

REVIEW AND SYNTHESIS

Self-structuring in spatial evolutionary ecology

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Abstract

Spatial self-structuring has been a focus of recent interest among evolutionary ecologists. We review recent developments in the study of the interplay between spatial self-structuring and evolution. We first discuss the relative merits of the various theoretical approaches to spatial modelling in ecology. Second, we synthesize the main theoretical studies of the evolution of cooperation in spatially structured populations. We show that population viscosity is generally beneficial to cooperation, because cooperators can reap additional benefits from being clustered. A similar mechanism can explain the evolution of honest communication and of reduced virulence in host–parasite interactions. We also discuss some recent innovative empirical results that test these theories. Third, we show the relevance of these results to the general field of evolutionary ecology. An important conclusion is that kin selection is the main process that drives evolution of cooperation in viscous populations. Many results of kin selection theory can be recovered as emergent properties of spatial ecological dynamics. We discuss the implications of these results for the study of multilevel selection and evolutionary transitions. We conclude by sketching some perspectives for future research, with a particular emphasis on the topics of evolutionary branching, criticality, spatial fluctuations and experimental tests of theoretical predictions.

Space is the place – Sun Ra

Keywords

Cooperation, kin selection, levels of selection, spatial structure, virulence, viscous population.

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INTRODUCTION

Most theories in ecology, and in evolutionary ecology, either do not consider space at all (effectively assuming that individuals encounter each other randomly) or suppose that populations face some form or other of underlying environmental heterogeneity. However, it is becoming increasingly clear that spatial or social structure can emerge spontaneously as a consequence of interactions between individuals. Spatial self-structuring has become a focus of interest for ecologists, fuelling both ecological and evolutionary lines of questioning. The purpose of this review was to tie together the ecological and evolutionary research on spatial self-structuring by examining what the latest spatially explicit ecological models have taught us about evolution.

Two independent papers illustrate the essential aspects of the developments we review in this article. A first groundbreaking contribution was published by Boerlijst & Hogeweg (1991). It has been suggested that hypercycles, self-replicating molecules cyclically linked by catalysis, have

played a pivotal role in the emergence of life, but Maynard Smith (1979) showed that they collapse when exploited by parasites. Boerlijst & Hogeweg (1991) demonstrated that, when placed in a spatial setting, hypercycles form rotating spiral structures that protect them against ‘selfish’ molecules that give no catalytic support, but receive catalytic support from other molecules. In other words, spatial self-structuring changes the evolutionary outcome, and leads to selection of ‘altruistic’ traits. The results are best understood by observing that selection acts ‘at the level of the spiral’.

Another important insight was generated by Durrett & Levin’s (1994a) comparative study of different methods for modelling spatial structure, in which they introduce interacting particle systems (a theoretical approach originally developed for statistical physics) as a formalism that captures essential features of both patch models and reaction-diffusion equations. Comparing the different approaches, they note that different spatial models can lead to radically different predictions about the ecological dynamics of a population, and make the important point

that spatial models must take into account individuality, and the associated demographic stochasticity. This has led to a radical transformation of the field of spatial ecology over the last two decades. Combined with the advent of modern computing facilities, this conceptual breakthrough has fuelled much interest in the analysis of stochastic, individual-based spatial ecological models.

Though both articles have space and individuality as essential ingredients, they are very different in scope and style. While the latter focuses on the consequences of individuality for ecological dynamics, the first paper stresses the evolutionary consequences of the multilevel selection that may result. As we will discuss in some detail, these two approaches have merged as new ecological models with both spatial structure and individuality have been used to address evolutionary questions. Our aim in this study was to review what models of the ecological process of spatial self-structuring have taught us about the feedback loop between ecology and evolution. We show that individuality and multilevel selection are essential to understand evolution in spatially structured populations, as highlighted by these seminal papers.

We begin by reviewing the various theoretical approaches to spatial ecological modelling, and discuss their implications in an evolutionary context. We then summarize the main results achieved by merging spatial ecology and evolution, with a special emphasis on the evolution of cooperation, as the significance of the new approach is most apparent there. We discuss these results in the light of kin, group and multilevel selection, and sketch some perspectives for future empirical and theoretical work.

SETTING THE STAGE

Spatial models in ecology

Theoretical ecologists have been using many different approaches to model the dynamics of spatially structured populations (Tilman & Kareiva 1997; Dieckmann *et al.* 2000). The classical modelling approaches are reaction-diffusion models and patch-structured models (metapopulations, coupled-map lattices and deme-structured populations). The advantage of these approaches is that they are amenable to mathematical analysis, but this sometimes comes at the expense of various simplifying assumptions that limit their applicability, in particular in evolutionary contexts.

More recently, the advent of modern computing facilities has encouraged ecologists to turn to individual-based spatial simulations, such as Multi-Agent Systems (MAS; Gotts *et al.* 2003) and Probabilistic Cellular Automata (PCA; Durrett & Levin 1994a,b). In PCA, space is represented by a network of sites, and the state of the network is updated through probabilistic rules representing stochastic demographic

events (birth, death, movement, etc.). In spatial MAS, individuals are typically represented as computer program entities (memory structures) that move as points across a continuous space (though lattices are also often used; Grim *et al.* 1999; Gotts *et al.* 2003). As yet, this technique has not often been applied to evolutionary problems (but see Grim *et al.* 1999) and we will focus on the PCA approach. To get analytical insight into the results of stochastic simulations, new modelling approaches have been developed, such as spatial moment analysis for PCA (Matsuda *et al.* 1992; Rand 1999; van Baalen 2000) and point processes analysis (Bolker & Pacala 1997, 1999; Fournier & Méléard 2004).

Spatial models in evolution

All these spatial ecological models make different assumptions with respect to time and space (continuous vs. discrete), the volume of individuals, dispersal and, most importantly for our purpose, individuality. Models that do not take fully into account the discreteness of individuals (Box 1) allow for the existence of so-called 'nano-individuals' that can diffuse into the entire space domain, irrespective of the selective pressures (the 'atto-fox' problem; Mollison 1991). We argue that spatial ecological models that preserve individuality (Box 2) are best suited to yield valuable insight on the selective pressures generated by spatial self-structuring. As this review will be slightly biased towards PCA, we also provide an additional toolbox to give the reader some details about the analysis of these models (Box 3).

Spatial self-structuring vs. spatial heterogeneity

Spatial structure can be the result of two distinct processes (Fig. 1). First, it can result from externally imposed constraints, such as heterogeneity in resource distribution, physical barriers, alternation of habitats of different quality, spatial variation in physical characteristics (humidity, temperature and salinity). Second, it can emerge from intrinsic ecological dynamics in an otherwise homogeneous environment. In this review, we focus on the evolutionary consequences of such spatial self-structuring, and do not address the question of spatial heterogeneity resulting from external variations of the environment.

The feedback loop between ecology and evolution

Spatial self-structuring is likely to play an important role in the feedback loop between ecology and evolution. Because the behaviour of individuals affects their local environment, the local structure of an individual's environment depends on the traits of this individual. In turn, the environment imposes selective pressures on the individuals that affect the evolution of the trait. Models that study the interplay of

Box 1 Models without individuality**Mean-field models**

The easiest approach to modelling spatial structure is to ignore it. Classical ecological models consider that populations are well mixed (individuals move very fast and can interact with any individual in the population). Then, only one variable $n(t)$ is needed to describe the dynamics of a single, unstructured population.

Metapopulations and coupled-map lattices

Classical models of metapopulations represent space implicitly by assuming that the population is distributed over patches that are coupled by migratory fluxes (Hanski & Gilpin 1997). Coupled-map lattices represent an extension in which patches occupy the nodes of a network. In each patch, the local dynamics of the subpopulation has a reaction term derived from the mean-field model, and a coupling term that accounts for emigration to and immigration from neighbouring patches. Coupled-map lattices are usually treated in discrete time. Individuality is not preserved in this approach, as each site can contain a continuous number of individuals.

Reaction-diffusion models

In these spatial models (Fife 1979), space is represented explicitly as a continuous arena. The population density is measured at location \mathbf{x} (where \mathbf{x} is a vector of coordinates) and time t . To describe the dynamics of the density $n(\mathbf{x}, t)$, partial differential equations (or more generally integro-differential equations) are needed. The time evolution of $n(\mathbf{x}, t)$ has two components. The reaction term is derived from the mean-field model and describes the local dynamics of the population at \mathbf{x} . The diffusion term represents the migration or spread of the population at \mathbf{x} to nearby locations. Reaction-diffusion models give rise to interesting wave-like phenomena and spatial pattern formation. From an evolutionary perspective, however, they lack individuality. Locally, population density is a continuous variable, so that these models allow for the existence of 'nano-individuals' that can diffuse into the entire spatial domain.

spatial ecological dynamics and evolution may help to shed some light on the feedback loop between ecology and evolution.

Maybe the most obvious way to understand the feedback loop between ecology and evolution is to think about dispersal. In a temporally constant environment, dispersal can be beneficial because it decreases competition and inbreeding. On the other hand, dispersal is also a costly behaviour, because it can increase the mortality of dispersers or decrease their fecundity if they land on bad habitats. If the local habitat is saturated, individuals may then benefit

Box 2 Models with individuality**Patch models with individuality**

A further extension of the metapopulation framework makes the more realistic assumption that each site can only be occupied by a discrete number of individuals (0, 1, 2, ...; Metz & Gyllenberg 2001; Cadet *et al.* 2003). Deme-structured models represent a related approach in which the number of individuals per patch (or deme) is often assumed to be fixed [see Rousset (2004) for a synthesis].

Moment or correlation equations

In the last 20 years, statistical physics has inspired new modelling techniques to ecologists (Dieckmann *et al.* 2000). In these approaches, individuality is preserved and space is considered explicitly, either as a continuous arena, or as a network of sites. These models give a deterministic analytical representation of individual-based spatial models.

Discrete space

Lattice models are PCA: space is represented by a network of sites, each site can be empty or occupied by usually at most one individual, and transitions from one state to another are stochastic. Various spatial moments can be computed, such as the expected density p_i of sites in state i , the expected density p_{ij} of pairs of sites in state $i-j$, or the expected density p_{ijk} of triplets. From these global densities, we can compute local densities, such as $q_{i|j} = p_{ij}/p_j$ which gives the expected number of i individuals around a j individual. The dynamics of the first-order moment p_i will then depends on second-order moments such as p_{ij} and in turn, the dynamics of p_{ij} will be a function of higher-order moments, which yields an infinite system of ordinary differential equations.

Continuous space

In *spatial point processes*, discrete individuals are represented by a Dirac function $\delta(x)$ (which takes a non-zero value only at location x). As in the discrete case, spatial moments can be computed, such as spatial mean values and spatial covariances between two locations. These models lead to an infinite system of integro-differential equations, and are well suited to compare theoretical predictions to empirical data. However, until now, the use of spatial point processes in evolutionary ecology has been limited, due to some mathematical difficulties, in particular in the derivation of invasion conditions.

from investing into dispersal strategies. Thus, ecological processes (habitat saturation) result in selection for increased dispersal. However, increasing dispersal will decrease habitat saturation, and thus modify ecological conditions. In turn, low habitat saturation may select for

Box 3 Analysing lattice models**Simulations**

Stochastic simulations are a natural way to analyse PCA such as lattice models. However, as individuality (and thus stochasticity) is preserved, the computation time is proportional to the size of the lattice and may be prohibitive. Another important drawback of simulations of spatial models is that they yield results that tend to be difficult to analyse and generalize. This problem calls for more analytical approaches such as moment equations.

Moment closure approximations

Moment equations are based on the notion that one can describe the state of a population by an infinite hierarchy of spatial moments (Box 2). Moment closure approximations (MCA) allow one to obtain a closed system, typically by approximating third- and higher-order moments in terms of second- and first-order moments only. This method is called 'pair approximation' in lattice models (Matsuda *et al.* 1992; Rand 1999; van Baalen 2000). Of course, MCA introduce errors in the description of spatial dynamics, but despite this, they give some welcome insight. Note however that MCA are not always needed. Especially in an evolutionary context, much analytical insight can be gained by using the unclosed equations for the expected densities of individuals, and MCA may only be needed to get quantitative results (Lion & van Baalen 2007).

Birth-death process on a lattice

Consider a lattice where each site can be either empty (\emptyset) or occupied by an individual (\times). Individuals can reproduce to an empty neighbouring site at rate b , or die at rate d . The dynamics of the expected density of individuals is (Matsuda *et al.* 1992):

$$\frac{dp_{\times}}{dt} = (bq_{\emptyset/\times} - d)p_{\times} \quad (a)$$

This equation is exact, in the sense that no MCA is needed in the derivation. However, the dynamics of the local density $q_{\emptyset/\times}$ depend on higher-order moments. By writing an equation for the dynamics of $q_{\emptyset/\times}$ and $q_{\times/\times}$, and using an appropriate MCA, one can obtain a deterministic approximation of the spatial birth-death process.

The mean-field approximation

From eqn a, a closed system can be obtained by making a first-order MCA $q_{\emptyset/\times} \approx p_{\emptyset} = 1 - p_{\times}$, which yields

$$\frac{dp_{\times}}{dt} = (b(1 - p_{\times}) - d)p_{\times} \quad (b)$$

which is the logistic equation. The first-order MCA is also termed the mean-field approximation, and is expected to describe the dynamics of well-mixed populations. It is actually the hidden assumption behind classical models of non-spatial population dynamics.

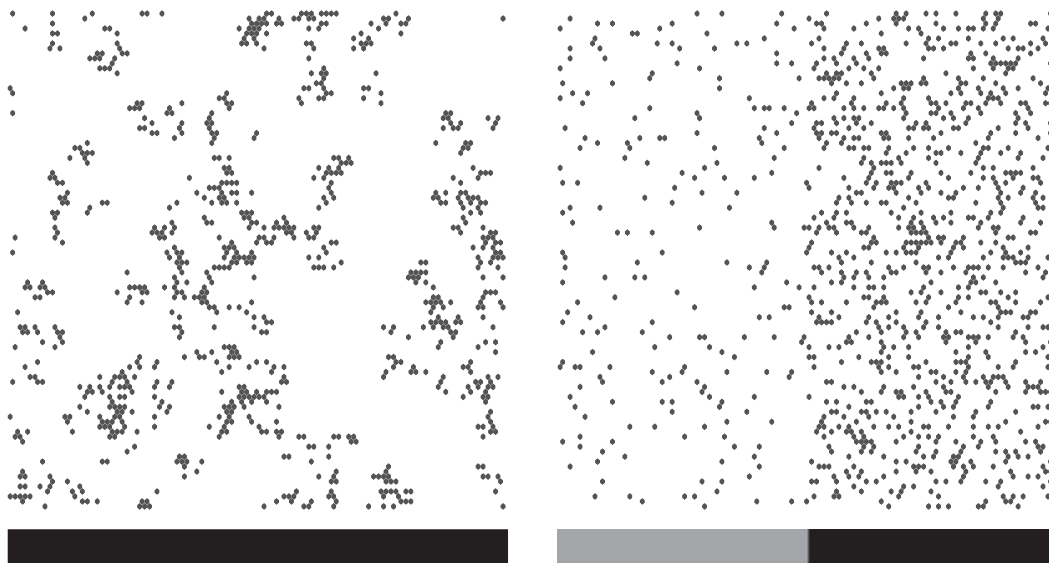


Figure 1 Spatial self-structuring vs. spatial heterogeneity. Left: typical snapshot of a spatial birth-death process on a lattice with local dispersal, and a local Allee effect (to make spatial structure more apparent). Right: typical snapshot of a birth-death process on a lattice with global dispersal and a lower probability of establishment in the left-hand region of the lattice. In this case, spatial structure is created by environmental conditions.

lower dispersal rates. To gain insight into the potential evolutionary outcomes, it is necessary to model in detail the interplay between ecological and evolutionary dynamics. In the next section, we will review what such detailed ecological modelling has taught us about the interplay of ecological processes and selective pressures.

SPACE AND THE FEEDBACK LOOP BETWEEN ECOLOGY AND EVOLUTION

In this section, we focus on the evolution of cooperation, and address in turn several topics (altruism and other social dilemmas, communication and parasite virulence). Our aim was to highlight their most salient contributions to our understanding of the role of spatial ecological processes in evolution.

Altruism and the role of local population regulation

The evolution of altruism is a fundamental puzzle in the Darwinian theory of evolution: because a selfish individual can benefit from altruistic behaviours without paying the cost, altruism should be counter-selected under strict individual selection in the absence of mechanisms counter-balancing the fitness cost of altruism. Ever since Hamilton (1964) conjectured that cooperation should evolve more readily in viscous populations (e.g. population with limited dispersal), many theoretical studies have used spatial models to investigate the evolution of altruism.

Hamilton's verbal argument was at first dismissed by theoretical studies which stressed that the accrued benefits reaped through local interactions can be nullified by the increased local competition due to spatial clustering (Wilson 1977; Michod 1982; Wilson *et al.* 1992). In the wake of these studies, several authors have developed patch-structured models to investigate the effect of population viscosity on the evolution of altruism.

The scale of cooperation and competition

In a patch model with constant patch size and non-overlapping generations, Taylor (1992a) found that the selective force on altruism is the same as in the well-mixed population. The general interpretation is that, for altruism to evolve, an altruistic group must be able to export altruists into neighbouring groups (Grafen 1984; Wilson *et al.* 1992), i.e. the population must be elastic. This is the case for instance if patches can be empty (Taylor 1992b). Kelly (1992, 1994) have generalized these models to allow for density regulation and mating to take place over distinct spatial scales, and argue that Taylor's (1992b) conclusions hold more generally whenever regulation operates at a larger spatial scale than mating. Thus, the appropriate scale at which to study the evolution of altruism in spatially

structured populations is the 'regulation scale' [e.g. the 'dispersal neighbourhood' of Wilson *et al.* (1992) and the 'economic neighbourhood' of Queller (1994)]. West *et al.* (2002) have reviewed these studies and concluded that the crucial point for the evolution of altruism in viscous populations is that competition must occur more globally among the whole population than cooperation. As we will discuss below, this effect can be rather subtle.

Demographic stochasticity and habitat saturation

Later on, studies have started investigating the evolution of altruism using stochastic, individual-based, continuous-time models, and have achieved seemingly different results. Following the seminal paper of Matsuda *et al.* (1992), van Baalen & Rand (1998) used moment equations to show that altruism can evolve in a spatially structured population if the aggregation of altruists is sufficient to outweigh the costs of altruism. When population viscosity decreases (for instance if migration increases), the clustering of altruists decreases and eventually vanishes in the limit of a well-mixed population. The same holds when the size of the interaction neighbourhood is increased (so that in the limit of a very large neighbourhood, the mean-field limit is recovered), a result that was also attained by Ifti *et al.* (2004) using a model without demographic stochasticity. In a systematic investigation of the joint evolution of altruism and mobility, Le Galliard *et al.* (2003, 2005) further show that strict selfishness is maintained only under very restricted conditions, and point out that local clustering and habitat saturation are the key mediators of the evolution of altruism and mobility. Because empty sites are available for the spread of altruists, the selective pressure generated by competition for space may become negligible [but see Lion & van Baalen (2007)].

These studies show that population regulation (resulting from competition for space or other forms of density dependence) is a crucial ecological factor mediating the evolution of altruism. The key issue is habitat saturation, which measures the strength of competition on altruists. Depending on the form of density dependence, local competition need not be detrimental to altruists in viscous population.

Social dilemmas and the role of network interactions

Implicit in these models is the fact that interactions between individuals take the form of a continuous Prisoner's Dilemma (PD) game, in which the intensity of cooperation can vary continuously. Other models have more explicitly analysed spatial games as an ecological framework for social dilemmas (including altruism). Spatial evolutionary game theory can be traced back to Axelrod (1984) and include works by Nowak & May (1992), Killingback & Doebeli (1996) and Killingback *et al.* (1999). The distinctive feature

of these studies is that they rely on a deterministic synchronous updating [but see Nowak *et al.* (1994) and Killingback *et al.* (1999)], and, most important, assume a constant population size. The Iterated PD was studied by Nakamaru *et al.* (1997), who showed that ‘tit-for-tat’ players form clusters that make it easier for the tit-for-tat strategy to spread in a selfish population of ‘always-defect’ player, thus allowing the emergence of cooperation [see also Ferrière & Michod (1995)]. Other games played in space have also been analysed, such as Public Goods (PG) games (Brandt *et al.* 2003) or the Snowdrift (SD) game (Hauert & Doebeli 2004). The general conclusion is that spatial structure is beneficial to the evolution of cooperation in PD and PG games, but that it can be detrimental in the SD game (Hauert & Doebeli 2004; Doebeli & Hauert 2005; Hauert 2006). Indeed, in the spatial PD, cooperators form compact clusters, whereas in the spatial SD game, cooperators form filament-like clusters, which yields a lower local advantage to cooperators (Hauert & Doebeli 2004).

Much attention has been given recently to ‘evolutionary graph theory’, which aims at investigating the impact of

graph topology on the evolution of cooperation. Lieberman *et al.* (2005) stress that graph structure can have important consequences on the probability of fixation of a mutant: some graphs can act as amplifiers, and others as suppressors of selection. Taylor *et al.* (2007a) [see also Grafen (2007) and Lehmann *et al.* (2007b)] have recently shown that, for a large class of finite graphs with constant population size, cooperation evolves if the benefit-to-cost ratio is above a threshold that depends on the total number of sites and on the average weight of an edge, thus generalizing more specific results (Ohtsuki *et al.* 2006; Ohtsuki & Nowak 2006). In the perspectives, we will discuss several recent studies that investigate the joint evolution of graph topology and cooperation.

A variety of techniques has been used to study the evolution of altruism in spatial ecologies, producing insights into the role of population regulation and interaction network in the evolution of social traits. Thanks to the diversity of approaches, we begin to have a better understanding of the various ecological factors that can affect the evolution of altruism (Box 4).

Box 4 Ecological factors that promote altruism in viscous populations

Individuality

Individuality and stochasticity have been shown to be critical to the evolution of altruism (Goodnight 1992; Di Paolo 2000). This is because in models that do not preserve individuality, such as reaction-diffusion models, selfish nano-individuals will diffuse into the entire spatial domain and exploit altruists everywhere. In such models, altruists do not stand a chance [Ferrière & Michod (1995) provide an exception, but in their model of a spatial iterated game, reciprocity offsets the advantage of selfish nano-individuals].

Population regulation

In a population with constant size, habitat saturation and competition for space are high, which may preclude the spread of altruism. When empty sites (and thus demographic fluctuations) are allowed, competition is alleviated because population elasticity increases, and the conditions for the evolution of altruism become less stringent (Perrin & Lehmann 2001; Le Galliard *et al.* 2003, 2005; Lehmann *et al.* 2006; Lion & van Baalen 2007).

An important consequence of constant population size is that reproduction and mortality are correlated events, so that PCA and spatial games make very different assumptions on the form of density dependence. The evolution of altruism in PCA will depend critically on whether the benefits and costs of altruism affect survival or mortality (Nakamaru & Iwasa 2005; Lehmann *et al.* 2006; Lion & van Baalen 2007). In spatial games, the main criterion will be

whether birth takes place before or after the death of an individual (Hauert 2006; Taylor *et al.* 2007a).

Overlapping generations

When individuals can survive from one generation to the next, evolution of altruism is favoured because the clustering of altruists increases (Taylor & Irwin 2000; Irwin & Taylor 2001; Lehmann *et al.* 2007b). Similarly, altruism evolves more readily in spatial games with asynchronous updating than with synchronous updating (Hauert & Doebeli 2004).

Spatial structure

Obviously, the conditions under which altruism evolves in stochastic spatial models with asynchronous updating are quite favourable, because of the added positive effect of overlapping generations and population fluctuation. However, the important point is that, when the migration rate or the proportion of global interactions is increased, the advantage to altruists decreases. In the limit where spatial structure is completely destroyed, only selfishness is an evolutionarily stable strategy, as in the mean-field model. Thus, the evolution of altruism in these models relies on spatial structure, although the range of parameters over which selfishness is evolutionary stable will often be wider in models with constant population size and non-overlapping generations. Importantly, models of evolutionary graph theory show that the topology and heterogeneity of the interaction network play a crucial role in shaping the selective pressures on altruism.

Communication and the role of spatial fluctuations

As Hamilton (1963) already realized in his seminal article on the evolution of altruism, altruists can potentially greatly improve their chances if they can recognize each other. Their problem, as was stressed by Dawkins (1982), is that the recognition system they use renders them vulnerable to cheaters. Krakauer & Pagel (1995) have shown that their clustered spatial distribution can protect the honest signalers from exploitation by the cheaters. More recently, van Baalen & Jansen (2003) demonstrated that the evolutionary end result need not be stable but exhibits (local) fluctuations that reflect the dynamically changing pattern (locally a communication system invades, their code gets 'broken' by cheats, a new communication system invades and so on). Jansen & van Baalen (2006) showed that altruism can dynamically maintain itself if there are sufficiently many different communication systems to choose from (for instance different beard colours to advertise altruism). Their analysis suggests that the heterogeneity at which the system saturates (at the global level) reflects something about the intensity of conflicting interests in the interaction between individuals relative to their common interests (served by honest communication). Models of the evolutionary ecology of communication (or more generally tag-based cooperation) thus point to the role of dynamical spatial patterns and fluctuations in shaping the selective pressures on the traits, and suggest that there may be some ecological signature of these selective pressures.

Virulence and the role of trophic interactions

There has been much interest in the impact of spatial or social structure on parasite evolution, and the general result is that local clustering leads to reduced levels of virulence compared with well-mixed populations (Claessen & de Roos 1995; Boots & Sasaki 1999, 2000; Haraguchi & Sasaki 2000; van Baalen 2002; O'Keefe & Antonovics 2002; Read & Keeling 2003; Kamo & Boots 2004; O'Keefe 2005).

Indeed, when transmission is local, pathogens that increase host mortality too much, spread too fast, reduce host fertility or cause host immunity, can cause local extinction of the population of susceptible hosts (Rand *et al.* 1995; Boots & Sasaki 2001; van Ballegooijen & Boerlijst 2004). More generally, in spatially structured populations, evolution favours more prudent strategies for the exploitation of the local host supply (van Baalen 2002). Any factor that disrupts host clustering can be expected to lead to reduced levels of host exploitation. Reduced host clustering can be caused by an increase in host migration or dispersal (Boots & Sasaki 2000; O'Keefe & Antonovics 2002; Lion *et al.* 2006), transmission scale (Boots & Sasaki 1999; Kamo & Boots 2006), number of contacts (van Baalen 2002), host

fecundity or network randomness (van Baalen 2002; Lion *et al.* 2006). It has also been shown that an intermediate level of transmission can evolve in the absence of cost or trade-off, irrespective of the route of transmission. This occurs for instance when the parasite increases the range to which propagules are dispersed (Kamo & Boots 2006) or manipulates host dispersal distance while keeping transmission local (Lion *et al.* 2006). In both cases, selection will favour parasites that strike the optimal balance between local exploitation of a cluster of hosts and transmission to distant clusters. Reducing the intensity of exploitation of a cluster of hosts is a form of cooperation between the parasites that infect the cluster.

From the point of view of the parasite, a spatially structured host population represents a heterogeneous resource. Models of spatial host–parasite interactions are thus a special case of resource–consumer interactions, and suggest that the emergence of spatial heterogeneity in the resource will strongly affect the evolution of ecological traits that simultaneously affect different trophic levels (such as virulence or predation rate). In particular, prudent exploitation of the local resource supply is likely to be favoured. A crucial aspect of these interactions is that spatial heterogeneity is dynamic and self-structured, and results from the complex interaction between the endogenous dynamics of resource and consumer.

Population viscosity, habitat saturation and the scale of competition

Theoretical studies of the evolution of altruism and virulence all point to the fact that altruism, honest communication or reduced virulence will evolve more readily when population viscosity is high. As population viscosity decreases and spatial structure is destroyed, the evolutionary pressures change, because the advantage conferred by local clustering decreases. There will exist a critical viscosity above which cooperation is counter-selected. As the population moves closer to well mixed, the evolutionary pressures will collapse to those obtained in non-spatial models.

The fact that the selective pressures on a trait (e.g. cooperation) depend on migration rate, dispersal distance or network structure has been repeatedly stressed by all the studies we have just discussed. The main message is thus that spatial self-structuring leads to the emergence of new selective pressures on cooperation, which can be either positive (local cooperation) or negative (local competition), but that the conditions for the evolution of cooperation will in general be more favourable in viscous populations than in well-mixed populations.

This advantage may be rather subtle, but is often decisive. For instance, in apparent contrast with the 'scale argument'

(Queller 1994; West *et al.* 2002), altruism can evolve even when both competition and altruistic interactions take place locally. The point, actually, is not so much whether competition occurs locally or globally, but whether the scale of competition is large enough compared to the scale at which altruistic interactions occur. Importantly, the ratio between these two scales need not be very different from 1. This effect can be difficult to capture, however. We argue that it is often ecologically more intuitive to think in terms of related dynamical ecological variables, such as habitat saturation (Le Galliard *et al.* 2005).

Note that fewer studies have investigated what happens when mobility can jointly evolve with cooperation, but the results so far suggest that our understanding of the feedback loop between population viscosity and cooperation is far from complete (Koella 2000; Le Galliard *et al.* 2003, 2005; Kamo *et al.* 2006). Leturque & Rousset (2003) and Wild & Taylor (2004) provide related analyses of the joint evolution of sex ratio and dispersal, in which the overproduction of females can be argued to be an altruistic trait.

Experimental studies of the evolutionary ecology of viscous populations

Most empirical studies on the effect of spatial structure on selection have focused on spatial heterogeneity caused by habitats having different productivities, or environmental gradients. A typical example is Rainey & Travisano's (1998) study of adaptive radiation in *Pseudomonas fluorescens*, in which different morphs evolve in an unshaken medium (because of a vertical oxygen gradient), but not in a well-mixed medium. On the other hand, experimental evidence for the role of spatial self-structuring predicted by theoretical models is scarce, but several recent clever experiments have confirmed some of the main predictions reviewed in this article. In this section, we review two major breakthroughs.

Kerr *et al.* (2006) have studied the interaction between a host (*Escherichia coli*) and its parasite (T4 phage) embedded in a plate which imposed a metapopulation structure. The spatial structure of the population was manipulated through periodic transfers between wells according to two 'migration' schemes: in the local migration treatment, transfers were limited to the nearest neighbours of a well, while in the global migration treatment, transfers occurred with the same probability, but to any random well in the metapopulation. The main result was that more rapacious phages evolved in the global treatment, whereas the local treatment selected for more prudent phages. The authors interpreted their results as an example of a 'tragedy of the commons': wells containing rapacious phages in the local treatment are overexploited and 'burn out' before spreading. This finding is in agreement with the results of a stochastic cellular

automaton in the same paper, but also with the general message of our review of spatial models of virulence evolution that local dispersal should favour more prudent exploitation of the hosts.

Arguably, the spatial structure of the population in this experimental study is quite different from a lattice model as each well contains a large number of individuals. While the experience proves that spatial structure can alter the selective pressures on virulence, it does not manipulate the viscosity of the host population itself. In a recent study, Boots & Meador (2007) have provided what is to our knowledge the first empirical manipulation of population viscosity. The authors have conducted microevolutionary experiments in populations of larvae of the Indian Meal Moth infected by a virus. By manipulating the viscosity of the food medium in which the larvae live (from soft to hard), the authors could reduce the dispersal of larvae, leading to clustering of the host population. Host infectivity decreased in the hard medium and increased in the soft medium, in accordance with the prediction that virulence should decrease with decreased host dispersal. Interestingly, for an intermediate viscosity of the medium, virulence tended to evolve to higher levels. Although this latter effect was not statistically significant, it may be in accordance with recent theoretical findings (Kamo & Boots 2006). This study paves the way for stimulating interactions between theoretical and empirical approaches.

SPATIAL ECOLOGY OF KIN AND GROUP SELECTION

Until now, we have not talked about kin selection or group selection. This could give the false impression that these processes do not play a role in the evolution of cooperation in spatially structured populations. There is an unnecessary confusion on this point in the literature. Some authors have argued that demographic stochasticity and spatial structure create a different regime in which kin selection does not apply (Di Paolo 1999; Wenseleers 2006), or that evolution of cooperation stems from a distinct mechanism labelled 'network reciprocity' (Nowak 2006). The aim of this section was to show that kin selection is a fundamental process in spatially structured ecologies.

Viscous populations

When Hamilton (1964) coined the term 'viscous populations' to describe populations with limited dispersal, he made the crucial point that, in such populations, offspring will tend to be close to their parents, so that clusters of related individuals should develop, and altruism should be favoured by kin selection as individuals would meet, on balance, more related individuals than non-related

individuals. As we have seen, this hypothesis was challenged by early patch-structured models, on the basis that population viscosity also increases competition between relatives, which can impede the spread of altruism. However, stochastic individual-based models have shown that, under certain conditions, the balance can be easily tipped in favour of altruism.

Evolution of cooperation in viscous populations can be interpreted using three main arguments: kin selection, group selection (clusters of altruists do better) or network reciprocity. We argue that these three arguments are in a large measure equivalent. This can be shown either with a top-down approach, by showing that the results of evolutionary graph theory can be retrieved as special cases of a general kin selection model (Rousset 2004; Grafen 2007; Lehmann *et al.* 2007b; Taylor *et al.* 2007a); or with a bottom-up approach, by showing that relatedness and Hamilton's rule can be recovered as emergent properties of the ecological spatial dynamics (van Baalen & Rand 1998; Lion & van Baalen 2007). We focus on the latter approach, which we think is often more intuitive, and discuss briefly at a later stage the limits and merits of each approach.

Invasion

When a mutant appears in a viscous population, stochastic demographic processes will tend to lead to the emergence of a cluster of mutants, with a local structure that is characterized by spatial statistics (Fig. 2). For instance, in a lattice model, one can use statistics such as aggregation (the local density $q_{M/M}$ of mutants experienced by an average mutant) and local saturation (the local density $q_{o/M}$ of empty sites experienced by an average mutant). The initial clustering of mutants implies that the local density $q_{M/M}$ is much larger than the global density \bar{p}_M . Therefore, Matsuda *et al.* (1992) have shown that, when the mutants are rare, the local densities change faster than the global densities, and the cluster reaches a stationary local structure while the mutants are still rare (Fig. 2).

Let us consider individuals living on a regular network of sites where each site can be either empty or occupied. Reproduction is asexual and conditional to the availability of empty sites in the neighbourhood of an individual. Then a mutant will invade if its per-capita growth rate λ (or any relevant invasion criterion) is positive. Using correlation equations, the invasion condition then reads (Matsuda *et al.* 1992; van Baalen & Rand 1998)

$$\lambda = b_M q_{o/M} - d_M > 0, \quad (1)$$

where b_M and d_M are the birth and death rates of a mutant and possibly depend on an individual's environment. Here, $q_{o/M}$ gives the local density of empty sites experienced by the mutants in the cluster, and is determined by the structure of the invading cluster. As we will

explain in more detail in the section on multilevel selection, this implies that we have defined fitness at the level of the invading cluster.

Relatedness

The local density $q_{M/M}$ gives a measure of mutant clustering, but is also the conditional probability that the recipient of an altruistic act is a mutant, given that the donor is a mutant. As shown by Day & Taylor (1998), this is a measure of relatedness for a rare mutant ($p_M \approx 0$). When the mutant is not rare, relatedness can be computed as a function of local density $q_{M/M}$ and other spatial statistics (Lion & van Baalen 2007). This means that relatedness is not a fixed parameter, but a spatio-temporal variable which depends on demographic and ecological parameters and variables, although in practice the computation can be complex (for instance with diploid genetics).

Hamilton's rule

Let us now consider that individuals have a trait x that represent the investment into altruism. Altruism increases recipient's survival and decreases donor's fecundity. If a mutant M with investment y appears in a selfish resident population R with investment $x = 0$, we know from eqn 1 that it will invade if $\lambda > 0$. Under an assumption of weak selection, altruism evolves if the selection gradient $\partial\lambda/\partial y$ is positive. Then, it can be shown (van Baalen & Rand 1998; Le Galliard *et al.* 2003; Lion & van Baalen 2007) that the condition for the spread of altruism takes the form

$$\frac{\partial B}{\partial y} q_{M/M} > - \frac{\partial(b_M q_{o/M})}{\partial y} \quad (2)$$

where $q_{M/M}$ and the partial derivatives are evaluated at $x = y = 0$ (the mutant is only slightly altruistic, i.e. the mutant is close to the resident). Here, B represents the benefits of altruism, b_M is the birth rate of a mutant and $q_{o/M}$ is the local density of empty sites in the neighbourhood of a mutant, so that $b_M q_{o/M}$ is the reproductive output of a mutant.

In words, altruism spreads if the marginal benefit of altruism ($\partial B/\partial y$), weighted by relatedness $q_{M/M}$, is greater than the marginal cost of altruism [$\partial(b_M q_{o/M})/\partial y$], i.e. how much does a slight increase in altruism reduce the fecundity of the donor. This means that we have recovered Hamilton's rule as an emergent property of the ecological spatial dynamics.

In this version of Hamilton's rule, relatedness and the benefits and costs of altruism are not constant, but depend on the demographic and ecological parameters. Moreover, we see that altruism has a twofold cost: it has a direct physiological cost (fecundity b_M is decreased), and an

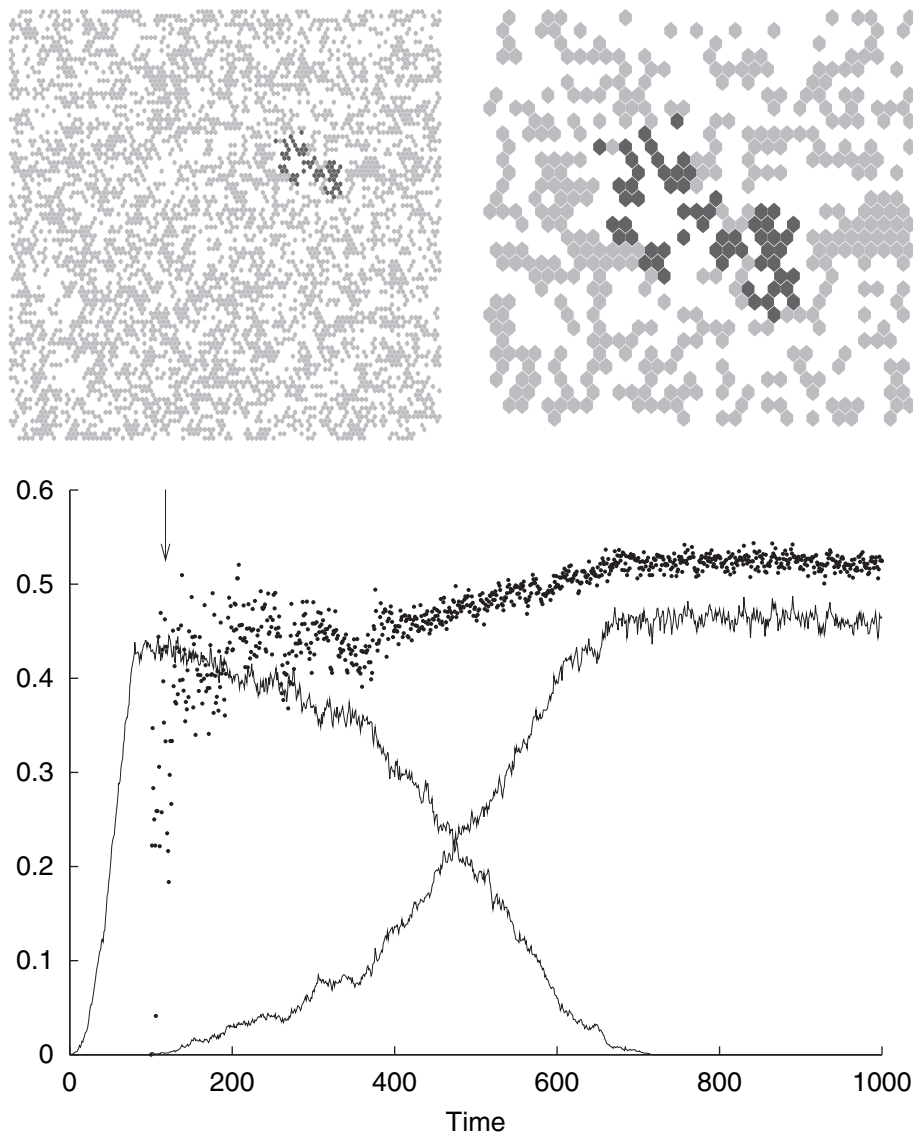


Figure 2 Invasion of a rare mutant in a resident population. A birth-death-migration process on a triangular lattice (each site has six neighbours) has been simulated. At first, a single type R is present and the population settles onto an attractor. At $t = 100$, a rare mutant M with a slightly greater reproduction rate is introduced, and invades. The top panel shows a snapshot of the lattice shortly after the mutant has been introduced, and a zoom on the cluster of mutants. The bottom panel shows the dynamics of the global densities of resident and mutant types (solid lines) and of the local aggregation of mutants $q_{M/M}$ (dots). While the mutant is still rare (arrow), the local clustering of mutants quickly reaches a quasi-equilibrium. This indicates that the cluster of mutants has a precise structure that can be defined using appropriate statistics. Demographic parameters: $b_R = 2$, $b_M = 2.1$, $d = 1$, $m = 1$. Lattice size: 100×100 .

indirect ecological cost (because altruism increases the survival of neighbours, it also decreases the availability of empty sites, so that competition for space increases). Thus, kin competition also emerges from the analysis, and is shown to be related to habitat saturation (Le Galliard *et al.* 2005). When population viscosity decreases (for instance if dispersal increases), $q_{M/M}$ decreases and eventually vanishes, and so does kin competition. The net effect will be that the direction of selection on altruism is reversed (Fig. 3). In the

mean-field limit, the condition for the invasion of altruism collapses to $0 > -(1-p_R) (\partial b_M / \partial j)$, so that selfishness is the sole evolutionary outcome.

Because invasion of altruists in a selfish population depends on the clustering of altruists when rare, i.e. on relatedness, spatial versions of Hamilton's rule are expected to be a general feature of spatial models for the evolution of altruism, (see Lion & van Baalen (2007) for an extension to class-structured populations).

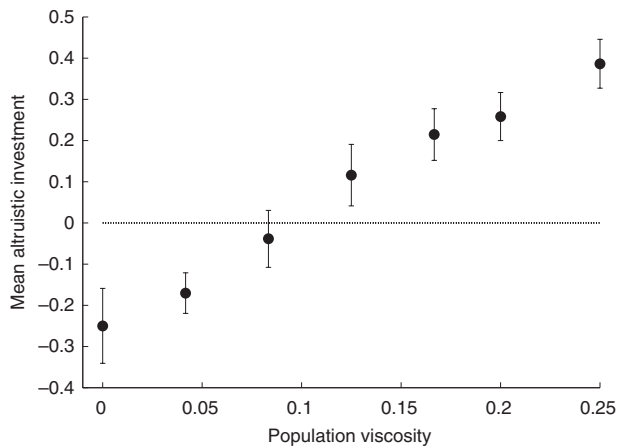


Figure 3 Mean altruistic investment in a stochastic, age-structured evolutionary model after 30 000 generations, as a function of population viscosity. When investment is positive adults help juvenile neighbours ('care'), when it is negative they actually harm them ('cannibalism') [see Lion & van Baalen (2007) for more details].

The important point is that the precise form of the benefits and the costs is complex and depends on the demographic and ecological processes in a subtle way (Rousset 2004; Lehmann *et al.* 2007b). For instance, the marginal benefits and costs of altruism in equation (2) take different forms depending on whether altruism increases survival or fecundity (Le Galliard *et al.* 2003; Lion & van Baalen 2007). Note also that kin recognition or kin discrimination are not necessary for kin selection to operate (Mateo 2004; van Baalen & Jansen 2006). Spatial models for the evolution of cooperation show that altruism will be favoured if one meets, on balance, more related than non-related individuals, but that altruistic acts need not be preferentially directed towards relatives.

Extension to virulence

In spatially structured populations, local transmission of a parasite gives rise to clusters of related parasites, i.e. patches of hosts infected by the same strain of parasites. To understand why reduced levels of host exploitation are favoured by natural selection, we must focus on this cluster of related parasites. The explanation is then that hypovirulent parasites are favoured not because it pays 'the' parasite more to be nice to 'its' host, but rather because clusters of hypovirulent parasites exploit their local host supply more efficiently than clusters of hypervirulent parasites. In other words, the mechanism is group selection, or equivalently, because parasites in the cluster tend to be related, kin selection. Thus, reduced virulence evolves if between-host relatedness of parasites increases. Factors that decrease between-host relatedness (e.g. increased dispersal of host or

parasite) can then be expected to lead to an increase in host exploitation (van Baalen 2002).

Ecological kin selection

On a more conceptual level, spatial models have a more general contribution to evolutionary biology, because they give another sound base to the idea that group and kin selection are but two sides of the same coin (Grafen 1984), and they show that kin selection theory is implicitly rooted in ecology. Inclusive fitness is computed on a group of related individuals that has an ecological (e.g. spatial) dimension. The fact that the same concepts can be derived either from a bottom-up or from a top-down approach is reassuring as to the solidity of kin selection theory, although we argue that it is often simpler and more intuitive to start from ecological principles.

Other approaches

The field of spatial evolutionary genetics pioneered by Rousset and co-workers (Rousset & Billiard 2000; Rousset 2004; Lehmann *et al.* 2007b; Taylor *et al.* 2007b) is a good example of top-down approach. One of the main advantages of this approach is that exact analytical results can be derived using sophisticated population genetics methods, potentially without relying on some assumptions of evolutionary game theory (for instance mutant rarity). However, until now, the application of this technique to populations with fluctuating size has proven unwieldy (but see Rousset & Ronce 2004; Lehmann *et al.* 2006). At this point, it seems that the top-down approach applies more easily to populations with constant local size, and the bottom-up approach to populations with demographic fluctuations [see also Jansen & Vitalis (2007)]. This calls for further modelling work.

SPATIAL ECOLOGY OF MULTILEVEL SELECTION

It has long been recognized that kin selection is a special form of multilevel selection (Hamilton 1975; Frank 1998; Sober & Wilson 1998; Lehmann *et al.* 2007a). In this section, we discuss what spatial models can teach us about multilevel selection and evolutionary transitions (Maynard Smith & Szathmáry 1995; Keller 1999).

Emergence of new units of selection

A crucial aspect of spatially structured populations is that rare mutants can interact with each other, because local stochastic processes lead to the emergence of clusters. The fate of a mutant in a viscous population thus depends on whether the cluster of mutants expands or decays, which can be accounted for by defining fitness at the level of the

cluster. As we have seen previously, this is not fundamentally different from the way inclusive fitness is computed.

Correlation equations represent one way to obtain an analytical expression of fitness that takes into account spatial clustering (van Baalen & Rand 1998). The technique relies on the simultaneous computation of a measure of fitness and of the local structure of the invading cluster. These two objects are obtained as a pair of eigenvalue and eigenvector, which entails that if the fitness is positive, the cluster will grow while keeping a characteristic structure (much like a stable age distribution in well-mixed age-structured populations). Thus, the cluster can be seen as the associated unit of selection (van Baalen & Rand 1998), i.e. the level of organization at which fitness is defined. In Dawkins's (1976) terms, the cluster is a vehicle for selection, since, obviously, the cluster lacks the ability to replicate itself. Because we are interested in whether a mutant can invade or not, we use the concept of invasion fitness, which means that the unit of selection can be defined as the unit of invasion.

Spatial self-structuring has thus the important effect of altering selective pressures by lifting the operation of natural selection from the individual level to a higher level of organization. In contrast to models of group selection, which allow to partition individual fitness into within- and between-group components, it is more difficult to identify individual and group components in spatial models, because the 'group' in this case is not an ingredient of the model, but an emergent property.

It can be speculated that the emergence of new units of selection through spatial self-structuring is quite general, and does not depend on the structure of the model. However, the precise structure of the unit of selection will depend on the assumptions of the model. For instance, the models used by Boerlijst & Hogeweg (1991) and Boerlijst *et al.* (1993) are deterministic coupled map lattices which allow one to identify spirals as the relevant unit of selection. In stochastic models with a more continuous spatial structure, the unit of selection is a cluster with a characteristic statistical structure, but no precise geometric shape.

Common good

Interactions between individuals (in particular, local interactions) inevitably lead to the emergence of a 'common good' (Keller 1999; van Baalen & Jansen 2001). Individuals can cooperate by investing into the common good, or, in stark contrast, by agreeing on sacrificing the common good (van Baalen & Jansen 2001). The outcome of the interaction is thus determined by the balance between the common good and the individuals' private interests. New levels of organization can emerge when lower-level units sacrifice part of their private interests to bolster the common good (Maynard Smith & Szathmary 1995; Keller 1999).

Spatial evolutionary models provide a coherent framework in which to look at the question of such evolutionary transitions [see also studies of pre-biotic evolution by Hogeweg (1994) and Hogeweg & Takeuchi (2003)]. Spatial self-structuring leads to the emergence of a common good between individuals in a cluster, and creates positive selective pressures for investing into the common good at the expense of the individuals' private interests. This leads to the emergence of cooperation between lower-level units. It also represents a natural mechanism by which fitness can be reorganized and move from the lower level (here, the individual) to the higher level (here, the cluster) (Michod 2000).

PERSPECTIVES

Theory on evolution in spatially structured populations has developed into a large body of literature, solving some old puzzles, but also raising new questions. We conclude this review by sketching some directions for future work.

Evolution of cooperation

Because of the variety of modelling approaches used to study the evolution of altruism, attempts to assess the relative merits and the links between the different theoretical frameworks are still in infancy. In Box 4, we give an overview of the ecological factors that have been shown to affect the selective pressures on altruism. This list is certainly not complete, and further work is needed to achieve a comprehensive synthesis of the intricate feedback loop between ecological processes (dispersal, habitat saturation and life cycle) and the evolution of cooperative traits.

The study of the joint evolution of social structure and cooperation is an interesting avenue of research. Several recent papers have demonstrated that cooperation can be favoured in heterogeneous populations, in which some individuals have more interactions than others (as is often the case in natural populations; Santos *et al.* 2006a). Such heterogeneity can result from the joint evolution of graph topology and cooperation (Santos *et al.* 2006b,c).

Evolutionary branching and speciation

Spatial structure is one of the main ingredients of allopatric speciation, a theory that explains the origin of new species by geographic isolation leading to separate evolution of subpopulations in different habitats. In models of allopatric speciation, spatial structure is thus externally imposed.

Sympatric speciation, on the other hand, assumes that disruptive selection and reproductive isolation can occur in a single habitat. Disruptive selection can happen if

frequency-dependent ecological interactions drive the population to a fitness minimum, at which point the population may split into two diverging phenotypic clusters. This phenomenon is called evolutionary branching. Interestingly, virtually all studies showing evolutionary branching and sympatric speciation have focused on well-mixed populations, or populations in spatially heterogeneous environment. The effect of spatial self-structuring appears to have been barely touched.

A notable exception is Magori *et al.* (2005), who have shown that evolutionary branching is possible in a lattice model of asymmetric competition, but in a more limited range of parameters than in the mean-field model. Similar results have been obtained in a spatial model of the SD game (S. Lion, unpublished results) in which interactions can take place globally or locally. As interactions become more localized, the stability of the evolutionary singularity changes, and the branching point becomes an ESS (Fig. 4). These results are consistent with those obtained in models of deme-structured populations that show that limited dispersal inhibits evolutionary branching (Day 2001; Ajar 2003). Note however that these latter studies assume that local populations have a fixed size. As we have seen, population regulation can have important consequences on the evolution of cooperation, and the same can be expected to be true for coexistence and evolutionary branching.

We believe that one of the major challenges faced by the theory of adaptive dynamics is to elucidate the impact of spatial self-structuring on evolutionary branching. From these early results, it seems that spatial structure can reverse or alter the selective pressures and hamper disruptive selection, which, because of the appeal of allopatric speciation, can seem counter-intuitive, and also contradicts some empirical studies that show that limited dispersal could promote coexistence in several taxa, including bacteria (Kerr *et al.* 2002) and ants (Yu *et al.* 2001). As in the study of cooperation, we expect that the predictions will critically depend on whether the model allows empty sites or not, and on demographic stochasticity that can itself inhibit evolutionary branching (Claessen *et al.* 2007).

Trade-offs

The interaction between the ecological conditions and the trade-offs between two traits determines the evolutionary fate of a population. Spatial self-structuring can have important effects on this interaction, as it can lead to emergent trade-offs at the level of the cluster (Rand *et al.* 1995; Harada 1999; van Ballegooijen & Boerlijst 2004; Lion *et al.* 2006). Moreover, it has been recently stressed that spatial self-structuring could also significantly alter the interaction between ecological dynamics and the existing trade-offs, which may have important consequences on the

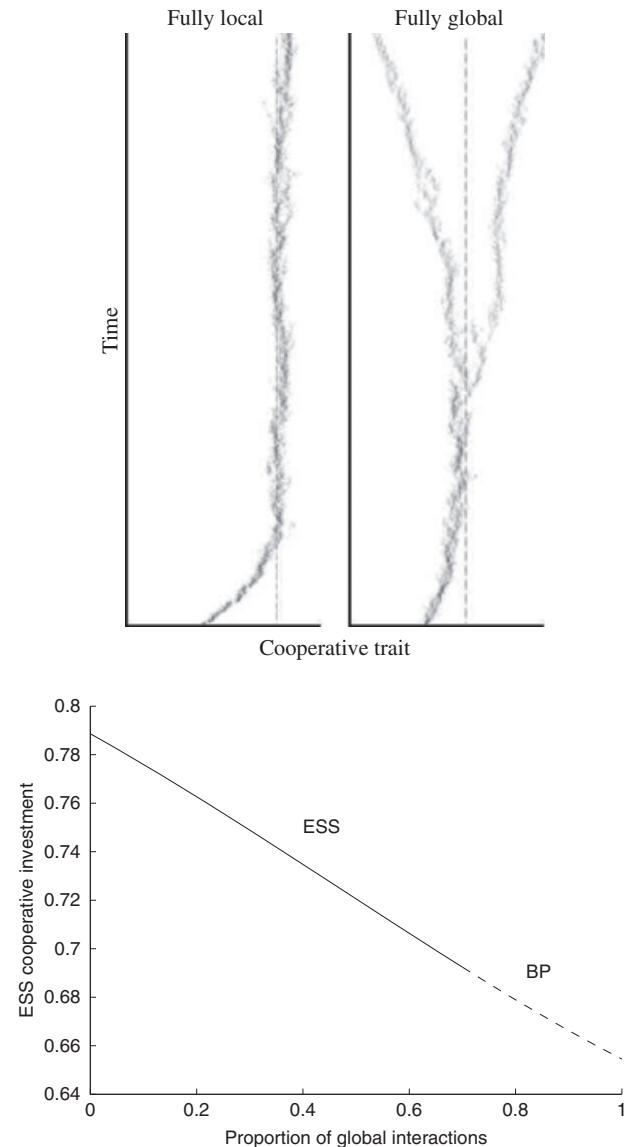


Figure 4 Effect of the scale of interactions on evolutionary branching in a continuous snowdrift game. Individuals on a random network play the snowdrift game of Doebeli *et al.* (2004) either locally or globally. Each site has four neighbours. Individuals reproduce at rate $b = 2$, and die at rate $d = 1$. The payoffs of the game are scaled by a parameter $k = 0.2$ with parameters $b_2 = -1.4$, $b_1 = 7$, $c_2 = -1.7$, $c_1 = 4.56$ (see Doebeli *et al.*, 2004). When interactions are fully global, evolutionary branching (BP) occurs as in Doebeli *et al.* (2004), but as interactions become more local, the evolutionary singularity becomes an ESS.

validity of predictions based primarily upon the shape of a given trade-off (Kamo *et al.* 2006). In some cases, the precise functional form of a trade-off does not affect the evolutionary outcome in a well-mixed population, but, when the population is spatially structured, it can lead to very different predictions, ranging from ESS to evolutionary

branching (S. Lion and M. van Baalen, in preparation). We believe that the study of the interplay between spatial structure and the shape of trade-offs will help getting insight on the assumptions and consequences of these trade-offs.

Evolutionary suicide, extinction and evolution to criticality

Evolutionary suicide is a process by which directional selection drives the entire population extinct (Ferrière *et al.* 2002; Dieckmann & Ferrière 2004). This occurs when the evolutionary trajectory crosses the boundary of the viability domain. Spatial self-structuring is likely to have an important impact on evolutionary suicide. First, new regions of extinction in parameter space can emerge as a consequence of spatial structure (Boots & Sasaki 2001). Second, spatial self-structuring itself can cause the emergence of implicit trade-offs that can collide with the extinction boundary (Rand *et al.* 1995; van Ballegooijen & Boerlijst 2004). These two processes driven by spatial self-structuring can combine and may strongly affect the possibility of evolutionary suicide. Because most natural populations possess some form or other of spatial self-structuring, this is likely to be of crucial importance in conservation biology (Ferrière *et al.* 2004), and triggers the question of whether spatial structure increases or decreases the probability of extinction.

On a more conceptual note, one may wonder if evolution can bring a population to a critical state, a phenomenon called 'self-evolved criticality' (SEC) by Rand *et al.* (1995). Evolution to the border of extinction is an example of SEC. Spatial ecological models typically exhibit a phase transition in parameter space between persistence and extinction of at least one type of individuals. Rand *et al.* (1995) have shown that evolution of parasite transmission could drive the parasite population on the verge of extinction. This happens because the critical ecological state is an attractor for the evolutionary dynamics. It is well known from statistical physics that continuous phase transition, in which the transition from persistence to extinction is gradual, are associated with criticality: at the point where the transition takes place, the system exhibit scale invariance, and many variables display a power-law behaviour (Hinrichsen 2000). More generally, criticality can also be statistical in the sense that, on the evolutionary attractor, the distribution of some events or variables follows a power law [see Stollenwerk & Jansen (2003) for an example].

Note that, although SEC involves characteristic power laws, it is a different process from 'self-organized criticality' (SOC; Bak *et al.* 1988). In SOC, the ecological system self-organizes to reach a critical state. In SEC, the *evolutionary* dynamics drives the ecological system to an *ecological* critical state, so that SEC is the result of an eco-evolutionary feedback process. While there has been increasing interest in criticality in ecological systems in the last 20 years (Pascual

& Guichard 2005), the question of whether populations can evolve to a critical state has received less attention [but see Rand *et al.* (1995), Socolar *et al.* (2001), see also Caraco *et al.* (2006) for an example where SEC is inhibited by spatial structure]. Further research on this topic could provide a sound evolutionary mechanism for the occurrence of scale-free patterns in nature.

There are two main reasons why spatial modelling could yield fruitful contributions to this field. First, many spatial ecological models are likely to bear a close relationship with the class of directed percolation models which have been extensively studied in statistical physics and are characterized by a continuous phase transition (Hinrichsen 2000; Hauert & Szabó 2005). Second, near a critical point, several spatial statistics, such as the correlation length, are expected to diverge, which suggests that some spatial patterns can be good indicators that a population is about to go extinct (Oborny *et al.* 2005; Pascual & Guichard 2005; Kéfi *et al.* 2007; Scanlon *et al.* 2007). Note that divergence of correlation lengths has the important consequence for modellers that MCAs and simulations on small-size lattices will become less reliable on the verge of extinction. This calls for refined mathematical methods that can deal with this problem and allow to make accurate quantitative predictions.

Spatial fluctuations

Much of the current theory in evolutionary game theory and adaptive dynamics is built (at least in practice) upon the assumption that evolution occurs at a much slower pace than ecology [but see Marrow *et al.* (1992); Dieckmann & Law (1996); Champagnat *et al.* (2006)]. It is becoming increasingly clear, however, that the ecological and evolutionary timescales need not be so different, and may even be overlapping (van der Laan & Hogeweg 1995; Hairston *et al.* 2005; Champagnat *et al.* 2006). A fundamental problem is that a mutant that is similar to the resident will have very similar dynamics as well. If the resident is at equilibrium, the mutant's dynamics will therefore be slow (and thus much slower than typical for most ecological processes). One important consequence is that mutant dynamics tend to be strongly affected by demographic stochasticity (Metz & Gyllenberg 2001; Cadet *et al.* 2003). In practice this means that the density of the mutant will exhibit strong fluctuations with, given that absolute numbers will be small, a significant probability of extinction. The closer the mutant is to the resident, the larger these fluctuations will be and, moreover, their size will tend to be distributed according to a power law (Stollenwerk & Jansen 2003; Ferrière *et al.* 2006). The importance of such fluctuations has already been demonstrated for the evolution of infectious diseases, where these fluctuations allow multiple, individually

counterselected mutations to appear in combination which may help strains to cross adaptive valleys (Antia *et al.* 2003; Iwasa *et al.* 2004), something they would not be able to do otherwise unless present in excessively large numbers (Taddei *et al.* 1997).

It is obvious that in a spatially explicit setting such fluctuations will have a spatial dimension as well. However, to our knowledge, no one has explicitly addressed the question of how to characterize these fluctuations nor analysed what consequences they might have. They are likely to be significant, however. Consider a spatially structured population in which mutation generates slightly disadvantageous mutants. Because the mutations are disadvantageous, we know that they will disappear on the long run, but before disappearing they may have persisted for some time and spread quite far. If the mutation rate is low, this may give rise to a genetic patchwork or mosaic, which is important because if the mutation would have affected a socially relevant trait it will have time to encounter other carriers in large numbers, enhancing the efficiency of kin selection. If the mutation rate is higher, the effect is counteracted because locally more mutants emerge, to the effect that each of them encounters fewer copies of itself reducing the strength of kin selection.

This effect is likely the more pronounced the more complicated the spatial dynamics of the system. If the system self-organizes into some characteristic spatial structure, low mutation rates will pitch these structures against each other (thus strengthening selection for social coherence), whereas high mutation rates are likely to favour traits that reproduce at the expense of these structures [counterselecting social coherence, thus blocking potentially major evolutionary transitions (Maynard Smith & Szathmáry 1995)].

Whatever the consequences for social evolution and kin selection, considering the size of spatial fluctuations will help us to better understand the role of patterns in ecology and evolution. Recently, the use of so-called 'neutral models' has been advocated to interpret species distributions in tropical forests (Hubbell 2001). The problem is that such neutral models are not structurally stable so that even small modifications can utterly destroy the resulting patterns. Developing a 'nearly neutral' approach is much more in line with biological reality: many mutants (or similar species, in an ecosystem context) will have slow global dynamics and may therefore occasionally create patches with high local abundances even if they are bound to disappear in the long term.

The spatial scale of selection

What is the relevant spatial scale at which to measure (and identify) natural selection? One of the main insights resulting from the new approaches that we discuss is that selection may operate at intermediate levels, such as a

cluster of individuals. This calls for new methods to identify and quantify the unit of selection and for refined definitions of fitness. Spatial moment analysis already has provided us with analytical insight on the ecological and evolutionary behaviour of spatial models, but many open questions remain. First, modellers need to develop new spatial statistics and MCAs that are valid both in an ecological and an evolutionary context. Further research should in particular provide empiricists with statistical tools to measure and identify the scale of selection in the field. Fruitful results can be expected from a close interaction with mathematicians and physicists, who have already an extensive knowledge of these techniques. Second, we still have a limited understanding of the process of invasion in spatially structured populations, in particular when stochasticity is taken into account. Third, it could be useful to extend the concepts of fitness and unit of selection to the case where large-scale spatial self-structuring occur. In a more empirical perspective, spatial point processes (moment equations in continuous space) are more suited to fitting empirical data than lattice models, as they allow to represent more realistic dispersal and interaction kernels. Extending this framework so that it can account for invasion more naturally is one of the big challenges for theoretical spatial ecologists [see for instance Bolker & Pacala (1999); Fournier & Méléard (2004); Murrell *et al.* (2004); Champagnat & Méléard (2007)].

Testing theory

Despite the paucity of empirical studies that have addressed the evolutionary consequences of spatial self-structuring, we feel confident that the growing theoretical interest for this question will prompt many innovative experiments that will shed much light on this important aspect of the eco-evolutionary feedback loop. Microbial or arthropod host populations infected by micro-organisms seem to be promising model systems in this respect, because the spatial dynamics is very close to the assumptions of lattice models of host–parasite interactions. By manipulating the viscosity of the medium, one could test the impact of spatial structure on other cooperative traits, such as the production of public goods (e.g. siderophore production in bacteria) or cooperative swarming, which are usually studied by directly manipulating the level of relatedness (Griffin *et al.* 2004). Many unicellular organisms present examples of cooperative traits and are very practical for laboratory studies, which make them good model organisms for investigating empirically the impact of population viscosity and spatial structure on the evolution of cooperation. In particular, many of the predictions we have reviewed can be tested by experimental studies of virulence evolution in host–parasite experimental systems (Boots & Meador 2007). In a broader perspective,

colonial organisms such as the volvocine algae have proved to be good experimental systems to study the interplay of motility, cooperation and multilevel selection [Michod (2007) and references therein].

We can conclude that this field, which has until now been almost entirely driven by theory, has reached a point at which innovative empirical studies are needed to test predictions and generate new problems for theoreticians.

The major transitions in evolution

Not only can spatial models help to shed a new light onto old Darwinian puzzles such as the evolution of altruism, but they can also help to bridge gaps between distant fields (for instance between spatial games and the theory of kin selection) and bring seemingly different evolutionary problems into the unifying framework of multilevel selection. As virtually no population is well mixed at all levels of organization, the insights we discuss in this review apply to many different systems.

The recognition that multilevel selection can be a major force driving evolution in viscous populations should also foster new perspectives on evolutionary transitions. Because cooperation, relatedness and spatial proximity between lower-level units are necessary for the formation of higher-level units of selection, it is quite fascinating to realize that the three processes are intricately linked. Maybe this will lead to a major conceptual and philosophical breakthrough in the way we think about fitness and levels of selection... or maybe not, but at least we hope this review will have convinced the reader of the relevance of studying evolution in a spatial ecological context.

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