Improving the method of moments for two-species spatial Lotka-Volterra models

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Goal

To identify optimal moment closures for describing two interacting spatially structured populations.

Background and Motivation

Spatial models offer new insights and ideas in ecology and evolutionary biology. The rapid development of computer technology nowadays allows for the exploration of spatially explicit, site- or individual-based models that are designed to describe complex ecological processes in extrinsically or intrinsically structured populations (Levin 1976; Hamilton and May 1977; Crowley 1981). Local interactions and dispersal, often described by individual-based stochastic processes, result in new, and sometimes surprising departures from traditional mean-field descriptions. For instance, spatially explicit counterparts of mean-field models often predict the survival of apparently disadvantageous traits, the evolution of altruistic phenotypes, and reveal the macroscopic structure observed also in field-experiments (Nowak and Sigmund 1992; Durrett and Levin 1994; Oborny and Bartha 1995; Czaran 1997; Dieckmann, Law and Metz 2000).
However, realizations of spatially explicit models contain a vast amount of information. It is therefore difficult to extract those essential degrees of freedom that are needed to parsimoniously specify the current state of the system and to predict its expected change. Relaxation projections are used to identify suitable sets of state variables, which provide salient extra information beyond mean densities. Correlation densities have proven useful in providing such necessary additional information about the spatial structure of an ecological system (Dieckmann, Law and Metz 2000). By describing the dynamics of correlation densities it also becomes possible to predict the long-term dynamics of such systems. Moment closures, needed for describing the dynamics of correlation densities, play a central role in relaxation projections. It has been observed that under particular circumstances certain moment closures provide more accurate descriptions than others. Yet, the criteria for choosing the most appropriate moment closure for a given system currently are almost entirely unclear.

Research questions

For describing the correlation dynamics of a given order we must take into account higher-order correlation densities: correlation dynamics of order i depend on correlation densities of order 1, …, i+1. This recursive relation between correlation densities (or moments) is called a moment hierarchy. Fortunately, higher-order terms usually contain no essential extra information, so we may truncate the moment hierarchy by expressing correlation densities of order i+1 through correlation densities of order 1,..., i. Such a relaxation projection can be defined by using several alternative moment closures.

Here we focus on expressing triplet densities $\tilde{T}$ in terms of singlet densities N and pair densities $\tilde{C}$. There exist four such candidate moment closures:

1. $$\tilde{T}_{ijk}(\xi,\xi') = \tilde{C}_{ij}(\xi)N_k + \tilde{C}_{ik}(\xi')N_j + \tilde{C}_{jk}(\xi'-\xi)N_i - 2N_iN_jN_k$$

2.a $$\tilde{T}_{ijk}(\xi,\xi') = \tilde{C}_{ij}(\xi)\tilde{C}_{ik}(\xi')/N_i$$

2.b. $$\tilde{T}_{ijk}(\xi,\xi') = \frac{1}{2}\left[\tilde{C}_{ij}(\xi)\tilde{C}_{ik}(\xi')/N_i + \tilde{C}_{ij}(\xi)\tilde{C}_{jk}(\xi'-\xi)/N_j + \tilde{C}_{ik}(\xi')\tilde{C}_{jk}(\xi'-\xi)/N_k - N_iN_jN_k\right]$$

3. $$\tilde{T}_{ijk}(\xi,\xi') = \tilde{C}_{ij}(\xi)\tilde{C}_{ik}(\xi')\tilde{C}_{jk}(\xi'-\xi)/(N_iN_jN_k)$$

The indices *i*, *j*, and *k* refer to the different species that may coexist in the considered ecological system. Vectors ξ and ξ' denote the distances between individuals *i* and *j*, and between individuals *i* and *k*, respectively. The four closures above are referred to as the power-1, asymmetric power-2, symmetric power-2, and power-3 moment closure, respectively**.**

The above closures obey two consistency conditions, which provide criteria for valid moment closures:

- Condition (C1). In the absence of any pair correlations, individuals in triplets must also be assumed to be uncorrelated.
- Condition (C2). Because attention is focused on small-scale spatial structure, pairs of individuals separated by large distance are assumed to be uncorrelated.

These closures, originally introduced for continuous space, are easily applied to dynamics in discrete space. In this case elements of the distance vectors may take their values only from a discrete set, in our case they may take integer values.

In this project we plan to identify the most suitable moment closure for a flexible class of spatially explicit two-species Lotka-Volterra models on square lattices. For this purpose we will investigate the four candidate closures above, as well as variants that result from assigning different weights to the terms on the right-hand side of these closures. The goal is to determine how the considered ecological setting affects the optimal choice for these weights.

Method and work plan

We will study a two-species Lotka-Volterra model on a two-layered square lattice with asynchronous updating. There exist occupied and empty sites on the lattices of both species. The elementary ecological processes in this model are birth, death, and movement events. Each individual gives birth to a new individual, dies, or changes state with an adjacent site at constant rates, depending on whether their site on the other species' layer is occupied or not. By choosing different values for these rate parameters, a wide range of ecological interactions – including competition, mutualism, and predator-prey relations – can be investigated.

We will perform numerical simulations of these systems with different parameter settings. On this basis, we will measure average singlet densities, pair densities, and triplet densities. Values for the latter will then be compared to those obtained by different approximation methods (moment closures). In this way, optimal weights can be estimated through linear regression.

Previous studies suggest that power-2 provide the best match (Dieckmann, Law and Metz 2000). Specifically, we therefore plan to investigate this kind of closure in two ways. First, tentative evidence indicates that the optimal weight of the three terms in Equation 2.b depends on the relative demographic timescales of the two interacting species. To confirm this hypothesis we will simulate systems with such different relative demographic timescales and compare them by approximations that are based on different weight values. Second, weights can be assigned to the three terms in Equation 2.b in a configuration-dependent way by using different weight values for different triplet configurations. To clarify whether or not such a generalization is worthwhile will be one focus of our study.

Relevance and link to ADN's research plan

Obtaining better insight into criteria for choosing moment closures has important repercussions for the efficient modeling of spatial ecological systems. Moreover, pair approximation techniques and corresponding moment closures play a critical role in the studies on spatial invasion fitness conducted by the Adaptive Dynamics Network.

Expected output and publication

The proposed research is planned to result in a jointly authored paper by the end of the YSSP.

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