

Parameter Sensitivity In A Lattice Ecosystem With Intraguild Predation

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Abstract: Ecosystem stability is an important issue in conservation of biodiversity. The stability of prey-predator systems or competitive systems has been studied extensively. However, natural communities are far more complex than those simple ecosystems. Intraguild predation presents a sound example of a complex ecosystem with both competition and predation. The 3-species ecosystem with intraguild predation is the simplest such complex ecosystem. We studied the spatial pattern dynamics in the 3-species ecosystems with intraguild predation using the lattice version of the Lotka-Volterra model. A food web consists of plant, pure consumer (prey) and predatory consumer, where the latter two consumers show intraguild predation. The simulation of the lattice model shows complex patterns of phase transition with various parameter-dependence. The outcomes depend on the combination of these two reproductive parameters. This suggests that the stability of this ecosystem depends on the environmental parameters of the component species. Our results suggest that the discussion of stability based on the ecosystem structure could be meaningless unless all ecological and life history parameters of the component species are included. Our results indicate that a small human activity may have a relatively large impact on ecosystems by changing the ecological conditions of their component species.

Keywords: *Intraguild predation, phase transition, lattice model, prey-predator ecosystem*

1. INTRODUCTION

One of the major issues in ecological studies is the stability and complexity of ecosystems (Paine, 1966; May, 1973; Pimm, 1991; Ives and Gross, 2000). Many traditional theoretical studies have explored the possible relationships between the structure of the food web and the ecosystem stability. However, no conclusive results have been obtained from these studies (Pimm, 1991). As a model ecosystem, predator-prey systems have been extensively studied both empirically and theoretically (May, 1973; Pimm, 1991; Hofbauer and Sigmund, 1988; Hance and Impe, 1998). These systems often exhibit some regularity. However, multi-species cyclic systems often reveal some parameter dependence (Tainaka, 1988, 1994, 1991).

Natural ecosystems are usually far more complex and difficult to analyze, and studies of complex ecosystems are essential in understanding natural communities. Natural food webs usually consist of a network of species with many connections. For example, an omnivore predator eats both plants and herbivores (animals and insects). Such connections in a food web are often called intraguild predation, and are common in natural communities (Holt and Polis, 1997). In order to understand natural ecosystems, we study a three-species complex

model ecosystem with intraguild predation. It is the 'simplest' complex food web we can build.

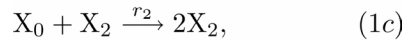
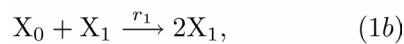
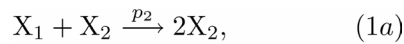
The spatio-tempo dynamics of ecosystems is one of most intriguing problems arising in complex systems (Shigesada and Teramoto, 1986; Harada and Iwasa, 1994; Caswell and Cohen, 1995). Species form various spatial patterns such as order or random (disorder) distributions. Space is also limited in many ecosystems, such as ecosystems with plants, and space is usually a very important limiting factor of ecosystems. Therefore, we use a lattice model of a simple intraguild predation system to study the basic features of complex ecosystems.

In this article, we build a three-species lattice ecosystem with intraguild predation. We demonstrate that phase transition appears in all three species with a slight change in environmental parameters of the two consumer species. We show that the equilibrium densities of all three species, including extinction of some species, depend at least on the combination of the reproductive parameters of the two consumers. The stability of model ecosystems is discussed in terms of parameter sensitivity of the component species. We also discuss human impacts on natural ecosystems.

2. THE MODEL

Here a plant-consumer ecosystem that includes intraguild predation (IGP) in the consumer guild (grazers, plant-eaters) is studied (Fig. 1). The ecosystem consists of three species, plant species X_0 , a 'prey' consumer X_1 , and a predatory consumer X_2 . This model ecosystem can be viewed in many ways. For example, (1) X_1 and X_2 are species under resource competition with intraguild predation of X_1 by X_2 . Or (2) X_1 and X_2 are prey and predator, respectively, with extra herbivory (reproduction) of X_2 on X_0 . This system is also viewed as (3) a destructed cyclic system by an additional "jump-over" herbivory. (4) The species X_0 can be also viewed as a vacant site and two herbivore species occupy it. In any interpretation, the model ecosystem studied here is one of the simpler, but general food web ecosystems.

Consider a two-dimensional lattice consisting of three species. Each lattice site is labeled by X_1 , X_2 , or X_0 , where X_1 (or X_2) is the site occupied by a 'prey' consumer (or a predatory consumer), and X_0 represents a plant species (or a vacant site). We assume the following interaction (Hofbauer and Sigmund, 1988; Tainaka, 1994; Satulovsky and Tome, 1994; Sutherland and Jacobs, 1994):



where X_i means an individual of species i for $i = 0, 1, 2$. Equation (1a) represents a predator-prey relationship that is the intraguild predation in this ecosystem, and p_2 is the predation rate of X_2 . The animal consumer species X_1 and X_2 reproduce offspring by eating (grazing) plant species X_0 . The parameter r_j is the reproduction rate of animal X_j for $j = 1$ and 2 and m denotes the death rate of predator species X_2 . When species X_2 dies, it is served for plant species X_0 . Species X_0 and X_1 can be considered as a producer and a consumer, respectively. We set $p_2 = 1$ and $m = 0.6$ for all simulations.

We apply a method used on the lattice Lotka-Volterra model (LLVM) (Tainaka, 1988; Matsuda et al., 1992). The evolution method for the lattice model is defined as follows:

- (1) Distribute two species, X_1 and X_2 , over some square-lattice of points in such a way that each point is occupied by only one individual.

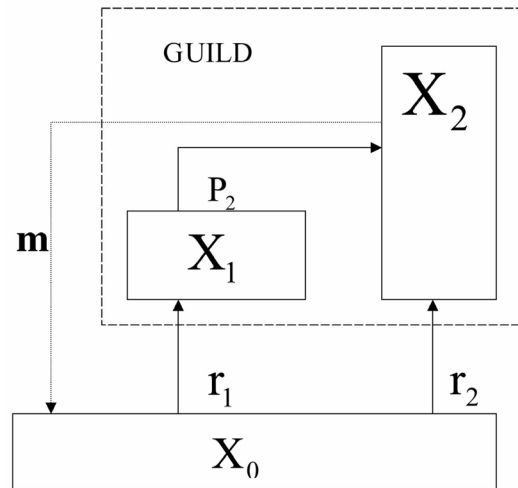


Figure 1. A schematic diagram of an ecosystem with intraguild predation. The ecosystem consists of a plant X_0 , a pure consumer (prey) X_1 and a predatory consumer X_2 . The environmental parameters, r_1 and r_2 , are reproduction rates of X_1 and X_2 , respectively. p_2 is the predation rate of X_2 , and m is the mortality rate of X_2 .

- (2) The following two reaction processes are performed.

- (i) We perform a single particle reaction (1d). Choose one square-lattice point randomly; if the point is occupied by an X particle, it will become O at the rate m .

- (ii) Next, we perform a two-body reaction, that is, the reactions (1a), (1b) and (1c) above. Select one square-lattice point randomly, and then specify one of the nearest-neighbor points. Let the pair react according to (1a), (1b) and (1c); for example, if a pair of points occupied by X_1 and X_2 are picked up, the former point will become of X_2 . Here we employ periodic boundary conditions.

- (3) Repeat step 2) $L \times L$ times, where $L \times L$ is the total number of the square-lattice sites. This step is called a Monte Carlo step (Tainaka, 1988). In this paper, we set $L = 100$.

- (4) Repeat the step (3) for 1000-2000 Monte Carlo steps.

3. SIMULATION RESULTS

We carried out simulation runs of the LLVM model for various values of the parameters. The population dynamics of all three species reach their stationary (equilibrium)

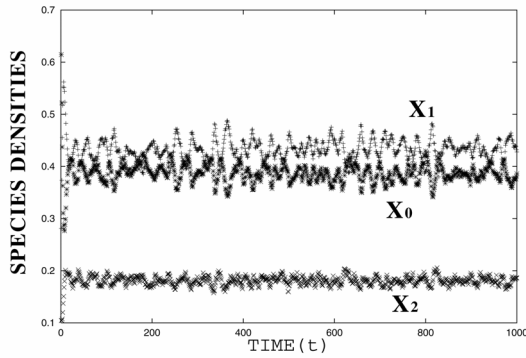


Figure 2. Temporal evolution of a 3-species lattice ecosystem with intraguild predation. The generation time t is measured as Monte Carlo step in the simulation. The densities of a plant X_0 , a prey consumer X_1 and a predatory consumer X_2 are plotted against 1000 generations.

densities in a few generations (Monte Carlo steps) and then fluctuate around them (Fig. 2).

In Fig. 3, the steady state densities of X_1 and X_2 are plotted against reproduction rates of either r_1 or r_2 . Simulation results of for the LLVM, clearly reveal very complex behaviour. The steady-state densities of all three species are highly dependent on the combination of both r_1 and r_2 in a very complex manner. We also can find that species remain in existence or go extinct depending on the values of the parameters of r_1 and r_2 . Such extinction is called phase transition.

A parameter sensitivity appears in the density of X_1 . In Fig. 3(c), the density of X_1 increases with r_1 increasing, if r_2 is 0.5 or larger. However, the density of X_1 decreases with an increase of r_1 if r_2 is 0.3 or smaller. The latter result is paradoxical since the prey density decreases in spite of an increase in prey reproductive rate. The r_1 -dependence of X_1 is strongly effected by r_2 .

We also observe a twisting behavior. Fig. 3(d) shows that all curves are crossing around $r_2=0.4$. We call this a twisting profile: any pair of curves are intersecting near $r_2=0.4$. The r_2 -dependence of X_1 sensitively depends on r_1 .

Another parameter sensitivity appears in X_2 (Figs. 3(e) and 3(f)), reflecting some trends of X_1 . If r_2 is at or below 0.5, the X_2 density increases gradually with r_1 . However, if r_2 is above 0.7, it becomes almost independent of r_1 . This is expected because X_1 is extinct at that level of r_2 . As a result of the r_2 -sensitivity of X_1 and X_2 , the density of X_0 changes with an increase in r_1 and r_2 (Figs. 3(a) and 3(b)). Furthermore, we also see the twisting profiles in

species X_0 , while X_2 shows no such phenomenon (Figs. 3(c) and 3(e)).

4. DISSCUTION

We have analyzed a spatial ecosystem composed of a plant, a prey consumer and a predatory consumer. For all species, the population dynamics show that the densities approach their steady-state values.

These steady-state densities reveal highly complex parameter sensitivity. For example, the extinction of a prey consumer is sensitive to an environmental parameter (Fig. 3).

Four typical examples of stationary patterns of the lattice ecosystem are shown in Fig. 4. These figures indicate the parameter sensitivity of the steady state densities on r_1 and r_2 . In fig. 4(a) three species coexist. However, if r_2 is increasing, X_1 is extinction. (fig. 4(b) and 4(c)) But, if r_1 is increasing, three species can coexist (fig 4(d))

In fig. 5, the phase diagram is shown against both parameters r_1 and r_2 . The stability and complexity of communities and/or ecosystems becomes a very important issue in conservation (Pimm, 1991). Traditional studies of ecosystems often tried to correlate the stability to the shape (network structure) of food webs (Paine, 1966). Our results show that the stability depends not only on the shapes, but also on the parameter conditions of the food web network. Even if the ecosystems are identical in their shapes/structures, different parameter settings may result in different equilibriums and/or stabilities. In natural communities, a slight environmental change in one species often has a strong effect on another species (Pimm, 1991).

Our results also show highly complex phase transitions, probably due to the spatial structure of the lattice model. This also complicates the outcomes of ecosystem dynamics in general. We also evaluated the mean-field version of this ecosystem (unpublished results). These results show rather simple parameter dependence (see also (Satulovsky and Tome, 1994; Hance and Impe, 1998)), unlike paradoxical aversions and twisting in the current lattice simulations (Fig. 3).

Our results imply that the prediction of complex ecosystem stability cannot be made solely by the community structures. Instead it may also depend on environmental factors.

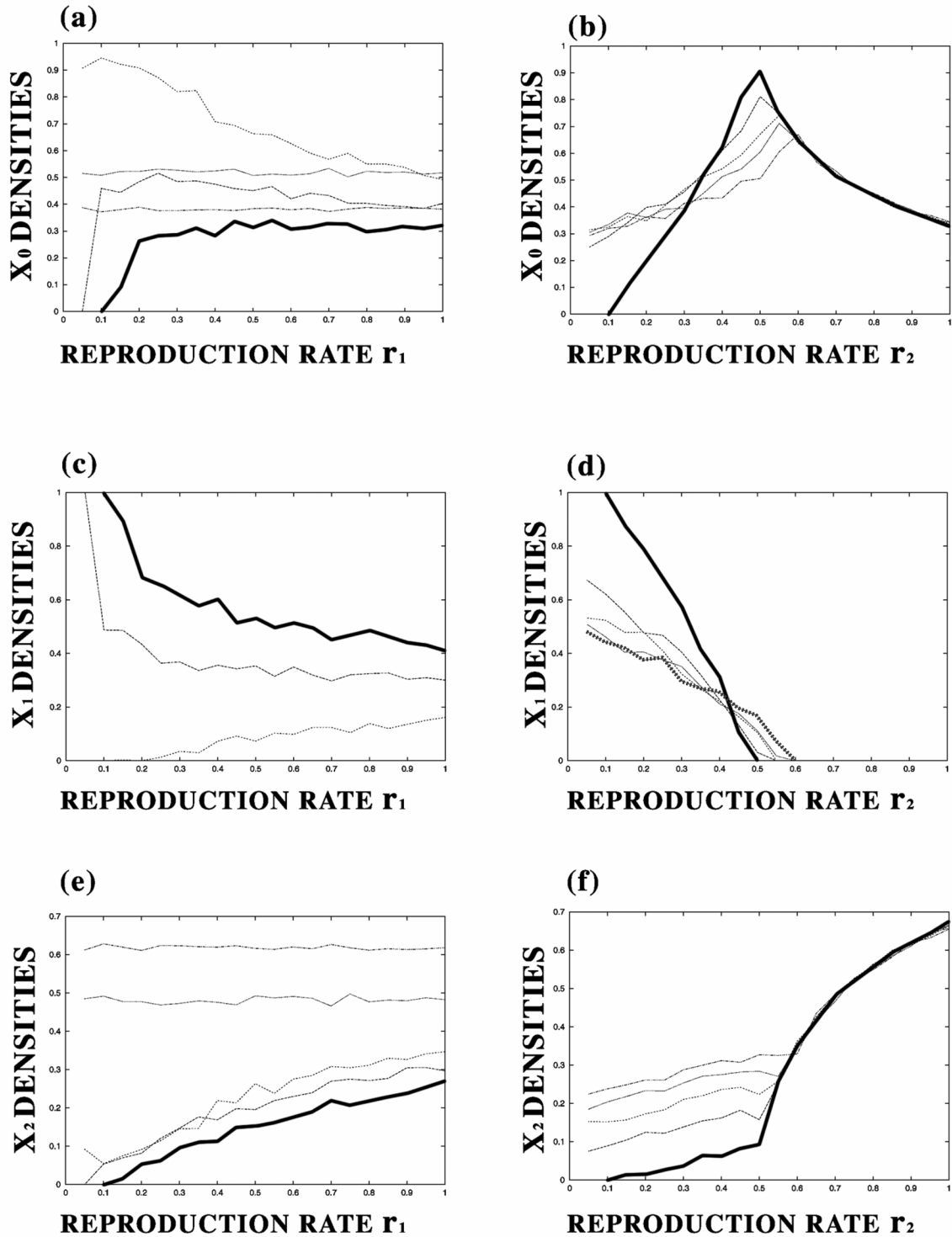
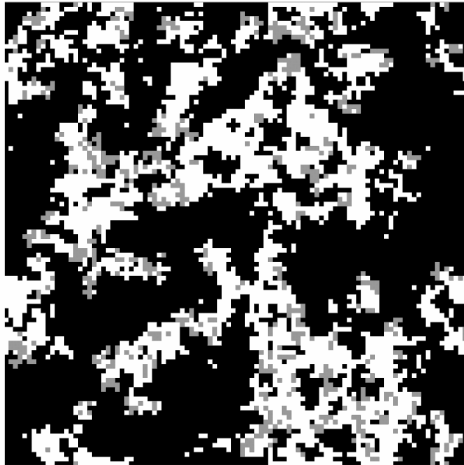


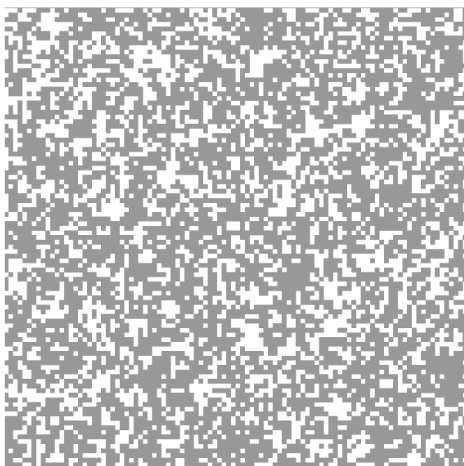
Figure 2. Simulation results of steady state densities of a 3-species lattice ecosystem with intraguild predation. (a): density of X_0 against r_1 at the values of $r_2 = 0.1$ (bottom bold line), 0.3 (next curved line), 0.5 (upper line), 0.7 (upper level line) and 0.9 (lower level line); (b): density of X_0 against r_2 at the values of $r_1 = 0.1$ (bold line with highest peak), 0.3, 0.5, 0.7 and 0.9 (line with lowest peak). (c): density of X_1 against r_1 at the values of $r_2 = 0.1$ (upper bold line), 0.3, 0.5 (bottom line); (d): density of X_1 against r_2 at the values of $r_1 = 0.1$ (upper bold line), 0.3, 0.5, 0.7 and 0.9 (bottom bold line); (e): density of X_2 against r_1 at the values of $r_2 = 0.1$ (bottom bold line), 0.3, 0.5, 0.7 and 0.9 (upper line); and (f): density of X_2 against r_2 at the values of $r_1 = 0.1$ (bottom bold line), 0.3, 0.5, 0.7 and 0.9 (upper line). Some of the lines are mixed up because of simulation time and lattice size. The two other parameters are set: $p_2 = 1$ and $m = 0.6$.



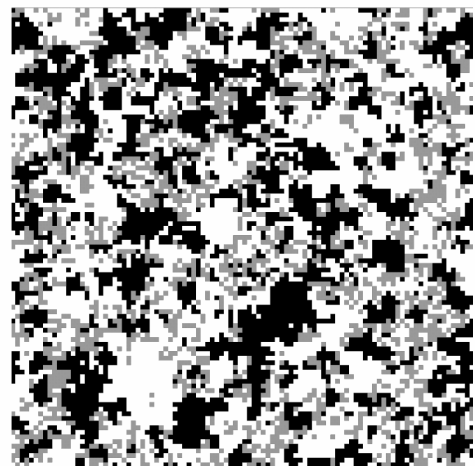
(a)



(b)



(c)



(d)

Figure 4. Snapshots of typical stationary patterns of a 3-species lattice ecosystem with intraguild predation. The parameter conditions are (a): $r_1 = 0.1$ and $r_2 = 0.2$; (b): $r_1 = 0.1$ and $r_2 = 0.5$; (c): $r_1 = 0.1$ and $r_2 = 0.9$; and (d): $r_1 = 0.5$ and $r_2 = 0.2$. The white, black and grey represent the species X_0 , X_1 and X_2 , respectively.

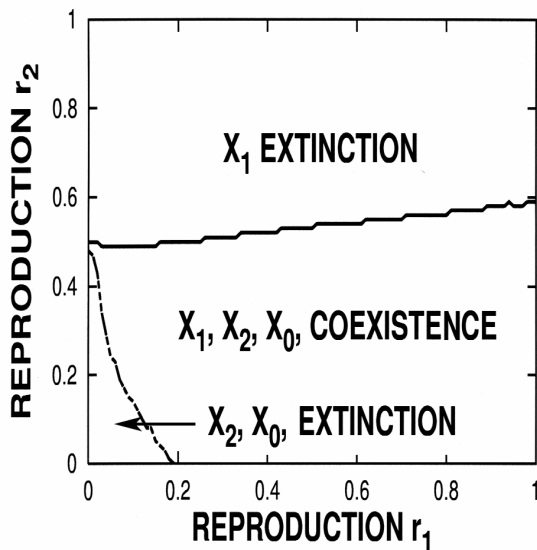


Figure 5. The phase diagram of a 3-species lattice ecosystem with intraguild predation.

Our results imply that the prediction of complex ecosystems stability cannot be made solely by the community structures. Instead it may also depend on environmental factors.

Our results also suggest that the discussion of stability based on the ecosystem structure could be meaningless unless all ecological and life history parameters of the component species are included. This could be a serious problem for the conservation of natural communities. Human activity has a great impact on ecosystems and changes the environmental conditions of the ecosystems. Such environmental changes usually alter the ecological and life history parameters of a species, even if the ecosystems appear to be same. Therefore, a slight human activity may act destructively through the changes in species-specific parameters of the component species in ecosystems.

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