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## Evolutionary games in deme structured, finite populations

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## ABSTRACT

We describe a fairly general model for the evolutionary dynamics in a sub-divided (or deme structured) population with migration and mutation. The number and size of demes are finite and fixed. The fitness of each individual is determined by pairwise interactions with other members of the same deme. The dynamics within demes can be modeled according to a broad range of evolutionary processes. With a probability proportional to fitness, individuals migrate to another deme. Mutations occur randomly. In the limit of few migrations and even rarer mutations we derive a simple analytic condition for selection to favor one strategic type over another. In particular, we show that the Pareto efficient type is favored when competition within demes is sufficiently weak. We then apply the general results to the prisoner's dilemma game and discuss selected dynamics and the conditions for cooperation to prevail.

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## 1. Introduction

Evolutionary dynamics in viscous populations (Wilson et al., 1992; Kelly, 1992), island models (Taylor et al., 2000; Wakeley, 2003) or deme structured populations (Wilson, 1977; Nunney, 1985) has a long history in evolutionary biology and is a classic in population genetics (Wright, 1931). Of particular interest is the effect of population structure on the evolution of cooperation – for recent reviews see e.g. Nowak et al. (2010); Szabó and Fáth (2007). The object of the present paper is to help to understand the emergence and maintenance of traits that benefit the group but are costly to the individual.

We introduce a simple stochastic model that describes the evolution of a finite population that is divided into independent subunits, termed demes. The size and number of demes are constant. There are two types of individuals: *A* and *B*. Individuals interact in pairs and only with other members of the same deme. This determines their fitness and drives the evolutionary dynamics. In addition, our model allows for mutations between the two types as well as for migrations from one deme to another. The mutation rate is constant but the migration rate is proportional to fitness. Hence, demes with a higher average fitness also have a higher reproductive output than those with lower average fitness. This type of evolutionary dynamics in subdivided populations has also been termed 'hard selection' (see e.g. Christiansen, 1975; Wade, 1985; Lessard, 2009) because the number of migrants depends on the fitness of individuals within a deme – as opposed to 'soft selection' where each

deme produces, on average, the same number of migrants. A similar ecological feedback can be achieved if the deme size (or population density) depends on the average fitness (Hauert et al., 2008; Wakano et al., 2009) or if demes represent a transient aggregation of individuals (Fletcher and Zwick, 2004).

To compare the overall success of the two strategic types, we consider the long-run behavior of the dynamics. If the time average of the fraction of type *A* individuals is larger than that of type *B*, we say type *A* is favored in the deme model. For small mutation and migration rates but with mutation being rarer than migration, we derive a simple criterion for type *A* to be favored based on the fixation probability of a single mutant within a deme and the fitness values obtained in homogeneous demes. Our selection result is very general and covers any fixed population size, any number of demes and any intensity of selection and is moreover applicable to a broad class of processes describing evolutionary dynamics within the demes. We focus on the frequency-dependent Moran process (Nowak et al., 2004) and on the pairwise comparison process (Traulsen et al., 2005).

As an application, we consider the evolution of cooperation. In the prisoner's dilemma defection is the dominant strategy but groups of cooperators outperform groups of defectors. This generates a conflict of interest referred to as social dilemmas (Dawes, 1980; Hauert et al., 2006). In the present context this means that defectors have a selective advantage within demes. However, for each deme there is a small but positive probability that cooperators take over due to stochastic effects. Whenever they do, they have a higher fitness than members of demes containing only defectors. Therefore, there will be more migrations from cooperator demes to defector demes than in the opposite direction. Thus, on the two levels of the evolutionary dynamics, selection

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works in different directions: against cooperators within demes and in favor of cooperators between demes.

For the frequency-dependent Moran process, it turns out that deme structure is not sufficient to support cooperation in the prisoner's dilemma. Defection is favored for any number of demes and any population size. On the other hand, under the pairwise comparison process, cooperation may be favored in the deme model depending on the strength of competition within demes. Our analytical results hold in the limit of small mutation and migration rates, but all the findings are substantiated by extensive individual based simulations for fixed positive rates.

## 2. The model

We consider a finite population of size  $M$  that is divided into  $D$  demes of equal size  $N$  ( $M = D \cdot N$ ). Each individual is either of type  $A$  or  $B$ . At each point in time  $t$ , one of three possible actions takes place: (i) the composition in one randomly selected deme changes according to some frequency-dependent process, as described below. The states of the other demes remain unchanged. (ii) With probability  $\mu$  one individual migrates. Specifically, with a probability proportional to fitness, one individual of the entire population is chosen to produce an offspring of the same type. The offspring then migrates to one of the other demes and replaces a randomly chosen individual of that deme. (iii) With probability  $\nu$ , a mutation occurs, that is, one individual is replaced by an individual of the opposite type. All individuals are equally likely to mutate.

In the absence of mutation and migration we consider the evolution in each deme individually. In each deme, the two states where only type  $A$  or only type  $B$  is present are absorbing. Eventually a deme reaches either one of the absorbing states from any initial composition. Examples of evolutionary processes that satisfy these requirements include the frequency-dependent Moran process (Nowak et al., 2004), the pairwise comparison process (Traulsen et al., 2005), the frequency-dependent Wright–Fisher process (Imhof and Nowak, 2006), and certain imitation and aspiration processes (e.g. Binmore and Samuelson, 1997; Schlag, 1998; Fudenberg and Imhof, 2008).

For migration rates  $\mu > 0$ , the entire population has only two absorbing states where either all individuals are of type  $A$  or all individuals are of type  $B$ . If  $\mu$  is small, all demes are homogeneous when a migration occurs. Let  $\rho_{AB}$  denote the probability that a single migrant of type  $B$  takes over a deme that consists otherwise of type  $A$  only. Similarly, let  $\rho_{BA}$  be the corresponding fixation probability for a single migrant of type  $A$ . For all the processes above (with the exception of the Wright–Fisher process) simple explicit formulas for  $\rho_{AB}$  and  $\rho_{BA}$  are known. The rate at which a deme produces migrants is determined by the fitness of its members –  $F_A$  for a homogeneous deme of type  $A$  and  $F_B$  for type  $B$  demes. The time evolution of the number of homogeneous demes of a particular type naturally recovers the Moran process (Moran, 1962).

For mutation rates  $\nu > 0$  no absorbing states remain and instead every state is reached with a certain probability. In the limit of rare migration  $\mu \rightarrow 0$  and rare mutations  $\nu \rightarrow 0$ , but such that migrations occur much more often than mutations ( $\mu \gg \nu$ ), the population spends almost all the time in the homogeneous states with all individuals of type  $A$  or all of type  $B$ . In this limit, we provide an analytical derivation of the fraction of time,  $f_A$ , spent in the state with all  $A$ 's and  $f_B = 1 - f_A$  spent with all  $B$ 's.

### 2.1. The simplified chain

We describe the evolution of the population by a homogeneous discrete-time Markov chain  $\{X(t) : t = 0, 1, \dots\}$  with state

space  $\mathcal{X} = \{0, \dots, N\}^D$ . The  $i$ th component of  $X(t)$  is the number of type  $A$  individuals in deme  $i$  at time  $t$ . Clearly, in the absence of mutation and migration, the set of absorbing states of  $\{X(t)\}$  is  $\mathcal{A} = \{0, N\}^D$ . If the mutation probability  $\nu$  is positive, then  $\{X(t)\}$  is ergodic and has a unique invariant distribution, which describes the long-run proportion of time that  $\{X(t)\}$  spends in each state.

We assume that the ratio of the migration probability  $\mu$  to the mutation probability  $\nu$  is fixed. Write  $\mu = \mu_0 \varepsilon$  and  $\nu = \nu_0 \varepsilon$  for some fixed  $\mu_0 \geq 0$  and  $\nu_0 > 0$ . We denote the transition probabilities of  $\{X(t)\}$  by  $p_\varepsilon(x, x')$ ,  $\varepsilon \geq 0$ , and the ergodic distribution by  $\pi_\varepsilon$ ,  $\varepsilon > 0$ . If  $\varepsilon = 0$ , then the states in  $\mathcal{A}$  are absorbing. This implies that for small  $\varepsilon > 0$ ,  $\{X(t)\}$  spends almost all the time in  $\mathcal{A}$ , so that

$$\lim_{\varepsilon \rightarrow 0} \pi_\varepsilon(x) = 0 \quad \text{for all } x \in \mathcal{X} \setminus \mathcal{A}. \tag{1}$$

To determine the proportion of time that  $X(t)$  spends at the individual states of  $\mathcal{A}$  we consider a simpler Markov chain that records only transitions of  $\{X(t)\}$  between states in  $\mathcal{A}$  but ignores the details of these transitions. Specifically, we follow the approach of Fudenberg and Imhof (2006) and consider a Markov chain with reduced state space  $\mathcal{A}$  and transition probabilities  $\Lambda(x, y)$  given by  $\Lambda(x, y) = \sum_{x' \in S(x)} \tau(x, x') \rho(x', y)$  for  $x \neq y$  and  $\Lambda(x, x) = 1 - \sum_{y \neq x} \Lambda(x, y)$ , where  $S(x)$  is the set of states in  $\mathcal{X} \setminus \{x\}$  that  $\{X(t)\}$  can reach from  $x$  in a single step by mutation or migration;  $\tau(x, x') = \lim_{\varepsilon \rightarrow 0} p_\varepsilon(x, x') / \varepsilon$  and  $\rho(x', y)$  is the probability that starting from  $x'$ ,  $\{X(t)\}$  gets absorbed at  $y$  when there are no mutations or migrations.

If  $(\lambda(x) : x \in \mathcal{A})$  is the unique invariant distribution for this chain, then the limit of the ergodic distribution of  $\{X(t)\}$  for small mutation probabilities is given by

$$\lim_{\varepsilon \rightarrow 0} \pi_\varepsilon(x) = \lambda(x), \quad x \in \mathcal{A}, \tag{2}$$

see Theorem 2 of Fudenberg and Imhof (2006) for details.

To calculate  $\Lambda(x, y)$ , fix a state  $x \in \mathcal{A}$ . Suppose that  $k$  entries of  $x$  are equal to  $N$  and the other  $D - k$  entries are 0. That is, if  $X(0) = x$ , there are  $k$  pure  $A$  demes and  $D - k$  pure  $B$  demes. Then there are  $D$  states other than  $x$  itself which  $\{X(t)\}$  can reach from  $x$  in one step:  $k$  states where a single individual of type  $B$  occurs in one of the  $k$   $A$  demes and  $D - k$  states with one individual of type  $A$  in one of the  $D - k$   $B$  demes. Suppose that  $x'$  is a state of the second type. The chance that a mutant of type  $A$  occurs in a given  $B$  deme is  $\nu/D$ . The overall fitness of the population is  $kN F_A + (D - k)N F_B$ , where  $F_A, F_B$  denotes the fitness of members of pure  $A$  and pure  $B$  demes, respectively. The chance that an individual of type  $A$  migrates to a given  $B$  deme is given by

$$\mu \frac{k F_A}{k F_A + (D - k) F_B} \frac{1}{D - 1}. \tag{3}$$

Hence

$$\tau(x, x') = \nu_0 \frac{1}{D} + \mu_0 \frac{k F_A}{k F_A + (D - k) F_B} \frac{1}{D - 1}. \tag{4}$$

Suppose now that  $X(1) = x'$ . Then there are two states where  $\{X(t)\}$  can get absorbed in the absence of mutation and migration: either at  $x$  or at the state  $y'$ , say, where the single individual of type  $A$  successfully invaded the  $B$  deme and has overtaken that deme. Clearly,  $\rho(x', y') = \rho_{BA}$ , and so

$$\Lambda(x, y') = \left[ \nu_0 \frac{1}{D} + \mu_0 \frac{k F_A}{k F_A + (D - k) F_B} \frac{1}{D - 1} \right] \rho_{BA}. \tag{5}$$

Similarly, if  $y''$  denotes one of the  $k$  states obtained from  $x$  by replacing an  $A$  deme with a  $B$  deme,

$$\Lambda(x, y'') = \left[ \nu_0 \frac{1}{D} + \mu_0 \frac{(D - k) F_B}{k F_A + (D - k) F_B} \frac{1}{D - 1} \right] \rho_{AB}. \tag{6}$$

The remaining transition probabilities  $\Lambda(x, y)$ , where  $y$  differs from  $x$  in more than one position, are zero.

To calculate  $(\lambda(x) : x \in \mathcal{A})$ , recall that all demes are pure and either of type *A* or type *B* such that we can further simplify the chain by lumping together those states in  $\mathcal{A}$  that have the same number of pure demes of each type. Thus for  $k = 0, \dots, D$ , let  $A_k$  denote the set of all  $x \in \mathcal{A}$  with  $k$  entries equal to *N*. The states of the lumped process are  $A_0, \dots, A_D$  and the probability of a transition from  $A_k$  to  $A_\ell$  is

$$\hat{p}_{k\ell} = \sum_{y \in A_\ell} A(x, y), \tag{7}$$

where  $x$  is any state in  $A_k$ . Note that the expression on the right-hand side does not depend on the choice of  $x \in A_k$ , so that the lumped process is a well-defined Markov chain (Kemeny and Snell, 1960, p. 124). Moreover, the chain so obtained is a birth-death process with

$$\hat{p}_{k,k+1} = (D-k) \left[ v_0 \frac{1}{D} + \mu_0 \frac{kF_A}{kF_A + (D-k)F_B} \frac{1}{D-1} \right] \rho_{BA}, \quad k = 0, \dots, D-1, \tag{8}$$

$$\hat{p}_{k,k-1} = k \left[ v_0 \frac{1}{D} + \mu_0 \frac{(D-k)F_B}{kF_A + (D-k)F_B} \frac{1}{D-1} \right] \rho_{AB}, \quad k = 1, \dots, D, \tag{9}$$

$$\hat{p}_{kk} = 1 - \hat{p}_{k,k-1} - \hat{p}_{k,k+1}, \quad k = 1, \dots, D-1, \tag{10}$$

and the boundary conditions

$$\hat{p}_{00} = 1 - \hat{p}_{01}, \quad \hat{p}_{DD} = 1 - \hat{p}_{D,D-1}. \tag{11}$$

The invariant distribution for the lumped process is given by  $(\phi_0, \dots, \phi_D)$ , where

$$\phi_k = \phi_0 \prod_{i=1}^k \frac{\hat{p}_{i-1,i}}{\hat{p}_{i,i-1}}, \quad k = 1, \dots, D, \tag{12}$$

and  $\phi_0$  is chosen such that  $\phi_0 + \dots + \phi_D = 1$  (Ewens, 2004, p. 91). Hence

$$\lambda(x) = \frac{\phi_k}{|A_k|} = \frac{k!(D-k)!}{D!} \phi_k \quad \text{for all } x \in A_k. \tag{13}$$

If migrations occur much more often than mutations, that is,  $v_0 \ll \mu_0$ , then for small  $\varepsilon$ ,  $\{X(t)\}$  spends almost all the time at the states  $ALL A = (N, \dots, N)$  and  $ALL B = (0, \dots, 0)$ . Thus,

$$\lim_{\varepsilon \rightarrow 0} \frac{p_\varepsilon(ALL A)}{p_\varepsilon(ALL B)} = \frac{\lambda(ALL A)}{\lambda(ALL B)} = \frac{\phi_D}{\phi_0} \approx \left( \frac{\rho_{BA}}{\rho_{AB}} \right)^D \left( \frac{F_A}{F_B} \right)^{D-1}. \tag{14}$$

The fraction of time that the population spends at  $ALL A$  is simply  $f_A = \phi_D$ . In the above limit,  $\phi_i \rightarrow 0$ ,  $i = 1, \dots, D-1$  and  $\phi_0 + \phi_D \rightarrow 1$  holds such that  $f_A$  equally denotes the average fraction of cooperators in the population and is given by:

$$f_A = \left( 1 + \frac{F_A}{F_B} \left( \frac{\rho_{AB} F_B}{\rho_{BA} F_A} \right)^D \right)^{-1}. \tag{15}$$

Selection is said to favor *A* if the population spends more time with all individuals of type *A* than with all of type *B*. If the population is not subdivided ( $D=1$ ), then selection favors *A* if and only if  $\rho_{BA} > \rho_{AB}$  (Fudenberg et al., 2006). However, our analysis shows that for subdivided populations selection may favor *A* even if  $\rho_{BA} < \rho_{AB}$  provided that  $F_A > F_B$  and there are sufficiently many demes  $D$ . This holds whenever  $f_A > \frac{1}{2}$  or, equivalently, if:

$$\frac{\rho_{BA}}{\rho_{AB}} > \left( \frac{F_B}{F_A} \right)^{1-1/D}. \tag{16}$$

Thus, even though type *A* may be selected against on the deme level ( $\rho_{BA} < \rho_{AB}$ ) it may still be favored on the population level if demes of type *A* have a sufficiently high reproductive output as compared to demes of type *B* such as to compensate for selective disadvantages when individuals of type *A* and *B* compete within a single deme.

## 2.2. Weak competition within demes

According to our analysis Eq. (16), selection always favors the Pareto efficient type if the population is divided into two or more demes and competition within demes is sufficiently weak. Specifically, suppose the fixation probabilities  $\rho_{BA}$  and  $\rho_{AB}$  depend continuously on the strength of competition  $\beta$  such that they converge to  $1/N$  as  $\beta \rightarrow 0$ . In this limit the dynamics within each deme corresponds to neutral drift and the left-hand side of (16) converges to 1. If type *A* is Pareto efficient, that is,  $F_A > F_B$ , and if there are at least two demes, then condition (16) is satisfied if  $\beta$  is sufficiently small. Therefore, selection favors *A* for weak competition. Note that if selection favors a Pareto efficient type for a certain intensity  $\beta_0$  and a certain number of demes  $D_0$ , then the type is also favored for the same intensity  $\beta_0$  and any number of demes  $D \geq D_0$ . In particular, if an efficient type is favored in a single deme, then the type continues to be favored for any number of demes of the same size.

## 2.3. Levels of selection

Because selection acts differently on the level of demes within a population and on the level of individuals within a deme, such scenarios are often referred to as group selection (Leigh, 1983; Wynne-Edwards, 1986; Ono et al., 2003), multi-level selection (Frank, 1998; Keller, 1999; Traulsen and Nowak, 2006) or sometimes spatial selection (Wang et al., 2011). However, we note that in our framework the unit of selection remains the individual but the successful spreading of group beneficial traits can be mediated by selective advantages arising at the level of demes. This can be viewed as an essential first step towards the major transitions in the evolutionary history of life (Maynard Smith and Szathmary, 1995), which has repeatedly lead to the integration of lower level units into higher level entities as exemplified by the transitions from genes to chromosomes, or from uni-cellular to multi-cellular organisms as well as the transition from individuals to societies. At least in the first two examples this transition is accompanied by a change in the unit of selection – shifting from lower level units to higher level entities.

The most prominent example of such opposing selective forces is, of course, represented by the problem of cooperation in social dilemmas and the prisoner’s dilemma in particular.

## 3. Applications to the problem of cooperation

Let us consider pairwise interactions characterized by the general  $2 \times 2$  payoff matrix

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}. \tag{17}$$

If two individuals of type *A* interact, each gets  $a$ , two type *B* players receive  $d$  each and if an *A* player meets a *B* player, the former gets  $b$  and the latter  $c$ . Suppose that type *A* corresponds to cooperation and type *B* to defection, then the prisoner’s dilemma is defined by the payoff ranking  $c > a > d > b$ . Thus, irrespective of the other player’s decision it is always better to defect and hence defection is the dominant strategy. However, mutual cooperation is preferred over mutual defection ( $a > d$ ).

In a deme with  $j$  individuals of type *A* (and  $N-j$  of type *B*) the average payoff of an *A* player is given by  $\pi_A(j) = ((j-1)a + (N-j)b)/(N-1)$  and for a *B* player by  $\pi_B(j) = (jc + (N-1-j)d)/(N-1)$ . The fitness of each individual is determined by its average payoff and must be non-negative in order to be biologically meaningful. Here we consider two popular and mathematically convenient mappings: (i) the fitness is given by  $\exp(\omega\pi_A(j))$  and

$\exp(\omega\pi_B(j))$ , respectively, where  $0 \leq \omega < \infty$  determines the intensity of selection on fitness differences between A and B types (Traulsen et al., 2008); (ii) the fitness is given by the convex combination of the static baseline fitness, which is normalized to 1 for all players, and the average payoffs,  $1-w+w\pi_A(j)$  and  $1-w+w\pi_B(j)$ , respectively (Nowak et al., 2004). The intensity of selection  $0 \leq w \leq w_{\max} \leq 1$  determines the relative weight of the static and dynamic fitness components. The maximum selection intensity  $w_{\max}$  ensures that fitness remains non-negative in case one or more entries in the payoff matrix (17) are negative and is given by  $w_{\max} = 1/(1 - \min\{0, a, b, c, d\})$ . Alternatively, the payoffs in Eq. (17) can be rescaled by adding a constant or a scalar multiplication. Both operations leave the replicator dynamics (Hofbauer and Sigmund, 1998) in infinite populations unchanged and in finite populations they essentially correspond to adjusting the baseline fitness and selection strength,  $w$ .

Note that the derivation of Eq. (16) involves only mild assumptions on the dynamics within the demes and none on the payoff-to-fitness mapping, so that we can test its predictive power for different scenarios. First we consider the frequency-dependent Moran process (Nowak et al., 2004) and then turn to the pairwise comparison process (Szabó and Töke, 1998; Traulsen et al., 2006).

### 3.1. Moran process

If the dynamics in each deme is given by the frequency-dependent Moran process (Nowak et al., 2004; Traulsen and Hauert, 2009), then an explicit expression can be derived for the fraction of time,  $f_A$ , that the population spends in a homogeneous state A (see Eq. (15)).

#### 3.1.1. Linear fitness, $1-w+w\pi_A(j)$

The fixation probability  $\rho_{AB}$  ( $\rho_{BA}$ ) of a single defector (cooperator) in a cooperator (defector) deme is given by:

$$\rho_{AB} = \left( 1 + \sum_{i=1}^{N-1} \prod_{j=1}^i \frac{1-w+w\pi_A(N-j)}{1-w+w\pi_B(N-j)} \right)^{-1} \quad (18)$$

$$\rho_{BA} = \left( 1 + \sum_{i=1}^{N-1} \prod_{j=1}^i \frac{1-w+w\pi_B(j)}{1-w+w\pi_A(j)} \right)^{-1} \quad (19)$$

and the ratio simplifies to

$$\begin{aligned} \frac{\rho_{AB}}{\rho_{BA}} &= \prod_{j=1}^{N-1} \frac{1-w+w\pi_B(N-j)}{1-w+w\pi_A(N-j)} \\ &= \left( \frac{c-d}{a-b} \right)^{N-1} \frac{1-w+wc}{1-w+wd} \frac{\Gamma\left(\frac{(N-1)(1-w+wc)}{(c-d)w}\right) \Gamma\left(\frac{(N-1)(1-w+wb)}{(a-b)w}\right)}{\Gamma\left(\frac{(N-1)(1-w+wd)}{(c-d)w}\right) \Gamma\left(\frac{(N-1)(1-w+wa)}{(a-b)w}\right)}. \end{aligned} \quad (20)$$

It is easy to see that for the Moran process cooperation is never favored in the prisoner's dilemma because the payoff of defectors always exceeds the payoff of cooperators,  $\pi_A(j) < \pi_B(j)$  for all  $j \in \{1, 2, \dots, N-1\}$ . The characteristic payoff ranking ( $b < d$  and  $c > a$ , in particular) allows to derive a lower bound for the fixation probability  $\rho_{AB}$  of a single defector in a cooperator population:

$$\begin{aligned} \frac{1}{\rho_{AB}} &< 1 + \sum_{i=1}^{N-1} \prod_{j=1}^i \frac{1-w+w(dj+a(N-1-j))/(N-1)}{1-w+w(d(j-1)+a(N-j))/(N-1)} \\ &= 1 + \sum_{i=1}^{N-1} \frac{1-w+w(di+a(N-1-i))/(N-1)}{1-w+wa} \\ &= \frac{N}{2} \left( \frac{1-w+wd}{1-w+wa} + 1 \right) = \frac{N}{2} \left( \frac{F_B}{F_A} + 1 \right), \end{aligned} \quad (21)$$

where  $F_A, F_B$  denote the fitness of individuals in pure A and B demes, respectively. Similarly, an upper bound is obtained for the fixation probability  $\rho_{BA}$  of a single cooperator in a defector population:

$$\frac{1}{\rho_{BA}} > \frac{N}{2} \left( \frac{F_A}{F_B} + 1 \right) \quad (22)$$

and hence

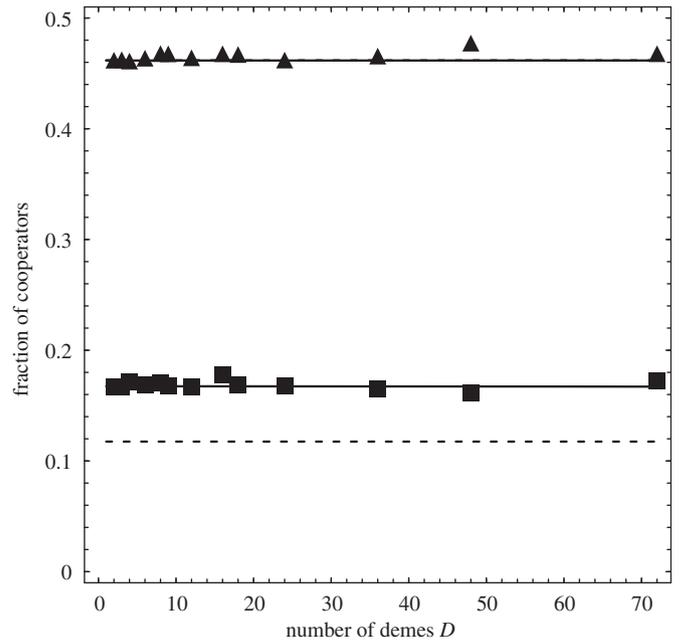
$$\frac{\rho_{BA}}{\rho_{AB}} < \frac{F_B}{F_A} < \left( \frac{F_B}{F_A} \right)^{1-1/D} \quad (23)$$

follows for all  $D \geq 1$  and  $0 < w \leq 1$  because  $a > d$ . Consequently, condition (16) is never satisfied. Increasing the number of demes barely affects the time spent in the state with all cooperators (see Fig. 1). In fact, there is even a weak trend in the opposite direction such that increasing the number of demes  $D$  actually impedes cooperation (note that this trend is too weak to be visible in Fig. 1).

In the weak selection limit ( $w \rightarrow 0$ ), the average time spent in the cooperative state becomes particularly simple:

$$f_A = \frac{1}{2} - \frac{w}{8} (2(a-d) - D \cdot N(a+b-c-d)). \quad (24)$$

Again, it is easy to see that  $f_A < \frac{1}{2}$  always holds for the payoff ranking of the prisoner's dilemma. Interestingly, in this limit,  $f_A$  only depends on the population size  $M = D \cdot N$  and not on the number or size of the demes. Consequently, deme structured populations are insufficient to enable selection to favor cooperation.



**Fig. 1.** Effects of deme structures in finite populations on the evolution of cooperation in the frequency-dependent Moran process. Cooperation is never favored and the system always spends more time in a state with all defectors than in a state with all cooperators. Decreasing the cost-to-benefit ratio of cooperation,  $r$ , or decreasing the selection strength,  $w$ , increases the average time spent in the cooperative state. Rather surprisingly, however, the time in the cooperative state barely depends on the number of demes. Parameters:  $M=144$ ,  $a=1$ ,  $b=0$ ,  $c=1+r$ ,  $d=r$  with  $r=0.1$  and a selection strength  $w=0.1$  (simulation data ■) as well as for weak selection  $w=0.01$  (▲). The solid lines indicate the analytical solution (see Eq. (15)) and the dashed line marks the weak selection approximation (see Eq. (25)) for  $w=0.1$  but is indistinguishable from the solid line for  $w=0.01$ . For the simulations the mutation rate was  $\nu = 10^{-6}$ , the migration rate  $\mu = 10^{-2}$  and the results were averaged over  $10^9$ – $10^{10}$  generations.

### 3.1.2. Exponential fitness, $\exp(\omega\pi_A(j))$

In this case the fixation probability  $\rho_{AB}$  ( $\rho_{BA}$ ) of a single defector (cooperator) in a cooperator (defector) deme is given by:

$$\begin{aligned}\rho_{AB} &= \left(1 + \sum_{i=1}^{N-1} \prod_{j=1}^i \exp(\omega(\pi_A(N-j) - \pi_B(N-j)))\right)^{-1} \\ &= \left(1 + \sum_{i=1}^{N-1} \prod_{j=1}^i \exp\left(\frac{\omega}{N-1}(j(c-a+b-d) + N(a-c) + d-a)\right)\right)^{-1} \\ &= \left(\sum_{i=0}^{N-1} \exp(\omega i(u+v))\right)^{-1}\end{aligned}\quad (26)$$

$$\rho_{BA} = \left(\sum_{i=0}^{N-1} \exp(\omega i(u+v))\right)^{-1}\quad (27)$$

with  $u = (c-a+b-d)/[2(N-1)]$ ,  $v = (N(a-c)+d-a)/(N-1)$ ,  $v' = (N(d-b)+a-d)/(N-1)$ .

The fixation probabilities become particularly simple in the special case of ‘equal gains from switching’, that is, if  $c-a=d-b$  (Nowak and Sigmund, 1990). This states that the payoff gain achieved by switching from cooperation to defection against a cooperator is the same as the gain from switching strategies against a defector. A prominent case of equal-gains-from-switching for the prisoner’s dilemma occurs if cooperation incurs costs  $C$  to the actor and provides a benefit  $B > C > 0$  to the recipient, i.e. if  $a=B-C$ ,  $b=-C$ ,  $c=B$ , and  $d=0$ . These payoffs can be conveniently rescaled to  $a=1$ ,  $b=0$ ,  $c=1+r$ ,  $d=r$  where  $r=C/B \in (0,1)$  denotes the cost-to-benefit ratio. In this case,  $u=0$  and  $v=-v'=-r-1/(N-1) < 0$  holds and hence

$$\rho_{AB} = \left(\sum_{i=0}^{N-1} \exp(\omega i v)\right)^{-1} = \frac{e^{\omega v} - 1}{e^{\omega N v} - 1}\quad (28)$$

$$\rho_{BA} = \frac{e^{-\omega v} - 1}{e^{-\omega N v} - 1}\quad (29)$$

and the ratio simplifies to

$$\frac{\rho_{BA}}{\rho_{AB}} = \exp(\omega(N-1)v).\quad (30)$$

According to Eq. (15) the average fraction of cooperators in the population amounts to

$$f_A = (1 + \exp(\omega(D(d-a-(N-1)v)+a-d)))^{-1}.\quad (31)$$

For the cost–benefit formulation of the prisoner’s dilemma, the exponent in Eq. (31),  $D(d-a-(N-1)v)+a-d = D \cdot Nr - r + 1$ , is always positive and depends only on the total population size  $M = D \cdot N$ . Hence, the fraction of cooperators remains unaffected by deme structures and, moreover,  $f_A < \frac{1}{2}$  always holds.

### 3.2. Pairwise comparison

In the pairwise comparison process a randomly selected focal individual is replaced by clonal offspring of another randomly picked model individual with a probability that depends on the fitness difference between the model and the focal individual. Instead of modeling genetic transmission of the strategic type where the clonal offspring of the model replaces the focal individual, we could similarly consider cultural evolution where the focal individual occasionally reassesses its strategy and imitates other members of the same deme depending on their performance. A particularly interesting updating procedure is given by the Fermi function (Szabó and Tóke, 1998; Traulsen et al., 2006), where the focal individual adopts the strategy of the

model (through imitation or inheritance) with probability

$$P_{f \rightarrow m} = \frac{1}{1 + e^{-\beta(P_m - P_f)}}.$$

$P_m, P_f$  denote the fitness of the model and the focal individual and  $\beta$  represents a noise term that corresponds to the strength of competition within demes. For small  $\beta$ , competition is weak and the focal individual has only marginal preferences for the better performing strategy. In contrast, for large  $\beta$ , competition is strong such that the focal individual readily adopts any strategy that performs at least marginally better but basically never switches to a worse performing one. Note that in this scenario the exponential payoff-to-fitness mapping neither provides additional insights nor admits further analysis and hence we focus solely on the linear mapping.

The general results of Section 2.2 show that for  $D > 1$  cooperation is favored in the prisoner’s dilemma for any  $0 < w \leq w_{\max}$  if  $\beta$  is sufficiently small. Again, in the special case of ‘equal gains from switching’ a particularly simple, explicit threshold for  $\beta$  can be derived for the prisoner’s dilemma with costs and benefits. With  $a=1$ ,  $b=0$ ,  $c=1+r$ ,  $d=r$  where  $r=C/B \in [0,1]$  denotes the cost-to-benefit ratio of cooperation, we have  $w_{\max} = 1$  and condition (16) simplifies to:

$$\exp\left[-\beta \frac{N-1}{N} w(1+(N-1)r)\right] > (1-w(1-r))^{1-1/D}.$$

Hence, cooperation dominates if competition is sufficiently weak:

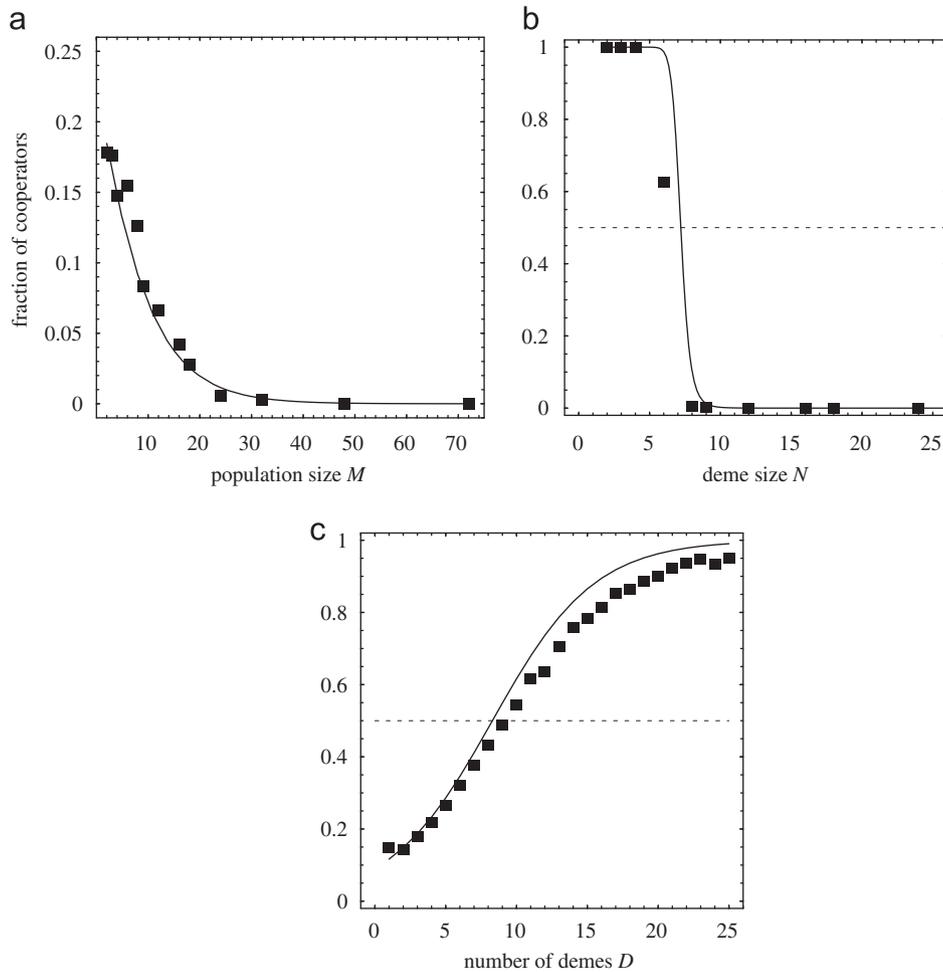
$$\beta < -\frac{(D-1)N}{D(N-1)} \cdot \frac{\ln(1-w(1-r))}{w(1+(N-1)r)}.\quad (32)$$

Note that in unstructured populations ( $D=1$ ) condition (32) is never satisfied (see Fig. 2a). In contrast, cooperation can dominate in deme structured populations even though cooperation is dominated in every single deme provided that there is a sufficient number of demes (see Fig. 2b, c). The reason for this outcome is that for weak competition, the higher reproductive output of cooperative demes can offset the disadvantage of cooperators in mixed demes. The average fraction of cooperators in a finite, deme structured population is shown in Fig. 3 as a function of the selection strength  $w$ , the strength of competition  $\beta$ , and the number of demes  $D$ .

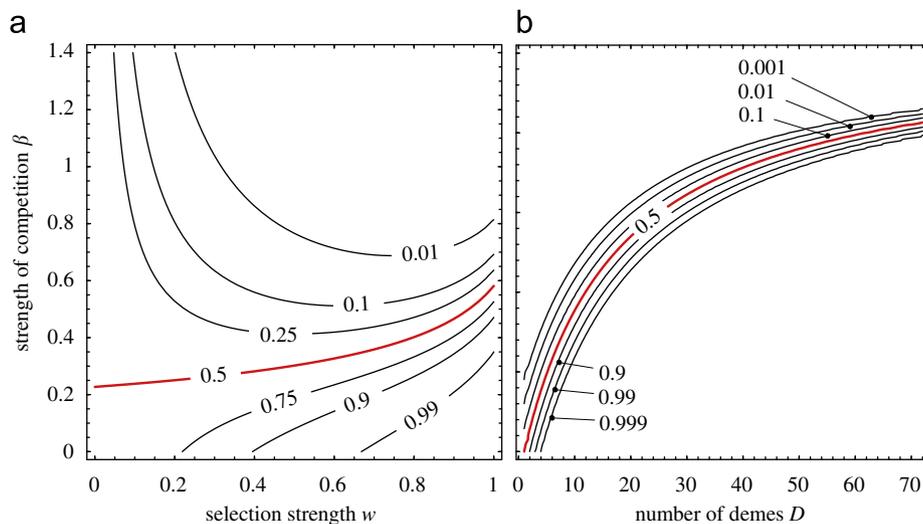
Note that for equal-gains-from-switching, the pairwise comparison process becomes equivalent to the original, frequency-independent Moran process (Moran, 1962; Traulsen et al., 2006) with a fixed resident fitness of 1 and a fixed mutant fitness of  $s = \exp[-\beta w(1+r(N-1))/(N-1)]$ . For the prisoner’s dilemma  $s < 1$  holds, which confirms that selection acts against cooperation in each deme but on the population level the odds may nevertheless be in favor of cooperators.

## 4. Conclusions

In contrast to infinite populations, rare mutations in finite populations can maintain Pareto efficiency even if this is a strictly dominated outcome (Nowak et al., 2004; Fudenberg et al., 2006). However, the fraction of time the population spends in the Pareto efficient state cannot exceed  $\frac{1}{2}$  and decreases exponentially with system size. This outcome changes considerably for populations that are subdivided into separate demes with limited migration among them. In this limit, the simple condition (16) determines whether the Pareto efficient outcome is favored. Most importantly, this condition is independent of the details of the evolutionary dynamics. In particular, it holds regardless of the fact that the Moran process (Nowak et al., 2004), Wright–Fisher process (Imhof and Nowak, 2006), pairwise comparison (Traulsen et al., 2005) or imitation dynamics (Binmore and Samuelson, 1997; Fudenberg and Imhof, 2008), may obviously result in different



**Fig. 2.** (a) In well-mixed populations ( $D=1$ ) playing the prisoner's dilemma, the average frequency of cooperators rapidly decreases with increasing population size  $M$  (simulation data, ■; analytical approximation, solid line). (b) In a population of fixed size ( $M=144$ ) cooperators can prevail for sufficiently large numbers of demes,  $D$  (and hence small  $N$ ). The strength of competition,  $\beta$ , was chosen such that for demes of size  $N \leq 6$  ( $D \geq 24$ ) the population spends more time cooperating. (c) For an increasing number of demes of fixed size ( $N=6$ ) the fraction of cooperators steadily increases.  $\beta$  was chosen such that the odds should change in favor of cooperation for  $D > 8$ . Parameters:  $r=0.1$ ,  $w=1$ ,  $\nu=10^{-6}$ , averages over  $10^8$ – $10^9$  generations; (a)  $D=1$ ; (b)  $M=144$ ,  $\beta=0.741$ ,  $\mu=10^{-2}$ ; (c)  $M=D \cdot N$ ,  $N=6$ ,  $\beta=1.35$ ,  $\mu=10^{-3}$ .



**Fig. 3.** Average fraction of cooperators (contour levels) as a function of the strength of competition  $\beta$  and (a) the selection strength  $w$  as well as (b) the number of demes  $D$ . The population size is constant  $M=144$  and the cost-to-benefit ratio is  $r=0.1$ . Above the bold (red) line defectors dominate and below cooperators are more frequent. (a) For sufficiently weak competition within demes,  $\beta$ , the system spends more time in the cooperative state. This effect becomes more pronounced for stronger selection,  $w$ . (b) Increasing the number of demes,  $D$ , strengthens the position of cooperators and they can prevail for a larger range of  $\beta$ . Parameters: (a)  $N=24$ ,  $D=6$ ; (b)  $N=144/D$ ,  $w=1$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

fixation probabilities of a single mutant strategy in one deme. Moreover, the Pareto efficient outcome is always favored if there are at least two demes and competition within demes is sufficiently weak.

The most prominent scenario where the Pareto efficient outcome cannot be achieved in the absence of supporting mechanisms is posed by the problem of cooperation as described by the prisoner's dilemma. Mutual cooperation is clearly the preferred outcome for both parties (Pareto optimum) but cooperation is dominated by defection because it is better to defect independent of the opponent's decision. The temptation of increased benefits for unilateral defection renders cooperation unstable – to the detriment of all. However, in deme structured populations cooperators may prevail and offset the inherent disadvantage against defectors because individuals in cooperative demes have a higher fitness and produce more offspring and more colonizing migrants, in particular.

Nevertheless, establishing cooperation remains challenging. For example, for the frequency-dependent Moran process (Nowak et al., 2004) cooperation is never favored and holds for linear or exponential payoff-to-fitness mappings (see Eqs. (24) and (31)). The intuitive reason is that the selection strength  $w$ , which determines the fitness differences between cooperators and defectors, has opposing effects on the evolutionary dynamics within and between demes. Lowering  $w$  promotes cooperation within demes by increasing the chance that a single cooperator succeeds in converting a defector deme. Conversely, increasing  $w$  promotes cooperation on the population level because cooperating demes have a much higher reproductive output. This echoes Taylor's (1992) conclusions that in deme structured populations the benefits of cooperation are canceled by competition among cooperators. In contrast, for the two-level Moran process in Traulsen and Nowak (2006) cooperation prevails more easily – specifically, in the limit of weak selection, if  $B/C > 1 + N/(D-2)$ . In this model demes essentially split into two with a probability proportional to fitness while eliminating another randomly chosen deme and hence cooperators only need to successfully invade a single deme.

In our model odds change in favor of cooperation when considering the pairwise comparison process (Traulsen et al., 2005, 2006). This process naturally introduces the strength of competition  $\beta$ . Within demes,  $\beta$  has the same effect as  $w$  but does not affect the reproductive output of demes. Hence, sufficiently weak competition in finite deme structured populations always leads to cooperation for any selection strength.

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