



Evolution of staying together in the context of diffusible public goods



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HIGHLIGHTS

- We study a model for public goods exchange incorporating staying together.
- Clusters of cooperators consume a fraction of their own public goods.
- Cooperators in large clusters have diminished access to external public goods.
- Cooperators and defectors can receive unequal payoff from consuming a public good.
- We derive conditions for the coevolution of cooperation and clustering.

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ABSTRACT

We study the coevolution of staying together and cooperation. Staying together means that replicating units do not separate after reproduction, but remain in proximity. For example, following cell division the two daughter cells may not fully separate but stay attached to each other. Repeated cell division thereby can lead to a simple multi-cellular complex. We assume that cooperators generate a diffusible public good, which can be absorbed by any cell in the system. The production of the public good entails a cost, while the absorption leads to a benefit. Defectors produce no public good. Defectors have a selective advantage unless a mechanism for evolution of cooperation is at work. Here we explore the idea that the public good produced by a cooperating cell is absorbed by cells of the same complex with a probability that depends on the size of the complex. Larger complexes are better at absorbing the public goods produced by their own individuals. We derive analytical conditions for the evolution of staying together, thereby studying the coevolution of clustering and cooperation. If cooperators and defectors differ in their intrinsic efficiency to absorb the public good, then we find multiple stable equilibria and the possibility for coexistence between cooperators and defectors. Finally we study the implications of disadvantages that might arise if complexes become too large.

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1. Introduction

A crucial question in biology is: what makes evolution constructive? Why does evolution generate more complicated life forms over time? How does evolution move to higher levels of organization? Examples of such constructive steps in evolution are the emergence of cellular replicators, of multi-cellular organisms, of animal societies and of human society (Maynard Smith and Szathmari, 1998; Carroll, 2001).

The fundamental mathematical tools of evolutionary dynamics (Nowak, 2006), such as the various approaches to study population genetics (Fisher, 1930; Wright, 1931; Haldane, 1932; Crow and Kimura,

2009), the quasi-species equation (Eigen and Schuster, 1977), the replicator equation (Hofbauer and Sigmund, 1998), the Moran process (Moran, 1962), the Wright–Fisher process (Fisher, 1930; Wright, 1931), or evolutionary graph theory (Lieberman et al., 2005) describe selection and mutation on a single level of organization. The search is on for deterministic equations or stochastic processes that describe how evolution can construct new levels of organization.

Tarnita et al. (2013) investigate two such mechanisms: staying together and coming together. Staying together means that individual replicators (for example cells) do not separate after reproduction but remain in the same complex (Kirk, 2003, 2005; Koschwanez et al., 2011; King, 2004). The emergence of a multi-cellular organism by repeated cell division starting from a single cell is an example of staying together (Rainey, 2007; Rossetti et al., 2011). As another example, among social insects, the standard method to form a colony is that offspring stay with their mother

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and help to produce further offspring (Wilson, 1971). In contrast, coming together describes the aggregation of individual replicators to form a complex (Hall-Stoodley et al., 2004; Kolter, 2010; Willensdorfer, 2008; Garcia and De Monte, 2012). For example, slime molds live as individual cells when food is abundant, but come together to form a single moving body when food is rare (Bonner, 2008). Also in insect colonies, there are cases where several fertilized females come together to form a colony (Gadagkar, 1994, 2001).

Previous work on staying together (Tarnita et al., 2013) mostly investigated the case of constant selection. Here we link staying together with a public goods game (Hardin, 1968; Sigmund et al., 2001; Hauert et al., 2008; Gore et al., 2009; Julou et al., 2013; Allen et al., 2014; Wakano et al., 2009). We assume that there are two types of cells: cooperators and defectors. Cooperators form aggregates by staying together. Moreover, cooperators produce a diffusible public good which can subsequently be absorbed by any cell in the system (Allen et al., 2014; Brandt et al., 2003; Gore et al., 2009; Driscoll and Pepper, 2010; Kummerli et al., 2009; Julou et al., 2013; Momeni et al., 2014). If cells are in the same complex then they have a higher chance to absorb each other's public good productions. Specifically we assume that a complex that consists of k many cells absorbs a fraction α_k of the public good that is produced by each of its own members. Thus the complex preferentially benefits from its own productions and releases only a fraction $1 - \alpha_k$ into the environment, which can then be absorbed by other individual cells or complexes. It is natural to assume that α_k is an increasing sequence in k . This is because the fraction of cells on the boundary of a cluster—the only region from which any diffusible public goods can escape the cluster—decreases with the number of cells in the cluster. In our model, defectors have no advantage to stay together, because they produce no public good. Therefore, we do not need to investigate complex formation of defectors. (An extension of our model in which defectors can cluster together is presented in Appendix A.)

In the absence of staying together, cooperators would be outcompeted by defectors. But staying together leads to a population structure that allows evolution of cooperation. It is known that cooperators can be favored over defectors in structured populations (Nowak and May, 1992; Nowak et al., 2010b; Ohtsuki et al., 2006; Allen and Nowak, 2012; Antal et al., 2009; Ferriere and Michod, 1996; Helbing and Yu, 2008; Herz, 1994; Nakamaru et al., 1997; Ohtsuki et al., 2007; Szabó and Töke, 1998; Szabó and Hauert, 2002; Szabó and Fath, 2007; Tarnita et al., 2009a, 2009b; Taylor et al., 2007; Damore and Gore, 2012; Killingback and Doebeli, 1996, 1998; van Baalen and Rand, 1998; Ifti et al., 2004; Santos and Pacheco, 2005). An exception is shown in Hauert and Doebeli (2004), where spatial structure is found to inhibit evolution of cooperation in certain situations with the snowdrift game. Our aim in this paper is to calculate conditions for the coevolution of cooperation and staying together.

Our paper is organized as follows. In Section 2 we introduce the basic model and study the evolutionary dynamics first for any intensity of selection and subsequently for weak selection. We derive simple analytic conditions for particular choices of the sequence α_k . In Section 3 we explore the case where cooperators and defectors differ in their efficacy to absorb the public good. In Section 4 we introduce disadvantages for complexes that are too large and derive optimal probabilities for staying together after reproduction. Section 5 is our conclusion.

2. Staying together and diffusible public goods

Inspired by evolution's propensity for creating structures with ever-increasing levels of complexity, we posit that cooperators can

cluster together to form complexes (Grosberg and Strathmann, 2007; Furusawa and Kaneko, 2000; Bell and Mooers, 1997; Tarnita et al., 2013; Michod, 1999, 2007; Rossetti et al., 2010). Each k -complex contains k cooperating units. Whenever a cooperator inside a k -complex reproduces, its offspring can stay together with its parent k -complex with probability q , yielding a $(k+1)$ -complex, or its offspring can instead form a new 1-complex with probability $1 - q$. Defectors do not cluster together after reproduction. These biological reactions are represented as



A_k represents a complex consisting of k cooperators and B represents a single defector. We choose fitnesses f_k and f_y that describe the production and absorption of public goods. Consider the following fitness functions:

$$\begin{aligned} f_k &= k \left[1 + w \left(-c + b \sum_{n \geq 1} n x_n \right) \right] \\ f_y &= 1 + w b \sum_{n \geq 1} n x_n \end{aligned} \quad (2)$$

These fitnesses describe a biological system in which each cooperator incurs a cost c to produce a unit of a public good. The public good may be absorbed by a cooperator, thus delivering a benefit b to its recipient. The public good may instead be absorbed by a defector, which then also receives a benefit b . The parameter w represents the intensity of selection. It measures how much the payoff of the public goods game contributes to the fitness of the individuals. If we denote x_k as the frequency of A_k 's and y as the frequency of B 's, then the kinetics of the biological reactions (1) are described by the following system of differential equations:

$$\begin{aligned} \dot{x}_1 &= (1 - q) \sum_{k \geq 1} f_k x_k - q f_1 x_1 - \phi x_1 \\ \dot{x}_k &= q f_{k-1} x_{k-1} - q f_k x_k - \phi x_k \\ \dot{y} &= f_y y - \phi y \end{aligned} \quad (3)$$

Looking at the equation for \dot{x}_1 , we see that x_1 increases whenever any complex makes a new unit which detaches from its parent complex. x_1 decreases whenever the offspring of a 1-complex stays together and forms a 2-complex. From the equation for \dot{x}_k with $k > 1$, a k -complex forms when a $(k-1)$ -complex makes a new unit which stays attached to its parent complex. A k -complex similarly disappears when a k -complex makes a new unit which stays attached to its parent, transforming the parent complex into a $(k+1)$ -complex. Here ϕ represents a density-dependent death rate and is used exactly as in the replicator and quasi-species (Eigen and Schuster, 1977; Hofbauer and Sigmund, 1998). We require that the total number of cells in the population remains constant: $\sum_{k \geq 1} k x_k + y = 1$. The ϕ that enforces this density constraint is $\phi = \sum_{k \geq 1} f_k x_k + f_y y$.

Complex formation in nature may have begun through neutral drift (Bonner, 1998; Tarnita et al., 2013). By choosing f_k to be proportional to k , and with $w=0$, each k -complex is equally efficient at producing k new cooperating units as k isolated defectors are at producing k additional defectors. Consequently, the k -complexes and the defectors are neutral variants in terms of selection (Tarnita et al., 2013). The death rate of cooperating units within k -complexes, $\phi k x_k$, equals the ratio of the number of cooperating units within k -complexes to the number of defectors, $k x_k / y$, multiplied by the death rate of defectors, ϕy . Thus the k -complexes and defectors are also neutral variants in terms of death. The parameters multiplied by w in the fitnesses (b and c in Eqs. (2)) therefore represent a nontrivial perturbation to the system's behavior in the limit $w \rightarrow 0$. Absent any

mechanism for cooperation, and for all $w > 0$, defectors will always outcompete cooperators.

Since cooperators within a k -complex are clustered together in physical space, larger k -complexes are likely more efficient at consuming their own internally produced goods. Public goods produced in the interior of a cluster are less likely to escape if there are a greater number of cells in the cluster. Indeed, there is growing evidence that spatial clustering enhances cooperation in microbial populations where public goods are exchanged (Kummerli et al., 2009; Julou et al., 2013; Momeni et al., 2014; Allison, 2005; Misevic et al., 2012; Buckling et al., 2007; Koschwanez et al., 2011; Allen et al., 2014; Gore et al., 2009; Damore and Gore, 2012). We modify our fitnesses to incorporate the advantage of clustering. A cooperating unit within a k -complex produces a public good at cost c and, with probability α_k , the public good is absorbed by a cooperating unit within the same k -complex (Fig. 1). The new fitness functions that reflect this internal consumption of public goods are

$$f_k \rightarrow f_k^\alpha = k \left[1 + w \left(-c + b\alpha_k + b \sum_{n \geq 1} (1 - \alpha_n) n x_n \right) \right]$$

$$f_y \rightarrow f_y^\alpha = 1 + wb \sum_{n \geq 1} (1 - \alpha_n) n x_n \quad (4)$$

Note that fitnesses (2) are a special case of fitnesses (4) with all $\alpha_k = 0$. Isolated cooperators are still less fit than defectors. If however α_k is a monotonically increasing function of complex size k , then larger k -complexes may become more efficient at producing k new cooperating units than single defectors are at producing additional defectors. In such a scenario, cooperation and construction are mutually reinforcing and can evolve simultaneously (Fig. 2).

In determining the benefit to a cooperator from consuming its complex's own goods, it is helpful to first consider a simple case: Assume that each of the k cooperators in a k -complex produces goods

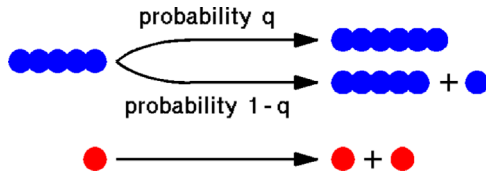


Fig. 1. Blue spheres are cooperating units and red spheres are defectors. Cooperators stay together after reproduction with probability q or separate with probability $1 - q$. Defectors always separate after reproduction. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

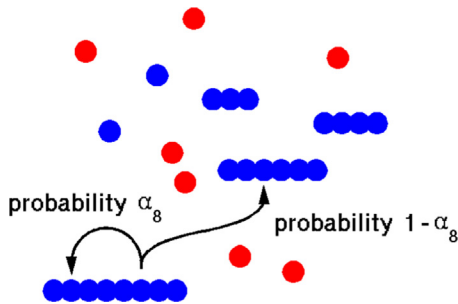


Fig. 2. Blue spheres are cooperating units and red spheres are defectors. Four cooperating complexes, two solitary cooperators, and seven defectors are shown. α_k is the probability that a public good will be consumed by a cooperator within the same complex as the cooperator that produced the good. In this example, a cooperator within the complex of size $k=8$ produces a unit of the public good. With probability α_8 , the good is consumed by a cooperator which is part of the same 8-complex. With probability $1 - \alpha_8$, the good is instead consumed by an external cooperator or defector (in this case a cooperator within the nearby 6-complex). Higher values of α_k represent increased efficiency and tend to promote cooperation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

at unit rate. A fraction α_k of the complex's goods are consumed within the complex. Each of the $k\alpha_k$ goods consumed within the complex is used by one of the k cooperators of the complex, delivering benefit b . Thus the internal benefit for a cooperator within the complex is $b k \alpha_k / k = b \alpha_k$. More generally, we emphasize two points: (1) our model is sensitive to interactions within a k -complex through the single parameter α_k and (2) the α_k 's are free parameters. Therefore, to describe k -complexes with more complicated internal interactions, one simply changes the value of α_k ; the mathematics of the model is preserved.

In our model for public goods production, diffusion, and reabsorption among k -complexes and solitary defectors, what is the critical benefit-to-cost ratio b/c needed for cooperation to evolve?

2.1. Any intensity of selection

Our mathematical analysis of the dynamical system (3) follows that of Tarnita et al. (2013). It is based on direct manipulation of the differential equations of staying together and cooperation. To simplify notation, define $S = S(\vec{\alpha}, \vec{x}) \equiv \sum_{n \geq 1} (1 - \alpha_n) n x_n$, which is the total amount of diffusing public goods. If the system consists entirely of defecting units, $y^* = 1$, then $\phi = 1$. Tarnita et al. (2013) found that, for frequency-independent fitnesses \tilde{f}_k of the k -complexes, and for $\phi = 1$, the all-defecting fixed point is stable to invasion by cooperators if

$$\frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{q \tilde{f}_k}{1 + q \tilde{f}_k} < 1 \quad (5)$$

In our evolutionary game, for y^* slightly less than one, the bS terms in Eqs. (4) make negligible contributions to the overall fitnesses of cooperating k -complexes and solitary defectors compared with the frequency-independent fitness terms. Therefore, Eq. (5) allows us to deduce the stability of the $y^* = 1$ equilibrium to infinitesimal perturbations. To simplify writing in what follows, we define two expressions:

$$F_k(X, Y) \equiv \frac{qk[1 + w(-c + b\alpha_k + X)]}{1 + wY + qk[1 + w(-c + b\alpha_k + X)]}$$

$$G(X, Y) \equiv -1 + \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n F_k(X, Y) \quad (6)$$

(Here, X and Y are just placeholders.) The condition for the $y^* = 1$ equilibrium to be asymptotically stable to invasion by cooperators is $G(0, 0) < 0$

If the system instead consists entirely of cooperating complexes, $y^* = 0$, then we can explicitly calculate ϕ as

$$\phi = \sum_{k \geq 1} f_k x_k = 1 + w(b - c)$$

At the $y^* = 0$ fixed point, the quantity S is maximum. This maximum value of S , denoted as S_{\max} , is given implicitly by

$$G(bS_{\max}, b - c) = 0 \quad (8)$$

Now consider the stability of the $y^* = 0$ fixed point. Note that for an infinitesimal perturbation to the $y^* = 0$ fixed point (i.e. $S = S_{\max} - \delta S$), $\dot{y} < 0$ holds if $1 + wb(S_{\max} - \delta S) < 1 + w(b - c) - \mathcal{O}(\delta S)$. In the limit $\delta S \rightarrow 0$, this condition becomes $bS_{\max} < b - c$. Thus, Eq. (8) allows us to determine the condition for asymptotic stability of the $y^* = 0$ equilibrium to invasion by defectors as

$$G(bS_{\max}, bS_{\max}) > 0 \quad (9)$$

2.2. Weak selection

Now examine in detail the weak-selection limit ($w \rightarrow 0$), where fundamental insights are gleaned. In Appendix B, we simplify $G(X, Y)$ by treating w as a small parameter in our equations. With

help from Lemma 1 (see Appendix C), we find that $G(X, Y)$ reduces to

$$G(X, Y) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + X - Y}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \quad (10)$$

We now derive a simple condition on b/c that must be satisfied for cooperation to evolve. Recalling Eq. (7), we can simply write the condition for the $y^* = 1$ fixed point to be stable to invasion by cooperators as

$$G(0, 0) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} < 0$$

This reduces to

$$\frac{b}{c} < \frac{\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}{\sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}} \quad (11)$$

Using Lemma 2 (see Appendix C), Eq. (11) simplifies to

$$\frac{b}{c} < \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1} \quad (12)$$

Now recall the condition (Eq. (9)) for stability of the opposite equilibrium, $y^* = 0$, to invasion by defectors:

$$G(bS_{\max}, bS_{\max}) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + bS_{\max} - bS_{\max}}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} > 0$$

Simplifying gives

$$\frac{b}{c} > \frac{\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}{\sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}$$

Again using Lemma 2, we can simplify this further:

$$\frac{b}{c} > \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1} \quad (13)$$

Eqs. (12) and (13) give the critical b/c ratios needed for asymptotic stability of the all-defecting and all-cooperating equilibria to invasion by the opposite type in the limit of weak selection, respectively. We see that instability of the defecting equilibrium to invasion by cooperators also means stability of the cooperating equilibrium to invasion by defectors.

We must now determine if mixed equilibria can exist. Consider Eqs. (3). If an equilibrium is mixed, then by definition we have $0 < y^* < 1$. But if $y > 0$, then for \dot{y} to equal zero, we must have $\phi = f_y$. Since $f_y = 1 + wbS^*$ with $S^* = \sum_{n \geq 1} (1 - \alpha_n)nx_n^*$, we have $\phi = 1 + wbS^*$. Setting all time derivatives to zero, Eqs. (3) then require that $G(bS^*, bS^*) = 0$. In the limit of weak selection, this becomes

$$G(bS^*, bS^*) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + bS^* - bS^*}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} = 0$$

Of course, the amount of externally diffusing goods for any mixed equilibrium, $0 < y^* < 1$, is less than the amount of externally diffusing goods if every cell is a cooperator, $y^* = 0$. Thus the inequality $0 < S^* < S_{\max}$ must also be satisfied. Note that for weak selection, we have

$$\frac{d}{dS} G(bS, bS) = 0$$

We see that the condition for a mixed equilibrium to exist is independent of the frequencies of cooperators and defectors in the population. We now know that there is competitive exclusion. Cooperators and defectors cannot coexist in this basic version of

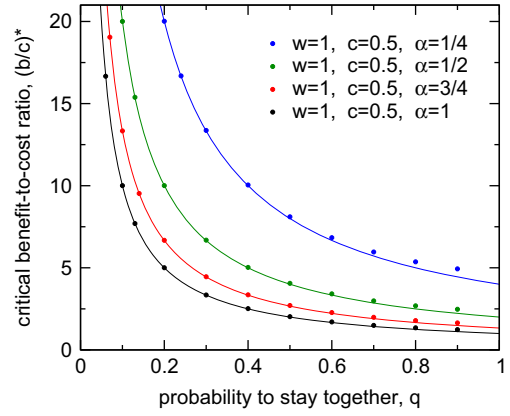


Fig. 3. Critical benefit-to-cost ratio needed for evolution of cooperation for $w=1$ (data points) plotted over the theoretical result for $w \rightarrow 0$ (solid curves). The critical b/c for $w \rightarrow 0$ accurately predicts the critical b/c for $w=1$, although there are noticeable discrepancies for large values of q . For our measurements with $w=1$, numerical errors are roughly the size of the data points.

the model. Cooperation arises if

$$\frac{b}{c} > \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1}$$

This result is general, holding for arbitrary internal efficiencies α_k . All else being equal, a system with a greater tendency q of newly produced cooperators to stay together within their parent k -complex typically requires a lower benefit-to-cost ratio in order for cooperation to evolve. A system further lowers its critical benefit-to-cost ratio by increasing the probability α_k that a public good is consumed within the same k -complex from which it originated (Fig. 3). For example, if all α_k are equal to zero, then cooperation cannot evolve for any finite value of the benefit-to-cost ratio b/c . This is reminiscent of the classic prisoner's dilemma. Note that if any one of the α_k values is strictly positive, then the critical value of b/c is finite and cooperation and construction can evolve concurrently. As the probabilities α_k of a k -complex consuming its own public good productions increase, the critical value of b/c generally decreases. At the other extreme, if all α_k are equal to 1, meaning that each cluster consumes all of its public good productions, then, using Lemma 2, we find that cooperation evolves if the much weaker condition $b > c$ is satisfied. These results support recent work (Allen et al., 2014) which found that cooperation in spatial games with diffusible goods is favored for small diffusion rates.

Recent experiments have revealed clustering phenotypes in microbes. Production of glue-like polymers by certain replicating strains of bacteria leads to clustering (Rainey and Rainey, 2003). Intricate cluster designs have also been observed through post-division adhesion in yeast (Ratcliff et al., 2012). We wonder if it is possible to determine q —the probability that a new reproductive bacterium or yeast cell remains physically attached to its parent—in these laboratory settings. This may form a starting point for experimentally exploring public goods exchange among undifferentiated cell clusters.

2.3. A specific example

To gain insight, it is helpful to consider a reasonable example for the sequence α_k . We choose

$$\alpha_k = \alpha \left(1 - \frac{1}{k} \right) \quad (14)$$

Since α_k is a probability, we require $0 \leq \alpha \leq 1$. Now our condition for cooperation becomes

$$\frac{b}{c} > \left[\frac{(1-q)^2 \alpha}{q} \left(\frac{q}{(1-q)^2} - \sum_{n \geq 1} \sum_{k=1}^n \frac{1}{k(1+kq)} \prod_{p=1}^n \frac{pq}{1+pq} \right) \right]^{-1} \quad (15)$$

Substituting Lemma 3 (see Appendix C) into condition (15), we obtain a strikingly simple condition for the evolution of cooperation:

$$\frac{b}{c} > \frac{1}{q\alpha}$$

The critical $(b/c)^*$ needed for cooperation decreases with (1) the probability q that new offspring remain with their parent complexes and (2) the probability α that a good is absorbed within the same complex that produced it. These two features are physically reasonable: (1) Offspring can remain with their parents by default (due to cells replicating in an environment with low diffusivity, scarcity of resources outside of the nest in animal societies, etc.). (2) Absorption of public goods is a first-passage process (Redner, 2001). Mean time to absorption of goods is lowest for cooperators that are in proximity. In our model, this suggests that cooperators within the same complex consume primarily their own public goods, which leads to α being strictly positive.

3. Bistability and coexistence of cooperators and defectors

The treatment thus far assumes that cooperating units and defectors receive the same benefit from absorbing a unit of public good. We now relax this assumption. Define a new parameter r that measures the ratio of the benefit gained by a defector receiving a unit of public good to the benefit gained by a cooperator receiving a unit of public good. To incorporate the parameter r , we modify the fitness function for defectors to be

$$f_y^\alpha \rightarrow f_y^{\alpha r} = 1 + wrb \sum_{n \geq 1} (1 - \alpha_n) n x_n$$

Note that the case $r < 1$ corresponds to a selective advantage for cooperators, while the case $r > 1$ corresponds to a selective advantage for defectors. Note that $r = 1$ reproduces the results of the previous section. How do values $r < 1$ and $r > 1$ affect the evolution of cooperation?

3.1. Any intensity of selection

Near the all-defecting equilibrium, $y^* = 1$, the total amount of externally diffusing public goods S is negligible. Just as for the case $r = 1$, the $y^* = 1$ equilibrium is stable to invasion by cooperators if $G(0, 0) < 0$, where the function $G(X, Y)$ is defined by Eq. (6).

At the all-cooperating equilibrium, S_{\max} is again given implicitly by Eq. (8). Note that for an infinitesimal perturbation to the $y^* = 0$ fixed point (i.e. $S = S_{\max} - \delta S$), $\dot{y} < 0$ holds if $1 + wrb(S_{\max} - \delta S) < 1 + w(b - c) - \mathcal{O}(\delta S)$. In the limit $\delta S \rightarrow 0$, this condition becomes $rbS_{\max} < b - c$. Thus, Eq. (8) again allows for determination of stability of the $y^* = 0$ equilibrium to invasion by defectors. The $y^* = 0$ equilibrium is now asymptotically stable if

$$G(bS_{\max}, rbS_{\max}) > 0$$

For any mixed equilibrium, $0 < y^* < 1$, we must have $\phi = 1 + wrbS^*$ to enforce $\dot{y} = 0$. Simplifying, the two conditions that must be satisfied for a mixed equilibrium to exist are

$$G(bS^*, rbS^*) = 0 \quad (16)$$

$$0 < S^* < S_{\max}$$

3.2. Weak selection

We reexamine the limit of weak selection, now with parameter $r < 1$ or $r > 1$. Notice that as $w \rightarrow 0$, the condition for stability of the all-defecting equilibrium to invasion by cooperators is as before:

$$\frac{b}{c} < \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1}$$

The all-cooperating equilibrium is stable to invasion by defectors if

$$G(bS_{\max}, rbS_{\max}) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + bS_{\max} - rbS_{\max}}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} > 0$$

Simplifying gives

$$\frac{b}{c} > \frac{\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}{\sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} + (1-r)S_{\max} \sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}$$

S_{\max} is independent of r . In the weak-selection limit, we can solve explicitly for S_{\max} . Using Eqs. (8) and (10)

$$G(bS_{\max}, b - c) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + bS_{\max} - (b - c)}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} = 0$$

So we obtain

$$S_{\max} = \frac{\sum_{n \geq 1} \sum_{k=1}^n \frac{1 - \alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}{\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}} \quad (17)$$

We find that the all-cooperating state is asymptotically stable to invasion by defectors if

$$\frac{b}{c} > \frac{\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}{\sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k + (1-r)(1 - \alpha_k)}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}$$

Again using Lemma 2, this simplifies to

$$\frac{b}{c} > \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k + (1-r)(1 - \alpha_k)}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1}$$

We must again determine if mixed equilibria can exist with weak selection. Recall Eq. (16):

$$G(bS^*, rbS^*) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + bS^* - rbS^*}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} = 0$$

$$0 < S^* < S_{\max}$$

The condition for a mixed equilibrium to exist now depends on the frequencies of cooperators and defectors in the population. Note that weak selection linearizes $G(bS, rbS)$ in S . We find

$$\frac{d}{dS} G(bS, rbS) = wb \frac{1-r}{1-q} \quad \text{which is } \begin{cases} > 0 & \text{if } r < 1 \\ = 0 & \text{if } r = 1 \\ < 0 & \text{if } r > 1. \end{cases} \quad (18)$$

Eq. (18) tells us that, if $r < 1$, and if the $y^* = 1$ fixed point is stable to invasion by cooperators, then there can exist at most one unstable mixed equilibrium. If $r > 1$, and if the $y^* = 1$ fixed point is unstable to invasion by cooperators, then there can exist at most one stable mixed equilibrium. Otherwise, there are no mixed equilibria. Therefore, introducing the parameter r allows multiple stable equilibria (if $r < 1$) and coexistence between cooperators and defectors (if $r > 1$).

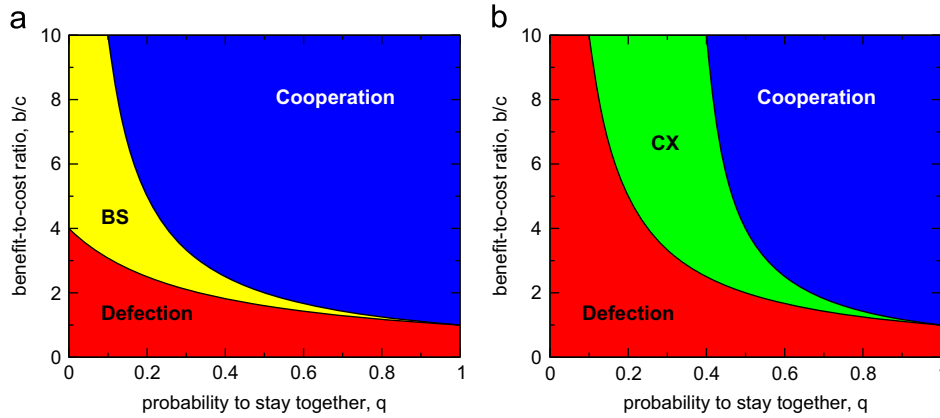


Fig. 4. (a) If cooperators benefit more from absorption of a public good than do defectors, then there are values of b/c for which the cooperating and defecting states are bistable (BS). (b) If defectors benefit more from absorption of a public good than do cooperators, then there are values of b/c for which cooperating complexes and defectors can coexist (CX).

We now summarize the behavior of the population for arbitrary internal efficiencies α_k . To simplify notation, define

$$H(r, q, \vec{\alpha}) \equiv \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k + (1-r)(1-\alpha_k)}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1}$$

- For $r < 1$: If $b/c < H(r, q, \vec{\alpha})$, then there is no mixed equilibrium, and the $y^* = 1$ equilibrium is stable. If $H(r, q, \vec{\alpha}) < b/c < H(1, q, \vec{\alpha})$, then there is a single unstable mixed equilibrium. If $b/c > H(1, q, \vec{\alpha})$, then there is no mixed equilibrium, and the $y^* = 0$ equilibrium is stable.
- For $r > 1$: If $b/c < H(1, q, \vec{\alpha})$, then there is no mixed equilibrium, and the $y^* = 1$ equilibrium is stable. If $H(1, q, \vec{\alpha}) < b/c < H(r, q, \vec{\alpha})$, then there is a single stable mixed equilibrium. If $b/c > H(r, q, \vec{\alpha})$, then there is no mixed equilibrium, and the $y^* = 0$ equilibrium is stable.
- For $r = 1$, there is one condition characterizing the system. The $y^* = 0$ fixed point is stable if $b/c > H(1, q, \vec{\alpha})$ and unstable otherwise. This is the result obtained in Section 2.

The parameter r is experimentally important and often overlooked in game-theoretic models of cooperation. The genes responsible for the distinction between cooperation and defection may generate additional phenotypic differences between cooperators and defectors. Thus the frequently used assumption that a defecting cell receives exactly the same payoff from consuming a public good as does a cooperating cell is not necessarily true.

3.3. A specific example

By using $\alpha_k = \alpha(1 - 1/k)$, we find that

$$H(r, q, \vec{\alpha}) \rightarrow H(r, q, \alpha) = \frac{1}{1 - r(1 - q\alpha)}$$

The behavior of this system for different values of the parameters b/c , q , and r is shown in Fig. 4.

4. Disadvantages for large complexes

The increased efficiency of larger complexes of cooperators compared with smaller complexes at consuming their own public goods allows for evolution of cooperation. But cooperators and defectors do not necessarily receive the same payoff from consuming a public good, and we model this payoff difference through the parameter r . For $r < 1$ or $r > 1$, we can have unstable

or stable mixed equilibria, respectively. Yet as seen in Figs. 3 and 4, the value of the staying-together probability q that minimizes the critical b/c for cooperation in our model with α_k and r is trivially equal to 1. Therefore the optimal strategy for cooperators is to form complexes that are as large as possible. We suspect that additional physical or biological mechanisms impose a cost for cooperating complexes getting too big.

To extend our model, we modify our fitness functions for k -complexes:

$$f_k^\alpha \rightarrow f_k^{\alpha\gamma} = k \left[1 + w \left(-c + b\alpha_k + b\gamma_k \sum_{n \geq 1} (1 - \alpha_n) n x_n \right) \right]$$

Larger k -complexes maintain their higher probability α_k for reabsorbing any locally produced public goods. However, there is now a cost γ_k for a cooperating complex getting too big: Larger complexes are not as efficient at consuming externally diffusing goods as are smaller complexes. This assumption is justifiable on physical grounds: As a complex grows, the fraction of cooperating units that reside on the surface of the complex decreases. Thus cooperators in the interior of the complex likely have reduced access to any externally diffusing public goods. The decrease in the surface area-to-volume ratio of a cluster with the size of the cluster is responsible both for the increase of α_k with k and for the decrease of γ_k with k . We would like to understand how the competing effects of α_k and γ_k modify the behaviors seen in Fig. 4.

4.1. Any intensity of selection

Start by redefining F and G (for arbitrary strength of selection) as

$$F_k(X, Y) \rightarrow F_k^\gamma(X, Y) \equiv \frac{qk[1 + w(-c + b\alpha_k + X\gamma_k)]}{1 + wY + qk[1 + w(-c + b\alpha_k + X\gamma_k)]}$$

$$G(X, Y) \rightarrow G^\gamma(X, Y) \equiv -1 + \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n F_k^\gamma(X, Y)$$

The condition for the $y^* = 1$ equilibrium to be stable to invasion by cooperators is $G^\gamma(0, 0) < 0$, which is identical to the corresponding condition found in Sections 2 and 3. For arbitrary intensity of selection, w , analyzing the cooperating fixed point is more difficult. From the rate equations (3), we must have $1 + wrbS_{\max} < \phi$ if the cooperating fixed point is stable. But determination of ϕ in the cooperating state is not so simple because ϕ depends on S_{\max} , which is implicitly a function of \vec{y} through the steady-state frequencies \vec{x}^* .

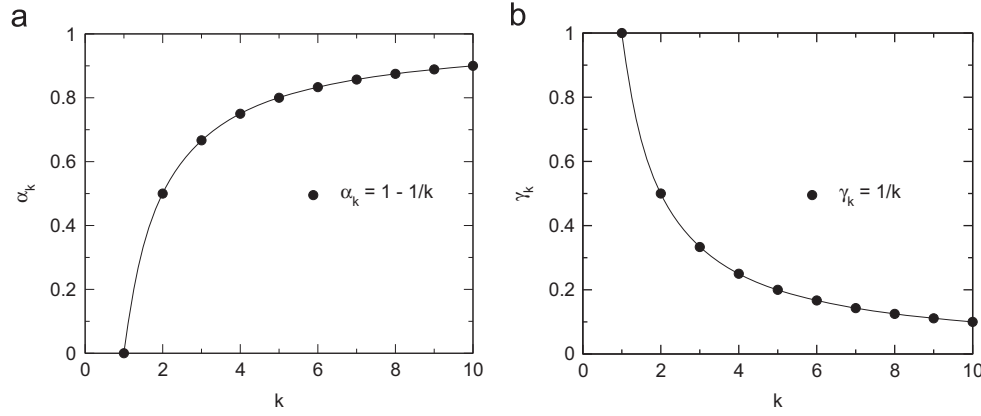


Fig. 5. (a) α_k increases monotonically while (b) γ_k decreases monotonically. These plots correspond to Eqs. (14) and (20) with $\alpha = 1$ and $\gamma = 1$, respectively. Note that k is discrete; the lines are a guide for the eye.

4.2. Weak selection

In Appendix B, we simplify the quantities $F_k^Y(X, Y)$ and $G^Y(X, Y)$ by assuming that the strength of selection, w , is small. Taking the limit $w \rightarrow 0$, we get

$$\begin{aligned} \sum_{n \geq 1} \prod_{k=1}^n F_k^Y(X, Y) &\approx \sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} + w \sum_{n \geq 1} \prod_{k=1}^n \frac{-c + b\alpha_k + X\gamma_k - Y}{1+kq} \\ &\times \prod_{p=1}^n \frac{pq}{1+pq} G^Y(X, Y) \\ &\approx w \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{-c + b\alpha_k + X\gamma_k - Y}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \end{aligned}$$

The condition for the $y^* = 1$ equilibrium to be stable to invasion by cooperators is exactly as before:

$$\frac{b}{c} < \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{\alpha_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1}$$

We now determine the stability of the cooperating fixed point. Note that for weak selection, the quantity of diffusing public goods at the cooperating fixed point, S_{\max} , is unaffected by the form of γ_k . To see why, we use the density constraint $\sum_{k \geq 1} kx_k^* = 1$ and the rate equations (3) to compute the steady-state distribution of x_k^* s:

$$x_k^* = \frac{1-q}{kq} \prod_{p=1}^k \frac{pq}{1+pq}$$

Since S_{\max} does not depend explicitly on $\vec{\gamma}$, and since, for $w \approx 0$, \vec{x}^* does not depend on $\vec{\gamma}$, we can use our result for S_{\max} from Section 3.

Similar to the calculation in Section 3, the cooperating fixed point is asymptotically stable if

$$G^Y(bS_{\max}, rS_{\max}) \approx w \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{-c + b\alpha_k + b\gamma_k S_{\max} - rS_{\max}}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} > 0$$

Rearranging gives

$$\frac{b}{c} > \frac{\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}{\sum_{n \geq 1} \sum_{k=1}^n \frac{\alpha_k + (\gamma_k - r)S_{\max}}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}}$$

Here S_{\max} is given by Eq. (17). We can use Lemma 2 to simplify this further:

$$\frac{b}{c} > \left[\frac{(1-q)^2}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{\alpha_k + (\gamma_k - r)S_{\max}}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \right]^{-1}$$

To determine if mixed equilibria can exist, we use the following equations, which must hold if $0 < y^* < 1$:

$$G^Y(bS^*, rS^*) \approx w \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{-c + b\alpha_k + b\gamma_k S^* - rS^*}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} = 0$$

$$0 < S^* < S_{\max}$$

Again, note that weak selection linearizes $G^Y(bS, rS)$ in S . We find

$$\frac{d}{dS} G^Y(bS, rS) = w \frac{1-q}{q} \left[\sum_{n \geq 1} \prod_{k=1}^n \frac{\gamma_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} - \frac{rq}{(1-q)^2} \right]$$

Note that this is positive, zero, or negative for all S . Thus for a given set of parameters, there can be at most one bistable equilibrium (if $d/dS G^Y(bS, rS) > 0$) or at most one coexisting equilibrium (if $d/dS G^Y(bS, rS) < 0$). (Details on the equations corresponding to mixed equilibria are presented in Appendix D.)

For general functions γ_k , the system can have different types of equilibria for different values of q . For example, we can locate a certain q for which mixed equilibria cannot exist, which is the solution to

$$\sum_{n \geq 1} \prod_{k=1}^n \frac{\gamma_k}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} = \frac{rq}{(1-q)^2} \tag{19}$$

Amazingly, the special value of q that satisfies this condition, denoted henceforth as q^* , is independent of the internal efficiencies α_k of the cooperating complexes.

4.3. A specific example

To develop intuition, we choose a reasonable form for γ_k :

$$\gamma_k = 1 - \gamma \left(1 - \frac{1}{k} \right) = 1 - \frac{\gamma}{\alpha} \alpha_k \tag{20}$$

Here $0 \leq \gamma \leq 1$. The functions (14) and (20) are presented graphically in Fig. 5.

Our conditions now simplify dramatically. Using our series identities in Appendix C and substituting our expression for S_{\max} , we find that the cooperating equilibrium is stable if

$$\frac{b}{c} > \frac{1}{1 - (r + q\gamma)(1 - q\alpha)} \tag{21}$$

We can solve Eq. (19) explicitly for q^* :

$$q^* = \frac{1-r}{\gamma}$$

Some other special values of q may be of interest. There may exist a value of $q = q_{\text{peak}}$ for which the critical b/c that guarantees stability of the cooperating state to invasion by defectors is maximal. By differentiating the denominator of (21) and setting the resulting expression to zero, we find

$$q_{\text{peak}} = \frac{\gamma - r\alpha}{2\alpha\gamma}$$

There may also exist a value of $q = q_{\text{max}}$ above which total cooperation is impossible. To find q_{max} , we set the denominator of (21) equal to zero and solve the resulting quadratic equation for

q . We find

$$q_{\text{max}} = \frac{1}{2\alpha\gamma} \left[\gamma - r\alpha - \sqrt{(\gamma - r\alpha)^2 - 4\alpha\gamma(1-r)} \right]$$

Of course, q^* , q_{peak} , and q_{max} do not all necessarily exist (i.e. do not all necessarily reside in the interval 0–1) for arbitrary values of α , r , and γ .

If defectors receive a greater or equal payoff from absorbing a public good compared with cooperators (i.e. $r \geq 1$), then the system admits defecting, coexisting, and cooperating equilibria, as in Fig. 6(a). If defectors receive a lesser payoff from absorbing a

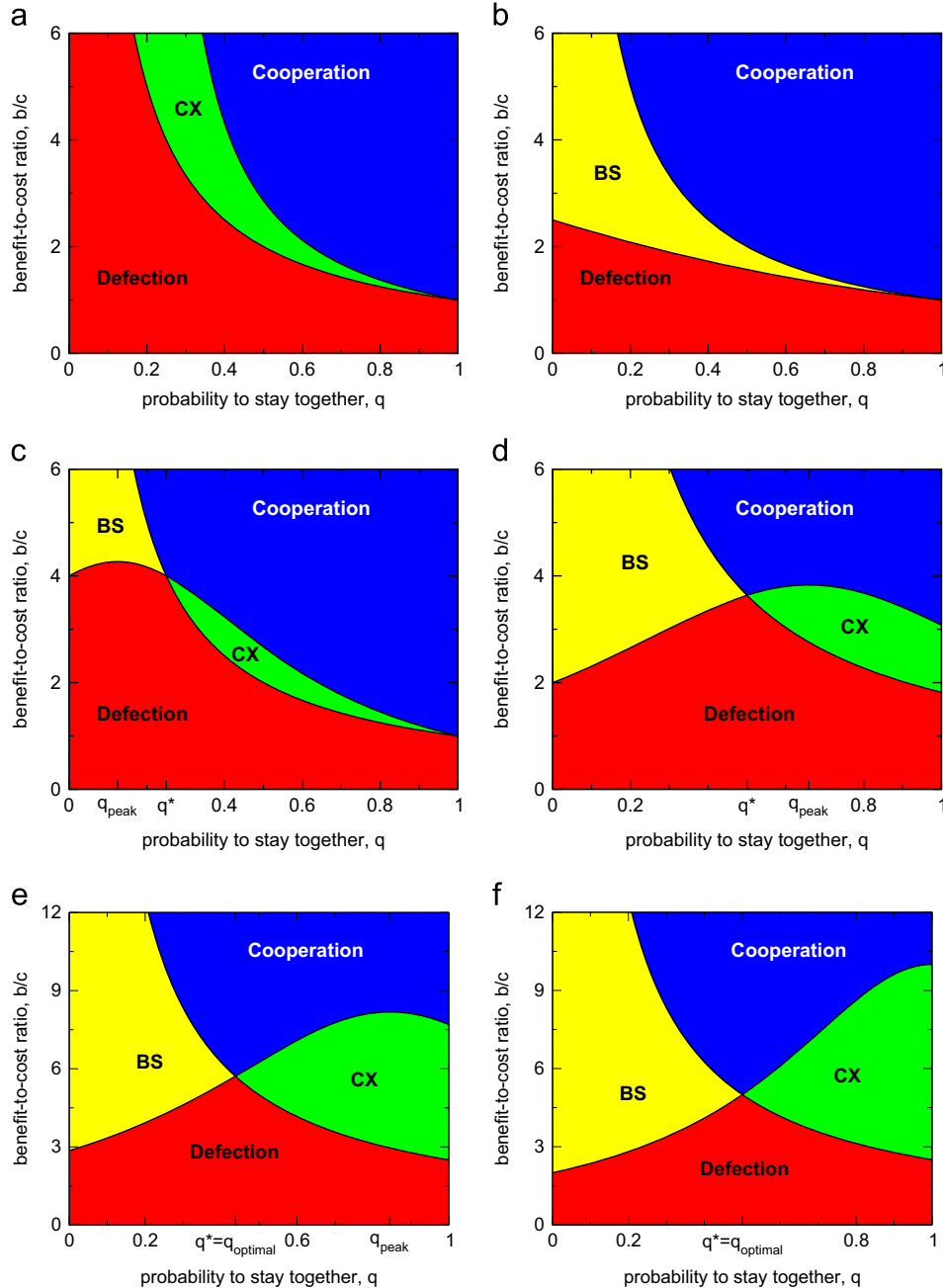


Fig. 6. Clustering of cooperators during exchange of public goods leads to rich behavior depending on the internal efficiency α , the defector-versus-cooperator benefit ratio r , and the external receptiveness γ . In these plots, red indicates defection, yellow indicates bistability (BS), green indicates coexistence (CX), and blue indicates cooperation. All four behaviors are possible for different values of the benefit-to-cost ratio b/c and the staying-together probability q . The boundary of the blue region represents the minimal b/c needed for total cooperation. (a) $\alpha = 1$, $r = 1.2$, $\gamma = 0.2$, (b) $\alpha = 1$, $r = 0.6$, $\gamma = 0.25$, (c) $\alpha = 1$, $r = 0.75$, $\gamma = 1$, (d) $\alpha = 0.55$, $r = 0.5$, $\gamma = 1$, (e) $\alpha = 0.4$, $r = 0.65$, $\gamma = 0.8$, and (f) $\alpha = 0.4$, $r = 0.5$, $\gamma = 1$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

public good than do cooperators (i.e. $r < 1$), then there are several cases to consider: If $q^* \geq 1$, then the system can only admit defecting, bistable, and cooperating equilibria, as in Fig. 6(b). If $q^* < 1$, then the system can also admit a coexisting equilibrium. For the case $q^* < 1$, the system's behavior can additionally be classified according to the following conditions:

- If $r\alpha - \gamma + 2\alpha(1-r) \geq 0$, then the critical b/c needed for cooperation to dominate is a monotonically decreasing function of q : $q_{\text{optimal}} = 1$ (Fig. 6(c)).
- If $r\alpha - \gamma + 2\alpha(1-r) < 0$ and $\gamma - \alpha(1-r) > \gamma(r+\gamma)(1-\alpha)$, then $q = q^*$ represents a local minimum of the critical b/c needed for cooperation to evolve. The global minimum of the critical b/c is at $q = q_{\text{optimal}} = 1$ (Fig. 6(d)).
- If $r\alpha - \gamma + 2\alpha(1-r) < 0$, $\gamma - \alpha(1-r) < \gamma(r+\gamma)(1-\alpha)$, and $0 < q_{\text{peak}} < 1$, then $q = 1$ represents a local minimum of the critical b/c needed for cooperation to evolve. The global minimum of the critical b/c is at $q = q_{\text{optimal}} = q^*$ (Fig. 6(e)).
- If $r\alpha - \gamma + 2\alpha(1-r) < 0$, $\gamma - \alpha(1-r) < \gamma(r+\gamma)(1-\alpha)$, and $q_{\text{peak}} \geq 1$, then $q_{\text{optimal}} = q^*$ is the value of q that is most favorable for evolution of cooperation (Fig. 6(f)).
- If $0 < q_{\text{max}} < 1$, then $q_{\text{optimal}} = q^*$ is the value of q that is most favorable for evolution of cooperation. Additionally, if $q > q_{\text{max}}$,

then total cooperation is always unstable to invasion by defectors (Fig. 7).

Intuitively, if $q < q_{\text{optimal}}$, then the population consists mostly of small complexes that are not efficient at internally consuming their own public good productions. But if $q > q_{\text{optimal}}$, then units within large complexes have difficulty absorbing externally diffusing public goods. Thus, the population most easily achieves simultaneous evolution of cooperation and evolution of construction if $q = q_{\text{optimal}}$.

We also simulated our general model for $w=1$ (Fig. 8). Our weak selection results provide a nice approximation to the system's behavior for $w=1$.

5. Discussion

Evolution is a constructive process, leading to life forms with increasing levels of complexity. Recent works have suggested that cooperators can outcompete defectors by clustering together—either on an arbitrary interaction graph or in physical space—both through theoretical analyses (Nowak and May, 1992; Nowak et al., 2010b; Ohtsuki et al., 2006; Allen et al., 2014; Wang et al., 2013; Gomez-Gardenes et al., 2012) and also in experiments (Julou et al., 2013; Rainey and Rainey, 2003; Gore et al., 2009; Ratcliff et al., 2012). Here we have developed a primitive model for the coevolution of cooperation and staying together. Cooperators produce public goods at a cost c . Cooperators prefer to cluster together because they retain a fraction α_k of their own public goods, with α_k increasing with complex size k . There is no advantage for defectors to stay together because they produce no public good. Cooperation and construction coevolve if the benefit-to-cost ratio b/c for exchange of goods exceeds a well-defined threshold that depends on q and $\bar{\alpha}$. We also investigate the situation where cooperators and defectors receive an unequal payoff from consuming a public good, which is modeled by a new parameter r . We find that bistability is possible if cooperators receive greater payoff from a public good ($r < 1$), while coexistence is possible if defectors receive greater payoff from a public good ($r > 1$). We further postulate that cooperators within larger clusters have diminished access γ_k to external goods. The resulting system may feature defecting, bistable, coexisting, or cooperating behavior (Damore and Gore, 2012). There may also be an optimal probability for staying together after reproduction, q_{optimal} , for which the system most easily achieves coevolution of cooperation and construction.

Our study provides new insights into cooperation in microbial populations, which can be investigated in the lab. Cooperation in the context of public goods occurs in bacterial colonies, when siderophores are emitted to fetch soluble iron. The fetched iron may be used by a bacterium that is not the producer of the absorbed iron-chelating molecule, leading to a public goods game. A recent study (Julou et al., 2013) found that *Pseudomonas aeruginosa* grown in solid habitats forms large clusters. Moreover, siderophore concentration was found to be highest at the center of a large cluster of bacteria. This is a consequence of the geometric fact that siderophore molecules produced by bacteria inside a cluster are absorbed quickly before they can escape the cluster, which affirms our assumption that α_k is an increasing function of complex size k . What happens if this experiment is repeated in an environment with a viscosity intermediate between that of an aqueous solution and a solid habitat? Presumably, patches of bacteria of varying size would form throughout the medium. For example, *Pseudomonas fluorescens* has demonstrated a clustering phenotype in spatially heterogeneous environments through overproduction of an adhesive polymer (Rainey and Rainey, 2003). Suppose that the average size of these bacterial clusters can be

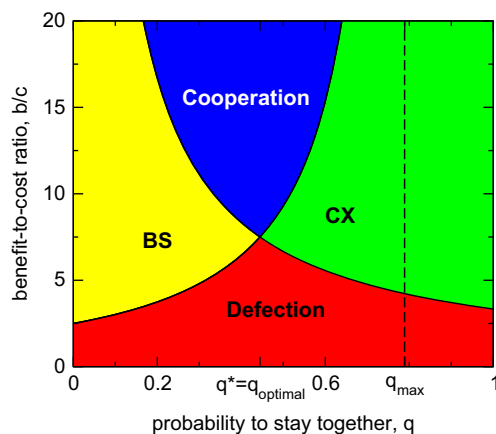


Fig. 7. $\alpha = 0.3$, $r = 0.6$, $\gamma = 0.9$. For these values of α , r , and γ , we have $q_{\text{optimal}} = 4/9$. For $q > q_{\text{max}} \approx 0.789$ (dotted line), complete cooperation is impossible regardless of the value of b/c .

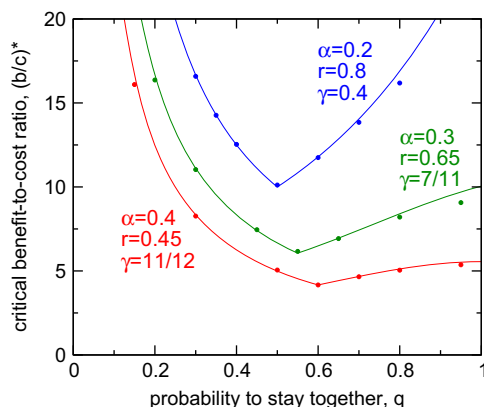


Fig. 8. Critical benefit-to-cost ratio needed for evolution of complete cooperation for $w=1$ (data points) plotted over the theoretical result for $w \rightarrow 0$ (solid curves) for our generalized model. The critical b/c for $w \rightarrow 0$ accurately predicts the critical b/c for $w=1$, although there are again noticeable discrepancies for some values of q . For our measurements with $w=1$, numerical errors are roughly the size of the data points.

experimentally controlled while maintaining the density of bacteria within each cluster. In our model, this would amount to varying the effective probability of staying together after reproduction (q) while keeping the sequence $\{\alpha_k\}$ constant.

Experimentalists observe a similar type of cooperation in budding yeast colonies (*Saccharomyces cerevisiae*) in glucose-limited environments. In another recent study (Gore et al., 2009), budding yeast cooperators produce invertase to hydrolyze sucrose. Most of the resulting monosaccharides (around 99%) diffuse away, ultimately being absorbed by other yeast cooperators or by defectors. Defectors do not produce invertase, but they may benefit from the public good productions of cooperators. Yeast cooperators and defectors are found to coexist in a well-mixed solution, and this coexistence is attributed to a nonlinear dependence of growth rate with the concentration of monosaccharides in the medium. As the abundance of cooperators increases, defectors become less dependent on the public good productions of cooperators. What happens if these experiments are repeated with an uneven spatial distribution of cooperators and defectors? Indeed, recent exciting experiments (Ratcliff et al., 2012) have succeeded in generating intricate slowflake-like clusters of *S. cerevisiae*—via postdivision adhesion—in the lab. Based on our model, we wonder if the average rate at which a yeast cell reproduces can be experimentally related to the spatial arrangement of cooperating clusters.

Interestingly, the cooperating strain in the experiments of Gore et al. is a histidine auxotroph. Thus by changing the histidine concentration, the cost of cooperation can be experimentally controlled. Is it possible to also modify the sensitivity of the defecting strain to monosaccharide consumption? If the yeast defectors could be made to benefit more from public good absorption than the yeast cooperators (amounting to having $r > 1$ in our model), then the predictions of Section 4 may be experimentally tested. Would it be possible to locate an optimal spatial distribution of cooperating clusters and defectors which maximizes the steady-state abundance of invertase-producing yeast relative to nonproducers?

Our model builds on recent work (Tarnita et al., 2013) and represents a starting point for exploring construction in evolutionary games. Tantalizing questions abound. For example, what happens if the offspring of cooperators within a cluster are allowed to mutate into defectors with some small probability? The within-group conflicts generated by cancerous defector cells within a large cooperating complex do not drastically modify the conditions needed for cooperation as long as the mutation rate is low enough. Our results are quite robust when applied to cooperation and construction in cellular systems (see Appendix A). As another example, is this system's qualitative behavior modified if q is not constant but is a function of complex size k ? If q increases with k —which is physically reasonable—then is cooperation more easily achieved for a smaller value of b/c ? Also, here we have a single metric for complexity in our game of public goods exchange—the complex size k . We can envision subcomplexes within complexes, such that the subcomplexes facilitate specialization and division of labor. Indeed, the world of staying together in evolutionary games is vast and deserving of serious exploration.

Acknowledgements

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Appendix A. Mutation of cooperators into defectors

As an extension to our model, we postulate two modifications: (1) Cooperators can mutate into defectors with some probability u .

(2) Cooperators and defectors can coexist within the same cluster. We are interested in how the resulting within-group conflicts may affect the evolutionary dynamics. With these modifications, our model may be reformulated with the following system of differential equations:

$$\begin{aligned}\dot{x}_{1,0} &= (1-q)(1-u)\sum f_{ij}x_{ij} - qf_{1,0}x_{1,0} - \phi x_{1,0} \\ \dot{x}_{0,1} &= (1-q)u\sum f_{ij}x_{ij} + (1-q)\sum g_{ij}x_{ij} - qg_{0,1}x_{0,1} - \phi x_{0,1} \\ \dot{x}_{i,0} &= q(1-u)f_{i-1,0}x_{i-1,0} - qf_{i,0}x_{i,0} - \phi x_{i,0} \\ \dot{x}_{0,j} &= qg_{0,j-1}x_{0,j-1} - qg_{0,j}x_{0,j} - \phi x_{0,j} \\ \dot{x}_{ij} &= q(1-u)f_{i-1,j}x_{i-1,j} + quf_{ij-1}x_{ij-1} + qg_{ij-1}x_{ij-1} \\ &\quad - q(f_{ij} + g_{ij})x_{ij} - \phi x_{ij}\end{aligned}$$

As before, q is the probability that a new reproductive—either a cooperator or a defector—stays within its parent complex. f_{ij} is the fitness of cooperators within a complex that contains i cooperators and j defectors. g_{ij} is the fitness of defectors within a complex that contains i cooperators and j defectors. We again assume that each cooperating unit produces a unit of a public good. The public good may be consumed by another cooperator or a defector within the same (i,j)-complex. The public good may instead be consumed by a cooperator or a defector elsewhere in the system. To mathematically describe this emission and absorption of public goods, we use the following fitness functions for cooperators and defectors:

$$\begin{aligned}f_{ij} &= i \left[1 + w \left(-c + b \frac{i-1}{i+j-1} \alpha_{i+j} + b \sum (1 - \alpha_{i+j}) i x_{ij} \right) \right] \\ g_{ij} &= j \left[1 + w \left(b \frac{i}{i+j-1} \alpha_{i+j} + b \sum (1 - \alpha_{i+j}) i x_{ij} \right) \right]\end{aligned}$$

α_k is the probability that a public good produced by a cooperator within a complex of k units is absorbed by another cooperator or a defector within the same complex. We also assume that γ_k is equal to 1 for all k ; i.e., cells within a complex absorb externally diffusing goods with the same efficacy regardless of the size of the complex they belong to.

Our numerical studies suggest that our predictions for critical b/c ratios needed for cooperation are accurate to within about 10% as long as the mutation rate u is less than around 10^{-3} . This error threshold is several orders of magnitude larger than the error rate of order 10^{-7} that is typical for inactivating a gene in DNA replication of cells. Thus, with the assumption $u=0$, our results in the main text form a robust description of staying together and cooperation in cellular systems. Detailed effects of a nonzero mutation rate u on the evolutionary dynamics will be explored in a future publication.

Appendix B. Weak selection

The two quantities $F_k(X, Y)$ and $G(X, Y)$ appear frequently in the mathematical analysis of cooperation with staying together. We define these quantities by

$$\begin{aligned}F_k(X, Y) &\equiv \frac{qk[1 + w(-c + b\alpha_k + X)]}{1 + wY + qk[1 + w(-c + b\alpha_k + X)]} \\ G(X, Y) &\equiv -1 + \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n F_k(X, Y)\end{aligned}\quad (B.1)$$

q is the probability that a new reproductive stays within its parent complex. b and c are the benefit and cost of absorption and production of the public good, respectively. α_k is the probability that a public good produced within a k -complex is absorbed by another unit within the same k -complex. X and Y are just placeholders that are substituted for in our various calculations. w represents the strength of selection.

We can simplify $F_k(X, Y)$ and $G(X, Y)$ if there is weak selection. This corresponds to having $w \ll 1$. We start by simplifying $F_k(X, Y)$. We expand the denominator in the small parameter w , keeping only terms of order 1 and of order w . We get

$$F_k(X, Y) \approx \frac{kq}{1+kq} + w \frac{kq}{(1+kq)^2} (-c + b\alpha_k + X - Y)$$

Therefore,

$$\sum_{n \geq 1} \prod_{k=1}^n F_k(X, Y) \approx \sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} \left[1 + w \frac{-c + b\alpha_k + X - Y}{1+kq} \right]$$

Again keeping only terms that are lowest order in w , we get

$$\sum_{n \geq 1} \prod_{k=1}^n F_k(X, Y) \approx \sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} + w \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + X - Y}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}$$

With these simplifications, $G(X, Y)$ becomes

$$G(X, Y) \approx -1 + \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} + w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + X - Y}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}$$

To simplify this further, we use **Lemma 1**:

$$\sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} = \frac{q}{1-q}$$

Note that $G(X, Y)$ then reduces to

$$G(X, Y) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + X - Y}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \quad (\text{B.2})$$

In **Section 4**, we introduce the parameter γ_k , which is the probability that a unit within a k -complex absorbs an externally diffusing public good that is incident upon the k -complex. For the more general calculations of **Section 4**, we redefine $F_k(X, Y)$ and $G(X, Y)$ as

$$F_k(X, Y) \rightarrow F_k^\gamma(X, Y) \equiv \frac{qk[1 + w(-c + b\alpha_k + X\gamma_k)]}{1 + wY + qk[1 + w(-c + b\alpha_k + X\gamma_k)]}$$

$$G(X, Y) \rightarrow G^\gamma(X, Y) \equiv -1 + \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n F_k^\gamma(X, Y)$$

Again, X and Y are just placeholders. They are substituted for in our calculations in **Section 4**. Taking the weak-selection limit, $w \rightarrow 0$, and following the steps above, we obtain

$$\sum_{n \geq 1} \prod_{k=1}^n F_k^\gamma(X, Y) \approx \sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} + w \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + X\gamma_k - Y}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq}$$

$$G^\gamma(X, Y) \approx w \frac{1-q}{q} \sum_{n \geq 1} \sum_{k=1}^n \frac{-c + b\alpha_k + X\gamma_k - Y}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} \quad (\text{B.3})$$

Appendix C. Series identities

The following three series identities allow many of our formulae and our critical b/c values needed for cooperation to be simplified.

Lemma 1.

$$\sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} = \frac{q}{1-q}$$

Proof. Define

$$R_n(q) \equiv (1+nq) \prod_{k=1}^n \frac{kq}{1+kq}$$

Note that $R_n(q)$ satisfies the recurrence relation

$$R_n(q) = (1-q) \prod_{k=1}^n \frac{kq}{1+kq} + R_{n+1}(q)$$

Therefore,

$$q = R_1(q) = (1-q) \sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} \quad \square$$

Lemma 2.

$$\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} = \frac{q}{(1-q)^2}$$

Proof.

$$\begin{aligned} \sum_{n \geq 1} \sum_{k=1}^n \frac{1}{1+kq} \prod_{p=1}^n \frac{pq}{1+pq} &= q \sum_{n \geq 1} \sum_{k=1}^n \frac{k}{(1+kq)^2} \prod_{p \neq k}^n \frac{pq}{1+pq} \\ &= q \frac{d}{dq} \left(\sum_{n \geq 1} \prod_{k=1}^n \frac{kq}{1+kq} \right) \\ &= q \frac{d}{dq} \left(\frac{q}{1-q} \right) = \frac{q}{(1-q)^2} \quad \square \end{aligned}$$

Lemma 3.

$$\sum_{n \geq 1} \sum_{k=1}^n \frac{1}{k(1+kq)} \prod_{p=1}^n \frac{pq}{1+pq} = \frac{q}{1-q}$$

Proof. By simply regrouping terms, this series can be written in the alternate form

$$\sum_{n \geq 1} \frac{1}{n(1+nq)} \sum_{p \geq n} \prod_{k=1}^p \frac{kq}{1+kq}$$

After using $R_n(q)$ from **Lemma 1**, this becomes

$$\frac{1}{1-q} \sum_{n \geq 1} \frac{R_n(q)}{n(1+nq)} = \frac{1}{1-q} \sum_{n \geq 1} \frac{1}{n} \prod_{k=1}^n \frac{kq}{1+kq}$$

Now define

$$T_n(q) \equiv \frac{R_n(q)}{n}$$

Note that $T_n(q)$ satisfies the recurrence relation

$$T_n(q) = \frac{1}{n} \prod_{k=1}^n \frac{kq}{1+kq} + T_{n+1}(q)$$

So we have

$$q = T_1(q) = \sum_{n \geq 1} \frac{1}{n} \prod_{k=1}^n \frac{kq}{1+kq} \quad \square$$

Appendix D. Mixed equilibria

As shown in the main text, with weak selection ($w \ll 1$), there generally can exist only a single mixed equilibrium for a given set of model parameters. The single mixed equilibrium can be either unstable (corresponding to bistability of the two pure equilibria) or stable (corresponding to coexistence of cooperators and defectors). For arbitrary strength of selection w , we have not succeeded in determining the number of mixed equilibria that our model admits. Mathematically, this corresponds to finding the number of sequences of cluster frequencies $\{x_k^*\}$ that satisfy

$$G'(bs^*, rbs^*) = -1 + \frac{1-q}{q} \sum_{n \geq 1} \prod_{k=1}^n \frac{qk[1 + w(-c + b\alpha_k + by_k s^*)]}{1 + wrbs^* + qk[1 + w(-c + b\alpha_k + by_k s^*)]} = 0$$

There is a simpler condition for existence of a mixed equilibrium that can be derived for arbitrary strength of selection. Note that, from Eqs. (3), in order for \dot{y} to equal zero with a mixed equilibrium, we must have $\phi = f_y = 1 + wrbs^*$. If the frequencies of all clusters are to sum to one, then we must also have $\phi = \sum f_k x_k + f_y y$. In addition, recall two simple identities:

$$\begin{aligned} \sum kx_k^* &= 1 - y^* \\ \sum k\alpha_k x_k^* &= 1 - y^* - S^* \end{aligned}$$

Substituting for f_k and f_y , and using the above identities, we find that the following equation must be satisfied by the cluster frequencies $\{x_k^*\}$ for any mixed equilibrium:

$$(1 - y^*)[c + b(rS^* - 1)] = bS^*(\sum \gamma_k x_k^* - 1)$$

We can specialize this condition to the case of all $\gamma_k = 1$:

$$(1 - y^*)[c + b(rS^* - 1)] = -by^*S^*$$

If we further assume that cooperators and defectors receive the same benefit from consuming the public good, i.e. $r=1$, then we find that the system stops evolving in time if:

$$b\sum k\alpha_k x_k^* = c\sum kx_k^*$$

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