Trophic interactions affect the population dynamics and risk of extinction of basal species in food webs

Tomas Jonsson *, Patrik Karlsson, Annie Jonsson

Ecological Modelling Group, Systems Biology Research Centre, University of Skövde, P.O. Box 408, SE-541 28 Skövde, Sweden

ABSTRACT

This paper addresses effects of trophic complexity on basal species, in a Lotka–Volterra model with stochasticity. We use simple food web modules, with three trophic levels, and expose every species to random environmental stochasticity and analyze (1) the effect of the position of strong trophic interactions on temporal fluctuations in basal species' abundances and (2) the relationship between fluctuation patterns and extinction risk. First, the numerical simulations showed that basal species do not simply track the environment, i.e. species dynamics do not simply mirror the characteristics of the applied environmental stochasticity. Second, the extinction risk of species was related to the fluctuation patterns of the species.

More specifically, we show (i) that despite being forced by random stochasticity without temporal autocorrelation (i.e. white noise), there is significant temporal autocorrelation in the time series of all basal species' abundances (i.e. the spectra of basal species are red-shifted), (ii) the degree of temporal autocorrelation in basal species time series is affected by food web structure and (iii) the degree of temporal autocorrelation tend to be correlated to the extinction risks of basal species.

Our results emphasize the role of food web structure and species interactions in modifying the response of species to environmental variability. To shed some light on the mechanisms we compare the observed pattern in abundances of basal species with analytically predicted patterns and show that the change in the predicted pattern due to the addition of strong trophic interactions is correlated to the extinction risk of the basal species. We conclude that much remain to be understood about the mechanisms behind the interaction among environmental variability, species interactions, population dynamics and vulnerability before we quantitatively can predict, for example, effects of climate change on species and ecological communities. Here, however, we point out a new possible approach for identifying species that are vulnerable to environmental stochasticity by checking the degree of temporal autocorrelation in the time series of species. Increased autocorrelation in population fluctuations can be an indication of increased extinction risk.

1. Introduction

The abiotic environment of most species is spatially as well as temporally variable. It has been shown that characteristics of environmental variability affect population dynamics and thus the risk of extinction in population models (Tuljapurkar, 1982; Mode and Jacobson, 1987; Halley, 1996; Ripa and Lundberg, 1996) as well as laboratory populations (Petchey, 2000; Pike et al., 2004). Thus, environmental variability undoubtedly affects species and potentially also the functioning of the ecosystems that the species are a part of. Understanding how characteristics of environmental variability (such as spectral colour) affect the dynamics and

extinction risk of populations is therefore an important task for the science of ecology. This effort is becoming more urgent in the light of anticipated climate change which is predicted to include changes in the variability and correlation structure (colour) of the environment (Wigley et al., 1998; Karl and Trenberth, 2003). Thus to understand and predict consequences of climate change on biodiversity and ecosystem functioning (Petchey et al., 1999) requires, among other things, an understanding of the mechanisms by which environmental variability affects species in ecological communities.

Time series of natural animal population have been found to exhibit red-shifted power spectra, i.e. a high degree of auto-correlation (Pimm and Redfearn, 1988; Ariño and Pimm, 1995; Sugihara, 1995; Halley, 1996; Inchausti and Halley, 2002). Suggestions for this observed red-shift include extrinsic factors such as environmental forcing (Lawton, 1988; Sugihara, 1996) and

---

* Corresponding author. Tel.: +46 500 448636; fax: +46 500 448499.
E-mail address: tomas.jonsson@his.se (T. Jonsson).

species interactions (Ripa et al., 1998), or characters intrinsic to populations, such as growth rate (Kaitala et al., 1997), the interaction between density dependence and demographic stochasticity (Miramontes and Rohani, 1998) and positive temporal autocorrelation between successive generations (Petchey, 2000). Cohen (1995) pointed out that contrary to real time series, the population dynamics of some well-known population models tended to display blue fluctuations (i.e. negative autocorrelation and a dominance of high frequencies in the power spectra). Later it was demonstrated that modifications of the single population models studied by Cohen, e.g. by adding delayed density-dependence (Kaitala and Ranta, 1996) or including a spatial dimension (White et al., 1996), can change the power spectra profoundly. These studies initiated an interest in the characteristics of the power spectra of real, as well as model-generated population time series, and what happens when a system is exposed to environmental stochasticity. Not surprising, it has been shown that a noise signal that propagates through a network (e.g. an ecological community) gets filtered through interactions between nodes (species) implying that the structure of a food web may have an effect on spectral colour of populations (Ripa et al., 1998; Xu and Li, 2002; Greenman and Benton, 2005), which would add further complexity to the discussion about the origin of the spectral colour of population dynamics.

With respect to extinctions, biotic factors that act directly on populations are rather well examined through studies focusing on how species vulnerability is affected by genetics, demographic variability (Shaffer, 1981), life history characteristics such as growth rate and longevity (Lande, 1993; Ripa and Lundberg, 2000; Jonsson and Ebenman, 2001; Fisher and Owens, 2004) or the spatial distribution of a population (Hanski et al., 1994). Extinction risk of real populations subjected to various environmental regimes have rarely been examined because of scarcity of field data (long population time series) and difficulties in performing adequate field and laboratory experiments (but see Belovsky et al., 1999; Pike et al., 2004). Theoretical studies of extinction risk due to environmental variability have predominantly practiced a single-species setting, initially using uncorrelated stochasticity (i.e. white noise, Leigh, 1981; Lande, 1993) and later comparing the effects of blue, white and red environmental noise on extinction risk (e.g. Ripa and Lundberg, 1996; Halley and Kunin, 1999; Heino et al., 2000). These and other studies (Petchey et al., 1997; Cuddington and Yodzis, 1999; Ripa and Heino, 1999; Ripa and Lundberg, 2000; Schwager et al., 2006) have confirmed that the extinction risk of a species is affected by the type of environmental variability and the life history or spatial distribution of a species. Although it is acknowledged that species interactions may be important, few multi-species modelling studies have focused on how species interactions may modulate the extinction risk of species due to environmental variability.

With respect to non-animal populations, long time series of trophically interacting primary producer species (i.e. not in isolation in a laboratory) are, to our knowledge, scarce and as a consequence analyses of the spectral characteristics of such time series absent. At the same time, theoretical studies have modelled the effect of environmental variability on producer population dynamics and extinctions using competitive communities void of trophic interactions (e.g. Ruokolainen et al., 2007). However, we are aware of no study that have analyzed the effect of stochasticity on characteristics of population dynamics of basal species, and subsequently their vulnerability to extinction, in a food web setting (i.e. in communities with trophic interactions). Thus, here we focus on how food web structure, more specifically the position of strong trophic interactions, affect characteristics of the population dynamics and extinction risk of primary producer species exposed to both trophic interactions and temporally uncorrelated stochasticity. A first study

of the effect of food web structure and stochastic forcing on the vulnerability to extinction of consumer species was presented by Jonsson et al. (2006) and this issue will be further addressed and discussed elsewhere (Jonsson et al. in prep.).

To summarize, here we focus on the interaction between food web structure and environmental variability by studying: (i) how the population dynamics of basal species, as measured by the power spectra of fluctuations in abundances, in six-species Lotka–Volterra food web models that are exposed to temporally uncorrelated stochasticity, are affected by the position of strong trophic interactions, and (ii) if changes in the spectral characteristics of basal species time series due to strong trophic interactions are correlated to increased vulnerability of populations.

We show that time series of primary producer species in our study are affected by the position of strong trophic interactions in unexpected ways and that extinction risks of these species tend to be negatively correlated to the spectral density regression coefficient.

2. Methods

2.1. The model

Species dynamics were modelled by coupled continuous-time differential equations of Lotka–Volterra type with stochasticity:

$$\frac{dN_i}{dt} = N_i \left(b_i + \sum_{j=1}^{6} a_{ij} N_j \right) + \beta_i(\tau) \tag{1}$$

Here N_i is the abundance of species i, b_i is the density-independent per capita growth or mortality rate of species i, a_{ij} is the per capita effect of species j on the per capita growth rate of species i (being negative if j is a predator on i and positive if j is a prey to i), a_{ii}-values are always negative, representing negative density-dependence. β represents a stochastic term (see Section 2.2 below) that changes each integer time step, τ. Basic parameter values used for Eq. (1) (before the addition of strong trophic interactions, see Section 2.3 below) are summarized in Table 1. All producer species have the same growth rate b_i, and in absence of interspecific competition they only differ in which predator species they are consumed by. To reflect the longer generation times often observed at higher trophic levels (Peters, 1983) the absolute magnitude of b_i decreases with increasing trophic position of consumers. Furthermore, predator effects (a_{ij}) and prey effects (a_{ji}) are not equal in size and interaction strength ratios ($|a_{ij}|/a_{ji}|$) decrease with trophic position of the consumer. This was chosen to reflect the unique pattern in the distribution of interaction strengths claimed to be found in real food webs (DeRuiter et al., 1995), which could be caused by differences in body size between consumers and their resources (Jonsson and Ebenman, 1998; Emmerson and Raffaelli, 2004) and/or realistic distributions of biomass (Neutel et al., 2002). This particular parameter setting has been used elsewhere (Jonsson et al., 2006; Karlsson et al., 2007).

2.2. Stochasticity

Stochasticity (β) of species i was represented as

$$\beta_i(\tau) = \delta(\tau) \alpha \Pi_i, \tag{2}$$

where τ is the integer value of time (t), $\delta(\tau)$ is a time-specific random number from a specific probability distribution, α is a constant representing the maximum addition or reduction in growth rate of a species relative to the gross production of a species and Π_i is the "equilibrium gross production of species i" (i.e. the gross production of a species at system equilibrium, or in other