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LETTER

Linear analysis solves two puzzles in population dynamics: the route to extinction and extinction in coloured environments

Jörgen Ripa[1] **and Mikko Heino**[2]
[1]*Department of Theoretical Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden.*
E-mail: jorgen.ripa@teorekol.lu.se
[2]*Division of Population Biology, Box 17, FIN-00014 University of Helsinki, Finland.*

Abstract

In this paper, we give simple explanations to two unsolved puzzles that have emerged in recent theoretical studies in population dynamics. First, the tendency of some model populations to go extinct from high population densities, and second, the positive effect of autocorrelated environments on extinction risks for some model populations. Both phenomena are given general explanations by simple, linear, stochastic models. We emphasize the predictive and explanatory power of such models.

Keywords

Autocorrelation, environmental stochasticity, extinction risk, linear models, stochastic population dynamics

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INTRODUCTION

Population extinctions is an important topic of ecological research, not only for its importance in population ecology, but also as the focus of conservation biology. Theoretical studies of population extinctions necessarily involve population dynamic models including environmental stochasticity, demographic (including genetic) stochasticity, or both. Recent theoretical analyses of extinction processes and the dependence on the environmental autocorrelation have arrived at a couple of partly counter-intuitive conclusions. We will here recapitulate these puzzling results and present simple solutions.

THE FIRST PUZZLE

Roughgarden (1975), Gyllenberg *et al.* (1994), and Ripa & Lundberg (1996) noted the tendency of some model populations to go extinct from high population densities, even above carrying capacity. Most population extinctions occurred as sudden crashes, and not as the more gradual extinctions one would expect, both from data and intuition. This raised the question of whether current population dynamic models are unable to describe population extinctions, or if data on extinction dynamics are too scarce or misinterpreted and our intuition fails. The former would seriously undermine many theoretical results in conservation biology. The latter would call for extensive re-analysis of extinction data, more sampling, and, most important, rethinking our common assumptions on how most extinctions occur.

THE SECOND PUZZLE

The importance of the temporal autocorrelation of the environment has been underlined in several theoretical studies lately (Mode & Jacobson 1987a, b; Ripa & Lundberg 1996; Johst & Wissel 1997; Heino 1998). Ripa & Lundberg (1996) noted that increased environmental autocorrelation decreased the extinction risk of their model population. Other studies showed opposite (Johst & Wissel 1997) or indecisive (Mode & Jacobson 1987a, b; Petchey *et al.* 1997; Heino 1998) results. Ripa & Lundberg's result was also in contrast to the intuitive argument, that increased environmental autocorrelation would lead to long runs of bad years, and therefore increase extinction risk (Petchey *et al.* 1997). Faced with an increasing body of evidence for autocorrelated environments (Steele 1988; Halley 1996; Lawton 1997), the question whether models with uncorrelated noise underestimate or overestimate extinction risks becomes increasingly significant.

SOLVING THE FIRST PUZZLE

Roughgarden (1975) noted that population crashes from high densities were more prevalent in populations with high intrinsic growth rate, or high "responsiveness" to environmental changes. Later, examining pre-extinction

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densities of different population models, Petchey *et al.* (1997) and Ripa & Lundberg (unpublished work) showed that the intrinsic dynamics of the populations did play an important role. In general, populations with overcompensatory growth went extinct from high densities, whereas model populations with slower, undercompensatory growth went extinct from low densities, well below carrying capacity. A very simple explanation can be put forward. Assume a general stochastic, one species, discrete time, population dynamic model:

$$N_{t+1} = f(N_t, z_t) \tag{1}$$

Population size at time t is denoted N_t, z_t is a stochastic environmental parameter with mean z^*, and f is the recruitment function. Choose as an approximate average population size $N^* = f(N^*, z^*)$, the equilibrium population size, had the parameter z been fixed at its mean. Using N^* as a linearization point, a linear approximation of equation 1 is:

$$X_{t+1} = aX_t + b\phi t, \tag{2}$$

where $X_t = N_t - N^*$, $a = \partial f(N^*, z^*)/\partial N$, $b = \partial f(N^*, z^*)/\partial z$, and $\phi_t = z_t - z^*$. Equation 2 is a first order auto-regressive process (AR(1)), with well-known statistical properties (Box & Jenkins 1970) largely depending on the coefficient a, the slope of the recruitment function at equilibrium. Populations with overcompensatory (undercompensatory) growth have negative (positive) slopes at equilibrium, hence the coefficient a is negative (positive). A negative a leads to alternating dynamics, where high densities tend to be followed by low densities and vice versa. The autocorrelation function of such dynamics shows strong negative autocorrelation in the first time lag. Consequently, a *very* low population size, such as an extinction, would have a high probability of being preceded by a very high population size. Exactly the opposite result holds for a positive a, or undercompensatory growth; extinctions are preceded by low population densities. These results are valid for the linear approximation and can be assumed to hold for most nonlinear models. The conclusion follows that a simple linear analysis predicts the result of computer simulations and extensive analysis in earlier studies (Petchey *et al.* 1997; Ripa & Lundberg, unpublished work): extinctions in overcompensating population models occur from high densities, and extinctions in undercompensating population models appear more gradually, after a period of decline.

As many populations do have positively autocorrelated dynamics (Pimm & Redfearn 1988), be it from autocorrelated environments, undercompensatory growth, or other characteristics of their biology (such as age structure), it is probable that they also go extinct from low densities, as data and intuition tell us.

SOLVING THE SECOND PUZZLE

The influence of autocorrelated environments on extinction risks was more thoroughly studied by Petchey *et al.* (1997) and Heino (1998). These studies revealed that intrinsic dynamics or population structure again play an important role. Overcompensating populations gain viability from positively autocorrelated environments [except for a special case with random growth rate, commented by Heino *et al.* (unpublished work)], while undercompensating populations experience increasing extinction risk as the environmental autocorrelation increases. Spatial structure makes a population respond to environmental autocorrelation in the same way as an undercompensating, single population (Petchey *et al.* 1997; Heino 1998). Ripa & Lundberg (1996) only studied overcompensating population models, hence the unambiguous result.

Again, a linear analysis can explain the phenomenon. As it turned out, the necessary calculations were done by Roughgarden more than two decades ago (Roughgarden 1975), assuming a linear, autoregressive process for the environment:

$$\phi_{t+1} = \alpha\phi_t + \varepsilon_t, \tag{3}$$

where the ε_t are independent normally distributed random numbers with zero mean and variance σ^2. The coefficient α is the "noise equivalent" to a in equation 2. A positive α produces a positively autocorrelated time series. Inserting equation 3 in equation 2 gives an autoregressive process with autoregressive disturbances – a linear approximation of a population with autocorrelated environment. Roughgarden (1975) analytically calculated the variance of such a population. A generalization of Roughgarden's result yields:

$$Var(X_t) = \frac{1 + a\alpha}{(1 - a^2)(1 - a\alpha)} b^2 \, Var(\phi_t) \tag{4}$$

According to equation 4, the variance of an overcompensating population (negative a) decreases as the environmental autocorrelation (α) increases, which explains the decreased extinction risk observed in model populations (Fig. 1). The opposite is true for undercompensating populations (Fig. 1). Note that this is only valid if the variance of the environment, ϕ_t, is kept constant by adjusting σ^2 as α changes (see Ripa & Lundberg 1996). Also note the importance of the parameter b, the *responsiveness* of the population size to a change in the environment [$b = \partial f(N^*, z^*)/\partial z$], which can depend on the same parameters that determine a.

In the case of spatial structure, with several subpopulations connected through migration, a global extinction requires the simultaneous extinction of all subpopulations. Thus, it is really the dynamics of the number of existing

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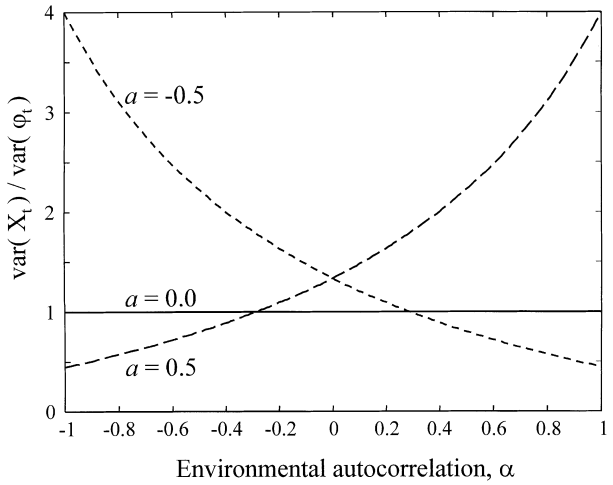


Figure 1 The ratio between the variance of the population size (X_t) and the variance of the environment (z_t), as a function of the environmental autocorrelation (α), according to equation 4. Ratios for three different values of the slope of the recruitment function (a) are shown, corresponding to overcompensating ($a = -0.5$), compensating ($a = 0$) and undercompensating ($a = +0.5$) population dynamics. The responsiveness to environmental change (b) is set to 1.

subpopulations, or occupied patches, that is relevant for global extinction risks. These dynamics may be totally different from the local dynamics of each patch, and it is quite safe to assume that it is "undercompensating" in its nature, which makes a metapopulation respond to environmental autocorrelation in the same way as an undercompensating single population.

DISCUSSION

Linear analysis provides us with strict mathematical explanations for some oddities in dynamics of simple model populations. Such mathematical explanations are not very useful outside their own abstract realm, unless they can be interpreted in more biological terms. A brief intuitive explanation of equation 4 proceeds as follows.

An undercompensating population is a "slow tracker" of the environment. The population averages out abrupt changes in environment. For this kind of population a slowly changing environment, with potential for runs of bad years, is more devastating than a negatively autocorrelated environment with isolated bad years. An overcompensating population, on the other hand, suffers greatly from a negatively autocorrelated environment. It overreacts to the current environment, faces in the next time step a totally different environment, overreacts again, and so on.

This explanation is perhaps more appealing to the human mind than equation 4, but the mathematical result gives the mere handwaving reasoning the necessary theoretical support, and provides more precise predictions. Equation 4 also reveals that the observed phenomenon is not a result of obscure nonlinearities. Our strictly linear assumptions are sufficient to predict the general behaviour of different nonlinear models. It is interesting to note that we can predict patterns of extinction risks even though extinctions occur far away from equilibrium, where the linear approximations usually deviate substantially from the real model. Of course, the complete nonlinear models are required to predict their respective behaviour in more detail.

The success of the linear analyses above demonstrates the explanatory and predictive power of stochastic linear approximations of population dynamic models. This point is also emphasized in other recent work (Horwood 1983; Taylor 1992, 1993a, b; Ives 1995; Ives & Jansen 1998; Ripa *et al.* 1998). We think that the basics of this statistical theory should be in the "mathematical toolbox" of every population biologist. It can prevent excessive simulations and certainly helps in understanding population dynamic phenomena.

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BIOSKETCH

Jörgen Ripa does theoretical work mainly on stochastic population dynamic models, with special interest in extinction risk assessments, model formulation of environmental stochsticity, autocorrelated environments, and analysis of linear stochastic models.

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