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Evolutionary game theory: Theoretical concepts and applications to microbial communities

Erwin Frey *

Ludwig-Maximilians-Universität München, Arnold Sommerfeld Center for Theoretical Physics and Center for NanoScience, Theresienstrasse 37, D-80333 Munich, Germany

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ABSTRACT

Ecological systems are complex assemblies of large numbers of individuals, interacting competitively under multifaceted environmental conditions. Recent studies using microbial laboratory communities have revealed some of the self-organization principles underneath the complexity of these systems. A major role of the inherent stochasticity of its dynamics and the spatial segregation of different interacting species into distinct patterns has thereby been established. It ensures the viability of microbial colonies by allowing for species diversity, cooperative behavior and other kinds of "social" behavior.

A synthesis of evolutionary game theory, nonlinear dynamics, and the theory of stochastic processes provides the mathematical tools and a conceptual framework for a deeper understanding of these ecological systems. We give an introduction into the modern formulation of these theories and illustrate their effectiveness focussing on selected examples of microbial systems. Intrinsic fluctuations, stemming from the discreteness of individuals, are ubiquitous, and can have an important impact on the stability of ecosystems. In the absence of speciation, extinction of species is unavoidable. It may, however, take very long times. We provide a general concept for defining survival and extinction on ecological time-scales. Spatial degrees of freedom come with a certain mobility of individuals. When the latter is sufficiently high, bacterial community structures can be understood through mapping individual-based models, in a continuum approach, onto stochastic partial differential equations. These allow progress using methods of nonlinear dynamics such as bifurcation analysis and invariant manifolds. We conclude with a perspective on the current challenges in quantifying bacterial pattern formation, and how this might have an impact on fundamental research in non-equilibrium physics.

1. Introduction

This article is intended as an introduction into the concepts and the mathematical framework of evolutionary game theory, seen with the eyes of a theoretical physicist. It grew out of a series of lectures on this topic given at various summer schools in the year 2009.[1] Therefore, it is not meant to be a complete review of the field but rather a personal, and hopefully pedagogical, collection of ideas and concepts intended for an audience of advanced students.

* Tel.: +49 0 89 2180 4537.
E-mail address: frey@lmu.de.

[1] International Summer School Fundamental Problems in Statistical Physics XII, August 31–September 11, 2009, Leuven, Belgium; Boulder School for Condensed Matter and Materials Physics, "Nonequilibrium Statistical Mechanics: Fundamental Problems and Applications", July 6–31, 2009, Boulder, Colorado; WE-Heraeus Summerschool 2009, "Steps in Evolution: Perspectives from Physics, Biochemistry and Cell Biology 150 Years after Darwin", June 28–July 5, 2009, Jacobs University Bremen.

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The first chapter gives an introduction into the theory of games. We will start with "strategic games", mainly to introduce some basic terminology, and then quickly move to "evolutionary game theory". The latter is the natural framework for the evolutionary dynamics of populations consisting of multiple interacting species, where the success of a given individual depends on the behavior of the surrounding ones. It is most naturally formulated in the language of nonlinear dynamics, where the game theory terms "Nash equilibrium" or "evolutionary stable strategy" map onto "fixed points" of ordinary nonlinear differential equations. Illustrations of these concepts are given in terms of two-strategy games and the cyclic Lotka–Volterra model, also known as the "rock–paper–scissors" game. We conclude this first chapter by an (incomplete) overview of game-theoretical problems in biology, mainly taken from the field of microbiology.

A deterministic description of populations of interacting individuals in terms of nonlinear differential equations, however, misses some important features of actual ecological systems. The molecular processes underlying the interaction between individuals are often inherently stochastic and the number of individuals is always discrete. As a consequence, there are random fluctuations in the composition of the population which can have an important impact on the stability of ecosystems. In the absence of speciation, extinction of species is unavoidable. It may, however, take very long times. Our second chapter starts with some elementary, but very important, notes on extinction times. These ideas are then illustrated for two-strategy games, whose stochastic dynamics is still amenable to an exact solution. Finally, we provide a general concept for defining survival and extinction on an ecological time scale which should be generally applicable.

Section 3, introducing the May–Leonard model, serves two purposes. On one hand, it shows how a two-step cyclic competition, split into a selection and reproduction step, modifies the nonlinear dynamics from neutral orbits, as observed in the cyclic Lotka–Volterra model, to an unstable spiral. This teaches that the details of the molecular interactions between individuals may matter and periodic orbits are, in general, non-generic in population dynamics. On the other hand, the May–Leonard model serves to introduce some more advanced concepts from non-linear dynamics: linear stability analysis, invariant manifolds, and normal forms. In addition, the analysis will also serve as a necessary prerequisite for the analysis of spatial games in the subsequent chapter. Section 3 is mainly technical and may be skipped in a first reading.

Cyclic competition of species, as metaphorically described by the children's game "rock–paper–scissors", is an intriguing motif of species interactions. Laboratory experiments on populations consisting of different bacterial strains of *Escherichia coli* have shown that bacteria can coexist if a low mobility enables the segregation of the different strains and thereby the formation of patterns [1]. In Section 4 we analyze the impact of stochasticity and an individual's mobility on the stability of diversity as well as the emerging patterns. Within a spatially-extended version of the May–Leonard model we demonstrate the existence of a sharp mobility threshold, such that diversity is maintained below, but jeopardized above that value. Computer simulations of the ensuing stochastic cellular automaton show that entangled rotating spiral waves accompany biodiversity. These findings are rationalized using stochastic partial differential equations (SPDE), which are reduced to a complex Ginzburg–Landau equation (CGLE) upon mapping the SPDE onto the reactive manifold of the nonlinear dynamics.

In Section 5, we conclude with a perspective on the current challenges in quantifying bacterial pattern formation and how this might have an impact on fundamental research in non-equilibrium physics.

1.1. Strategic games

Classical Game Theory [2] describes the behavior of rational players. It attempts to mathematically capture behaviors in strategic situations, in which an individual's success in making choices depends on the choices of others. A classical example of a strategic game is the *prisoner's dilemma*. In its classical form, it is presented as follows[2]:

"Two suspects of a crime are arrested by the police. The police have insufficient evidence for a conviction, and, having separated both prisoners, visit each of them to offer the same deal. If one testifies (defects from the other) for the prosecution against the other and the other remains silent (cooperates with the other), the betrayer goes free and the silent accomplice receives the full 10-year sentence. If both remain silent, both prisoners are sentenced to only 1 year in jail for a minor charge. If each betrays the other, each receives a five-year sentence. Each prisoner must choose to betray the other or to remain silent. Each one is assured that the other would not know about the betrayal before the end of the investigation. How should the prisoners act?"

The situation is best illustrated in what is called a "payoff matrix" which in the classical formulation is rather a "cost matrix":

P	Cooperator (C)	Defector (D)
C	1 year	10 years
D	0 years	5 years

Here rows and columns correspond to player (suspect) 1 and 2, respectively. The entries give the prison sentence for player 1; this is sufficient information since the game is symmetric. Imagine you are player 1, and that player 2 is playing the strategy "cooperate". Then you are obviously better off to play "defect" since you can get free. Now imagine player 2 is playing "defect". Then you are still better off to defect since 5 years in prison is better than 10 years in prison. If both players are rational players a dilemma arises since both will analyze the situation in the same way and come to the conclusion that

[2] This description is taken from Wikipedia: http://en.wikipedia.org/wiki/Prisoner's_dilemma.