The effect of autocorrelation in environmental variability on the persistence of populations: an experimental test

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Despite its significance regarding the conservation and management of biological resources, the body of theory predicting that the correlation between successive environmental states can profoundly influence extinction has not been empirically validated. Identical clonal populations from a model experimental system based on the collembolan *Folsomia candida* were used in the present study to investigate the effect of environmental autocorrelation on time to extinction. Environmental variation was imposed by variable implementation (present/absent) of a culling procedure according to treatments that represented six patterns of environmental autocorrelation. The average number of culling events was held constant across treatments but, as environmental autocorrelation increased, longer runs of both favourable and unfavourable culling tended to occur. While no difference was found among the survival functions for the various treatments, the time taken for 50% of the component populations to become extinct decreased significantly with increasing environmental autocorrelation. Similarly, analysis of all extinct populations demonstrated that time to extinction was shortened as environmental autocorrelation increased. However, this acceleration of extinction can be fully offset if sequential introduction is used in place of simultaneous introduction when founding the populations.

Keywords: extinction risk; autocorrelation; red noise; environmental stochasticity; population viability

1. INTRODUCTION

The magnitude of environmental variation is widely acknowledged to be a crucial determinant of the dynamics of small populations (Leigh 1981; Goodman 1987; Lande 1993). Although it was initially assumed that this variation might be essentially random, it is now recognized that environmental fluctuations are usually temporally correlated (Nisbet & Gurney 1982; Cohen 1995; Halley 1996). A string of recent theoretical investigations has indicated that this environmental autocorrelation is also likely to be critical to the growth and decline of populations (Goodman 1987; Mode & Jacobson 1987; Rotenberg 1987; Caswell & Cohen 1995; Halley 1996; Johst & Wissel 1997; Petchey *et al.* 1997; Halley & Kunin 1999; Morales 1999; Petchey 2000; Holt *et al.* 2003).

Patterns in environmental variation are commonly described by using colour terminology based on analogy to the composition of light. White environmental variation is created when states of all frequencies in the environmental spectrum have equal influence, just as white light is created when photons of all frequencies in the visible spectrum have equal densities. There is no correlation between successive environmental states in such white noise. The more ecologically common situation is that infrequent environmental states have a disproportionately greater influence on populations than occasional or frequent states (i.e. the environmental noise spectrum is biased towards

low frequencies, or reddened). A consequence of having such long-term environmental oscillations is that the component states that produce them will usually be correlated with preceding states. It is also theoretically possible that populations could be subject to 'bluish' environments in which high-frequency environmental fluctuations would provide the dominant influence. In such cases, successive environmental states will be negatively correlated.

Theory has thus far been the predominant tool for predicting the influence of environmental autocorrelation on populations. The great majority of studies have concentrated on the issue of how interference between environmental noise colour and nonlinear processes may influence the regulation of large populations. Only a small subset of these studies has explicitly examined extinction in this context. It is predicted that, when population dynamics are overcompensatory, increased environmental autocorrelation will increase persistence, whereas autocorrelation will reduce persistence in populations with undercompensatory dynamics (Ripa & Lundberg 1996; Petchey *et al.* 1997). The related findings of Morales (1999) demonstrated that reddened noise increased extinction risk when the environmental variation affected the growth rate, but that it decreased extinction risk when the carrying capacity was affected. Johst & Wissel (1997) emphasized that the effects of increasing temporal correlation in environmental noise are highly dependent on the noise magnitude. Gonzalez & Holt (2002) used a protistan model system to provide empirical support for their theory that increased environmental autocorrelation can increase

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Table 1. The environmental variation treatments used in the experiment.
(Culling rates for the two sub-treatments of treatment 6 are given in parentheses.)

treatment	starting state	probability of remaining in previous state	average culling rate	environmental treatment	colour
1	culling/respice	0	0.5	alternation	—
2	culling/respice	1/4	0.5	negative autocorrelation	bluish
3	culling/respice	1/2	0.5	no autocorrelation	white
4	culling/respice	2/3	0.5	positive autocorrelation	reddish
5	culling/respice	5/6	0.5	positive autocorrelation	reddish
6(a)	respice	1	0.5(0)	constant	—
(b)	culling		(1)		

population size in open-sink populations. Their prediction for closed-sink environments was that increased autocorrelation would enhance extinction. Indeed, in general, the prediction has been that increasing temporal correlation leads to increasing extinction risk (Mode & Jacobson 1987; Rotenberg 1987; Wichmann *et al.* 2003). The analysis of Inchausti & Halley (2003) was able to provide limited support for this prediction, using a multi-species population database to compare the reddening of population variability to the quasi-extinction time (the time it took for a 90% reduction in population to occur).

Although the precedent has been to deal with processes relevant to large populations, many naturally occurring cases of populations facing a risk of extinction involve relatively small populations, which are likely to be characterized by quite different population dynamics. Haccou & Vatutin (2003) dealt with the case of newly founded populations and were able to make predictions about the probability of ultimate extinction in response to different levels of environmental autocorrelation. They concurred with Wichmann *et al.* (2003) that negatively autocorrelated environments often decrease extinction risk, while positively autocorrelated environments may promote it. In addition, Haccou & Vatutin (2003) were able to show that environments with independently sequenced states may be expected to exert an intermediate effect. Significantly, the authors also provided evidence that, in positively autocorrelated environments, extinction risk can be markedly reduced if sequential rather than simultaneous introduction is used when founding the population. The reduction in extinction was expected to decrease significantly in negatively autocorrelated environments.

The current theoretical framework has thus begun to provide tools for predicting the probability of ultimate extinction. However, the effect of environmental autocorrelation on time to extinction has not been addressed. A forecasting tool for this relationship would hold tremendous utility. Although such a theoretical tool has not yet been developed, we might reasonably speculate that qualitatively similar trends to those expected for ultimate extinction may apply: increasing environmental autocorrelation may reduce time to extinction. We set out to (i) empirically test the validity of the theoretically predicted effect of autocorrelation on ultimate extinction, and (ii) extend our current knowledge by using a model biological system to produce a prediction for the relationship between

autocorrelation and time to extinction. Small clonal populations of springtails were used to assess these issues simultaneously with an examination of how the type of introduction (simultaneous versus sequential) may alter the observed effects. Findings on these issues hold immediate repercussions for the management and conservation of biological resources.

2. MATERIAL AND METHODS

(a) *Study organism*

Populations were composed of a single clone of the parthenogenetic collembolan species *Folsomia candida* (Willem) and were kept at 95–100% humidity and $21 \pm 0.5^\circ\text{C}$ with food (yeast pellets) available *ad libitum*. Under these conditions, eggs hatched *ca.* 10 days after laying and individuals became sexually mature 16 days after hatching. Populations were reared on a flat, wet plaster substrate inside sealed cylindrical phials 50 mm in diameter. This two-dimensional, circular substrate allowed population size to be easily quantified and facilitated a standardized technique for applying environmental variation—culling by surface area, which is described in § 2b.

(b) *Experimental design*

One hundred and forty populations were used in the experiment and each of these was founded by the introduction of five mature adults of *F. candida*. Seventy populations were founded by simultaneous introduction in which all five individuals were inserted on day 1 and 70 populations were founded by sequential introduction in which one individual was inserted on each of days 1, 5, 9, 13 and 17 of the experiment. Populations were tracked every 2 days for 66 days. Within each of the two subsets of 70 populations defined by introduction type, seven identical environmental variation treatments were applied to each of 10 replicate populations. Environmental variation was artificially induced by culling the individuals (including eggs) found on a contiguous, but randomly selected, area representing one-third of the surface of the rearing substrate. This culling had the potential to occur every two days, but the realized occurrence was adjusted according to treatment as set out in table 1.

Treatments 1–5 thus represented those exposed to environmental state changes. Equal numbers of replicate populations from each of these five treatments were assigned to each of the two possible starting states to prevent the amplification of initial inadvertent biases. Every two days, for each population, it was determined if culling should occur by taking a random number between 0 and 1 and comparing it with the pre-assigned probability of a

population's remaining in with previous state. If the number fell outside the stated probability, a state change was implemented. At the time of this assessment, and following culling if it took place, the number of adult individuals present was recorded and the presence or absence of nymphs and eggs was noted. If none of these remained, a population was declared extinct.

(c) Analysis

The survival responses of each population were assessed by plotting Kaplan–Meier survival curves and the differences between these were examined using Cox proportional hazards regressions. Treatments 1–5 were of particular interest because it was in these that the environmental state actually varied (within the scope permitted by the autocorrelation values pre-assigned to each). For these treatments, time to extinction was modelled using the following three factors.

- (i) *The probability of changing state.* This corresponds to the factor *treatment*, but provides for greater statistical power by allowing the degree of autocorrelation to be treated as a continuous variable.
- (ii) *Introduction type:* simultaneous or sequential.
- (iii) *Realized culling rate.* This was calculated by dividing the number of culling events by the total number of culling opportunities that had occurred before the population went extinct or the experiment ended.

Time values at which 50% of populations had become extinct were also recorded for each of the 12 population groups defined by the two types of introduction and the six different probabilities of remaining in the previous state. (To arrive at values for the population groups subjected to an environmental autocorrelation probability of 1, treatments 6a and 6b were combined.) This information was used in regression analysis as an indicator of how extinction rate may change with changing environmental autocorrelation and according to the type of introduction used to found the populations.

In an attempt to identify if components of recent history, for example runs of bad luck, directly contributed to extinction, the number of sequential culling events broken no more than once by a respite was calculated on day 42 for populations founded by simultaneous introduction. (Day 42 was chosen because approximately half of the populations were extinct at this time.) For extinct populations, the index was calculated for the days preceding extinction. For populations extant on day 42, the index was calculated backwards from day 40. This index, along with the realized culling rate, the introduction type, and the probability of remaining in the preceding state were used as predictor variables in a logistic regression against extinction status.

3. RESULTS

By the end of the experiment, 99 out of the 140 populations had become extinct. Survival analysis of the populations according to treatment and introduction type demonstrated that treatment 6a (the zero culling treatment in which no population became extinct) and treatment 6b (the constant culling treatment in which every population became extinct) were different both from one another and from the five other treatments. As treatments 6a and 6b represent the two states possible in the extreme case of absolute environmental autocorrelation (i.e. with a probability of 1 of remaining in the previous state), they were subsequently pooled in order to provide an indication of this extreme

Figure 1. Kaplan–Meier survival curves for each of the six treatments in populations founded by either (a) simultaneous or (b) sequential introduction of five adult springtails. The solid line gives the survival curve estimated from 10 populations (20 populations for treatment 6), dashed lines indicate 95% confidence bands, and diamonds (with value labels) indicate times at which 50% of the populations had gone extinct.

Figure 2. The effect of environmental autocorrelation on time to extinction in populations that became extinct on or before day 56 of the experiment. Data for (a) simultaneous and (b) sequential introduction are presented separately.

case's average effect. The survival curves for each of the autocorrelation treatments are set out in figure 1.

Ensuing survival analyses (parametric and non-parametric) which excluded treatments 6a and 6b failed to differentiate between any of the remaining curves based on probability of remaining in the previous state, introduction type or realized culling rate (or interactions between these factors, $p > 0.12$ in every case).

Regression analysis upon values for time to extinction of 50% of populations (indicated by filled diamonds in figure 1) demonstrated that this measure decreased with increasing environmental autocorrelation in populations founded by simultaneous introduction ($F_{1,4} = 17.79$, $p = 0.014$) whereas no trend was apparent in populations founded by sequential introduction ($F_{1,4} = 0.12$, $p = 0.75$). Similarly, regression analyses that were limited to populations that had become extinct within the first 28, 42, 56 or 66 days of the experiment all demonstrated one clear relationship between time to extinction and environmental autocorrelation. Data on populations that had become extinct within the first eight weeks of the experiment (on or before day 56, $n = 70$) have been arbitrarily selected for presentation. In populations founded simultaneously, the time to extinction decreased as the probability of remaining in the previous state increased ($F_{1,34} = 23.55$, $p < 0.001$; figure 2). By contrast, in populations founded sequentially, no trend was evident ($F_{1,32} = 0.019$, $p = 0.89$).

The logistic regression model for extinction status on day 42 found that the three-way interaction between (i) realized culling rate, (ii) introduction type and (iii) probability of remaining in the preceding state was significant ($F_{1,85} = 6.33$, $p = 0.012$). This indicates that the realized culling rate had a different influence on extinction status in simultaneously and sequentially founded populations, as well as on the different treatments within each of these groups. Sub-analysis found that the interaction between

the realized culling rate and environmental autocorrelation was significant only in a subset (notably treatments 4 and 5) of the sequentially founded populations. Recent history, as indicated by the chain of culling events immediately preceding extinction, was not found to exert a significant effect.

The negative relationship between environmental autocorrelation and time to extinction is likely to be related to the fact that variation in realized culling rates increased with increasingly positive environmental autocorrelation (figure 3), such that the culling level was often considerably greater or less than the level observed for uncorrelated or negatively autocorrelated environments.

4. DISCUSSION

The results suggest that the probability of ultimate extinction does increase with increasing environmental autocorrelation as expected, but there is insufficient statistical power to demonstrate this conclusively by comparing survival functions. However, a probable indicator of the probability of ultimate extinction (i.e. the time taken for 50% of populations to become extinct) provided empirical confirmation of the theoretical prediction. Our experiment also demonstrated the existence of a strong trend between environmental autocorrelation and time to extinction. Provided that extinction did occur, it tended to occur more quickly in environments that were positively autocorrelated. This finding calls for new theoretical developments to explain the precise details of the population processes that may underlie it (see Lande *et al.* 2003, pp. 33–34 for a possible approach).

The distinction between extinct and non-extinct trajectories made in our analysis of time to extinction is grounded in the theory of stochastic population dynamics (for which Caswell (2001) and Lande *et al.* (2003) provide comprehensive reviews). Small populations face non-zero

Figure 3. The spread in realized culling rates with increasing environmental autocorrelation. Box plots indicate medians, interquartile intervals and ranges of the rate values found within each of the six treatments. Open circles represent extinct populations and filled circles represent populations that remained extant at the end of the experiment.

probabilities of extinction in stochastic environments despite having positive growth rates because the effects of good and bad luck are most asymmetric at the earliest population stages. A run of bad luck should have little effect on a growing population that has persisted long enough to reach a large size whereas the same run may well cause extinction at an earlier stage when the population is still small. This asymmetry is the source of the somewhat non-intuitive prediction that mean time to extinction is shorter in faster-growing populations (e.g. Lande & Orzack 1988). In essence, extinction of growing populations tends to occur 'early or never' and it is this generalization that induced us to limit one part of our analysis to those population trajectories that became extinct over the course of the experiment.

The realized culling rate for the whole experimental period was found to influence extinction status predominantly in those treatments that were characterized by both sequential foundation and strong positive environmental autocorrelation. This result is consistent with expectations because an interaction between a high realized culling rate and a high environmental autocorrelation is equivalent to a long run of environmental bad luck. The asymmetric penalties that accompany such runs of bad luck may thus well have been responsible for the documented influence. The effect of these interacting terms was not seen in the simultaneously founded populations, as it may not have had the opportunity to arise. In such nascent populations in which potentially large stochastic effects are not offset by time-averaged introductions, single events or very short event sequences (that are below the limits of detection) may have pre-emptive influences on extinction. The fact that the chain length of culling events immediately preceding extinction did not have a significant effect on extinction may also indicate that the population dynamics of the study system often provided at least a partial buffer

against perturbations over periods shorter than the entire experimental duration. As one might expect, the additional role of luck, which determined how many springtails fell within the area to be culled, was also crucial. For example, two out of the three populations to go extinct before day 20 experienced a chain of five successive culling events. However, a number of equivalent populations also experienced such chain lengths but, by chance, enough individuals in these other populations were fortunate enough to fall outside the culling area and thus avoid extinction. The third population to become extinct before day 20 was exposed to culling only half of the time but, through bad luck, all individuals had fallen within the culling area by the time four non-consecutive culling events had occurred.

The current results thus provide strong indications that increasingly positive environmental autocorrelation may result in greater extinction risks. This finding bears significant repercussions for the conservation and management of biological resources and merits further verification at even larger experimental scales. Nevertheless, the potential for sequential introduction to counter hastened extinction trajectories in positively autocorrelated environments is remarkably clear. However, the sequences that maximize the population establishment probabilities of sequential introductions remain to be elucidated (although Haccou & Iwasa (1996) have provided a starting point with their theoretical demonstration that progressively increasing the lag between successive sequential introductions may reduce the chance of extinction in independently varying environments). The expeditious development of methods for determining the optimal timing and magnitude of sequential introductions on a case-by-case basis is thus warranted.

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