Coexistence of productive and non-productive populations by fluctuation-driven spatio-temporal patterns

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ABSTRACT

Cooperative interactions, their stability and evolution, provide an interesting context in which to study the interface between cellular and population levels of organization. Here we study a public goods model relevant to microorganism populations actively extracting a growth resource from their environment. Cells can display one of two phenotypes — a productive phenotype that extracts the resources at a cost, and a non-productive phenotype that only consumes the same resource. Both proliferate and are free to move by diffusion; growth rate and diffusion coefficient depend only weakly phenotype. We analyze the continuous differential equation model as well as simulate stochastically the full dynamics. We find that the two sub-populations, which cannot coexist in a well-mixed environment, develop spatio-temporal patterns that enable long-term coexistence in the shared environment. These patterns are purely fluctuation-driven, as the corresponding continuous spatial system does not display Turing instability. The average stability of coexistence patterns derives from a dynamic mechanism in which the producing sub-population equilibrates with the environmental resource and holds it close to an extinction transition of the other sub-population, causing it to constantly hover around this transition. Thus the ecological interactions support a mechanism reminiscent of self-organized criticality; power-law distributions and long-range correlations are found. The results are discussed in the context of general pattern formation and critical behavior in ecology as well as in an experimental context.

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1. Introduction

Cooperative behavior of individuals in nature has attracted the interest of scientists for many years (Axelrod and Hamilton, 1981; Michod and Roze, 2001; Nowak, 2006). The evolution and stability of cooperation is sometimes formulated as a dilemma or conflict between the optimal strategy of the individual and that of the population. More generally, cooperative interactions and their stability provide a fascinating context in which to investigate the relations between these two levels of organization — the individual and the population. Indeed, a biological population is more than a collection of individuals: it is characterized by its interactions — direct and indirect, by its memory through inheritance, and by its relation with the environment (Moore et al., 2013; Stolovicki and Braun, 2011). Therefore, phenomena at the population level,

including evolutionary dynamics and long-term stability of individual traits, are necessarily affected by all these ingredients.

Populations of microorganisms provide a valuable model system to study cooperative interactions. Much is known about the mechanisms underlying microbial cooperative behavior: mutations, gene expression and other processes affect cellular behavior, which in turn affects the environment and feeds back on the individual dynamics (Kummerli et al., 2009; Elhanati et al., 2011). Thus these systems offer concrete test cases for many fundamental issues at the intersection between the individual, the population and the environment. Microbial populations have the great advantage of allowing controlled experiments, where predictions can be tested quantitatively; at the same time the detailed biological knowledge about the processes involved places severe constraints on the models relevant to these systems (Schuster et al., 2010; Damore and Gore, 2012). Indeed previous work has shown that conclusions drawn on fundamental problems may depend subtly on details of realization of the particular biological system. In the present work we focus on models appropriate for microbial interactions taking into account carefully the constraints that they pose.

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One important type of cooperative interaction is induced by the production of public goods: in a population inhabiting a shared environment, individuals depend on a resource for their growth or survival. The resource can be produced or actively extracted from the environment by the individuals, generally at some cost. Once produced, it is shared by other population members as well, thus defining a setting with some degree of cooperation. The more general problem known as public goods cooperation has been considered in several different contexts, from abstract game theory in which encounter rules are defined (Hauert et al., 2006, 2008), through theoretical evolutionary models (Doebeli et al., 2004) and to biophysical aspects of microorganism model systems that secrete resource-extracting molecules outside the cell boundaries (Craig Maclean and Brandon, 2008; Gore et al., 2009; Kummerli et al., 2009; Velicer and Vos, 2009). In general it is by now well established that various mechanisms at the population level can break the symmetry between producers and non-producers, supporting privileged share of the resource to the productive individuals, or inducing assortment of sub-populations, thus enabling coexistence of productive and non-productive phenotypes in the same environment (Nowak, 2006; Damore and Gore, 2012). Spatial structure and mobility, for example, is one such mechanism that has a strong effect on the public goods problem in its various levels of abstraction (Hamilton, 1971; Eshel, 1972; Nowak et al., 1994; Irwin and Taylor, 2001; Perc et al., 2013). Intuitively, when cells are proliferating in different regions in space, and if the cooperative trait is inherited, then it will be directed mainly towards other cooperators. However, different mechanisms can support coexistence in a spatially extended environment and, once again, their fundamental nature may depend on the details of the system.

Previous work on spatial public goods dynamics has focused on a class of models derived from the public goods game in economy, where a well-defined group interacts by individual contribution and a reward common to the group (Wakano, 2007; Wakano et al., 2009; Wakano and Hauert, 2011). This model was transformed to partial differential equations and coexistence was found in one of two possible cases: (A) coexistence already emerges in the mean field ordinary differential equation (ODE); (B) there is no coexistence in the mean field, but a Turing instability in the spatial model described by partial differential equations (PDE) induces spatial patterns of coexistence. In this case, as is typical of the Turing mechanism, the diffusion coefficients of the producers and non-producers must differ greatly (Wakano and Hauert, 2011).

In the context of microbial populations there is no biological justification to assume a difference in diffusion coefficient between different physiological states or even different strains of the same organism. Thus, an argument is needed for the more general case, where diffusion is not strongly dependent on the production of common goods, and where co-existence is impossible in the mean field. We here present and study such a model, which is quite generally suited for microbial populations actively extracting a growth resource from the environment.

In a well-mixed environment with homogeneous interactions, the model exhibits an extreme "tragedy of the commons" scenario: non-productive individuals have a higher fitness, take over the population, and cause extinction due to the extreme dependence of growth on the extracted resource. This is the only fixed point of the well-mixed system, sharpening the question of rescue from the tragedy of extinction. The model has been proposed and studied previously in the presence of strategy changes induced by gene expression, either random or by environmental feedback; then, co-existence can be stabilized in a well-mixed system (Elhanati et al., 2011). Here we resort to the basic resource-extraction dynamics without change of strategy, but in the presence of spatial and demographic fluctuations.

Embedding the populations in space in a continuous dynamical system description with diffusion does not induce non-homogeneous solutions; namely, there is no Turing instability (in contrast to other studied systems of spatial public good games (Wakano et al., 2009)). However, we find that when the discrete stochastic nature of the interactions is taken into account, mobility in space and demographic noise drive the system to a solution where spatio-temporal patterns prevail and allow a nontrivial coexistence of the productive and non-productive sub-populations in a large region of parameter space. The mechanism underlying this phenomenon is based on the existence of an absorbing state extinction transition, a slow timescale of competition, and the stochastic dynamics characteristic of a discrete population of cells. We propose an analogy of this mechanism to self-organized criticality and discuss its relation spatio-temporal patterns found in other ecological models.

2. Methods

2.1. Numerical integration of ODE and PDE

The ODEs were solved numerically using the Matlab fourth-order Runge Kutta (Jameson et al., 1981), as applied in the MATLAB ode45 function assuming non-stiff equations (Hanselman and Littlefield, 1997). The partial differential equations (PDEs) were solved using a fourth-order Runge Kutta on a two-dimensional 100×100 square lattice, with periodic boundary conditions. The diffusion scheme that was used was a second-order leapfrog scheme (Alexander, 1977).

2.2. Stochastic simulation

Monte Carlo simulations of the studied model were performed on a two-dimensional 100×100 square lattice with periodic boundary conditions. We initiated the reactants at random positions and enacted each reaction separately. We computed at each lattice point the probability of each reaction and performed reactions according to the prescribed probabilities. At high reaction rates, we used a Poisson approximation (Aparicio and Solari, 2001). The simulation updating was asynchronous (i.e. the lattice sites were updated one at a time with a random order). In each time interval (dt) all lattice sites were updated based on the current values in the lattice. The dynamics were simulated for different parameter values. The lattice size used was the two-dimensional 100×100 unless otherwise noted. The simulation was described in detail in previous publications (Agranovich et al., 2006; Behar et al., 2012; Davidovich and Louzoun, 2013).

3. Model presentation

Our model describes a population of microorganisms in an environment that allows growth in principle; however the growth resource is not directly available for the cells to metabolize but rather needs to be actively extracted. This situation is encountered, for example, when complex sugars need to be hydrolyzed by enzyme secretion (Carlson and Botstein, 1982; Jones et al., 1992) or iron needs to be chelated (Hider and Kong, 2010). The cooperative public goods problem is formalized in this context as follows: one type of cell, with a population size N_P, produces the growth resource, while the other type, with a population size N_{NP} does not. The two sub-populations consume the resource C and proliferate following resource consumption. It is important that the resource is absolutely essential for growth, as further discussed below. The fitness difference between the two sub-populations is modeled as a lower net death rate of the non-productive type, representing the cost or internal resources invested to create the growth resource C.