

REPORT

Effects of environmental variation on extinction and establishment

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Abstract

Theoretical models predict that increasing environmental variation increases the probability of extinction, decreases the probability of establishment, and influences the distribution of times to extinction or establishment. We conducted an experiment with 281 independent populations of *Daphnia magna* under controlled laboratory conditions to test these predictions. Consistent with the theory, the fraction of populations going extinct increased and the fraction of populations establishing self-sustaining populations decreased under higher levels of environmental variation compared with controls. Time to extinction decreased under higher levels of environmental variation, but we found no effect on time to establishment. These results are consistent with theoretical predictions from models of extinction. They therefore support the use of stochastic population models to predict the fates of introductions of non-indigenous species or native endangered species based on historic fluctuations and/or expected future conditions.

Keywords

Daphnia magna, demographic stochasticity, environmental variability, population viability analysis, probability of extinction, PVA, risk analysis, time to extinction.

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INTRODUCTION

Stochastic population growth has long been a topic of theoretical concern (Bailey 1964; Lewontin & Cohen 1969) and is presently of significant practical importance for predicting the fates of introduced and endangered populations (Haccou & Iwasa 1996; Morris & Doak 2002; Lande *et al.* 2003). However, despite the widespread use of stochastic models for predicting future population growth, model predictions are only beginning to be validated with observational and experimental data (Belovsky *et al.* 1999; Brook *et al.* 2000; McCarthy *et al.* 2001; Holmes & Fagan 2002). Most of these studies (e.g. Brook *et al.* 2000; Holmes & Fagan 2002) have focused on the accuracy of quantitative estimates of extinction probability in natural populations and did not control for other factors like environmental variation. Results from an experiment in which environmental variation was manipulated along with initial population size and carrying capacity suggest that environmental variation can have an effect on population persistence time (Belovsky *et al.* 1999). However, the analysis of that experiment did not entirely separate environmental variation from carrying capacity because the two treatments were not fully

crossed, preventing direct inferences about its effect on population fates.

The theory of population growth in variable environments predicts that increasing variation in environmental variables will increase the probability of extinction and decrease the average time to extinction (Tuljapurkar & Orzack 1980; Nisbet & Gurney 1982; Lande & Orzack 1988; Lande *et al.* 2003). As it has recently been proposed that stochastic models of population growth are a reasonable method for conducting risk analysis for biological invasions (Wilson 2000; National Research Council 2002), we further suggest that environmental variation will lead to a decrease in the probability of establishment and an increase in the time to establishment. In this study we address these hypotheses experimentally by manipulating environmental variation in laboratory microcosms and tracking the extinction and establishment dynamics of small populations over time. We further observe that a population tracking frequent large fluctuations in the environment will tend, on average, to be further from carrying capacity than populations subject only to small environmental fluctuations. We suppose therefore that the chances of being re-jeopardized (i.e. of declining to small population size) or of going extinct after having attained a 'viable' population size will also tend

to increase with environmental variation. Therefore, we also tested two additional hypotheses: (1) that the probability of being re-jeopardized after having established would increase with environmental variation and (2) that the probability of going extinct after having established would increase with environmental variation.

MATERIALS AND METHODS

Experimental design

The experiment comprised three treatments, which differed in the variation in the amount of food provided. Experimental microcosms were plastic containers filled with *c.* 750 ml of groundwater and inoculated with five parthenogenetic (female) individuals of *Daphnia magna*, no more than two of which were adults. Our experimental set-up, which limits the maximum population size to reasonably small numbers ($\ll 100$), imitates the common conservation situation in which larger organisms are confined to habitat fragments. The small size and short lifespan of *Daphnia* allowed us to conduct an experiment with reasonable statistical power.

Microcosms were maintained in a greenhouse for 104 days (15 August 2001 to 26 November 2001) and were arranged on three shelf units; any microclimate differences were controlled by blocking in groups of 10 or 15. The food resource, *Selenastrum* sp., was cultured in a dilute solution of alga-gro[®] medium (Carolina Biological Supply Company, Burlington, NC, USA). Variability in food was manipulated for each microcosm independently according to three treatments (low, medium and high). Populations were fed once per day for the duration of the experiment by independently drawing food volume for each population from a randomly generated lognormal distribution with specified mean and variance so that feeding history was unique for each of 281 populations. A different distribution was generated for each treatment level, with arithmetic mean constant across treatments (average = 2.2 ml) and standard deviation distributed according to treatment level ($\sigma_{\text{low}} = 0$, $\sigma_{\text{medium}} = 2.2$, $\sigma_{\text{high}} = 4.4$). Thus, the coefficient of variation (CV) in food resource over time was *c.* 0, 1 or 2 by treatment. Control populations were maintained at relatively high population sizes for the duration of the experiment to ensure that the accumulation of metabolites did not adversely affect environmental conditions.

Populations were inspected everyday. Although extinction may be difficult to determine in the field, the size of an extinct population is unambiguous in principle ($n = 0$). Establishment, in contrast, is a vague concept. We considered a population 'established' for $n \geq 10$ individuals, the theoretical probability of extinction for which, according to a linear birth–death process with birth rate 0.34 and death rate, 0.07 (average rates observed in our experiment), is

1.37×10^{-7} (Renshaw 1991). Hence, all populations were categorized daily as extinct ($n = 0$), established ($n \geq 10$) or in jeopardy ($0 < n < 10$) for the duration of our experiment.

Statistical analysis

Analysis of extinction and establishment probabilities was accomplished by randomly assigning populations to one of 10 replicates within the treatment level. Within each replicate the following statistics were calculated: proportion of microcosms that reached extinction, proportion of microcosms that reached establishment, proportion of populations re-jeopardized after establishment, and proportion of populations that reached extinction after having first established. Proportion data were arcsine-square root transformed for statistical analysis. Analysis of variance using treatment level as a categorical variable was accomplished with the PROC GLM procedure in SAS 8.02 (SAS Institute, Inc., Cary, NC, USA) and Tukey's multiple comparisons tests ($\alpha = 0.05$).

Time to extinction and time to establishment, so-called 'first passage times' (Dennis 2002), were defined as the number of days until a population reached $n = 0$ and $n = 10$, respectively. All populations were tracked until either they established or went extinct. Pearson's correlation, Spearman's rank correlation and Kendall's τ were used to examine the relationship between the distribution of food resource and first passage times.

RESULTS

Extinction and establishment probabilities

The effect of variation in food resource on the probability of extinction was marginally insignificant ($P = 0.0877$). In contrast, the effect of variation in food resource on the probability of establishment was highly significant ($P = 0.0052$). Both relationships were in the expected direction: increasing variability increased the probability of extinction and decreased the probability of establishment. For establishment, the effect of the high variation treatment was significantly different from the low and medium variation treatments, although these treatments were not different from each other (Fig. 1). Treatment level had no detectable effect on the proportion of populations re-jeopardized (range of means across populations was 0.67–1.0) or on the proportion of populations going extinct after having first established (0–0.67).

Time to extinction and time to establishment

Time to extinction was significantly correlated with variation in the food resource ($P = 0.0076$, Pearson's $\rho = -0.20$),

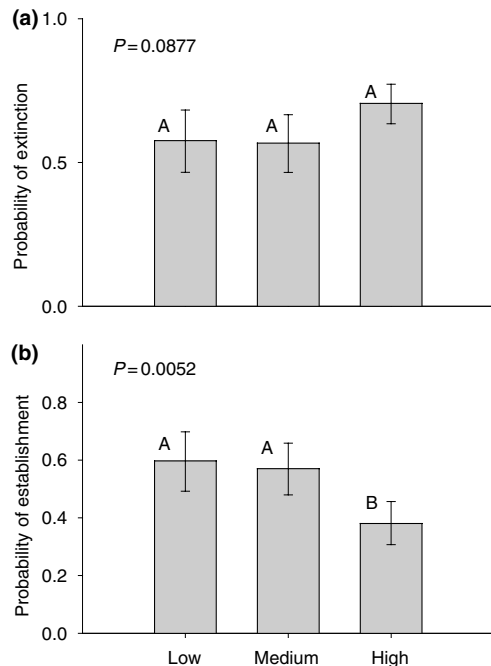


Figure 1 Probability of extinction (a) and establishment (b) for three levels of variability in food. Bars with different letters are significantly different from each other (Tukey's multiple comparison test $\alpha = 0.05$).

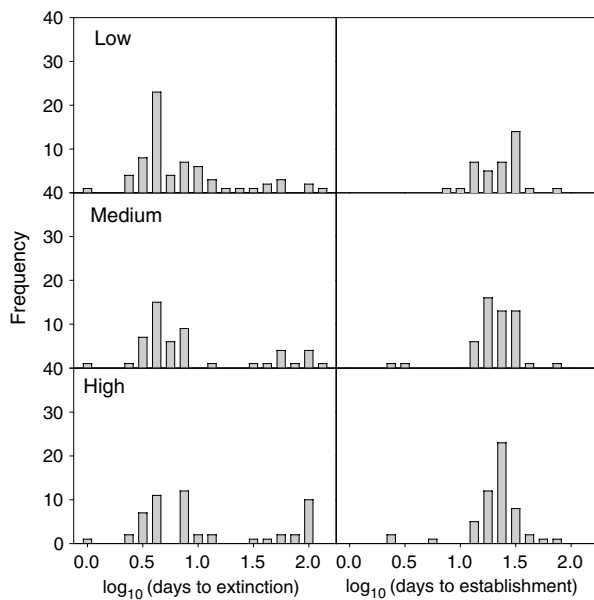


Figure 2 Frequency distribution of time to extinction and establishment for three levels of variability in food.

although there was no detectable effect on time to establishment (Fig. 2). The frequency distributions of time to extinction were not normally distributed, exhibiting a

concentration of extinctions in the short-term with fat tails (Fig. 2; notice the transformation of the x-axis). Inspection of Fig. 2 suggests that the correlation between time to extinction and environmental variation might be driven by the tails of the distribution, rather than by the more frequent extinctions that occurred in short times. To explore this possibility, we examined the correlation between time to extinction for all populations that went extinct by the 15th day and variation in the food resource. The lack of a significant result ($P = 0.7077$, Pearson's $\rho = -0.03$) supports our suspicion that the fat-tailed extinction times caused the correlation above. The consequence of asymmetric extinction times is that residuals were not normally distributed, violating the interpretation of a correlation as a least-squares hypothesis test. Two nonparametric tests for this relationship, Spearman's rank correlation ($P = 0.0791$) and Kendall's τ ($P = 0.0744$), were both marginally insignificant. The fat-tailed distributions of time to extinction that we observed (Fig. 2) are characteristic of the negative exponential (Mangel & Tier 1993) and inverse Gaussian (Dennis *et al.* 1991) distributions predicted by theory, have led previous investigators to suggest that the median is a better indicator of the central tendency of time to extinction (Dennis *et al.* 1991). Summarizing our data in this way reduces our sample size to $n = 3$ with the median probability of extinction as a function of treatment environmental variation falling perfectly on a straight line ($R^2 = 1.0$; $y = -\sigma/\bar{x} + 6.0$).

DISCUSSION

The results presented here confirm the theoretical predictions that probabilities of extinction and establishment and the distribution of time to extinction can be affected by environmental variation and that the consequences of these effects can be measured. The qualitative effect in our experiment is consistent with theory: increasing variation increases the probability of extinction, decreases the probability of establishment and decreases the time to extinction. Contrary to our hypothesis, time to establishment was not affected by environmental variation.

The findings of this study are important for two reasons. First, we have provided the first unequivocal experimental evidence to confirm the longstanding prediction from the theory of stochastic population growth that increasing environmental variation increases the probability of extinction and decreases the time to extinction. Second, two unpredicted results emerged in our analysis. The effects of low and moderate environmental variation were indistinguishable, although the effect of high variation was pronounced. One possible explanation for this result is that our experimental treatments were not representative of natural conditions. We rejected this possibility after com-

paring our experimental treatments with levels of natural variation in chlorophyll *a* in seven moderate-sized North American lakes for over 20 years. For this comparison, we obtained data from the North Temperature Lakes Long Term Ecological Research (LTER) site (<http://www.limnology.wisc.edu/>). These data comprised 140 annual time series of chlorophyll *a*. We calculated the CV over time for each of these time series, after first averaging sampling stations for each sampling day. For consistency, only chlorophyll *a* values from the top 10 m of the water column were included. Our experimental treatments were clearly representative of these time series, which exhibited CVs ranging from 0.34 to 1.94 (Fig. 3). Another, untested possible explanation for the lack of difference between low and medium treatments is that populations have the capacity to buffer low levels of environmental variation, but not high levels, and that the response of population growth to environmental variation is therefore nonlinear. Mechanisms that could produce a buffering effect occur at both the physiological level (e.g. energy reserves) and at the population level (e.g. storage effects or population inertia).

Our second unexpected result was that time to establishment was not affected by environmental variation. This conflicts with the prediction of the Lewontin–Cohen model (1969) in which the dominant effect of environmental variation is to diminish realized population growth rate. Moreover, this effect is preserved in all the more recently developed models (e.g. Tuljapurkar & Orzack 1980; Lande & Orzack 1988; Lande *et al.* 2003) and in this respect is a consistent prediction of stochastic theory. Although we do not know the reasons as to why environmental variation failed to have this effect in our experiment, we speculate that the average reduction predicted by these models might

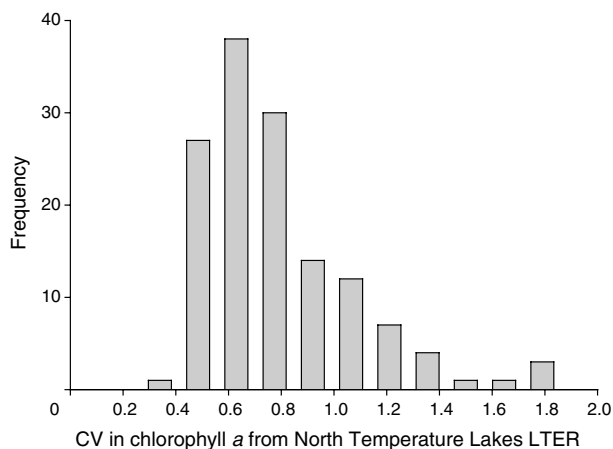


Figure 3 Histogram of the coefficient of variation for 140 annual time series of phytoplankton chlorophyll *a*.

be negligible in very small populations, which are dominated by demographic stochasticity. This implies that discrete techniques are more appropriate than the usual diffusion approximations for modelling small populations such as ours (Ludwig 1996).

To further explore the relevance of these results to natural populations, we examined the relationship between variation in chlorophyll *a* and consumer (392 annual time series of *Daphnia* spp.) abundance in the LTER field data. We compared the CVs for each of 10 *Daphnia* species with $CV_{chl\alpha}$ using Spearman rank correlation. Surprisingly, both the abundance ($P < 0.0001$; $\rho = 0.20$) and variation in abundance ($P < 0.0001$; $\rho = 0.28$) of *Daphnia* were positively correlated with variation in chlorophyll *a*, a result that awaits theoretical explanation. Thus, while a full quantitative assessment of the robustness of the theory of population growth in variable environments remains incomplete, our results, which are consistent with the general predictions of theory, signify its fruitfulness in practice. In light of the urgency of applications of theory to the management of both non-indigenous and endangered species, we believe that our results support its careful but continued use.

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