Stability Of Specialists Feeding On A Generalist

Tomoyuki Sakata, Kei-ichi Tainaka, Yu Ito and Jin Yoshimura
Department of Systems Engineering, Shizuoka University

Abstract: The investigation of ecosystem stability of competing species is important not only to forecast the effect of ecological management but also to conserve biospecies. So far, it is well known that competing species can coexist, when they respectively live in different microhabitats. However, such species-specific differentiation does not always hold, if competing species interact with a generalist that can live in a variety of microhabitats. In the present paper, we study stability of two competing specialists by two metapopulation models, that is, island and lattice models. Computer simulations reveal that both models are not always stable. Moreover, we find that all species coexist, when a cyclic balance similar to the paper-scissors-rock game holds. The difference of results between lattice model and mean-field theory is discussed.
*Keywords: lattice model, ecosystem stability, metapopulation dynamics, different microhabitats*

1. INTRODUCTION

The study of ecological stability between competing species is a continuing topic to ecologists. It is well known that competing species can coexist, when they live in different microhabitats (Begon et al., 1996). The species can coexist because of species-specific differentiation in microhabitat. However, such specialists may not always coexist, if they interact with a generalist that can live in a variety of microhabitats. The purpose of the present article is to discuss the stability of competing specialists that feed on the same generalist. We find that our system does not always stable, and that specialists and generalist coexist under a cyclic balance similar to the paper-scissors-rock game.

From the terms of specialist-generalist system, ecologists may associate with the theory of so called "competition-colonization tradeoff"(Wilson and Yoshimura, 1994). In this case, specialists are competing with generalists. Our system, however, differs from usual specialist-generalist systems, because specialists feed on a generalist that live in both microhabitats. An example is the system of MacArthur (1958). He has illustrated that several different birds have fed on insects in different microhabitats even in a single tree. Each specialist (bird) feeds on in a specific microhabitat, whereas the generalist (insect) can live in different microhabitats. Namely, the direct resource (generalist) of specialists has no species-specific differentiation. Another example of our model is insect-plant system. Insects (specialists) exploit a common resource (plant: generalist). The insects have species-specific differentiation in microhabitat, while the

plant does not have.
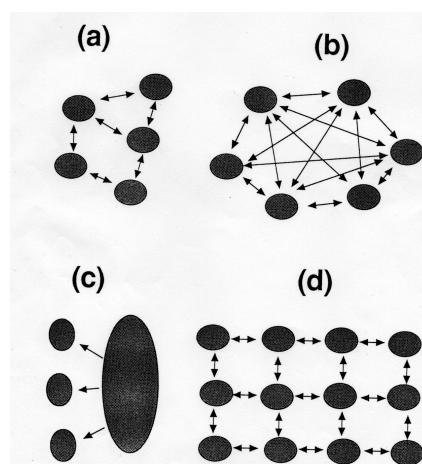
Figure 1. Several patch models. The arrows denote the direction that biological individuals can migrate. (a) stepping stones: each patch interacts with several patches; (b) islands: interaction is allowed between any pair of patches (Levins, 1969); (c) continent and islands: migration occurs from a large continent to small islands (Boorman and Levitt, 1980); (d) lattice: each patch can interact with the adjacent patches (Hassel et al., 1991; Caswell and Cohen, 1995). In the present paper, we apply the island (b) and lattice (d) models. In the case of lattice model, each patch is allowed to interact with z adjacent patches ($z = 4$ for square lattice).

We apply a metapopulation (patch) model; each patch represents a microhabitat. Heretofore, several patch models (Figure 1) have been presented

by many authors (Hanski and Gilpin, 1997; Levin, 1974; Maynard Simith, 1982). We use the island (Levins, 1969) and lattice (Hassel et al., 1991; Caswell and Cohen, 1995) models as illustrated in Figure 1 (b) and (d), respectively. The Lotka-Volterra equation (LVE) is applied to the former, and "lattice Lotka-Volterra model"(LLVM) (Tainaka, 1988, 1989; Matsuda et al., 1992) is applied to the latter. Note that our patch systems are entirely deferent from usual patch models (Hanski and Gilpin, 1997; Durrett and Levin, 1994): we use LVE and LLVM not for the population dynamics inside each patch but for between-patch (interdemic) dynamics.
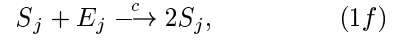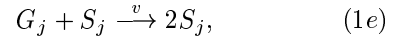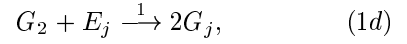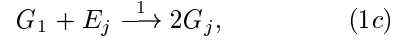
2. MODEL

Consider two specialists S_1 and S_2 and one generalist G which live on square lattice space. Each lattice site (patch) represents a microhabitat; there are two kinds for microhabitat. The specialist S_j lives in the specific microhabitat j ($j = 1, 2$), while the generalist can live in both microhabitats. Both specialists exploit a single generalist (G) as a resource. Each patch (lattice site) takes one of six states, that is, S_j, G_j and E_j. Here, S_j (G_j) denotes the patch of specialist (generalist) in microhabitat j, and E_j means the empty patch of habitat j. While S_1 and S_2 are different species, both G_1 and G_2 represent a single species.
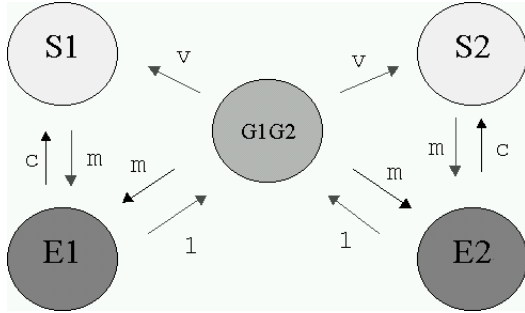
Figure 2. Schematic illustration of patch interaction. The symbols S_j and G_j represent specialist and generalist that live in microhabitat j, respectively, and E_j is the empty patch of microhabitat j. The arrows have the same meanings as in the reactions (1a) – (1f). For example, the process (1e) changes G_j into S_j, so that there are two arrows from G_j to S_j.

We study the following patch reactions:

$$S_j \xrightarrow{m} E_j. \qquad (1a)$$

$$G_j \xrightarrow{m} E_j. \qquad (1b)$$

$$G_1 + E_j \xrightarrow{1} 2G_j, \qquad (1c)$$

$$G_2 + E_j \xrightarrow{1} 2G_j, \qquad (1d)$$

$$G_j + S_j \xrightarrow{v} 2S_j, \qquad (1e)$$

$$S_j + E_j \xrightarrow{c} 2S_j, \qquad (1f)$$

The first two reactions (1a) and (1b) represent the patch extinction of S_j and G_j, respectively. The reaction (1c) means the "colonization"process of species G_j: if some individuals of G_1 migrate into an empty patch E_j, then its population size may grow up in this patch; the generalist G_1 can reproduce in both habitats 1 and 2. The reaction (1d) also denote the colonization of G_2. The fifth reaction (1e) means the herbivory or predation of species S_j: if individuals of S_j migrate into the patch G_j, the population size of S_j (G_j) immediately increases (decreases). This is because the specialist S_j feeds on the generalist G_j in the habitat j. The last reaction (1f) denotes direct growth; we add this for a generality.

We assume that the rates of processes (1a) – (1f) are given by m, m, 1, 1, v, c, respectively, as illustrated in Figure 2. The parameters m means the extinction (mortality) rate of species, and it takes the same value for any species. Moreover, we assume that the colonization rate c takes a small value; it is found that the last interaction (1f) can be omitted ($c = 0$), so long as c is small. The invasion rate v is always put unity ($v = 1$).

There are variety of modelings for our specialist-generalist system. Strictly speaking, our model (1) is slightly different from the microhabitat system presented by MacArthur (1958). In the latter case, the insect (generalist) can move from one microhabitat to the other; in other words, transformation (migration) between G_1 and G_2 easily occurs by the movement. An example of our model is insect-plant system. two insects (specialists) commonly exploit a plant (generalist). The insects have species-specific differentiation in microhabitat; for instance, S_1 (S_2) lives in humid (arid) environment. On the other hand, the plant grows in any environment.

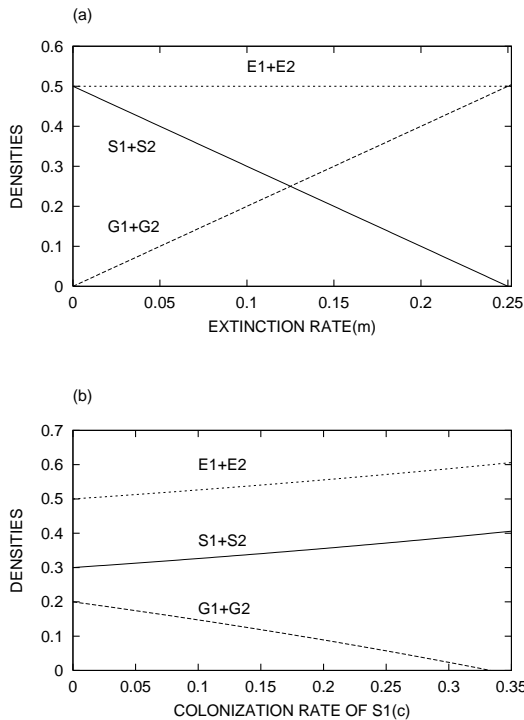Simulation is carried out as follows:

1) Initially, we distribute six kinds of states over a square-lattice. In this paper, we set that the population size of microhabitat 1 is slightly higher than that of microhabitat 2.

2) Reactions (1a) - (1f) are performed in the following two steps.
i) First, a single particle reactions, the processes (1a) and (1b), are performed. Choose one lattice site randomly, and let it react according to (1a) and (1b). For example, if the S_1 site is picked up, it will become E_1 by the rate m. ii) Next, we perform two-body reactions, namely, reactions (1c) - (1f). Choose one lattice site randomly, and then specify one of four nearest-neighbor sites. Let them react according to (1c) - (1f). For example, if you pick up a pair of sites labeled by S_1 and G_1, the latter site will become S_1 by a probability (rate) v. Here we employ periodic boundary conditions.

3) Repeat step 2) by $L \times L$ times, where $L \times L$ is the total number of the square-lattice sites. This step is called Monte Carlo step (Tainaka, 1988). In this paper, we set $L = 100$ and $L = 200$.

4) Repeat step 3) for 1000 – 2000 Monte Carlo steps. It is note that the population size of resource 1 or 2 does not change though out our simulation: the density of resource 1 is slightly higher than that of resource 2.

3. RESULTS OF ISLAND MODEL

Since interaction between any pair of patches is allowed in island model, the population dynamics is expressed by a Lotka-Volterra equation (LVE) (Hofbauer and Sigmund, 1988):

$$\dot{P}_{\mathrm{Sj}} = 2vP_{\mathrm{Sj}}P_{\mathrm{Gj}} + 2cP_{\mathrm{Sj}}P_{\mathrm{Ej}} - mP_{\mathrm{Sj}}, \quad (2a)$$

$$\dot{P}_{\mathrm{Gj}} = 2(P_{\mathrm{G1}} + P_{\mathrm{G2}})P_{\mathrm{Ej}} - 2vP_{\mathrm{Sj}}P_{\mathrm{Gj}} - mP_{\mathrm{Gj}}, \quad (2b)$$

$$\dot{P}_{\mathrm{Ej}} = m(P_{\mathrm{Gj}} + P_{\mathrm{Sj}}) - 2c(P_{\mathrm{S1}} + P_{\mathrm{S2}})P_{\mathrm{Ej}}$$
$$-2(P_{\mathrm{G1}} + P_{\mathrm{G2}})P_{\mathrm{Ej}} \quad (2c)$$

where the dots denote the derivative with respect to the time t which is measured by the Monte Carlo step, P_i is the density of patch i (i =S1, S2, G1, G2, E1, E2), and j represents the resource ($j = 1, 2$). Note that the total density is unity:

$$\Sigma_i P_i = 1. \quad (2d)$$

Each term in (2) comes from respective reaction in (2). For example, the first term in the right-hand side of (2a) is originated in the reaction (2a), where the factor 2 denotes that there are two ways for the left-hand side of (2a); that is, S1+G1 and G1+S1.

To obtain the steady-state solution, we set all the time derivatives in (2) to be zero:

$$2vP_{\mathrm{Sj}}P_{\mathrm{Gj}} + 2cP_{\mathrm{Sj}}P_{\mathrm{Ej}} = mP_{\mathrm{Sj}}, \quad (3a)$$

$$2(P_{\mathrm{G1}} + P_{\mathrm{G2}})P_{\mathrm{Ej}} = 2vP_{\mathrm{Sj}}P_{\mathrm{Gj}} + mP_{\mathrm{Gj}}, \quad (3b)$$

$$m(P_{\mathrm{Gj}} + P_{\mathrm{Sj}}) = 2c(P_{\mathrm{S1}} + P_{\mathrm{S2}})P_{\mathrm{Ej}}$$
$$+2(P_{\mathrm{G1}} + P_{\mathrm{G2}})P_{\mathrm{Ej}} \quad (3c)$$

If we put

$$P_{\mathrm{S}} = P_{\mathrm{S1}} + P_{\mathrm{S2}},$$
$$P_{\mathrm{G}} = P_{\mathrm{G1}} + P_{\mathrm{G2}},$$
$$P_{\mathrm{E}} = P_{\mathrm{E1}} + P_{\mathrm{E2}},$$

then we can easily obtain non-trivial densities in stationary state. It follows that

$$P_{\mathrm{S}} = 1/\alpha - 2m/v, \quad (4a)$$

$$P_{\mathrm{G}} = 2m/v - c/\alpha, \quad (4b)$$

$$P_{\mathrm{E}} = v/\alpha, \quad (4c)$$

where $\alpha = 1 + v - c$.

In Figure 5, steady-state densities for island model is depicted. Figure 5 predicts the following results:

1) When the extinction rate m of species takes large values, then specialists go extinct.

Figure 3. Steady-state densities for island model. The densities are theoretically given by equation (4). The horizontal axis denotes (a) the mortality rate m, or (b) the colonization rate c of specialist. The symbols S_j, G_j and E_j have the same meanings as in Figure 2.

2) When the colonization rate c of specialists takes large values, then the generalist goes extinct.

Hence, we can roughly discuss the stability of island model. Since S is stronger than G, the cyclic balance similar to the paper-scissors-rock game is necessary as follows: E is stronger than S, whereas it is weaker than G.

4.   RESULTS OF LATTICE MODEL

Simulations for lattice model (LLVM) are carried out for various values of the parameters c and m. (We fix $v = 1$.) It is found from the simulation that the population dynamics exhibits the stable focus.

In Figure 4, typical population dynamics are illustrated. The lattice system evolves into a stationary state, where all densities become constant in time, but always experience fluctuations. Spatial pattern is also self-organized into a stationary state, but the configuration of patch distribution dynamically varies: the specialists run after the generalist.

In Figure 5, the steady-state densities of six states are plotted against the extinction rate m. It is found from Figure 5 that the steady-state densities of specialists (P_S) decreases with the increase of m. On the other hand, the density of generalist (P_G) increases with m. Such behaviors can be qualitatively predicted by island model (see Figure 3). However, the behavior of P_E differs between lattice and island models: the latter predicts that P_E is independent of m, while in the lattice model, P_E complicatedly depends on m.
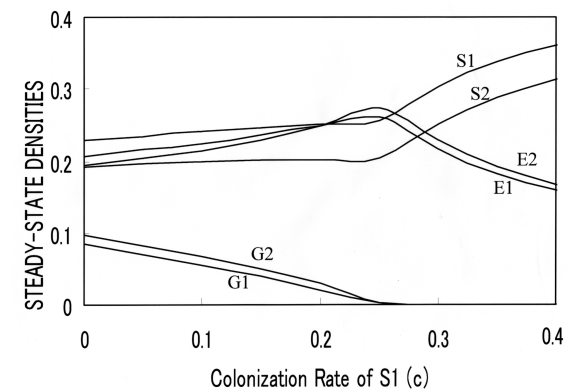
In Figure 6, the steady-state densities are plotted against the colonization rate c of specialists. Figure 6 indicates that the island theory well predicts the dependence of c. If c takes larger values than a critical value c_{crit}, then the generalist goes extinct. This result illustrates that for the stability of lattice model, the cyclic balance similar to the paper-scissors-rock game is necessary. If the parameter c increases, S becomes stronger than E: the cyclic balance is broken. On the other hand, there is qualitative difference between island and lattice models. For example, the density of E1 and E2 are not constant in the lattice model.
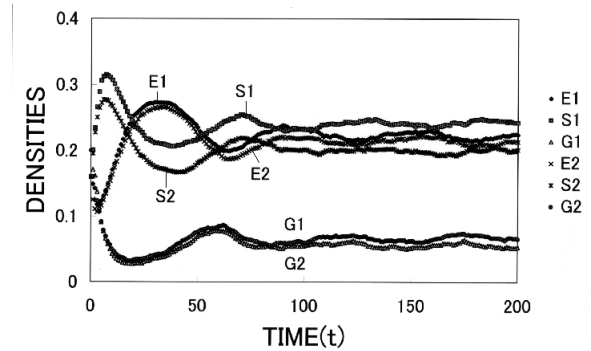
Figure 4. Time dependences of all patches. An example of population dynamics on lattice space are shown. The time is measured by the unit of Monte Carlo step. The system evolves into a stationary state.
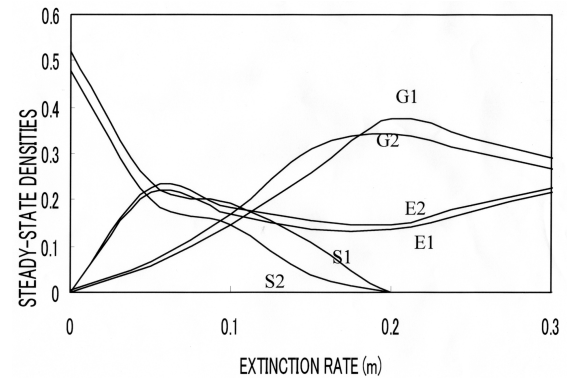
Figure 5. The patch densities in stationary state. The steady-state densities of all patches are plotted against the extinction rate of species (m). If m takes large values, then both specialists go extinct. This is well predicted by mean-field theory.


Figure 6. The steady-state densities are depicted against the colonization rate of specialist S_1 or S_2 (c). If the parameter c takes large values, then generalist goes extinct. This extinction is also predicted by mean-field theory.

5. CONCLUDING REMARKS

In general, competing species can coexist, when they live in different microhabitats (Begon et al., 1996). The species can coexist because of species-specific differentiation in microhabitat. However, such specialists may not always coexist, if they interact with a generalist that can live in a variety of microhabitats. In the present paper, We have developed patch model to study stability of competing specialists that feed on the same generalist. Both island and lattice models reveals that our system does not always stable, and that specialists and generalist coexist under a cyclic balance similar to the paper-scissors-rock game (Figure 7). The specialist S is always stronger than G, while it is changed to E. On the other hand, G can easily colonizes into the empty patch E.

For example, the stability in Figure 6 can be roughly explained by the rule of paper-scissors-rock game. If the parameter c takes small values, then generalist (G) goes extinct, where this parameter denotes the colonization rate of specialist S_1. Namely, in the case of a large value of parameter c, the net flow from S to E becomes weak. Hence the cyclic balance is broken: this lead to the extinction of generalist (G). On the other hand, when the parameter c takes small values, no extinction occurs. In such cases, the cyclic balance always holds. Finally, it should be emphasized that two types of extinction shown in Figures 5 and 6 are well predicted by mean-field theory (Figure 3).
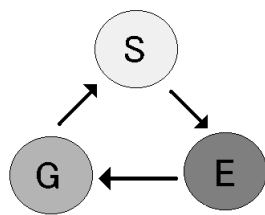
Figure 7. Mechanism of stability. Specialists (S) are stronger than generalists (G). On the other hand, generalists (G) have a skill that can get a variety of resources; G has higher ability of colonization than S to get empty patches (E). Hence, this cyclic balance just corresponds to the paper-scissors-rock game.

6. REFERENCES

Begon, M., J. L. Harper, and C. R. Townsend. *Ecology*. Blackwell Science, Oxford, 1996.

Boorman, S. A. and P. R. Levitt. *The Genetics of Altruism*. Academic Press, New York, 1980.

Caswell, H. and J. E. Cohen. Red, white and blue:environmental variance spectra and coexistence in metapopulations. *J. theor. Biol.*, 176: 301–316, 1995.

Durrett, R. and S. Levin. The importance of being discrete (and spatial). *Theor. popul. Biol.*, 46: 363–394, 1994.

Hanski, I. and M. Gilpin. *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, San Diego, 1997.

Hassel, M. P., H. N. COMINS, and R. M. MAY. Spatial structure and chaos in metapopulation dynamics. *Nature*, 353:255–258, 1991.

Hofbauer, J. and K. Sigmund. *The theory of evolution and dynamical systems*. Cambridge Univ. Press, Cambridge, 1988.

Levin, S. A. Dispersion and population interactions. *Am. Nat.*, 108:202–228, 1974.

Levins, R. Some demographic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. America*, 15:237–240, 1969.

MacArthur, R. Population ecology of some warblers of north eastern coniferous forests. *Ecology*, 39:599–619, 1958.

Matsuda, H., N. Ogita, A. Sasaki, and K. Sato. Statistical mechanics of population: the lattice lotka-volterra model. *Prog. theor. Phys.*, 88:1035–1049, 1992.

Maynard Simith, J. *Evolutionary Genetics*. Cambridge Univ. Press., Cambridge, 1982.

Tainaka, K. Lattice model for the lotka-volterra system. *J. Phys. Soc. Jpn.*, 57:2588–2590, 1988.

Tainaka, K. Stationary pattern of vortices or strings in biological systems: lattice version of the lotka-volterra model. *Phys. Rev. Lett.*, 63:2688–2691, 1989.

Wilson, D. S. and J. Yoshimura. On the coexistence of specialists and generalists. *American Naturalist*, 144:692–707, 1994.