



A simple population theory for mutualism by the use of lattice gas model

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ABSTRACT

The population dynamics of species interactions provides valuable information for life sciences. Lotka–Volterra equations (LVEs) are known to be the most popular model, and they are mainly applied to the systems of predation and competition. However, LVEs often fail to catch the population dynamics of mutualism; the population sizes of species increase infinitely under certain condition (divergence problem). Furthermore, LVEs never predicts the Allee effect in the systems of obligate mutualism. Instead of LVEs, several models have been presented for mutualism; unfortunately, they are rather complicated. It is, therefore, necessary to introduce a simpler theory for mutualism. In the present paper, we apply the lattice gas model which corresponds to the mean-field theory of the usual lattice model. The derived equations are cubic and contain only essential features for mutualism. In the case of obligate mutualism, the dynamics exhibits the Allee effect, and it is almost the same as in the male–female systems. In our model, the population sizes never increase infinitely, because our model contains not only intra- but also interspecific competitions. If the density of one species increases disproportionately in respect of its mutual partners, then this might imply downward pressure on the population abundance of the mutual partner species and such feedback would eventually act as a controlling influence on the population abundance of either species. We discuss several assumptions in our model; in particular, if both species can occupy in each cell simultaneously, then the interspecific competition disappears.

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1. Introduction

All species on the earth are closely related to other species. In a simple view, the interaction between a pair of species can be classified into three typical categories: predation (one gains and the other suffers: “+”, “−”), competition (−, −) and mutualism (+, +) (Begon et al., 2006). In recent years, the concern for mutualism is growing, since most of the World’s biomass is dependent on mutualism (e.g., Pellmyr and Huth, 2002; Bashary and Bronstein, 2004; Begon et al., 2006). For example, microbial species influence on the abundances and ecological functions of related species (Madigan et al., 2000; Keller and Surette, 2006; Goto et al., 2010). Many bacterial species coexist in a syntrophic association (obligate mutualism); that is, one species lives off the products of another species. So far, mathematical models for mutualisms have often been neglected in many ecological textbooks.

The most famous model of population dynamics is a series of Lotka–Volterra equations (LVEs) (e.g., Lotka, 1925; Volterra, 1926; Takeuchi, 1996; Hofbauer and Sigmund, 1998). In many textbooks,

LVEs are referred as basic models for both predation and competition. When LVEs were applied to mutualism, they were given by

$$\frac{dx}{dt} = \frac{r_X x (K_X - x + \alpha_Y y)}{K_X} \quad (1a)$$

$$\frac{dy}{dt} = \frac{r_Y y (K_Y - y + \alpha_X x)}{K_Y} \quad (1b)$$

where x and y indicate the population sizes (densities) of symbiotic species X and Y , respectively, and r_j , K_j , α_j are parameters ($j = X, Y$). It is known that the positive stable equilibrium exists, only when $\alpha_X \alpha_Y < 1$ (Takeuchi, 1996). However, if $\alpha_X \alpha_Y > 1$, the population sizes of both x and y increase infinitely (“divergence problem”). Moreover, LVEs never predict Allee effects for obligate mutualism. These problems can be avoided by several models (Wright, 1989; Doebeli, 2002; Tainaka et al., 2003; Hammerstein, 2003; Amarasekare, 2004; Courchamp et al., 2008; Holland and DeAngelis, 2010). However, these models are rather complicated; they use fractional equations or nonlinear equations of higher order; not only the analytic solutions are difficult to obtain, but also the resultant solutions are difficult to interpret. In order to understand the basic features of mutualism, it is necessary to build a simpler mathematic model.

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The Allee effect has been first introduced for a single-species by W.C. Allee (Allee, 1930). His main interest was the influence of density on population dynamics, especially in aquatic organisms. When the population size of a species becomes below a critical number, the risk of extinction increases drastically. Such a threshold effect is termed Allee effect (Odum, 1953; Courchamp et al., 2008). Since his pioneering work, many ecologists studied the Allee effect (Lamont et al., 1993; Groom, 1998; Davis et al., 2002; Angulo et al., 2007; Tanaka et al., 2009; Nariai et al., 2011). The most typical population model for an Allee effect has been represented by

$$\frac{dx}{dt} = Rx(x - a)(b - x) \tag{2}$$

where x indicates the population size of a species, and the parameters R , a and b are positive ($a < b$) (Lewis and Kareiva, 1993; Courchamp et al., 2008). Eq. (2) has three equilibriums; both $x = 0$ and $x = b$ are stable, while $x = a$ is unstable. The species survives (goes extinct) for $x > a$ ($x \leq a$). Hence, the parameter a means a minimum size of viable population and b the stable equilibrium density. Note R is a parameter related to the initial growth rate (discussed later). Our theory for obligate mutualism can derive Eq. (2) for both species.

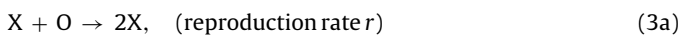
In the present paper, we apply “lattice gas model” or “lattice gas automaton” which is a kind of individual-based models on a lattice (Frisch et al., 1986; Dieter, 2000; Hagiwara et al., 2011). The lattice gas model (lattice gas automaton) differs from the usual “lattice model”. The difference between lattice and lattice gas models lies in the range of interaction: in lattice model, the interaction occurs between adjacent lattice sites (“local interaction”), whereas in lattice gas model it occurs between any pair of lattice sites (“global interaction”). In most cases, the dynamics of lattice models cannot be expressed by mathematical equations. In contrast, that of lattice gas model is usually represented by differential equations that are called the mean-field theory of lattice model. Such equations are served for multiple uses. In order to build a simple mathematical model of mutualism, we here apply the lattice gas model.

In the next section, we review the correspondence relation between lattice and lattice gas models. In ecology, the lattice gas model (mean-field theory of lattice model) usually corresponds to LVEs (Tainaka, 1988, 1989; Matsuda et al., 1992). We apply such a correspondence to mutualism. In Section 3, we build a simple lattice gas model for mutualism. In Sections 4 and 5, we derive the mean-field theories which are represented by cubic equations. Section 5 is devoted to report the results for obligate mutualism. In Section 5, we deal with general cases of mutualism. The phase diagram and typical types of population dynamics are elucidated.

2. Theoretical rationale

In recent years, lattice models are widely applied in the field of ecology. On a lattice, simulations are performed under either local or global interactions. In the former case, an interaction occurs between adjacent lattice sites. The latter case is called lattice gas model, where an interaction occurs between any pair of lattice sites.

For simplicity, we first consider a single-species system. It is well known that the most canonical model is the logistic equation (Verhulst, 1838). A lattice version of logistic equation is called “contact process” (Harris, 1974; Liggett, 1985; Konno, 1994) which is defined as follows:



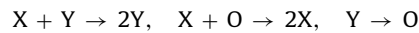
where X denotes an individual of a species (or the site occupied by a species), and O is the empty site. The first (second) reaction means the birth (death) processes of X . In the lattice model, the

first reaction occurs between adjacent lattice sites. In the lattice gas model, it occurs between any pair of sites, and its dynamics can be represented by the following rate equation:

$$\frac{dx}{dt} = rx(1 - x) - mx \tag{4}$$

where x and $(1 - x)$ are the densities of species and empty sites, respectively. The first and second terms in the right hand side come from the birth and death processes. Eq. (4) can be rewritten by the logistic equation $dx/dt = Rx(1 - x/K)$, where $R = r - m$ and $K = r/(r - m)$.

For two-species system, the lattice version of Lotka–Volterra models have been studied by several authors (Satulovsky and Tome, 1994; Nakagiri et al., 2001). A typical lattice version of prey–predator system has been introduced as follows (Tainaka and Fukazawa, 1992):



where X and Y denote prey and predator, respectively. The above reactions represent the predation of Y , reproduction of X , and death of Y , in order. The mean-field theory corresponds to LVEs in prey–predator system with density effect. Similarly, lattice versions of competition system have been presented by several authors (Matsuda et al., 1992; Neuhauser, 1992; Tainaka et al., 2004; Kawai et al., 2008). Their mean-field theories correspond to the LVEs of competition. Hence, it is expected that a canonical theory for mutualism can be derived from a canonical lattice gas model.

3. Model

Let us consider a system consisting of two species X and Y . Each lattice site is labeled by X , Y or O , where O means the empty site. The reactions are defined by



where the reactions (5a) and (5c) respectively denote the birth and death processes of species X , and B_X (m_X) denotes the birth (mortality) rate of species X . Similarly, the reactions (5b) and (5d) have the same meanings for species Y . The birth rates should be indicated as follows:

$$B_X = r_X + \varepsilon_{XY} \tag{6a}$$

$$B_Y = r_Y + \varepsilon_{YX} \tag{6b}$$

where x (y) is the density of species X (Y). The parameters r_X and r_Y are the reproduction rates without the other species, and ε_X and ε_Y denote mutualistic effects on the reproduction rates. Hence, the birth rate of one species increases with the density of the other species. If species Y is absent, then the reaction (5) is equivalent to the contact process [the reaction (3)]. In the limiting case ($\varepsilon_X, \varepsilon_Y$) \rightarrow (0,0), the system (5) becomes a competition model called “multiple contact process” (Neuhauser, 1992). In this case, two species cannot coexist; because of reaction (5a), both species compete with each other to get empty sites (exploitative competition).

We explain the simulation procedure of lattice gas model for mutualism. Reaction processes are performed in the following two steps:

- i) Two lattice sites are chosen randomly and independently. The pair sites obey the reaction (5a). For example, if chosen sites are

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