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Original Research Article

Temporal scales of resource variability: Effects on population dynamics of structured populations

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ABSTRACT

I develop a two-class continuous-time model with juveniles and adults, with both potentially reproducing, to investigate the role of large variability on population dynamics and persistence. By specializing to the case of resources that are periodic in time and only at two different levels, I am able to show using a combination of analytic and numerical techniques the effect of different temporal scales of resource variability on persistence and dynamics. I focus on either very rapid variation or very slow variation in resource levels. I assume that the effect of resources is to alter the fecundity. If survivorship is the same for the two stages and fecundity is higher for the adult class than the juvenile class, then the population grows more rapidly with rapid variation in resource levels. However, if the fecundity is higher for the juvenile class, then the population grows more rapidly with slow variation in resources. These results, and results for variation in fecundity with stage, show the extreme contrast between population dynamics with a single class and with more than one class, or expressed differently the strong interaction between life histories and variability.

1. Introduction

Most ecological theory ignores large temporal variation in resource availability, although there have been exceptions (Tuljapurkar, 1985, 1990). Yet it has become increasingly recognized that large temporal variation in resources is common and this variation can have large effects on population dynamics. Examples of varying resources have been carefully reviewed (Yang et al., 2010; Yang and Naeem, 2008), and the examples range across a wide variety of terrestrial and aquatic habitats as well as a wide range of taxa.

An important question is how temporal variation in resource availability affects the persistence and population dynamics of species which depend on these variable resources. It is clear that temporal variation in resources could affect species persistence. It is also intuitively clear that if there is a period of essentially no resources longer than the maximum lifespan of the consumer species, the consumer species will go extinct. But, determining the exact nature of the interaction between consumer life histories and temporal resource variability that would determine persistence or extinction will provide insights into important questions of how changes in variability of resources will affect species in the future. General theoretical approaches to impacts of resource variability on population dynamics were reviewed by Holt (2008), who pointed out the limitations of current theory.

In a previous paper (Hastings, 2012), I used a simple model of a single species to begin studying how the relationship between life history of a consumer and the nature of temporal variability of resources could affect persistence. The model reflected a species with a fixed lifespan and was based on a simple integral equation that could also be written as a delay equation. I assumed that resources were measured on a scale that directly reflected their contribution to fecundity. I showed that if resources varied on a very short time scale, the arithmetic mean of resource levels determined persistence, while if resources only varied on a very long time scale the geometric mean of resource levels determined persistence. I additionally showed that if fecundity was independent of age and the lifetime of the consumer was exponentially distributed (i.e., if age structure was ignored) then once again persistence was determined by the arithmetic mean of resource levels. Since the geometric mean of resource levels is always less than or equal to the arithmetic mean of resource levels, this showed a potentially large effect of resource variability. In particular, for resources that varied slowly (relative to lifespan), small increases in resource variability at times when the level was very low could have a large effect. This result echoed classic results for a simple discrete time model with no age structure (Lewontin and Cohen, 1969). However, these results (Hastings, 2012) were based on models for two particular life histories, leaving open the more general question of what general classes of life histories

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would lead to the persistence of a species being affected by temporal variation in resources. This would require a more flexible model, and the study of such a model is the subject of the current paper.

Other important earlier work on temporal variation (Tuljapurkar, 1985, 1990) used approaches based on matrix models. In the work that is closest to the approach here, based on cyclic variation in life histories, Tuljapurkar obtained results comparing the growth rate with different lengths of cycle periods. These results will provide an interesting contrast for the results here, since the variability here can be more rapid than the single time step possible with a matrix model.

Once again, since my goal is a heuristic understanding, I will use a very simple modeling approach that allows fecundity and survivorship to potentially be age dependent, as the previous work (Hastings, 2012) showed that such age dependence was critical. The simplest model that is possible is one with two age classes, essentially juveniles and adults, with a rate of maturation from the juvenile class to the adult class, and all individuals born as juveniles. I have previously used such an approach, which is essentially a variation of the linear chain trick to mimic delay equations, to look at interactions between two species (Hastings, 1983).

I will begin with a more general model and then make a series of simplifying assumptions. The primary analysis will focus on two cases that are the same ones that were the focus of my earlier model (Hastings, 2012): very rapid changes in resource levels or very slow changes in resource levels. Here rapid or slow is relative to the lifespan of the consumer. A goal of the analysis will be to determine how robust the conclusions from the earlier model are to changes in the description of the life history of the organism and to explicit inclusion of variability in fecundity and survivorship with stage.

2. Models

The model here is one with two classes, juvenile and adult. For the consumer species, let the population level of the juvenile class be $n_1(t)$ and the population level of the adult class be $n_2(t)$. I will initially denote the level of a time varying resource to be $R(t)$. Note that since the goal here is simply to focus on persistence, the consumer species can be assumed to be rare. Thus, I can ignore any effect of the consumer species on the resource level, which is equivalent to linearizing about the zero equilibrium for the consumer species. Then

$$\begin{aligned}\frac{dn_1}{dt} &= M_1(R(t))n_1 + M_2(R(t))n_2 - \mu_1(R(t))n_1 - \gamma(R(t))n_1 \\ \frac{dn_2(t)}{dt} &= \gamma(R(t))n_1 - \mu_2(R(t))n_2\end{aligned} \tag{1}$$

is a general density independent model describing population dynamics with resource dependence. Here M_i is a function giving the fecundity of age class i as a function of the resource level, μ_i is the mortality rate of class i as a function of the resource level, and γ is the resource dependent maturity rate.

3. Analysis and results

3.1. Model simplification and general results

Since the models introduced are linear (or essentially since the models have been linearized about the zero solution), the analysis will be to determine the stability or instability of the zero solution. The general model is obviously too general, even though it is linear in the population size, to allow a meaningful analysis. Therefore I will make a number of simplifying assumptions that will lead to an analysis that will provide heuristic results. In particular, I will restrict attention to a special form of variation in the resource level, namely that it is periodic in time and piecewise constant:

$$R(t+T) = R(t) \tag{2}$$

and

$$R(t) = R_i \quad \text{for } t_{i-1} < t < t_i \tag{3}$$

where i is 1 or more and $T = t_n - t_0$.

Although this is a model which could be analyzed using the theory of Floquet multipliers (Gökçek, 2004; Klausmeier, 2008), I will simplify further before analysis so heuristic results easily emerge.

I will assume that there are only two different resource levels so in Eq. (3), n is 2. Additionally I will assume that in one of the resource regimes, the 'bad' regime, no reproduction occurs ($M_1 = M_2 = 0$), and that the time this resource regime occurs is a fraction $1-\theta$ of the total time. In the other resource regime, the 'good' regime, the fecundity of juveniles is m_1, the fecundity of adults is m_2, and this regime occurs a fraction θ of the total time.

The two different regimes can be represented by matrices representing the linear dynamics of the consumer species, with the death rates of juveniles and adults represented by μ_1 and μ_2, respectively, and the maturation rate denoted by γ. The two matrices, denoted A and B, respectively, for the 'good' and the 'bad' environments are then

$$A \equiv \begin{pmatrix} -\mu_1 - \gamma + m_1 & m_2 \\ \gamma & -\mu_2 \end{pmatrix} \tag{4}$$

and

$$B \equiv \begin{pmatrix} -\mu_1 - \gamma & 0 \\ \gamma & -\mu_2 \end{pmatrix} \tag{5}$$

Before proceeding with the analysis I will note that the analysis is most interesting if the population increases in the 'good' environment and decreases in the 'bad'. It is clear that the leading eigenvalue in the 'bad' environment is negative, so I am assuming the matrix (4) has a real eigenvalue greater than zero (that this eigenvalue is real can be deduced from the fact that the off-diagonal elements are both positive, Horn and Johnson, 1990).

I will look at two extreme cases in terms of the temporal scale of variability, and determine the life histories under which the persistence conditions vary. I will consider rapid variation in the resource regimes or very slow variation. Obviously, it would be important to consider dynamics for intermediates rates of variation, but since the goal here is to demonstrate the direction of the change in growth rates potentially caused by variability, it is sufficient (and much simpler) to focus only on the two endpoints.

3.2. Rapid resource variation

If the time scale of variability is very short, then the dynamics of the system are determined by the arithmetic average of the different resource regimes, weighted by the time spent in these regimes. This is easy to see, or can be carefully proven (Gökçek, 2004). Thus, in the limit as the time of the switches between environments, T, goes to zero, the dynamics of the system are governed by the eigenvalues of the matrix

$$\theta A + (1-\theta)B = \begin{pmatrix} -\mu - \gamma + \theta m_1 & \theta m_2 \\ \gamma & -\mu_2 \end{pmatrix} \tag{6}$$

and persistence is determined by whether or not the matrix has an eigenvalue with a positive real part.