Evolutionary Ecology Research, 2006, **8**: 629–642

The role of rare species in the community stability of a model ecosystem

Jin Yoshimura,[1,2,3]* Kei-ichi Tainaka,[1] Takanori Suzuki,[1] Yukio Sakisaka,[2]
Nariyuki Nakagiri,[1,4] Tatsuya Togashi[2] and Tatsuo Miyazaki[2]

[1]*Department of Systems Engineering, Faculty of Engineering, Shizuoka University, Hamamatsu 432-8561, Japan,* [2]*Marine Biosystems Research Center, Chiba University, Uchiura, Kamogawa, Chiba 299-5502, Japan,* [3]*Department of Environmental and Forest Biology, State University of New York, Syracuse, NY 13210, USA and* [4]*School of Human Science and Environment, University of Hyogo, Himeji 670-0092, Japan*

ABSTRACT

Question: Is a rare or low-density species important for the balance of an ecosystem?

Features of the model: Perturbation experiments on a model lattice with two common species and one low-density species.

Key variables: The low-density species is preyed upon by one of the common species, but it eats the other common species. Meanwhile, the latter common species is eaten by the first common species. Thus the relationship between the three species is cyclic, corresponding to the 'rock–paper–scissors' game. Control experiments include only two common species. Perturbation is introduced by decreasing the rate of reproduction of one of the common species.

Simulation results: The outcome of perturbations depends strongly on both the low-density species and the perturbation strengths. The responses to perturbation are often paradoxical and different from those expected from the mean-field or global version of the lattice model.

Conclusions: The presence of a low-density species can alter the balance of an ecosystem. The conservation biology and management practice of natural ecosystems may be hindered if less common, unattractive species are ignored.

Keywords: community structure, lattice ecosystems, low-density species, perturbation.

INTRODUCTION

Most natural ecosystems contain a few species that are common and many species that are less common (Andrewartha and Birch, 1954; Elton, 1966; MacArthur and Wilson, 1967; Rosenzweig, 1995; Myers *et al.*, 2000; Magurran and Henderson, 2003). In the conservation of natural ecosystems, however, we often ignore less common (or rare) species unless they are the target species (Soulé, 1986; Gaston, 1994). When an ecosystem is disturbed by some external factor such as climate change or

---

* Author to whom all correspondence should be addressed. e-mail: jin@sys.eng.shizuoka.ac.jp

human habitat destruction, it may undergo a marked change in community structure (Pimm, 1991). The common species are often thought to be the critical element affecting the outcome of such environmental disturbances (Pickett and White, 1985; Stiling, 1999). However, less common species may be equally influential, for example keystone species (Paine, 1966; Lawton and Brown, 1993). With the introduction of a low-density species, the food-web balance of the ecosystem could become qualitatively different. Here, we show that an ecological response to an applied perturbation is drastically altered by the presence of a low-density species.

As a result of human management, ecosystems often become stressed or perturbed. The investigation of such perturbations is important for forecasting the effects of human management and for understanding community interactions (Paine, 1966; May, 1973; Tilman and Downing, 1994). The most familiar perturbation is the 'press' perturbation: one or more quantities are increased or decreased. An example of press perturbation is enrichment. In the upper part of Fig. 1, the rate of reproduction of a target species is suddenly increased at some point in time. Immediately after the perturbation, the population size of the target species is increased. Later, however, its population size decreases. This unexpected response of enrichment is called the 'paradox of enrichment', after Rosenzweig (1971), who presented the first model of this paradox. However, the mechanisms underlying his model are rather complicated; a much simpler lattice version of the paradox of enrichment is proposed by Tainaka (1994). Press perturbation is a useful tool to assess the stability of model ecosystems.

It is well known that the reaction of an ecosystem to a perturbation consists of both short- and long-term responses (Bender, 1984). The short-term 'direct' response flows directly from the cause. In contrast, the long-term 'indirect' response is more difficult to predict (Yodzis, 1988; Pimm, 1991; Schmitz, 1997).

The study of indirect effects is growing exponentially (Krivtsov, 2001; Nakagiri *et al.*, 2001; DeWitt and Langerhans, 2003; Itoh and Tainaka, 2004; Nakagiri and Tainaka, 2004). Some methods, such as network analysis, have been used to quantify indirect effects (Abarca-Arenas and Ulanowicz, 2002). In many ecological studies, indirect effects arise by linking two or more direct effects via a species involved in both interactions (Wootton, 1993).

Here, we explore the role of a low-density species in a model lattice ecosystem in introducing a perturbation that affects a common species. The initial lattice ecosystem

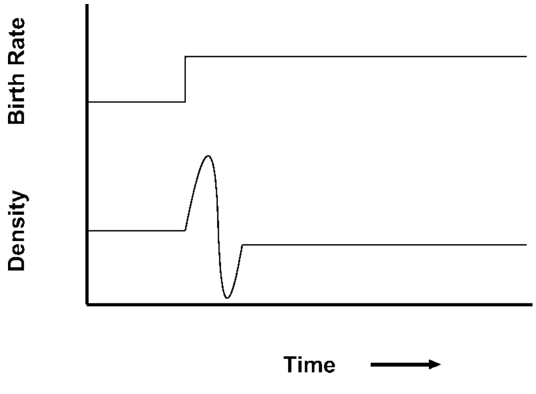


Fig. 1. Schematic representation of the perturbation experiment. (Upper trace) At some moment the rate of reproduction of a target species is suddenly increased. (Lower trace) The response of the target species. Despite the increase in birth rate, the density of the species decreases (the paradox of enrichment).

consists of prey, predator and vacant site (plant) (Tainaka, 1994). We introduce a third, low-density species that is preyed upon by the common prey but which preys on the common predator, resulting in indirect effects between the three species. The relationship between the three species is cyclic, corresponding to the 'rock–paper–scissors' game (Itoh, 1973; Tainaka, 1988).

We chose the 'rock–paper–scissors' game as a model ecosystem for two reasons. First, the model makes for a simple ecosystem. A more complicated model would have made analysis of the results more difficult. The second reason is the relationship between the network structure and stability of the ecosystem. Were we to introduce a rare species that interacts with only one other species in the ecosystem (a species at a terminal node), it might be completely unimportant. A good candidate (in terms of its effect on the stability of community dynamics) would be a species with interactions (connections) with many other species. Such connections might well affect the stability of the whole ecosystem. This led us to choose a rare species with many nodes. The simplest ecosystem with a rare species should contain at least three species, and the most connections achieved by the rare species will be those with the other two species. Thus a three-species network is the best network for the model ecosystem. We also require a model ecosystem that is initially stable. The 'rock–paper–scissors' lattice game does have cyclic stability (Tainaka, 1988). Recent studies of lattice ecosystems imply that real ecosystems may attain stability through a combination of many cyclic networks or relationships (Tainaka, 1994; Schmitz, 1997; Sakata and Tainaka, 2001). Thus we believe that the 'rock–paper–scissors' game can be used as a canonical model of ecosystems.

To assess the effects of the low-density species, perturbation experiments are performed. We decrease the rate of reproduction of one common species to compare the eventual community structures with and without the low-density species. We also vary the perturbation strength and compare the outcomes. The mean-field version of the lattice model is also analysed. Based on the complex results, we discuss the role of a less common species in natural communities and its implications for conservation practice.

THE MODELS

We consider two ecosystems, I and II. Ecosystem I consists of two species, prey X and predator Y (Tainaka, 1994). In ecosystem II, a third species, Z, is introduced. If species Z goes extinct, ecosystem II will then be equivalent to ecosystem I. Let us first explain ecosystem I:

$$\mathrm{X} + \mathrm{Y} \rightarrow 2\mathrm{Y} \text{ (rate: 1)} \tag{1a}$$

$$\mathrm{X} + \mathrm{O} \rightarrow 2\mathrm{X} \text{ (rate: } r_1\text{)} \tag{1b}$$

$$\mathrm{Y} + \mathrm{O} \rightarrow 2\mathrm{Y} \text{ (rate: } r_2\text{)} \tag{1c}$$

$$\mathrm{X} \rightarrow \mathrm{O} \text{ (rate: } d_1\text{)} \tag{1d}$$

$$\mathrm{Y} \rightarrow \mathrm{O} \text{ (rate: } d_2\text{)} \tag{1e}$$

where O represents an empty site. Interaction (1a) means the predation of Y; species Y produces its offspring by eating X. Interactions (1b) and (1c) denote reproduction of species X and Y respectively, while (1d) and (1e) are the death processes.

In contrast, ecosystem II contains several interactions in addition to (1a)–(1e):

$$\mathrm{Y} + \mathrm{Z} \rightarrow 2\mathrm{Z}\ (\text{rate: } 1) \tag{2a}$$

$$\mathrm{Z} + \mathrm{X} \rightarrow 2\mathrm{X}\ (\text{rate: } 1) \tag{2b}$$

$$\mathrm{Z} + \mathrm{O} \rightarrow 2\mathrm{Z}\ (\text{rate: } r_3) \tag{2c}$$

$$\mathrm{Z} \rightarrow \mathrm{O}\ (\text{rate: } d_3) \tag{2d}$$

where interactions (2a) and (2b) represent predation, and interactions (2c) and (2d) are the rate of reproduction and death process of species Z respectively. In our analyses, the steady-state density of Z was kept the lowest of the three species. We achieved this by adjusting the growth/death parameters not only of Z, but also of X and Y in the ecosystem (Fig. 2).

Schematic representations of our ecosystems are shown in Fig. 2, where (a) and (b) represent ecosystems I and II respectively. Ecosystem II tacitly contains the cyclic strength of the 'rock–paper–scissors' game (or 'paper–scissors–stone' game) (Itoh, 1973; Tainaka, 1988). Species X eats species Z but is eaten by species Y. In contrast, the scarce, introduced species Z eats Y. The relationships in the 'paper–scissors–stone' game symbolically represent ecological balance. A concrete example of this relationship is that of side-blotched lizards (Sinervo and Lively, 1996). There are three morpho-species of males distinguished by the colour of their throat: orange, blue and yellow. Orange-throated males dominate blue-throated males, blue-throated males dominate yellow-throated males, and yellow-throated males, which resemble females in morphology, dominate orange-throated males. The relationships among the males are represented by the 'paper–scissors–stone' game.

Another example of the 'paper–scissors–stone' game is the microbiological community reported by Kerr *et al.* (2002). Their system comprises three kinds of *Escherichia coli*: colicin-producing (C), colicin-sensitive (S) and resistant (R) bacteria. The colicin-sensitive bacteria are at the greatest advantage in terms of growth rate, but they are beaten by the

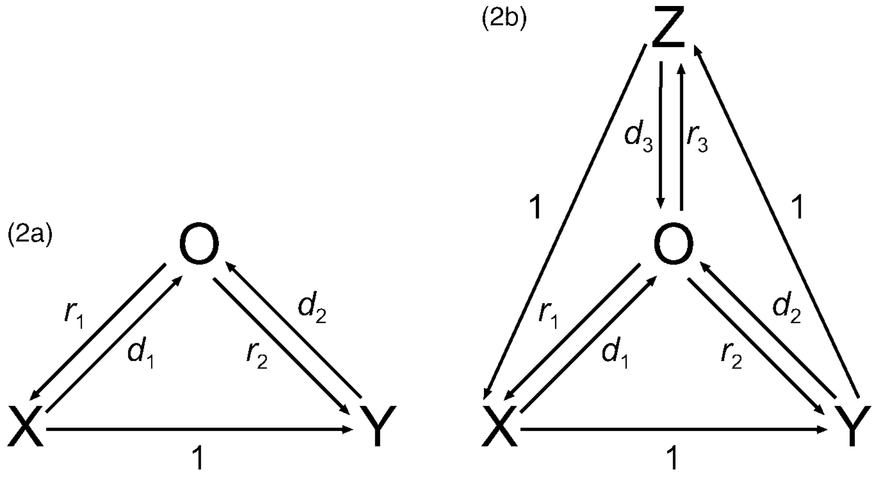


Fig. 2. The models. (a) Ecosystem I: two abundant species, X and Y. (b) Ecosystem II: a rare species Z is introduced into ecosystem I.

colicin-producing bacteria because of colicin, a toxin. Owing to the growth rate advantage, the colicin-sensitive (resistant) bacteria are stronger than the resistant (colicin-producing) bacteria. Kerr *et al.* showed experimentally that the three kinds of bacteria co-existed in the case of a local interaction but not a global (long-range) one. These results were predicted by Itoh (1973) for the global case and by Tainaka (1988) for the local one.

We apply a lattice Lotka-Volterra model (Tainaka, 1988; Nakagiri *et al.*, 2001), of which the global version is a mean-field theory called the 'Lotka-Volterra equation'. In the lattice model a local interaction between adjacent lattice sites is assumed, whereas with the mean-field simulation a global interaction occurs between any pair of lattice sites. This lattice model differs from cellular automata: in the former processing is asynchronous, whereas with the latter it is synchronous. The natural ecosystem is usually asynchronous. The results of the lattice Lotka-Volterra model differ qualitatively from those of the mean-field theories.

Our simulation model is defined as follows:

- First, we distribute individuals on a square-lattice such that each lattice site (cell) is occupied by a single individual of one of two, or one of three, species.
- Second, reaction processes are performed in two steps: (i) Perform two-body reactions [e.g. reactions (1a), (1b) and (1c)]. Select one square-lattice point at random, and then specify one of its four neighbouring sites. Let the pair react according to two-body reactions. For example, if the pair comprises X and O, then the latter becomes X at rate r_1. (ii) Perform the single-body reactions (1d) and (1e). Choose one square-lattice point at random. If the point is occupied by X, then it becomes O at rate d_1.
- Third, repeat step 2 $L \times L$ times, where $L \times L$ is the total number of square-lattice sites. Here, we set $L = 100$. This step is called the 'Monte Carlo step' (Tainaka, 1988).
- Fourth, repeat step 3 for 2500×10^4 Monte Carlo steps.

In the mean-field simulation, almost all procedures of the lattice model are unchanged. However, two-body reactions can take place between any pair of lattice sites. We also solve the mean-field prediction (Lotka-Volterra equation) analytically.

PERTURBATION EXPERIMENTS

In perturbation experiments, the rate of reproduction r_1 of species X is suddenly decreased. In the two-species ecosystem a single perturbation is applied at time $t = 1500$. Before the perturbation, we set $r_1 = 0.8$. Then the ecosystem evolves into a stationary state. After the perturbation, r_1 is suddenly decreased from 0.8 to one of four values (i.e. 0.1, 0.16, 0.24, 0.34). In contrast, in the three-species ecosystem two types of perturbation are applied sequentially. Two species, X and Y, are at the initial state ($t = 0$). The first perturbation ($t = 500$) introduces species Z: several empty sites are changed into Z. Then the ecosystem achieves a new stationary state. In this state, all three species co-exist, where Z has the lowest density. The second perturbation is applied at $t = 1500$. Before the second perturbation, we always set $r_1 = 0.8$. After the perturbation, r_1 is suddenly decreased from 0.8 to one of four values (i.e. 0.1, 0.16, 0.24, 0.34). Hence the second perturbation is the same as in the two-species ecosystem.

MEAN-FIELD THEORY

We first describe the theoretical prediction of mean-field theory. If the total number of lattice sites is sufficiently large, we can build the population dynamics (rate equation) for mean-field simulation.

Let x, y and z be the densities of species X, Y and Z respectively. In the two-species ecosystem (ecosystem I), we have the following rate equations:

$$\mathrm{d}x/\mathrm{d}t = r_1 x(1 - x - y) - d_1 x - xy \tag{3a}$$

$$\mathrm{d}y/\mathrm{d}t = r_2 y(1 - x - y) - d_2 y + xy \tag{3b}$$

where the first, second and third terms on the right-hand side of the equations correspond to the rate of reproduction, death and predation respectively, and factor $(1 - x - y)$ denotes the density of empty sites.

In the three-species ecosystem (ecosystem II), we have:

$$\mathrm{d}x/\mathrm{d}t = r_1 x(1 - x - y) - d_1 x - xy + xz \tag{4a}$$

$$\mathrm{d}y/\mathrm{d}t = r_2 y(1 - x - y) - d_2 y + xy - yz \tag{4b}$$

$$\mathrm{d}z/\mathrm{d}t = r_1 z(1 - x - y) - d_3 z - xz + yz \tag{4c}$$

Together, equations (3) and (4) are called the Lotka-Volterra model.

The steady-state solution for mean-field theory can be obtained by setting all the time derivatives in (3) to zero. The non-zero values of such densities are given by

$$0 = r_1(1 - x - y) - d_1 - y \tag{5a}$$

$$0 = r_2(1 - x - y) - d_2 + x \tag{5b}$$

for ecosystem I and by

$$0 = r_1(1 - x - y) - d_1 - y + z \tag{6a}$$

$$0 = r_2(1 - x - y) - d_2 + x - z \tag{6b}$$

$$0 = r_2(1 - x - y) - d_3 - x + y \tag{6c}$$

for ecosystem II. In Fig. 3, the steady-state densities are plotted against the rate of reproduction of species X, where Fig. 3a and Fig. 3b show the results for the two- and three-species ecosystem respectively. When the value of r_1 decreases, the density of X decreases. Moreover, we find that the density of Y (or Z) decreases (or increases) in line with the decrease in r_1.

RESULTS OF THE LATTICE MODEL

We first describe the results before the perturbation ($t < 1500$). Computer simulations reveal that the ecosystem achieves a stationary state. Under various initial conditions, the ecosystem reaches the identical state. Typical examples of stationary distribution before perturbation are shown in Fig. 4 ($r_1 = 0.9$). In the stationary state, the spatial distribution of individuals varies widely, whereas the density of each species is usually near constant. After the perturbation, the ecosystem reaches different final states, depending on the values of the parameters.

First, we report the results for the two-species ecosystem (ecosystem I). Figure 5 illustrates the time dependence of species densities, where the model parameters are $r_2 = 0.4$, $d_1 = 0.1$ and $d_2 = 0.25$. Figure 6 displays typical spatial patterns at the final stationary state ($t = 3000$). In Fig. 7, steady-state densities at the final stationary state are shown plotted against perturbation strength (r_1), where $r_2 = 0.4$, $d_1 = 0.1$ and $d_2 = 0.25$ in Fig. 7a and $r_2 = 0.4$, $d_1 = 0.1$ and $d_2 = 0.3$ in Fig. 7b. Moreover, we use $r_1 = 0.9$ and 0.8 before the perturbation in Fig. 7a and Fig. 7b respectively. Hence for the two-species ecosystem (Figs. 5–7), we obtain the following results:

1. If the perturbation is strong, or if r_1 after the perturbation takes a small value, the densities of both species X and species Y decrease.
2. In Fig. 7a, species X (prey) goes extinct, but species Y (predator) survives. These results can be predicted by mean-field theory, as shown in Fig. 3a. However, for the other set of parameters, results (1) and (2) are changed completely, as shown in Fig. 7b.
3. When the perturbation becomes strong, species X increases (the paradox of enrichment), but species Y goes extinct.
4. If the perturbation is too strong, both species X and species Y go extinct.

Hence the response of the lattice system is complicated.

For the three-species ecosystem (ecosystem II), the responses are even more complex. Figures 8–10 display the results of the perturbation experiments, where a single parameter set ($r_2 = 0.4$, $r_3 = 0.9$, $d_1 = 0.1$, $d_2 = 0.25$, $d_3 = 0.05$) is used. These three figures indicate that:

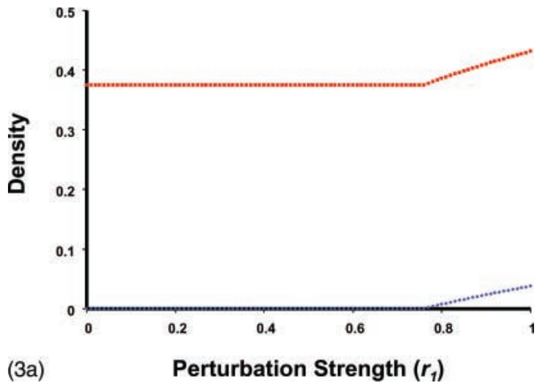
1. When the rate of reproduction r_1 after the perturbation takes a value higher than 0.2, all three species (X, Y and Z) survive.
2. For the range $r_1 = 0.18$–0.2, species Z goes extinct.
3. For the range $r_1 = 0.155$–0.175, both species Y and species Z go extinct.
4. When r_1 takes a value smaller than 0.15, species Y goes extinct.

Although the rate of reproduction (r_1) of species X is decreased, the density of X increases in certain regions. Since predator Y goes extinct indirectly, its prey X is suddenly increased. Hence several types of indirect effects are observed.

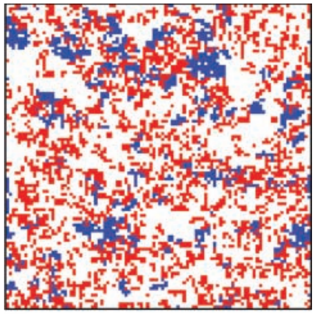
DISCUSSION

Our results demonstrate that a low-density (rare) species may play an important role in the balance of an ecosystem. This occurs as a result of the cyclic nature of ecosystem II with the introduction of species Z. The difference in ecosystems I and II is a kind of parity law in model ecosystems (Sakata and Tainaka, 2001). Natural ecosystems are usually extremely complex, and we often ignore low-density species in such ecosystems. However, these low-density species can play a critical role in the balance/stability of the ecosystem if they introduce cyclic relationships. Thus it would be unwise to ignore low-density species in the conservation and management of natural ecosystems.

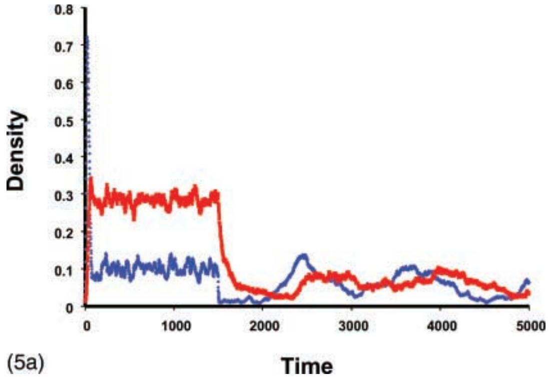
The concept of low-density species here is, in many respects, similar to that of keystone species (Paine, 1966; Lawton and Brown, 1993). The starfish in Paine's (1966) removal experiment is a low-density species. However, there is one difference between Paine's and the current model.



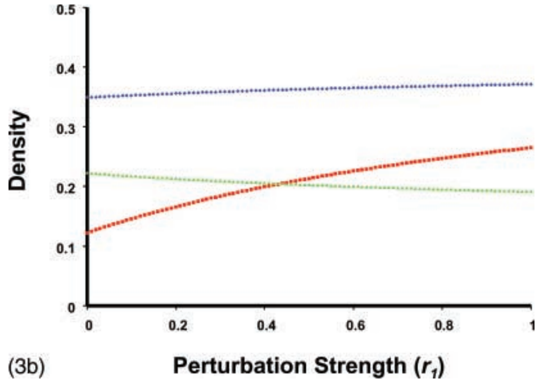
(3a)



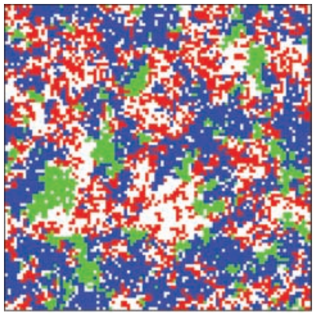
(4a)



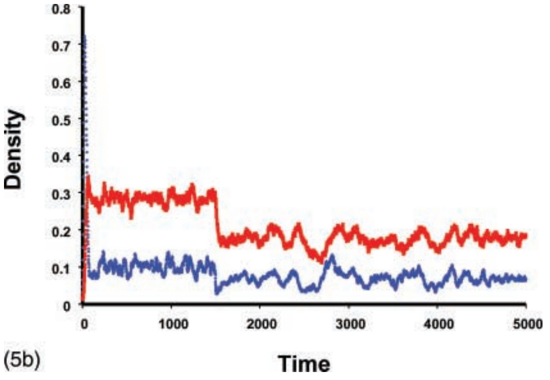
(5a)



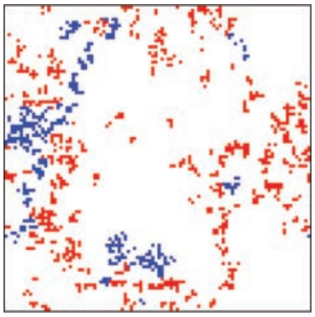
(3b)



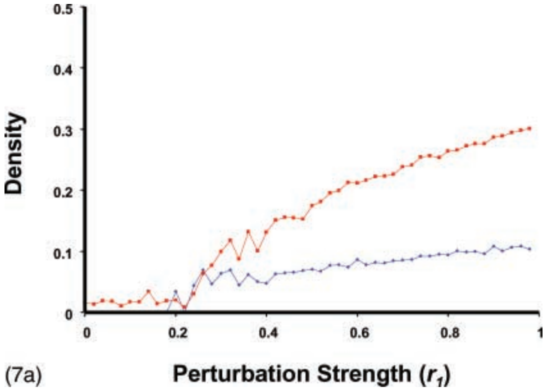
(4b)



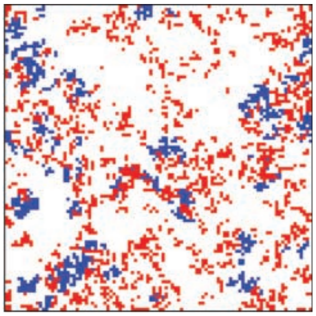
(5b)



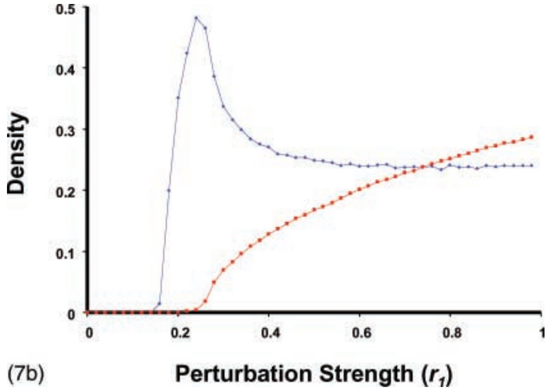
(6a)



(7a)



(6b)



(7b)

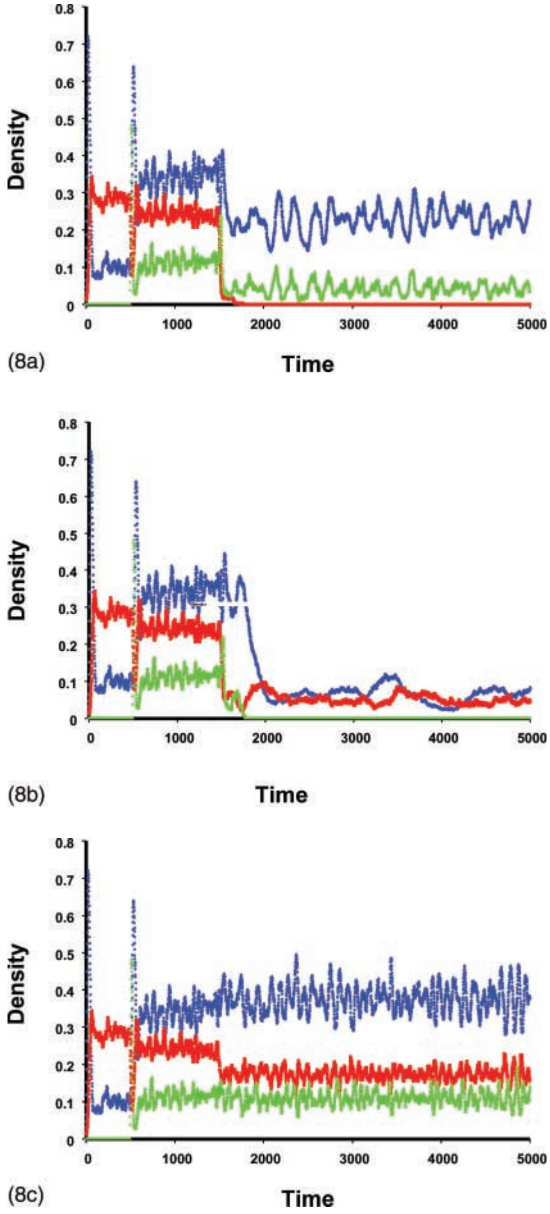
Fig. 3. Steady-state density of species X (blue), Y (red) and Z (green) plotted against the rate of reproduction (r_1) of species X using mean-field theory. (a) Two-species ecosystem (ecosystem I); (b) three-species ecosystem (ecosystem II).

Fig. 4. Typical spatial patterns of (a) two-species ecosystem and (b) three-species ecosystem at the stationary state (species X: blue; species Y: red; species Z: green; $t = 1000$). Before the perturbation ($r_1 = 0.9$), the system evolves into a stationary state.

Fig. 5. Population dynamics of the perturbation experiment in a two-species lattice system (species X: blue; species Y: red). Model parameters are as follows: $r_2 = 0.4$, $d_1 = 0.1$, $d_2 = 0.25$. At $t = 1500$, the perturbation is applied from $r_1 = 0.9$ to (a) $r_1 = 0.23$ or (b) $r_1 = 0.5$.

Fig. 6. Stationary patterns for Fig. 5 (species X: blue; species Y: red; $t = 3000$). At $t = 1500$, the perturbation is applied from $r_1 = 0.9$ to (a) $r_1 = 0.23$ or (b) $r_1 = 0.5$.

Fig. 7. The stationary densities of the two-species lattice system (species X: blue; species Y: red) plotted against the birth rate (r_1) of species X ($t = 3000$). Model parameters are as follows: (a) $r_2 = 0.4$, $d_1 = 0.1$, $d_2 = 0.25$, and before perturbation $r_1 = 0.9$; (b) $r_2 = 0.4$, $d_1 = 0.1$, $d_2 = 0.3$, and before perturbation $r_1 = 0.8$.



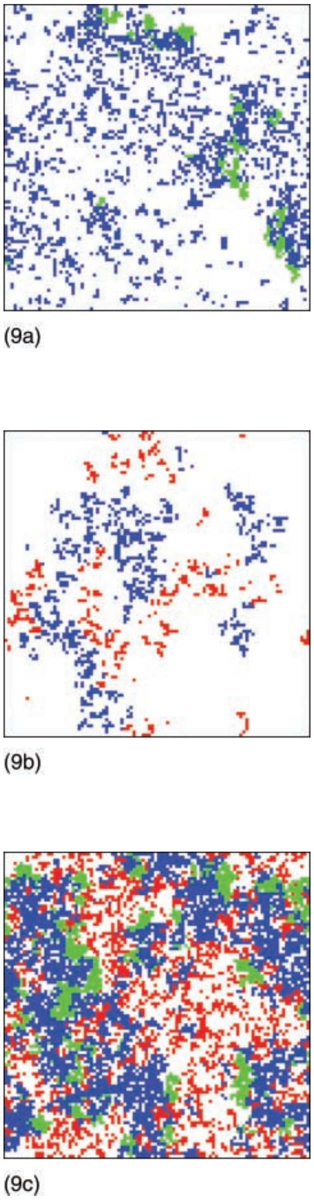


Fig. 8. Population dynamics in the three-species lattice system (species X: blue; species Y: red; species Z: green). Model parameters are as follows: $r_2 = 0.4$, $r_3 = 0.9$, $d_1 = 0.1$, $d_2 = 0.25$, $d_3 = 0.05$. At $t = 500$, the rare species (green) is introduced. At $t = 1500$, the perturbation is applied from $r_1 = 0.9$ to (a) $r_1 = 0.14$, (b) $r_1 = 0.20$ or (c) $r_1 = 0.5$. Before the perturbation, the system remains in a stationary state ($r_1 = 0.9$).

Fig. 9. Stationary patterns for Fig. 8 (species X: blue; species Y: red; species Z: green; $t = 3000$). At $t = 1500$, the perturbation is applied from $r_1 = 0.9$ to (a) $r_1 = 0.14$, (b) $r_1 = 0.20$ or (c) $r_1 = 0.5$. The surviving species are entirely different, depending on a slight change in perturbation strength (r_1).

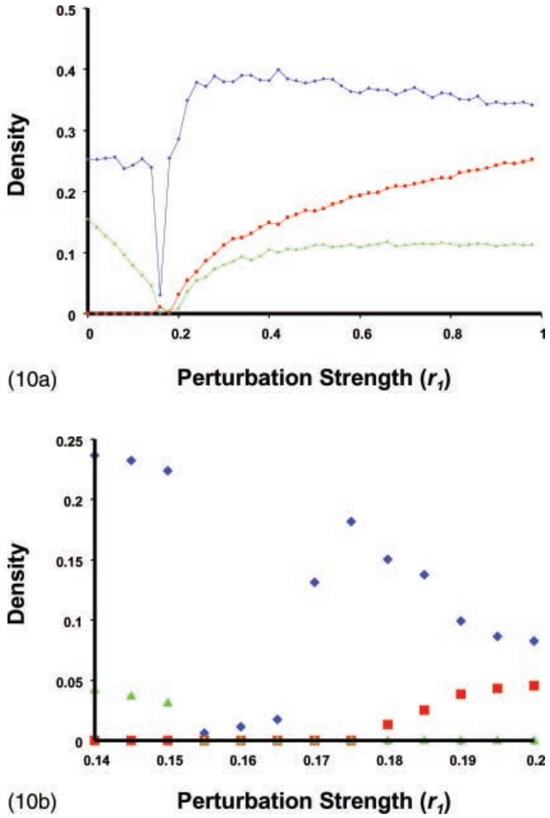


Fig. 10. The stationary densities of the three-species lattice system (species X: blue; species Y: red; species Z: green) plotted against the birth rate (r_1) of species X ($t = 3000$). Model parameters are as in Figs. 8 and 9. (a) $r_1 = 0$–1. (b) Enlargement of (a) for $r_1 = 0.14$–2.0.

Our focus is the effects of a low-density species on perturbation. The addition and removal of a starfish, for example, does not change the structure of a community, unlike the direct changes observed when a starfish is removed (Paine, 1966; Lawton and Brown, 1993). The difference becomes apparent only when the environment is exposed to a strong perturbation. We believe that this can be considered a new type of keystone species, albeit one that is very difficult to detect.

The strength of a perturbation also affects the outcome. In ecosystem I, the order of extinction is in line with the mean-field results (Fig. 4). However, the simulation results in ecosystem II are much more complex and unpredictable (Figs. 2a, 3a), and cannot be predicted from mean-field theory. This highlights the unpredictable nature of ecosystem dynamics (May, 1973; Pimm, 1991).

Ecosystem II is a rather simple ecosystem consisting of three species (or four species if one includes empty sites). The main characteristic of this ecosystem is the 'paper–scissors–stone' game relationship among species X, Y and Z. This may be a rare occurrence in a simple ecosystem, but the implications of our model are far more important. The networks of natural ecosystems are far more complex, with complicated food webs and other interactions. Many cyclic (or 'paper–scissors–stone' game) interactions are embedded in such complex networks (see, for example, Elton, 1966; Pimm, 1991). Ecosystem stability appears to be achieved by many such cyclic interactions in its network (Tainaka, 1988, 1994). For example, a food chain contains some cyclic interactions via the death of individuals.

The results of the present study indicate that low-density species may be an important part of such finely balanced cyclic food webs. When we view an ecosystem as a balanced combination of many cyclic networks (interactions), removing a node species could, even if it is rare, alter the nature of the whole ecosystem. If a low-density species is involved in one such cyclic interaction, the extinction/removal of that species could alter the main properties of the ecosystem. Being of 'low density' or 'rare' does not mean 'unimportant' for ecosystem stability.

The results of the present study also raise the following questions:

1. Does the rare node species always have an important role in the cyclic structure of ecosystem networks and the resulting response to perturbations? If not always, then when and where is it important?
2. If the rare species is at a terminal node in the ecosystem network (connected to one other species only), can it affect the cyclic structure of the ecosystem? It is clear that a rare species in a cyclic network can have a profound effect in perturbation experiments. But if the rare species is at a terminal node, it may never be important.
3. What kinds of rare species can or cannot affect the cyclic network properties of an entire ecosystem?

The stability of communities and ecosystems is one of the most important issues in community ecology and conservation biology yet to be resolved (Pimm, 1991; Rosenzweig, 1995). If as we suspect cyclic balance is the key to stability, the current approach may be a new way of examining the stability of ecosystems. One should note, however, that the cyclic stability (balance) of the 'paper–stone–scissors' game system is different from the concept of mathematical equilibrium (Tainaka, 1988). There is still no mathematical solution for cyclic balance even in the simplest 'paper–stone–scissors' game model. Simulation studies have shown that cyclic balance often puts up strong resistance to perturbations. We now have a new tool to study the stability of ecosystems. The rare species can be used to test the cyclic balance of various simple model ecosystems.

A low-density species can be a key species in an ecosystem, exhibiting extreme parameter sensitivities for the stability/steady state of ecosystems (Yodzis, 1988). The possibility of such extreme sensitivity allows for the breakdown/change of the effective cyclic network. This implies great difficulty forecasting ecosystems (Elton, 1966; Pimm, 1991). It is clear that the parity of food webs often leads to the opposite response in the dynamics (Sakata and Tainaka, 2001). The current approach is a new way of looking at and organizing the stability of a community network.

We are faced with a loss of diversity in most natural communities (Rosenzweig, 1995). It is therefore important to recognize that any slight modification to the environment by human activity could hamper conservation practice.

ACKNOWLEDGEMENTS

This research was supported in part by several Japanese Ministry of Culture and Science grants-in-aid to J.Y., K.T., Y.S., T.T. and T.M.

REFERENCES

Abarca-Arenas, L.G. and Ulanowicz, R.E. 2002. The effects of taxonomic aggregation on network analysis. *Ecol. Model.*, **149**: 285–296.

Andrewartha, H.G. and Birch, L.C. 1954. *The Distribution and Abundance of Animals*. Chicago, IL: University of Chicago Press.

Bender, E.A. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology*, **65**: 1–13.

DeWitt, T.J. and Langerhans, R.B. 2003. Multiple prey traits, multiple predators: keys to understanding complex community dynamics. *J. Sea Res.*, **49**: 143–155.

Elton, C.S. 1966. *The Pattern of Animal Communities*. London: Chapman & Hall.

Gaston, K.J. *Rarity*. London: Chapman & Hall.

Itoh, Y. 1973. On a ruin problem with interaction. *Ann. Inst. Stat. Math.*, **25**: 635–641.

Itoh, Y. and Tainaka, K. 2004. Spatial enhancement of population uncertainty in model ecosystems. *J. Phys. Soc. Jap.*, **73**: 53–59.

Kerr, B., Riley, M.A., Feldman, M.W. and Bohannan, B.J.M. 2002. Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors. *Nature*, **418**: 171–174.

Krivtsov, V. 2001. Study of cause-and-effect relationships in the formation of biocenoses: their use for the control of eutrophication. *Russ. J. Ecol.*, **32**: 230–234.

Lawton, J.H. and Brown, V.K. 1993. Redundancy in ecosystems. In *Biodiversity and Ecosystem Function* (E.D. Schulze and H.A. Mooney, eds.), pp. 255–270. New York: Springer.

MacArthur, R.H. and Wilson, E.O. 1967. The Theory of Island Biogeography. Princeton, NJ: Princeton University Press.

Magurran, A.E. and Henderson, P.A. 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature*, **422**: 714–716.

May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton University Press.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonsseca, G.A.B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, **403**: 853–858.

Nakagiri, N. and Tainaka, K. Indirect effects of habitat destruction in model ecosystems. *Ecol. Model.*, **174**: 103–114.

Nakagiri, N., Tainaka, K. and Tao, T. 2001. Indirect relation between extinction and habitat destruction. *Ecol. Model.*, **137**: 109–118.

Paine, R.T. 1966. Food web complexity and species diversity. *Am. Nat.*, **100**: 65–75.

Pickett, S.T.A. and White, P.S., eds. 1985. *The Ecology of Natural Disturbance as Patch Dynamics*. New York: Academic Press.

Pimm, S.L. 1991. *Food Webs*. London: Chapman & Hall.

Rosenzweig, M.L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, **171**: 385–387.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Sakata, T. and Tainaka, K. 2001. Long-term forecast and parity law in interacting particle systems. *Systems Analysis Modelling Simulation* (*SAMS*), **41**: 719–733.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. *Ecology*, **78**: 55–69.

Sinervo, B. and Lively, C.M. 1996. The rock–paper–scissors game and the evolution of alternative male strategies. *Nature*, **380**: 240–243.

Soulé, M.E. 1986. *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA: Sinauer Associates.

Stiling, P. 1999. *Ecology*, 3rd edn. London: Prentice-Hall.

Tainaka, K. 1988. Lattice model for the Lotka-Volterra system. *J. Phys. Soc. Jap.*, **57**: 2588–2590.

Tainaka, K. 1994. Intrinsic uncertainty in ecological catastrophe. *J. Theor. Biol.*, **166**: 91–99.

Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature*, **367**: 363–365.

Wootton, J.T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *Am. Nat.*, **141**: 71–89.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology*, **69**: 508–515.