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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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DETECTING POPULATION-LEVEL CONSEQUENCES OF ONGOING ENVIRONMENTAL CHANGE WITHOUT LONG-TERM MONITORING

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Abstract. The frequent lack of correspondence between measured population stage structures and those predicted from demographic models has usually been seen as an embarrassment, resulting from poor data, or a testimony to the failings of overly simplistic models. However, such mismatches can also arise due to natural or anthropogenic changes in the environment, thus providing the data needed to test hypotheses about the ecological effects of local or global environmental change. Here, we present a method that allows this type of comparison to rigorously test for the population-level effects of past and ongoing environmental change in situations where no long-term monitoring data exist. Our approach hinges on the fact that changing environmental conditions will cause population size structure to lag behind that predicted by current demographic rates. We first develop the methods needed to calculate the likelihood of an observed population structure, given different stochastic models of demography responding to environmental changes. We next use simulated data to explore the method's power in the face of estimation errors in current vital rates, environmental noise, and other complications. We conclude that this method holds promise when applied to slowly growing, long-lived species and when model structures are used that allow for realistic time lags in population structure. Researchers using this approach should also be careful to assess the importance of other phenomena (rare catastrophes, recent founding of populations, genetic changes, and density dependence) that may compromise the method's accuracy. Although large data sets are required for the method to be accurate and powerful, the data required will be readily obtainable for abundant and easily sampled species. While most ecological efforts to detect global environmental changes have focused on long-term monitoring, or indicators such as tree rings that are unique to organisms not present in all biomes, this method allows tests for past and ongoing changes in situations where neither past monitoring data nor unique indicator species are available.

Key words: climate; demographic modeling; demography; environmental change; global change; likelihood; matrix; population structure; stochastic demography.

INTRODUCTION

There is general agreement that anthropogenic environmental changes have already affected most areas of the world, and that these impacts will become increasingly pronounced over the next century (Schneider 1993, Vitousek 1994, Vitousek et al. 1996). These changes include global phenomena, such as atmospheric warming, ozone depletion, and higher CO_2 concentrations, as well as more localized impacts such as nitrogen deposition, acid precipitation, introduced species, grazing pressure, and selective harvesting. However, what the consequences of these changes will be for individuals, populations, and communities is far from clear (Kareiva et al. 1993, Korner and Bazzaz 1996, Walker and Steffen 1996). In part, this uncertainty arises because the predicted regional-scale (i.e., continental or subcontinental) changes in temperature, for example, are on less firm footing than are global predictions (Houghton et al. 1990, Tao et al. 1996). In addition, many simultaneous anthropogenic changes will result in a mix of negative effects (e.g., the consequences of elevated levels of ultraviolet (UV) radiation caused by ozone depletion) and positive effects

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(e.g., the amelioration of arctic and alpine environments by global warming and the enhancement of photosynthesis due to enrichment of atmospheric CO_2) on native species and communities. In the face of this uncertainty, there is a considerable need for new data and new methodologies to quantify the effects of environmental changes. Here, we present a method that can be used to detect the population-level effects of past and ongoing environmental changes in the absence of any long-term monitoring data, thus providing a firmer empirical footing for future predictions. The data requirements of this technique are substantial, but not unrealistic, for common, easily sampled species. While, in our *Discussion*, we will focus on climatic changes, the method is just as useful for detecting more localized population-level responses to anthropogenic impacts or naturally occurring changes in local environments.

Exploration of the results of environmental change can be focused on individual, population, community, or ecosystem responses. However, most studies of global environmental change have focused on traits of individuals (e.g., growth, Tissue and Oechel [1987], Havstrom et al. [1993]; or reproduction, Wookey et al. [1993]) or ecosystem-level features (e.g., total biomass, Harte and Shaw [1995]), while relatively few studies have examined population-level changes, such as trends in the size distributions or numbers of individuals (Korner and Bazzaz 1996). For example, we are aware of only two studies that have documented population responses of herbaceous plants to ongoing climatic warming in the field. Fowbert and Lewis Smith (1994) and Lewis Smith (1994) have recently argued that the signature of climate change can be detected by examining entire populations of herbaceous plants. Taking advantage of long-term censuses of the only two native species of Antarctic vascular plants, pearlwort (*Colobanthus quitensis*) and hairgrass (*Deschampsia antarctica*), they were able to show that the numbers of individuals in two populations of each species have increased in the past two to three decades, a trend that paralleled increases in temperature at their study sites. Searching for shifts in the historical ranges of species (Grabherr et al. 1994, Parmesan 1996) provides another population-scale approach to detecting biotic responses to environmental change. These two studies provide some of the most convincing data directly documenting population-level climatic change. However, the data used in these studies, i.e., very long-term censuses, are currently unavailable for most species and locales.

In the current paper, we propose a new method that will allow ecologists to search for the population-level consequences of past environmental change in the absence of long-term data. While the method will not work for all species, it is sensitive enough to measure the effects of environmental change for many plants and animals. Conveniently, it may be especially appropriate for species such as long-lived herbaceous perennial plants that characterize those biomes (e.g., arctic and alpine tundra) that are depauperate in the woody species commonly relied upon as long-term detectors of environmental change. Thus, the technique provides a natural complement to existing methodologies in the detection of environmental change and its ecological consequences. The method uses the fact that species will manifest responses to changing environments not only in individual demographic rates, but also in the distribution of the sizes or ages of individuals within populations, and that for long-lived and slowly growing species, population structure can lag far behind that predicted from current demographic rates. In a nutshell, the idea is that, by determining the degree to which the current size distribution in a population does not accord with current demographic rates (i.e., reproduction, growth, and survival), we can estimate recent changes in demographic rates, even when we have no way of directly determining the size or structure of the population at any time in the past. While the comparison of actual and predicted size or age distributions is straightforward (Caswell 1989), it has most often been viewed as a simple check on the validity of demographic models, with mismatches seen as mere annoyances. Our goal is to turn these ''mismatches'' into a virtue, thereby facilitating tests of specific hypotheses about the strength and speed of multiple effects of environmental change.

We begin by describing the general approach, and then develop the modeling and statistical tools needed to perform these analyses using real field data. We next present the results of simulation studies designed to illustrate both the problems and potential of the method, and finally discuss what biological prerequisites, data requirements, and modeling considerations are most important to make this a powerful approach for evaluating environmental change.

Methods

Background and overview

It is difficult to directly infer the population-level consequences of environmental change. Invasive species, increased temperature, higher UV intensity, and elevated CO_2 levels will all affect rates of growth, reproduction, and survival, and these effects will differ depending upon the size or age of each individual. The simplest and best established methods for extrapolating population behavior from such multiple effects on individual performance use population matrix models, in which size, age, or some other predictor of individual performance is used to classify individuals (Werner and Caswell 1977, Bierzychudek 1982, Caswell 1989, Menges 1990, Doak 1992, Schemske et al. 1994, Morris and Doak 1998). Matrix models yield two related but distinct predictions about population behavior: (1) the overall rate of population growth, and (2) the ex-

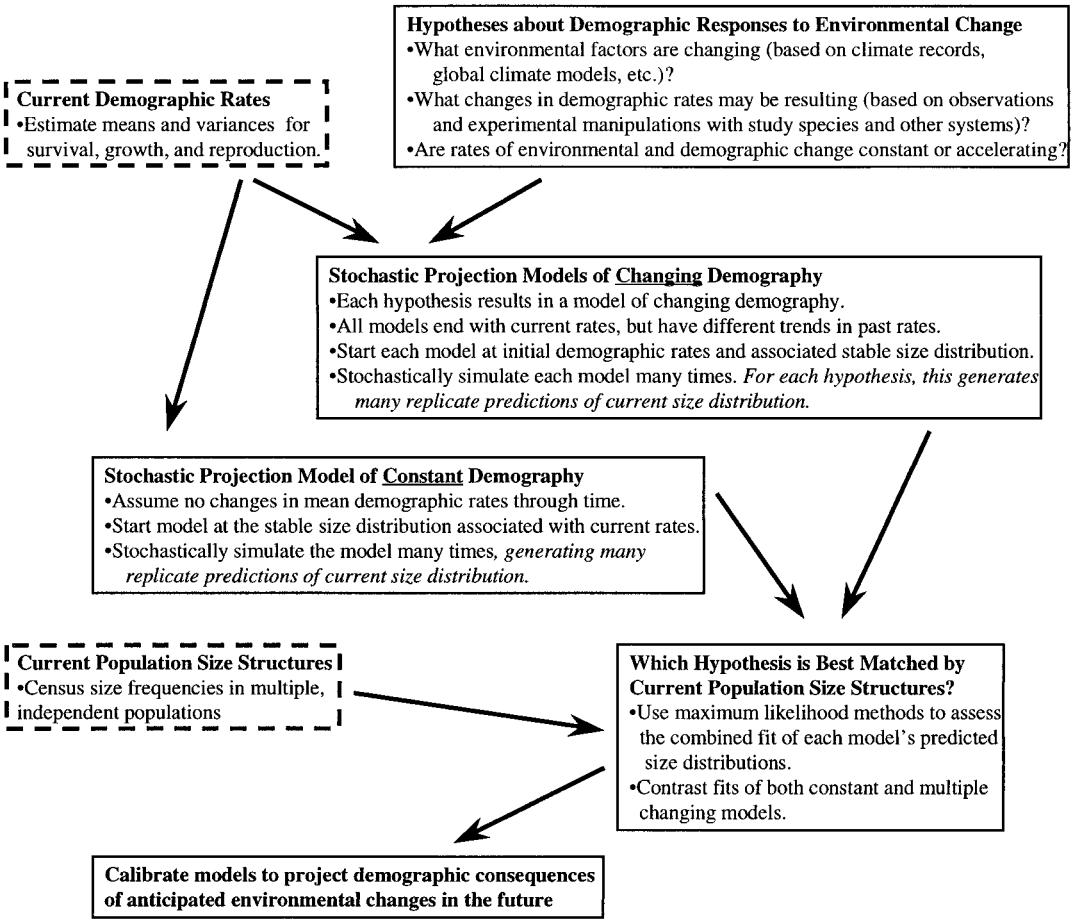

FIG. 1. Flow diagram of data collection and analysis steps needed to test the predictions of demographic models of environmental change against current population size structures. Dashed boxes indicate the direct field data used to construct and test models of demographic change.

pected stage distribution of individuals in the population (i.e., the relative frequency of individuals of different stages; henceforth, we will assume size-based stages for convenience). At their simplest, such models assume that demographic rates are constant from year to year. When this is the case, the models predict that the population will grow or shrink at a constant rate and that the relative abundance of individuals in different stages will stay the same; this constant set of proportions of differently sized individuals is commonly termed the Stable Stage Distribution (SSD). While matrix models with stochastic variation (but no long-term trends) in demographic rates do not predict stable population structures, they can be used to generate a range of likely size distributions that can be compared with an observed population structure (Tuljapurkar 1990). If mean vital rates are changing deterministically through time, the range of likely size distributions will shift, but will still be more or less predictable at any given point in time.

Our method starts with the collection of the current size distribution of a population and the collection of the actual current demographic rates, as measured over the course of a few years. We then test the fit of the current observed size structure of a population against both (1) the predictions of a stochastic matrix model that assumes the mean values of demographic rates have not deviated from their current values over time; and (2) a suite of alternative stochastic models that incorporate different scenarios of how mean demographic rates may have changed in the recent past. In making this comparison, we see each model of stable or changing demographic rates as a separate hypothesis, which makes predictions about population structure, and the current population structure as the data against which to test these hypotheses. If demographic rates are on average changing through time (such as they may be with climate or other environmental change), then the size distribution of individuals will be shifting as well, lagging behind current rates and reflecting the combined influences of both past and present demographic rates. In this situation, a matrix model built with current demographic rates should yield relatively poor predictions of current population

structure, and models that include shifting rates through time should provide better predictions. Conversely, if environmental changes have not significantly affected a population, then demographic rates should have remained the same, on average, over the past several decades, and a matrix model built with these current demographic rates should accurately predict the current size distribution. In this way, the measurement and comparison of current demographic rates and current population structure can potentially provide a powerful tool for detecting the effects of past and current environmental change.

Fig. 1 provides a summary of the steps needed to perform the tests just described. While the basic idea is simple, its fruitful application depends upon the use of population models that incorporate realistic environmental variation in demographic rates, as well as the establishment of clear statistical criteria with which to judge the fit between model predictions and population structure. While simple static matrix models make clear predictions about population size distributions, there is often substantial variation in vital rates from year to year. This variation is of two distinct types: (1) stochastic variation around mean values, and (2) long-term trends in the mean values, due to forces such as climatic change. It is the later that we wish to test, but, to do so, we must also acknowledge and account for the former. An additional complication that must be considered is the uncertainty in our estimates of mean vital rates. Essentially, this means that each of the comparisons we advocate becomes a statistical exercise, judging the current size distribution against a frequency distribution of possible size distributions that is determined, not just by environmentally induced changes in rates, but also by the random variation and the uncertainty in each vital rate. Thus, predictions of expected size distributions must come from stochastic simulations of structured population models that allow changing mean values for different vital rates, along with random fluctuations in rates from year to year and uncertainty in mean rates. Many studies have now been published using different methods to simulate stochastic matrices. In the work we present, a modified version of the model described in Doak et al. (1994) is employed, allowing each vital rate used in the matrix to vary each year of the simulation, according to a prescribed mean and variance, and allowing correlated variation between different rates. This model was altered to permit the mean value for each vital rate to change through time, and also to incorporate uncertainty in current demographic rates due to sampling error. With such a model in hand, the next requirement is an objective test of the fit of the model predictions to an observed size distribution. We now turn to the development of a statistical test to compare the size distributions predicted by alternative stochastic models, using population structures measured in the field.

A strong test of fit between stochastic model predictions and measured size distributions

There are several statistics available to test for the match between a predicted and an actual frequency distribution. Two of these, Keyfitz's delta and Cohen's cumulative distance tests, have been proposed specifically to test the fit between the SSD predicted by a matrix model and an observed stage distribution (Caswell 1989). In addition, Pearson chi-square, likelihood-ratio chi-square (*G* [goodness-of-fit] tests), and Kolmogorov–Smirnov tests are all frequently suggested for the testing of empirical vs. predicted frequency distributions (Sokal and Rolhf 1995). However, in their simplest forms, none of these tests is quite adequate for our purposes. This is because of the need to incorporate environmental variation and measurement error into our models; each ''model'' (a set of assumptions about the current values of all the vital rates, their rates of change in the past, and the magnitudes of environmental variation in each) is stochastic, and thus can provide an infinite number of predictions concerning the observed size distribution. In addition, we need to account for uncertainties in our estimates of current demographic rates, which will also affect model predictions of size structures. Our goal is to devise a means to determine whether the observed size distribution is more likely to lie within the range of distributions predicted by one model vs. another. For these comparisons, we adopt a likelihood approach, based upon the multinomial distribution, also the basis of the *G* test. Using this distribution assumes that size distributions estimated from field data come from measurements of randomly sampled individuals that are part of much larger populations.

We begin by calling any set of assumptions about the changing values of demographic rates a model, M_i, where i ranges from 1 to the number of scenarios of environmental change we aim to test. In particular, this suite of models includes both the model of constant mean demographic rates, as well as multiple models incorporating reasonable guesses about changing rates (Fig. 1). In the language of hypothesis testing, the model of constant rates is the null hypothesis, while the models of changing rates are a set of differing, alternative hypotheses. Each model, or hypothesis, can predict many different size distributions, due to the particular sequence of randomly varying matrices that are generated over time, and the uncertainty we have in knowing the actual current demographic rates, upon which all projections of past and changing rates are based. To include these sources of variation, M_i must be simulated many times to produce a large number, k, of replicate predicted size distributions, $\mathbf{p}_{i1}$, $\mathbf{p}_{i2}$, $\mathbf{p}_{i3}$, . . . , $\mathbf{p}_{ik}$, where $\mathbf{p}_{ij}$ is a vector containing the proportions of individuals in each size class for run j of model i. For each replicate of the model, we randomly choose a set of mean current rates (based upon estimated grand

means and standard errors for each vital rate), plus a realized sequence of yearly rates through time (based upon our estimates of the effects of hypothesized environmental change, plus variation about the mean rates due to environmental stochasticity). Assuming for the moment that we have a single observed size distribution vector, **d**, the likelihood of observing this distribution, given k simulated predictions based on model M_i, is approximated by

$$L(\mathbf{d}\,|\,M_i) = \sum_{j=1}^{k} [\,f(\mathbf{p}_{ij})L(\mathbf{d}\,|\,\mathbf{p}_{ij})] \tag{1}$$

where $f(\mathbf{p}_{ij})$ is the relative frequency of the predicted distribution $\mathbf{p}_{ij}$ among the predictions of model M_i; and $L(\mathbf{d}\,|\,\mathbf{p}_{ij})$ is the likelihood of the data, given only one replicate run of the model (which yields a single predicted size distribution). In words, the total likelihood is estimated by the weighted average of the likelihoods of the data, given each of the k stochastic predictions of model M_i. Since we will rely upon extensive simulation to estimate the distribution of the $\mathbf{p}_{ij}$'s, $f(\mathbf{p}_{ij})$ will equal $1/k$ for all k runs of the model, and Eq. 1 becomes

$$L(\mathbf{d}\,|\,M_i) = \frac{1}{k}\sum_{j=1}^{k} [L(\mathbf{d}\,|\,\mathbf{p}_{ij})]. \tag{2}$$

As mentioned, we use the multinomial distribution to estimate the individual likelihoods, $L(\mathbf{d}\,|\,M_i)$. If run j of model M_i predicts that the fractions $\mathbf{p}_{ij}(0)$, $\mathbf{p}_{ij}(1)$, $\mathbf{p}_{ij}(2)$, . . . , $\mathbf{p}_{ij}(s)$ of the population that will be found in size classes 0, 1, . . . , s, and the observed N individuals are distributed as $d(0)$, $d(1)$, $d(2)$, $d(3)$, . . . , $d(s)$ individuals in each class (where $N = \Sigma_{n=1}^{s}\, d(n)$; and $d(n)$ is the number of individuals in size class n), then the probability of the data under the predicted distribution is determined by a multinomial distribution:

$$L(\mathbf{d}\,|\,\mathbf{p}_{ij}) = \frac{N!}{d(0)!d(1)!\cdots d(\mathbf{s})!}\mathbf{p}_{ij}(0)^{d(0)}\cdot\mathbf{p}_{ij}(1)^{d(1)}\cdots\mathbf{p}_{ij}(s)^{d(s)}. \tag{3}$$

Thus, substituting Eq. 3 into Eq. 2, we can estimate the total likelihood for a model M_i, given the data.

If observed size distribution vectors $\mathbf{d}_1$, $\mathbf{d}_2$, . . . , $\mathbf{d}_m$ are available for m replicate populations, which we assume have experienced the same average environmental trends in the past, then the estimated model likelihood becomes the product of the likelihoods of the model given each data set (i.e., each replicate population):

$$L(\mathbf{d}_1, \mathbf{d}_2, \ldots, \mathbf{d}_m\,|\,M_i) = \prod_{i=1}^{m} [L(\mathbf{d}_i\,|\,M_i)]. \tag{4}$$

Several final points need to be mentioned. First, throughout the rest of the paper we will be reporting not estimates of likelihoods, but rather of negative log-likelihoods, denoted $\mathcal{L}$, as is standard practice (Edwards 1992). The model with the *smallest* negative log-likelihood provides the best fit to an observed size distribution. In addition to providing a relative measure of model fit, negative log-likelihood values allow us to test statistically whether a model i (with negative log-likelihood $\mathcal{L}_i$) fits an observed size distribution significantly worse than does the best fit model (for which the negative log likelihood, $\mathcal{L}_{\text{best}}$, is by definition lower than for any other model being tested). This result comes from a likelihood ratio test, which makes use of the fact that the quantity $G = 2(\mathcal{L}_i - \mathcal{L}_{\text{best}})$ has an asymptotic chi-square distribution with df = 1 (Stuart and Ord 1991). Because the critical value of $\chi^2_1 = 3.84$, at a significance level of $\alpha = 0.05$, there is only a 5% chance that comparing the predictions of an alternative model to an observed size distribution would produce a negative log-likelihood value that differs from $\mathcal{L}_{\text{best}}$ by ≥ 1.92 ($=3.84/2$) if, in fact, the alternative model actually predicts the data as well as the best fit model. Said another way, using this critical value means that there is a 5% probability that we will incorrectly reject the true model in favor of some other modeled rate of change. Thus, we can use an upper cutoff of 1.92 to identify those models whose likelihoods are close enough to the best fit model that they cannot be rejected statistically; this suite of models forms a 95% confidence interval that brackets the most likely scenarios of past change (Hudson 1971, Hilborn and Mangel 1997). If this interval does not include the model with no change, we would have strong statistical support for the claim that demographic rates have indeed been changing.

Simulation Tests

Approach and basic results

The method just outlined should, in theory, allow one to test for past and ongoing environmental change. The question remains, how accurate and sensitive is this procedure? To begin to provide an answer and to stimulate further research, we present preliminary tests using simulated data for a generic long-lived, slowly growing plant. In these tests, we generated size distributions with known rates of change in specific demographic rates, and then used the method to determine how well we could detect the signature of these changing rates.

There are a vast number of possible effects of changing environments on different combinations of demographic rates, as well as many factors that can confound detection of changes in demography. In this paper, we limit our tests to two possible sets of changing demographic rates that mimic an amelioration of environmental conditions (such as warming temperature in an arctic ecosystem): (1) decreases through time in the mortality rates of all but the smallest size class, and

TABLE 1. Mean demographic rates used in simulation tests. For constant rates, $\lambda = 1.056$. See *Simulation tests: Approach and basic results* for explanation of stochastic simulations using these rates.

Class	Mortality rates (yr^{-1})	Growth rates (yr^{-1})	Seedling production (no. seedlings/ parent plant)
0	0.90	1	0
1	0.40	0.8	0
2	0.20	0.8	0
3	0.10	0.4	1
4	0.05	0.2	2
5	0.05	0.1	4
6	0.05	0.1	6
7	0.05	0.1	8
8	0.05	0.1	8
9	0.10	0	8

(2) increases through time in the growth rates of all but the smallest size class. Using these changes, we first explore a baseline set of simulations. In *Simulation tests: Complications and limitations*, we extend these simulations to address three factors likely to undermine the power of the method: high temporal variation in demographic rates, inaccurate measurement of current demographic rates, and construction of matrices that ''compress'' size structure into a small number of categories.

For these tests, we constructed a set of simplified demographic rates that would be typical for a long-lived perennial plant, with high juvenile mortality, low adult mortality, and low transition rates among 10 size classes (Table 1). The tests involve two parts. First, we generated ''observed'' current size distributions from known patterns of change in demographic rates. Because of environmental stochasticity, a range of observed size distributions could result from a given scenario of demographic change. Thus, we generated 1000 size distributions for each scenario. We then applied our method to see if we could recover the signal of demographic change built into these observed distributions.

We first describe simulation tests, including modest environmental variation and ignoring sampling uncertainty in estimates of current demographic rates. (We will use these as a baseline to assess the impact of sampling uncertainty). The 1000 simulated observed size distributions were constructed to be samples with a total of 3000 individuals in the nine largest size classes. The exact number of individuals is somewhat arbitrary, the point being to sample sufficient numbers to obtain a highly accurate estimate of the actual, current population structure. Our model structure assumes that, over one year, a surviving plant can only remain the same size or grow one size larger. The probability that a plant in size class x survives and grows into class $x + 1$ is thus $s_x g_x$, while the probability of surviving and remaining the same size is $s_x(1 - g_x)$, where s_x and g_x are the stage specific survival and growth probabilities, respectively. For the initial simulations, we assume that each year there is uncorrelated random variation in all growth and mortality rates, with standard deviations equal to 10% of the mean for each rate (CV = 10%); for all simulations, each fertility value was picked randomly each year to equal the mean, 50% of the mean, or 150% of the mean (which mimics the high interannual variation in fecundity shown by many arctic, alpine, and desert plants). All annual changes in mean vital rates were constant, linear additions, or subtractions that were proportional to a rate's final value. Each simulation started at the stable size distribution predicted by its initial vital rates, and all ended with the same final mean rates. Thus, high rates of change correspond to past demographic rates that are more deviant from the final mean rates common to all simulations. All simulated size distributions are the result of 20 yr of changing rates. For mortalities, we generated size distributions from three sets of simulations: no changes in mean rates, or higher rates having occurred in the past (at two possible levels). These higher rates were calculated as linear changes, such that in each past year mean rates were higher than final mean values by either by 1 or 2% of the final value per year. For example, assuming 1% yearly changes, one year ago the present a rate equaled 1.01 times its current value, and 10 years ago it equaled 1.10 times its current value. For growth rates, we also generated three sets of size distributions resulting from either no changes, or past rates that were lower than current values by 2 or 3% per year. We deliberately simulated yearly changes of small magnitude, as would be expected for natural populations experiencing subtle environmental trends (e.g., climatic warming).

Next, we ran a second set of simulations to make ''predicted'' size distributions, based upon different models of environmentally induced demographic change. These models all used the same variation in fertilities described for the ''observed'' cases, and all used standard deviations in growth and mortality rates equal to 10% of mean values. For mortalities, we ran models with past rates differing from current values by between -2.5 and $+4$% per year; for growth rates, we ran models with past rates differing from current values by between -4.5 and $+4.5$% per year. All simulations ran for 20 yr, starting at the stable size distribution predicted by the initial vital rates. Six thousand replicates were run for each model, and these predicted distributions were then compared to the observed size distributions as follows. Based upon the 1000 observed distributions, we calculated (using Eq. 2 or 4) a negative log-likelihood for each of the models being tested (including the ''true'' model), identified the best fit model (which, due to environmental stochasticity, was not always the true model), and then tested whether we could reject each of the other models when compared to the best fit model, using the likelihood ratio test.

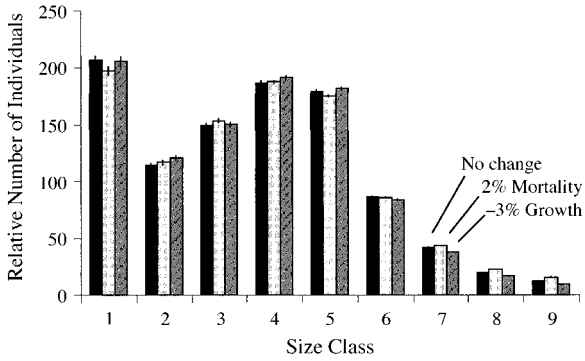

FIG. 2. Stage structures from models of changing or constant environments. Relative numbers (mean ± 1 SE) of individuals in size classes 1–9 for models of environments with no directional change, past mortality rates higher than current rates by 2% per year, and past growth rates lower than current rates by 3% per year. Results are based upon 1000 simulated data sets for each scenario. Simulations were for 20 yr and assumed moderate random environmental variation in growth and mortality rates (CV = 10% for all rates).

The method is a success if, over an entire set of 1000 observed size distributions, the true model and others close to it are rarely rejected, and models far from the true model are rejected in a firm majority of cases.

In performing these tests of actual vs. predicted size distributions, we used each set of 1000 observed distributions in three different ways, in order to assess how many size distributions one would need to sample in order to achieve powerful results. Specifically, we either fit each of the 1000 observed size distributions separately (using Eq. 2), fit 100 sets of 10 distributions each (using Eq. 4), or fit 50 sets of 20 distributions each (using Eq. 4). These alternative exercises correspond to collecting size data from either 1, 10, or 20 populations within a single region, each of which would experience similar, but not identical, environmental changes.

Before examining the stochastic simulations, it is important to note that there are actually multiple ways to test each model against the data. The basic multinomial probabilities for each model can be calculated for all size classes, or for only a subset of the classes. The benefit in using a subset of the data is that, for many long-lived organisms, the smaller, shorter duration size classes are the hardest to accurately sample in the field and will also be the most buffeted by yearly environmental variation (hence census data will yield estimates of their current frequency in the population that are less certain than estimates for larger size classes). Thus, calculating probabilities for only the larger size classes may give better estimates of relative model fit than will consideration of all classes; conversely, the smaller the number of classes that are considered, the smaller are the sample sizes used to estimate model fit. The models used here have realistically high variation in annual reproduction, and the resulting wide variation in numbers in the smaller size classes means that tests based upon larger classes are more robust; we report results using classes 5–9 to test the models against the simulated data.

The observed size distributions generated by different scenarios of changing demography differ in small, but highly consistent, ways (Fig. 2). In spite of the modest nature of the differences seen in these initial tests, for which the ''true'' amount of annual variation in demographic rates is moderate (i.e., CV = 10%) and demographic models are accurate (i.e., correct values for final rates and a realistic number of size categories are used to test for changing rates), the method was quite powerful (Fig. 3). The ability of a single population's size distribution to correctly distinguish models with differing rates is fairly low (Fig. 3A, B); but, as data from either 10 (Fig. 3C, D) or 20 (Fig. 3E, F) populations are utilized simultaneously to test against model predictions, the models with changing rates are usually able to reject observed size distributions with no change or change in the opposite direction, for both changing mortality and growth rates. Simultaneous fitting of multiple distributions also results in a closer match to the expected 5% rejection rate of the true models, showing better approximation to the correct likelihood function. Overall, the ability to differentiate between these models is striking, because even the highest rate of change we used to generate observed size distributions amounted to only a 3% change in demographic rates per year, and operated in the face of significant annual variation in all demographic rates. These results also emphasize that it is important to use size distribution data from several replicate populations to test models of demographic change.

Complications and limitations

While the results reported thus far are encouraging, we used additional simulations to explore more complicated, and realistic, scenarios. These suggest that the method is surprisingly robust to, though not unaffected by, two potential problems (high levels of environmental stochasticity and estimation error of current rates), while they reveal one factor (model ''compression'') that will hopelessly erode the usefulness of the method. First, increased annual variation in demographic rates somewhat weakens, but does not doom, the method. For mortality rates, increasing the coefficients of variation for all demographic rates from 10% to 25% results in a substantially broader range of accepted rates of change (compare Fig. 4A with Fig. 3E). However, the same increase in environmental variation had little influence on the power to detect changing growth rates (compare Fig. 4B with Fig. 3F). For both sets of results, the estimation of the correct likelihood functions is also somewhat worsened, as evidenced by the >5% rejection rates of the true models, indicating that more extensive model replication would be needed to achieve highly accurate estimates of true rejection

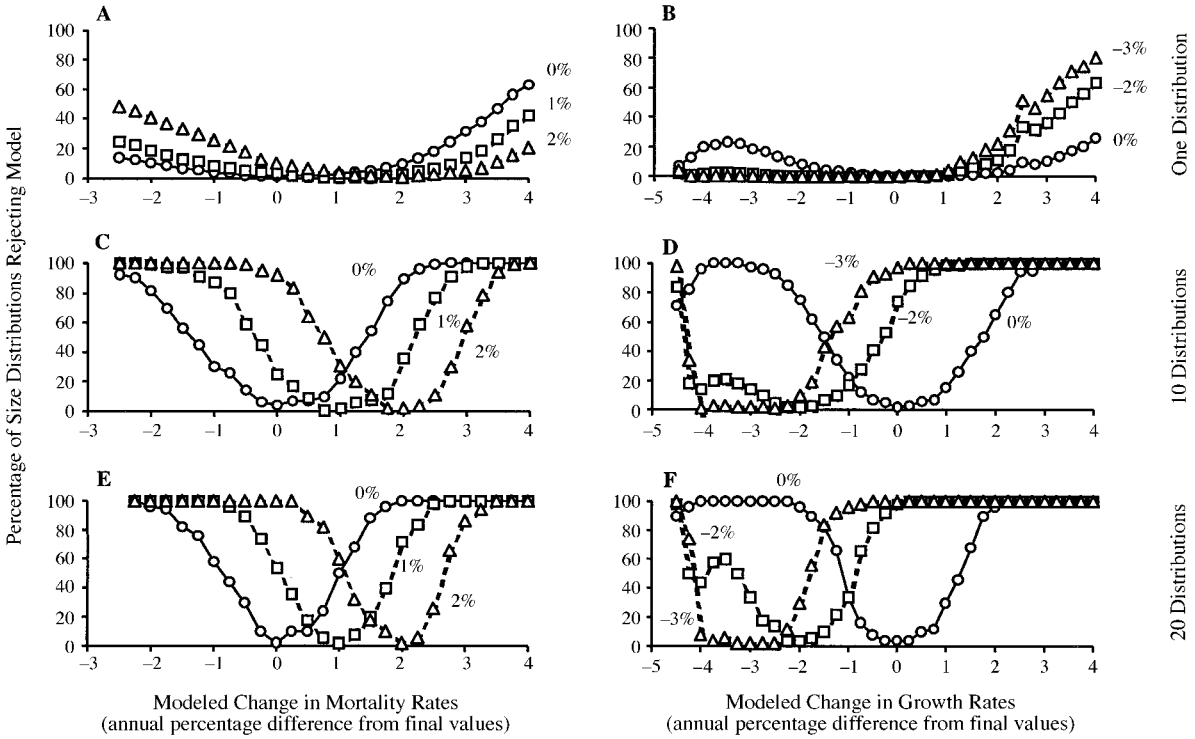

FIG. 3. Results of simulation tests for a generic long-lived plant. Each graph shows the percentage of simulated ''observed'' size distributions (or sets of distributions) that rejected each model of demographic change. Steeper sided ''valleys'' indicate more power to distinguish the best fit model in the ''valley bottom.'' Lines show results for population size data resulting from simulations with past mortality rates higher than current rates by 0%, 1%, or 2% per year (○, □, and △, respectively), or past growth rates lower than current rates by 0%, 2%, or 3% per year year (○, □, and △, respectively). The CV of all rates was 10%. (A and B): Results for changing mortality and growth rates, respectively, fitting population size structures to models individually (n = 1000 ''observed'' population size distributions). (C and D): Fits using data for sets of ten population structures each (n = 100 sets of size data). (E and F): Fits using data for sets of 20 population structures each (n = 50 sets of size data).

rates. While these results show that the method can cope with substantial random environmental variation, even higher stochasticity, or incorrect estimation of variation, can fatally weaken the comparisons (D. F. Doak and W. Morris, *unpublished data*), cautioning that we should only apply the method to species with demographic rates that are not too volatile across years.

To examine the method's ability to handle errors in the measurement of current demographic rates (or equivalently, variation in demographic rates among replicate populations), we next created new sets of 1000 simulated size distributions resulting from different rates and types of demographic change. To include measurement error, for each simulation we generated a different set of current mean rates by picking the final mean value for each growth and survival rate from a beta distribution (with grand means equal to the values in Table 1 and CV = 5%). Thus, all simulated data sets were created using somewhat different current and past mean rates. In creating these ''observed'' size distributions, we again assumed that environmental variation was moderate (CV = 10%), but added biological realism by forcing correlations in the annual deviations of different demographic rates (r^2 = 0.64 for all pairs of rates). To test these observed size distributions, we ran new sets of model simulations, each also including random variation in estimated current rates (CV = 5%). For each modeled type and rate of change, we ran 20 000 replicates, which was the minimum needed to generate relatively stable results with this new source of variation. For these tests, it also proved essential to perform simultaneous fits of >20 size distributions to give convincing results. Furthermore, we calculated not only the separate rejection of each modeled rate of change by each set of size distributions (Fig. 4C, D; data point symbols), but also the percentage of sets that did not accept any of three adjacent models (Fig. 4C, D; dashed and dotted lines). While including measurement uncertainty results in somewhat weaker, and far noisier, comparisons, the method maintains its ability to distinguish correct and incorrect models for changes in both mortality and growth rates. Thus, we find that uncertainty in measurements of current demography does not fatally undermine the method, although it does demand that size distribution data be collected from multiple popula-

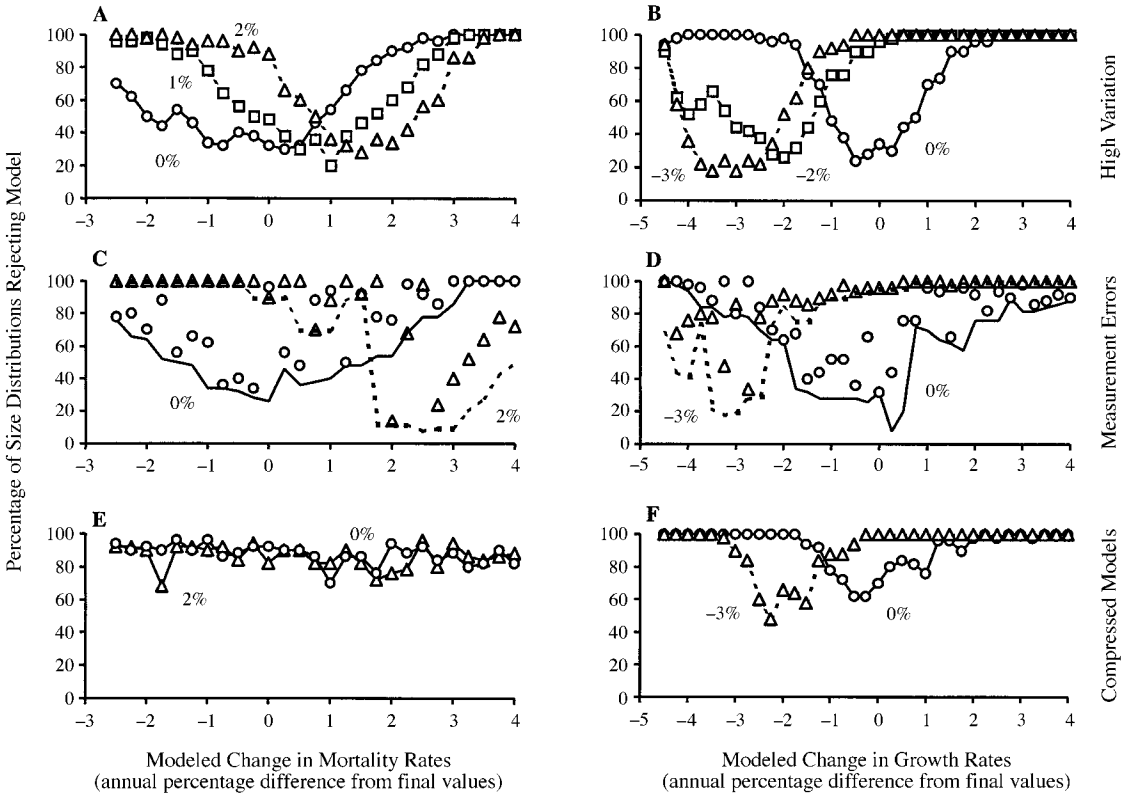

FIG. 4. Results of simulation tests for a generic long-lived plant showing effects of additional complications on the comparison of observed and predicted size distributions. Each graph shows the percentage of simulated ''observed'' size distributions that rejected each model of demographic change. Lines show results for data simulating past mortality rates higher than current rates by 0%, 1%, or 2% per year, or past growth rates lower than current rates by 0%, 2%, or 3% per year (see Fig. 3 for symbol definitions). All model rejection rates are based upon 50 sets of 20 ''observed'' size distributions each. (A and B): Fits for sets of size distributions with changing mortality and growth rates, respectively, with high random fluctuations in demographic rates (CV = 25%; compare with Fig. 4A, B). (C and D): Fits for sets of size distributions incorporating errors (CV = 5%) in measurements of current mortality and growth rates. Symbols show percent rejection of individual models, while lines show the percentage of distributions that do not accept any of three adjacent models. (E and F): Fits for sets of observed size distributions when model results are based upon ''compressed'' size structures that combine size classes (five classes vs. the 10 used to generate the observed size distributions).

tions, and that the model simulations used to test the observed distributions both include this uncertainty and be extensively replicated.

Finally, we consider the problem of inaccurate model structure, in which the number of size classes used is much lower than that representing ''reality.'' To do this, we ran compressed models for changing growth and mortalities that were based upon only five classes, each equivalent to two of the classes in Table 1 (i.e., classes 0 and 1, 2 and 3, etc.), with rates appropriately combined from those of the underlying classes (cf. Enright et al. 1995). These compressed models essentially negate the ability of the method to accurately identify changes in mortality rates and substantially weaken tests for changing growth, at least for the relatively low rates of annual change we tested (Fig. 4E, F). For both of the ''true'' rates of mortality change, no models are accepted by even 50% of the sets of 20 size distributions, and there is no perceivable pattern in model rejections (Fig. 4E). Models of changing growth rates show some ability to distinguish size distributions, but here too even the correct models are rejected at very high rates (Fig. 4F). For all of these simulations, we used accurate estimates of demographic rates, and moderate levels of annual environmental variation (CV = 10%), so the only factor reducing the power of the method from that shown in Fig. 3 is the compression of size classes. The severe effect of using a small number of size classes probably arises for two reasons. First, it destroys the ability of the population size structure to preserve the clear, but subtle, signals of changing demography seen in Fig. 2 (see *Prerequisite 1*). Second, by reducing the number of size categories, it reduces the statistical power to distinguish between alternative size distributions.

With these results in mind, we turn now to a more general discussion of the major biological and modeling prerequisites needed for our approach to work. Specifically, we discuss two issues: (1) the life history characteristics needed to permit extended time lags in

TABLE 2. Estimates of damping ratio and times to convergence for population matrices of herbaceous plant species.

Species	No. of stages	Magnitude of: λ_1	Magnitude of: λ_2	Damping ratio, ρ	t_{20} (yr)	Reference
Calochortus obispoensis	3	1.023	0.369	2.775	2.94	Fiedler 1987
Calochortus tiburonensis	3	1.156	0.732	1.580	6.55	Fiedler 1987
Andropogon semiberberis	4	1.252	0.332	3.769	2.26	Silva et al. 1991
Calochortus albus	4	1.542	0.782	1.973	4.41	Fiedler 1987
Calochortus pulchellus	4	1.135	0.658	1.725	5.49	Fiedler 1987
Coryphantha robbinsorum	4	1.052	0.642	1.638	6.07	Schmalzel et al.
Erythronium japonicum	4	1.076	0.571	1.886	4.72	Kawano et al. 1987
Danthonia sericea	6	1.209	0.723	1.675	5.81	Moloney 1988
Panax quinquefolium	6	1.026	0.685	1.499	7.40	Charron and Gagnon 1991
Pedicularis furbushiae	6	1.274	0.672	1.896	4.68	Menges 1990
Potentilla anserina	6	1.328	0.757	1.755	5.33	Eriksson 1988
Allium monanthum	7	1.588	0.265	5.996	1.67	Kowano et al. 1987
Arisaema triphyllum	7	1.113	0.726	1.561	6.73	Bierzychudek 1982
Disporum smilacinum	7	1.428	0.425	3.357	2.47	Kawano et al. 1987
Calathea ovandensis	80	0.992	0.551	1.800	5.10	Horvitz and Schemske 1995
Disporum sessile	12	1.072	0.582	1.843	4.90	Kawano et al. 1987
Silene acaulis	12	1.009	0.962	1.050	62.01	Morris and Doak 1998
Erythronium japonicum	13	1.055	0.820	1.286	11.92	Kawano et al. 1987
Viola fimbriatula	14	1.422	0.848	1.677	5.79	Solbrig et al. 1988
Armeria maritima	17	1.060	0.877	1.209	15.80	Lefebvre and Chandler-Mortimer 1984
Arisaema serratum	19	0.995	0.756	1.315	10.94	Kinoshita 1987
Chamaelirium luteum	24	1.020	0.979	1.041	73.89	Meagher 1982

Notes: Before calculation of eigenvalues, we corrected published matrices that included a redundant seed stage (see Caswell 1989, Silvertown et al. 1993), and we followed Silvertown et al. in using averaged values to construct single matrices when multiple years or populations were studied. Key: λ_1 = dominant eigenvalue; λ_2 = subdominant eigenvalue; ρ = damping ratio; t_{20} = time until the contribution of the dominant eigenvalue to changes in population growth and structure is 20 $\times$ more important than that of any other eigenvalue.

population structure, along with the modeling framework needed to simulate these effects; and, (2) the problems posed by several extrinsic factors that can weaken or bias the method's ability to infer changes in demography caused by environmental change.

PREREQUISITE 1: LONG LAG TIMES IN CONVERGENCE TO THE STABLE STAGE DISTRIBUTION

Matrix models predict that if vital rates are changed, a population's stage distribution will eventually converge to a new stable stage distribution. If vital rates are gradually changing through time, a population's stage distribution may lag far behind that predicted by current vital rates, or it may ''keep up'' with the SSD predicted by current rates. Clearly, our method relies upon the existence of a significant lag, causing a mismatch between the current stage distribution and current predicted SSD. Biologically, species that show slow adjustment of stage distributions to changing conditions are those with high adult survival, slow growth, and relatively long prereproductive periods (Caswell 1989). Thus, arctic, alpine and desert perennials, many trees and shrubs, long-lived vertebrate species, and some slowly growing clonal invertebrates are among the most suitable species for these analyses.

Mathematically, a population matrix can be analyzed in several ways to estimate how quickly a population will converge to SSD (reviewed in Caswell [1989]). The most commonly used of these measures is the damping ratio, ρ, the ratio of the magnitude of the dominant eigenvalue of the population matrix (which will be a real number for most realistic projection matrices; Caswell 1989) to the magnitude of the subdominant eigenvalue (which is often a complex number). To illustrate the general range of convergence times, we calculated ρ for matrices based upon data for 22 herbaceous plant species (Table 2). The damping ratio can be used to calculate a measure of the lag time (in years) for convergence to the SSD. Specifically, we calculated $t_{20} = \ln(20/\ln(\rho))$, which is the predicted time needed for the dominant eigenvalue to become $\geq 20\times$ more important than any other eigenvalue in determining population growth and structure. For many of the published matrices in Table 2, the predicted convergence times are relatively short, and thus these matrices are not likely to give powerful results using our approach. However, it is crucial to point out that damping ratios are influenced not only by the life history of the species in question, but also by the matrix structure researchers choose to adopt. Matrix modelers have a tendency to make highly compressed models; that is, ones with a few broad size categories and relatively low rates of transition between them. While the degree to which size structure is compressed, if done properly, has no effect on most uses of matrix models, it has a large effect on damping ratios and convergence times. One published example of this effect is Crowder et al.'s (1994) study of loggerhead sea turtles. In this case, a five-stage size transition matrix has a damping ratio of 1.2758 and predicts 12 yr until the dominant eigenvalue overrides the others by a factor of 20, while a full 54 $\times$ 54 age-based matrix has a damping ratio of 1.0228

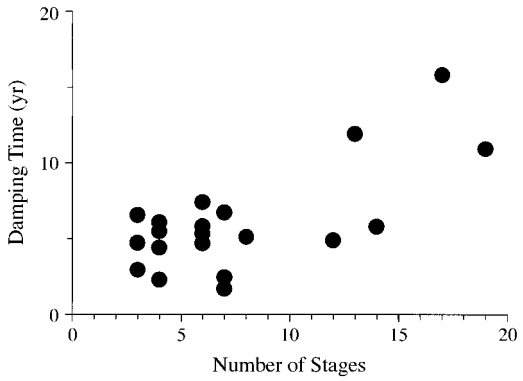

FIG. 5. Effect of matrix model structure on convergence times. Damping time, t_{20} (the number of years needed for the effect of the dominant eigenvalue on population structure to be $\geq 20\times$ higher than the effect of any other eigenvalue) is plotted against number of size or age stages in a matrix. Data are from studies listed in Table 2, excluding two species with outlying damping times (*Chamaelirium luteum* and *Silene acaulis*).

and predicts 133 yr for equivalent convergence to occur. Similarly, increasing the number of stages from 4 to 13 in models for the forb *Erythronium japonicum* (Kawano et al. 1982, Kawano et al. 1987) more than doubles the convergence time (Table 2).

Considering the range of plant species in Table 2, some species had short convergence times, regardless of the number of stages in the underlying matrix, but long convergence times were predicted only when a relatively large number of stages were used. Of the matrices in Table 2, only 7 of 22 had ≥ 10 stages, yet two of these seven, and none of the other 15, had t_{20} values >20 yr. Furthermore, even after removing these two outliers, the remaining 20 matrices showed a strong correlation between t_{20} and the number of stages (Fig. 5; $r = 0.701$, $P < 0.01$). The lesson from this survey is that detecting environmental changes will rely both upon picking species that have the right life history characteristics to show lag times in population structure and, just as importantly, upon making models capable of accurately capturing these lag times. It may neither be possible nor desirable to make models with extremely narrow size categories for most species (Moloney 1986). Furthermore, expanding the size of the projection matrix will come at a cost of larger censuses required to assure adequate sample sizes in each stage. Still, making models with size categories that reflect the amount of growth that individuals can undergo in a single year is crucial to the modeling of realistic time lag effects and, hence, to successfully probe for the impacts of environmental change.

PREREQUISITE 2: MINIMIZING SPURIOUS EFFECTS (UNUSUAL CATASTROPHIC EVENTS, DEMOGRAPHIC FOUNDER EFFECTS, DENSITY DEPENDENCE, AND GENETIC CHANGE)

As shown in our simulation studies, comparison of population structure and demographic rates can be quite robust to moderate environmental variation in demographic rates. However, although quite rare, ''catastrophic'' events are a major force in shaping the structure of a population. It may be extremely difficult to detect effects of slowly changing mean vital rates, for two reasons. First, if catastrophes are frequent, population structure may often be far from convergence to any stable structure. Second, such catastrophic events may make it difficult to collect the data needed to estimate the frequency and effects of important environmental variation. For example, although saguaro cacti are extremely long lived and slowly growing, the size structures of these populations are largely controlled by rare, but catastrophic, freezing events (Steenbergh and Lowe 1977, 1983). Thus, the current size structure of saguaro populations will rarely be close to that predicted by current vital rates, but this mismatch will be due to episodic events and not gradual environmental change. Other examples of such confounding environmental effects include rare forest fires and infrequent, but severe, avalanches. While some types of ''rare catastrophes'' will occur in almost all environments, the best species to use for the methods presented here are ones that are highly buffered against these events. In addition, sampling many populations for size structure will also help to preclude this problem, assuming that the sites are far enough apart that there is little chance they will experience simultaneous catastrophes, but close enough to experience similar regional changes in demographic rates.

Similar to catastrophes are effects on population stage structure due to the recent founding of populations. Thus, it is best to look for environmental change effects in populations old enough that they are unlikely to show persistent effects of initial colonization. One simple way to do this is to use the estimate of population growth from a matrix model to calculate how much time would be needed to arrive at the current number of individuals; if the population is predicted to have been in existence for far longer than the convergence time predicted from the damping ratio, then it is probably free from persistent founder effects.

If population density has a significant effect on demographic rates, then changes in densities over time may also confound or obscure any effects due to directional environmental trends. This problem is slightly different from the previous two, because it is inherent to most matrix models, which generally do not incorporate density dependence. There are three ways to avoid serious problems due to density effects. First, it is likely that selecting species with the biological characteristics we have already identified as most desirable, i.e., long lifetimes and slow growth, will favor those for which density changes very little over the time periods important for these analyses. Second, it is often known, albeit qualitatively, if population density has been (for example) increasing over time. For such a population, better fit of a model that includes improving

demographic rates (e.g., increasing growth rates) would argue against strong demographic effects of intraspecific competition and would build confidence that density dependence had not seriously compromised the method (although it might have reduced the apparent magnitude of environmentally induced demographic changes). Finally, it is possible to construct density-dependent models to use with our method. However, we view this as perhaps the least practical solution, since accurate estimation of parameters for density-dependent models is exceedingly difficult, especially for the slowly growing species most suited to this work. In addition to these ways of avoiding density dependence, in many situations it may be possible to test for the importance of density dependence as a major factor in changing demographic rates, using short-term experimental or observational data.

Finally, as with density effects, evolutionary change may lead to shifting demographic rates in the absence of any environmental changes. While the method we have outlined could still be used to test for such demographic changes, we would be in error if we concluded that they were environmentally driven. To avoid this error, we should not use populations likely to experience genetic changes unrelated to environmental trends, such as small populations subjected to random genetic drift or newly founded populations experiencing strong directional selection imposed by a novel (but unchanging) local environment. Fortunately, many of the features we have advocated will reduce these potentially confounding effects of genetic change. Sampling only large populations, as is statistically prudent, will also reduce the likelihood that demographic changes are due to random genetic drift. Similarly, avoiding newly founded populations and using perennial species (whose long generation times retard the response to selection) will help to guard against confounding effects of natural selection. Nevertheless, researchers must always consider genetic change as an alternative hypothesis when testing for environmental effects on demography.

In sum, we recommend careful consideration of the biology of the focal species, and the sampling program used to study it, in order to prevent these confounding effects from seriously compromising efforts to detect population responses to environmental change.

Discussion

The past decade has seen an explosion of studies examining the potential effects of ongoing environmental change on various ecological variables (for major reviews, see Strain 1987, Bazzaz 1990, Woodward et al. 1991, Chapin et al. 1992, Kareiva et al. 1993, Curtis 1996, Koch and Mooney 1996, Korner and Bazzaz 1996, Walker and Steffen 1996, and others too numerous to list here). Most of these studies have quantified attributes of either individual plants or entire ecosystems. In addition, a number of researchers have used tree ring analysis to detect or predict biotic responses to a modified climate, especially for subalpine, northern temperate, and taiga zones (Peterson et al. 1990, Villalba et al. 1994, Ettl and Peterson 1995). While these extensive studies have clearly documented potential impacts of environmental change at the individual level, they do not necessarily provide accurate predictions about the population-level effects of changing environments (McGraw and Fetcher 1992), and there have been far fewer studies explicitly focused on the population level. Most population-level studies have been restricted to single-species greenhouse and growth chamber experiments (Bazzaz et al. 1992, Morse and Bazzaz 1994) although some of these studies have incorporated interspecific competition (Bazzaz and Garbutt 1988; also see reviews of direct CO_2 effects by Strain and Cure [1985], Strain [1987], Bazzaz [1990], and Woodward et al. [1991]). Thus, although there has been much progress made in the study of global change, little of this attention has focused on population processes, and even less on population dynamics in natural situations (but see Fraser et al. 1992, Fowbert and Lewis Smith 1994, Grabherr et al. 1994, Lewis Smith 1994, Chapin et al. 1995, Parmesan 1996).

In this paper we have tried to illustrate the potential power of rigorous comparisons of size distributions and demographic models for the study of environmental change, and also to highlight some of the important considerations needed when using this approach. In particular, several criteria must be met by both the model structure and the biology of a species in order for these tests to have reasonable power. Most importantly, only species with life histories that can generate significant time lags in size structures will be good candidates for the method. An important corollary to this requirement is that the model formulation must not obscure biologically realistic time lags in size structure. In particular, highly compressed model structure will hopelessly weaken tests of demographic change. Just as model structure must be adequate for this analysis to be most useful, so must enough data be available to permit strong tests of the models. Although the technique does not require long-term data, it does require careful collection of population and individual data to accurately test the models. Future tests of environmental change hypotheses using this method should involve the collection of large data sets on population structure, and do so over many populations spread over large areas, just as the use of palynological data to detect vegetational change must include sampling from many sites (Gramlich and Davis 1993). In addition, it is important to obtain good estimates of demographic rates from at least a few sites that span the ecological range of the populations being examined. As our simulations including measurement error show, while demographic data must be of fairly high quality, the method can still work with realistic uncertainty in estimates of vital rates. Thus, quite practical amounts of data

collection should allow convincing, statistically powerful tests of widespread changes in demography resulting from environmental change. In sum, these considerations mean that the method should most appropriately be applied not just to long-lived species, but in particular to ones that are locally common and easily censused, so that large data sets can be assembled at reasonable cost.

With carefully collected data and appropriate models, we believe that the method that we have presented will allow comparisons of population structure and demographic processes (i.e., growth, survival, and recruitment) to provide a tractable bioassay for climatic and other environmental impacts on long-lived species. Our principal goal here has been to set forth a rigorous statistical method with which to test hypotheses concerning changing environments. Clearly, more work can and should be done to explore the effects of model structure on damping ratios, sensitivity of model power to the number of size classes used, biased model fits, and other issues involved with model construction and testing, as well as collection of better empirical data to use with these models. We are currently collecting the data needed to apply these tests to *Silene acaulis*, a slowly growing circumboreal cushion plant living in both high alpine and arctic tundra communities. This method has most promise for the study of species like this tundra perennial, which lives in areas where significant environmental change has occurred and is predicted to continue (Foster 1989, Chapman and Walsh 1993, Myneni et al. 1997, Overpeck et al. 1997). Few long-term data exist, and other methods of inferring biotic effects of environmental change (e.g., tree ring data) are nonexistent. In the interest of clarity, we have tested only very simplistic models of environmental change in this paper, varying at most one type of demographic rate at a time. However, with data collected for the purpose of these tests, much more sophisticated models that incorporate multiple effects of environmental change can be built and tested. Indeed, it is in this context that the maximum likelihood method may have its greatest use, since multiple changes in different rates will have effects on size distributions that are difficult to intuit or to test in any other fashion.

Finally, it is important to point out that the most important aspect of documenting past change is to improve the accuracy with which we can predict future trends in population size and structure due to environmental change. While our method tests hypotheses about environmental changes in the past, it can also play an important role in the prediction and monitoring of ongoing and future environmental changes. Specifically, it allows the estimation of current and past demographic rates, and their responses to environmental changes, pemitting estimation of which effects may be most severe or easiest to observe in the coming decades. Thus, we hope to extend current research on global changes by the incorporation of rigorous population-level approaches. In addition, our approach can be of value in all situations where changes in demography or population-level characteristics are of importance, but where there are no long term data sets available to test for past change. Such situations include estimation of the impacts of previously introduced plants and herbivores on native species, assessment of the improvement or worsening circumstances of endangered species, and the study of population changes during natural successional processes. Thus, we hope that this method can turn what has been a nuisance to ecologists, i.e., the mismatch between demography and size structure, into a useful tool for the anticipation of population responses to environmental changes.

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