FORECASTING EXTINCTION RISK WITH NONSTATIONARY MATRIX MODELS

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Abstract. Matrix population growth models are standard tools for forecasting population change and for managing rare species, but they are less useful for predicting extinction risk in the face of changing environmental conditions. Deterministic models provide point estimates of λ, the finite rate of increase, as well as measures of matrix sensitivity and elasticity. Stationary matrix models can be used to estimate extinction risk in a variable environment, but they assume that the matrix elements are randomly sampled from a stationary (i.e., non-changing) distribution. Here we outline a method for using nonstationary matrix models to construct realistic forecasts of population fluctuation in changing environments. Our method requires three pieces of data: (1) field estimates of transition matrix elements, (2) experimental data on the demographic responses of populations to altered environmental conditions, and (3) forecasting data on environmental drivers. These three pieces of data are combined to generate a series of sequential transition matrices that emulate a pattern of long-term change in environmental drivers. Realistic estimates of population persistence and extinction risk can be derived from stochastic permutations of such a model. We illustrate the steps of this analysis with data from two populations of *Sarracenia purpurea* growing in northern New England. *Sarracenia purpurea* is a perennial carnivorous plant that is potentially at risk of local extinction because of increased nitrogen deposition. Long-term monitoring records or models of environmental change can be used to generate time series of driver variables under different scenarios of changing environments. Both manipulative and natural experiments can be used to construct a linking function that describes how matrix parameters change as a function of the environmental driver. This synthetic modeling approach provides quantitative estimates of extinction probability that have an explicit mechanistic basis.

Key words: conservation; demography; extinction; life table response experiment; matrix model; nitrogen deposition; N:P ratio; ombrotrophic bogs; population viability analysis; response-surface design; Sarracenia; *time series.*

INTRODUCTION

Population viability analysis (PVA) is used to forecast extinction risks of local populations under variable or changing environmental conditions (Boyce 1992, Beissinger and McCullough 2002). Matrix population growth models potentially are an important tool for such forecasts (e.g., Olmsted and Alvarez-Buylla 1995, Silvertown et al. 1996, Cortes 2000). In a simple stage-based matrix model, individuals are classified into discrete stages, and transitions between stages are estimated from observed rates of recruitment, persistence, growth, or shrinkage. The model formulation is flexible and can be tailored to a variety of life histories and demographic data (Caswell 2000).

Deterministic matrix models that assume no migration or density dependence provide estimates of the equilibrium size structure of the population, the finite rate of increase (λ), and other eigenvalues that measure damping ratios and the speed of population recovery from perturbations (Caswell 2000). Sensitivity, elasticity, and loop analyses often are used in conjunction with these deterministic matrix models to reveal which transitions and life history loops have the greatest absolute or proportional effects on population growth rate (de Kroon et al. 1986, van Groenendael et al. 1994). This information can inform management strategies aimed at increasing λ by efficiently targeting particular life history stages or transitions (Heppell et al. 1996, Marmontel et al. 1997, Wisdom and Mills 1997).

In spite of the widespread use of elasticity, sensitivity, and loop analyses, their value for conservation biologists may be limited—they are applicable only if the populations of interest are in deterministic environments, or if they are in stochastic environments in

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which the sampled parameters are stationary and the population has reached equilibrium (Benton and Grant 1996). Most populations, however, are neither in deterministic environments nor in equilibrium conditions in stochastic environments. Realistic and successful application of PVA requires different analytical tools to forecast how nonequilibrium populations will respond to changing environmental conditions (Doak and Morris 1999).

In this paper, we describe and illustrate a method for modeling population change and producing realistic forecasts of population growth and extinction risk in a continuously changing environment. Such models are directly relevant to managing declining species in the face of increased atmospheric concentrations of CO_2, increased deposition rates of nitrogen, and other long-term environmental changes that ultimately reflect the exponentially increasing human population (Gilland 2002, Penn 2003).

Elsewhere, we have published the basic formulation and results of such a model for populations of the northern pitcher plant *Sarracenia purpurea* (Gotelli and Ellison 2002). The growth, morphology, and reproduction of this perennial carnivorous plant is affected dramatically by increasing levels of nitrogen (N) deposition (Ellison and Gotelli 2002). However, Gotelli and Ellison (2002) did not discuss the general strategy and detailed methods of building forecasting models for population dynamics in changing environments. Here, we describe in detail the steps necessary for constructing and analyzing these kinds of forecasting models. We illustrate each step with data from populations of *S. purpurea*. Our approach is similar to Anderson et al. (1995), who incorporated environmental driving variables into projection matrix models via logistic regression. Dennis and Otten (2000) also incorporated environmental drivers in the context of a stationary model. Our emphasis is on the way that experimental data on population responses and time-series data on environmental drivers can be incorporated into such models.

Begin with a Basic Matrix Model

Formulating the model

Matrix model formulation begins by classifying the individuals of a population into a set of *s* discrete stages. These stages may be based on the size, age, sex, reproductive status, or life history status of an individual. Vandemeer (1978) and Moloney (1986) discuss some of the issues involved in identifying stages for matrix model formulation. If the *s* stages represent an arbitrary classification of an underlying continuous variable such as body size or age, the model can be recast as an equivalent individual-based model that uses continuous growth functions (e.g., Łomnicki 1999, Uchmański 1999, Walters et al. 2002). Hybrid models that combine matrix models with individual-based models (Picard et al. 2001) allow for the separate assessment of population dynamics of numerous small or young individuals (the matrix component) and less common large or old individuals (the individual-based component). However, the discrete stage formulation that we present here is simpler to implement and the data required are gathered more easily.

Once the *s* stages have been established, a square *s* × *s* transition matrix **A** is created:

$$\mathbf{A} = \begin{pmatrix} F_{11} & F_{12} & F_{13} & \cdots & F_{1s} \\ p_{21} & p_{22} & p_{23} & \cdots & p_{2s} \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ p_{s1} & p_{s2} & p_{s3} & \cdots & p_{ss} \end{pmatrix}.$$

Each element p_{ij} of **A** represents the fraction of individuals in stage *j* (the columns) at time *t* that are in stage *i* (the rows) at time *t* + 1. The p_{ij}s can usually be interpreted directly as transition probabilities. The elements F_{1j} in the first row of the matrix are not necessarily probabilities that, like the p_{ij}s, range from 0 to ≤ 1.00, but may represent fecundities, the average number of offspring (stage *i* = 1) at time *t* + 1 produced by individuals in stage *j* at time *t*. Transitions that cannot or do not occur directly in a single time step are represented by zeroes in the matrix. The diagonal elements of the matrix specify the probability of persistence, which is the chance that an individual in stage *j* at time *t* remains in stage *j* at time *t* + 1. The time step of the model is a fixed constant identified by the investigator. The population size, and age or stage structure at time *t*, are represented in a column vector $\mathbf{n}_t$ with *s* rows and 1 column. Each element of this vector is the number of individuals in a particular age or stage class *i* at time *t*. Population growth is computed using matrix multiplication:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t. \tag{1}$$

Note that Eq. 1 is a model of exponential growth and does not include terms for density dependence. The finite rate of increase of the population λ can be estimated as the dominant eigenvalue of **A**, and the first eigenvector represents the stable age or stage structure of the population. The instantaneous rate of increase *r* equals the natural logarithm of λ.

Elasticity analysis measures the relative change in λ caused by a proportional change in any of the matrix elements (de Kroon et al.1986). The elasticity e_{ij} of either transition p_{ij} or fecundity F_{ij} is calculated as

$$e_{1j} = \frac{F_{1j}}{\lambda} \frac{d\lambda}{dF_{1j}}$$

$$e_{ij} = \frac{p_{ij}}{\lambda} \frac{d\lambda}{dp_{ij}} \qquad i \neq 1. \tag{2}$$

Elasticity elements for a transition matrix sum to 1.0.

TABLE 1. Annual transition matrices for *Sarracenia purpurea* populations at Hawley Bog, Massachusetts, USA, and Molly Bog, Vermont, USA.

	Stage at year t			
Stage at year $t + 1$	Recruit	Juvenile	Non-flowering adult	Flowering adult
Hawley Bog†				
Recruit	0.0000 (0)	0.0000 (0)	0.0000 (0)	4.0000 (0)
Juvenile	0.1000 (2)	0.9540 (61)	0.0900 (2)	0.0000 (0)
Non-flowering adult	0.0000 (0)	0.0360 (3)	0.7010 (18)	0.8375 (5)
Flowering adult	0.0000 (0)	0.0000 (0)	0.1802 (6)	0.1610 (1)
Molly Bog‡				
Recruit	0.0000 (0)	0.0000 (0)	0.0000 (0)	4.0000 (2)
Juvenile	0.1000 (2)	0.8540 (44)	0.1770 (6)	0.0000 (0)
Non-flowering adult	0.0000 (0)	0.1310 (8)	0.7080 (27)	0.6660 (4)
Flowering adult	0.0000 (0)	0.0000 (0)	0.1000 (5)	0.3070 (2)

Notes: The first entry in each cell is the average annual transition rate between each pair of stages in the model. The entry in parentheses is the percentage of elasticity of the transition, a measure of its relative contribution to population growth rate.
† $r = 0.00456$.
‡ $r = 0.00554$.

Stochastic matrix models (Wisdom et al. 2000) can be used to incorporate temporal variation in environmental conditions. Stochastic matrix models differ from deterministic ones in that the transition probabilities vary randomly from one time-step to the next and are sampled from a specified probability distribution with parameters estimated for each transition element (Pfister 1998). Thus, the growth equation is rewritten as

$$\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t. \qquad (3)$$

Now the matrix **A** is no longer a constant, but is also subscripted with t to indicate that that the matrix values are different in each time step. However, note that all of these matrix elements are sampled from an unchanging (i.e., stationary) distribution with constant means, variances, and covariances for each matrix element.

Although they are straightforward in concept, the behavior of stochastic matrix models is sensitive to the probability functions used to model vital rates (Kaye and Pike 2003), the inclusion of density dependence (Grant and Benton 2000), and the presence of covariance among vital rates (van Tienderen 1995, Benton and Grant 1996). In such stochastic models, average estimates of λ or of elasticities may give misleading results (Tuljapurkar et al. 2003). Most critically, these stochastic models assume that vital rates are sampled from a stationary distribution, which will not be the case in a chronically changing environment.

Estimating the transition probabilities

We illustrate the procedure for estimating the transition probabilities and fecundities of **A** with data from *Sarracenia purpurea*, a long-lived perennial plant that grows in ombrotrophic (rain-fed) bogs in the northeastern United States and Canada (Schnell 2002). Gross (2002) considers the general problem of optimal sampling strategies for estimating F_{1j} and p_{ij} from available field data. The physiology, growth, and demography of *S. purpurea* are very sensitive to changes in nitrogen availability (Ellison and Gotelli 2002). Botanical carnivory evolved as an adaptation to low-N environments (Givnish et al. 1984), but there is growing evidence that anthropogenic N is affecting many aspects of growth and plants currently may be becoming phosphorus-limited because of chronic atmospheric deposition of N (Wakefield et al. 2005).

We began our study by classifying individual plants into one of four stages: recruits (seedlings), juveniles, non-flowering adults, or flowering adults. Adults were defined as plants >10 cm in rosette diameter, the minimum size at which we have observed plants to flower. At each of two sites in New England (Hawley Bog, Massachusetts, and Molly Bog, Vermont) we located and tagged 100 juvenile and 100 non-flowering adult plants that were located in the center of the bog and were not crowded by neighboring plants. These populations have been censused annually since 1998. At each census, we record the presence, size, and flowering status of each surviving individual in our marked sample. Recruitment transitions were estimated separately from measures of seed set and controlled plantings. Transitions for adult flowering plants were estimated from those non-flowering plants in the first year that flowered in the second season. See Gotelli and Ellison (2002) for complete details on sampling design and methods.

We estimated the average values for the elements of the transition matrix from the first two censuses (1998–1999 and 1999–2000; Table 1). The p_{ij}s for each interval were estimated directly as the average number of individuals in stage i at time $t + 1$ divided by the number of individuals in stage j at time t. Recruitment (the F_{1j}s in the transition matrix) was estimated as the

product of seed production (mean = 1000 seeds per plant) and establishment probability, which was estimated from controlled plantings in the field.

Instantaneous growth rates estimated from these matrices were $r = \log(\lambda) = 0.00456$ individuals·individual^{-1}·yr^{-1} at Hawley Bog and $r = 0.00554$ individuals·individual^{-1}·yr^{-1} at Molly Bog. The corresponding doubling times of these two populations would be 152 and 125 yr, respectively. Stochastic matrix models of these populations (N. J. Gotelli and A. M. Ellison, *unpublished analysis*) generated distributions of r with average growth rates slightly less than 0.0, and fairly wide confidence intervals that included 0.0.

Elasticity analysis revealed that recruitment made a relatively small contribution to population growth rate, and that λ was most sensitive to changes in the persistence probabilities of juvenile and non-flowering adult plants (Table 1). These results are typical for matrix model analyses of other long-lived perennial plants and invertebrates (Caswell 1986, Gotelli 1991, Enright et al. 1995).

Conduct a Life Table Response Experiment

Rationale and experimental design

Life table response experiments (LTREs) establish populations in different environmental conditions, and allow for statistical hypothesis tests of differences in λ or r among environments (Caswell 1989). In the field or laboratory, individuals are raised under constant environmental conditions in two or more experimental treatments. Growth, survivorship, and reproduction are measured and used to estimate **A** for each treatment. Statistical tests for differences in λ are based on bootstrapping or jackknifing procedures (Efron 1981).

LTREs may have limited utility for forecasting purposes, however. In nature, environmental variation is continuous in time and space, and often cannot be represented by simple stochastic parameters sampled from stationary distributions. Life stage simulation analysis (LSA) has been used to model stochastic environments and to incorporate simple patterns of environmental variation (Gotelli 1991, Wisdom et al. 2000). A limited number of different matrix types can be built to represent different environments (Bierzychudek 1982), such as fire (Hoffmann 1999, Brewer 2001) or disturbance regimes (Pascarella and Horvitz 1998), and these different matrix types are randomly sampled to represent a set of alternating environmental regimes. However, even these simulations model equilibrium conditions and do not accurately describe environmental change, which includes short-term, year-to-year fluctuations superimposed on long-term chronic changes.

Impact of environmental change on population growth of S. purpurea

We used a standard ANOVA-style LTRE to investigate the role of nitrogen on the population growth
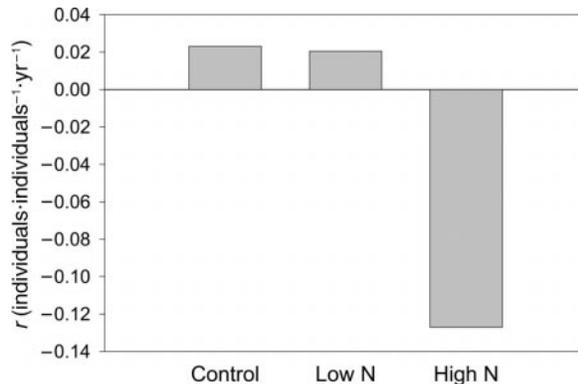

FIG. 1. Estimated r for *Sarracenia purpurea* populations in different nitrogen treatments of a life table response experiment. The figure is modified from Gotelli and Ellison (2002).

rate of *S. purpurea*. At Hawley Bog, 90 juvenile and 90 adult plants were selected haphazardly and 10 of each were assigned randomly to nine treatments: two control treatments (distilled H$_2$O or 10% concentration of micronutrients from Hoagland's solution); two N treatments (0.1 mg/L NH$_4$-N or 1.0 mg/L NH$_4$-N as NH$_4$Cl); two P treatments (0.025 mg/L PO$_4$-P or 0.25 mg/L PO$_4$-P as NaH$_2$PO$_4$); and three treatments in which we altered the N:P ratio (low [1:2.5], medium [4:1], and high [40:1]). Treatments were maintained for two years in an ecological "press" experiment. Here, we discuss the results of only the control and N addition treatments. Experimental details are given in Gotelli and Ellison (2002).

Sarracenia is N limited, and its growth, reproduction, and survivorship are sensitive to the N:P ratio of precipitation, prey, and pore water (Gotelli and Ellison 2002, Ellison and Gotelli 2002, Wakefield et al. 2005). Time-series data on P inputs to bogs are not available, so we built our model based only on N deposition rates and used experimental data only from the control (distilled water), low N, and high N treatments. Population growth rates were highest for the control and low-N treatments, and lowest for the high N treatment (Fig. 1). A bootstrapping model incorporating random measurement error established that the differences in growth rates among treatments were statistically significant (Gotelli and Ellison 2002).

This labor-intensive LTRE confirmed that increasing N deposition could lead to negative growth rates of *S. purpurea* populations, possibly leading to their local extinction. However, this information by itself is not very useful for forecasting population growth rate. Like the basic demographic analysis, the LTRE only predicts growth under equilibrium conditions in different nutrient environments. However, nutrient deposition rates vary substantially on an annual basis. Over a time scale of decades, rates have increased substantially and will continue to do so, perhaps at an accelerated rate. It is

this type of mixture of short-term variability and long-term trend in environmental change in N deposition that must be modeled in order to realistically predict the fate of populations.

Forecast Environmental Change

Time-series modeling

To model population growth in a changing environment, we first need a simple model of how the environment itself changes with time. We use the variable D_t to indicate the level of an environmental driver D measured at time t. D might be any variable that we suspect will influence population viability in the long-run, such as nitrogen availability, CO_2 concentration, or temperature. We seek a simple model to describe how D changes with time:

$$D_t = f(t). \qquad (4)$$

The function $f(t)$ might come from simple forecasts, such as projected rates of increase in global nitrogen over the next century (Galloway and Cowling 2002, Hungate et al. 2003). However, the best source of data for modeling future changes is existing time series of environmental variables that are recorded as part of long-term environmental monitoring.

To forecast temporal variation in D, we use two simple models:

$$D_t = \alpha + \beta t + \varepsilon_t \qquad (5)$$

$$D_t = \alpha + \beta D_{t-1} + \varepsilon_t. \qquad (6)$$

In both equations, α and β are parameters (constants), and ε_t is a normal random variable with a mean of zero and a variance of σ^2 [$\varepsilon_t \sim \mathcal{N}(0, \sigma^2)$]. Eq. 5 is a simple linear model of D vs. time, whereas Eq. 6 is a first-order autoregressive model. Even relatively short time-series data for environmental drivers can be fit easily to these equations with standard statistical software. In Eq. 6, if the constant α is set to zero, the constant β is a simple multiplier that represents a fixed percentage increase or decrease in an environmental driver. For example, if $\alpha = 0.0$ and $\beta = 1.02$, the level of the environmental driver increases, on average, 2% per year. Eq. 5 also can be modified to accommodate a constant percentage change by regressing $\ln(D)$ against t.

Using time-series data or other sources, the equations can be fitted as

$$\hat{D}_t = a + bt \qquad (7)$$

$$\hat{D}_t = a + bD_{t-1} \qquad (8)$$

where a and b are the estimated coefficients.

The values of the fitted coefficients a and b are actually not critical, because we will vary them to create different scenarios for environmental change. We also estimate the variance $\hat{\sigma}^2$ of the error term ε_i. This var-

iance describes the annual variation in the environmental driver that populations will experience. Moreover, the autoregressive model (Eq. 8) generates a time series of D values that are autocorrelated with one another, whereas, in the linear model (Eq. 7), the values of D from one year to the next are entirely independent. Although both the linear and autoregressive model fit the short time series in Fig. 2 equally well, the autocorrelation has important consequences for the pattern of population fluctuation generated by the model.

Predicted nitrogen deposition at Hawley and Molly bogs

Fig. 2 illustrates annual deposition rates of NO_3 and NH_4 measured by the National Atmospheric Deposition Program at permanent monitoring stations in Quabbin, Massachusetts and Shelburne, Vermont (data *available online*).[4] These two sites are respectively within 60 km of the Massachusetts and Vermont populations of *S. purpurea* that we are studying. Before fitting the models, we combined NO_3 and NH_4 data to give estimates of total nitrogen deposition, as our experiments were based on concentration of total N, rather than concentrations of a particular form of inorganic nitrogen. We fit separate models for each of the two sites.

The estimated parameters of the first-order linear models (Eq. 5) fit to the total nitrogen deposition data were $a = 0.391$, $b = -20.004$ mg N/L, and $\hat{\sigma}^2$ of $\varepsilon = 0.0056$ at Quabbin, and $a = 0.477$, $b = -20.001$ mg N/L and $\hat{\sigma}^2$ of $\varepsilon = 0.0042$ at Shelburne. For these linear models, the expected initial value is equivalent to the intercept a. To fit the autoregressive model (Eq. 6) to the data from each site, the observed 1998 N deposition levels were used as the initial points in the time series, and the intercept a was fixed at zero. The estimated coefficients of the autoregressive models were $b = 0.953$ and $\hat{\sigma}^2$ of $\varepsilon = 0.0018$ at Quabbin, and $b = 0.979$ and $\hat{\sigma}^2$ of $\varepsilon = 0.0250$ at Shelburne.

These estimated parameters for $\hat{\sigma}^2$ were used to simulate time series in nitrogen deposition that describe different scenarios for realistic models of environmental change (different values of b). For example, Fig. 3 depicts three realizations of the autoregressive model for scenarios of no change, small annual increases, or small annual decreases in nitrogen deposition at Shelburne.

Link the LTRE with Forecasted Environmental Change

Time series of nonstationary transition matrices

The key step in the construction of a matrix model that is responsive to environmental change is to link the demographic response of populations to altered environmental conditions (quantified by the LTRE) with the annual pattern of fluctuation in the environmental
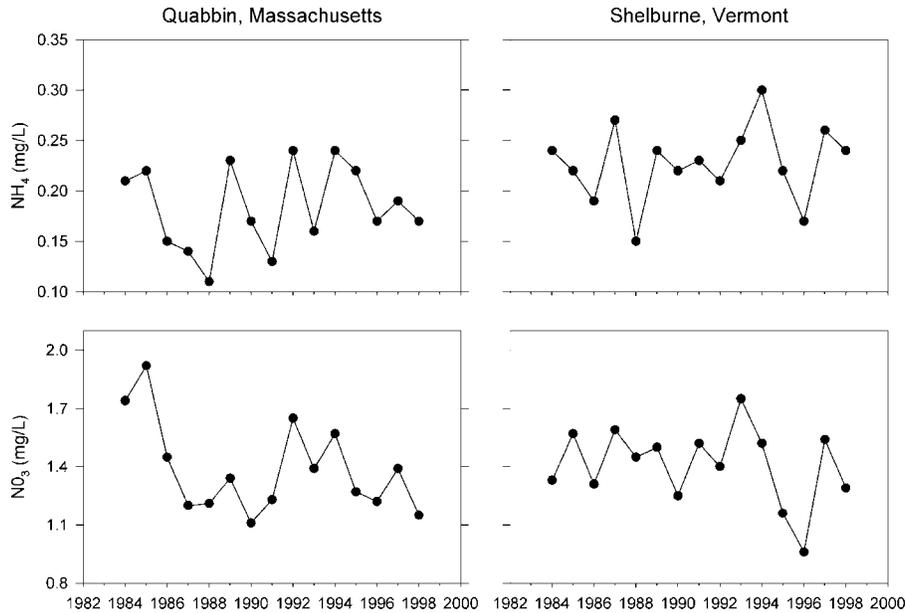
[4] ⟨http://nadp.sws.uiuc.edu/⟩

Quabbin, Massachusetts   Shelburne, Vermont

FIG. 2. Time-series trajectories for annual ammonium (NH_4) and nitrate (NO_3) deposition rates measured at NADP (National Atmospheric Deposition Program) monitoring sites in Quabbin, Massachusetts, USA, and Shelburne, Vermont, USA (1984–1998). Data are from the NADP (see footnote 4).

driver (forecast by the time-series models). We use a linking function that specifies each matrix transition element p_{ij} (or F_{1j}) as a function of the environmental conditions:

$$P_{ij} = f(D_t) \equiv \{f[g(t)]\} \qquad (9)$$

where $g(t)$ is, for example, Eq. 5 or 6. Population growth is then described as

$$\mathbf{n}_{t+1} = \mathbf{A}_t^* n_t = [p_{ij}(t)]n_t. \qquad (10)$$

Note that $\mathbf{A}^*$ varies with time, but is a deterministic function of D, the environmental driver. Stochasticity is introduced through the variance of the error term of D.

Graphically, each transition element is plotted against the continuous variable D. There is a unique function for each transition element because not all transitions respond identically to changes in D. Each treatment in the LTRE specifies a different level of D and therefore determines a single point in this graph. For transition probabilities, Eq. 9 describes a monotonic function bounded between 0.0 and 1.0. This function specifies the matrix transition at time step t (i.e., p_{ijt}) associated with environmental conditions D_t at time step t.

Transition functions for Sarracenia purpurea

Because there were only three treatments from the LTRE experiment that could be used for the linking function (control, low N, high N), we were forced to fit a continuous function to three data points (Fig. 4). To do this, we assumed that (1) all transition responses were linear on a logarithmic scale of N concentration;

(2) above a concentration that was 10× higher than our high N treatment, all plants died, so that if N > 10 mg/L then $p_{ij} = 0.0$ for all transitions; (3) below the lowest measured N concentration of the distilled water added in the control treatment (0.01 mg/L), p_{ij} values did not change any further; (4) response values between the three measured points could be fit by simple linear interpolation. This approach yielded 16 transition functions, one for each element in the 4 × 4 transition matrix. Our experiment did not generate any
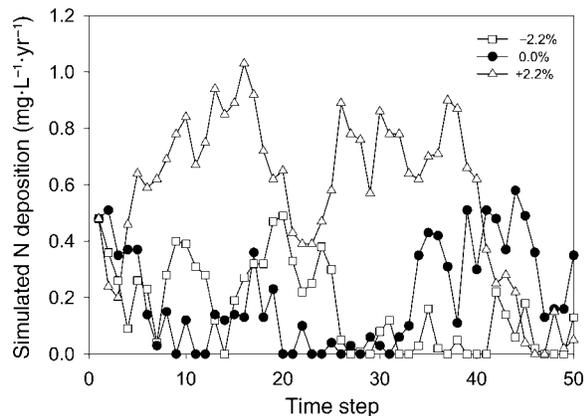

FIG. 3. Simulated time-series trajectories for total nitrogen (N) deposition at Shelburne, Vermont. The simulated autoregressive model is $N_{t+1} = \beta N_t + \varepsilon_t$, where $\varepsilon \sim \mathcal{N}(0, 0.0250)$. The three estimated coefficients of $b = 0.978$, $b = 0.000$, and $b = 1.022$ correspond to scenarios of annual average change in N deposition of −2.2%, 0.0%, and +2.2%, respectively.
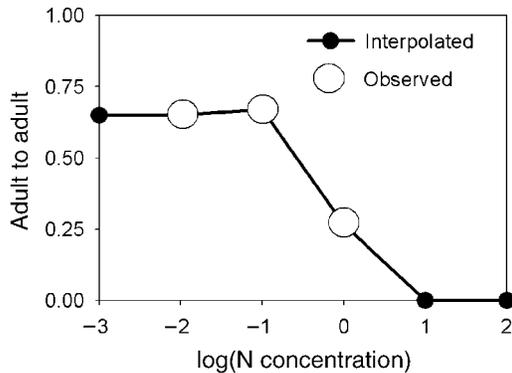
FIG. 4. Sample calculation of transition functions for the nonstationary population growth model. The x-axis is the $\log_{10}$(concentration of nitrogen). The y-axis is the persistence transition for adult plants (the probability that a non-flowering adult plant persists as a non-flowering adult plant from one year to the next). The three open circles are the observed experimental values from the nutrient addition experiment. The solid circles and solid line are the interpolated values for unobserved transition probabilities. The figure is from Gotelli and Ellison (2002).

information on recruitment, so we assumed those transitions were unaffected by N deposition. Obviously, fitting a continuous function to only three data points is not very satisfactory, and we discuss alternative designs for more informative LTREs in *Discussion*.

FORECAST POPULATION GROWTH AND EXTINCTION RISK

A forecasting algorithm

With a form (Fig. 4) for the linking function (Eq. 9) in hand, it is straightforward to simulate population responses to realistic or hypothesized long-term trajectories of changes in the environmental drive D. This is done in the following sequence of operations:

1) Supply parameters (slope and intercept coefficients) for the time-series model (Eq. 4 or 5) to represent a particular environmental scenario (e.g., a 1% annual increase in N deposition). Note that the initial matrix is not based on the measured transitions (Table 1), but on the matrix created by specifying the initial levels of the environmental driver D_0.

2) Use a random-number generator to create the error term ε_t in Eq. 5 or 6. This error term, along with the specified coefficients yields a time series of environmental coefficients D_t.

3) Use the linking function (Eq. 9) to create a sequential series of transition matrices $\mathbf{A}_t^*$. Each transition matrix represents the population response to the environmental conditions at time t.

4) From field measurements, estimate the initial population vector $\mathbf{n}_0$, the number of individuals in each stage class of the model.

5) Estimate population size using Eq. 10, updating $\mathbf{A}_t^*$ (from step 3) at each iteration.

6) Determine whether the population has gone extinct (or fallen below some specified minimum viable population size V) by the end of the simulation. Alternatively, allow the simulation to continue until the population has fallen below V and use that number of time steps as the estimate of the life span of the population.

7) Repeat steps 2–6 to create a series of 1000 (or more) iterated population tracks. Because of the random error term in the time-series model, each sequence of environmental drivers D_t will differ, so there will be different outcomes for population growth as well.

Predictions of extinction risk for pitcher plants

Fig. 5 summarizes extinction risk after 100 years for the two populations at Molly and Hawley Bog under different scenarios of nitrogen deposition. These analyses are based on the autoregressive model (Eq. 6) for the nitrogen time series. Estimated initial population sizes at both Hawley and Molly Bog exceeded 10 000 individuals Assuming current average deposition levels continue to hold (0% change on the x-axis of Fig. 5), extinction risks are substantially higher at Molly Bog because N deposition rates in 1998 (the starting point for the simulations) were much higher there than at Hawley Bog. In the autoregressive model, the variance estimate $\hat{\sigma}^2$ for Hawley Bog is smaller than for Molly Bog, which may explain the greater sensitivity of extinction risk in Hawley Bog to increases in N. The analysis indicates that even modest increases in N deposition can lead to substantial long-term risks of extinction, although there are important differences in population sensitivity to changing conditions, reflecting spatial variation in the magnitude and variability of N deposition. Finally, analysis of simulated population structure reveals that the error structure of the
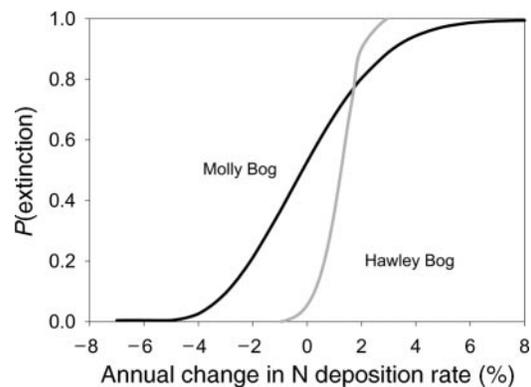

FIG. 5. Probability of extinction after 100 years as a function of changes in annual N deposition rate for Molly Bog, Vermont (black line) and Hawley Bog, Massachusetts (gray line). Extinction probability was estimated as the fraction of 1000 simulated populations that declined below 1 individual after 100 time steps in the model. N deposition time series were based on estimated parameters from monitoring stations at Shelburne, Vermont, and Quabbin, Massachusetts.

TABLE 2. Summary of three kinds of matrix models for population growth.

Factor	Deterministic model	Stationary stochastic model	Nonstationary stochastic model
Population growth	$n_{t+1} = An_t$	$n_{t+1} = A_t n_t$	$n_{t+1} = A*n_t$
Matrix elements	F_{1j}, p_{ij} fixed	$F_{1j}(t) \sim \mathcal{N}(\mu_{F_{1j}}, \sigma^2_{F_{1j}})$	$F_{1j}(t) = L_{F_{1j}}(D_t)$
		$p_{ij}(t) \sim \mathcal{N}(\mu_{p_{ij}}, \sigma^2_{p_{ij}})$	$p_{ij}(t) = L_{p_{ij}}(D_t)$
Temporal variation	none	Matrix elements vary randomly through time and are drawn from a stationary distribution.	Matrix elements change through time as a deterministic function of an environmental driver D.
Incorporation of enviromental variation	none	Implicit in variances and covariances of matrix elements.	Modeled via linking function $L(D_t)$ for each matrix element.
Determinants of extinction risk $P(E)$	$P(E) = 1.0$ if $\lambda < 1.0$ $P(E) = 0.0$ if $\lambda \geq 1.0$	Depends on $\bar{\lambda}$ and variances and covariances of matrix elements.	Depends on initial size structure of population (n_0), initial level of environmental driver D_0, time series model for D_t and the linking function L.

model for environmental change (D_t) has interesting consequences for the pattern of population growth. In particular, the autocorrelated time series for nitrogen imposes short-term population cycles on a long-term pattern of exponential decline (see Fig. 3 in Gotelli and Ellison 2002).

DISCUSSION

Table 2 highlights the differences among simple deterministic models, stochastic stationary models, and the stochastic nonstationary models we propose. The modeling framework we have outlined effectively links short-term demographic measurements, life-table response experiments, and time-series data on environmental drivers to produce realistic population forecasts. Although these models are based on short-term data, they have a strong mechanistic basis, and they can be used with available data to forecast extinction risk under different scenarios of environmental change. Our method does require data from life table response experiments or appropriate ''natural experiments,'' and these are always challenging to design and execute. Nevertheless, the method we have proposed is feasible within the 3–5 yr duration of a typical grant proposal. Fitting a model based on 3–5 yr of data from field experiments and forecasting models may give more reliable predictions than an 8–10 yr demographic monitoring study that does not incorporate experimental results.

A retrospective on how to design field experiments for modeling studies

When we began this work, our initial focus was on estimating the effects of different nutrient regimes on population growth rate of *Sarracenia*. To this end, we used a well-replicated standard ANOVA design for an LTRE with nine experimental treatments and 20 plants (10 adults and 10 juveniles) assigned randomly to each treatment. This design was appropriate and powerful for testing the null hypothesis that λ does not differ among different treatment regimes any more than expected by chance.

Unfortunately, we did not begin the modeling work until after the experiment was completed. With hindsight, this is not the order we should have done it in, but we suspect that is the sequence that most ecologists would follow. Once we began assembling the time-series data on nitrogen and building the nonstationary model, it became apparent that our experimental design was less than ideal. Because long-term data on P inputs were not available, we could only model changes in N deposition and therefore could use data from only three of our nine experimental treatments (distilled water control, low N, and high N; Fig. 1). Although these three treatments had a total of 60 replicates, there were effectively only three nitrogen levels used. To create the linking function, we were therefore forced to fit a line through these three data points (Fig. 4). Although we could have used logit or probit models or other sophisticated curve-fitting algorithms, the results would not be that different than the simple ''connect the dots'' piecewise construction that we used. Obviously, we need more than three data points to confidently estimate the linking function. What should we have done differently?

This retrospective look at our experimental design highlights a common problem: conventional ANOVA designs may not be the best choice for estimating model parameters. In our case, in spite of multiple treatments and large sample sizes, we ended up with only three data points from which we had to estimate a continuous function. The general problem is that a continuous variable (nitrogen concentration) was shoehorned into a set of discrete categories in order to match a conventional ANOVA design.

A better approach would have been a regression or response-surface design (e.g., Inouye 2001). Rather than replicate a few arbitrarily chosen levels of nitrogen concentration, each plant could have been assigned a unique nitrogen concentration, spanning the range of

biologically relevant concentrations. Then we could have fit a logistic regression or used any of a number of nonlinear fitting methods to model transition elements as a function of N. Inouye (2001) and Gotelli and Ellison (2004) discuss many other advantages of response-surface designs. Although conventional ANOVA designs are powerful, they are also a kind of intellectual straightjacket (Werner 1998); ecologists need to consider other experimental designs in order to estimate model parameters more efficiently.

Caveats

Some of the usual caveats that apply to matrix models apply to our analysis as well: the model does not include density dependence, migration, or spatial variation, although these factors can certainly be incorporated if the biology warrants it. For *Sarracenia*, there is little evidence of density dependence (Brewer 1999), the isolated bogs in northern New England are unlikely to be influenced much by migration, and small-scale variation in local demographic rates does not appear to be strong (N. J. Gotelli and A. M. Ellison, *unpublished data*). The model we have presented here also does not directly incorporate covariance in demographic rates. However, nonzero covariances are indirectly generated because of covariation in the response of demographic parameters to variation in N deposition rates. Indeed, in the context of this model, the variance-covariance matrix of demographic rates is an epiphenomenon that reflects population responses to changing environmental conditions, and may change depending on what time interval the population is sampled over.

Another challenge in analyzing changing environmental conditions is that populations may have already been exposed to chronic changes in the past. For example, nitrogen deposition rates have been high in the United States. for the past few decades, and in Europe for much longer than that. If populations are already stressed when measurements and experiments are initiated, the responses may be very different from populations that had not been exposed to stressful levels of environmental drivers. It may also be difficult to calibrate measured levels of an environmental driver, such as nitrogen, with biologically reactive levels that are perceived by organisms. For *Sarracenia*, correlations of plant morphology and measured levels of pore water NH_4 in a set of 26 New England bogs are consistent with experimental manipulations of pitcher water N (Ellison and Gotelli 2002).

One important limitation is that our model does not produce confidence intervals on probabilities of extinction. We can only generate point estimates of extinction probabilities (Fig. 5) because our model assumes that all individuals in the population have identical growth trajectories that are described by the simple matrix model. Variation in population growth is imposed only through variation in the environmental

driver D_t, and its effects on the transition matrix. Models that incorporate individual variation (Clarke et al. 2003, Kendall and Fox 2003) can be used to generate confidence intervals for such estimates. Recent approaches to Bayesian parameter estimation for matrix models also are promising (Gross et al. 2002).

We have taken a piecewise approach to modeling by estimating terms for each model component in isolation. An integrated modeling framework, such as a state-space model, could simultaneously account for measurement and process error (e.g., Staples et al. 2004), which we have not done. Relatively little theoretical work has been done on parameter estimation in nonstationary systems. Halley's (2003) studies of "parameter drift" suggest that changing conditions may lead to better parameter estimates and tighter confidence intervals, but Ellner (2003) uses a different model formulation and arrives at more pessimistic conclusions.

Perhaps the most serious limitation to the method we propose is that the analysis cannot be easily carried out using "canned" statistical software routines. We programmed our model in Delphi (an object-oriented version of Pascal), and the compiled stand-alone software for our model is available (Supplement). However, that model is very specific to our system. That seems only fitting if we want to generate biologically realistic forecasts for specific systems. We also note that the results of such models may be system-specific. Although the *Sarracenia* populations at Hawley and Molly Bog have similar measured transition matrices and projected growth rates (Gotelli and Ellison 2002), the background deposition rates of nitrogen are very different, leading to different scenarios of extinction risk at each site. These results suggest that it may be difficult to generalize the results of a population viability analysis from one population to another.

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SUPPLEMENT

Executable Delphi source code and the compiled program for the nonstationary matrix model projection (*Ecological Archives* A016-004-S1).