



Stochastic evolution of staying together

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HIGHLIGHTS

- Staying together is a crucial operation for construction of complexity in biology.
- Staying together means that cells do not separate after division.
- We study the evolution of staying together.
- We explore a stochastic process with finite population size.
- We derive exact results for the limit of weak selection.

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ABSTRACT

Staying together means that replicating units do not separate after reproduction, but remain attached to each other or in close proximity. Staying together is a driving force for evolution of complexity, including the evolution of multi-cellularity and eusociality. We analyze the fixation probability of a mutant that has the ability to stay together. We assume that the size of the complex affects the reproductive rate of its units and the probability of staying together. We examine the combined effect of natural selection and random drift on the emergence of staying together in a finite sized population. The number of states in the underlying stochastic process is an exponential function of population size. We develop a framework for any intensity of selection and give closed form solutions for special cases. We derive general results for the limit of weak selection.

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1. Introduction

This paper is part of the effort to explore how staying together (ST) can contribute to the emergence of complexity in evolution (Tarnita et al., 2013; Olejarz and Nowak, in press). ST means that reproductive units do not separate, but stay together. For example, cells that have divided can remain attached to each other forming multi-cellular filaments or aggregates. ST in the context of cellular division can therefore lead to the evolution of multi-cellularity, which is a major topic of investigation (Bell and Mooers, 1997; Bonner, 1998, 2008; Maynard Smith and Szathmari, 1998; Michod, 1999, 2007; Furusawa and Kaneko, 2000; Carroll, 2001; Pfeiffer and Bonhoeffer, 2003; Kirk, 2003, 2005; King, 2004; Grosberg and Strathmann, 2007; Rainey, 2007; Willensdorfer, 2008; Kolter, 2010; Rossetti et al., 2010, 2011; Koschwanez et al., 2011; Ratcliff et al., 2012, 2013; Norman et al., 2013). Another example of ST is that the offspring of a social insect do not leave the nest but stay with their mother and participate in raising further offspring

(Wilson, 1971; Gadagkar, 1994, 2001; Hunt, 2007; Hölldobler and Wilson, 2009). ST in the context of subsocial insects is a trajectory for the evolution of eusociality (Nowak et al., 2010a). Another example of ST is that reproducing intra-cellular symbionts remain in the same host cell. The evolution of eukarya by endosymbiosis (Margulis, 1981) is a form of staying together (Tarnita et al., 2013). At the dawn of life protocells enable a staying together of RNA sequences that replicate inside them (Chen et al., 2005; Bianconi et al., 2013). It is therefore of great interest to study fundamental aspects of the evolutionary dynamics of staying together. Previous work has focused on deterministic evolutionary dynamics (Tarnita et al., 2013; Olejarz and Nowak, in press). Here we develop a stochastic approach.

We study the fixation of ST in a population of finite size, N . We introduce a single mutant that has the ability to stay together and calculate the probability that it reaches fixation in a population where the resident type does not stay together.

Our paper is structured as follows. In Section 2, we describe the basic model and key results. In Section 3, we show the underlying mathematical ideas and derivation of our results. In Section 4, we provide a brief summary and outlook for future research. The Appendix contains detailed derivations.

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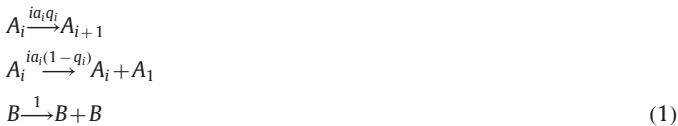
2. Model and key results

We consider a population of constant and finite size, N . There are two types: A has the ability to form complexes by staying together (ST), while B only exists in single units. We use the notation A_i to describe a complex of size i . The largest conceivable complex size is given by the size of the population, N . In this case the entire population would consist of a single complex.

We assume that the rate of reproduction of A units depends on the size of the complex. An A unit in a complex of size i has reproductive rate a_i . In comparison a B unit has a fixed reproductive rate, 1, which determines the time scale.

If a unit within A_i reproduces, there are two possibilities: (i) the new unit can stay with the complex, in which case we obtain a complex that has grown in size, A_{i+1} ; or (ii) the new unit leaves the complex, in which case we obtain an additional new complex of size one, A_1 . The former happens with probability q_i while the latter happens with probability $1 - q_i$. Thus, both the rate of reproduction and the probability of ST can depend on the size of the complex.

Reproduction in our system is described by the following biological reactions:



In any one time step we choose a random unit for reproduction proportional to fitness and simultaneously we choose a random unit to die. If a unit in a complex A_i (with $i \geq 2$) dies, then we obtain a complex that is one unit smaller, A_{i-1} . If an A_1 unit dies then this complex disappears. Similarly if a B unit dies, the total number of B units in the whole population decreases by one.

Death in our system is described by the following biological reactions:



In contrast to the previous work on staying together which was based on deterministic equations (Tarnita et al., 2013; Olejarz and Nowak, in press), we do not consider the removal (death) of entire complexes. Instead in our system individual units die to ensure constant population size. This assumption facilitates the analysis of the stochastic process (Fig. 1).

The above notation for the biological reactions in our system is borrowed from chemical kinetics. Note however that we do not use this notation to describe a time continuous process, but a discrete one. Moreover, in our model there is always exactly one birth and one death event to ensure that the population size is strictly constant as in the Moran (1962) process.

Unlike the Moran process (for two types) our system has a very large number of states. If we denote by x_i the number of complexes of type A_i and by y the number of B units in the population, then a state of the process is given by a vector $(x_1, x_2, \dots, x_N, y)$ subject to the constraint:

$$y + \sum_{i=1}^N ix_i = N. \quad (3)$$

The total number of states grows exponentially with population size, N .

The main biological question that we want to answer is the following. We introduce one A_1 unit in a population of $N - 1$ many B units and ask what is the probability that the lineage arising

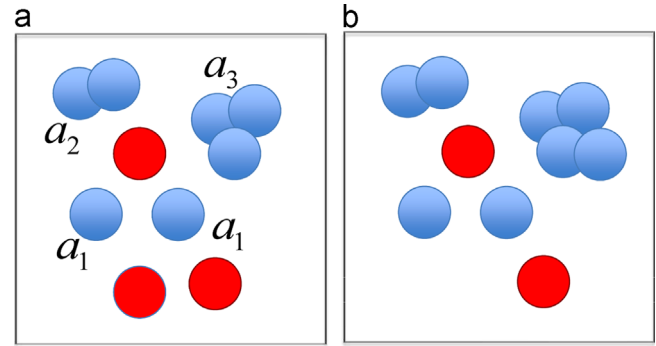


Fig. 1. Stochastic evolution of staying together. Blue spheres represent A units (cells) that have the ability to stay together after reproduction. Red spheres represent B units which always separate. (a) The fitness values of units depend on their type and for A units also on the size of the complex in which they are in. An A unit in a complex of size i has reproductive rate a_i . B units have reproductive rate 1. (b) In any one time step a random unit is chosen for reproduction proportional to fitness and a random unit is chosen for death. The total population size (total number of all units) remains constant. In this example, an A unit in the complex of size 3 has reproduced; this complex has now size 4. A B unit has died. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

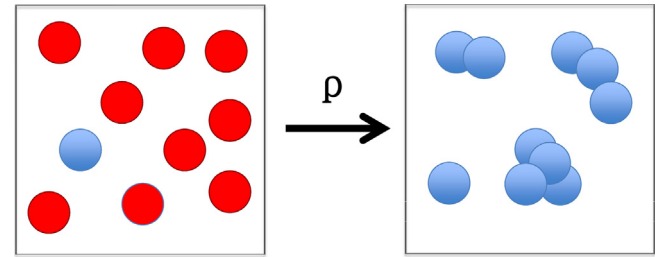


Fig. 2. We introduce a single A unit (blue) in a population of B units (red). The probability that the stochastic processes eventually reach a state where all units in the population are of type A is called the fixation probability, ρ , of A . Note that there is a single absorbing state of only B units, but there are many states that have the property of consisting of only A units. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

from this single A unit takes over the whole population? Thus, we want to calculate the fixation probability of A . There is either fixation or extinction. Let ρ be the probability that starting with one A unit the process eventually reaches a state where all units are of type A and type B has become extinct (Fig. 2).

Let us consider a simple case first. If q_i 's are all 1, then A units always stay together. Since we start with a single A_1 complex, at any time we have only at most one A complex. Hence the state space of our stochastic process is simply given by the total number of A units, $i = 0, 1, \dots, N$. There are two absorbing states, 0 and N , while the remaining states, $i = 1, \dots, N - 1$, are transient. Using standard methods (Karlin and Taylor, 1975; Nowak, 2006), we obtain

$$\rho = \left[1 + \frac{1}{a_1} + \frac{1}{a_1 a_2} + \dots + \frac{1}{a_1 a_2 \dots a_{N-1}} \right]^{-1}. \quad (4)$$

For our general system we can derive an analytic expression for the fixation probability in the limit of weak selection. In this limit, we assume that the reproductive rate of all units is very close to 1. We introduce the notation $a_i = 1 + ws_i$, where s_i is the payoff (fitness contribution) for being in a complex of size i and w is the intensity of selection. For $w = 0$ we have neutrality. The limit of weak selection is given by $w \rightarrow 0$. For studying weak selection, we assume that w is small enough so that higher order terms of w are

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