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The evolution of juvenile-adult interactions in populations structured in age and space

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ABSTRACT

We study the evolution of a spatially structured population with two age classes using spatial moment equations. In the model, adults can either help juveniles by increasing their survival, or adopt a cannibalistic behaviour and consume juveniles. While cannibalism is the sole evolutionary outcome when the population is well-mixed, both cannibalism and parental care can be evolutionarily stable if the population is viscous. Our analysis allows us to make two main technical points. First, we present a method to define invasion fitness in class-structured viscous populations, which allows us to apply adaptive dynamics methodology. Second, we show that ordinary pair approximation introduces an important quantitative bias in the evolutionary model, even on random networks. We propose a correction to the ordinary pair approximation that yields quantitative accuracy, and discuss how the bias associated with this approach is precisely what allows us to identify subtle aspects associated with the evolutionary dynamics of spatially structured populations.

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1. Introduction

Spatial ecological dynamics have been the focus of an increasing number of studies (Tilman and Kareiva, 1997; Dieckmann et al., 2000). The advent of modern computing facilities has allowed ecologists to explore ever more complex models, and to reveal how spatial structure can give rise to particular patterns (Hassell et al., 1991; Real and McElhany, 1996; de Roos et al., 1998) or modify the conditions of coexistence of species (Hassell et al., 1994; Keeling, 1999, 2005). However, stochastic computer simulations lack the tractability of traditional non-spatial models. In particular, assessing explicit invasion criteria from simulations is often a difficult undertaking.

To bridge the gap between non-spatial models and simulations, several spatial analytical models have been introduced. These include patch models Hassell et al. (1991); reaction-diffusion equations (Skellam, 1951; Fife, 1979); models of metapopulations (Hanski and Gilpin, 1997) and deme-structured populations (Malécot, 1975; Metz and Gyllenberg, 2001; Rousset, 2004); and, more recently, moment (or correlation) equations, often known as pair approximation models (Matsuda et al., 1992; Bolker and Pacala, 1997; van Baalen and Rand, 1998; Rand, 1999; van Baalen, 2000). Comparison of different modelling approaches is often a good way to bring to light the most salient features of a given spatial stochastic model (Durrett and Levin, 1994a; Wilson, 1998). An alternative route is to develop a modelling framework that tries to capture the most interesting aspects of the simulations models, while ignoring less relevant information. In this perspective, moment equations seem an efficient analytical approach, as they retain two fundamental assumptions of spatial stochastic simulations: spatial structure and individuality (Durrett and Levin, 1994b; Lion and van Baalen, 2008). Moreover, even in complex scenarios, they can be used to derive analytical invasion criteria that can be contrasted with the non-spatial criteria to obtain some insight into the underlying ecological processes (Bolker and Pacala, 1997; van Baalen and Rand, 1998; Boots and Sasaki, 1999; Le Galliard et al., 2003; Lion and van Baalen, 2007).

Early on, those analytical approaches to spatial ecological dynamics were embedded in evolutionary models exploring the interplay between spatial self-structuring and evolution. Building on the earlier observations that spatial self-structuring can act as a template for evolution (Hogeweg, 1989; Kauffman, 1993; Boerlijst et al., 1993; Rand et al., 1995; Keeling and Rand, 1995), this has led to many studies exploring the impact of spatial structure on the evolution of cooperation (Matsuda et al., 1992; Harada et al., 1995; van Baalen and Rand, 1998; Le Galliard et al., 2003, 2005; Hauert,

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2006); parasite virulence (Boots and Sasaki, 1999; van Baalen, 2002; Read and Keeling, 2002; Kamo et al., 2007); or competitive ability (Iwasa et al., 1998; Mágori et al., 2005). Central to those models is the realisation that spatial structure is a key component of the eco-evolutionary feedback loop: the evolution of a trait shapes the local structure of the population, which in turn creates new selective pressures on the trait (for a review see Lion and van Baalen (2008)).

Models using moment equations to describe spatial dynamics have proven to be particularly well suited to the framework of adaptive dynamics (Metz et al., 1992, 1996; Geritz et al., 1998; Le Galliard et al., 2003, 2005; Mágori et al., 2005; Kamo et al., 2007). In this paper, we pursue that fruitful line of work and extend previous studies by investigating how to make the link between ecological dynamics and evolution when the population is not only spatially structured, but also structured in discrete classes (age, size, etc.). The fact that we model evolution using adaptive dynamics theory does not preclude the use of spatial moment equations in other models of evolution, such as population genetics (Lion and Gandon, in prep.).

A common aspect of the spatial evolutionary models that we have discussed so far is that populations tend to be unstructured in age or stage. This is of course a simplifying assumption to facilitate the analysis, but there is no doubt that age or stage structure can have far-reaching consequences (Caswell, 2001). Analysis of appropriate (typically non-spatial) models has led to the notion of a stable age (or stage) distribution: any growing or declining population will approach a particular distribution over the age or stage classes (the difference between them being that the amount of time spent in an age class is fixed, but is variable in a stage class) (Caswell, 2001). Up until recently, space and class (age or stage) structure have been mainly considered separately (but see Neubert and Caswell (2000)), but there are reasons to suspect that they may interact in subtle ways. Lion and van Baalen (2007) already published an analysis of a spatial class-structured model to study under what conditions juvenile cannibalism gives way to parental care, by assessing the selective pressures that act on such viscous class-structured populations. In the model, an adult can invest resources to help surrounding juveniles (irrespective of whether they are actually its own offspring). A continuum of strategies ranging from cannibalism to care for juveniles can be explored. The aim of the present paper is to offer a more technical and detailed account of our modelling approach, to extend the study by investigating the long-term evolutionary outcomes, and to pay attention to a number of issues that arise in this type of analysis.

We first analyse a non-spatial version of this model, and show that cannibalism is the sole possible evolutionary outcome in the absence of spatial structure. We contrast this conclusion with the result of stochastic simulations that show that parental care can evolve in a viscous population. The analysis of the spatial model then addresses three points. First, we provide a general definition of invasion fitness for populations that are structured both in discrete classes and in space. Second, we demonstrate how this general result can be used to derive an analytical expression for the selection gradient that takes into account spatial structure and gives valuable information about the selective pressures on adult investment. Third, we compare our analytical predictions to the results of stochastic simulations, and we show that ordinary pair approximation (Matsuda et al., 1992) results in an important bias that can be corrected using an improved moment closure approximation. This leads us to discuss the impact of higher-order spatial correlations on the evolution of spatially structured populations.

2. A model of parental investment

2.1. Life cycle assumptions

We consider a population subdivided into two age classes: juveniles (J) and adults (A). Individuals live on an infinite network of sites, in which every site is connected to n neighbouring sites. Each site can be empty (o) or occupied by one individual.

We assume overlapping generations, and formalise the dynamics in continuous time. Juveniles become adults at a constant maturation rate μ. Adults can reproduce at rate b_A. Juveniles are sent to a random neighbouring site and survive only if the site is empty. The background mortality rates of juveniles and adults are d_J and d_A respectively. This defines a spatial birth–death-maturation process. Mobility of individuals at rates m_J and m_A can also be included in this framework, but for the sake of simplicity we will restrict our analysis to the limiting case of a sessile population.

A crucial aspect of the model is that adults can increase or decrease the mortality rate of juvenile neighbours. In other words, adults can either kill (or eat) a juvenile that occupies a neighbouring site, or invest into caring for it, through protection or food supply. We monitor adult investment using a single parameter c. A positive investment ($c > 0$) corresponds to what we call *parental care* and decreases juvenile mortality, while a negative investment ($c < 0$) corresponds to *infanticide* or *cannibalism*. The investment has an efficiency β. Mathematically, this verbal definition translates into the following expression for the death rate $\delta_J(x)$ of a juvenile located at site x

$$\delta_J(x) = d_J - \beta c \frac{n_A(x)}{n},$$

where $n_A(x)$ denotes the number of adults around site x. Obviously, we do not want negative rates of juvenile mortality, so we need to set an upper limit for c. Because $n_A(x)/n$ is below 1, a conservative choice is to take $c < d_J/\beta$, which will be assumed throughout the paper.

Because of stochasticity, $n_A(x)/n$ will fluctuate around an average value $q_{A/J}$, that represents the *local density* of adults around a juvenile, that is the expected proportion of adults in the neighbourhood of a juvenile. Averaging $\delta_J(x)$ over all sites x harbouring a juvenile, we obtain the following expression for the expected death rate of a juvenile

$$\delta_J = d_J - \beta c\, q_{A/J}. \tag{1}$$

In a well-mixed population, with no spatial structure, the expected density of adults around a juvenile is simply p_A, the global density of adults in the population, in which case the average death rate will be $\delta_J = d_J - \beta c p_A$ (In the following, we consistently use p_i to denote the global density of type i, and $q_{i/j}$ to denote the local density of type i as experienced by a j-type individual).

Another central assumption is that cannibalised juveniles ($c < 0$) represent a source of energy for adults, and caring for juveniles bears a cost to the donor. We therefore assume a trade-off between adult reproduction b_A and adult (positive or negative) investment c. Details are unnecessary at this stage, and it is sufficient to know that this trade-off will be negative (e.g., reproduction decreases with care, and may or may not increase with infanticide or cannibalism). Therefore, the reader must keep in mind that, throughout the paper, b_A is a function of adult investment c and of the local environment of adults.

2.2. Non-spatial model

2.2.1. Ecological dynamics

The mean-field approximation of the birth–death-maturation process assumes that there is no spatial structure, that is, the

population is well-mixed. Under this assumption, local densities $q_{i/j}$ are equal to the global densities p_i, so the dynamics of a monomorphic resident population is given by

$$\begin{cases} \dfrac{dp_J}{dt} = b_A(1-p_A-p_J)p_A - (\delta_J+\mu)p_J \\ \dfrac{dp_A}{dt} = \mu p_J - d_A p_A \end{cases} \tag{2}$$

where $\delta_J = d_J - \beta c p_A$. Density-dependence of the reproduction term in the first equation arises as a consequence of competition.

The system has a trivial equilibrium corresponding to extinction, which is stable if $b_0 < d_A(d_J+\mu)/\mu$. Otherwise the system has a unique stable equilibrium (p_J^*, p_A^*), that satisfies biologically meaningful conditions for the parameter values and the trade-off curves we consider in this paper.

2.2.2. Non-spatial selection gradient

When a rare mutant (J', A') appears within the population, we may assume that as long as the mutant is rare, the resident population will not significantly deviate from its attractor. In other words, the resident dynamics are not affected by the mutant. On the other hand, the mutant does experience the resident, so mutant juveniles can be cared for (or preyed on) by both resident and mutant adults. The death rate of mutant juveniles is therefore

$$\delta_{J'} = d_{J'} - \beta c\, p_A - \beta c'\, p_{A'}.$$

We make the important assumption that adults can only discriminate between juveniles and adults, but not between resident and mutant juveniles. Thus, there is no kin discrimination. For a rare mutant, $p_{A'} \approx 0$ (and $p_{J'} \approx 0$), and the mutant contribution to the death rate vanishes

$$\delta_{J'} = d_{J'} - \beta c\, p_A^*.$$

The invasion dynamics of the mutant are linear and can be written in matrix form (Appendix A):

$$\frac{d}{dt}\begin{pmatrix} p_{J'} \\ p_{A'} \end{pmatrix} = \begin{pmatrix} -(\delta_{J'}+\mu') & b_{A'}(1-p_A^*-p_J^*) \\ \mu' & -d_{A'} \end{pmatrix}\begin{pmatrix} p_{J'} \\ p_{A'} \end{pmatrix}. \tag{3}$$

We are interested in the dominant eigenvalue λ of the invasion matrix $\boldsymbol{M}$. In general, λ can be obtained as the solution of a second-order equation. We shall restrict our attention to the case where the mutant is close to the resident (weak selection), in which case a first-order approximation of λ can be obtained as (Genkai-Kato and Yamamura, 1999)

$$\lambda \approx \frac{\det \boldsymbol{M}}{\operatorname{tr} \boldsymbol{M}}$$

where $\det \boldsymbol{M}$ is the determinant of the invasion matrix, and $\operatorname{tr} \boldsymbol{M}$ is its trace. In Appendix A, we show that the selection gradient then takes the form

$$\frac{\partial \lambda}{\partial c'} = \frac{d_A}{b_A}\frac{d_J - \beta c p_A^* + \mu}{d_A + d_J - \beta c p_A^* + \mu}\frac{\partial b_{A'}}{\partial c'} \tag{4}$$

where the partial derivatives are evaluated at $c' = c$. This result implies that the selection gradient has the same sign as $\partial b_{A'}/\partial c'$. Therefore, if there is a negative trade-off between adult investment and adult reproduction, the selection gradient is negative. Consequently, in the non-spatial model, parental care cannot evolve. If reproduction is enhanced by a negative investment, cannibalism will even be favoured. Thus, if parental care can evolve in the spatial version of the model, we know that it will be the consequence of spatial structure.

2.3. Spatially extended model

2.3.1. Invasion analysis

To investigate the potential impact of spatial structure on this model, stochastic simulations of the full spatial model can be performed. In Fig. 1, we present the results of two typical simulation runs of an invasion: starting with a small number of juveniles and adults with no adult investment ($c = 0$), we let the dynamics of this resident population reach an attractor ($t = 100$). We then introduce juveniles and adults of a second type (invaders), at a low global density. The adult invaders care for resident and invading juveniles with investment $c' = 0.5$, but because care is costly, invaders have a lower reproduction rate than residents. The invasion dynamics we present were performed on a triangular lattice (Fig. 1(a)–(b)) and on a regular random network (Fig. 1(c)–(d)).

In contrast with the non-spatial model, we observe that invaders increase in number and displace the residents. Because in the non-spatial model, such an invasion would never be successful, this invasion analysis indicates that spatial structure alters the selective pressures on parental care, and makes it possible for parental care to evolve. Note also that invasion is much slower on the triangular lattice than on the random network, showing the importance of network topology (and population viscosity) on the speed of evolution.

2.3.2. Moment equations

Extensive computer simulations of this model, while feasible, do not lead to easily generalisable understanding of the underlying eco-evolutionary processes. Analytical insight can be obtained by deriving a deterministic approximation of this model.

Any spatial distribution can be described by a hierarchy of moments, where the first moment represents the global density of single sites of each type, the second moment the correlation between neighbouring sites, and so forth. Changes in the spatial distribution thus imply corresponding changes in the spatial moments. Differential equations that describe the dynamics of spatial moments are called correlation equations (Rand, 1999). Mean-field models are actually a first-moment approximation of the spatial process, obtained by approximating higher-order moments in terms of first moments only.

We use the densities p_i (density of type i), p_{ij} (density of pairs of neighbouring sites ij), and higher-order statistics such as p_{ijk} (triplet densities). From these global densities p_i, p_{ij} and p_{ijk}, we can compute the local densities:

$$q_{i/j} = \frac{p_{ij}}{p_j} \quad \text{and} \quad q_{i/jk} = \frac{p_{ijk}}{p_{jk}}.$$

Differential equations for the dynamics of the global densities can be derived (van Baalen, 2000). These equations are not closed, in the sense that the equations for the pairs will involve third-order correlations $q_{i/jk}$. The aim of spatial moment equations is to derive a low-dimensional approximation of the dynamics by closing the system using moment closure approximations (Dieckmann and Law, 2000; Law et al., 2003; Murrell et al., 2004). Usually, the system is closed at the level of pairs, and the set of moment closures used in this case is called pair approximation (Rand, 1999). Other closures are possible, such as triple approximations, but in practice they tend to yield unwieldy systems of equations (Morris, 1997). Pair approximation amounts to approximating local densities of the form $q_{i/jk}$ with second-order local densities $q_{x/y}$. For instance, the ordinary pair approximation postulates $q_{i/jk} \approx q_{i/j}$ (Matsuda et al., 1992), but improved approximations may be used (Sato et al., 1994; van Baalen, 2000). The usual expectation is that ordinary pair approximation is best suited for random networks, while more regular network structures (e.g. lattices) are best described using improved approximations that take into account network geometry (van Baalen, 2000). We shall discuss this assertion later on in the paper.

Fig. 1. Invasion dynamics — In a resident population with no adult investment, invaders with a positive investment ($c' = 0.5$) are introduced at $t = 100$ (arrow) and invade, despite the cost of helping. Dynamics of global densities of juvenile (open circles) and adult (filled circles) individuals are presented (a) on a triangular lattice, and (c) on a regular random network ($n = 6$). (b) Typical cluster of mutant individuals (black) invading the resident population (grey) on a triangular lattice. Small hexagons represent juveniles, and large hexagons represent adults. (d) Dynamics of the global density of mutant juveniles p_{AJ} (filled circles) and of the local density of mutant juveniles experienced by mutant adults $q_{J'/A'}$ (open circles) on a regular random network. Parameters as in Table 1. Details on the cost function used in the simulations are given in Section 4.

2.3.3. Ecological dynamics

Using these notations, the dynamics of the expected global densities of juveniles and adults in a monomorphic population are given by:

$$\begin{cases} \dfrac{dp_J}{dt} = b_A q_{o/A} p_A - (d_J + \mu - \beta c q_{A/J}) p_J \\ \dfrac{dp_A}{dt} = \mu p_J - d_A p_A \end{cases} \tag{5}$$

where the first term in the first equation represents density-dependent reproduction (in the mean-field limit, $q_{o/A} = p_o = 1 - p_J - p_A$, and we recover a classical logistic growth term). It is important to note that those equations exactly describe the expected changes in the densities of juvenile and adults. The problem is that they depend, through the $q_{i/j}$'s, on pair densities, that is, on higher moments. Thus, the system is not closed, and we will need to choose a particular moment closure approximation to solve it numerically.

As in the non-spatial model, extinction is the only stable population equilibrium for some combinations of parameters. Otherwise, the population settles onto a unique stable positive equilibrium. We denote the global and local densities at equilibrium with a star (p_J^*, p_A^*, $q_{o/A}^*$, etc.). Appendix B gives the explicit expressions of some local densities under the ordinary pair approximation. In this paper, we shall restrict our attention to regions of parameter space in which the population is viable.

3. Spatial invasion fitness in class-structured populations

Following Metz et al. (1992), we set out in this section to derive the invasion fitness of a rare mutant (J', A') with adult investment c' in a resident population at equilibrium. More generally, we provide a general result that can be used to compute the spatial invasion fitness of a mutant in class-structured viscous populations.

3.1. Relaxation principle

As shown by Matsuda et al. (1992), we note that the local densities experienced by the mutant are fast variables that equilibrate relatively quickly when the mutant is still rare (Fig. 2). Therefore, the invasion dynamics quickly relax to a relaxation manifold on which fewer variables are needed to describe the system, as typical in spatial ecological models (see also Dieckmann et al. (2000)). As explained by van Baalen and Rand (1998), we can define spatial invasion fitness on this relaxation (or invasion) manifold (Ferrière and Le Galliard, 2001). More generally, such a separation of time scales is expected to be a general feature of mutant dynamics in spatially structured populations under weak selection (Rousset, 2004, 2006; Lion and Gandon, 2009). In fact, the more similar the invader to the resident, the slower the dynamics of invasion, and the longer the system stays close to the invasion manifold (compare for instance Figs. 1(d) and 2).

One can distinguish three phases in the invasion process of a rare mutant. First, the mutant individuals (J', A') undergo a