



Dynamical Systems Approach to Higher-level Heritability

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Abstract. To explain higher-level heritability, we propose a dynamical systems approach, based on simulations of the high-dimensional replicator equation with mutation dynamics. We assume that all variants are generated from within the groups of variants through mutations. Simulating the equation with a random interaction matrix and possible variants, we report that this system tends to have many attractors, of fixed point, chaotic and quasiperiodic type. In a chaotic attractor, special gene-like variants appear to control the heritability of the system, in the sense that removal of the variants would easily enable the system to depart from the attractor. Those variants do not predominate in the population size, but have the lowest net reproduction and mutation rates on average. Because their rate of growth is small, they are named neutral phenotypes. Additionally, combinatorial effects of these neutral variants to the entire system are reported.

Key words: chaos, evolvability, neutral phenotype, replicator dynamics

1. Introduction

Over the years, experimental studies of higher level group selection have been carried out [1]. Many of them have reported that there are significant responses against group selection with heritable variations. In practice, the heritability of soil/aquatic ecosystems is studied by the successive selection and generation of new system units by taking the previously-selected ones as the parents. In contrast to individual selection mechanisms, an ecosystem has no genetic base. Therefore, heritability at the ecosystem level is not very reliable, as is observed in the experiments by Swenson et al. [2]. This unreliable but still heritable nature of information in Swenson's higher-level systems is attributed to a network of microbes underlying the system. Indeed, Yokoyama [3] reported that topological changes in a network of microbes explains the soil-borne diseases caused by repetitive monoculture.

Compared with genetic systems, we can't easily replicate a soil ecosystem. This unstable nature of replication is, however, an important factor in the context of evolutionary systems. Since a complete replicator cannot reproduce a new one, no further evolution occurs. However, at the same time, overly unreliable replicators cannot survive [4]. We define the capability of replicators to evolve as evolvability.

How does each replicating microbe contribute to the stability of replication and evolvability of the entire system? In the following, we use a model of replicator dynamics to study the switching of an attractor by the removal of phenotypic variables.

2. Replicator Dynamics

The replicator equation was initially proposed by Maynard Smith [5] and was developed thereafter to describe evolutionary dynamics (see e.g. Hofbauer [6]). The equation describes the evolution over time of the relative frequency of, for example, phenotypes, and it is equivalent to the Lotka-Volterra equation. It is now widely accepted as a basic model equation applicable from ecosystems to game-playing systems. Some new observations have been reported recently, and an issue related to the present one is found in Tokita and Yasutomi's experiment [7]. They studied the threshold effect: a phenotype whose population size is lower than the given threshold must be removed from the system. As the result, the model avoids the heteroclinic instability inherent in the original system. The system now shows several universal phenomena. However, by compensation, it loses rich temporal behaviours and many degrees of freedom.

We instead study the effect of mutation processes in the replicator system. The mutation process naturally gives a lower bound to each amount of phenotype [8, 9]. A mutation process from one phenotype to another is introduced in the original replicator model as follows:

$$\frac{dx_i}{dt} = x_i \left(\sum_j a_{ij} x_j - \sum_k \sum_j x_k a_{kj} x_j \right) - \mu x_i + \frac{\mu}{N-1} \sum_{j \neq i} x_j. \quad (1)$$

where $\sum x_i = 1$.

The first two terms devote that the growth rate is proportional to the difference of fitness from the population average. The remaining terms can be recognized as mutations among phenotypes. We assume that every phenotype is generated by others with the same rate. Controlling parameters of this system are the structure of the interaction matrix $\{a_{ij}\}$ and the mutation coefficient μ . We study a system with a randomly generated matrix. The initial distribution of phenotypes also determines the reachable attractors.

3. Dominant, Recessive and Neutral Phenotypes

Relative frequencies of most phenotypes generally vary from the lowest order (limited by the mutation effect) to the order of unity. No single phenotype dominates the population eventually, as it is immediately out-competed by the others. However, we found that some replicator systems can have (1) coexistence of different kinds of attractors (chaotic (C), periodic (P), quasi-periodic (QP) and fixed point (F)),

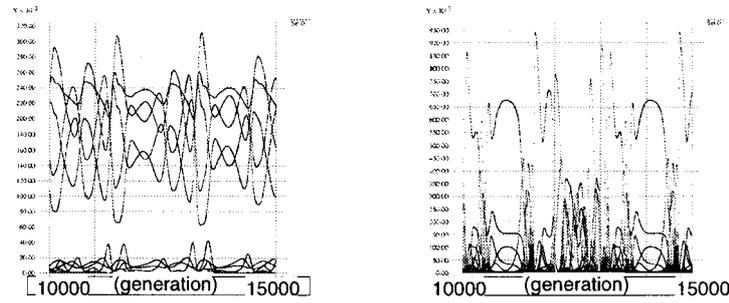


Figure 1. Temporal evolution of phenotype frequencies in chaotic (left) and quasi-periodic attractors (right). $\mu = 0.0125$ and a_{ij} is assigned a random number from $(-2.5, 2.5)$. Through the paper, we only study these parameter values.

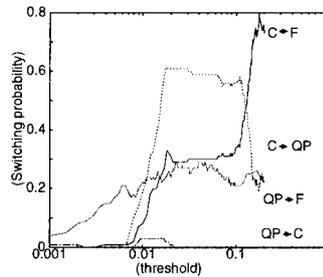


Figure 2. Switching probabilities among attractors. After a system attains an attractor, phenotypes whose frequencies are lower than a given threshold (X-axis) are removed. Renormalizing the rest of phenotypes, we restart the system to see which attractor it attains. Each switching probability (Y-axis) is computed by averaging over 100 different states for each threshold value. When it attains a fixed point attractor, it never switches to other attractors.

and (2) a few phenotypes in those attractors can dominate the population. (see the left figure of Figure 1).

Because any phenotype can be continually supplied through mutation, each attractor has all phenotypes. Only their relative frequencies and time structures differ. Let us suppose we try to select for and replicate attractors.

We assume that replication of attractors has to sacrifice their less frequent phenotypes. In Figure 2, the switching probabilities among attractors are computed against the removal threshold. An attractor is called a stable replicator if it can rebuild a whole structure from dominant phenotypes. This is true for fixed-point attractors, but not for others. For the quasi-periodic state, we always have incomplete replication, even for the lower thresholds. However, for the chaotic attractor, there exists a clear threshold around 0.005. Below this threshold, the replication seems to be perfect, while above it there are dominant phenotypes and it is difficult to reorganize the entire state from them.

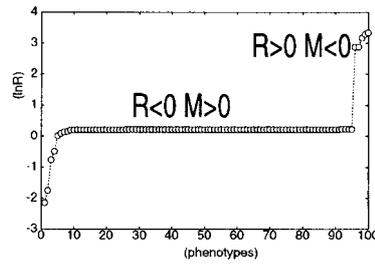


Figure 3. A net reproduction rate (R) averaged over 10000 time generations is computed for each phenotype for the chaotic attractor (see Figure 1). The absolute values of R s in a log-scale are sorted according to their amplitudes.

Our conclusion from this observation is that the relative abundance of phenotypes does not simply correspond to the significance in the stability of attractor. It means that we have to pay attention to these invisible minor phenotypes even when there are dominant ones in the ecosystem replication experiments. We thus investigate the net reproduction rate of each phenotype to see its contribution to the stability of the whole. A net reproduction rate (R) is defined by the time-average of the first two terms in Equation (1). A phenotype behaves as a prey on average when R becomes negative, whereas a positive R implies that a phenotype behaves like a predator on average. We also define an averaged mutation flow (M) by averaging over the contributions from the mutation terms. On long time averages, R becomes equal to $-M$. Using these new values, we can classify phenotypes into dominant ($R > 0$, $M < 0$), recessive ($R < 0$, $M > 0$), and neutral groups (small R and M). Because the dominant group exploits others and produces variants and the recessive ones are only exploited by the dominants, the indices are logical. Sorting by the amplitudes of R s, we rank them in Figure 3 using a log-scale. The left ends with the lowest R s in Figure 3 constitute a **neutral** group, because they have small contributions to the rate of growth from both reproduction and mutation. We found that this group never dominates the population; however, removal of the phenotypes belonging to the group controls the stability of the attractor as if these phenotypes were the parameters of the equation. This neutral group provides the lower threshold value especially for the chaotic attractor switching in Figure 2.

4. Control by Neutral Phenotypes

To study the effect of the neutral group, we conducted another experiment, in which we specifically selected and removed neutral phenotypes from the population. Those phenotypes are immediately recovered through mutation; however, the attractor itself may change after some transient periods (see Figure 4). The impact of each phenotype on attractor switching is, interestingly, correlated with its neutrality (i.e., the smallness of R). Simultaneous removal of several neutral

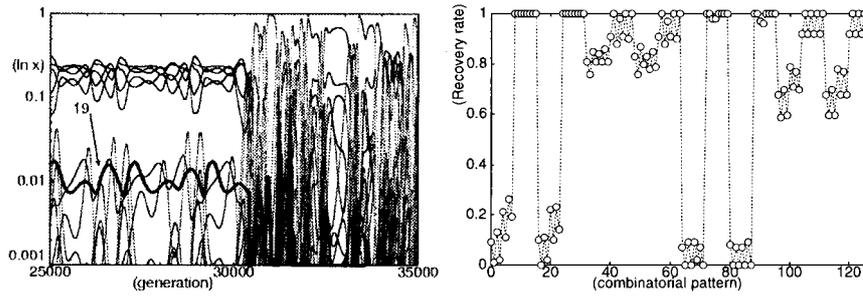


Figure 4. On the left is a time-based evolution of population in a log scale, plotted against generation steps. Every phenotype is superimposed. When phenotype 19 (with a wider line) is removed at generation 30000, the entire structure abruptly collapses and switches to a quasi-periodic attractor. On the right is a result of controlling neutral phenotypes of the seven lowest R rates. We have used 127 combinatorial removing/non-removing events of those seven neutral types. The vertical line denotes the recovery rate of the chaotic attractor after the combinatorial removal of the phenotypes. The combinatorial pattern is decimally encoded on the horizontal line. We have examined 100 events for each combination and the recovery rate has been averaged. See for example number 87, which corresponds to a removal of phenotypes 19 and 76, and the resultant rate is zero: that is, it never recovered the original attractor.

phenotypes will combinatorially cause an attractor switching event (see captions in Figure 4 right figure). For example, a system sometimes switches to other attractors only when two neutral phenotypes are simultaneously removed.

This kind of combinatorial effect implies that a network of neutral phenotypes exists. The matrix elements show that those neutral phenotypes are mostly parasitizing on the dominant phenotypes. Since dominant phenotypes are mostly mutually cooperative, those neutral ones cannot overtake the population. However, a subtle dynamic balance between networks of neutral and dominant types provides the phenomena that we have described.

5. Discussion

To conclude, we have shown that stable replication of some attractors is controlled not simply by dominant phenotypes but also by neutral ones. Removal of a large number of individuals to cause attractor switching may correspond to a large external perturbation. However, the removal of neutral phenotypes may be a subtle perturbation, but its result can be large. In this sense, the switch by neutral types provides a non-trivial mechanism that may be related to the notion of keystone phenotypes in ecosystems (see e.g. [10]). A keystone phenotype has been discussed for a long time, but its existence and function has never been explicitly discussed theoretically. Keystone species do not have to have a large population size, but rather neutrality against other species is important. Hence, the keystone species may act as a gene or a parameter in a higher level ecosystem. That a neutral, thereby minor species, can control the entire system has also been reported in different

systems (see e.g. [11, 12]). A detailed study of the present model and the function of neutral phenotypes will be reported elsewhere.

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