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Neutral phenotypes as network keystone species

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Abstract The concept of network keystone species is proposed. A set of phenotypes constitute a network that acts as a functional keystone. When an ecosystem forms a large, complex network that changes temporally, it is generally difficult to tell which will become a keystone species. Based on simulations of abstract ecosystems, phenotypes were classified to show that neutral phenotypes, or slowly reproducing phenotypes, are candidates for keystone species. I show that the removal of neutral phenotypes breaks up an attractor state and produces significant impacts on the stability of an attractor, in spite of small population size. The effect of partial removal of neutral phenotypes, and the combinatorial effects of keystone species, are reported in detail.

Keywords Replicator equation · Population dynamics · Neutral phenotypes · Chaos attractor · Keystone

Introduction

The definition of keystone species is still controversial amongst ecologists. Power et al. (1996) defines keystone species as those species whose existence has an effect on an ecosystem that is disproportionately large, relative to its population size within that ecosystem. However, as would be expected, keystone species are context dependent (see e.g. Payton et al. 2002). Whether or not a species can function as a keystone species is dependent on the composition of the entire ecosystem. If the ecosystem changes its species composition, different species may become keystone species. Therefore, a keystone species is not just a simple characteristic of its own properties.

Recently, various functional networks have been studied, which are characterized by a scale-free property link (Barabasi 2002). A scale-free network is characterized by the property that network connectivity obeys a power law function. A few nodes exhibit a high number of connections, while most nodes have relatively few connections. The Internet is a good example of where a well-connected hub node works as keystone species, in the sense that the removal of the hub node will catastrophically crash the network. Thus, it can be argued that it is important to protect the hub nodes from cyber attacks. The scale-free network with hubs, provides a keystone example of the characteristics of a special network topology.

On the other hand, another kind of keystone species exists that is only accessible dynamically. Ecosystems potentially have many equilibrium states (attractors), e.g. different species composition, even for the same network topology. This paper considers an ecosystem with multiple attractors and keystone species analyzes as dynamic and network objects. Knowing that an ecosystem is generally dynamic, it is important to know the dynamic nature of keystone species.

Classic keystone species, e.g. starfish or sea otters, are all predators. When an ecosystem is modeled as a randomly connected network, the situation is far more complex. Some species become top predators in the abstract ecosystem, but some species are simultaneously prey and predator. As shown in the simulations, these intermediate layer species can become keystone species. Furthermore, it will be shown that the degree of keystone ‘species-ness’ changes from species to species and over time. The effect of keystone species cannot be attributed to a single species (Wilson and Halupka 1995). The effect is essentially network-based. Whether species A can function as a keystone species or not is dependent on species B. It will be shown in this paper that (1) keystone species functions as a network, (2) neutral species are the candidates that comprise the keystone network, and (3) a partial and combinatorial removal of the neutral species determines the fate of the system.

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A potential application of this theory might be microbial networks in soil or water (Swenson et al. 2000; Yokoyama 2000; Grayston et al. 2001; Carpenter et al. 1985). This is because they are freely interacting with each other and their phenotypic variation is expected to be high. The other reason for using microbial networks as a model ecosystem is that temporal variation has recently been described and studied for this ecosystem (Huisman and Weissing 2001). As described below, an ecosystem model with bi-directional mutation among “species” is developed. Species are treated as phenotypic variations or indirect dispersal effects behind the model ecosystem. First, the model equation is introduced. In the following sections, the evidence of keystone species, the notion of neutral species and the synergetic effect of keystone species is shown. Lastly, the same model equation, but with no mutation terms, was studied.

Replicator dynamics with mutation terms

The time-based evolution of phenotypes of species was simulated by a 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 recently been reported (Chawanya 1995, 1996), where the unexpectedly rich behavior of this equation has been revealed. For example, a strange hierarchy of attractors has been noted, 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 dysfunctional biological behavior into the system. For example, the relative abundance of a phenotype decreasing to the order of e^{-100} is thought to be unrealistic. A solution 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 a result, the model avoids the heteroclinic instability inherent in the original system (Tokita and Yasutomi 1999). The system presents some universal phenomena, however by compensation, it loses aspects of its rich dynamics.

In this paper the effect of mutation processes were studied in the original replicator system. It was assumed that the mutation process accounts for the phenotypic and genetic variation observed in microbial communities. It is known that soil or aquatic microbes have considerable variation (Demezas et al. 1995). Such variation is proposed to determine the functioning and stability of terrestrial ecosystems (see, e.g. Grayston et al. 2001). In the last section of this paper, population diversity was examined by introducing new phenotypes

from outside the system. But we mainly focus on the internal mechanism of mutation processes. In the first three sections, the diversity of intraspecific variations was studied by introducing bi-directional mutation process among different phenotypes. However, the mutation term is also interpreted as a dispersal term for each phenotype. It becomes an emigration term when its frequency (x_i) is less than the average frequency ($1/N \sum x_k$). Otherwise, it becomes an immigration term. A more practical advantage is that the mutation process naturally gives a lower boundary to each amount of phenotype, so that unrealistic behavior can be avoided (Ikegami and Yoshikawa 1995; Hashimoto and Ikegami 2001). The present simulation studies the effect of keystone species by removing target species from the system. However, without the mutation term, this results in a monotonic decrease in the number of species, which is an unrealistic assumption.

Considering these perspectives, the replicator dynamics of the model were studied by including the mutation processes.

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

where $\sum x_i = 1$ and the total number of variables is given by N . Throughout this paper $N=100$.

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. It was assumed that every phenotype was produced at the same rate. This second term was then rewritten as $\mu N/(N-1)(1/N - x_i)$ i.e., a conditional dispersal (source) term of the first order (x_i) as described above.

The controlling parameters of this system are the structure of the interaction matrix $\{ a_{ij} \}$ and the mutation coefficient μ . a_{ij} was randomly generated from $(-2.5, 2.5)$. The number and kinds of attractors was highly dependent on the matrix and the mutation rate. In total, there are basically $N^2 + 1$ independent parameters. Throughout the paper, an example of the interaction matrix that was studied has keystone species as described below. In total, there are basically $N^2 + 1$ independent parameters. The initial distribution of the phenotypes also determined the reachable attractors.

Kinds of attractors and hierarchy of phenotypes

The behavior of the equation is characterized by the long-term temporal structure of the phenotypes, i.e. kinds of attractors. An attractor with no time-dependent behavior, is called a fixed-point attractor. The other attractors have time-dependent behaviors with different

stabilities. In particular, some attractors show chaotic instabilities showing aperiodic temporal variation of population frequencies. Such chaotic attractors in ecosystems have been studied both theoretically [see, e.g. Kaneko and Ikegami 1992; Ikegami and Kaneko 1992] and a review of lynx dynamics by Gamarra and Sole (2000)] and experimentally (see, e.g. Dennis et al. 2001; Turchin and Ellner 2000).

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. Attention was paid to the hierarchical organization of the phenotypes that constituted each attractor.

The results show that for most attractors, the relative frequency of each phenotype changed from the lowest order (limited by the mutation effect) to the order of unity, except for fixed-point states. Generally no single phenotype completely dominated the population, as it was immediately out-competed by the others, except for the fixed-point cases. A kind of attractor has been automatically detected by computing the first Lyapunov exponent (λ) and the time-averaged momentum ($\sum_i x_i^2$) (See Fig. 1).

Several time-dependent attractors were found to have a clear hierarchical or food web structure. Several phenotypes eventually dominated the population in some chaotic attractors. Such an attractor can be observed by carefully tuning the interaction matrix with a mutation rate, and an initial state of the population. This matrix also enables several quasi-periodic/periodic attractors and fixed-point ones with different phenotype compositions.

The interaction matrix was searched under the condition where $\mu=0.0125$ and each matrix element was assigned a random number from $(-2.5, +2.5)$. It was difficult to find a matrix structure that had time-dependent attractors with clear separation between dominant and recessive phenotypes. Through this paper, we focus

on the rare interaction matrix that has this characteristic.

Note that dominant phenotypes have relatively larger abundances compared with the other phenotypes. A classification of phenotypes is quantitatively defined in the next section.

Classification of phenotypes

The dynamics of each phenotype were governed by Eq. 1. However, by analyzing its functional role, each phenotype was classified into one of three categories; dominant, recessive and others. The dominant group exploits others and becomes the main source of variants. Conversely, the recessive ones are only exploited by the dominants. They are also produced via dominants through mutation processes. Besides the dominant and recessive ones, there are sometimes unclassifiable phenotypes. These change their functional role temporally and can be both dominant and recessive.

The right-hand side of Eq. 1 was initially decomposed into two parts, the reproduction term (the first and second terms) and the mutation term (the last two terms). By computing the time-based average of the reproduction term, a net reproduction rate was obtained as;

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

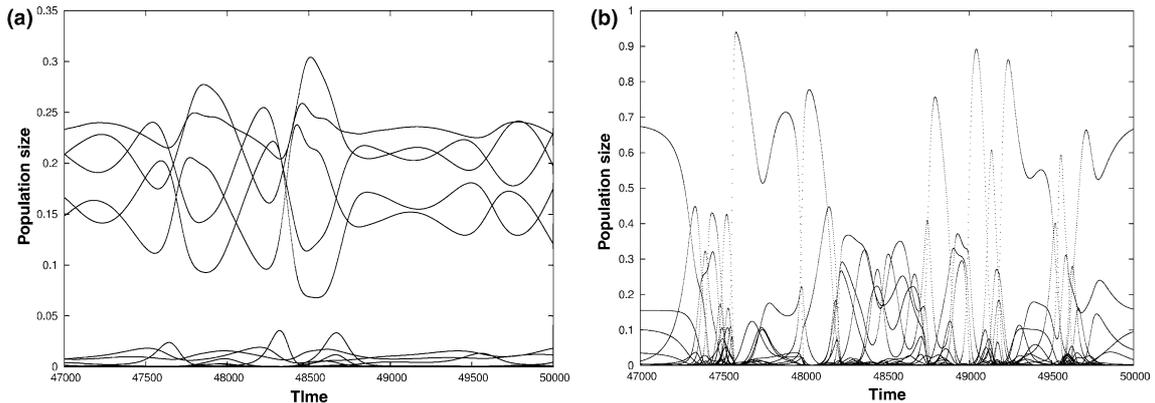
$$R_i(T) = \lim_{T \rightarrow \infty} \frac{1}{T} r_i(T) \quad (3)$$

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

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

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

Fig. 1 Two kinds of attractors are depicted by the time evolution of all phenotypes. They are chaotic (*left*) and quasi-periodic (*right*). The chaotic attractor has its Lyapunov exponent (λ)=0.000853 and the time-averaged sum of second momentum ($\sum_i x_i^2$)=0.193, whereas the quasi-periodic attractor has $\lambda=0.0$ and $\sum_i x_i^2=0.376$



$$= \frac{\mu N}{N-1} \left(\frac{1}{N} - \langle x_i \rangle \right) \quad (6)$$

gave a genetic flow from the other phenotypes. In particular, the last form of M_i denotes that the quantifier is proportional to the time-average of the abundance $\langle x_i \rangle$. On the long-term average, R_i becomes equal to $-M_i$, if the average is taken within an attractor. That is because by definition the time average of each $d x_i / d t$ converges to a zero value. Since $R_i + M_i = 0$ should hold, the absolute value of R_i is defined as A_i .

Using the quantifiers (R_i , M_i), phenotypes were classified into dominant (+, -), recessive (-, +) and neutral groups (ϵ , ϵ), where $\epsilon < 1$ is a small value.

This classification was sufficient for classifying the attractors with the dominant phenotypes. But the population size can vary strongly for other attractors. As for the other quantifier, the alternating rate was adopted between the positive and negative values of the derivatives, \dot{r}_i or \dot{m}_i . Practically, the number of the sign alternation (B_i) was defined as,

$$B_i = \lim_{T \rightarrow \infty} \frac{1}{T} \int_{\tau}^{\tau+T} dt \Theta(\dot{r}_i(t)) - \Theta(\dot{m}_i(t)) \quad (7)$$

where $\Theta(x) = 1$ ($x > 0$) and 0 (*otherwise*). This is also given as a time-averaged quantity.

Strong dominant phenotypes tended to have large B_i values, and in particular, ever-dominating phenotypes have exactly $B_i = 1$. On the other hand, recessive phenotypes had negative B_i values. Completely dominated phenotypes had $B_i = -1$. Phenotypes that changed their

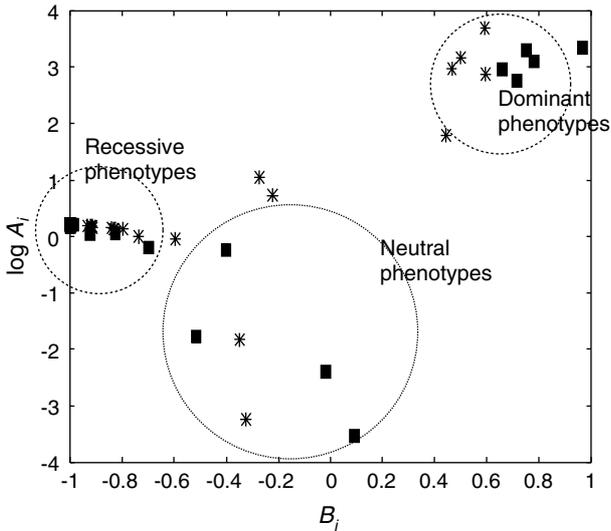


Fig. 2 A characteristic measure of B_i , $\ln(A_i)$, averaged over 10,000 time generations, was computed for each phenotype. The squares correspond to the chaotic attractor and the asterisks to a quasi-periodic one. Most points of recessive phenotypes degenerated at the same point as shown in the figure

functional role temporally had $B_i = 0$ as the ultimate case.

Using A_i and B_i , the characteristics of each phenotype was plotted on the A–B plane in Fig. 2. In the chaotic attractor, dominant phenotypes exist close to the $B_i = 1$ and larger A_i values. Recessive phenotypes were found at $B_i = -1$ with smaller A_i values. The neutral phenotypes were found around $B_i = 0$ with much smaller A_i values. A set of phenotypes that constitutes a quasi-periodic attractor also showed a similar classification as depicted in Fig. 2. Therefore, it can be seen that this classification, due to the quantifiers, makes sense.

What is important 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, even when in spite of their relative small frequencies are small. This aspect fits the definition of a keystone species by Power et al. (1996). In the following sections, it will be shown that neutral phenotypes, such as keystone species, have dynamic natures and so the neutral phenotypes themselves form a sub-network.

Keystone species as a network of neutral phenotypes

Keystone phenotypes usually become apparent when their removal or disappearance from a particular ecosystem causes a significant change in it. For the present system, the significant effects are defined by the transition of attractors. If the removal of a non-dominant phenotype causes transitions of the attractor, the phenotype was called a keystone species. If this is so, the relative abundance of any given phenotypes does not simply correspond to its significance for the stability of the attractor. This means that attention must be paid to the roles of these minor phenotypes, which cannot dominate the system, but nevertheless control its entire

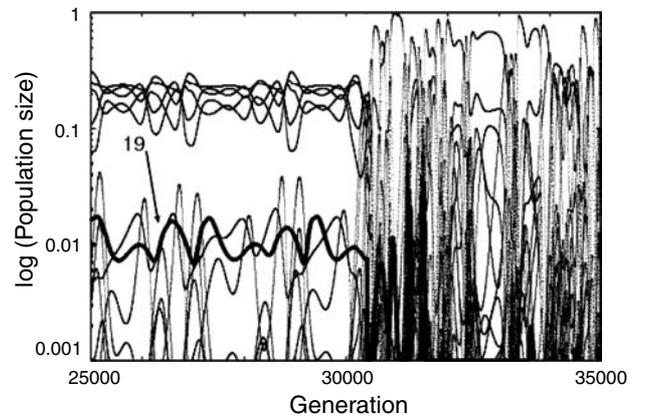


Fig. 3 A time-based evolution of population in a log-scale, plotted against generation steps. Every phenotype is superimposed. When phenotype #19 (with a wider line) was removed at generation 30,000, the entire structure abruptly collapsed and switched to a quasi-periodic attractor

stability. Phenotypes were specifically selected and removed from the population. Practically, a phenotype was removed by turning the population size to a zero value at a given time step. The rest of the population sizes were renormalized at the same time.

The results show that removing dominant phenotypes produced a large effect on the system and that removing recessive phenotypes did not have any effect. Interestingly, the impact of each phenotype on attractor switching was correlated with its neutrality (i.e., the smallness of A_i or B_i distributed around a zero value). Since there is a production term via other phenotypes, removed phenotypes will never be extinguished. However, the attractor itself may change after some transient period. The relative abundance of the neutral phenotypes of the chaotic attractor was low, but the impact was far larger than expected (Fig. 3). In this example, a neutral phenotype with the second smallest R_i value (phenotype 19) was removed from the system.

While Paine's original (1966) and other keystone concepts are still limited to a single phenotype, the combined effects of keystone species, i.e. of neutral phenotypes, were studied with small A_i values. In this case, phenotypes with smaller A_i values had smaller absolute B_i values. Simultaneous removal of several neutral phenotypes combined to cause an attractor-switching event as in Fig. 4. The seven phenotypes with the lowest A_i values were selected and all 127 patterns of combinatorial removal of those phenotypes were tested. By putting the seven neutral phenotypes in order, a binary representation of the removed set of phenotypes was produced. This was done by setting

$$y_a(t) = (\Theta(x_{13}(t)), \Theta(x_{15}(t)), \Theta(x_{16}(t)), \Theta(x_{19}(t)), \Theta(x_{64}(t)), \Theta(x_{76}(t)), \Theta(x_{87}(t))), \quad (8)$$

where the subscript a runs from 0 to 127 and the string, $y_{42}(t) = [0101010]$ is read as a removal of phenotypes 13, 16, 64 and 87 with keeping 15, 19 and 76. Figure 4 shows that phenotypes 19, 76 and 87 were the three most effective ones that constitute the keystone network in the attractor. As can be seen in Fig. 4, there were approximately four recovery patterns and phenotype 19 was the most efficient. But the entire effect of phenotype 19 was affected by phenotypes 87 and 76. For example, the recovery rate of (###0#10) and (###0#01) was very different from those of (###0#00) and (###0#11). Therefore, whether phenotype 19 can function as a keystone species is also a function of those phenotypes. Therefore, it is proposed that these three phenotypes form a keystone network.

From Fig. 2 we know that 76 and 19 are phenotypes with the two smallest A_i values and phenotypes 87 and 13 are the next strongest neutral phenotypes. However, the removal of a single phenotype 76 did not cause any destruction; only when this was coupled with phenotype 19 did it cause a drastic change. It appears that the simultaneous removal of the other phenotypes often weakened the cooperative actions of phenotypes 19 and 76. It should also be noted that when the neutrality was weakened, the contribution to the system stability was also weakened. This is implied by the fact that the less neutral phenotypes such as 13, 15, 16, 64 and 87 were less effective as keystone species.

This kind of combinatorial effect implies the existence of a network of neutral phenotypes. Since dominant phenotypes are mostly mutually cooperative, having large A values, they are insensitive to small population changes. The recessive phenotypes with negative R values are also insensitive to small population changes. Only neutral phenotypes are sensitive to small changes. A subtle dynamic balance exists in networks of neutral phenotypes. It is hypothesized that the removal of a neutral phenotype release other neutral phenotypes faster than other dominant or recessive ones. Figure 5 shows how a single neutral phenotype causes a cascading impact on the whole system after a certain time lag.

A phenotype can work as a keystone without being fully removed. For example, the effective phenotype 19 caused the attractor to collapse, even following a 50% decrease in its population size. However, how much has to be removed to cause the attractor to collapse is highly dependent on the timing. The composition of the other phenotypes determines the critical size.

If a pair of neutral phenotypes are only partially removed, it is possible to see the cooperative effect in detail. Figure 6 depicts how the critical boundary is determined as a function of both removed amount of phenotypes. There are several important observations from this experiment. That is, a new attractor becomes accessible by a partial removal. The regions close to a

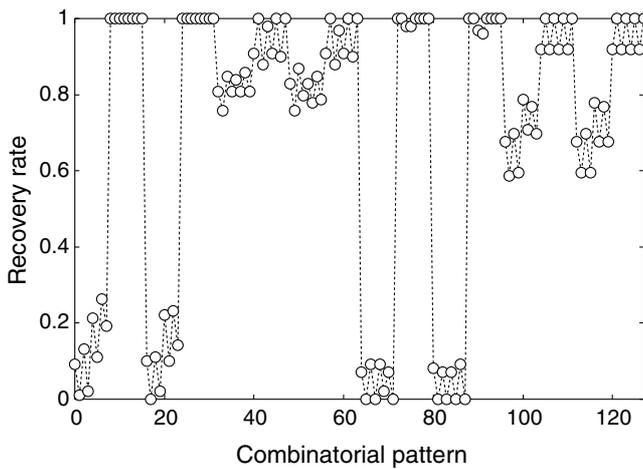
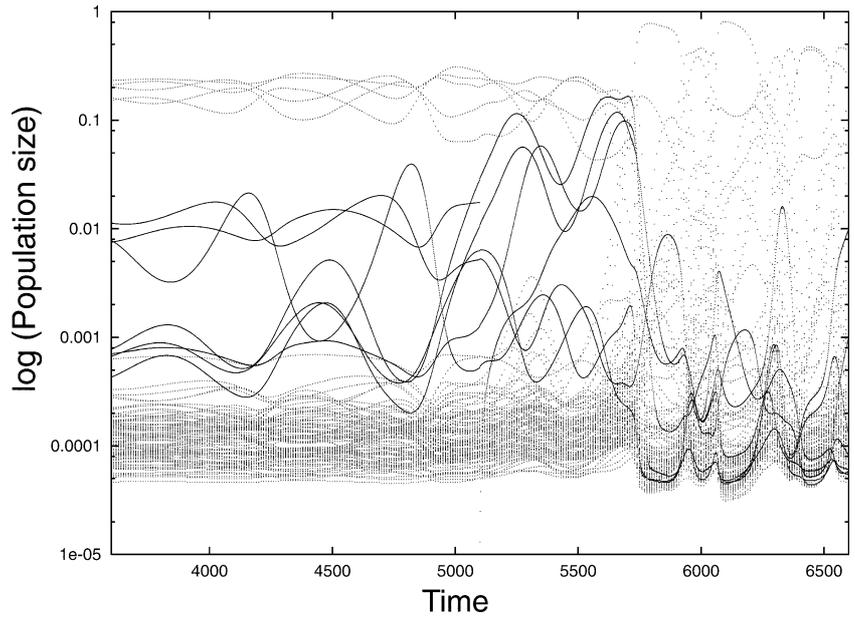


Fig. 4 The combinatorial pattern is decimally encoded on the horizontal line. One-hundred events were examined for each combination and the recovery rate has been averaged. The recovery rate became zero when the chaotic attractor never recovered. In the figure, the four most unstable regions are labeled with the associated binary string, (###0#00), (###0#10), (###0#01) and (###0#11), where # denotes either 0 or 1. Here the effective neutral phenotypes are #19, #76 and #87

Fig. 5 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 neutral phenotype 19 was removed at time step 5200, the other neutral phenotypes increased their abundance and reached the order of the dominant phenotypes at around step 5700. Then a drastic change occurred, and the attractor switched



full removal almost always drive a system to the same attractor that is reached following a complete removal. However, the partial removal allows new attractors. Those new attractors (either quasi-periodic or fixed points) are found around the boundary of the partial removals in Fig. 6.

Indeed, the effect of the prime keystone 19 was sensitive to the frequency of 76. Figure 7 depicts two cases;

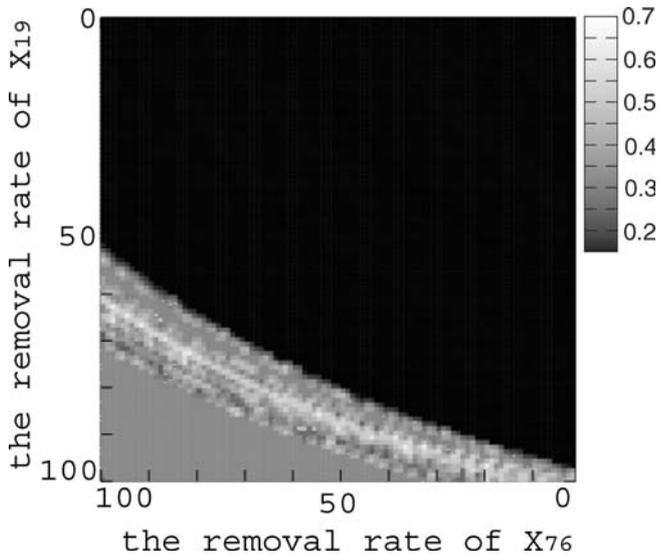


Fig. 6 Removing phenotypes from the system when it is in the chaotic attractor leads to transitions between attractors. Here, we plot the effect of partially removing two phenotypes at the same time. The x, y coordinates give, respectively, the amount of phenotypes x_{76} and x_{19} removed while the color of a point shows the attractor reached shortly after the removal takes place. The *right upper corner* corresponds to the original chaotic attractor and the *lower left corner* corresponds to a quasi-periodic attractor. At the boundary region, there exist several attractors, including fixed points

removing a phenotype 19 with 50% of its frequency, the effect in the case of removing a phenotype 76 with 60% and that of 50% was studied. In the former case, the attractor collapsed, but in the latter case, it was sustained. Therefore, a small difference in the second keystone species determined the keystone functional. The conclusion here is that the role of keystone species must be studied in terms of the sub-network of keystone species. The interesting aspect of the combinatorial effect of keystone species may reflect a complex and high-dimensional basin boundary, which has also been reported by Huisman and Weissing (2001).

Keystone phenotypes with no mutation terms

Instead of introducing mutation terms, it is worthwhile searching for the keystone phenomena in the original replicator equation with the extinction threshold. The evolution of keystone species in the open-environment is also briefly reported.

The behavior of the original equation was studied by putting $\mu=0$ in Eq. 1, but taking $a_{ii}=-1$ for all i in the interaction matrix. Each phenotype is interacting with the other phenotypes with a probability C , which is called the connectance of the network. In this model, $C=0.1$ was chosen to have a clear effect of keystone species. In particular, to increase the diversity of the system, suppressing the connectance at the lower value is crucial (Iwata 2003). By randomly generating the off-diagonal elements of the interaction matrix with a normal distribution $N(0, 1)$ but with $C=0.1$, a system was found with a keystone species in the above sense. For simplicity, a fixed-point attractor was studied. Since this equation has no mutation term and the attractor is a fixed point, every $A_i (=R_i)$ and B_i value of the phenotypes became 0. In order to avoid heteroclinic instability,

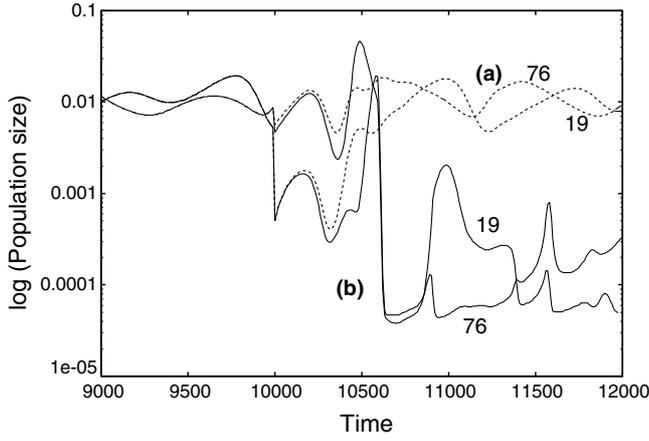
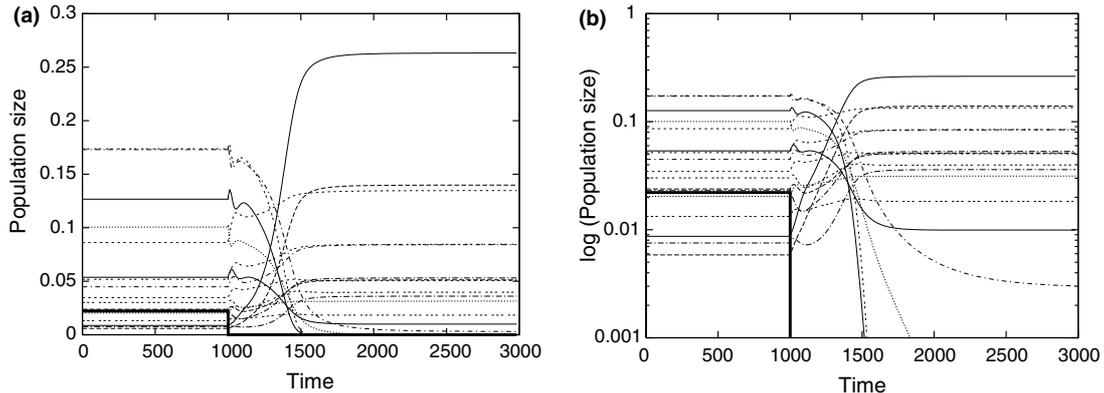


Fig. 7 The time evolution of population size of phenotypes 19 and 76 is depicted in the two partial removal cases of **a** and **b**. Ninety percent of phenotype 19 was removed along with 50% of phenotype 76 for case **a**, and 60% of phenotype 76 for case **b** at 10,000 time steps. The amplitude of the perturbation between **a** and **b** is small, but the outcome is different. In **a**, it returned to the same attractor, but in **b**, it jumped onto a new attractor. This case is a quasi-periodic attractor

the extinction boundary (σ) was introduced to the population size. Species whose population size was lower than the threshold were removed from the system. Once a phenotype was removed, there was no chance for it to come back.

An initial example is the removal of single phenotype. In this example, removal of a single phenotype releases two lower population value phenotypes (see Fig. 8). When the populations become similar in size to the other phenotypes, the system showed a drastic change. Therefore, the potential keystone species may comprise a network as has been discussed in the preceding sections (See Fig. 5).

Fig. 8 The removal of a single phenotype at time 1,000 will release a pair of far less abundant phenotypes. They exponentially increase in size, and when they reach a certain level, a drastic change occurs. Since any given population size is not bound by the mutation flow, this effectively demonstrates how extinction affects the system. Normal scale (**a**) and logarithmic scale (**b**). The extinction boundary δ was given at $1e-8$. Here the time step unit here is ten steps



Secondly, the functional role of keystones was described in an open evolutionary context. For this purpose, new phenotypes were added into the replicator system to observe the evolution of keystone species (Iwata 2003). In each generation, the system was added a new phenotypes after the system was settled down to an attractor. The interaction matrix element of the inserted phenotype was randomly assigned with $N(0, 1)$ and the initial population size was set at $\delta=1e-7$. The extinction boundary (σ) was given at $1e-8$. The connectance C was set at 0.1 as in the first experiment. Figure 9 shows an example of how the total number of phenotypes varied in time and where the potential keystone species appeared. However, it should be noted that the meaning of “time” is different from the previous examples, where the time steps exactly correspond to the time steps of Eq. 1. On the other hand, time step merely implies a successive event of introducing mutants after the system mostly settles down to an attractor in Fig. 9.

The effect of potential keystone species was examined by removing it from the system. As for the measure of keystone species, the net difference of phenotype composition was computed before and after the removal of a phenotype. Practically, the impact on the entire network was measured by the quantity;

$$\sqrt{\sum_{i=1}^{i=N} (x_i^{\text{before}} - x_i^{\text{after}})^2}.$$

If the difference was larger than 50% of that given by the dominant phenotypes, and the population size of the removed phenotypes was lower than 25% of the most dominant phenotypes, it was defined as a keystone species. As shown in the previous section, the effect of keystone species was basically a network function. Therefore, the measure is a tentative one.

The results show that keystone species appeared in 66 systems out of 1,000 trials. Four systems had 3 keystone species, 17 systems had 2 keystone species, and 57 systems had 1 keystone species. The keystone species also emerged around the critical size of the system, at which a mass extinction occurs. In other words, the emergence of the keystone species triggered the mass extinction. The result may not be surprising, but it adds a new mechanism of mass extinction. A spontaneous mass ex-

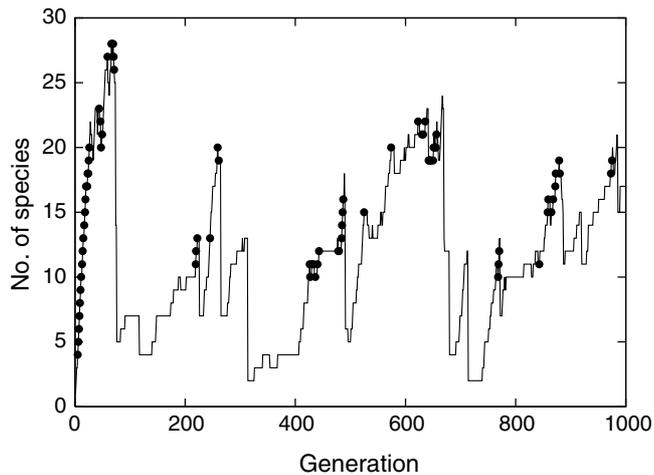


Fig. 9 Evolution of diversity (line) and the existence of keystone species (circle). At each generation, every single phenotype is removed to test the impact after 10,000 time steps, where the system has settled down to an attractor

tion requires a keystone species, which is given as a natural cause of evolutionary dynamics.

Discussion

In conclusion, it has been shown that the removal of some phenotypes caused a subtle perturbation of the system, but the results can be large compared with its perturbation amplitude. The candidates of such phenotypes are neutral in the sense that they are neither predator nor prey. They are neutrally wandering in an ecosystem network. In this sense, the attractor switch by neutral types produces a non-trivial mechanism, related to the notion of keystone species.

Furthermore, it has been shown that there is a net effect of several neutral phenotypes. The net effect was affected by the pattern of removed phenotypes, which is named a combinatorial effect. The existence of such a combinatorial effect implies that neutral phenotypes formed a sub-network, in which neutral phenotypes mutually suppressed each other. This view may be generic, as the original replicator system also showed the same kind of behavior.

Finally, it is important to discuss the emergence of keystone species in an evolutionary context. As has been briefly discussed, keystone species tend to appear at the critical stage of an ecosystem. If some neutral phenotypes, acting as keystone species can work as genes or parameters, this should be evolutionarily favorable, 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 resetting 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. Also, if keystone species form a network, a fine-tuning of the directions of the attractor switching can be expected. The point here is that the switching mechanism 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. The relationship between a keystone species and the concept of evolvability will be reported elsewhere.

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References

- Barabasi A (2002) LINKED: the new science of networks. Perseus, Cambridge
- Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. *BioScience* 35:634–639
- Chawanya T (1995) A new type of irregular motion in a class of game dynamics systems. *Prog Theor Phys* 163:163–179
- Chawanya T (1996) Infinitely many attractors in game dynamics system. *Prog Theor Phys* 679:679–684
- Demezas DH, Reardon TB, Gibson AH, Watson JM (1995) Diversity and genetic relationships among a natural population of *Rhizobium leguminosarum* bv. *trifolii* isolated from *Trifolium subterraneum* L. *Mol Ecol* 4:209–220
- Dennis B, Desharnais RA, Cushing JM, Henson SM, Costantino RF (2001) Estimating chaos and complete dynamics in an insect population. *Ecol Monogr* 71:277–303
- Gamarra HGP, Sole RV (2000) Bifurcations and chaos in ecology: lynx returns revisited. *Ecol Lett* 3:114–121
- Grayston SJ, Griffith GS, Mawdsley JL, Campbell CD and Bardgett RD (2001) Accounting for variability in soil microbial communities of temperate upland grassland ecosystems. *Soil Biol Biochem* 33:533–551
- Hashimoto K, Ikegami T (2001) Heteroclinic Chaos, Chaotic itinerancy and neutral attractors in symmetrical replicator equations with mutations. *J Phys Soc Jpn* 70:349–352
- Hofbauer J (1981) On the occurrence of limit cycles in the Volterra-Lotka equation. *Nonlin Anal* 5:1003–1007
- Huisman J, Weissing FJ (2001) Fundamental unpredictability in multispecies competition. *Am Nat* 157:488–494
- Ikegami T, Hashimoto K (2002) Dynamical systems approach to higher-level heritability. *J Biol Phys* 28:799–804
- Ikegami T, Kaneko K (1992) Evolution of host-parasitoid network through homeochaotic dynamics. *Chaos* 2:397–408
- Ikegami T, Yoshikawa E (1995) Chaos and evolution of cooperative behavior in a host-parasite game. In: Yamaguchi M (ed) Towards the harnessing of chaos, vol 63. Springer, Tokyo, pp 63–72
- Ikegami T, Iwata T, Hashimoto K (2003) A network of dynamic keystone species. In: Standish RK, Bedau MA, Abbass HA (eds) Artificial life. VIII. MIT, Cambridge, pp 216–222
- Iwata T (2003) Measuring keystone species. Master Thesis, University of Tokyo, Department of general systems studies
- Kaneko K, Ikegami T (1992) Homeochaos: dynamics stability of a symbiotic network with population dynamics and evolving mutation rates. *Physica* 56D:406–429
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65–75

- Payton IJ, Fenner M, Lee WG (2002) Keystone species: the concept and its relevance for conservation management in New Zealand. Department of Conservation, Wellington, New Zealand
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *BioScience* 46:609–620
- Smith JM (1982) *Evolution and the theory of games*. Cambridge University Press, Cambridge
- Swenson W, Wilson DS, Elias R (2000) Artificial ecosystem selection. *Proc Natl Acad Sci USA* 97:9110–9114
- Tokita K, Yasutomi A (1999) Mass extinction in a dynamical system of evolution with variable dimension. *Phys Rev* 60:682–687
- Turchin P, Ellner SP (2000) Living on the edge of chaos: population dynamics of Fennoscandian voles. *Ecology* 81:3099–3116
- Willson MF, Halupka KC (1995) Anadromous fish as keystone species in vertebrate communities. *Conserv Biol* 9:489–497
- Yokoyama K (2000) Presented at the Mathematical Biology Meeting (Hamamatsu, October 2000)