

# Modes of migration and multilevel selection in evolutionary multiplayer games

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## Abstract

The evolution of cooperation in group-structured populations has received much attention, but little is known about the effects of different modes of migration of individuals between groups. Here, we have incorporated four different modes of migration that differ in the degree of coordination among the individuals. For each mode of migration, we identify the set of multiplayer games in which the cooperative strategy has higher fixation probability than defection. The comparison shows that the set of games under which cooperation may evolve generally expands depending upon the degree of coordination among the migrating individuals. Weak altruism can evolve under all modes of individual migration, provided that the benefit to cost ratio is high enough. Strong altruism, however, evolves only if the mode of migration involves coordination of individual actions. Depending upon the migration frequency and degree of coordination among individuals, conditions that allow selection to work at the level of groups can be established.

*Keywords:* altruism, cooperation, migration, multilevel selection

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# 1. Introduction

Cooperation can be defined as “a joint action for mutual benefit” (16; 43; 10; 62). Participation in a cooperative act is generally costly to cooperators (27; 6; 10). Therefore, cooperators have lower fitness than non-cooperators (defectors) and, thus, should be eliminated by natural selection. Nevertheless, cooperation is widespread in nature (11; 53; 74). How cooperation evolves and is maintained in the face of selfishness has been the subject of intensive investigation (27; 71; 6; 47; 67).

In a group-structured population, members of cooperative groups have a selective advantage over the members of non-cooperative groups. This advantage can make the evolution of cooperation possible (28; 71; 65; 47). The essential idea is that population structure channels cooperation preferentially to other cooperators (20; 19). Wilson and Wilson (73) formulated this as: “Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary.” However, the interplay between these effects is important because it determines whether cooperation will evolve.

Group structure by itself does not provide an advantage to cooperation (23) - indeed within groups, selfish types have an advantage over cooperating types (71). For cooperating types to be maintained, groups must participate in some kind of birth and death process. Individuals arising within one group must have an opportunity to become a member of another group. There are many ways by which this may occur. For instance, in standard trait group models (71; 5; 22), individuals within groups are released into a global pool and then randomly form new groups. Alternatively groups may fragment (65). A further possibility is that individuals from one group may migrate to another (9; 37; 31; 32). Via the process of migration, groups themselves do not reproduce in a conventional sense, but the effects are parallel.

In this study we consider models where an individual may become a member of another group by migration between groups. Individuals migrating from one group to another may fixate in the new group, or be eradicated as a consequence of individual-level selection. A defecting individual has a higher probability of fixation in a group of cooperators than does a cooperating individual in a group of defectors, thus individual-level selection favours defectors. However, individuals in groups of cooperators are more productive than in groups of defectors, and therefore groups of cooperators release more migrants than do groups of defectors. Thus, while previous studies

have shown that migration makes cooperation more difficult to evolve (because it brings about the mixing of groups (65)), recent work shows that rare migration can favor cooperation (32). Here, we consider a range of modes by which migration might occur and describe ensuing effects on the evolution of cooperation.

Migration can be implemented in multiple ways: individuals may migrate individually, or in clumps; subsequent migrations may or may not be influenced by previous ones; migration may be triggered by signals perceived by individuals, or may be influenced by the group. In this study we compare different modes of migration. For each mode, we identify the games in which cooperation is evolutionarily successful, i.e., where selection at the group level is strong enough to overcome selection at the individual level. The comparison between modes of migration shows that the set of games in which cooperation evolves generally expands with increasing degrees of coordination surrounding the migration process.

## 2. Evolutionary dynamics within a single group

We make the assumption that individuals live in a population with a fixed number of groups. The interactions between all individuals within a group are determined by a multiplayer game. The payoff of each individual depends on its strategy and the composition of the group. Each individual can be either a cooperator ( $C$ ) or a defector ( $D$ ). The size of the game is equal to group size. Thus, all players sharing the same strategy within a group have the same payoff. More specifically, the payoff of a cooperator in a group with  $i$  cooperators and  $n - i$  defectors is  $a_i$ , and the payoff of a defector in a group with  $i$  cooperators and  $n - i$  defectors is  $b_i$ . Thus, a game is completely determined by two sequences,  $a_1, \dots, a_n$ , and  $b_0, \dots, b_{n-1}$  (38; 25).

We use an exponential function to map payoff to fitness. The fitnesses of cooperators and defectors in a group with  $i$  cooperators are therefore  $e^{wa_i}$  and  $e^{wb_i}$ , respectively (66). Here,  $w$  measures the intensity of selection. For  $w = 0$ , selection is neutral. For  $w \ll 1$ , the fitness is approximately linear in payoffs. For large  $w$ , small differences in payoffs lead to large fitness differences.

The evolutionary dynamics are governed by a Moran process. At each time step a single individual in the population is chosen for reproduction with probability proportional to fitness (45; 48). This chosen individual produces identical offspring, replacing a randomly chosen individual. Thus,

74 population size is kept constant. For such a process, the probability for a  
75 single cooperator to take over the whole population,  $\phi_C$ , can be calculated  
76 exactly, as well as the probability of a single defector taking over the whole  
77 population,  $\phi_D$  (24; 64). These fixation probabilities form the basis of our  
78 measure of success for each strategy.

79 In order to compare the evolutionary success of the two strategies  $C$  and  
80  $D$ , we examine whether  $\phi_C > \phi_D$ . Thus, the value of  $\phi_C/\phi_D$  determines  
81 which strategy is more common. For a ratio greater than 1, cooperation is  
82 favoured over defection. If the ratio is less than 1, defection is favoured. The  
83 fixation probabilities of cooperators and defectors in the Moran process with  
84 exponential mapping are (36; 48; 66)

$$\phi_C = \frac{1}{1 + \sum_{j=1}^{n-1} \prod_{i=1}^j e^{w(b_i - a_i)}} \quad (1)$$

$$\phi_D = \frac{1}{1 + \sum_{j=1}^{n-1} \prod_{i=1}^j e^{w(a_i - b_i)}}. \quad (2)$$

86 The ratio of the fixation probabilities is given by (46)

$$\frac{\phi_C}{\phi_D} = \prod_{i=1}^{n-1} \frac{e^{wa_i}}{e^{wb_i}} = e^{w \sum_{i=1}^{n-1} (a_i - b_i)}. \quad (3)$$

87 Whether this ratio is greater than 1 (i.e. cooperators are favoured) depends  
88 solely on the sign of

$$\Lambda_0 = \sum_{i=1}^{n-1} (a_i - b_i). \quad (4)$$

89 This is a generalization of the classic result of risk dominance to multiplayer  
90 games (35; 48; 21; 3; 40; 26). For a positive  $\Lambda_0$ , cooperation is favoured in  
91 terms of the fixation probability, while a negative  $\Lambda_0$  means that defectors  
92 are selected. We will use such  $\Lambda$  values for comparing the different migration  
93 modes.

### 94 3. Migration modes

95 We now extend this analysis to multiple groups, and include migration  
96 between groups (see Fig. 1). Consider  $m$  different groups, each with a fixed

group size of  $n$ . We discuss several different modes of migration that individuals can use to move between groups.

The rate of migration between groups is assumed to be very small compared to the rate of fixation of a strategy within a group. This implies that migration events typically occur only when groups are homogeneous (65; 66). Under this time-scale separation, fixation events in the whole population occur in two stages: first a strategy fixes inside a group – with probability  $\phi_C$  ( $\phi_D$ ) for cooperators (defectors) – and then in the whole population – with probability  $\Phi_C$  ( $\Phi_D$ ) for groups of cooperators (defectors).

We use Eqs. (1) and (2) to compute  $\phi_C$  and  $\phi_D$  at the individual level. At the group level, the fixation probabilities  $\Phi_C$  and  $\Phi_D$  depend on the mode of migration. Expressions for these probabilities are generally simpler than for the probabilities at the individual level due to the fact that all individuals within a group have the same fitness when migration occurs (see Appendix A.2-Appendix A.5 for details).

The ratio of fixation probabilities in the structured population (analogous to Eq. (3)) is then given by  $\frac{\phi_C \Phi_C}{\phi_D \Phi_D}$  (65).

Here we present a brief derivation of fixation probabilities and corresponding “sign sums”  $\Lambda$ . A different  $\Lambda$  will be calculated for each migration mode (See Appendix A.1 – Appendix A.5 for details).

### 3.1. Single individual migration

As in Traulsen and Nowak (65), we assume that offspring are added to the parent group with probability  $1 - \lambda$ , or to a randomly chosen group with probability  $\lambda$ . This is the simplest migration process, with  $\lambda$  being the migration probability. Due to  $\lambda \ll 1$ , we consider the probability that a group where the mutant has fixed will send out a migrant that will become a member another group. This probability is equal to  $ne^{w_{a_n}}\lambda$  for groups of cooperators, and  $ne^{w_{b_0}}\lambda$  for groups of defectors. For the fixation probabilities at the group level, we obtain the ratio

$$\frac{\Phi_C}{\Phi_D} = \prod_{j=1}^{m-1} \frac{ne^{w_{a_n}}\lambda\phi_C}{ne^{w_{b_0}}\lambda\phi_D} = e^{w(m-1)(a_n-b_0+\sum_{i=1}^{n-1}(a_i-b_i))}. \quad (5)$$

Combining Eqs. (3) and (5) we obtain

$$\frac{\phi_C \Phi_C}{\phi_D \Phi_D} = e^{w((m-1)(a_n-b_0)+m\sum_{i=1}^{n-1}(a_i-b_i))}. \quad (6)$$

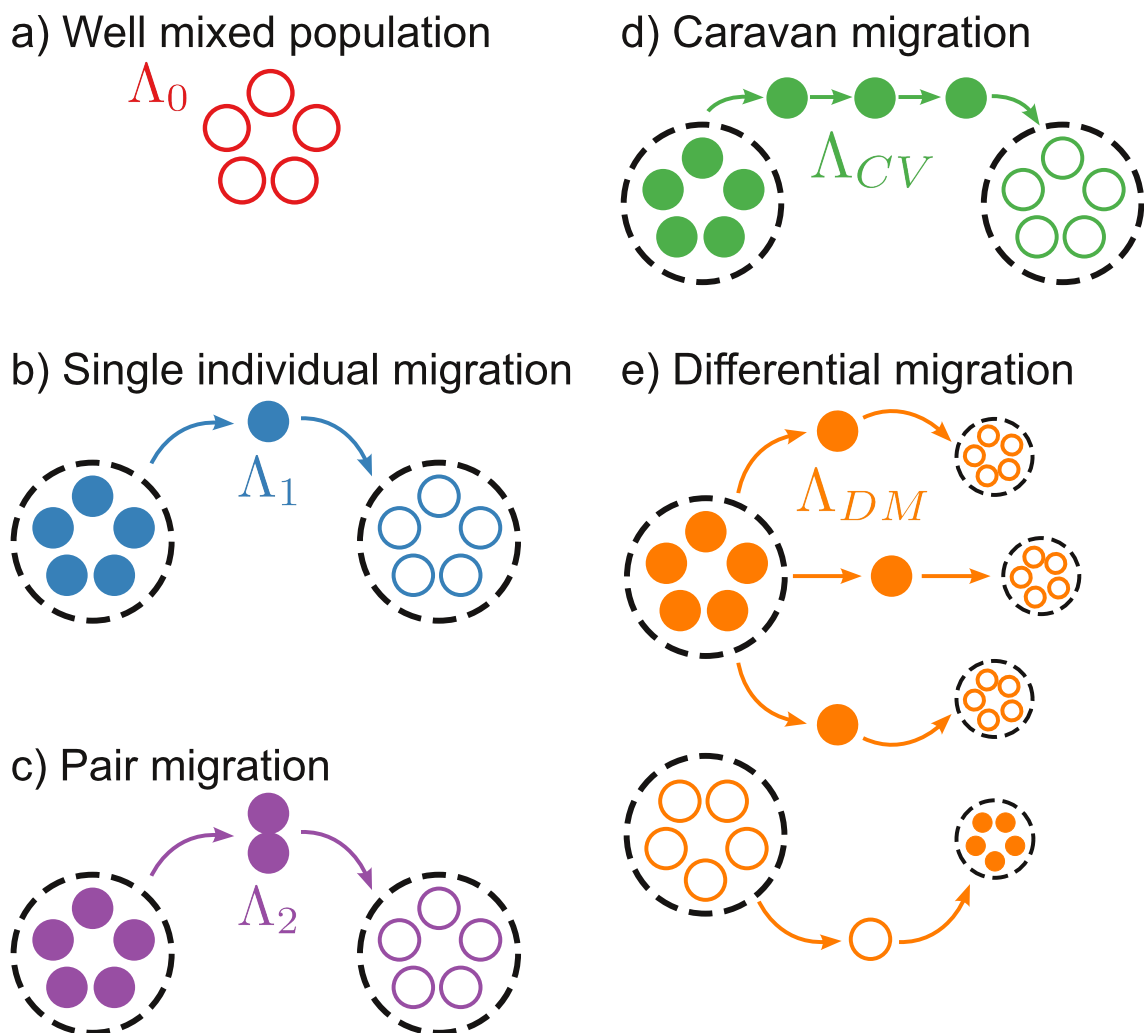


Figure 1: **Different modes of migration.** Closed circles represent cooperators, open circles represent defectors, dotted line circles represent groups. (a) *Well mixed population*, where no migration is possible. (b) *Single individual migration mode*, where each individual migrates independently. (c) *Pair migration mode*, where individuals migrate in pairs. (d) *Caravan migration mode*, where multiple migrants go to the same group. (e) *Differential migration mode*, where cooperators have higher chances to migrate than defectors. In each case, the quantity  $\Lambda$  determines whether cooperation evolves or not, cf. Fig. 2.

127 Here, the outcome of evolution is determined by the sign of  $\Lambda_1$ , given by

$$\Lambda_1 = (m - 1)(a_n - b_0) + m \sum_{i=1}^{n-1} (a_i - b_i) = (m - 1)(a_n - b_0) + m\Lambda_0 \quad (7)$$

128 The equation for the sign sum  $\Lambda_1$  contains the sign sum of the single group  
129 mode,  $\Lambda_0$ , as the second term. The first term  $(m - 1)(a_n - b_0)$  is proportional  
130 to the fitness difference of the purely cooperative group and the purely de-  
131 fecting group, and describes the effect of group migration. Eq. 7 explicitly  
132 expresses conditions for selection to favor cooperation in the single individual  
133 migration mode (31) through payoffs from a multiplayer game that is played  
134 within groups.

135 Groups of cooperators send out more migrants than groups containing  
136 high frequencies of defecting types, which means that cooperative strategies  
137 gain an advantage in the face of migration. The effect of migration depends  
138 on the number of groups  $m$  in a population. The relative weight of the  
139 new term in comparison with the lower-level selection term  $\sum_{i=1}^{n-1} (a_i - b_i)$   
140 depends only weakly on the number of groups  $m$ . With decreasing number  
141 of the groups,  $\Lambda_1$  approaches  $\Lambda_0$ , and for  $m = 1$  both are identical.

### 142 3.2. Pair migration

143 Another mode of migration is one where migrants leave simultaneously.  
144 For this mode we assume that every migration event carries propagules of a  
145 finite number. For illustrative purposes, we discuss propagules of size 2 or  
146 ‘pair migration’. In this case, we consider the probability that two deviating  
147 individuals take over the population. The sign sum is

$$\Lambda_2 = \Lambda_1 + \frac{m - 1}{w} \ln \left[ \frac{1 + e^{-w(a_1 - b_1)}}{1 + e^{w(a_{n-1} - b_{n-1})}} \right] \quad (8)$$

148 The additional term, now including the selection coefficient, may be positive  
149 or negative, depending on the payoff comparison in groups with 1 and  $n - 1$   
150 individuals of each type. For a game where cooperators receive a lower pay-  
151 off than defectors in the same group, this additional term is always positive.  
152 Therefore the increase of invading propagule size from 1 to 2 benefits coop-  
153 erators. The sign sums can be calculated for propagules of arbitrary size in  
154 a similar fashion.

### 155 3.3. Caravan migration

156 Next, we assume that a new migrant might follow a previous migrant  
 157 with a probability  $p$ . This causes a caravan effect, whereby migrants invade  
 158 the same group with a probability greater than random. Due to the time  
 159 scale separation assumption, a migrant is fixed or eliminated from the group  
 160 before the next migrant arrives. Therefore, the caravan migration mode  
 161 considers multiple migrations of single individuals, whereas the propagule  
 162 mode of migration considers simultaneous migration of multiple individuals.  
 163 For simplicity we introduce an additional time scale separation to the caravan  
 164 migration model: all follow-up migrants arrive at the recipient group earlier  
 165 than migrants from any other group. The caravan migration mode represents  
 166 biological systems in which migrants may leave some record of their migration  
 167 that stimulates the production of further individuals within the group to  
 168 follow the first departed migrant. This approximates a situation where, for  
 169 example, an ant leaves a chemical trail (33). This is the simplest example of  
 170 the model in which all players in the group coordinate their actions.

171 The probability that the number of migrants entering the same group is  
 172 equal to  $k$  is given by

$$P(k) = p^{k-1}(1 - p). \quad (9)$$

173 The probability that at least one migrant is successful is equal to

$$\phi_C^{\text{Caravan}} = 1 - \sum_{k=1}^{\infty} P(k)(1 - \phi_C)^k = \frac{\phi_C}{1 - p(1 - \phi_C)}. \quad (10)$$

174 Here  $\phi_C^{\text{Caravan}}$  is the probability of a successful invasion of a group of defectors  
 175 by a cooperative group.

176 Similarly, the expected probability of the opposite event is  $\frac{\phi_D}{1 - p(1 - \phi_D)}$ .  
 177 Thus, the ratio of fixation probabilities at the group level is

$$\frac{\Phi_C}{\Phi_D} = \prod_{j=1}^{m-1} \frac{ne^{w_{a_n}} \lambda \phi_C (1 - p(1 - \phi_D))}{ne^{w_{b_0}} \lambda \phi_D (1 - p(1 - \phi_C))}. \quad (11)$$

178 If  $p \gg 1 - \phi$ , the probability that the group invaded by the first migrant is  
 179 eventually taken over approaches 1, such that the result becomes independent  
 180 of  $\phi_C$  and  $\phi_D$ . The group that receives the first migrant will be invaded with  
 181 a probability equal to 1. The flow of migrants from one group to another



182 means that the invaded group will be converted with a probability equal to  
183 1. The ratio of fixation probabilities at the group level in this limit is

$$\frac{\Phi_C}{\Phi_D} = \prod_{j=1}^{m-1} \frac{ne^{wa_n}\lambda}{ne^{wb_0}\lambda} = e^{w(m-1)(a_n-b_0)}. \quad (12)$$

184 The sign sum (see Eq. (7)) for this mode is then

$$\Lambda_{CV} = (m-1)(a_n - b_0) + \sum_{j=1}^{n-1} (a_j - b_j) = \Lambda_1 - (m-1)\Lambda_0. \quad (13)$$

185 This is larger than in the migration mode for a single individual  $\Lambda_1$ , as  
186  $\Lambda_0 < 0$  for traits that are disadvantageous at the individual level ( $a_i < b_i$ ).  
187 An increase in the number of groups in a population significantly increases  
188 the advantage to cooperators caused by this migration process. Since the  
189 caravan mode effectively displaces the accepting group with a copy of the  
190 donor group, the result obtained here is mathematically equivalent to those  
191 of Traulsen and Nowak (65), where it was assumed that a group splits and  
192 displaces a randomly selected group.

### 193 3.4. Differential migration

194 In the earlier migration modes we have assumed that the migration rate  
195 is independent of the type of emigrant. Here we relax this assumption. For  
196 example, a group of cooperators may increase the migration rate of its mem-  
197 bers, therefore increasing the fitness of the group as a whole. Biologically,  
198 this could be envisioned to occur via secretion of a chemical signal promoting  
199 newly emerged individuals to leave the parent group.

200 In this mode, let  $\lambda_C$  be the migration rate of  $C$  types, and  $\lambda_D$  be the  
201 migration rate of  $D$  types. Assuming that the time scale separation is not  
202 violated by increased migration rates, we calculate the ratio of fixation prob-  
203 abilities on the group level as

$$\frac{\Phi_c}{\Phi_d} = \prod_{j=1}^{m-1} \frac{ne^{wa_n}\lambda_C}{ne^{wb_0}\lambda_D} = e^{w(m-1)(a_n-b_0 + \frac{\ln(\lambda_C/\lambda_D)}{w})}. \quad (14)$$

204 Therefore, the sign sum in this mode is

$$\Lambda_{DM} = \Lambda_1 + \frac{m-1}{w} \ln \left( \frac{\lambda_C}{\lambda_D} \right). \quad (15)$$

205 The difference in migration rates ( $\lambda_C > \lambda_D$ ) provides an advantage to co-  
 206 operating groups, which emits proportionally more migrants in this mode.  
 207 This is reflected in an additional term  $\ln \left( \frac{\lambda_C}{\lambda_D} \right)$ , which can shift the balance  
 208 of selection in favour of cooperators. Interestingly, the overall sign sum  $\Lambda_{DM}$   
 209 may still be negative, despite the fact that groups of cooperators produce  
 210 more migrant offspring than groups of defectors. This can be explained by  
 211 the fact that the raw number of migrant offspring is not a determinant of  
 212 evolutionary success, instead the number of successfully invaded migrants  
 213 is a defining characteristic of evolution in our model. As such, even if the  
 214 number of migrants emitted by the cooperating group might be high, the fix-  
 215 ation process occurring by means of selection at the individual level favours  
 216 defectors. The interplay of these two factors does not necessarily promote  
 217 cooperation even in the differential migration mode, where cooperators are  
 218 considered to have an advantage.

## 219 4. Social dilemmas

220 To be more concrete, we now apply the results of the previous sections  
 221 to different social dilemma games (12; 6; 38; 47). In social dilemma games,  
 222 the average payoff to players increases with the number of cooperators, but  
 223 defectors gain higher payoff than cooperators. An example of a pairwise  
 224 social dilemma is the prisoner’s dilemma, which is extensively used for the  
 225 study of the evolution of cooperation (6; 44; 15). For our purposes, it is  
 226 useful to differentiate between weak and strong altruism.

### 227 4.1. Weak and strong altruism

228 Weak altruism is a situation where cooperators provide an advantage to  
 229 the group, but regardless of the group composition, cooperators have lower  
 230 payoff than defectors (72; 38). Therefore, the payoffs under weakly altruistic  
 231 interactions have two properties,

- 232 1. If the number of cooperative players increases, the payoffs of all players  
 233 increase. That is  $a_i < a_{i+1}$  and  $b_i < b_{i+1}$ .
- 234 2. Cooperators have lower payoff than defectors. That is  $a_i < b_i$ .

235 Since  $a_i < b_i$ , then, consequently,  $\Lambda_0 < 0$ . Unsurprisingly, weak altruism  
236 does not arise in the absence of selection at the group level.

237 In the case of single migrants, the migration-related term in the sign sum  
238  $\Lambda_1$  (Eq. (7)) can balance, and even overcome, the term that represents lower  
239 level selection. Thus, weak altruism can be favoured in simple migration  
240 settings. Similar arguments hold for the pair migration, caravan migration  
241 and differential migration modes.

242 Strong altruism (72), also termed as focal complement altruism (38), are  
243 interactions where switching to cooperation always entails a loss of repro-  
244 ductive success. A well-known example of strong altruism is the prisoner's  
245 dilemma where strongly altruistic interactions are characterized by two prop-  
246 erties:

- 247 1. If the number of cooperative players increases, the payoffs of all players  
248 increase. That is  $a_i < a_{i+1}$  and  $b_i < b_{i+1}$ .
- 249 2. If a player switches from defection to cooperation, their payoff de-  
250 creases. That is  $a_i < b_{i-1}$ .

251 Strong altruism is always disadvantageous in populations without struc-  
252 ture, i.e.  $\Lambda_0 < 0$ . In addition, we find that

$$\Lambda_1 = (m-1)(a_n - b_0) + m \sum_{i=1}^{n-1} (a_i - b_i) = \underbrace{-(a_n - b_0)}_{<0} + m \sum_{i=1}^n \underbrace{a_i - b_{i-1}}_{<0} < 0, \quad (16)$$

253 which means that strong altruism is also disfavoured with simple individual-  
254 based migration. This result generalizes previous findings that cooperation  
255 in the Prisoner's dilemma game cannot evolve when migration involves just  
256 a single individual (31).

257 For pair migration,  $\Lambda_2$  can become positive due to the additional term  
258 that is present in  $\Lambda_2$  (see Eq. 8). Also for caravan migration, cooperation  
259 can be favored due to the additional positive term  $-(m-1)\Lambda_0$ .

260 Next, we discuss more specific examples of social dilemmas.

## 261 4.2. Public goods games

262 Pairwise games, such as the prisoner's dilemma, where only two players  
263 participate in each game round, cannot represent cooperation with synergis-  
264 tic interactions. With synergistic interactions, multiple cooperators amplify

each other’s contributions, thus providing higher benefit than they would produce independently. To encompass these kinds of interactions, we utilize *multiplayer games*, where multiple players are taken into account in the payoff calculation (30; 40; 26).

Public goods games are a type of multiplayer game where each player can make a donation to a public pool. The collected amount is then multiplied, and evenly shared amongst all players, including those that decided not to make a donation. Weak and strong altruism can be naturally represented by self-returning benefit and self-excluding benefit games, respectively (59; 14). In self-returning benefit games, the public goods are shared among all participants; therefore, a proportional part of a donation returns to contributors as a part of their payoff. In this case, all players receive the same share of a public good, but defectors save the cost of donation. Therefore self-returning benefit games represent weak altruism. In self-excluding benefit games, a donation by a focal individual is only shared among other participants; therefore, the payoff of this focal player depends only on the donation of others. In self-excluding benefit games, switching from cooperation to defection does not change the received amount of the public goods, but saves the cost of cooperation. This makes cooperation in self-excluding benefit games strongly altruistic.

We start with the simplest public goods game. Here, the reward to cooperators increases linearly with the number of cooperators. Cooperative individuals pay a cost  $\gamma$ , in order to provide a benefit  $\beta$ . This benefit is either split amongst the rest of the group, in the linear self-excluding game (LSE game); or split among the whole group, in the linear self-returning game (LSR game). A defecting individual does not pay the cost, but reaps the benefits from other cooperators. The LSR game is weakly altruistic, see Table 1. The LSE game is strongly altruistic, and can be viewed as a multiplayer generalization of the standard prisoner’s dilemma.

In addition, we consider non-linear public goods games. If there are synergies in the production of the public goods, each additional donation can provide more benefits than the previous one. Likewise, if the marginal benefit decreases with the number of donations, the benefits are discounted and become saturated as the number of cooperators increase. These so-called non-linear public goods games have been extensively analyzed (18; 7; 30; 69; 50; 25; 70; 4; 51; 55; 1).

In the simplest version of the game incorporating synergy and discounting, the first cooperator in the group pays a cost  $\gamma$  to generate  $\beta$  units of

Table 1: Payoffs and their differences for the linear self-returning (LSR), the linear self-excluding (LSE), the synergy/discounting self-returning (SDSR), and the synergy/discounting self-excluding (SDSE) public goods games.  $a_i$  is the payoff to a cooperator in a group of size  $n$  with  $i$  cooperators, and  $b_i$  is the payoff for a defector. The sum of the payoff difference  $a_i - b_i$  determines the value of  $\Lambda_0$  (see Eq. 4). Switching from defection to cooperation leads to a payoff difference  $a_i - b_{i-1}$ . Switching always decreases payoffs for the self-excluding benefit games (LSE and SDSE); however, the change in payoff for the self-returning benefit games (LSR and SDSR) can be positive and therefore cooperators could have a higher fixation rate than defectors in these games.

	LSR	LSE	SDSR	SDSE
$a_i$	$\frac{i}{n}\beta - \gamma$	$\frac{i-1}{n-1}\beta - \gamma$	$\frac{\beta}{n} \frac{1-\zeta^i}{1-\zeta} - \gamma$	$\frac{\beta}{n-1} \frac{1-\zeta^{i-1}}{1-\zeta} - \gamma$
$b_i$	$\frac{i}{n}\beta$	$\frac{i}{n-1}\beta$	$\frac{\beta}{n} \frac{1-\zeta^i}{1-\zeta}$	$\frac{\beta}{n-1} \frac{1-\zeta^i}{1-\zeta}$
$a_i - b_i$	$-\gamma < 0$	$-\frac{\beta}{n-1} - \gamma < 0$	$-\gamma < 0$	$-\frac{\beta}{n-1}\zeta^{i-1} - \gamma < 0$
$a_i - b_{i-1}$	$\frac{\beta}{n} - \gamma$	$-\gamma < 0$	$\frac{\beta}{n}\zeta^{i-1} - \gamma$	$-\gamma < 0$
Altruism	Weak	Strong	Weak	Strong

a public good. Each additional cooperator present in the group provides  $\zeta$  times the public good than the previous one. If  $\zeta > 1$ , then cooperators act synergistically. If  $\zeta < 1$ , benefits are discounted. Again, donations can be either shared among all players (synergy/discounting game with self-returning benefit, or SDSR game), or only among other players and excluding the donor (synergy/discounting game with self-excluding benefit, or SDSE game).

The payoffs  $a_i$  and  $b_i$  to players in these games (LSR, LSE, SDSR and SDSE) and their differences are presented in Table 1. For each of these games we derive the conditions for the evolution of cooperation under different migration schemes (see Section 3). The sign sums for each combination of game and migration mode are presented in Tables 2 (for self-returning games) and 3 (for self-excluding games).

Sign sums as functions of benefit  $\beta$  for different games and modes of migration are presented in Fig. 2. In the well mixed model, cooperation is evolutionary unsuccessful in all games ( $\Lambda_0 < 0$ ).

For the games representing weak altruism (LSR and SDSR), cooperation may be successful in all migration modes, provided that the benefit to cost

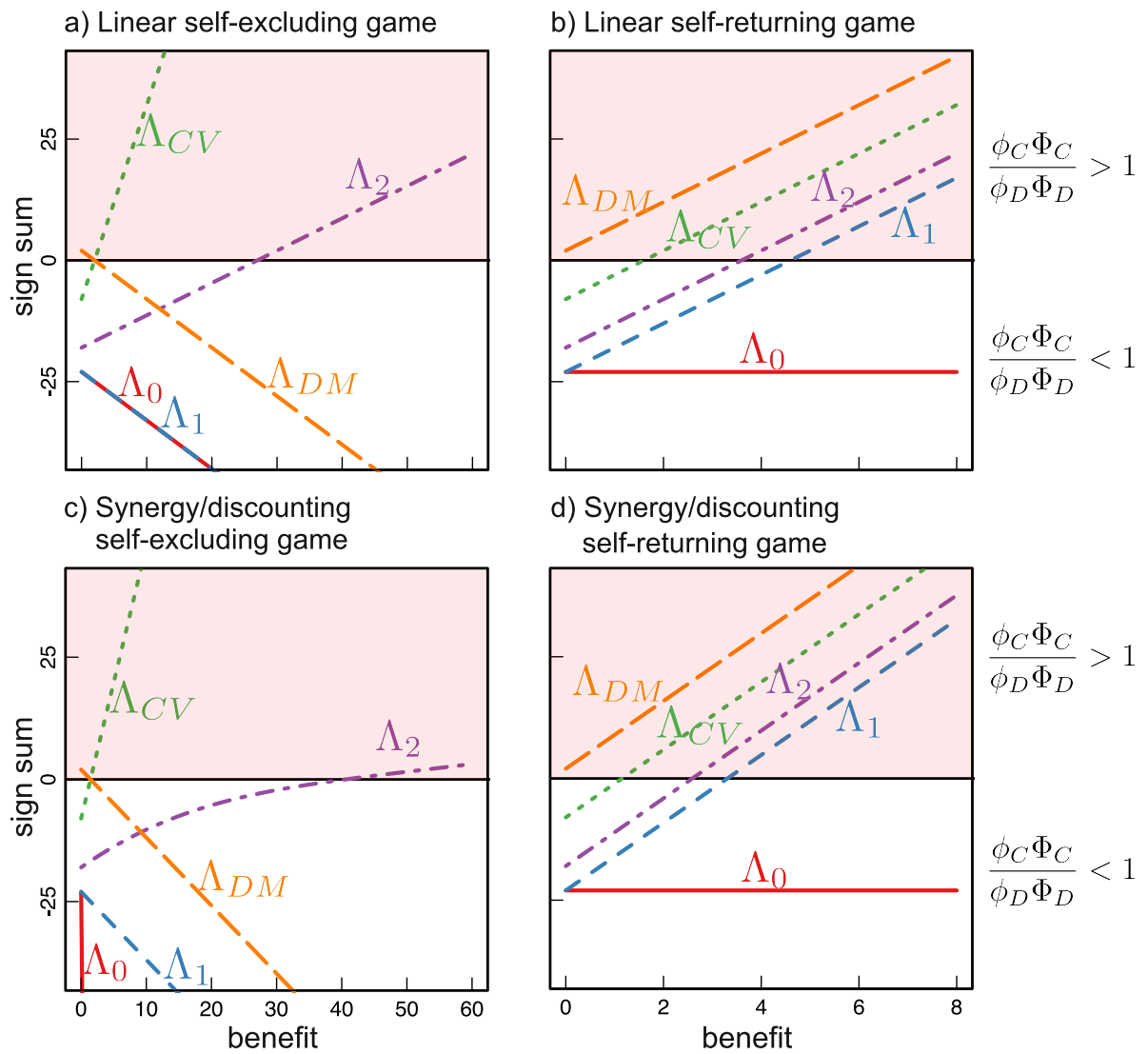


Figure 2: **The evolution of cooperation does not always become easier with increasing benefit  $\beta$ .** Cooperation is advantageous in terms of fixation probabilities if the sign sum  $\Lambda$  calculated for migration modes (lines) is positive (shaded region). In the well mixed case,  $\Lambda_0$  decreases in self-excluding games and stays constant for self-returning games. In the single individual migration mode and the differential migration mode, cooperation becomes easier with increasing benefit in the self-returning case, but harder in the self-excluding case. In the pair migration mode and in caravan migration, cooperation becomes easier with increasing benefit for all games with the current parameter set. ( $n = 24$  for the well mixed population,  $m_A = 6$  and  $n = 4$  in migration models,  $\zeta = 1.35$ , intensity of selection  $w = 0.1$ , cost of cooperation  $\gamma = 1$ , group migration bonus factor in differential migration mode  $w^{-1} \ln(\lambda_C/\lambda_D) = 5$ , colors as in Fig. 1).

Table 2: Sign sums for self-returning games (weak altruism) in a well mixed population and under different modes of migration.

	LSR	SDSR
$\Lambda_0$	$-(n-1)\gamma$	$-(n-1)\gamma$
$\Lambda_1$	$(m-1)\beta - (mn-1)\gamma$	$(m-1)\frac{\beta}{n}\frac{1-\zeta^n}{1-\zeta} - (mn-1)\gamma$
$\Lambda_2$	$(m-1)\beta - m(n-1)\gamma$	$(m-1)\frac{\beta}{n}\frac{1-\zeta^n}{1-\zeta} - m(n-1)\gamma$
$\Lambda_{CV}$	$(m-1)\beta - (m+n-2)\gamma$	$(m-1)\frac{\beta}{n}\frac{1-\zeta^n}{1-\zeta} - (m+n-2)\gamma$
$\Lambda_{DM}$	$(m-1)\left(\beta + \frac{\ln(\lambda_C/\lambda_D)}{w}\right) - (mn-1)\gamma$	$(m-1)\left(\frac{\beta}{n}\frac{1-\zeta^n}{1-\zeta} + \frac{\ln(\lambda_C/\lambda_D)}{w}\right) - (mn-1)\gamma$

ratio is large enough. Clearly, increasing synergy in self-returning games favours cooperation.

For the games representing strong altruism (LSE and SDSE), even for the individual migration mode, cooperators have no selective advantage ( $\Lambda_1 < 0$ ). For the pair migration and caravan migration modes, strong altruism may have a selective advantage over defection and in LSE game this is possible if the benefit to cost ratio is high enough. Under differential migration strong altruism also can have a selective advantage in the LSE game. However, the prerequisites for this are restrictive: the group migration bonus factor  $w^{-1} \ln(\lambda_C/\lambda_D)$  must be high enough to ensure a strong implicit advantage to cooperators. Interestingly, an increase in the benefit to cost ratio works against cooperation under this mode of migration.

At the qualitative level, the difference between linear and non-linear games from the same migration scheme are minor, with a few notable exceptions. Strongly altruistic, non-linear SDSE games, can promote cooperation in the pair migration mode at high values of benefit  $\beta$  (the sign sum in this case cannot be reduced to benefit to cost ratio) only if the number of groups  $m$  is high enough (Appendix A.6). The minimal number of groups necessary for the success of cooperation for this game increases with the increase of the synergy. Therefore synergistic interactions work against cooperation success in the pair migration mode.

In the caravan migration mode, the SDSE game, similar to the linear LSE game, promotes cooperation if the benefit to cost ratio ( $\beta/\gamma$ ) is high enough. However, synergy of cooperators makes cooperation successful at lower values

Table 3: Sign sums for self-excluding public good games (strong altruism) in a well mixed population and under different modes of migration.

	LSE	SDSE
$\Lambda_0$	$-\beta - (n-1)\gamma$	$-\frac{\beta}{n-1} \frac{1-\zeta^{n-1}}{1-\zeta} - (n-1)\gamma$
$\Lambda_1$	$-\beta - (mn-1)\gamma$	$-\frac{\beta}{n-1} \frac{1-\zeta^{n-1}}{1-\zeta} - (mn-1)\gamma$
$\Lambda_2$	$\beta \frac{m-n}{n-1} - m(n-1)\gamma$	$-\frac{\beta}{n-1} \frac{1-\zeta^{n-1}}{1-\zeta} - (mn-1)\gamma + \frac{m-1}{w} \ln \left[ \frac{1+e^{w(\frac{\beta}{n-1}+\gamma)}}{1+e^{-w(\frac{\beta}{n-1}\zeta^{n-2}+\gamma)}} \right]$
$\Lambda_{CV}$	$(m-2)\beta - (m+n-2)\gamma$	$(m-2) \frac{\beta}{n-1} \frac{1-\zeta^{n-1}}{1-\zeta} - (m+n-2)\gamma$
$\Lambda_{DM}$	$(m-1) \frac{\ln(\lambda_C/\lambda_D)}{w} - \beta - (mn-1)\gamma$	$(m-1) \frac{\ln(\lambda_C/\lambda_D)}{w} - \frac{\beta}{n-1} \frac{1-\zeta^{n-1}}{1-\zeta} - (mn-1)\gamma$

of benefit to cost ratio than in the LSE game. Finally, in the SDSE game with differential migration, as well as in the LSE game, the advantage of cooperation depends on the group migration bonus factor, while both high benefit to cost ratio and synergy work against cooperation.

Synergy always favours cooperation in weakly altruistic self-returning games (LSR and SDSR); however, it may work against cooperation in strongly altruistic LSE and SDSE games under certain modes of migration. Intuitively, cooperation will be enhanced if the benefit provided by a cooperator is large or if there is more synergy between cooperators (larger  $\beta$ , larger or increasing  $\zeta$ ). Counterintuitively, in self-excluding games this works against cooperation (49). Consider the prisoner's dilemma game, played by one cooperator and one defector. An increase in the amount of benefit produced by cooperator  $\beta$  leads only to an increase in the payoff to the defector; thereby harming cooperation. Furthermore, in a multiplayer game, an increasing  $\zeta$  just provides more benefit for defectors to exploit, as it does not return benefit to the contributor. This shows that cheaper cooperation can benefit defectors.

In all four games, for all values of the benefit to cost ratio, defection is favoured (negative sign sums) in well mixed populations. This illustrates that even weak altruism is less successful than defection in the absence of population structure. The standard migration mode allows LSR and SDSR games to have a positive sign sum if the benefit to cost ratio is large enough. However, cooperators in LSE and SDSE games, being strongly altruistic are



367 always disadvantageous, independent of the benefit to cost ratio.

## 368 5. Discussion

369 We have shown that migration, even in the absence of coordination be-  
 370 tween individuals, promotes the evolution of weakly altruistic cooperation.  
 371 The single individual migration mode presented here is not based on pro-  
 372 cesses that involve an entire group (65), or specific structure of groups (42).  
 373 Our results indicate that cooperation may emerge by means of group-level  
 374 selection even if selection is conducted by the non-coordinated actions of in-  
 375 dividuals. In other words, selection on the group level can be mediated by  
 376 population structure alone.

377 In modes where migration involves the coordinated actions of multiple  
 378 individuals, cooperation can evolve in a much wider range of games than in  
 379 the single individual migration mode. In the pair, caravan and differential  
 380 migration modes, strong altruism can be favored. Also, in weakly altruistic  
 381 games the range of parameters promoting the evolution of cooperation is  
 382 extended: the domain of benefit to cost ratio with positive sign sums becomes  
 383 wider than in the single individual migration mode (see Figure 2 panels  
 384 b and d). Thus, introduction of coordination between individuals' actions  
 385 substantially extends the set of conditions under which cooperation may  
 386 evolve.

387 Throughout this manuscript, we have concentrated on the exponential  
 388 payoff to fitness mapping, which allows a very compact representation of  
 389 the sign sums. However, many of our results hold for more general payoff  
 390 to fitness mappings (75; 76). For example, for any mapping in which the  
 391 number of emitted migrants is proportional to the reproductive output of  
 392 the players within the group the single individual migration mode can favor  
 393 weak altruism, but not strong altruism, see Appendix B. This is in contrast  
 394 to a scenario of a pairwise comparison process (31; 32), where production  
 395 of migrants moving between groups depends directly on payoffs, but the  
 396 competition between types within the group depends on differences between  
 397 individual payoffs.

398 The evolution of cooperation under limited coordination of individuals'  
 399 actions may have particular importance for understanding early stages of the  
 400 evolution of multicellularity. While details remain unclear, there is general  
 401 agreement that the earliest stages involved the evolution of simple, undif-  
 402 ferentiated groups of cooperating cells (68; 57; 52; 2; 39; 29). In theoretical

models of the evolution of cooperation, the mechanistic details surrounding the re-distribution of individuals among groups are often overlooked. Two broad kinds of group formation are generally considered: groups originating from growth of a single individual, referred to as “staying together”, and groups formed by aggregation of individuals, referred to as “coming together” (63). An example of the “staying together” mode is fragmentation (65), as found in the algae *Gonium pectorale* (61). The “coming together” mode is utilized by slime molds (8) and in trait group models (71). Multiple individual modes of group formation can be constructed within these two kinds (71; 5; 52; 65; 54; 22; 41; 60; 63), including those in which ‘staying together’ is combined with migration events that establish new groups (56; 41; 58; 29). From a mechanistic point of view, modes of individual assignment, considered in the previous paragraph, are typically assumed to arise by the coordinated actions of multiple individuals in the group. However, early cellular groups were most likely unable to act as a single coordinated unit, and as such recurrence of these groups was presumably conducted by unregulated actions of individual cells (13).

Based on our results, one can perform a classification of multilevel selection models based on the level of complexity of the interactions between groups. The first class consists of models in which processes between groups are mediated by a single individual, such as the single individual migration mode and metapopulation models (17; 34). As shown here, these kinds of models can promote weak altruism, but not strong altruism. The second class of models are those in which between-group processes involve several individuals, or even whole groups. Examples include the pair, caravan and differential migration modes, and also the splitting of whole groups (65). In the context of the early stages of the evolution of multicellularity, the first class of models likely have particular importance, as the multi-individual actions of the second class generally require coordinated activity, which might not be available for early groups.

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## 438 Appendix A. Derivation of sign sums

### 439 Appendix A.1. Derivation of $\Lambda_0$

440 The fixation probability for one individual of the two strategies in a well  
441 mixed population is equal to (46; 64)

$$\begin{aligned}\phi_C &= \frac{1}{1 + \sum_{j=1}^{n-1} \prod_{i=1}^j \frac{e^{wb_i}}{e^{wa_i}}} \\ \phi_D &= \frac{1}{1 + \sum_{j=1}^{n-1} \prod_{i=1}^j \frac{e^{wa_{n-i}}}{e^{wb_{n-i}}}}.\end{aligned}\tag{A.1}$$

442 The ratio of these fixation probabilities is

$$\frac{\phi_C}{\phi_D} = \prod_{i=1}^{n-1} \frac{e^{wa_i}}{e^{wb_i}} = e^{w \sum_{i=1}^{n-1} (a_i - b_i)} = e^{w\Lambda_0}.\tag{A.2}$$

443 Here,  $\Lambda_0 = \sum_{i=1}^{n-1} (a_i - b_i)$  is the sign sum for a well mixed population, as  
444 stated previously, for example by (40) and (25).

### 445 Appendix A.2. Derivation of $\Lambda_1$

446 For group structure and small migration rates, the trait of interest first  
447 needs to fix in a group ( $\phi_C$ ) and then that group needs to fix in the population  
448 ( $\Phi_C$ ). The total fixation probability ratio is thus equal to  $\frac{\Phi_C}{\Phi_D} \frac{\phi_C}{\phi_D}$  (65). Here  
449  $\frac{\phi_C}{\phi_D}$  is calculated according to Eq. (A.2). The ratio  $\frac{\Phi_C}{\Phi_D}$  is calculated as

$$\frac{\Phi_C}{\Phi_D} = \prod_{j=1}^{m-1} \frac{ne^{wa_n} \lambda \phi_C}{ne^{wb_0} \lambda \phi_D} = \prod_{j=1}^{m-1} \left( \frac{e^{wa_n}}{e^{wb_0}} e^{w\Lambda_0} \right) = e^{w(m-1)(a_n - b_0 + \Lambda_0)}.\tag{A.3}$$

450 Therefore the total fixation probability ratio is

$$\frac{\phi_C}{\phi_D} \frac{\Phi_C}{\Phi_D} = e^{w\Lambda_0} e^{w(m-1)(a_n - b_0 + \Lambda_0)} = e^{w((a_n - b_0)(m-1) + m \sum_{i=1}^{n-1} (a_i - b_i))}.\tag{A.4}$$

451 Thus, the sign sum for the single individual migration mode is

$$\Lambda_1 = (a_n - b_0)(m - 1) + m \sum_{i=1}^{n-1} (a_i - b_i).\tag{A.5}$$

### 452 *Appendix A.3. Derivation of $\Lambda_2$*

453 In the pair migration mode, the individual-level fixation probabilities are  
 454 different from the single individual migration mode because the initial state  
 455 of the group with mixed composition after accepting a migrant is  $n-2$  players  
 456 of the base type and two players of the invading type. Therefore, the fixation  
 457 probabilities are not equal to the ones presented in Eq. (A.1). According to  
 458 (46), the fixation probabilities  $\phi^i$  for an initial number of  $i$  individuals solves  
 459 the recurrence equation

$$\phi^i = \phi^i(1 - T^{i+} - T^{i-}) + \phi^{i-1}T^{i-} + \phi^{i+1}T^{i+}. \quad (\text{A.6})$$

460 Here  $T^{i+} = \dots$  and  $T^{i-} = \dots$  are probabilities to increase or decrease the  
 461 number of players with a chosen strategy if there are currently  $i$  players.  
 462 Because  $\phi^0 = 0$ ,  $\phi^2$  is

$$\phi_C^2 = \phi_C^1 \left( 1 + \frac{T^{1-}}{T^{1+}} \right) = \phi_C^1 (1 + e^{-w(a_1-b_1)}) \quad (\text{A.7})$$

$$\phi_D^2 = \phi_D^1 \left( 1 + \frac{T^{(n-1)+}}{T^{(n-1)-}} \right) = \phi_D^1 (1 + e^{w(a_{n-1}-b_{n-1})}). \quad (\text{A.8})$$

463 Therefore, the ratio of individual-level fixation probabilities in the pair mi-  
 464 gration mode is

$$\frac{\phi_C^2}{\phi_D^2} = \frac{\phi_C^1}{\phi_D^1} \frac{1 + e^{-w(a_1-b_1)}}{1 + e^{w(a_{n-1}-b_{n-1})}} = \exp \left[ w\Lambda_0 + \ln \left[ \frac{1 + e^{-w(a_1-b_1)}}{1 + e^{w(a_{n-1}-b_{n-1})}} \right] \right]. \quad (\text{A.9})$$

465 The total ratio of fixation probabilities (taking into account that the invading  
 466 strategy starts with one player in the first group, and with two players in all  
 467 following migration invasions) is

$$\frac{\phi_C^1}{\phi_D^1} \frac{\Phi_c}{\Phi_d} = e^{w \left( (a_n-b_0)(m-1) + m \sum_{i=1}^{n-1} (a_i-b_i) + (m-1) \frac{1}{w} \ln \left[ \frac{1+e^{-w(a_1-b_1)}}{1+e^{w(a_{n-1}-b_{n-1})}} \right] \right)} \quad (\text{A.10})$$

468 and the sign sum is

$$\Lambda_2 = (a_n - b_0)(m - 1) + m \sum_{i=1}^{n-1} (a_i - b_i) + (m - 1) \frac{1}{w} \ln \left( \frac{1 + e^{-w(a_1-b_1)}}{1 + e^{w(a_{n-1}-b_{n-1})}} \right). \quad (\text{A.11})$$

469 *Appendix A.4. Derivation of  $\Lambda_{CV}$*

470 In the caravan migration mode with large  $p$ , the probability of successful  
471 invasion of one group into another is equal to 1. Therefore, the ratio of  
472 group-level fixation probabilities is

$$\frac{\Phi_C}{\Phi_D} = \prod_{j=1}^{m-1} \frac{ne^{wa_n}\lambda}{ne^{wb_0}\lambda} = e^{w(a_n-b_0)(m-1)}. \quad (\text{A.12})$$

473 This way the total fixation probabilities ratio is

$$\frac{\phi_C}{\phi_D} \frac{\Phi_C}{\Phi_D} = e^{w\Lambda_0} e^{w(a_n-b_0)(m-1)} = e^{w((a_n-b_0)(m-1) + \sum_{i=1}^{n-1} (a_i-b_i))} \quad (\text{A.13})$$

474 and the sign sum in the caravan migration mode is

$$\Lambda_{CV} = (a_n - b_0)(m - 1) + \sum_{i=1}^{n-1} (a_i - b_i). \quad (\text{A.14})$$

475 *Appendix A.5. Derivation of  $\Lambda_{DM}$*

476 In the differential migration mode, the groups have control over the mi-  
477 gration probabilities of the players. This affects the fixation probabilities at  
478 the group level. The migration probabilities no longer cancel,

$$\frac{\Phi_C}{\Phi_D} = \prod_{j=1}^{m-1} \frac{ne^{wa_n}\lambda_C\phi_C}{ne^{wb_0}\lambda_D\phi_D} = \prod_{j=1}^{m-1} \left( \frac{e^{wa_n}}{e^{wb_0}} e^{w\Lambda_0 + \ln\left(\frac{\lambda_C}{\lambda_D}\right)} \right) = \exp \left[ w(m-1) \left( a_n - b_0 + \Lambda_0 + \frac{1}{w} \ln \left( \frac{\lambda_C}{\lambda_D} \right) \right) \right] \quad (\text{A.15})$$

479 Therefore, the total fixation probability ratio is

$$\frac{\phi_C}{\phi_D} \frac{\Phi_C}{\Phi_D} = e^{w(m-1) \left( a_n - b_0 + \Lambda_0 + \frac{1}{w} \ln \left( \frac{\lambda_C}{\lambda_D} \right) \right) + w\Lambda_0} \quad (\text{A.16})$$

480 and the sign sum becomes

$$\Lambda_{DM} = \left( a_n - b_0 + \frac{\ln \left( \frac{\lambda_C}{\lambda_D} \right)}{w} \right) (m - 1) + m \sum_{i=1}^{n-1} (a_i - b_i). \quad (\text{A.17})$$

## 481 Appendix A.6. The SDSE game in the pair migration mode

482 The sign sum for the SDSE game in the pair migration mode is:

$$\Lambda_2^{SDSE} = -\frac{\beta}{n-1} \frac{1-\zeta^{n-1}}{1-\zeta} - \gamma(mn-1) + \frac{m-1}{w} \ln \left[ \frac{1 + e^{w(\frac{\beta}{n-1} + \gamma)}}{1 + e^{-w(\frac{\beta}{n-1} \zeta^{n-2} + \gamma)}} \right]. \quad (\text{A.18})$$

483 If benefit  $\beta$  is high enough ( $\beta \gg n-1, \beta \gg \frac{n-1}{\zeta^{n-1}}$ ), then the sign sum  
484 approaches

$$\Lambda_2^{SDSE} \approx \frac{\beta}{n-1} \left( m-1 - \frac{1-\zeta^{n-1}}{1-\zeta} \right) - \gamma m(n-1). \quad (\text{A.19})$$

485 Therefore, the sign sum is positive at high benefit values, if the number of  
486 groups  $m$  is high enough:  $m > 1 + \frac{1-\zeta^{n-1}}{1-\zeta}$ . In the case of the discounting  
487 game ( $\zeta < 1$ ), this condition is more restrictive than  $m \geq 2$ , which is always  
488 required in multilevel selection models.

## 489 Appendix B. Other payoff to fitness mappings

490 Strong altruism is at a disadvantage in the single individual migration  
491 mode, when we use the exponential payoff to fitness mapping (66). Here we  
492 show that this result holds true with any mapping.

493 In terms of fitness, strong altruism is characterized by two properties:

- 494 1. If the number of cooperative players increases, the payoffs of all play-  
495 ers increase. That is  $f_a(i) < f_a(i+1)$  and  $f_b(i) < f_b(i+1)$ , where  
496  $f_a(i)$  ( $f_b(i)$ ) is the fitness of cooperators (defectors) in a group with  $i$   
497 cooperators.
- 498 2. If a player switches from defection to cooperation, their payoff de-  
499 creases. That is  $f_a(i) < f_b(i-1)$ .

500 The ratio of fixation probabilities in the structured population is given  
501 by  $\frac{\phi_c}{\phi_d} \cdot \frac{\Phi_c}{\Phi_d}$  (65). We calculate each term separately.

502 The ratio of fixation probabilities of a single cell in a group of opposite  
503 composition (36; 46) is

$$\frac{\phi_C}{\phi_D} = \prod_{i=1}^{n-1} \frac{f_a(i)}{f_b(i)}. \quad (\text{B.1})$$

504 The ratio of fixation probabilities of a single group in a population of  
505 opposite composition is

$$\frac{\Phi_C}{\Phi_D} = \prod_{j=1}^{m-1} \frac{n f_a(n) \lambda \phi_C}{n f_b(0) \lambda \phi_D} = \left( \frac{f_a(n)}{f_b(0)} \prod_{i=1}^{n-1} \frac{f_a(i)}{f_b(i)} \right)^{m-1}. \quad (\text{B.2})$$

506 Combining Eqs. (B.1) and (B.2) we get the ratio of fixation probabilities of  
507 a single cell in a population of opposite composition:

$$\frac{\phi_C \Phi_C}{\phi_D \Phi_D} = \prod_{i=1}^{n-1} \frac{f_a(i)}{f_b(i)} \cdot \left( \frac{f_a(n)}{f_b(0)} \prod_{i=1}^{n-1} \frac{f_a(i)}{f_b(i)} \right)^{m-1} = \frac{f_b(0)}{f_a(n)} \cdot \left( \frac{f_a(n)}{f_b(0)} \prod_{i=1}^{n-1} \frac{f_a(i)}{f_b(i)} \right)^m. \quad (\text{B.3})$$

508 Expression in parenthesis can be rewritten:

$$\frac{f_a(n)}{f_b(0)} \prod_{i=1}^{n-1} \frac{f_a(i)}{f_b(i)} = \frac{f_a(n) \prod_{i=1}^{n-1} f_a(i)}{f_b(0) \prod_{i=1}^{n-1} f_b(i)} = \frac{\prod_{i=1}^n f_a(i)}{\prod_{i=0}^{n-1} f_b(i)} = \prod_{i=1}^n \frac{f_a(i)}{f_b(i-1)}. \quad (\text{B.4})$$

509 Thus, the fixation probabilities ratio is equal to

$$\frac{\phi_C \Phi_C}{\phi_D \Phi_D} = \underbrace{\frac{f_b(0)}{f_a(n)}}_{<1} \cdot \left( \prod_{i=1}^n \underbrace{\frac{f_a(i)}{f_b(i-1)}}_{<1} \right)^m < 1. \quad (\text{B.5})$$

510 So, the inability of the strong altruism to emerge in a single individual  
511 migration mode holds true for all possible payoff to fitness mappings.

## 512 References

- 513 [1] Abou Chakra M, Traulsen A. Under high stakes and uncertainty the  
514 rich should lend the poor a helping hand. *Journal of Theoretical Biology*  
515 2014;341:123–30.
- 516 [2] Aledo JC. An early and anaerobic scenario for the transition to undiffer-  
517 entiated multicellularity. *Journal of molecular evolution* 2008;67(2):145–  
518 53.

- 519 [3] Antal T, Nowak M, Traulsen A. Strategy abundance in  $2 \times 2$  games for  
520 arbitrary mutation rates. *Journal of Theoretical Biology* 2009;257:340–4.
- 521 [4] Archetti M, Scheuring I. Review: Evolution of cooperation in one-shot  
522 social dilemmas without assortment. *Journal of Theoretical Biology*  
523 2012;299:9–20.
- 524 [5] Avilés L. Solving the freeloader's paradox: genetic associations and  
525 frequency-dependent selection in the evolution of cooperation among  
526 nonrelatives. *Proceedings of the National Academy of Sciences of the*  
527 *United States of America* 2002;99(22):14268–73.
- 528 [6] Axelrod R, Hamilton W. The evolution of cooperation. *Science*  
529 1981;211(4489):1390–6.
- 530 [7] Bach LA, Helvik T, Christiansen FB. The evolution of  $n$ -player coop-  
531 eration - threshold games and ESS bifurcations. *Journal of Theoretical*  
532 *Biology* 2006;238:426–34.
- 533 [8] Bonner J. *The Cellular Slime Molds*. Princeton University Press, Prince-  
534 ton, NJ, 1959.
- 535 [9] Christiansen FB Hard and soft selection in a subdivided population.  
536 *American Naturalist* 109: 11–6.
- 537 [10] Clements K, Stephens D. Testing models of non-kin cooperation: mutu-  
538 alism and the prisoner's dilemma. *Animal Behaviour* 1995;50(2):527–35.
- 539 [11] Crespi B. The evolution of social behavior in microorganisms. *Trends*  
540 *in Ecology and Evolution* 2001;16(4):178–83.
- 541 [12] Dawes RM. Social dilemmas. *Annual Review of Psychology* 1980;31:169–  
542 93.
- 543 [13] De Monte S, Rainey P. Nascent multicellular life and the emergence of  
544 individuality. *Journal of Biosciences* 2014;39(2):237–48.
- 545 [14] De Silva H, Hauert C, Traulsen A, Sigmund K. Freedom, enforcement,  
546 and the social dilemma of strong altruism. *Journal of Evolutionary*  
547 *Economics* 2010;20:203–17.



- 548 [15] Dugatkin L. Cooperation Among Animals: An Evolutionary Perspective  
549 (Oxford Series in Ecology and Evolution). Oxford University Press,  
550 Oxford, 1997.
- 551 [16] Dugatkin L, Mesterton-Gibbons M, Alasdair I. Beyond the prisoner's  
552 dilemma: Toward models to discriminate among mechanisms of cooper-  
553 ation in nature. Trends in Ecology and Evolution 1992;7(6):202–5.
- 554 [17] Eshel I. On the neighbor effect and the evolution of altruistic traits.  
555 Theoretical Population Biology 1972;3:258–77.
- 556 [18] Eshel I, Motro U. The three brothers' problem: kin selection with more  
557 than one potential helper. 1. The case of immediate help. American  
558 Naturalist 1988;132(4):550–66.
- 559 [19] Fletcher J, Doebeli M. A simple and general explanation for the evolu-  
560 tion of altruism. Proceedings of the Royal Society B 2009;276:13–9.
- 561 [20] Fletcher JA, Zwick M, Doebeli M, Wilson DS. What's wrong with  
562 inclusive fitness? Trends in Ecology and Evolution 2006;21:597–8.
- 563 [21] Fudenberg D, Nowak M, Taylor C, Imhof L. Evolutionary game dy-  
564 namics in finite populations with strong selection and weak mutation.  
565 Theoretical Population Biology 2006;70:352–63.
- 566 [22] Garcia T, De Monte S. Group formation and the evolution of sociality.  
567 Evolution 2013;67(1):131–41.
- 568 [23] Godfrey-Smith P. Darwinian Populations and Natural Selection. Oxford  
569 University Press, Oxford, 2009.
- 570 [24] Goel N, Richter-Dyn N. Stochastic Models in Biology. Academic Press,  
571 New York, 1974.
- 572 [25] Gokhale CS, Traulsen A. Evolutionary games in the multiverse. Pro-  
573 ceedings of the National Academy of Sciences USA 2010;107:5500–4.
- 574 [26] Gokhale CS, Traulsen A. Evolutionary multiplayer games. Dynamic  
575 Games and Applications 2014;.
- 576 [27] Hamilton W. The evolution of altruistic behavior. American Naturalist  
577 1963;97(896):354–6.

- 578 [28] Hamilton WD. The genetical evolution of social behavior I and II. Jour-  
579 nal of Theoretical Biology 1964;7:1–16 + 17–52.
- 580 [29] Hammerschmidt K, Rose C, Kerr B, Rainey P. Life cycles, fitness decou-  
581 pling and the evolution of multicellularity. Nature 2014;515(7525):75–9.
- 582 [30] Hauert C, Michor F, Nowak M, Doebeli M. Synergy and discount-  
583 ing of cooperation in social dilemmas. Journal of Theoretical Biology  
584 2006;239:195–202.
- 585 [31] Hauert C, Imhof L. Evolutionary games in deme structured, finite pop-  
586 ulations. Journal of theoretical biology 2012;299:106–12.
- 587 [32] Hauert C, Chen Y, Imhof L. Fixation Times in Deme Structured, Fi-  
588 nite Populations with Rare Migration. Journal of Statistical Physics  
589 2014;156:739–59.
- 590 [33] Hölldobler B, Wilson E. The Ants. Belknap Press, 1990.
- 591 [34] Hui C, McGeoch MA. Spatial patterns of prisoner’s dilemma game in  
592 metapopulations. Bulletin of Mathematical Biology 2007;69(2):659–76.
- 593 [35] Kandori M, Mailath GJ, Rob R. Learning, mutation, and long run  
594 equilibria in games. Econometrica 1993;61:29–56.
- 595 [36] Karlin S, Taylor HMA. A First Course in Stochastic Processes. 2nd ed.  
596 London: Academic, 1975.
- 597 [37] Kelly JK. Restricted migration and the evolution of altruism. Evolution  
598 1992;46:1492–5.
- 599 [38] Kerr B, Godfrey-Smith P, Feldman MW. What is altruism? TREE  
600 2004;19(3):135–40.
- 601 [39] Koschwanez J.H., Foster K.R., Murray A.W. Improved use of a public  
602 good selects for the evolution of undifferentiated multicellularity. Elife  
603 2013;2:e00367.
- 604 [40] Kurokawa S, Ihara Y. Emergence of cooperation in public goods games.  
605 Proceedings of the Royal Society B 2009;276:1379–84.

- 606 [41] Libby E., Rainey P. A conceptual framework for the evolutionary origins  
607 of multicellularity. *Physical Biology* 2013;10(3):035001.
- 608 [42] Libby E., Ratcliff W., Travisano M., Kerr B. Geometry shapes  
609 evolution of early multicellularity. *PLoS Computational Biology*  
610 2014;10(9):e1003803.
- 611 [43] Mesterton-Gibbons M, Dugatkin L. Cooperation among unrelated  
612 individuals: evolutionary factors. *Quarterly Review of Biology*  
613 1992;67(3):267–81.
- 614 [44] Milinski M. Tit for tat in sticklebacks and the evolution of cooperation.  
615 *Nature* 1987;325(6103):433–5.
- 616 [45] Moran PAP. The estimation of the parameters of a birth and death pro-  
617 cess. *Journal of the Royal Statistical Society: Series B* 1953;15(2):241–5.
- 618 [46] Nowak M. *Evolutionary Dynamics*. Cambridge MA: Harvard University  
619 Press, 2006.
- 620 [47] Nowak M. Five rules for the evolution of cooperation. *Science*  
621 2006;314(5805):1560–3.
- 622 [48] Nowak M, Sasaki A, Taylor C, Fudenberg D. Emergence of cooperation  
623 and evolutionary stability in finite populations. *Nature* 2004;428:646–50.
- 624 [49] Ohtsuki H. Does synergy rescue the evolution of cooperation? an  
625 analysis for homogeneous populations with non-overlapping generations.  
626 *Journal of Theoretical Biology* 2012;307:20–8.
- 627 [50] Pacheco JM, Santos FC, Souza MO, Skyrms B. Evolutionary dynamics  
628 of collective action in n-person stag hunt dilemmas. *Proceedings of the*  
629 *Royal Society B* 2009;276:315–21.
- 630 [51] Peña J. Group size diversity in public goods games. *Evolution*  
631 2012;66:623–36.
- 632 [52] Pfeiffer T, Bonhoeffer S. An evolutionary scenario for the transition to  
633 undifferentiated multicellularity. *Proceedings of the National Academy*  
634 *of Sciences of the United States of America* 2003;100(3):1095–8.

- 635 [53] Porat D, Chadwick-Furman N. Effects of anemonefish on giant sea  
636 anemones: expansion behavior, growth, and survival. *Hydrobiologia*  
637 2004;530(1–3):513–20.
- 638 [54] Powers S, Penn A, Watson R. The concurrent evolution of coop-  
639 eration and the population structures that support it. *Evolution*  
640 2011;65(6):1527–43.
- 641 [55] Purcell J, Brelsford A, Avilés L. Co-evolution between sociality and  
642 dispersal: The role of synergistic cooperative benefits. *Journal of The-*  
643 *oretical Biology* 2012;312C:44–54.
- 644 [56] Rainey PB, Kerr B. Cheats as first propagules: A new hypothesis for  
645 the evolution of individuality during the transition from single cells to  
646 multicellularity. *BioEssays* 2010;32(10):872–80.
- 647 [57] Rainey PB, Rainey K. Evolution of cooperation and conflict in experi-  
648 mental bacterial populations. *Nature* 2003;425(6953):72–4.
- 649 [58] Ratcliff W, Herron M, Howell K, Pentz J, Rosenzweig F, Travisano M.  
650 Experimental evolution of an alternating uni-and multicellular life cycle  
651 in *Chlamydomonas reinhardtii*. *Nature Communications* 2013;4.
- 652 [59] Sigmund K. The calculus of selfishness. Princeton Univ. Press, 2010.
- 653 [60] Simon B, Fletcher JA, Doebeli M. Towards a general theory of group  
654 selection. *Evolution* 2013;67(6):1561–72.
- 655 [61] Stein J. A morphologic and genetic study of *Gonium pectorale*. *Ameri-*  
656 *can Journal of Botany* 1958;45:664–72.
- 657 [62] Stephens D, Anderson J. Reply to roberts: cooperation is an outcome,  
658 not a mechanism. *Animal Behaviour* 1997;53(6):1363–4.
- 659 [63] Tarnita C, Taubes C, Nowak M. Evolutionary construction by stay-  
660 ing together and coming together. *Journal of Theoretical Biology*  
661 2013;320:10–22.
- 662 [64] Traulsen A, Hauert C. Stochastic evolutionary game dynamics. In:  
663 Schuster HG, editor. *Reviews of Nonlinear Dynamics and Complexity*.  
664 Weinheim: Wiley-VCH; volume 2; 2009. p. 25–61.

- 665 [65] Traulsen A, Nowak M. Evolution of cooperation by multi-level selection.  
666 Proceedings of the National Academy of Sciences of the United States  
667 of America 2006;103:10952–5.
- 668 [66] Traulsen A, Shores N, Nowak M. Analytical results for individual  
669 and group selection of any intensity. Bulletin of Mathematical Biology  
670 2008;70:1410–24.
- 671 [67] van Veelen M. Group selection, kin selection, altruism and cooperation:  
672 when inclusive fitness is right and when it can be wrong. Journal of  
673 Theoretical Biology 2009;259(3):589–600.
- 674 [68] Velicer GJ, Yuen-tsu NY. Evolution of novel cooperative swarming in  
675 the bacterium myxococcus xanthus. Nature 2003;425(6953):75–8.
- 676 [69] Wakano J, Nowak M, Hauert C. Spatial dynamics of ecological pub-  
677 lic goods. Proceedings of the National Academy of Sciences USA  
678 2009;106:7910–4.
- 679 [70] Wakano JY, Hauert C. Pattern formation and chaos in spatial ecological  
680 public goods games. Journal of Theoretical Biology 2011;268(1):30–8.
- 681 [71] Wilson D. A theory of group selection. Proceedings of the National  
682 Academy of Sciences of the United States of America 1975;72(1):143–6.
- 683 [72] Wilson D. The natural selection of populations and communities. Ben-  
684 jamin/Cummings, Menlo Park, CA, 1980.
- 685 [73] Wilson DS, Wilson EO. Rethinking the theoretical foundation of socio-  
686 biology. Quarterly Review of Biology 2007;82:327–48.
- 687 [74] Wingreen N., Levin S. Cooperation among microorganisms. PLoS Biol-  
688 ogy 2006;4(9):e299.
- 689 [75] Wu B., Altrock P.M., Wang L., Traulsen A. Universality of weak elec-  
690 tion. Physical Review E 2010;82:046106.
- 691 [76] Wu B., Bauer B., Galla T., Traulsen A. Fitness-based models  
692 and pairwise comparison models of evolutionary games are typically  
693 different—even in unstructured populations. New Journal of Physics  
694 2015;17(2):023043.