

Effects of habitat destruction in model ecosystems: Parity law depending on species richness

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ABSTRACT

Habitat destruction is one of the primary causes of recent mass extinction of biospecies. Even if the destruction is limited to a local and small area, the cumulative destruction increases the risk of extinction. In this paper, we explore the effect of habitat destruction in lattice ecosystems composed of multiple species. Simulations reveal a parity law: the response of the system shows different behaviors by whether the species richness of system is even or odd. The mean-field theory partially predicts such a parity law.

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1. Introduction

Many species go extinct in recent history; one of main causes of such a mass extinction is the destruction of habitat (Frankel and Soule, 1981; Wilson, 1992; Tilman and Downing, 1994; Seabloom et al., 2002; Montoya et al., 2008). Even if the destruction is restricted within a local and small area, its accumulation increases the risk of extinction (Bascompte and Sole, 1996; Boswell et al., 1998; Tilman et al., 1997; Nakagiri et al., 2001a). The many researchers have studied a cause of the extinction under the local destruction of habitat (Bascompte and Sole, 1998a; Ryall and Fahrig, 2005, 2006).

It has been found that a cause-and-effect relation between the destruction of the habitat and extinction is not so simple (Nakagiri et al., 2001a,b, 2005; Nakagiri and Tainaka 2004; Su et al., 2009). Due to the so-called “indirect effect” (Yodzis, 1988; Heithaus et al., 2008), the long-term response of ecosystem to external perturbations (stresses) becomes usually complicated. However, the so-called “parity law” is one of exceptional cases: the long-term response can be roughly predicted by simple rules.

The parity law for model ecosystem has been first reported by Kobayashi and Tainaka (1997). They changed the values of parameters, such as reproduction or mortality rate of a target species, and found the parity law: the steady-state density of each species increased or decreased by whether the species richness n was even

or odd. Since this work, some authors reported the similar parity law for different models (Tainaka and Sakata, 1999; Sato et al., 2002; Nagata et al., 2008). However, they never dealt with the destruction of habitat.

Even if the habitat destruction is limited to a local and small area, its accumulation increases the risk of extinction (Bascompte and Sole, 1996; Boswell et al., 1998; Tilman et al., 1997; Nakagiri et al., 2001a). So far, two kinds of models for local destruction had been applied on a square lattice (Nakagiri et al., 2005). One is the “site destruction”, where species cannot live in the destroyed sites (Boswell et al., 1998; Tilman et al., 1997; Ives et al., 1998; Bascompte and Sole, 1996, 1998b; Hill and Caswell, 1999; Hiebler, 2000). The other is the “bond destruction” by which interactions between neighboring lattice sites are prohibited (Tao et al., 1999; Nakagiri et al., 2001a,b, 2005; Nakagiri and Tainaka 2004). The site and bond destruction are respectively called “site and bond percolation networks” in the network epidemiology (Moore and Newman, 2000). The purpose of the present paper is to illustrate a parity law for bond destruction.

The bond destruction has first introduced by Tao et al. (1999). They dealt with a single species system called the contact process (Harris, 1974; Liggett, 1985; Konno, 1994) on bond percolation network:



where X meant the site occupied by a species, and O was the empty site. The reaction (1a) and (1b) denoted birth and death process of

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single species X , respectively. Reaction (1a) occurred between adjacent lattice sites, but it was disturbed by bond destruction (“barrier”). Tao et al. (1999) found that the steady-state density of X was decreased with the increase of barrier density D .

Nakagiri et al. (2001a) applied the same bond destruction to a two-species (prey–predator) system:



where X and Y meant the sites occupied by prey and predators, respectively. These reactions respectively represented the reproduction of X , predation of Y and death of Y . The barrier was assumed to prohibit only the reaction (2a). Simulations revealed that the steady-state density of X increased in spite of the increase of barrier density D .

Hence, the responses of X to the increase of D are just opposite between single- and two-species systems. In this article, we extend the bond percolation network to the multiple- species system introduced by Nagata et al. (2008). This system contains n kinds of species ($n = 1, 2, \dots, 6$). In the next section, we explain the model and method in detail. Section 3 is devoted to explain the mean-field theory. In Section 4, we describe the simulation results of lattice model to report a parity law. Conclusions and discussions are described in the final section.

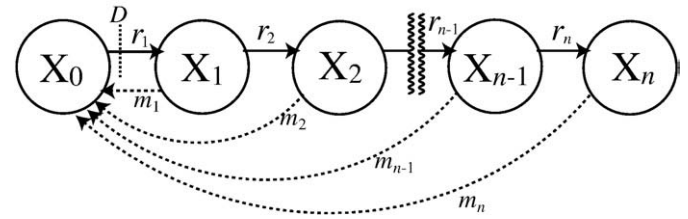


Fig. 1. The schematic diagrams of cyclic model ecosystems (3). Here D indicates the destruction of habitat. The system consists of n kinds of species ($X_i, 1 \leq i \leq n$) and empty (X_0). The parameters r_i and m_i respectively denote the reproduction and mortality rates of species i .

2. Model and method

2.1. Model

We consider the ecosystem composed of n species on the square lattice ($n = 1, 2, \dots, 6$) (Nagata et al., 2008):



where X_i means an individual of species i ($i = 1, \dots, n$) and X_0 represents the vacant site. The reaction (3a) means that the species i reproduces offspring by eating species $i - 1$. The parameters r_i is the reproduction rate of X_i ; in this paper, we always put $r_i = 1$. The reaction (3b) represents death process of species i , and the parameters m_i is the mortality rate of X_i . The schematic diagram of this system is shown in Fig. 1. The species 1 represents a producer, but

Table 1
Coexisting region and equilibrium densities for mean-field theory.

n	Coexisting region	Inner equilibrium point
1	$0 < m < 2r$	$x_0 = 2r - m$
2	$0 < m < 2r - m_i$	$x_0 = \frac{m}{2r}, x_1 = \frac{1}{4r}(2r - m - m_i)$
3	$0 < m < r - m_i$	$x_0 = \frac{r - m}{2r}, x_1 = \frac{m}{2r},$ $x_2 = \frac{r - m - m_i}{2r}$
4	$0 < m < r - 2m_i$	$x_0 = \frac{m + m_i}{2r}, x_1 = \frac{2r - 2m - m_i}{6r},$ $x_2 = \frac{m}{2r}, x_3 = \frac{r - m - 2m_i}{3r}$
5	$0 < m < \frac{2r}{3} - 2m_i$	$x_0 = \frac{2r - 3m}{6r}, x_1 = \frac{m - m_i}{2r},$ $x_2 = \frac{2r - 3m - 3m_i}{6r}, x_3 = \frac{m}{2r},$ $x_4 = \frac{2r - 3m - 6m_i}{6r}$
6	$0 < m < \frac{2r}{3} - 3m_i$	$x_0 = \frac{m + 2m_i}{2r}, x_1 = \frac{2r - 3m - m_i}{8r},$ $x_2 = \frac{m + m_i}{2r}, x_3 = \frac{2r - 3m - 5m_i}{8r},$ $x_4 = \frac{m}{2r}, x_5 = \frac{2r - 3m - 9m_i}{8r}$

m (m_i): mortality rate of top predator (the other species).

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