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Evolution of cooperation mediated by limiting resources: Connecting resource based models and evolutionary game theory

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Abstract

Recent studies have shown that constraints on available resources may play an important role in the evolution of cooperation, especially when individuals do not posses the capacity to recognize other individuals, memory or other developed abilities, as it is the case of most unicellular organisms, algae or even plants. We analyze the evolution of cooperation in the case of a limiting resource which is necessary for reproduction and survival. We show that, if the strategies determine a prisoner's dilemma, the outcome of the interactions may be modified by the limitation of resources allowing cooperators to invade the entire population. Analytic expressions for the region of cooperation are provided. Furthermore we derive expressions for the connection between fitness, as understood in evolutionary game theory, and resource exchanges, which may be of help to link evolutionary game theoretical results with resource based models.

Keywords: Evolutionary game theory; cooperation; limiting resources; prisoner's dilemma.

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1. INTRODUCTION

Since Darwin published the theory of natural selection (Darwin 1859), the question of how cooperation is established and evolves has centered the attention of many scientists, as it seems to contradict the principle of maximizing one's own fitness. The first mechanism found to promote cooperation, kin selection (Hamilton 1964), states the conditions that make beneficial to help individuals sharing your own genes, even if it is costly for yourself. Later studies focused in how cooperation evolves in the absence of genetic relatedness. Two main frameworks are widely used for this purpose.

The first framework is evolutionary game theory (Maynard Smith & Price 1973, Maynard Smith 1982, Hofbauer & Sigmund 2003), which models the interactions from an individual's point of view, centering attention on the strategies of the interacting agents but without regarding directly to ecological dynamics. In it, the payoffs obtained by individuals after an interaction are expressed as fitness, which are usually fixed values determined by the strategies of the interacting individuals and do not depend explicitly on environmental factors. The study of the prisoner's dilemma (PD) game using this framework (Doebeli & Hauert 2005, see caption of Table 1) allowed scientists to find new mechanisms for the evolution of cooperation, such as direct and indirect reciprocity (Trivers 1971, Axelrod & Hamilton 1981, Nowak & Sigmund 1998), the existence of interaction networks (Ohtsuki et al. 2006, Roca et al. 2009) or the existence of the so called green beards (Riolo et al. 2001). These mechanisms require the existence of assortment between cooperative individuals (Fletcher & Doebeli 2009), which allows them to avoid the exploitation by selfish ones, also called defectors. In order to achieve this assortment, the mechanisms require individuals to have developed features such as memory, capacity to recognize their partners or ability

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to use reputation concepts. Though there exist some examples of organisms that posses a gene able to cause the complex effect necessary for the green-beard effect (Riolo et al. 2001, Queller et al. 2003), namely genes causing behaviours that benefit individuals containing identical genes (Gardner & West 2010), thus creating assortment, the requirement of developed abilities prevents most of the previous mechanisms to be applicable to simple forms of life, such as bacteria, algae or even plants. Indeed, the cooperation necessary for the first major transitions in evolution (Maynard Smith & Szathmáry 1995), such as the one leading from eukaryote to prokaryote cells or from unicellular organisms to multicellularity, is likely to have happened in the absence of those evolved features.

The second framework, so called ecological, resource based or resources framework, includes Lotka-Volterra like models and resource-ratio theory (MacArthur 1972, Tilman 1982, Chase & Leibold 2003). This framework models the ecological systems as a whole, including environmental features, such as the existence of limiting resources, but usually makes specific assumptions about the interactions among individuals. Experimental studies (Craig MacLean & Gudelj 2006, Brockhurst et al. 2010) as well as analyses using the ecological framework, have shown that the limitation of resources might be important to explain cooperative behaviours in bacteria, plants, insects and even animals that do not posses enough information as to decide not to act as parasites. Some of these results are: the tradeoff between rate and yield of metabolic pathways, as that of aerobic and anaerobic bacteria, may foster cooperation in a two dimensional world (Pfeiffer et al. 2001, Pfeiffer & Bonhoeffer 2003, Craig MacLean & Gudelj 2006); if trade of resources is possible, long term relationships allow cooperative plants to evolve (Mazancourt & Schwartz 2010); if the resource for

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which insects compete is the empty space left to lay eggs and they are not able to recognize their own eggs, cooperation, defection and coexistence are allowed (Mesterton-Gibbons 1991); if the individuals have the choice to parasite food items from their partners (kleptoparasitism, Broom & Ruxton 1998) all individuals will end up either always parasitizing or never doing it, and if the information about the amounts of food they will obtain is restricted, populations of cooperative individuals may evolve depending on the past history of the system (Broom & Rychtar 2009).

While evolutionary game theory has demonstrated to be a very powerful tool to express qualitatively the necessary conditions for cooperation to evolve, the difficulty to check its predictions has led to a big gap between theory and experimental proof. The lack of a clear connection between environmental factors and fitness has contributed to this problem. On the other hand, most models used in the ecological framework study the evolution of complex behaviors in an environment where resources are present in a finite amount, but the complexity of such behaviors makes it difficult to see how the limitation of resources influences the evolution of cooperation because several mechanisms promoting cooperation act simultaneously.

Here we present a simplified model of a population of individuals whose genetically inherited strategies fulfil a PD, but where the availability of a limiting resource, which is necessary for their survival and reproduction, may modify the expected outcome of the interactions. The model directly resembles kleptoparasitic behaviours, which are widely observed in nature (Iyengar 2008), but it does not intend to model any specific kleptoparasitic situation. Instead, it seeks two main objectives. The first one is to expose the logic under which cooperation may evolve if there is a limiting resource that constraints the parasitic ability of the individuals, independently of the nature of the

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limiting resource and the specific situation under study. The second objective is to find connections between evolutionary game theoretical results and resource based models.

We show that in the absence of resource limitation the parasitic strategy determines a PD and thus the dynamics leads to the extinction of cooperators. However, when the resource limitation is taken into account, the game is modified so that cooperators may invade the population. Recently, it has been proved that mutation and selection acting not only on the strategies but on the game is able to provide an escape from the PD (Worden & Levin 2007). Our model also provides an escape from the PD by modifying the game structure, but the modification roots on constraints on availability of resources rather than in mutation and selection of strategies and matrix payoffs.

Additionally, we derive equations that connect resource exchanges and fitness as defined in evolutionary game theory, and check the validity of the replicator equation (Schuster & Sigmund 1983) to describe the time evolution of the system. This connection might be important to incorporate ecological factors into evolutionary game theory by understanding how the payoffs depend on available resources, and to design experiments to test evolutionary game theoretical predictions. It could also lead ecologists to include more accurate behavioural features on resource based models and benefit from the high amount of results obtained in evolutionary game theory in the last decades.

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2. THE MODEL

The model consists of a well mixed population of self-replicating individuals that receive resources from the environment and exchange resources through interactions. Each individual is represented by its internal amount of resources and its strategy,

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namely to cooperate or defect: defectors parasite resources from the interaction partner at a cost to themselves, cooperators do not. In order to maintain living functions, every time step individuals dissipate an amount of resources E_l. If the internal amount of resources of an individual surpasses a certain bound, E_s, it splits into two identical copies with half its internal amount of resources; if it is exhausted, the individual dies. Neither genetic relatedness nor special abilities are assumed.

2.1. Environment and resource allocation

In order to study the influence of resource limitation in the evolution of cooperation, we assume for simplicity that the environment supplies resources at a constant rate. Every time step, the environment generates an approximately constant amount of resources E_T to be shared among all individuals in the population. Each individual receives a random portion uniformly distributed on the interval $[0, 2E_T/N]$, where N denotes the number of individuals in the population. In this way, we allow for variations in the resource intake of individuals while keeping an approximately constant total yield E_T in the population. Other resource assignation methods were also tested providing the same results.

In contrast to most models, where the number of individuals in the population is kept constant, in the present one it evolves in time and its equilibrium value depends on the composition of the final population. The reason for this is that, in equilibrium, the resources that enter the system compensate the ones that are dissipated. Since defectors dissipate resources at a higher rate than cooperators (see next subsection) the amount of individuals that the environment is able to sustain depends on the fraction of defectors in the final population. In the simple case when it only contains cooperators, the equilibrium size is $N=E_T/E_l$.

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2.2. Interactions

The defective strategy is characterized by two quantities: the cost spent (E_c) for getting a reward (E_r) from the co-player. Both quantities are inherited without mutation and supply the payoffs of the interaction whenever the internal resources of the two players surpass the corresponding values, E_c and E_r. If resources were unlimited, the internal resources of individuals would be high and those values would describe the amount of resources actually exchanged. However, under limited resources, this is not always the case. We then assume: (i) if the internal resources of a defector are smaller than the cost E_c, it does not pay the cost nor receives the reward; and (ii) if the interaction partner of the defector has internal resources below E_r, the defector extracts the entire amount of resources of the co-player. Note that, in contrast to previous models (Broom & Ruxton 1998, Broom & Rychtar 2009), here individuals do not possess the ability to decide whether they act as defectors (parasites) or not: if they have the chance (enough resources), they do. Some modifications of the rule were also tested, such as allowing parasites to spend lower costs than E_c if their internal resources are smaller than this amount and then getting proportional rewards; they yield similar results.

The interesting case obviously requires $E_r > E_c > 0$, otherwise defectors have no chance to survive. For simplicity, we will consider situations in which the interactions are simultaneous, though results are the same for not simultaneous interactions (see Appendix). For unlimited resources, the interaction matrix can thus be directly written and fulfils the requirements of a simplified prisoner's dilemma (see Table 1), with defectors paying a cost E_c and obtaining a net reward $\Delta E = E_r - E_c > 0$. However, under limited resource supply, the interactions with cooperators whose internal resources are

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lower than E_r make the average reward actually obtained by defectors E'_r to fall below the value expected from their inherited strategy, $E'_r<E_r$. Since E'_r depends on the distribution of resources within the population of cooperators, which in turn depends on the action of defectors, its value is not known a priori. The change in E'_r modifies accordingly the average net reward got by defectors in an interaction $\Delta E'=E'_r-E_c$. Therefore, resource limitation modifies the payoffs of interactions and, if eventually $\Delta E'$ became negative, the game would no longer be a PD and cooperation would become dominant. Because E'_r is not known, but determined by the dynamics, it turns out quite difficult to predict analytically the fate of the population. Instead, we have performed extensive numerical simulations.

2.3. Numerical simulations

Simulation runs started with population compositions ranging from 5% to 90% of cooperators, and sizes close to the estimated equilibrium values for such proportion of individuals. The initial internal resources of individuals was taken from a uniformly random distribution on the interval $[0,E_s]$, whereas other initial distributions have been analysed yielding the same results. The value of E_T was chosen to ensure big populations ($N\sim10^4$ individuals) in order to avoid finite size effects while keeping feasible simulation times. The amount of resources required for splitting was taken $E_s=1000$. The dynamics is implemented as follows. Every *interaction* time step, six individuals are chosen at random: (a) two of them receive an amount of resources E_p from the environment, independently calculated for each one, (b) two of them interact and (c) two of them dissipate an amount of resources E_l. This process is repeated N/2 times for, in average, all individuals to have captured resources, interacted, and

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dissipated resources, once. This defines one time step of the simulation. Simulations run a maximum of 1000 time steps and stop if a homogeneous population is reached before.

The latter dynamics thus describes a completely asynchronous updating method with overlapping generations in order to prevent spurious correlations (see Szabo & Fath 2007). Note that asynchronous updating mimics the dynamics observed in nature where, with few exceptions, individuals do not feed, interact and reproduce at the same time, but with fixed mean ratios between the different actions. Other updating methods were also tested obtaining the same results (see Appendix).

Finally, let us note that the model presented here contains 5 parameters. One of them, say E_s, sets the scale of resources, and E_T only affects the number of individuals in equilibrium (provided it is big enough), but not its composition. Therefore, the fate of the population in the model is characterized by three parameters: the a priori defector's cost E_c and net benefit $\Delta E=E_r-E_c$, and the amount of resources dissipated by the individuals to keep alive E_l. We have performed simulations covering the whole parameters space.

3. RESULTS

Simulations show that, when resources are limited, there exist situations in which selfish individuals die out despite the genetically inherited strategies determine a PD under unlimited resources (Fig. 1).

The dynamics leads to two different regions in the parameter space: one where the system ends up in a population of only cooperators at essentially large costs E_c, and another with a population of only defectors (Figs. 2). The biggest regions of cooperation are found for dissipation of resources around $E_l \approx 0.4 \cdot E_s$, while increasing or decreasing

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it diminishes the region of cooperation. There is little dependence on the initial fraction of cooperators; the bigger the fraction, the bigger the region of cooperation. This dependence increases as E_l approaches the splitting bound E_s. However, except from extreme cases of very high resource dissipation, $E_l \sim E_s$, and very low initial fraction of cooperators (smaller than a 10%) one observes regions where cooperators invade the entire population in all simulations.

Modifications in the updating method as well as in the definitions of interactions and resource allocation were also tested: distributing the resources in identical portions among all individuals $E_p=E_T/N$; giving portions of a constant size E_p with a probability $p=E_T/NE_p$; allowing defectors to get a proportional reward to the cost spent in case their internal amount of resources was lower than E_c; or defining not simultaneous interactions (see Appendix). The results obtained in all cases showed similar or slightly bigger regions of cooperation. In the case in which individuals may spend lower costs than E_c and get proportional rewards, the regions of cooperation do not depend on the initial fraction of cooperators.

4. DISCUSSION

The genetically determined prisoner's dilemma structure of the resource exchanges among cooperators and defectors, which matches the real resource exchanges in the absence of limitation of resources, may lead to the prediction that selfish parasitic individuals have a larger resource intake than cooperative ones and thus reproduce quicker. However, as simulations show, the existence of a limiting resource modifies the outcomes of the interactions allowing cooperators to overcome defectors in the case of a well mixed population and with non-iterated interactions.

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4.1. Depletion of resources and survival of cooperation

The invasive capability of cooperators when there is a limitation in the available resources is due to the subsequent distribution of internal resources in the population. This distribution modifies the outcome of the interactions by lowering the average reward E'_r actually obtained by parasites from cooperators, because some cooperators have internal resources below E_r. Neither the value of E'_r nor the distribution of internal resources are known a priori, but are the result of the dynamics. Simulations show that, in some cases, the dynamics leads a defector's average reward E'_r to be smaller than the defector's cost E_c, so that its net reward $\Delta E' = E'_r - E_c$ becomes negative over all the simulation time, and defection is not favored any more by natural selection. In this case the resource payoff matrix no longer obeys the prisoner's dilemma structure found in the absence of resources limitation. This happens in the regions where cooperation invades the entire population in Figs 2.

In contrast to previous results found for the case in which the limiting resource did not rule the death dynamics (Mesterton-Gibbons 1991, Requejo and Camacho 2010), no stable coexistence between cooperators and defectors is observed in the present model. This change in the behaviour of the system when deaths and reproduction are ruled by the same limiting resource comes from the fact that defectors are not only able to steal resources from their co-players, but to kill them if the latter ones have no resources after interacting.

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4.2. Analytic expressions

As mentioned before, an exact analytical treatment of the model is quite difficult because of the interdependence of E'_r and the cooperator's distribution of internal resources. We next provide a quantitative analysis that will allow us to estimate the region in the parameter space where cooperation becomes dominant.

The condition for cooperation to outperform defection is

$$E_c > E'_r, \tag{4.1}$$

i.e. the cost per interaction of the selfish individual must be bigger than the average amount of resources obtained from a cooperative individual. Let us call $P(E^C<E_r)$ the probability that a cooperator has an internal amount of resources lower than E_r. The mean payoff for a defector playing against a cooperator can be written as $E'_r = P(E^C>E_r)\cdot E_r + P(E^C<E_r)\cdot \overline{E}_r$, where $\overline{E}_r$ is the mean internal amount of resources of cooperators in the region $E<E_r$. This may be rewritten as

$$E'_r = E_r - P(E^C<E_r)\cdot(E_r - \overline{E}_r). \tag{4.2}$$

If the distribution of resources were known, one could derive from this equation the analytic expression for the region where cooperation is dominant. As an example, for the case shown in Fig. 2a the distribution of resources may be taken at a first approximation as uniform (see Fig. 3a). For uniform distributions, the mean amount of resources that selfish individuals steal from cooperators is $E'_r = E_r - E_r^2/2E_s$, which after a few calculations yields

$$E_c > (2E_s\cdot\Delta E)^{1/2} - \Delta E. \tag{4.3}$$

Fig. 2a shows that this approximation is in good agreement with simulation results.

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For other values of the dissipation of resources E_l the internal distributions of resources cannot be approximated as uniform (Fig. 3b). Then, stepwise distributions are good approximations to calculate the region where selfishness is suppressed (Fig. 2b).

4.3. Connecting resources and fitness

The usual framework in evolutionary game theory expresses the payoffs in terms of fitness. This framework can be recovered in our resource scenario by comparing the fitness matrix, in which cooperators pay a cost c in order to provide a benefit b to the co-player, with the one in terms of resources. To do so, let us notice that in the model the greater the resource intake by an individual, the faster it reaches the splitting bound E_s and reproduces. Therefore, the resource income rate is proportional to the reproductive rate and may be translated into fitness. In the Appendix we derive the specific values of the payoff matrix describing the resource exchanges when a finite resource supply is taken into account. As expected, the interaction terms are described by the cost E_c and the average rewards E'_r and $\Delta E'=E'_r-E_c$. All these terms, however, appear multiplied by the factor $p\equiv P(E^D>E_c)$, namely the probability that a defector actually performs a parasitic action (table 2). Naturally, being factor p in all terms of the payoff matrix, it does not modify the structure of the game (see Appendix for more details). Comparing the payoff matrixes in the two formulations, i.e. resources and evolutionary game theoretical or fitness, a relationship between both frameworks can be derived (table 2).

These relationships can be used to check the validity of the replicator equation on its evolutionary game theoretical form to describe the dynamics in the model (Schuster & Sigmund 1983)

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$$\frac{\mathrm{d}\rho}{\mathrm{dt}} = \rho \cdot (\pi_C - \bar{\pi}) , \tag{4.4}$$

where ρ is the fraction of cooperators, π_C their fitness and $\bar{\pi}$ the mean population fitness. According to Table 2, this equation writes

$$\frac{\mathrm{d}\rho}{\mathrm{dt}} = - a' \Delta \mathrm{E}' \rho \cdot (1 - \rho) , \tag{4.5}$$

with $a' = ap$. The factor $p=P(E^D>E_c)$ depends on the distribution of internal resources in the population of defectors. By assuming that stationary distributions are rapidly achieved (this is confirmed by simulations), the factor a' and $\Delta E'=E'_r-E_c$ can be approximated as constants. One may thus predict the mean time evolution of the system for any set of parameters E_r, E_c whenever the constant a' relating resources and fitness is known. In our simulations we do not know its value in advance. However, good agreement between the replicator equation and the simulations can be observed in Fig. 4, where the a' value has been obtained by a numerical fit using the simulation data. In the cases where the resources exchanged during the interactions are much smaller than those necessary to split, $E_r,E_c<<E_s$, the internal resources of most individuals surpass those values and the payoffs are not modified. Then, the result of extinction of cooperation expected for a PD in well mixed populations is recovered as $\Delta E'=\Delta E>0$. To calculate the value of $\Delta E'$ in the cases in which the payoffs are modified, one may use Eq. (4.2).

However, as the genetically determined quantities (in the sense that they are fixed before starting the game) are the values of E_r and E_c related to the selfish strategy, which might be measured in experiments designed to avoid external influences on the payoffs, it would be useful to find a rule for the evolution of cooperation based only on these a priori determined quantities. Using the equations in Table 2 one may find the

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corresponding fitness values for these quantities associated to the parasitic strategy, namely $b_p=a{\cdot}p{\cdot}E_r$ for the reward, $c_p=a{\cdot}p{\cdot}\Delta E$ for the cost. Then, writing the constant a in units of E_s condition (4.3) reduces to

$$b_p > (2{\cdot}a{\cdot}p{\cdot}c_p)^{1/2} \tag{4.6}$$

This inequality is similar to previously found rules to describe the evolution of cooperation. Indeed, the rules relating to kin selection (Hamilton 1964), direct and indirect reciprocity, network reciprocity and group selection can be written as: b/c>1/r (Nowak 2006). Equation (4.6) suggests that, as a first order approximation, a rule for the evolution of cooperation based on statistical analyses and including the effect of environmental or morphological constraints might be written as

$$b_p/c_p^{\,S} > (\lambda{\cdot}a)^S \tag{4.7}$$

where λ, S and a are constants related to the statistical properties of the system under study and the reproductive dynamics of the population.

5. CONCLUSIONS

We have analysed the influence of the limitation of resources in the evolution of cooperative behaviours in the case in which selfish individuals perform parasitic acts, and have shown that, although the genetically inherited strategies define a PD under unlimited resources, resource constraints may modify the structure of the game so that cooperation becomes the dominant strategy. Thus, resource limitation permits the survival of cooperation in well mixed populations, without repeated encounters between the same two individuals and in the absence of either genetic relatedness, memory, or other special abilities. This suggests that the limitation of resources is an important element to be taken into account when studying the evolution of cooperation of simple

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entities, such as viruses, unicellular organisms or plants, and makes our results suitable for studying the evolution of cooperation in early evolutionary stages, and thereafter the associated transitions in evolution, as those from prokaryote to eukaryote cells or from unicellular to multicellular organisms. More generally, these results might be applicable to any system in which reproduction and death are ruled by a limiting resource, and with the restrictions that the strategies are fixed before starting the game and that the benefits and costs for defecting are disassociated.

We have used two different frameworks in this study, the resources framework and the (evolutionary game theoretical) fitness framework. In the first one selfish individuals pay the cost, while in the latter cooperators are the individuals paying it. This might seem contradictory; however, selection is totally unaware of who is the individual acting and selects behaviours by the results of the actions. Therefore, as both matrixes determine the same outcome, there is no contradiction on it, and individuals that seem not to pay the cost in some situations might be seen as cooperators paying a cost in the fitness framework. Indeed, our simulations show that the dynamics in the model is well described by the replicator equation of evolutionary game theory both, when resource exchanges satisfy a PD so that cooperators die out, and also when resource constraints make cooperation dominant and defectors are extinguished.

Finally, we have found a simple rule for the evolution of cooperation based only on the fitness translation of the inherited strategies. The use of equations connecting resources and fitness may facilitate the design of experiments to test evolutionary game theoretical predictions and we hope they will help in establishing the necessary communication between evolutionary game theoretical researchers and experimental biologists, as well as to introduce more detailed behavioural and ecological features in

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the models, all of this in order to continue expanding our knowledge on how altruistic, mutualistic and parasitic behaviours evolved and gave rise to the diversity present in the natural world.

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Appendix A. Payoff matrix calculation.

We now evaluate the average payoff obtained by each player in a time step. Interactions are defined as simultaneous between both players. Defectors pay a cost E_c to steal a maximum reward E_r from the co-player. Furthermore (i) if the internal resources of a defector are smaller than the cost E_c, it does not pay the cost nor receives the reward; and (ii) if the interaction partner of the defector has internal resources $E_{int}<E_r$, the defector extracts the entire amount of resources of the co-player. Thus, the reward obtained by a defector when interacting with individual i is $E_r^i=\min(E_r,E_{int}^i)$. Accordingly, if individuals j and k interact, the variation of their internal resources after interacting can be written as:

$$\Delta E^j = q^j\cdot(E_r^k - E_c) - q^k\cdot E_r^j, \qquad \Delta E^k = q^k\cdot(E_r^j - E_c) - q^j\cdot E_r^k. \tag{A1}$$

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Here $q^i = 1$ if individual i is a defector with resources above the cost E_c, i.e. it is an individual able to perform a parasitic action, and $q^i = 0$ otherwise. Below we provide the variation of internal resources of the players as supplied by eq. (A1) for all possible interaction couples:

i) Interaction CD:

$$\Delta E^C = -q^D \cdot E_r^C, \qquad \Delta E^D = q^D \cdot (E_r^C - E_c). \tag{A2}$$

ii) Interaction CC:

$$\Delta E^{C1} = 0, \qquad \Delta E^{C2} = 0 \tag{A3}$$

iii) Interaction DD:

$$\Delta E^{D1} = q^{D1} \cdot (E_r^{D2} - E_c) - q^{D2} \cdot E_r^{D1}, \qquad \Delta E^{D2} = q^{D2} \cdot (E_r^{D1} - E_c) - q^{D1} \cdot E_r^{D2} \tag{A4}$$

Averaging Eqs. (A2)-(A4) over the entire population one finds the average payoffs obtained by each player in a time step, i.e. the terms in the payoff matrix. The average of E_r^C is, by definition, E'_r; and the average of q^D supplies $P(E^D>E_c)$, the fraction of defectors that possess resources above the cost. Then, by calling $p \equiv P(E^D>E_c)$ the terms in the payoff matrix write:

i) Interaction CD:

$$\Delta E^C = -p \cdot E'_r, \qquad \Delta E^D = p \cdot (E'_r - E_c). \tag{A5}$$

ii) Interaction CC:

$$\Delta E^C = 0 \tag{A6}$$

iii) Interaction DD:

$$\Delta E^D = -p \cdot E_c \tag{A7}$$

Therefore, the payoff matrix of resource exchanges due to interactions in a time step reads

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$$\begin{array}{c} \\ C \\ D \end{array} \begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} 0 & -p\cdot E'_r \\ p\cdot\Delta E' & -p\cdot E_c \end{pmatrix} \end{array}$$

The condition for cooperators to dominate defectors (Mesterton-Gibbons 1991, Nowak 2006) is then $E_c>E'_r$ (Eq. (4.1)).

The decrease of defectors' rewards due to the distribution of internal resources of cooperators is included in the term E'_r, while the decrease in the capacity of defectors to act as parasites is included in the term $p=P(E^D>E_c)$, related to their distribution of internal resources. Note that the first term may alter the structure of the payoffs, meanwhile the last term only affects the time scale of the simulations by reducing the net number of effective interactions, i.e. interactions in which defectors actually behave as parasites. To obtain the total exchange of resources for individuals in a time step, one must add the average portion E_p received from the environment and substract the dissipated resources E_l, i.e one must add $E_0 =E_p-E_l$. This provides the resource payoff matrix displayed in table 2.

Note that, if the interactions are defined with one individual as actor and one as recipient of the act, which would model not simultaneous interactions, the calculation of the payoffs is similar but a 0.5 factor appears multiplying the term p. This happens because the individuals act only half of the times and receive the act the other half. However, as this factor multiplies each matrix element, it does not modify the structure of the game but only the time scale of the dynamics, which now becomes slower. We have checked that the use of this method does not modify the simulation results.

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Nevertheless, since our extensive simulations over the parameter space are very time consuming, they have been carried out using simultaneous interactions.

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Fig 1. Time evolution of the fraction of cooperators for several parameter values and initial conditions of the model. The genetically determined strategies of the individuals fulfil a simplified PD (see Table 1). However, the limitation of resources may modify the payoff structure of the interactions, allowing cooperators to invade the entire population. Stable coexistence is not observed. While the invasion capacity of cooperation depends on its initial frequency in some situations, this dependence is very small for low E_l, being cooperation the dominant strategy in many situations (see figure 2).

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Fig. 2. Regions of cooperation and defection. The final fraction of cooperators ρ is displayed as a function of the parasite strategy, i.e. resources cost (E_c) and net benefit ($\Delta E = E_r - E_c$). In black, the fraction of cooperators is 1; in white it is 0. Whenever costs and net benefits are small enough, i.e. when the limitation of resources does not influence the payoffs, defectors invade the entire population, as expected for a PD. However, one observes a well defined region where cooperation overcomes defection. In this region the initial PD is modified by the lack of resources, which leads to negative net benefits for defectors and allows the system to evolve towards homogeneous populations of cooperators. Solid lines show the analytical prediction for the frontier between both regions. In (a) the dissipation of resources for keeping alive is $E_l \approx 0.4 \cdot E_s$; in (b) $E_l \approx 0.02 \cdot E_s$. In all cases, simulations start with a 50% of cooperators. The results have been averaged over 50 realizations.

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Fig. 3. Internal distribution of resources for cooperators. Cumulative resource histograms for parameter values close to the boundaries between regions of cooperation and defection (see Fig. 2) for (a) $E_l \approx 0.4 \cdot E_s$ and (b) $E_l \approx 0.02 \cdot E_s$. In (a) the histograms do not depend on the point of the boundary chosen (only two points are displayed for clarity), and can be approximated by a straight line, i.e. a uniform distribution. This approximation is used to derive the analytical prediction shown in Fig. 2a. In (b) the histograms are point dependent. To derive the analytical prediction of the boundary in Fig 2b a mean histogram was obtained and approximated by a stepwise distribution. This rough approximation is again in good agreement with the results.

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Fig. 4. Connection between resource and fitness frameworks and test of the replicator equation. The decreasing solid line shows the time evolution for simulations with ΔE = 16, E_c = 1; in this case (E_c, $\Delta E << E_s$ = 1000) the payoffs are not altered and the dynamics results in the extinction of cooperators, as expected for a well mixed PD. The increasing solid line shows the time evolution in a region where the distribution of internal resources modifies the payoffs and drives defectors to extinction (ΔE = 16 and E_c = 161). Solid lines show the mean time evolution averaged over 20 realizations. Dashed lines show the analytical predictions by using the best fit value for parameter a' (see Eq. (4.5)).

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Table 1. Payoff matrix under unlimited resources. In an interaction between two players, defectors pay a cost E_c and obtain a reward E_r. If we call P_{XY} the payoff for strategy X playing against strategy Y, the payoff rank required for a Prisoner's Dilemma (PD) is $P_{DC}>P_{CC}>P_{DD}>P_{CD}$. For a simplified PD, the condition $P_{DC}-P_{CC}=P_{DD}-P_{CD}$, also known as equal gains from switching, must be fulfilled. In our simulations, $E_r>E_c>0$, so that the interaction matrix satisfies a simplified PD.

Table 2. Relationship between resource exchanges and fitness. The resource income is proportional to the reproductive rate and may be translated into fitness. Comparing the payoff matrixes in the two formulations, i.e. resources and evolutionary game theoretical or fitness, a relationship between both frameworks can be derived (see text for parameter definitions). $E_0=E_p-E_l$ describes the resources exchanged with the environment and the factor p the probability that the defector parasitizes resources from the co-player in a time step, i.e. the fraction of defectors with internal resources above the cost. Note that the addition of a constant k to all payoffs in the standard formulation of game theory does not modify the replicator dynamics, whereas allows relating resources and fitness. In the relationships, a denotes the proportionality constant between both quantities. The relationship between cost to net benefit ratios in both formulations does not depend on the values of k and a.

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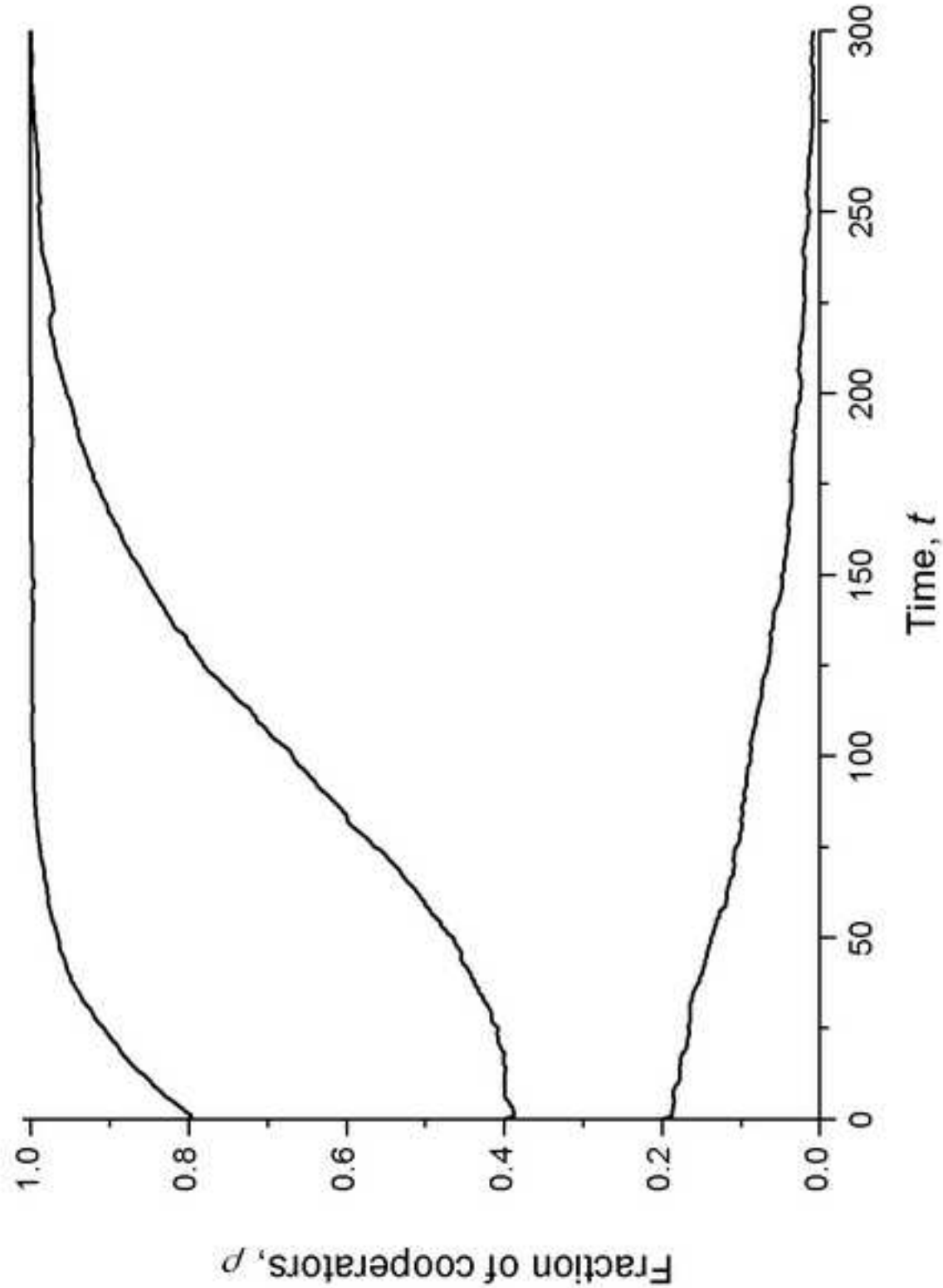


Figure 1

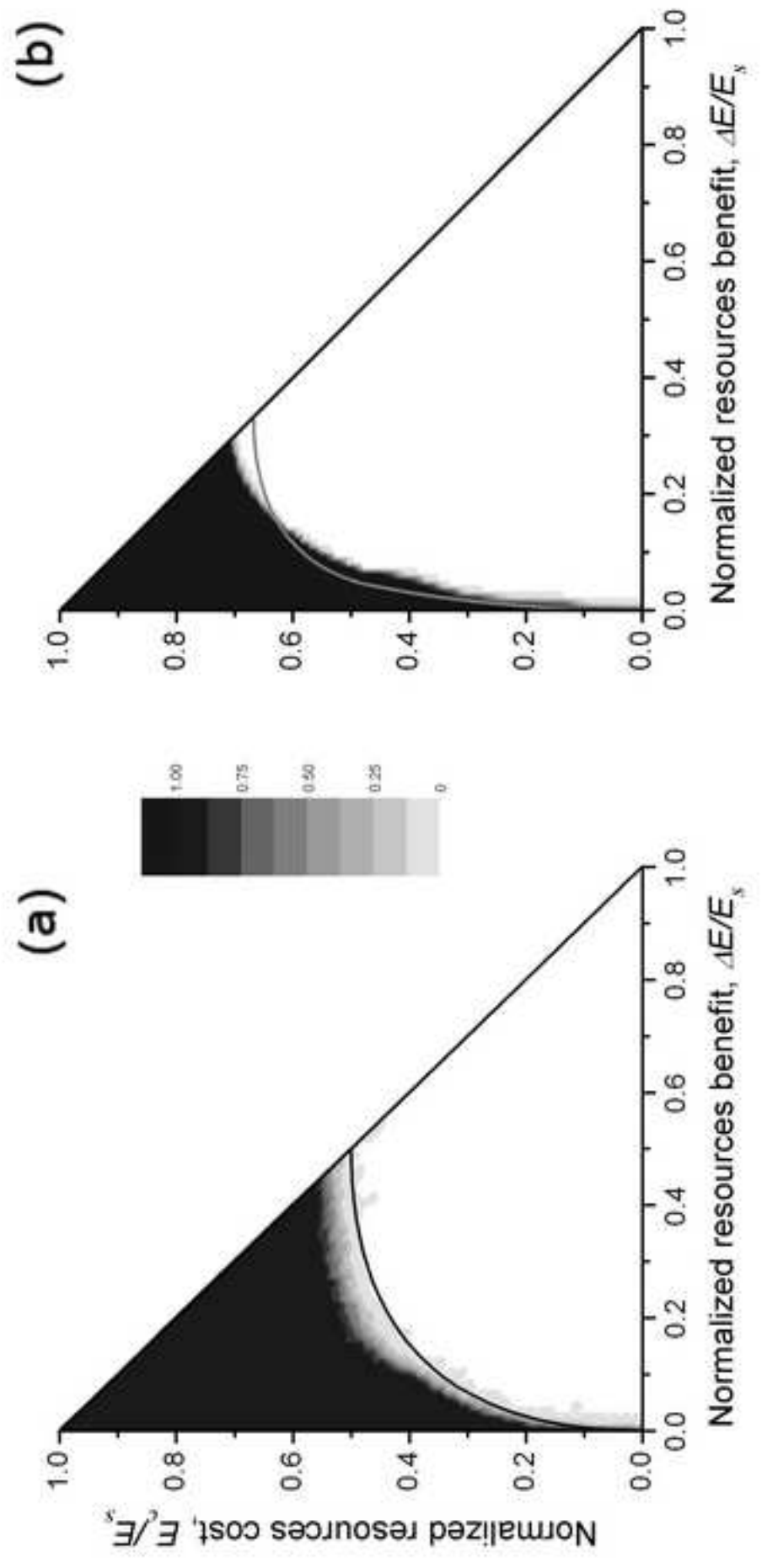

(a)
(b)
Normalized resources cost, E_c/E_s
Normalized resources benefit, $\Delta E/E_s$
Normalized resources benefit, $\Delta E/E_s$
1.00
0.75
0.50
0.25
0
0.0
0.2
0.4
0.6
0.8
1.0

Figure 2

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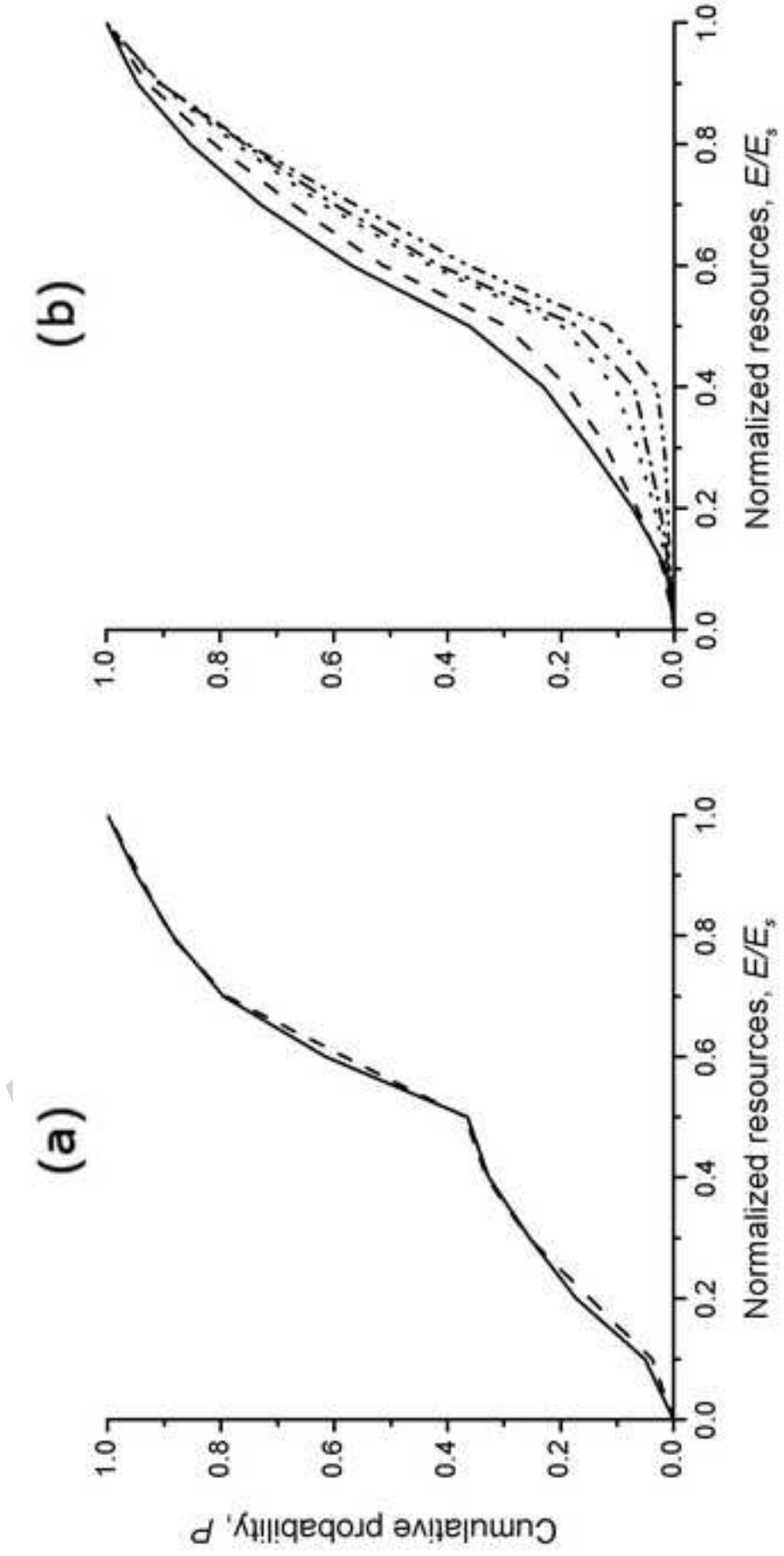


Figure 3

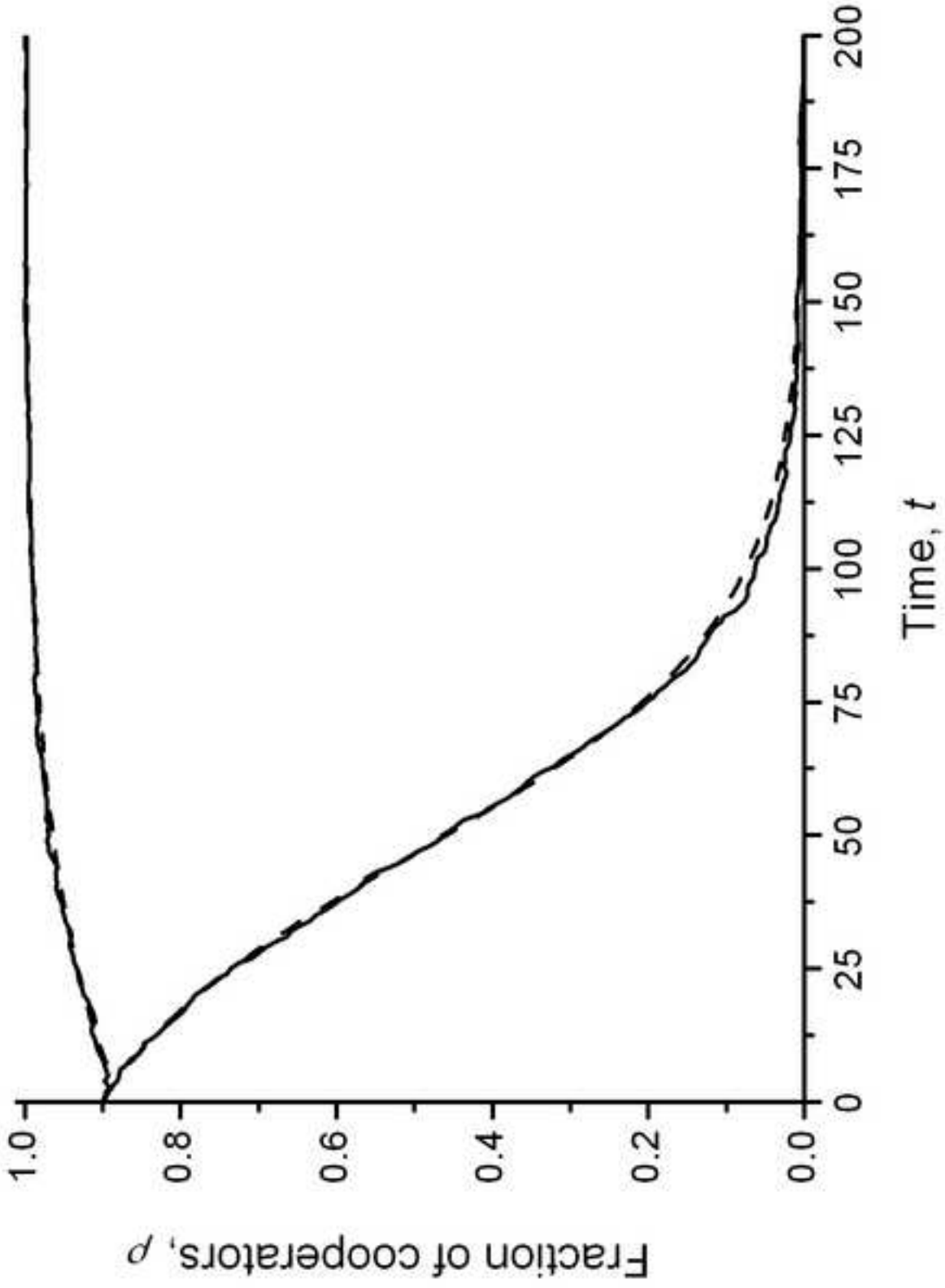

Fraction of cooperators, ρ
1.0
0.8
0.6
0.4
0.2
0.0
0
25
50
75
100
125
150
175
200
Time, t

Figure 4

Table 1

	C	D
C	0	$-E_r$
D	$\Delta E = E_r - E_c$	$-E_c$

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Table 2

Resources framework

	C	D
C	E_0	$E_0 - pE_r'$
D	$E_0 + p\Delta E'$	$E_0 - pE_c$

Fitness framework

	C	D
C	$k + b - c$	$k - c$
D	$k + b$	k

Relationship between both frameworks

$b = a \cdot p \cdot E_r'$, $c = a \cdot p \cdot \Delta E'$, $k = a \cdot (E_0 - p \cdot E_c)$,

$\Delta E'/E_c = c/(b-c)$

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