

Ecological public goods games: Cooperation and bifurcation

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Abstract

The Public Goods Game is one of the most popular models for studying the origin and maintenance of cooperation. In its simplest form, this evolutionary game has two regimes: defection goes to fixation if the multiplication factor r is smaller than the interaction group size N , whereas cooperation goes to fixation if the multiplication factor r is larger than the interaction group size N . Hauert et al. [Hauert, C., Holmes, M., Doebeli, M., 2006a. Evolutionary games and population dynamics: Maintenance of cooperation in public goods games. *Proc. R. Soc. Lond. B* 273, 2565–2570] have introduced the *Ecological Public Goods Game* by viewing the payoffs from the evolutionary game as birth rates in a population dynamic model. This results in a feedback between ecological and evolutionary dynamics: if defectors are prevalent, birth rates are low and population densities decline, which leads to smaller interaction groups for the Public Goods game, and hence to dominance of cooperators, with a concomitant increase in birth rates and population densities. This feedback can lead to stable co-existence between cooperators and defectors. Here we provide a detailed analysis of the dynamics of the *Ecological Public Goods Game*, showing that the model exhibits various types of bifurcations, including supercritical Hopf bifurcations, which result in stable limit cycles, and hence in oscillatory co-existence of cooperators and defectors. These results show that including population dynamics in evolutionary games can have important consequences for the evolutionary dynamics of cooperation.

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1. Introduction

The Public Goods Game (Kagel & Roth, 1995) is a classical mathematical metaphor illustrating the problem of cooperation and cheating (Colman, 1995; Dugatkin, 1997; Doebeli & Hauert, 2005). In its simplest form, the game has two strategies: cooperate (C) and defect (D). It is played in interaction groups of size N , in which each cooperator contributes to the public good at a cost c to itself. Each contribution increases the common resource by rc , where r determines the efficiency of investments and the attractiveness of the public good. If there are k cooperators in the given interaction group, the total amount of public goods produced is krc . This public good is

distributed equally among the N members of the group. Thus, in the given group, the defector's payoff is

$$P_D(k) = \frac{rkc}{N}, \quad (1)$$

whereas the cooperator's payoff is

$$P_C(k) = P_D(k) - c. \quad (2)$$

Two things immediately follow from these payoff expressions. First, if $r \leq 1$, then $P_C(N) \leq 0 = P_D(0)$, hence cooperation is always doomed. For the Public Goods game one therefore always assumes $r > 1$. Second, in any given interaction group, cooperators always do worse than defectors. To determine the fate of cooperators and defectors on a population wide scale, we thus need to take into account that the composition of interaction groups is variable.

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In the following, we always assume that interaction groups are formed randomly. Let x be the frequency of cooperators in the population. For any given focal individual, the probability that it finds itself in an interaction group in which k of the other $N - 1$ members are cooperators is

$$\binom{N-1}{k} x^k (1-x)^{N-1-k}. \quad (3)$$

Thus, on average, the focal player encounters $x(N - 1)$ cooperators among its $N - 1$ interaction partners — independent of whether the focal individual is a cooperator or a defector. As a consequence, all that matters for determining the outcome of the evolutionary game is what the focal individual receives from its own action. By definition, a defector receives a payoff of zero from its own action, hence its expected payoff f_D is

$$f_D = \frac{r}{N} x(N - 1), \quad (4)$$

where the costs of cooperation are henceforth set to $c = 1$. A cooperator receives a payoff of $r/N - 1$ from its own contribution to the public good, hence the expected payoff of a cooperator is

$$f_C = \frac{r}{N} x(N - 1) - 1 + \frac{r}{N}. \quad (5)$$

These expressions for f_D and f_C immediately show that with random interactions, defectors win the evolutionary game (and go to fixation) if and only if $r < N$, i.e., if the multiplication factor is smaller than the size of interaction groups. If $r > N$, cooperators win and defectors go to extinction (Hauert et al., 2006c). However, also note that even for $r > N$ defectors are better off than cooperators in every interaction group that contains both types.

The basic idea in Hauert et al. (2006a) was that if the public goods game is combined with ecological dynamics, then changing population densities could lead to changes in the effective size $S \leq N$ of the interaction groups. More precisely, large population densities result in large effective interaction groups ($S > r$), and hence leads to situations in which defection is favored evolutionarily. But the decline of cooperators also reduces the returns from the public good, which decreases game payoffs and hence lowers birth rates and reduces population densities. On the other hand, low population densities result in small effective interaction groups ($S < r$), and hence leads to situations in which cooperation is favored evolutionarily. Thus the production of the public good increases, which increases game payoffs and birth rates and triggers an increase in the population density. This feedback between ecological and evolutionary dynamics can lead to the co-existence of cooperators and defectors at an ecologically and evolutionarily stable equilibrium (Hauert et al., 2006a). In particular, including ecological dynamics in evolutionary game theory models could be a fundamental mechanism promoting the evolutionary origin and maintenance of cooperation.

In principle, the aforementioned feedback between ecological and evolutionary dynamics opens up the possibility of oscillatory dynamics, and in particular of cyclic co-existence of

cooperators and defectors (Hauert et al., 2006b). In the present paper we complete the study of Hauert et al. (2006a) and provide a detailed analysis of all dynamical regimes, including a proof of the existence of cyclic co-existence.

2. Model and results

Following Hauert et al. (2006a), we consider a large well-mixed population in which individuals interact in randomly formed interaction groups. We denote the density of cooperators by x and the density of defectors by y , and we incorporate population dynamics by adding a third dynamic variable z for “vacant space”, assuming that $x + y + z = 1$. Thus, $x + y$ is the total population density, which can vary between 0 and 1. Cooperators and defectors have per capita birth rates that are determined by the game interactions and by the amount of available vacant space. Specifically, the per capita birth rate of cooperators is $z(f_C + b)$, and the per capita birth rate of defectors is $z(f_D + b)$, where f_C and f_D are the average payoffs from game interactions for cooperators and defectors, as described below. The parameter b denotes a baseline birth rate, which is assumed to be the same for cooperators and defectors. If we assume in addition that both cooperators and defectors have the same constant per capita death rate, we arrive at the following dynamics for x , y and z :

$$\dot{x} = x(z(f_C + b) - d) \quad (6a)$$

$$\dot{y} = y(z(f_D + b) - d) \quad (6b)$$

$$\dot{z} = -\dot{x} - \dot{y} = (x + y)(d - zb) - z(xf_C + yf_D). \quad (6c)$$

Note that Eq. (6c) is simply a consequence of the fact that $x + y + z = 1$ at all times. Also note that choosing density-independent death rates does not impose any restrictions on the dynamics of the system. Mathematically, any density-dependent death rate could be translated into a change in the density-dependent birth rate combined with a constant death rate. If the death rate d is variable such that the population density remains constant ($\dot{z} = 0$) then Eq. (6) reduces to the replicator dynamics (Hofbauer & Sigmund, 1998). Finally, we note that in principle, the parameter b must be chosen such that $b + f_C \geq 0$ and $b + f_D \geq 0$ are satisfied, lest the terms $z(f_C + b)$ and $z(f_D + b)$ cannot be interpreted as per capita birth rates. This can be achieved by ensuring that $b + f_C \geq 0$ in the limit $y \rightarrow 1$ since this case results in the lowest payoffs from the public good (see below). However, we point out that our analysis shows that theoretically, the constraint on b is unimportant, and no qualitatively new dynamic regimes occur when the constraint is dropped.

To determine the payoffs f_C and f_D , we assume that interaction groups are formed by interpreting the densities x , y and z as probabilities for drawing a particular strategy and for failing to find a participant, respectively. Specifically, we assume that interaction groups of nominal size N are formed randomly such that the available N places are filled with either cooperators or defectors, or are left empty, according to the probabilities x , y and z . In particular, for $z > 0$ the average effective group size is less than N . The chance that an individual finds itself in a group of size S is given by:

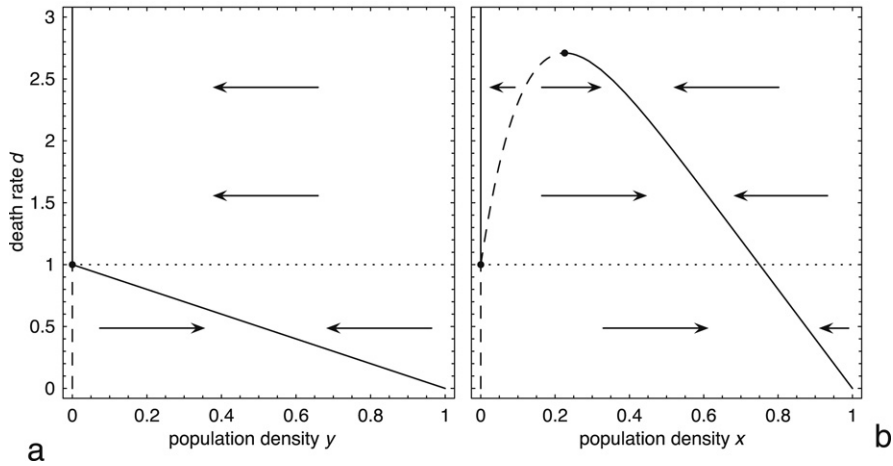


Fig. 1. Dynamics of homogeneous defector **a** and cooperator **b** populations interacting in ecological public goods games with $N = 8$, $r = 4$. The location of stable (solid line) and unstable (dashed line) fixed points are shown for different death rates d and a baseline birthrate of $b = 1$ (the horizontal dotted line marks $d = b$). **a** Defectors cannot survive on their own if $d > b$ and the population goes to extinction. However, for $d < b$ defectors persist at an equilibrium density $1 - d/b$. **b** Cooperators can handle much higher death rates due to the fitness benefits from cooperation. However, this requires sufficiently high population densities because otherwise cooperative interactions are too rare. The threshold density is indicated by the unstable equilibrium at low densities. For $b > d$ this threshold disappears and cooperators persist irrespective of their initial density. Note that the equilibrium density of cooperators is always substantially higher than that of defectors because of the higher fitness of cooperators.

$$\binom{N-1}{S-1} (1-z)^{S-1} z^{N-S}. \quad (7)$$

If an individual finds itself in a group of size S , it faces k cooperators and $S-1-k$ defectors among its $S-1$ interaction partners with probability

$$\left(\frac{x}{1-z}\right)^k \left(\frac{y}{1-z}\right)^{S-1-k} \binom{S-1}{k}. \quad (8)$$

Based on the probabilities given in Eq. (8), one can calculate the expected payoff for cooperators and defectors in interaction groups of size S , which can then be used, together with the probability distribution for S given by Eq. (7), to calculate the average payoffs f_C and f_D :

$$f_D = r \frac{x}{1-z} \left(1 - \frac{1-z^N}{N(1-z)}\right) \quad (9a)$$

$$f_C = f_D - F(z), \quad (9b)$$

where

$$F(z) = 1 + (r-1)z^{N-1} - \frac{r}{N} \frac{1-z^N}{1-z}. \quad (10)$$

A detailed derivation of these expressions can be found in Hauert et al. (2006a, 2002a).

Denoting by $q = x/(x+y)$ the fraction of cooperators in the population, Eq. (6) can be transformed into

$$\dot{q} = \frac{\dot{x}y - \dot{y}x}{(1-z)^2} = -zq(1-q)F(z) \quad (11a)$$

$$\dot{z} = -(1-z)(z(b+q(r-1)(1-z^{N-1})) - d). \quad (11b)$$

This is the dynamical system that we aim to characterize in this paper.

2.1. Homogeneous populations

In the absence of cooperators ($q = 0$) the population dynamics (11) reduce to

$$\dot{z} = -(1-z)(zb - d) \quad (12)$$

with the trivial equilibrium $z_1^* = 1$ and potentially a second one at $z_2^* = d/b$. If the death rate d exceeds the baseline birthrate b , z_1^* is the only equilibrium and is stable, i.e. the population goes to extinction. Thus, in this case, the survival of defectors hinges on the presence of cooperators that can be exploited. However, if $b > d$ defectors can survive on their own at an equilibrium density $y^* = 1 - z_2^*$ (see Fig. 1(a)).

Conversely, in the absence of defectors ($q = 1$) the population dynamics are given by:

$$\dot{z} = -(1-z)(z(b + (r-1)(1-z^{N-1})) - d), \quad (13)$$

which is dynamically more interesting. Again, the system has a trivial equilibrium at $z_1^* = 1$, but in addition there are up to two non-trivial and analytically inaccessible equilibria z_2^* , z_3^* . To prove that there exist at most two interior equilibria, consider $g(z) = \dot{z}/(1-z)$ with $g(0) = d > 0$, $g(1) = d - b$ and $g''(z) = (N-1)N(r-1)z^{N-2} > 0$. It follows that if $d < b$ exactly one equilibrium exists, and if $d > b$ at most two equilibria exist. The maximum death rate d_{\max} for which pure cooperator populations persist is determined by the minimum of $g(z) - d$: $d_{\max} = (N-1)/N[(b+r-1)/(N(r-1))]^{1/(N-1)}(b+r-1)$. Fig. 1(b) illustrates the three different scenarios: (i) for $d > d_{\max}$ the fitness benefits from cooperative interactions cannot compensate the death rate and cooperators go to extinction; z_1^* is the only equilibrium, and it is stable. (ii) For $d_{\max} > d > b$, the dynamics are bistable: cooperators can survive for sufficiently high initial densities, but if initial cooperator densities lie below a threshold, too few interactions take place, so that the fitness benefits from cooperation are insufficient to

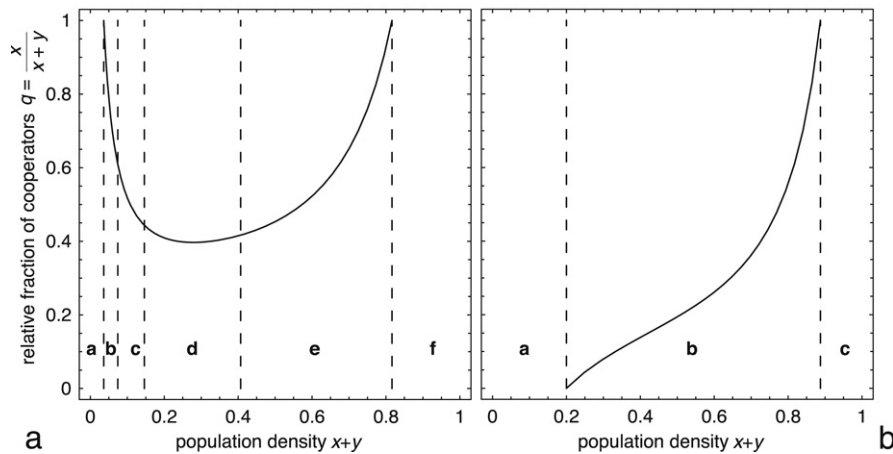


Fig. 2. Bifurcations and dynamical regimes (separated by dashed lines) in heterogeneous populations of cooperators and defectors interacting in ecological public goods games with $N = 8$, $b = 1$ and the multiplication factor r as the bifurcation parameter. The solid line indicates the location of the interior fixed point \mathbf{Q} as a function of r . **a** For $b < d$ ($b = 1$, $d = 1.2$) increasing r produces the following dynamical scenarios (see text for details): (a) no \mathbf{Q} , extinction; (b) \mathbf{Q} unstable node, extinction; (c) \mathbf{Q} unstable focus, extinction. A Hopf bifurcation occurs between regimes (c) and (d). If it is supercritical, stable limit cycles appear as r approaches r_{Hopf} and cooperators and defectors can co-exist in everlasting oscillations. (d) \mathbf{Q} stable focus, co-existence. If the Hopf bifurcation is subcritical, the basin of attraction of \mathbf{Q} is bounded by an unstable limited cycle close to the bifurcation point ($r > r_{\text{Hopf}}$). (e) \mathbf{Q} stable node, co-existence; (f) no \mathbf{Q} , cooperation. For unfavorable initial conditions, the population goes to extinction even for (d)–(f). **b** The dynamics are considerably less rich for $b > d$ ($b = 1$, $d = 0.8$) but extinction no longer occurs. The following scenarios are observed for increasing r : (a) no \mathbf{Q} , defection; (b) \mathbf{Q} stable, co-existence; (c) no \mathbf{Q} , cooperation.

offset the death rate and the population disappears. In ecology the positive correlation between population density and per capita growth rate is known as the Allee effect (Stephens, 1999). In the presence of Allee effects, populations become prone to extinction at low densities, typically due to difficulties in finding mating partners. In the present model, the Allee effect is due to difficulties in finding interaction partners for the public goods game. (iii) Finally, for $b > d$ the threshold density capable of sustaining cooperation disappears and cooperators always survive ($z_1^* = 0$ is unstable). Note that the equilibrium density of pure cooperator populations is always higher than that of pure defector populations because of the fitness benefits from cooperative interactions.

2.2. Heterogeneous populations

In heterogeneous populations an interior fixed point $\mathbf{Q} = (\hat{q}, \hat{z})$ with $0 < \hat{q}, \hat{z} < 1$ may appear, at which cooperators and defectors co-exist. The presence (or absence) of \mathbf{Q} results in a rich variety of dynamical scenarios, including Hopf bifurcations accompanied by stable or unstable limit cycles. It turns out that the multiplication factor r serves as a convenient bifurcation parameter. For increasing r , the system undergoes a series of bifurcations. The trajectory of \mathbf{Q} together with the different dynamical regimes are shown in Fig. 2. For $b < d$ starting with small r , the following sequence of bifurcations and dynamical scenarios occurs (numerical thresholds of r are given for $N = 8$, $c = 1$, $b = 1$, $d = 1.2$):

(a) $r < r_{\text{trans}_1} \approx 2.077$: No interior fixed point exists. Along $q = 1$, i.e. in the absence of defectors (cf. Fig. 1(b)), two fixed points occur: an unstable node at lower densities and a saddle node at higher densities, which is stable along $q = 1$ but prone to invasion by defectors. The population invariably goes to extinction.

(b) $r_{\text{trans}_1} < r < r_{\text{nf}} \approx 2.166$: *Transcritical bifurcation* — for $r = r_{\text{trans}_1}$ a transcritical bifurcation occurs through which the interior fixed point \mathbf{Q} enters the phase plane and is an unstable node (for $r < r_{\text{trans}_1}$, the fixed point \mathbf{Q} also exists but $\hat{q} > 1$ holds). With the appearance of \mathbf{Q} the unstable node along $q = 1$ turns into a saddle node. The population still goes to extinction.

(c) $r_{\text{nf}} < r < r_{\text{Hopf}} \approx 2.366$: for $r = r_{\text{nf}}$ the fixed point \mathbf{Q} changes from an unstable node into an unstable focus — no changes along $q = 1$. The population keeps going to extinction but when starting in the vicinity of \mathbf{Q} the densities of cooperators and defectors exhibit oscillations of increasing amplitude. If the system undergoes a supercritical Hopf bifurcation for $r = r_{\text{Hopf}}$ then a stable limit cycle appears as r approaches r_{Hopf} from below and cooperators and defectors can stably co-exist in everlasting oscillations. However, the basin of attraction of the stable limit cycle remains limited and the population may not be able to recover from unfavorable initial conditions. Thus, when starting from low initial densities or high relative abundance of defectors, the population goes to extinction. The amplitude of the oscillations decreases for $r \rightarrow r_{\text{Hopf}}$.

(d) $r_{\text{Hopf}} < r < r_{\text{fn}} \approx 3.52$: *Hopf bifurcation* — for $r = r_{\text{Hopf}}$ a Hopf bifurcation occurs and \mathbf{Q} turns into a stable focus. The population can survive with cooperators and defectors co-existing. The system converges to \mathbf{Q} with oscillations of decreasing amplitude. If the Hopf bifurcation is subcritical then co-existence occurs only when starting in the vicinity of \mathbf{Q} , i.e. in the interior of the unstable limit cycle. The size of the limit cycle or the basin of attraction of \mathbf{Q} quickly increases with r . Unfavorable initial conditions always drive the population to extinction.

(e) $r_{\text{fn}} < r < r_{\text{trans}_2} \approx 6.530$: for $r = r_{\text{fn}}$ the fixed point \mathbf{Q} changes from a stable focus into a stable node. Cooperators and defectors co-exist but no longer show a tendency to

oscillate in the vicinity of \mathbf{Q} . As before, unfavorable initial conditions result in extinction.

- (f) $r > r_{\text{trans}_2}$: *Transcritical bifurcation* — the interior fixed point \mathbf{Q} leaves the phase plane and the saddle node at higher densities along $q = 1$ turns into a stable node (for $r > r_{\text{trans}_2}$ \mathbf{Q} still exists but $\hat{q} > 1$ holds). Cooperation becomes dominant and defectors disappear. However, even now the population goes to extinction for unfavorable initial conditions.

Depending on the parameter values N, b and d , not all six dynamical scenarios described above may be observed. For example, for larger d no Hopf bifurcation occurs, and if d exceeds d_{max} the interior fixed point \mathbf{Q} never appears, and the fixed points along $q = 1$ disappear, so that the population invariably goes to extinction.

If the birth rate exceeds the death rate ($b > d$), then the dynamics of the system become less interesting with fewer dynamical regimes but the system is never driven to extinction (numerical thresholds of r are given for $N = 8, b = 1, d = 0.8$):

- (a) $r < r_{\text{trans}_1} \approx 2.546$: No interior fixed point exists. In the absence of defectors ($q = 1$), a saddle point exists, which is stable along $q = 1$ (cf. Fig. 1(b)) but prone to invasion by defectors. Along $q = 0$ (no cooperators) a stable node exists (cf. Fig. 1(a)). Consequently, cooperators go to extinction and only defectors survive.
- (b) $r_{\text{trans}_1} < r < r_{\text{trans}_2} \approx 7.098$: *Transcritical bifurcation* — the interior fixed point \mathbf{Q} enters the phase plane and is always stable. At the same time, the stable node along $q = 0$ (no cooperators) turns into a saddle node (remaining stable along $q = 0$). Thus, cooperators and defectors co-exist in a globally stable equilibrium. The equilibrium density of cooperators increases with r .
- (c) $r > r_{\text{trans}_2}$: *Transcritical bifurcation* — the interior fixed point leaves the phase plane, which turns the saddle node along $q = 1$ (no defectors) into a stable node. Cooperation becomes the dominant strategy.

The most interesting dynamics occur in the vicinity of the Hopf bifurcation ($b < d$) and a detailed analysis follows.

3. Analysis

A complete analysis of the dynamics in heterogeneous populations is impossible in general. Already the coordinates of the interior fixed point $\mathbf{Q} = (\hat{q}, \hat{z})$ are analytically inaccessible, because $F(\hat{z}) = 0$ cannot be solved analytically for arbitrary N . However, we can determine the uniqueness and stability of \mathbf{Q} (see Section 3.1) and in the special case with $b = 0$ the Hopf bifurcation can be analyzed in detail (see Section 3.2).

\mathbf{Q} is unique for $r > 2$, because $F(z) = 0$ admits only a single root in $[0, 1)$ (Hauert et al., 2002a) and because \hat{z} is linear in q (see Eq. (11)). For $r \leq 2$, $F(z)$ has no root in $[0, 1)$ and \mathbf{Q} does not exist. Note that \hat{z} is independent of b and d but \hat{q} is not. Thus, even if $r > 2$, the fixed point \mathbf{Q} may not exist because $\hat{q} \notin (0, 1)$. The Jacobian matrix of our dynamical system (11) at a fixed point $\mathbf{Q} = (\hat{q}, \hat{z})$ is given in Box I.

Note that $\det \mathbf{J} > 0$ always holds because $F'(\hat{z}) < 0$ (Hauert et al., 2002a).

3.1. Stability of \mathbf{Q}

Let us first consider the simpler scenario with $b > d$ and prove the stability of \mathbf{Q} . \mathbf{Q} is stable if both eigenvalues λ_{\pm} of \mathbf{J} have a negative real part: $\lambda_{\pm} = (\text{tr } \mathbf{J} \pm \sqrt{(\text{tr } \mathbf{J})^2 - \det \mathbf{J}}) / 2$. Since $\det \mathbf{J} > 0$ always holds, it is sufficient to show that $\text{tr } \mathbf{J} < 0$. $\text{tr } \mathbf{J}$ has the same sign as $g(z) = d(Nz^{N-1} - 1) - bz^N(N-1)$. Solving $g'(z) = 0$ yields $z = d/b$ and noting that $g''(d/b) < 0$ holds, we know that $g(z)$ has a maximum at $z = d/b$ with $g(d/b) = d((d/b)^{N-1} - 1)$ such that $\max_z g(z) < 0$ and thus \mathbf{Q} is always stable.

In the dynamically richer case with $b < d$ we prove that \mathbf{Q} is stable for $r > r_{\text{Hopf}}$. First we note that \hat{z} is a decreasing function of r . Consider the Taylor expansion of $F(z)$ (see Eq. (10)) around \mathbf{Q} in terms of $r = r_{\mathbf{Q}} + \delta r$ and $z = \hat{z} + \delta z$ using $F(r_{\mathbf{Q}}, \hat{z}) = 0$:

$$F(r, z) = \frac{\partial F}{\partial r} \delta r + \frac{\partial F}{\partial z} \delta z + h.o.t. \tag{14}$$

Since $F(r, \hat{z}) = 0$ holds at any equilibrium, it follows that $\partial F / \partial r \delta r = -\partial F / \partial z \delta z$, up to first order. The coefficients of δr and δz are both negative at \mathbf{Q} : $\partial F / \partial r$ reduces to $(\hat{z}^{N-1} - 1) / r < 0$ and $\partial F / \partial z$ is simply $F'(\hat{z}) < 0$ (see above). Hence, an increase in r ($\delta r > 0$) results in a decrease in \hat{z} ($\delta z < 0$).

Second, we show that $\text{tr } \mathbf{J} > 0$ holds for $\hat{z} > \hat{z}_{\text{Hopf}}$. At the Hopf bifurcation $\text{tr } \mathbf{J} = 0$ holds and

$$\frac{d}{dz} \text{tr } \mathbf{J} \Big|_{z=\hat{z}_{\text{Hopf}}} = -\frac{1 - \hat{z}_{\text{Hopf}}}{1 - \hat{z}_{\text{Hopf}}^{N-1}} N(N-1) \hat{z}_{\text{Hopf}}^{N-3} (b \hat{z}_{\text{Hopf}} - d) \tag{15}$$

is positive whenever $b < d$. Thus, $\text{tr } \mathbf{J}$ is increasing in \hat{z} and decreasing in r such that for $r > r_{\text{Hopf}}$, $\text{tr } \mathbf{J} < 0$ holds and \mathbf{Q} is stable. Moreover, this proves that the Hopf bifurcation is unique.

3.2. Hopf bifurcation

For the existence of a Hopf bifurcation, it is necessary and sufficient that the trace of the Jacobian \mathbf{J} vanishes ($\text{tr } \mathbf{J} = 0$) and that $\det \mathbf{J} > 0$. In non-linear systems Hopf bifurcations can be either supercritical or subcritical, i.e. give rise to stable or unstable limit cycles in the vicinity of the Hopf bifurcation. The two scenarios are distinguished based on the sign of the Lyapunov coefficient l_1 (Kuznetsov, 2004), which captures effects of non-linear terms at the bifurcation point. Up to first order, \mathbf{Q}_{Hopf} is neutrally stable. However, due to higher order terms, \mathbf{Q}_{Hopf} can still be attracting ($l_1 < 0$). In this case the bifurcation is supercritical and a stable limit cycle appears when \mathbf{Q} becomes unstable (for $r < r_{\text{Hopf}}$). Conversely, if \mathbf{Q}_{Hopf} is repelling ($l_1 > 0$) then the bifurcation is subcritical and an unstable limit cycle appears after \mathbf{Q} becomes stable (for $r > r_{\text{Hopf}}$).

In the special case $b = 0$ it is possible to explicitly derive both coordinates of \mathbf{Q}_{Hopf} thus allowing for a more detailed analysis. The $\text{tr } \mathbf{J}$ vanishes for $\hat{z} \in (0, 1)$ only if $1 - N\hat{z}^{N-1} = 0$

$$\mathbf{J} = \begin{pmatrix} 0 & -(1 - \hat{q})\hat{q}\hat{z}F'(\hat{z}) \\ -(r - 1)(1 - \hat{z})\hat{z}(1 - \hat{z}^{N-1}) & -\frac{1 - \hat{z}}{\hat{z}(1 - \hat{z}^{N-1})} (d(1 - N\hat{z}^{N-1}) + b\hat{z}^N(N - 1)) \end{pmatrix}$$

Box I.

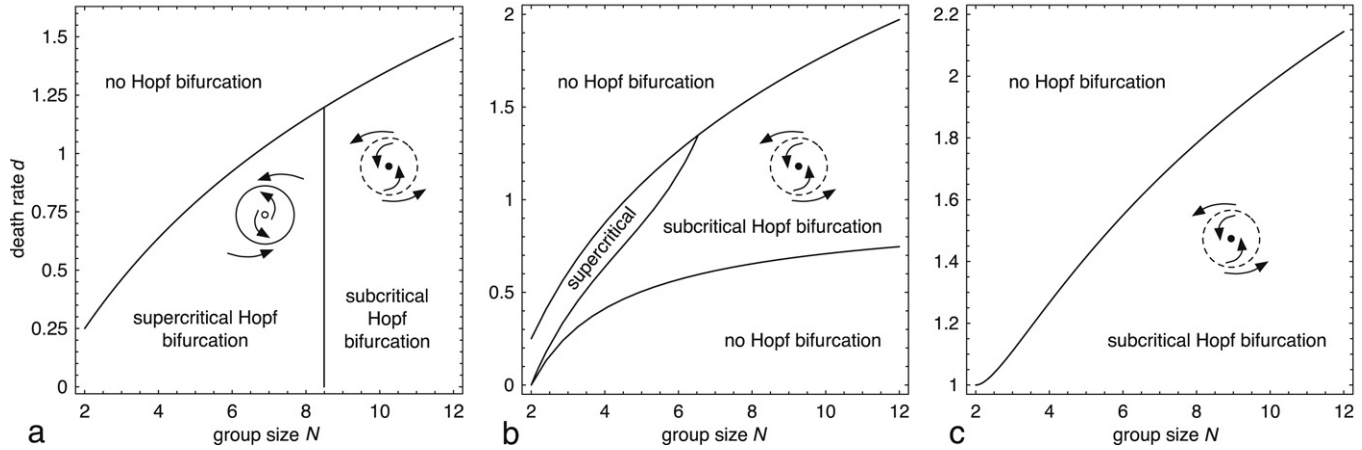


Fig. 3. Hopf bifurcations and first Lyapunov coefficient l_1 as a function of the group size N and the death rate d for different birth rates b . For sufficiently large d , Hopf bifurcations no longer occur. This threshold corresponds to the condition that the interior fixed point \mathbf{Q} exists, i.e. $\hat{q} < 1$. **a** In the special case with $b = 0$ the Hopf bifurcation can be analyzed in detail (see text) and occurs at $r = r_{\text{Hopf}} = N(N^{\frac{1}{N-1}} - 1)$. For $N < N^* \approx 8.493$ the bifurcation is supercritical and stable limit cycles are observed for r slightly smaller than r_{Hopf} . Similarly, for $N > N^*$ the bifurcation is subcritical as reflected in unstable limit cycles for r slightly above r_{Hopf} . **b** Setting $b = b_0 = 1 - r/N$ denotes the minimal b that ensures compatibility with the interpretation of Eq. (6) in terms of per capita birth and death rates. For very small d no Hopf bifurcations occur because $d < b$ holds (cf. Fig. 2(b)). The region of supercritical Hopf bifurcations and stable limit cycles is considerably smaller and for $N \geq 7$ all bifurcations are subcritical. **c** Setting $b = 1$ corresponds to the minimal birthrate that is compatible with all group sizes N . In that case, stable limit cycles no longer occur. Instead, the Hopf bifurcation is always subcritical and accompanied by unstable limit cycles.

and thus yields $\hat{z} = N^{-\frac{1}{N-1}}$. Using $F(\hat{z}) = 0$ we obtain $r_{\text{Hopf}} = N(N^{\frac{1}{N-1}} - 1)$ and finally inserting \hat{z} and r_{Hopf} into Eq. (11) returns the other coordinate of \mathbf{Q}_{Hopf} :

$$\hat{q} = \frac{dN^{\frac{N}{N-1}}}{(N - 1)(N^{\frac{N}{N-1}} - N - 1)}. \tag{16}$$

The Jacobian \mathbf{J} at the bifurcation point can be written as

$$\mathbf{J} = \begin{pmatrix} 0 & -(1 - \hat{q})\hat{q}\frac{N - 1}{N} \frac{r_{\text{Hopf}}(1 - \hat{z}) - 1}{1 - \hat{z}} \\ -\frac{(1 - \hat{z})d}{\hat{q}} & 0 \end{pmatrix} \tag{17}$$

with eigenvalues $\lambda_{\pm} = \pm i\omega$ and

$$\omega = \sqrt{-\frac{d}{N}(N - 1)(1 - \hat{q})(r_{\text{Hopf}}(1 - \hat{z}) - 1)} > 0.$$

Following Kuznetsov (2004), we obtain the first Lyapunov coefficient l_1 as:

$$l_1 = -\frac{d^2(1 - \hat{q})(N - 1)^2(r_{\text{Hopf}} - 1)(1 - \hat{z})^2}{4\hat{q}N^2\hat{z}^2\omega^5} \times (-\hat{q}(N - 1)(r_{\text{Hopf}} - 1)(1 - r_{\text{Hopf}}(1 - \hat{z}))\hat{z}^2 + dN(2 - (N - 3)\hat{z} + N\hat{z}^2 - 2r_{\text{Hopf}}(1 - \hat{z}^2))). \tag{18}$$

The detailed derivation of l_1 is available in the online supplement.

For all \mathbf{Q} in the interior ($0 < \hat{q}, \hat{z} < 1$), the first factor of l_1 is always negative and the sign of l_1 depends only on the second term. Upon inserting \hat{q}, \hat{z} and r_{Hopf} , it becomes clear that the sign of l_1 is exclusively determined by N , more precisely by the sign of the following expression:

$$N - 2(1 + N^{\frac{1}{N-1}}) + N^{\frac{N}{N-1}} (2N^{\frac{1}{N-1}} - 3). \tag{19}$$

This expression has a single real root with $N^* = 8.493$, such that supercritical Hopf bifurcations ($l_1 < 0$) occur for $N < N^*$ and subcritical bifurcations ($l_1 > 0$) for $N > N^*$ as shown in Fig. 3(a). At $\mathbf{B} = (r_{\text{Hopf}}, N^*)$ we have strong evidence that the system undergoes a Bautin bifurcation (or generalized Hopf bifurcation) (Kuznetsov, 2004; Guckenheimer & Kuznetsov, 2007) because at r_{Hopf} the eigenvalues λ_{\pm} are purely imaginary, the first Lyapunov coefficient l_1 vanishes at N^* and finally, numerical analysis yields a non-vanishing second Lyapunov coefficient, $l_2 < 0$. Thus, nothing changes in the supercritical case ($N < N^*$) but in the subcritical case ($N > N^*$) an interesting sequence of dynamical scenarios occurs in the vicinity of \mathbf{B} as we increase r : For $r < r_{\text{Hopf}}$, the co-existence equilibrium \mathbf{Q} is unstable, surrounded by a stable limit cycle. As $r \rightarrow r_{\text{Hopf}}$, the amplitude of the limit cycle decreases and at r_{Hopf} the stability of \mathbf{Q} changes. For $r > r_{\text{Hopf}}$, \mathbf{Q} is surrounded by a pair of limit cycles, an unstable inner cycle and a stable outer cycle. For increasing r , the two limit cycles collide and disappear in a saddle-node bifurcation of periodic orbits, which leaves just the stable \mathbf{Q} behind. These interesting dynamical

features have already been observed in Hauert et al. (2006b) but only now we can attribute them to an underlying Bautin bifurcation. The dynamics can be further explored using the *VirtualLabs* (Hauert, 2007).

3.3. Numerical extensions ($b > 0$)

The first Lyapunov coefficient l_1 is analytically inaccessible for $b > 0$. But, as mentioned before, setting $b = 0$ violates the interpretation of $z(f_C + b)$ and $z(f_D + b)$ in Eq. (6) in terms of per capita birth rates, because $z(b + f_C)$ can become negative for small q and large z . Thus, it is important to know how increasing b affects the dynamics. Our numerical analysis indicates that $b = 0$ produces the richest dynamics and that the dynamics becomes simpler for larger b . For example, the region of supercritical bifurcations decreases and eventually disappears for increasing baseline birth rates b . To ensure that birth rates are positive for all q and z , the baseline birth rate b has to exceed $b_0 = -\min f_C = 1 - r/N$. The numerical results for $b = b_0$ are shown in Fig. 3(b). Setting $b = 1$ ensures compatibility ($z(f_C + b) \geq 0$) for all parameter values r, N because $\min f_C = -1$ for $N \rightarrow \infty$. In this case, numerical investigations suggest that $l_1 > 0$ always holds and supercritical Hopf bifurcations no longer occur (see Fig. 3(c)).

We also note that the Bautin bifurcation, which yields multiple stable and unstable limit cycles (see Section 3.2), does not seem to occur for larger b . Again the dynamics appear to become simpler and, in particular, for $b > b_0$ no scenarios with multiple limit cycles have been found.

4. Conclusions

The Public Goods game is commonly used for studying the evolution and maintenance of cooperation. In its simplest form, this evolutionary game has two regimes: defection goes to fixation if the multiplication factor r is smaller than the interaction group size N , whereas cooperation goes to fixation if the multiplication factor r is larger than the interaction group size N . Our premise was to start with a scenario in which $r < N$, where N is the “nominal” interaction group size, and then to assume that the effective interaction group size S can vary by incorporating population dynamics into the Public Goods game. This is done in such a way that a prevalence of defectors in the population leads to low birth rates and hence to a decline in the population size. This in turn generates smaller effective interaction group sizes S , for which $r > S$ holds, and hence leads to situations in which cooperation dominates. A prevalence of cooperation then leads to higher birth rates, and hence to an increase in the population size. In this way, incorporating population dynamics based on the payoffs received from game interactions creates a feedback loop through which cooperation can be maintained in the population.

In this paper we presented a detailed analysis of the *Ecological Public Goods Game* (Hauert et al., 2006a,b). We confirm that under suitable conditions, a stable equilibrium \mathbf{Q} is found at which cooperators and defectors co-exist. At \mathbf{Q} , the payoffs of cooperators and defectors are equal ($F(\hat{z}) = 0$),

which implies that the effective interaction group size S must satisfy $r = S$ (cf. Eqs. (4) and (5)). We show here that this equilibrium appears and disappears through transcritical bifurcations, and that the model can exhibit subcritical or supercritical Hopf bifurcations. The latter case is particularly interesting because it results in a stable limit cycle, and hence in oscillatory co-existence of cooperators and defectors. Cyclic co-existence of different strategies in evolutionary games is well known from the Rock–Paper–Scissors Game, or from voluntary Public Goods games (Hauert et al., 2002b) but in the absence of population structures this has not been reported for games with only cooperators and defectors. Thus, the existence of stable limit cycles in the *Ecological Public Goods Game* appears to be a significant finding, which shows that including population dynamics in evolutionary games can have important consequences for the evolutionary dynamics of cooperation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tpb.2007.11.007.

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