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

product of seed production (mean 5 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 5 log(λ) 5 0.00456 individuals·individual^{21}·yr^{21} at Hawley Bog and r 5 0.00554 individuals·individual^{21}·yr^{21} 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 Stochastic matrix models of these populations (N. J. Gotelli and A. M. Ellison, *unpublished analysis*) generated distributions of r with average growth rates slightly less than 0.0, and fairly wide confidence intervals that included 0.0.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).
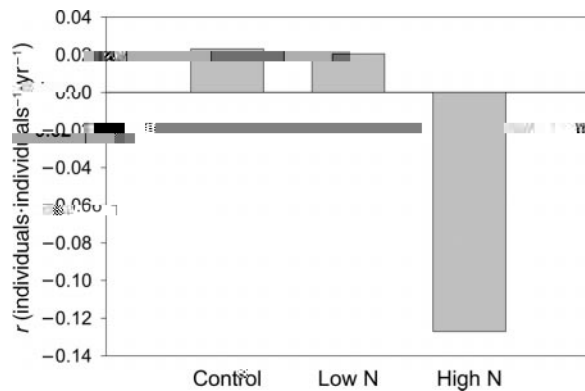

FIG. 1. Estimated r for *Sarracenia purpurea* populations in different nitrogen treatments of a life table response experiment. The figure is modified from Gotelli and Ellison (2002).

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:

$$D_t = a + bt + \epsilon_t \qquad (5)$$

$$D_t = a + bD_{t-1} + \epsilon_t. \qquad (6)$$

In both equations, a and b are parameters (constants), and ϵ_t is a normal random variable with a mean of zero and a variance of σ^2 [$\epsilon_t \sim \mathcal{N}(0, \sigma^2)$]. 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 a is set to zero, the constant b
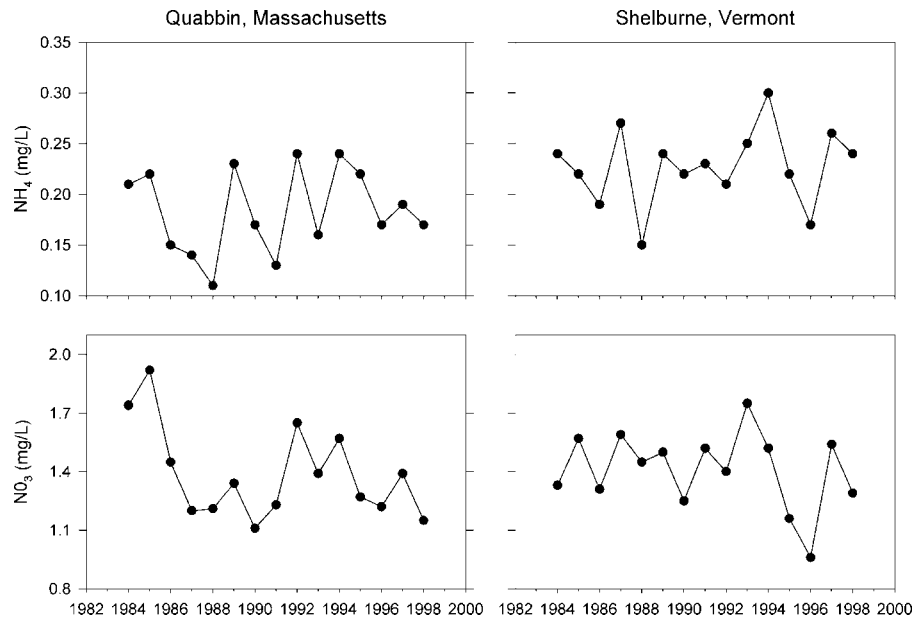
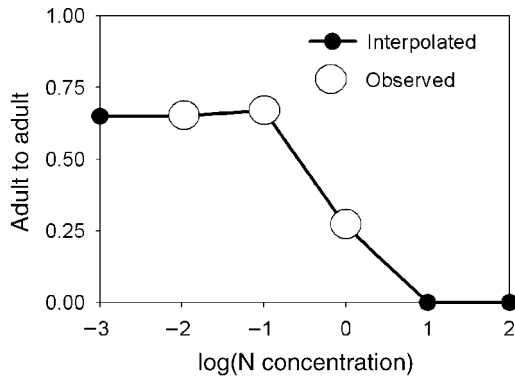FIG. 2.   Time-series trajectories for annual ammonium (NH$_4$) and nitrate (NO

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).
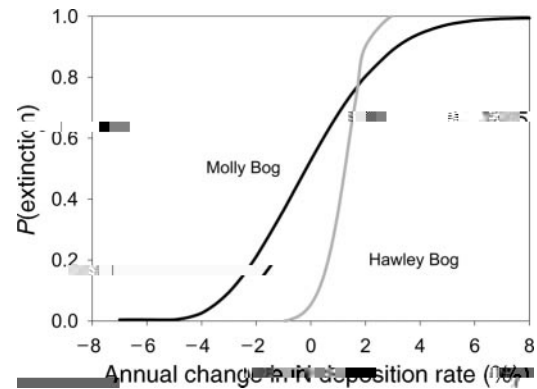

FIG. 5. Probability of extinction after 100 years as a function of changes in annual N deposition rate for Molly Bog,

Table

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

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