

Individual-Based Model of a Forest with Spatial Structure and Gene Flow

Akio TAKENAKA

*Environmental Biology Division, National Institute for Environmental Studies,
Tsukuba 305-0053, Japan*

Abstract—An individual-based model of a forest with a spatial structure has been developed. The objective is to reproduce the dynamics of a forest composed of multiple species with genetic variations within each species. Using the model, the possible consequences of a climate change was investigated. The results of the simulation study suggests the following: 1) The degree of overlap of the potential habitat ranges of different species affects the mode of the movement of the realized habitat in response to the climate change. A large overlap increases the inertia of the current distribution pattern. 2) Species diversity in the trees is reduced during the movement of the vegetation zones due to the founder effect, i.e., one or a few species which happened to be dominant near the front line dominates in the invaded area.

INTRODUCTION

The response of the spatial distribution pattern of vegetation to climate change is of great importance in the effort to predict the effects of global warming on terrestrial ecosystems. It is also of interest for understanding the current vegetation pattern because it has gone through the climate changes in the glacial and interglacial periods as well as the Dansgaard-Oeschger cycle during the last glacial period (Taylor *et al.*, 1992). However, the time scale of forest dynamics is long and experimental studies are often not practical. Thus, model simulation is an indispensable tool for the study of the effects of climate changes on forest ecosystems.

There have been various modeling approaches to forest ecosystems. One of them is an individual-based model (Chertov *et al.*, 1999). Tree-based models have been developed for various types of forests. Shugart and Smith (1992) argued that important phenomena in the context of global changes are captured in individual-based models, but not in other models.

Recently, more attention has been paid to the significance of genetic variations in an ecological context (Huenneke, 1991). Genetic variation may play an important role when plants are subjected to a heterogeneous environment. An individual-based model of a forest with spatial structure has been developed, which takes genetic variations into account. Using this model, the dynamic responses of forest communities to climate changes were investigated.

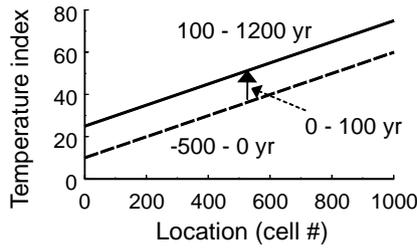


Fig. 1. Simulated “warming” of the climate. There is a linear gradient of the “temperature index” from 10 (cool climate) to 60 (warm climate) along the long side of the lattice (cell #1 to 1000). After 500 years, the index gradually rises by 15 over the entire area for a period of 100 years. This corresponds to the horizontal shift in temperature regime by 300 cells. After the warming, the new temperature regime prevails for 1100 years.

MODEL DESCRIPTION

A forest is represented as a 2-D lattice. In the present study, a 1000×100 lattice is used. It is a 2-D array of “cells”, each of which can sustain a tree at most. There is a temperature regime gradient along the long side of the lattice. The temperature condition is expressed by a hypothetical index labeled “temperature index”. A smaller index value indicates a cooler climate. To simulate the warming of the climate, the spatial pattern of the temperature index was changed as shown in Fig. 1.

Three groups of tree species are assumed. Each group consists of five species. The three groups differ in their suitable temperature regimes. The temperature condition affects the fecundity of a tree (amounts of seeds and pollen a tree makes). The optimal temperature index was 20, 40 and 60 for the tree species of groups 1, 2 and 3, respectively. The fecundity decreases with the difference between the optimal temperature index for a tree and the temperature index of the cell it occupies. The range of the temperature index when the fecundity of a tree is positive is the potential habitat of the tree. The width of the potential habitat was assumed 25 over the range (optimal ± 12.5).

Each tree has a pair of alleles (genes), which determines the optimal temperature index for the tree. For example, the optimal temperature index of a tree with a pair of alleles (24, 36) is $(24 + 36)/2 = 30$. A new tree inherits the alleles from the parent trees.

Trees die stochastically (mortality = 0.02 yr^{-1}). A new tree which sprouts from a seed randomly chosen from those dispersed from neighboring mature trees (age ≥ 25 years) occupies the vacated cell. The densities of seeds and pollen dispersed from a mature tree follow an exponential function

$$\text{density} = c \exp(-kx)$$

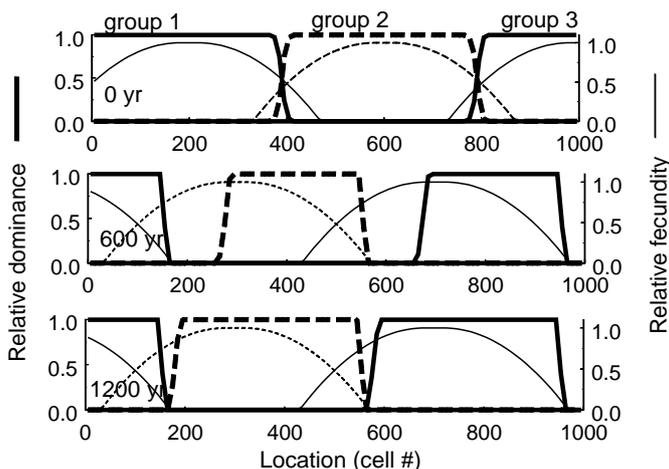


Fig. 2. Spatial patterns of species group dominance along the long side of the lattice with temperature gradient. Thick lines indicate the relative dominance of the species groups; thin lines indicate relative fecundity of the species groups.

where x is the distance from the source tree, and c and k are constants. In the present study, k is assumed 0.4 for seeds and 0.2 for pollen. The maximum dispersal distance is 8 cells for seeds and 12 for pollen. Thus, it takes at least twice the time for tree maturation (25 years) for the movement of the distribution range of a tree species by 16 cells.

SIMULATION RESULTS AND DISCUSSION

Movement of distribution range of trees in response to climate change

Initially, 15 species of trees (five species each for each of the three groups) were uniformly distributed over the entire lattice. The optimal temperature index was 20, 40 and 60 for the tree species of groups 1, 2 and 3, respectively. The fecundity of a species was positive within the range of temperature index of (optimal ± 12.5). No genetic variation was given for the first simulation. During the 500 years with stable conditions, a clear spatial pattern had emerged (Fig. 2). The three species groups were spatially ordered forming forest zones corresponding to their adapted temperature conditions. The forest zones moved gradually toward the cool end of the lattice (less cell #) in response to the simulated warming. The movement was slower than that of the environment because of the limitation of seed dispersal.

During the movement of the forest zones, temporal vacant zones appeared between forest zones. The trees formerly occupying the area were no longer capable of reproduction after the warming. The area remained vacant until the seeds of the tree species adapted to the area reached there.

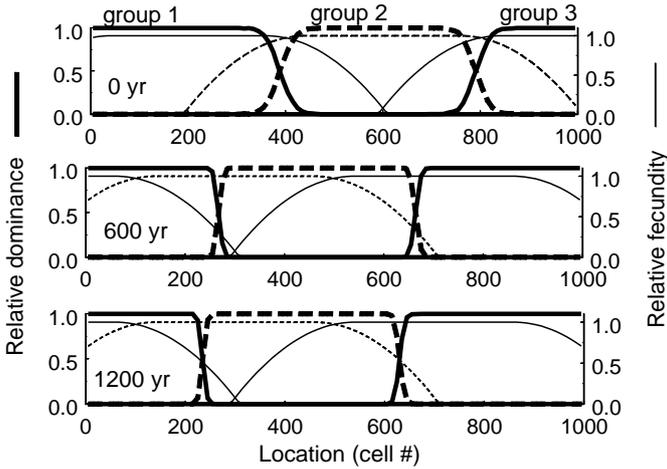


Fig. 3. Spatial patterns of species group dominance along the long side of the lattice. Within each species, there is a genetic variation in the optimal temperature index (mean ± 8). The other details are as in Fig. 2.

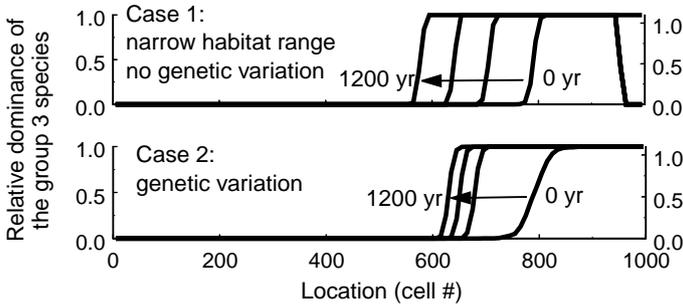


Fig. 4. Movement of the realized habitat of the group 3 species in response to the warming. Top, no genetic variation; bottom, with genetic variation in the optimal temperature index.

The mode of the movement of the forest zone was different in the second simulation with within-species genetic variation (Fig. 3). In this simulation, a genetic variation in the optimal temperature index over the range (mean ± 8) is given for each species. Due to this variation, there are large overlaps of the potential habitat ranges of neighboring forest zones. The realized borders of the forest zones were determined as a result of competitive interactions among the tree species. In this case, a change in the temperature regime reduced the fecundity of the originally dominant tree species near the warm border of their distribution, but their fecundity was still positive. Thus, no vacant zone was

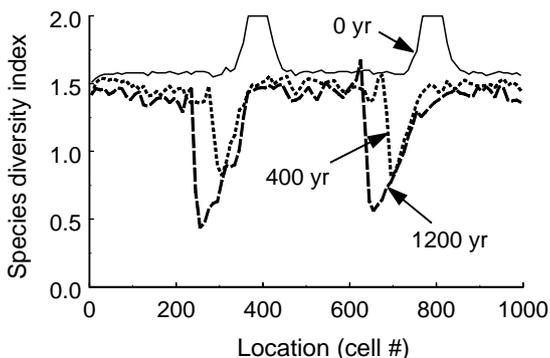


Fig. 5. Spatial pattern of the Shannon index of species diversity.

formed as in the first simulation. Movement of the forest zones depends on the gap formation (creation of vacant cells by the stochastic death of trees). Furthermore, there are trees of the formerly dominant forest zone, which keep on dispersing seeds into the gap. Consequently, the movement of forest zones cannot be as swift as in the first simulation. The difference in the rate of the movement of the forest zones due to the genetic variation is illustrated in Fig. 4. The large inertia of the spatial distribution of the forest zones agrees with the results of Kohyama and Shigesada (1995) who used a size structure-based model.

Similar results as in the second simulation were obtained when each tree can reproduce under wider temperature index range (optimal ± 20.0) (data not shown). We can conclude that the degree of overlap of the potential habitat range of neighboring species affects the mode of vegetation movement in response to climate changes. If the overlap is small, the movement is seed dispersal limited. If it is large, the gap dependent regeneration causes a large inertia to the vegetation pattern.

In the second simulation with genetic variation, a spatial genetic structure emerged along the temperature gradient. In response to the warming, the structure gradually moved like the movement of the species groups. The dispersal of both seeds and pollen are concerned with the movement of the genetic structure.

Changes in species diversity

The Shannon index, I , of species diversity was calculated for each band with 10-cell width (Fig. 5). The index is defined as

$$I = -\sum p_i \ln(p_i) \quad (i = 1, 2, \dots \text{number of species})$$

where p_i is the relative abundance of the i -th species. The diversity was low in the area where a new species group invaded in response to the environmental change. In this area, only one or a few species dominate. This is due to the founder effect,

i.e., one or a few species, which happened to be dominant near the border of the forest zone, dominated the newly invaded area.

The above results may have relevance not only to the future response of vegetation to climate changes, but also to those in the past. As the changes in temperature are greater in the higher latitude regions, it is likely that the founder effect was more pronounced in the higher latitude regions, where the amplitude of temperature change was larger. The current gradient of species diversity of forests from highly diversified tropical forests to the boreal forests dominated by a few tree species agrees with this hypothesis.

The application range of the model

The 1000×100 lattice used in the present study is large enough to represent the vertical distribution pattern of vegetation zones along mountain slopes. Although it is two orders smaller than that required for the study of the latitudinal distribution pattern of vegetation, enlargement of the lattice by an order or two is within the computation power of personal computers.

Relevance of genetic factors in the dynamics of biodiversity and extinction processes has been well recognized (Sih *et al.*, 2000). Molecular techniques for the detection of the gene flow among individuals have made significant progress in recent years. As trees are sessile and the gene flow strongly depends on the distance among trees, individual-based models with a spatial structure and gene flow are promising tools to make full use of the field data.

REFERENCES

- Chertov, O. G., Komarov, A. S. and Karev, G. P. (1999) "*Modern Approaches in Forest Ecosystem Modelling*" Brill, Netherland.
- Huenneke, L. F. (1991) Ecological implications of genetic variation in plant populations. In "*Genetics and Conservation of Rare Plants*" (D. A. Falk and K. E. Holsinger eds.), Oxford Univ. Press, pp. 31–44.
- Kohyama, T. and Shigesada, N. (1995) A size-distribution-based model of forest dynamics along a latitudinal environmental gradient. *Vegetatio* **121**: 117–126.
- Shugart, H. H. and Smith, T. M. (1992) The potential for application of individual-based simulation models for assessing the effects of global change. *Annu. Rev. Ecol. Syst.* **23**: 15–38.
- Sih, A., Jonsson, B. G. and Luikart, G. (2000) Habitat loss: ecological, evolutionary and genetic consequences. *TREE* **15**: 132–134.
- Taylor, K. C. *et al.* (1992) The 'flickering switch' of the late Pleistocene climate change. *Nature* **361**: 432–436.