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Lattice models of habitat destruction in a prey-predator system

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Abstract: In recent decades, species extinction has become one of the most important issues in ecology and conservation biology. Such extinctions are mainly caused by habitat destruction. The destruction has no possibility of recovery for endangered species unless the destroyed habitat is restored. Furthermore, even if the destruction is restricted to a local area, its accumulation increases the risk of extinction. Habitat destruction not only reduces the habitat area but also fragments the habitat. In the present article, we introduce three types of destruction models. i) Bond destruction: the fragmentation occurs, but habitat area is never reduced. ii) Random site destruction: both fragmentation and area loss occur. iii) Rectangular site destruction: the habitat area is reduced, but fragmentation never occurs. We apply a lattice system composed of prey and predator, and compare the effects of the three types of habitat destructions. Simulations reveal that outcomes entirely differ for the different models. The density of prey or predator undergo complicated changes by destructions. The habitat fragmentation is much more serious for species extinction than the area loss of habitat. In our simulation, extinction only occurs for fragmentation models. For the random site destruction, we universally obtain a "40% criterion": when the proportion of destroyed sites exceed percolation transition (40%), the risk of species extinction suddenly increases. Moreover, we find an asymmetric effects on predator and prey. In all destruction models, the steady-state density of predator tends to decrease with the increase of the magnitude (D) of the destruction. In contrast, the effect on prey is rather opposite: prey density usually increases with increasing D.

Keywords: *Stochastic cellular automaton, area loss of habitat, habitat fragmentation, prey and predator, percolation transition*

1. INTRODUCTION

In recent years, species extinction has become one of the most important issues in conservation biology. In ecological studies of endangered species, habitat destruction has been confirmed as an important factor causing extinction (Frankel and Soule, 1981; Soule, 1987; Wilson, 1992; Ryall and Fahrig, 2005). Furthermore, such habitat destruction has no possibility of recovery for endangered species without intervention (Noss and Murphy, 1995).

To explore the effect of habitat destruction, several approaches have been studied (Tilman and Downing, 1994; Bascompte and Sole, 1997; Ryall and Fahrig, 2006; Alwan, 2011; Coudrain et al., 2013). The first example is the area reduction of habitat. When the area is decreased, the total number of species is reduced ("species-area curve") (Arrhenius, 1921). The second example is random site destruction on a lattice (Tilman et al., 1997; Ives et al., 1998; Bascompte and Sole, 1998; Hiebeler, 2000; Liao et al., 2013). In this case, species cannot live in destroyed site (cell). The third example is bond destruction, where the interaction (link) between neighboring cells is prohibited (Tao et al., 1999; Nakagiri et al., 2001a; 2001b; 2005; 2010; Nakagiri and Tainaka, 2004). These models have been separately studied under restricted conditions. In the present paper, we deal with various destruction models and compare the effects of the type of destruction. It is found that the effect of habitat destruction is entirely differ if the type of destruction is changed.

In the next section, we describe a prey-predator system, and explain three main and nine sub-models of habitat destruction. Section 3 is devoted to the reporting of the simulation results. It is found that the habitat fragmentation is much more serious for species extinction than the habitat loss. In most cases, the density of predator is decreased with the increase of destruction ratio (D). In contrast, prey density tends to increase with increasing D. However, if predator goes extinct, prey decreases with increasing D. In the final section, we discuss the relation between habitat destruction and the critical conditions of survival.

2. THE MODEL

2.1. Prey-predator system

Consider a preys and predators on a lattice. Birth and death processes update the lattice:

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

$$\mathrm{X} + \mathrm{O} \rightarrow 2\mathrm{X} \qquad (\text{rate: } r), \qquad (1b)$$

$$j \rightarrow \mathrm{O} \qquad (\text{rate: } m_j), \qquad (1c)$$

where X, Y and O denote prey, predator and empty cells (j=X or Y). The reactions (1a) and (1b) are birth processes of species Y and X, respectively; the parameter p is the predation rate of Y and r is the reproduction rate of X. The death process is defined by (1c), where m_j is the mortality rate of species j.

Simulations are carried out as follows:

1. Initially, we randomly distribute two kinds of species, X and Y on a square-lattice in such a way that each lattice site is occupied by only one individual. Here, we employ periodic boundary conditions.
2. Each reaction process is performed in the following two-step process:
   (1) We perform birth processes (1a) and (1b). Choose one cell randomly, and then specify its adjacent sell. For example, when the pair of selected cells are occupied by Y and X, then the cell X will become Y by the rate *p*. When *p*=2, the step of *p*=1 in probability is repeated twice.
   (2) Next we perform the death process (1c). Choose one square-lattice site randomly. If the site is occupied by species j, then it becomes O by the rate m_j.
3. Repeat steps (1) and (2) for 3000 Monte Carlo steps (MCS), where 1 MCS means that both steps (1) and (2) are repeated *L*x*L* times (Tainaka, 1988; 1989; Tainaka and Nakagiri, 2000). Here, lattice size (*L*) is set to $L = 100$.

2.2. Destruction scenario

Models of habitat destruction are classified into three main cases:

i) Bond destruction,

ii) Random site destruction,

iii) Rectangular site destruction.

In the model i), a destroyed bond ("barrier"), located at the boundary between two neighboring cells, prohibits the interactions between both cells. The boundary becomes a barrier with probability D . Hence, the habitat area is never reduced for bond destruction. Note that there are three possibilities for bond destruction: the barrier prohibits reaction (1a), reaction (1b), or both reactions (1a) and (1b). If the barrier only disturbs reaction (1a), we say that the destruction only disturbs the predator. This is because reaction (1a) only affects the birth process of predator. Hence, the bond destruction contains three sub-models: the barrier disturbs predator, prey and both species.

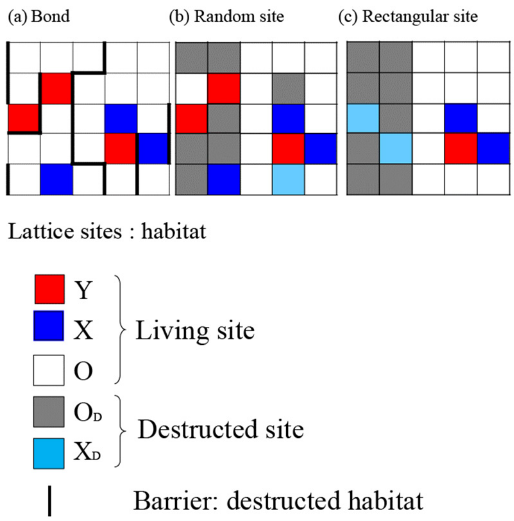

Figure 1. Schematic depiction of the type of habitat destruction. (a) bond destruction, (b) random site destruction, and (c) rectangular site destruction. In (a), thick lines denote "barriers" which prohibit the interactions between both sides of cells. Both (b) and (c) display site destruction, where predator cannot live.

In model ii), each cell is destructed with probability D ; species cannot live in a destroyed site. The site destruction model also has three types of sub-models: predator, prey or both species cannot live inside the destroyed site. In model iii), the site (cell) is also destroyed with the probability D , but all destroyed sites are arranged to form a rectangular. Figure 1 illustrates three types of destruction. In Figure 1 (a), bond-destruction model is displayed; the interaction between adjacent cells are prohibited. The barrier is randomly put with probability D. Each site (cell) takes one of three states: prey (X), predator (Y) and empty (O). Figure 1 (b) and (c) show a site-destruction model; in these cases, the destruction only disturbs the survival of predator. Each cell is thus one of four states: prey, predator, empty and destroyed cells. The destroyed cell is either X_D or O_D. Here X_D (O_D) denotes the destroyed cell in which prey (no species) survives. In Figure 1 (b), we randomly arrange destroyed sites with probability D. In Figure 1 (c), the destroyed cells are arranged to form a rectangle. Hence, both site destruction models ii) and iii) cause area loss of habitat. In the models i) and ii), the habitat fragmentation occurs.

3. RESULTS

3.1. Case that bond destruction disturbs only predators

First, we report the case that bond destruction only disturbs the birth process of predator [reaction (1a)]. In Figure 2, a typical result of bond destruction is depicted, where both densities of prey (blue) and predator (red) are plotted. By an external factor (perturbation), the value of D is suddenly increased from 0 to 0.3 at $t = 0$. Before the perturbation ($t < 0$), the system stays in an equilibrium. We say "equilibrium" (or stationary state), when all densities take almost constant values. Just after the perturbation, the density of predator (Y) decreases, but later it increases in a new equilibrium. In spite of the increase of D , the density of Y eventually increases (paradox). This paradox can be explained as follows: by the perturbation, the prey density increases, so that the predators easily catch preys at new equilibrium.

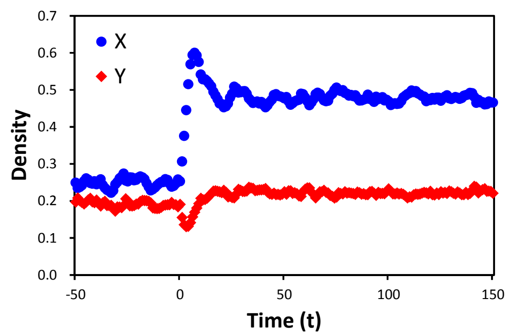

Figure 2. A typical result of bond destruction which disturbs the birth process of predator only [reaction (1a)]. The time course of both species X (blue) and Y (red) are depicted. At t=0, the destruction ratio D (barrier density) suddenly increases from 0 to 0.3. We set r=1.0, p=2.0, $m_X = 0.05$ and $m_Y = 0.6$ (100×100 lattice).

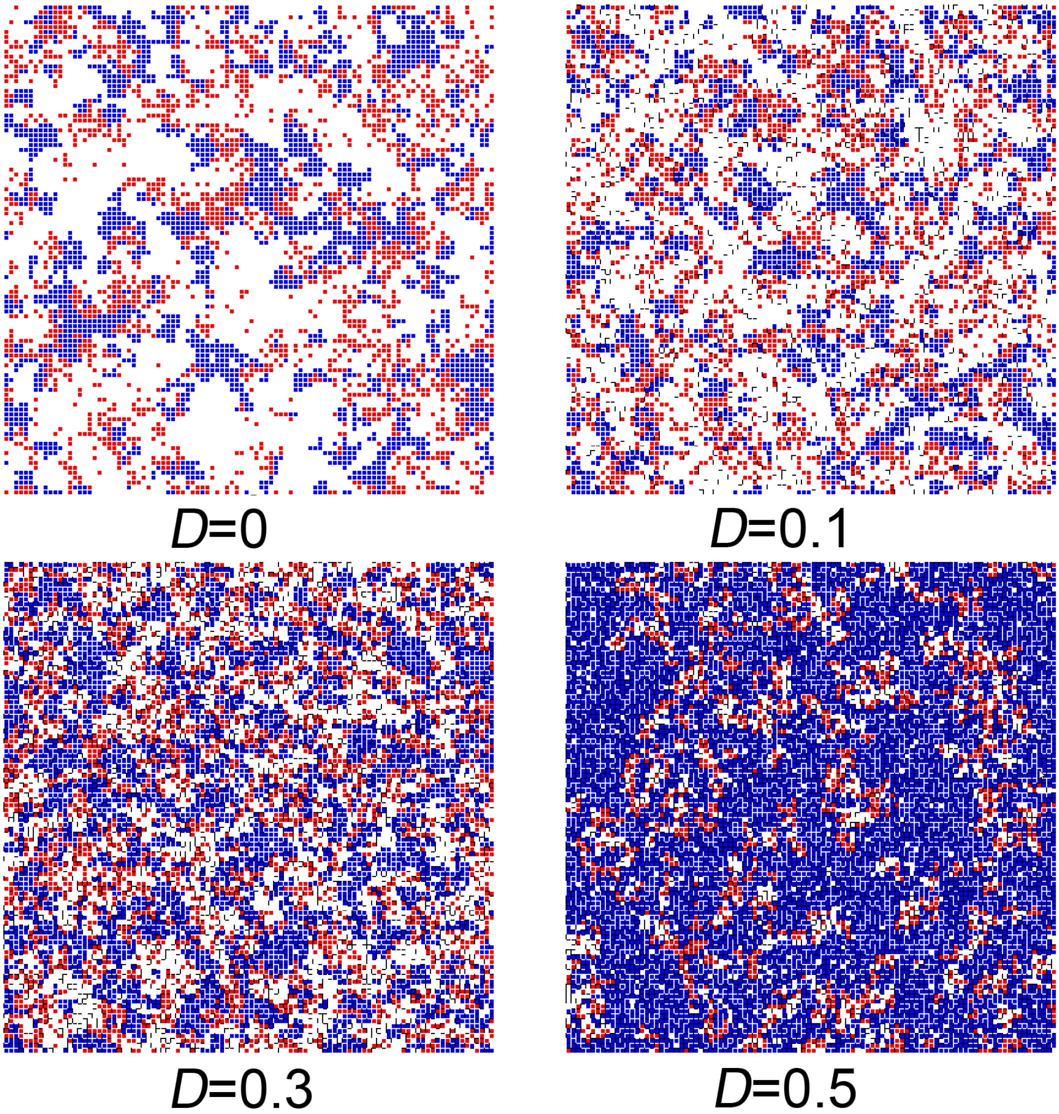

Figure 3. Typical spatial patterns in the stationary state for four bond rates D (t=3000). Bond destruction only disturbs the birth process of the predator. The prey (X), the predator (Y) and empty (O) sites are indicated by blue, red and white, respectively. Barriers are represented by thick black lines.

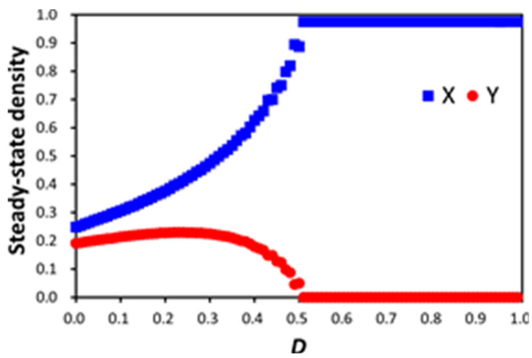

Figure 4. The steady-state densities of prey $x(eq)$ and predator $y(eq)$ are plotted against D. Each plot is obtained by the long time average in the stationary state (2000 $\leq$ t<3000).

Figures 3 and 4 display the spatial pattern and both densities at equilibrium, respectively. When the value of *D* increases, the density of predator (red color) sensitively changes. When *D* exceed the threshold ($D \approx 0.51$), predators go extinct, and almost all cells are occupied by prey (blue color).

3.2. Cases of site destructions

Next, we report cases for random and rectangular site destruction which disturb only predators. In Figures. 5 and 6, simulation results at equilibrium are illustrated. In the case of random site destruction, predators go extinct at $D \approx 0.46$. This value of *D* is less than the extinction point for bond destruction $(D \approx 0.51)$. In the case of rectangular site

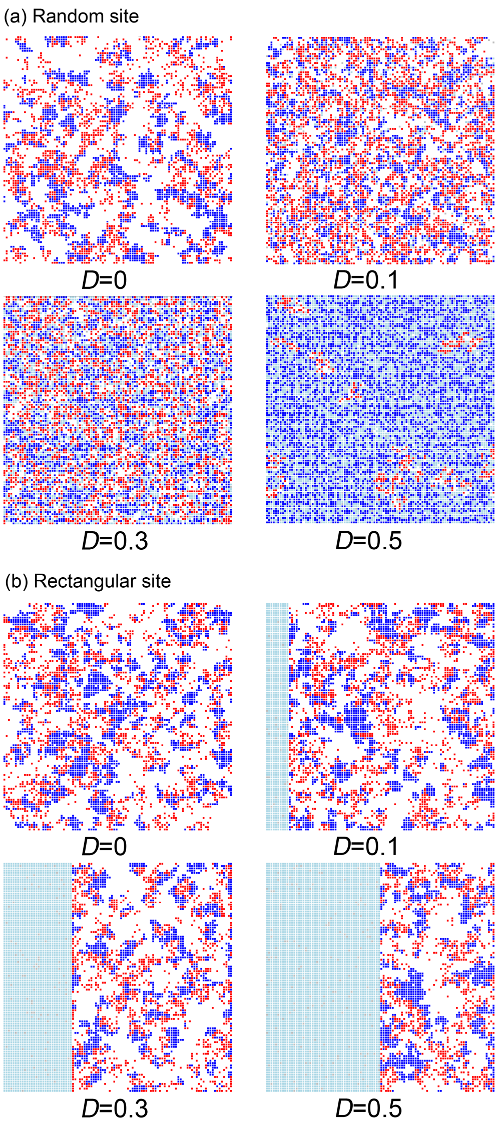

Figure 5. Same as Figure 3, but for the site destructions. (a) random site destruction. (b) rectangular site destruction. The destruction disturbs only predators.

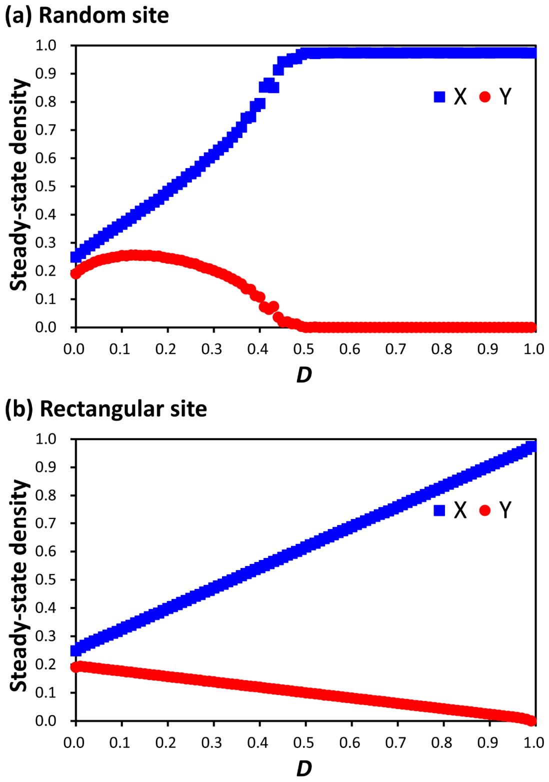

Figure 6. Same as Figure 4, but for the site destructions. (a) Random site destruction, (b) rectangular site destruction. The destruction disturbs only predators.

destruction, predators survive ($D \approx 0.99$). Heretofore, destruction disturbs only predators. It is found that habitat fragmentation is much more serious for species extinction than area loss.

3.3. General cases

We report results in general cases. The effects of habitat destructions are summarized in Table 1. Here both $x(eq)$ and $y(eq)$ mean the equilibrium densities of prey (X) and predator (Y), respectively; the sign + (or –) denotes that the density increases (or decreases) with increasing D. The symbol ± means the case as in Figure 4: $y(eq)$ increases, but later it decreases with the increase of D. Figure 7 illustrates the results, where the destruction disturbs both prey and

Table 1. Change of equilibrium densities with increasing of D.

Destruction	(a) Bond destruction			(b) Random site			(c) Rectangular site		
Disturbance	Predator	Prey	Both	Predator	Prey	Both	Predator	Prey	Both
Figures	Figure 4		Figure7a	Figure6a		Figure7b	Figure6b		Figure7c
$x(eq)$	+	±	±	±	±	±	+	−	−
$y(eq)$	±	−	−	±	−	−	−	−	−

predator. In these cases, the steady-state density of predator simply decreases with the increase of D. The critical ratios that predators go extinct are found at $D \approx 0.4$, $D \approx 0.32$ and $D \approx 0.97$ for Figure 7 (a), (b) and (c), respectively. Hence, we obtain the same outcome that the fragmentation is much more serious for species extinction compared to the area loss without fragmentation. The prey density shows more complicated behavior (Table 1). When predators survive, the steady-state densities of prey increases with D for fragmentation models (a) and (b); however, it decreases with D in the absence of predator. On the other hand, the effect of rectangular site destruction is simple: both species decrease with the increase of D [Figure 7 (c)].

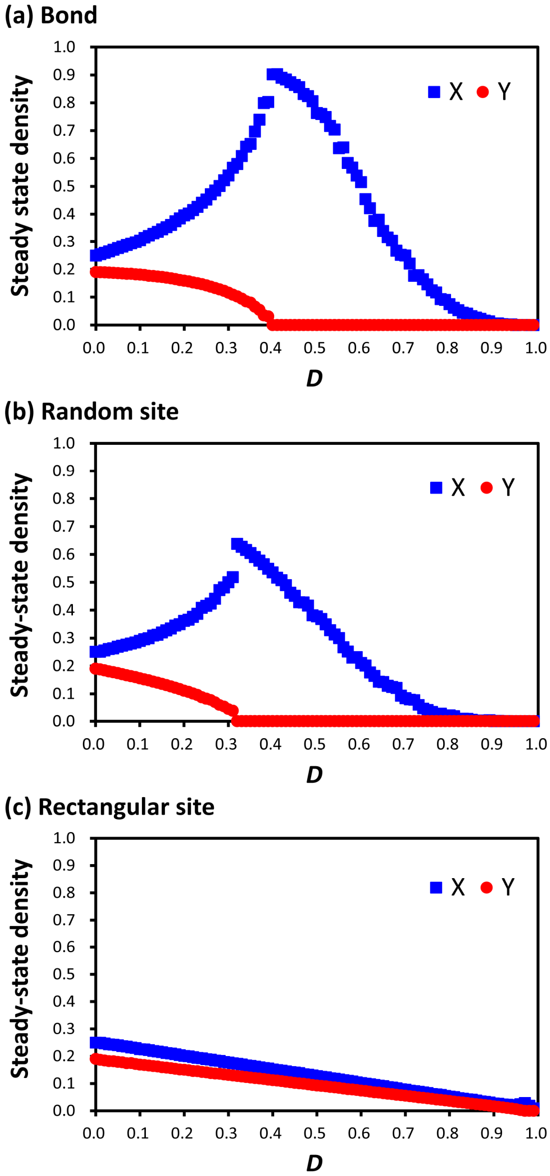

Figure 7. Effects of habitat destructions. The bond or site destruction prohibits the birth processes of both species. (a) Bond destruction, (b) random site destruction, and (c) rectangular site destruction. The steady-state densities are plotted against the ratio *D*.

4. CONCLUSION AND DISCUSSIONS

Habitat destruction is a key determinant of species extinction. Its main factors are habitat fragmentation and area loss (Ryall and Fahrig, 2006). We apply various destruction models to a prey-predator system. Computer simulations reveal that the habitat fragmentation is much more serious for species extinction than area loss. The effect of destruction is not simple. The density of prey or predator changes in complicated ways due to the increase in destruction ratio (D). The steady-state densities also change in various ways (Table 1). In general, the equilibrium density $y(eq)$ of the predator has a tendency to decrease with increasing D. On the other hand, the steady-state density $x(eq)$ of the prey always increase with D, so long as predators survives. When predators go extinct, the response becomes opposite; namely $x(eq)$ tends to decrease.

We discuss the relation between habitat destruction and the critical conditions of survival. The extinction closely related to the fragmentation of habitat. It is also associated with "percolation transition" in physics (Stauffer, 1994; Nakagiri et al., 2005). The percolation transition occurs at D>1/2 for bond destruction, and D≈0.6 for random site destruction. When the destroyed rate (D) exceeds the transition point, the largest cluster (connection) of destroyed bonds or sites can reach the system size. In the case of bond destruction, the habitat fragmentation can occur for D>1/2. On the other hand, in the case of random site destruction, the percolation of destroyed cells can occur for $D>0.6$. Similarly, the habitable cells also percolate (connect), when $(1-D)>0.6$. In other word, the fragmentation of habitat occurs, when D is larger than 0.4. Thus we lead to the "40% criterion": when the proportion of destroyed site exceeds about 40%, species suddenly faces extinction. This criterion is also observed in other models (Sakisaka et al., 2010).

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