

Indirect effect of habitat destruction on ecosystems

N. Nakagiri and K. Tainaka^a

^a *Department of Systems Engineering, Shizuoka University, Jyohoku 3-5-1, Hamamatsu, Japan,
nakagiri@kei2.sys.eng.shizuoka.ac.jp*

Abstract: Habitat destruction is one of the primary causes of species extinction in recent history. Even if the destruction is restricted to a local and small area, its accumulation increases the risk of extinction. To study local destruction of habitat, we present a lattice ecosystem composed of prey (X) and predator (Y). This system corresponds to a lattice version of the Lotka-Volterra model, where interaction is allowed between neighboring lattice points. The lattice is partly destroyed, and destructed sites or barriers are randomly located between adjacent lattice points with the probability p . The barrier interrupts the reproduction of X, but the species Y suffers no direct damage by barriers. This system exhibits an extinction due to an indirect effect: when the density p of barriers increases, the species Y goes extinct. On the other hand, an initial suppression of X may later lead to the increase of X. The predator Y decreases in spite of the increase of X. These results cannot be explained by a mean-field theory such as the Lotka-Volterra equation. We discuss that endangered species may become extinct by a slight perturbation to their habitat.

Keywords: indirect effect; lattice model; percolation; perturbation; habitat destruction

1 INTRODUCTION

Human beings have various influences on natural ecosystems. Such influences often cause the loss of biodiversity. In recent years, loss of biodiversity become one of the most important issues in ecology and conservation biology, as a global environmental problem.

In ecological studies of endangered species, over-hunting was considered as a most important factor of extinction. [Wilson, 1992; Soule, 1987; Batabyal, 1998] However, recently environmental and habitat destruction was realized to be an equally important factor causing extinction. [Soule, 1986; Frankel and Soule, 1981; Soule, 1987] Furthermore, such habitat destruction has no possibility of recovery for endangered species unless the destructed habitat is reconstructed that is currently almost impossible. [Frankel and Soule, 1981; Soule, 1987] We also recognize that natural habitats/ecosystems on the earth have been already completely modified and in a sense destructed in part, even in the deep forests of Amazon or ice fields of the North Pole. [Soule, 1986; Frankel and Soule, 1981; Soule, 1987]

Global habitat destruction is always damaging to

the species. The effects of habitat destructions have been studied empirically or theoretically, e.g., species-area curves [MacArthur and Wilson, 1967; Durrett and Levin, 1996; Ney-Nifle and Mangel, 1999] and species-habitat principle [Noss and Murphy, 1995]. But many local (restricted) small destructions should be equally critical to the endangered species.

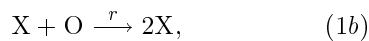
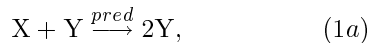
Habitat destruction by man is the fastest of Through out the evolutionary history of life, habitat destruction by man is the fastest and strongest damages on natural ecosystems. The most important cause of extinction in the present days should be habitat destruction directly or not directly. [Frankel and Soule, 1981] This implies that the causal relation between species extinction and local destruction of habitat is very complicated. It may be impossible to know the origin of the extinction because of “the indirect effect” [Yodzis, 1988; Pimm, 1993; Tainaka, 1994; Schmitz, 1997]. The purpose of the present article is to illustrate such an indirect relation between extinction and habitat destruction.

Recently, co-workers in our laboratory presented a papers on “contact percolation process” [Tao et al., 1999]. In this work, the contact process [Harris,

1974; Liggett, 1985, 1994], which denotes birth and death processes of a single species X, was carried out on a partially destroyed lattice. The destroyed sites, or *barriers*, are located on the boundary between neighboring lattice sites, and they represent local destruction of habitat. The reproduction of X is prohibited by barriers. With the increase in the number of barriers, the steady-state density of X is decreased, and eventually X becomes extinct. Namely, this system exhibited a phase transition between a phase where the species survived and a phase where it was extinct. The phase boundary between survival and extinct phases was found to be represented by a scaling law of mean-field theory (MFT). In the present paper, we apply the same destroyed lattice to a more complicated system which contains two kinds of species; through the interaction between both species, the effect of habitat destruction in this system becomes entirely different from that in the contact percolation process.

2 THE MODEL

We focus on a predator-prey system [Hofbauer and Sigmund, 1988; Pacheco et al., 1997; Hance and Van Impe, 1998]. Consider a two-dimensional lattice consisting of two species of prey (X) and predator (Y). Each lattice site is labeled by X, Y, or O, where X (or Y) is the site occupied by prey (or predator), and O represents the vacant site. We assume the following interaction [Hofbauer and Sigmund, 1988; Tainaka and Fukazawa, 1992; Tainaka, 1994; Satulovsky and Tome, 1994; Sutherland and Jacobs, 1994]:



The above reactions respectively represent the predation (*pred*), reproduction of prey (*r*) and the death (d_X, d_Y) of prey and predator.

The destroyed sites, or *barriers*, are put on the boundary (link) between neighboring lattice sites, where the barrier means the local destruction of habitat. For simplicity, we randomly put barriers in such a way that each link has a barrier by the probability p . Thus, p measures the intensity of habitat destruction. We assume that the interactions (1a) and (1b) occurs between adjacent lattice points, and that the barrier prohibits only (1b). Namely, the destruction only disturbs the reproduction of prey

(X); in contrast predators (Y) receive no direct damage. It is well known in the field of physics that the barrier distribution shows *percolation transition* [Stauffer, 1985; Sahimi, 1993]. When p takes an extremely small value, no barriers may connect with each other. On the contrary, when p takes a large value (near unity), almost all barriers are connected. Below, we call *cluster* for a clump of connected barriers, and *percolation* in the case that the largest cluster reaches the whole size of system. The probability of percolation takes a nonzero value, when p exceeds a critical point p_c ; this value is given by $p_c = 0.5$ in our case (*link percolation* in a square lattice). Percolation ecologically means that the habitat region of species X may be fragmented into small segments for $p > p_c$.

We carry out a perturbation experiment [Paine, 1966; May, 1973; Pimm, 1993; Tilman and Downing, 1994; Yokozawa et al., 1999] by computer simulation of a lattice model. In this paper, we apply the lattice Lotka-Volterra model [Tainaka, 1988; Matsuda et al., 1992; Itoh and Tainaka, 1994]. Before the perturbation, the system is assumed to stay in a stationary state of $p = 0$. At time $t = 0$ the barrier density is jumped from zero to a nonzero value of p as schematically. We record the population sizes of both species X and Y for $t > 0$.

Evolution method of lattice model is defined as follows:

(1) Distribute two kinds of species, X and Y, over some square-lattice points in such a way that each point is occupied by only one individual (particle).

(2) Each reaction process is performed in the following two steps.

(i) We perform a single particle reactions (1c) and (1d). Choose one square-lattice point randomly; if the point is occupied by a X (or Y) particle, it will become O by a probability d_X (or d_Y).

(ii) Next, we perform two-body reaction, that is, the reactions (1a) and (1b). Select one square-lattice point randomly, and then specify one of the nearest-neighbor points. The number of these points is called the coordinate number (z); for square-lattice, this is given by $z = 4$. When the pair of selected points are X and O, and when there is no barrier (barrier) between them, then the latter point will become X by a probability r . On the other hand, the barrier never effects the predation of Y: when the selected points are X and Y, the former point becomes Y. 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 a Monte Carlo step [Tainaka, 1988, 1989]. In this paper, we set $L = 100$.

(4) Repeat the step (3) for 1000 – 2000 Monte Carlo steps.

3 MEAN-FIELD THEORY

We first describe theoretical results of MFT which is called Lotka-Volterra equation [Hofbauer and Sigmund, 1988; Takeuchi, 1996]. Time evolution in the mean-field limit ($P_{ij} = P_i P_j$) is represented by

$$\dot{P}_X = -2P_X P_Y + 2r(1-p)P_X P_O - d_X P_X, \quad (2a)$$

$$\dot{P}_Y = 2P_X P_Y - d_Y P_Y, \quad (2b)$$

where P_X , P_Y and P_O are densities of X, Y and O, respectively ($P_O = 1 - P_X - P_Y$), and the dots denote the derivatives with respect to the time t which is measured by the Monte Carlo step [Tainaka, 1988, 1989]. In the above equations, the effect of barrier connection (cluster formation) is neglected; the factor $1 - p$ in (2a) denotes the probability that the barrier is absent. This factor can be obtained from the coordinate number z which is the number of nearest neighbors ($z = 4$ for square lattice). The *effective* coordinate number $\langle z \rangle$ which takes into account the effect of barrier. The mean value $\langle z \rangle$ averaging over z can be obtained by

$$\langle z \rangle = \sum_{z=1}^4 z \binom{4}{z} (1-p)^z p^{4-z}.$$

It follows $\langle z \rangle = 4(1-p)$. Thus, the probability that the barrier is absent is given by $\langle z \rangle / 4 = (1-p)$.

The densities of both P_X and P_Y reach the stationary values. When $d < 2$, they are expressed by

$$P_X = \frac{d_Y}{2}, \quad P_Y = \frac{r(1-p)(1 - \frac{d_X}{2} - \frac{d_Y}{2r(1-p)})}{1 + r(1-p)}. \quad (3)$$

When $d > 2$, we have $P_X = 1$ and $P_Y = 0$. According to the linear stability analysis [Hofbauer and Sigmund, 1988], the steady-state densities (3) are stable in the case $d < 2$. Hence, we can answer the result of the perturbation experiment. Just after

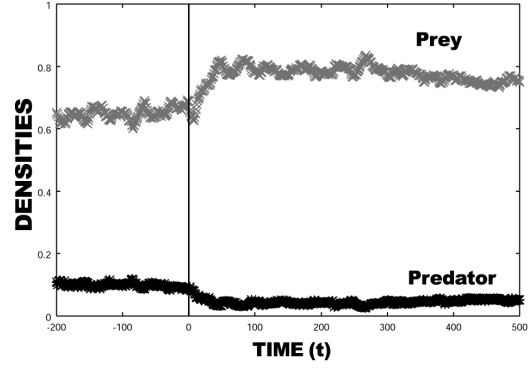


Figure 1: An example of population dynamics for the lattice model (100×100). The time dependence of both species X and Y are shown, where the applied perturbation is that the barrier density p is jumped from zero to 0.2. We put $r = 0.5$, $d_X = 0.05$ and $d_Y = 0.6$. Perturbation starts at $t=0$.

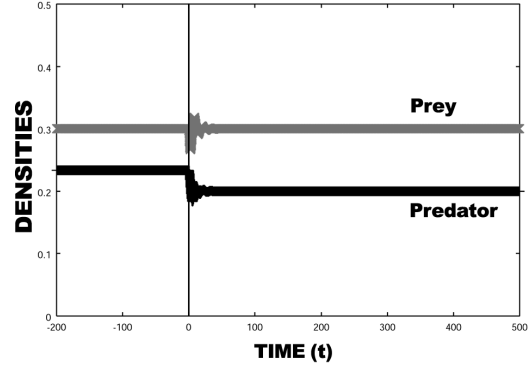


Figure 2: Same as Fig. 1, but the result of MFT. Perturbation starts at $t=0$.

the perturbation, the abundance of prey X always decreases (short-term response), but the steady-state density of X is unchanged by p ; during a long period, the prey population recovers the same density as before the perturbation (long-term response). On the other hand, the steady-state density of Y is decreased with increasing p . Note that Y never becomes extinct for any value of p ($0 < p < 1$).

4 SIMULATION RESULTS

We describe the result of perturbation experiments in the lattice model. Before the perturbation, the system is assumed to be in a stationary state. After the perturbation, the system changes into the other stationary state. In Fig. 1, a typical example of time dependence of densities of both species is plotted,

where the value of p is jumped from 0 to 0.2 at time $t = 0$. Just after this perturbation, the prey X decreases, but later, it increases in a new stationary state. Fig. 2 shows the result of mean field theory is also depicted. The theory predicts that the prey X increases in a new stationary state after it decreases. In Fig. 3, typical spatial patterns in stationary state are illustrated for several values of p . It is found that the steady-state density of Y decreases with increasing p ; in particular, Y becomes extinct for large values of p . Figures 4 and 5 show the plots of densities of both species X and Y in the stationary states for various value of p , where the results of MFT is also depicted. The lattice model in Figs. 4 and 5 reveals the following results:

- i) With the increase of barrier density p , the density P_Y of predator decreases. Especially, when $p > p_0$, the predator becomes extinct.
- ii) The prey density P_X increases with p , and it takes the maximum value at $p = p_0$. When $p > p_0$, the prey density conversely decreases with p .

The species Y goes extinct, even though it suffers no direct damage by barriers, and there exist a lot of prey. Moreover, we find from Figs. 4 and 5 that the density P_X (or P_Y) for the lattice model is much larger (or smaller) than that predicted by MFT.

When the species Y becomes extinct ($p > p_0$), our system (1) is represented only by reaction (1b). It is therefore thought that the prey (X) occupies the whole lattice points. Nevertheless, this argument is not true: X cannot increase, since the fragmentation of habitat of X becomes severe for a large value of p . In particular, when p exceeds the percolation transition p_c ($p_c = 1/2$), the prey X is enclosed in small segments. Hence, the prey density decreases with increasing p (Fig. 4). In the theory (MFT), the effect of fragmentation is not taken into account.

5 CONCLUSION

In summary, we have developed a model ecosystem consisting of prey X and predator Y . The destroyed sites or barriers represents the local destruction of habitat as introduced in the contact percolation process [Tao et al., 1999]. The system in the present article exhibits an extinction due to indirect effect: although predators suffer no direct damage by the destruction, they go extinct. In both cases of the present model and contact percolation process, the barriers give the same influence on

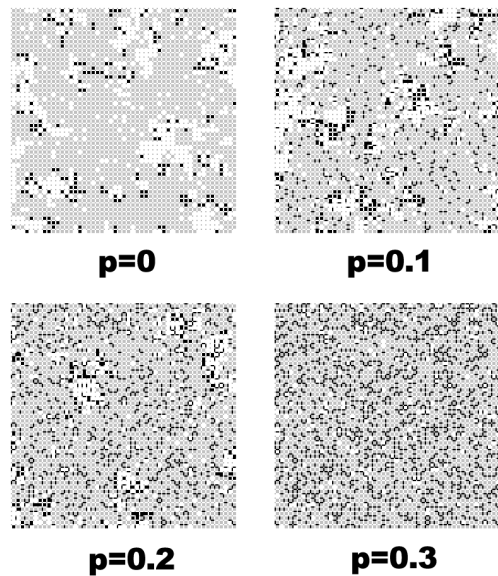


Figure 3: Typical spatial patterns of lattice model for various values of p ($r = 0.5$, $d_X = 0.05$ and $d_Y = 0.6$). The grey and black mean the sites occupied by X and Y , respectively; and the white represents the vacant site (O).

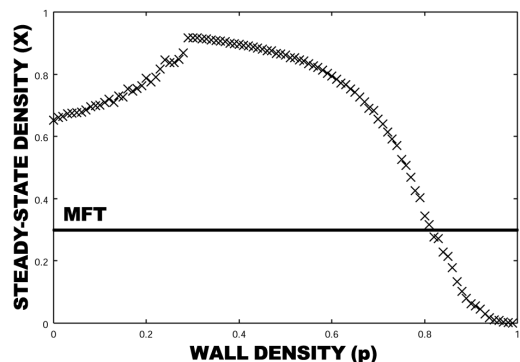


Figure 4: The steady-state density of species X is plotted against the barrier density p ($r = 0.5$, $d_X = 0.05$ and $d_Y = 0.6$). The theoretical results of the MFT is also shown. Each plot is obtained by the long-time average in the stationary state ($200 < t \leq 1000$) with 100×100 lattice.

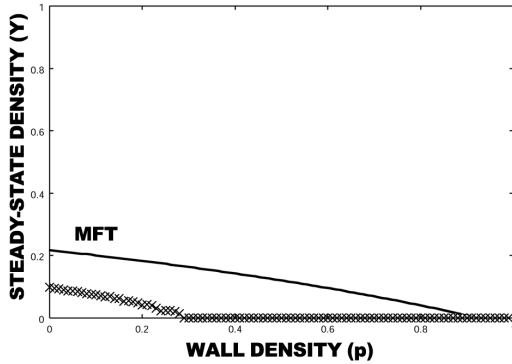


Figure 5: Same as Fig. 4, but the vertical axis denotes the steady-state density of species Y.

the short-term response of species X. However, the long-term effect of barriers are entirely different between both models: in the contact percolation process, the steady-state density of X was intuitively decreased by the increase of the number of barriers. On the other hand, in the case of the present model, an initial damage and suppression of prey X may later lead to enhancement of the prey population; the steady-state density of X increases with p (see Fig. 4 for $p < p_0$). In this article, we put $r = 0.5$, $d_X = 0.05$ and $d_Y = 0.6$. For other values of parameters r and d , the species Y (X) usually decreases (increases). The MFT never sufficiently explain results of our simulation.

In the absence of predators ($p > p_0$), prey conversely decrease. This result is related to the percolation transition [Stauffer, 1985; Sahimi, 1993]. When p takes an extremely small value, no barriers may connect with each other. On the contrary, when p takes a large value, almost all barriers are connected. The probability of percolation takes a nonzero value, when p exceeds a transition point p_c ; $p_c = 0.5$ in our lattice. With increasing p , the prey X is therefore enclosed in small segments (see Fig. 3). In particular, p exceeds the percolation transition p_c ($p_c = 1/2$), the habitat region of X becomes small. Hence, the prey density decreases with increasing p (Fig. 4). In the system (1), the death process of X is ignored. If we introduce the death of X, then this species may go extinct for $p > p_c$.

The extinction of predator (Y) observed in simulation thought to be understood by the following argument: The only way that species Y may reproduce is by consuming X. A domain containing only Y is unstable, due to the death of predators [reaction (1c)]. The species Y will eventually die out, unless there is an influx of prey (X) into the region. As the den-

sity p of barriers increases, such an influx thought to become impossible, and Y goes extinct. However, this argument is not completely correct, since the steady-state density of prey increases with the increase of p . More refined theories and arguments are necessary to explain the extinction of Y.

So far, we considered the press perturbation that the barrier density is jumped from zero to a nonzero value of p . Now we can consider more general cases; namely, p is increased from p_1 to p_2 . If $p_1 < p_0 < p_2$ is satisfied, then the species Y becomes extinct; no matter how the difference $p_2 - p_1$ is small, the extinction occurs. When there is an endangered species, it may become extinct by a slight perturbation to its habitat.

In conclusion, we emphasize that the approaches of modeling and simulation are useful to study the real relationships between habitat destruction and species extinction. At least we can count the following three advantages of the present approach over empirical studies: (i) in our case of theory or simulation, we have found the true cause of extinction; in the present work, Y goes extinct by the increase of p . In wild habitats, however, no one may believe such an indirect effect, since the prey population increases. (ii) in real ecosystems, it takes a very long time to know the long-term response. (iii) we cannot carry out real experiments of extinction, if species is to be conserved.

As we show, indirect extinction is easily happen in a simple ecosystem. Real ecosystems are far more complex than any ecosystem models. However, the basic principle should be same in any ecosystem. Our results suggest that indirect effects may play an important role in habitat destruction. Many known unexpected extinction may be due to such an indirect effect in an ecosystem. Therefore, we should keep in mind that the conservation of a species (especially an endangered species) may not be achieved without the conservation of the whole ecosystem in which the species inhabits. Thus we state that the conservation of the entire ecosystem is the only certain method of conserving the species inhabiting in it.

REFERENCES

- Batabyal, A. An optimal stopping approach to the conservation of biodiversity. *Ecological Modelling*, 105:293–298, 1998.
- Durrett, R. and S. Levin. Spatial model for the species-area curves. *J. Theor. Biol.*, 179:119–127,

- 1996.
- Frankel, O. and M. Soule. *Conservation and evolution*. Cambridge Univ. Press, Cambridge, 1981.
- Hance, T. and G. Van Impe. The influence of initial age structure on predator-prey interaction. *Ecol. Mod.*, 114:195–211, 1998.
- Harris, T. Contact interaction on a lattice. *Ann. Prob.*, 2:969–988, 1974.
- Hofbauer, J. and K. Sigmund. *The theory of evolution and dynamical systems*. Cambridge Univ. Press, Cambridge, 1988.
- Itoh, Y. and K. Tainaka. Stochastic limit cycle with power-law spectrum. *Phys. Lett. A*, 189:37–42, 1994.
- Liggett, T. *Interacting Particle Systems*. Springer-Verlag, Berlin, 1985.
- Liggett, T. *Phase transition of interacting particle systems*. World Scientific, Singapore, 1994.
- MacArthur, R. and E. Wilson. *The theory of island biogeography*. Princeton Univ. Press, Princeton, NJ, 1967.
- 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.
- May, R. M. *Stability and Complexity in Model Ecosystems*. Princeton Univ. Press, Princeton, 1973.
- Ney-Nifle, M. and M. Mangel. Species-area curves based on geographic range and occupancy. *J. Theor. Biol.*, 196:327–342, 1999.
- Noss, R. F. and D. D. Murphy. Endangered species left homeless in sweet home. *Conserv. Biol.*, 9: 229–231, 1995.
- Pacheco, J., C. Rodriguez, and I. Fernandez. Hopf bifurcations in predator-prey systems with social predator behavior. *Ecol. Mod.*, 105:83–87, 1997.
- Paine, R. Food web complexity and species diversity. *Amer. Nat.*, 100:65–75, 1966.
- Pimm, S. *Discussion: understanding indirect effects: is it possible? In: Mutualism and Community Organization*. Oxford Univ. Press, Oxford, kawanaabe, h., cohen, j. e. and iwasaki, k. edition, 1993.
- Sahimi, M. *Applications of percolation theory*. Taylor & Francis, London, 1993.
- Satulovsky, J. E. and T. Tome. Stochastic lattice gas model for a predator-prey system. *Phys. Rev. E*, 49:5073–5079, 1994.
- Schmitz, O. Press perturbations and the predictability of ecological interactions in a food web. *Ecology*, 78:55–69, 1997.
- Soule, M. *Conservation biology*. Cambridge Univ. Press, Cambridge, 1986.
- Soule, M. *Viable populations for conservation*. Cambridge Univ. Press, Cambridge, 1987.
- Stauffer, D. *Introduction to percolation theory*. Taylor & Francis, London, 1985.
- Sutherland, B. and A. Jacobs. Self-organization and scaling in a lattice prey-predator model. *Complex Systems*, 8:385–405, 1994.
- 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.
- Tainaka, K. Intrinsic uncertainty in ecological catastrophe. *J. theor. Biol.*, 166:91–99, 1994.
- Tainaka, K. and S. Fukazawa. Spatial pattern in a chemical reaction system: prey and predator in the position-fixed limit. *J. Phys. Soc. Jpn.*, 61: 1891–1894, 1992.
- Takeuchi, Y. *Gloval dynamical properties of lotka-voltera systems*. World Scientific, Singapore, 1996.
- Tao, T., K. Tainaka, and H. Nishimori. Contact percolation process: contact process on a destructed lattice. *J. Phys. Soc. Jpn.*, 68:326–329, 1999.
- Tilman, D. and J. Downing. Biodiversity and stability in grassland. *Nature*, 367:363–365, 1994.
- Wilson, E. *The diversity of life*. Harvard Univ. Press, Cambridge, MA., 1992.
- Yodzis, P. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology*, 69:508–515, 1988.
- Yokozawa, M., Y. Kubota, and T. Hara. Effects of competition mode on the spatial pattern dynamics of wave regeneration in subalpine tree stands. *Ecol. Mod.*, 118:73–86, 1999.