

Heterogeneity in background fitness acts as a suppressor of selection

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We introduce the concept of heterogeneity in background fitness to evolutionary dynamics in finite populations. Background fitness is specific to an individual but not linked to its strategy. It can be thought of as a property that is related to the physical or societal position of an individual, but is not dependent on the strategy that is adopted in the evolutionary process under consideration. In our model, an individual's total fitness is the sum of its background fitness and the fitness derived from using a specific strategy. This approach has important implications for the imitation of behavioural strategies: if we imitate others for their success, but can only adopt their behaviour and not their social and economic ties, we may imitate in vain. We study the effect of heterogeneity in background fitness on the fixation of a mutant strategy with constant fitness. We find that heterogeneity suppresses selection, but also decreases the time until a novel strategy either takes over the population or is lost again. We derive analytical solutions of the fixation probability in small populations. In the case of large total background fitness in a population with maximum inequality, we find a particularly simple approximation of the fixation probability. Numerical simulations suggest that this simple approximation also holds for larger population sizes.

Keywords: evolutionary dynamics, background fitness, wealth, inequality, heterogeneity, intensity of selection

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1. Introduction

Evolutionary dynamics explores how strategies change over time and space in structured or unstructured populations (Bürger, 2000; Cressman, 2003; Durrett and Levin, 1994; Fu et al., 2007; Helbing, 2010; Hofbauer and Sigmund, 2003; 1988; Imhof and Nowak, 2006; Maynard-Smith, 1993; Nowak, 2006; Nowak and May, 1992; Nowak and Sigmund, 2004; Samuelson, 1998; Traulsen and Nowak, 2006; Weibull, 1997). These strategies can be alleles in a genetic context or behaviours in social interactions (Nowak, Tarnita, and Wilson, 2010; Tarnita et al., 2012). In the simplest case, these strategies have a fixed fitness. Even in this case, population structure can have subtle influences, suppressing or amplifying selection (Allen and Tarnita, 2012; Bürger, 2000; Cressman, 2003; Helbing, 2010; Hofbauer and Sigmund, 2003; 1988; Imhof and Nowak, 2006; Lieberman et al., 2005; Nowak, 2006; Nowak and Sigmund, 2004; Nowak, Tarnita, and Antal, 2010; Ohtsuki et al., 2006; Ohtsuki and Nowak, 2006; Samuelson, 1998; Skyrms and Pemantle, 2000; Tarnita et al., 2009; 2011; Traulsen et al., 2005; Weibull, 1997). One important aspect of many real-world population structures is that different physical locations or positions in society have different value (Nowak, 2012): A good breeding site may give a breeding bird an advantage that is sometimes connected to its own behaviour (Kokko, 2002) but sometimes also independent of its own behaviour (Misenhelter and Rotenberry, 2000). A good school district can be influential for one's career progression (Cullen et al., 2005). Inherited wealth may positively affect reproductive success (Essock-Vitale, 1984). We consider evolutionary dynamics in such a setting and ask how heterogeneity in the implicit value of different physical or societal positions affects the evolutionary dynamics. Our model does not include explicit spatial structure, but only considers different values for each position. In a biological context, this would mean that nesting site quality can crucially contribute to the spreading of new mutations, in addition to behavioural or physiological change associated with this mutation. In a social interpretation, it would mean that we imitate successful individuals, assuming their success derives from a behaviour we might be able to copy. It may also be the case, however, that we not only imitate those who are successful due to their behaviour, but also those who are successful due to heritage or their social and economic ties. In the latter case, the imitation may be in vain, but this does not preclude strategies from spreading.

In our approach, we assume that fitness is the sum of the background fitness associated with a certain position (or location) and the fitness derived from the strategy of an individual. We assume that

a strategy can spread from any position to any other position through individuals copying each other. Thus, we can use the convenient mathematical properties of well-mixed, unstructured populations when it comes to the changes in the abundance of a strategy. At the same time, however, the distribution in background fitness allows to address an important aspect of population structure that has not been considered in this context so far. In contrast, spatial and social heterogeneity has been considered in the case of evolutionary dynamics in degree-heterogeneous networks (Cavaliere et al., 2011; Lieberman et al., 2005; Ohtsuki et al., 2006; Perc and Szolnoki, 2008; Poncela et al., 2009; Santos and Pacheco, 2011; 2005; Santos et al., 2012; 2008; Szabó and Fátth, 2007; Szabó and Szolnoki, 2012). Another source of heterogeneity arises from different kinds of interactions within the population (Chatterjee et al., 2012; Fu et al., 2008; McNamara et al., 2004; Rand et al., 2013; Taylor and Nowak, 2006; Traulsen et al., 2007; Wang et al., 2010). Also in population genetics, heterogeneity in offspring number and nest sites has been addressed (Eldon and Wakeley, 2005; Lessard, 2007; Wakeley, 2008).

Our model is based on a Markov chain with two absorbing states – a new strategy is eventually either lost or reaches fixation in a finite population. In homogeneous populations, the transition matrix of these processes reduces to a tri-diagonal matrix, leading to closed expressions for the time to absorption or the probability to reach a certain state (Altrock and Traulsen, 2009; Nowak et al., 2004). In the case of heterogeneous wealth distribution, such an approach fails and these quantities typically must be inferred numerically based on standard methods (Grinstead and Snell, 1997). However, the same method leads to a full analytical solution in closed form for small populations. For larger populations, the corresponding analytical expressions become cumbersome, but a Taylor expansion of the small population result in the important limit of large heterogeneity gives us an approximation that numerically also holds for larger populations. Throughout this paper, we adopt terms (e.g. “wealth”, “rich”, “poor”, “inequality” etc.) inspired by economics and sociology. But a biological meaning for each of these words can readily be inferred (e.g. “resources”, “high quality of nest site”, “low quality of nest site”, “heterogeneous nest site qualities” etc.).

2. An evolutionary process with heterogeneous background fitness

We assume a finite population of size N with two types A and B. Evolution proceeds by selecting one individual proportional to its total fitness to reproduce asexually. Its identical offspring replaces another individual chosen with uniform probability to die (Moran, 1962). This implies that in each time

step, the number of individuals of a certain type can change at most by ± 1 . Hence, the dynamics can be captured by a simple birth-death process, which allows calculating the probability of fixation and the associated time as well as several related quantities in closed form analytically (Antal and Scheuring, 2006; Nowak et al., 2004). When mutations arise infrequently, the fixation probability is a relevant measure to describe the average abundance of types in a mutation-selection equilibrium (Fudenberg and Imhof, 2006; Wu et al., 2012). In this case, a mutant will fixate or go extinct before another mutant arises. Thus, the system effectively reduces to an evolutionary process jumping between the two absorbing states where all individuals use the same strategy.

An individual's total fitness f is the sum of that individual's background fitness b and the fitness derived from the strategy s the individual has chosen:

$$f_i = b_i + s_i \tag{1}$$

where i ($0 \leq i \leq N$) denotes an individual in the population. Note that we assume that the strategy of the individual has an impact on the fitness that is only dependent on the individual's type. We assume no frequency-dependent interactions between types, such that $s_i > 0$ is a fixed number. Due to heterogeneities in the background fitness b_i , however, our state space is not only determined by the number of individuals of one type, but also by the unique position of each individual. Therefore the transition matrix is no longer tri-diagonal, excluding many analytical approaches based on this property. Thus, calculating a closed form for the absorption probabilities and times becomes much more cumbersome.

We assume that an offspring inherits its parent's strategy, but it does not receive its parent's background fitness. Instead, the offspring "inherits" the background fitness of the individual who was chosen for death and thus previously occupied the same location. In other words, the topology of background fitness remains unchanged over time, but strategies evolve on top of the background fitness topology. The fixed background topology thus represents a static environment in which the strategies change due to biological or cultural reproduction. Such an environment could be breeding sites in biology (Misenhelter and Rotenberry, 2000) or economic wealth in human society (Wolff, 2002).

3. Background fitness effectively reduces intensity of selection

We assume there exist two strategies A and B. If $s_A > s_B$ there is constant selection for type A and if $s_A < s_B$ selection favours B. Thus $s_A = s_B$ is the neutral case. Without loss of generality, we assume that strategy B's fitness is always $s_B = 1$. All values of strategy fitness and background fitness are non-negative.

We are interested in the fixation probability of a single mutant of type A in a population of $N - 1$ individuals of type B. Let ρ_i and τ_i denote the fixation probability and average absorption time of type A if the mutant arises in location i , and let ρ and τ denote the average fixation probability and absorption time of type A if the mutation arises at a random location in the population:

$$\rho = \frac{1}{N} \sum_{i=1}^N \rho_i \quad (2)$$

$$\tau = \frac{1}{N} \sum_{i=1}^N \tau_i \quad (3)$$

We combine an analytical approach, which is feasible for small populations only, with computational approaches. Numerically, we compute properties from the exact transition matrix of the Markov Chain and run stochastic agent-based simulations. Agent-based simulations proceed as follows: in every time step, one individual is selected proportional to fitness to reproduce and one individual is selected at random to die, until the population has reached a homogeneous state in which all individual are of type A or B. We average over m realisations for every possible initial location of the mutant to calculate ρ_i . Thus, the fixation probability of a randomly arising mutant ρ is the average over Nm realisations.

We are interested in the effect that heterogeneous background fitness has on the fixation probability ρ of a randomly arising mutant. We expect that heterogeneity in background fitness modulates and neutralises the effects of selection on a strategy, similar to some population structures (Lieberman et al., 2005; Traulsen et al., 2005) or the introduction of a random number of interactions in evolutionary games (Traulsen et al., 2007). Intuitively, the strength of selection becomes effectively weaker when any background fitness is introduced. This is because the total fitness of an individual is no longer just derived from using a strategy, but also from a fixed, non-negative background fitness (see Equation (1)). Depending on their relative value, either strategy-dependent fitness or individual background fitness may have a greater impact on the total fitness.

Second, if there exists any heterogeneity in background fitness, richer individuals will be favoured over poorer individuals and thus mutants arising in rich individuals are more likely to spread. This is especially important if background fitness values are large compared to the strategy payoff values. Moreover, the effect of heterogeneity on fixation ought to be largest when the total background fitness in the population is very unequally distributed among individuals of a population. We speak of *perfect inequality* when one individual j in a population possesses the entire wealth $K = \sum_{i=1}^N b_i$ in the population (Keister and Moller, 2000): $b_j = K$ and $b_i = 0$ for all remaining individuals.

An intuitive prediction is that for a large enough value of total background fitness K in the population and under perfect inequality, the probability of fixation approaches the case of neutral drift, $1/N$. In other words, if the total amount of background fitness is large and all of it is in the possession of one individual j , then fixation of type A occurs *only if* the mutant arises in individual j . Mutations arise at a random position in the population, and therefore the probability of fixation must converge to $1/N$.

We numerically confirm this hypothesis of perfect inequality (Figure 1): We vary the fitness r of the mutant type A in a population of size $N = 30$ to find the fixation probability for 4 values of the rich individual's wealth, b_1 . For $b_1 = 0$, we recover the well known results for constant selection of a mutant with fitness r in a *homogeneous* population. As b_1 increases, the fixation probability increases for disadvantageous mutants, $r < 1$, and decreases for advantageous mutants, $r > 1$. In other words, by increasing the amount the rich individual possesses, fixation of the randomly arising mutant strategy becomes less dependent on the strategy's advantage or disadvantage and more dependent on the origin of the mutation: The quality of an individual's position, not its strategy, becomes the determinant for evolutionary success. For $b_1 = 100$, the probability of fixation is already very close to the neutral case where $s_1 = s_2$. This is an example of how high inequality in background wealth suppresses selection.

4. Unequal wealth distributions suppress selection more than an equal distribution

We note that in Figure 1, as the wealth of the only rich individual b_1 increases, so does the total wealth K . In other words, the total wealth in the population is increasing but all of it is in the possession of one individual. All of the examples with $b_1 > 1$ in Figure 1 are thus examples of perfect inequality, although the extent to which the rich individual possesses more background wealth varies greatly. But

this raises the question if selection is suppressed because the total wealth has increased or because inequality has increased.

We therefore separate the effects of K and b_1 on fixation. To this end, we are not only interested in the fixation probability of type A when $b_1 = K$ but also when wealth is distributed differently in the population. Wealth can be distributed in many different ways within the population. We focus on those distributions where the total wealth is split by an increasing number of individuals within the population. That is, in the most unequal case, the total wealth is in the hands of one individual ($j = 1$). The same amount of total wealth is then successively owned by two players ($j = 2$), then by three ($j = 3$), and so on, until it is split evenly among all individuals ($j = 15$) (Figure 2).

We clearly observe that both forces are driving the suppression of selection (Figure 2): the total amount of wealth in the population and also the inequality in the distribution of the total wealth within the population affect the effective intensity of selection. An increase in the total wealth in the population also leads to the probability of any fixation being closer to neutrality: it defines the possible magnitude to which selection can be suppressed at a minimum and at a maximum. How much selection is suppressed is then entirely determined by the inequality in wealth distribution. The more unequal the wealth is distributed, the more selection is suppressed (i.e. closer to neutrality within the possible magnitude defined by the total wealth). Conversely, the more equally wealthy everyone is, the less the effect of selection suppression is.

If there exists no background wealth, heterogeneity is obviously absent and has no effect. As background wealth increases, inequality suppresses selection at a faster rate than does equality of the same total wealth K , which leads to the observed disparity of fixation probabilities in the middle section of K (Figure 2). This trend, however, is bound by a global minimum (that is, neutral drift) for both inequality and equality. Hence, as total background wealth becomes very large, selection is suppressed to a similar extent by both inequality and equality because neither can suppress selection below $1/N$.

These results show that selection is suppressed when background wealth is added. Intuitively, this makes sense because with higher background fitness, the addition of a small fitness value from the strategy has little impact. This effect is amplified by an unequal allocation of wealth within the population. To understand the exact mechanism, we use an analytical approach to study heterogeneity.

We analytically solve the fixation probabilities in populations of size $N = 3, 4$ and 5 . We also provide an approximation that numerically holds in the limiting case for larger population sizes.

5. Perfect inequality is a strong suppressor of selection

Based on the Markov Chain process, we construct a stochastic transition matrix \mathcal{M} such that \mathcal{M}_{jk} is the transition probability to go from j to k ; $j, k \in \{1, \dots, 2^N\}$. The state space of the transition matrix is described by all possible binary strings of 1s (A) and 0s (B). The absorption probabilities ρ_i into A are the elements of the eigenvector to the largest eigenvalue of \mathcal{M} (Grinstead and Snell, 1997). We find the fixation probability ρ and absorption time τ of a randomly arising mutant numerically based on Equations 2 and 3.

The transition matrix is of size $2^N \times 2^N$. Therefore closed analytical solutions of our model are only feasible for small N . We use numerical solutions based on the transition matrix because, in contrast to stochastic agent-based simulations, solutions derived directly from the Markov Chain process are exact and do not require a large number of realisations. For an analytical solution, which leads to results that can be interpreted most easily, we rearrange the matrix elements in \mathcal{M} into its canonical form and derive the fundamental matrix containing information on all transient states (Grinstead and Snell, 1997). In the canonical form, states are renumbered such that the p transient states come first, followed by the two absorbing states where all individuals use the same strategy.

$$\mathcal{M} = \begin{pmatrix} Q & \mathcal{R} \\ \mathcal{O} & J \end{pmatrix} \quad (4)$$

where J is a 2×2 identity matrix (once all individuals use the same strategy, the state is not left again), \mathcal{O} is a $p \times 2$ zero matrix (one cannot escape from an absorbing state), \mathcal{R} is a non-zero $2 \times p$ matrix describing fixation, and Q is a $p \times p$ matrix describing the dynamics within the transient states. Here $p = 2^{N-1}$ is the number of unique positions of all individuals in a population of size N .

For an absorbing Matrix Chain, there exists an inverse \mathcal{N} of the matrix $J - Q$. \mathcal{N} is called the fundamental matrix of \mathcal{M} , and $\mathcal{N} = J + Q + Q^2 + \dots$ (Grinstead and Snell, 1997). Each entry \mathcal{N}_{ij} of \mathcal{N} contains the expected number of time steps the chain is in state j , given that it starts in state i . Hence, the time to absorption τ_i , given that the process starts in state i , is the sum over all entries of \mathcal{N}

in row i . Let γ_{ij} be the probability that the process will be absorbed in the absorbing state j , given that it starts in the transient state i . Let γ be the $p \times 2$ matrix with entries γ_{ij} :

$$\gamma = \mathcal{NR} \quad (5)$$

Specifically, we speak of a fixation probability ρ if the process begins in a transient state i where only 1 mutant exists. This is only the case for a subset of entries in γ . The size of this subset depends only on the distribution of the background fitness.

We can perform the above procedure analytically and thus obtain a closed solution of our model in the case of small population sizes $N = 3, 4$ and 5 . While analytical solutions for larger population sizes are theoretically attainable, they come in intricate form and are very difficult to interpret beyond $N = 5$. This is because the starting point for an analytical solution is the transition matrix and the analytical procedure implies that we need to find an analytical form for its eigenvector. As noted above, the transition matrix is of size $2^N \times 2^N$. Therefore, this procedure quickly becomes very cumbersome as N increases.

We calculate the exact solutions for the fixation probabilities ρ for $N = 3$ for any arbitrary background wealth distribution $\mathcal{K} = (b_1, b_2, b_3)$ from Equation (5). Despite the small population size, the exact general solution for an arbitrary wealth distribution spans multiple pages.[†] For ease of reading, we therefore only print the solution in the case of perfect inequality and simplify our notation: we set $b_1 = b$ for the rich individual and $b_2 = b_3 = 0$ for the two poor individuals. We then obtain for the fixation probability of the rich individual:

$$\rho_{rich} = \frac{(1+b)(r^3(7+7b+2b^2)+2r^4(2+b)+(1+b)(2+b)^2)}{2(2+3b+b^2)+r(11+16b+9b^2+2b^3)+r^2(15+22b+16b^2+6b^3+b^4)+r^3(11+16b+9b^2+2b^3)+2r^4(2+3b+b^2)} \quad (6)$$

Similarly, for each of the two poor individuals, we find:

$$\rho_{poor} = \frac{r^2(4+3b+b^2)+r^3(7+8b+4b^2+b^3)+2r^4(2+3b+b^2)}{2(2+3b+b^2)+r(11+16b+9b^2+2b^3)+r^2(15+22b+16b^2+6b^3+b^4)+r^3(11+16b+9b^2+2b^3)+2r^4(2+3b+b^2)} \quad (7)$$

[†] A complete solution can be obtained from ohauser@fas.harvard.edu.

Finally, using Equation 2, we can also calculate the fixation probability of a randomly arising mutant

$$\rho = \frac{1}{3}(\rho_{rich} + 2\rho_{poor}):$$

$$\rho = \frac{r^2(12+18b+15b^2+6b^3+b^4)+r^3(21+30b+17b^2+4b^3)+6r^4(2+3b+b^2)}{3(2(2+3b+b^2)+r(11+16b+9b^2+2b^3))+r^2(15+22b+16b^2+6b^3+b^4)+r^3(11+16b+9b^2+2b^3)+2r^4(2+3b+b^2)} \quad (8)$$

When $b = 0$, no background wealth is present in the population and Equations (6), (7) and (8) reduce to the well known fixation probability in the case of a homogeneous environment without any

background wealth, $\frac{1-\frac{1}{r}}{1-\frac{1}{r^3}}$.

Furthermore, the analytical solution approaches $1/N$ in the limit of $b \rightarrow \infty$ (Figure 3a), which is also expected from our argument above: When the total wealth in the population is large and one individual owns all this wealth, fixation can only occur if the mutation arises in the position with high background fitness (Figure 3b).

The exact solutions from the Markov Chain process provide very useful insight into the evolutionary dynamics in a heterogeneous population. They are, however, long and complicated to interpret. We therefore also present approximated solutions that are more intuitive and easily derived from previous results. For each of the three population sizes $N = 3, 4$ and 5 , we find the first-order Taylor approximations for large b for the equations corresponding to (6), (7), and (8):

$$\rho_{rich} \approx 1 - \frac{N-1}{rb} \quad (9)$$

$$\rho_{poor} \approx \frac{r}{b} \quad (10)$$

$$\rho \approx \frac{1}{N} + \frac{N-1}{N} \frac{r}{b} \left(1 - \frac{1}{r^2}\right) \quad (11)$$

For very large b , only the leading term in Equation (11) prevails, $\rho \approx 1/N$, which is in agreement with the limiting case discussed above. We find that the first order approximations work very well for small populations with high population wealth under perfect inequality (for instance, the fixation probability of a randomly arising mutant using Equation (11) for $N = 3$ is shown in Figure 4a). Moreover, numerical simulations suggest that the Taylor approximations are also in reasonable agreement with slightly larger population sizes (Figure 4b,c). In general, we expect this approximation to hold for

larger N if the wealth of the rich individual also increases. That is, $1/b$ enters in a similar way as r does in the weak selection approximation of the fixation probability under constant selection, $\rho = \frac{1-\frac{1}{r}}{1-\frac{1}{rN}}$.

In that case, the approximation is valid only for $N(r-1) \ll 1$. Similarly, in the present case the convergence radius also depends on N , b and r . For example, in the case of large r , $(N-3)r^2/((1+r)b) \ll 1$ is required.

6. Time to absorption decreases in a wealthy population under perfect inequality

In addition to the probability of fixation of a mutant, we are also interested in how fast the mutant either fixates or goes extinct. The absorption time measures how many time steps need to be taken on average to reach either of the two absorbing states – that is, either a state of all A or all B individuals. It can be calculated from summing over the line corresponding to the initial condition in the fundamental matrix \mathcal{N} of the Markov process (Grinstead and Snell, 1997).

In a population of size $N = 3$, the unconditional absorption times of a rich and poor individual are, respectively:

$$\tau_{rich} = \frac{3(4(2+3b+b^2)+r(30+52b+34b^2+8b^3))+r^2(48+80b+55b^2+18b^3+3b^4)+r^3(37+54b+27b^2+6b^3)+6r^4(2+3b+b^2)}{2(2(2+3b+b^2)+r(11+16b+9b^2+2b^3))+r^2(15+22b+16b^2+6b^3+b^4)+r^3(11+16b+9b^2+2b^3)+2r^4(2+3b+b^2)}$$

(12)

$$\tau_{poor} = \frac{3(4(2+3b+b^2)+2r(15+20b+9b^2+2b^3))+r^2(48+65b+41b^2+12b^3+2b^4)+r^3(37+54b+30b^2+7b^3)+6r^4(2+3b+b^2)}{2(2(2+3b+b^2)+r(11+16b+9b^2+2b^3))+r^2(15+22b+16b^2+6b^3+b^4)+r^3(11+16b+9b^2+2b^3)+2r^4(2+3b+b^2)}$$

(13)

The unconditional absorption time of a randomly arising mutant (Equation 3) thus is:

$$\tau = \frac{12(2+3b+b^2)+2r(45+66b+35b^2+8b^3)+r^2(144+210b+137b^2+42b^3+7b^4)+r^3(111+162b+87b^2+20b^3)+18r^4(2+3b+b^2)}{2(2(2+3b+b^2)+r(11+16b+9b^2+2b^3))+r^2(15+22b+16b^2+6b^3+b^4)+r^3(11+16b+9b^2+2b^3)+2r^4(2+3b+b^2)}$$

(14)

Again, these three equations reduce to the well-known result from homogeneous populations for $b = 0$ (Altrock and Traulsen, 2009).

When we look at the absorption time of a randomly arising mutant (Equation (14)), we find that higher inequality leads to fewer time steps until absorption (Figure 5a), relative to the same amount of wealth being equally distributed among all individuals. When we look at the individual components of the absorption time, we find that mutations arising in poor individuals generally absorb more quickly than equally wealthy individuals or rich individuals (Figure 5b). Intuitively, the higher the inequality in a population, the quicker the poor individuals absorb back into the resident state. This is a consequence of inequality as it hinders poor individuals from fixating and fosters their extinction.

The absorption time of the rich individual depends on the relative advantage that the background wealth bestows on it. When the background wealth of the rich individual is comparable to the payoff values of the competing strategies, the time to absorption is longer. This is because the advantage from background wealth is small and rich individuals are therefore only selected slightly more often for reproduction than poor individuals.

As the wealth advantage increases, however, the time to absorption decreases rapidly. The advantage that the background wealth provides to the rich individual increases and selection favours this individual for reproduction. The rich individual's strategies reach fixation more often and more quickly than the poor individuals' strategies.

7. Discussion

We have shown that heterogeneity in background fitness reduces selection regardless of the strategy payoff. Background fitness is a concept that has been previously proposed to incorporate environmental or otherwise contributing factors to competitiveness, fitness and evolutionary survival (Dayton-Johnson and Bardhan, 2002; Deng et al., 2011; Knez and Camerer, 1995; McNamara et al., 2004). Equal background reduces the intensity of selection: the payoff values of each strategy are scaled proportionally to the homogeneous background fitness of all individuals (Deng et al., 2011; Nowak et al., 2004). We focus on shifting the distribution of background fitness among individuals in a population. A heterogeneous distribution of background fitness is a possible way to address this issue. Such heterogeneities may exist in economic, social, cultural, or other dimensions that are all prevalent in nature and society (Bardhan and Dayton-Johnson, 2002; Chen et al., 2007; Droz et al., 2009; Norton and Ariely, 2011; Perc and Szolnoki, 2008; Santos et al., 2008).

Our results show that inequalities in background fitness can lead to suppressed selection. Many types of suppressors of selection are known (Antal et al., 2006; Lieberman et al., 2005; Nowak et al., 2003; Traulsen et al., 2005). The largest extent to which selection can be suppressed is if the affected trait fixates at random in a population, neutralising the effects derived from fitness entirely (Nowak et al., 2003). We show that large inequality can lead to this kind of neutral drift. Our work complements an existing literature in population genetics on heritable traits when selection is weak and elements of population structure are heterogeneous (Eldon and Wakeley, 2005; Lessard, 2007).

The evolution of frequency-dependent traits, such as cooperation, under heterogeneous background fitness is another interesting aspect alongside constant selection for a heritable trait. It has been argued that inequality can either increase cooperation in the public goods management (Olson, 1965; Ruttan and Mulder, 1999; Wang et al., 2010) or, much in contrast, lead to the downfall of cooperation (Varughese and Ostrom, 2001). Neither effect has been discussed in the context of evolutionary biology. Our work provides a first step towards (constant) evolutionary games in a finite population, by separating out the effects of interaction from the background fitness of individuals.

Moreover, evolutionary game theory has received much attention on networks (Abramson and Kuperman, 2001; Fu et al., 2008; Lieberman et al., 2005; Perc and Szolnoki, 2010; Santos and Pacheco, 2005; Szabó and Fáth, 2007; Van Segbroeck et al., 2009; Zschaler et al., 2010). Many networks have been studied in regards to imitation of traits or spread of pathogens or emotions (Christakis and Fowler, 2007; Fowler and Christakis, 2008; Hill et al., 2010; Keeling and Eames, 2005). Recently the interest in directed networks (Masuda and Ohtsuki, 2009) or degree-heterogeneous networks has increased (Antal et al., 2006; Cavaliere et al., 2011; Santos et al., 2006) and produced stimulating results. It would be interesting finding the connection between heterogeneous background fitness and heterogeneous networks.

In our model, we have also shown that absorption times under constant selection are negatively affected by heterogeneous background fitness. In other words, the more inequality exists, the faster absorption takes place. This stands in contrast to findings on a graph with heterogeneous edge weights in which the mean absorption time increases (Voelkl, 2010). While heterogeneity leads to an increase of absorption time in some models (Frean et al., 2013), it can be a catalyst to determine whether or not a strategy goes to fixation. We find that, when fixation time is very fast in an unequal population, often the mutant went extinct after arising in a poor individual. This is the case because a

poor individual is unlikely to be selected for reproduction when inequality in background fitness is large.

Finally, the co-evolution of background fitness and strategic fitness could lead to interesting dynamics. The tendency that individuals in different classes of background fitness might show towards choosing an appropriate strategy is a crucial feature of many real-world examples, such as differences in votes between social classes over tax reforms (Ogburn and Peterson, 1916). Other evidence comes from field studies (Bardhan and Dayton-Johnson, 2002; Bardhan, 1984) that show that head-end and tail-end farmers in irrigation systems derive different incentives from their location, which in turn influences their strategy whether or not to cooperate.

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References

- Abramson, G., Kuperman, M., 2001. Social games in a social network. *Phys. Rev. E* 63, 030901.
- Allen, B., Tarnita, C., 2012. Measures of success in a class of evolutionary models with fixed population size and structure. *Journal of mathematical biology* 1–35.
- Altrock, P., Traulsen, A., 2009. Fixation times in evolutionary games under weak selection. *New J. Phys.* 11, 013012.
- Antal, T., Redner, S., Sood, V., 2006. Evolutionary Dynamics on Degree-Heterogeneous Graphs. *Phys. Rev. Lett.* 96, 188104.
- Antal, T., Scheuring, I., 2006. Fixation of Strategies for an Evolutionary Game in Finite Populations. *Bull. Math. Biol.* 68, 1923–1944.
- Bardhan, P., Dayton-Johnson, J., 2002. Unequal irrigators: heterogeneity and commons management in large-scale multivariate research. *The drama of the commons* 87–112.
- Bardhan, P.K., 1984. *Land, labor, and rural poverty: Essays in development economics.*
- Bürger, R., 2000. *The Mathematical Theory of Selection, Recombination, and Mutation.* John Wiley, Chichester, New York.
- Cavaliere, M., Sedwards, S., Tarnita, C.E., Nowak, M.A., Csikász-Nagy, A., 2011. Prosperity is associated with instability in dynamical networks. *Journal of Theoretical Biology.*
- Chatterjee, K., Zufferey, D., Nowak, M.A., 2012. Evolutionary game dynamics in populations with different learners. *Journal of Theoretical Biology* 301, 161–173.
- Chen, X., Fu, F., Wang, L., Chen, T., 2007. Evolutionary game dynamics in inhomogeneous populations. arXiv eprint.
- Christakis, N.A., Fowler, J.H., 2007. The spread of obesity in a large social network over 32 years. *New England journal of medicine* 357, 370–379.
- Cressman, R., 2003. Evolutionary dynamics and extensive form games 5.
- Cullen, J.B., Jacob, B.A., Levitt, S.D., 2005. The impact of school choice on student outcomes: an analysis of the Chicago Public Schools. *Journal of Public Economics* 89, 729–760.
- Dayton-Johnson, J., Bardhan, P., 2002. Inequality and Conservation on the Local Commons: A Theoretical Exercise. *The Economic Journal* 112, 577–602.
- Deng, L., Tang, W., Zhang, J., 2011. The coevolutionary ultimatum game on different network topologies. *Physica A: Statistical Mechanics and its Applications* 390, 4227–4235.
- Droz, M., Szwabiński, J., Szabó, G., 2009. Motion of influential players can support cooperation in prisoner's dilemma. *The European Physical Journal B-Condensed Matter and Complex Systems* 71, 579–585.
- Durrett, R., Levin, S., 1994. The importance of being discrete (and spatial). *Theoretical Population Biology* 46, 363–394.
- Eldon, B., Wakeley, J., 2005. Coalescent Processes When the Distribution of Offspring Number Among Individuals Is Highly Skewed. *Genetics* 172, 2621–2633.
- Essock-Vitale, S.M., 1984. The Reproductive Success of Wealthy Americans. *Ethology and Sociobiology* 5, 45–49.
- Fowler, J.H., Christakis, N.A., 2008. The dynamic spread of happiness in a large social network. *BMJ: British medical journal* 337, a2338.
- Frean, M., Rainey, P.B., Traulsen, A., 2013. The effect of population structure on the rate of evolution. *Proceedings of the Royal Society B: Biological Sciences* 280.
- Fu, F., Hauert, C., Nowak, M.A., Wang, L., 2008. Reputation-based partner choice promotes cooperation in social networks. *Phys. Rev. E* 78, 026117.
- Fu, F., Liu, L.-H., Wang, L., 2007. Evolutionary Prisoner's Dilemma on heterogeneous Newman-Watts small-world network. *The European Physical Journal B-Condensed Matter and Complex Systems* 56, 367–372.
- Fudenberg, D., Imhof, L.A., 2006. Imitation processes with small mutations. *Journal of Economic Theory* 131, 251–262.
- Grinstead, C.M., Snell, J.L., 1997. *Introduction to probability.* American Mathematical Society.
- Helbing, D., 2010. *Quantitative sociodynamics: Stochastic methods and models of social interaction processes.*
- Hill, A.L., Rand, D.G., Nowak, M.A., Christakis, N.A., Hill, A.L., Rand, D.G., Nowak, M.A., Christakis, N.A., 2010. Emotions as infectious diseases in a large social network: the SISa model. *Proceedings of the Royal Society B: Biological Sciences* 277, 3827–3835.
- Hofbauer, J., Sigmund, K., 1988. *The theory of evolution and dynamical systems. Mathematical aspects of selection.* Cambridge University Press, New York, NY.
- Hofbauer, J., Sigmund, K., 2003. *Evolutionary game dynamics.* Bulletin of the American Mathematical

- Society 40, 479.
- Imhof, L.A., Nowak, M.A., 2006. Evolutionary game dynamics in a Wright-Fisher process. *Journal of mathematical biology* 52, 667–681.
- Keeling, M.J., Eames, K.T., 2005. Networks and epidemic models. *Journal of the Royal Society Interface* 2, 295–307.
- Keister, L.A., Moller, S., 2000. Wealth Inequality in the United States. *Annual Review of Sociology* 26 IS -, 63–81.
- Knez, M.J., Camerer, C.F., 1995. Outside options and social comparison in three-player ultimatum game experiments. *Games and Economic Behavior* 10, 65–94.
- Kokko, H., 2002. Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68, 940–950.
- Lessard, S., 2007. Cooperation is less likely to evolve in a finite population with a highly skewed distribution of family size. *Proceedings of the Royal Society B: Biological Sciences* 274, 1861–1865.
- Lieberman, E., Hauert, C., Nowak, M.A., 2005. Evolutionary dynamics on graphs. *Nature* 433, 309–312.
- Masuda, N., Ohtsuki, H., 2009. Evolutionary dynamics and fixation probabilities in directed networks. *New J. Phys.* 11, 033012.
- Maynard-Smith, J., 1993. *Evolution and the Theory of Games*.
- McNamara, J.M., Barta, Z., Houston, A.I., 2004. Variation in behaviour promotes cooperation in the Prisoner's Dilemma game. *Nature* 428, 745–748.
- Misenhelter, M.D., Rotenberry, J.T., 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81, 2892–2901.
- Moran, P.A.P., 1962. The statistical processes of evolutionary theory. *The statistical processes of evolutionary theory*.
- Norton, M.I., Ariely, D., 2011. Building a Better America--One Wealth Quintile at a Time. *Perspectives on Psychological Science* 6, 9–12.
- Nowak, M.A., 2006. *Evolutionary dynamics: exploring the equations of life*. Belknap Press.
- Nowak, M.A., 2012. Evolving cooperation. *Journal of Theoretical Biology* 299, 1–8.
- Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. *Nature* 359, 826–829.
- Nowak, M.A., Michor, F., Iwasa, Y., 2003. The linear process of somatic evolution. *Proceedings of the National Academy of Sciences* 100, 14966–14969.
- Nowak, M.A., Sasaki, A., Taylor, C., Fudenberg, D., 2004. Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428, 646–650.
- Nowak, M.A., Sigmund, K., 2004. Evolutionary dynamics of biological games. *Science* 303, 793.
- Nowak, M.A., Tarnita, C.E., Antal, T., 2010. Evolutionary dynamics in structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 19–30.
- Nowak, M.A., Tarnita, C.E., Wilson, E.O., 2010. The evolution of eusociality. *Nature* 466, 1057–1062.
- Ogburn, W.F., Peterson, D., 1916. *Political Thought of Social Classes*. *Political Science Quarterly* 300–317.
- Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A., 2006. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441, 502–505.
- Ohtsuki, H., Nowak, M.A., 2006. Evolutionary games on cycles. *Proceedings of the Royal Society B: Biological Sciences* 273, 2249–2256.
- Olson, M., 1965. *The logic of collective action: public goods and the theory of groups*. 124.
- Perc, M., Szolnoki, A., 2008. Social diversity and promotion of cooperation in the spatial prisoner's dilemma game. *Phys. Rev. E* 77, 011904.
- Perc, M., Szolnoki, A., 2010. Coevolutionary games-A mini review. *Biosystems* 99, 109–125.
- Poncela, J., Gómez-Gardeñes, J., Traulsen, A., Moreno, Y., 2009. Evolutionary game dynamics in a growing structured population. *New J. Phys.* 11, 083031.
- Rand, D.G., Tarnita, C.E., Ohtsuki, H., Nowak, M.A., 2013. Evolution of fairness in the one-shot anonymous Ultimatum Game. *Proceedings of the National Academy of Sciences*.
- Ruttan, L.M., Mulder, M.B., 1999. Are East African Pastoralists Truly Conservationists? 1. *Current Anthropology* 40, 621–652.
- Samuelson, L., 1998. Evolutionary games and equilibrium selection 1.
- Santos, F.C., Pacheco, J.M., 2005. Scale-Free Networks Provide a Unifying Framework for the Emergence of Cooperation. *Phys. Rev. Lett.* 95, 098104.
- Santos, F.C., Pacheco, J.M., 2011. Risk of collective failure provides an escape from the tragedy of the commons. *Proceedings of the National Academy of Sciences* 108, 10421–10425.
- Santos, F.C., Pacheco, J.M., Lenaerts, T., 2006. Evolutionary dynamics of social dilemmas in

- structured heterogeneous populations. *Proceedings of the National Academy of Sciences* 103, 3490–3494.
- Santos, F.C., Pinheiro, F.L., Lenaerts, T., Pacheco, J.M., 2012. The role of diversity in the evolution of cooperation. *Journal of Theoretical Biology* 299, 88–96.
- Santos, F.C., Santos, M.D., Pacheco, J.M., 2008. Social diversity promotes the emergence of cooperation in public goods games. *Nature* 454, 213–216.
- Skyrms, B., Pemantle, R., 2000. A dynamic model of social network formation. *Proceedings of the National Academy of Sciences* 97, 9340–9346.
- Szabó, G., Fáth, G., 2007. Evolutionary games on graphs. *Physics Reports* 446, 97–216.
- Szabó, G., Szolnoki, A., 2012. Selfishness, fraternity, and other-regarding preference in spatial evolutionary games. *Journal of Theoretical Biology* 299, 81–87.
- Tarnita, C.E., Ohtsuki, H., Antal, T., Fu, F., Nowak, M.A., 2009. Strategy selection in structured populations. *Journal of Theoretical Biology* 259, 570–581.
- Tarnita, C.E., Taubes, C.H., Nowak, M.A., 2012. Evolutionary construction by staying together and coming together. *Journal of Theoretical Biology*.
- Tarnita, C.E., Wage, N., Nowak, M.A., 2011. Multiple strategies in structured populations. *Proceedings of the National Academy of Sciences* 108, 2334–2337.
- Taylor, C., Nowak, M.A., 2006. Evolutionary game dynamics with non-uniform interaction rates. *Theoretical Population Biology* 69, 243–252.
- Traulsen, A., Nowak, M.A., 2006. Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences* 103, 10952–10955.
- Traulsen, A., Nowak, M.A., Pacheco, J.M., 2007. Stochastic payoff evaluation increases the temperature of selection. *Journal of Theoretical Biology* 244, 349–356.
- Traulsen, A., Pacheco, J.M., Nowak, M.A., 2007. Pairwise comparison and selection temperature in evolutionary game dynamics. *Journal of Theoretical Biology* 246, 522–529.
- Traulsen, A., Sengupta, A.M., Nowak, M.A., 2005. Stochastic evolutionary dynamics on two levels. *Journal of Theoretical Biology* 235, 393–401.
- Van Segbroeck, S., Santos, F.C., Lenaerts, T., Pacheco, J.M., 2009. Reacting differently to adverse ties promotes cooperation in social networks. *Phys. Rev. Lett.* 102, 58105.
- Varughese, G., Ostrom, E., 2001. The contested role of heterogeneity in collective action: some evidence from community forestry in Nepal. *World development* 29, 747–765.
- Voelkl, B., 2010. The “Hawk-Dove” Game and the Speed of the Evolutionary Process in Small Heterogeneous Populations. *Games* 1, 103–116.
- Wakeley, J., 2008. Coalescent theory.
- Wang, J., Fu, F., Wang, L., 2010. Effects of heterogeneous wealth distribution on public cooperation with collective risk. *Phys. Rev. E* 82, 016102.
- Weibull, J.W., 1997. *Evolutionary game theory*.
- Wolff, E.N., 2002. Inheritances and wealth inequality, 1989–1998. *The American Economic Review* 92, 260–264.
- Wu, B., Gokhale, C.S., Wang, L., Traulsen, A., 2012. How small are small mutation rates? *Journal of mathematical biology* 64, 803–827.
- Zschaler, G., Traulsen, A., Gross, T., 2010. A homoclinic route to asymptotic full cooperation in adaptive networks and its failure. *New J. Phys.* 12, 093015.

Figure Captions

Figure 1. Constant selection is suppressed as inequality in background fitness increases. A mutant with fitness r arises in a population of size $N = 30$. The population is heterogeneous: b_1 denotes the background fitness of one individual, while all others have background fitness θ . For $b_1 = \theta$, we recover the well known fixation probability under constant selection, $\frac{1-r}{1-r^N}$ (solid line). For very high background fitness and large inequality, $b_1 \gg \theta$, the fixation probability of a randomly arising mutant approaches $1/N$. Thus, selection is suppressed through the introduction of heterogeneous background fitness (symbols denote individual-based simulations averaged over 30,000 realisations).

Figure 2. Increasing a population's total wealth suppresses selection. Inequality amplifies the effect that wealth has on the fixation probability. As the total wealth in a population of $N = 15$ increases, the fixation probabilities of any wealth distribution shift towards neutral drift. A wealth distribution here refers to the number of rich actors j that share the total wealth in the population. The fewer rich people own the total population wealth (the smaller j), the more selection is suppressed. Perfect inequality ($j = 1$) is the strongest suppressor of selection, regardless of the total wealth K . In contrast, when all individuals are equally wealthy, the fixation probability is least suppressed for any given total wealth in the population ($j = 15$). Lines show the fixation probabilities in a homogeneous population and neutral drift.

Figure 3. In a population of size $N = 3$, the fixation probability of a randomly arising mutant approaches $1/3$ as inequality increases because the mutation can only fixate if it arises in the wealthy individual. a) For disadvantageous ($r = 0.5$) and advantageous mutant ($r = 2$), selection is suppressed and approaches neutrality $1/N = 1/3$ for high inequality, $b \gg 1$. b) As inequality increases, the probability of fixation of mutant $r = 2$ increases for the wealthy individual and decreases for all others. This argument holds for any value of r .

Figure 4. If inequality and background fitness are large, a simple approximation of the rate of evolution is derived from the analytical solution for small N . Numerically, it is also reasonable for larger N . a) For a randomly arising mutant in $N = 3$, the fixation probability can be approximated as $\rho \approx \frac{1}{N} + \frac{N-1}{N} \frac{r}{b} \left(1 - \frac{1}{r^2}\right)$ for large b . b) Although the approximation is analytically derived only for population sizes $N \leq 5$, it also appears to hold for slightly larger N , such as $N = 10$ and, for very large background wealth, $N = 30$. Legend: solid lines are exact (Markov Chain) solutions, dashed lines are first order Taylor expansions of the solutions for large inequality and symbols represent agent-based simulations over $30,000$ realisations.

Figure 5. The absorption time of a randomly arising mutant decreases with inequality. a) In contrast to a population with equal wealth distribution, inequality reduces the number of time steps that a randomly arising mutant in a population of $N = 3$ makes on average to absorption. b) This effect in reduction of absorption time is driven primarily by the fast extinction of poor individuals when inequality disfavours them. In contrast, if inequality exists but it is small, richer individuals take longer to fixate than if all were equal. This is because the advantage from background wealth is small and rich individuals are therefore only selected slightly more often for reproduction than poor individuals.