Population dynamics of intraguild predation in a lattice gas system

Yuanshi Wang, Hong Wu*

School of Mathematics and Computational Science, Sun Yat-sen University, Guangzhou 510275, PR China

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ABSTRACT

In the system of intraguild predation (IGP) we are concerned with, species that are in a predator–prey relationship, also compete for shared resources (space or food). While several models have been established to characterize IGP, mechanisms by which IG prey and IG predator can coexist in IGP systems with spatial competition, have not been shown. This paper considers an IGP model, which is derived from reactions on lattice and has a form similar to that of Lotka–Volterra equations. Dynamics of the model demonstrate properties of IGP and mechanisms by which the IGP leads to coexistence of species and occurrence of alternative states. Intermediate predation is shown to lead to persistence of the predator, while extremely big predation can lead to extinction of one/both species and extremely small predation can lead to extinction of the predator. Numerical computations confirm and extend our results. While empirical observations typically exhibit coexistence of IG predator and IG prey, theoretical analysis in this work demonstrates exact conditions under which this coexistence can occur.

1. Introduction

Intraguild predation (IGP) occurs between species in the same community which utilize similar resources (space or food), and thus there is competition between them. IGP is classified as asymmetrical or symmetrical. In asymmetrical IGP, one species consistently preys upon the other. But in symmetrical IGP, either species can prey upon the other. In this work, we are concerned with asymmetrical IGP. For convenience, we call it as IGP in the following discussions. IGP has been widely observed in both terrestrial and aquatic communities [27]. For examples, there exists IGP between large mammalian carnivores. Large canines and felines are the mammal groups often involved in IGP, with larger species such as lions and gray wolves preying upon smaller species such as foxes and lynx [14]. Coyotes function as predators on gray foxes and bobcats in North America [3]. Since empirical observations typically exhibit coexistence of IG predator and IG prey, an interesting question has been focused on that under which conditions the coexistence can occur [16,17].

Several models have been established to characterize IGP. Holt and Polis [5] formed a three-specie model of IGP with Holling Type I functional response, in which two species that have a predator–prey relationship, also compete for a shared resource. They also formed a two-species system, which is an extension of the exploitative competition model introduced by Schoener [19,20]. Theoretical analysis demonstrated a general criterion for coexistence in IGP that IG prey

should be superior at exploitive competition for the shared resource, whereas the IG predator should gain significantly from the IG prey. Local stability analysis and numerical computations also showed that at intermediate levels of environmental productivity, there exist alternative states (either IG prey dominance or IG predator dominance, or either the IG predator dominance or coexistence). Ruggieri and Schreiber [18] considered the Schoener–Polis–Holt model, in which IG prey and IG predator compete for resources (food). A global analysis exhibits six dynamics of the model. Okuyama [28] studied IGP in a spatial setting by establishing a lattice IGP model. For homogeneous resources, pair approximation was used to study the effect of spatially structured species interactions. The qualitative results of the pair approximation model predicted coexistence of the species over a wider range of parameters than the non-spatial model. Takimoto et al. [22,23] analyzed models of IGP with three and four dimensions, and demonstrated complex but systematic sequences of alternative states along a productivity gradient, where sufficient conditions that determine which sequences to occur, are clarified. Takimoto et al. [24] presented a Levins-type patch occupancy model of IGP. Theoretical analysis exhibited conditions for feasibility of each equilibrium, while numerical computations displayed both equilibrium stability and food-chain length with different strength of local IGP. The model showed that ecosystem size can promote coexistence and increase food-chain length even when local IGP is strong, which is consistent with empirical patterns. Kang and Wedekin [7] formed a model of IGP with Holling Type III functional response. Sufficient conditions are provided for persistence and extinction of species in all possible situations and multiple attractors and periodic oscillations are exhibited. For other relevant work, we refer to

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* Corresponding author. Tel.: +86 2084034848.
E-mail address: wuhong@mail.sysu.edu.cn (H. Wu).

Refs. [1–3,10,13]. As far as we know, mechanisms by which IG prey and IG predator can coexist in IGP models with spatial competition, have not been shown. Therefore, forming an appropriate model of IGP with spatial competition and demonstrating its properties are necessary.

In this work, we use a lattice gas model to describe IGP. The lattice gas model is individual-based and is different from the classical "lattice model". Since the lattice model characterizes local interactions occurring between adjacent sites on a lattice, the lattice gas model describes interactions between any pair of lattice sites and the interactions occur randomly and independently [21]. While dynamics of lattice models cannot be described by mathematical equations, dynamics of lattice gas models are usually depicted by differential equations when the lattice is sufficiently large, which are called the mean-field theory of lattice model. These equations have been widely applied in characterizing competition, predation and mutualism in biology for years. For example, a lattice version of predator–prey model was presented by Nakagiri et al. [11] and dynamics of the model exhibit conditions under which the species can coexist and under which the predator would be excluded by competition of the prey. A typical lattice version of competition model has also been studied by several authors [8,9,12]. In a recent study, a lattice version of mutualism-competition model was introduced by Iwata et al. [6]. In the two-species system, spatial competition is considered and the space where the two species live, is assumed to be divided into many sites and is regarded as a lattice. Since each site can be occupied by one individual of the populations, the species are competitive for sites on the lattice. The species are also mutualistic since each of them produces resources for the other. The benefit of the mutualism is represented by the increased reproduction rate of both species populations. Dynamics of the mixed mutualism-competition model demonstrate that when the mutualistic effects vary, interaction outcomes between the species can change among mutualism, parasitism and competition in a smooth fashion.

Inspired by the work of Nakagiri et al. [11] and Iwata et al. [6], we apply a lattice version of predation-competition model to describe IGP. The model focuses on spatial competition. The space occupied by the population is regarded as a lattice and each site can be occupied by one individual of the species. Thus, the species are competitive for sites on the lattice. The species are also involved in a predator–prey relationship since predation can occur as a predator meets the prey. Similar to Ref. [6], the benefit of the predation is represented by the increased reproduction rate of the predator. Dynamics of the model demonstrate properties of IGP and mechanisms by which the IGP leads to persistence/extinction of species: (i) In IGP where IG predator cannot survive in the absence of IG prey, when the efficiency of predator in converting its consumption into fitness is high, the predator can persist. When the efficiency is intermediate, the predator can persist if it has a high initial density; if the initial density is low, the predator goes to extinction. When the efficiency is low, the predator will go to extinction. (ii) In IGP where IG predator can survive in the absence of IG prey, when the efficiency of predator is high, the IGP can enhance population density of predator. When the efficiency is low, the predator can persist if its population density is large. Otherwise, the predator will be driven into extinction by its prey through competition. (iii) Intermediate predation can lead to persistence of the predator, while extremely big predation can lead to extinction of one/both species and extremely small predation can lead to extinction of the predator. Saddle-node bifurcation and pitchfork bifurcation in the model are demonstrated, while numerical computations confirm and extend our results.
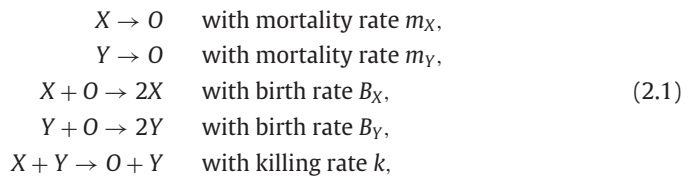
The paper is organized as follows. The model is described in Section 2. Sections 3 and 4 show dynamics of the model. Discussion is in Section 5.

2. Model

In this section, we form the lattice gas model of IGP and exhibit boundedness of solutions and nonexistence of periodic orbit of the model.

Let X and Y represent the prey and predator, respectively. A site on a lattice is labeled by X (or Y) if it is occupied by an individual of species X (or Y). When a site is empty, it is labeled by O. On the lattice, any pair of sites can interact randomly and independently. When there is only one species on the lattice, the interactions can be described by contact process [4]. For example, in the system of species X, if a site is occupied by X, then it will become O in a mortality rate m_X. If sites X and O interact, then the site O will become X in a birth rate B_X. A similar discussion can be given for the one-species system of Y. Moreover, when the prey X and predator Y emerge on the same lattice, predation can occur: X would be killed and consumed if it meets Y, which promotes the growth of Y.

Therefore, reactions on the lattice of species X and Y can be depicted as follows:

$$\begin{aligned}
X &\to O & \text{with mortality rate } m_X, \\
Y &\to O & \text{with mortality rate } m_Y, \\
X + O &\to 2X & \text{with birth rate } B_X, \\
Y + O &\to 2Y & \text{with birth rate } B_Y, \\
X + Y &\to O + Y & \text{with killing rate } k,
\end{aligned} \tag{2.1}$$

where the first and second reactions respectively describe the mortality processes of species X and Y, while the third and fourth reactions respectively characterize their birth processes. The fifth reaction represents the predation of species Y on X, in which species X is killed by Y and the site occupied by X becomes empty.

When the lattice size is large, reactions of (2.1) are usually described by differential equations, which are called lattice models of mean-field theory [6,26]:

$$\begin{aligned}
\frac{dx}{dt} &= -m_X x + B_X x(1 - x - y) - kxy, \\
\frac{dy}{dt} &= -m_Y y + B_Y y(1 - x - y),
\end{aligned} \tag{2.2}$$

where x and y represent fractions of sites occupied by species X and Y, respectively. The factor $(1 - x - y)$ is the fraction of empty sites. Since one site can be occupied by one individual, x and y represent the sizes of population densities of species X and Y. For convenience, x and y are called densities of the two species. The first and second terms in the righthand side of each equation come from the mortality and birth processes, while the third term in the first equation comes from the predation process. Thus, the lattice gas model (2.2) has the same form as Lotka–Volterra equations. Parameters m_X and m_Y respectively represent mortality rates of species X and Y, and the birth rates are defined by

$$B_X = r_X, \quad B_Y = r_Y + \bar{e}kx,$$

where r_X (r_Y) denotes the birth rate of species X (Y) in the absence of the other. Parameter k represents the killing rate of species Y on X, while $\bar{e}$ denotes the efficiency of Y in converting the consumption into fitness. In the following discussion, we denote

$$e = \bar{e}k.$$

In system (2.2), we assume $r_Y \geq 0$ and all other parameters are positive. We consider solutions $(x(t), y(t))$ of (2.2) with initial values $x(0) > 0, y(0) > 0$. Thus we have $x(t) > 0, y(t) > 0$ as $t > 0$. When $r_X \leq m_X$, we have $dx/dt < 0$ by the first equation of (2.2). Then species X goes to extinction and system (2.2) becomes a one-species system