

# The Coexistence of Plankton Species with Various Nutrient Conditions: A Lattice Simulation Model

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**Abstract:** In aquatic ecosystems, species diversity is known to be higher in poor nutrient conditions. The enrichment of nutrition often induces the loss of biodiversity. This phenomenon is called the paradox of enrichment, since higher nutrient levels can support more species. Furthermore, the species diversity is usually high in most natural communities of phytoplankton. However, the niches of planktonic algae seem almost identical in apparently homogeneous, aquatic environments. Therefore, the high species diversity of phytoplankton is incomprehensible and called the paradox of plankton. Mathematical studies show that local coexistence of competitive species is rare. In a competitive community, the most superior species eliminates all the inferior species in the long run. Experimental results using chemostats also support this theoretical prediction. Thus we have no sound explanation for the local coexistence of many planktonic species in low nutrient conditions. Here we build a lattice model of ten planktonic species. All ten species are under competition for space in a relatively large lattice space. We report a few cases of simulation run. Simulation shows that, in an ecological time scale, coexistence of many species is observed when all species have low identical birth rates. We also show that, when the average birth rates are high, the most superior species exclude all the inferior species immediately. Our results suggest that competition for space does not function among species, when the densities of species are extremely low. The results of current simulation experiments may be related to the paradox of enrichment as well as that of plankton.

**Keywords:** Paradox of plankton; Species diversity; Coexistence; Lattice model; Paradox of enrichment

## 1. INTRODUCTION

Enrichment is empirically known to reduce the level of species diversity of animal and plant communities. However, a community should be able to support more species with enrichment because of increased productivity. Therefore, the loss of biodiversity with enrichment is counterintuitive and called the paradox of enrichment [Rosenzweig, 1975, 1995, Tilman, 1982]. Here we limit our argument in the aquatic ecosystems.

In the aquatic systems, the loss of biodiversity is often correlated with enrichment of water conditions [Ogawa and Ichimura, 1984a, 1984b, Ogawa, 1988]. High biodiversity is observed in still waters with low nutrients. Recent pollution due to domestic and factory wastewaters increases the nutrient levels of almost all aquatic systems, invoking the serious enrichment problem.

The nutrient concentrations are low in most well-preserved aquatic ecosystems. The species diversities of phytoplankton are usually high in these ecosystems. Because water environment is homogeneous and the niches of phytoplankton are almost identical, the most superior species should exclude all the rest of inferior species. However, it seems that many species of phytoplankton usually coexist in a single natural aquatic ecosystem without apparent competitive exclusions. This unexplainable phenomenon is called the paradox of plankton after Hutchinson [1961].

In contrast with the observed high diversity in natural aquatic ecosystems, theoretical studies predict that local coexistence of species is highly limited. Many mathematical analyses and simulations show that local coexistence of competitive species is usually impossible unless interspecific competition is weaker than intraspecific competition. Simulation experiments

usually show that the outcomes are the dominance of a single species resulting in the exclusion of all the rest (inferior) species.

To explain the extreme diversity in some communities, external factors are suggested, such as climatic changes, immigration from other habitats. Many mathematical models and theories try to achieve coexistence of many species by means of external factors, such as environmental changes (stochasticity), immigration of adjacent individuals. However, such external factors do not necessarily seem to be applicable to the diversity of plankton. Many empirical studies of small pond and lake ecosystems with low nutrient still waters show high species diversity. There seems no indication of external factors in these ecosystems in general.

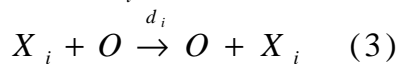
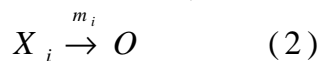
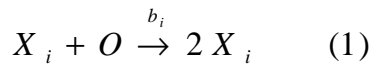
Thus we have three-fold mysteries in the planktonic communities with low nutrient conditions: (1) paradox of enrichment, (2) paradox of plankton and (3) competitive exclusion of species with identical niches.

In this paper, we built a simulation model of ten planktonic species in a large lattice habitat. We assumed that the competition between planktonic species (or individuals) is achieved through the growth difference of species. We carried out quite a few simulation runs with various birth rates, keeping the constant death rate. We show a typical dynamics of low and high nutrition conditions. In low nutrient conditions, we show that many species persist and coexist in ecological time. In high nutrient conditions, we show the case of instant elimination of all the inferior species by the most superior species. We discuss the implication of the current simulation trials in relation to the paradoxes of enrichment and plankton.

## 2. LATTICE MODEL OF MULTIPLE COMPETITIVE SPECIES

### 2.1 Lattice Model

We consider a competitive ecosystem of ten planktonic species ( $S_i$ ;  $i = 1, \dots, 10$ ) on a large square lattice (500×500 cells). Birth and death processes are given by



where each lattice site is either occupied by species  $S_i$  ( $X_i$ ) or empty ( $O$ ). The reactions (1), (2) and (3) simulate reproduction (birth), death, and dispersal (movement), respectively. The parameters  $b_i$  and  $m_i$

represent the birth and death rates of an individual, respectively. All parameters are kept constant during a simulation run. The death rate  $m_i$  is kept at  $m_i = 0.3$  for all simulations. The parameter  $d_i$  represents the accidental dispersal (movement) rate of an individual, where an individual move to one cell to another, randomly. The dispersal is implemented to prevent clumping or extreme aggregation, simulating an aquatic system. The reaction is carried out in two ways: the contact process (CP) where interaction occurs between adjoining lattices [Harris, 1974] and the mean-field simulation (MFS) where interaction globally occurs between any pair of lattices.

We study two distinct growth conditions assuming low and high productivities. In the high productivity, we assume that all species have species-specific birth rates, while in the low productivity, all species have the identical low birth rate due to the critical threshold for growth rates. We set  $b_i = 0.5$  ( $i = 1, \dots, 10$ ) for the low productivity. At this birth rate, the net growth (reproductive) rate is positive, but very close to zero. For the high productivity, we set  $b_i = 1.01 - 0.01i$  ( $i = 1, \dots, 10$ ). Here  $\max b_i = b_1 = 1.00$ , and  $\min b_i = b_{10} = 0.91$ .

### 2.2 Simulation Procedure

The simulation procedures for the contact process (CP) are as follows:

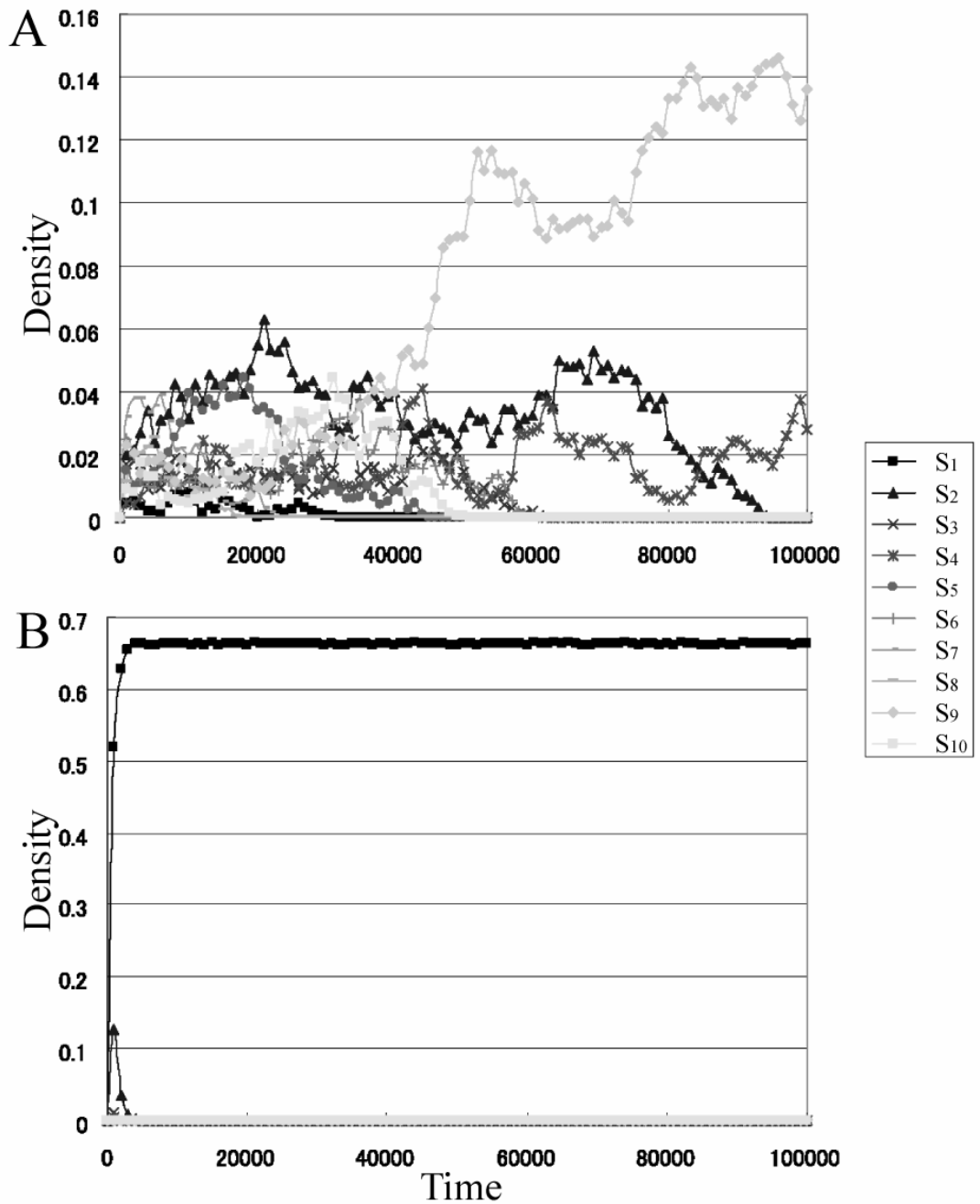
(I) Algal cells are distributed randomly over some square-lattice points in such a way that each point is occupied by only one individual cell, if the point is occupied. The initial density of  $X_i$  is set to 0.0001 for all simulations.

(II) Each reaction process is performed in the following three steps.

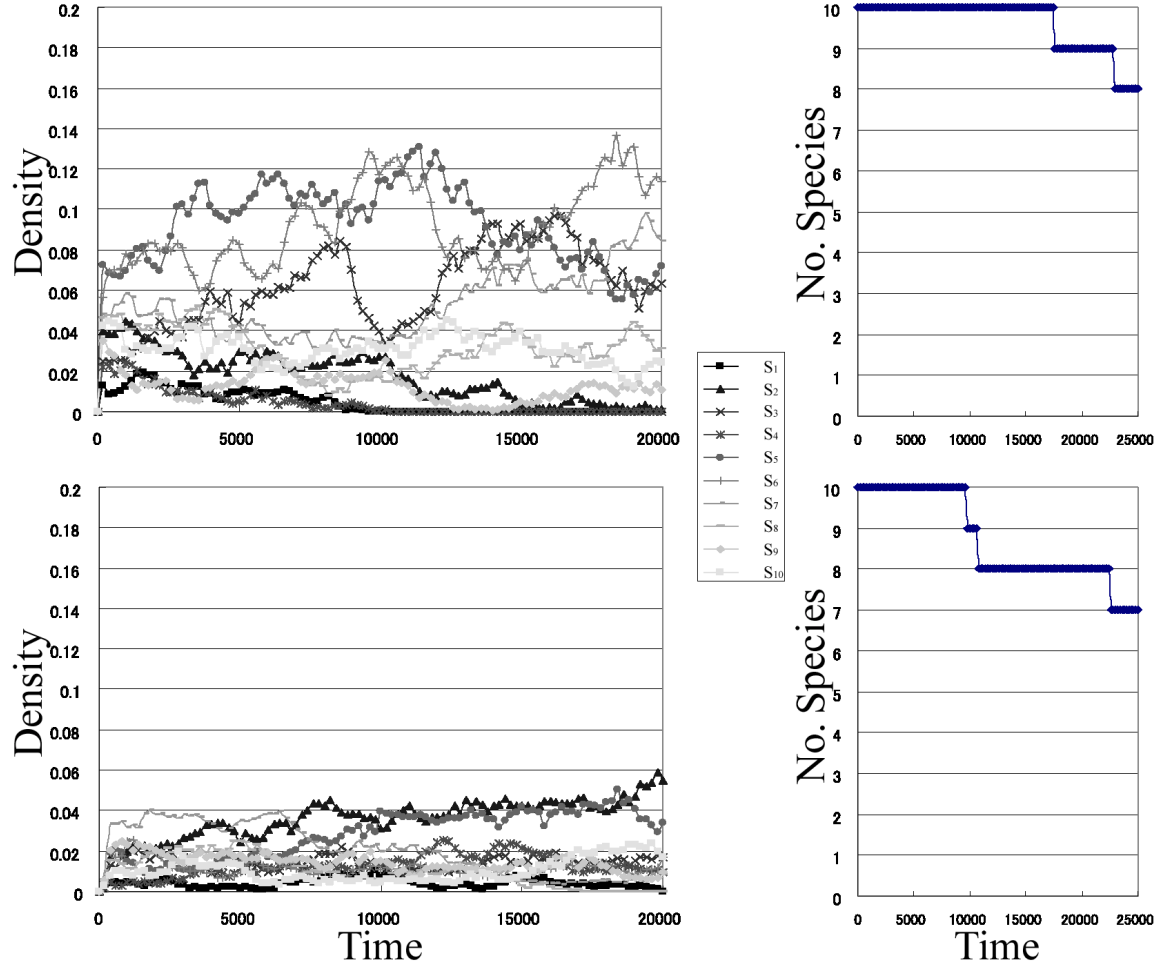
(i) We perform the single body reaction (2). Choose one square-lattice point randomly. Let change the point to  $O$  with probability  $m_i$ , if it is occupied by a  $X_i$  individual.

(ii) Next, we perform the two-body reaction (1). Select one point randomly and specify one of adjacent points. Here the adjacent site is set as the Neumann neighbors (4 sites: up, down, left and right). If the selected pair is  $X_i$  and  $O$ , then the latter point will become  $X_i$  with probability  $b_i$ . Here we employ periodic boundary conditions.

(iii) At last, we perform the two-body reaction (3). Select one point randomly. If the selected point is  $X_i$ , then we choose another point randomly. If the second point is not occupied ( $O$ ), then we move  $X_i$  to the second site (interchange  $X_i$  and  $O$ ).



**Figure 1.** A typical result of population dynamics for the lattice ecosystem of ten competitive species  $S_i$  ( $i = 1, \dots, 10$ ). A: the contact process. An identical low birth rate  $b_i = 0.5$  is assumed for all species, implying a poor nutrient condition. At this birth rate, the net growth (reproductive) rate is positive, but very close to zero. B: the contact process. High different birth rates are assumed for ten species, such that  $b_i = 1.01 - 0.01i$  ( $i = 1, \dots, 10$ ). Here  $\max b_i = b_1 = 1.00$ , and  $\min b_i = b_{10} = 0.91$ . C: the mean-field simulation (MFS) for A. D: the mean-field simulation (MFS) for B. The death rate  $m_i = 0.3$  and the dispersal rate  $d_i = 0.01$ . The time is measured by the Monte Carlo step. The total number of square-lattice sites is  $500 \times 500$ .



**Figure 2.** Temporal dynamics of ten competitive species in the spatial ecosystems in ecological time with an identical low birth rate  $b_i = 0.5$ . Top: the contact process model (exerted from Fig. 1A). Bottom: the mean-field simulation (MFS). The density of each species (left cells) and the remaining number of species (right cells) is plotted against time evolution. Up to 20,000 Monte Carlo steps are shown.

(III) Repeat the step (II) by  $L \times L$  times, where  $L \times L$  is the total number of the square-lattice sites. Here we set  $L = 500$ . This step is called a Monte Carlo step [Tainaka, 1988]

(IV) Repeat the step (III) for a specific length, that is 100,000 Monte Carlo steps.

In the case of mean-field simulation (MFS), the above procedure is slightly different. In the contact process, the interaction (1) occurs between adjacent lattice sites. However, in the MFS, the long-ranged (global) interaction is allowed: the reaction (1) takes place between any pair of lattice sites. The second sentence in Step (ii) is changed as follows:

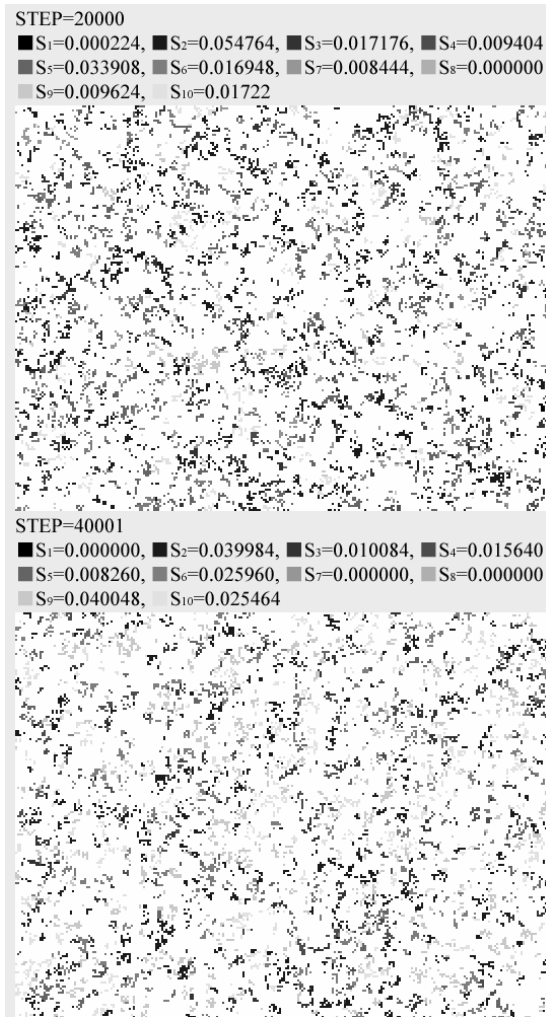
(ii') ... Two lattice sites are randomly and independently selected.

Note also that the reaction (3) has no meaning (effect) on the dynamics in the MFS.

### 3. RESULTS

We run a long-term simulation for various birth rate conditions, while keeping the death rate constant at  $m_i = 0.3$ . A typical example of long-term dynamics is shown in Fig. 1 for both low and high birth rates.

There is a threshold value for birth rates to achieve positive or net reproductive rates, resulting in zero net growth where the birth and death rates are balanced. When the birth rates are slightly lower than this threshold value (for example,  $b_i = 0.49$ ), all species go extinct quite rapidly. In an ecological time scale of about 10,000 time steps (Monte Carlo



**Figure 3.** Snapshots of a temporal pattern in the lattice model (CP) of Fig. 1 at a time point (top: 20,000, bottom: 40,001). The birth rate  $b_i = 0.5$ . The density of  $S_i$  are listed above. The 100x100 sites are cut from 500x500 sites.

steps, almost all species still coexist in the ecosystem, when the birth rate is positive, but close to zero growth rates ( $b_i = 0.50$ ; Fig. 1A). In much longer time scales, most species are eliminated by chance, as a random walk.

In contrast, when the birth rates are significantly higher, all inferior species are immediately excluded by the most superior species in a very short time much shorter than 5,000 time steps (Fig. 1B). When the birth rates are high and different among species, only one dominant species with the highest growth rate eliminate all the rest species immediately in almost any simulation. This happens irrespective of the simulation methods (either contact process models or mean-field simulations).

Fig. 2 shows the results of the contact process and the mean field simulation in which the birth rate is close to zero growth rate value. Note that the dynamics of up to 20,000 time steps is long enough to cover ecological time scales. In both the contact process and the mean-field simulation, the coexistence of most species is maintained in these time steps (Fig. 2). Between the two simulations, there are only slight differences in the average density and extinction dynamics. In the contact process, the average density is slightly higher (Fig. 2, top-left) than that of the mean-field simulation (Fig. 2, bottom-left). The remaining number of species is also higher in the contact process (Fig. 2, top-right) in contrast with that in the mean-field simulation (Fig. 2, bottom-right).

These slight differences should be due to the spatial structure of lattice model in the reaction (e.g. step (II)). Fig. 3 shows the temporal pattern dynamics of Fig. 1 at a time point of 20,000 and 40,001 time steps. Fig. 3 clearly shows clumping tendency. It indicates the effects of lattice spatial structure on the coexistence trends in Fig. 2.

We also tested various conditions in birth rates. For example, we run the simulation with low variable birth rates ( $b_i = 0.49 + 0.01i$ ). In the low density, the effects of the 0.01 differences in birth rate on the dynamics are extraordinary. All the inferior species are instantly eliminated from the ecosystem. The elimination rate is a few times faster than that in the high birth rates. The implication of variability (differences) in low and high birth rates will be discussed in detail later in the discussion.

#### 4. DISCUSSION

In the current simulations, we vary birth rates of ten species to see the persistence and coexistence of species in ecological time scales. When the birth rates of ten species are identical, most species coexist. However, a slight difference are introduced, the species with the highest growth rate eliminate all other species. In natural ecosystems of poor nutrient conditions, growth rates are closely zero and virtually no species variability in growth rate is expected [see e.g., Tilman, 1982]. Thus the coexistence in ecological time scale in our simulation is understandable in nutrient-limited aquatic systems. In contrast, in nutrient-rich conditions, the species-specific growth rates should be extremely variable [Kuwata and Miyazaki, 2000]. Thus, the elimination of all the inferior species should take place due to the competitive interaction between species.

The lattice size ( $500 \times 500$ ) in our simulation is larger than usual lattice models, but it is still extremely small in comparison with the real sizes of natural aquatic ecosystems. The total densities of plankton in natural ecosystems are lower in several magnitudes than those in our low-density simulation. Due to the computational limitation of lattice size ( $500 \times 500$ ), it is impossible to get the stable steady state with lower birth rates (closer to the threshold value). The general trends we observed in the lattice simulation could be much more significant in the natural ecosystems.

Our simulation shows that the local coexistence of phytoplanktonic species in ecological time may be achieved by the internal factors alone. The coexistence in the ecosystem is virtually not coexistence at the same site in the lattice; rather almost all individual planktonic species survive and reproduce independently from other species due to the vast space between them. Low nutrient conditions of natural ecosystems may prohibit the reproduction to reach the high density that incurred competitive interaction.

Even though the current simulations are limited and only trial runs with limited combinations of parameters are carried out, these results indicate that local coexistence of many species in very low birth rates is possible, while the instant elimination of all inferior species by a single dominant species is also possible. Thus the mechanisms underlining the current lattice model may relate to the paradox of enrichment, as well as that of plankton.

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