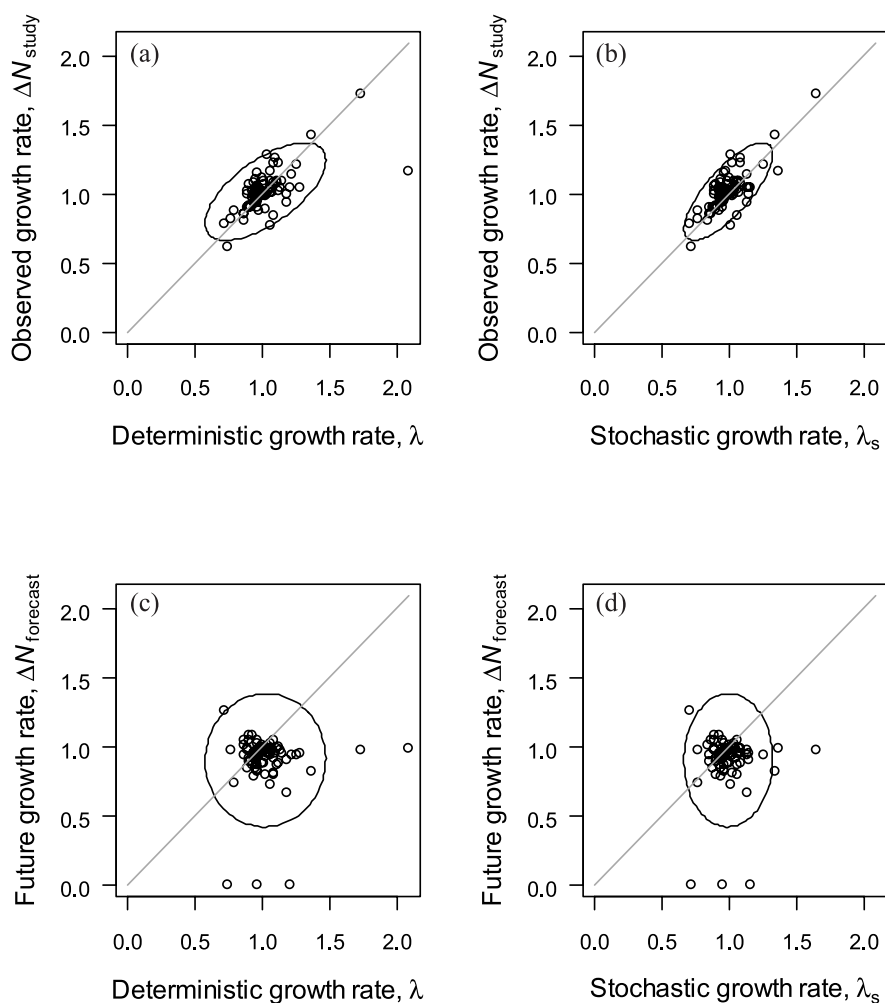


Figure 2. (a, c) Deterministic and (b, d) stochastic population growth rates (λ and λ_s , respectively) versus population growth rates during (a, b) data-collection and (c, d) forecast intervals (ΔN_{study} and $\Delta N_{\text{forecast}}$, respectively). Ellipses indicate 90% confidence intervals of correlations, and lines are the 1:1 association that would be expected if forecasts were unbiased and precise.

Covariates calculated from the demographic data were not strongly associated with prediction error. Models based on fewer annual matrices tended to forecast larger population sizes than we observed ($t = 1.92$, $p = 0.06$). No other covariates of prediction error (shorter forecast period, larger number of plants per stage class [weighted by reproductive value], or longer lifespan) significantly predicted forecast accuracy (Table 2). These results suggest that forecasts could be improved by including more data, but only if those data increased the time period.

We detected density dependence. On average, density dependence was negative (Fig. 4a) (range of β values: -0.525 – 0.132 [Supporting Information]). However, β was not associated with prediction error in the expected direction (Supporting Information) (bootstrap $p = 0.50$) (Fig. 4b). The β values were also uncorrelated with signed and absolute prediction error ($r = -0.021$, $p = 0.85$, and $r = 0.123$, $p = 0.27$, respectively). Therefore, there was little evidence that use of density-dependent models would substantially improve forecasts.

In contrast, the analyses of temperature and precipitation data supported the hypothesis that models did

not forecast future population sizes due to temporal environmental change. Temperature and precipitation differed more between the data-collection and forecast periods than expected on the basis of temporally uncorrelated interannual variation alone (Fig. 4c) (observed vs. expected change between the data collection and forecast periods for mean annual precipitation [$t = 2.62$, $p = 0.01$], mean daily maximum temperature [$t = 3.85$, $p < 0.001$], variance in annual precipitation [$t = 4.30$, $p < 0.001$], and variance in daily maximum temperature [$t = 1.21$, $p = 0.16$]). Furthermore, prediction error was associated with environmental differences between the 2 periods (correlation of observed vs. expected $r = 0.51$, likelihood-ratio test of multiple regression with 4 environmental covariates compared with a null model: $\chi^2 = 13.4$, $df = 4$, $p = 0.01$). The covariate most strongly associated with poor forecasts was the change in variance of annual precipitation (Fig. 4d) ($t = 2.01$, $p = 0.05$). However, because these climate variables were strongly correlated, it was not possible to attribute poor forecasts to changes in any particular variable.

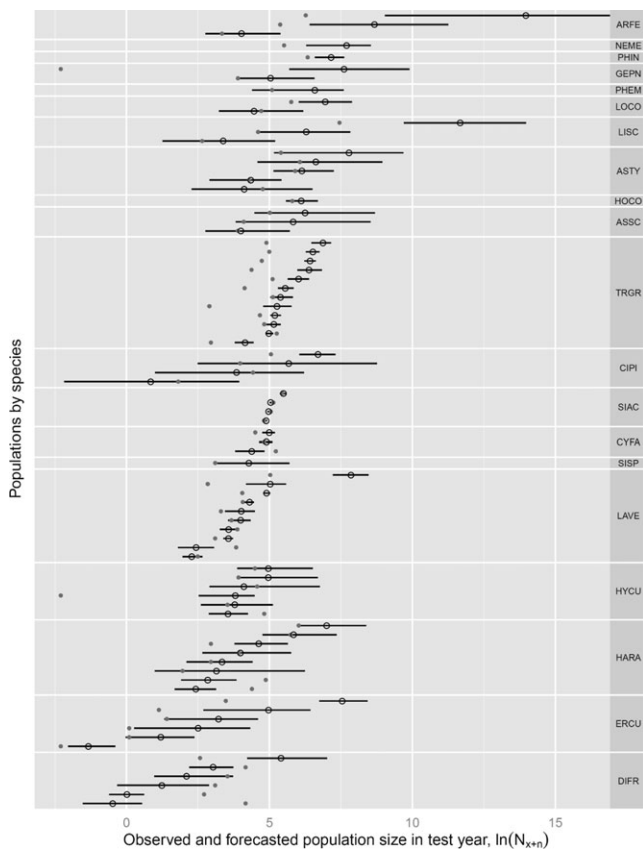


Figure 3. Observed population size at the end of the forecast period (filled circles, N_{x+n}) in relation to forecasted population size from population models (open circles, \hat{N}_{x+n}) (lines, 95% forecast limits). Species codes appear opposite populations of each species and are defined in Supporting Information.

Discussion

Our results point to 3 broad conclusions about the use and interpretation of population models. First, very simple demographic models are an ecologically meaningful way to integrate multiple aspects of individual performance into a single metric of population status. This conclusion implies that simple population models work well for common uses such as projecting population growth rates under current conditions and assessing the net consequences of management alternatives. In this light, more complicated approaches such as integral projection models (Rees & Ellner 2009), transient analysis (Ezard et al. 2010), and serially correlated variance structures (Tuljapurkar et al. 2009) could be viewed as a way to further improve these relatively good projections.

Second, in contrast to the findings of Brook et al. (2000), simple models failed to forecast the future of the populations we studied. The time horizons for these 2 studies were similar. The animals studied by Brook et al. (2000) had a median maximum age of 12 years (range

4–50; see their Supplementary Table 2) and a median forecast period of 10.5 years (range 7–28), whereas the plants in our study had a median conditional total lifespan of 12 years (range 5–326) and median forecast period of 10 years (range 5–18). Our conclusions about forecasting ability may be less favorable because we evaluated the ability of models to predict individual population fates, whereas Brook et al. (2000) based their conclusions on ensemble predictions, which are expected to be more precise (Ellner et al. 2002). Still, predictions for individual populations should show the same trends as ensemble predictions (Ellner et al. 2002), and forecasts were not correlated with observations in our analyses (Fig. 2). One possible explanation is that habitat selection by animals could moderate environmental change, making forecasts for animal populations more accurate than those for plants. In addition, Brook et al. (2000) based their analysis on extensive data sets (Coulson et al. 2001) for which model structures could be tailored to match species-specific biology. In practice, management plans are often made for animal and plant species whose life histories are poorly known (Harding et al. 2001) or on the basis of generic density-independent matrix population models (e.g., Biek et al. 2002; Ellis & Elphick 2007; Morris et al. 2011). Therefore, we strongly caution against the expectation that reliable forecasts can be made from simple population models.

Third, our results shed light on 2 ecological mechanisms that are generally expected to be responsible for poor forecasts. The effect of the first, density dependence, was partially supported by our analyses; asymptotic population growth rates calculated from annual transition matrices tended to be lower in years with more plants. Vital rates of most plants are expected to decline as density increases (Freckleton & Watkinson 2002). However, correlations of vital rates with density do not always imply classical density dependence. For example, density dependence of *Phyllanthus emblica* was positive and was caused by decreasing habitat quality (Supporting Information). This site has been colonized by mistletoe (*Taxillus tomentosus*) in the canopy, which reduces growth, reproduction, and survival of *P. emblica*, and by an understory shrub that limits recruitment. As these invasive species have become more abundant, *P. emblica*'s population size and vital rates have declined (Ticktin et al. 2012). As another example, one of our species, *Astragalus scaphoides*, alternates between years with high flowering and high dormancy (Crone et al. 2005, 2009b). Over decades, one would not expect model forecasts to deviate systematically from observations due to this kind of rapid population cycle. In principle, one could develop species-specific models by regressing individual vital rates against population size for each species and using these models to forecast population dynamics. Such models are relatively rare in plant ecology (Crone et al. 2011), can be problematic to

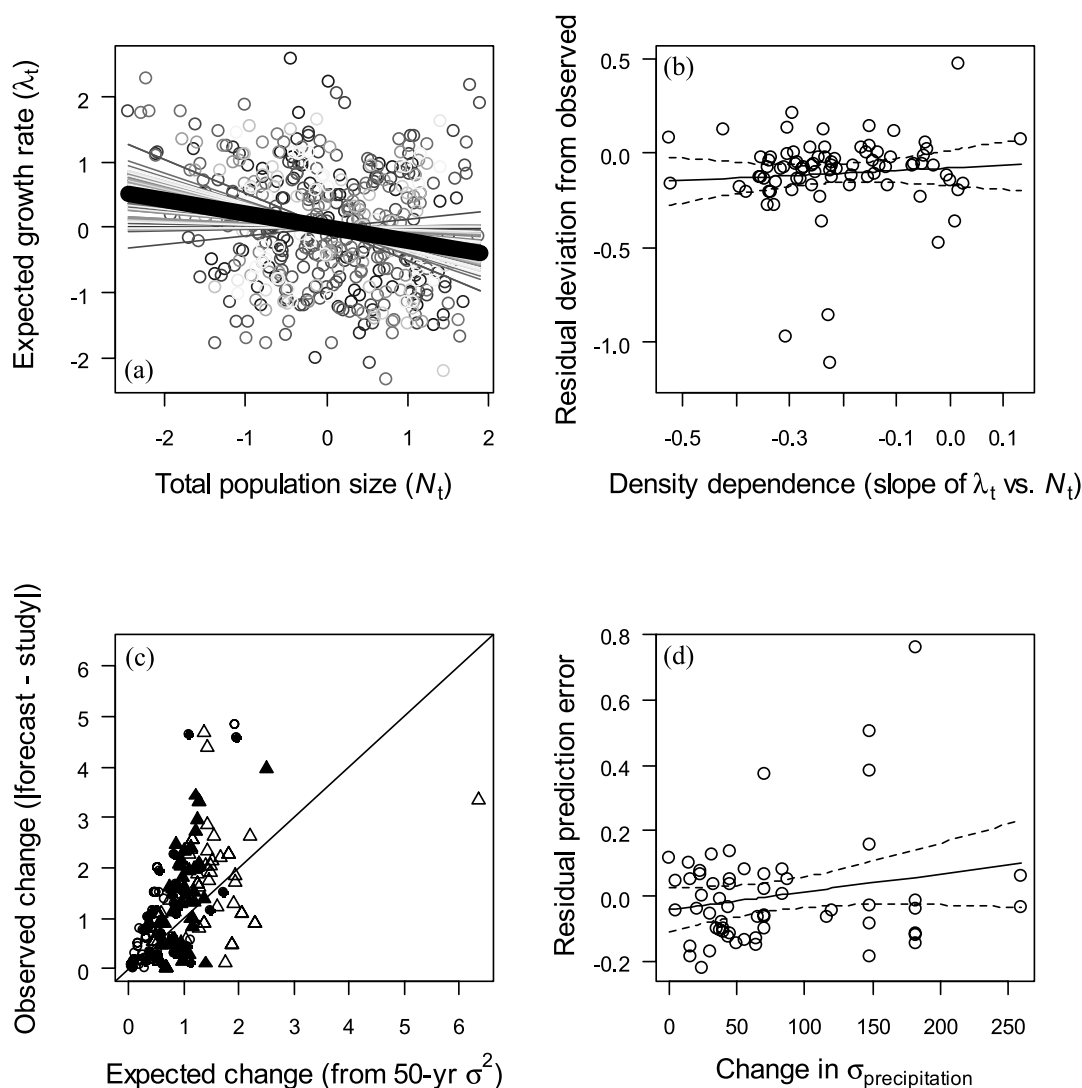


Figure 4. (a) Density dependence estimated as the slope of expected population growth rate (i.e., leading eigenvalue of the matrix associated with that year versus population size in each year) (different shading indicates different species; thin lines, fitted functions for populations; thick line, mean relation across populations and species). Fitted functions for individual populations are presented separately in Supporting Information. (b) Density dependence versus signed prediction error (residuals of a regression model with $[\Delta N_{\text{study}} - 1]$ as a predictor). (c) Observed versus expected change between the data-collection and forecast periods for mean annual precipitation (closed circle), mean daily maximum temperature (closed triangle), variance in annual precipitation (open circle), and variance in daily maximum temperature (open triangle) (line, 1:1 line shown for comparison). (d) Forecast error versus change in the standard deviation of precipitation regimes (lines, fitted function from linear model with confidence limits).

implement and interpret (Evans & Davis 2011), and are beyond the scope of this paper. However, further analyses could be done with our published database (Ellis et al. 2012).

Of the mechanisms we evaluated, the most plausible explanation for why our forecasts failed appears to be that the future environment differs from that of the past. Temperature and precipitation affect plant growth, survival, and reproduction across many taxa (Schauber et al. 2002; Huxman et al. 2004), but they are only 2 of many

possible environmental features that could change in unexpected ways over relatively short periods (Carpenter 2002; Doak et al. 2008). In some cases, one can make realistic predictions of the dynamics of physical and biotic environments and use these to drive population models (Menges 2000; Quintana-Ascencio et al. 2003; Gotelli & Ellison 2006). Linking demographic patterns to their drivers and incorporating these effects into demographic forecasts is likely to be the best way to improve forecasts. However, tight associations between vital rates and

environmental drivers can be difficult to detect (Knape & de Valpine 2011). For example, we reviewed 396 published demographic models for plants before designing the methods for this paper (Crone et al. 2011). Only 52 (13.1%) of these linked demographic responses to a potential environmental driver. Environmental change can also be difficult to forecast; for example, for populations in our data set, average conditions tended to be cooler—not warmer, as might be expected—during the forecast versus data-collection period (paired t test: $t = -1.60$, $p = 0.12$).

On the basis of our results, there does not seem to be a single simple solution that can dramatically improve model forecasts for plant populations in general. Therefore, in situations in which extensive system-specific models are not feasible, one should not expect precise model forecasts. Inability to forecast the future does not mean populations cannot be managed, however. Rather than using models to provide precise forecasts, management alternatives can be assessed on the basis of their ability to avoid undesirable outcomes (such as extinction of endangered species) over a broad range of uncertainty about a species' biology and future environmental conditions (Rosenberg & Restrepo 1994; Pielke & Conant 2003).

Acknowledgments

This work was conducted as a part of the Testing Matrix Models Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by the National Science Foundation (grant#EF-0553768), the University of California, Santa Barbara, and the State of California.

Supporting Information

A table of species included in our analyses (Appendix S1), detailed rationale for analyses of density dependence (Appendix S2), and population-specific results of our analysis of density dependence (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

- Adams, V. M., D. M. Marsh, and J. S. Knox. 2005. Importance of the seed bank for population viability and population monitoring in a threatened wetland herb. *Biological Conservation* 124:425–436.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- Biek, R., W. C. Funk, B. A. Maxell, and L. S. Mills. 2002. What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conservation Biology* 16:728–734.
- Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. *Ecological Applications* 9:1278–1287.
- Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akcakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385–387.
- Carpenter, S. R. 2002. Ecological futures: building an ecology of the long now. *Ecology* 83:2069–2083.
- Caswell, H. 1989. *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, MA.
- Caswell, H. 2001. *Matrix population models: construction, analysis and interpretation*. 2nd edition. Sinauer Associates, Sunderland, MA.
- Clark, J. S., et al. 2001. Ecological forecasts: an emerging imperative. *Science* 293:657–660.
- Cochran, M. E., and S. Ellner. 1992. Simple methods for calculating age-based life-history parameters for stage-structured populations. *Ecological Monographs* 62:345–364.
- Coulson, T., G. M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population viability analysis. *Trends in Ecology & Evolution* 16:219–221.
- Crone, E. E., M. Marler, and D. E. Pearson. 2009a. Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts. *Journal of Applied Ecology* 46:673–682.
- Crone, E. E., et al. 2011. How do plant ecologists use matrix population models? *Ecology Letters* 14:1–8.
- Crone, E. E., E. Miller, and A. Sala. 2009b. How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters* 12:1119–1126.
- Crone, E. E., L. Polansky, and P. Lesica. 2005. Empirical models of pollen limitation, resource acquisition, and mast seeding by a bee-pollinated wildflower. *The American Naturalist* 166:396–408.
- Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea-turtles and implications for conservation. *Ecology* 68:1412–1423.
- Daly, C., W. Gibson, M. Doggett, and J. Smith. 2010. Near-real-time high-resolution monthly average maximum/minimum temperature for the conterminous United States. The PRISM Climate Group, Oregon.
- Doak, D. F., et al. 2008. Understanding and predicting ecological dynamics: are major surprises inevitable? *Ecology* 89:952–961.
- Ellis, M. M., and C. S. Elphick. 2007. Using a stochastic model to examine the ecological, economic and ethical consequences of population control in a charismatic invasive species: mute swans in North America. *Journal of Applied Ecology* 44:312–322.
- Ellis, M. M., et al. 2012. Matrix population models from 20 long-term studies of perennial plant populations. *Ecology* 93:951.
- Ellner, S. P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. *Conservation Biology* 16:258–261.
- Ellner, S. P., and E. E. Holmes. 2008. Commentary on Holmes et al. (2007): resolving the debate on when extinction risk is predictable. *Ecology Letters* 11:E1–E5.
- Engen, S., R. Lande, B. E. Saether, and F. S. Dobson. 2009. Reproductive value and the stochastic demography of age-structured populations. *The American Naturalist* 174:795–804.
- Evans, J. A., and A. S. Davis. 2011. Consequences of parameterization and structure of applied demographic models: a comment on Pardini et al. (2009). *Ecological Applications* 21:608–613.
- Ezard, T. H. G., J. M. Bullock, H. J. Dalglish, A. Millon, F. Pelletier, A. Ozgul, and D. N. Koons. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. *Journal of Applied Ecology* 47:515–523.
- Farrington, S. J., R. M. Muzika, D. Drees, and T. M. Knight. 2009. Interactive effects of harvest and deer herbivory on the population dynamics of American ginseng. *Conservation Biology* 23:719–728.

- Freckleton, R. P., and A. R. Watkinson. 2002. Are weed population dynamics chaotic? *Journal of Applied Ecology* **39**:699–707.
- Gotelli, N. J., and A. M. Ellison. 2006. Forecasting extinction risk with nonstationary matrix models. *Ecological Applications* **16**:51–61.
- Harding, E. K., et al. 2001. The scientific foundations of habitat conservation plans: a quantitative assessment. *Conservation Biology* **15**:488–500.
- Huxman, T. E., et al. 2004. Convergence across biomes to a common rain-use efficiency. *Nature* **429**:651–654.
- Kaye, T. N., and D. A. Pyke. 2003. The effect of stochastic technique on estimates of population viability from transition matrix models. *Ecology* **84**:1464–1476.
- Kendall, B. E., and G. A. Fox. 2002. Variation among individuals and reduced demographic stochasticity. *Conservation Biology* **16**:109–116.
- Kephart, S. R., and C. Paladino. 1997. Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var *oraria* (Caryophyllaceae). *American Journal of Botany* **84**:179–189.
- Knap, J., and P. de Valpine. 2011. Effects of weather and climate on the dynamics of animal population time series. *Proceedings of the Royal Society B-Biological Sciences* **278**:985–992.
- Lennartsson, T., and J. G. B. Oostermeijer. 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *Journal of Ecology* **89**:451–463.
- Lesica, P. 1987. A technique for monitoring nonrhizomatous perennial plant species in permanent belt transects. *Natural Areas Journal* **7**:65–68.
- Lindborg, R., and J. Ehrlén. 2002. Evaluating the extinction risk of a perennial herb: demographic data versus historical records. *Conservation Biology* **16**:683–690.
- Menges, E. S. 2000. Population viability analyses in plants: challenges and opportunities. *Trends in Ecology & Evolution* **15**:51–56.
- Morris, J. A., K. W. Shertzer, and J. A. Rice. 2011. A stage-based matrix population model of invasive lionfish with implications for control. *Biological Invasions* **13**:7–12.
- Morris, W. F., P. L. Block, B. R. Hudgens, L. C. Moyle and J. R. Stinchcombe. 2002. Population viability analysis in endangered species recovery plans: past use and future improvements. *Ecological Applications* **12**:708–712.
- Morris, W. F., and D. F. Doak. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates, Sunderland, MA.
- Neel, M. C., A. K. Leidner, A. Haines, D. D. Goble, and J. M. Scott. 2012. By the numbers: How is recovery defined by the US Endangered Species Act? *BioScience* **62**:646–657.
- Pielke, R. A., and R. T. Conant. 2003. Best practices in prediction for decision-making: lessons from the atmospheric and earth sciences. *Ecology* **84**:1351–1358.
- Quintana-Ascencio, P. F., E. S. Menges, and C. W. Weekley. 2003. A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida rosemary scrub. *Conservation Biology* **17**:433–449.
- Rees, M., and S. P. Ellner. 2009. Integral projection models for populations in temporally varying environments. *Ecological Monographs* **79**:575–594.
- Rosenberg, A. A., and V. R. Restrepo. 1994. Uncertainty and risk evaluation in stock assessment: advice for US marine fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:2715–2720.
- Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* **83**:1214–1225.
- Schemske, D. W., B. C. Husband, M. H. Ruckelshaus, C. Goodwillie, I. M. Parker, and J. G. Bishop. 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75**:584–606.
- Schodelbauerova, I., R. L. Tremblay, and P. Kindlmann. 2010. Prediction vs. reality: Can a PVA model predict population persistence 13 years later? *Biodiversity and Conservation* **19**:637–650.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. W. H. Freeman, New York.
- Stubben, C. J., and Milligan, B. G. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* **22**:11.
- Ticktin, T., R. Ganesan, M. Paramesh, and S. Setty. 2012. Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees. *Journal of Applied Ecology* **49**:774–784.
- Tuljapourkar, S., J. M. Gaillard, and T. Coulson. 2009. From stochastic environments to life histories and back. *Philosophical Transactions of the Royal Society B-Biological Sciences* **364**:1499–1509.
- Tuljapourkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. *The American Naturalist* **162**:489–502.
- Tuljapourkar, S. D. 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theoretical Population Biology* **21**:114–140.
- Van Mantgem, P. J., and N. L. Stephenson. 2005. The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. *Journal of Ecology* **93**:737–747.

