



Heterogeneity in background fitness acts as a suppressor of selection



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HIGHLIGHTS

- We introduce the concept of heterogeneity in background fitness to evolutionary dynamics.
- We study the fixation of a new mutant in a finite population.
- The distribution of background fitness impacts the mutant's fixation probability.
- Inequality in background fitness is a strong suppressor of selection.

ARTICLE INFO

Article history:

Received 19 March 2013

Received in revised form

25 September 2013

Accepted 23 October 2013

Available online 7 November 2013

Keywords:

Evolutionary dynamics

Background fitness

Wealth

Inequality

Heterogeneity

Intensity of selection

ABSTRACT

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.

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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 et al., 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 et al., 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

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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 Fáth, 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., 2007a,b; 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”, and “inequality”) 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”, and “heterogeneous nest site qualities”).

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:

$$f_i = b_i + s_i \quad (1)$$

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 Rothenberry, 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 state in which all individual are of type A or B. We average over m realisations for every possible initial location

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