Advances in Complex Systems
Vol. 15, Suppl. No. 1 (2012) 1250059 (27 pages)
© World Scientific Publishing Company
DOI: 10.1142/S0219525912500592

OPTIMAL MIGRATION PROMOTES THE OUTBREAK OF COOPERATION IN HETEROGENEOUS POPULATIONS

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Received 6 February 2012
Revised 23 April 2012
Published 4 June 2012

We consider a population of agents that are heterogeneous with respect to (i) their strategy when interacting n_g times with other agents in an iterated prisoners dilemma game, (ii) their spatial location on K different islands. After each generation, agents adopt strategies proportional to their average payoff received. Assuming a mix of two cooperating and two defecting strategies, we first investigate for isolated islands the conditions for an exclusive domination of each of these strategies and their possible coexistence. This allows to define a threshold frequency for cooperation that, dependent on n_g and the initial mix of strategies, describes the outbreak of cooperation in the absence of migration. We then allow migration of a fixed fraction of the population after each generation. Assuming a worst case scenario where all islands are occupied by defecting strategies, whereas only one island is occupied by cooperators at the threshold frequency, we determine the optimal migration rate that allows the outbreak of cooperation on *all* islands. We further find that the threshold frequency divided by the number of islands, i.e., the relative effort for invading defecting islands with cooperators decreases with the number of islands. We also show that there is only a small bandwidth of migration rates, to allow the outbreak of cooperation. Larger migration rates destroy cooperation.

Keywords: Migration; cooperation; iterated prisoners dilemma.

1. Introduction

Human Migration, i.e., the movement of large numbers of people out of, or into specific geographical areas, is seen as one of the biggest challenges that face the human societies in the 21st century. On one hand, part of the human population has reasons to *emigrate* into countries which provide a "better" life — on the other hand, industrialized countries cannot sustain their current situation without the *immigration* of people. The real problem arises because the "demand" and the "supply" side cannot be matched. Industrialized countries fear that immigrants do not contribute to their further economic growth but, on the contrary, deplete their wealth by taking advantage of a social security, health, and educational system which they did not contribute to.

If we move this problem on the more abstract level of a game-theoretical model, we can distinguish between two types of agents: those *cooperating*, i.e., being able to integrate in a society and to contribute to a common good, namely economic growth, and those *defecting*, i.e., without the ability to socially integrate and thus depleting a common good at the cost of the cooperating agents. Certainly, based on their past experience, agents can adapt, i.e., they can change their strategy from defection to cooperation and vice versa dependent on the payoff they receive in a given environment. The question for an industrialized country would be then to define an optimal immigration rate that (a) does not destroy the common good, and (b) allows agents to adapt to the assumed cooperative environment within one or two generations, even if they may have not immigrated with a cooperative strategy.

The problems of cooperation and defection and the payoff-dependent adoption of strategies have been discussed in the framework of the Prisoner's dilemma (PD) and the iterated PD (IPD) game (see Sec. 2). With our paper, we add to this framework the ability to migrate between different countries ("islands"). Our aim is to reveal optimal conditions for the migration of agents such that cooperating strategies can take over even on those islands where they were initially not present.

We note that migration was previously studied in a game-theoretical context by different authors [6, 10]. Our work differs from these attempts in various respects. First of all, we do not assume that migration is based on the anticipated success [6, 7] — this shifts the conceptual problem of the "outbreak of cooperation" to proposing rules with nonlocal information such that two cooperators meet at the same place, from which cooperating clusters can grow. We also do not make migration dependent on local variables such as the number of defectors in the neighborhood [10] or random choices of "empty" places [6, 10]. In fact, human migration is rarely targeted at less densely crowded places, it is rather the opposite. Further, we do not assume one-shot games such as the PD, but instead consider the IPD in which the number n_g of repeated interaction as well as the mix of up to eight different strategies plays a crucial role.

Eventually, we do not use an agent-based model in which update and migration rules are freely defined, to study their impact on computer simulations on a lattice. Our approach proposes a population based model in which subpopulations are defined with respect to (i) their interaction strategy, and (ii) their spatial location. The consideration of separated "islands" allows a coarse-grained implementation of spatial structures which is in between a lattice or network approach and a meanfield description. It is known that spatial structures have an impact on the outbreak of cooperation [11, 15, 16], but their influence varies with other degrees of freedom, such as update rules, synchronization, interaction topology, payoff matrix.

Therefore, in this paper we adopt mostly standard assumptions about the interaction type (IPD with n_g encounters) and interaction topology (panmictic subpopulations), strategy adoption (replication proportional to payoff), and migration (fixed fraction of the population). To understand the basic dynamics, we first investigate "isolated" islands (no migration) to find out about the conditions for the "outbreak of cooperation" without external influence. This "outbreak" is defined as the critical point (strategy mix, number of encounters n_g) beyond which a whole island is going to be occupied by cooperating agents, if agents adopt strategies proportional to their average payoff. Then, we add migration between islands to this dynamics to find out under which conditions the outbreak of cooperation can be enhanced. It is important to note that migration does not distinguish between strategies or islands, i.e., there are no better suited strategies for immigration, or bad places with high emigration rates — which we consider as artificial assumptions to explain the "outbreak of cooperation".

To determine the robustness of our findings, we always consider worst case scenarios, i.e., initial settings in which most islands have either an entirely defective subpopulation, or at least a defective majority. We further control for important parameters such as the pool of available strategies s, the number of interactions n_g or the number of islands K, for which critical conditions are derived. Our finding that migration is indeed able to boost the outbreak of cooperation is remarkable both because it is based on minimal assumptions about the dynamics and because it follows from a quite systematic investigation of the underlying conditions.

2. Rules of the Game

2.1. *Strategic interaction*

Let us investigate a population of N agents divided into subpopulations on K different islands which imply a coarse-grained spatial structure, i.e., $N = \sum_k^K N_k$. Agents at island k are assumed to interact with the $N_k - 1$ other agents on their island (*panmictic population*). But, in general we assume that migration between the islands is possible, with the respective migration rates given by m_{uv}. These define the fraction of the agent population at island u that migrates to island v in a given time interval. Figure 1 shows the case of three different locations.

Our model basically considers two different time scales for interaction and migration. We define a *generation* G to be the time in which each agent has interacted with all other $N_k - 1$ agents a given number of times, denotes as n_g. Thus the total number of interactions during each generation in the panmictic population is roughly $N_k^2/2 \times n_g$. At any given time, agent i can interact only with one other agent in a "two-person game". But during one generation G, it interacts with all other $N_k - 1$ agents n_g times (repeated two-person game).

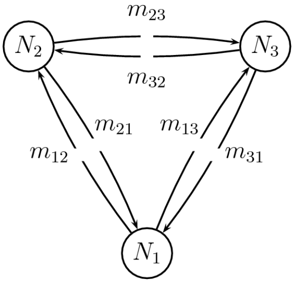

Fig. 1. Subpopulations N_k (with different strategies) are spatially distributed on k islands from where they can migrate at rates m_{uv}.

For the interaction, we adopt the well known *iterative prisoner's dilemma* (IPD) from game theory. At each encounter between agents i and j, both have two actions to choose from, either to *collaborate* (C) or to *defect* (D), *without knowing* the action chosen by their counterpart. The outcome of that interaction is described in the following payoff matrix:

$$\begin{array}{ccc} & \mathbf{C} & \mathbf{D} \\ \mathbf{C} & (R,R) & (S,T) \\ \mathbf{D} & (T,S) & (P,P) \end{array} \tag{1}$$

If both agents have chosen to collaborate, then they both receive the payoff R. If one of the agents chose to defect and the other one to cooperate, then the defecting agent receives the payoff T and the cooperating the payoff S. If both defect, they both receive the payoff P. In the special class of *Prisoner's Dilemma* (PD) games, the payoffs have to fullfil the following two inequations:

$$T > R > P > S; \quad 2R > S + T \tag{2}$$

which are met by the standard values $T = 5$, $R = 3$, $P = 1$, $S = 0$. This means in a cooperating environment, a defector will get the highest payoff.

For $n_g = 1$ ("one-shot" game) choosing action D is unbeatable, because it rewards the higher payoff for agent i no matter if the opponent chooses C or D. At the same time, the payoff for *both agents i and j* is maximized when both cooperate. A simple analysis shows that defection is a so-called *evolutionary stable strategy* (ESS) in a one-shot PD. If the number of cooperators and defectors in the population is given by N^c and $N^d = N - N^c$ respectively, then the expected average payoff for cooperators will be $a^c = (R \times N^c + S \times N^d)/N$. Similarly the expected average payoff for defectors will be $a^d = (T \times N^c + P \times N^d)/N$. Since $T > R$ and $P > S$, a^d is always larger than a^c for a given number N^c, and pure defection would be optimal in a one-shot game. Even one defector is sufficient to invade the complete population of $N - 1$ cooperators.

But in a *consecutive* game with short *memory*, both agents, by simply choosing D, would end up earning less than they would earn by cooperating. Thus, the number of games n_g two agents play together becomes important. This makes sense only if the agents can remember the previous choices of their opponents, i.e., if they have a memory of $n_m \leq n_g - 1$ steps. Then, for the *iterated Prisoner's Dilemma* (IPD), they are able to develop different *strategies* based on their past experiences with their opponents. We note that the IPD game was studied both in the context of a panmictic population ([1, 4, 5, 12, 14, 23]) and assuming a spatial population structure [3, 18, 19].

Usually, in an IPD only a *one-step* memory is taken into account. Based on the known previous choice of its opponent, either C or D, agent i has then the choice between *eight* different strategies. Following a notation introduced in [13], these strategies are coded in a 3-bit binary string $[I^o|I^cI^d]$ which always refers to *cooperation.* The first bit represents the *initial* choice of agent i: it is 1 if agent i has *cooperated*, and 0 if it has defected initially. The two other values always refer to the previous choice of agent j. I^c is set to 1 if agent i chooses to cooperate given that agent j has cooperated before and 0 otherwise. I^d is similarly set to 1 if agent i chooses to cooperate given that agent j has defected before and 0 otherwise.

Both I^c and I^d can be also interpreted as *probabilities* to choose the respective action given the knowledge of the previous choice of the opponent, i.e., $\{0 \leq I_p, I^d \leq 1\}$ in the stochastic case. In the *deterministic* case considered in this paper, I^d and I^c are either 0 or 1. Out of the eight possible strategies, to keep our results in a tractable manner, we consider the following four strategies $z^{(s)}$ $(s = 1, 2, 3, 4)$:

$$\begin{aligned} z^{(1)} &: \quad [1|10] \quad \mathrm{TFT} \\ z^{(2)} &: \quad [0|00] \quad \mathrm{ALL-D} \\ z^{(3)} &: \quad [1|11] \quad \mathrm{ALL-C} \\ z^{(4)} &: \quad [0|01] \quad \mathrm{A-TFT} \end{aligned} \tag{3}$$

These four strategies were also considered originally in the famous paper by Axelrod and Hamilton [1]. Hence, we will extend these investigations by later adding migration to the game. We note that all eight strategies have been discussed in [17]. In this paper we have dropped those variants that differ only in the first move but then continue as described in the following. The strategies ALL-D and ALL-C are obvious: for $z^{(2)}$ agent i always chooses to defect regardless of the previous choices of agent j, $z^{(3)}$ follows likewise. These two strategies represent the limit case of *no memory*, i.e., agent i is simply "fixed" as a cooperator or a defector.

The most interesting strategy $z^{(1)}$, known as "tit for tat" (TFT), means that agent i initially cooperates and continues to do so, given that agent j was also cooperative in the previous move. However if agent j was defective in the previous move, agent i chooses to be defective, too. This strategy was shown to be the most successful one in iterated Prisoners Dilemmas [1]. If initially two cooperative agents meet, they stay cooperative (forever, in a deterministic game), this way maximizing their average payoff. This encourages other agents to adopt TFT. Hence, the "outbreak of cooperation" in a community of N agents occurs as the amplification of a cooperative initial fluctuation.

The fourth possible strategy $z^{(4)}$ is just the negation of the most successful one, therefore named Anti-TFT. It means that agent i starts as a defector and continues to be so, as long as it meets with cooperative agents j, this way receiving the highest possible payoff T. But, if it meets an agent that has previously defected, it changes its "behavior" to cooperation. This makes some sense, since the loss in payoff is not that much — P would be just slightly higher than S. On the other hand, if the collaborative agent meets again with another cooperative agent, the payoff would be R, which is a much higher gain. So, this strategy, while not making sense in the first place, may end up with a higher payoff in those cases where defecting and cooperating strategies are equally present. We will later show that A-TFT in the long run benefits agents playing ALL-D and therefore will create a more difficult environment for the invasion of cooperation, i.e., considering all four strategies captures a worst-case scenario for the outbreak of cooperation which we deem interesting to study (instead of giving rational arguments in favor of A-TFT).

2.2. *Dynamics of replication and migration*

In this paper, we are interested in how the frequencies of the different strategies would evolve in the agent community. The fraction of agents choosing strategy $z^{(s)}$ on island k is defined as $f_k^{(s)}(t) = N_k^{(s)}(t)/N_k$, where the different strategies are given by Eq. (3). Similarly, the *total fraction* of agents playing strategy $z^{(s)}$ in the *whole* system, is given as $f^{(s)}(t) = N^{(s)}(t)/N$. For the dynamics we may assume that during each generation G every agent behaves according to a fixed strategy picked up from the pool of possible strategies. This strategy can be changed only after one generation is completed. The "update" rule for the strategy is simply given by the success of different strategies during the past generation. As the evaluation criteria, we choose the average payoff $a_k^{(s)}$, each strategy has received during the last generation on island k. This will be compared with the total average payoff $\bar{a}_k$ that gives an estimate of the overall dynamics on that island:

$$\bar{a}_k(t) = \sum_{s=1}^{4} a_k^{(s)}(t) f_k^{(s)}(t); \quad \sum_{s=1}^{4} f_k^{(s)}(t) = 1. \tag{4}$$

For the evolution of the frequencies of the different strategies, the following dynamics is postulated:

$$f_k^{(s)}(G+1) = \frac{a_k^{(s)}(G)}{\bar{a}_k(G)} f_k^{(s)}(G). \tag{5}$$

It means that in the next generation $G+1$ the share of agents choosing a particular strategy $z^{(s)}$ has grown/shrunk — i.e., strategy $z^{(s)}$ has replicated — according to the *relative* performance of this strategy on island k during the previous generation G. In population dynamics, this is known as *fitness-proportional selection* [8], we adopt it here since the relative performance of a certain strategy can be also interpreted as its *fitness*.

The dynamics of Eq. (5) does not take into account that agents can migrate between the K islands. For simplicity, we assume that each island k is occupied by the same number of agents $N_k = N/K$ and migration can occur between any two islands with a constant and equal migration rate $m_{uv} \equiv m/(K-1)$. We interpret $m \in \{0, 1\}$ as the total fraction of the agent population at any given island that migrates to other islands in a given time interval, namely one generation. In a first approximation, we assume that migration only occurs *after* a generation is completed, i.e., at fixed times G, $G+1$.

While the fraction m is fixed (but controlled for, afterwards), the *composition* of the migrating subpopulation across the existing strategies $z^{(s)}$ is not. We assume this composition to be proportional to the fraction $f_k^{(s)}$ of these strategies at island k at the time when generation G is completed and migration occurs, to affect the dynamics during the next time interval $G+1$. This means migration changes the fraction $f_k^{(s)}(G+1)$ by an additional amount $\mathcal{F}$ representing the difference between the influx and the outflux of the agents playing strategy $z^{(s)}$:

$$\mathcal{F}_k^{(s)}(G) = -m f_k^{(s)}(G) + \frac{m}{K-1} \sum_{j=1, j\neq k}^{K} f_j^{(s)}(G) \tag{6}$$

which defines the complete dynamics by the following set of iterative equations:

$$f_k^{(s)}(G+1) = \frac{a_k^{(s)}(G)}{\bar{a}_k(G)} f_k^{(s)}(G) + \mathcal{F}_k^{(s)}(G). \tag{7}$$

Using $\mathcal{F}(0) = 0$ and an equal share $f_k^s(0)$ for each strategy on each island as initial conditions, the dynamics is completely determined if we know the respective average payoffs which are derived in the following section. We note that, in general, the fixpoints of a difference equation may not characterize its asymptotic behavior, while it holds for the given simplified case.

2.3. *Determining the payoffs of repeated interaction*

In a deterministic game, we are able to calculate the average payoff $a_i^{(rq)}$ that is received *by agent* i playing strategy $z^{(r)}$, $r \in s$, n_g times with an agent j playing strategy $z^{(q)}$, $q \in s$. For $s = 1, 2, 3, 4$, the results are given in the 4×4 payoff matrix of Eq. (8). Note that the matrix is not symmetric, since it gives the average payoff of agent i. r refers to the row and q to the column of Eq. (8).

$$\mathbf{a}_i = \frac{1}{n_g} \begin{bmatrix} n_g R & S + (n_g-1)P & n_g R & a^{(14)} \\ T + (n_g-1)P & n_g P & n_g T & P + (n_g-1)T \\ n_g R & n_g S & n_g R & n_g S \\ a^{(41)} & P + (n_g-1)S & n_g T & a^{(44)} \end{bmatrix} \tag{8}$$

where

$$a^{(14)} = (n_g \mathrm{div} 4)\mathcal{P} + \sum_{k=1}^{(n_g \mathrm{rem} 4)} b_k; \quad a^{(41)} = (n_g \mathrm{div} 4)\mathcal{P} + \sum_{k=1}^{(n_g \mathrm{rem} 4)} c_k$$

$$a^{(44)} = (n_g \mathrm{div} 2)(P+R) + \sum_{k=1}^{(n_g \mathrm{rem} 2)} d_k. \tag{9}$$

The symbols T, R, P and S refer to the payoff matrix of the two-person game, Eq. (1). Further, we have used $n_g = (n_g \mathrm{div} y)y + (n_g \,\mathrm{rem}\, y)$, with $0 \leq (n_g \,\mathrm{rem}\, y) < y$. $(n_g \,\mathrm{div}\, y)$ means the *integer* part of the division n_g/y, i.e., $(n_g \,\mathrm{div}\, 4) = 4$ for $n_g = 18$; while $(n_g \,\mathrm{rem}\, y)$ means the *remainder*, i.e., $(n_g \,\mathrm{rem}\, 4) = 2$ for $n_g = 18$. The constants appearing are defined as follows:

$$\begin{gathered} \mathcal{P} = T + R + P + S; \quad b_1 = S; \quad b_2 = P; \quad b_3 = T; \quad b_4 = R \\ c_1 = T; \quad c_2 = P; \quad c_3 = S; \quad c_4 = R \; d_1 = P; \quad d_2 = R. \end{gathered} \tag{10}$$

To verify how the matrix entries of Eq. (8) are derived we have provided a number of illustrative examples shown in Appendix A.

With the known average payoff resulting from each possible interaction, the average payoff per strategy at island k is simply given as:

$$a_k^{(s)} = \sum_{r=1}^{4} a^{(rs)} f_k^{(r)}; \quad \sum_{r=1}^{4} f_k^{(r)} = 1 \quad (s = 1, \ldots, 4), \tag{11}$$

where $f_k^{(r)}$ denotes the fraction of agents playing strategy $z^{(r)}$ at island k and the $a^{(rs)}$ are given in Eq. (8). Strictly speaking, Eq. (11) has to consider the fact that an agent does not play against itself. This would lead to a correction term of the order of $a^{(ss)}/N$, which is small and therefore neglected here.

2.4. *Calculating the fixpoints*

With the above specifications we are now able to solve the dynamic equations with respect to the fraction of agents $f_k^{(s)}(t)$ playing strategy $z^{(s)}$. Here, we are mostly interested in the impact of migration on the prevalence of certain strategies, therefore we will discuss first the case *without* migration, Eq. (5), which should be used as a reference for the case *with* migration, Eq. (7). Also, we are mostly interested in the *stationary* solutions of the respective dynamics, i.e., in the fixpoints $f_k^{(s)}$ reached after a sufficiently large number of generations. Our focus is then on three issues which crucially determine the long-term outcome:

(i) the initial frequencies of strategies $f^{(s)}(0)$,
(ii) the number of repeated interactions, n_g, as this enters the payoff matrix, Eq. (8) and therefore affects the average payoff per strategy, Eq. (11)
(iii) the impact of the migration rate m on the prevailing strategies.

The stationary values of $f_k^{(s)}$ are reached if the different frequencies do not change anymore in the new generation. This leads to the stationary condition:

$$f_k^{(s)}(G+1) = f_k^{(s)}(G) = f_k^{(s)}, \tag{12}$$

where $f_k^{(s)}$ shall denote the stationary (i.e., asymptotic) frequency of strategy $z^{(s)}$, in contrast to $f_k^{(s)}(0)$ that denotes the initial frequency. For the full dynamics which includes migration, Eq. (7), we solve this condition numerically. But for the case without migration, Eq. (5), the stationary condition leads to $\bar{a}_k f_k^{(s)} = a_k^{(s)} f_k^{(s)}$, which reduces to the quite simple expression $\bar{a}_k = a_k^{(s)}$ only if $f_k^{(s)} \neq 0$.

To further discuss the case of isolated islands, we drop the index k. For $m = 0$ Eq. (12) with Eq. (5) basically yields two different types of solutions, which could be either stable or unstable:

(i) the exclusive dominance of any *one* strategy $z^{(q)}$ ($q \in s$) while all other strategies $z^{(r)}$, $r \neq q$, have disappeared, i.e.,

$$f^{(q)} = 1; \quad \bar{a}_k = a^{(q)} \quad \text{and} \quad f^{(r)} = 0 \quad \text{for } r \neq q \tag{13}$$

(ii) the co-existence of some (or all) of the strategies $z^{(q)}$, $z^{(r)}$ with the *same average payoff* $\bar{a}$, but probably *different frequencies of agents*, $f^{(q)}$, $f^{(r)}$, i.e.,

$$\sum_{i=1}^{4} a^{(iq)} f^{(i)} = \sum_{i=1}^{4} a^{(ir)} f^{(i)} \tag{14}$$

In the deterministic case considered here it solely depends on the initial conditions $f^{(s)}(G = 0)$, which of the possible stationary solutions will be eventually reached. After we know the *basins of attraction*, i.e., the range of possible initial conditions that lead to a given stationary solution and the *separatrix* dividing them, we could tell from the outset which strategies will be adopted by the population, and which strategies will disappear. Therefore, in the next section we will calculate the basins of attraction for the case of isolated islands, to compare these later on for the case of migration which, as we will see, shifts these basins considerably.

3. No Migration: Coexistence and Dominance of Strategies

For isolated islands, condition (12) leads to $s = 4$ coupled equations, which follow from Eq. (4) with Eq. (11). In addition, we have the boundary condition $\sum_s f^{(s)} = 1$, which leads to three independent variables $f^{(1)}$, $f^{(2)}$, $f^{(3)}$. The separatrix then appears as a two-dimensional *plane* in this three-dimensional space, which will be hard to calculate analytically. In order to elucidate this multi-dimensional problem, we discuss in Appendix B the case of only two possible strategies, where the separatrix appears as a *point* in the one-dimensional space, and in Appendix C the case of three possible strategies, where the separatrix appears as a *line* in the two-dimensional space. Here, we continue with the full problem of four possible strategies.

Compared to Appendix C, strategy $z^{(4)} = $ A-TFT is added which in the long run benefits agents playing ALL-D and therefore will decrease the basins of attraction of the cooperating strategies, i.e., considering A-TFT as an additional strategy will create a more difficult environment for the invasion of cooperation, therefore it will be very interesting to see, under what conditions cooperation can survive also in the worst case. The stationary solutions for the frequencies $f^{(s)}$ result from the following set of coupled equations:

$$\begin{gathered}\bar{a} = \sum_{s=1}^{4} a^{(s)} f^{(s)} = \sum_{s=1}^{4} \left(\sum_{r=1}^{4} a^{(rs)} f^{(r)} \right) f^{(s)} \\ \bar{a} f^{(i)} - (a^{(i1)} f^{(1)} + a^{(i2)} f^{(2)} + a^{(i3)} f^{(3)} + a^{(i4)} f^{(4)}) f^{(i)} = 0 \quad (i = 1,2,3,4) \\ f^{(1)} + f^{(2)} + f^{(3)} + f^{(4)} = 1.\end{gathered} \tag{15}$$

The matrix elements $a^{(rq)}$ can be calculated from Eq. (8). With $n_g = 4$ we find the following stationary solutions:

$$\begin{array}{ll} \text{(i)} & f^{(1)} = 1, \quad f^{(2)} = 0, \quad f^{(3)} = 0, \quad f^{(4)} = 0 \quad \text{(stable)} \\ & f^{(1)} = 0, \quad f^{(2)} = 1, \quad f^{(3)} = 0, \quad f^{(4)} = 0 \quad \text{(stable)} \\ & f^{(1)} = 0, \quad f^{(2)} = 0, \quad f^{(3)} = 1, \quad f^{(4)} = 0 \quad \text{(unstable)} \\ & f^{(1)} = 0, \quad f^{(2)} = 0, \quad f^{(3)} = 0, \quad f^{(4)} = 1 \quad \text{(unstable)} \\ \text{(ii)} & f^{(1)}_{\text{thr}} = 0.2, \quad f^{(2)}_{\text{thr}} = 0.8, \quad f^{(3)} = 0, \quad f^{(4)} = 0 \quad (\text{for } n_g = 4) \quad \text{(unstable)} \\ & f^{(1)} = 1.0 - f^{(3)} (0 \le f^{(3)} \le 1), \quad f^{(2)} = 0, \quad f^{(4)} = 0 \quad \text{(stable)}. \end{array} \tag{16}$$

We note that the stationary solutions also cover the results of the two-strategy case, Appendix B and the three-strategy case, Appendix C. We find solutions of type (i) where one strategy is exclusively dominating the whole population. However, the solution of all agents playing $z^{(4)} = $ A-TFT is also an unstable attractor, because a small perturbation by agents playing either strategy ALL-D or TFT will lead to the invasion of that respective strategy into the whole A-TFT population. To see this, we also refer to the payoffs received in the respective interactions, Eqs. (A.3) and (A.4). From the solutions (ii) that describe the coexistence of strategies we further see that the addition of strategy $z^{(4)} = $ A-TFT does not lead to new coexisting states compared to the case of two strategies, Appendix B and three strategies, Appendix C. There is only a coexistence between strategies $z^{(1)} = $ TFT and $z^{(3)} = $ ALL-C, which is stable as long as no spontaneous mutations towards ALL-D or A-TFT occur.

The separatrix that distinguishes between the different attractors is in the given case a two-dimensional plane in the three-dimensional space of independent frequencies with $\sum_s f^{(s)} = 1$. With respect to the cooperative strategy TFT it defines the *threshold frequency* $f^{(1)}_{\text{thr}} = f^{(1)}(G = 0)$ that has to be reached initially, in order to allow the system to converge to a fully cooperative state, $f^{(1)}(G \to \infty) = 1$. Because of the n_g-dependence of the payoff matrix, Eqs. (8), (B.1) $f^{(1)}_{\text{thr}}$ strongly

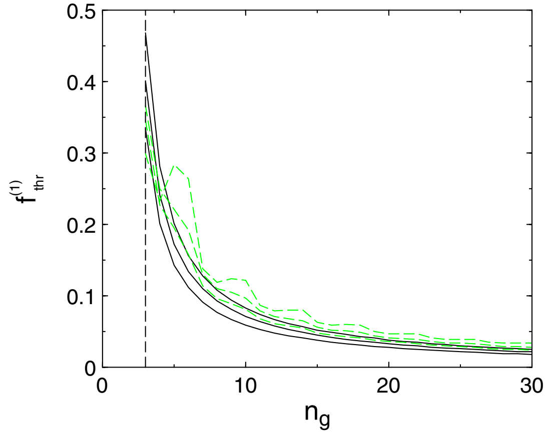

Fig. 2. Threshold frequency $f^{(1)}_{\text{thr}} = f^{(1)}(0)$ of agents playing strategy $z^{(1)} = \text{TFT}$ versus number of interactions n_g between each two agents, in the case of four strategies. For $f^{(1)}(0) \geq f^{(1)}_{\text{thr}}$, the TFT strategy will be adopted by the whole population, while for $f^{(1)}(0) \leq f^{(1)}_{\text{thr}}$ the $z^{(2)} = \text{ALL-D}$ strategy will be adopted by the whole population.

decreases with the number of encounters n_g, as shown in Fig. 2. In agreement with known results from evolutionary game theory [5, 16], for a sufficiently large number of interactions the whole population will adopt the cooperative strategy, this way increasing the average payoff. The important point to notice here is the quantitative analysis which allows us to determine, for a given *finite* number of n_g, the threshold initial frequency $f^{(1)}_{\text{thr}}$ of agents playing TFT, in order let cooperation invade the whole population. Or else, for a given initial frequency $f^{(1)}(0)$, we are able to determine the *minimum number of interactions*, $n_g^{\min}$, to let the whole population adopt the TFT strategy.

To get some further insights, we find it more convenient to present two-dimensional graphical projections of this three-dimensional space, where the separatrix naturally appears as a line. The most interesting projection is the $f^{(1)} - f^{(2)}$ projection, since it allows us to compare the results with the previous cases. The results are shown Fig. 3. They have been obtained by numerically solving Eq. (5) for the full range of initial frequencies, $0 \leq f^{(s)}(0) \leq 1$. In the stationary limit, the average payoff was then evaluated to find out to which basin of attraction the solution belongs.

The calculation of the basins of attraction in Fig. 3 are done for a fixed number of interactions, $n_g = 4$, but for a varying initial frequency of agents playing strategy $z^{(4)} = \text{A-TFT}$. Of course, this sets limits to the *maximum* initial frequencies $f^{(1)}(0) = 1 - f^{(3)}(0)$ and $f^{(2)}(0) = 1 - f^{(3)}(0)$, therefore in Fig. 3 we have scaled the $f^{(s)}(0)$-axes by the maximum possible value, which should be noticed when comparing the figures. For a small initial frequency of A-TFT [Fig. 3 (left)] we find the picture rather similar to the case of three strategies shown in Appendix C,

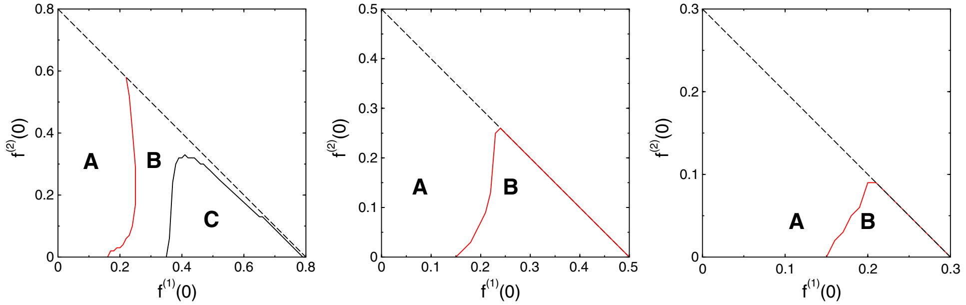

Fig. 3. Basins of attraction, i.e., range of initial frequencies $f^{(s)}(0)$ that lead to a particluar stable solution, Eq. (16), in the case of four strategies. A: adoption of $z^{(2)}$ = ALL-D strategy in the whole population, B: adoption of $z^{(1)}$ = TFT strategy in the whole population, C: coexistence of both $z^{(1)}$ = TFT and $z^{(3)}$ = ALL-C strategies. $f^{(3)}(0) = 1 - f^{(1)}(0) - f^{(2)}(0)$, $n_g = 4$. (left) $f^{(4)}(0) = 0.2$, (middle) $f^{(4)}(0) = 0.5$, (right) $f^{(4)}(0) = 0.7$.

however the separation line between the basins of attraction A (defection) and $B + C$ (cooperation) is now a nonlinear function, different from Eq. (C.3).

With an increasing initial frequency of A-TFT, we find that the basin of attraction of defection is naturally decreasing in absolute size, but it is increasing *relative* to the basin of attraction of cooperation. That means that an increase in the fraction of agents initially playing A-TFT always benefits the adoption of the ALL-D strategy, at the end. A similar conclusion can be drawn also for the number of agents initially playing ALL-C. We notice that with an increasing initial frequency of A-TFT region C, that describes the coexistence of both strategies TFT and ALL-C, ceases to exist, i.e., strategy ALL-C has vanished for the benefit of strategy ALL-D. This can also be understood by looking at the average payoff matrix, Eq. (8). If an agent playing ALL-D meets with an agent playing ALL-C, it gets the maximum payoff, T, while it gets almost the maximum payoff $(P + (n_g - 1)T)/n_g$ when it meets an agent playing A-TFT. Thus, strategy ALL-D will eventually invade the population of agents playing either ALL-C or A-TFT, or, in other words, the presence of strategies like ALL-C and A-TFT in the population helps strategy ALL-D to invade.

Eventually, we have also calculated numerically the relative size of each basin of attraction as shown in Fig. 4 for two different values of $n_g = 4$ and $n_g \to \infty$. Here the relative sizes a, b, c and d refer to the three-dimensional space of all possible initial conditions (which is different from Fig. 9 where they refer to the areas A, B and C shown, thus Eq. (C.4) does not apply here). When $n_g = 4$, the ALL-D basin "a" is slightly bigger than the cooperative basin "d" as shown in contrast to Fig. 10. With $n_g \to \infty$, the size of the ALL-D basin "a" becomes pretty small as compared to cooperative basin "d".

To conclude this analysis, we have shown for the case of isolated islands (no migration) what are the critical initial conditions for cooperative strategies, such as ALL-C, TFT to be adopted by the whole agent population. Dependent on the

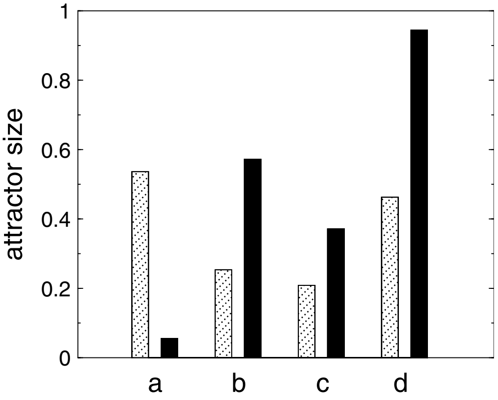

Fig. 4. Relative size of the basins of attraction. "a" represents the size of the ALL-D basin, "b" represents the size of the TFT basin, "c" represents the size of TFT + ALL-C basin and "d" represents the size of cooperative basin (i.e., b + c). The left bars (shaded area) refer to $n_g = 4$, while the right bars (black area) refer to $n_g \to \infty$. Thus, the change indicates the influence of n_g on the size of the basins of attraction.

number of interactions n_g, we can tell the minimum initial frequency of TFT, $f^{(1)}(0)$ that has to be reached to ensure an cooperative outcome dependent on the initial mix of strategies (details of the two and three strategy case are provided in Appendix B and Appendix C). In the limit of small n_g, while one may naively assume that an initial increase of the ALL-C strategy benefits cooperation, at the end, this analysis shows that with the involvement of A-TFT it eventually benefits defection in the system, which is an interesting finding by itself. In the following, we will investigate how this picture changes if we add the possibility of migration.

4. Migration: The Rise and Fall of Cooperation

4.1. *The role of migration*

The previous section has shown that an increase of the number of interaction n_g always supports the prevalence of cooperating strategies, such as ALL-C and TFT. Therefore, in the following we will concentrate the analysis on the critical conditions which occur for small n_g. We fix $n_g = 4$ (note that $n_g = 3$ is the threshold number of interaction to allow the replication of cooperating strategies at all, see Appendix B and Fig. 2.

To understand how migration affects the existing equilibrium states, let us start with the simple example shown in Fig. 5. We take the setup of Fig. 1 and consider only two strategies, $z^{(1)} = \text{TFT}$ and $z^{(2)} = \text{ALL-D}$, but different initial conditions on the three islands. As the detailed analysis of Appendix B has shown, below an initial frequency $f^{(1)}(0) = 0.2$ the only stable stationary state is $f^{(1)} = 0$, $f^{(2)} = 1$. Hence, if no migration is possible, with the given initial conditions shown in Fig. 5(i) the three islands converge into a final state shown in Fig. 5(iia) where ALL-D prevails in two islands, while in one TFT dominates because that island started

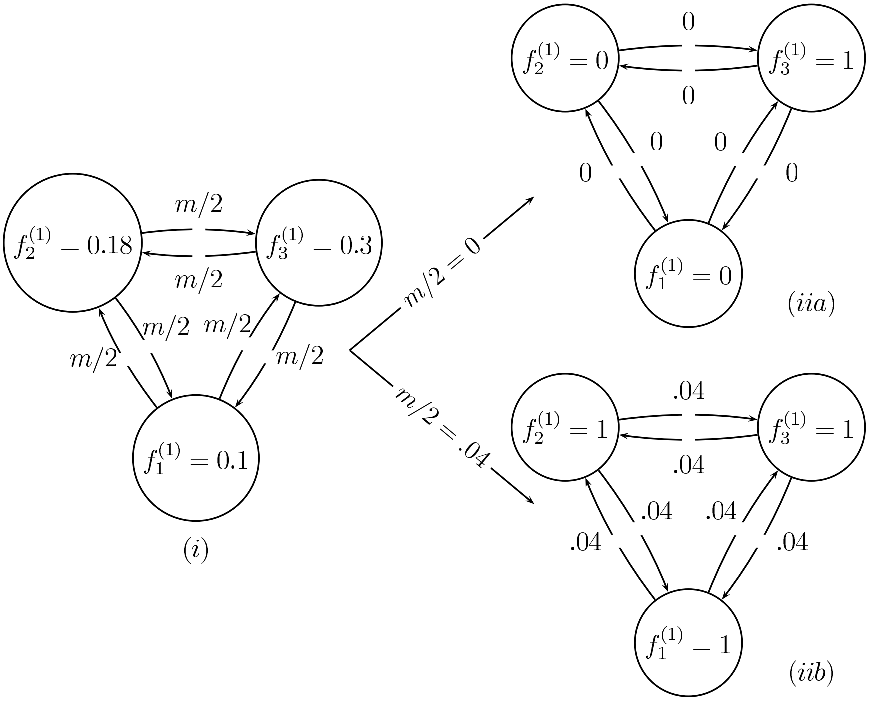

Fig. 5. Migration between the three islands enhances the outbreak of cooperation. (i) Initial state ($G = 0$) using two strategies. The defective strategy ALL-D has the majority on all islands. (ii) Final state ($G \to \infty$) (a) without and (b) with a small migration rate. In (a) only one island has adopted cooperation, in (b) all three islands have adopted cooperation.

from an initial condition above the threshold. If we however introduce a rather small migration rate of $m/2 = 0.04$ all three islands are eventually dominated by the cooperating strategy, TFT, as shown in Fig. 5(iib). Hence, even with a rather small advantage on *one* island ($f^{(1)}(0) = 0.3$ is just above the threshold of 0.2), a small migration was able to induce a transition toward TFT instead of a relaxation into ALL-D on *all* islands.

It is precisely this kind of phenomenon that we would like to understand better regarding the critical conditions involved. In particular, we concentrate on the impact of the migration rate on the threshold value of TFT, to still observe the outbreak of cooperation. The results are found numerically, by iterating the set of Eq. (7), for $n_g = 4$ and K islands that have the same total number of agents, but different initial strategy distributions.

Figure 6 shows results of the two strategies case, TFT and ALL-D, for $K = 5$ and three different migration rates, in terms of the average payoff $\bar{a}_k$. As explained in Appendix B $\bar{a}_k = 1$ means that ALL-D invades the entire population, whereas $\bar{a}_k = 3$ is achieved when TFT takes over. Figure 6(left) with $m = 0$ is used for comparison only, as it shows the result predicted in Appendix B, i.e., three islands

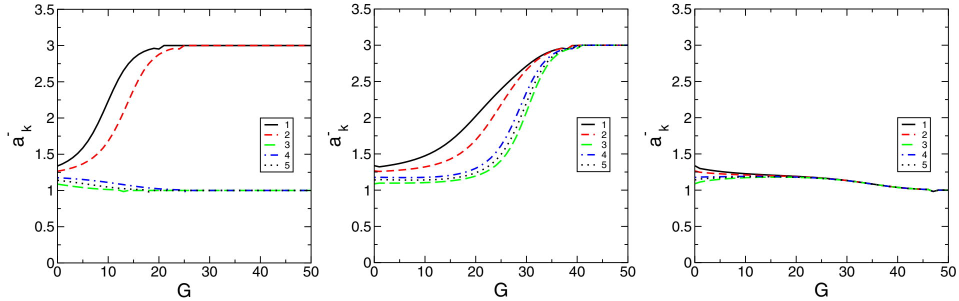

Fig. 6. Evolution of the average payoff in the $K = 5$ island model for different migration rates m: (left) $m = 0.0$, (middle) $m = 0.08$, (right) $m = 0.2$. Parameters: Panmictic population in $K = 5$ island model consisting of TFT and ALL-D. Initial frequencies of TFT: $f_1^{(1)} = 0.3, f_2^{(1)} = 0.25, f_3^{(1)} = 0.1, f_4^{(1)} = 0.18, f_5^{(1)} = 0.15$ and $f_k^{(2)} = 1 - f_k^{(1)}$.

which have a frequency of TFT below the threshold value of 0.2 are taken over by agents playing ALL-D. The remaining two islands are invaded by TFT. This result changes in Fig. 6(middle), where we allow migration of $m = 0.08$ between islands. Then all islands become populated solely by TFT which is indicated by $\bar{a}_k = 3$. However, if we further increase the migration rate to $m = 0.2$, the *opposite* result occurs. In this case ALL-D invades all islands as shown in Fig. 6(right) where $\bar{a}_k = 1$. These results suggest that there exists *an optimal range for* m that ensures the outbreak of cooperation, which will be further investigated in the following sections.

4.2. *How migration influences cooperation*

We continue our discussion for the case of two strategies, TFT and ALL-D, and now assume that for $K = 6$ $(K - 1)$ islands are initially dominated by strategy ALL-D, i.e., $f_k^{(1)}(0) = 0$ for $k \in 2, \ldots, 6$, while the *first* island $k = 1$ is initially populated by both TFT and ALL-D, i.e., $0 < f_1^{(1)}(0) < 1$. We then vary the migration rate m for different initial frequencies $f_1^{(1)}(0)$ to study numerically under which condition the outbreak of cooperation on all islands can be obtained. The results are shown in Fig. 7. For very small m, the average payoff $\bar{a}$ just reflects the mix of the initial strategies. But, as the middle part of Fig. 7 shows, for a certain value of the initial frequency $f_1^{(1)}(0)$, we find a spike $\bar{a} = 3$ at a particular value of m that indicates the *outbreak of cooperation*, thanks to an *optimal migration rate*. One would assume that increasing the initial fraction of TFT would further boost cooperation but, as Fig. 7 (right) clearly shows, the "bandwidth" of optimal migration rates m is rather limited. Precisely, if $f_1^{(1)}(0) = 0.40$ the bandwidth of optimal migration rates is $0.07 \leq m \leq 0.095$ which is to be compared to the maximum bandwidth $0.07 \leq m \leq 0.155$ for $f_1^{(1)}(0) = 1$. This makes sense because a large migration rate may have a contrary effect: While cooperative agents are "exported" to other islands, the same number of defective agents are "imported",

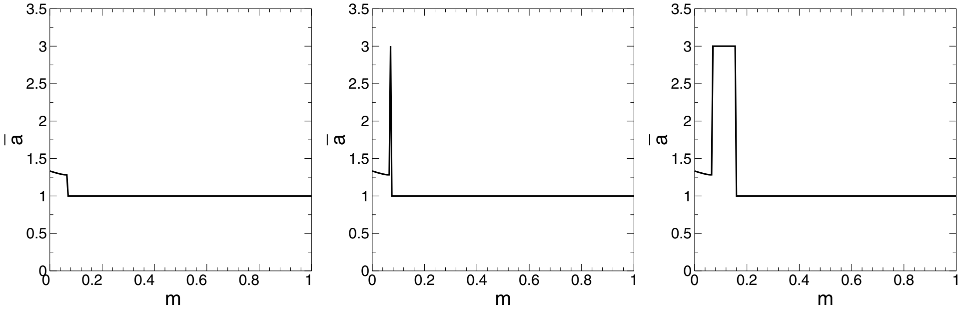

Fig. 7. Increasing $f_1^{(1)}(G=0)$ leads to increasing bandwidth of m in which cooperation will emerge in the system. From left to right: (1) $f_1^{(1)}(G=0)=0.31$ (2) $f_1^{(1)}(G=0)=0.32$ (3) $f_1^{(1)}(G=0)=0.40$ (4) $f_1^{(1)}(G=0)=1.00$. Parameters: $n_g=4$, $K=6$.

which may reduce the fraction of TFT below the critical threshold. Hence, there is a nonmonotonous relation between m and the outbreak of cooperation.

4.3. *Calculating the threshold frequency*

We are now interested in finding the *minimum initial frequency* $f_1^{(1)}(0)$ that will lead to invasion of cooperation on all $K-1$ islands, when varying the migration rate m. We define this as the *threshold frequency*, $f_{\rm thr}^K$:

$$f_{\rm thr}^K(m^K) = \min_{f_1^{(1)}} f_1^{(1)}(G=0) \tag{17}$$

$$\text{with } f_k^{(1)}(G=0)=0\ \forall\, k\in 2,\ldots,K; \quad f_k^{(1)}(G=\infty)=1\ \forall\, k\in K.$$

For each $f_{\rm thr}^K$, there exists a specific value of the migration rate $m^K\in[0,1]$ such that the outbreak of cooperation happens on all islands. m^K denotes the the smallest value of the bandwidth of optimal migration rates shown in Fig. 7, i.e., for fixed n_g and a given number of islands K with the initial conditions specified in Eq. (17), there exist a tuple of critical values $(f_{\rm thr}^K, m^K)$ which determine the *outbreak of cooperation*. The outbreak shown in Fig. 7(middle) for $K=6$ is observed for $(f_{\rm thr}^K, m^K)=(0.32, 0.07)$. This leads us to the question, how the threshold value and the critical migration rate change if we change the number of islands.

The results of exhaustive numerical calculations which had to search for the outbreak of cooperation on the whole $(K, f_1^{(1)}(0), m)$ parameter space are shown in Fig. 8(left). Obviously, for $K=1$ the threshold frequency results from the analysis given in Appendix B. If the number of islands increases, $f_1^{(1)}(0)$ has to increase as well, in order to be able to "export" cooperating agents while still staying above the theshold. This increase, however, is nonlinear in K. Precisely, as can be verified in Fig. 8,

$$f_{\rm thr}^K = K^3A_0 - K^2(2A_0A_1) + K(A_0A_1^2 + A_2). \tag{18}$$

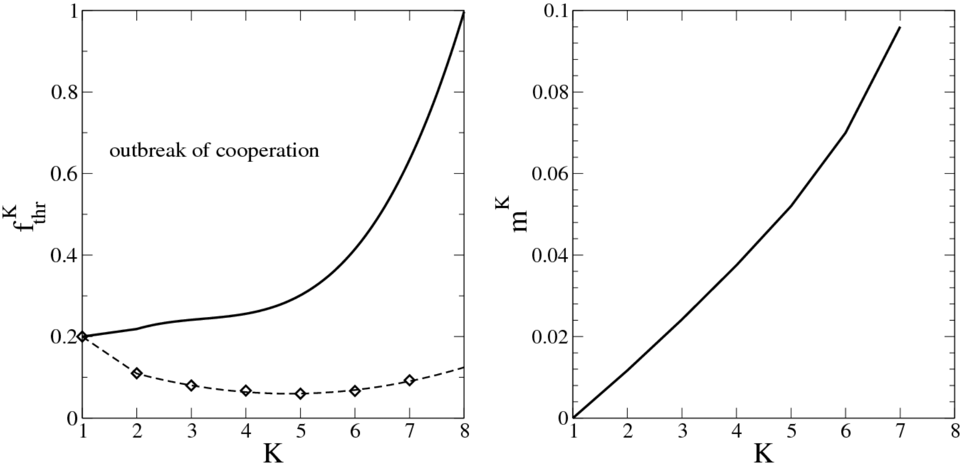

Fig. 8. (left) Threshold frequency $f_{\rm thr}^K$ (black line) and relative effort $f_{\rm thr}^K/K$ (dashed line) dependent on the number of islands K. Symbols represent results of numerical calculations. Fitted values of Eq. (18) $A_0 = 0.006$, $A_1 = 4.798$, $A_2 = 0.060$. (right) Optimal migration rate m^K dependent on the number of islands K.

The values of the constants A_n depend implicitly also on the payoff matrix, Eq. (1), which defines the comparative advantage of each strategy for reproduction and invasion, subsequently. Plotting $f_{\rm thr}^K/K$ we see that for $2 \leq K \leq 6$, with every new island added the *relative effort* to invade the new one with cooperators *decreases*, while for $K \geq 6$ this effort *increases* quadratically with K. However, the effort of invading other islands with cooperators always stays below the threshold of an isolated island, which is 0.2. This is a direct consequence of the combined processes of migration and reproduction. Newly arriving cooperative agents will reproduce on the other islands, this way reaching the threshold value the before the next generation is ready for migration. Hence, *diversification of the reproduction sites* for cooperating agents lower the relative effort for the outbreak of cooperation and makes it more favorable.

As a second consequence of the nonlinear dependency, the export of cooperation from *one* island to $K-1$ other islands is only possible for a limited number of islands, because of the two effects already mentioned above, i.e., the "export" of cooperating agents and the "import" of defecting agents both decrease the fraction of cooperating agents below the threshold frequency. Hence, for the two strategy case discussed here, $K = 8$ already leads to the collapse of exporting cooperation.

The critical migration rate m^K dependent on the number of islands is shown in Fig. 8(right). We recall that this gives the minimal fraction of the population that has to migrate in order to allow the outbreak of cooperation on any island. If $f_1^{(1)}(0) = f_{\rm thr}^K$ it is at the same the maximum fraction to not let cooperation collapse back home, i.e. it is the optimal migration rate [see Fig. 7(middle)].

Eventually, one can ask how the outbreak of cooperation $(f^K_{\rm thr}, m^K)$ is affected if instead of the two strategies TFT, ALL-D three or four strategies are considered. In general, the presence of both ALL-C and A-TFT favors the invasion of ALL-D at the end, whereas the presence of A-TFT favors the invasion of TFT — thus we can expect that the thresholds are slightly higher or lower in such cases. A more involved discussion is presented in Appendix D.

5. Conclusion

Before summarizing our findings, we wish to comment on a related strand of literature about multi-level selection in populations [20, 22]. There, quite similar to the setup presented in our paper, a population consisting of several groups (subpopulations) was considered where interaction only occurs between agents of the same subpopulation. The fitness of agents was determined by the payoff obtained from an evolutionary game, simply chosen as a non-iterative Prisoner's Dilemma, and their reproduction was assumed to be dependent on their payoff according to a Moran process [21]. Further a stochastic dynamics was considered.

In addition to these differences (PD, Moran process, stochastic dynamics), also a separate group dynamics was assumed. Groups can split when reaching a certain size, which denotes a amplified replication process at the group level. Precisely, groups that contain fitter agents reach the critical size faster and, therefore, split more often. This concept leads to selection among groups, although only individuals reproduce. It allows for the emergence of higher level selection (group) from lower level reproduction (agents). It was shown [20, 22] that cooperation in such a setting is favored if the size of groups is small whereas the number of groups is large. Migration does *not* support the outbreak of cooperation in this model because it favors the invasion of defectors rather than of cooperators.

In contrast to these investigations, we have contributed to the analysis of evolutionary (deterministic) IPD games in two different domains:

(i) For the meanfield limit, represented by a panmictic population where each agent interacts with $N-1$ other agents n_g times, a quantitative investigation of the basins of attraction was provided. Dependent on the initial mix of two cooperative (ALL-C, TFT) and two defective (ALL-D, A-TFT) strategies and the number of interactions n_g, we could derive the critical conditions (threshold frequencies) under which the outbreak of cooperation can be expected in a panmictic population. A detailed analysis of the two, three and four strategy cases helped to better understand the contribution of each strategy on the final outcome.

(ii) Using the "unperturbed" (or meanfield) limit as a reference point, the impact of migration on the outbreak of cooperation in a spatially distributed system could be quantified. We found that there is a bandwidth of optimal migration rates which lead to the induction (or "export") of cooperation to a number of islands which otherwise would converge to defection. We were able to determine the critical conditions f_{thr}^K, m^K which guarantee the outbreak of cooperation in a worst case scenario. Remarkably, the relative effort f_{thr}/K to export cooperation to defecting islands was decreasing with K in some range and always stayed below the critical value for an isolated island, i.e., effectively it became easier to turn defecting into cooperating islands, provided the optimal migration rate was reached.

It is important to note that the outbreak of cooperation is not enforced by a maximal migration rate but, as stated above, by a small range of optimal migration rates. This is because migration, different from other approaches, is not seen as an unidirectional dynamics, where agents just move to a "better" place. Instead, our model is based on the assumption that it is a *bidirectional* process, which we deem a more realistic assumptions when considering a dynamics over many generations. In fact, agents, or their offsprings, which have obtained certain skills or wealth at their immigration country, quite often decide to start new buisiness back home at their origin country — because their new capabilities give them a considerable advantage there, while it is only a marginal advantage in their immigration country. This assumption is in line with many policies about immigration/education of foreigners in a country, to give indirect support for development and to allow future business with those countries, where some agents with positive experience have resettled. At the end, as we have shown in our paper, it remarkably helps to spread "cooperation" globally, if the number of breeding places for such a strategy is increased (above a minimum threshold).

Acknowledgment

This work on the outbreak of cooperation was supported by the COST-Action MP0801 *Physics of Competition and Conflicts*. F.S. announces financial support from the Swiss State Secretariat for Education and Research SER C09.0055.

Appendix A. Calculating the Average Payoff

In order to illustrate Eq. (8), let us look at two agents i and j. If both of them play strategy $z^{(1)}$, TFT, then, during the n_g different "iterations", their choices are as follows:

$$\begin{array}{rr} & 1\;\;2\;\;3\;\;4\;\cdots n_g \\ \text{payoff } a_i^{(11)} & : R\;R\;R\;R\cdots\;R \\ i\qquad (TFT) & : C\;C\;C\;C\cdots\;C \\ j\qquad (TFT) & : C\;C\;C\;C\cdots\;C \\ \text{payoff } a_j^{(11)} & : R\;R\;R\;R\cdots\;R. \end{array} \tag{A.1}$$

Consequently, the average payoff for both agents i and j is $a_i^{(11)} = a_j^{(11)} = R$. If agent i playing TFT meets with an agent j playing strategy $z^{(2)}$ (ALL-D) the series of choices would be:

$$\begin{array}{rl}
 & 1\ \ 2\ \ 3\ \ 4\ \cdots n_g \\
\text{payoff } a_i^{(12)} : & S\ \ P\ \ P\ \ P \cdots\ \ P \\
i \qquad (TFT) : & C\ \ D\ \ D\ \ D \cdots\ \ D \\
j\ (ALL-D) : & D\ \ D\ \ D\ \ D \cdots\ \ D \\
\text{payoff } a_j^{(21)} : & T\ \ P\ \ P\ \ P \cdots\ \ P,
\end{array} \tag{A.2}$$

which leads to an average payoff for agent i of $a_i^{(12)} = [S + (n_g - 1)P]/n_g$, while the average payoff for agent j is $a_j^{(21)} = [T + (n_g - 1)P]/n_g$.

If agent i playing A-TFT interacts with agent j playing ALL-D, the series of choices reads:

$$\begin{array}{rl}
 & 1\ \ 2\ \ 3\ \ 4\ \cdots n_g \\
\text{payoff } a_i^{(42)} : & P\ \ S\ \ S\ \ S \cdots\ \ S \\
i\ (A-TFT) : & D\ \ C\ \ C\ \ C \cdots\ \ C \\
j\ (ALL-D) : & D\ \ D\ \ D\ \ D \cdots\ \ D \\
\text{payoff } a_j^{(24)} : & P\ \ T\ \ T\ \ T \cdots\ \ T.
\end{array} \tag{A.3}$$

That means the average payoff for agent i is $a_i^{(42)} = [P + (n_g - 1)S]/n_g$, while the average payoff for agent j is $a_j^{(24)} = [P + (n_g - 1)T]/n_g$. The remaining cases can be explained similarly. Only the three more complex cases are given below. $a_i^{(14)}$ follows from:

$$\begin{array}{rl}
 & 1\ \ 2\ \ 3\ \ 4\ \ 5\ \ 6\ \ 7\ \ 8\ \cdots \\
\text{payoff } a_i^{(14)} : & S\ \ P\ \ T\ \ R\ \ S\ \ P\ \ T\ \ R \cdots \\
i \qquad (TFT) : & C\ \ D\ \ D\ \ C\ \ C\ \ D\ \ D\ \ C \cdots \\
j\ (A-TFT) : & D\ \ D\ \ C\ \ C\ \ D\ \ D\ \ C\ \ C \cdots \\
\text{payoff } a_j^{(41)} : & T\ \ P\ \ S\ \ R\ \ T\ \ P\ \ S\ \ R \cdots
\end{array} \tag{A.4}$$

Here, the average payoff of agent i results from a repeated payoff series $SPTR$, and the value of n_g defines when this series is truncated. Similarly, the series for $a_i^{(41)}$ is $TPSR$. Thus, the first term of $a_i^{(rq)}$, Eq. (9) calculates all *completed* payoff series (n_g div 4), while the second term calculates the remaining payoffs (n_g rem 4).

For $a_i^{(44)}$, we find eventually:

$$\begin{array}{rl}
 & 1\ \ 2\ \ 3\ \ 4\ \cdots \\
\text{payoff } a_i^{(44)} : & P\ \ R\ \ P\ \ R \cdots \\
i\ (A-TFT) : & D\ \ C\ \ D\ \ C \cdots \\
j\ (A-TFT) : & D\ \ C\ \ D\ \ C \cdots \\
\text{payoff } a_j^{(44)} : & P\ \ R\ \ P\ \ R \cdots
\end{array} \tag{A.5}$$

Here, the period of the payoff series is just 2 instead of 4, and the expression for $a_i^{(44)} = a_j^{(44)}$, Eq. (9) follows accordingly.

Appendix B. Two Strategies: TFT and ALL-D

We assume that the population consists of only two strategies: $z^{(1)} = \text{TFT}$ and $z^{(2)} = \text{ALL-D}$, Eq. (3). This is an interesting combination since defection is known to be the only equilibrium in an one-shot PD game, while TFT fares well in a repeated PD interaction, given there is a critical number of encounters (discussed below).

The average payoff $a_i^{(rq)}$ received by agent i playing strategy $z^{(q)}$ $(q \in 1, 2)$ results from Eq. (8). Choosing $n_g = 4$ we find:

$$\begin{bmatrix} a^{(11)} & a^{(12)} \\ a^{(21)} & a^{(22)} \end{bmatrix} = \begin{bmatrix} 3.0 & 0.75 \\ 2.0 & 1.0 \end{bmatrix}. \tag{B.1}$$

Applying Eqs. (4) and (11), we find for the total average payoff:

$$\bar{a} = a^{(11)} {f^{(1)}}^2 + (a^{(12)} + a^{(21)}) f^{(1)} f^{(2)} + a^{(22)} {f^{(2)}}^2 \tag{B.2}$$

On the other hand, it follows from the stationary condition (12):

$$\begin{aligned} \bar{a} f^{(i)} - (a^{(i1)} f^{(1)} + a^{(i2)} f^{(2)}) f^{(i)} = 0 \quad (i = 1, 2) \\ f^{(1)} + f^{(2)} = 1. \end{aligned} \tag{B.3}$$

The combined Eqs. (B.2), (B.3) have to be solved simultaneously for the possible stationary frequencies $f^{(1)}$, $f^{(2)}$. As the result we find:

$$\begin{aligned} &\text{(i)} \quad f^{(1)} = 0, \quad f^{(2)} = 1 \quad \text{(stable)} \\ &\phantom{\text{(i)}} \quad f^{(1)} = 1, \quad f^{(2)} = 0 \quad \text{(stable)} \\ &\text{(ii)} \quad f^{(1)}_{\text{thr}} = 0.2, \quad f^{(2)}_{\text{thr}} = 0.8 \quad (\text{for } n_g = 4) \quad \text{(unstable)} \end{aligned} \tag{B.4}$$

Solution (i) implies that either strategy ALL-D or TFT invades the population completely, which are the two stable attractors of the system in the case of only two strategies. On the other hand, solution (ii) describes the coexistence of the two strategies with different frequencies within the total population. In the given case, it is is an unstable point attractor that separates the basins of two stable attractors, and therefore acts as a separatrix here, i.e., for an initial frequency $f^{(1)}(0) \leq 0.2$ of strategy $z^{(1)} = \text{TFT}$, the dynamics of the system will converge into a stationary state that is entirely dominated by strategy ALL-D (where the payoff per agent is $\bar{a} = P = 1$), whereas in the opposite case the population will entirely adopt strategy TFT (average payoff $\bar{a} = R = 3$).

The threshold value $f^{(s)}_{\text{thr}}$ strongly decreases with the number of encounters n_g, as shown in Fig. 2 for the case of four strategies. This raises the question about the critical n_g for which TFT could invade the whole population. Let us compare the average payoffs of the strategies $z^{(1)} = \text{TFT}$ and $z^{(2)} = \text{ALL-D}$:

$$\begin{aligned} a^{(1)} &= a^{(11)} f^{(1)} + a^{(12)} f^{(2)} \\ a^{(2)} &= a^{(12)} f^{(1)} + a^{(22)} f^{(2)}. \end{aligned} \tag{B.5}$$

The respective values of $a^{(rq)}$ can be calculated from Eq. (8) for different numbers of n_g. We find that only the elements $a^{(12)}$ and $a^{(21)}$ change with n_g, as follows:

$$\begin{array}{c|c|c|c|c} n_g & 1 & 2 & 3 & \cdots \\ \hline a^{(12)} & 0.0 & 0.5 & 0.677 & \cdots \\ a^{(21)} & 5.0 & 3.0 & 2.333 & \cdots \end{array} \tag{B.6}$$

With $a^{(11)} = 3.0$ and $a^{(22)} = 1.0$, we find for $n_g = 1$ that $a^{(21)} > a^{(11)}, a^{(22)} > a^{(12)}$. This implies that $a^{(2)} > a^{(1)}$ for all possible initial frequencies of the two strategies in the population. Thus, from the dynamics of Eq. (5) (fitness-proportional selection) the extinction of the strategy TFT results, in agreement with the known results. For $n_g = 2$ we find $a^{(21)} = a^{(11)}$, $a^{(22)} > a^{(12)}$, which again implies that $a^{(2)} > a^{(1)}$ for all possible initial frequencies of the two strategies in the population, i.e., the extinction of strategy TFT. However, for $n_g = 3$, we find $a^{(21)} < a^{(11)}$, $a^{(22)} > a^{(12)}$. Thus, there exist some initial frequencies of the two strategies for which $a^{(1)} > a^{(2)}$ results, i.e., we can conclude that for the given payoff matrix $n_g^{\mathrm{thr}} = 3$ is the *threshold value* for the number of interactions between each two agents that may lead to the invasion of cooperation in the whole population.

Appendix C. Three Strategies: TFT, ALL-D and ALL-C

When strategy $z^{(3)} =$ ALL-C is added to the previous strategies $z^{(1)} =$ TFT and $z^{(2)} =$ ALL-D, agents playing ALL-D will benefit from agents playing ALL-C. Therefore, if the frequency of agents playing ALL-C is increased in the initial population, it can be expected that the basin of attraction of the TFT strategy will shrink, while the basin of attraction of the ALL-D strategy will grow, compared to the case of two strategies, discussed in Appendix B. The stationary frequencies have now to be calculated from the following set of coupled equations that result from Eqs. (4), (11) and the stationary condition (12):

$$\begin{gathered} \bar{a} = \sum_{s=1}^{3} a^{(s)} f^{(s)} = \sum_{s=1}^{3} \left(\sum_{r=1}^{3} a^{(rs)} f^{(r)} \right) f^{(s)} \\ \bar{a} f^{(i)} - (a^{(i1)} f^{(1)} + a^{(i2)} f^{(2)} + a^{(i3)} f^{(3)}) f^{(i)} = 0 \quad (i = 1, 2, 3) \\ f^{(1)} + f^{(2)} + f^{(3)} = 1 \end{gathered} \tag{C.1}$$

The matrix elements $a^{(rq)}$ can be calculated from Eq. (8). With $n_g = 4$ we find the following stationary solutions:

$$\begin{array}{ll} \text{(i)} & f^{(1)} = 1, \quad f^{(2)} = 0, \quad f^{(3)} = 0 \quad \text{(stable)} \\ & f^{(1)} = 0, \quad f^{(2)} = 1, \quad f^{(3)} = 0 \quad \text{(stable)} \\ & f^{(1)} = 0, \quad f^{(2)} = 0, \quad f^{(3)} = 1 \quad \text{(unstable)} \\ \text{(ii)} & f^{(1)}_{\mathrm{thr}} = 0.2, \quad f^{(2)}_{\mathrm{thr}} = 0.8, \quad f^{(3)} = 0 \quad (\text{for } n_g = 4) \quad \text{(unstable)} \\ & f^{(1)} = 1.0 - f^{(3)} (0 \le f^{(3)} \le 1), \quad f^{(2)} = 0 \quad \text{(stable)} \end{array} \tag{C.2}$$

We note that a mean-field analysis of the three-strategy case was also dicussed in [24] and, assuming extensions such as mutations and fluctuations, analyzed further in [2, 9]. We consider the deterministc case here. Solutions (i) imply that either strategy TFT or ALL-D or ALL-C invades the entire population. We note that only the first two solutions are stable ones, while the last point-attractor $f^{(3)} = 1$, $f^{(1)} = f^{(2)} = 0$ is an unstable one, because any small pertubation (i.e., the invasion of one defecting agent) will transfer the cooperating system into a defecting one.

The first of the solutions (ii) describing coexisting strategies is already known from the investigation in Appendix B to be an unstable one. In the absense of the third strategy, it defines the separatrix point. The second solution (ii) however is a stable one, indicating that both agents playing TFT and ALL-C can coexist in the panmictic population. Note that there is neither a stable nor an unstable coexistence of all three strategies.

The separatrix that divides the different basins of attraction is now a line in a two-dimensional space of the initial frequencies. But different from Appendix B the stationary solutions of Eq. (C.2) do not give further information about the separatrices. In order to calculate the different basins of attraction, we therefore have numerically solved Eq. (5) for the full range of initial frequencies: $0 \le f^{(1)}(0) \le 1$, $0 \le f^{(2)}(0) \le 1$, $f^{(3)}(0) = 1 - f^{(1)}(0) - f^{(2)}(0)$, and have evaluated the average payoff in the stationary limit. If $\bar{a} = P$, obviously the whole population has adopted strategy $z^{(2)} =$ ALL-D. Similarly, if $\bar{a} = R$ and $f^{(1)} = 1$, the whole population has adopted strategy $z^{(1)} =$ TFT. However, if $\bar{a} = R$ and $f^{(1)} < 1$, then there is a coexistence of agents playing strategy $z^{(1)} =$ TFT and $z^{(3)} =$ ALL-C.

The basins of attraction are shown in Fig. 9 for two different values of $n_g = 4$ and $n_g \to \infty$. In the latter case, $a^{(12)} = a^{(21)} = 1$ results for the payoffs in Eq. (8). For $n_g = 4$ we can distinguish between three different regions in Fig. 9. Region A denotes the range of initial frequencies $f^{(s)}(0)$ that lead to the adoption of the $z^{(2)} =$ ALL-D strategy in the whole population, region B denotes the range of initial frequencies that lead to the adoption of the $z^{(1)} =$ TFT strategy in the whole population, while region C denotes the range of initial frequencies that lead to the coexistence of both $z^{(1)} =$ TFT and $z^{(3)} =$ ALL-C strategies.

Since regions B and C both describe the adoption of cooperating strategies in the population, the most interesting line in Fig. 9 is the separatrix between region A (all defectors) and region B (all cooperators). We can easily interpret this line based on our previous analysis of the two-strategy case, Appendix B. The diagonal in Fig. 9 represents $f^{(1)} + f^{(2)} = 1$, i.e., a population with only two strategies, $z^{(1)} =$ TFT and $z^{(2)} =$ ALL-D. Thus, the separatrix line between regions A and B starts from the separatrix point $f^{(1)} = 0.2$, $f^{(2)} = 0.8$, $f^{(3)} = 0$, Eq. (C.2). Further below the diagonal, the frequency $f^{(3)}$ of the strategy $z^{(3)} =$ ALL-C increases in the initial population, which in turn increases the threshold frequency $f^{(1)}$ necessary for the invasion of the $z^{(1)} =$ TFT strategy. In a certain range of frequencies, the separatrix

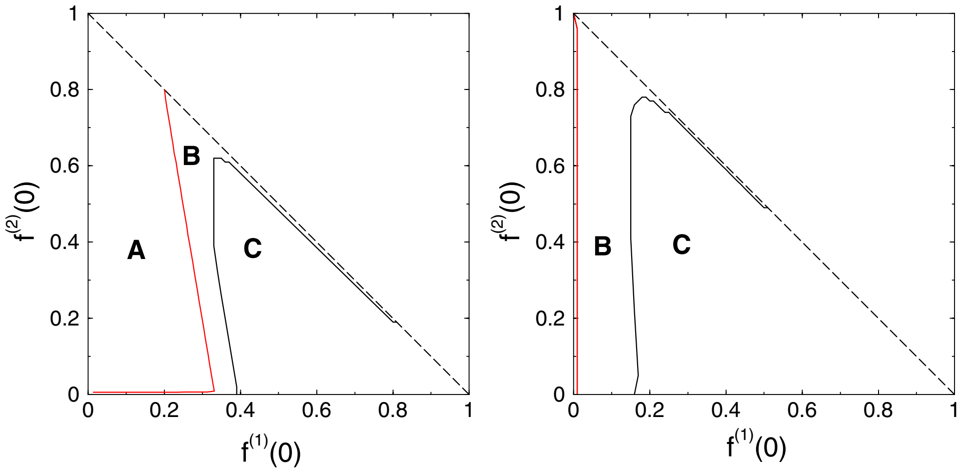

Fig. 9. Basins of attraction, i.e., range of initial frequencies $f^{(s)}(0)$ that lead to a particular stable solution, Eq. (C.2). A: adoption of $z^{(2)}$ = ALL-D strategy in the whole population, B: adoption of $z^{(1)}$ = TFT strategy in the whole population, C: coexistence of both $z^{(1)}$ = TFT and $z^{(3)}$ = ALL-C strategies. $f^{(3)}(0) = 1 - f^{(1)}(0) - f^{(2)}(0)$. (left) $n_g = 4$, (right) $n_g \to \infty$.

line between defection and cooperation can be described by a linear relation, found numerically as:

$$f^{(2)} = -6.1538 f^{(1)} + 2.0308 \quad \text{for } 0.2 \leq f^{(1)} \leq 0.31. \tag{C.3}$$

However, we notice that the separatrix line between regions A and B never hits the x-axis. For very low values of $f^{(2)}(0)$, i.e., close to the x-axis, it makes a sharp turn towards the origin. This means that for a vanishing initial frequency of ALL-D there will be no route to the respective attraction region A, which is obviously correct.

The influence of the parameter n_g is shown by comparing the left ($n_g = 4$) and the right part ($n_g = \infty$) of Fig. 9. In the latter case the basin of attraction A (exclusive domination of strategy $z^{(2)}$ = ALL-D) becomes very small. In order to further quantify the influence of n_g on the dominating strategies in the stationary limit, we have also calculated the relative size of each basin of attraction. If F_A, F_B and F_C denote the area of the regions A, B and C in Fig. 9, the relative sizes are defined as follows:

$$a = \frac{F_A}{F_{\text{tot}}}; \quad b = \frac{F_B}{F_{\text{tot}}}; \quad c = \frac{F_C}{F_{\text{tot}}}; \quad d = \frac{F_B + F_C}{F_{\text{tot}}}; \quad F_{\text{tot}} = F_A + F_B + F_C \tag{C.4}$$

The results are shown in Fig. 10 for the two different values of n_g.

In Fig. 10, d, Eq. (C.4) denotes the relative size of the basin of attraction for cooperation resulting from both solutions, domination of $z^{(1)}$ = TFT and coexistence of $z^{(1)}$ = TFT and $z^{(3)}$ = ALL-C. As we see, for $n_g = 4$, the cooperative basin d only has about the same size as the basin of attraction for defection a, that mean that about half of the possible initial conditions will lead to a population

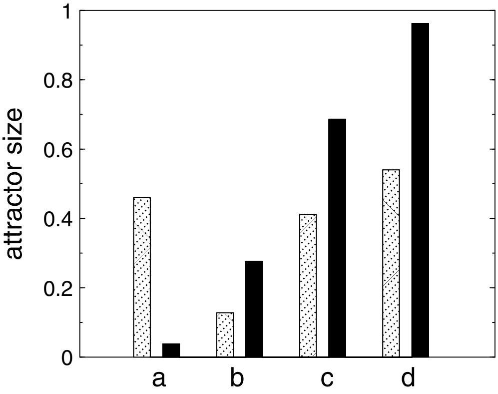

Fig. 10. Relative size, Eq. (C.4) of the basins of attraction shown in Fig. 9. The left bars (shaded area) refer to $n_g = 4$ (Fig. 9 left), while the right bars (black area) refer to $n_g \to \infty$ (Fig. 9 right). Thus, the change indicates the influence of n_g on the size of the basins of attraction.

of defecting agents, at the end. Only for $n_g \to \infty$ the size of the defection basin becomes insignificant as compared to the cooperative basin. This again explains the role of n_g in influencing cooperation.

Appendix D. Threshold Frequencies for Three and Four Strategies

In Sec. 4.3, we computed the critical conditions for the outbreak of cooperation (f^K_{thr}, m^K) in the presence of only two strategies, ALL-D and TFT. If we consider the two additional strategies ALL-C and A-TFT, Eq. (3), these critical conditions change dependent on the initial values of the four strategies and their distribution

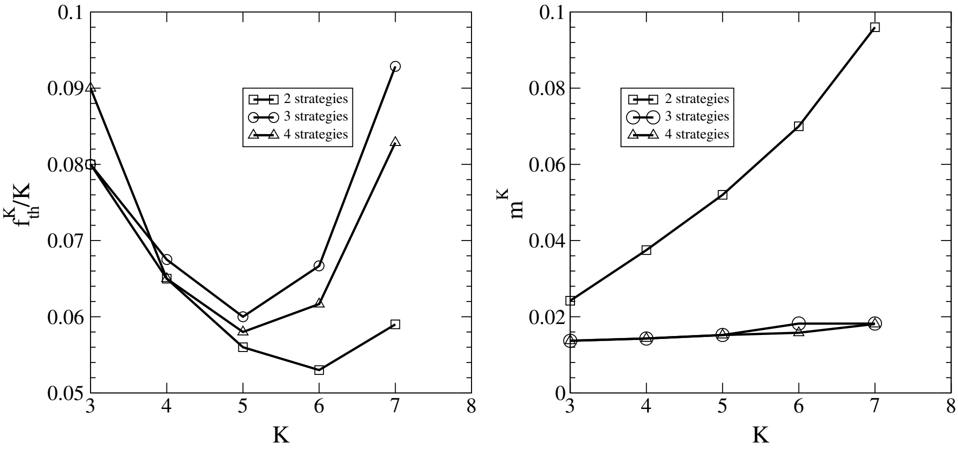

Fig. 11. (left) Threshold f^K_{thr} versus number of islands K. (right) Migration rate m versus number of islands K. Migration can only promote cooperation if the number of islands is $K \leq 7$.

on the different islands. Thus, instead of a complete investigations we only discuss the following sample configurations with $\sum_s f_k^{(s)}(0) = 1$:

(i) *three* strategies, TFT, ALL-D, ALL-C. $f_1^{(1)}(0) > 0, f_1^{(2)}(0) = 1 - f_1^{(1)}(0)$, $f_2^{(3)}(0) = 1$, $f_k^{(2)}(0) = 1$ with $k \geq 3$.
(ii) *four* strategies, TFT, ALL-D, ALL-C, A-TFT. $f_1^{(1)}(0) > 0, f_1^{(2)}(0) = 1 - f_1^{(1)}(0)$, $f_2^{(3)}(0) = 1$, $f_3^{(4)} = 1$, $f_k^{(2)}(0) = 1$ with $k \geq 4$.

These initial conditions imply that $K \geq 3$. The results of extensive calculations of the relative effort f_{thr}^K/K and the critical migration rate m^K are shown in Fig. 11 and can be compared to the two strategy case, Eq. (17).

Again, we notice that the relative effort to invade other islands by agents playing TFT is nonmonotonously dependent on K and always stays below the threshold values observed without migration, as given in Sec. 2.4, Appendix C. Regarding the impact of the different strategies on the outbreak of cooperation, we see that in the presence of ALL-C ALL-D benefits more than TFT in terms of payoff which raises the threshold frequency. However, adding A-TFT benefits ALL-D less than adding ALL-C, which lowers the threshold frequency. This explains why the curve for the *four* strategy case is in between the curves corresponding to *two* and *three* strategies. From Fig. 11(right) the optimal migration rate is found to be almost constant for three and four strategies in contrast to the two strategy case.

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