

Coexistence of Cooperators and Defectors in Well Mixed Populations Mediated by Limiting Resources

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Traditionally, resource limitation in evolutionary game theory is assumed just to impose a constant population size. Here we show that resource limitations may generate dynamical payoffs able to alter an original prisoner's dilemma, and to allow for the stable coexistence between unconditional cooperators and defectors in well-mixed populations. This is a consequence of a self-organizing process that turns the interaction payoff matrix into evolutionary neutral, and represents a resource-based control mechanism preventing the spread of defectors. To our knowledge, this is the first example of coexistence in well-mixed populations with a game structure different from a snowdrift game.

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Cooperative behavior is common in nature, and necessary for the evolutionary appearance of higher selective units—such as eukaryotic cells or multicellular life—from simpler components [1]. However, the survival of the fittest under the action of natural selection seems to foster selfish behavior, taking advantage of other individuals [2,3]. It is therefore intriguing how cooperative behaviors can emerge and survive in a world ruled by natural selection. This issue is frequently addressed in the context of evolutionary game theory, where the prisoner's dilemma (PD) game [4] has been used as a paradigm for understanding the evolution of cooperation, as its simplified noniterated version is the worst scenario for the survival of cooperation [5]; if interactions between individuals follow a PD and reproductive success grows with payoffs, cooperative behavior is led to extinction in large well-mixed populations [5,6]. In the last decades some mechanisms have been found allowing cooperative behaviors to survive in the absence of genetic relatedness, but none of them works for the simplified PD in the absence of features such as memory [7,8], reputation gain [9], network structure [10–12], or other sensory inputs [13,14].

Here we study the influence of resource limitation on the emergence of cooperation. We find that in addition to imposing a finite population size, as usually assumed in evolutionary game theory [4,5,7–15], it may generate dynamic payoffs [16–18]. In the absence of resource limitation, the interactions between cooperators and defectors fulfil a simplified PD, as determined by the selfish strategy, and thus cooperators extinguish, as expected in evolving well-mixed populations. Surprisingly, resource limitation may drive a self-organizing process that allows for stable coexistence

between cooperators and defectors. In contrast to previous studies including ecological features, in which coexistence happens only in public goods games with variable interaction group sizes [19], it is transient [20] or requires spatial structure [21,22], here we find stable coexistence for

pairwise interactions without population structure. This stable coexistence resembles the homeostatic equilibrium in the daisy world [23,24], as both are mediated by environmental factors driving the system out from equilibrium.

In order to study this, we develop a model consisting of an evolving well-mixed population of self-replicating individuals that receive resources from the environment and exchange resources during interactions. No population structure, memory, learning abilities, or any other sensory inputs are assumed. Each individual i is represented by its internal amount of resources E_i and its strategy, namely, cooperate (C) or defect (D). The internal amount of resources may be interpreted as the amount that belongs to it, independently of why or how. The environment provides resources in portions E_0^i per unit time to randomly chosen individuals independently of their strategy, thus, not modifying the structure of the payoffs. For simplicity, we impose a constant total resource influx E_T , though results also apply for non constant fluxes (see [25]). If the amount of resources of an individual exceeds a value E_s , it splits into two identical copies with half its internal amount of resources.

Defectors are characterized by the maximum amount of resources associated to an interaction: the cost spent (E_c) for stealing a reward (E_r) from the coplayer. If the internal resources of a defector are smaller than the cost E_c , it does not pay the cost nor receive the reward. If the interaction partner has resources below the reward, the entire amount of resources is sequestered. We assume that these quantities are inherited without mutation; they represent physiologic, morphologic or genetic characteristics intrinsic to individuals and cannot be modified by choice.

We consider large populations, simultaneous interactions and $E_r > E_c > 0$, although the same results are obtained if one assumes that every interaction is carried out by a donor and received by the coplayer [18]. The interaction matrix determined by the strategies is thus

$$\begin{array}{c} C \\ D \end{array} \begin{array}{cc} C & D \\ \left(\begin{array}{cc} 0 & -E_r \\ \Delta E & -E_c \end{array} \right) \end{array} \quad (1)$$

and equals a simplified PD, with defectors paying a cost E_c and obtaining a net reward $\Delta E = E_r - E_c > 0$ (payoffs for the row player, we will omit C and D in the following matrices).

Finally, we assume that the limiting resource necessary for reproduction provides no advantage for keeping alive; therefore deaths occur at random with a frequency (rate) f relative to receiving resources and interacting, which happen equally frequently.

According to the PD structure of resource exchanges among cooperators and defectors in the absence of resources limitation, defectors should have a larger resource intake, reaching faster the splitting bound E_s and thus reproducing quicker (i.e., fitness is proportional to resource exchanges). Therefore one would expect homogeneous populations of defectors as the outcome of the evolutionary process. However, the limitation of resources generates a distribution of resources among individuals in the population. As a consequence, the average reward stolen from cooperators E'_r may decrease below E_r , since the internal resources of some cooperators may fall below this quantity, thus modifying the payoffs. If the net average benefit of defectors $\Delta E' = E'_r - E_c$ remains negative over all the time, the payoff matrix does not correspond to a PD anymore; it is turned into a harmony game and cooperation becomes the dominant strategy. Simulations show that the model yields the latter behavior and also, more interestingly, stable coexistence of cooperation and defection (Fig. 1); see [25] for details on the simulations. Dominance of cooperation was already found in a previous model assuming that resources are necessary for keeping alive [18] which, however, did not provide coexistence.

Coexistence in this scenario requires a complex feedback process whose exact analysis is quite difficult because of the complex nonlinearities involved in the dynamics. However, a simple quantitative reasoning exhibits the logic of this feedback and allows for an analytic estimation of the final stable state of the system. Let us note that an increase in the number of defectors over the equilibrium value would cause an overexploitation of cooperators, thus, reducing their resource content. This would have two effects: (i) it would reduce cooperators' reproduction rate (fitness) because they become farther from the splitting bound E_s , and (ii) it would also decrease the average reward obtained by defectors, which thereby reduces their fitness. If the second effect dominates over the first one, then stable coexistence becomes possible, as the feedback pushes the system back to equilibrium. A similar argument applies for a decrease in the number of defectors.

The entire system is in equilibrium when the resource influxes and outfluxes in the populations of both

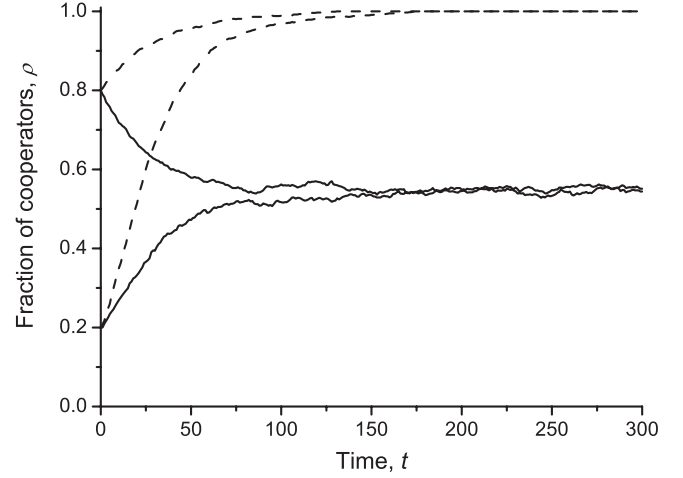


FIG. 1. Simulation results for the evolution of the fraction of cooperators ρ for two different values of the reward E_r and cost E_c associated to the selfish strategy (averaged over 10 runs). In some cases the simplified PD payoff structure is modified by the limitation of resources, which allows for coexistence of cooperation and defection (solid line) and dominance of cooperation (dashed line). The final stable states are independent of the initial ρ and N . Parameters: $f = 1$, $E_s = 1000$, $E_T = 8200000$, $E_c = 660$; solid line, $\Delta E = 310$; dashed line, $\Delta E = 10$.

cooperators and defectors cancel out. The balance of resources in these subpopulations contains three contributions: environmental supply, deaths, and interactions. They are expressed in the following equations

$$\frac{dE^C}{dt} = N_C[E_0 - f\bar{E}^C - pE'_r(1 - \rho)], \quad (2)$$

$$\frac{dE^D}{dt} = N_D[E_0 - f\bar{E}^D - pE_c + pE'_r\rho]. \quad (3)$$

E^j , \bar{E}^j and N_j denote, respectively, the total resource content, average resources per individual, and number of individuals of the subpopulations $j = C, D$; $E_0 = E_T/N$ is the mean amount of resources received by an individual per unit time, with $N = N_C + N_D$ the instantaneous population size; $\rho = N_C/N$ is the fraction of cooperators; f is the death probability per individual and interaction, and p the fraction of the population of defectors able to pay the cost (i.e., with $E_i > E_c$).

In equilibrium, the populations of cooperators and defectors become constant in time so that the resource pools E^D and E^C reach a constant value. One thus finds the equilibrium condition

$$p(E'_r - E_c) = f[\bar{E}^D - \bar{E}^C]. \quad (4)$$

This shows that the coexistence depends on the death frequency f . For simplicity, we will assume in this analytic derivation that deaths happen much less frequently than interactions, i.e., the limit $f \rightarrow 0$; this corresponds to many interactions in a lifetime, when the effects of interactions

become more relevant. Other f values are studied through simulations [25]. Since ρ never equals zero due to the constant resource influx, Eq. (4) reduces in this limit to

$$E_c = E'_r, \quad (5)$$

which states that, in equilibrium, the cost paid by defectors equals the reward stolen from cooperators. In order to analytically predict the region of coexistence in the parameters space and the corresponding population composition, we need to know the average reward E'_r in terms of the parameters E_r and E_c . This implies the calculation of the equilibrium distribution of resources for cooperators, which is a difficult task due to the nonlinearities involved in the dynamics. Instead, we can give a rough heuristic estimate as follows. The lower the fraction of cooperators in the population, the more frequent any cooperator meets a defector, thereby cooperators become overexploited and their average internal resources decrease. Thus, the average reward E'_r is expected to decrease as ρ decreases. We assume a linear relationship between both quantities, $E'_r = \alpha\rho$, with α a positive constant. For the moment, we consider that when ρ is close to 1, the effect of defectors is expected to be small, so that at first order, we approximate the resource distribution of cooperators as uniform. For uniform distributions [25], one finds $E'_r = E_r - E_r^2/(2E_s)$. We thus propose

$$E'_r = \rho \left(E_r - \frac{E_r^2}{2E_s} \right). \quad (6)$$

By combining Eq. (6) with Eq. (5), one obtains an expression for the equilibrium fraction of cooperators

$$\rho = \frac{E_c}{E_r - E_r^2/2E_s}. \quad (7)$$

In order to analyze in detail the behavior of the model, we have performed extensive numerical simulations covering the whole parameters space. They confirm the stability of the coexistence for all death frequencies, and show that the final stable state is independent of the initial conditions and resource influx (and thus, final population size) [25]. Figures 2(a) and 2(b) show a good qualitative agreement between the predicted ρ and the outcome of the simulations. Deviations root in the linear approximation assumed in Eq. (6) (see [25]).

Let us notice that the obtained stable coexistence between cooperators and defectors presents a new outcome in the context of two-player games, where a stable mixed state is only expected in Snowdrift (or Hawk-Dove) games, which have a payoff structure different from ours. In general, symmetric two-player games can be described through the interaction matrix [26]

$$\begin{pmatrix} 0 & a \\ b & 0 \end{pmatrix}, \quad (8)$$

where coefficients a and b are assumed to be constant. Applying the replicator equation [6,15,26] to analyze the evolution of the population, three cases are possible [see Fig. 2(c)]: (i) dominance of one strategy (when a and b differ in sign); this is the case of the noniterated PD, where defection always wins; (ii) bistability (if both a and b are negative); in this case the final state is homogeneous and depends on initial conditions; this is what happens in stag hunt games, where coordinating with the partner pays; and (iii) coexistence (if both a and b are positive); this is what

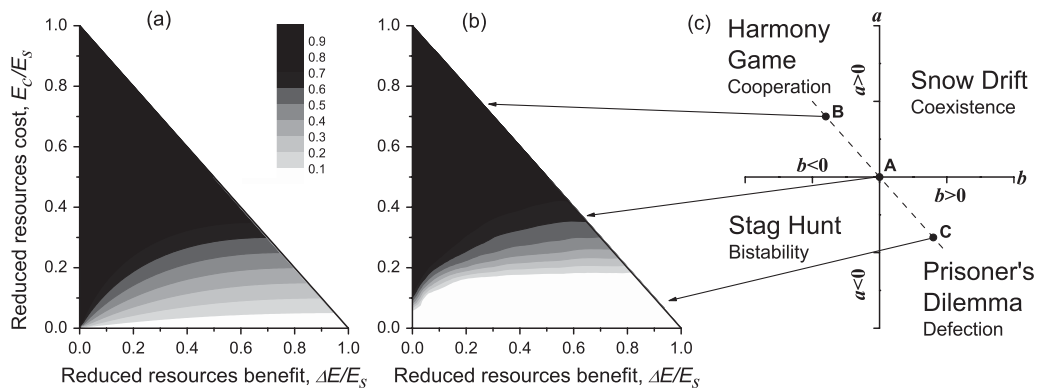


FIG. 2. Final fraction of cooperators ρ represented in terms of resources cost (E_c) and net benefit ($\Delta E = E_r - E_c$) of the selfish strategy. In black $\rho = 1$, in white $\rho = 0$. One observes well defined regions of coexistence of cooperation and defection, as well as regions where cooperation is the dominant strategy. In (a) prediction according to Eq. (7) (see [25] for a highly improved analytical prediction); in (b) results of agent-based simulations averaged over 50 runs ($f = 0.01$, $E_s = 1000$, $E_T = 420\,000$). In (c) we show the different games corresponding to a 2×2 matrix; the dashed line shows the places where the payoffs in the model lay [see Eq. (10)]. Point A denotes the final payoffs for coexistence states, where the payoff matrix is evolutionary neutral; points B and C are examples of final payoffs for situations where cooperation and defection are dominant, respectively.

occurs in Snowdrift games, when it always pays to play the opposite of the coplayer.

In our model, fitness is directly proportional to resource exchanges, because individuals reproduce when their resources overcome an upper bound that is the same for cooperators and defectors. Resource exchanges come from the environment and from interactions. The resource supply from the environment is the same for defectors and cooperators; it just provides a constant to all fitness values and can be omitted in the fitness matrix. The latter is thus ruled by the average resources exchanged through interactions, which aside from a scale factor translating resource exchanges to fitness, is [18]

$$\begin{pmatrix} 0 & -pE'_r \\ p\Delta E' & -pE_c \end{pmatrix}. \quad (9)$$

As stated above, p stands for the fraction of defectors whose resources exceed the cost E_c . Let us note that this factor does not change the payoff structure in any case, as it multiplies all payoffs, and it only modifies the time scale of the dynamics. The interaction matrix can be rewritten in the form of matrix (8) by adding pE_c to the second column (as adding a constant to a column does not affect the replicator dynamics [6,26]):

$$\begin{pmatrix} 0 & -p\Delta E' \\ p\Delta E' & 0 \end{pmatrix}, \quad (10)$$

i.e., $a = -b = -p\Delta E'$. According to the classification given above, this payoff matrix leads to dominance of one strategy whenever $p\Delta E' \neq 0$. In the absence of resource limitation, $\Delta E' = \Delta E > 0$ and we have a PD. If resources are limited, there exists a wide range of parameters for which the $\Delta E'$ is tuned to zero for a specific mixture of cooperators and defectors [see Figs. 2(a) and 2(b)]; thus, the stable equilibrium is the result of a dynamical self-organizing process and not of the game structure itself [see Fig. 2(c)].

We can use the payoff matrix (10) to gain further insight into the stability of the coexistence state found in our model. In Eq. (6) we proposed the rough estimate $E'_r = \alpha\rho$ for the net benefit of defectors, with $\alpha > 0$. Thus, we have $\Delta E' = \alpha\rho - E_c$. Aside from a positive factor relating fitness and payoffs in Eq. (10), the replicator equation yields

$$\frac{d\rho}{dt} = -\rho(1-\rho)p\Delta E = p\rho(1-\rho)(E_c - \alpha\rho), \quad (11)$$

which supplies three equilibria, $\rho = 0, 1$, and E_c/α . Since $p > 0$, the mixed state is the stable one for $0 < E_c/\alpha < 1$, in agreement with the stability of the coexistence states observed in the simulations.

We have presented a scenario which allows for stable coexistence of unconditional cooperators and defectors in well-mixed populations under pairwise interactions. This result is quite robust, since it does not depend on initial

conditions, and it is also observed in small populations—though in this case fluctuations may lead to the extinction of one strategy—and under nonconstant influx of resources [25]. This stable coexistence roots on a self-organizing process which implicitly includes the environment, and it is the feedback induced by environmental constraints and defectors' behavior which turns the payoff matrix into evolutionary neutral and allows for the stability of the system. The evolutionary neutrality of the system (environment + individuals) and its stability as a whole, might be a first step towards the emergence of new units of selection by providing a self-organizing mechanism preventing the spread of selfish mutants alternative to central control (see [1]).

Let us also remark that, in contrast to previous models in evolutionary dynamics, the model presented here explicitly sets the issue in a nonequilibrium context, where a (resource) flux drives the system out from equilibrium. The observed self-organized coexistence state may be seen as another example of the self-organizing processes found in nonequilibrium systems such as, for instance, the unexpected oscillations in Belusov-Zhabotinsky reactions. This perspective may bear interest in economic contexts, another classical field of evolutionary game theory, where some authors claim that economic systems should be modeled as open, nonlinear nonequilibrium systems instead of the closed, equilibrium view dominant in traditional economics [27,28].

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