

# Evolutionary dynamics of collective action in spatially structured populations

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## Abstract

Many models proposed to study the evolution of collective action rely on a formalism that represents social interactions as  $n$ -player games between individuals adopting discrete actions such as cooperate and defect. Despite the importance of spatial structure in biological collective action, the analysis of  $n$ -player games in spatially structured populations has so far proved elusive. We address this problem by considering mixed strategies and by integrating discrete-action  $n$ -player games into the direct fitness approach of social evolution theory. This allows to conveniently identify convergence stable strategies and to capture the effect of population structure by a single structure coefficient, namely, the pairwise (scaled) relatedness among interacting individuals. As an application, we use our mathematical framework to investigate collective action problems associated with the provision of three different kinds of collective goods, paradigmatic of a vast array of helping traits in nature: “public goods” (both providers and shirkers can use the good, e.g., alarm calls), “club goods” (only providers can use the good, e.g., participation in collective hunting), and “charity goods” (only shirkers can use the good, e.g., altruistic sacrifice). We show that relatedness promotes the evolution of collective action in different ways depending on the kind of collective good and its economies of scale. Our findings highlight the importance of explicitly accounting for relatedness, the kind of collective good, and the economies of scale in theoretical and empirical studies of the evolution of collective action.

**Keywords.**  $n$ -player games; games between relatives; relatedness; inclusive fitness

# 1 Introduction

1

2 Collective action occurs when individuals work together to provide a collective good (Olson, 1971).  
3 Examples abound in the social and natural sciences: humans collectively build houses, roads, walls, and  
4 mobilize armies to make war; bacteria secrete enzymes that benefit other bacteria; sterile ant workers  
5 build the nest and raise the brood of the queen; lions work together to catch large game. Yet cooperation  
6 of this kind poses a collective action problem: if individual effort is costly there is an incentive to reduce or  
7 withdraw one's effort, but if enough individuals follow this logic the collective good will not be provided.

8 Much research in the social sciences has identified mechanisms for solving collective action problems,  
9 including privatization and property rights, reciprocity in repeated interactions, and institutions (Hardin,  
10 1982; Sugden, 1986; Taylor, 1987; Ostrom, 2003). The principles behind these mechanisms have also been  
11 explored in evolutionary biology (Boyd and Richerson, 1988; Nunn and Lewis, 2001; Strassmann and  
12 Queller, 2014) where it has been further emphasized that individual effort in cooperation should also  
13 increase as the relatedness between interactants increases (Hamilton, 1964). As social interactions often  
14 occur between relatives (because of spatial structure, kin recognition, or both; Rousset 2004; Bourke  
15 2011) it is thought that relatedness plays a central role for solving collective action problems in biology.  
16 In particular, relatedness has been identified as the main mechanism of conflict resolution in the fraternal  
17 major transitions in evolution, i.e., those resulting from associations of relatives, such as the transitions  
18 from unicellularity to multicellularity, or from autarky to eusociality (Queller, 2000).

19 Mathematical models of collective action in spatially structured populations or between relatives often  
20 assume that strategies are defined in a continuous action space, such as effort invested into the provision  
21 of a public good or level of restraint in resource exploitation (Frank, 1995; Foster, 2004; Lehmann, 2008;  
22 Frank, 2010; Cornforth et al., 2012). This allows for a straightforward application of the direct fitness  
23 method (Taylor and Frank, 1996; Rousset, 2004) to investigate the effects of relatedness on the evolution  
24 of collective action. Contrastingly, many evolutionary models of collective action between unrelated  
25 individuals (Boyd and Richerson, 1988; Dugatkin, 1990; Motro, 1991; Bach et al., 2006; Hauert et al.,  
26 2006; Pacheco et al., 2009; Archetti and Scheuring, 2011; Sasaki and Uchida, 2014) represent interactions  
27 as  $n$ -player games in discrete action spaces (e.g., individuals play either "cooperate" or "defect"). These  
28 models can be mathematically involved, as identifying polymorphic equilibria might require solving  
29 polynomial equations of degree  $n - 1$ , for which there are no general analytical solutions if  $n \geq 6$ .

30 Here we integrate two-action  $n$ -player mixed strategy game-theoretic models into the direct fitness  
31 method of social evolution theory (Taylor and Frank, 1996; Rousset, 2004), which allows for studying the  
32 effect of spatial structure on convergence stability by using pairwise relatedness. Several shape-preserving  
33 properties of polynomials in Bernstein form (Farouki, 2012) then allow us to characterize convergence  
34 stable strategies with a minimum of mathematical effort. Our framework delivers tractable formulas  
35 for games between relatives which differ from the corresponding formulas for games between unrelated

36 individuals only in that “inclusive payoffs” (the payoff to self plus relatedness times the sum of payoffs  
37 to others) rather than solely standard payoffs must be taken into account. For a large class of games,  
38 convergence stable strategies can then be identified by a straightforward adaptation of existing results for  
39 games between unrelated individuals (Peña et al., 2014).

40 As an application of our modeling framework, we study the effects of relatedness on the evolution of  
41 collective action under different assumptions on the kind of collective good and its economies of scale,  
42 thus covering a wide array of biologically meaningful situations. To this aim, we distinguish between three  
43 kinds of collective goods: (i) “public goods” where all individuals in the group can use the good, e.g.,  
44 alarm calls in vertebrates (Searcy and Nowicki, 2005) and the secretion of diffusible beneficial compounds  
45 in bacteria (Griffin et al., 2004; Gore et al., 2009; Cordero et al., 2012); (ii) “club goods” where only  
46 providers can use the good (Sandler and Tschirhart, 1997), e.g., cooperative hunting (Packer and Rutan,  
47 1988) where the benefits of a successful hunt go to individuals joining collective action but not to solitary  
48 individuals; and (iii) “charity goods” where only nonproviders can use the good, e.g., eusociality in  
49 Hymenoptera (Bourke and Franks, 1995) where sterile workers provide a good benefiting only queens.

50 For all three kinds of goods, we consider three classes of production functions giving the amount  
51 of good created as a function of the total level of effort and hence describing the associated economies  
52 of scale: (i) linear (constant returns to scale), (ii) decelerating (diminishing returns to scale), and  
53 (iii) accelerating (increasing returns to scale). Although linear production functions are often assumed  
54 because of mathematical simplicity, collective goods are often characterized by either decelerating or  
55 accelerating functions, so that the net effect of several individuals behaving socially is more or less  
56 than the sum of individual effects. In other words, social interactions can be characterized by (either  
57 positive or negative) synergy. For instance, enzyme production in microbial collective action is likely to  
58 be nonlinear, as in the cases of invertase hydrolyzing disaccharides into glucose in the budding yeast  
59 *Saccharomyces cerevisiae* (Gore et al., 2009) or virulence factors triggering gut inflammation in the  
60 pathogen *Salmonella typhimurium* (Ackermann et al., 2008). In the former case, the relationship between  
61 growth rate and glucose concentration in yeast has been reported to be decelerating, i.e., invertase  
62 production has diminishing returns to scale (Gore et al., 2009, Fig. 3.c); in the latter case, the relationship  
63 between the level of expression of virulence factors and inflammation intensity appears to be accelerating,  
64 i.e., it exhibits increasing returns to scale (Ackermann et al., 2008, Fig. 2.d).

65 We show that the effect of relatedness on the provision of collective goods, although always positive,  
66 critically depends on the kind of good (public, club, or charity) and on its economies of scale (linear,  
67 decelerating or accelerating production functions). Moreover, we show that relatedness and economies of  
68 scale can interact in nontrivial ways, leading to patterns of frequency dependence and dynamical portraits  
69 that cannot arise when considering any of these two factors in isolation. We discuss the predictions of our  
70 models, their implications for empirical and theoretical work, and their connections with the broader

71 literature on the evolution of helping.

## 72 2 Model

### 73 2.1 Population structure

74 We consider a homogeneous group-structured population with a finite number of groups each containing  
 75 an identical number of haploid individuals. Spatial structure may follow a variety of schemes, including  
 76 the island model of dispersal (Wright, 1931), the isolation-by-distance model (Malécot, 1975), the haystack  
 77 model (Maynard Smith, 1964), models where groups split into daughter groups and compete against each  
 78 other (Gardner and West, 2006; Traulsen and Nowak, 2006; Lehmann et al., 2007b), and evolutionary  
 79 graphs (Ohtsuki et al., 2006; Taylor et al., 2007; Lehmann et al., 2007a). We leave particular details of  
 80 the life history (e.g., whether generations are overlapping or non-overlapping) and population structure  
 81 (e.g., the dispersal distribution) unspecified as they do not affect our analysis. All that is required is  
 82 that the “selection gradient” can be written in a form proportional to (4) below. For this, we refer the  
 83 interested reader to Rousset (2004); Lehmann and Rousset (2010); Van Cleve (2015).

### 84 2.2 Social interactions

85 Within groups, individuals participate in an  $n$ -player game with two available actions:  $A$  (e.g., “cooper-  
 86 ation”) and  $B$  (e.g., “defection”). We denote by  $a_k$  the payoff to an  $A$ -player when  $k = 0, 1, \dots, n - 1$   
 87 co-players choose  $A$  (and hence  $n - 1 - k$  co-players choose  $B$ ). Likewise, we denote by  $b_k$  the payoff to a  
 88  $B$ -player when  $k$  co-players choose  $A$ . These payoffs can be represented as a table of the form:

Opposing $A$ -players	0	1	...	$k$	...	$n - 1$
89 payoff to $A$	$a_0$	$a_1$	...	$a_k$	...	$a_{n-1}$
payoff to $B$	$b_0$	$b_1$	...	$b_k$	...	$b_{n-1}$

90 Individuals implement mixed strategies, i.e., they play  $A$  with probability  $z$  (and  $B$  with probability  
 91  $1 - z$ ). The set of available strategies is then the interval  $[0, 1]$ . At any given time only two strategies are  
 92 present in the population:  $z$  and  $z + \delta$ . Denoting by  $z_\bullet$  the strategy of a focal individual and by  $z_{\ell(\bullet)}$  the  
 93 strategy of its  $\ell$ -th co-player, the expected payoff  $\pi$  to the focal can be written as

$$94 \quad \pi(z_\bullet, z_{1(\bullet)}, z_{2(\bullet)}, \dots, z_{n-1(\bullet)}) = \sum_{k=0}^{n-1} \phi_k(z_{1(\bullet)}, z_{2(\bullet)}, \dots, z_{n-1(\bullet)}) [z_\bullet a_k + (1 - z_\bullet) b_k], \quad (1)$$

95 where  $\phi_k$  is the probability that exactly  $k$  co-players play action  $A$ . A first-order Taylor-series expansion  
 96 about the average strategy  $z_\circ = \sum_{\ell=1}^{n-1} z_{\ell(\bullet)} / (n - 1)$  of co-players shows that, to first order in  $\delta$ , the

97 probability  $\phi_k$  is given by a binomial distribution with parameters  $n - 1$  and  $z_o$ , i.e.,

$$98 \quad \phi_k(z_1(\bullet), z_2(\bullet), \dots, z_{n-1}(\bullet)) = \binom{n-1}{k} z_o^k (1 - z_o)^{n-1-k} + O(\delta^2). \quad (2)$$

99 Substituting (2) into (1) and discarding second and higher order terms, we obtain

$$100 \quad \pi(z_\bullet, z_o) = \sum_{k=0}^{n-1} \binom{n-1}{k} z_o^k (1 - z_o)^{n-1-k} [z_\bullet a_k + (1 - z_\bullet) b_k] \quad (3)$$

101 for the payoff of a focal individual as a function of the focal's strategy  $z_\bullet$  and the average strategy  $z_o$  of  
102 co-players.

### 103 **2.3 Evolutionary dynamics, scaled relatedness, and Hamilton's rule**

104 We are interested in the long-term evolutionary attractors of the probability  $z$  of playing  $A$ . To derive  
105 them, we consider a population of residents playing  $z$  in which a single mutant playing  $z + \delta$  appears  
106 due to mutation, and denote by  $\rho(\delta, z)$  the fixation probability of the mutant. We take the phenotypic  
107 selection gradient  $\mathcal{S}(z) = (d\rho/d\delta)_{\delta=0}$  as measure of evolutionary success (Rousset and Billiard 2000, p.  
108 819; Van Cleve 2015, Section 2.5); indeed,  $\mathcal{S}(z) > 0$  entails that the fixation probability of the mutant  
109 is greater than that of a neutral mutant under so-called “ $\delta$ -weak” selection (Wild and Traulsen, 2007).  
110 Letting the expected relative fecundity of an adult be equal to its expected payoff (i.e., the payoffs from  
111 the game have fecundity effects; Taylor and Irwin 2000), the selection gradient  $\mathcal{S}(z)$  can be shown to be  
112 proportional to what we call in this paper the “gain function”

$$113 \quad \mathcal{G}(z) = \underbrace{\frac{\partial \pi(z_\bullet, z_o)}{\partial z_\bullet} \Big|_{z_\bullet = z_o = z}}_{\text{direct effect, } -\mathcal{C}(z)} + \kappa \underbrace{\frac{\partial \pi(z_\bullet, z_o)}{\partial z_o} \Big|_{z_\bullet = z_o = z}}_{\text{indirect effect, } \mathcal{B}(z)} = -\mathcal{C}(z) + \kappa \mathcal{B}(z) \quad (4)$$

114 (for a derivation, see e.g., Van Cleve and Lehmann 2013, Eq. 7, or Van Cleve 2015, Eq. 73).

115 The gain function  $\mathcal{G}(z)$  is determined by three components. First, the direct effect  $-\mathcal{C}(z)$  describing  
116 the change in expected payoff resulting from the focal infinitesimally changing its own strategy. Second,  
117 the indirect effect  $\mathcal{B}(z)$  describing the change in expected payoff of the focal resulting from the focal's  
118 co-players changing their strategy infinitesimally. Third, the indirect effect is weighted by the scaled  
119 relatedness coefficient  $\kappa$ , which is a measure of relatedness between the focal individual and its neighbors,  
120 demographically scaled so as to capture the effects of local competition on selection (Queller, 1994;  
121 Lehmann and Rousset, 2010).

122 Scaled relatedness  $\kappa$  is a function of demographic parameters such as the migration rate, group size,  
123 and vital rates of individuals or groups, but is independent of the evolving trait  $z$  and the payoffs from  
124 the game. In general,  $\kappa$  can take a value between  $-1$  and  $1$ , depending on the demographic assumptions

125 (Lehmann and Rousset, 2010; Van Cleve and Lehmann, 2013). For instance, in a model where groups  
126 split into daughter groups and compete against each other (Traulsen and Nowak, 2006), scaled relatedness  
127 can be shown to be given by (Lehmann et al., 2007b)

$$128 \quad \kappa = \frac{q - [2q/g + m/(ng)]}{m/ng - 1 + q(n + g - 2)/g}, \quad (5)$$

129 where  $g$  is the number of groups,  $n$  is group size,  $q$  is the splitting rate at which groups form propagules,  
130 and  $m$  is the migration rate (Van Cleve and Lehmann, 2013, Eq. B.4). Scaled relatedness coefficients have  
131 been evaluated for many spatially structured populations and demographic assumptions (see Lehmann  
132 and Rousset 2010; Van Cleve and Lehmann 2013 and references therein). In Appendix A we contribute  
133 to this literature by calculating values of scaled relatedness for several variants of the haystack model. In  
134 the subsequent analysis we treat  $\kappa$  as a parameter.

135 The gain function (4) is sufficient to characterize convergence stable strategies (i.e., strategies towards  
136 which selection locally drives the population by successive allelic replacements; Christiansen 1991; Geritz  
137 et al. 1998) under a trait substitution dynamic (Rousset and Billiard, 2000; Rousset, 2004). In our context,  
138 candidate convergence stable strategies are either singular strategies (i.e., values  $z^*$  for which  $\mathcal{G}(z^*) = 0$ ),  
139 or the two pure strategies  $z = 0$  and  $z = 1$ . In particular, a singular strategy  $z^*$  is convergence stable  
140 (or an attractor) if  $d\mathcal{G}(z)/dz|_{z=z^*} < 0$  and convergence unstable (or a repeller) if  $d\mathcal{G}(z)/dz|_{z=z^*} > 0$ .  
141 Regarding the endpoints,  $z = 0$  (resp.  $z = 1$ ) is convergence stable if  $\mathcal{G}(0) < 0$  (resp.  $\mathcal{G}(1) > 0$ ).

142 Finally, let us also note that the condition for a mutant to be favored by selection,  $-\mathcal{C} + \kappa\mathcal{B} > 0$ , can  
143 be understood as a demographically scaled form of the marginal version of Hamilton's rule (Lehmann  
144 and Rousset, 2010), with  $\mathcal{C}$  corresponding to the marginal direct costs and  $\mathcal{B}$  to the marginal indirect  
145 benefits of expressing an increased probability of playing action  $A$ . This scaled version of Hamilton's rule  
146 partitions the selection gradient in fecundity effects and scaled relatedness, in contrast to the partition on  
147 fitness effects and genetic relatedness of the classical formalism (i.e.,  $-c + rb > 0$ , where  $c$  and  $b$  are the  
148 direct and indirect fitness effects, and  $r$  is relatedness). Social evolution theory classifies social behaviors  
149 as altruistic, cooperative (or mutually beneficial), selfish, and spiteful, according to the signs of direct  
150 fitness costs and benefits (Hamilton, 1964; Rousset, 2004; West et al., 2007). A similar classification of  
151 social behaviors can be done according to the behavior's effect on the direct and indirect components of  
152 marginal payoff (or fecundity). In order to avoid ambiguities, we refer to the resulting social behaviors as  
153 "payoff altruistic" ( $\mathcal{C} > 0$  and  $\mathcal{B} > 0$ ), "payoff cooperative" ( $\mathcal{C} < 0$  and  $\mathcal{B} > 0$ ), "payoff selfish" ( $\mathcal{C} < 0$  and  
154  $\mathcal{B} < 0$ ), and "payoff spiteful" ( $\mathcal{C} > 0$  and  $\mathcal{B} < 0$ ).

### 3 Games between relatives

We start by deriving compact expressions for the direct effect  $-\mathcal{C}(z)$ , the indirect effect  $\mathcal{B}(z)$ , and the gain function  $\mathcal{G}(z)$  in terms of the payoffs  $a_k$  and  $b_k$  of the game. These expressions provide the foundation for our subsequent analysis.

Imagine a focal individual playing  $B$  in a group where  $k$  of its co-players play  $A$ . Suppose that the focal switches its action to  $A$  while co-players hold fixed their actions, thus changing its payoff from  $b_k$  to  $a_k$ . As a consequence, the focal experiences a “direct gain from switching” given by

$$d_k = a_k - b_k, \quad k = 0, 1, \dots, n - 1. \quad (6)$$

At the same time, each of the co-players playing  $A$  experiences a change in payoff given by  $\Delta a_{k-1} = a_k - a_{k-1}$  and each of the co-players playing  $B$  experiences a change in payoff given by  $\Delta b_k = b_{k+1} - b_k$ . Taken as a block, co-players experience a change in payoff given by

$$e_k = k\Delta a_{k-1} + (n - 1 - k)\Delta b_k, \quad k = 0, 1, \dots, n - 1, \quad (7)$$

where we set  $a_{-1} = b_{n+1} = 0$ . From the focal’s perspective, this change in payoffs represents an “indirect gain from switching” to the focal if co-players are relatives. Adding up direct and indirect gains weighted by  $\kappa$  allows us to define the “inclusive gains from switching”

$$f_k = d_k + \kappa e_k, \quad k = 0, 1, \dots, n - 1, \quad (8)$$

in a group where  $k$  out of the  $n - 1$  co-players play  $A$ .

We show in Appendix B that the direct, indirect, and net effects appearing in (4) are indeed given by

$$-\mathcal{C}(z) = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} d_k, \quad (9a)$$

$$\mathcal{B}(z) = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} e_k, \quad (9b)$$

and

$$\mathcal{G}(z) = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} f_k, \quad (10)$$

that is, as the expected values of the relevant gains from switching when the number of co-players playing  $A$  is distributed according to a binomial distribution with parameters  $n - 1$  and  $z$ .

It follows from (10) that games between relatives are mathematically equivalent to transformed games



181 between unrelated individuals, where “inclusive payoffs” take the place of standard, or personal, payoffs.

182 Indeed, consider a game in which  $A$ -players and  $B$ -players respectively obtain payoffs

$$183 \quad a'_k = a_k + \kappa [ka_k + (n - 1 - k)b_{k+1}], \quad (11a)$$

$$184 \quad b'_k = b_k + \kappa [ka_{k-1} + (n - 1 - k)b_k], \quad (11b)$$

186 when  $k$  co-players play  $A$ . Payoffs  $a'_k$  and  $b'_k$  can be understood as inclusive payoffs consisting of the payoff  
 187 obtained by a focal plus  $\kappa$  times the sum of the payoffs obtained by the focal’s co-players. Using (6)–(7)  
 188 we can rewrite (8) as  $f_k = a'_k - b'_k$ , so that the inclusive gains from switching are identical to the direct  
 189 gains from switching in a game with payoff structure given by (11).

190 This observation has two relevant consequences. First, existing results on the evolutionarily stable  
 191 strategies of games between unrelated individuals (Peña et al., 2014), which are based on the observation  
 192 that the right side of (10) is a polynomial in Bernstein form (Farouki, 2012), also apply here, provided  
 193 that the inclusive gains from switching  $f_k$  are used instead of the standard (direct) gains from switching  $d_k$   
 194 in the formula for the gain function, and that evolutionary stability is understood as convergence stability.  
 195 For a large class of games, these results allow us to identify convergence stable strategies from a direct  
 196 inspection of the sign pattern of the inclusive gains from switching  $f_k$ . Second, we can interpret the effect  
 197 of relatedness as inducing the payoff transformation  $a_k \rightarrow a'_k$ ,  $b_k \rightarrow b'_k$ . For  $n = 2$ , such transformation is  
 198 the classic result of two-player games between relatives (Hamilton, 1971; Grafen, 1979; Day and Taylor,  
 199 1998)

$$200 \quad \begin{pmatrix} a'_0 & a'_1 \\ b'_0 & b'_1 \end{pmatrix} = \begin{pmatrix} a_0 + \kappa b_1 & (1 + \kappa)a_1 \\ (1 + \kappa)b_0 & b_1 + \kappa a_0 \end{pmatrix},$$

201 where the payoff of the focal is augmented by adding  $\kappa$  times the payoff of the co-player.

## 202 **4 The evolution of collective action**

203 Let us now apply our model to the evolution of collective action. To this end, we let action  $A$  (“provide”)   
 204 be associated with some effort in collective action, action  $B$  (“shirk”) with no effort, and refer to  $A$ -players   
 205 as “providers” and to  $B$ -players as “shirkers”. Each provider incurs a cost  $\gamma > 0$  in order for a collective   
 206 good of value  $\beta_j$  to be created, where  $j$  is the total number of providers. We assume that the collective   
 207 good fails to be created if no individual works ( $\beta_0 = 0$ ), and that the value of the collective good  $\beta_j$  is   
 208 increasing in the number of providers ( $\Delta\beta_j = \beta_{j+1} - \beta_j \geq 0$ ). We distinguish between three kinds of   
 209 collective goods, depending on which individuals have access to the good: (i) “public goods”, (ii) “club   
 210 goods”, and (iii) “charity goods”. Fig. 1 illustrates these three kinds of collective goods and Table 1

211 provides the corresponding payoffs and gains from switching.

212 Economies of scale are incorporated in the model through the properties of the production function  
213  $\beta_j$ . We investigate three functional forms (Fig. 2): (i) linear ( $\beta_j = \beta j$  for some  $\beta > 0$ , so that  $\Delta\beta_j$  is  
214 constant), (ii) decelerating ( $\Delta\beta_j$  is decreasing in  $j$ ), and (iii) accelerating ( $\Delta\beta_j$  is increasing in  $j$ ). We also  
215 say that returns to scale are respectively (i) constant, (ii) diminishing, or (iii) increasing. To illustrate  
216 the effects of economies of scale, we consider the “geometric production function”:

$$217 \quad \beta_j = \beta \sum_{\ell=0}^{j-1} \lambda^\ell, \quad (12)$$

218 with  $\beta > 0$  and  $\lambda > 0$ , for which returns to scale are constant when  $\lambda = 1$ , decreasing when  $\lambda < 1$ , and  
219 increasing when  $\lambda > 1$  (Fig. 2).

220 For all three kinds of collective goods, the indirect gains from switching are always nonnegative, hence  
221 the indirect effect  $\mathcal{B}(z)$  is nonnegative for all  $z$ . Consequently, participation in collective action is either  
222 payoff altruistic or payoff cooperative, and the selection gradient is increasing in  $\kappa$ . The provision of  
223 each kind of collective good however leads to a different collective action problem, as it is reflected in the  
224 different payoff structures of the corresponding games (Table 1). In particular, while the provision of  
225 charity goods is payoff altruistic for all  $z$ , the provision of public and club goods can be either payoff  
226 altruistic or payoff cooperative, depending on the parameters of the game and the resident strategy  $z$ .

227 In the following, we characterize the evolutionary dynamics of each of these three kinds of collective  
228 action problems and investigate the effects of (scaled) relatedness on the set of evolutionary attractors.  
229 Although many of our results also extend to the case of negative relatedness, for simplicity we restrict  
230 attention to nonnegative relatedness ( $\kappa \geq 0$ ). It will be shown that the evolutionary dynamics fall  
231 into one of the following five dynamical regimes: (i) “null provision” ( $z = 0$  is the only attractor), (ii)  
232 “full provision” ( $z = 1$  is the only attractor), (iii) “coexistence” (there is a unique singular strategy  $z^*$   
233 which is attracting), (iv) “bistability” ( $z = 0$  and  $z = 1$  are both attracting, with a singular repeller  $z^*$   
234 dividing their basins of attraction), and (v) “bistable coexistence” ( $z = 0$  is attracting,  $z = 1$  is repelling,  
235 and there are two singular strategies  $z_L$  and  $z_R$ , satisfying  $z_L < z_R$ , such that  $z_L$  is a repeller and  $z_R$   
236 is an attractor). Regimes (i)-(iv) are those classical from  $2 \times 2$  games (Cressman, 2003, Section 2.2),  
237 while bistable coexistence can only arise for interactions with more than two players (indeed, bistable  
238 coexistence requires the polynomial  $\mathcal{G}(z)$  to have two sign changes, which is only possible if  $n > 2$ ; Broom  
239 et al. 1997; Gokhale and Traulsen 2014).

## 240 4.1 Linear production functions

241 To isolate the effects of the kind of collective good, we begin our analysis with the case where the  
242 production function takes the linear form  $\beta_j = \beta j$ , i.e.,  $\lambda = 1$  in (12). For all three kinds of collective

243 goods, the gain function can then be written as

$$244 \quad \mathcal{G}(z) = (n - 1) [-C + \kappa B + (1 + \kappa)Dz].$$

245 The parameter  $C > 0$  may be thought of as the “effective cost” per co-player of joining collective action  
246 alone. We have  $C = \gamma/(n - 1)$  when a focal provider is not among the beneficiaries of the collective  
247 good (charity goods) and  $C = (\gamma - \beta)/(n - 1)$  otherwise (public and club goods). The parameter  $B \geq 0$   
248 measures the incremental benefit accruing to each co-player of a focal provider when none of the co-players  
249 joins collective action. We thus have  $B = 0$  for club goods and  $B = \beta$  otherwise. Finally,  $D$  is null for  
250 public goods ( $D = 0$ ), positive for club goods ( $D = \beta$ ), and negative for charity goods ( $D = -\beta$ ).

251 Depending on the values of these parameters, we obtain the following characterization of the resulting  
252 evolutionary dynamics:

- 253 1. For public goods ( $D = 0$ ) selection is frequency independent. There is null provision if  $-C + \kappa B < 0$ ,  
254 and full provision if  $-C + \kappa B > 0$ .
- 255 2. For club goods ( $D > 0$ ) selection is positive frequency-dependent. There is null provision if  
256  $-C + \kappa B + (1 + \kappa)D \leq 0$ , and full provision if  $-C + \kappa B \geq 0$ . If  $-C + \kappa B < 0 < -C + \kappa B + (1 + \kappa)D$ ,  
257 there is bistability: both  $z = 0$  and  $z = 1$  are attractors and the singular strategy

$$258 \quad z^* = \frac{C - \kappa B}{(1 + \kappa)D} \tag{13}$$

259 is a repeller.

- 260 3. For charity goods ( $D < 0$ ), selection is negative frequency-dependent. There is null provision if  
261  $-C + \kappa B \leq 0$ , and full provision if  $-C + \kappa B + (1 + \kappa)D \geq 0$ . If  $-C + \kappa B + (1 + \kappa)D < 0 < -C + \kappa B$ ,  
262 there is coexistence: both  $z = 0$  and  $z = 1$  are repellers and the singular strategy  $z^*$  is the only  
263 attractor.

264 This analysis reveals three important points. First, in the absence of economies of scale the gain  
265 function is linear in  $z$ , which allows for a straightforward analysis of the evolutionary dynamics for all  
266 three kinds of collective action. Second, because of the linearity of the gain function, the evolutionary  
267 dynamics of such games fall into one of the four classical dynamical regimes arising from  $2 \times 2$  games.  
268 Third, which of these dynamical regimes arises is determined by relatedness and the kind of good in  
269 a simple way. For all kinds of collective action, there is null provision when relatedness is low. For  
270 public goods provision, high values of relatedness lead to full provision. For club and charity goods, high  
271 relatedness also promotes collective action, leading to either bistability (club goods) or to the coexistence  
272 of providers and shirkers.

## 273 4.2 Public goods with accelerating and decelerating production functions

274 How do economies of scale change the evolutionary dynamics of public goods provision? Substituting the  
 275 inclusive gains from switching given in Table 1 into (10) we obtain

$$276 \quad \mathcal{G}(z) = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} \{-\gamma + [1 + \kappa(n-1)] \Delta\beta_k\}. \quad (14)$$

277 If the production function is decelerating,  $\Delta\beta_k$  is decreasing in  $k$ , implying that  $\mathcal{G}(z)$  is decreasing in  
 278  $z$  (Peña et al., 2014, Remark 3). Similarly, if the production function is accelerating,  $\Delta\beta_k$  is increasing  
 279 in  $k$ , so that  $\mathcal{G}(z)$  is increasing in  $z$ . In both cases the evolutionary dynamics are easily characterized  
 280 by applying existing results for public goods games between unrelated individuals (Peña et al., 2014,  
 281 Section 4.3): with accelerating production functions, there is null provision if  $\gamma \geq [1 + \kappa(n-1)]\Delta\beta_0$ ,  
 282 and full provision if  $\gamma \leq [1 + \kappa(n-1)]\Delta\beta_{n-1}$ . If  $[1 + \kappa(n-1)]\Delta\beta_{n-1} < \gamma < [1 + \kappa(n-1)]\Delta\beta_0$ , there is  
 283 coexistence. With decelerating production functions, there is null provision if  $\gamma \geq [1 + \kappa(n-1)]\Delta\beta_{n-1}$ ,  
 284 and full provision if  $\gamma \leq [1 + \kappa(n-1)]\Delta\beta_0$ . If  $[1 + \kappa(n-1)]\Delta\beta_0 < \gamma < [1 + \kappa(n-1)]\Delta\beta_{n-1}$ , there is  
 285 bistability.

286 The effect of relatedness on the evolution of public goods provision can be better grasped by noting  
 287 that multiplying and dividing (14) by  $1 + \kappa(n-1)$  we obtain

$$288 \quad \mathcal{G}(z) = [1 + \kappa(n-1)] \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} (-\tilde{\gamma} + \Delta\beta_k), \quad (15)$$

289 where  $\tilde{\gamma} = \gamma/[1 + \kappa(n-1)]$ . This is (up to multiplication by a positive constant) equivalent to the gain  
 290 function of a public goods game with constant cost  $\tilde{\gamma}$  between unrelated individuals, which has been  
 291 analyzed under different assumptions on the shape of the production function  $\beta_k$  (Motro, 1991; Bach  
 292 et al., 2006; Hauert et al., 2006; Pacheco et al., 2009; Archetti and Scheuring, 2011; Peña et al., 2014).  
 293 Hence, the effects of relatedness can be understood as affecting only the cost of cooperation, while leaving  
 294 economies of scale and patterns of frequency dependence unchanged.

295 To illustrate the evolutionary dynamics of public goods games, consider a geometric production  
 296 function (12) with  $\lambda \neq 1$  (see Table 2 for a summary of the results and Appendix C for a derivation). We  
 297 find that there are two critical cost-to-benefit ratios:

$$298 \quad \varepsilon = \min(1 + \kappa(n-1), \lambda^{n-1}[1 + \kappa(n-1)]) \quad \text{and} \quad \vartheta = \max(1 + \kappa(n-1), \lambda^{n-1}[1 + \kappa(n-1)]), \quad (16)$$

299 such that for small costs ( $\gamma/\beta \leq \varepsilon$ ) there is full provision and for large costs ( $\gamma/\beta \geq \vartheta$ ) there is null

300 provision. For intermediate costs ( $\varepsilon < \gamma/\beta < \vartheta$ ), there is a singular strategy given by

$$301 \quad z^* = \frac{1}{1-\lambda} \left[ 1 - \left( \frac{\gamma}{\beta[1+\kappa(n-1)]} \right)^{\frac{1}{n-1}} \right], \quad (17)$$

302 such that there is coexistence if returns to scale are diminishing ( $\lambda < 1$ ) and bistability if returns to scale  
 303 are increasing ( $\lambda > 1$ ). For a given cost-to-benefit ratio  $\gamma/\beta$ , higher relatedness makes the region in the  
 304 parameter space where cooperation (resp. defection) dominates larger (resp. smaller). Moreover,  $z^*$  is an  
 305 increasing (resp. decreasing) function of  $\kappa$  when  $\lambda < 1$  (resp.  $\lambda > 1$ ), meaning that the proportion of  
 306 providers at the internal attractor (resp. the size of the basin of attraction of  $z = 1$ ) is larger for higher  $\kappa$   
 307 (Fig. 3.a and 3.d).

### 308 4.3 Club goods with accelerating and decelerating production functions

309 For club goods the direct gains from switching  $d_k$  (cf. Table 1) are increasing in  $k$  independently of  
 310 any economies of scale. This implies that the direct effect  $-\mathcal{C}(z)$  is positive frequency-dependent. If  
 311 the production function is accelerating, the indirect gains from switching  $e_k$  are also increasing in  $k$ ,  
 312 so that the indirect effect  $\mathcal{B}(z)$  is also positive frequency-dependent. For  $\kappa \geq 0$  this ensures that, just  
 313 as when economies of scale are absent, the gain function  $\mathcal{G}(z)$  is positive frequency-dependent. Hence,  
 314 the evolutionary dynamics are qualitatively identical to those arising from linear production functions:  
 315 for low relatedness, there is null provision; for high relatedness, there is bistability (see Fig. 3.e for an  
 316 illustration and Appendix D.1 for proofs).

317 If the production function is decelerating, the indirect gains from switching  $e_k$  may still be increasing  
 318 in  $k$  because the incremental benefit  $\Delta\beta_k$  accrues to a larger number of recipients as  $k$  increases. In such  
 319 a scenario, always applicable when  $n = 2$ , the evolutionary dynamics are again qualitatively identical  
 320 to those arising when economies of scale are absent. A different picture emerges if the number of  
 321 players is greater than two and returns to scale are diminishing. In this case,  $\mathcal{B}(z)$  can be negative  
 322 frequency-dependent for some  $z$ , and hence (for sufficiently high values of  $\kappa$ ) so can be  $\mathcal{G}(z)$ . Depending  
 323 on the value of relatedness, which modulates how the frequency dependence of  $\mathcal{B}(z)$  interacts with that of  
 324  $\mathcal{C}(z)$ , and on the particular shape of the production function, this can give rise to evolutionary dynamics  
 325 different from those discussed in Section 4.1. In particular, bistable coexistence is possible.

326 As an example, consider the geometric production function (12) with  $\lambda \neq 1$  (see Table 2 for a summary  
 327 of results and Appendix D.2 for proofs). Defining the critical returns-to-scale value

$$328 \quad \xi = \frac{\kappa(n-2)}{1+\kappa(n-1)}, \quad (18)$$

329 and the two critical cost-to-benefit ratios

$$330 \quad \varsigma = \frac{1 - \lambda^n}{1 - \lambda} + \kappa(n - 1)\lambda^{n-1}, \quad \text{and} \quad \tau = \frac{1}{1 - \lambda} \left[ 1 + \lambda\kappa \left( \frac{(n - 2)\kappa}{1 + \kappa(n - 1)} \right)^{n-2} \right], \quad (19)$$

331 which satisfy  $\xi < 1$  and  $\varsigma < \tau$ , our result can be stated as follows. For  $\lambda \geq \xi$  the evolutionary dynamics  
 332 depends on how the cost-to-benefit ratio  $\gamma/\beta$  compares to 1 and to  $\varsigma$ . If  $\gamma/\beta \leq 1$  (low costs), there is full  
 333 provision, while if  $\gamma/\beta \geq \varsigma$  (high costs), there is null provision. If  $1 < \gamma/\beta < \varsigma$  (intermediate costs), there  
 334 is bistability. For  $\lambda < \xi$ , the classification of possible evolutionary dynamics is as in the case  $\lambda \geq \xi$ , except  
 335 that, if  $\varsigma < \gamma/\beta < \tau$ , there is bistable coexistence, with  $z = 0$  convergence stable,  $z = 1$  convergence  
 336 unstable, and two singular strategies  $z_L$  (convergence unstable) and  $z_R$  (convergence stable) satisfying  
 337  $0 < z_L < z_R < 1$ . Although we have not been able to obtain closed form expressions for the singular  
 338 strategies ( $z^*$  in the case of bistability;  $z_L$  and  $z_R$  in the case of bistable coexistence), numerical values of  
 339 their locations can be obtained by searching for roots of  $\mathcal{G}(z)$  in the interval  $(0, 1)$ , as we illustrate in Fig.  
 340 3.b and Fig. 3.e.

341 The critical values  $\xi$ ,  $\varsigma$ , and  $\tau$  are all increasing functions of  $\kappa \geq 0$ . Hence, with larger relatedness  $\kappa$ ,  
 342 the regions of the parameter space where some level of collective action is convergence stable expand  
 343 at the expense of the region of dominant nonprovision. Moreover, inside these regions the convergence  
 344 stable positive probability of providing increases with  $\kappa$  (Fig. 3.b). When the production function is  
 345 “sufficiently” decelerating ( $\lambda < \xi$ ) and for intermediate cost-to-benefit ratios ( $\varsigma < \gamma/\beta < \tau$ ), relatedness  
 346 and economies of scale interact in a nontrivial way, leading to saddle-node bifurcations whereby two  
 347 singular strategies appear as  $\kappa$  increases (Fig. 3.b).

#### 348 4.4 Charity goods with accelerating and decelerating production functions

349 For charity goods the direct gains from switching  $d_k$  (cf. Table 1) are always decreasing in  $k$ , so that the  
 350 direct effect  $-\mathcal{C}(z)$  is negative frequency-dependent.

351 From the formulas given in Table 1, it is clear that the direct gains from switching  $d_k$  are always  
 352 decreasing in  $k$ . Hence, the direct effect  $-\mathcal{C}(z)$  is negative frequency-dependent. If the production  
 353 function is decelerating, the indirect gains from switching  $e_k$  are also decreasing in  $k$ , implying that the  
 354 indirect effect  $\mathcal{B}(z)$  is also negative frequency-dependent and that the same is true for the gain function  
 355  $\mathcal{G}(z) = -\mathcal{C}(z) + \kappa\mathcal{B}(z)$ . Hence, diminishing returns to scale lead to evolutionary dynamics that are  
 356 qualitatively identical to those arising when economies of scale are absent: for low relatedness, there is  
 357 null provision, and for sufficiently high relatedness, a unique interior attractor appears (see Appendix E.1  
 358 and Fig. 3.c).

359 If the production function is accelerating, the indirect gains from switching  $e_k$  may still be decreasing in  
 360  $k$  because the incremental benefit  $\Delta\beta_k$  accrues to a smaller number of recipients ( $n - 1 - k$ ) as  $k$  increases.

361 In such a scenario, always applicable when  $n = 2$ , the evolutionary dynamics are again qualitatively  
 362 identical to those arising when economies of scale are absent. A different picture emerges if  $n > 2$  holds  
 363 and the economies of scale are sufficiently strong. In this case,  $\mathcal{B}(z)$  can be positive frequency-dependent  
 364 for some  $z$ , and hence (for sufficiently high values of  $\kappa$ ) so can be  $\mathcal{G}(z)$ . Similarly to the case of club  
 365 goods provision with diminishing returns to scale, this pattern of frequency dependence can give rise to  
 366 bistable coexistence. For a concrete example, consider again the geometric production function (12) with  
 367  $\lambda \neq 1$  (see Table 2 for a summary of results, and Appendix E.2 for proofs). In this case, the evolutionary  
 368 dynamics for  $n > 2$  depend on the critical value

$$369 \quad \varrho = \frac{1 + \kappa(n - 1)}{\kappa(n - 2)}, \quad (20)$$

370 and on the two critical cost-to-benefit ratios

$$371 \quad \zeta = \kappa(n - 1), \quad \text{and} \quad \eta = \frac{1}{\lambda - 1} \left[ 1 + \lambda \kappa \left( \frac{(n - 2)\lambda \kappa}{1 + \kappa(n - 1)} \right)^{n-2} \right], \quad (21)$$

372 which satisfy  $\varrho > 1$  and  $\zeta < \eta$ .

373 With these definitions our results can be stated as follows. For  $\lambda \leq \varrho$  the dynamical outcome depends  
 374 on how the cost-to-benefit ratio  $\gamma/\beta$  compares to  $\zeta$ . If  $\gamma/\beta \geq \zeta$  (high costs), there is null provision, while  
 375 if  $\gamma/\beta < \zeta$  (low costs), there is coexistence. For  $\lambda > \varrho$ , the dynamical outcome also depends on how the  
 376 cost-to-benefit ratio  $\gamma/\beta$  compares to  $\eta$ . If  $\gamma/\beta \geq \eta$  (high costs), there is null provision. If  $\gamma/\beta \leq \zeta$  (low  
 377 costs), we have coexistence. In the remaining case ( $\zeta < \gamma/\beta < \eta$ , intermediate costs) the dynamics are  
 378 characterized by bistable coexistence. Closed form expressions for the singular strategies ( $z^*$  in the case  
 379 of coexistence;  $z_L$  and  $z_R$  in the case of bistable coexistence) are not available, but we can find their  
 380 values numerically, as we illustrate in Fig. 3.c and Fig. 3.f.

381 It is evident from the dependence of  $\varrho$ ,  $\zeta$ , and  $\eta$  on  $\kappa$  that relatedness plays an important role in  
 382 determining the convergence stable level(s) of expression of helping. With higher  $\kappa$ , the regions of the  
 383 parameter space where some  $z > 0$  is convergence stable expand at the expense of the region of dominant  
 384 nonprovision. This is so because  $\zeta$  and  $\eta$  are increasing functions of  $\kappa$ , and  $\varrho$  is a decreasing function of  $\kappa$ .  
 385 Moreover, inside these regions the stable non-zero probability of providing is bigger the higher  $\kappa$  (see Fig.  
 386 3.c and 3.f). Three cases can be more precisely distinguished as for the effects of increasing  $\kappa$ . First,  
 387  $z = 0$  can remain stable irrespective of the value of relatedness, which characterizes high cost-to-benefit  
 388 ratios. Second, the system can undergo a transcritical bifurcation, destabilizing  $z = 0$  and leading to the  
 389 appearance of a unique interior attractor (Fig. 3.c). This happens when  $\lambda$  and  $\gamma/\beta$  are relatively small.  
 390 Third, there is a range of intermediate cost-to-benefit ratios such that, for sufficiently large values of  $\lambda$ ,  
 391 the system undergoes a saddle-node bifurcation, whereby two singular strategies appear (Fig. 3.f). In  
 392 this latter case, economies of scale are strong enough to interact with the kind of good and relatedness in

393 a nontrivial way.

## 394 4.5 Connections with previous models

395 Our formalization and analysis of specific collective action problems are connected to a number of results  
396 in the literature of cooperation and helping; we discuss these connections in the following paragraphs.

397 Our results on public goods games with geometric production functions (Section 4.2 and Appendix C)  
398 extend the model studied in (Hauert et al., 2006, p. 198) from the particular case of interactions between  
399 unrelated individuals ( $\kappa = 0$ ) to the case of related individuals ( $\kappa \neq 0$ ) and recover the result in (Archetti,  
400 2009, p. 476) in the limit  $\lambda \rightarrow 0$ , where the game is known as the “volunteer’s dilemma” (Diekmann, 1985).  
401 Although we restricted our attention to the cases of linear, decelerating, and accelerating production  
402 functions, it is clear that (15) applies to production functions  $\beta_j$  of any shape. Hence, results about  
403 the stability of equilibria in public goods games with threshold and sigmoid production functions (Bach  
404 et al., 2006; Pacheco et al., 2009; Archetti and Scheuring, 2011; Peña et al., 2014) carry over to games in  
405 spatially structured populations.

406 Ackermann et al. (2008) considered a model of “self-destructive cooperation”, which can be reinter-  
407 preted as a charity goods game with no economies of scale in a particular version of the haystack model  
408 of population structure (Appendix A). In this model we have  $\kappa = (n - N)/(n(N - 1))$ , where  $N$  is the  
409 number of founders and  $n \geq N$  is the number of offspring among which the game is played. Identifying  
410 our  $\gamma$  and  $\beta$  with (respectively) their  $\beta$  and  $b$ , the main result of Ackermann et al. (2008), given by Eq. 7  
411 in their supplementary material, is recovered as a particular case of our result (13). The fact that in this  
412 example  $\kappa$  is a probability of coalescence within groups shows that social interactions effectively occur  
413 between family members, and hence that kin selection is crucial to the understanding of self-destructive  
414 cooperation (Gardner and Kümmerli 2008; see also Rodrigues and Gardner, 2013).

415 Eshel and Motro (1988) consider a model in which one individual in the group needs help, which can  
416 be provided (action  $A$ ) or denied (action  $B$ ) by its  $n - 1$  neighbors: a situation Eshel and Motro call  
417 the “three brothers’ problem” when  $n = 3$ . Suppose that the cost for each helper is a constant  $\varepsilon > 0$   
418 independent on the number of volunteers (the “risk for each volunteer”, denoted by  $c$  in Eshel and Motro  
419 1988) and that the benefit for the individual in need when  $k$  co-players offer help is given by  $v_k$  (the  
420 “gain function”, denoted by  $b_k$  in Eshel and Motro 1988). Then, if individuals need help at random,  
421 the payoffs for helping ( $A$ ) and not helping ( $B$ ) are given by  $a_k = -\varepsilon(n - 1)/n + v_k/n$  and  $b_k = v_k/n$ .  
422 Defining  $\gamma = \varepsilon(n - 1)/n$  and  $\beta_k = v_k/(n - 1)$ , we have  $a_k = -\gamma + \beta_k$  and  $b_k = \beta_k$ . Comparing these with  
423 the payoffs for public goods games in Table 1, it is apparent that the key difference between the case  
424 considered by Eshel and Motro (1988) and the public goods games considered here is that a provider  
425 cannot benefit from its own helping behavior. As we show in Appendix F, our results for public goods  
426 games carry over to such “other-only” goods games (Pepper, 2000). In particular, our results for public



427 goods games with geometric benefits can be used to recover Results 1, 2, and 3 of Eshel and Motro (1988).  
428 Finally, Van Cleve and Lehmann (2013) discuss an  $n$ -player coordination game. They assume payoffs  
429 given by  $a_k = 1 + S(R/S)^{k/(n-1)}$  and  $b_k = 1 + P(T/P)^{k/(n-1)}$ , for positive  $R, S, T$ , and  $P$ , satisfying  
430  $R > T$ ,  $P > S$  and  $P > T$ . It is easy to check that both the direct effect  $-\mathcal{C}(z)$  and the indirect effect  
431  $\mathcal{B}(z)$  are strictly increasing functions of  $z$  having exactly one sign change. This implies that, for  $\kappa \geq 0$ ,  
432 the evolutionary dynamics are characterized by bistability. Importantly, and in contrast to the kinds  
433 of collective action analyzed in this article, expressing the payoff dominant action  $A$  does not always  
434 qualify as either payoff altruistic or payoff cooperative, as  $\mathcal{B}(z)$  is negative for some interval  $z \in [0, \hat{z})$ .  
435 As a result, increasing relatedness  $\kappa$  can have mixed effects on the location of the interior convergence  
436 unstable equilibrium  $z^*$ . Both of these predictions are well supported by the numerical results reported  
437 by Van Cleve and Lehmann (2013), where increasing  $\kappa$  leads to a steady increase in  $z^*$  for  $R = 2$ ,  $S = 0.5$ ,  
438  $P = 1.5$ ,  $T = 0.25$ , and a steady decrease in  $z^*$  for  $R = 2$ ,  $S = 0.5$ ,  $P = 1.5$ ,  $T = 1.25$  (see their Fig. 5).  
439 This illustrates the fact that scaled relatedness (and hence spatial structure) plays an important role not  
440 only in the specific context of collective action problems but also in the more general context of nonlinear  
441  $n$ -player games.

## 442 5 Discussion

443 Many discrete-action, nonlinear  $n$ -player games have been proposed to study the evolutionary dynamics of  
444 collective action in well-mixed populations (Boyd and Richerson, 1988; Dugatkin, 1990; Motro, 1991; Bach  
445 et al., 2006; Hauert et al., 2006; Pacheco et al., 2009; Archetti and Scheuring, 2011; Peña et al., 2014).  
446 We extended these models to the more general case of spatially structured populations by integrating  
447 them into the direct fitness approach of kin selection theory (Taylor and Frank, 1996; Rousset, 2004;  
448 Lehmann and Rousset, 2010; Van Cleve, 2015). We showed that convergence stable strategies for games  
449 between relatives are equivalent to those of transformed games between unrelated individuals, where the  
450 payoffs of the transformed game can be interpreted as “inclusive payoffs” given by the original payoffs to  
451 self plus scaled relatedness times the sum of original payoffs to others. The evolutionary attractors of  
452 games in spatially and family structured populations can then be obtained from existing results on games  
453 in well-mixed populations (Peña et al., 2014).

454 We applied these general results to the evolution of collective action under different assumptions on  
455 the kind of collective good and its economies of scale, thereby unifying and extending previous analyses.  
456 We considered three kinds of collective goods, illustrative of different kinds of helping traits in nature.  
457 Firstly, public goods (both providers and shirkers have access to the good) for which the collective action  
458 problem is the well known free-rider problem (i.e., shirkers are cheaters who benefit from the good without  
459 helping to create it). Secondly, club goods (only providers have access to the good) for which there is no

460 longer a free-rider but a coordination problem (i.e., individuals might prefer to stay alone rather than join  
461 a risky collective activity). Thirdly, charity goods (only shirkers use the good) for which the collective  
462 action problem takes the form of an altruism problem (i.e., individuals would prefer to enjoy the collective  
463 good rather than provide it for others).

464 We showed that relatedness can help solving each of these collective action problems, but that such  
465 effect takes different forms, depending on the kind of good and on its economies of scale. Simply put:  
466 relatedness transforms different collective action problems into different games. For public goods this  
467 transformation does not qualitatively affect the evolutionary dynamics, as it only reduces the cost  
468 of providing but otherwise leaves economies of scale (and hence patterns of frequency dependence)  
469 unaffected. Contrastingly, for club goods with diminishing returns and charity goods with increasing  
470 returns, relatedness can change patterns of frequency dependence in a nontrivial way. In particular,  
471 increasing relatedness can induce a saddle-node bifurcation resulting in the creation of an attracting  
472 equilibrium with positive helping and a repelling helping threshold.

473 This type of evolutionary dynamics, that we call bistable coexistence, is different from usual scenarios  
474 of frequency dependence in that selection favors mutants at some intermediate frequencies, but neither  
475 when rare nor common. Bistable coexistence had been previously predicted in models of public goods  
476 provision with sigmoidal production functions both in unstructured (Bach et al., 2006; Archetti and  
477 Scheuring, 2011) and structured (Cornforth et al., 2012) populations. Our results show that bistable  
478 coexistence can also arise in models of club goods with diminishing returns and of charity goods with  
479 increasing returns when interactants are related. Participation in cooperative hunting illustrates the first  
480 of these situations: cooperative hunting is a club good (as hunted prey is available to hunters but not to  
481 solitary individuals) and is likely to exhibit diminishing returns because hunting success is subadditive  
482 in the number of hunters (Packer and Ruttan, 1988, Figs. 4-9). Eusociality in insects illustrates the  
483 second of these situations: eusociality is a charity good (as the benefits of the good created by workers  
484 are enjoyed only by reproducing queens) and is likely to exhibit increasing returns because of division of  
485 labor and other factors (Pamilo, 1991; Fromhage and Kokko, 2011). Our results suggest that bistable  
486 coexistence might be more common than previously considered, thus expanding the repertoire of types of  
487 frequency-dependence selection beyond classic paradigms of either stabilizing (negative) or disruptive  
488 (positive) frequency-dependent selection (Levin et al., 1988).

489 Our results have implications for theoretical and empirical work on microbial cooperation. Although  
490 most research in this area has focused on public goods dilemmas (Griffin et al., 2004; Gore et al., 2009;  
491 Cordero et al., 2012), club and charity goods can also be present in microbial interactions. First, cases  
492 of “altruistic sacrifice” (West et al., 2006), “self-destructive cooperation” (Ackermann et al., 2008), and  
493 “bacterial charity work” (Lee et al., 2010), by which providers release chemical substances that benefit  
494 shirkers, are clear examples of charity goods. Second, “greenbeards” (Gardner and West, 2010; Queller,

2011), where providers produce an excludable good such as adherence or food sources (Smukalla et al., 2008; White and Winans, 2007), can be taken as examples of club goods. In all these examples, economies of scale are likely to be present, and hence also the scope for the complex interaction between relatedness and the shape of the production function predicted by our model. In particular, the possibility of bistable coexistence has to be acknowledged and taken into account both in models and experiments. Under bistable coexistence, even if providers are less fit than shirkers both when rare and when common, they are fitter than shirkers for some intermediate frequencies. Consequently, competition experiments should test for different starting frequencies before ruling out the possibility of polymorphic equilibria where providers and shirkers coexist. More generally, we encourage empirical work explicitly aimed at identifying club and charity goods and at measuring occurrences of economies of scale (i.e., nonlinear payoffs) in microbial systems.

We assumed that the actions implemented by players are discrete. This is in contrast to standard models of games between relatives, which assume a continuum of pure actions in the form of continuous amounts of effort devoted to some social activity. Such continuous-action models have the advantage that fitness or payoff functions (the counterparts to (3)) can be assumed to take simple forms that facilitate mathematical analysis. On the other hand, there are situations where individuals can express only few morphs (e.g., worker and queen in the eusocial Hymenoptera; Wheeler 1986), behavioral tactics (e.g., “producers” and “scroungers” in *Passer domesticus*; Barnard and Sibly 1981) or phenotypic states (e.g., capsulated and non-capsulated cells in *Pseudomonas fluorescens*; Beaumont et al. 2009). These situations are more conveniently handled by means of a discrete-action model like the one presented here. This being said, we expect our qualitative results about the interaction between kind of good, economies of scale, and relatedness to carry over to continuous-action models.

We assumed that the number of interacting individuals  $n$  is constant. However, changes in density will inevitably lead to fluctuating group sizes, with low densities resulting in small group sizes and high densities resulting in large group sizes. It is clear from the dependence of the critical cost-to-benefit ratios and the critical returns-to-scale parameters on group size (Table 2) that the effects of varying group sizes on the evolutionary dynamics of collective action will critically depend on the the kind of good and its economies of scale. It would be interesting to integrate this phenomenon into our model, thus extending previous work on the effects of group size in the evolution of helping (Motro, 1991; Brännström et al., 2011; Peña, 2012; Shen et al., 2014).

We assumed that players play mixed strategies and that the phenotypic deviation  $\delta$  is small (i.e., “ $\delta$ -weak” selection; Wild and Traulsen 2007), which is sufficient to characterize convergence stability but insufficient to characterize the fixation probability of a mutant when mutations have strong effects on phenotypes. This last scenario may occur when individuals can only express either full provision or null provision so that, say, mutants always play  $A$  and residents always play  $B$ . In these cases, a different

530 limit of weak selection (i.e., “*w*-weak” selection; Wild and Traulsen 2007) might be more appropriate  
531 to model the evolutionary dynamics. For general nonlinear *n*-player games in structured populations  
532 the evolutionary dynamics will then depend not only on relatedness but also on higher-order genetic  
533 interactions (Ohtsuki, 2014). The analysis of such evolutionary games under strong mutation effects and  
534 possibly strong selection remains to be done. This could be partly carried out by using invasion fitness  
535 proxies such as the basic reproductive number for subdivided populations (Metz and Gyllenberg, 2001;  
536 Ajar, 2003).

537 Collective action problems in nature are likely to be more diverse than the usually assumed model of  
538 public goods provision with constant returns to scale. Given the local demographic structure of biological  
539 populations, interactions between relatives are also likely to be the rule rather than the exception.  
540 Empirical work on the evolution of altruism and cooperation should thus aim at measuring the relatedness  
541 of interactants, the kind of good, and the associated economies of scale, as it is the interaction between  
542 these three factors which will determine the evolutionary dynamics of collective action in real biological  
543 systems.

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## A The haystack model

546

547 Many models of social evolution (Matessi and Jayakar, 1976; Wilson, 1987; Taylor and Wilson, 1988;  
548 Fletcher and Zwick, 2004; Ackermann et al., 2008; Powers et al., 2011; Cremer et al., 2012) have assumed  
549 variants of the haystack model (Maynard Smith, 1964), where several rounds of unregulated reproduction  
550 occur within groups before a round of complete dispersal. In these cases, as we will see below, the scaled  
551 relatedness coefficient  $\kappa$  takes the simpler interpretation of the coalescence probability of the gene lineage  
552 of two interacting individuals in their group. Here we calculate  $\kappa$  for different variants of the haystack  
553 model.

554 The haystack model can be seen as a special case of the island model where dispersal is complete and  
555 where dispersing progeny compete globally. In this context, the fecundity of an adult individual is the  
556 number of its offspring reaching the stage of global density-dependent competition. The conception of  
557 offspring may occur in a single or over multiple rounds of reproduction, so that a growth phase within  
558 patches is possible. We let  $N$  denote the number of founders (or lineages, or seeds) on a patch.

559 Two cases need to be distinguished when it comes to social interactions. First, the game can be played  
560 between the founders. In this case

$$561 \quad \kappa = 0, \tag{A.1}$$

562 since relatedness is zero among founders on a patch and there is no local competition. Second, the game  
563 can be played between offspring after reproduction and right before their dispersal. In this case two  
564 individuals are related if they descend from the same founder. Since there is no local competition,  $\kappa$  is  
565 directly the relatedness between two interacting offspring and is obtained as the probability that the  
566 two ancestral lineages of two randomly sampled offspring coalesce in the same founder. (Relatedness in  
567 the island model is defined as the cumulative coalescence probability over several generations, see e.g.,  
568 Rousset 2004, but owing to complete dispersal gene lineages can only coalesce in founders.)

569 In order to evaluate  $\kappa$  for the second case, we assume that, after growth, exactly  $N_o$  offspring are  
570 produced and that the game is played between them ( $n = N_o$ ). Founders, however, may contribute a  
571 variable number of offspring. Let us denote by  $O_i$  the random number of offspring descending from the  
572 founder  $i = 1, 2, \dots, N$  on a representative patch after reproduction, i.e.,  $O_i$  is the size of lineage  $i$ . Owing  
573 to our assumption that the total number of offspring is fixed, we have  $N_o = O_1 + O_2 + \dots + O_N$ , where  
574 the  $O_i$ 's are exchangeable random variables. The coalescence probability  $\kappa$  can then be computed as the  
575 expectation of the ratio of the total number of ways of sampling two offspring from the same founding  
576 parent to the total number of ways of sampling two offspring:

$$577 \quad \kappa = \mathbb{E} \left[ \sum_{i=1}^N \frac{O_i(O_i - 1)}{N_o(N_o - 1)} \right] = N \left( \frac{\sigma^2 + \mu^2 - \mu}{N_o(N_o - 1)} \right), \tag{A.2}$$

578 where the second equality follows from exchangeability,  $\mu = E[O_i]$  is the expected number of offspring  
579 descending from any founder  $i$ , and  $\sigma^2 = E[(O_i - \mu)^2]$  is the corresponding variance. Due to the fact  
580 that the total number of offspring is fixed, we also necessarily have  $\mu = N_o/N$  (i.e.,  $N_o = E[N_o] =$   
581  $E[O_1 + O_2 + \dots + O_N] = N\mu$ ), whereby

$$582 \quad \kappa = \frac{N_o - N}{N(N_o - 1)} + \frac{\sigma^2 N}{N_o(N_o - 1)}, \quad (\text{A.3})$$

583 which holds for any neutral growth process.

584 We now consider three different cases:

585 1. Suppose that there is no variation in offspring production between founders, as in the life cycle  
586 described by Ackermann et al. (2008). Then  $\sigma^2 = 0$ , and (A.3) simplifies to

$$587 \quad \kappa = \frac{N_o - N}{N(N_o - 1)}. \quad (\text{A.4})$$

588 2. Suppose that each of the  $N_o$  offspring has an equal chance of descending from any founder, so  
589 that each offspring is the result of a sampling event (with replacement) from a parent among the  
590  $N$  founders. Then, the offspring number distribution is binomial with parameters  $N_o$  and  $1/N$ ,  
591 whereby  $\sigma^2 = (1 - 1/N)N_o/N$ . Substituting into (A.3) we get

$$592 \quad \kappa = \frac{1}{N}. \quad (\text{A.5})$$

593 In more biological terms, this corresponds to a situation where individuals produce offspring  
594 according to a Poisson process and where exactly  $N_o$  individuals are kept for social interactions  
595 (i.e., the conditional branching process of population genetics; Ewens 2004).

596 3. Suppose that the offspring distribution follows a beta-binomial distribution, with number of trials  
597  $N_o$  and shape parameters  $\alpha > 0$  and  $\beta = \alpha(N - 1)$ . Then,  $\mu = N_o/N$  and

$$598 \quad \sigma^2 = \frac{N_o(N - 1)(\alpha N + N_o)}{N^2(1 + \alpha N)},$$

599 which yields

$$600 \quad \kappa = \frac{1 + \alpha}{1 + \alpha N}. \quad (\text{A.6})$$

601 In more biological terms, this reproductive scheme results from a situation where individuals produce  
602 offspring according to a negative binomial distribution (larger variance than Poisson, which is  
603 recovered when  $\alpha \rightarrow \infty$ ), and where exactly  $N_o$  individuals are kept for social interactions.

## B Gains from switching and the gain function

In the following we establish the expressions for  $-\mathcal{C}(z)$  and  $\mathcal{B}(z)$  given in (9); the expression for  $\mathcal{G}(z)$  (10) is then immediate from the definition of  $f_k$  (8) and the identity  $\mathcal{G}(z) = -\mathcal{C}(z) + \kappa\mathcal{B}(z)$ .

Recalling the definitions of  $\mathcal{C}(z)$  and  $\mathcal{B}(z)$  from (4) as well as the definitions of  $d_k$  and  $e_k$  from (6)–(7) we need to show

$$\left. \frac{\partial \pi(z_\bullet, z_o)}{\partial z_\bullet} \right|_{z_\bullet = z_o = z} = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} [a_k - b_k], \quad (\text{B.1})$$

$$\left. \frac{\partial \pi(z_\bullet, z_o)}{\partial z_o} \right|_{z_\bullet = z_o = z} = \sum_{k=0}^{n-1} \binom{n-1}{k} z^k (1-z)^{n-1-k} [k\Delta a_{k-1} + (n-1-k)\Delta b_k], \quad (\text{B.2})$$

where the function  $\pi$  has been defined in (3). (B.1) follows directly by taking the partial derivative of  $\pi$  with respect to  $z_\bullet$  and evaluating at  $z_\bullet = z_o = z$ , so it remains to establish (B.2).

Our derivation of (B.2) uses properties of polynomials in Bernstein form. Such polynomials, which in general can be written as  $\sum_{k=0}^m \binom{m}{k} x^k (1-x)^{m-k} c_k$  for  $x \in [0, 1]$ , satisfy (Farouki, 2012, p. 391)

$$\frac{d}{dx} \sum_{k=0}^m \binom{m}{k} x^k (1-x)^{m-k} c_k = m \sum_{k=0}^{m-1} \binom{m-1}{k} x^k (1-x)^{m-1-k} \Delta c_k.$$

Applying this property to (3) and evaluating the resulting partial derivative at  $z_\bullet = z_o = z$ , yields

$$\begin{aligned} \left. \frac{\partial \pi(z_\bullet, z_o)}{\partial z_o} \right|_{z_\bullet = z_o = z} &= (n-1)z \sum_{k=0}^{n-2} \binom{n-2}{k} z^k (1-z)^{n-2-k} \Delta a_k \\ &+ (n-1)(1-z) \sum_{k=0}^{n-2} \binom{n-2}{k} z^k (1-z)^{n-2-k} \Delta b_k. \end{aligned} \quad (\text{B.3})$$

In order to obtain (B.2) from (B.3) it then suffices to establish

$$x \sum_{k=0}^{m-1} \binom{m-1}{k} x^k (1-x)^{m-1-k} c_k = \sum_{k=0}^m \binom{m}{k} x^k (1-x)^{m-k} \frac{k c_{k-1}}{m} \quad (\text{B.4})$$

and

$$(1-x) \sum_{k=0}^{m-1} \binom{m-1}{k} x^k (1-x)^{m-1-k} c_k = \sum_{k=0}^m \binom{m}{k} x^k (1-x)^{m-k} \frac{(m-k)c_k}{m}, \quad (\text{B.5})$$

as applying these identities to the terms on the right side of (B.3) yields the right side of (B.2).

Let us prove (B.4) ((B.5) is proven in a similar way). Starting from the left side of (B.4), we multiply and divide by  $m/(k+1)$  and distribute  $x$  to obtain

$$x \sum_{k=0}^{m-1} \binom{m-1}{k} x^k (1-x)^{m-1-k} c_k = \sum_{k=0}^{m-1} \frac{m}{k+1} \binom{m-1}{k} x^{k+1} (1-x)^{m-(k+1)} c_k \frac{k+1}{m}.$$

629 Applying the identity  $\binom{r}{k} = \frac{r}{k} \binom{r-1}{k-1}$  and changing the index of summation to  $k = k + 1$ , we get

$$630 \quad x \sum_{k=0}^{m-1} \binom{m-1}{k} x^k (1-x)^{m-1-k} c_k = \sum_{k=1}^m \binom{m}{k} x^k (1-x)^{m-k} \frac{k c_{k-1}}{m}.$$

631 Finally, changing the lower index of the sum by noting that the summand is zero when  $k = 0$  gives (B.4).

## 632 C Public goods games with geometric production function

633 For a geometric production function, we have  $\Delta\beta_k = \beta\lambda^k$ , so that the inclusive gains from switching for  
 634 public goods games are given by  $f_k = -\gamma + [1 + \kappa(n-1)]\beta\lambda^k$ . Substituting this expression into (10) and  
 635 using the formula for the probability generating function of a binomial random variable, we obtain

$$636 \quad \mathcal{G}(z) = -\gamma + [1 + \kappa(n-1)]\beta(1-z+\lambda z)^{n-1}. \quad (\text{C.1})$$

637 As  $\mathcal{G}(z)$  is either decreasing ( $\lambda < 1$ ) or increasing ( $\lambda > 1$ ) in  $z$ ,  $A$  (resp.  $B$ ) is a dominant strategy if  
 638 and only if  $\min[\mathcal{G}(0), \mathcal{G}(1)] \geq 0$  (resp. if and only if  $\max[\mathcal{G}(0), \mathcal{G}(1)] \leq 0$ ). Using (C.1) to calculate  $\mathcal{G}(0)$   
 639 and  $\mathcal{G}(1)$  then yields the critical cost-to-benefit ratios  $\varepsilon = \min[\mathcal{G}(0), \mathcal{G}(1)]$  and  $\vartheta = \max[\mathcal{G}(0), \mathcal{G}(1)]$  given  
 640 in (16). The value of  $z^*$  given in (17) is obtained by solving  $\mathcal{G}(z^*) = 0$ .

## 641 D Club goods games

642 For club goods games, the inclusive gains from switching are given by

$$643 \quad f_k = -\gamma + \beta_{k+1} + \kappa k \Delta\beta_k. \quad (\text{D.1})$$

### 644 D.1 Accelerating production function

645 In the case where the production function is accelerating, we have the following general result.

646 **Result 1** (Club goods games with accelerating production function). *Let  $f_k$  be given by (D.1) with  $\beta_k$   
 647 and  $\Delta\beta_k$  increasing in  $k$ . Moreover, let  $\kappa \geq 0$ . Then*

- 648 1. *If  $\gamma \leq \beta_1$ ,  $z = 1$  is the only convergence stable strategy (full provision).*
- 649 2. *If  $\beta_1 < \gamma < \beta_n + \kappa(n-1)\Delta\beta_{n-1}$ , both  $z = 0$  and  $z = 1$  are convergence stable and there is a unique  
 650 convergence unstable strategy  $z^* \in (0, 1)$  (bistability).*
- 651 3. *If  $\gamma \geq \beta_n + \kappa(n-1)\Delta\beta_{n-1}$ ,  $z = 0$  is the only convergence stable strategy (null provision).*



652 The assumptions in the statement of the result imply that  $f_k$  is increasing in  $k$ . In particular, we have  
 653  $f_0 < f_{n-1}$ . The sign pattern of the inclusive gain sequence thus depends on the values of its endpoints in  
 654 the following way. If  $f_0 \geq 0$  (which holds if and only if  $\gamma \leq \beta_1$ ),  $f_k$  has no sign changes and a positive  
 655 initial sign. If  $f_{n-1} \leq 0$  (which holds if and only if  $\gamma \geq \beta_n + \kappa(n-1)\Delta\beta_{n-1}$ ),  $f_k$  has no sign changes and  
 656 a negative initial sign. If  $f_0 < 0 < f_{n-1}$  (which holds if and only if  $\beta_1 < \gamma < \beta_n + \kappa(n-1)\Delta\beta_{n-1}$ )  $f_k$  has  
 657 one sign change and a negative initial sign. Result 1 follows from these observations upon applying Peña  
 658 et al. 2014, Result 3.

## 659 D.2 Geometric production function

660 For a geometric production function, we obtain the following result.

661 **Result 2** (Club goods games with geometric production function). *Let  $f_k$  be given by (D.1) with  $\beta_k$*   
 662 *given by (12). Also, let  $\kappa \geq 0$  and  $n > 2$  (the cases  $\kappa < 0$  or  $n = 2$  are trivial). Moreover, let  $\xi$ ,  $\varsigma$  and  $\tau$*   
 663 *be defined by (18) and (19). Then*

664 1. *If  $\lambda \geq \xi$ ,  $\mathcal{G}(z)$  is nondecreasing in  $z$ . Furthermore*

665 (a) *If  $\gamma/\beta \leq 1$ ,  $z = 1$  is the only convergence stable strategy (full provision).*

666 (b) *If  $1 < \gamma/\beta < \varsigma$ , both  $z = 0$  and  $z = 1$  are convergence stable and there is a unique convergence*  
 667 *unstable strategy  $z^* \in (0, 1)$  (bistability).*

668 (c) *If  $\gamma/\beta \geq \varsigma$ ,  $z = 0$  is the only convergence stable strategy (null provision).*

669 2. *If  $\lambda < \xi$ ,  $\mathcal{G}(z)$  is unimodal in  $z$ , with mode given by  $\hat{z} = \frac{1+\kappa}{[1+\kappa(n-1)](1-\lambda)}$ . Furthermore*

670 (a) *If  $\gamma/\beta \leq 1$ ,  $z = 1$  is the only convergence stable strategy (full provision).*

671 (b) *If  $1 < \gamma/\beta \leq \varsigma$ , both  $z = 0$  and  $z = 1$  are convergence stable and there is a unique convergence*  
 672 *unstable strategy  $z^* \in (0, \hat{z})$  (bistability).*

673 (c) *If  $\varsigma < \gamma/\beta < \tau$ , there are two singular strategies  $z_L$  and  $z_R$  satisfying  $0 < z_L < \hat{z} < z_R < 1$ .*  
 674 *The strategies  $z = 0$  and  $z_R$  are convergence stable, whereas  $z_L$  and  $z = 1$  are convergence*  
 675 *unstable (bistable coexistence).*

676 (d) *If  $\gamma/\beta \geq \tau$ ,  $z = 0$  is the only convergence stable strategy (null provision).*

677 Observing that  $\xi < 1$  holds and ignoring the trivial case  $\lambda = 1$ , there are three cases to consider: (i)  
 678  $\lambda > 1$ , (ii)  $1 > \lambda \geq \xi$ , and (iii)  $\xi > \lambda$ .

679 For  $\lambda > 1$  the production function is accelerating and hence Result 1 applies with  $\beta_1 = \beta$  and  
 680  $\beta_n + \kappa(n-1)\Delta\beta_{n-1} = \beta\varsigma$ . This yields Result 2.1 for the case  $\lambda > 1$ .

681 To obtain the results for the remaining two cases, we calculate the first and second forward differences  
 682 of the production function (12) and substitute them into

$$683 \quad \Delta f_k = \Delta \beta_{k+1} + \kappa \{ (k+1) \Delta^2 \beta_k + \Delta \beta_k \}, \quad k = 0, 1, \dots, n-2,$$

684 to obtain

$$685 \quad \Delta f_k = \beta \lambda^k [\lambda(1 + \kappa) + \kappa(\lambda - 1)k], \quad k = 0, 1, \dots, n-2.$$

686 For  $\lambda < 1$ , the sequence  $\Delta f_k$  is decreasing in  $k$  and hence can have at most one sign change. Moreover,  
 687 as  $\Delta f_0 = \beta \lambda(1 + \kappa) > 0$  always holds true, the initial sign of  $\Delta f_k$  is positive and whether or not the  
 688 sequence  $\Delta f_k$  has a sign change depends solely on how  $\Delta f_{n-2}$  compares to zero. Observe, too, that for  
 689  $\lambda < 1$  we have  $\varsigma > 1$  as  $\lambda^n < \lambda$  holds.

690 Consider the case  $\xi \leq \lambda < 1$ . By the definition of  $\xi$  (18) this implies  $\Delta f_{n-2} \geq 0$ . In this case  $\Delta f_k$   
 691 has no sign changes and  $f_k$  is nondecreasing. The sign pattern of the inclusive gain sequence can then  
 692 be determined by looking at how the signs of its endpoints depend on the cost-to-benefit ratio  $\gamma/\beta$ . If  
 693  $\gamma/\beta \leq 1$ , then  $f_0 \geq 0$ , implying that  $f_k$  has no sign changes and its initial sign is positive. If  $\gamma/\beta \geq \varsigma$ ,  
 694 then  $f_{n-1} \leq 0$  and hence  $f_k$  has no sign changes and its initial sign is negative. If  $1 < \gamma/\beta < \varsigma$ , then  
 695  $f_0 < 0 < f_{n-1}$ , i.e.,  $f_k$  has one sign change and its initial sign is negative. Result 2.1 then follows from  
 696 an application of Peña et al. 2014, Result 3.

697 For  $\lambda < \xi$  we have  $\Delta f_{n-2} < 0$ , implying that  $\Delta f_k$  has one sign change from  $+$  to  $-$ , i.e.,  $f_k$  is  
 698 unimodal. Hence, the gain function  $\mathcal{G}(z)$  is also unimodal (Peña et al., 2014, Section 3.4.3) with mode  $\hat{z}$   
 699 determined by  $\mathcal{G}'(\hat{z}) = 0$ . Using the assumption of geometric benefits, we can express  $\mathcal{G}(z)$  in closed form  
 700 as

$$701 \quad \mathcal{G}(z) = -\gamma + \frac{\beta}{1-\lambda} + \beta \lambda \left\{ [1 + \kappa(n-1)]z - \frac{1}{1-\lambda} \right\} (1-z + \lambda z)^{n-2},$$

702 with corresponding derivative

$$703 \quad \mathcal{G}'(z) = (n-1)\beta \lambda \{ 1 + \kappa - (1-\lambda)[1 + \kappa(n-1)]z \} (1-z + \lambda z)^{n-3}.$$

704 Solving  $\mathcal{G}'(\hat{z}) = 0$  then yields  $\hat{z}$  as given in Result 2.2. The corresponding maximal value of the gain  
 705 function is

$$706 \quad \mathcal{G}(\hat{z}) = -\gamma + \frac{\beta}{1-\lambda} \left[ 1 + \lambda \kappa \left( \frac{(n-2)\kappa}{1 + \kappa(n-1)} \right)^{n-2} \right].$$

707 Result 2.2 then follows from applying Peña et al. 2014, Result 5. In particular, if  $\gamma/\beta \leq 1$ , we also have

708  $\gamma/\beta < \varsigma$ , ensuring that  $f_0 \geq 0$  and  $f_{n-1} > 0$  hold (with unimodality then implying that the gain function  
709 is positive throughout). If  $1 < \gamma/\beta \leq \varsigma$ , we have  $f_0 < 0$  and  $f_{n-1} \geq 0$  (with unimodality then implying  
710  $\mathcal{G}(\hat{z}) > 0$ ). If  $\varsigma < \gamma/\beta$ , we have  $f_0 < 0$  and  $f_{n-1} < 0$ . Upon noticing that  $\mathcal{G}(\hat{z}) \leq 0$  is satisfied if and only  
711 if  $\gamma/\beta \geq \tau$  holds, this yields the final two cases in Result 2.2.

## 712 E Charity goods games

713 For charity goods games, the inclusive gains from switching are given by

$$714 \quad f_k = -\gamma - \beta_k + \kappa(n-1-k)\Delta\beta_k. \quad (\text{E.1})$$

### 715 E.1 Decelerating production function

716 If the production function is decelerating, we have the following general result.

717 **Result 3** (Charity goods games with decelerating production function). *Let  $f_k$  be given by (E.1) with*  
718  *$\beta_0 = 0$ ,  $\beta_k$  increasing and  $\Delta\beta_k$  decreasing in  $k$ . Moreover, let  $\kappa \geq 0$  (the case  $\kappa < 0$  is trivial). Then*

- 719 1. *If  $\gamma \geq \kappa(n-1)\Delta\beta_0$ ,  $z = 0$  is the only convergence stable strategy (null provision).*
- 720 2. *If  $\gamma < \kappa(n-1)\Delta\beta_0$ , both  $z = 0$  and  $z = 1$  are convergence unstable and there is a unique convergence*  
721 *stable strategy  $z^* \in (0, 1)$  (coexistence).*

722 The arguments used for deriving this result are analogous to those used for deriving the results for  
723 the case of club goods with accelerating production function (Result 1 in Appendix D). The assumptions  
724 in the statement imply that  $f_k$  is decreasing in  $k$ . In particular, we have  $f_{n-1} < f_0$ . Consequently, if  
725  $f_0 \leq 0$  (which holds if and only if  $\gamma \geq \kappa(n-1)\Delta\beta_0$ ) the inclusive gain sequence has no sign changes and  
726 its initial sign is negative. Observing that  $f_{n-1} = -\gamma - \beta_{n-1} < 0$  always holds true, the inequality  $f_0 > 0$   
727 (which holds if and only if  $\gamma < \kappa(n-1)\Delta\beta_0$ ) implies that the decreasing sequence  $f_k$  has one sign change  
728 and that its initial sign is positive. Result 3 is then obtained by an application of Peña et al. 2014, Result  
729 3.

### 730 E.2 Geometric production function

731 For a geometric production function, we obtain the following result.

732 **Result 4** (Charity goods games with geometric production function). *Let  $f_k$  be given by (E.1) with  $\beta_k$*   
733 *given by (12) and let  $\kappa \geq 0$  and  $n > 2$  (the cases  $\kappa < 0$  or  $n = 2$  are trivial). Moreover, let  $\varrho$ ,  $\zeta$  and  $\eta$  be*  
734 *defined by (20) and (21). Then*

- 735 1. *If  $\lambda \leq \varrho$ ,  $\mathcal{G}(z)$  is nonincreasing in  $z$ . Furthermore:*

736 (a) If  $\gamma/\beta < \zeta$ , both  $z = 0$  and  $z = 1$  are convergence unstable and there is a unique convergence  
737 stable strategy  $z^* \in (0, 1)$  (coexistence).

738 (b) If  $\gamma/\beta \geq \zeta$ ,  $z = 0$  is the only convergence stable strategy (null provision).

739 2. If  $\lambda > \varrho$ ,  $\mathcal{G}(z)$  is unimodal in  $z$  with mode given by  $\hat{z} = \frac{\kappa[(n-2)\lambda - (n-1)] - 1}{[1 + \kappa(n-1)](\lambda-1)}$ . Furthermore:

740 (a) If  $\gamma/\beta \leq \zeta$ , both  $z = 0$  and  $z = 1$  are convergence unstable and there is a unique convergence  
741 stable strategy  $\hat{z} < z^* < 1$  (coexistence).

742 (b) If  $\zeta < \gamma/\beta < \eta$ , there are two singular strategies  $z_L$  and  $z_R$  satisfying  $0 < z_L < \hat{z} < z_R < 1$ .  
743 The strategies  $z = 0$  and  $z_R$  are convergence stable, whereas  $z_L$  and  $z = 1$  are convergence  
744 unstable (bistable coexistence).

745 (c) If  $\gamma/\beta \geq \eta$ , then  $z = 0$  is the only convergence stable strategy (null provision).

746 The arguments used for deriving this result are analogous to those used for deriving the results for  
747 club goods games with geometric production function (Result 2 in Appendix D). Observing that  $\varrho > 1$   
748 holds for  $\kappa \geq 0$  and that the case  $\lambda = 1$  (constant returns to scale) is trivial, we can prove this result by  
749 considering three cases: (i)  $\lambda < 1$ , (ii)  $1 < \lambda \leq \varrho$ , and (iii)  $\varrho < \lambda$ .

750 For  $\lambda < 1$ , the production function is decelerating and hence Result 3 applies with  $\Delta\beta_0 = \beta$ . Recalling  
751 the definition of  $\zeta = \kappa(n-1)$  from (21) and rearranging, this yields Result 4.1 for the case  $\lambda \leq 1 < \varrho$ .

752 To obtain the result for the remaining two cases, we calculate the first and second forward differences  
753 of the benefit sequence (12) and substitute them into

$$754 \quad \Delta f_k = -(1 + \kappa)\Delta\beta_k + \kappa(n-2-k)\Delta^2\beta_k, \quad k = 0, 1, \dots, n-2.$$

755 to obtain

$$756 \quad \Delta f_k = \beta\lambda^k \{ \kappa [(n-2)\lambda - (n-1)] - 1 + \kappa(1-\lambda)k \}, \quad k = 0, 1, \dots, n-2.$$

757 For  $\lambda > 1$ , the sequence  $\Delta f_k$  is decreasing in  $k$  and hence can have at most one sign change. Moreover,  
758 since  $\Delta f_{n-2} = -\beta\lambda^{n-2}(1 + \kappa) < 0$  always holds true, the sign pattern of  $\Delta f_k$  depends exclusively on  
759 how  $\Delta f_0 = \beta \{ \kappa [(n-2)\lambda - (n-1)] - 1 \}$  compares to zero. Observe, too, that  $f_{n-1} < 0$  always holds  
760 true and that the sign of  $f_0$  is identical to the sign of  $\zeta - \gamma/\beta$ .

761 Consider the case  $1 < \lambda \leq \varrho$ . Recalling the definition of  $\varrho$  (20) we then have  $\Delta f_0 \leq 0$ , implying that  
762  $\Delta f_k$  has no sign changes and that its initial sign is negative, i.e.,  $f_k$  is nonincreasing. Hence, if  $f_0 \leq 0$   
763 (which holds if and only if  $\gamma/\beta \geq \zeta$ ), the inclusive gain sequence has no sign changes and its initial sign is  
764 negative. Otherwise, that is, if  $\gamma/\beta < \zeta$  holds, we have  $f_0 > 0 > f_{n-1}$  so that the inclusive gain sequence  
765 has one sign change and its initial sign is positive. Result 4.1 then follows from Peña et al. 2014, Result 3.

766 For  $\lambda > \varrho$  we have  $\Delta f_0 > 0$ , implying that  $\Delta f_k$  has one sign change from + to -, i.e.,  $f_k$  is unimodal.  
 767 This implies that the gain function  $\mathcal{G}(z)$  is also unimodal with its mode  $\hat{z}$  being determined by  $\mathcal{G}'(\hat{z}) = 0$   
 768 (Peña et al., 2014, Section 3.4.3). Using the assumption of geometric benefits, we can express  $\mathcal{G}(z)$  in  
 769 closed form as

$$770 \quad \mathcal{G}(z) = -\gamma + \frac{\beta}{\lambda - 1} + \beta \left\{ \kappa(n - 1) - \frac{1}{\lambda - 1} - [1 + \kappa(n - 1)]z \right\} (1 - z + \lambda z)^{n-2}$$

771 with corresponding derivative

$$772 \quad \mathcal{G}'(z) = (n - 1)\beta(\lambda - 1)(1 - z + \lambda z)^{n-3} \left\{ \kappa(n - 2) - \frac{1 + \kappa}{\lambda - 1} - [1 + \kappa(n - 1)]z \right\}.$$

773 Solving  $\mathcal{G}'(\hat{z}) = 0$  then yields  $\hat{z}$  as given in Result 4.2. The corresponding maximal value of the gain  
 774 function is

$$775 \quad \mathcal{G}(\hat{z}) = -\gamma + \frac{\beta}{\lambda - 1} \left[ 1 + \kappa \lambda \left( \frac{(n - 2)\kappa\lambda}{1 + \kappa(n - 1)} \right)^{n-2} \right].$$

776 Result 4.2 follows from an application of Peña et al. 2014, Result 5 upon noticing that  $f_0 \geq 0$  (precluding  
 777 the stability of  $z = 0$  and ensuring  $\mathcal{G}(\hat{z}) > 0$ ) holds if and only if  $\gamma/\beta \leq \zeta$  and that  $\mathcal{G}(\hat{z}) \leq 0$  (ensuring  
 778 that  $B$  dominates  $A$ ) is satisfied if and only if  $\gamma/\beta \geq \eta$ . (We note that the range of cost-to-benefit ratios  
 779  $\gamma/\beta$  for which bistable coexistence occurs is nonempty, that is  $\eta > \zeta$  holds. Otherwise there would exist  
 780 a ratio  $\gamma/\beta$  satisfying both  $\gamma/\beta \leq \zeta$  and  $\gamma/\beta \geq \eta$  which in light of Result 4.2.(a) and Result 4.2.(c) is  
 781 impossible.)

## 782 F Other-only goods games

783 In other-only goods games, providers are automatically excluded from the consumption of the good they  
 784 create, although they can still reap the benefits of goods created by other providers in their group. Payoffs  
 785 for such games are given by  $a_k = -\gamma + \beta_k$  and  $b_k = \beta_k$ , so that the inclusive gains from switching are  
 786 given by  $f_k = -\gamma + \kappa [k\Delta\beta_{k-1} + (n - 1 - k)\Delta\beta_k]$ .

787 For this payoff constellation, it is straightforward to obtain the indirect benefits  $\mathcal{B}(z)$  from (B.3) in  
 788 Appendix B. Indeed, observing that  $\Delta a_k = \Delta b_k = \Delta\beta_k$  holds for all  $k$ , we have

$$789 \quad \mathcal{B}(z) = \frac{\partial \pi(z_\bullet, z_o)}{\partial z_o} \Big|_{z_\bullet = z_o = z} = \sum_{k=0}^{n-2} \binom{n-2}{k} z^k (1 - z)^{n-2-k} (n - 1) \Delta\beta_k.$$

790 Using (9a) and the fact that  $a_k - b_k = -\gamma$ , we have that the direct benefit is given by  $-\mathcal{C}(z) = -\gamma$ .

791 Substituting these expressions for  $\mathcal{C}(z)$  and  $\mathcal{B}(z)$  into (4), we obtain

$$792 \quad \mathcal{G}(z) = \sum_{k=0}^{n-2} \binom{n-2}{k} z^k (1-z)^{n-2-k} [-\gamma + \kappa(n-1)\Delta\beta_k]. \quad (\text{F.1})$$

793 If  $\kappa \leq 0$ , our assumption that the production function  $\beta_k$  is increasing implies that  $\mathcal{G}(z)$  is always  
794 negative, so that  $z = 0$  is the only convergence stable strategy (null provision).

795 To analyze the case where  $\kappa \geq 0$ , it is convenient to observe that (F.1) is of a similar form as (14).  
796 The only differences are that the summation in (F.1) extends from 0 to  $n-2$  (rather than to  $n-1$ ) and  
797 that the term multiplying the incremental benefit  $\Delta\beta_k$  is given by  $\kappa(n-1)$  (rather than by  $1 + \kappa(n-1)$ ).  
798 All the results obtained for public goods games can thus be easily translated to the case of other-only  
799 goods games.

800 Specifically, we have the following characterization of the resulting evolutionary dynamics. With  
801 constant returns to scale, selection is frequency-independent with null provision if  $\kappa < \gamma/[(n-1)\beta]$  and  
802 full provision if  $\kappa > \gamma/[(n-1)\beta]$ . With diminishing returns to scale, the gain function is decreasing  
803 in  $z$  (negative frequency dependence). There is null provision if  $\gamma \geq \kappa(n-1)\Delta\beta_0$ , and full provision if  
804  $\gamma \leq \kappa(n-1)\Delta\beta_{n-2}$ . If  $\kappa(n-1)\Delta\beta_{n-2} < \gamma < \kappa(n-1)\Delta\beta_0$  holds, there is coexistence. With increasing  
805 returns to scale, the gain function is increasing in  $z$  (positive frequency dependence). There is null provision  
806 if  $\gamma \geq \kappa(n-1)\Delta\beta_{n-2}$ , and full provision if  $\gamma \leq \kappa(n-1)\Delta\beta_0$ . If  $\kappa(n-1)\Delta\beta_0 < \gamma < \kappa(n-1)\Delta\beta_{n-2}$ , there  
807 is bistability.

808 If the production function is geometric (12), the gain function is given by

$$809 \quad \mathcal{G}(z) = -\gamma + \kappa(n-1)\beta(1-z + \lambda z)^{n-2},$$

810 so that, for  $\lambda \neq 1$ , the evolutionary dynamics are similar to the case of public goods games after redefining  
811 the critical cost-to-benefit ratios as

$$812 \quad \varepsilon = \min(\kappa(n-1), \lambda^{n-2}\kappa(n-1)) \quad \text{and} \quad \vartheta = \max(\kappa(n-1), \lambda^{n-2}\kappa(n-1))$$

813 and letting

$$814 \quad z^* = \frac{1}{1-\lambda} \left[ 1 - \left( \frac{\gamma}{\beta\kappa(n-1)} \right)^{\frac{1}{n-2}} \right].$$

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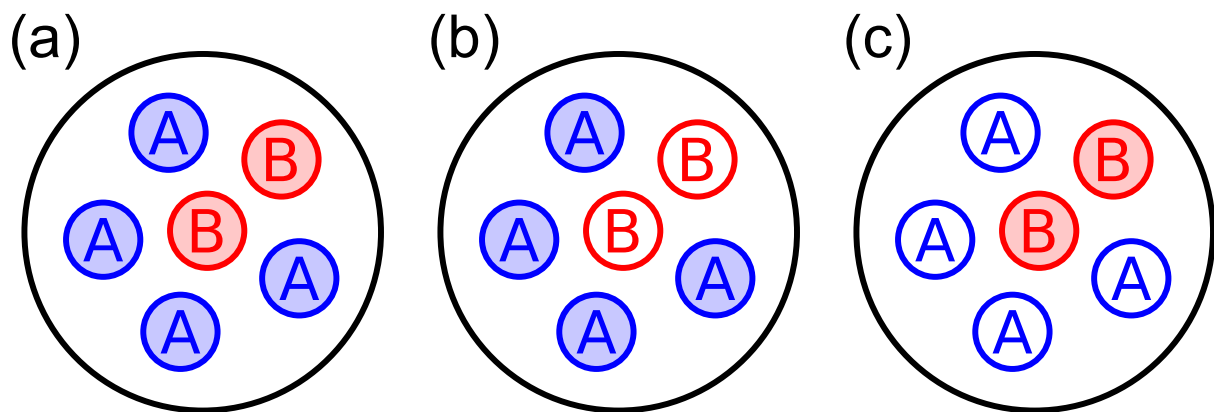


Figure 1: Three kinds of collective goods. Providers ( $A$ ) and shirkers ( $B$ ) interact socially. Providers (e.g., vigilants, cooperative hunters, or sterile workers) work together to create a collective good (e.g., alarm calls, increased hunting success, or nest defense), which can be used exclusively by a subset of individuals in the group (filled circles). Shirkers do not make any effort in collective action. *a*, Public goods (both providers and shirkers use the good). *b*, Club goods (only providers use the good). *c*, Charity goods (only shirkers use the good).

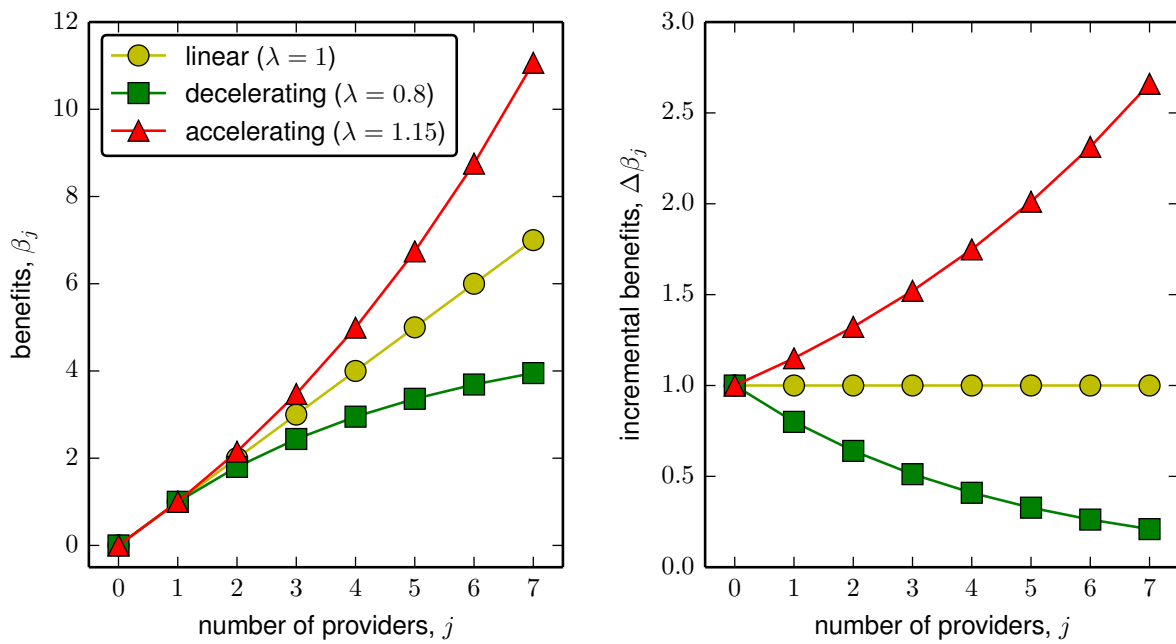


Figure 2: Linear, decelerating and accelerating production functions (here, geometric production functions as given by (12) with different values for the returns-to-scale parameter  $\lambda$ ). *Left panel*, benefits  $\beta_j$  from the collective good are additive for linear functions, subadditive for decelerating functions and superadditive for accelerating functions. *Right panel*, incremental benefits  $\Delta\beta_j$  from the collective good are constant for linear functions (constant returns to scale), decreasing for decelerating functions (diminishing returns to scale), and increasing for accelerating functions (increasing returns to scale).

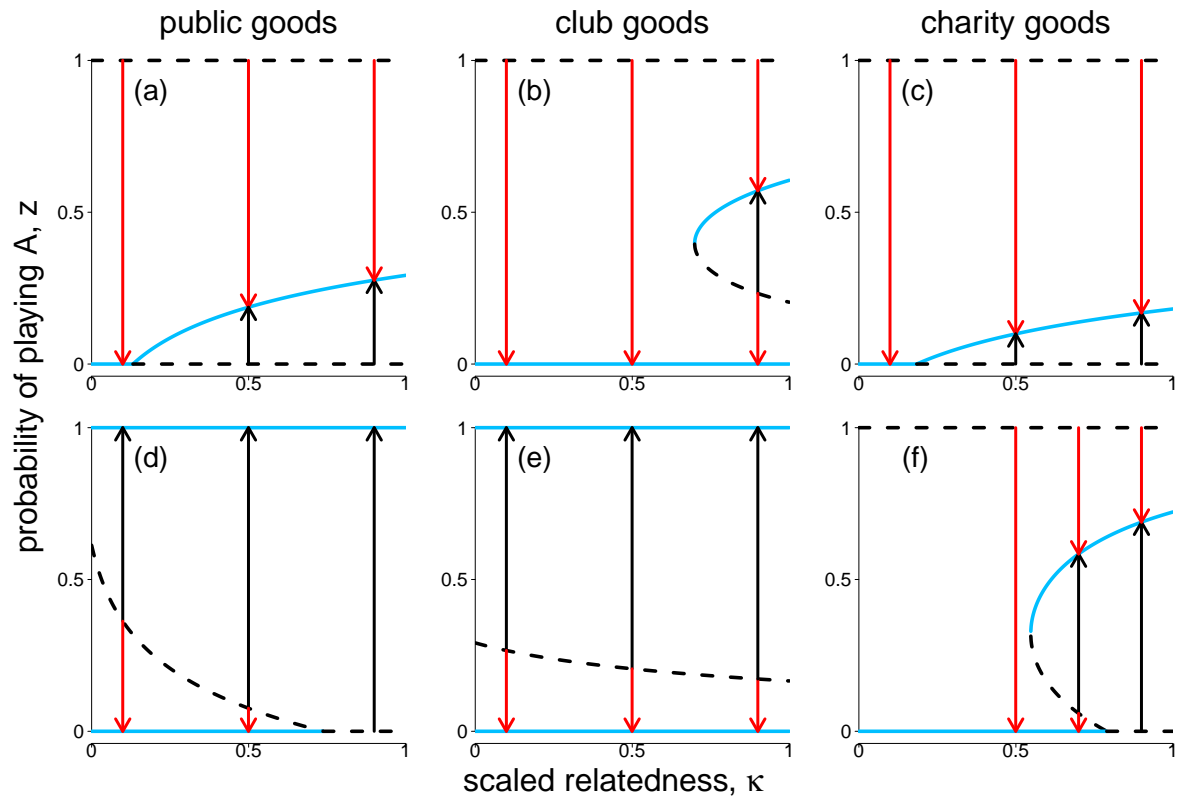


Figure 3: Bifurcation plots illustrating the evolutionary dynamics of collective action for public (*a, d*), club (*b, e*), and charity (*c, f*) goods with geometric production function. The scaled relatedness coefficient  $\kappa \geq 0$  serves as a control parameter. Arrows indicate the direction of evolution for the probability of providing. Solid lines stand for convergence stable equilibria; dashed lines for convergence unstable equilibria. *a, b, c*, Diminishing returns to scale ( $\lambda = 0.7$ ) and low cost-to-benefit ratio ( $\gamma/\beta = 3.5$ ). *d, e, f*, Increasing returns to scale ( $\lambda = 1.25$ ) and high cost-to-benefit ratio ( $\gamma/\beta = 15$ ). In all plots,  $n = 20$ . The central arrows, for which  $\kappa = 0.5$ , could correspond, for example, to a group splitting model with infinitely many groups ( $g \rightarrow \infty$ ) and splitting probability equal to the migration rate  $q = m$  (5), or to a particular case of the haystack model with two founders (A.5).

kind of good	payoffs to $A$ ( $a_k$ )	payoffs to $B$ ( $b_k$ )	direct gains ( $d_k$ )	indirect gains ( $e_k$ )	inclusive gains ( $f_k$ )
public	$-\gamma + \beta_{k+1}$	$\beta_k$	$-\gamma + \Delta\beta_k$	$(n-1)\Delta\beta_k$	$-\gamma + (1 + \kappa(n-1))\Delta\beta_k$
club	$-\gamma + \beta_{k+1}$	$0$	$-\gamma + \beta_{k+1}$	$k\Delta\beta_k$	$-\gamma + \beta_{k+1} + \kappa k\Delta\beta_k$
charity	$-\gamma$	$\beta_k$	$-\gamma - \beta_k$	$(n-1-k)\Delta\beta_k$	$-\gamma - \beta_k + \kappa(n-1-k)\Delta\beta_k$

Table 1: Payoff structures and gains from switching for the three classes of collective action problems. In each case providers incur a cost  $\gamma > 0$  to create a collective good of value  $\beta_j \geq 0$ , where  $j$  is the number of providers in the group. The number of providers experienced by a focal is  $j = k$  if the focal is a shirker (action  $B$ ), and  $j = k + 1$  if it is a provider (action  $A$ ). Direct gains ( $d_k$ ) and indirect gains ( $e_k$ ) are calculated by substituting the formulas for  $a_k$  and  $b_k$  into (6) and (7). Inclusive gains from switching ( $f_k$ ) are then obtained from (8).



public goods	$\lambda < 1$		$\lambda > 1$	
	$\gamma/\beta \leq \varepsilon$	full provision	$\gamma/\beta \leq \varepsilon$	full provision
	$\varepsilon < \gamma/\beta < \vartheta$	coexistence	$\varepsilon < \gamma/\beta < \vartheta$	bistability
	$\gamma/\beta \geq \vartheta$	null provision	$\gamma/\beta \geq \vartheta$	null provision
club goods	$\lambda < 1/\varrho$		$\lambda \geq 1/\varrho$	
	$\gamma/\beta \leq 1$	full provision	$\gamma/\beta \leq 1$	full provision
	$1 < \gamma/\beta < \varsigma$	bistability	$1 < \gamma/\beta < \varsigma$	bistability
	$\varsigma \leq \gamma/\beta < \tau$	bistable coexistence	$\gamma/\beta \geq \varsigma$	null provision
$\gamma/\beta \geq \tau$	null provision			
charity goods	$\lambda \leq \varrho$		$\lambda > \varrho$	
	$\gamma/\beta < \zeta$	coexistence	$\gamma/\beta < \zeta$	coexistence
	$\gamma/\beta \geq \zeta$	null provision	$\zeta \leq \gamma/\beta < \eta$	bistable coexistence
			$\gamma/\beta \geq \eta$	null provision

Table 2: Dynamical regimes of collective action for the case of geometric production functions. The dynamical outcome depends on the type of good, the magnitude of the returns-to-scale parameter  $\lambda$ , and the cost-to-benefit ratio  $\gamma/\beta$ . The results hold for  $\kappa \geq 0$  and  $n > 2$ . The critical cost-to-benefit ratios are given by  $\zeta = \kappa(n-1)$ ,  $\varepsilon = \min(1 + \zeta, \lambda^{n-1}(1 + \zeta))$ ,  $\vartheta = \max(1 + \zeta, \lambda^{n-1}(1 + \zeta))$ ,  $\eta = [1/(\lambda-1)] \left\{ 1 + \lambda\kappa [(n-2)\lambda\kappa/(1+\zeta)]^{n-2} \right\}$ ,  $\varsigma = (1 - \lambda^n)/(1 - \lambda) + \zeta\lambda^{n-1}$ ,  $\tau = [1/(1-\lambda)] \left\{ 1 + \lambda\kappa [(n-2)\kappa/(1+\zeta)]^{n-2} \right\}$ . The critical returns-to-scale parameters are  $\xi = \kappa(n-2)/[1 + \kappa(n-1)]$  and  $\varrho = 1/\xi$ .