

## Evolutionary Symmetries in Populations Undergoing Moran Processes

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This summer I had the pleasure of working with Dr. Wes Maciejewski and Dr. Christoph Hauert on evolutionary game theory. Evolutionary game theory provides the tools to predict how a population will evolve over time based on the interactions of individuals, and the manner in which the population updates. For this project, we were interested in examining how a population's structure, updating process, selection criteria, and the strength of selection affect the evolutionary process. By examining this question we are able to identify symmetries between processes, and gain insight into how these four components of a population affect evolution.

To examine what traits affect evolution, we must first make a population mathematically definable. In nature, the dynamics and structure of a population are often complex (Kareiva *et al.* 1990); however, we can imagine some general ways in which a population may be organized. The population may be well-mixed where all individuals interact with one another, or there may be structure to the population where each individual interacts with only a certain set of neighbours. Of these structured populations, they may exist on regular graphs where all individuals interact with the same number of neighbours, or they may exist on more complex heterogeneous graphs where the number of interactions an individual has is dependent on its position. The type of structure, and the number of interactions in a population will likely affect its evolution.

Once population structure is established, we can imagine different ways in which the population updates over time. The Moran Process is one commonly-used updating process in the study of evolution (Moran 1958). Here, a population is imagined to consist of two types of individuals, *A*s and *B*s, possessing different traits. At each time step, one individual in the population is chosen to reproduce and one individual is chosen to die. We can predict that the order in which birth and death occurs, and the way in which individuals are selected for each of these two events will affect the evolution of a population.

In terms of selection, we limit ourselves to thinking of selection acting on one of two traits: fecundity or survival. By fecundity we mean the ability of an individual to give birth, and by survival we mean the ability of an individual to continue living. If selection acts on fecundity then this will affect who is chosen to give birth, and if selection acts on survival then this will affect who is chosen to die. For these selection criteria, we assume that the fecundity or survival of an individual depends on its type, either *A* or *B*, and its interactions with its neighbours. Every interaction garners a particular payoff according to the general payoff matrix of **Figure 1**, which we then scale by a coefficient representing the strength of selection. The greater the strength of selection, the more impact these interactions have on the selection process.

	<i>A</i>	<i>B</i>
<i>A</i>	<i>a</i>	<i>b</i>
<i>B</i>	<i>c</i>	<i>d</i>

**Figure 1:** general payoff matrix for interactions between *A* and *B* type individuals. If two *A*-types interact then both receive a payoff of *a*. If an *A*-type and a *B*-type interact then the *A*-type will receive a payoff of *b* and the *B*-type will receive a payoff of *c*. If two *B*-types interact then both receive a payoff of *d*.

These variables in the updating process allow us to imagine four different Moran-based updating processes which we then can apply to well-mixed populations, populations on regular graphs, and heterogeneous populations:

1. The birth-death fecundity process (BDF): One individual from the population is first selected to give birth based on its relative fecundity to the population. The new offspring then replaces a random neighbour who is chosen to die.
2. the death-birth fecundity process (DBF): One individual is first randomly selected to die. A neighbouring individual is then selected to give birth and fill the vacant spot based on its relative fecundity to the set of neighbours.
3. the birth-death survival process (BDS): One individual is first randomly selected to give birth. The new offspring then replaces a neighbouring individual who is selected to die based on its relative survival to its neighbours.
4. the death-birth survival process (DBS): One individual is first selected to die based on its relative survival to the population. A neighbouring individual is then randomly selected to give birth and place an offspring at the vacant spot.

When carrying out the analysis for each updating process and population structure, we imagine the population consisting entirely of *B*-type individuals to which a random mutation occurs and an *A*-type individual appears. We are interested in finding the probability that this population evolves into an all-*A*-type population with every *B*-type individual being displaced by an *A*-type over time; we can then see whether different processes produce different or the same evolutionary outcome.

To predict the results of this analysis, first notice that with our four updating processes, selection acts at one of two levels. When selection occurs in the first step it acts at the population level, and when selection occurs in the second step, it acts at the neighbour level. Our results show that this distinction greatly impacts whether different updating processes produce the same or different fixation probabilities.

In the well-mixed population, selection, regardless of whether it occurs in the first step or second, will be at the population level since an individual's neighbours are the entire population. As a result, all four updating processes produce the same fixation probability and we say one evolutionary process exists in well-mixed populations.

On the cycle-graph, arguably the simplest regular graph, we see a pairing of processes. The BDF and DBS processes produce the same fixation probability, both having selection occur in the first step, and the DBF and BDS processes produce the same fixation probability, both having selection occur in the second step. Despite this result, the second pairing of DBF and BDS only occurs when we assume the population is experiencing weak selection. Under strong selection, the symmetry breaks down and we have DBF and BDS producing separate fixation probabilities due to the increased influence of the

fecundity or survival payoff. Although yet to be proven, these results for the cycle graph are expected to hold for all regular graphs.

Finally for heterogeneous graphs, all processes produce unique fixation probabilities. This is true for all strengths of selection. These unique fixation probabilities are produced due to the structure of the graph and the fact that not all nodes can be considered equal. Not all individuals have an equal number of neighbours meaning the number of interactions contributing to the payoff an individual receives is not equal. Selection therefore acts on each individual in a different way. Similarly, the fixation probability now depends on where the mutation first arises which creates variability between processes.

By identifying these symmetries and determining in which scenarios the population structure, updating process, selection criteria, and the strength of selection affect the evolutionary process, we gain information into how we should examine populations. In the natural world, populations may not have defined structure (Kareiva *et al.* 1990), may have variable numbers of births and deaths (Johnson & Parker 1995), experience variable strengths of selection depending on environmental and current population conditions (Hoekstra *et al.* 2001), and the selection process may not solely be on either fecundity or survival, but some mix of the two (Potti *et al.* 2013). Our results show that as the complexity of the population structure increases, the evolution of the population becomes more dependent on the prescribed updating process. This means that while we may be able to examine well-mixed populations with a single updating process and get a clear picture of evolution, more complex populations should be examined with multiple updating processes to get the full spectrum of possible evolutionary outcomes. As the complexity of population structure increases we also have to become more aware of how we want to define population updating because, as seen, it leads to different results. Further work in this area can be done by examining other evolutionary traits besides fixation probability, such as fixation time, as well as seeing how a population responds when selection acts on both fecundity and survival rather than just one or the other. This work will allow for a more realistic representation of natural populations and help in the understanding of the evolutionary process.

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