



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

$$\delta_J = d_J - \beta c q_{A/J}. \quad (1)$$

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

$$\begin{cases} \frac{dp_j}{dt} = b_A(1 - p_A - p_j)p_A - (\delta_j + \mu)p_j \\ \frac{dp_A}{dt} = \mu p_j - d_A p_A \end{cases} \quad (2)$$

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):

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

We are interested in the dominant eigenvalue λ of the invasion matrix \mathbf{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)

$$\lambda \approx \frac{\det \mathbf{M}}{\text{tr} \mathbf{M}}$$

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

$$\frac{\partial \lambda}{\partial c'} = \frac{d_A}{b_A} \frac{d_j - \beta c p_A^* + \mu}{d_A + d_j - \beta c p_A^* + \mu} \frac{\partial b_{A'}}{\partial c'} \quad (4)$$

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.

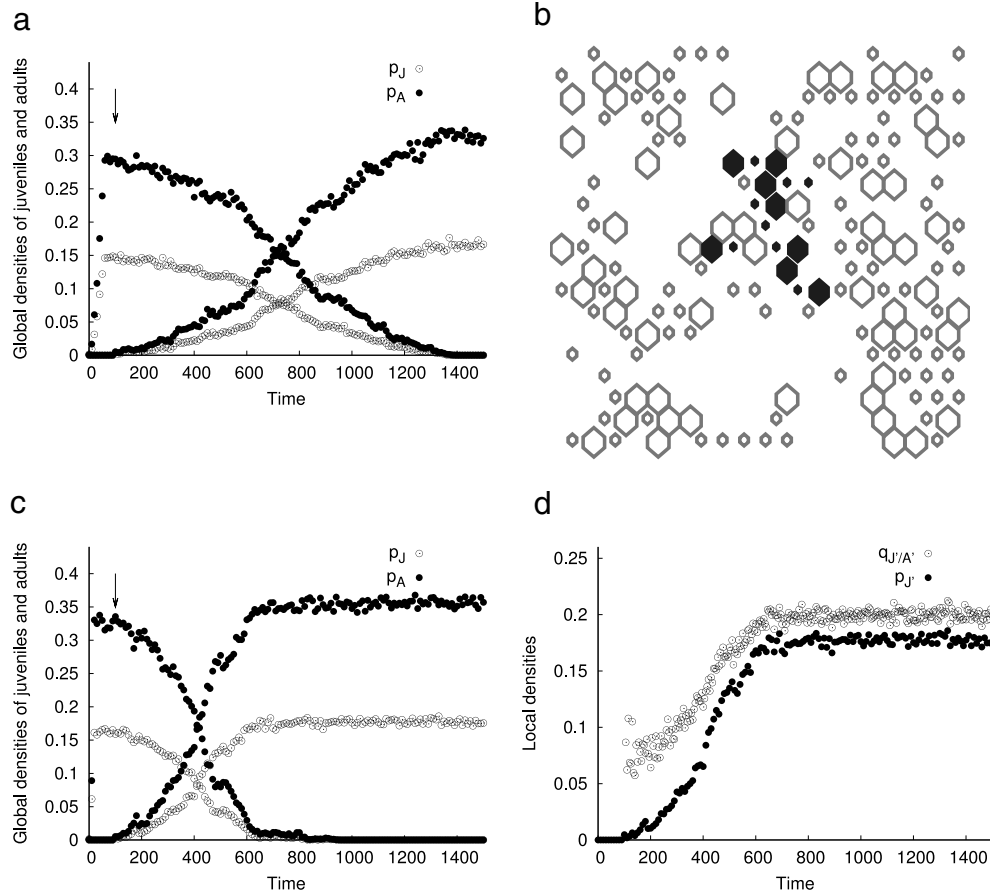


Fig. 1. Invasion dynamics – In a resident population with no adult investment, invaders with a positive investment ($c' = 0.5$) are introduced at $t = 100$ (arrow) and invade, despite the cost of helping. Dynamics of global densities of juvenile (open circles) and adult (filled circles) individuals are presented (a) on a 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. (c) 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:

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

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_{ij} '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

Table 1
Symbols and description of the model.

Type	Symbol	Description	Default value
Space	n	Number of nearest neighbours	6
	ϕ	Probability to draw a neighbour at random	$1/n$
	$\bar{\phi}$	Probability to draw a neighbour at random among $n - 1$	$1 - \phi$
Demography	b_0	Background birth rate	4
	d_j	Background death rate of juveniles	1.5
	d_A	Background death rate of adults	1
	b_A	Average birth rate of adults	
	δ_j	Average death rate of juveniles	
	μ	Maturation rate	2
	m_j	Juvenile migration rate	
	m_A	Adult migration rate	
	c	Adult investment	
	β	Efficiency of adult investment	1.5
	k	Intensity of the cost of parental care	0.1
	Variables	p_i	Global density of type i
p_{ij}		Global density of pairs of connected sites ij	
p_{ijk}		Global density of triplets of connected sites ijk	
$n_i(x)$		Number of neighbours of site x that are in state i	
$q_{i/j}$		Local density of type i as seen by type j	
$q_{i/jk}$		Local density of type i as seen by a j individual that has a k neighbour	

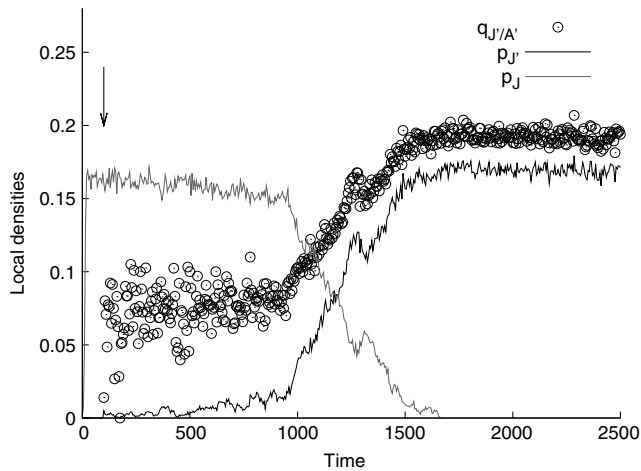


Fig. 2. Invasion dynamics and relaxation principle – The same experiment as in Fig. 1 is performed on a random regular network ($n = 6$), and the dynamics of the global densities of resident (grey line) and invader (black line) juveniles are shown, along with the dynamics of the local density $q_{J'/A'}$ (dots). We choose a lower value for the invaders' investment ($c' = 0.2$) so that the replacement of the resident is much slower. All other parameters as in Table 1, except that the cost of helping is lower ($k = 0.02$). Details on the cost function used in the simulations are given in Section 4.

highly stochastic process during which the mutant subpopulation either can go extinct, or can establish locally and reach a stable local structure. Second, as long as they are rare, the mutant subpopulation stay on the invasion manifold and retain this structure characterised by quasi-equilibrium values of the local densities, denoted by $\tilde{q}_{i/J'}$ and $\tilde{q}_{i/A'}$ for any type i . At this stage, spatial invasion fitness can be computed, and determines the issue of the third phase. A positive invasion fitness indicates successful invasion of the mutant: the mutant cluster grows (initially) exponentially and displaces the resident. A negative invasion fitness means that the mutant dies out. Note that this description of the invasion process hinges upon the assumption of large population size (Proulx and Day, 2001).

3.2. Invasion dynamics

As long as the mutants (J', A') are globally rare, we can decouple their dynamics from that of the residents, and assume that the resident population stay on the stable attractor ($p_A^*, p_J^*, \mathbf{q}^*$). The invasion dynamics are therefore governed by a vector \mathbf{p}_M of ten pair densities ($p_{oJ'}, p_{JJ'}, p_{AJ'}, p_{J'J'}, p_{A'J'}, p_{oA'}, p_{JA'}, p_{AA'}, p_{J'A'}, p_{A'A'}$). The dynamics of \mathbf{p}_M can be expressed in matrix form (van Baalen and Rand, 1998)

$$\frac{d\mathbf{p}_M}{dt} = \mathbf{M}(\mathbf{q})\mathbf{p}_M.$$

The invasion matrix $\mathbf{M}(\mathbf{q})$ depends only on the vector of local densities \mathbf{q} . Therefore, over a fast time scale, it quickly converges to a constant matrix $\tilde{\mathbf{M}} = \mathbf{M}(\tilde{\mathbf{q}})$. The dominant eigenvalue of $\tilde{\mathbf{M}}$ gives the spatial invasion fitness.

Most previous studies have studied invasion in a viscous population using an unstructured mutant. In this case, the dominant eigenvalue of $\tilde{\mathbf{M}}$ is equal to the per-capita growth rate of the mutant evaluated on the relaxation manifold (see Appendix C). This useful fact allows to gain insight into the selective pressures on the trait without computing the whole invasion matrix. A similar result holds when the mutant subpopulation is class-structured. In Appendix C, we show that, once the system has relaxed, the per-capita growth rate of each class of mutant individuals is equal to the dominant eigenvalue λ of the matrix $\tilde{\mathbf{M}}$. Thus, for the particular model we consider, spatial invasion fitness λ satisfies

$$\lambda = \frac{1}{p_{J'}} \frac{dp_{J'}}{dt} = \frac{1}{p_{A'}} \frac{dp_{A'}}{dt} \quad (6)$$

where the per-capita growth rates are evaluated on the relaxation manifold. In words, this means that once the mutant has reached a quasi-equilibrium structure, a positive invasion fitness implies that the class structured mutant subpopulation grows exponentially as would an unstructured population. In much the same way as population growth in well-mixed class-structured populations is associated with a stable stage distribution (Caswell, 2001), this exponential growth is associated with a characteristic spatial structure, which is given by a suitably normalised right eigenvector associated with λ (Appendix C).

3.3. Structure of the invading cluster

Mutant individuals in viscous populations form clusters that grow (Fig. 1(b)). Ultimately, the properties of the cluster will determine the success or failure of the invasion. As van Baalen and Rand (1998) have shown, the invasion fitness λ and the local structure $\tilde{\mathbf{q}}$ of the invading cluster must be computed simultaneously on the relaxation manifold from an eigenvalue equation. They argue that the right eigenvector associated with λ characterises the unit of selection in a viscous population (see Lion and van Baalen (2007) for further discussion). In populations with no class structure, a normalised eigenvector is simply $\tilde{\mathbf{q}}$, the vector of quasi-equilibrium local densities. In class-structured viscous populations, the right eigenvector contains information on both the local structure and the class structure of the mutant subpopulation (Appendix C).

Note that the class structure of the invading mutant cluster is determined by its local structure. Indeed, because $p_{J'A'} = q_{J'/A'} p_{A'} = q_{A'/J'} p_{J'}$, we can also use those spatial statistics to characterise the ratio juveniles/adults of the invading cluster

$$\tilde{w}_{J'/A'} = \frac{p_{J'}}{p_{A'}} = \frac{\tilde{q}_{J'/A'}}{\tilde{q}_{A'/J'}}$$

or the proportion of juveniles or adults within the invading cluster

$$\tilde{w}_{J'} = \frac{p_{J'}}{p_{J'} + p_{A'}} = \frac{\tilde{q}_{J'/A'}}{\tilde{q}_{J'/A'} + \tilde{q}_{A'/J'}}$$

$$\tilde{w}_{A'} = \frac{p_{A'}}{p_{J'} + p_{A'}} = \frac{\tilde{q}_{A'/J'}}{\tilde{q}_{J'/A'} + \tilde{q}_{A'/J'}}.$$

There is a close parallel with non-spatial class-structured populations, where the long-term dynamics of the mutant subpopulation is described by the growth rate of the mutant and by a stable stage distribution. Interestingly, in spatially structured populations, the stable stage distribution ($w_{J'}, w_{A'}$) results directly from the relaxation of the spatial dynamics. Note that there is a close analogy with the work of Neubert and Caswell (2000), who provide a method to compute the stage-structure of the travelling wave of an invading species.

Because mutants are initially clustered, the class structure $\tilde{w}_{J'/A'}$ of the invading mutant subpopulation is in general different from the equilibrium stage distribution $w_{J'/A}^*$ of the resident population. Of course, the closer the invader and the resident, the smaller the discrepancy between $\tilde{w}_{J'/A'}$ and $w_{J'/A}^*$. For a neutral invader that is identical to the resident, the class distribution during the invasion phase will be equal to the equilibrium class distribution.

4. The evolution of adult investment

Having defined invasion fitness in class-structured viscous populations, we are now equipped to ask standard questions of evolutionary game theory and adaptive dynamics regarding the convergence and evolutionarily stability of evolutionary singularities, which are points at which the selection gradient vanishes (Maynard Smith, 1982; Eshel, 1983; Metz et al., 1996; Geritz et al., 1998; Rousset, 2004). In this section, we derive an analytical expression for the selection gradient in our model, and investigate numerically the stability properties of its evolutionary singularities.

4.1. Invasion fitness

The invasion dynamics of a rare mutant (J', A') can be summed up in the following two equations

$$\begin{cases} \frac{dp_{J'}}{dt} = b_{A'} q_{o/A'} p_{A'} - (d_{J'} + \mu' - \beta c q_{A/J'} - \beta c' q_{A'/J'}) p_{J'} \\ \frac{dp_{A'}}{dt} = \mu' p_{J'} - d_{A'} p_{A'}. \end{cases} \quad (7)$$

From the first equation, we observe that a mutant juvenile will experience the presence of both resident and mutant adults. This is in sharp contrast with what happens in the mean-field model, in which a rare mutant perceives the environment as set by the resident only. In viscous populations, mutants form clusters, so the environment they experience is characterised by both the resident and the mutant individuals.

We know that on the invasion manifold, the invasion fitness is equal to the per-capita growth rates of J' and A' . Hence, because $p_{J'}/p_{A'} = q_{J'/A'}/q_{A'/J'} = \tilde{w}_{J'/A'}$, we have

$$\lambda = \frac{b_{A'} \tilde{q}_{o/A'}}{\tilde{w}_{J'/A'}} - (d_{J'} + \mu' - \beta c \tilde{q}_{A/J'} - \beta c' \tilde{q}_{A'/J'}) \quad (8)$$

$$\lambda = \mu' \tilde{w}_{J'/A'} - d_{A'}. \quad (9)$$

In principle, we can obtain the spatial invasion fitness for any couple of resident and mutant traits by numerically solving for the pseudo-equilibrium local densities $\tilde{q}_{o/A'}$, $\tilde{q}_{A'/J'}$ and $\tilde{q}_{J'/A'}$ and substituting those equivalently into Eq. (8) or Eq. (9). This method can be used to compute Pairwise Invasibility Plots (PIP) (Geritz et al., 1998). However, to shed more light on the selective pressures responsible for the evolution of parental care, we shall take one further analytical step.

4.2. Selection gradient

Combining Eqs. (8) and (9) by eliminating the ratio $\tilde{w}_{J'/A'}$, we obtain the following equation implicitly defining λ

$$\lambda = b_{A'} \tilde{q}_{o/A'} \frac{\mu'}{d_{A'} + \lambda} - (d_{J'} + \mu' - \beta c \tilde{q}_{A/J'} - \beta c' \tilde{q}_{A'/J'}). \quad (10)$$

Our goal is to solve Eq. (10) in the special case where the mutant is close to the resident.

When rare, a neutral mutant (a mutant that is identical to the resident in all aspects, except for a neutral inherited tag) will quickly reach a characteristic quasi-equilibrium structure \bar{q} . (Note that we use the bar symbol instead of the tilde to denote the quasi-equilibrium local densities of a neutral mutant.) Given a resident population with trait c , one can make a first-order Taylor-expansion of the structure of the invading mutant subpopulation with trait $c' = c + \epsilon$ for $\epsilon \approx 0$:

$$\bar{q}(c + \epsilon) = \bar{q} + \epsilon \frac{\partial \bar{q}}{\partial c}(c) + o(\epsilon).$$

Obviously, if the mutant is identical to the resident, it will experience the same density of empty sites, thus $\bar{q}_{o/A'} = q_{o/A}^*$, where the star denotes the value of the resident local density at equilibrium. Likewise, the total density of adults perceived by a neutral mutant juvenile will be equal to $q_{A/J}^*$. However, as the mutant experiences both mutant and resident adults, we have $\bar{q}_{A/J'} + \bar{q}_{A'/J'} = q_{A/J}^*$.

Assuming that the mutant deviates only slightly from neutrality (i.e. the mutant is close to the resident), we can obtain a first-order Taylor expansion of Eq. (10). This yields the following expression of the selection gradient (Appendix D, Eq. (D.1))

$$\frac{\partial \lambda}{\partial c'} \propto \beta \bar{q}_{A'/J'} + \frac{\mu}{d_A} \frac{\partial b_{A'} \tilde{q}_{o/A'}}{\partial c'} + \beta c \frac{\partial}{\partial c'} (\bar{q}_{A/J'} + \bar{q}_{A'/J'}). \quad (11)$$

In the mean-field limit, the latter equation collapses to Eq. (4). Indeed, in a well-mixed population, $\bar{q}_{A'/J'} \approx p_{A'} \approx 0$, and the first term is zero. Likewise, the third term vanishes, because $\bar{q}_{A/J'} + \bar{q}_{A'/J'} \approx p_A + p_{A'} \approx p_A^*$, which does not depend on the mutant trait. Finally, since $\bar{q}_{o/A'} \approx p_o^* = 1 - p_J^* - p_{A'}^*$, the second term becomes proportional to $\partial b_{A'}/\partial c'$, which is the result of Eq. (4).

Eq. (11) allows one to identify the selective pressures at work on adult investment. In a separate paper (Lion and van Baalen, 2007), we discuss in detail the ecological implications of this invasion condition, and show that we can interpret this expression as a variant of Hamilton's rule.

4.3. Neutral local structure of the cluster of mutants

Under neutrality ($c' = c$), an analytical expression for the local density $\bar{q}_{J'/A'}$ can be obtained (Appendix E)

$$\bar{q}_{J'/A'} = \phi \frac{b_A q_{o/A}^*}{\mu + d_J + d_A - \beta c (\phi + \bar{\phi} \tilde{q}_{A'/J}^*)}. \quad (12)$$

This also gives $\bar{q}_{A'/J'}$ because $\bar{q}_{A'/J'}/\bar{q}_{J'/A'} = \mu/d_A$. To derive this expression, we use two approximations, namely we set two higher-order local densities ($q_{A'/oA'}$ and $q_{A'/oA}$) to zero. The simplifying assumption is that correlations between non-neighbouring sites can be ignored. As we will show later on, this assumption cannot be safely made in invading subpopulations.

We first note that, by taking the mean-field limit ($\phi \rightarrow 0$) in Eq. (12), we recover the fact that $\bar{q}_{J'/A'}$ tends towards zero in non-spatial models. In the spatial model, combining Eqs. (12) and (B.6) yields in the limit of low investment

$$\bar{q}_{J'/A'} = \phi \frac{d_A}{\mu} \frac{d_J + \mu}{d_A + d_J + \mu}. \quad (13)$$

In the general case where adult investment is not negligible, ordinary pair approximation can be used in Eq. (12) to obtain a (complicated) expression for $\bar{q}_{J'/A'}$ as a function of demographic parameters and adult investment c .

It is important to note that, while obtaining Eqs. (12) and (13) requires that we make some assumptions on the local structure of the invading cluster, the only approximation used to derive the selection gradient (11) is the assumption of small mutations (weak selection), that is, we assume the mutant is close to the resident. Higher-order moments are not neglected, but encompassed in local densities.

4.4. Trade-off between adult investment and adult reproduction

In order to make predictions about the evolutionary outcomes of the model, we need to specify a trade-off between adult investment and adult reproduction. We assume that the reproduction rate is a decreasing function of investment, which means that parental care decreases the reproduction rate and cannibalism increases it. In particular, we choose the following functional relationship

$$b_A(x) = b_0 - \gamma(c) \frac{n_J(x)}{n}. \quad (14)$$

Thus, a resident adult at site x with investment c has a negative or positive payoff $\gamma(c)$ only if it has juveniles in its neighbourhood.

To derive the average birth rate, we need to average $b_A(x)$ over all sites occupied by an adult that effectively reproduces, meaning that we need to take the average over all pairs in state A_0 . This leads the following expression for the average birth rate

$$b_A = b_0 - \gamma(c) \bar{\phi} q_{J/A_0}$$

where $\bar{\phi} = 1 - \phi = (n - 1)/n$ is a discounting factor taking into account the fact that at least one site in the neighbourhood is empty (see Appendix A in van Baalen and Rand (1998) for a discussion).

For a mutant adult, we obtain a similar expression for $b_{A'}$, except that the mutant adults interact with both mutant and resident juveniles

$$b_{A'} = b_0 - \gamma(c') \bar{\phi} (q_{J/A'_0} + q_{J'/A'_0}).$$

In the following, we shall assume that the cost of parental care is accelerating and the benefit of cannibalism is decelerating, which can be captured smoothly by the functional form $\gamma(c) = k(\exp(c) - 1)$. In the discussion we shall briefly review the consequences of choosing other trade-off functions.

4.5. Pair approximation vs. stochastic simulations

In this section, we choose to close the equations using the ordinary pair approximation (Matsuda et al., 1992), setting

$$q_{i/jk} \approx q_{i/j}.$$

In Fig. 3, we present the predictions of the adaptive dynamics model under the ordinary pair approximation. We find that the evolutionary singularity is convergent-stable (CSS) and evolutionarily stable (ESS), as shown by a typical PIP (Geritz et al., 1998). Thus, starting from low or high values of the trait, evolution will bring the trait to a resting point that may correspond to a positive level of investment (low values of k), or to a negative level of investment (high values of k).

Fig. 3 shows that the qualitative predictions are borne out by evolutionary stochastic simulations on regular random networks. However, the quantitative accuracy of ordinary pair approximation is poor, since ordinary pair approximation consistently underestimates the ESS on a regular random network, on which it is often

expected to be accurate. Such an important bias can usually be explained by systematic errors introduced by the ordinary pair approximation in the evaluation of the local structure of the cluster of mutants. In the next section, we introduce a correction to the ordinary pair approximation that allows the analytical model to match the results of the simulations.

4.6. Clustering of rare mutants and improved pair approximation

Application of adaptive dynamics methodology to spatially structured populations rests upon two necessary steps. First, we need to compute the ecological attractor for the resident monomorphic population. Second, we have to calculate the local structure of the invading cluster of mutants.

It is known that some important features of the initial clustering of rare mutants can be left out by ordinary pair approximation (Sato et al., 1994). For instance, ordinary pair approximation will approximate the local density $q_{A'/oA'}$ as $q_{A'/o}$, which vanishes when the mutant is rare. But since an empty site neighbouring a mutant adult is likely to belong to a clump of empty sites and mutants, $q_{A'/oA'}$ can be expected to be non-zero even when the mutant is rare. To get a better idea of why this is the case, we can have a look at the schematic cluster in Fig. 4, which consists of four black sites (\times) embedded in a matrix of empty sites. As explained in the caption, the local density $q_{\times/o}$ is $O(1/N)$, where N is the total number of sites, but the local density $q_{\times/o\times}$ is $O(1)$. Then, even when the number of occupied sites becomes vanishingly small, the density $q_{\times/o\times}$ can remain positive.

Because of stochastic fluctuations, it is difficult to compute $q_{A'/oA'}$ from stochastic simulations when the mutant is rare. However, our simulations suggest that, even on a random network, $q_{A'/oA'}$ is not negligible, although the quantitative deviation appears to be rather small (results not shown). To take this effect into account, and check whether it is sufficient to explain the bad quantitative performance of ordinary pair approximation, we introduce an improved pair approximation. The idea is to set $q_{A'/oA'}$ to a non-zero value and to modify other local densities so that conservation rules hold. In our model, $q_{A'/oA'}$ is likely to have an important role, because it will be directly connected to the ability of mutant adults to reproduce. In particular, the full expression for inter-age relatedness depends on $\bar{q}_{A'/oA'}$

$$\bar{q}_{J'/A'} = \frac{b_A q_{o/A}^* (\phi + \bar{\phi} \bar{q}_{A'/oA'})}{\mu + d_J + d_A - \beta c (\phi + \bar{\phi} q_{A'/JA}^*)}. \quad (15)$$

If $\bar{q}_{A'/oA'}$ is negligible, we recover Eq. (12). This will be the case if we use ordinary pair approximation. However, if $\bar{q}_{A'/oA'}$ has a small positive value, inter-age relatedness is predicted to be higher, and thus the positive selective pressure on parental care is greater.

This observation inspired the following correction to the ordinary pair approximation: all triple local densities are approximated as $q_{i/jk} \approx q_{i/j}$ except

$$\bar{q}_{A/oA'} = (1 - \nu) q_{A/o}^*$$

$$\bar{q}_{A'/oA'} = \nu q_{A'/o}^*.$$

When ν tends towards zero, we recover ordinary pair approximation ($\bar{q}_{A'/oA'} = 0$ and $\bar{q}_{A/oA'} = q_{A/o}^* \approx q_{A'/oA}^*$). We can take into account the clustering of rare mutant adults by setting ν to a non-zero positive value. As ν increases, the accuracy of our approximation improves across the whole range of the cost parameter k . In Fig. 3b, we show that there exists a value of ν for which the evolutionarily stable investment predicted by our improved pair approximation matches very accurately the results of stochastic simulations. In Fig. 3b, we used $\nu = 0.13$, which leads to a slight overestimation of the value $q_{A'/oA'}$ computed from simulations (results not shown), but yields a better prediction of the evolutionary endpoints.

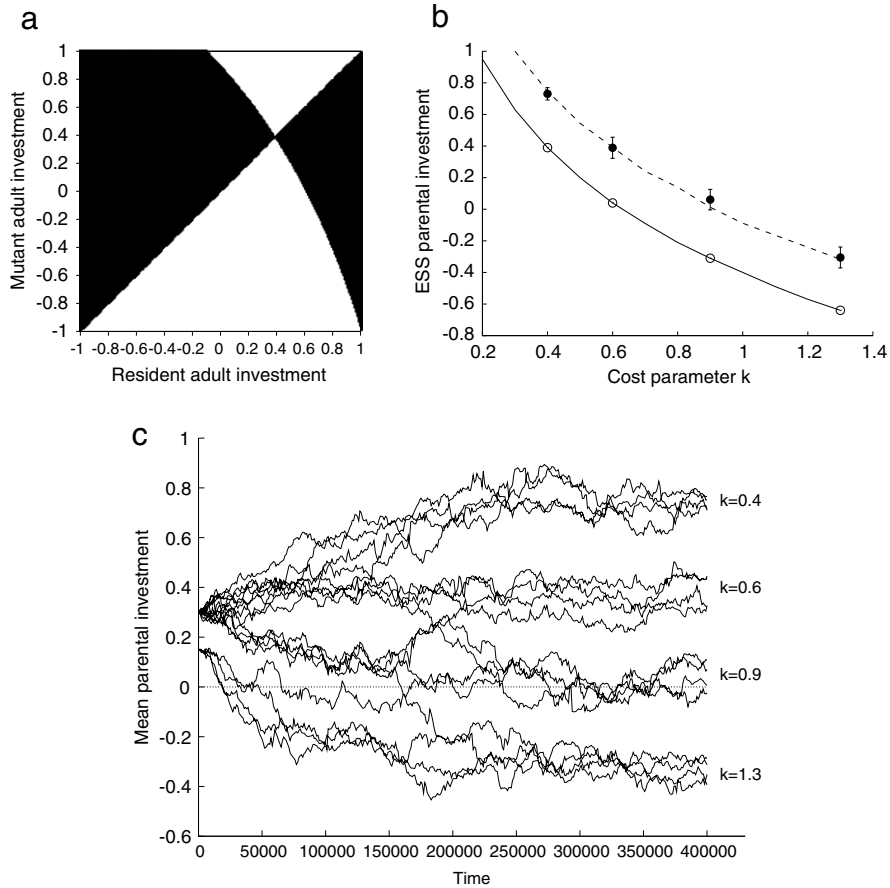


Fig. 3. (a) Pairwise invasibility plot ($k = 0.4$). (b) ESS adult investment for various values of k , as predicted under the pair approximation (continuous line and empty circles) and obtained from stochastic simulations (filled circles with error bars indicating the mean and standard deviation across 10 runs). The dashed line indicate the predictions of an improved pair approximation (see main text). (c) Evolution of mean adult investment for increasing values of k (top to bottom: $k = 0.4, 0.6, 0.9, 1.3$). Four stochastic trajectories are shown in each case, starting from initial conditions 0.3, except for $k = 1.3$ where the initial value of the trait was 0.15 to allow all simulations to reach the attractor on a similar timescale. Parameters as in Table 1.

4.7. The evolutionary consequences of higher-order correlations

Our analysis highlights the evolutionary role of triple correlations, and shows that even a very slight error on the prediction of some triplet correlations in the invading cluster can be sufficient to cause important deviations between analytical predictions and stochastic simulations. Alternatively, one might want to take a more optimistic view to this problem, and consider that this means that only a small correction may be needed to achieve quantitative accuracy.

It is important to notice that our results go somewhat against the expectation that ordinary pair approximation should be accurate on regular random networks, because their local structure resembles that of a tree, on which there are no short loops (Szabó and Fátth, 2007); whereas improved pair approximations would be needed on lattices, which are characterised by a higher degree of clustering (Sato et al., 1994; van Baalen, 2000). Here, we have shown that even on random networks, the initial clustering of mutants causes some correlations to deviate from the value predicted by ordinary pair approximation, causing corrections to be necessary.

What is usually not fully acknowledged is that the accuracy of ordinary pair approximation on random regular networks also depends on the demographic process used to model population dynamics. As an example, consider the equilibrium structure of the resident population in our model. On a random regular network (Fig. 5, top panel), the local densities are extremely well predicted by ordinary pair approximation, but the triple correlations $T_{ijk} =$

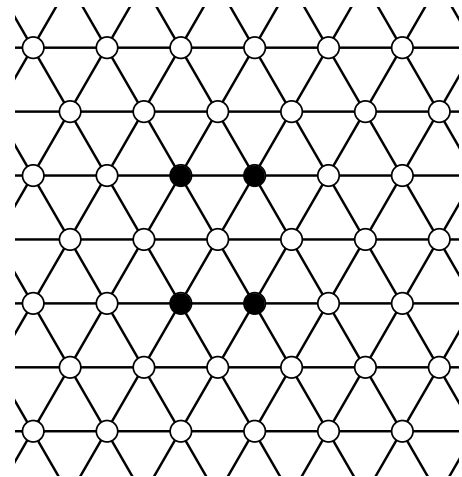


Fig. 4. Schematic cluster on a triangular lattice of N sites. Four occupied sites (\times , filled circles) are embedded in a matrix of empty sites (o , white circles) as shown. We then have $N - 4$ empty sites, and we can count $20 \times o$ pairs and $10 \times o \times o$ triples. If we compute the density of occupied sites in the neighbourhood of an empty site, we obtain $q_{\times/o} = p_{o \times} / p_o = (20 / (6N)) / ((N - 4) / N) = 10 / (3(N - 4))$ which vanishes when N is large, while the local density $q_{\times/o \times} = p_{\times o \times} / p_{o \times} = (10 / (30N)) / (20 / (6N)) = 1 / 10$.

$q_{i/jk} / q_{ij}$ deviate significantly from the predicted value 1. This effect is rather subtle if we contrast it with what happens on a lattice (Fig. 5, bottom panel), in which case, as expected, the

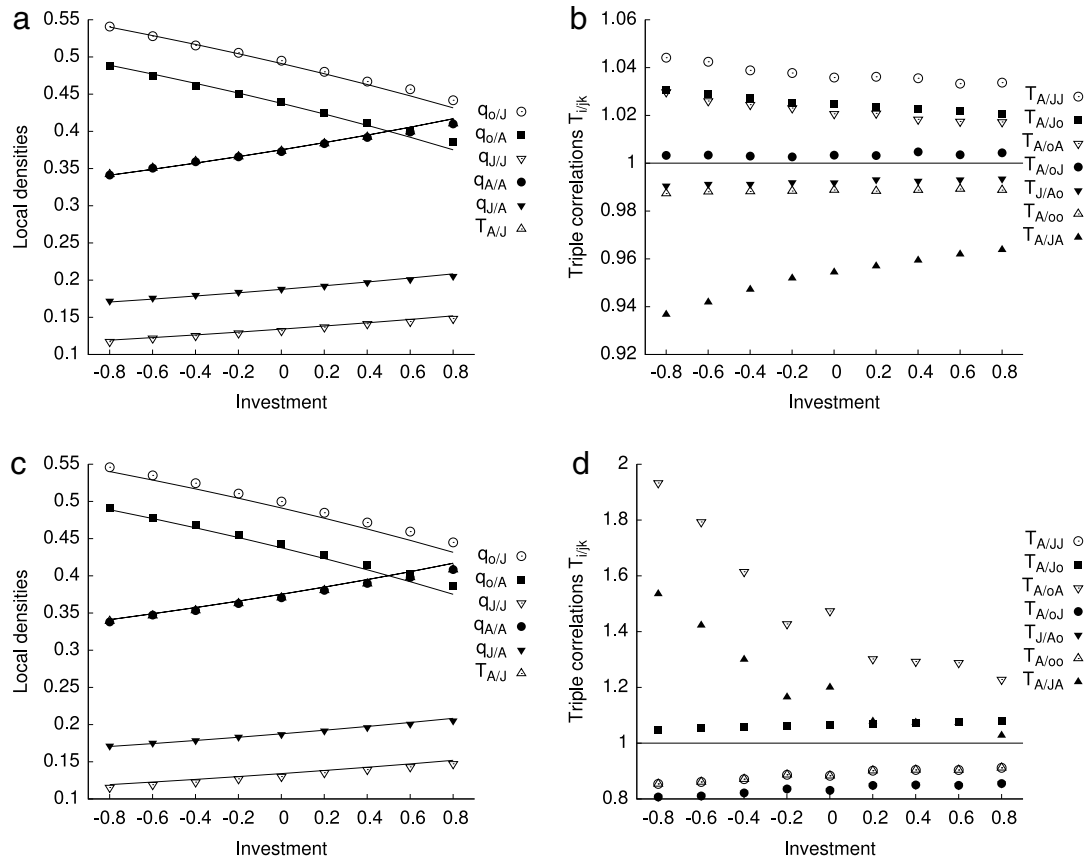


Fig. 5. Local structure of the resident population at equilibrium for different levels of adult investment and an exponential trade-off. Left panel: Local densities q_{ij} as predicted using ordinary pair approximation (lines) and as obtained from stochastic simulations (points). Right panel: Triplet correlations obtained from stochastic simulations. A deviation from 1 indicates that ordinary pair approximation does not hold. ((a)–(b)) Regular random network with 6 neighbours. ((c)–(d)) Triangular lattice. Parameters as in Table 1 except $k = 0.4$.

deviations for triple correlations are more important. However, in models of altruistic interactions with no age structure on random networks, such as those studied by van Baalen and Rand (1998) and Le Galliard et al. (2003, 2005), the triple correlations T_{ijk} do not differ significantly from 1 (results not shown), which indicates that the bias we observe in the age-structured population is a direct consequence of class structure. Thus, life cycle assumptions may have a subtle impact on higher-order correlations, and thus on the performance of moment closure approximations. We note that this effect will be missed if one is only interested in accurately predicting the equilibrium values of the first- and second-order spatial moments, so one cannot expect a moment closure approximation that is accurate in an ecological context to perform necessarily well when using the same ecological model in an evolutionary setting.

We conclude by stressing that spatial correlations beyond the level of pairs can have a significant evolutionary impact, either because they determine the success of the invading cluster, as we showed in the previous section, or because demographic processes can lead to a higher degree of spatial structuring than expected from topological considerations. How much the two levels may interplay is largely model-dependent. In our model for instance, taking into account the triple correlations when computing the equilibrium densities of the resident population did not lead to any significant improvement in predicting the ESS value on a random regular network, and we are fairly confident that much of the observed discrepancy between simulations and ordinary pair approximation is due to the correlations between mutant adults and empty sites within the invading cluster.

5. Discussion

This paper proposes a general method to study the evolution of class-structured viscous populations using a combination of moment closure techniques and adaptive dynamics. Central to our approach is the definition of spatial invasion fitness. We apply this general concept to the evolution of interactions between juveniles and adults and discuss the choice of moment closure approximations and their relevance to evolutionary models.

5.1. The evolution of parental investment

In a well-mixed population, parental care is always counter-selected because individuals do not interact with their own offspring. In the absence of any other mechanism, we can therefore expect cannibalism of juveniles to evolve in non-spatial models. On the other hand, in viscous populations, offspring dispersal is limited. As a consequence, mutant adults tend to be surrounded by mutant juveniles, and parental care can evolve if the costs are not too high. This corroborates previous studies on the evolution of cooperation that showed that spatial structure generally favours the evolution of cooperation (see Lion and van Baalen (2008) for a review, and Doebeli and Hauert (2005) for a discussion). We argue elsewhere that these results are not produced by some network-specific mechanism (e.g. Nowak (2006)), but can be understood as a form of kin selection (Lion and van Baalen, 2007, 2008). In this paper, we show that the endpoint of the evolution of adult investment is given by an evolutionarily stable level of investment. At the ESS, adults may either care for juveniles, or cannibalise them depending on the cost of helping and the benefits of cannibalism.

The generality of our results is limited to a certain extent by the particular shape of the trade-off we assume between adult investment and adult reproduction. Clearly, the trade-off relationship we chose, with accelerating costs of helping and saturating benefits of cannibalism, is only one of many plausible trade-off relationships. However, finding a mathematical function that describes a biologically meaningful trade-off while keeping some tractable analytical properties is a difficult undertaking. This is due in part to the fact that we model adult investment as a continuous trait that may be either negative or positive. Assuming that cannibalism and helping are coded by two different (and jointly evolving) traits could actually alleviate the difficulty of choosing an adequate trade-off function, at the expense of increased complexity in the evolutionary analysis.

Although we did not address this difficulty in our article, preliminary results do show that our results are sensitive to the shape of the trade-off between adult investment and adult reproduction. With saturating costs of parental care, for instance, the model may exhibit an evolutionary repellor, and the evolutionary dynamics become bistable: if the population starts off from below the singularity, it will evolve towards cannibalism; otherwise, parental care will evolve (results not shown). The robustness of this result to perturbations of the trade-off curve remains to be investigated.

The evolutionary importance of trade-off shapes is well recognised in well-mixed populations (de Mazancourt and Dieckmann, 2004; Kisdi, 2006), and its importance in viscous populations has recently been stressed by Kamo et al. (2007) in the case of the evolution of parasite virulence. Compared with non-spatial models, a further complication arises in viscous populations because spatial structuring leads to new selective pressures or even creates emergent trade-offs (van Ballegooijen and Boerlijst, 2004). Further modelling work is needed to understand how these emergent patterns may combine with the physiological trade-off of classical evolutionary theory, and give rise to a complex pattern of costs and benefits.

Finally, we want to stress that, as often in spatial demographic models, different predictions on the evolution of adult investment should be expected under different life cycle assumptions, for instance if the costs of helping affect adult survival instead of adult reproduction. Another assumption in our model is that these costs are density-dependent (an individual pays a reproduction cost only if there are juveniles in her neighbourhood), but one could also imagine that costs are unconditional, for example if care is mediated through the release of juvenile-specific resources into the environment, in a density-independent manner. Thus, a deeper understanding of the evolution of adult investment would necessitate a careful analysis of the impact of life cycle assumptions, density dependence, and physiological trade-offs on the selective pressures on adult investment.

5.2. Spatial invasion fitness

Evolution proceeds through the repeated appearance and spread of new mutations. To assess the evolutionary success of a mutation, we therefore need a measure of the probability of invasion of a rare mutant. Such invasion analysis is the basis of game-theoretic modelling (Maynard Smith, 1982; Eshel, 1983), and allows a rigorous definition of fitness. In finite populations, fixation probabilities will provide the correct measure of fitness (Proulx and Day, 2001). In infinite (or large enough) populations, the growth rate of the mutant when rare is typically used (Metz et al., 1992).

In spatially structured (viscous) populations, things are more complicated because, even when globally rare, the mutant may be locally abundant. Indeed, when a mutant arises in a spatially

structured population, it will tend to form clusters because reproduction is a local process (Fig. 1(b)). The interaction of a mutant with other mutants will therefore not be negligible, in clear contrast with what happens in well-mixed populations. This does not preclude however the use of the growth rate of a rare mutant as the invasion fitness, except that we have to shift the concepts up to the cluster level (van Baalen and Rand, 1998). Rarity should then be understood as “global” rarity, and invasion fitness should be defined as the growth rate of the cluster of (globally rare) mutants. The cluster is thus the relevant unit of invasion (van Baalen and Rand, 1998).

In general, this is a complicated problem, because the invasion dynamics of the mutant must be described by a highly non-linear system of equations. However, for a rare mutant (or under weak selection, see Lion and Gandon (2009)), the local densities experienced by the mutant are fast variables, whereas the global densities are slow variables (Matsuda et al., 1992). Separation of time scales implies that the local densities quickly reach a quasi-equilibrium while the mutant is still rare, and invasion can thus be approximated by a linear process. We show in this paper that, even when the populations are structured in discrete stages, this relaxation property can be used to derive a unique measure of invasion fitness, that can be obtained equivalently as the per-capita growth rate of any mutant class, or as the dominant eigenvalue of the invasion matrix. The elements of the associated eigenvector describe the structure of the invading cluster, both in terms of space and stage. In other words, in class-structured viscous populations, the fate of a mutant is ultimately determined by the properties of a cluster, the spatial and demographic structures of which are a consequence of the relaxation of the spatial ecological dynamics.

There are some limitations to our method. In particular, we assume a sufficiently large network of sites, harbouring a large population, but extension to finite populations should be possible, provided that proper care be taken when computing the fixation probability of a mutant. Although the derivation of spatial moment equations in finite populations is a more difficult task, the equations obtained are very similar (Stollenwerk, 2005), so it should be possible to use a similar argument of separation of time scales to make progress (see Rousset (2006) for a discussion). The development of a finite population extension to the methods we describe here might also be needed to fully characterise the invasion of a rare mutant, which, due to the small number of individuals, is an inherently stochastic process. Ultimately, the assumption of mutant rarity may be relaxed, as a similar separation of time scales occurs under weak selection (Rousset, 2006; Lion and Gandon, 2009).

5.3. Moment closure approximations

Deriving an analytical expression for invasion success is an important first step, even when component quantities are still unknown. For instance, we can infer different selection pressures even when we cannot yet calculate them precisely. To make quantitative predictions, however, for instance to compute an ESS value, we must be able to numerically evaluate invasion fitness. The difficulty we encounter here is that the invasion dynamics of the mutant typically depend on higher-order spatial correlations (e.g. triples, or more complex configurations), so the system is not closed in mathematical terms.

Moment closure approximations, such as pair approximations, circumvent the problem by setting higher-order spatial correlations to zero. Ever since the introduction of moment equations to theoretical ecology, however, it has been pointed out that moment closure approximations could neglect some key aspects of spatial structure (Sato et al., 1994). The main reason is that, basically, not

every spatial configuration can be expressed in terms of pairs. This is obvious if we think of large-scale structures such as spiral waves (Boerlijst et al., 1993), but an important conclusion of early studies of pair approximation techniques was that it is true as soon as we move beyond the level of pairs. An additional insight of our work is that the accuracy of moment closure approximations depends not only on network topology, but also on life cycle assumptions.

Indeed, the evolutionary effect of higher-order spatial correlations will depend strongly on population dynamics and on the feedback loop between ecology and evolution. Contrasting different models may be instructive in this respect. For instance, ordinary pair approximation only yields a rough estimate of the ESS in our model whereas it is quite accurate in the lattice model of host-parasite interactions studied by Kamo et al. (2007). At first glance, one could rather expect the reverse to hold true, because the lattice structure assumed by Kamo et al. (2007) introduces correlations that ordinary pair approximations cannot take into account. However, those correlations may not be very relevant to the evolution of virulence, for instance if they affect local densities that have a weak impact on the fitness of mutants.

It should also be realised that the accuracy of moment closure approximations in an ecological context tells us little about their predictive power in an evolutionary context. As we showed in this work, moment closure approximations may predict accurately the dynamics of low-order spatial correlations such as p_i and $q_{i/j}$, but they may also neglect some crucial information about the dynamics of higher-order correlations that may be determinant for the evolutionary dynamics, although irrelevant for most ecological purposes.

In this study, we consider a modified pair approximation to understand what causes the difference between the predictions of our analytical model and the results of our evolutionary stochastic simulations (an alternative approach, based on a triple approximation, is discussed in Lion (in press)). Our improved pair approximation has thus allowed us to identify an important evolutionary factor that is missed by ordinary pair approximation. Clearly, other factors may play a role, and further studies are needed to provide a rigorous account of the error terms introduced by moment closure approximations (Morris, 1997; Rand, 1999). Sensitivity analysis could be used in a more general theory to identify the regions of parameter and functional space where these error terms are negligible. However, we believe that the goal of evolutionary models based on spatial moment equations should be to try and understand the selection process rather than to provide quantitatively accurate results. Our results demonstrate that observing a discrepancy between explicit simulation results and approximation is not a mere ‘failure’ of the latter, but rather a useful indication that helps us to identify more subtle but essential aspects of the system. For instance, we can conclude that class-structured population may generate non-negligible triple correlations that may have important evolutionary consequences.

Our analysis therefore teaches us two important lessons for spatial evolutionary ecology. The first is that higher-order spatial correlations can have crucial evolutionary consequences, and that predicting evolutionary dynamics may require a more precise analysis than is usually needed to predict ecological dynamics. The second reason is that, when selection is weak, a slight error in the computation of the local structure of the invading cluster may translate into large quantitative differences between analytical models and stochastic simulations. This is an important point, because it implies that errors caused by moment closure approximations will increase as we approach the singular point. Clearly, this calls for new moment closure techniques that are less sensitive to this important problem (see for instance (Petermann and De Los Rios, 2004; Murrell et al., 2004)), or for alternative methods of deriving moment equations in space (Ovaskainen and Cornell, 2006).

5.4. Conclusions

Our approach provides a general framework in which to investigate the consequences of spatial structure and ecological dynamics on the evolution of traits. In a separate paper (Lion and van Baalen, 2007), we show that we can use this framework to recover some classical results of kin selection theory. As emphasised by Le Galliard et al. (2005), the type of spatial ecological models we study in this paper, coupled with evolutionary frameworks such as adaptive dynamics or population genetics, can help us tie together the effects of demographic fluctuations, habitat saturation, local interactions, kin selection, kin competition and dispersal. A distinct benefit of such an approach is that it allows one to recover some classical results of the literature (such as Hamilton’s rule) as emergent properties of the eco-evolutionary dynamics, as well as to offer much-needed insight on the interplay between spatial dynamics and selection.

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Appendix A. Selection gradient in the non-spatial model

The invasion dynamics of the mutant are given by

$$\begin{cases} \frac{dp_{j'}}{dt} = b_{A'}(1 - p_j - p_A - p_{j'} - p_{A'})p_{A'} - (\delta_{j'} + \mu')p_{j'} \\ \frac{dp_{A'}}{dt} = \mu'p_{j'} - d_{A'}p_{A'} \end{cases} \quad (\text{A.1})$$

where $\delta_{j'} = d_{j'} - \beta c p_A - \beta c' p_{A'}$. Assuming that the mutant is rare ($p_{j'} \approx 0$ and $p_{A'} \approx 0$) and that the resident population is on the non-trivial equilibrium (p_j^*, p_A^*), we can rewrite Eq. (A.1) in matrix form

$$\begin{aligned} \frac{d}{dt} \begin{pmatrix} p_{j'} \\ p_{A'} \end{pmatrix} &= \begin{pmatrix} \beta c p_A^* - (d_{j'} + \mu') & b_{A'}(1 - p_A^* - p_{j'}^*) \\ \mu' & -d_{A'} \end{pmatrix} \begin{pmatrix} p_{j'} \\ p_{A'} \end{pmatrix} \\ &= \mathbf{M} \begin{pmatrix} p_{j'} \\ p_{A'} \end{pmatrix}. \end{aligned}$$

We are interested in the dominant eigenvalue λ of the invasion matrix \mathbf{M} . For a mutant close to the resident, we can use a first order approximation of λ Genkai-Kato and Yamamura (1999)

$$\lambda \approx \frac{\det \mathbf{M}}{\text{tr} \mathbf{M}}$$

with

$$\det \mathbf{M} = d_{A'}((d_{j'} + \mu') - \beta c p_A^*) - \mu' b_{A'}(1 - p_A^* - p_{j'}^*)$$

$$\text{tr} \mathbf{M} = \beta c p_A^* - (d_{A'} + d_{j'} + \mu').$$

Let us further assume that there is a trade-off between adult reproduction and adult investment, and that all other demographic traits are fixed. Then, the trace of the matrix is

$$\text{tr} \mathbf{M} = -(d_A + \mu + d_j - \beta c p_A^*)$$

which is always negative because we assume $\beta c < d_j$. The determinant of \mathbf{M} reads

$$\det \mathbf{M} = d_A(d_j - \beta c p_A^* + \mu) - \mu b_{A'}(1 - p_A^* - p_{j'}^*).$$

We can use Eq. (2) in the main text to get the equilibrium condition for the resident

$$1 - p_J^* - p_A^* = \frac{d_J - \beta c p_A^* + \mu}{b_A} \frac{p_J}{p_A} = (d_J - \beta c p_A^* + \mu) \frac{d_A}{\mu b_A}.$$

Thus, the determinant of the invasion matrix can be recast into the much simpler form

$$\det \mathbf{M} = \frac{d_A}{b_A} (d_J - \beta c p_A^* + \mu) (b_A - b_{A'}).$$

For a mutant close to the resident, we therefore have

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

where $\Delta b_{A'} = b_{A'} - b_A$, which leads to the following expression for the selection gradient

$$\frac{\partial \lambda}{\partial c'} = \frac{d_A}{b_A} \frac{d_J - \beta c p_A^* + \mu}{d_A + d_J - \beta c p_A^* + \mu} \frac{\partial b_{A'}}{\partial c'} \quad (\text{A.2})$$

where the factor in front of the partial derivative is always positive for $\beta c < d_J$.

Appendix B. Spatial structure of the resident population at equilibrium

We will derive some useful equilibrium densities for the resident in the spatial model. From Eq. (5), we get

$$\frac{\mu}{d_A} = \frac{p_A^*}{p_J^*} = \frac{q_{A/J}^*}{q_{J/A}^*}. \quad (\text{B.1})$$

The dynamics of pairs AA is given by the following equation

$$\frac{dp_{AA}}{dt} = 2\mu p_{JA} - 2d_A p_{AA}.$$

At equilibrium, the right-hand side is zero, which leads

$$\frac{q_{A/A}^*}{q_{J/A}^*} = \frac{\mu}{d_A}. \quad (\text{B.2})$$

Equating Eqs. (B.1) and (B.2), we obtain the following condition

$$q_{A/A}^* = q_{A/J}^* = \frac{\mu}{d_A} q_{J/A}^*. \quad (\text{B.3})$$

Conservation requires that

$$q_{o/A}^* + q_{A/A}^* + q_{J/A}^* = 1.$$

Using Eq. (B.3), we can rewrite the latter equation as

$$q_{o/A}^* = 1 - \left(1 + \frac{d_A}{\mu}\right) q_{A/J}^*$$

and plug this into Eq. (5) in the main text to obtain

$$b_A \frac{\mu}{d_A} \left(1 - \left(1 + \frac{d_A}{\mu}\right) q_{A/J}^*\right) = (d_J + \mu - \beta c q_{A/J}^*). \quad (\text{B.4})$$

Solving Eq. (B.4) gives after some rearrangements

$$q_{A/J}^* = q_{A/A}^* = \frac{d_J + \mu - \mu b_A/d_A}{\beta c - b_A - \mu b_A/d_A} \quad (\text{B.5})$$

and

$$q_{o/A}^* = \frac{\beta c - (1 + d_A/\mu)(d_J + \mu)}{\beta c - b_A - \mu b_A/d_A}. \quad (\text{B.6})$$

Note that the right-hand side of Eq. (B.5) also gives the equilibrium density of adults in the non-spatial model.

Appendix C. Spatial invasion fitness in viscous populations

No class structure

The invasion dynamics of a mutant M described by a single state can be written in matrix form (van Baalen and Rand, 1998)

$$\frac{d\mathbf{p}_M}{dt} = \mathbf{M}(\mathbf{q}_M)\mathbf{p}_M$$

where \mathbf{p}_M is a vector of pair densities (p_{xM}) and \mathbf{q}_M is a vector of local densities ($q_{x/M}$). (In general, the matrix M will also depend on triple local densities, but this does not affect our conclusions.) By definition, we have

$$\mathbf{p}_M = p_M \mathbf{q}_M \quad (\text{C.1})$$

where p_M is the global density of the mutant. The mutant invasion dynamics quickly relax to a relaxation manifold on which $\mathbf{q}_M = \tilde{\mathbf{q}}$, where $\tilde{\mathbf{q}}$ is obtained as the solution of $d\mathbf{q}_M/dt = \mathbf{0}$. On this invasion manifold, the dynamics of M are linear

$$\frac{d\mathbf{p}_M}{dt} = \mathbf{M}(\tilde{\mathbf{q}})\mathbf{p}_M = \tilde{\mathbf{M}}\mathbf{p}_M.$$

Differentiation of Eq. (C.1) yields

$$\frac{d\mathbf{q}_M}{dt} = \mathbf{M}(\mathbf{q}_M)\mathbf{q}_M - \left(\frac{1}{p_M} \frac{dp_M}{dt}\right) \mathbf{q}_M$$

and we obtain

$$\tilde{\mathbf{M}}\tilde{\mathbf{q}} - \tilde{\lambda}\tilde{\mathbf{q}} = \mathbf{0}$$

where $\tilde{\lambda}$ is the per-capita growth rate $\frac{1}{p_M} \frac{dp_M}{dt}$ taken at $\mathbf{q}_M = \tilde{\mathbf{q}}$. Consequently

$$\frac{d\mathbf{p}_M}{dt} = \tilde{\mathbf{M}}\mathbf{p}_M = \tilde{\mathbf{M}}\mathbf{q}_M p_M = \tilde{\lambda}\mathbf{q}_M p_M = \tilde{\lambda}\mathbf{p}_M$$

and $\tilde{\lambda}$ is the long-term growth rate of the mutant when rare. More precisely, $\tilde{\lambda}$ is the dominant eigenvalue of $\tilde{\mathbf{M}}$, and $\tilde{\mathbf{q}}$ is an associated eigenvector that gives the local structure of the invading cluster.

Class structure

Let us now assume that we need several states to describe the invading mutant. For the sake of simplicity, we only address the case where two states M_1 and M_2 are required, but the result readily extends to the case where the mutant population consists of n classes. We introduce the vector \mathbf{p}_M as the vector

$$\mathbf{p}_M = \begin{pmatrix} p_{M_1} \\ p_{M_2} \end{pmatrix}$$

where $\mathbf{p}_{M_i} = (p_{xM_i})$. Likewise, we define

$$\mathbf{q}_M = \begin{pmatrix} q_{M_1} \\ q_{M_2} \end{pmatrix}, \quad \mathbf{P} = \begin{pmatrix} p_{M_1} \mathbf{I} & \mathbf{0} \\ \mathbf{0} & p_{M_2} \mathbf{I} \end{pmatrix}.$$

Consequently, we have $\mathbf{p}_M = \mathbf{P}\mathbf{q}_M$. The dynamics of invasion of (M_1, M_2) quickly relax to a relaxation manifold where $\mathbf{p}_M = \mathbf{P}\tilde{\mathbf{q}}$ where $\tilde{\mathbf{q}}$ is the solution of $d\mathbf{q}_M/dt = \mathbf{0}$. Note that

$$\frac{d\mathbf{q}_M}{dt} = \mathbf{P}^{-1} \frac{d\mathbf{p}_M}{dt} - \Lambda(\mathbf{q}_M)\mathbf{q}_M$$

where

$$\Lambda(\mathbf{q}_M) = \begin{pmatrix} \left(\frac{1}{p_{M_1}} \frac{dp_{M_1}}{dt}\right) \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \left(\frac{1}{p_{M_2}} \frac{dp_{M_2}}{dt}\right) \mathbf{I} \end{pmatrix}.$$

Then, because \mathbf{P} and $\Lambda(\mathbf{q}_M)$ commute

$$\frac{d\mathbf{q}_M}{dt} = \mathbf{0} \Leftrightarrow \frac{d\mathbf{p}_M}{dt} = \Lambda(\tilde{\mathbf{q}})\mathbf{p}_M.$$

Thus, on the relaxation manifold, the invasion dynamics are

$$\frac{d\mathbf{p}_M}{dt} = \tilde{\Lambda}\mathbf{p}_M.$$

However, because of the symmetric relationship $p_{M_1M_2} = p_{M_2M_1}$, we can obtain a stronger result. Let λ_1 and λ_2 be the per-capita growth rates of M_1 and M_2 respectively. We have

$$\frac{dq_{M_1/M_2}}{dt} = \frac{1}{p_{M_2}} \frac{dp_{M_1M_2}}{dt} - \lambda_2 q_{M_1/M_2}$$

and

$$\frac{dq_{M_2/M_1}}{dt} = \frac{1}{p_{M_1}} \frac{dp_{M_1M_2}}{dt} - \lambda_1 q_{M_2/M_1}.$$

On the relaxation manifold, the derivatives of the local densities vanish, and we have

$$\frac{dp_{M_1M_2}}{dt} = \lambda_2 p_{M_1M_2} = \lambda_1 p_{M_1M_2}.$$

Hence, on the relaxation manifold, $\lambda_1 = \lambda_2 = \tilde{\lambda}$ and we have finally very simple invasion dynamics

$$\frac{d\mathbf{p}_M}{dt} = \tilde{\lambda}\mathbf{p}_M.$$

Thus, in the case of a stage-structured mutant, we can equivalently define spatial invasion fitness as the per-capita growth rate of M_1 or M_2 on the relaxation manifold. Alternatively, $\tilde{\lambda}$ can be obtained as the solution of the following eigenvalue equation

$$\tilde{\mathbf{M}}\mathbf{p}_M = \tilde{\lambda}\mathbf{p}_M.$$

A normalised eigenvector associated with $\tilde{\lambda}$ is given by

$$\tilde{\mathbf{u}} = \tilde{w}_1 \begin{pmatrix} \tilde{\mathbf{q}}_{M_1} \\ \mathbf{0} \end{pmatrix} + \tilde{w}_2 \begin{pmatrix} \mathbf{0} \\ \tilde{\mathbf{q}}_{M_2} \end{pmatrix}$$

where w_1 (resp. w_2) gives the proportion of mutants of class 1 (resp. class 2) in the mutant subpopulation, and \tilde{w}_1 and \tilde{w}_2 are the corresponding values on the relaxation manifold. Because $p_{M_1M_2} = q_{M_1/M_2} p_{M_2} = q_{M_2/M_1} p_{M_1}$, it follows that

$$w_1 = \frac{p_{M_1}}{p_{M_1} + p_{M_2}} = \frac{q_{M_1/M_2}}{q_{M_1/M_2} + q_{M_2/M_1}}$$

and a similar expression for $w_2 = 1 - w_1$ is obtained by permuting 1 and 2.

Appendix D. Selection gradient in the spatial model

Our starting point is Eq. (10):

$$\lambda = b_{A'} \tilde{q}_{o/A'} \frac{\mu'}{d_{A'} + \lambda} - (d_{J'} + \mu' - \beta c \tilde{q}_{A/J'} - \beta c' \tilde{q}_{A'/J'}).$$

Now, because the resident fitness is zero, we have

$$0 = b_A q_{o/A} \frac{\mu}{d_A} - (d_J + \mu - \beta c q_{A/J}^* - \beta c' q_{A'/J}^*).$$

We assume a trade-off between adult reproduction and adult investment, and that all other demographic rates are equal. Therefore, subtracting the last two equations, we obtain

$$\lambda = b_{A'} \tilde{q}_{o/A'} \frac{\mu}{d_A + \lambda} - b_A q_{o/A} \frac{\mu}{d_A} + \beta (c \tilde{q}_{A/J'} + c' \tilde{q}_{A'/J'} - c q_{A/J}^*).$$

Under the assumption that the mutant is close to the resident ($c' = c + \partial c$), $\lambda = \partial \lambda$ is close to zero. Invasion statistics $\tilde{q}_{o/A'}$, $\tilde{q}_{A/J'}$ and $\tilde{q}_{A'/J'}$ can be Taylor-expanded as follows

$$\tilde{q}_{o/A'} = q_{o/A}^* + \partial \tilde{q}_{o/A'}$$

$$\tilde{q}_{A/J'} = \bar{q}_{A/J'} + \partial \tilde{q}_{A/J'}$$

$$\tilde{q}_{A'/J'} = \bar{q}_{A'/J'} + \partial \tilde{q}_{A'/J'}$$

where the bar symbol denotes the local densities of a neutral mutant, identical to the resident, as explained in the main text. Using the fact that $\bar{q}_{A/J'} + \bar{q}_{A'/J'} = q_{A/J}^*$, we obtain after some rearrangements

$$\begin{aligned} \left(1 + b_A \frac{\mu}{d_A} q_{o/A}^*\right) \frac{\partial \lambda}{\partial c'} &= \beta \bar{q}_{A'/J'} + \frac{\mu}{d_A} q_{o/A}^* \frac{\partial b_A}{\partial c'} + \frac{\mu b_A}{d_A} \frac{\partial \tilde{q}_{o/A'}}{\partial c'} \\ &+ \beta c \left(\frac{\partial \tilde{q}_{A/J'}}{\partial c'} + \frac{\partial \tilde{q}_{A'/J'}}{\partial c'} \right). \end{aligned} \quad (\text{D.1})$$

Appendix E. The structure of the invading cluster for a neutral mutant

In this appendix, we derive an explicit solution for the local density $\tilde{q}_{J'/A'}$ of a neutral mutant. The fitness of a neutral mutant being zero, $\tilde{q}_{A'/J'}$ can be obtained as the solution of the system

$$\frac{d\mathbf{p}}{dt} = \mathbf{0}$$

where \mathbf{p} is a vector of mutant pair densities.

For the system we consider, an analytical solution can be found. We have

$$\begin{aligned} \frac{dp_{J'J'}}{dt} &= 2(\bar{\phi} b_{A'} q_{A'/oJ'}) p_{oJ'} \\ &- 2(\mu + d_{J'} - \bar{\phi} \beta c q_{A/J'} - \bar{\phi} \beta c' q_{A'/J'}) p_{J'J'} \end{aligned}$$

$$\begin{aligned} \frac{dp_{J'A'}}{dt} &= (\phi b_{A'} + \bar{\phi} b_{A'} q_{A'/oA'}) p_{oA'} + \mu p_{J'J'} \\ &- (d_{J'} + \mu + d_{A'} - \phi \beta c - \bar{\phi} \beta c q_{A/J'} - \bar{\phi} \beta c' q_{A'/J'}) p_{J'A'}. \end{aligned}$$

For a rare neutral mutant, we obtain, because for $\tilde{q}_{o/A'} \approx q_{o/A}^*$ and $\tilde{q}_{o/J'A'} \approx q_{o/JA}^*$

$$\begin{aligned} 0 &= (\bar{\phi} b_{A'} \bar{q}_{A'/oJ'}) p_{oJ'} - (\mu + d_{J'} - \bar{\phi} \beta c (\tilde{q}_{A/J'} + \tilde{q}_{A'/J'})) p_{J'J'} \\ 0 &= (\phi b_{A'} + \bar{\phi} b_{A'} \bar{q}_{A'/oA'}) p_{oA'} + \mu p_{J'J'} \\ &- (d_{J'} + \mu + d_{A'} - \phi \beta c - \bar{\phi} \beta c (\bar{q}_{A/J'} + \bar{q}_{A'/J'})) p_{J'A'}. \end{aligned}$$

Because $\bar{q}_{A/J'} + \bar{q}_{A'/J'} = q_{A/J}^*$, the first equation yields

$$\tilde{q}_{J'/J'} = \frac{\bar{\phi} b_{A'} \bar{q}_{A'/oJ'} \bar{q}_{o/J'}}{\mu + d_{J'} - \bar{\phi} \beta c q_{A/J}^*}$$

and we can use this in the second equation to find, after dividing by $p_{A'}$ and using $\bar{q}_{A/J'} + \bar{q}_{A'/J'} = q_{A/J}^*$,

$$\begin{aligned} (\phi b_{A'} + \bar{\phi} b_{A'} \bar{q}_{A'/oA'}) \bar{q}_{o/A'} + d_A \frac{\bar{\phi} b_{A'} \bar{q}_{A'/oJ'} \bar{q}_{o/J'}}{\mu + d_{J'} - \bar{\phi} \beta c q_{A/J}^*} \\ - (d_{J'} + \mu + d_{A'} - \phi \beta c - \bar{\phi} \beta c q_{A/J}^*) \tilde{q}_{J'/A'} = 0 \end{aligned}$$

which finally leads to

$$\tilde{q}_{J'/A'} = \frac{(\phi + \bar{\phi} \bar{q}_{A'/oA'}) b_A q_{o/A}^* + \frac{d_A}{\mu + d_{J'} - \bar{\phi} \beta c q_{A/J}^*} \bar{\phi} b_{A'} \bar{q}_{A'/oJ'} \bar{q}_{o/J}^*}{\mu + d_{J'} + d_A - \beta c (\phi + \bar{\phi} q_{A/J}^*)}.$$

Extensive numerical simulations indicate that it is safe to neglect $\tilde{q}_{A'/oJ'}$. This allows one to simplify the expression into

$$\tilde{q}_{J'/A'} = \frac{(\phi + \bar{\phi} \bar{q}_{A'/oA'}) b_A q_{o/A}^*}{\mu + d_{J'} + d_A - \beta c (\phi + \bar{\phi} q_{A/J}^*)}.$$

If we neglect also $\bar{q}_{A'/oA'}$, we recover Eq. (12), but we discuss in the main text why this would lead to a bias in the estimate of $\bar{q}_{i/A'}$. Finally, under ordinary pair approximation ($q_{i/jk} \approx q_{i/j}$) and in the limit of low investment, we can use the results of Appendix B to find Eq. (13).

References

- Boerlijst, M.C., Lamers, M.E., Hogeweg, P., 1993. Evolutionary consequences of spiral waves in a Host–Parasitoid system. *Proceedings of the Royal Society of London B* 253, 15–18.
- Bolker, B., Pacala, S.W., 1997. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theoretical Population Biology* 52, 179–197.
- Boots, M., Sasaki, A., 1999. 'Small worlds' and the evolution of virulence: Infection occurs locally and at a distance. *Proceedings of the Royal Society of London B* 266, 1933–1938.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, Mass.
- de Mazancourt, C., Dieckmann, U., 2004. Trade-off geometries and frequency-dependent selection. *American Naturalist* 164, 765–778.
- de Roos, A.M., McCauley, E., Wilson, W.G., 1998. Pattern formation and the spatial scale of interaction between predators and their prey. *Theoretical Population Biology* 53 (2), 108–130.
- Dieckmann, U., Law, R., 2000. Relaxation projections and the method of moments. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), *Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press, pp. 412–455.
- Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), 2000. *Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press.
- Doebeli, M., Hauert, C., 2005. Models of cooperation based on the prisoner's dilemma and the snowdrift game. *Ecology Letters* 8, 748–766.
- Durrett, R., Levin, S.A., 1994a. Stochastic spatial models — a user's guide to ecological applications. *Philosophical Transactions of the Royal Society B* 343 (1305), 329–350.
- Durrett, R., Levin, S.A., 1994b. The importance of being discrete (and spatial). *Theoretical Population Biology* 46, 363–394.
- Eshel, I., 1983. Evolutionary and continuous stability. *Journal of Theoretical Biology* 103, 99–111.
- Fife, P., 1979. Mathematical aspects of reacting–diffusing systems. In: *Lecture Notes on Biomathematics*, vol. 28. Springer.
- Ferrière, R., Le Galliard, J.F., 2001. Invasion fitness and adaptive dynamics in spatial population models. In: Clobert, J., Dhondt, A., Danchin, E., Nichols, J. (Eds.), *Dispersal*. Oxford University Press, pp. 57–79.
- Le Galliard, J.-F., Ferrière, R., Dieckmann, U., 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* 57 (1), 1–17.
- Le Galliard, J.-F., Ferrière, R., Dieckmann, U., 2005. Adaptive evolution of social traits: Origin, trajectories, and correlations of altruism and mobility. *American Naturalist* 165 (2), 206–224.
- Genkai-Kato, M., Yamamura, N., 1999. Evolution of mutualistic symbiosis without vertical transmission. *Theoretical Population Biology* 55 (3), 309–323.
- Geritz, S.A.H., Kisdi, É., Meszéna, G., Metz, J.A.J., 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary ecology* 12, 35–57.
- Hanski, I., Gilpin, M.E. (Eds.), 1997. *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press.
- Harada, Y., Ezoe, H., Iwasa, Y., Matsuda, H., Sato, K., 1995. Population persistence and spatially limited social interaction. *Theoretical Population Biology* 48, 65–91.
- Hassell, M., Comins, H.N., May, R.M., 1991. Spatial structure and chaos in insect population dynamics. *Nature* 6341 (255–258).
- Hassell, M., Comins, H.N., May, R.M., 1994. Species coexistence and self-organizing spatial dynamics. *Nature* 370 (6487), 290–292.
- Hauert, C., 2006. Spatial effects in social dilemmas. *Journal of Theoretical Biology* 240 (4), 627–636.
- Hogeweg, P., 1989. Simplicity and complexity in mirror universes. *Biosystems* 23, 231–246.
- Iwasa, Y., Nakamaru, M., Levin, S.A., 1998. Allelopathy of bacteria in a lattice population: Competition between colicin-sensitive and colicin-producing strains. *Evolutionary Ecology* 12, 785–802.
- Kamo, M., Sasaki, A., Boots, M., 2007. The role of trade-off shapes in the evolution of parasites in spatial host populations: An approximate analytical approach. *Journal of Theoretical Biology* 244, 588–596.
- Kauffman, S.A., 1993. *The Origins of Order*. Oxford University Press, New-York.
- Keeling, M.J., 1999. The effects of local spatial structure on epidemiological invasions. *Proceedings of the Royal Society London B* 266, 859–867.
- Keeling, M.J., 2005. The implications of network structure for epidemic dynamics. *Theoretical Population Biology* 67, 1–8.
- Keeling, M.J., Rand, D.A., 1995. A spatial mechanism for the evolution and maintenance of sexual reproduction. *Oikos* 74, 414–424.
- Kisdi, É., 2006. Trade-off geometries and the adaptive dynamics of two co-evolving species. *Evolutionary Ecology Research* 8, 959–973.
- Law, R., Murrell, D.J., Dieckmann, U., 2003. Population growth in space and time: Spatial logistic equations. *Ecology* 84 (1), 252–262.
- Lion, S., Relatedness in spatially structured populations with empty sites: An approach based on spatial moment equations, *Journal of theoretical Biology* (in press).
- Lion, S., Gandon, S., 2009. Habitat saturation and the spatial evolutionary ecology of altruism. *Journal of Evolutionary Biology* 22, 1487–1502.
- Lion, S., van Baalen, M., 2007. From infanticide to parental care: Why spatial structure can help adults be good parents. *American Naturalist* 170 (2), E26–E46.
- Lion, S., van Baalen, M., 2008. Self-structuring in spatial evolutionary ecology. *Ecology Letters* 11 (3), 277–295.
- Mágori, K., Szabó, P., Mizera, F., Meszéna, G., 2005. Adaptive dynamics on a lattice: Role of spatiality in competition, co-existence and evolutionary branching. *Evolutionary Ecology Research* 7, 1–21.
- Malécot, G., 1975. Heterozygosity and relationship in regularly subdivided populations. *Theoretical Population Biology* 8, 212–241.
- Matsuda, H., Ogita, N., Sasaki, A., Sato, K., 1992. Statistical-mechanics of population — the lattice Lotka–Volterra model. *Progress in Theoretical Physics* 88, 1035–1049.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press.
- Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A., van Heerwaarden, J.S., 1996. Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn–Lunel, S.M. (Eds.), *Stochastic and Spatial Structures of Dynamical Systems*. Elsevier, North–Holland, pp. 183–231.
- Metz, J.A.J., Gyllenberg, M., 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proceedings of the Royal Society of London B* 268, 499–508.
- Metz, J.A.J., Nisbet, R.M., Geritz, S.A.H., 1992. How should we define fitness for general ecological scenarios. *Trends in Ecology Evolution* 7, 198–202.
- Morris, A.J., 1997. Representing spatial interactions in simple ecological models. Ph.D. Thesis. University of Warwick.
- Murrell, D.J., Dieckmann, U., Law, R., 2004. On moment closures for population dynamics in continuous space. *Journal of Theoretical Biology* 229 (3), 421–432.
- Neubert, M.G., Caswell, H., 2000. Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* 81 (6), 1613–1628.
- Nowak, M.A., 2006. Five rules for the evolution of cooperation. *Science* 314, 1560–1563.
- Ovaskainen, O., Cornell, S.J., 2006. Asymptotically exact analysis of stochastic metapopulation dynamics with explicit spatial structure. *Theoretical Population Biology* 69 (1), 13–33.
- Petermann, T., De Los Rios, P., 2004. Cluster approximations for epidemic processes: A systematic description of correlations beyond the pair level. *Journal of Theoretical Biology* 229, 1–11.
- Proulx, S.R., Day, T., 2001. What can invasion analyses tell us about evolution under stochasticity in finite populations? *Selection* 2 (2), 1–15.
- Rand, D.A., 1999. Correlation equations and pair approximation for spatial ecologies. In: McGlade, J. (Ed.), *Advanced Ecological Theory*. Oxford: Blackwell, pp. 100–142.
- Rand, D.A., Keeling, M., Wilson, H.B., 1995. Invasion, stability and evolution to criticality in spatially extended, artificial host–pathogen ecologies. *Proceedings of the Royal Society of London B* 259, 55–63.
- Read, J.M., Keeling, M.J., 2002. Disease evolution on networks: The role of contact structure. *Proceedings of the Royal Society of London B* 270, 699–798.
- Real, L.A., McElhany, P., 1996. Spatial pattern and process in plant–pathogen interactions. *Ecology* 77 (4), 1011–1025.
- Rousset, F., 2004. *Genetic Structure and Selection in Subdivided Populations*. Princeton University Press.
- Rousset, F., 2006. Separation of time scales, fixation probabilities and convergence to evolutionarily stable states under isolation by distance. *Theoretical Population Biology* 69 (2), 165–179.
- Sato, K., Matsuda, H., Sasaki, A., 1994. Pathogen invasion and host extinction in lattice structured populations. *Journal of Mathematical Biology* 32, 251–268.
- Skellam, J., 1951. Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Stollenwerk, N., 2005. Criticality in epidemics: The mathematics of sandpiles explains uncertainty in epidemic outbreaks. In: Baeza–Yates, R., Glaz, J., Gzyl, H., Huesler, J., Palacios, J.L. (Eds.), *Recent Advances in Applied Probability*. Kluwer Academic Publishers, Boston, MA, pp. 455–494.
- Szabó, G., Fáth, G., 2007. Evolutionary games on graphs. *Physics Reports* 446, 97–216.
- Tilman, D., Kareiva, P. (Eds.), 1997. *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press.
- van Baalen, M., 2000. Pair approximation for different spatial geometries. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press, pp. 359–387.
- van Baalen, M., 2002. Contact networks and the evolution of virulence. In: Dieckmann, U., Metz, J.A.J., Sabelis, M.W., Sigmund, K. (Eds.), *Adaptive Dynamics of Infectious Diseases. In Pursuit of Virulence Management*. Cambridge University Press, pp. 85–103.
- van Baalen, M., Rand, D.A., 1998. The unit of selection in viscous populations and the evolution of altruism. *Journal of Theoretical Biology* 193, 631–648.
- van Ballegoijen, W.M., Boerlijst, M.C., 2004. Emergent trade-offs and selection for outbreak frequency in spatial epidemics. *Proceedings of the National Academy of Sciences* 101, 18246–18250.
- Wilson, W.G., 1998. Resolving discrepancies between deterministic population models and individual-based simulations. *American Naturalist* 151, 116–134.