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## Moment equations in spatial evolutionary ecology

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## HIGHLIGHTS

- I review the toolkit of moment equations for spatial evolutionary models.
- I first show how to derive spatial moment equations from first principles.
- Using adaptive dynamics methodology, the selection gradient can be calculated in terms of measures of genetic and demographic structure.
- I discuss the connection with inclusive fitness theory and sketch perspectives for future work.

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## ABSTRACT

How should we model evolution in spatially structured populations? Here, I review an evolutionary ecology approach based on the technique of spatial moment equations. I first provide a mathematical underpinning to the derivation of equations for the densities of various spatial configurations in network-based models. I then show how this spatial ecological framework can be coupled with an adaptive dynamics approach to compute the invasion fitness of a rare mutant in a resident population at equilibrium. Under the additional assumption that mutations have small phenotypic effects, I show that the selection gradient can be expressed as a function of neutral measures of genetic and demographic structure. I discuss the connections between this approach and inclusive fitness theory, as well as the applicability and limits of this technique. My main message is that spatial moment equations can be used as a means to obtain compact qualitative arguments about the evolution of life-history traits for a variety of life cycles.

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## 1. Introduction

Classical evolutionary models usually rely on the assumption that the population is well-mixed, thus neglecting the role of spatial structuring in the evolutionary process. In recent years, a growing number of studies have addressed this shortcoming by investigating evolution in spatially or socially structured populations (for reviews, see Rousset, 2004; Lion and van Baalen, 2008).

Over the years, a wide range of techniques have been introduced to tackle this important question (Tilman and Kareiva, 1997; Dieckmann et al., 2000; Rousset, 2004). Individual-based (or agent-based) simulations are a natural framework in which to explore the role of local interactions or limited dispersal on the evolution of a trait, and still form the backbone of virtually all studies in spatial evolutionary ecology. Pure simulation studies, however, usually have some downsides. First, it may be easy to get lost into unnecessary details of the biological process, thereby

increasing the difficulty of picking up the biological signal from the simulation noise. Second, the danger is great of interpreting the outcome of simulations using appealing verbal arguments instead of either testing one's hypotheses using simulation experiments, or providing an analytical underpinning to the results.

Although analytical models of spatial evolutionary dynamics are notoriously difficult to handle, a fair number of successful approaches have been introduced in the field over the years. Three main analytical frameworks exist to this date: metapopulation models with large local population sizes (Metz and Gyllenberg, 2001; Jansen and Vitis, 2007); models of deme-structured populations with finite and constant local populations (see Rousset, 2004; Rousset and Ronce, 2004; Lehmann et al., 2006 for extensions to populations with fluctuating demography); and spatial moment equations (Matsuda et al., 1992; Bolker and Pacala, 1997; Van Baalen and Rand, 1998; Rand, 1999; Law and Dieckmann, 2000; Lion and van Baalen, 2008).

The aim of spatial moment equations is to derive equations for the dynamics of spatial moments. This approach can be applied to discrete space (stochastic processes on networks, Matsuda et al., 1992; Rand, 1999; Van Baalen, 2000) or to continuous space (spatial point

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processes, Bolker and Pacala, 1997, 1999; Law and Dieckmann, 2000). In discrete space, one will typically track the densities of sites in a given state (densities of singlets), the densities of pairs of sites, the densities of triplets of sites, and so on. In continuous space, equations for the global densities of different types, along with the dynamics of spatial correlations between two or more types, are needed. Both frameworks have their respective merits and limitations, but, to my knowledge, only a very restricted number of studies have modelled evolutionary dynamics in continuous space (see e.g. North et al., 2011; Barraquand and Murrell, 2012a,b). I will therefore focus my review on discrete-space models and briefly outline the most salient similarities of continuous-space models in Box 1.

#### Box 1–Moment equations in continuous space: an overview.

In contrast with reaction–diffusion equations, moment-based ecological models in continuous space represent populations as a finite configuration of (marked) discrete points in the real plane (Bolker and Pacala, 1997; Bolker, 1999; Bolker and Pacala, 1999; Dieckmann and Law, 2000; Law and Dieckmann, 2000; Murrell et al., 2004; Champagnat and Méléard, 2007; Ovaskainen et al., 2014). As in the discrete-space case, one is interested in how the state of the population (the configuration) changes as a result of various events. However, this task is mathematically challenging in continuous space because the space of such configurations is infinite and we need to consider a measure-valued Markov process (Champagnat and Méléard, 2007; Ovaskainen et al., 2014). The generator of this Markov process allows us to derive equations for the time evolution of various observables, as in the discrete case.

For the SIS model in continuous space, one may for instance track the total densities of hosts infected by the resident ( $\bar{I}$ ) and mutant ( $\bar{I}'$ ) parasite respectively. We have (Bolker, 1999)

$$\frac{d\bar{I}}{dt} = \beta(\bar{S}\bar{I} + \bar{c}_{SI}) - \gamma\bar{I}, \quad (a)$$

$$\frac{d\bar{I}'}{dt} = \beta'(\bar{S}\bar{I}' + \bar{c}_{S'I'}) - \gamma'\bar{I}', \quad (b)$$

where  $\bar{S}$  is the total density of susceptible hosts, and

$$\bar{c}_{Sx} = 2 \int_0^\infty U(r) c_{Sx}(r) dr$$

is the average covariance between susceptible hosts and infected hosts of a given type, weighted by the infection kernel  $U(r)$  describing the probability that a parasite propagule lands at distance  $r$  from a focal individual.

Eq. (b) allows us to derive the following expression for the invasion fitness:

$$\lambda' = \beta' \left( \bar{S} + \frac{\bar{c}_{S'I'}}{\bar{I}'} \right) - \gamma' \quad (c)$$

The term between brackets is the continuous-space analogous of  $q_{S'I'}$  in Eq. (9). The main difference is that the average covariance is a centred moment and therefore the effect of space is expressed as a deviation from the non-spatial density  $\bar{S}$ . However, the biological interpretations are similar.

To proceed from (c), one may derive equations for the dynamics of spatial covariances  $c_{S'I'}(r)$ ,  $c_{I'I'}(r)$ ,  $c_{I'I}(r)$ . These spatial covariances describe the demographic and genetic structuring of the parasite population. Estimates for relatedness at different distances could in principle be obtained from the dynamics of these covariances (see Robledo-Arnuncio and Rousset, 2010 for another approach). As in the discrete case, the equations for the spatial covariances will depend on higher-order spatial moments and moment closure approximations can be used to reduce the dimensionality of the system (Dieckmann and Law, 2000; Murrell et al., 2004). Under weak selection, quasi-equilibrium approximations

could also be used to make analytical progress by treating  $\bar{c}_{S'I'}$  as a fast variable, as the local densities  $q_{x'I'}$  in the discrete-space models. Although it appears that the additional mathematical complexity has so far limited the use of moment-based continuous-space models in evolutionary ecology, recent studies (e.g. North et al., 2011; Barraquand and Murrell 2012a, b) pave the way for a fruitful development of these techniques.

The demarch of spatial moment equations is very similar to the use of moment equations in quantitative genetics, in which one seeks to derive equations for the dynamics of the mean, variance, and higher-order moments of the distribution of the evolving trait. As in quantitative genetics, one is ultimately faced with an infinite system of equations that needs to be closed using an appropriate moment closure approximation. In quantitative genetics, the distribution of the trait is often assumed to be Gaussian (Lande, 1976; Lande and Arnold, 1983; Abrams, 2001; Day and Proulx, 2004). Thus, only the mean and variance of the distribution are needed. In spatial models, alternative moment closure approximations, such as the pair approximation, have been developed for both discrete-space and continuous-space models (Matsuda et al., 1992; Sato et al., 1994; Bolker and Pacala, 1999; Rand, 1999; Dieckmann and Law, 2000; Van Baalen, 2000; Ellner, 2001; Murrell et al., 2004).

The purpose of this paper is to provide a methods-minded review of the use of moment equations in spatial evolutionary ecology. My main motivation is to dissipate the confusion about the inner workings of the method and make it more palatable to the average (theoretical) biologist. Currently, the use of spatial moment equations is hampered by several obstacles. First, different authors use different approaches and notations. Second, the link to biological concepts such as inclusive fitness theory is still not well understood. Third, the popularisation of the technique under the misleading label “pair approximation” has been instrumental in spreading the misconception that the method may only be applied to interactions between pairs of individuals, or is inherently flawed because it necessarily ignores larger-scale spatial patterns. Lastly, new technical developments of the approach have usually been introduced in the literature as new biological questions were investigated, so that, overall, progress in this area has been brought forward by a fruitful wave of pluralism, but largely outside a well-defined and consistent theoretical framework.

Throughout this review, I will use a running example of a simple SIS epidemiological model (also known as the contact process in the mathematical literature, Harris, 1974; Liggett, 1985; Neuhauser, 1992). This review consists of two parts that are largely independent of one another. Readers familiar with the derivation of spatial moment equations should feel free to directly jump to the second part. In the first part, I focus on ecological dynamics and show how deterministic moment equations can be derived from first principles, using a microscopic description of the stochastic process. I first unfold the general machinery, then apply the result to the SIS epidemiological model (or contact process). In the second part, I show how spatial moment equations can be coupled with an adaptive dynamics evolutionary framework to derive analytical approximations for the direction of selection in terms of local measures of genetic and demographic structure. The approach is general, but for the sake of simplicity, I mostly discuss the application to the SIS model. The result for the SIS model is particularly simple, both mathematically and biologically, but further extensions and complications are reviewed in the discussion.

## 2. Ecological dynamics

Spatial moment equations may be thought of as deterministic approximations of a stochastic individual-based process in space.

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