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# On the Local Coexistence of Species in Plant Communities

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**Abstract:** Coexistence of many competitive species is very common in natural plant communities. For example, almost all forests and grasslands consist of various species. Extremely high biodiversity is seen in tropical rain forests. Grassland communities also often consist of many species. In plant communities, spatially competitive species of plants coexist in a mosaic pattern. Communities with a single species are very extremely rare in nature. However, mathematical studies show that the local coexistence of spatially competitive species is rarely achieved even with two competitive species. Many studies have introduced external factors to promote coexistence, such as immigration of seeds, seed dormancy, spatial heterogeneity and stochastic environments. Certainly coexistence is achieved under some circumstance in these models. However, we lack the evidence of such external factors in many plant communities. Natural coexistence of competitive species seems more prevailing than that expected from that with external reasoning. Therefore, it is reasonable to consider the possibility of internal factors promoting local coexistence of competitive species. Here we consider a plant community of two spatially competitive species in a lattice environment. We simulate the competitive interactions between the two species. Unlike the traditional models, we assume that the competition between the two species induces the replacement/takeover of one species by the other. This competitive superiority means that the reaction acts like predation in a mathematical context. We show that such replacement allows the local coexistence of two locally competitive species to some extent. Competitive interaction may take a various form of mathematical relations in spatially competitive communities. The rarity of coexistence in previous models may be the artefact of the Lotka-Volterra type competition.

**Keywords:** Competition; Species diversity; Local coexistence; Lattice modelling; Plant communities

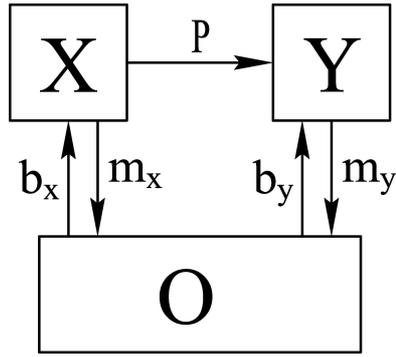
## 1. INTRODUCTION

Wild communities and ecosystems usually consist of many species [Wilson, 1992; Rosenzweig, 1995; Peterson et al., 1998]. Communities or ecosystems with one or few species are very rare in nature. Coexistence of a large number of species is almost universal in natural communities and ecosystems. It is well known that food webs can support several species [May, 1973; Peterson et al 1998].

Species diversity is also high in plant communities, where plant species are spatially competitive in nature [Tilman, 1982]. For example, individual plants in terrestrial plant communities always compete for light or space to grow, e.g., grasslands and tropical rainforest. Spatial competition is also

seen in animal communities of tidal zones or aquatic ecosystems. These communities consist of so many competing species, yet they are coexisting. Thus communities with many competitive species are universal in nature [Tilman, 1982; Shiyomi and Yoshimura, 2000].

In contrast, almost all theoretical studies imply that local coexistence of competitive species is a highly restricted case and rarely predicted [MacArthur and Wilson, 1967; Wilson and Yoshimura, 1994]. Local coexistence of competitive species may be achieved in many different mechanisms that allow animals and plants to coexist with high diversity and density. However, local coexistence is rarely achieved among spatially competitive species.



**Figure 1.** A schematic relation of a plant community of an inferior species  $X$ , a superior species  $Y$  and vacant site  $O$  ( $b_x$ ,  $b_y$ ,  $m_x$  and  $m_y$  are birth and death rates of  $X$  and  $Y$ , respectively.  $P$  is the replacement/takeover rate of  $X$  by  $Y$ ).

Local coexistence of plant species seems to be almost impossible except when some external maintaining factors such as immigration, spatial heterogeneity and temporal stochasticity [MacArthur and Levins, 1967; Wilson and Yoshimura, 1994]. Competitive interactions must lead to the exclusion of all the inferior species in plant communities [Harada and Iwasa, 1994; Harada, 1999].

In contrast, many grassland communities show extremely high diversity of species without strong external factors [Shiyomi and Yoshimura, 2000; Shiyomi, Takahashi and Yoshimura, 2000]. In some grassland communities, almost no external factors are detected, but local coexistence of many species is maintained over many years. Thus we expect some internal factors promoting local coexistence of spatially competing species in grasslands. High species diversity of competitive species is also found in tropical rainforests and aquatic ecosystems [Wilson, 1992].

Recently lattice simulation models have been used to study the spatial dynamics of communities and ecosystems in ecological studies [Tainaka, 1988; 1989; 2003]. Competitive interactions in lattice models also lead to competitive exclusion of spatially competing species [Harada and Iwasa, 1994; Harada, 1999].

Here we build a lattice model of two plant species to examine the possibility of local coexistence. The two plant species compete for space (cell or site in the lattice) as an exploitive competition. Once the site is occupied, the other species have no chance of seed dispersal as in a grassland community.

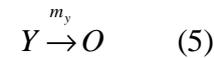
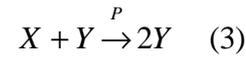
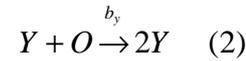
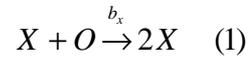
Unlike the traditional models, we introduce the third factor: the competitive replacement or takeover of one species by the other. Without

replacement, local coexistence is impossible in the current lattice model, as predicted. However, we show that, by the introduction of replacement process, local coexistence of competitive plant species becomes feasible. We discuss the discrepancy between mathematical theories and real ecological interactions. We also discuss the mechanisms of local coexistence in terms of ecosystem structure.

## 2. LATTICE MODEL OF COMPETITIVE COMMUNITIES

### 2.1 Model of Competitive Interaction

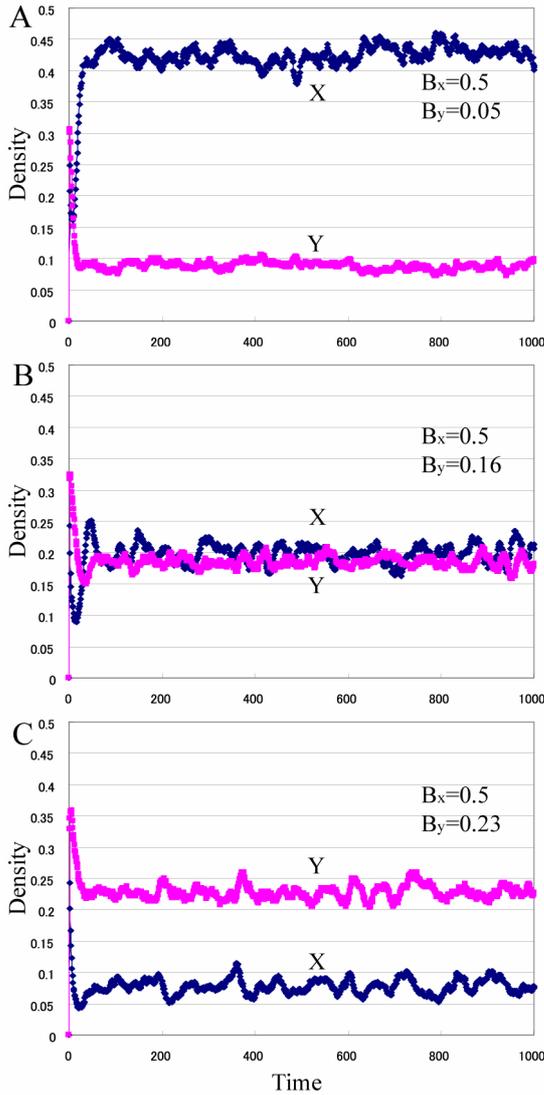
Here, we consider a simple community composed of two species  $X$  and  $Y$  in a two-dimensional lattice habitat. Interactions between species is defined as follows (Fig. 1):



where  $X$  and  $Y$  means individuals (or covers) of a plant species with seed reproduction, and  $O$ , a vacant site [Tainaka, 1988, 2003]. Each lattice site is either occupied by a plant (cover)  $X$  or  $Y$  or vacant ( $O$ ). A large individual may cover a few sites and two small plants of a single species may occupy a site.

The above equations represent respectively, reproduction of seeds (1) and (2), competitive replacement of  $X$  by  $Y$  (3), and death (4) and (5). The parameters  $b_x$  and  $b_y$  represent the birth rates of a  $X$ - and  $Y$ -individual, respectively. The parameters  $m_x$  and  $m_y$  represent the death rates of a  $X$ - and  $Y$ -individual, respectively. In the current simulation, we kept the death rates identical and constant, that is  $m_x = m_y = 0.1$ . We varied the birth rates of both species to change the competitive ability of species, since it is determined by the birth/death ratios [Tainaka, 1988].

The parameter  $P$  in Eq. (3) represents the replacement/inviation rate of an  $X$ -individual by a  $Y$ -individual. The replacement process [Eq. (3)] is functionally equivalent to a predator-prey relationship. When  $P = 0$ , the model becomes pure Lattice Lotka-Volterra competition among species  $X$  and  $Y$  [Harada and Iwasa, 1994; Harada, 1999].



**Figure 2.** A typical population dynamics of spatially competitive species with replacement. The birth rate of  $Y$  is varied in A, B and C. The parameters not shown are replacement rate  $P = 0.4$ , and mortality rates  $m_x = m_y = 0.2$ .

We carried out a computer simulation. In this paper, we apply a method of lattice Lotka-Volterra model (LLVM), similar to a contact process model [Tainaka, 1988; 1989; 2003]. If replacement reaction (Equation (3)) has no site specificity, it becomes a mean-field theory called the Lotka-Volterra equation. We record the population sizes of both species  $X$  and  $Y$ .

## 2.2 Simulation Procedures of Lattice Model

Population dynamics processing of the lattice model is explained as follows:

(1) Initially, we randomly distribute particles of two species on a square lattice, where each lattice site is either vacant ( $O$ ) or occupied by a single species  $X$  or  $Y$ .

(2) Reaction processes are performed in the following three steps:

A) We perform the reproduction processes (1) and (2). Choose one lattice site randomly. If the point is occupied by  $X$  or  $Y$ , choose one lattice site again randomly. If this second site is vacant ( $O$ ), it becomes  $X$  or  $Y$  with the probability  $b_x$  or  $b_y$ . Here we employ periodic boundary conditions such that the edges are connected to the opposite edges.

B) Next, we perform a one-body reactions (4) and (5). We chose one lattice site randomly; if the point is occupied by  $X$  or  $Y$ , then it becomes  $O$  at the death rate  $m_x$  or  $m_y$ .

C) We perform a replacement reaction (3). Chose one lattice site randomly, and then select one of the four nearest neighbour points (Neumann neighbours). If the two selected points are one  $X$  and one  $Y$ ,  $X$  is replaced by  $Y$  with probability  $P$ .

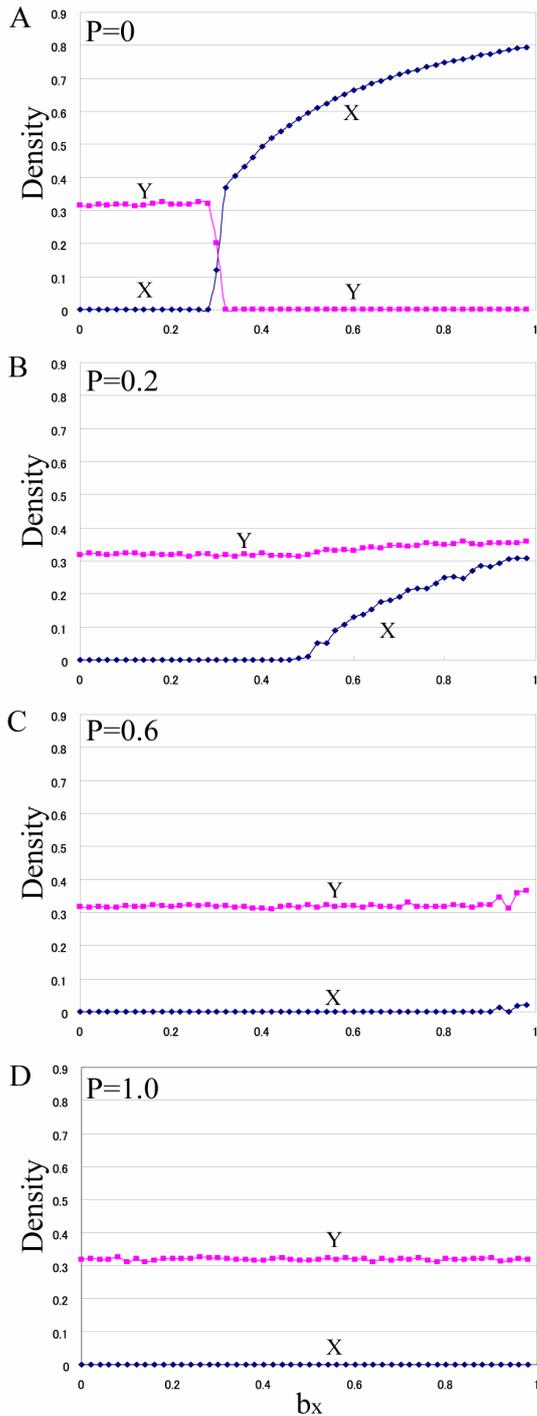
(3) Repeat step (2)  $L \times L$  times, where  $L \times L$  is the total number of square-lattice sites. This step is called a Monte Carlo step. In this paper, we set  $L = 100$ .

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

## 3. RESULTS

We carried out simulations for square lattices for various parameter combinations. We first describe simulation results where each species has no interaction ( $P = 0$ ). Without replacement, competitive exclusion always takes place. The species with a higher birth/death ratio always wins if the initial densities of both species are sufficiently high. If the ratio of the two species are identical, the temporal dynamics becomes random walk and the exclusion takes place in a long run depending on the total lattice size, and the winning probability is one half. If one species have a slightly higher ratio, it will exclude the other species quite rapidly. Thus the competition for space in the lattice model is quite keen.

When the replacement probability ( $P > 0$ ) is introduced, the coexistence of species may be induced (Fig. 2). In our example, since species  $Y$  is superior, coexistence appears when the birth rate of  $Y$  is smaller than that of  $X$ . The steady state



**Figure 3.** The steady state densities of X and Y plotted against the X's birth rate  $b_x$  with various replacement rates  $P$ . A:  $P = 0$ . B:  $P = 0.2$ , C:  $P = 0.6$ , D:  $P = 1.0$ . The Y's birth rate is constant at  $b_y = 0.3$ . The mortality rates  $m_x = m_y = 0.2$ .

densities of both species also depend on the combinations of the birth rates and the replacement rate (compare Fig. 2A, 2B and 2C).

In Figure 3, the steady-state densities of species X and Y are plotted against the birth rate of species X while keeping the birth rate of Y constant a low

rate. This figure shows the distinctive nature of replacement effects. When the replacement  $P = 0$ , the competition between the two species is extremely keen and the winner of competitive exclusion is sharply switched at  $b_x = b_x = 0.3$  (Fig. 3A). However, the replacement is once introduced, the pattern of steady state densities changes completely (Fig. 3B-3D).

When  $P = 0.2$ , both X and Y coexist when the birth rate of X is sufficiently high ( $b_x > 0.5$  in Fig. 3B). Interestingly, at the same time, the density of Y is slightly increased with the birth rate of X. This increase is the effect of replacement reaction. When the replacement rate is further increased to  $P = 0.6$ , the coexistence is marginally possible when  $b_x \gg 0.95$  (Fig. 3C). When it further increased to  $P = 1.0$ , no coexistence becomes possible and X is always eliminated (Fig. 3D). Fig. 3 also shows that coexistence is possible only in some intermediate range of  $P$ .

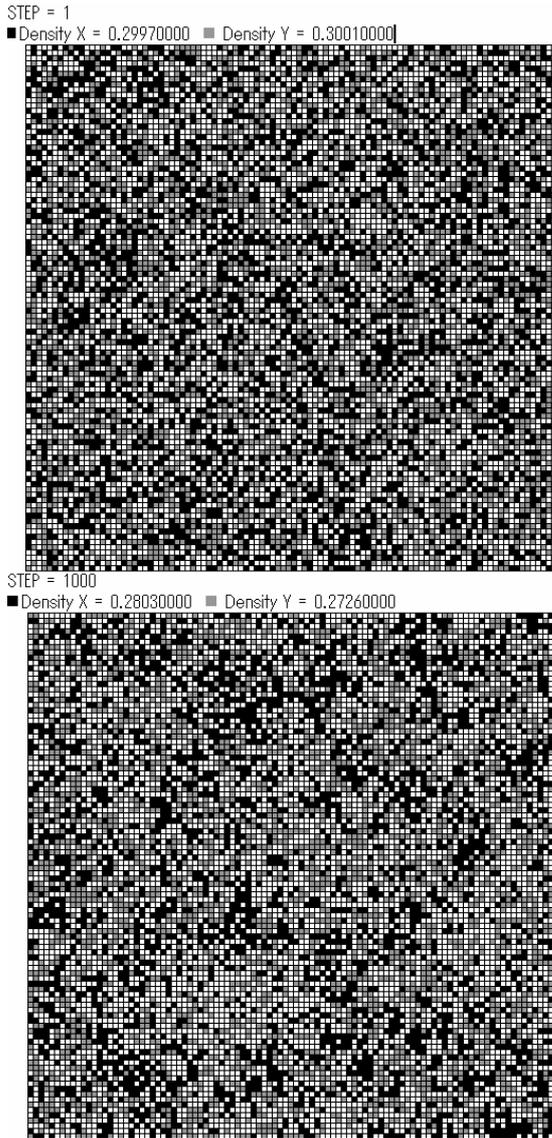
Thus, in a lattice environment, stable coexistence of two species becomes possible under a range of direct replacement interactions, as long as the two species are approximately equal in their relative strengths (Figs. 3B).

The distribution pattern at the steady states shows the clumping tendencies of X and Y (Fig. 4). Both X and Y aggregate compared with the initial random distribution. However, the aggregation tendency is much stronger in Y, probably because Y chases and eats up X individuals.

#### 4. DISCUSSIONS

Mathematical and simulation studies show that the coexistence of competing species is not very likely in general because of competitive exclusions (MacArthur and Wilson 1967; Tilman 1982). For example, in a Lotka-Volterra competition system, the coexistence of two species is only possible when the degree of interspecific density effects is smaller than that of intraspecific ones. Mutual exclusion is always a common outcome in many competitive models.

Competitive exclusion is fierce when the two species are competing for space, when space is limited (Fig. 3A). Laboratory experiments on competition in a closed system also show that competitive exclusion is a most likely outcome, e.g., grain beetles, an aquarium, bacterial cultures, chemostats [Kuwata and Miyazaki, 2000]. Our simulation experiments show that spatial coexistence is indeed impossible if competition for space is the Lotka-Volterra type (Fig. 3A). Therefore, mathematical and simulation studies



**Figure 4.** A snapshot of typical stationary patterns for the lattice competitive communities. Left: the initial distribution. Right: the distribution pattern at time step  $t = 1000$ . The steady state densities are about 0.28 for both species. The parameters are  $b_x = 0.8$ ,  $b_y = 0.1$ ,  $P = 0.3$ . The mortality rates  $m_x = m_y = 0.2$ .

agree well with laboratory experiments. The local coexistence of competitive species is rarely possible, as predicted in the previous studies.

In contrast, almost all natural competitive communities show high species diversity [Wilson 1992; Rosenzweig, 1995; Shiyomi and Yoshimura, 2000]. We then face the paradox of local coexistence of many competitive species. Theory tells us that most competitive communities should be pure communities, whilst observation tells us that almost all plant communities have high species

diversity. There should be some general reasons or mechanisms for local coexistence of plant species.

Many mathematical and simulation models have been developed and explored to show the local coexistence of plant (or spatially competitive) species. These models include some forms of external factors, such as heterogeneity in space and time, temporal disturbances or destruction of local habitats, immigration, dispersal or movements between isolated patches and variations in microhabitat structure [Tilman, 1988; Rosenzweig, 1995; Peterson et al., 1998]. These models show some level of local coexistence. However, we find the evidence of such external factors in plant communities. For example, isolated grasslands often consist of many species of grasses and herbs. There is neither indications of a heavy load of seed immigration nor the variability in habitats maintaining the stable species components in the grassland communities [Shiyomi, Takahashi and Yoshimura, 2000].

In this paper, we closely examine the nature of competitive interaction between the plant species. In grasslands, plant species always compete for space. Some species is stronger or superior in competitive ability and shading and invading the neighbouring plants. From such a fact, we introduce the replacement/takeover process between the two species,. Here one species Y is superior in competitive ability (replacement ability). With the replacement process, coexistence becomes feasible in a relatively wide range of parameter space (Fig. 2 and 3).

The replacement process is functionally equivalent to prey-predator interaction. In prey-predator systems, coexistence of several to many species is generally possible [May, 1973]. This means that competitive coexistence may be maintained by a mechanism similar to that of predator-prey interactions. However, we should note that, in the current lattice model, the replacement reaction is weak unlike the predator-prey systems of the most traditional studies. Interestingly, coexistence tends to appear when the replacement rates are not in the extreme values (Fig. 3). Predator-prey communities is known to have high biodiversity in oligotrophic environments [Rosenzweig, 1995]. Mathematically such relationships may be seen among competing plant species in grassland communities.

In grassland communities, the exact distribution of each plant species are dynamically changing over the years, but the overall community structure seems stable with multiple species coexistence [Tilman and Downing, 1994; Shiyomi and Yoshimura, 2000]. Frequent burning may also

promote the coexistence by promoting such replacements [Tilman, 1988]. In the actual dynamics, temporal invasion of one plant species by another should be frequent. Here the tradeoff between reproductive superiority and replacement ability allows the coexistence of species.

## 5. CONCLUSIONS

We could conclude that local coexistence is possible even when two plant species are competing for space. The species diversity in many plant communities may be functionally different from that of the strict Lotka-Volterra type. In the current case, the replacement or takeover interactions are functionally identical to predator-prey interactions.

There may be some other types of competitive interactions that allow the coexistence of plant species. Our studies imply that the current mathematical expression of competitive interaction is not at least adequate for the competitive interactions in plant communities. Extraordinary biodiversity in tropical rainforest may be maintained by different mechanisms. However, close examinations of species interactions are necessary to reveal the mechanisms of coexistence of so many diverse species of trees.

The external factors may be some contributing factors as in many animal studies [Peterson et al., 1998]. However, we find no evidence of the widespread co-occurrence of such factors in most diverse plant communities. We believe that some forms of internal mechanisms should be in many plant communities, as nature is so diverse in life (Wilson, 1992).

## 6. ACKNOWLEDGEMENTS

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