A phenomenological analysis of eco-evolutionary coupling under dilution.

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May 11, 2017

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 [A. Sanchez, J. Gore, PLOs Biology, 11 (4), e1001547 (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 by Tao and Cressman Y. Tao, R. Cressman, Bull. Math. Biol. 69, 1377 - 1399 (2007). Its original version takes into account changes of the total population density while the individuals experience pairwise Prisoner’s Dilemma game. The extension devised here contains a dilution factor to be conform with the experimental procedure, in addition of a term accounting for Allee effects. Differently from 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.

Keywords: eco-evolutionary dynamics; game theory; cooperation; dilution

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1 Introduction

Ecological and evolutionary dynamics taking place at similar timescale 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 [1]. Microbes have always been considered as promising candidates to exhibit eco-evolutionary cyclic process although the experimental confirmation of such expectations occurred only a few years ago investigating mixed population of budding yeast \textit{Saccharomyces cerevisiae} [2]. The individuals in these populations that posses the gene SUC2 \textit{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 ”\textit{cheaters}”, do not have the gene SUC2. Despite of this, cheaters may still be benefited by the products, sucrose and fructose left available in the medium by the cooperators, as a \textit{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 special, 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 the their relevance in the context of the dilemma of cooperation in biology [3].

In another set of related experiments [4] one examined questions regarding changes on 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, this procedure shall be equivalent to produce changes on the intrinsic mortality rate of the population since it consists on 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 $\theta$ which also determines the behavior of the observed equilibrium points. A turning point bifurcation is identified in these data, occurring at the value of $\theta$ for which these equilibrium points coalesce [4].
Traditionally, such questions regarding the evolution of cooperation in competing populations have been addressed theoretically based on evolutionary game theory \cite{5} 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 \cite{6}, \cite{7}, \cite{8}. 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 \cite{9}.

In general terms, the long-time behavior observed in the experimental data in \cite{2} has been predicted by some of these eco-evolutionary models \cite{6}, \cite{7}. Yet, coexistence of cooperators and cheaters has been achieved using the Prisoner’s Dilemma Game (PDG) in such context only under favorable conditions for assortative encounters \cite{10} or cooperation among individuals in groups of all possible sizes.

Conversely, the eco-evolutionary model proposed in Ref.\cite{11} has been conceived in the absence of structured populations, kin selection, or assortative encounters. Yet, limitations of resources are not described by Lotka-Volterra equations, but are introduced directly into the elements of the payoff matrix that defines the game, expressing rewards and costs in terms of resources exchanged between each pair of individuals. The dynamic payoffs constructed in this way set conditions under which the population composed of two defined types of individuals is driven to a stable coexistence. The nature of both the competition investigated by the model and the predicted equilibrium, however, show no correspondence with the system 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 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) [12]. 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 pairwise PDG 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 [13] and differences on 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 indicate that both its equilibrium and dynamic properties reproduce remarkably well the details reported in both experimental works [2] and [4]. 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 PDG. 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 5.
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

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

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

The curly brackets include the total fitness of each population. The dependence of the fitness on \( \beta \) and on the parameters \( a_{ij}, i, j = 1, 2 \) comprise precisely the original model proposed in Ref. \[12\]. \( \beta \) 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 \[12\] 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 (PDG). 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 \[9\] the PDG payoff matrix is expressed as:

\[
\begin{pmatrix}
Co & Ch \\
Co & B - C & -C \\
Ch & B & 0
\end{pmatrix}
\]

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
to the production of these substances which is spent by cooperators only.

The remaining factors in (1) modify the original equations in Ref. [12], as explained next:

i) The factor \((\frac{N}{A} - 1)\) was introduced following the suggestions made by the authors of the experiments [2], 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 the benefit promoted by the cooperators would be shared among all other individuals present in the population at each time. This is introduced into the equations above as a strong Allee like effect that depends on the parameter \(A\) setting the scale at which such effects are expected to be relevant [13]. It affects negatively the rates for small population i.e., far from the carrying capacity of the system, \(\beta^{-1}\).

ii) The two constants \(\lambda\) and \(\delta\) for cooperators and cheaters, respectively distinguishes the intrinsic per-capita growth rates. Such difference has also been noticed in the experimental data and thus included by the authors in the analysis accompanying the experimental report [2].

iii) The factor linear in \(n_1\) in the first equation (or \(n_2\) in the second), with a proportionality constant \(\nu\) intends to reproduce the protocol of dilution introduced in the experiments [2]. According to this, the quantity of individuals removed after each interval of 24 hours corresponds to a fraction of the total present in the mixture at that instant of time.

Adding the two equations in (1) with the definition \(p \equiv p_1\) and using the payoffs as in (2) it results

\[
\dot{\hat{N}} = \hat{N} \left\{ \left(\frac{N}{A} - 1\right) [p(B - C) + (1 - \beta N)(p(\lambda - \delta) + \delta)] - \nu \right\} \tag{3}
\]

The expression for the time evolution of the frequency of cooperators \(p\) can then be derived with the aid of the identity \(\dot{n}_1 = \hat{p}N + p\hat{N}\), yielding

\[
\dot{p} = p(1 - p) \left(\frac{N}{A} - 1\right) [-C + (\lambda - \delta)(1 - \beta N)]. \tag{4}
\]

The system comprising the above non-linear equations (3) and (4) couples the two quantities \(N\) and \(p\) which are the focus of the cited experiments. This pair of equations constitutes the basis for the phenomenological analysis we perform hereafter. We emphasize that for intrinsic growth rates \(\lambda = \delta = 1\) and in the absence of both, dilution (\(\nu = 0\)) and Allee effects, these equations reduce
to the deterministic version of the equations proposed by Tao and Cressman \[12\]. These same conditions are necessary (but not sufficient) for this model to reduce to the deterministic equations of Frey and col. \[8\] to examine the transient behavior of cooperators.

3 Analysis

The non-trivial equilibrium points of the dynamics described by Equations \((3)\) and \((4)\), denoted as \((N(i), p(i))\), \(i = 1, 2, 3\) are listed below:

\[
p(1) = 0 \quad N_{(1)}^{\pm} = \frac{A}{2\beta} \left[ \left( \frac{1}{A} + \beta \right) \pm \sqrt{\left( \frac{1}{A} - \beta \right)^2 - 4 \frac{3\nu}{A^3}} \right] \quad (a)
\]

\[
p(2) = 1 \quad N_{(2)}^{\pm} = \frac{A}{2\beta} \left[ \left( \frac{1+(B-C)/\lambda}{A} + \beta \right) \pm \sqrt{\left( \frac{1+(B-C)/\lambda}{A} - \beta \right)^2 - 4 \frac{3\nu}{A^3}} \right] \quad (b)
\]

\[
p(3) = \frac{1}{\beta} \left( \frac{\nu}{(N(3)/A-1) - \frac{C}{\lambda} \delta} \right) \quad N(3) = \frac{1}{\beta} \left( 1 - \frac{C}{\lambda} \delta \right) \quad (c)
\]

\[
N(3) = \frac{1}{\beta} \left( 1 - \frac{C}{\lambda} \delta \right) \quad (5)
\]

In addition, the dynamics may drive the entire population to extinction since \(N = 0\) is also an equilibrium for all \(p \in [0, 1]\). The nature of each of these non-trivial points \((N(i), p(i))\) shall be determined, as usual, by linear analysis of Eqs. \((3)\) and \((4)\) examining the properties of the corresponding eigenvalues of the Jacobian matrix:

\[
J |_{(N(i), p(i))} = \left( \begin{array}{cc}
\frac{\partial N}{\partial N} & \frac{\partial N}{\partial p} \\
\frac{\partial p}{\partial N} & \frac{\partial p}{\partial p} 
\end{array} \right) |_{(N(i), p(i))} \quad (6)
\]

evaluated at each of these points \((N(i), p(i))\). If not otherwise specified, \(\nu\) shall be taken as a controlling parameter in the analysis of the two equilibrium points at the line \(p = p(1) = 1\).

The numerical values for the remaining parameters are adjusted phenomenologically by identifying each one of the equilibrium points observed in \[2\], namely \(\{(5.96 \times 10^4, 1), (516, 1), (5.78 \times 10^4, 0.086)\}\) with the corresponding expressions in the set \(\{ (N_{(2)}^+, 1), (N_{(2)}^-, 1), (N(3), p(3)) \}\). \[5\]. The

\[1\] The two sets of equations coincide if, in addition to the conditions stated in the text, both the strength of selection \(s\) and the global birth fitness function \(\nu\) introduced in Ref. \[8\] are taken equal to the unity.
two points located at \( p = 1 \) indicate two monomorphic equilibria, and the one internal characterize coexistence of the two populations. This procedure set the values of the parameters that will be used in the subsequent analysis. The results are compiled in Table 1. Using these parameters, we notice that \( N_{(1)}^\pm \) assume complex values, from what we conclude that the predicted equilibria at \((N_{(1)}^+, 0)\) and \((N_{(1)}^-, 0)\) are meaningless in the present context.

The numerical value for \( \beta \) is specified separately considering the two experiments. For the single population case [4], we found \( \beta = 5.831 \times 10^{-6} \). This has been obtained using the parameters in Table 1 and adjusting the two monomorphic equilibrium \(((N_{(2)}^+, 1), (N_{(2)}^-, 1))\) at the respective experimental points \((1.75 \times 10^5, 1), (1.5 \times 10^3, 1)\). For the experiments performed with both cooperators and cheaters [2], the two-population case, we found \( \beta = 1.7185 \times 10^{-5} \). These results are in consonance with the analysis performed by the authors of the experiments: their data indicate that the carrying capacity of the system with isolated population of cooperators is larger than the carrying capacity for the mixture of cooperators and cheaters. In turn, this suggests that under these experimental conditions, the cooperators are more efficient in using the available resources in the absence of cheaters.

3.1 The single population case

We shall now examine the data from the experiments reported in Ref. [4]. In these experiments one observes the properties of yeast populations of cooperators, in the absence of the cheaters, with respect to changes in the considered dilution factor \( \theta \). From the perspective of the present
model, this corresponds to fix \( p = 1 \) in the above equations and then examine the behavior of the solutions under changes on \( \nu \).

Notice first that for \( p = 1 \) (absence of cheaters) one has \( \frac{\partial p}{\partial N} = 0 \). Thus, the corresponding eigenvalues of \( J|_{(N(i),p(i))}, i = 1,2 \) are real. Each of the two equilibrium points at \( p = 1 \), i.e. \((N^\pm(2),1)\), represents a monomorphic equilibrium such that

\[
\begin{align*}
\left( \frac{\partial N}{\partial N} \right)_{(N^+_i,1)} & = -\Delta_2 N^+_i < 0 \\
\left( \frac{\partial N}{\partial N} \right)_{(N^-_i,1)} & = +\Delta_2 N^-_i > 0
\end{align*}
\]

with \( \Delta_2 \equiv \sqrt{\left(\frac{1+(B-C)/A - \beta}{A}\right)^2 - 4\frac{\beta \nu}{A^2}} \). From this we conclude that \((N^+_i,1)\) is stable (attracting) whereas \((N^-_i,1)\) is unstable (repelling) equilibrium point.

We then examine the behavior of \( N^+_i \) and \( N^-_i \), Eqs. (5 (b)) as functions of the dilution \( \nu \), the remaining parameters fixed as in Table 1. The results are shown in Figure 1. The shape of the curves reproduces the referred experimental study in which one identifies a turning point bifurcation [14]. Our results predict this bifurcation and explain its origin as occurring at a value of \( \nu \) for which \( \Delta_2 = 0 \) so that the points \((N^+_i,1)\) and \((N^-_i,1)\) coalesce.

![Figure 1](image.png)

**Figure 1:** The behavior of the equilibrium points \((N^+_i,1)\) (solid) and \((N^-_i,1)\) (dashed) as the parameter \( \nu \) changes.

Let us now examine the time evolution of the density of cooperators \( n_1(t) \) for \( p = 1 \), as solutions
to

\[ n_1 = n_1 \left\{ \left( \frac{n_1}{A} - 1 \right) \left[ (B - C) + (1 - \beta n_1) \lambda \right] - \nu \right\}. \]  

(8)

Numerical results for \( n_1(t) \), obtained from this equation using \( \nu = 507.21 \) and \( \nu = 2480.0 \) (corresponding to the experimental \( \theta = 750 \) and \( \theta = 1400 \), respectively) are shown in Figures. 2(a) and 2(b) for several initial population densities \( n_1(0) \). In Figure 2(a) we see that the trajectories initiating at relative high densities approach the stable equilibrium point \( (N^+_{(2)}, 1) \), whereas the populations initiating at densities below the unstable equilibrium point \( (N^-_{(2)}, 1) \) go extinct. Because \( N^-_{(2)} \) increases with \( \nu \) (see expression (5) (b)) we explain in this way the data indicating that increasing \( \nu \) may drive population to extinction even for those high initial values for which it would have been survived if \( \nu \) were lower, see Figure 2(b).

Figure 2: Time evolution \( n_1(t) \) of single populations of yeast cooperators according to Eqs. (1) for \( p = 1 \). Population go extinct if initial conditions \( n_1(0) \) are chosen below \( N^-_{(2)} \) (dashed); otherwise population is driven to the stable equilibrium \( N^+_{(2)} \) (solid)

The results in Figures 1 and 2 suggest that the model proposed here describes very accurately the behavior of the single populations of cooperator yeast, as studied in [4]. In turn, this supports the idea that the analytical results for \( N^+_{(2)} \) and \( N^-_{(2)} \) as functions of the parameters may be useful to foresee the conditions leading to the critical slowing down of these populations under external perturbations, as expressed in the experiments through the dilution protocol.
3.2 The two population case

We use the numerical values in Table 1, also $\beta = 1.7185 \times 10^{-5}$ as specified above, and $\nu = 73.9$ to proceed into the phenomenological analysis of the experimental data in Ref. [2]. A global view of the $N \times p$ phase space of the model, Eqs. (3) and (4), can be achieved by means of the nullclines represented in Figure 3. The $N$-nullclines are obtained from the solutions to the equation (3) for $\dot{N} = 0$, which are: i) the line $N = 0$ (not represented) and ii) the curve defined by the set of points $(N, p)$ satisfying

$$\left(\frac{N}{A} - 1\right)\left[p(B - C) + (1 - \beta N)(p(\lambda - \delta) + \delta)\right] - \nu = 0. \quad (9)$$

A trace of this curve is shown in Figure 3 (solid). The $p$-nullclines also depicted on the same figure (dashed) correspond to the solutions to the equation $\dot{p} = 0$, resulting $p = 0$, $p = 1$, $N = A$ and $N = (\lambda - \delta - C)/(\beta(\lambda - \delta))$.

Figure 3: The set of $N$-nullclines (solid) and the $p$-nullclines (dashed) represented on the $(N \times p)$ phase diagram.

The entire set of equilibrium points predicted by the model are depicted at the encounters of the $p$-nullclines with the $N$-nullclines. It is worth noticing in these results that the shape of curve defined by the set of points satisfying (9), seems to approach very well the trace of the curve identified by the authors of the experiments as a separatrix [2]. In fact, our results indicate that starting from values above this curve and for $p < 1$ the population is driven to the internal
equilibrium at \((N(3), p(3))\) representing coexistence of cheaters and cooperators. This is illustrated in Figure 4, which shows the outcomes of numerical solutions to (3) and (4) for the time evolution \(N(t)\) and \(p(t)\), represented parametrically on the phase diagram \(N \times p\) for several initial conditions \((N(0), p(0))\).

![Figure 4: Time evolution of mixed populations of yeast represented parametrically on the \((N \times p)\) phase space for diverse initial conditions \((N(0), p(0))\). The arrows point to the direction of the dynamics as the time increases. The two points used as references are \(N_3 = 57800\) and \(\beta^{-1} = 58190\) (indicated).](image)

The complete phase diagram of the model is represented in Figure 5. These results should be compared qualitatively and also quantitatively with the corresponding diagrams obtained experimentally for the two population case.

The nature of the internal equilibrium point \((N(3), p(3))\) shall be disclosed through the eigenvalues \(\Gamma^{\pm}\) of the Jacobian matrix \(J|_{(N(3), p(3))}\) evaluated at the referred point. Defining \(Q(3) = \left(\frac{N(3)}{A} - 1\right)\), we write

\[
J|_{(N(3), p(3))} = \begin{pmatrix}
\frac{N(3)}{Q(3)} \left(\frac{\nu}{A} - \beta(\lambda p(3) + \delta(1 - p(3)))(Q(3))^2\right) & N(3)Q(3)B \\
-\beta p(3)(1 - p(3))Q(3)(\lambda - \delta) & 0
\end{pmatrix}
\]

and the corresponding eigenvalues as \(\Gamma^{\pm} = X \pm \frac{1}{2} \sqrt{\Delta}\), where
The complete phase diagram of the model. The insert shows the field near the internal equilibrium point represented by the simulated trajectories that illustrate the spiraling dynamics following different initial conditions.

\[ X = \frac{N_{(3)}}{2Q_{(3)}} \left[ \frac{\nu}{A} - \beta(\lambda p_{(3)} + \delta(1 - p_{(3)}))(Q_{(3)})^2 \right] \]

\[ \Delta = \left( \frac{N_{(3)}}{Q_{(3)}} \left[ \frac{\nu}{A} - \beta(\lambda p_{(3)} + \delta(1 - p_{(3)}))(Q_{(3)})^2 \right] \right)^2 - 4N_{(3)}p_{(3)}(1 - p_{(3)})B\beta(\lambda - \delta)(Q_{(3)})^2 \]  

(11)

Since \( p = p_{(3)} \) is the only non-trivial equilibrium solution for the frequency of cooperators (i.e., different from \( p = 0 \) or \( p = 1 \)), it is suggestive to look for the conditions under which \((N_{(3)}, p_{(3)})\) exhibit properties of an attractive node as identified in the experimental data, and also as suggested in Figure 5 (see insert). This requires \( \Delta < 0 \) and \( X < 0 \). Indeed, these two conditions are fulfilled by the numerical choices for the parameters as in Table 1.

In retrospective, this means that by identifying the coordinates of the equilibrium points predicted by the model with the corresponding experimental, one concludes that the internal equilibrium point predicted theoretically is an attractive node, precisely as observed. We can also obtain from our results that in contrast to the equilibrium points at \( p = 1 \) there is no bifurcation associated with \((N_{(3)}, p_{(3)})\) since it remains attractive for all positive \( \nu \).
4 Discussion

Observe that for equal growth rates \( \lambda = \delta \), Eqs. (3) and (4) present no solutions for internal equilibrium points. The invasion condition for fixation of cooperation, namely \( \frac{1}{n_1} \frac{dn_1}{dt} > \frac{1}{n_2} \frac{dn_2}{dt} \) is equivalent to \((\lambda - \delta)(1 - \beta N) > C\) which can be satisfied if \( \lambda \neq \delta \) for a certain range of parameters in all regions of the phase plane for which \( N < 1/\beta \). Conversely, even taking \( \lambda \neq \delta \), and also \( B \neq C \) such that \( B, C > 0 \), but in the absence of the factor controlling Allee effects, one would still find a solution to the internal equilibrium \((N(3), p(3))\) although in this case the bifurcation predicted at the projection line \( p = 1 \) would be suppressed.

The existence of the attractive node as a result from an eco-evolutionary feedback can be understood by examining the behavior of the different contributions to Eqs. (3) and (4). For \( N \gtrsim 1/\beta \), the environment effects weighted by the difference between the intrinsic growth rates \((\lambda - \delta)(1 - \beta N)\) dominates the dynamics: the entire population and in particular the density of cooperators in the population decrease fast since \((\lambda - \delta)\) is large and positive. As \( N \) decreases reaching values such that \( N \lesssim 1/\beta \), then \( N \) continues decreasing while dilution effects dominates. The frequency \( p \) however, can revert its behavior since the cost \(-C\) represented in (4) contributing negatively to the fitness of cooperators can be overcome by the growth rate contribution. As \( p \) increases, both the game and intrinsic growth rate contributions in Eq. (3) will eventually overcome the effects of dilution so that the population as a whole increases until reaching the carrying capacity. At this point the behavior of \( N \) would follow the sum of the contribution due to the game, namely \( p(B - C) \) and the one due to dilution. While this combination assumes positive values, \( N \) continues to increase until \((\lambda - \delta)(1 - \beta N)\) dominates the dynamics with a large negative contribution and the feedback cycle resumes. What is important to notice is that this behavior is largely anchored on the process of dilution and on the difference between the intrinsic growth rates. This comes in addition to the effects more often discussed in the literature regarding the contributions to the fitness due to the Lotka-Volterra and game at different regions of the phase space.

The behavior of the solutions near \((N_3, p_3)\) can also be investigated from the point of view of the two populations, equations (11). For this we define an effective game, with payoffs \( \overline{a_{ij}} \) \( i, j = 1, 2 \) being functions of both \( N \) and \( \nu \), such that
where $ECo$ and $ECh$ refer to effective cooperation and effective defect (cheat) strategies, respectively. With these definitions we rewrite Eqs. (1) as

\begin{align*}
\dot{n}_1 &= n_1 \left( \overline{a}_{11} p + \overline{a}_{12} (1 - p) \right) \equiv n_1 F_1(N, p) \\
\dot{n}_2 &= n_2 \left( \overline{a}_{21} p + \overline{a}_{22} (1 - p) \right) \equiv n_2 F_2(N, p)
\end{align*}

expressing in this way the fitness for cooperators $F_1(N, p)$ and for cheaters $F_2(N, p)$ in terms of the effective payoffs $\overline{a}_{ij}$. In turn, the time variations $\dot{N}$ and $\dot{p}$ can be expressed in terms of $F_1$ and $F_2$ as

\begin{align*}
\dot{N} &= n_1 F_1 + n_2 F_2 \\
\dot{p} &= p(1 - p)(F_1 - F_2)
\end{align*}

Because we want to examine the behavior of this effective game near $(N(3), p(3))$ we observe in particular that

\begin{align*}
\overline{a}_{11}(N(3)) &= \overline{a}_{21}(N(3)) = \left( B + C \frac{\delta}{\lambda + \delta} \right) Q(3) - \nu \\
\overline{a}_{12}(N(3)) &= \overline{a}_{22}(N(3)) = \left( C \frac{\delta}{\lambda + \delta} \right) Q(3) - \nu.
\end{align*}

From this, it follows that $F_1(N(3), p) = F_2(N(3), p)$ for all $p \in [0, 1]$. Evidently, for variable $N$ the condition $F_1 = F_2$ is not sufficient to characterize equilibrium as it would be the case of the replicator dynamics for which $N$ is a conserved quantity \cite{9}. For variable $N$, the required condition for equilibrium is that $F_1 = F_2 = 0$ which is fulfilled at the point $(N(3), p(3))$.

The four entries of the effective payoff matrix (12) are represented in Figure 6 as functions of $N$, near $N(3)$. The parameters used in the plot are those from in Table 1, $\beta = 1.7185 \times 10^{-5}$ and $\nu = 73.9$. Observe that the line $N = N(3)$ (dashed) sets out two regions within each of which
the effective payoffs characterize different games. For \( N \gtrsim N_3 \) the inequalities \( \overline{a}_{21}(N) > \overline{a}_{11}(N) > \overline{a}_{22}(N) > \overline{a}_{12}(N) \) hold so that in this region the effective game corresponds to a PDG for which the effective defect is an ESS (Evolutionary Stable Strategy), the dominant strategy for both players. In the region for which \( N \lesssim N(3) \) one has \( \overline{a}_{11}(N) > \overline{a}_{21}(N) > \overline{a}_{12}(N) > \overline{a}_{22}(N) \) corresponding to a Harmony game for which the dominant strategy for both players is the effective cooperation, the ESS in this case. At \( N = N(3) \), one has \( \overline{a}_{11}(N(3)) = \overline{a}_{21}(N(3)) \) and \( \overline{a}_{12}(N(3)) = \overline{a}_{22}(N(3)) \) indicating that both effective defect and effective cooperation are Nash equilibria at the coexistence condition but none of these is an ESS.

A similar analysis has been performed in Ref. [11]. Although the eco-evolutionary model there has also been conceived in the absence of structured populations, the correspondence to our analysis is not immediate because their dynamic payoff matrix has been defined \emph{a priori}, directly in terms of the resources exchanged between pairs of individuals. The effective matrix built up here comprises the original game, the dilution factor and the ecological effects, what allowed us to evaluate separately each contribution to the dynamics discussed here.

Figure 6: Effective payoffs \( \overline{a}_{ij}, i, j = 1, 2 \) as functions of \( N \), near \( N_3 \) (dashed). The regions where the strategies characterize different games are explicitly indicated. For Harmony game it is limited by \( N_3 \) and the solution \( N \) to \( \overline{a}_{12} = \overline{a}_{21} \) (left dotted). For PD Game it is limited by \( N_3 \) and the solution \( N \) to \( \overline{a}_{11} = \overline{a}_{22} \) (right dotted).
5 Conclusions

The phenomenological analysis presented above suggests that the dilution process introduced into the considered experiments primarily to examine properties of resilience of the populations under changing environments, may be crucial for observing coexistence of cooperators and cheaters in the mixed population of yeast. The analytical results have been achieved in terms of parameters strictly related to the populations traits or to their interactions with the environment. The strength of dilution is a control parameter. We believe that this study can be useful to make further predictions on the properties of such systems under different conditions. For example, it shall be of interest to examine the limits for population extinction by analyzing the behavior of the N-nullcline Eq.9, with respect to changes in the diverse parameters. This curve appears to approach very well the trace of the separatrix identified in the data.

The analysis of the defined effective game offers an alternative to understand the outcomes of the dynamics in terms of the nature of strategies that change within each region of the considered phase space.

6 Acknowledgements

The financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Brazil under Grant No. 2015/17395-3 is gratefully acknowledged.

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