A Role Of A Low-Density Species On The Community Outcomes In A Model Ecosystem

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Abstract: The balance of ecosystems may be altered with/without a less common species. We explore the role of a low-density species in a model ecosystem by perturbation experiments. We build a lattice ecosystem of two common species with/without one low-density species. Consider a two-dimensional lattice consisting of prey, predator and vacant site. We introduce the third low-density species that is preyed by the common prey, while eats the common predator. The relationship among three species is cyclic, corresponding to the Rock-Paper-Scissors game. We perform perturbation experiments by decreasing the reproduction rate of one common species. We then compare the resulting community structures and evaluate the effects of the low-density species and the perturbation strength on the model ecosystems. The simulation results are dependent on both the low-density species and perturbation strengths. The results are often paradoxical and different from those expected from the mean field version of the lattice model. Our results imply that the conservation biology and management practice of natural ecosystems may be hindered if less common unattractive species are ignored. Furthermore, an introduction of a new species may alter the ecosystem balance without changing the apparent structures of the community.

Keywords: *Low-density species; Community structure; Perturbation; Lattice ecosystems*

1. INTRODUCTION

Most natural ecosystems consist of many species; some of them are usually rare and others are common (Elton, 1966). In the conservation practice of natural ecosystems, however, we often ignore less common (or rare) specie s, except target species (Soulé, 1986, Gaston 1994). When an ecosystem is disturbed by external factors such as climatic changes or human habitat destruction, it may undergo a large change in community structure (Pimm, 1991). Here we often expect that the common species are the critical factor affecting the outcome of such environmental disturbances (Pickett and White, 1985, Stiling, 1999). However, less common species may be equally influential. With an introduction of a low-density species, the food-web balance of the ecosystem may become qualitatively different.

We explore the role of a low-density species in a lattice ecosystem introducing the perturbation on a common species. The initial lattice ecosystem consists of prey, predator and vacant site (plant). As an experiment, we introduce the third low-density species that is preyed by the common prey, while predate on the common predator. The relationship among three species is cyclic, corresponding the Rock-Paper-Scissors game (Itoh, 1973, Tainaka, 1988). An example of such relation is three kinds of fish; namely saury, mackerel and sardine. As a control, no new species are introduced. We use the lattice version of cyclic ecosystems to study the functional response of a model ecosystem (Tainaka, 1988).

To evaluate the effects of the low-density species, perturbation experiments are performed. We perform perturbation experiments by decreasing the reproductive rate of one common species and compare the eventual community structures with/without the low-density species. We also change the perturbation strength and compare the outcomes. The mean field version of the lattice model is also analyzed (Tainaka, 1988). From the complex outcome, we discuss the role/effects of a less common species in natural communities and its implications on our conservation practice.

2. THE MODEL

We consider two ecosystems I and II. The system I is composed of two species; that is prey X and predator Y. In the system II, the third species Z is introduced to the system I. If the species Z goes extinct, the system I becomes equivalent to the system I.

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

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

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

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

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

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

On the other hand, the system II contains not only the reactions (1a) - (1e) but also the following interactions:

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

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

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

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

where the reactions (2a) and (2b) represent the predation, and (2c) and (2d) are reproduction and death processes of species Z, respectively. In our analyses, we kept the steady state density of Z lowest among the three species. This is achieved by adjusting the growth/death parameters of not only Z, but also X and Y in the ecosystems (Fig. 1).

Our ecosystems are schematically illustrated in Fig. 1. The system II tacitly contains the cyclic strength of rock-paper-scissors game, or paper-scissors-stone game (PSSG) (Tainaka, 1988; Itoh, 1973). The species X eats Z, but it is beaten by Y. On the other hand, the introduced species Z can eat Y. The relation of PSSG symbolically represents ecological balance. A concrete example of this relation is the case of side-blotched lizards (Sinervo and Lively, 1996); there are three morpho-species of males distinguished by colors of throat: orange, blue and yellow. Males with orange throats are dominant to males with blue; blue males are dominant over yellow males; yellow males resemble females in morphology and prevail the orange males. The relation among three males is represented by the PSSG rule.

Another example of PSSG is a microbiological community reported by (Kerr, et al 2002). Their system is composed of three kinds of *Escherichia coli*; that is, colicin-producing (C), colicin-sensitive (S), and resistant (R) bacteria. The bacteria S has the highest advantage for growth rate, but it is beaten by C because of colicin (toxin). Due to the growth-rate advantage, S (or R) is stronger than R (or C).

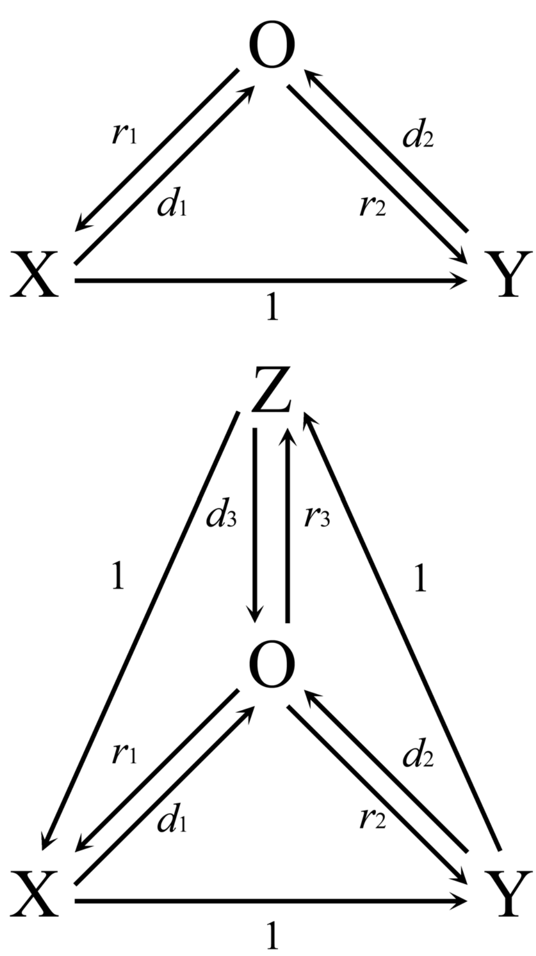

Figure 1. Model ecosystems with/without an introduced species. Top: before introduction, and Bottom: after introduction. O: vacant site, X and Y: common species, and Z: an introduced rare species. Letter r_i, d_i and i represent reproduction, death and predation (invasion) and the associated numbers denoted species.

We apply a method of lattice Lotka-Volterra model (LLVM) (Tainaka, 1988; Nakagiri, et al, 2001) which has a mean-field theory called Lotka-Volterra equation. This lattice model differs from the cellular automata; in the former case, processing is asynchronous, while the latter is synchronous. The natural ecosystem is usually asynchronous. Various results of LLVM are qualitatively different from the prediction of non-spatial theories. Evolution method of lattice model is defined as follows:

1) Initially, we distribute individuals on a square-lattice in such a way that each lattice site (cell) is occupied by a single individual of one of two or three species.

2) Reaction processes are performed in the following two steps.

(i) We perform two-body reactions; examples are the reactions (1a), (1b) and (1c). Select one square-lattice point randomly, and then specify one of four neighbor sites. Let the pair react according to two-body reactions. For example, if the pair is X and O, then the latter is changed into X by the rate r_1.

(ii) Next, we perform the single body reactions; an example is the reaction (1d). Choose one square-lattice point randomly; if the point is occupied by X, then it becomes O by the rate d_1.

3) Repeat step 2) by L × L times, where L × L is the total number of the square-lattice sites. This step is called as Monte Carlo step (Tainaka, 1988). In this paper, we set L=100.

4) Repeat the step 3) for 2500 Monte Carlo steps.

In the present paper, we study a perturbation experiment. at time t=1500, the value of parameter r_1 is jumped from 0.8 to a nonzero value. Then we record the density of all species.

3. PERTURBATION EXPERIMENTS

By computer, we carry out perturbation experiments, where the reproduction rate r_1 of species X is suddenly decreased. In the case of 2-species system, a single perturbation is applied at time t=1500. Before the perturbation, we set r_1=0.8; then the system evolves into a stationary state. After the perturbation, the value of r_1 is suddenly decreased from 0.8 to one of the four values (0.1, 0.16, 0.24 and 0.34).

In the case of 3-species system, two types of perturbation are applied subsequently. There are two species X and Y at the initial state (t=0). By the first perturbation (t=500), the species Z is introduced: several empty sites (O) are changed into Z. Then, the system evolves into a new stationary state. In this state, three species X, Y and Z coexist. The second perturbation is applied at t=1500. Before the second perturbation, we always set r_1=0.8. After the perturbation, the value of r_1 is suddenly decreased from 0.8 to one of the four values (0.1, 0.16, 0.24 and 0.34). Hence, the second perturbation is the same as in the 2-species system.

4. RESULTS

The results of perturbation experiments are reported (Fig. 2). First, we describe the result before the perturbation (t<1500). Computer simulations reveal that the system evolves into a stationary state. Under various initial conditions, the system reaches the identical state. Typical examples of stationary distribution before perturbation are shown at the top two boxes in Fig. 3. In stationary state, the spatial distribution of individuals varies greatly, whereas the density of each species almost constant in the average.

After the perturbation, the system reaches different final states, depending on the values of parameters. Final stationary patterns (t=2000) are illustrated in the lower 8 boxes in Fig. 3. The time dependences of species densities are depicted in Fig. 2 for the different values of r_1.

In the case of 2-species system (the left column in Fig. 2), we obtain the following results. When the reproduction rate r_1 (= r) after the perturbation takes 0.1 and 0.16, both species go extinct (Fig. 2 Top-Left and Upper-middle-Left). However, when r_1=0.24, the species Y goes extinct (Fig. 2 Lower-middle-Left). On the other hand the species X does not go extinct. Note that r_1=0.8 before the perturbation. Despite the reproduction rate r_1 of species X is decreased, the density of X increases. Since the predator Y becomes extinct indirectly, its prey X is abruptly increased. Furthermore, in the case of r_1=0.34, no species goes extinct (Bottom-Left). In the final case, two types of indirect effect are observed: 1) the predator Y does not become extinct; nevertheless, the density of X after the perturbation becomes higher than that before the perturbation. 2) the steady-state density of Y is eventually decreased by the perturbation.

In the case of 3-species system, we obtain entirely different results (see the right column in Fig. 2). Despite the same perturbation applied at t=1500, surviving species are different between 2- and 3-species systems. (i) When r_1=0.1, the species Y goes extinct: both species X and Z survive (Fig. 2 Top-Right). (ii) When r_1=0.16, the species Y and Z go extinct: only species X survives (Fig. 2 Upper-middle-Right). (iii) In the case of r_1=0.24, the species Z goes extinct: both species X and Y survive (Fig. 2 Lower-middle-Right). (iv) When r_1=0.34, no species goes extinct: three species X, Y and Z survive (Fig. 2 Bottom-Right). Hence, the perturbation (the decrease of reproduction rate of X) brings about various types of extinction indirectly.

Comparing the temporal dynamics between 2- and 3-species systems of Fig. 2, the responses of perturbation experiments are qualitatively different. The response profiles against different values of r are distinctively different between 2- and 3-species systems. Thus the existence of species Z alters the properties of ecosystems.

The mean-field version of the lattice model is also calculated for r_1 (Fig. 4). In the 2-species system,

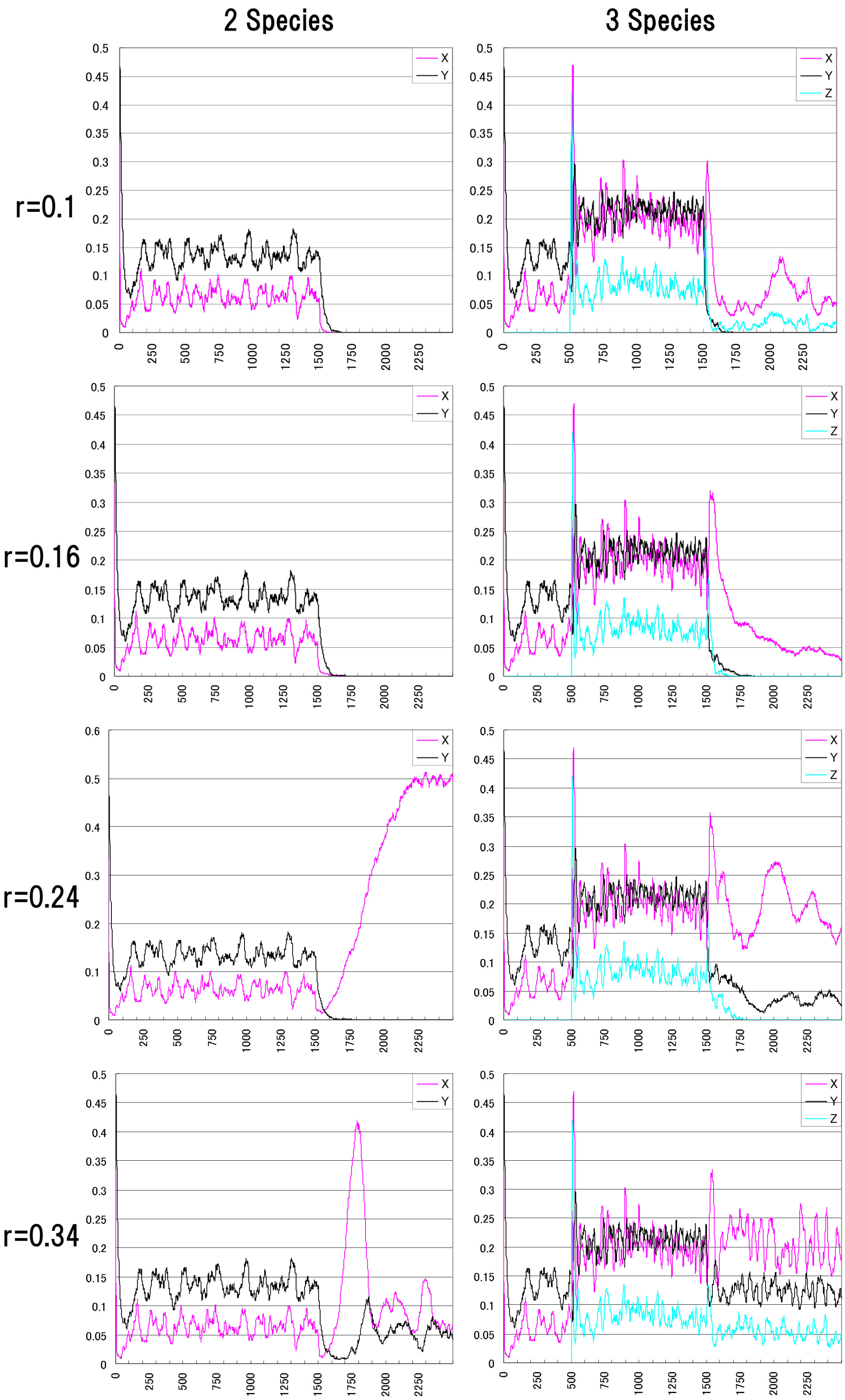

Figure 2. The time dependence of the total densities of X, Y and Z for a square-lattice system (100x100). At time t=1500 MCS, the initial reproduction rate r_1=0.8 of X is changed to r=0.1, 0.16, 0.24 or 0.34 (from top to bottom). The 2-species system (left columns) is control and species Z is introduced at t=500 for 3-species system (right columns). (r_1, r_2, d_1, d_2) = (0.8,0.4,0.1,0.3) and for 3-species system at t=500, (r_3, d_3)=(0.8,0.1).

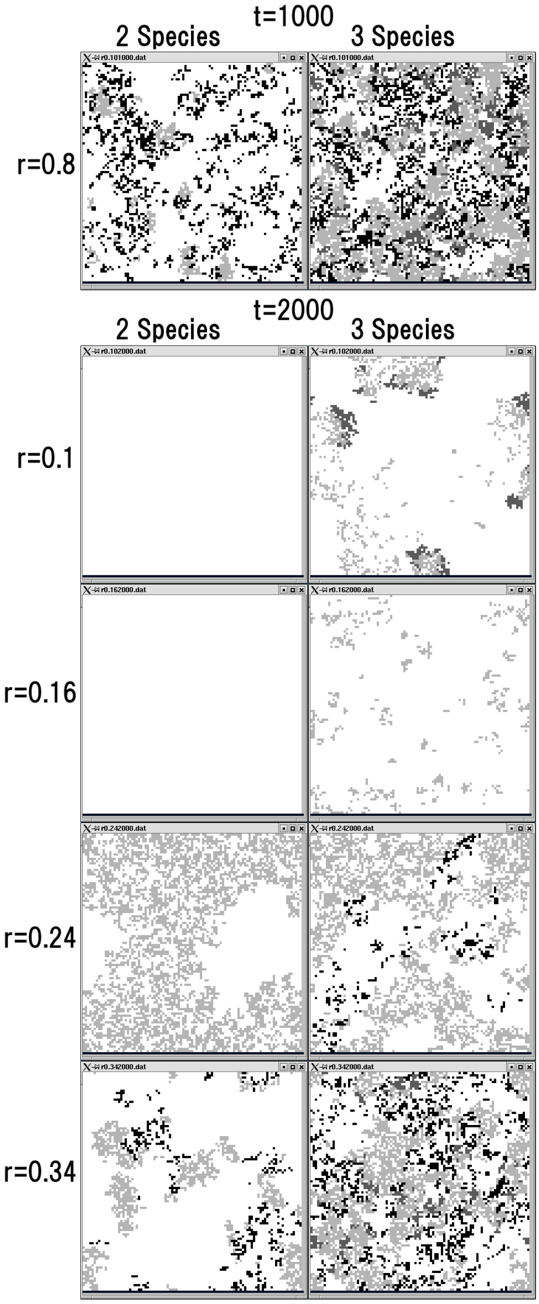

Figure 3. Snapshots of typical spatial patterns of a square-lattice system (100x100). The points of light gray, black, dirk gray and white represent X, Y, Z and O, respectively. Left columns: 2-species system; right columns: 3-species system; top two boxes: t=1000; and lower six boxes: t=2000. The initial parameter settings are (r_1, r_2, d_1, d_2) = (0.8,0.4,0.1,0.3) for all systems, and at t=500, (r_3, d_3)=(0.8,0.1) for 3-species system. At t=1500, r_1=0.8 is changed to r=0.1, 0.16, 0.24 or 0.34 (from top to bottom).

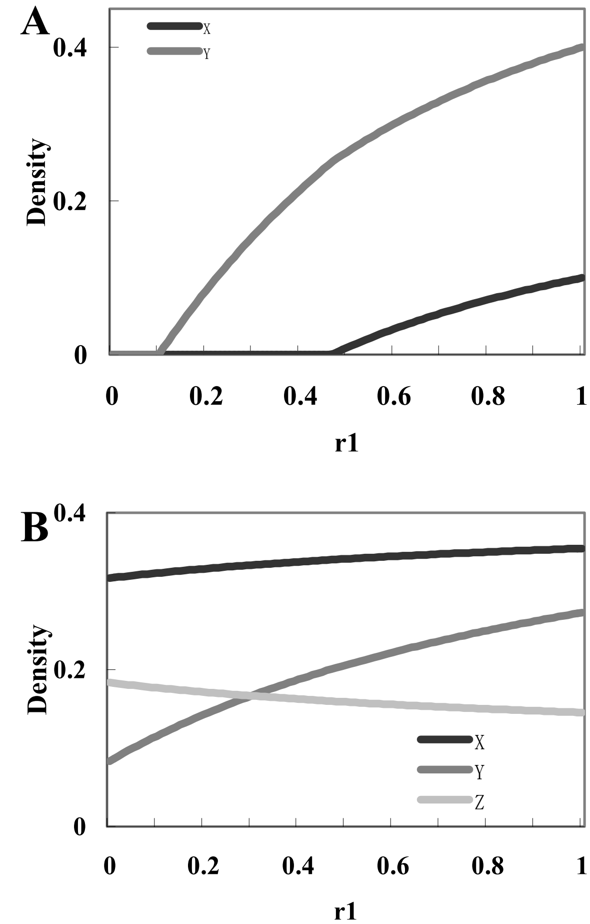

Figure 4. The steady-state densities of each species are plotted against the reproduction rate r_1 of species X for the mean-field version of the lattice system. For detail settings see Fig. 2.

the mean-field results agree well with the lattice counterparts. However, in the 3-species system, the mean-field version shows no extinction of species (no phase transition in Fig. 4), while perturbation simulations in the lattice model shows variable extinction of species with different levels of perturbation (complex phase transitions in Figs. 2 and 3).

5. DISCUSSIONS

Our results demonstrate that a rare species may play an important role in the balance of the whole ecosystem. This happens due to the cyclic nature of ecosystem II with the introduced species Z. The difference in the two ecosystems (I and II) is a kind of parity law in model ecosystems (Sakata and Tainaka, 2001). Natural ecosystems are usually extremely complex. We often ignore rare or low-density species in such ecosystems. However, these rare species can become critical in the balance/stability of the introduced ecosystem, by introducing cyclic relations. Thus ignoring rare species may be hazardous in conservation and management of natural ecosystems.

The strength of perturbation also affects the outcomes. In ecosystem I, the order of extinction is in agreement with the mean-field results (Fig. 4). However, The simulation results in ecosystem II are far more complex and unpredictable (Figs. 2 and 3 left columns). These results are not predictable at all from their mean-field counterparts (Tainaka, 1988). This exemplifies the unpredictable nature of ecosystems dynamics (May, 1973, Pimm, 1991).

The current systems are a rather simple system consisting of 3 or 4 species (including empty sites). The main characteristics of this ecosystem is the PSSG relation among X, Y and Z. This may be rare in a simple ecosystem (for example, see the method section). However, our implications are far more important. The networks of natural ecosystems are far more complex with complicated food webs and other interactions. Many cyclic (or PSSG) interactions are imbedded in such complex networks, e.g., see (Elton, 1966, Pimm, 1991).

The ecosystem stability is achieved by such cyclic interactions in its network. For example, a food chain contains some cyclic interactions via the death of individuals. If one of the low-density species is at one of such cyclic interactions, the extinction/removal of such species may alter the major properties of the ecosystem. Thus “low density” or “rare” does not mean unimportant in the ecosystem stability.

The current result also indicates the extreme parameter sensitivities for the stability/steady state of ecosystems. Sensitivity analyses may play a key role in the stability and diversity analyses of ecosystems and communities. It may imply the extreme difficulty of ecosystem forecasts, if not impossible at all (Elton, 1966, Pimm, 1991).

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7. REFERENCES

Elton, C. S., The pattern of animal communities, Chapman and Hall, London, 1966.

Gaston, K.J., Rarity, Chapman & Hall, London, 1994.

Itoh, Y., On a ruin problem with interaction, *Annals of the Institute of Statistical Mathematics*, 25, 635-641, 1973.

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

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

Nakagiri, N., K. Tainaka, and T. Tao, Indirect relation between species extinction and habitat destruction, *Ecological Modelling*, 137, 109-118, 2001.

Pickett, S. T. A., and P. S. White, eds., The ecology of natural disturbance as patch dynamics, Academic Press, New York, 1985

Pimm, S., Food web, Chicago University Press, Chicago, 1991.

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

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

Soulé, M. E., Conservation biology: the science of scarcity and diversity, Sinauer, Sunderland, 1986.

Stiling, P., Ecology, third edition, Prentice Hall International, London, 1999.

Tainaka, K., Lattice model for the lotka-volterra system, Journal of Physical Society of Japan, 57, 2588-2590, 1988.