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A phenomenological analysis of eco-evolutionary coupling under dilution

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ABSTRACT

Evolutionary dynamics experienced by mixed microbial populations of cooperators and cheaters has been examined in experiments in the literature using a protocol of periodic dilution to investigate the properties of resilience and adaptability to environmental changes. Data depicted on an appropriate phase diagram indicate, among other features, a stable equilibrium point at which cooperators and cheaters coexist (Sanchez and Gore, 2013). We present here a phenomenological analysis of these data focusing on an eco-evolutionary-game perspective. To that end, we work on an extension of the model proposed in Tao and Cressman (2007). It's original version takes into account changes of the total population density while the individuals experience a pairwise Prisoners Dilemma game. The extension devised here contains a dilution parameter to conform with the experimental procedure, in addition to a term accounting for Allee effects. In contrast to other descriptions proposed in similar contexts, however, the model here does not account for assortative encounters, group or kin selection. Nonetheless, it describes surprisingly well both qualitatively and quantitatively the features of the observed phase diagram. We discuss these results in terms of the behavior of an effective payoff matrix defined accordingly.

1. Introduction

Ecological and evolutionary dynamics taking place at similar timescales may drive certain interacting populations of individuals to an eco-evolutionary feedback, a situation under which ecological limitations may control evolutionary changes and vice-versa (Post and Palkovacs, 2009). Microbes have always been considered as promising candidates to exhibit eco-evolutionary cyclic processes although the experimental confirmation of such expectations occurred only a few years ago in an investigation of mixed population of budding yeast *Saccharomyces cerevisiae* (Sanchez and Gore, 2013). The individuals in these populations that posses the gene SUC2 *cooperate* since they codify for the production of *invertase*, an important enzyme to the process of the hydrolysis of sucrose into fructose and glucose, helping yeast to improve the use of the sucrose present in the medium. The other individuals considered in the experiments, the *"cheaters"*, do not have the gene SUC2. Despite this, cheaters may still benefit from the products, sucrose and fructose, left available in the medium by the cooperators, as a *public good*, avoiding in this way the cost of production. Data released from these experiments show the behavior of the fraction (frequency) $p(t)$ of cooperators present in the sample at each time t, analyzed as a function of the total population density $N(t)$. In particular, one can identify in these data a stable *coexistence equilibrium* reached by the two populations in the long-time regime. These results drew considerable attention in the literature due to their relevance in the context of the *dilemma of cooperation* in biology (Allen and Nowak, 2013).

In another set of related experiments (Dai et al., 2012), the authors examined questions regarding changes in resilience of single populations consisting only of the referred cooperators subject to dilution, the strength of which has been used as a controlling parameter. According to the authors, changing the level of dilution shall be equivalent to produce changes on the intrinsic mortality rate of the population since it consists of a periodic removal of a certain number of individuals in proportion to the quantity present at each instant of time. The evolution of the single population of cooperators was examined there under these conditions for diverse initial population sizes and different values of a defined *dilution factor* θ which also determines the behavior of the observed equilibrium points. A turning point bifurcation is identified in these data, occurring at the value of θ for which these equilibrium points coalesce (Dai et al., 2012).

Traditionally, such questions regarding the evolution of cooperation in competing populations have being addressed theoretically

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based on *evolutionary game theory* (Nowak and Sigmund, 2004) coupled to classical models from ecology (Lotka–Volterra) to take into account variations of the size N of the entire population under environment constraints, see for example (Cremer et al., 2011; Hauert et al., 2008; Zhang and Hui, 2011). This kind of formulation extends the dynamics described by the *replicator equation* conceived on the basis of evolutionary game theory for *pairwise encounters*, to describe exclusively evolutionary aspects of populations of constant sizes (Nowak, 2006).

In general terms, the long-time behavior observed in the experimental data in Sanchez and Gore (2013) has been predicted by some of these *eco-evolutionary models* (Hauert et al., 2008; Zhang and Hui, 2011). Yet, coexistence of cooperators and cheaters has been achieved using the *Prisoner's Dilemma Game* (PD Game) in such a context only under favorable conditions for assortative encounters (Bergstrom, 2003) or cooperation among individuals in groups of all possible sizes.

Conversely, the eco-evolutionary model proposed in Requejo and Camacho (2012) has been conceived in the absence of structured populations, kin selection, or assortative encounters. Yet, ecological contributions to the dynamics in this model are not described by Lotka–Volterra equations. Instead, the authors use a different representation in which ecological contributions are introduced into the elements of the payoff matrix defining with these an effective game. The dynamic payoffs assembled in this way set conditions under which the two kinds of individuals that compose the entire population are driven to a stable coexistence. Apparently however, the kind of competition among the different individuals investigated there show no correspondence with the quantities investigated in the experiments mentioned above.

A rather simple model has been proposed by the same authors of the experiments to explain their data. It is based entirely on Lotka–Volterra equations expressing competition for external resources but in the absence of a game. Because there are indications in the data suggesting that the maximum per-capita growth rate (or *intrinsic growth rate*) differs for each population, such differences are introduced into their model as the only way to distinguish cooperators from cheaters. In addition, the authors assume that these intrinsic growth rates change when the population reaches a certain critical density $N = N_C$, introduced as an external input. Thus, the complete model devised there comprises four equations to describe the time variation of the densities of cooperators and cheaters, two of them for total population density values $N < N_C$ and the other two with different parameters, for $N > N_C$. Dilution is not explicitly introduced into these equations but it is implemented in the numerical simulation for studying the dynamics.

Here, we resume the more traditional eco-evolutionary view on the basis of the model introduced by Tao and Cressman (TC). This model has been formulated originally to study stochastic effects on the evolution of competitive populations. Its deterministic limit accounts for variations of the total density N through Lotka–Volterra dynamics while individuals experience the pairwise PD Game in the absence of assortative encounters, group or kin selection. The long time dynamics of this model does not predict stability of cooperators, as expected. In the present work, we extend the deterministic version of this model to proceed into a phenomenological analysis of the aforementioned experiments. We explicitly introduce into the original TC model an extra factor to account for the dilution protocol. Also in addition to a Lotka–Volterra contribution that enters in the original formulation as a N-dependent background fitness, we take into account Allee effects (Stephens and Sutherland, 1999) and differences in the intrinsic growth rates of each population which, however, are conserved along the entire dynamics.

In Section 2 we explain our model and argue that it meets the requirements to describe specificities of the experiments. The analysis presented in Section 3 indicates that both its equilibrium and dynamic properties reproduce remarkably well the details reported in both experimental works (Dai et al., 2012; Sanchez and Gore, 2013). The consistence between these two phenomenological studies suggests that the model is surprisingly robust. To our knowledge, this is the first time that eco-evolutionary feedback resulting in coexistence is predicted on the basis of the original pairwise PD Game. The analysis presented in Section 4 in terms of the properties of an effective game defined accordingly, allows us to understand the maintenance of cooperation in the long time regime in terms of a Nash equilibrium between two competing populations that depends on N. Concluding remarks are in Section 6.

2. Eco-evolutionary model with dilution

We consider the time evolution of well mixed microbial populations of interacting cooperators and defectors (cheaters). Let $n_i(t)$ be the density (number of individuals per unit volume) of cooperators $(i = 1)$ and cheaters $(i = 2)$ present in the mixture of fixed volume at each time t. Then $N(t) = n_1(t) + n_2(t)$ is the total population density and $p_i(t) = n_i(t)/N(t),\ i = 1, 2$ the corresponding frequencies. We express the time variation of individual densities as:

$$\dot{n}_1 = n_1\left\{\left(\frac{N}{A} - 1\right)[(a_{11}p_1 + a_{12}p_2 + \lambda(1 - \beta N)] - \nu\right\}, \tag{1a}$$

$$\dot{n}_2 = n_2\left\{\left(\frac{N}{A} - 1\right)[(a_{21}p_1 + a_{22}p_2) + \delta(1 - \beta N)] - \nu\right\}. \tag{1b}$$

The curly brackets include the total *fitness* of each population. The dependence of the fitness on β and on the parameters $a_{ij}, i, j = 1, 2$ comprise precisely the original model proposed in Tao and Cressman (2007). β can be interpreted as the inverse of *carrying capacity* of the system. Thus, the factor $(1 - \beta N)$ in each of the equations above represents the usual Lotka–Volterra factor imposing limitations on population growth at relative high values of N, due to environment constraints. As noticed by the authors Tao and Cressman (2007), it can be ascribed, in the context, to a *background fitness* for both populations. The *payoff matrix* elements a_{ij} are constants representing the effects on fitness due to the interactions between any pair of individuals that play a *game* chosen to coincide with the *Prisoner's Dilemma Game (PD Game)*. Each a_{ij} is interpreted as the reward for each individual, either a cooperator (Co) or a cheater (Ch), that undergoes pairwise disputes. Following the usual representation of Nowak (2006) the PD Game payoff matrix is expressed as:

$$\begin{array}{c} \\ Co \\ Ch \end{array}\begin{pmatrix} Co & Ch \\ B - C & -C \\ B & 0 \end{pmatrix}, \tag{2}$$

with $B, C > 0$ and $B > C$. The constant B is a measure of the benefit received by a player in disputes (encounters) with a cooperator. In the present case, it corresponds to the benefit after using the considered substances (fructose and glucose). C is a measure of the total cost associated with the production of these substances which is spent by cooperators only.

The remaining factors in Eq. (1) modify the original equations of Tao and Cressman (2007), as explained next:

(i) The factor $(\frac{N}{A} - 1)$ was introduced following the suggestions made by the authors of the experiments (Sanchez and Gore, 2013), based on evidences in the data indicating that a minimum population size is needed to transform the environment into glucose rich. Only under this favorable condition would the benefit promoted by the cooperators be