

A Network of Dynamic Keystone Species

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Abstract

A concept of dynamic keystone species is proposed based on simulation studies of replicator equations. We report that the variables of this equation can be categorized into three groups based on their individual dynamic behaviour. They are dominant, neutral and recessive phenotypes. Because the growth rates are small in average, they are termed neutral phenotypes.

Especially with a chaotic attractor, neutral phenotypes work as keystone species to control the stability of the system. The removal of neutral phenotypes may be a subtle perturbation, but it can have a large effect compared with its relative abundance, as it triggers an attractor switch. We also report that these neutral phenotypes form a network that can provide combinatorial effects on the attractor switch. A mere topological structure of the interacting matrix is not sufficient for determining which may be a keystone species; instead, it is determined by the kind of the attractors they organize.

Introduction

Even without a genetic basis, experimental studies have reported that there are quasi-heritable properties in ecosystems (Goodnight 2000). In particular, Swenson's group has reported that small soil and aquatic ecosystems can show significant responses against certain artificial selection pressures (Swenson, Wilson, & Elias 2000). In their experiments, successive selections of system units were conducted with respect to pH (aquatic systems) or surface biomass (soil systems). Then, new units were reproduced by taking the selected units as parents, in which sexual recombination effects can also be taken into account. In contrast to individual selection mechanisms, an ecosystem has no genetic base. Therefore, heritability at the ecosystem level is not very reliable, as was observed in Swenson's experiments. This unreliable but still heritable nature of information in Swenson's system is well known in agriculture. For example, if one continually plants the same crops in the same area, the quality of the soil will decay. Moreover, it is known that soil-borne diseases are exacerbated by repetitive monoculture. We attribute those qualitative

and heritable features of ecosystems to underlying networks of microbes. Indeed Yokoyama argues that topological changes in a microbe network may explain the existence of soil-borne diseases (Yokoyama 2000).

In this paper, we simulate the dynamics of the underlying microbe network (preliminary results have been published in Ikegami and Hashimoto (2002)). However, we do not pay attention here to the topological nature of the network. Rather, we focus on the dynamic nature of the microbes that constitute the network. In other words, we study the hierarchical nature of the (chemical) species constituting the network with respect to its contribution to the system's stability. We first propose a dynamic definition of a keystone species. Such species are usually noticed when they are removed from an ecosystem or when their disappearance from an ecosystem causes a significant change to it. Second, we demonstrate some combinatorial effects of those keystone species. We show that the keystone species actually consists of a sub-network, providing a combinatorial effect on a system when it is removed. We show that partial removal of any keystone species releases the other keystone species, resulting in a drastic change to the entire system.

Replicator dynamics

We simulated the time-based evolution of phenotypes of (chemical) species by the replicator equation. The reproduction rate of each phenotype was assumed to be proportional to the difference between the individual gain and the average gain of the whole system. The replicator equation is equivalent to the Lotka-Volterra equation with some variable transformations. This equation was initially proposed by Maynard Smith (1982) and was developed thereafter to describe generic evolutionary dynamics (for example see Hofbauer (1981)).

Some new observations have been reported recently (Chawanya 1995; 1996), where unexpectedly rich behaviour of this equation has been revealed. For example, we note a strange hierarchy of attractors even within a system of only a few degrees of freedom. The mechanism is attributed to the heteroclinic cycle underlying the equation. However, this cycle also brings dysfunc-

tional biological behaviour into the system. For example, the relative abundance of phenotype falling down to the order of e^{-100} is thought unrealistic. A remedy is to introduce a removal threshold into the system; 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 (Tokita & Yasutomi 1999). The system presents some universal phenomena, however by compensation it loses aspects of rich dynamics.

We studied the effect of mutation processes in the original replicator system. The mutation process naturally gives a lower boundary to each amount of phenotype, so that it can also avoid dysfunctional behaviour (Ikegami & Yoshikawa 1995; Hashimoto & Ikegami 2001). A mutation process from one phenotype to another was 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 $\sum x_i = 1$ and the total number of variables is given by N . Throughout this paper, we take $N = 100$.

The first two terms express the idea that the growth rate of any phenotype is proportional to the difference between its fitness and the average fitness. The remaining terms can be recognized as mutations among phenotypes. We assume that every phenotype is produced with the same rate. This second term is then rewritten as $\frac{\mu N}{N-1} (\frac{1}{N} - x_i)$, that is, a source term of the first order (x_i).

The controlling parameters of this system are the structure of the interaction matrix $\{a_{ij}\}$ and the mutation coefficient μ . Therefore, we basically have $N^2 + 1$ independent parameters. The initial distribution of phenotypes also determines the reachable attractors.

Kinds of Attractors and Hierarchy of Species

The equation can have more than one attractor when the number of possible phenotypes is sufficiently large or when the interaction matrix is carefully selected. We paid attention to the hierarchical organization of phenotypes that constitute each attractor.

The results show that, for most attractors the relative frequency of each phenotype changes from the lowest order (limited by the mutation effect) to the order of unity except for fixed-point states. Generally no single phenotype dominates the population eventually, as it is immediately out-competed by the others, except for the trivial fixed-point cases. However, we found that several phenotypes can also dominate the population in a chaotic attractor. Such an attractor can be observed by carefully tuning the interaction matrix with a mutation

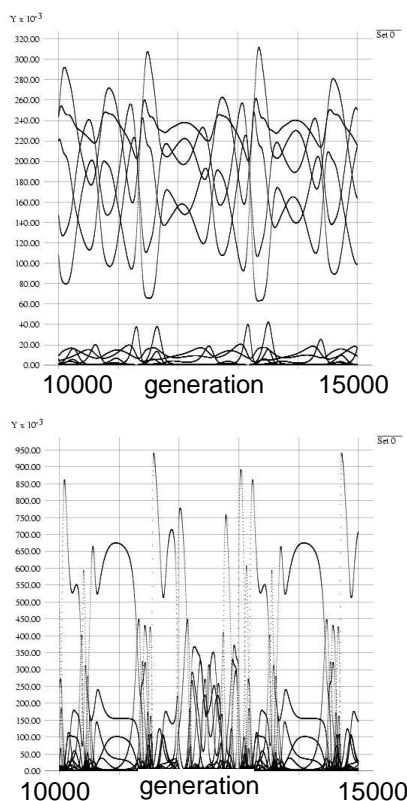


Figure 1: Temporal evolution of phenotype frequencies in chaotic (above) and quasi-periodic attractors (below). $\mu = 0.0125$ and a_{ij} has been assigned a random number from $(-2.5 \text{ to } +2.5)$. We only studied these values in this paper.

rate and an initial state. (see the upper figure of Fig. 1). This matrix also enables several quasi-periodic/periodic attractors and fixed-point ones. The interaction matrix was searched under the condition where $\mu = 0.0125$ and each matrix element was assigned a random number from $(-2.5 \text{ to } +2.5)$. It is difficult to find a matrix structure that has attractors with clear separation between dominant and recessive phenotypes. Note that dominant phenotypes have relatively larger abundances compared with the other phenotypes.

Let us suppose that we try to select for and replicate attractors as in the case of Swenson's experiment. We assume that replication of attractors has to sacrifice infrequent phenotypes below some given threshold. Because replication at an ecological level is assumed to be a macro-operational process, we cannot select for rare communities whose abundance is below the threshold.

In Fig. 2, the switching probabilities among attractors are computed against the removal threshold. The phenotypes whose abundance below the given threshold will be removed at a given time step. Below, a kind of attractor has been automatically detected by comput-

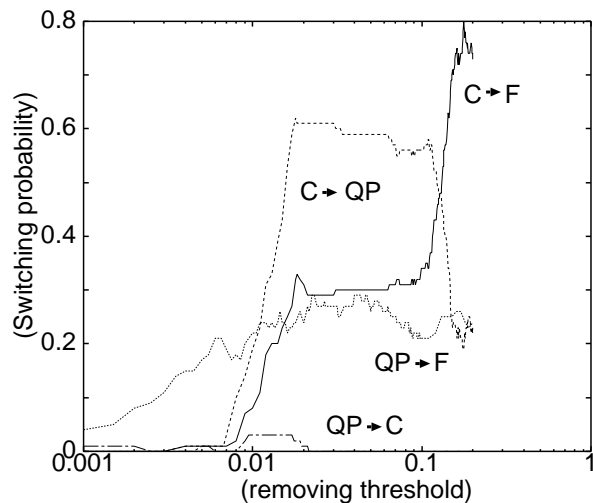


Figure 2: Switching probabilities among chaotic(C), quasi periodic (QP) and fixed point (F) attractors. After a system attains an attractor, phenotypes whose frequency are lower than a given threshold (X-axis) are removed. Renormalizing the rest of the phenotypes, we restart the system to see which attractor 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.

ing the first Lyapunov exponent and the time-averaged momentum ($\sum_i x_i^2$).

An attractor is called a stable replicator if it can recover after the removal of infrequent phenotypes. In particular, a fixed point attractor can rebuild a whole structure from dominant phenotypes. However, this is not true for the other attractors. For the quasi-periodic attractors, we have a non-negligible probability of switching to the other attractors, even for small thresholds. However, for the chaotic attractor, there exists a clear threshold around 0.005. Below this threshold, replication seems to be perfect, while above it there are dominant phenotypes and it is getting difficult to reorganize the entire state from them. However, this threshold is much smaller than the average abundance of the dominant phenotypes.

Our conclusion from this observation is that the relative abundance of any given phenotypes does not simply correspond to its significance for the stability of the attractor. This means that we have to pay attention to the roles of these minor phenotypes, which cannot dominate the system but nevertheless control its entire stability. For the chaotic attractor, the effective removal threshold emerges around a value of 0.005, which is much smaller than the order of the dominant phenotypes (about 0.2). Therefore, between the lowest threshold and the average amount of the dominant phenotypes, we have a certain

class of phenotype that can control the system's stability. In the (quasi) periodic attractors, it is difficult to label such phenotypes as we have no everlasting dominant forms. However, the significance of phenotypes varies from one to the other with reference to the removal event. To characterize these better, we have introduced some macro quantities to classify the phenotypes that constitute attractors.

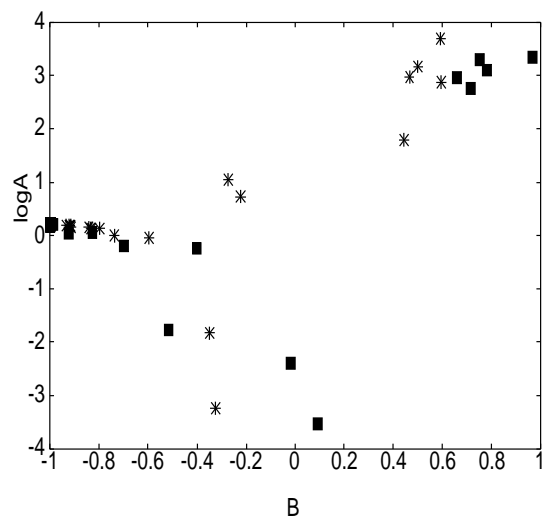


Figure 3: A characteristic measure of $(B_i, \ln(A_i))$ averaged over 10000 time generations has been computed for each phenotype. The square symbols correspond to the chaotic attractor and the other symbol to a quasi-periodic one.

Classification of phenotypes

The dynamics of each phenotype are governed by equation (1). We first decompose the right-hand side of the equation into two parts, the reproduction term (the first and second term) and the mutation term (the last two terms). By computing the time-based average of the reproduction term, we obtain a net reproduction rate as;

$$r_i(T) = \int_{\tau}^{\tau+T} dt (x_i (\sum_j a_{ij} x_j - \sum_{lm} x_l a_{lm} x_m)), \quad (2)$$

$$R_i(T) = \lim_{T \rightarrow \infty} \frac{1}{T} r_i(T) \quad (3)$$

that characterizes the frequency-dependent selection in this system. The time average of the mutation term

$$m_i(T) = \int_{\tau}^{\tau+T} dt \frac{\mu N}{N-1} (\frac{1}{N} - x_i), \quad (4)$$

$$M_i = \lim_{T \rightarrow \infty} m_i(T)/T \quad (5)$$

$$= \frac{\mu N}{N-1} (\frac{1}{N} - \langle x_i \rangle)$$

gives a genetic flow from the other phenotypes. In particular, the last form of M_i denotes that the quantifier is almost proportional to the time average of the abundance $\langle x_i \rangle$. On the long time average, R_i becomes equal to $-M_i$, if the average is taken within an attractor. That is because the time average of each dx_i/dt converges to a zero value by definition.

Using these quantifiers (R_i, M_i), we can classify phenotypes into dominant (+, -), recessive (-, +) and neutral groups (ϵ, ϵ), where $\epsilon \ll 1$ is a small value. The dominant group exploits others and produces variants. In addition, the recessive ones are only exploited by the dominants. Therefore, we see that this classification, due to the quantifiers, makes sense.

This classification is sufficient for classifying the attractors with the dominant phenotypes. However, those without everlasting dominant phenotypes require another quantifier. Actually, when the time oscillation shows rugged peaks, those quantifiers may lose too much information for the attractor state.

The other quantifier, for example, is the alternating rate between positive and negative values of the derivatives, \dot{r}_i or \dot{m}_i . We use the $\Theta(x)$ function, where $\Theta(x) = 1(x > 0)$ and 0 (otherwise), to define the second quantifier. Practically, we define the number of sign alternation (B_i) as,

$$B_i = \lim_{T \rightarrow \infty} \frac{1}{T} \int_{\tau}^{\tau+T} dt \Theta(\dot{r}_i(t)) - \Theta(\dot{m}_i(t)) \quad (6)$$

This is also given as a time-averaged quantity. Dominant phenotypes tend to have large B_i values, and in particular completely dominating phenotypes have $B_i = 1$. On the other hand, recessive phenotypes have negative B_i values. Completely dominated phenotypes have $B_i = -1$. Neutral phenotypes should have a value of B_i that is not equal to 1 or -1 . The ideal neutral case might be $B_i = 0$. Since $R_i + M_i = 0$ should hold, we define the absolute value of R_i as A_i . It is true that A_i and B_i basically provide similar information, so that either is sufficient in general. However, as we have described, it is very rare to have such attractors that have everlasting phenotypes. Most attractors are (quasi) periodic without having dominant phenotypes. We cannot always distinguish dominant phenotypes from others in terms of population size, however, they may be defined as dominant phenotypes by the quantity B_i . Thus, the measure (A_i, B_i) may work in such generic cases.

Using A_i and B_i , we plot the characteristics of each phenotypes on the A-B plane in Fig.3. In the chaotic attractor, dominant phenotypes exist close to $B_I = 1$ and larger A_i values. Recessive phenotypes are found at $B = -1$ with smaller A_i values. The neutral phenotypes are found around $B_I = 0$ with much smaller A_i values. A set of phenotypes that constitutes a quasi-periodic attractor also shows a similar classification as depicted in

Fig.3.

What is important here is that the removal of some neutral phenotypes disintegrates the whole system. In particular, neutral phenotypes in the chaotic attractor can produce significant impacts on the stability of the attractor, and even their relative frequencies are small. This aspect fits the definition of a **keystone species** by Power et al. (1996) In the following sections, we study the effects of neutral phenotypes on the whole system. We will show that neutral phenotypes, as keystone species, have dynamic natures and so the neutral phenotypes themselves form a sub-network.

Keystone species as a network of neutral phenotypes

Following Paine's definition (1966), a keystone species provides a larger impact on its ecological system than would be expected from its relative abundance. A good example of keystone species is the sea otter found widely in the Northern Pacific ocean. Since Paine's paper was published, many studies have been performed on the effects of keystone species (see for example (Power & others 1996; Carpenter 1985)). Keystone phenotypes are usually made apparent when their removal or disappearance from a particular ecosystem causes a significant change to it. Thus the notion of keystone species is important in conservation biology.

As we noted in the preceding section, attractor switching occurs by removing less-abundant phenotypes. Here we concentrate more on individual phenotypes to see their impact on the whole system. To do this, we specifically selected and removed phenotypes from the population. The results show that removing dominant phenotypes produces a large effect on the system and that removing recessive phenotypes does not have any effect. The impact of each phenotype on attractor switching is, interestingly, correlated with its neutrality (i.e., the smallness of A_i). Those phenotypes are recovered immediately through mutation, however the attractor itself may change after some transient periods. The relative abundance of the neutral phenotypes is the lowest, specially for the chaotic attractor, but the impact is far larger than expected (Fig.4). In this example, a neutral phenotype with the second smallest R_i value (phenotype 19) is removed from the system.

While Paine's original and other keystone concepts are still limited to a single phenotypes, we have studied the combined effects of keystone species, i.e. of neutral phenotypes with small A_i values. Simultaneous removal of several neutral phenotypes combine to cause an attractor-switching event as in Figure5. We selected phenotypes with the seven lowest A_i values and tested all 127 patterns of combinatorial removal of those phenotypes. By putting the seven neutral phenotypes in order, we produced a binary representation of the removed set

of phenotype. This was done by setting

$$y_a(t) = (\Theta(x_{13}(t)), \Theta(x_{15}(t)), \Theta(x_{16}(t)), \Theta(x_{19}(t)), \Theta(x_{64}(t)), \Theta(x_{76}(t)), \Theta(x_{87}(t))), \quad (7)$$

where the subscript a runs from 0 to 127 and the string, $y_{42}(t) = [0101010]$ is read as a removal of the phenotypes 13,16,64 and 87, for example. Fig.5 shows that the phenotypes 19 and 76 are the two most salient ones that constitute keystones in the attractor with the two smallest A_i values. However, the removal of a single phenotype 76 does not cause any destruction; only when this is coupled with phenotype 19 does it cause a drastic change. Thus it appears that the simultaneous removal of other phenotypes often weakens the cooperative actions of phenotypes 19 and 76.

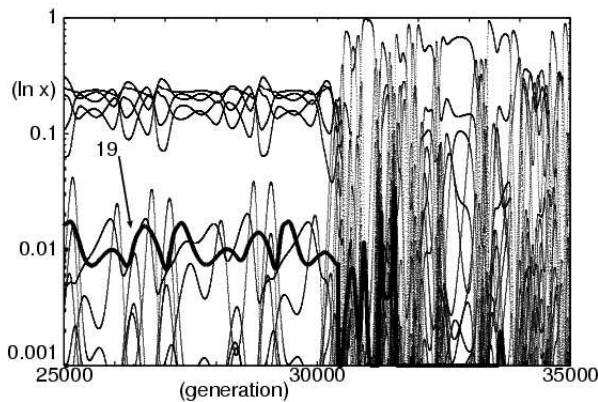


Figure 4: A time-based evolution of population in a log scale, plotted against generation steps. Every phenotype is superimposed. When phenotype #19 (with a wider line) is removed at generation 30000, the entire structure abruptly collapses and switches to a quasi-periodic attractor.

This kind of combinatorial effect implies the existence of a network of neutral phenotypes. Because dominant phenotypes are mostly mutually cooperative, having large A values, they are insensitive to small population changes. On the other hand, if the recessive phenotypes have negative R values, they are also insensitive to small population changes. However, a subtle dynamic balance exists in networks of neutral phenotypes. Therefore, the removal of a neutral phenotype does not release either dominant or recessive ones but only other neutral phenotypes. In Figure6, we show how a single neutral phenotype causes a cascading impact on the whole system after a certain time lag.

Keystone phenotypes in a mutation-free system

To compare the result of the preceding sections with the original replicator dynamics, we briefly describe here a

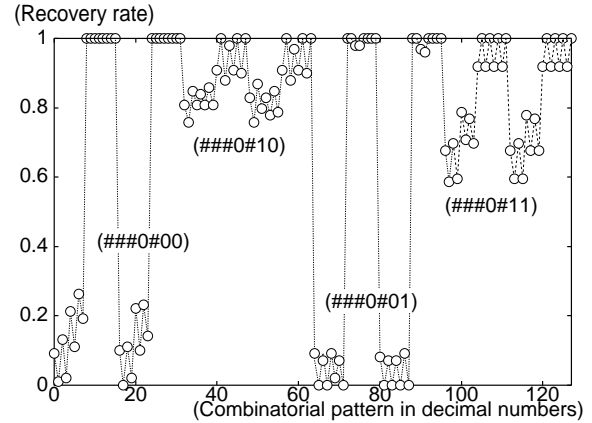


Figure 5: The combinatorial pattern is decimally encoded on the horizontal line. We have examined 100 events for each combination and the recovery rate has been averaged. The recovery rate becomes zero when the chaotic attractor is never recovered. In the figure, the four most unstable regions are labelled with the associated binary string, ($###0#00$), ($###0#10$), ($###0#01$) and ($###0#11$), where # denotes either 0 or 1. Here the salient neutral phenotypes are #19, #76 and #87.

specific version of an original replicator equation without mutation terms. Putting $\mu = 0$ in the equation (1) but taking $a_{ii} = -1$ for all i in the interaction matrix, we study the fate of the system. By randomly generating the off-diagonal elements of the interaction matrix, we find a system with a keystone species in the above sense. Unlike the previous system, a fixed-point attractor is studied here. Other dynamics are not often observed, due to the structure of the diagonal elements of the interaction matrix.

The relaxation time to the attractor is so long that a removal experiment was conducted during the transient time of the attractor. Since this equation has no mutation term and the attractor is a fixed point, every $A_i (= R_i)$ and B_i value of phenotypes becomes zero. Thus, every visible phenotype is neutral in this sense. As is expected from the basic nature of the replicator equation, removal of a single phenotype cannot produce a large impact on the other phenotypes, given the relatively larger population, and it can only affect the lower population value phenotypes. Removal of a single phenotype releases two far lower population value phenotypes (see Fig.7). When the population becomes comparable in size to other phenotypes, the system shows a drastic change. The same scenario holds true here, but we have not checked the combinatorial effect in this case.

The keystone species in the replicator equation with mutation terms have more dynamic natures than those in this section. As a result, the neutral phenotypes consti-

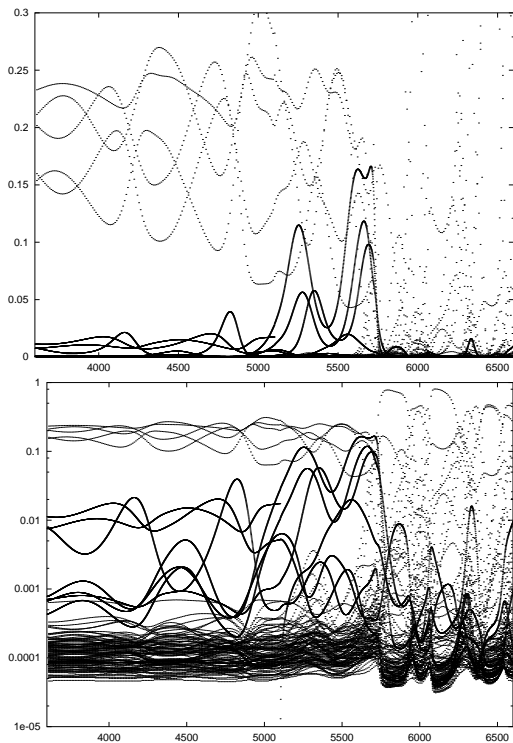


Figure 6: Relative abundance is plotted against time steps in a bar (above) and in a log scale (below). Neutral phenotypes are denoted with darker lines in the middle area (x_i is in the range of 0.01–0.001). After the neutral phenotype 19 is removed at time step 5200, other neutral phenotypes increase their abundance and reach the order of the dominant phenotypes at around step 5700. Then a drastic change occurs, and the attractor switches.

tute a complex basin boundary for the attractor. It can be shown that the basin boundary becomes glassy-like for neutral phenotypes. On the other hand, of particular interest here — lacking a mutation term — is the release of significantly small phenotypes compared with the former model.

Discussion

To conclude, we have shown that the removal of neutral phenotypes may produce a subtle perturbation to the system, but the results can be large compared with its relative abundance. In this sense, the attractor switch by neutral types produces a non-trivial mechanism, related to the notion of keystone species. Further, we have shown a combinatorial effect of such neutral phenotypes on the system’s stability.

The existence of such a combinatorial effect implies that neutral phenotypes form a sub-network in which neutral phenotypes mutually suppress each other. The keystone species acts as a gene or a system’s parameter in this higher level ecosystem. That a neutral, and

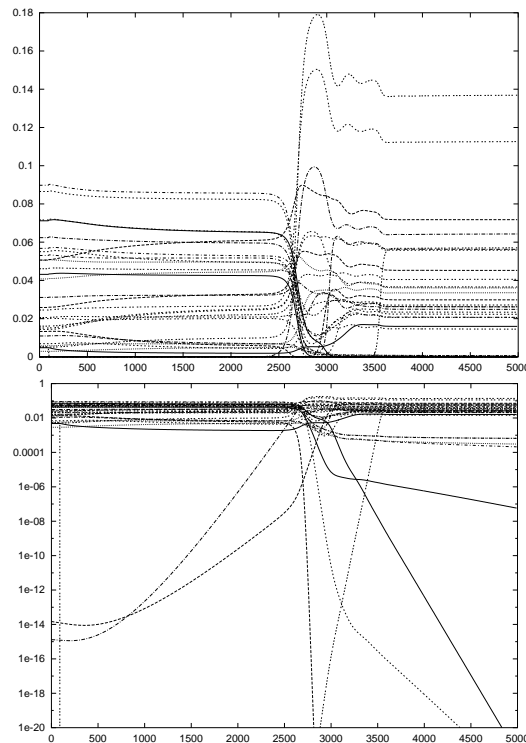


Figure 7: The removal of a single phenotype (of abundance = 0.00527) at time =100 will release a pair of far less abundant phenotypes. They increase in size exponentially and, when they reach a certain level, a drastic change occurs. Because any given population size is not bounded by the mutation flow, this demonstrates effectively how removal affects the system. Normal scale a) and logarithmic scale b).

thereby minor phenotype, can control the entire system has also been reported in different systems (see for example (Kaneko & Yomo 2002; Hogeweg 1998)).

The relationship between a keystone species and the concept of evolvability (Ikegami 1999) is worth discussing here. If some neutral phenotypes acting as keystone species can work as genes or parameters, this should be evolutionary favourable, as to evolve an ecosystem as a selective unit, some mechanisms are needed to reset the whole system. If this requires the removal of dominant phenotypes, the re-setting of the system requires major changes and it cannot occur spontaneously. However, if the resetting only requires the removal of phenotypes with small population sizes, it may occur spontaneously. In this sense, those keystone species may have developed as an evolutionary switch for higher order ecosystems to produce internal evolvability. A point here is that the switch is not a static notion with one degree of freedom, but it has a dynamic nature made possible by many degrees of freedom, i.e. there must be a network of neutral phenotypes.

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