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Fixation Times in Deme Structured, Finite Populations with Rare Migration

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Abstract Population structure affects both the outcome and the speed of evolutionary dynamics. Here we consider a finite population that is divided into subpopulations called demes. The dynamics within the demes are stochastic and frequency-dependent. Individuals can adopt one of two strategic types, A or B. The fitness of each individual is determined by interactions with other individuals in the same deme. With small probability, proportional to fitness, individuals migrate to other demes. The outcome of these dynamics has been studied earlier by analyzing the fixation probability of a single mutant in an otherwise homogeneous population. These results give only a partial picture of the dynamics, because the time when fixation occurs can be exceedingly large. In this paper, we study the impact of deme structures on the speed of evolution. We derive analytical approximations of fixation times in the limit of rare migration and rare mutation. In this limit, the conditional fixation time of a single A mutant in a B population is the same as that of a single B in an A population. For the prisoner's dilemma game, simulation results fit very well with our analytical predictions and demonstrate that fixation takes place in a moderate amount of time as compared to the expected waiting time until a mutant successfully invades and fixates. The simulations also confirm that the conditional fixation time of a single cooperator is indeed the same as that of a single defector.

Keywords Game theory · Cooperation · Subdivided populations · Stochastic dynamics · Speed of evolution

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1 Introduction

The structure of a population has the potential for profound effects on the evolutionary trajectory. This is a classic in population genetics [18,43]. Traditional models for population structures include viscous populations [16,42], lattices or networks [17,21,25], island models [11,32,39] or deme structured populations [14,24,30,37,41] with a particular focus on diffusion approximations [5,26,40]. One reason for the strong interest in structured populations is that they provide a simple, yet natural way to resolve the conundrum of cooperation as characterized by the prisoner's dilemma: in the absence of population structures individuals randomly interact with other members of the population and cooperative behaviour, which is costly to the actor and provides benefits to others, is doomed because it generates a social dilemma [6,15], where each individual faces the temptation to defect and avoid the costs of cooperation—in spite of the fact that everyone would be better off had everyone cooperated. However, spatial structure and limited local interactions represent one way of creating positive assortment [9,21] such that cooperators are more likely to interact with other cooperators, which can be sufficient to offset their losses from interacting with defectors.

In the absence of mutational processes any finite population eventually ends up in a homogeneous state with a single trait (or strategy) due to demographic noise and the trait is said to have reached fixation. Often it is assumed that mutation events are sufficiently rare such that a mutant will always have disappeared or reached fixation before the next mutation arises. Hence the mutational process does not interfere with the spreading (or disappearance) of resident and mutant types. In this case, a crucial determinant for evolutionary success is the probability that a single mutant succeeds in taking over the entire population [22]. This allows us to reduce the evolutionary process to an embedded Markov chain over all homogeneous states to determine the stationary distribution, i.e. the probabilities to find the population in each homogeneous state or the relative sojourn times [12,13]. However, evolutionary success is not solely based on fixation probabilities. In particular, high fixation probabilities do not imply a speedy take-over but the time to fixation determines how infrequent the occurrence of mutants needs to be, to be considered rare. Therefore it is important to complement fixation probabilities with fixation times [3,29]. More specifically, mutations need to occur far less frequently than the average time it takes a mutant to successfully invade and take over a population—otherwise the invasion and mutation processes interfere. However, under frequency-dependent selection, fixation times can easily become exceedingly large [1,2,7,38] such that the required mutation rates may be too small to remain biologically meaningful. Consequently, the concept of fixation may no longer be feasible and might be better replaced by an equilibrium analysis or by considering average abundances of different types [36].

Here we extend a stochastic model for the evolution of a finite population, which is subdivided into independent subunits often termed demes [14] and determine the fixation times. More specifically, we derive analytical expressions for (conditional) fixation times in the limit of rare migration and even rarer mutation. This determines the time scales on which migration and mutation events need to occur for the approximation to hold. Or, equivalently, the inverse conditional fixation time quantifies under which conditions migration and/or mutation can be considered rare events. Moreover, under general assumptions on the evolutionary dynamics within demes, we prove that the surprising symmetry in conditional fixation times [3,19,29] extends to deme structured populations. Finally, we demonstrate that the analytical approximations are in good agreement with simulation based results and show that the symmetry in conditional fixation times extends (approximately) to arbitrary migration rates.

2 The Model

Here we consider a finite population of constant size M that is divided into $D \geq 2$ subpopulations or demes of equal size $N \geq 2$ ($M = D \cdot N$). There are two types of individuals, A and B. Within each deme all individuals engage in pairwise interactions. The payoffs for the different interactions are given by the payoff matrix

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \tag{1}$$

indicating that two A types obtain the payoff a each, an A type interacting with a B type gets b whereas the B type gets c and two B types end up with d each. The payoff of each individual translates into its fitness or reproductive success. In a deme with j individuals of type A (and $N - j$ of type B), the payoff of A and B types is $\pi_A(j) = ((j-1)a + (N-j)b)/(N-1)$ and $\pi_B(j) = (j\,c + (N-j-1)d)/(N-1)$, respectively. Their fitness (or fecundity) is given by $f_A(j) = \exp(w\,\pi_A(j))$ and $f_B(j) = \exp(w\,\pi_B(j))$. The parameter $w > 0$ indicates the strength of selection on fitness differences arising from the different strategic types. For weak selection, $w \ll 1$, the fitness is given by $f_A(j) \approx 1 + w\,\pi_A(j)$, $f_B(j) \approx 1 + w\,\pi_B(j)$, respectively, and represents a combination of a constant baseline fitness, which is normalized to 1, and the frequency-dependent payoffs. In the limit $w \to 0$ everyone has the same (baseline) fitness. Based on individual fitness, the composition of each deme changes according to a stochastic evolutionary process such as the frequency-dependent Moran process [20,22] or pairwise comparison processes [34], see Sect. 4.

No interactions occur between individuals in different demes. However, offspring can migrate from one deme to another with probability μ. Occasionally, with probability ν, an individual may also mutate and spontaneously switch its strategic type from A to B or vice versa. Throughout the text we assume that mutation and migration events are both rare, $\mu, \nu \ll 1$, such that invasion attempts are isolated events and the invasion of a particular deme will have succeeded (or failed) before the next attempt occurs.

In the limit of rare mutation and rare migration, the population dynamics is reflected in the probabilities that the number i of homogeneous demes of type A increases, Q_i^+, or decreases, Q_i^-. With probabilities

$$p_A(i) = \frac{i\ F_A}{i\ F_A + (D-i)F_B} \tag{2a}$$

$$p_B(i) = \frac{(D-i)F_B}{i\ F_A + (D-i)F_B} = 1 - p_A(i) \tag{2b}$$

an A type or B type, respectively, is chosen for reproduction, where $F_A = f_A(N) = \exp(w\,a)$, $F_B = f_B(0) = \exp(w\,d)$ denote the fitness of A and B type individuals in a homogeneous A and B deme, respectively. With small probability the offspring mutates spontaneously into the other type or migrates into another deme. More specifically, Q_i^+ denotes the probability that a single homogeneous deme of B types is successfully invaded (and taken over) by A types. This occurs if either an A offspring migrates to a B deme or if the offspring of a B type mutates into an A type:

$$Q_i^+ = \rho_A \left(\nu\ p_B(i) + \mu\ p_A(i) \cdot \frac{D-i}{D} \right), \tag{3}$$

where ρ_A denotes the fixation probability of a single A type in a homogeneous B deme. Similarly, Q_i^- indicates the probability that one of the i demes of type A is taken over by B types

$$Q_i^- = \rho_B \left(\nu \; p_A(i) + \mu \; p_B(i) \cdot \frac{i}{D} \right) \tag{4}$$

and ρ_B is the probability that a single B individual takes over an otherwise homogeneous A deme. Finally, with probability $1 - Q_i^+ - Q_i^-$ the number of homogeneous demes remains unchanged – either because neither a mutation nor migration event occurred or because the invasion attempt was unsuccessful.

2.1 Rare mutation & rare migration

If $i = 0$ or $i = D$ the population is homogeneous. Without mutations, that is $\nu = 0$, these states are absorbing. For $\mu \ll 1$ the population spends most of its time in states where all demes are homogeneous, either of type A or of type B. This means that a migrant will have succeeded and taken over a deme or failed and disappeared before the next migration takes place. For $0 < \nu \ll \mu \ll 1$ mutation events are even rarer than migrations and hence the population will have reached one of the absorbing homogeneous states of $all-A$ or $all-B$ types before the next mutation arises. Consequently, the population is homogeneous most of the time. More specifically, we consider $\nu = \epsilon\nu_0$ and $\mu = \epsilon\mu_0$ in the limit $\epsilon \to 0$ and $\nu_0/\mu_0 \to 0$ [14].

3 Dynamics on the Level of Demes

3.1 Fixation Probabilities

The evolutionary process on the level of demes corresponds to a Moran process [20]. If there are i homogeneous demes of type A (and $D - i$ of type B) then the fixation probability of A's is given by

$$\Psi_i = \frac{1 + \sum_{k=1}^{i-1} \prod_{j=1}^{k} \frac{Q_j^-}{Q_j^+}}{1 + \sum_{k=1}^{D-1} \prod_{j=1}^{k} \frac{Q_j^-}{Q_j^+}} = \Psi_1 \left(1 + \sum_{k=1}^{i-1} \prod_{j=1}^{k} \frac{Q_j^-}{Q_j^+} \right). \tag{5}$$

Similarly, $\tilde{\Psi}_{D-i} = 1 - \Psi_{D-i}$ denotes the fixation probability of B's from i homogeneous demes of type A. The fixation probability of a single type A individual in a deme structured population then becomes $\rho_A \Psi_1$ and for a single B type it is $\rho_B \tilde{\Psi}_{D-1}$.

3.1.1 Rare Mutation

In the limit of rare mutation, the evolutionary process becomes equivalent to a Moran process with constant selection. More specifically, for $\nu \ll \mu$ the ratio Q_i^-/Q_i^+ reduces to a constant, $\eta = (F_B\rho_B)/(F_A\rho_A)$. The fixation probability of A's if there are i homogeneous demes of type A then reduces to

$$\Psi_i \approx \frac{1 - \eta^i}{1 - \eta^D}, \tag{6}$$

which has been derived in [14]. This results in a simple and general condition under which evolution favours the A types, without any assumptions on the dynamics within each deme:

$$\frac{\rho_A}{\rho_B} > \left(\frac{F_B}{F_A}\right)^{1-\frac{1}{D}}. \tag{7}$$

If condition (7) holds, then, in the long run, the population spends more time in the homogeneous A state than in the homogeneous B state – or, equivalently, the average fraction of A's in the population exceeds $1/2$.

Note that Eqs. (3), (4) link both mutation and migration events to the reproduction of a member of the population (cf. Eq. (2a)). This is slightly different but biologically more plausible than the setup in Hauert & Imhof [14], where mutations are random events. However, in the limit of rare mutation and even rarer migration, the two approaches converge and yield the same results.

3.2 Fixation Times

The unconditional fixation time, τ_i, denotes the expected time to reach either one of the homogeneous states given an initial state of the population with i homogeneous demes of type A (and $D-i$ demes of type B). The fixation time can be expressed as a recursive relation in terms of the probabilities that the number of A demes increases, Q_i^+, or decreases, Q_i^- by one, or stays the same (with probability $1 - Q_i^+ - Q_i^-$). Note that in either case, the time to fixation is incremented by the average time between *successful* invasion attempts based on the average time of an unsuccessful attempt as well as the time between subsequent events, which is denoted by γ_i. This yields:

$$\tau_i = Q_i^-(\tau_{i-1} + \beta) + Q_i^+(\tau_{i+1} + \alpha) + (1 - Q_i^- - Q_i^+)\tau_i + \gamma_i, \tag{8}$$

where α denotes the *conditional* fixation time of a single A type in an otherwise homogeneous deme of type B, i.e. the fixation time of the A type, provided that fixation is reached. Similarly, β denotes the conditional fixation time of a single B type in a homogeneous deme of type A. Note that Eq. (8) does not depend on the details of the dynamics within demes, which only affects the time increments α, β and γ_i (see Sect. 4). Consequently, the chain represented by Eq. (8) is similar to the original, frequency-independent Moran process [20], with the difference that time increments are not uniform.

The recursive relation, Eq. (8), states that the time to fixation given i demes of type A corresponds to the probability Q_i^- that the number of A demes is reduced to $i-1$, which takes the time β, plus the time it takes from the new state to reach fixation, τ_{i-1}. Similarly, with probability Q_i^+ the number of A demes is increased to $i+1$, which takes the time α, plus the new time to fixation τ_{i+1}. In analogy to the conditional fixation times α and β we define their complements $\bar{\alpha}$, $\bar{\beta}$ as the conditional fixation time of a single A (B) type that fails to invade a B (A) deme, i.e. the average time it takes a B (A) deme to successfully prevent an invasion attempt by an A (B) type.

With probability $1 - Q_i^- - Q_i^+$ the number of A demes remains unchanged. This applies to several events: (1) an A migrant fails to invade a B deme, which takes, on average, the time $\bar{\alpha}$ for a B deme to successfully defend itself against invasion plus 1 for the migration event; (2) similarly, a B migrant may fail to invade an A deme, which takes the time $\bar{\beta} + 1$; (3) a mutation arises in an A deme and it takes the time $\bar{\alpha}$ for the A deme to successfully defend itself against the B mutant plus 1 for the mutation event; (4) similarly, a mutation arises in a B deme and fails to take over, which takes the time $\bar{\beta} + 1$; (5) the remaining events simply

increase the time by 1, i.e. if an A migrant ends up in an A deme, a B migrates to another B deme, or simply a reproduction event—if all demes are homogeneous, this does not lead to a change in the population composition. The probabilities for each event above are:

$$p_1 = \mu\ p_A(i)\frac{D-i}{D}(1-\rho_A) \tag{9a}$$

$$p_2 = \mu\ p_B(i)\frac{i}{D}(1-\rho_B) \tag{9b}$$

$$p_3 = \nu\ p_A(i)(1-\rho_B) \tag{9c}$$

$$p_4 = \nu\ p_B(i)(1-\rho_A) \tag{9d}$$

$$p_5 = \mu\left(p_A(i)\frac{i}{D} + p_B(i)\frac{D-i}{D}\right) + (1-\mu-\nu)(p_A(i)+p_B(i)). \tag{9e}$$

Note that the probabilities for the five events must add up to $1-Q_i^- - Q_i^+$. Hence the average time of an unsuccessful invasion attempt, γ_i, is given by:

$$\begin{aligned}\gamma_i &= (p_1+p_4)(\bar{\alpha}+1) + (p_2+p_3)(\bar{\beta}+1) + p_5\\ &= (\bar{\alpha}+1)(1-\rho_A)\left(\mu p_A(i)\frac{D-i}{D} + \nu p_B(i)\right)\\ &\quad + (\bar{\beta}+1)(1-\rho_B)\left(\mu p_B(i)\frac{i}{D} + \nu p_A(i)\right)\\ &\quad + \mu\left(p_A(i)\frac{i}{D} + p_B(i)\frac{D-i}{D}\right) + 1 - \mu - \nu.\end{aligned} \tag{10}$$

Following and extending Traulsen & Hauert [35] we rewrite the recursive Eq. (8) as

$$\underbrace{\tau_{i+1}-\tau_i}_{z_{i+1}} = \xi_i(\underbrace{\tau_i-\tau_{i-1}}_{z_i}) - \alpha - \xi_i\beta - \gamma_i\frac{1}{Q_i^+}, \tag{11}$$

where $\xi_i = Q_i^-/Q_i^+$. If $i=0$ or $i=D$ fixation of B types or A types has already occurred in the entire population and hence $\tau_0 = \tau_D = 0$. The recursion yields

$$z_1 = \tau_1 - \tau_0 = \tau_1 \tag{12a}$$

$$z_2 = \tau_2 - \tau_1 = \xi_1(z_1-\beta) - \alpha - \frac{\gamma_1}{Q_1^+} \tag{12b}$$

$$z_3 = \tau_3 - \tau_2 = \xi_2(z_2-\beta) - \alpha - \frac{\gamma_2}{Q_2^+} \tag{12c}$$

$$= \xi_2\xi_1(\tau_1-\beta) - \xi_2(\alpha+\beta+\frac{\gamma_1}{Q_1^+}) - \alpha - \frac{\gamma_2}{Q_2^+} \tag{12d}$$

$$\vdots$$

$$z_{k+1} = (\tau_1-\beta)\prod_{m=1}^{k}\xi_m - \sum_{l=1}^{k}\left(\alpha+\beta+\frac{\gamma_l}{Q_l^+}\right)\prod_{m=l+1}^{k}\xi_m + \beta. \tag{12e}$$

The sum of z_k is telescoping and using $\tau_D = 0$ we find

$$\sum_{k=i+1}^{D} z_k = \tau_{i+1} - \tau_i + \tau_{i+2} - \tau_{i+1} + \cdots + \tau_D - \tau_{D-1} = -\tau_i \tag{13}$$

In particular, this yields the fixation times starting from a single deme of type A

$$\tau_1 = -\sum_{k=2}^{D}(\tau_1 - \beta)\prod_{m=1}^{k-1}\xi_m + \sum_{k=2}^{D}\sum_{l=1}^{k-1}\left(\alpha + \beta + \frac{\gamma_l}{Q_l^+}\right)\prod_{m=l+1}^{k-1}\xi_m - \sum_{k=2}^{D}\beta \tag{14}$$

and hence, using Eq. (5) for the fixation probability of a single homogeneous deme, Ψ_1, yields

$$\tau_1 = (1 - D\Psi_1)\beta + \Psi_1\sum_{k=1}^{D-1}\sum_{l=1}^{k}\left(\alpha + \beta + \frac{\gamma_l}{Q_l^+}\right)\prod_{m=l+1}^{k}\xi_m. \tag{15}$$

More generally, the time to fixation τ_i of a population with i homogeneous demes of type A is

$$\tau_i = (\beta - \tau_1)\sum_{k=i}^{D-1}\prod_{m=1}^{k}\xi_m + \sum_{k=i}^{D-1}\sum_{l=1}^{k}\left(\alpha + \beta + \frac{\gamma_l}{Q_l^+}\right)\prod_{m=l+1}^{k}\xi_m - (D - i)\beta \tag{16}$$

and hence the fixation time given a single homogeneous B deme, τ_{D-1}, is

$$\begin{aligned}\tau_{D-1} = (D\tilde{\Psi}_{D-1} - 1)\beta - \tilde{\Psi}_{D-1}&\sum_{k=1}^{D-1}\sum_{l=1}^{k}\left(\alpha + \beta + \frac{\gamma_l}{Q_l^+}\right)\prod_{m=l+1}^{k}\xi_m \\ &+ \sum_{l=1}^{D-1}\left(\alpha + \beta + \frac{\gamma_l}{Q_l^+}\right)\prod_{m=l+1}^{D-1}\xi_m,\end{aligned} \tag{17}$$

where $\tilde{\Psi}_{D-1} = 1 - \Psi_{D-1}$ denotes the fixation probability of B types from a single homogeneous B deme.

In summary, the average fixation time of a single A type in a subdivided population with D demes of fixed size N is

$$\rho_A(\alpha + \tau_1) + (1 - \rho_A)\bar{\alpha}, \tag{18}$$

where α, $\bar{\alpha}$ account for the time it takes the mutant to either fixate in the first deme or disappear before reaching fixation. Similarly, the fixation time for a single B type is

$$\rho_B(\beta + \tau_{D-1}) + (1 - \rho_B)\bar{\beta}, \tag{19}$$

where β, $\bar{\beta}$ denote the conditional fixation and failure times for a single B mutant in the first A deme.

3.3 Conditional Fixation Times

Conditional fixation times indicate the time it takes for A (or B) types to take over the population, i.e. the fixation time of A (or B) types, provided that fixation of A (B) types indeed occurs.

3.3.1 Fixation of A Types

The conditional fixation time, τ_i^A, indicates the average time until A types have taken over the entire population for an initial configuration of the population with i homogeneous type

A demes (and $D-i$ demes of type B). Similar to the unconditional fixation time, Eq. (8), the conditional fixation time can be expressed through an analogous recursive relation for τ_i^A:

$$\Psi_i \tau_i^A = \Psi_{i-1} Q_i^- (\tau_{i-1}^A + \beta) + \Psi_{i+1} Q_i^+ (\tau_{i+1}^A + \alpha) + \Psi_i (1 - Q_i^- - Q_i^+) \tau_i^A + \Psi_i \gamma_i,$$

or

$$\underbrace{\Psi_{i+1}\tau_{i+1}^A - \Psi_i \tau_i^A}_{w_{i+1}} = \xi_i \underbrace{(\Psi_i \tau_i^A - \Psi_{i-1}\tau_{i-1}^A)}_{w_i} - \Psi_{i+1}\alpha - \Psi_{i-1}\xi_i \beta - \Psi_i \frac{\gamma_i}{Q_i^+}, \tag{20}$$

which has the same form as Eq. (11). A similar iteration yields:

$$w_k = \Psi_1 \tau_1^A \prod_{m=1}^{k-1} \xi_m - \sum_{l=1}^{k-1} \Psi_l \left(\alpha \xi_l + \beta + \frac{\gamma_l}{Q_l^+} \right) \prod_{m=l+1}^{k-1} \xi_m - (\alpha - \beta) \Psi_{k-1}, \tag{21}$$

using that at the boundaries $\Psi_0 \tau_0^A = \Psi_D \tau_D^A = 0$ holds because $\Psi_0 = 0$ (without any A's in the population they cannot reach fixation) and $\tau_D^A = 0$ (A's have already reached fixation). The sum over w_k is again telescoping, which yields $\sum_{k=i+1}^{D} w_k = -\Psi_i \tau_i^A$. Thus, the conditional fixation time of A types given a single, homogeneous A deme is:

$$\tau_1^A = \sum_{k=1}^{D-1} \sum_{l=1}^{k} \Psi_l \left(\alpha \xi_l + \beta + \frac{\gamma_l}{Q_l^+} \right) \prod_{m=l+1}^{k} \xi_m - (\alpha - \beta) \sum_{k=1}^{D-1} \Psi_k. \tag{22}$$

Consequently, the conditional fixation time of a single A individual in a homogeneous B population is

$$\alpha + \tau_1^A. \tag{23}$$

3.3.2 Fixation of B Types

Similar to Eq. (20), an analogous recursive relation for the conditional fixation times of B types can be derived. Using the shorthand $\tilde{\xi}_k = 1/\xi_k$ and $\tilde{\Psi}_k = 1 - \Psi_k$, which denotes the fixation probability of B types with k homogeneous A demes, we obtain an expression for the conditional fixation time, τ_1^B, when starting with a single homogeneous B deme:

$$\tau_{D-1}^B = \sum_{k=1}^{D-1} \sum_{l=1}^{k} \tilde{\Psi}_{D-l} \left(\alpha + \beta \tilde{\xi}_{D-l} + \frac{\gamma_{D-l}}{Q_{D-l}^-} \right) \prod_{m=l+1}^{k} \tilde{\xi}_{D-m} - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_{D-k}. \tag{24}$$

Comparison with Eq. (22) shows that the fixation times are symmetrical by exchanging $\alpha \leftrightarrow \beta$, $\Psi_k \leftrightarrow \tilde{\Psi}_k$, $\xi_k \leftrightarrow \tilde{\xi}_k$ and converting all indices from $i \leftrightarrow D-i$ with the exception of the sign of the second term. More importantly, however, the two conditional fixation times are actually equal:

$$\tau_1^A = \tau_{D-1}^B. \tag{25}$$

provided that $\alpha = \beta$ holds (see Appendix 3), i.e. the conditional fixation time within one deme of a single A type must be the same as that of a single B type. Even though this may appear to be a very restrictive constraint, it actually holds for any birth-death process with constant population size where the number of A (B) types changes at most by ± 1 (see Sect. 4). In particular, this includes the frequency-dependent Moran process, irrespective of the game [3,29], and other update rules that satisfy the detailed balance condition [29], as well as the Wright-Fisher process if selection is weak.

3.4 Rare Events

Recall that in the limit of rare mutation, $\nu \ll \mu$, the ratio $\xi_i = Q_i^-/Q_i^+$ reduces to a constant $\eta = (F_B\rho_B)/(F_A\rho_A)$. This results in considerable simplifications of the analytical expressions of the fixation times (see Appendix 1). More importantly, however, the fixation time scales inversely with the mutation rate $1/\mu$. This means that as μ decreases, opportunities to invade new demes dwindle and hence the fixation time increases and diverges in the limit $\mu \to 0$. Asymptotically, the fixation times scale as

$$\mu\,\tau_1 = \frac{D}{\rho_A}\sum_{l=1}^{D-1}\left(\frac{1}{l} + \frac{F_B}{F_A}\frac{1}{D-l}\right)\frac{1-\eta^l}{1-\eta^D} \tag{26a}$$

$$\mu\,\tau_{D-1} = \frac{D}{\rho_B}\sum_{l=1}^{D-1}\left(\frac{1}{l} + \frac{F_A}{F_B}\frac{1}{D-l}\right)\eta^{D-l}\frac{1-\eta^l}{1-\eta^D}. \tag{26b}$$

This means that whenever $\eta > 1$ (or $\rho_B F_B > \rho_A F_A$) then $\tau_1 > \tau_{D-1}$, at least for sufficiently small μ. Similarly, the conditional fixation times scale as

$$\mu\,\tau_1^A = \mu\,\tau_{D-1}^B = \frac{D}{\rho_A}\sum_{l=1}^{D-1}\left(\frac{1}{D-l} + \frac{F_B}{F_A}\frac{1}{l}\right)\frac{1-\eta^l}{1-\eta^D}\cdot\frac{1-\eta^{D-l}}{1-\eta}. \tag{27}$$

Note that irrespective of η, the conditional fixation time always exceeds both unconditional fixation times.

4 Dynamics on the Level of Individuals

The defining quantities for the dynamics on the level of demes are the fixation probabilities of a single A or B type in an otherwise homogeneous deme, ρ_A, ρ_B, as well as the average times of successful and unsuccessful invasion attempts, α, $\bar{\alpha}$ and β, $\bar{\beta}$, respectively, within a single deme.

4.1 Birth-Death Processes

Recall that the total population size, M, (and deme sizes N) remains constant and the number of A and B types changes at most by one in each time step. This applies, for example, if one individual is selected for reproduction and the clonal offspring displaces another individual in the population. Or, if an individual reassesses its strategic type and adopts the strategy of another individual in the population. The former case relates to biological reproduction and genetical inheritance, whereas the latter relates to cultural evolution and simple forms of learning mechanisms.

For such birth-death processes, explicit solutions for the fixation probabilities and (un)conditional fixation times are analytically accessible. The stochastic dynamics is reduced to the transition probabilities $T_i^{\pm}$, which indicates the probability that the number of A types, i, increases (or decreases) by one. The conditional fixation time, α, of a single A type in a B deme, i.e. the average time it takes the A type to successfully invade and take over the entire

deme, is given by:

$$\alpha = \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\Phi_l}{T_l^+} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+} \tag{28}$$

where Φ_l denotes the fixation probability of l A types (and $N-l$ B types) in a deme of size N:

$$\Phi_l = \frac{1 + \sum_{i=1}^{l-1} \prod_{j=1}^{i} \frac{T_j^-}{T_j^+}}{1 + \sum_{i=1}^{N-1} \prod_{j=1}^{i} \frac{T_j^-}{T_j^+}}. \tag{29}$$

The fixation probability of a single A type is denoted by $\rho_A = \Phi_1$ (for a review, see e.g. [35]).

Conversely, the average time of a failed invasion attempt, $\bar{\alpha}$, is the conditional fixation time of a single A type but conditioned on the event that all A's disappear. This is the average time it takes for a B deme to successfully defend itself against the invasion attempt of a single A type. We first note that the average, unconditional fixation time of a single A type, t_A, is given by:

$$t_A = \rho_A \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{1}{T_l^+} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+}. \tag{30}$$

Each invasion attempt of an A type succeeds with probability ρ_A and fails with probability $1-\rho_A$. Hence we have $t_A = \rho_A \alpha + (1-\rho_A)\bar{\alpha}$, where $\bar{\alpha}$ denotes the average time of a failed invasion attempt:

$$\begin{aligned} \bar{\alpha} &= \frac{t_A - \rho_A \alpha}{1-\rho_A} \\ &= \frac{\rho_A}{1-\rho_A} \left(\sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{1}{T_l^+} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+} - \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\Phi_l}{T_l^+} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+} \right) \\ &= \frac{\rho_A}{1-\rho_A} \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\tilde{\Phi}_l}{T_l^+} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+} \end{aligned} \tag{31}$$

Similarly, an invasion attempt of a single B type in an A deme succeeds with probability

$$\rho_B = \left(1 + \sum_{i=1}^{N-1} \prod_{j=1}^{i} \frac{T_j^+}{T_j^-} \right)^{-1}. \tag{32}$$

Note that $\rho_B = 1 - \Phi_{N-1}$ must hold, that is, the fixation probability of a single B type corresponds to the probability that $N-1$ individuals of type A fail to reach fixation. In analogy to Eq. (28), the conditional fixation time β is given by

$$\beta = \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\tilde{\Phi}_{N-l}}{T_{N-l}^-} \prod_{m=l+1}^{k} \frac{T_{N-m}^+}{T_{N-m}^-} \tag{33}$$

Comparing Eq. (28) and Eq. (33), we note that $\alpha = \beta$ holds for any birth-death process where the number of A and B types changes at most by one in each time step (see Appendix 2). In particular, note that this rather surprising symmetry holds irrespective of the game [3,29].

Similarly, the unconditional fixation time of a single B type in a deme of type A is

$$t_B = \rho_B \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{1}{T^-_{N-l}} \prod_{m=l+1}^{k} \frac{T^+_{N-m}}{T^-_{N-m}} \tag{34}$$

and leads to the average time, $\bar{\beta}$, of a failed invasion attempt of a B type by noting again that $t_B = \rho_B \beta + (1 - \rho_B)\bar{\beta}$ must hold:

$$\begin{aligned}
\bar{\beta} &= \frac{t_B - \rho_B \beta}{1 - \rho_B} \\
&= \frac{\rho_B}{1 - \rho_B} \left(\sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{1}{T^-_{N-l}} \prod_{m=l+1}^{k} \frac{T^+_{N-m}}{T^-_{N-m}} - \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\tilde{\Phi}_{N-l}}{T^-_{N-l}} \prod_{m=l+1}^{k} \frac{T^+_{N-m}}{T^-_{N-m}} \right) \\
&= \frac{\rho_B}{1 - \rho_B} \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\Phi_{N-l}}{T^-_{N-l}} \prod_{m=l+1}^{k} \frac{T^+_{N-m}}{T^-_{N-m}}.
\end{aligned} \tag{35}$$

Below we briefly discuss different approaches to modelling the stochastic dynamics within demes. This provides an opportunity to quantitatively compare our analytical predictions with simulation based data.

4.2 Moran Process

For the frequency-dependent Moran process [22] the transition probabilities are given by

$$T^+_i = \frac{N - i}{N} \left((1 - 2\nu) \frac{i f_A(i)}{i f_A(i) + (N - i) f_B(i)} + \nu \right) \tag{36a}$$

$$T^-_i = \frac{i}{N} \left((1 - 2\nu) \frac{(N - i) f_B(i)}{i f_A(i) + (N - i) f_B(i)} + \nu \right), \tag{36b}$$

which states that the number of A's increases (decreases) if (1) an A (B) type reproduces, no mutation occurs, and replaces a B (A) type or if (2) a B (A) type reproduces, the offspring mutates into an A (B) and again replaces a B (A) type. Mutations introduce a drift away from the homogeneous states with $i = 0$ and $i = N$ and hence increase the fixation time. Unfortunately, there is no similarly easy way to incorporate the effects of migrants on the dynamics within each deme. The number and type of migrants depends on the current composition of the entire population and hence, in general, the dynamics within one deme cannot be analyzed separately from the dynamics of the entire population. However, if the migration rate, μ, is sufficiently small then migrations are isolated events and do not affect the dynamics within each deme but only initiate new invasion attempts. This interpretation is confirmed through simulations and the good fit with the analytical approximation is illustrated for the prisoner's dilemma, see Fig. 1.

The present analysis hinges on the time-scale separation between the dynamics on the level of individuals in demes and demes in the population. To ensure that invasion attempts triggered by a mutant or a migrant remain isolated events requires $\nu, \mu \ll 1/\alpha$.

4.3 Pairwise Comparison Processes

Pairwise comparison processes are a broad and relevant class of update rules where a focal individual j and a model k are randomly selected from the population and a probabilistic comparison of their respective fitness determines whether the focal individuals switches

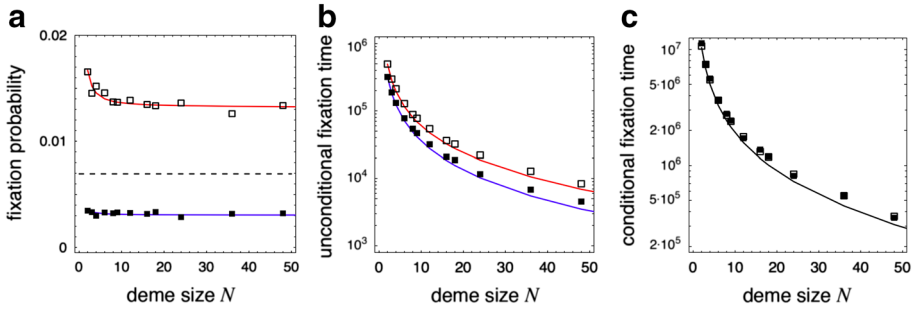

Fig. 1 Fixation probabilities and fixation times for the frequency-dependent Moran process for a population of fixed size, $M = 144$, as a function of the deme size. Within each deme, individuals engage in prisoner's dilemma interactions with $a = 1, b = 0, c = 1.1$, and $d = 0.1$ such that defection (B types) is dominant within demes but cooperative (A types) demes produce more migrants, $F_A > F_B$. **a** The fixation probability of cooperators (analytical approximation – *blue line*; simulation results – *filled symbols*) is always below the fixation probability of defectors (analytical approximation – *red line*; simulation results – *open symbols*) and also less than the neutral fixation probability (*dashed line*). The competitive advantage of cooperators between demes cannot compensate for their disadvantage within demes. **b** The unconditional fixation time of a single cooperator (*blue, filled symbols*) is consistently a little less than that of a single defector (*red, open symbols*). The reason is that with a high chance the cooperator does not even manage to take over the first deme and the population quickly fixates in the homogeneous $all-B$ state. **c** The conditional fixation times of cooperators and defectors are nevertheless equal.
Parameters: $M = 144$, $w = 0.1$, $\mu = 10^{-3}$, $\nu = 10^{-6}$ averaged over 10^5 runs once starting with a single A and once with a single B. (Color figure online)

strategy and adopts the strategy of the model, see e.g. [34]. The number of type A individuals changes only if the focal and the model individual have different types.

$$T_i^+ = \frac{N-i}{N}\left((1-\nu)\frac{i}{N}\gamma(f_B(i), f_A(i)) + \nu\right) \tag{37a}$$

$$T_i^- = \frac{i}{N}\left((1-\nu)\frac{N-i}{N}\gamma(f_A(i), f_B(i)) + \nu\right), \tag{37b}$$

where $\gamma(f_j, f_k)$ indicates the probability that the focal individual j adopts the model k's strategy in a deme with i individuals of type A. The number of A (B) types may increase if (1) the focal individual has type B (A) and the model is of type A (B), no mutation occurs and the focal adopts the model's strategy or (2) if the focal individual is of type B (A) and spontaneously changes its strategy to type A (B).

Examples of popular choices for $\gamma(f_j, f_k)$ include the local update process [33] with $\gamma(f_j, f_k) = \frac{1}{2} + \delta(f_k - f_j)$, where δ also specifies a selection strength but in contrast to w it affects only the dynamics within demes (cf. Eqs. (2a)-(4)). For $\delta \ll 1$ selection is weak and the dynamics within demes is dominated by random drift. For larger δ selection strength increases but an upper limit is imposed on δ by the requirement $0 \leq \gamma(f_j, f_k) \leq 1$. Another example is the Fermi process [4,28] with $\gamma(f_j, f_k) = 1/(1+\exp[-\delta(f_k - f_j)])$, see Fig. 2. Small δ recover the local update process and in the limit $\delta \to \infty$ the deterministic imitation dynamics is obtained [27,36].

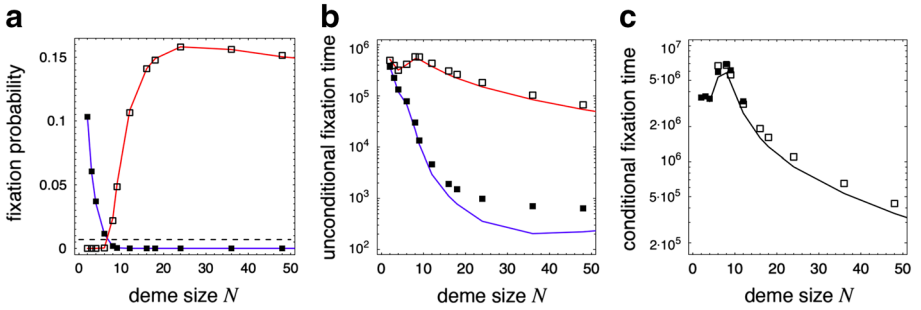

Fig. 2 Fixation probabilities and fixation times for a pairwise comparison process (Fermi process) for a population of fixed size, $M = 144$, as a function of the deme size. Setup is the same as in Fig. 1. **a** For small demes the fixation probability of cooperators (analytical approximation – *blue line*; simulation results – *filled symbols*) is higher than that of defectors (analytical approximation – *red line*; simulation results – *open symbols*) and also higher than the neutral fixation probability (*dashed line*) but for larger demes ($N \geq 8$) the converse holds. For small N and sufficiently weak selection within demes, the competitive advantage of cooperators between demes can outweigh their disadvantage within demes. **b** The unconditional fixation time of a single cooperator (*blue, filled symbols*) is always less than that of defectors (*red, open symbols*). However, for small N, where a single cooperator has a higher fixation probability than a single defector, the two fixation times are very similar. For larger N they rapidly differ by orders of magnitude. **c** The conditional fixation times are again equal and confirmed by the simulation data. However, due to the small fixation probabilities for cooperators and large N and defectors at small N, simulation data is only available in a limited region. Parameters: $M = 144$, $w = 0.1, \delta = 1.35, \mu = 10^{-3}, \nu = 10^{-6}$ averaged over 10^5 runs once starting with a single A and once with a single B. (Color figure online)

5 Symmetry of Conditional Fixation Times

A simple proof shows that the conditional fixation times of a single mutant of type A or B are identical for arbitrary birth-death processes with $T_i^+, T_i^- > 0$, $i = 1, \ldots, N-1$ and hence includes all dynamics described in Sect. 4. Again we assume that mutation and migration are rare events. More specifically, no further mutations occur until fixation takes place and, similarly, no migration occurs while one deme is inhomogeneous. This allows us to describe the deme dynamics by a Markov chain $\{X(t) : t = 0, 1, \ldots\}$ with state space $\{0, 1, \ldots, M\}$, where state x has the following interpretation: If x is a multiple of N, there are x/N homogeneous demes of type A and $D - x/N$ homogeneous demes of type B. If $x = kN + i$ with $k \in \{0, \ldots, D-1\}$ and $i \in \{1, \ldots, N-1\}$, there are k homogeneous demes of type A, $D - k - 1$ homogeneous demes of type B and there is exactly one mixed deme with i individuals of type A and $N - i$ individuals of type B. Using this chain, we do not need to keep track of which deme (if any) is mixed, which is of type A and which is of type B, as this is not important for the fixation times.

If x is not a multiple of N, $x = kN + i$ with $i \in \{1, \ldots, N-1\}$, then the next state is determined by the dynamics in the mixed deme, so that

$$
\begin{aligned}
P(X(t+1) = x+1 | X(t) = x) &= T_i^+, \\
P(X(t+1) = x-1 | X(t) = x) &= T_i^-, \\
P(X(t+1) = x | X(t) = x) &= 1 - T_i^+ - T_i^-.
\end{aligned}
$$

If x is a multiple of N, $x = kN$, then the next state is determined by a migration event

$$P(X(t+1) = x+1 | X(t) = x) = \frac{\mu}{D} \frac{k(D-k)F_A}{kF_A + (D-k)F_B},$$
$$P(X(t+1) = x-1 | X(t) = x) = \frac{\mu}{D} \frac{k(D-k)F_B}{kF_A + (D-k)F_B},$$
$$P(X(t+1) = x | X(t) = x) = 1 - P(X(t+1) = x \pm 1 | X(t) = x).$$

If $x = 0$ or $x = D\,N = M$ type B or type A has reached fixation. Another invasion attempt is initiated by a mutation event.

Thus, the transition matrix $[p_{xy}]$ with $x, y = 0, \ldots, M$ is a tridiagonal matrix and it follows from the results of Antal & Scheuring [3] or Taylor *et al.* [29] that t_1^A, the conditional fixation time of a single A type is equal to t_{M-1}^B, the conditional fixation time of a single B type. For the sake of completeness we give a short separate proof of the result used here.

Let π_x denote the probability that A takes over given the initial state is x. Let t_{xy} denote the expected time that the chain spends in state y before fixation takes place when the initial state is x. Let t_{xy}^A and t_{xy}^B denote the corresponding conditional expectation given that A and B, respectively, takes over. According to [8, Eqs. (2.159) and (2.153)],

$$\pi_x = t_{x,M-1}\, p_{M-1,M},$$
$$1 - \pi_x = t_{x1}\, p_{10},$$

and

$$t_{xy}^A = t_{xy} \frac{\pi_y}{\pi_x} = t_{xy} \frac{t_{y,M-1}}{t_{x,M-1}}, \tag{38a}$$

$$t_{xy}^B = t_{xy} \frac{1-\pi_y}{1-\pi_x} = t_{xy} \frac{t_{y1}}{t_{x1}}. \tag{38b}$$

Considering what happens on the first step, we see that $t_{xy} = \sum_{z=1}^{M-1} p_{xz} t_{zy}$ if $x \neq y$ and $t_{xx} = 1 + \sum_{z=1}^{M-1} p_{xz} t_{zx}$. Thus, in matrix notation, $\Theta = I + \Pi\Theta$, where $\Theta = [t_{xy}]$, $\Pi = [p_{xy}]$ with $x, y = 1, \ldots, M-1$ and I denotes the identity matrix. It follows that $\Theta = (I - \Pi)^{-1}$. Let Λ be the diagonal matrix with diagonal entries $\lambda_1, \ldots, \lambda_{M-1}$, where $\lambda_1 = 1$ and $\lambda_x = \prod_{y=1}^{x-1} p_{y,y+1}/p_{y+1,y}$ for $x \geq 2$. Using that Π is a tridiagonal matrix, one may verify that $\Pi = \Lambda^{-1}\Pi^T\Lambda$. Therefore,

$$\Theta = (I - \Pi)^{-1} = (I - \Lambda^{-1}\Pi^T\Lambda)^{-1} = \Lambda^{-1}(I - \Pi^T)^{-1}\Lambda = \Lambda^{-1}\Theta^T\Lambda.$$

Comparing the entries in position (x, y), we obtain that $t_{xy} = t_{yx}\lambda_y/\lambda_x$. It now follows from Eq. (38) that

$$t_{1y}^A = \frac{t_{y1}\,\lambda_y}{\lambda_1} \frac{t_{M-1,y}\,\lambda_{M-1}}{\lambda_y} \frac{\lambda_1}{t_{M-1,1}\,\lambda_{M-1}} = t_{M-1,y}^B.$$

Hence

$$t_1^A = \sum_{y=1}^{M-1} t_{1y}^A = \sum_{y=1}^{M-1} t_{M-1,y}^B = t_{M-1}^B.$$

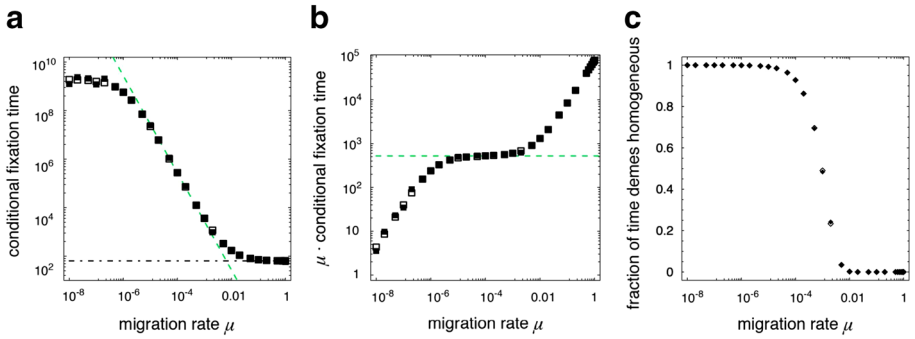

Fig. 3 Conditional fixation times for $D = 3$ demes of size $N = 100$ each ($M = 300$) as a function of the migration rate μ. Game parameters are the same as in Fig. 1 but with $\nu = 10^{-8}$ and averaged over 10^6 runs once starting with a single A and once with a single B. **a** conditional fixation times of a single A type (filled symbols) and a single B type (*open symbols*) remain very similar for any migration rate. The analytical approximation for rare mutation, $\nu \ll 1$ (*dashed green line*, cf. Eq. (27)), fits very well over a range of migration rates, μ. For very large migration rates the conditional fixation times approach those in an unstructured population (*dash-dotted line*). **b** scaling the conditional fixation times by the migration rate renders the analytical approximation (*dashed green line*) a constant. This highlights that the analytical approximation is best for intermediate migration rates, μ. For very small migration rates $\nu \ll \mu$ no longer holds and for large migration rates $\mu \ll 1$ is violated. In both cases the quality of the approximation is reduced. More specifically, at the upper end the approximation remains good even for $\mu > 1/(D \cdot N^2) = 3.3 \cdot 10^{-5}$ but for still larger migration rates, $\mu > 10^{-3}$, deviations rapidly increase. **c** for larger migration rates the demes remain heterogeneous for significant fractions of the time during successful invasion attempts. For example, for $\mu = 1/N = 0.01$ demes are homogeneous for merely a little over 0.2% of the time. Results are essentially identical for the pairwise comparison process (cf. Fig. 2), except that the plateau for the conditional fixation times in **b** occurs at smaller values (the analytical prediction changes from 522.7 to 470.5, not shown). (Color figure online)

6 Conclusions

Antal & Scheuring [3] and Taylor *et al.* [29] almost simultaneously reported the surprising finding that the conditional fixation times of a single A type in an otherwise homogeneous B population of constant finite size is the same as that of a single B type in an otherwise homogeneous A population. That is, provided that the single A type takes over the entire population, the average time is the same as the time it takes a single B type to take over, again provided that the B does reach fixation. This result is particularly surprising, because the symmetry holds for any game and for different kinds of evolutionary processes. Maruyama & Kimura [19] had proved a corresponding symmetry between the conditional fixation time of a beneficial allele and that of a deleterious allele in a diffusion model with frequency-independent selection.

Here we show that this symmetry extends to conditional fixation times in deme structured finite populations with frequency-dependent selection provided that mutation and migration events are rare. Note that the important difference between our setup and Antal & Scheuring [3] or Taylor *et al.* [29] is that their chain for the fixation times advances in uniform time steps (which corresponds to our dynamics within demes) but our chain on the level of demes advances in non-uniform time steps (as reflected by α, β, and γ_i in Eq. (8)). Our results hold for arbitrary dynamics within demes, provided that the deme size remains constant and the number of strategies of each type changes at most by one in one update. We illustrate our findings by deriving the actual (conditional) fixation times for the frequency-dependent Moran process [22], see Fig. 1, as well as a pairwise comparison process [34], see Fig. 2, for

the prisoner's dilemma. Figures 1 and 2 illustrate the very good agreement between analytical predictions and individual based simulations. Interestingly, in the Moran process the fixation probability is largely independent of the number of demes in a population of constant size, Fig. 1. Only if deme sizes are very small the fixation probability of cooperators is slightly increased but always remains below the fixation probability of a neutral mutant, $1/M$ [14].

The expected fixation time of cooperators is consistently smaller than that of defectors because invasion attempts of cooperators are likely to fail. For pairwise comparison processes, the disadvantage of cooperators within demes can be offset by the higher reproductive output and hence the increased production of migrants in homogeneous cooperator demes, provided that the selection strength within demes is sufficiently weak, Fig. 2. Interestingly, the conditional fixation time displays a peak near the point where the fixation probabilities of cooperators and defectors are approximately equal and equal to that of a neutral mutant, which relates to the fact that the payoff matrix satisfies equal-gains-from-switching [23,31]. In the present limit of rare migration and even rarer mutation the migration rate becomes a limiting factor such that all fixation times increase with the number of demes.

Our analytical results of fixation probabilities and fixation times crucially depend on the assumption that mutation events and, even more importantly, migration events are rare. More specifically, $\nu \ll \mu \ll 1$, such that all demes are homogeneous most of the time. In contrast to the diffusion approximations for subdivided populations developed in [5,26,40] our results do not require that the number of demes (nor the population size) is large and our results hold for any intensity of selection. Another difference between our contribution and much of the literature on diffusion approximations for population dynamics is that we allow selection to be frequency-dependent, which is crucial for the analysis of the evolution of cooperation.

In biological systems a migration rate of $\mu < 1/N$, i.e. on average one migrant per deme and generation, may already be considered rare. However, formally this does not imply that all demes would likely be homogeneous as this also depends on the number of demes as well as the fixation time within a single deme. Under neutral evolution, where all individuals have the same fitness, we can easily derive an upper bound for the migration rate such that demes are indeed homogeneous most of the time as required by the analytical approximation. In this case the conditional expected time for a single mutant to reach fixation in one deme is N^2 updates of that deme [3]. Because there are D demes in the population $D \cdot N^2$ updates are required. In order to render another migration event unlikely during those updates $\mu \ll 1/(D \cdot N^2)$ must hold. Note that this is a reasonable approximation whenever selection strength is weak but due to stochastic slowdown or speedup the threshold for μ may either be optimistic (for prisoner's dilemma type interactions) or conservative (for some co-existence games) [1,2].

From a biological perspective, the assumption of rare mutation is less problematic than assuming rare migration because the former occurs on an evolutionary time scale whereas the latter on an ecological time scale, which is usually much faster. In order to assess the quality of our analytical approximation under more realistic assumptions, we determined fixation times for migration rates $\mu \in [\nu, 1)$ through simulations, see Fig. 3. Most importantly, the simulations show that the conditional fixation time of a single A type and a single B type remain very similar for any migration rate. Moreover, fixation times are correctly predicted over a broad interval of μ. In fact, the order of magnitude remains valid for nearly any migration rate $\mu \in [\nu, 1)$. More specifically, the simulations also show that both limits, $\nu \ll \mu$, and $\mu \ll 1$, are important. For very small μ the approximation overestimates fixation times but underestimates them for μ close to 1. Moreover, Fig. 3c shows that the assumption of homogeneous demes is indeed valid for $\mu \lesssim 1/(D \cdot N^2)$, which means that the population is either waiting for a mutation or a migration event. For larger μ the

fraction of time that all demes are homogeneous during a successful invasion attempt steadily drops.

In order to determine evolutionary success in finite populations fixation probabilities play an essential role. The same applies to fixation times but in contrast they have received considerably less attention [10]. More specifically, fixation times can indicate whether the concept of fixation is reasonable or whether an analysis of the average abundance would be more adequate [36]. In particular, fixation times determine the time scale of mutations and quantify the conditions under which they can be considered rare and isolated events: $\nu \ll 1/(\alpha + \tau_1^A)$. Similarly, migration events are considered rare if $\mu \ll 1/\alpha$. The rate of evolution is traditionally determined by the expected waiting time for a mutant to arise and fixate: $1/(\nu\rho_A\Psi_1)$ and $1/(\nu\rho_B\Psi_{D-1})$. For the prisoner's dilemma our simulations show very good agreement even though the condition for isolated events is not always satisfied. The conditional fixation times remain moderate in comparison to the expected waiting times in the Moran process but can reach the same order of magnitude for the pairwise comparison process. However, note that the rate of evolution is limited by the mutation rate, ν, but in our analytical approximation essentially independent of the migration rate, μ, whereas the (conditional) fixation time is essentially independent of ν and limited by μ, see Eq. (26).

In contrast, in co-existence games, such as the snowdrift game, fixation times easily become enormous for larger populations [38] and hence the concept of fixation may no longer be meaningful. Similarly, treating mutations as isolated events for such large fixation times may require mutation rates that are too small to be biologically meaningful. In addition to the type of game, another crucial determinant of fixation times in deme structured populations is migration: for large migration rates the deme structure dissolves such that for co-existence games fixation becomes highly unlikely. Consequently, fixation times become exceedingly long. In contrast, for small migration rates the population consists of all homogeneous demes for most of the time and, again, fixation times become exceedingly long.

Only the combination of fixation probabilities and fixation times yield good measures for the effective rate of evolution, ξ [10]. In the present context this translates to

$$\xi = \frac{1}{\frac{1}{M\nu\rho_A\Psi_1} + \tau_1^A + \alpha}, \tag{39}$$

for a homogeneous population of B's. The traditional rate of evolution, $\xi = M\nu\rho_A\Psi_1$ is recovered, if mutation rates, ν, are small compared to the inverse fixation time, $\nu \ll (M\rho_A\Psi_1(\tau_1^A + \alpha))^{-1}$, or, equivalently, if fixation times, τ_1^A, are short (and, by extension, α is short, too) compared to the waiting time for the next mutation, $\tau_1^A + \alpha \ll (M\nu\rho_A\Psi_1)^{-1}$. In summary, the effective evolutionary success rate of a mutant A is determined by both, the waiting time for a successful mutant as well as its time to reach fixation.

Appendix 1: Rare Events

If migration is rare and mutation even rarer, $\nu \ll \mu \ll 1$ the asymptotic behaviour of the fixation times is determined by terms scaling as $1/\mu$. The only such terms in Eqs. (22), (24) are γ_i/Q_i^+ and, asymptotically, we can approximate $\gamma_i \approx 1$, which yields

$$\frac{\gamma_i}{Q_i^+} \approx \frac{D}{\mu\rho_A}\left(\frac{1}{D-i} + \frac{F_B}{F_A}\frac{1}{i}\right). \tag{40}$$

Using this approximation, the asymptotic fixation time for a single deme of type A, τ_1, becomes

$$\begin{aligned}\tau_1 &\approx \Psi_1 \frac{D}{\mu\rho_A}\sum_{k=1}^{D-1}\sum_{l=1}^{k}\left(\frac{1}{D-l}+\frac{F_B}{F_A}\frac{1}{l}\right)\eta^{k-l}\\ &= \frac{D}{\mu\rho_A}\sum_{l=1}^{D-1}\left(\frac{1}{D-l}+\frac{F_B}{F_A}\frac{1}{l}\right)\frac{1-\eta^{D-l}}{1-\eta^D}\end{aligned} \tag{41}$$

Similarly, the fixation time for a single deme of type B, τ_{D-1}, reduces to:

$$\begin{aligned}\tau_{D-1} &\approx \frac{D}{\mu\rho_A}\left[\sum_{l=1}^{D-1}\left(\frac{1}{D-l}+\frac{F_B}{F_A}\frac{1}{l}\right)\eta^{D-1-l}-\tilde{\Psi}_{D-1}\sum_{k=1}^{D-1}\sum_{l=1}^{k}\left(\frac{1}{D-l}+\frac{F_B}{F_A}\frac{1}{l}\right)\eta^{k-l}\right]\\ &= \frac{D}{\mu\rho_A}\sum_{l=1}^{D-1}\left(\frac{1}{D-l}+\frac{F_B}{F_A}\frac{1}{l}\right)\frac{1}{\eta}\frac{\eta^{D-l}-\eta^D}{1-\eta^D}\\ &= \frac{D}{\mu\rho_B}\sum_{l=1}^{D-1}\left(\frac{F_A}{F_B}\frac{1}{D-l}+\frac{1}{l}\right)\left(1-\frac{1-\eta^{D-l}}{1-\eta^D}\right)\end{aligned} \tag{42}$$

The asymptotic behaviour of the two conditional fixation times, τ_1^A and τ_{D-1}^B, must obviously be identical (see Appendix 3) and is similarly given by:

$$\begin{aligned}\tau_1^A &\approx \frac{D}{\mu\rho_A}\sum_{k=1}^{D-1}\sum_{l=1}^{k}\Psi_l\left(\frac{1}{D-l}+\frac{F_B}{F_A}\frac{1}{l}\right)\eta^{k-l}\\ &= \frac{D}{\mu\rho_A}\sum_{l=1}^{D-1}\left(\frac{1}{D-l}+\frac{F_B}{F_A}\frac{1}{l}\right)\frac{1-\eta^l}{1-\eta^D}\cdot\frac{1-\eta^{D-l}}{1-\eta}\end{aligned} \tag{43}$$

Appendix 2: $\alpha = \beta$

The necessary manipulations are similar to those demonstrating that $\tau_1^A = \tau_{D-1}^B$ holds (see Appendix 3).

$$\beta = \sum_{k=1}^{N-1}\sum_{l=1}^{k}\frac{\tilde{\Phi}_{N-l}}{T_{N-l}^-}\prod_{m=l+1}^{k}\frac{T_{N-m}^+}{T_{N-m}^-}$$

(switch summation over k and l; insert $\tilde{\Phi}_{N-l}$)

$$= \Phi_1\sum_{l=1}^{N-1}\sum_{k=l}^{N-1}\frac{1}{T_{N-l}^-}\sum_{i=N-l}^{N-1}\prod_{j=1}^{i}\frac{T_j^-}{T_j^+}\prod_{m=l+1}^{k}\frac{T_{N-m}^+}{T_{N-m}^-}$$

(change indices: $N-m\to m$ and $l\to N-l$)

$$= \Phi_1\sum_{l=1}^{N-1}\sum_{k=N-l}^{N-1}\frac{1}{T_l^-}\sum_{i=l}^{N-1}\prod_{j=1}^{i}\frac{T_j^-}{T_j^+}\prod_{m=N-k}^{l-1}\frac{T_m^+}{T_m^-}$$

(split the product over index j, the middle product over the index m is 1)

$$= \Phi_1 \sum_{l=1}^{N-1} \sum_{k=N-l}^{N-1} \frac{1}{T_l^-} \sum_{i=l}^{N-1} \prod_{j=1}^{N-k-1} \frac{T_j^-}{T_j^+} \prod_{m=N-k}^{l-1} \left(\frac{T_m^-}{T_m^+} \frac{T_m^+}{T_m^-} \right) \prod_{n=l}^{i} \frac{T_n^-}{T_n^+}$$

(factor out T_l^- / T_l^+; relabel $n \to m$)

$$= \Phi_1 \sum_{l=1}^{N-1} \sum_{k=N-l}^{N-1} \frac{1}{T_l^+} \sum_{i=l}^{N-1} \prod_{j=1}^{N-k-1} \frac{T_j^-}{T_j^+} \prod_{m=l+1}^{i} \frac{T_m^-}{T_m^+}$$

(switch summation over k and i; change index $k \to N-k$; separate term for $k=1$)

$$= \Phi_1 \sum_{l=1}^{N-1} \sum_{i=l}^{N-1} \frac{1}{T_l^+} \left[\sum_{k=2}^{l} \prod_{j=1}^{k-1} \frac{T_j^-}{T_j^+} + 1 \right] \prod_{m=l+1}^{i} \frac{T_m^-}{T_m^+}$$

(Φ_1 times the term in square brackets is Φ_l; switch summation over l and i; relabel $i \to k$)

$$= \sum_{k=1}^{N-1} \sum_{l=1}^{k} \frac{\Phi_l}{T_l^+} \prod_{m=l+1}^{k} \frac{T_m^-}{T_m^+} = \alpha. \tag{44}$$

Appendix 3: $\tau_1^A = \tau_{D-1}^B$

In order to show that the conditional fixation times are equal, we transform the formula for τ_{D-1}^B and recover τ_1^A – provided that $\alpha = \beta$ holds:

$$\tau_{D-1}^B = \sum_{k=1}^{D-1} \sum_{l=1}^{k} \tilde{\Psi}_{D-l} \left(\alpha + \beta \tilde{\xi}_{D-l} + \frac{\gamma_{D-l}}{Q_{D-l}^-} \right) \prod_{m=l+1}^{k} \tilde{\xi}_{D-m} - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_{D-k}$$

(switch summation over k and l; insert $\tilde{\Psi}_{D-l}$ in first term)

$$= \Psi_1 \sum_{l=1}^{D-1} \sum_{k=l}^{D-1} \sum_{i=D-l}^{D-1} \prod_{j=1}^{i} \xi_j \left(\alpha + \beta \tilde{\xi}_{D-l} + \frac{\gamma_{D-l}}{Q_{D-l}^-} \right) \prod_{m=l+1}^{k} \tilde{\xi}_{D-m} - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_k$$

(change indices: $D-m \to m$ and $l \to D-l$)

$$= \Psi_1 \sum_{l=1}^{D-1} \sum_{k=D-l}^{D-1} \sum_{i=l}^{D-1} \prod_{j=1}^{i} \xi_j \prod_{m=D-k}^{l-1} \tilde{\xi}_m \left(\alpha + \beta \tilde{\xi}_l + \frac{\gamma_l}{Q_l^-} \right) - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_k$$

(split the product over index j, the middle product over the index m is 1)

$$= \Psi_1 \sum_{l=1}^{D-1} \sum_{k=D-l}^{D-1} \sum_{i=l}^{D-1} \prod_{j=1}^{D-k-1} \xi_j \prod_{m=D-k}^{l-1} \xi_m \tilde{\xi}_m \prod_{n=l}^{i} \xi_n \left(\alpha + \beta \tilde{\xi}_l + \frac{\gamma_l}{Q_l^-} \right) - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_k$$

(factor out ξ_l; note $\xi_l / Q_l^- = 1/Q_l^+$)

$$= \Psi_1 \sum_{l=1}^{D-1} \sum_{k=D-l}^{D-1} \sum_{i=l}^{D-1} \prod_{j=1}^{D-k-1} \xi_j \left(\alpha \xi_l + \beta + \frac{\gamma_l}{Q_l^+} \right) \prod_{m=l+1}^{i} \xi_m - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_k$$

(switch summation over k and i; change index $k \to D - k$; separate term for $k = 1$)

$$= \Psi_1 \sum_{l=1}^{D-1} \sum_{i=l}^{D-1} \left[\sum_{k=2}^{l} \prod_{j=1}^{k-1} \xi_j + 1 \right] \left(\alpha \xi_l + \beta + \frac{\gamma_l}{Q_l^+} \right) \prod_{m=l+1}^{i} \xi_m - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_k$$

(Ψ_1 times the term in square brackets is Ψ_l; switch summation over l and i; relabel $i \to k$)

$$= \sum_{k=1}^{D-1} \sum_{l=1}^{k} \Psi_l \left(\alpha \xi_l + \beta + \frac{\gamma_l}{Q_l^+} \right) \prod_{m=l+1}^{k} \xi_m - (\alpha - \beta) \sum_{k=1}^{D-1} \tilde{\Psi}_k$$

$$= \tau_1^A + (\alpha - \beta) \sum_{k=1}^{D-1} (\Psi_k - \tilde{\Psi}_k) \tag{45}$$

In general, the sum $\sum_{k=1}^{D-1} (\Psi_k - \tilde{\Psi}_k)$ is non-vanishing but if $\alpha = \beta$ holds the difference disappears and the two conditional fixation probabilities are equal.

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