

Emergence and stability of cooperation in multi-public-good games

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Goal

To study the emergence and stability of cooperation in public-good games in which each player may contribute to two different public goods.

Background and motivation

The evolution and maintenance of cooperation among unrelated individuals in non-iterated games have been a major focus of evolutionary studies over the last decades. Models of cooperation are traditionally cast in the framework of game theory. In cooperation games, individuals receive a payoff according to their and their partners' strategies. One of the best studied cooperation games, the Prisoner's Dilemma, describes the interaction between two players: defection is the dominant strategy if interactions between individuals occur randomly over a large population (Maynard Smith 1982). However, despite the apparent disadvantage of cooperators in such games, cooperation is ubiquitous in nature and in human societies. Understanding why cooperation nevertheless evolves therefore is a challenging and important problem.

Many human endeavors require simultaneous cooperation of many individuals. Moreover, there are several biological situations, for example the production of biofilms or enzymes within bacterial communities, in which cooperative tasks are carried out jointly by several individuals (Nowak and Sigmund 2002; Rankin et al. 2007). These situations can be modeled by n -player analogues of the Prisoner's Dilemma, called public-good games. In classical public-good games, each individual has a personal pool of resources and decides how much of these to contribute to the public good (Hauert et al. 2002a 2002b; Bach et al. 2006). The invested resources from all individuals are then pooled and multiplied by a factor r ($1 < r < n$, where n is the number of players in the group); the multiplied amount is equally shared between all players, irrespective of their individual investments. The highest total payoff would thus be obtained if all individuals invested all their resources (full cooperation). However, to reduce their own costs, individuals have an incentive to avoid contributing to the public good (full defection), thereby potentially gaining a cost-free share of the public good resulting from the investments of others. Hence, as in the two-player Prisoner's Dilemma, the dominant strategy is defection. Recently, Doebeli et al. (2004) have extended the classical public-good game to incorporate non linear dependencies in both individual costs and common benefits. With this extension, defection is not always a dominant strategy, and cooperation can consequently evolve even in well-mixed populations. Doebeli et al. (2004) further found that, under some conditions, gradual evolution in cooperative investments results in evolutionary branching and in the emergence of coexisting low-investing and high-investing strategies.

All studies described above are based on the assumption of a single public good. In several biological and social situations, however, a community consisting of n individuals might depend on several different public goods, with each individual contributing to none, some, or all of these. A case in point is the community metabolism of bacterial communities, or the simultaneous dependence of advanced human societies in many public goods. In this project, I

will therefore consider an extension of the classical public-good game that allows each player to contribute to two public goods.

Research questions

The main goal of this project is to develop and explore multi-public-good games. As in simpler cooperation games, the key goal is to identify the circumstances that favor the emergence of cooperation. We can break this up into the following more specific questions:

- How does the total cooperative investment develop within the group?
- What is the effect of different nonlinearities in benefits and costs on the emergence and stability of cooperation when considering interactions among public goods?
- Will division of labor with regard to alternative contributions to the public goods naturally emerge within groups? What are the conditions for the emergence of specialists (who produce one public good) and generalists (who produce more than one public goods)?

If time allows, we will explore these questions also in a spatial setting. Spatial structure has been shown profoundly to affect the incentives for cooperation in classic public-good games and may thus have similarly important implications for multi-public-good games. Other potential extensions are the inclusion of punishment and of changing player densities.

Methods and work plan

Game dynamics

To understand the dynamics of multi-public-good games, we consider an individual-based model in which individuals within groups of n players ($n > 2$) can contribute to two public goods. We consider that these groups are assembled from a large population of $N > n$ players. At a constant rate, groups of n players are formed for which members are selected through an unbiased random draw from the population. Each player's strategy is characterized by the amounts x and y , respectively, it contributes to the first and second public good.

For each player i , total contributions X and Y determine the benefit B that is shared among the n players, while individual contributions x_i and y_i determine the costs C , resulting in the payoff

$$P_i = B(X, Y)/n - C(x_i, y_i),$$

where X and Y are the sum of x and y within a group,

$$X = \sum_{j=1}^n x_j \text{ and } Y = \sum_{j=1}^n y_j$$

The nonlinear functions

$$\begin{aligned} B(X, Y) &= b_1 A(X, Y) + b_2 A^2(X, Y), \\ C(x_i, y_i) &= c_1 a(x_i, y_i) + c_2 a^2(x_i, y_i), \end{aligned}$$

describe the benefits and costs of contributing to the two public goods. Without loss of generality, we can set $c_1 = 1$ by choosing the unit of contributions.

Contributions to public goods may interact synergistically or antagonistically, and may be essential or substitutable (Tilman 1980). In our model, we account for this range of interaction options by using generalized means,

$$A(X, Y) = \left(\frac{X^p + Y^p}{2} \right)^{1/p} \text{ and } a(x_i, y_i) = \left(\frac{x_i^q + y_i^q}{2} \right)^{1/q}.$$

In our analysis, we will consider all possible values for the parameters p and q , $-\infty < p, q < \infty$. As a result, the functions A and a can gradually be altered from the minimum norm ($p, q = -\infty$), to the harmonic mean ($p, q = -1$), geometric mean ($p, q = 0$), arithmetic mean ($p, q = 1$), and maximum norm ($p, q = \infty$) as special cases. In the particular case of perfectly substitutable public goods ($p, q = 1$), we recover the model studied by Doebeli et al. (2004), thus allowing the systematic comparison with earlier findings of the new results we will obtain.

Evolutionary dynamics

On a demographic time scale, players adopt the strategies of better-performing players. Two players i and j are randomly chosen and player i imitates the strategy of player j with probability $w_{ij} = 1/(1 + e^{-s(P_j - P_i)})$ depending on their payoff difference (Hauert et al. 2002a, 2002b; Sigmund et al. 2010), where $s > 0$ denotes the imitation strength (for $s \rightarrow \infty$, a more successful player is always imitated).

We will explore the evolution of investments x and y into the two public goods using adaptive-dynamics techniques (e.g., Geritz et al. 2004; Doebeli et al. 2004). We consider a resident strategy $z_r = (x_r, y_r)$ and a mutant strategy $z_m = (x_m, y_m)$. The frequencies of these strategies are denoted by p_r and p_m , respectively, with $p_r + p_m = 1$. As a consequence of the imitation dynamics described above, the frequencies of the resident and mutant subpopulations will follow the replicator equations

$$\frac{dp_k}{dt} = sp_k [P_k(p_r, p_m) - \bar{P}(p_r, p_m)]$$

for $k = r, m$. Here, $P_r(p_r, p_m)$ and $P_m(p_r, p_m)$ are the average payoffs of the resident strategy and mutant strategy, respectively, while $\bar{P}(p_r, p_m) = p_r P_r(p_r, p_m) + p_m P_m(p_r, p_m)$ is the average payoff in the population.

From the replicator dynamics, we derive the invasion fitness of the mutant strategy, i.e., the initial per capita growth rate of a rare mutant strategy z_m in a population of individuals with the resident strategy z_r ,

$$S_{z_r}(z_m) = \lim_{p_m \rightarrow 0^+} \frac{1}{p_m} \frac{dp_m}{dt} = s [P_m(1, 0) - P_r(1, 0)].$$

If $S_{z_r}(z_m) > 0$, the rare mutant strategy can spread in the resident population.

The long-term evolution of the resident strategy z_r is then described by the canonical equation of adaptive dynamics (Dieckmann and Law 1996),

$$\frac{dz_r}{dt} = \frac{1}{2} n \sigma^2(z_r) \frac{\partial}{\partial z_m} S_{z_r}(z_m) \Big|_{z_r=z_m},$$

where $\sigma^2(z_r)$ is the covariance matrix of mutational steps in the strategy z_r . In the simplest case, mutations in x and y are independent, uniform with respect to the strategy, and have the same variance.

An equilibrium point $z^* = (x^*, y^*)$ of the canonical equation is called an evolutionarily singular strategy. If z^* is attracting, it is said to be convergence stable. If the invasion-fitness landscape $S_{z^*}(z_m)$ has a local maximum around $z_m = z^*$, z^* is locally evolutionarily stable. If z^* is convergence stable but not locally evolutionarily stable, it is an evolutionary branching point.

Relevance and link to EEP's research plan

One of the most difficult scientific questions is the emergence and stability of cooperation in nature. IIASA's Evolution and Ecology Program has a long track-record of developing new perspectives in this area. My project thus contributes to EEP's research project on the *Evolution of Cooperation*. The anticipated results will assist in understanding the mechanisms that underpin cooperation at all biological levels, from molecules to human societies.

Expected output and publications

The results of this project are intended for publication in a co-authored article in an international scientific journal.

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