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A framework for modelling ecological communities and their interactions with the environment

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ABSTRACT

A generalized framework for representing the stochastic interactions between an ecological community and the environment is introduced. By modelling an ecosystem by a coupled system of stochastic differential equations, one can capture many of the ecosystem's salient features. For example, the framework permits each species within the community to have multiple developmental phases as well as for the environment to consist of several, interdependent environmental factors. This enables statistical inferences to be made on many pertinent ecological issues such as biodiversity and the allometric relationship between species abundance and biomass.

The framework gives accurate predictions of the population number cumulants over time whilst avoiding the negative transition rates that often beset traditional moment closure approaches. This framework is used to analyze a predator-prey model subject to random environmental fluctuations. The prey is assumed to have both an adult and larval phase with the adults vulnerable to predation. The results obtained for this model are in keeping with conventional ecological theory—the abundances of r-selected species are more erratic than those of K-selected species. In addition, the r-selected species abundances are more correlated to the environment than the K-selected species abundances.

1. Introduction

Ecological communities are governed by a complex web of interacting ecological mechanisms. These mechanisms can be classified into interspecific species interactions, intraspecific species interactions, species interactions with the environment and interactions between the environmental components. Ecological mechanisms have a direct bearing on wildlife management since commonly used conservation measures such as species richness, species viability and biomass are determined by the dynamics of the ecological communities. Hence, a modelling framework that is able to capture some of the complexities of real world systems should enable a deeper understanding of the aforementioned measures. This is vital for effective management of ecological systems.

Much work has focused on understanding the dynamics of ecological communities. This includes investigations into the assembly of ecological communities (see Luh and Pimm, 1993) where the factors that promote species coexistence are explored. Other studies are based on the ecosystem's food web (see Jonsson et al., 2010). This is useful as not only does a food web succinctly characterize the flow of nutrients between species, but it is also very helpful in understanding the allometric relationships that exist between species abundance, body size and biomass (see Cohen et al., 2003). Yet other works seek to explicitly model the spatial movement of species (see Austin, 2002; Morozov et al., 2008). Spatial models can provide insights into the mechanisms that promote species diversity (see Chave et al., 2002) and species persistence (see Keeling, 2000).

This paper presents an alternative approach to community modelling. The focus is on predicting the evolution of the species abundance cumulants over time. By treating the species abundance as a continuous random variable, Varughese and Fatti (2008) developed a diffusion approximation to the extended Kolmogorov equations of Marion et al. (2000). In this paper, this diffusion approximation is further extended to a coupled set of diffusion equations that can account for several interacting populations whilst still allowing for environmental stochasticity. However, the resulting system of equations is not only analytically intractable, but numerical solution of the system is also computationally demanding.

By applying moment closure procedures, the moment dynamics of a population can be predicted in a computationally tractable manner (see Whittle, 1957). Traditional moment closure methods assume a distributional form for the population numbers (see Whittle, 1957; Keeling, 2000). Often, distributional assumptions can cause the cumulants to have imaginary or negative steady-states (see Singh and Hespanha, 2006). This paper avoids making

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distributional assumptions. Instead, all cumulants above a certain order are assumed to be zero. For a single population, cumulant truncation yields a unique non-trivial positive real steady-state solution to the cumulants (see Singh and Hespanha, 2006).

The ability to predict the evolution of the population cumulants allows statistical inferences to be made on many topical ecological issues probed by the aforementioned approaches—for example, biodiversity measures and the relationship between species abundance and body mass. Furthermore, the model parameters can be statistically estimated (see De Valpine and Hastings, 2002). The parameter estimates and their confidence intervals can be used to test whether various hypothesized mechanisms are affecting the system as well as to infer the relative strengths of the ecological mechanisms that shape the community.

The coupled diffusion process, together with some underlying theory, is presented in Section 2. This is followed in Section 3 by a study of a hypothetical community consisting of two species where one of the species is assumed to have a larval and an adult development phase. In the adult phase, the species is susceptible to predation by the competing species. Both species are affected by the environment. The predictions under the coupled diffusion framework are shown to compare favourably with simulations. In Section 4, the results of the paper are discussed with conclusions being drawn in Section 5.

2. Modelling an ecological system as a set of coupled diffusion processes

Consider a single environmental factor ϕ that affects the population number N for a single species. Marion et al. (2000) assumed that only one of five events could possibly occur over an interval $(t, t+\Delta t)$:

- a birth with probability $B(N, \phi)\Delta t$,
- a death with probability $D(N, \phi)\Delta t$,
- the environmental condition improves by e with probability $x_e(\phi)$,
- the environmental condition deteriorates by $-e$ with probability $x_{-e}(\phi)$,
- the system remains unchanged over the interval.

Marion et al. (2000) showed that for such a system, the probability distribution function, $p_{N,\phi}(t)$ evolves according to the following equation:

$$\begin{aligned}\frac{\partial p_{N,\phi}(t)}{\partial t} &= B(N-1,\phi)\,p_{N-1,\phi}(t) + D(N+1,\phi)\,p_{N+1,\phi}(t)\\ &\quad - [B(N,\phi)+D(N,\phi)]\,p_{N,\phi}(t) - \frac{\partial}{\partial\phi}[\beta(\phi,t)\,p_{N,\phi}(t)]\\ &\quad + \frac{\partial p_{N,\phi}(t)}{\partial t} = B(N - \frac{1}{2}\frac{\partial^2}{\partial\phi^2}[\alpha(\phi,t)\,p_{N,\phi}(t)]\end{aligned} \tag{1}$$

where $\beta(\phi, t)$ and $\alpha(\phi, t)$ are the instantaneous mean and variance of ϕ, respectively.

$p_{N,\phi}(t)$ denotes the joint probability distribution of the population number (which is a discrete variable) and the environmental factor (which is assumed to be continuous). As such, $p_{N,\phi}(t)$ is an unusual joint distribution—its marginal distributions are discrete and continuous, respectively. The environmental probabilities are related to the instantaneous mean and variances by Marion et al. (2000):

$$\begin{aligned}x_e(\phi) &= \frac{1}{2A}(\alpha(\phi,t)+\beta(\phi,t)\Delta\phi) \quad \text{where } \Delta\phi^2 = A\Delta t,\ A > \alpha(\phi,t)\\ x_{-e}(\phi) &= \frac{1}{2A}(\alpha(\phi,t)-\beta(\phi,t)\Delta\phi)\end{aligned} \tag{2}$$

Varughese and Fatti (2008) derived a continuous approximation $\widehat{p}_{N,\phi}(t)$ to Eq. (1):

$$\begin{aligned}\frac{\partial \widehat{p}_{N,\phi}(t)}{\partial t} &= -\frac{\partial}{\partial N}[(B(N,\phi)-D(N,\phi))\,\widehat{p}_{N,\phi}(t)]\\ &\quad + \frac{1}{2}\frac{\partial^2}{\partial N^2}[(B(N,\phi)+D(N,\phi))\,\widehat{p}_{N,\phi}(t)] - \frac{\partial}{\partial\phi}[\beta(\phi,t)\,\widehat{p}_{N,\phi}(t)]\\ &\quad + \frac{1}{2}\frac{\partial^2}{\partial\phi^2}[\alpha(\phi,t)\,\widehat{p}_{N,\phi}(t)]\end{aligned} \tag{3}$$

Here, the population number is also treated as a continuous variable resulting in a standard joint probability distribution $\widehat{p}_{N,\phi}(t)$. A cursory examination of the form of Eq. (3) reveals that the population number N is now modelled as an diffusion process with instantaneous mean $B(N, \phi) - D(N, \phi)$ and instantaneous variance $B(N, \phi) + D(N, \phi)$. Varughese (2009) demonstrated that the diffusion approximation's predictions of the cumulant evolutions over time are very close to the predictions obtained from Eq. (1). Hence little is lost by using a diffusion approximation to represent the population numbers yet the diffusion approximation both avoids technical difficulties encountered by the extended Kolmogorov equations (such as negative transition rates—see Varughese and Fatti, 2008) as well as being less time consuming to implement for higher order cumulant studies.

Consider an ecological community consisting of n interacting populations as well as p interdependent environmental factors that affect (but are not affected) by the n populations. Let N_i denote the population number for the ith population and ϕ_i denote the ith environmental factor. If $\mathbf{N} = (N_1, N_2, \ldots, N_n)$ and $\Phi = (\phi_1, \phi_2, \ldots, \phi_p)$ then we can represent the birth and death rates for the ith population as $B_i(\mathbf{N}, \Phi)$ and $D_i(\mathbf{N}, \Phi)$, respectively. In addition, let $\alpha_i(\Phi, t)$ and $\beta_i(\Phi, t)$ denote the instantaneous mean and instantaneous variance respectively for the ith environmental factor.

The evolution of the ecological community's probability distribution can then be approximated by the following equation:

$$\begin{aligned}\frac{\partial \widehat{p}_{\mathbf{N},\boldsymbol{\Phi}}(t)}{\partial t} &= -\sum_{i=1}^{n}\frac{\partial}{\partial N_i}[(B_i(\mathbf{N},\boldsymbol{\Phi})-D_i(\mathbf{N},\boldsymbol{\Phi}))\,\widehat{p}_{\mathbf{N},\boldsymbol{\Phi}}(t)]\\ &\quad + \frac{1}{2}\sum_{i=1}^{n}\frac{\partial^2}{\partial N_i^2}[(B_i(\mathbf{N},\boldsymbol{\Phi})+D_i(\mathbf{N},\boldsymbol{\Phi}))\,\widehat{p}_{\mathbf{N},\boldsymbol{\Phi}}(t)]\\ &\quad - \sum_{i=1}^{p}\frac{\partial}{\partial\phi_i}[\beta_i(\boldsymbol{\Phi},t)\,\widehat{p}_{\mathbf{N},\boldsymbol{\Phi}}(t)] + \frac{1}{2}\sum_{i=1}^{p}\frac{\partial^2}{\partial\phi_i^2}[\alpha_i(\boldsymbol{\Phi},t)\,\widehat{p}_{\mathbf{N},\boldsymbol{\Phi}}(t)]\end{aligned} \tag{4}$$

It is assumed that the *instantaneous* covariances between the $n+p$ processes are zero. This does *not* imply that the processes are uncorrelated (see for example Fig. 3). Since the birth and death rates, as well as the instantaneous means and variances, are functions of the system $(\mathbf{N}, \Phi)$, Eq. (4) is capable of mimicking almost all of the correlation behaviour—for example, correlations due to inter-specific interactions—that can be exhibited by the more general model (with non-zero instantaneous covariances) whilst having far fewer parameters. Unfortunately, Eq. (4) is analytically intractable.

Though the populations and the environment are both represented by diffusion processes, the two are modelled in fundamentally different ways: the modelling of the environmental processes focuses on the processes' instantaneous mean and variance whilst with the species the focus is on the birth and death transition rates.

Like the probability distribution, the moment-generating function (MGF) characterizes the behaviour of the ecological system. Consider the random vector $\mathbf{X}(\mathbf{t}) = (X_1(t), X_2(t), \ldots, X_s(t))$ whose joint transition probabilities are given by:

$$P[\Delta\mathbf{X}(\mathbf{t}) = r|\mathbf{X}(t)] = f_r(\mathbf{X}(\mathbf{t}))\Delta t.$$