

Original Research Article

Persistence of mutualisms with bidirectional interactions in a two-species system

Shikun Wang^a, Yuanshi Wang^{b,*}^a School of Science, Zhejiang University, Hangzhou 310058, PR China^b School of Mathematics and Computational Science, Sun Yat-sen University, Guangzhou 510275, PR China

ARTICLE INFO

Article history:

Received 30 September 2014

Received in revised form 18 June 2015

Accepted 26 June 2015

Available online 18 July 2015

Keywords:

Mean-field theory

Lattice gas system

Cooperation

Stability

Coexistence

ABSTRACT

In Lotka–Volterra equations (LVEs) of mutualisms, population densities of mutualists will increase infinitely if the mutualisms between them are strong, which is called the divergence problem. In order to avoid the problem, a mutualism system of two species is analyzed in this work. The model is derived from reactions on lattice and has a form similar to that of LVEs. Population densities of species will not increase infinitely because of spatial limitation on the lattice. Stability analysis of the model demonstrates basic mechanisms by which the mutualisms lead to coexistence/extinction of the species. When in coexistence, intermediate mutualistic effect is shown to lead to the maximal density in certain parameter ranges, while a strong or weak mutualistic effect is not so good. Furthermore, the stability analysis exhibits that extremely strong/weak mutualisms will result in extinction of one/both species.

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1. Introduction

Mutualistic interactions are ubiquitous in nature, but they are not well understood theoretically (Neuhauser and Fargione, 2004). Among theoretical models established for mutualisms, Lotka–Volterra equations (LVEs) are the most famous. In the LVEs of mutualisms, mutualists can coexist at a steady state if mutualisms between them are weak. However, when the mutualisms are strong, the LVEs predict that population densities of the species increase infinitely, which is the so-called divergence problem (Iwata et al., 2011). The underlying reason is that in the mutualism system, each species is assumed to have only positive effect on the other without any negative feedback. This is not always true in natural environment. As pointed out by Agrawal et al., almost all of the interactions in nature are bidirectional (Agrawal et al., 2007). That is, there usually exist negative feedbacks in mutualisms.

Empirical observations demonstrate bidirectional interactions in many mutualism associations. In a cooperative association of bacteria, each species lives off products of another although neither of them can survive alone. Since they live in the same environment, there exists interspecific competition because of nutrient and spatial limitations (Keller and Surette, 2006; Cornforth and Foster, 2013). In particular, scientists are using

mutualistic bacteria as the key ingredient in a biological light bulb, a bacteria-powered light bulb that requires no electricity. “The Biobulb is essentially a closed ecosystem in a jar. It contains several different species of microorganisms, and each organism plays a role in the recycling of vital nutrients that each of the other microbes need to survive” (<http://news.discovery.com/tech/alternative-power-sources/bacteria-powered-light-bulb-is-electricity-free-130815.htm>). Those microorganisms feed the *Escherichia coli*, which will emit light. Gilbert’s study of interactions between Mullerian mimics exhibits that when the species are at low density, they are mutualistic since they facilitate the training of predators in recognizing unpalatable prey (Gilbert, 1983). However, when at high density, the species are competitive since they share resources. In pollination–mutualisms, plants provide nectar, pollen and other resources for pollinators, while pollinators transport pollen for the host plant. However, adult pollinators often lay eggs in flowers of the plant, from which larvae eat seeds and reduce the growth rate of plants (Wang et al., 2012). For more relevant works, we refer to Zhang (2003), Hernandez (1998), Wang and Wu (2011) and Wang and Wang (2015).

There are many models in describing mutualisms with bidirectional interactions, but most of them are difficult to be analyzed thoroughly. Thus, properties of mutualisms cannot be demonstrated as clearly as those shown by LVEs for competition/predation. Iwata et al. presented a lattice gas model of mutualisms, which is derived from reactions on lattice and has a form similar to that of LVEs (Iwata et al., 2011). While local stability analysis and

* Corresponding author. Tel.: +86 2084034848; fax: +86 20 84037978.
E-mail address: mcswws@mail.sysu.edu.cn (Y. Wang).

numerical simulations on the model display novel properties of mutualisms, global stability and complete simulations need to be shown. Therefore, a thorough analysis of the model is necessary to demonstrate more properties of mutualisms (Jones et al., 2012).

In this paper, the lattice gas model of mutualisms established by Iwata et al. (2011) is studied. Stability analysis of the model demonstrates basic mechanisms by which the mutualisms lead to coexistence/extinction of the species: (i) When neither species can survive in the absence of the other, the species can coexist if mutualisms between them are strong and population densities of the species are large, which describes the Allee effect in obligate mutualisms. (ii) When one species can persist in the absence of the other but the other cannot survive alone, the obligate species can survive if mutualism from the facultative one is strong, which implies that an obligate species can survive by cooperating with a facultative one. Even when the mutualism from the facultative one is intermediate, the obligate species can survive if its mutualistic effect on the facultative one is strong and its population density is large, which exhibits that an obligate species can survive by both strengthening its mutualistic effect on the other and enhancing its population density. (iii) When either species can survive in the absence of the other, a weak mutualism can lead to extinction of mutualists, which demonstrates a mechanism how an unbalanced mutualism leads to collapse of a cooperative association.

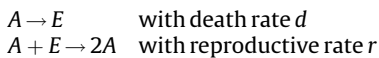
Furthermore, our analysis shows that extremely strong/weak mutualisms will result in extinction of one/both species, while strong mutualisms can lead to coexistence of species. When in coexistence, intermediate mutualistic effect is shown to lead to the maximal density in certain parameter ranges, while a strong or weak mutualistic effect is not so good. While seven typical types of dynamics of the system are displayed by simulations by Iwata et al. (2011), these types are confirmed by rigorous analysis in this paper and a new one is demonstrated (see Remark 3.3).

The paper is organized as follows. The model is characterized in Section 2. Section 3 displays global stability analysis. Discussion is in Section 4.

2. A lattice gas model

Lattice models have been applied in ecology in recent papers (Iwata et al., 2011). On the lattice, a site can be occupied by one individual of the species, while interactions between sites are classified into local and global ones. In local interactions, a site interacts with its adjacent sites, which means that the sites have common boundaries. In global interactions, a site interacts with any site on the lattice, which is called a lattice gas system.

Firstly, we consider a lattice gas system of one species *A*, where the interaction between sites is called “contact process” (Iwata et al., 2011):



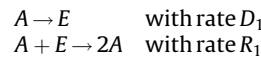
where *A* represents an individual of species *A* (i.e., a site occupied by *A*), and *E* is the empty site. The first and second reactions represent the death and reproductive processes, respectively. In a lattice model, the second reaction occurs between adjacent sites. In a lattice gas model, the second reaction occurs between any pair of sites on the lattice in a random and independent way. The lattice gas model can be depicted by

$$\frac{dN}{dt} = N[-d + kr(M - N)]$$

where *M* is the total number of sites on the lattice. Variables *N* and *M - N* represent the densities of species *A* and empty sites,

respectively. *k* is the possibility that an individual of species *A* meets an empty site, which is determined by searching ability of the species, etc. Thus, the second term “*kr(M - N)*” on the righthand side of the model describes the reproductive process: the new-born individuals (*r*) interact with the empty sites (*M - N*) in a random and independent way and the possibility that an individual meets an empty site is *k*, which forms the successful reproduction “*kr(M - N)*”. On the other hand, the first term “*-d*” describes the death process.

Second, in a lattice gas system of two species *A* and *B*, a site is labeled by *A* (*B*) if it is occupied by an individual of species *A* (*B*). If a site is empty, then it is labeled by *E*. The site occupied by species *A* (*B*) will become *E* in a death rate *D*₁ (*D*₂). On the lattice, reaction occurs between any pair of sites randomly and independently. When a site *A* meets an empty site *E*, the site *E* will become *A* in a reproductive rate *R*₁. Hence, the reactions in species *A* can be described by

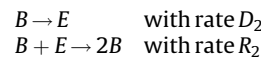


where the reproductive rate of *A* satisfies *R*₁ = *r*₁ + α₁*N*₂ (Iwata et al., 2011). Parameter *r*₁ represents the intrinsic growth rate of species *A* in the absence of *B*, and the term “α₁*N*₂” comes from the mutualism of species *B*, which is explained as follows. Here, the variable *N*₂ denotes the population density of species *B* and parameter α₁ represents the mutualistic effect of an individual of species *B* on the reproduction of *A*, which is defined by

$$\alpha_1 = e_A s_B$$

where *s*_{*B*} is the quantity of resources (or services) provided by an individual of species *B*, and *e*_{*A*} denotes the efficiency of species *A* in converting the resources into fitness. For example, in a cooperative association of bacteria *A* and *B*, *s*_{*B*} represents the quantity of products by an individual of *B* and *e*_{*A*} is the efficiency of *A* in converting the products into fitness. Thus, α₁*N*₂ denotes the mutualistic effects of bacteria *B* on the reproduction of *A*. Since *D*₁ denotes the death rate of *A*, we have *r*₁ > 0, α₁ > 0, *D*₁ > 0.

Similarly, reactions in species *B* can be described by



where *R*₂ = *r*₂ + α₂*N*₁. Parameters *r*₂ and α₂(= *e*_{*B*}*s*_{*A*}) represent the intrinsic growth rate of species *B*, mutualistic effect of species *A* on *B*, respectively. Variable *N*₁ denotes the population density of species *A*. Since *D*₂ denotes the death rate of *B*, we have *r*₂ > 0, α₂ > 0, *D*₂ > 0.

When the lattice size is sufficiently large, population dynamics of the lattice gas system are usually depicted by differential equations, which are called the mean-field theory of lattice model (Dieter, 2000). Let *M* be the total number of sites that can be colonized on the lattice. Then the number of empty sites is *M - N*₁ - *N*₂. Thus, the growth of the species can be described by

$$\begin{aligned} \frac{dN_1}{dt} &= N_1[-D_1 + k_1 R_1 (M - N_1 - N_2)] \\ \frac{dN_2}{dt} &= N_2[-D_2 + k_2 R_2 (M - N_1 - N_2)] \end{aligned} \tag{2.1}$$

where *R*₁ = *r*₁ + α₁*N*₂ and *R*₂ = *r*₂ + α₂*N*₁. The parameter *k*₁(*k*₂) represents the possibility that an individual of species *A*(*B*) meets an empty site. The first and second terms at the righthand sides of (2.1) denote the death and reproductive process of each species, respectively. Thus system (2.1) has a form similar to that of LVEs.

The maximal density that the species can approach is shown as follows. Let *N*₂ = 0 in the first equation of (2.1), we obtain

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