

## Consequences of fluctuating group size for the evolution of cooperation

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**Abstract** Studies of cooperation have traditionally focused on discrete games such as the well-known prisoner’s dilemma, in which players choose between two pure strategies: cooperation and defection. Increasingly, however, cooperation is being studied in continuous games that feature a continuum of strategies determining the level of cooperative investment. For the continuous snowdrift game it has been shown that a gradually evolving monomorphic population may undergo evolutionary branching, resulting in the emergence of a defector strategy that coexists with a cooperator strategy. This phenomenon has been dubbed the ‘tragedy of the commune’. Here we study the effects of fluctuating group size on the tragedy of the commune and derive analytical conditions for evolutionary branching. Our results show that the effects of fluctuating group size on evolutionary dynamics critically depend on the structure of payoff functions. This allows us to offer a general classification of games, elucidating when fluctuating group size helps or hinders cooperation.

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## 1 Introduction

Cooperation is ubiquitous in nature, and the cooperative integration of lower-level entities into higher-level units has been instrumental for the development of life on earth (Maynard Smith and Szathmary, 1995). While cooperation in the broad sense only implies joint action, the term is often used more strictly to describe situations in which cooperators help others at a cost to themselves. These interactions are typically vulnerable to cheating and exploitation by defectors that benefit without making costly cooperative contributions of their own. Cheating and exploitation are observed in viruses (Turner and Chao, 2003), bacteria (Rainey and Rainey, 2003), yeast (Greig and Travisano, 2004), amoebas (Buss, 1982; Dao et al, 2000; Strassmann et al, 2000), fish (Poulin and Vickery, 1995), and humans.

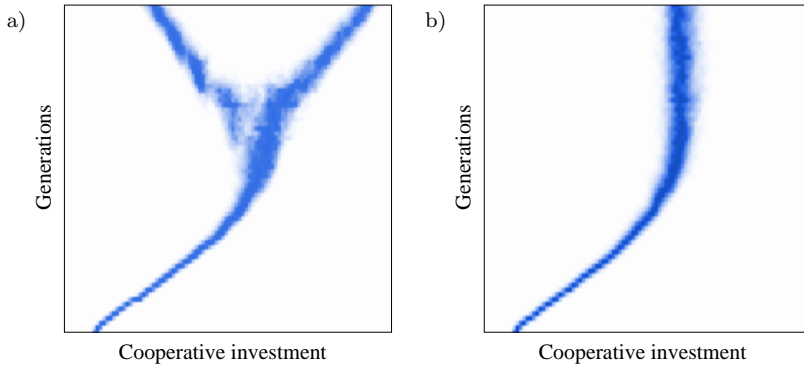
The persistence of cooperation in the presence of cheaters is not obvious, and at first glance it often appears as though the cheater rather than the cooperator has a higher fitness. Indeed, the well-known tragedy of the commons (Hardin, 1968) shows that even when cooperation is beneficial for the group, selection acting on the individual level often eliminates cooperation altogether. This has attracted significant scientific interest throughout the last decades, with explanations proposed for the origin and maintenance of cooperation falling into three main categories. First, kin selection (Hamilton, 1963, 1964, 1972) successfully explains many forms of cooperation among genetically related individuals. Second, selection on the level of groups (Wilson, 1980; Wilson and Dougatkin, 1997), through which subpopulations with non-cooperative individuals are at a reproductive disadvantage, promotes cooperation under certain conditions. Third, direct, indirect, or network reciprocation has been shown to foster cooperation (Trivers, 1971; Axelrod and Hamilton, 1981; Axelrod, 1984), even though the reliance of reciprocation on memorizing past behavior makes it applicable mainly to higher organisms. These mechanisms are further discussed in Nowak (2006).

Most game-theoretical studies of cooperation fall into the third category described above and revolve around a game known as the prisoner’s dilemma (Axelrod and Hamilton, 1981). The classic variant of this game is played by two players choosing between two pure strategies, cooperation or defection, but the game can be generalized to an arbitrary number of players (Kagel and Roth, 1995; Doebeli and Hauert, 2005) and to continuous degrees of cooperative contributions (Mar and Denis, 1994; Killingback et al, 1999). In the latter case, the cooperative contribution varies continuously and is represented by a real number  $r_1$ . The payoff for an  $r_1$ -strategist facing an  $r_2$ -strategist is  $B(r_2) - C(r_1)$ , where  $B$  and  $C$  are smooth and increasing functions that quantify the benefits and costs of cooperative contributions. Since cooperative investments do not directly benefit the acting individual, defection is the ra-

tional choice when the game is played only once. In many cases, however, it is more reasonable to assume that all players benefit equally from cooperative contributions. For example, the digestive enzymes produced by a cell of the yeast *Saccharomyces cerevisiae* can be used by all nearby cells, including the producing cell itself (Gore et al, 2009). Likewise, while the stalk produced by the amoeba *Dictyostelium discoideum* can be exploited by cheaters, it also vitally benefits the cooperators. Further examples of processes resulting in shared benefits are cooperative hunting, vigilance behavior, group foraging, and parental care (Kun et al, 2006). Situations where individuals directly benefit from cooperative acts that they perform can be described by the snowdrift game (Sugden, 1986), synonymously known as the hawk-dove game (Maynard Smith, 1982) or chicken game (Rapoport, 1966).

To better understand the evolution of cooperation and defection when all players are benefiting from cooperative contributions, Doebeli et al (2004) studied the snowdrift game with continuous investments. In this game, the payoff of an  $r_1$ -strategist facing an  $r_2$ -strategist is  $B(r_1 + r_2) - C(r_1)$ , where the functions  $B$  and  $C$  are chosen so that cooperation is better than defection in groups of defectors, but defection is advantageous in groups of cooperators. Consequently, cooperation in the snowdrift game always develops to some degree. However, assuming small mutations in continuous cooperative contributions, Doebeli et al (2004) showed that this gradual buildup of cooperation was sometimes followed by the emergence of cheaters with little or no cooperative contribution, while the remaining cooperators became even more cooperative. Similar results have been obtained by Brännström and Dieckmann (2005) in the context of the social amoeba *Dictyostelium*. When starvation is imminent, one or several strains of the amoeba aggregate to form fruiting bodies that enable spore dispersal (Raper, 1984; Fortunato et al, 2003). A strain, however, may forego investing into the stalk of the fruiting body and instead take a free ride on the investments of other strains. Brännström and Dieckmann (2005) modeled this process with spores as players and strains as strategies. In this model, the payoff of an  $r_1$ -strategist facing an  $r_2$ -strategist is multiplicative,  $B(r_1 + r_2)C(r_1)$ , with  $B$  an increasing and  $C$  a decreasing function of cooperative contributions. They showed that fluctuation in player numbers resulted in evolutionary branching and in the subsequent emergence and coexistence of low-investing cheaters and high-investing cooperators.

The work of Doebeli et al (2004) and Brännström and Dieckmann (2005) shows that selection on levels of cooperative investments need not always be stabilizing. Rather, initially monomorphic populations evolving in cooperation games may experience disruptive selection, resulting in evolutionary branching and the emergence of dimorphic evolutionary outcomes in which low-investing and high-investing individuals coexist. Doebeli et al (2004) investigated this evolutionary phenomenon, which they dubbed the *tragedy of the commune*, for games played in two-player groups. However, in many situations it is more natural to expect that interactions take place in groups of fluctuating size, for example, as a consequence of abstaining or of local interactions coupled with dispersal or movement. Since environmental fluctuations have been shown to



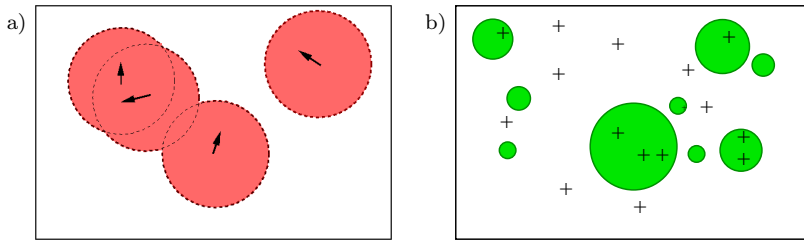
**Fig. 1** Individual-based simulations of a multi-player version of the continuous investment game proposed by Doebeli et al (2004). Parameters used here are identical to those used in Fig. 1A of Doebeli et al (2004). (a) The game played as a two-player game. Evolutionary branching leads to the emergence of cheaters, a characteristic process Doebeli et al (2004) dubbed the tragedy of the commune. (b) The game played with a random number of players (interactions taking place between either 1 or 3 players with equal probability). Although the average number of players is the same as before, evolutionary branching does not occur, and hence the tragedy of the commune is avoided. Note that although games with 1 player may seem odd, specific examples often allow a natural interpretation, e.g. single-clone aggregation in the case of *Dictyostelium*.

promote the coexistence of competing populations (Hutchinson, 1961) and to facilitate evolutionary branching in some models, such as the site-based model studied by Geritz et al (1998), one might expect that fluctuating group size would render the tragedy of the commune more likely. This, however, need not be the case. Figure 1 shows a multi-player extension of a game considered by Doebeli et al (2004), in which players interact in randomly formed groups that change between each interaction. When the size of these groups changes significantly from one interaction to the next, the tragedy of the commune no longer occurs.

The aim of this paper is to explore the evolutionary consequence of fluctuating group size for cooperation games. We first define a large class of games that includes the snowdrift game considered by Doebeli et al (2004), the *Dictyostelium* model conceived by Brännström and Dieckmann (2005), the prisoner’s dilemma, the stag hunt game, and other public goods (joint effort) games. For this class of games, we explore the evolutionary consequences of fluctuating group size for the establishment of cooperation and the tragedy of the commune.

## 2 Cooperation games with fluctuating group size

In this section we first explain why fluctuation in the size of groups of interacting players is generically expected in nature. We then introduce a class of cooperation games with continuous investments that incorporate fluctuating



**Fig. 2** Two examples of processes giving rise to fluctuations in the size of groups of interacting players. (a) Movement of individuals in conjunction with infrequent local interactions between nearby individuals give rise to games where groups are formed through contiguous overlap of interaction zones. (b) Players distributed over an area with interactions occurring among those players that occupy the patches marked with grey. A specific example is the dispersal of spores or seeds over an area containing many disconnected patches of suitable habitat.

group size. From the demographic dynamics resulting from the games in this class we determine the initial growth rate of a rare mutant strategy. This lays the foundation for our analysis of the evolutionary dynamics of cooperative investments. Finally, we describe the potential outcomes of gradual evolution in a monomorphic population with at most one interior singular strategy.

## 2.1 Fluctuating group size

Figure 2 depicts two situations in which variation in group size naturally occurs. First, movement and infrequent interactions between proximate players leads to a class of games where groups are formed through contiguous overlap of interaction zones. Though Fig. 2a depicts binary interactions, the interaction strength in general depends on factors such as distance between players. Second, Fig. 2b shows how a game is formed when players are repeatedly distributed onto patches of different sizes, giving rise to distinct groups of interacting players. Significant variation in patch size here leads to a wide distribution of the number of players in a group. This situation arises, for example, when spores or seeds are dispersed over an area with fragmented patches of suitable habitat. Our analysis will encompass both situations depicted in Fig. 2.

## 2.2 Payoffs in cooperation games

When a group of  $k$  players has been formed, we assume that each player contributes an amount or effort  $r_i$  towards the group's total effort  $r_1 + \dots + r_k$ . The contribution  $r_i$  is the strategy or trait value of a player and may optionally be constrained to an interval, e.g.  $0 \leq r_i \leq 1$ . We assume that the payoff  $P(r_i, r_s, k)$  for a focal individual playing strategy in a group of players with strategies may depend on the focal player's own contribution  $r_i$ ,

on the focal player's share of the total effort,  $r_s = (r_1 + \dots + r_k)/k$ , and on the number of individuals  $k$  in the group. By choosing  $P$  appropriately, we can recover all traditionally studied cooperation games. For example, the two-player prisoner's dilemma is obtained by choosing  $P(r_i, r_s, k) = B(kr_s - r_i) - C(r_i)$  with increasing functions  $B$  and  $C$ , and the public goods (joint effort) game by choosing  $P(r_i, r_s, k) = mr_s - r_i$  with a positive factor  $m$ .

We call a payoff function additive or multiplicative if, respectively, the effects of the first two arguments can be separated additively,  $P(r_i, r_s, k) = P_B(r_s, k) + P_C(r_i, k)$ , or multiplicatively,  $P(r_i, r_s, k) = P_B(r_s, k)P_C(r_i, k)$ . These two different types of payoff will play an important role in Sect. 3 when we examine the effect of fluctuating group size on the tragedy of the commune. When players pay a cost for making a cooperative contribution and benefit from their group's total effort, it is natural to assume that the payoff  $P$  decreases with  $r_i$  and increases with  $r_s$ ,

$$P_1(r_i, r_s, k) \leq 0 \text{ and } P_2(r_i, r_s, k) \geq 0, \quad (1)$$

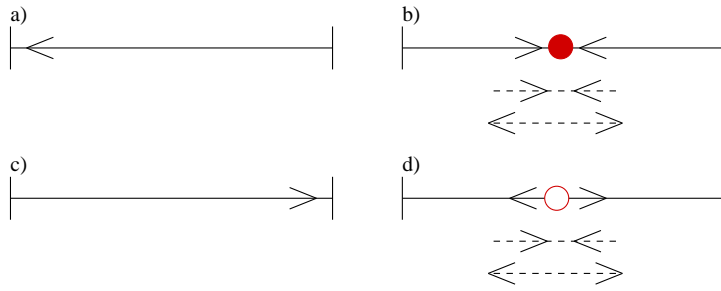
where the use of subindex in  $P_1$  and  $P_2$  denote the derivatives of the function with respect to its first and second argument respectively. Since this assumption is not needed for most of arguments below, it will be invoked only when analyzing the sign of mixed derivatives of multiplicative payoff functions.

### 2.3 Demographic dynamics in cooperation games

Based on the general specification of payoffs for players participating in cooperation games provided above, we now introduce the resultant demographic dynamics describing how player abundances change over time. For this we assume that, in successive generations, players are randomly distributed into groups of different size. The probability that an individual joins a game with  $k$  participants is  $p_k = kq_k/\langle k \rangle$ , where  $q_k$  is the fraction of groups with  $k$  players and  $\langle k \rangle = \sum_{k=1}^{\infty} kq_k$  is the average number of players in a group. Individuals then interact within the group and produce offspring in proportion to the payoff received. Survival to the next generation is density-dependent, but independent of trait values. Under these assumptions, the per capita growth rate of an initially rare mutant strategy  $m$  in an environment dominated by players with resident strategy  $r$  is

$$f(r, m) = \sum_{k=1}^{\infty} p_k \left( P \left( m, \frac{m + (k-1)r}{k}, k \right) - P(r, r, k) \right). \quad (2)$$

In adaptive dynamics theory, this quantity is known as invasion fitness (Metz et al, 1992). Equation (2), the derivation of which is provided in Appendix A, allows us to study the long-term evolution of trait values under mutation and selection (Metz et al, 1996; Dieckmann and Law, 1996; Geritz et al, 1998) and forms the foundation of our analysis of evolutionary dynamics in Sect. 3.



**Fig. 3** Classification of potential outcomes of gradual evolution in a monomorphic population with no interior singular strategy and one interior singular strategy. If no singular strategy exists (panels a and b), the system approaches the limit of low cooperation (panel a) or high cooperation (panel b). Convergence stable strategies allow for stationary dynamics at intermediate levels of cooperation if selection is stabilizing, or lead to dimorphic populations (c.f. Fig. 1a) if selection is disruptive (panel c). A singular strategy which is not convergence stable separates two basins of attraction for high and low cooperative investment respectively (panel d). Horizontal lines represent the level of cooperative investment and vertical lines boundary restriction, i.e. the minimum or maximum allowed cooperative investment. Circles represent singular strategies where directional selection ceases. Filled circles represent convergence stable singular strategies. The dashed lines beneath panels b and d indicates whether selection is stabilizing or disruptive.

## 2.4 Evolutionary dynamics in cooperation games

When mutational steps are small and rare, resident communities will successively be replaced by invading mutants with similar strategies and positive invasion fitness. Driven by directional selection, this process eventually ceases when evolution reaches a boundary strategy at which constraints prevent further evolution or at an interior strategy at which selection pressures vanish. Strategies of the latter type are called evolutionarily singular; in their vicinity, an initially monomorphic population may experience disruptive selection and thereby become dimorphic. Figure 1 illustrates how directional selection leads to a singular strategy at which selection is either disruptive (left panel) or stabilizing (right panel).

Assuming at most one interior singular strategy, there are only a finite number of qualitatively different possibilities for the evolutionary dynamics of a monomorphic population with individuals characterized by a single trait value. Figure 3 shows the relevant non-degenerate evolutionary outcomes. In Fig. 3a and 3c, gradual evolutionary change leads to a monomorphic population of full defectors (tragedy of the commons) or full cooperators respectively. This is also the case in Fig. 3d, but here the outcome depends on the initial condition (see e.g. Sumpter and Brännström, 2008). In Fig. 3b, gradual evolution will lead to cooperative investments near the interior singular strategy where selection can be stabilizing, resulting in an evolutionarily stable strategy. If selection is disruptive, however, the population will eventually become dimorphic (tragedy of the commune).

### 3 Evolutionary consequences of fluctuating group size

The initial growth rate of a rare mutant player with strategy  $m$  in an environment dominated by players with strategy  $r$ , (2), allows us to study the long-term consequences of small mutations and natural selection (Metz et al, 1996; Dieckmann and Law, 1996; Geritz et al, 1998). Below we assume that mutational steps are small and investigate the effect of fluctuating group size on the evolutionary of cooperation.

#### 3.1 Consequences for cooperative investments

The selection gradient  $g(r) = \frac{\partial}{\partial m}$ , being the derivative of the invasion fitness evaluated at  $m = r$ , contains information about which nearby strategies can invade a monomorphic population of players with cooperative investment  $r$ . When the selection gradient is positive (negative) more (less) cooperative strategies can invade. An invading strategy generically replaces the resident strategy and the population again becomes monomorphic (Geritz, 2005; Geritz et al, 2002). From (2) we derive the following expression for the selection gradient,

$$g(r) = \langle k \rangle^{-1} \sum_{k=1}^{\infty} k q_k \left[ P_1(r, r, k) + \frac{1}{k} P_2(r, r, k) \right],$$

where  $P_1$  and  $P_2$  as before denote the derivative of  $P$  with respect to the first and second argument respectively. In this expression  $\langle k \rangle$  is the average number of players in a group, and  $q_k$  is the probability that a group with  $k$  players is formed. Writing  $g_k(r)$  for the selection gradient with a fixed group size of  $k$  players we have,

$$g_k(r) = \left[ P_1(r, r, k) + \frac{1}{k} P_2(r, r, k) \right]. \quad (3)$$

We now introduce  $\varphi_k(r) = k g_k(r)$  so that we can apply Jensen's inequality, stating that the average of a convex function evaluated at various arguments is always larger or equal to that function evaluated at the average argument. Thus, if  $\varphi_k(r)$  is convex (accelerating) as a function of  $k$ , then

$$g(r) = \langle k \rangle^{-1} \sum_{k=1}^{\infty} q_k \varphi_k(r) \geq \langle k \rangle^{-1} \varphi_{\langle k \rangle}(r) = g_{\langle k \rangle}(r).$$

Thus, in this case, cooperation will be established more rapidly and reach higher levels when the group size of interacting players is variable, than when games are played in groups with a fixed size of  $\langle k \rangle$  players. If  $\varphi_k(r)$  is concave (decelerating) seen as a function of  $k$  whenever  $q_k > 0$  then the opposite is true: fluctuations in player numbers reduces cooperative development. With boundary conditions, fluctuations in group size can move singular strategies in or out of the allowed set of cooperative strategies, and thus prevent the evolution of cooperation altogether. However, in the following we show that



when the payoff depends only on the player's cooperative contribution and share of the common investment, the selection gradient is unchanged by fluctuating group size as long as the average number of players in a group remain constant.

### 3.2 Consequences for the tragedy of the commune

We now study the effect of fluctuating group size on the evolutionary dynamics, in particular the tragedy of the commune, near singular strategies for games where the payoff does not explicitly depend on group size, i.e.

$$P\left(r_i, \frac{r_1 + \dots + r_k}{k}, k\right) = P\left(r_i, \frac{r_1 + \dots + r_k}{k}\right). \quad (4)$$

For these games, the selection gradient vanishes for a strategy  $r^*$  whenever

$$\langle k \rangle P_1^* = -P_2^*, \quad (5)$$

where  $P_i^* = P_i(r^*, r^*)$  is the payoff  $P$  differentiated with respect to argument  $i$  and then evaluated at  $r = m = r^*$ . Since the only statistic of the distribution  $q_k$  that appears in (5) is the average number of players, fluctuating group size does not have any effect on the location of the singular strategies.

To understand the evolutionary dynamics of a monomorphic populations with strategy value close to the singular strategy  $r^*$  we need to know whether the strategy is convergence stable (nearby monomorphic populations evolve toward  $r^*$ ), and whether it is evolutionarily stable (selection is stabilizing rather than disruptive). Near a strategy which is convergence stable but not evolutionarily stable, a monomorphic population experiences disruptive selection and will eventually become dimorphic through evolutionary branching. In Appendix B we show that the singular strategy  $r^*$  is convergence stable if

$$\langle k \rangle P_{11}^* + (1 + \langle k \rangle) P_{12}^* + P_{22}^* < 0, \quad (6)$$

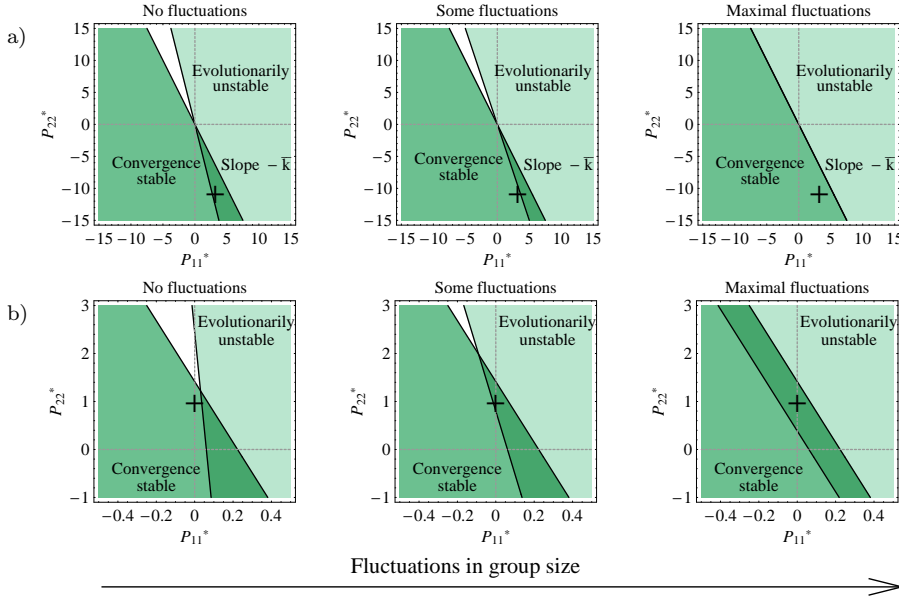
where  $P_{ij}^*$  is the payoff  $P$  differentiated twice, first with respect to argument  $i$  and then to argument  $j$ , and evaluated at  $r = m = r^*$ . The singular strategy is not evolutionarily stable if

$$\langle k \rangle P_{11}^* + 2P_{12}^* + \langle k^{-1} \rangle P_{22}^* > 0, \quad (7)$$

where

$$\langle k^{-1} \rangle = \sum_{k=1}^{\infty} \frac{q_k}{k}.$$

We will henceforth use  $\langle k^{-1} \rangle$  as a measure of the fluctuations in group size. It ranges from  $1/\langle k \rangle$  when a group of players always have the same size, to a maximal value of 1 which we will refer to as maximum variation in group size.



**Fig. 4** Evolutionary dynamics near the singular strategy  $r^*$  for combinations of  $P_{11}^*$  and  $P_{22}^*$  (second derivatives of the payoff function evaluated at the singular strategy) with fixed number of players (left panel) and variable number of players (middle and right panels). The dark gray area consists of the points  $(P_{11}^*, P_{22}^*)$  for which the singular strategy is convergence stable, (6), but not evolutionarily stable, (7), i.e. for which evolutionary branching eventually occurs. a) A multiplayer extension of the game considered by Doebeli et al (2004). The regions and the marker correspond to the parameters used to generate Fig. 1. The payoff  $P$  is additive (8) and consequently sufficient variation prevents evolutionary branching (middle and right panel). b) The *Dictyostelium* model. The regions and the marker correspond to parameters used by Brännström and Dieckmann (2005). The effect of the arguments in the payoff can be separated multiplicatively (9), and evolutionary branching does not occur without fluctuating group size.

### 3.2.1 Additive payoffs

We now analyze the special case where the effect of the two arguments in the payoff function can be separated additively,

$$P\left(r_i, \frac{r_1 + \dots + r_k}{k}\right) = B\left(\frac{r_1 + \dots + r_k}{k}\right) - C(r_i). \quad (8)$$

In cooperative games,  $B$  and  $C$  can be interpreted as the benefit and cost of a cooperative investment, respectively. Here the conditions in (1) means simply that both  $B$  and  $C$  are increasing functions. The separability between arguments implies that  $P_{12}^* = 0$  and it follows from (6) that the region of values in which  $P_{11}^*$  and  $P_{12}^*$  must lie for which the singular strategy is convergence stable consists of the points above the line

$$P_{22}^* = -\langle k \rangle P_{11}^*,$$

which is unaffected by variation in the number of players. The region for which the singular strategy is not evolutionarily stable, (7), is given by the points below the line

$$P_{22}^* = -\frac{\langle k \rangle}{\langle k-1 \rangle} P_{11}^*.$$

Here, the slope of the line defining the boundary of evolutionary stability changes from  $-\langle k \rangle^2$  to  $-\langle k \rangle$  as fluctuations in group size increase. This is shown in the three panels of Fig. 4a. The singular strategy  $r^*$  determines the values  $P_{11}^*$  and  $P_{22}^*$  that define a point in the plane. Evolutionarily branching, and hence the tragedy of the commune, eventually occurs when the singular point is convergence stable but not evolutionarily stable. This corresponds in Fig. 4a to the region marked with grey. Since this region lies exclusively in the fourth quadrant where  $P_{11}^* = -C''(r^*) > 0$  and  $P_{22}^* = B''(r^*) < 0$  it follows immediately that the tragedy of the commune can only occur when both the benefit,  $B$ , and the cost,  $C$ , are concave in a neighborhood of the singular point. Furthermore, we see that with additive payoffs fluctuating group size always reduces the parameter range in which evolutionary branching—and hence the tragedy of the commune—occurs. As the fluctuations increase, any point in the plane, including the marker which corresponds to the game studied by Doebeli et al (2004) (see also Fig. 1), eventually falls outside the region where evolutionary branching occurs. Hence, when the payoff is additive, the tragedy of the commune can always be avoided with sufficient fluctuation in group size.

In summary we have shown that in games with additive payoffs, or more generally in games with  $P_{12}^* = 0$ , fluctuations in group sizes generally reduce the parameter space where the tragedy of the commune can occur.

### 3.2.2 Multiplicative payoffs

For non-additive games the situation is considerably different, as illustrated by the *Dictyostelium* model conceived by Brännström and Dieckmann (2005). In this model the payoff is multiplicative,

$$P\left(r_i, \frac{r_1 + \dots + r_k}{k}\right) = B\left(\frac{r_1 + \dots + r_k}{k}\right) C(r_i). \quad (9)$$

Using an exponentially increasing function for the benefit and a linearly decreasing function for the cost, Brännström and Dieckmann (2005) derived an analytical condition showing that evolutionary branching only occurs with fluctuating group size. Fig. 4b shows why fluctuating group size is required. The slopes of the lines are the same as for additive games, but the line with constant slope now intersects the  $P_{22}^*$ -axis at the point  $-(1 + \langle k \rangle)P_{12}^*$  while the remaining line intersects at  $-2P_{12}^*/\langle k-1 \rangle$ . The effect that fluctuating group size has thus depends on the sign of  $P_{12}^*$ . For multiplicative payoffs,  $P_{12}^*$  is negative since  $P_{12}^* = B'(r^*)C'(r^*) < 0$ . With no fluctuations in group size, the region where evolutionary branching occurs lies entirely in the fourth quadrant. As

the fluctuations increase, the point of intersection  $-2P_{12}^*/\langle k^{-1} \rangle$  decreases from  $-\langle k \rangle^2 P_{12}^*$  to  $-\langle k \rangle P_{12}^*$ , which is below  $-(1 + \langle k \rangle)P_{12}^*$ . Thus, Brännström and Dieckmann (2005) did not find evolutionary branching without fluctuations in group size because they used a linear cost function. For sufficiently small values of  $P_{22}^*$ , evolutionary branching cannot occur without fluctuating group size.

The case  $P_{12}^* > 0$  is similar to additive games. In particular, sufficient fluctuation in group size will always prevent evolutionary branching and hence avoiding the tragedy of the commune.

### 3.3 Classifying the consequences of fluctuating group size

The preceding analysis shows that the sign of  $P_{12}^*$  has a profound impact on the evolutionary dynamics. When  $P_{12}^* \geq 0$  fluctuations in the number of players always reduces the parameter region for which evolutionary branching takes place, but when  $P_{12}^* < 0$  other outcomes are possible. To better understand the effect of fluctuating group size we combine inequalities (6) and (7), giving the following condition for the singular strategy to be convergence stable but not evolutionarily stable:

$$\langle k \rangle P_{12}^* + P_{22}^* < -\langle k \rangle P_{11}^* - P_{12}^* < P_{12}^* + \langle k^{-1} \rangle P_{22}^*. \quad (10)$$

Here only the term to the right changes with the degree of fluctuation in group size. It follows that a necessary condition for evolutionary branching when the number of players is fixed is

$$\langle k \rangle P_{12}^* + P_{22}^* < P_{12}^* + \frac{1}{\langle k \rangle} P_{22}^*. \quad (11)$$

Writing  $A = \langle k \rangle P_{12}^* + P_{22}^*$  and  $B = P_{12}^* + \langle k \rangle^{-1} P_{22}^*$  for the left and right hand side respectively, we can classify a game according to whether evolutionary branching is possible without variation in group size ( $A > B$ ) or not ( $A < B$ ). With maximum fluctuation in the number of players, we have the corresponding necessary condition,

$$\langle k \rangle P_{12}^* + P_{22}^* < P_{12}^* + P_{22}^*,$$

which simplifies to  $P_{12}^* < 0$ . Thus, we may further classify a game according to whether evolutionary branching is possible with maximal fluctuation in group size. Fig. 5 shows a graphical representation of the classifications. For each case, the range of values where the middle point of inequality (10) must lie for evolutionary branching to occur is plotted as a function of the degree of fluctuation in group size. When  $P_{12}^* < 0$ , which is the case for games with multiplicative payoffs, the effect that fluctuating group size group size has depends on whether condition (11) also holds. If it does not hold, fluctuating group size always reduces the region where evolutionary branching occurs. If

it does hold both outcomes are possible, and to distinguish between the two we need to check whether

$$P_{12}^* + \langle k^{-1} \rangle P_{22}^* < P_{12}^* + P_{22}^*,$$

which is the case if  $P_{22}^* > 0$ . In this case fluctuations in group size reduces the parameter range for which evolutionary branching occurs. If instead  $P_{22}^* < 0$ , fluctuations in group size promotes evolutionary branching.

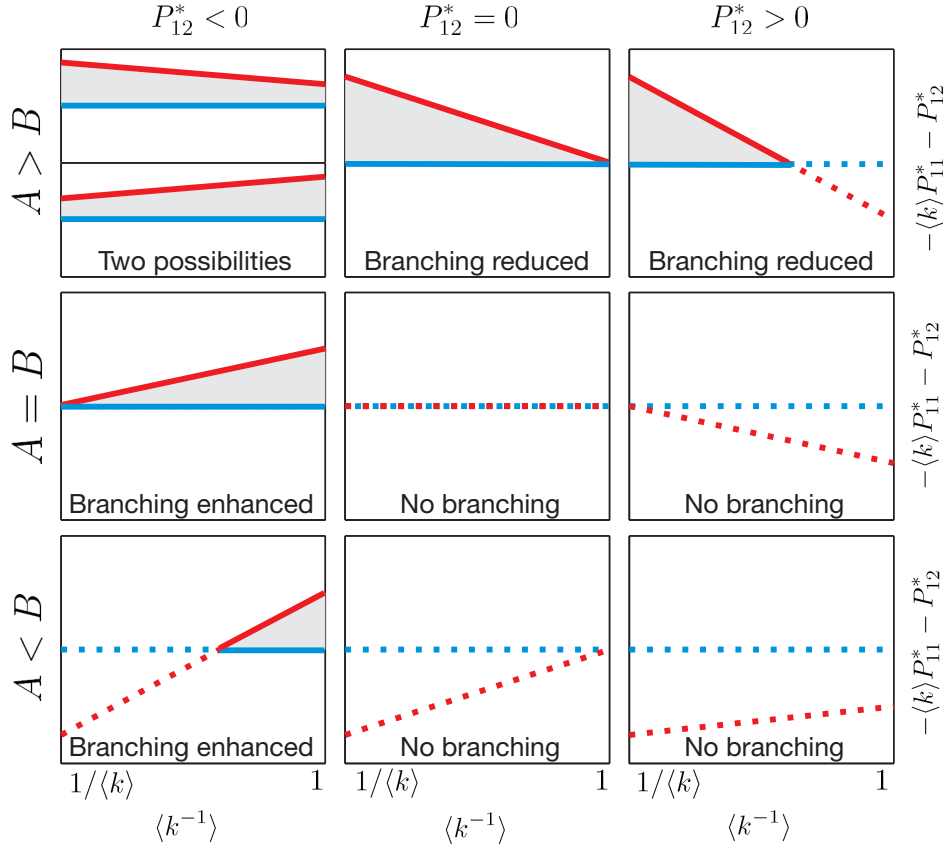
For additive games  $P_{12}^* = 0$  and we infer from Fig. 5 that fluctuations in the number of players always reduces the region where evolutionary branching occurs, consistent with the conclusions in Sect. 3.2.1.

## 4 Conclusions

Fluctuations are an inherent feature of population dynamics. In this paper we have studied the effect of fluctuating group size on the evolution of strategies in a large class of cooperative games. We have shown that, under rather general conditions, fluctuations in group size affect directional selection and hence the level of cooperative investment. To investigate the stability of singular strategies we have considered payoffs which do not explicitly depend on group size (4). For this class of games we have derived analytical criteria for the stability of singular strategies, showing that fluctuations in group size significantly affects the likelihood of evolutionary branching. Taken together, our results show that fluctuations in the size of groups of interacting individuals are potentially important for understanding both the classical tragedy of commons, and the tragedy of the commune.

A canonical assumption in models of cooperation is that the payoff can be written as a difference of a benefit function and a cost function. By applying the general criteria we have shown that sufficient fluctuations in group size can prevent evolutionary branching in these games. Fluctuations in group size promotes evolutionary branching only if the marginal gain to an individual for reducing its investment while keeping the total group investment constant increases with the size the group's investment ( $P_{12}^* < 0$  in the notation of Sect. 3). Moreover, the marginal cost to an individual for increasing its own investment while the group's investment remains constant must increase with the individual's investment, or at least only gradually decrease ( $P_{11}^* < \epsilon$  for a small positive  $\epsilon$ ), as otherwise fluctuations in group size will reduce the potential for evolutionary branching. Overall, these results indicate that the general effect of fluctuating group size in cooperative games is to reduce the risk of the tragedy of the commune, even though exceptions exist.

For investigating the stability of singular strategies, games where the communal investment are divided up between players are particularly accessible since the cooperative investment at the singular strategy is not affected by variation in group size. In more general games additional effects can arise. While fluctuations in group size still tend to stabilize games with additive payoffs, it can, as we have seen, lead to increased cooperation. Consequently,



**Fig. 5** The effect of fluctuating group size on the occurrence of evolutionary branching in games with payoff functions not explicitly depending on the group size can be classified using the values of  $P_{12}^*$ ,  $A = \langle k \rangle P_{12}^* + P_{22}^*$  and  $B = P_{12}^* + \langle k \rangle^{-1} P_{22}^*$ . Each panel shows the range of values in which the middle point of inequality (10) must lie for evolutionary branching to occur, as a function of  $\langle k^{-1} \rangle$  (fluctuation in group size). The blue and red dotted lines are the left and right hand side of inequality (10) respectively. When  $P_{12}^* \geq 0$  fluctuation in group size always reduces the region in which evolutionary branching occurs. If instead  $P_{12}^* < 0$  the effect that fluctuating group size has depends on whether  $A \leq B$  or  $A > B$ . In the former case, the region of branching increases with variation in the number of player, while information about  $P_{22}^*$  is needed to determine the role that fluctuating group size plays in the latter case (see Sect. 3.3 for details).

the singular strategy can shift to a region in which the payoff function has a different curvature. Therefore, one can certainly construct examples in which singular strategies in general common goods games with additive payoff are destabilized by fluctuations. However, for any given curvature, fluctuations will still have a stabilizing effect on general common goods games with additive payoff.

The results obtained in this study indicate that fluctuations in group size could significantly affect cooperation in real world systems by increasing or de-

creasing the cooperative investment, and by stabilizing cooperative strategies. However, so far only a handful of studies have considered the role of fluctuating group size for the evolution of cooperation (e.g. Hauert et al, 2006, 2002) and many questions remain unexplored, for example the effect of fluctuating group size in cooperative games where the communal investment is not divided up between the player, and the effect of arbitrarily large mutational steps. In light of the prominent role of functional forms of the payoff for the evolution of cooperation, studies addressing proper models formulations for real world cooperative systems are strongly desired.

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## A Demographic dynamics

We assume that there are  $n$  morphs in the population with trait values  $r_1, \dots, r_n$  and corresponding densities  $X_1, \dots, X_n$ . The population dynamics is assumed given by

$$\frac{X'_i(t)}{X_i(t)} = (\text{rate of participation in games}) \times \quad (12)$$

$$(\text{average individuals emerging from game}) - \mu(X_1 + \dots + X_n), \quad (13)$$

where  $\mu$  is included to allow for density dependence. Assume for simplicity that the rate at which an individual partakes in a game is 1, that an individual player participates in a  $k$ -player game a fraction  $p_k$  of the time, and that the participants are drawn at random from the population. The expected number of individuals with trait value  $r_i$  emerging from a game is then

$$R(r_i; X) = \sum_{k=1}^{\infty} p_k \sum_{1+k_1+\dots+k_n=k} \frac{(k-1)!}{k_1! \dots k_n!} \frac{X_1^{k_1} \dots X_n^{k_n}}{(X_1 + \dots + X_k)^{k-1}} P\left(r_i, \frac{\bar{W}(k_1, \dots, k_n)}{k}, k\right),$$

where  $P$  is the function for the payoff defined in Sect. 2.2 and  $\bar{W}(k_1, \dots, k_n)$  is the common investment produced by  $k_i$  individuals with trait value  $r_i$ ,  $1 \leq i \leq n$ . We then have

$$\frac{X'_i}{X_i} = R(r_i; X) - \mu(X_1 + \dots + X_n).$$

Now, let  $x_i$  be the frequency of trait value  $r_i$  in the population, i.e.,

$$x_i = \frac{X_i}{X_1 + \dots + X_k}.$$

Then

$$\frac{x'_i}{x_i} = \frac{X'_i}{X_i} - \frac{X'_1 + \dots + X'_n}{X_1 + \dots + X_n},$$

and so, with the obvious extension of the notation,

$$\frac{x'_i}{x_i} = R(r_i; x) - (x_1 R(r_1; x) + \dots + x_n R(r_n; x)), \quad (14)$$

which can be considered a generalization of the classical replicator equation (see e.g. Hofbauer and Sigmund, 1998).

## B Evolutionary dynamics

From (14) we deduce the initial increase in frequency for a rare mutant strategy  $m$  in an environment dominated by players with strategy  $r$ . Writing  $x_1 = x_r$ ,  $x_2 = x_m$ ,  $r_1 = r$  and  $r_2 = m$  when only two morphs are present, we have

$$R(m; x) = \sum_{k=1}^{\infty} p_k \sum_{j=0}^{k-1} \binom{k-1}{j} x_r^j x_m^{k-1-j} P \left( m, \frac{\tilde{W}(j, k-j)}{k}, k \right).$$

The invasion fitness of a rare mutant morph is then

$$f(r, m) = \lim_{x_m \rightarrow 0^+} \frac{x'_m}{x_m} = R(m; 1, 0) - R(r; 1, 0)$$

or

$$f(r, m) = \sum_{k=1}^{\infty} p_k \left[ P \left( m, \frac{\tilde{W}(1, k-1)}{k}, k \right) - P \left( r, \frac{\tilde{W}(1, k-1)}{k}, k \right) \right]. \quad (15)$$

In the arguments in Sect. 3 we assume that the total common investment equals the sum of individual contributions,

$$\tilde{W}(1, k-1) = m + (k-1)r, \quad (16)$$

and we also express all calculations in terms of the probability  $q_k$  that a game with  $k$  players is formed. This relates to the individual's probability  $p_k$  of joining a  $k$ -player game as

$$p_k = \frac{kq_k}{\sum_{k=1}^{\infty} kq_k} = \frac{kq_k}{\langle k \rangle}. \quad (17)$$

where  $\langle k \rangle$  is the average game size,  $\langle k \rangle = \sum kq_k$ . Substituting equations (16) and (17) into (15) yields

$$f(r, m) = \sum_{k=1}^{\infty} \frac{kq_k}{\langle k \rangle} \left[ P \left( m, \frac{m + (k-1)r}{k}, k \right) - P(r, r, k) \right]. \quad (18)$$

From the initial growth rate for rare mutants,  $f(r, m)$ , given by (18) we derive the selection gradient

$$g(r) = \frac{\partial f}{\partial m} \Big|_{m=r} = \langle k \rangle^{-1} \sum_{k=1}^{\infty} q_k [kP_1(r, r, k) - P_2(r, r, k)], \quad (19)$$

where  $P_i$  denotes the derivative with respect to argument  $i$ . Of particular interest are the singular strategies where directional selection ceases. This occurs at the points  $r^*$  for which the selection gradient vanishes, so that  $g(r^*) = 0$ . Below we use superscript  $*$  to denote that the first two arguments are evaluated at the singular strategy  $r^*$ . A singular strategy  $r^*$  is convergence stable if

$$g'(r^*) = \langle k \rangle^{-1} \sum_{k=1}^{\infty} q_k [kP_{11}^*(k) + (1+k)P_{12}^*(k) + P_{22}^*(k)] < 0, \quad (20)$$

in which case nearby monomorphic populations will evolve towards it. Disruptive selection occurs at the singular strategy if

$$\frac{\partial^2 f}{\partial m^2} \Big|_{m=r=r^*} = \langle k \rangle^{-1} \sum_{k=1}^{\infty} q_k \left[ kP_{11}^*(k) + 2P_{12}^*(k) + \frac{1}{k}P_{22}^*(k) \right] > 0. \quad (21)$$

We can combine (20) and (21) into a single criterion for the occurrence of an evolutionary branching point,

$$\sum_{k=1}^{\infty} q_k \left[ (1+k)P_{12}^*(k) + \frac{1}{k}P_{22}^*(k) \right] < - \sum_{k=1}^{\infty} kq_k P_{11}^*(k) \quad (22)$$

$$< \sum_{k=1}^{\infty} q_k \left[ 2P_{12}^*(k) + \frac{1}{k}P_{22}^*(k) \right]. \quad (23)$$



The left inequality is the condition for convergence stability (implying evolutionary attraction), while the right inequality is the condition for the absence of evolutionary stability (implying disruptive selection).

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