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FOREST-PEST INTERACTION DYNAMICS IN TEMPORAL AND SPATIAL DOMAINS

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IIASA
International Institute
for Applied Systems Analysis

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Preface

In this study mathematical models of forest-pest interaction dynamics in temporal and spatial domains are developed.

A comparison of models with different types of insect feeding and competition shows that properties of forest succession depend on insect feeding and competitive interactions within the species.

This study considers insect and seed spatial diffusion and transport and shows that the dispersion patterns of the species should not be ignored if a valid representation of reality is to be presented. In several particular cases traveling waves are obtained.

Parameter identification and inverse problems are discussed and finite-difference approximations and prepared software for the interactive exploration of developed models are briefly described. Some numerical results are presented.

B.R. Döös
Leader, Environment Program

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Introduction

Ecology and biology problems have become increasingly pressing. The only method of ecosystem research is simulation, as each ecosystem is unique and no full scale experiments are possible. A mathematical description of the essential ecological problems has only recently come into existence.

In the mathematical theory of ecological communities there are two major subjects:

1. the temporal dynamics of interacting populations, and
2. a spatial pattern of the community.

Historically, these subjects have been developed independently and, because of the mathematical difficulties, the majority of mathematical ecology models treat only temporal dynamics.

A spatial study of population dynamics began only recently. A study of the relations between structure and population dynamics is of critical importance, both to our general understanding of the behavior of the ecosystem and to our ability to manage such systems effectively.

The remarks of Okubo (1980) in his book, ***Diffusion and Ecological Problems: Mathematical Models***, merits consideration:

> "It may be optimistic, but I feel that through trial and error the use of mathematical models in the field of ecological diffusion will eventually lead to the establishment of laws and basic equations."

A mathematical treatment is indispensable if the dynamics of ecosystems are to be analyzed and predicted quantitatively. This fact is becoming more widely accepted (see, for example, Pielou, 1977; Clark, 1979; Levin, 1979,1981; Okubo, 1980; Hallam and Levin, 1986; Svirezhev, 1987).

When the model represents the ecosystem accurately, then an important aspect of the modelling is control of the biological system. A study of insect-forest systems is considered necessary for predicting forest dynamics and pest management (Bell, 1975; Holling et al., 1975; Holling and Dantzig, 1977).

Long-term relations between forest resistance and pest population cannot be described properly without consideration of spatial dynamics. It is difficult to overstate the necessity of taking into account the role of spatial heterogeneity where pest management is concerned. Even the best of long-term studies of local population dynamics fail to make sense in the absence of attention to insect dispersal. Consideration of spatial effects fundamentally changes our view of the organization of ecological communities. Models become aids to asking better questions and help focus scarce research funds, manpower, and opportunities, where they will do most good.

Studies of dispersal or spatial heterogeneity are complex but, at the same time, very urgent. A specific problem can sometimes be solved analytically but usually one must rely on computer calculations. Here the computer serves as the only possible tool for model treatment (Okubo, 1980).

Effective management of the forest-pest system requires an understanding of the consequences of alternative management strategies (Bell, 1975; Holling and Dantzig, 1977). Mathematical models of ecology give the possibility to consider different situations, to come to some conclusions, and to discuss implications for forest-pest management.

Of course, the main problem is creating a mathematical model of the object under study. An adequate model is half the success. It is necessary not only to write down all relevant mathematical relations, but also to have a clear idea as to which of these relations is of primary and secondary importance. The phenomenon, broken down into elementary physical processes, should not lose its integrity in the model.

As some authors point out (see, for example, Banks and Kareiva, 1983), before applying models to real experimental systems it appears necessary to test their performance against "data" generated by equations. Therefore, interactions between different components of the system are studied to determine a minimum set of necessary information about the system. So, initially, one should investigate the practical issues such as the amount of data required, the accuracy of the method, and the computational hazards. A large scale of complexity and detail may be necessary in order to discuss the main characteristics of the system.

Studying the effects of temporal and spatial dynamics requires additional data beyond the data needed for temporal models. Therefore, the problem of parameters and data becomes very important. It is urgent to study inverse problems and to apply estimation and optimization techniques.

The main purposes of mathematical models of ecosystems are: to search for partial solutions, to examine limiting cases, to provide qualitative dimensional analysis, to evaluate the dependence of the solution on various parameters - whether it is continuous or prone to increase unlimitedly, etc. Mathematical models for population try to describe the behavior of the system by using stable points, stable cycles and apparent chaos (May, 1976; Pielou, 1977; Svirezhev, 1987). Of special importance are the implications for pest outbreaks, where "catastrophes", in both the mathematical and the biological sense, may occur (May, 1976; Svirezhev, 1987).

The main goals of this paper are:

(i) to develop some temporal mathematical models of insect-forest dynamics by taking into account intraspecific competition;

(ii) to study spatial dynamics and heterogeneity;

(iii) to compare models which describe temporal and spatial dynamics of insect-forest systems with temporal models and to discuss considerations of space influence on the systems' behavior description.

Our intention in constructing mathematical models for insect-forest dynamics is to understand the way in which different kinds of biological and physical interactions affect the dynamics of forest and pest. This paper will try to point out what new information can be obtained by taking into account different nature effects and by studying spatial structure-population dynamics.

In Section I, the temporal dynamics of the system are considered. Intraspecific competition and cases where insects feed both on young and old trees are taken into account.

In Section II the models which describe both temporal and spatial dynamics with consideration to insect migration are presented.

In Section III, forest-pest interaction dynamics in heterogeneous environments is studied.

Section IV is devoted to the investigation of a model which describes two-age forest dynamics with seed dispersal.

As an analytical treatment may be carried out only in certain cases, it is necessary to provide a computer experiment. In Appendix A the finite-difference approximations, and in Appendix B the software which was prepared and used for numerical experiments, are briefly described.

I. Spatio-Temporal Forest-Pest Interaction Dynamics

1. Basic Model

The influence of insect pests on the age structure dynamics of forest systems has not been extensively studied in mathematical ecology. In Antonovsky et al. (1988) the temporal mathematical models of two-age forest, affected by insect-pest, are considered.

$$\begin{aligned}\dot{u} &= \rho v - (v-1)^2 u - su - \alpha u N,\\ \dot{v} &= u - hv - (1-\alpha) vN,\\ \dot{N} &= -\varepsilon N + \alpha B u N + (1-\alpha) CvN.\end{aligned} \tag{1}$$

Here u and v are densities of "young" and "old" trees; N is insect density, $\rho = \rho(v)$ is fertility of the species, $h = h(v)$ and $s = s(u)$ are death and aging rates, $\varepsilon = \varepsilon(u, v, N)$ is the mortality rate of insects, $B = B(u, N, b)$, $C = C(v, N, b)$, where b is a coefficient which represents a dependence of "young" tree mortality on the density of "old" trees.

Terms uN and vN represent the insect-forest interaction, α is a parameter and describes how insects feed. In [14] $\alpha = 0$ and $\alpha = 1$ only are considered. When $\alpha = 0$, system (1) describes the case of insects feeding only on "old" trees and when $\alpha = 1$, insects feed only on "young" trees.

In these models, cases in which insects feed both on "old" and "young" trees are not considered. In this paper different types of insects feeding are studied, therefore, let $\alpha \in [0,1]$.

Models in Antonovsky et al. (1988) do not consider intraspecific competition. The formation and maintenance of selfaggrandizing systems are the result of appropriate nonlinear couplings and of competition between the entities constituting the ecosystem. Competition becomes significant whenever the resources necessary for survival of biological components are limited. Therefore, competition is included in the models. When fertility of the "old" trees means seed production, seed dispersal is taken into consideration.

General "directed movement" mechanisms such as convection of seeds, and attractive phenomenon in population dispersal models, are taken into account.

Notice that the basic model in form (1) is obtained from the initial one by a linear change of variables. In this work, models obtained by the change of variables are studied.

2. General Model

Consider the so-called general model which is obtained from the mass balance laws and the basic model (see Fig. 1).

$$\begin{aligned} \frac{\partial u}{\partial t} &= \rho v - (v - 1)^2 u - su - \alpha u N \\ &\quad + \nabla (D_1 \nabla \rho v) - \nabla (\vec{V} \rho v), \\ \frac{\partial v}{\partial t} &= u - hv - (1 - \alpha)\, vN, \\ \frac{\partial N}{\partial t} &= - \varepsilon N + \alpha BuN + (1 - \alpha)\, CvN + \\ &\quad + \nabla (D_2 \nabla N) - \nabla (\vec{V} N), \end{aligned} \tag{2}$$

where t is time, x and y are the Cartesian spatial coordinates: $u = u(x,y,t)$, $v = v(x,y,t)$, $N = N(x,y,t)$. Functions $D_1 = D_1(v,x,y,t)$, $D_2 = (N,x,y,t)$ are the diffusion coefficients for seed and insects correspondingly. In general cases they may be determined in two directions:

$$D_i = \{D_i^x, D_i^y\}, \quad i = 1, 2.$$

The terms involving $\vec{V}$ represent a general "directed movement" mechanism. In general, the velocity $\vec{V} = \vec{V}(x,y,t)$ represents convective/advective movement. The terms $\nabla(D_1 \nabla \rho v)$ and $\nabla(D_2 \nabla N)$ represent seed and insect diffusion correspondingly.

Let us study system (2) in domain $\Omega \subset R^2$ at time $t > 0$ with initial and boundary conditions for $u, v, N, \geq 0,\ t \geq 0$.

For studying the system along with certain initial conditions

$$u\ (x,y,0) = u_0\,(x,y),\ \ v(x,y,0) = v_0\,(x,y),\ \ N\ (x,y,0) = N_0\,(x,y),$$

boundary conditions are considered.

2.1 Boundary Conditions

Nowadays, forest patches exist as more or less isolated islands surrounded by agricultural and urban land (Johnson et al., 1981). Spatial boundary conditions can be specified in various ways. Two types are studied (Okubo, 1980).

Let P be population density (ρv or N). Consider the following conditions at the boundary $\partial\ \Omega$.

a) Prescribed population densities at the boundary:

$$P\ (x,y,t) = F(t) \quad \text{at } \partial\ \Omega.$$

This condition represents a population reservoir at the boundary.

When a habitat is surrounded by a completely hostile environment, the boundary may be treated as an absorbing boundary, i.e. population density is equal to zero at the boundary:

$$P\ (x,y,t) = 0 \quad \text{at } \partial\ \Omega.$$

This condition means that there is no forest for insects and therefore no insects to feed on trees.

b) Prescribed flux across the boundary. Immigration or emigration across the boundary may be represented by the condition

$$-\nu \nabla P = W(t) \quad (\nu = D_1 \ \ or \ \ \nu = D_2) \text{ at } \partial \Omega.$$

Figure 2 illustrates how from one forest island, a new forest island may be obtained by means of seed transport - seed rain around a seed source. So if there is an outbreak of insects on one forest island, it may cause insect outbreaks on other forest islands. There is insect immigration for the second island and emigration for the first island.

When a habitat boundary is completely closed to the population - that means a fenced population. Its flux can be considered to be zero across the boundary (so-called reflecting boundary)

$$W(t) = 0 \text{ at } \partial \Omega.$$

This equation states that no flux of population occurs across the domain.

2.2 Different Types of Insect Diffusion Coefficient

In accordance with nature's processes, different types of insect diffusion may be considered.

(i) Isotropic diffusion with a constant diffusivity: $D_2 = const$.

(ii) The diffusivity is a function of trees ("old" and "young") densities:

$$D_2 = D_0 \, [alpha \ u + (1 - \alpha) v], \quad D_0 = const.$$

Many species of insects make use of smell, so attractive diffusion can be considered. The diffusivity increases with the density of tree increase.

(iii) The diffusivity is a function of insect density:

$$D_2 = D_2(N),$$

for example,

$$D_2 = D_0 \left[\frac{N}{N_0}\right]^m, \quad m > 0, \quad N_0 = N(x,y,0), \quad D_0 = const.$$

Therefore the diffusivity is high due to the high density of insects.

(iv) The combination of cases (ii) and (iii):

$$D_2 = D[\alpha u + (1 - \alpha) v] \left[\frac{N}{N_0}\right]^m, \quad D = const, \quad m > 0.$$

2.3 Different Types of Insect Death Rate

Different types of insect mortality are studied. Some important aspects of insect death concern the following:

(i) Death by natural causes only means that $\varepsilon = \varepsilon_0 = const$.

(ii) Death by intraspecific competition

a) $\varepsilon = \varepsilon_0 N$, $\varepsilon_0 = const$, therefore

$$\frac{\partial N}{\partial t} \sim - \varepsilon_0 N^2.$$

b) competition depends on feeding patterns:

$$\varepsilon = \frac{\varepsilon_0 N}{\alpha u + (1 - \alpha) v}$$ that means,

$$\frac{\partial N}{\partial t} \sim - \frac{\varepsilon_0 N^2}{\alpha u + (1 - \alpha) v}.$$

In this particular case, mortality is high due to low tree density.

(iii) Death by natural and intraspecific competition causes;

a) $\varepsilon = \varepsilon_1 + \varepsilon_0 N$, $\varepsilon_1 = const$, $\varepsilon_0 = const$, $\dfrac{\partial N}{\partial t} \sim - \varepsilon_1 N - \varepsilon_0 N^2$;

b) $\varepsilon = \varepsilon_1 + \dfrac{\varepsilon_0 N}{\alpha u + (1 - \alpha) v}$, $\dfrac{\partial N}{\partial t} \sim - \varepsilon_1 N - \dfrac{\varepsilon_0 N^2}{\alpha u + (1 - \alpha) v}$.

From a biological point of view, all of these cases mean considering different aspects of nature's processes. From a mathematical point of view, different types of diffusion equations (linear and nonlinear) are studied.

II. Temporal Dynamics

1. Consider an insect population which is closed to migration. Ignoring the effects of space, and therefore of wind and diffusion, we obtain system (1) from system (2). Let us study different types of insect mortality, the case when $\alpha \in [0,1]$ and all parameters are constant.

The main purpose of this study is to find out how the consideration of different nature processes influence the solution. Consider the following different models:

Model A:

Insect - forest dynamics with insect death by natural causes only: $\varepsilon = \varepsilon_0 = const$. When $\alpha = 0$ and $\alpha = 1$ the basic model is obtained.

Model B:

Insect - forest dynamics with insect death by intraspecific competition, without consideration of dependence on tree density (see (a) from (ii)).

Model C:

Insect - forest dynamics with insect death by intraspecific competition, which is dependent on tree density (case (b) from (ii)).

2. The stability of three models is studied. The main interest is not in the algebraic details but in the following questions: which factors determine the number of equilibrium points; will the system track environmental variations or will it average over them; which quantities in the equations are biologically significant?

Models A, B, and C have different numbers of equilibrium points but all of them have the same points as the model considered in Antonovsky et al. (1988). The origin $E_0 = (0,0,0)$ is always an equilibrium, it has no biological significance. On the invariant plane $N = 0$, there may exist either one or two equilibria with nonzero coordinates.

Table 1 illustrates the maximum possible number of equilibrium points for the different models. The number of these points depends on the order of the corresponding algebraic equation.

Table 1.

Model	$\alpha = 0$	$\alpha = 1$	$0 < \alpha < 1$
Basic	4	4	
A	4	4	7
B	6	5	7
C	7	6	11

Analytically and numerically, the relationship between the solution behavior, the number of equilibrium points, and the type of insect death are obtained.

The results of different models, numerically integrated by a computer, are presented in Figures 3-7. The parameters are chosen in accordance with Antonovsky et al. (1988). There are obvious qualitative differences between the computed solutions for different models. From Figures 3, 4, 5, and 6, it is easy to see how the effect of within-population competition influences the solution. From Figures 7 and 8, one can see how the structure of the solution depends on the varying of coefficient α. For different types of insect feeding (i.e., different values of α) different types of solutions are obtained. In Figures 7 and 8, the results of Model C are presented. All these figures illustrate that properties of forest succession depend on competitive interactions within and between species.

Therefore, different types of nonlinearities completely change the behavior of a system. But these different types of nonlinearities appear from complicating by a consideration of the natural world processes. This analysis of the models shows how necessary it is to take into account the physical characteristics of the medium, without which the model would be useless - obtained results would not be a valid representation of reality.

Future steps of presented model development are to study the case of parameter dependence on densities of trees and insects and to discuss how it effects the solution of the models.

3. Consider the stability of Model B for a particular case $\alpha = 1$. This means the forest-pest ecosystem with intraspecific competition ($\varepsilon = \varepsilon_0 N$), when insects feed on "young" trees only. From Table 1, one obtains evidence that there may exist from one to five equilibria in the first octant R_+^3:

$$E_0 = (0,0,0),\ E_1 = (u_1, v_1, 0),\ E_2 = (u_2, v_2, 0),$$
$$E_{3,4} = (u_{3,4}, v_{3,4}, N_{3,4}),$$

where

$$v_{1,2} = 1 \pm \sqrt{\frac{\rho - sh}{h}},\quad u_{1,2} = hv_{1,2},$$

$$v_{3,4} = 1 - \frac{q}{2} \pm \sqrt{\frac{q^2}{4} - q + \frac{\rho - sh}{h}},$$

$$u_{3,4} = hv_{3,4},\ N_{3,4} = qhv_{3,4},\quad q = \frac{B}{\varepsilon_0}.$$

Equilibrium $E_{1,2}$ appear in system (1) on the line

$$L_1 = \{(p,h),\ p = sh\}\ .$$

On the line

$$L_2 = \{(p,h):\ p = (s+1)h\}$$

equilibrium E_2 coalesces with equilibrium E_0 and disappears from R^3_+.

Equilibrium $E_{4,5}$ appears in system (1) on the line

$$L_3 = \{(p,h):\ p = sh - hq - \frac{hq^2}{4}\}\ .$$

On the line L_2 (if $q < 2$) equilibrium E_4 coalesces with equilibrium E_0 and disappears from R^3_+. If $q = 2$, there exists only equilibrium E_3, which coalesces with equilibrium E_0 on the line L_1 and disappears from R^3_+. If $q > 2$, there exist equilibrium E_3 only when $p > (s+1)h$. On the line L_2 it coalesces with E_0. Therefore, the parametric portrait of Model B differs from the corresponding portrait of the model described in Antonovsky et al. (1988). By means of linear stability theory parametric conditions are obtained.

In Figure 9, the solution numerically integrated by the computer is presented for a particular case ($\alpha = 1$) of Model B. Analytically, it is obtained that on line

$$L_5 = \{(p,s):\ p = sq + sh\}$$

exists equilibrium

$$E_* = (h + q, 1, q)\ ,$$

stable when certain conditions on the parameters take place.

III. Forest-Pest Interaction Dynamics in Heterogeneous Environments

A consideration of spatial effects may fundamentally change our view of the organization of the forest-pest system.

For the sake of simplicity, consider the one-dimensional diffusion-reaction system (2) with constant coefficients when non-diffusive terms are not included. This system provides different models as submodels and the most convenient starting point for a discussion of a mathematical modeling.

Let us study the following submodel of the spatio-temporal model (2). Consider forest-pest interaction dynamics in the one-dimensional domain $\Omega = [0,L]$ (see Fig. 10).

$$\frac{\partial u}{\partial t} = \rho v - (v-1)^2 u - su - a u N,$$

$$\frac{\partial v}{\partial t} = u - hv - (1-a) v N, \qquad (3)$$

$$\frac{\partial N}{\partial t} = -\varepsilon N + a b u N + (1-a) c v N + \frac{\partial}{\partial x}\left(D_2 \frac{\partial N}{\partial x}\right).$$

The main intent of this study is to consider the effects of diffusion (Hallam and Levin, 1986). Let $D_2 = const$, $a = 1$. System (3) has spatially uniform equilibrium. Note (U_*, V_*, N_*) is one of them. To study its stability with respect to small perturbations let $u = u_* + \tilde{u}$, $v = v_* + \tilde{v}$, $N = N_* + \tilde{N}$ and discard higher-order terms to obtain the linearized system:

$$\frac{\partial \tilde{u}}{\partial t} = -(s + (v_* - 1)^2 + bN_*)\,\tilde{u} - [-\rho + 2(v_* - 1)u_*]\,\tilde{v} - u_* N_*,$$

$$\frac{\partial \tilde{v}}{\partial t} = \tilde{u} - h\,\tilde{v}, \qquad (3.1)$$

$$\frac{\partial \tilde{N}}{\partial t} = -\varepsilon \tilde{N} + b\,\tilde{u}\,N_* + c\,u_* N_* \tilde{N} + D_2 \frac{\partial^2 \tilde{N}}{\partial x^2}.$$

Consideration of disturbances proportional to e^{ikx} gives the following results: If $F < F_{cr}$ then diffusion does not destabilize stable equilibrium.

For $F > F_{cr}$ a real positive eigenvalue λ of system (3.1) matrix and hence destabilization will occur for certain values of λ.

Here

$$F = F(u_{\bullet}, V_{\bullet}, N_{\bullet}, S, h, b, c) ,$$

$$F_{cr} = F_{cr}(U_{\bullet}, v_{\bullet}, N_{\bullet}, S, h, b, c, D_2) .$$

Exact formulae for F and F_{cr} are obtained. They are not present here because of algebraic complexity.

Thus, a pattern of diffusion can destabilize a uniform equilibrium of the forest-pest system. This adds another mechanism to those described by the temporal models.

IV. Seed Dispersal

1. Spatial Effects

One general study of forest island dynamics is the alteration of seed dispersal patterns which ultimately affect composition, structure, and successional development of forest patches. The inclusion of spatial effects on seed dispersal and the impacts of seed dispersal on the dynamics of forest islands are ecologically significant in rapidly changing landscapes (Johnson et al., 1981).

Consider the one-dimensional submodel of system (2) which describes two-age forest dynamics with seed dispersal by diffusion and wind:

$$\frac{\partial u}{\partial t} = \rho v - (v-1)^2 u + \frac{\partial}{\partial x}\left[D_1 \frac{\partial \rho v}{\partial x}\right] - \frac{\partial}{\partial x}(V \rho v) ,$$

$$\frac{\partial v}{\partial t} = u - hv. \tag{4}$$

When the same treatment is applied for system (4) as in (3) (i.e. based on linear stability theory), the following conclusion takes place. The system is more stable than the corresponding temporal model. For simplicity, seed transport by wind is ignored (V=0).

2. Travelling Waves

The diffusive system (4) for the existence of travelling waves is examined. Let all parameters be constant and nonnegative.

Stationary wave-form solutions of the systems propagating in the positive direction of x with speed c were sought, i.e.,

$$v(x,t) = v(\xi),\ u(x,t) = u(\xi),$$

where $\xi = x - ct$.

Without waste of community let $x \in [0,1]$. Then $-\infty < \xi \leq 1$. Substituting $v(\xi)$, $u(\xi)$ into (4) and looking for asymptotic situations as $t \to \infty$ and $\xi \to -\infty$ the following results are obtained: ($D_1^* = D,\rho$, $\rho = const$):

(i) $c^2 = D_1^*$, $h = 0$. There exist no less than two solutions. No bifurcation points.

(ii) $h = 0$, $\rho = 0$. The solution exists and $v \to 1$.

(iii) $c^2 = D_1^*$, $h > 0$.

When $\rho < sh$ the solution $v \to 0$.

When $sh < \rho < (s+1)h$ then $v \to 0$.

When $\rho > (s+1)h$ then $v \to 1 - \sqrt{\frac{\rho - sh}{h}}$.

When $\rho = sh$ then $v \to 1$.

Therefore, several particular cases are considered for which the existence of asymptotic travelling waves is proved.

V. On Parameter Estimation Problems

The use of a model in practice is often limited by the lack of exact values of parameters. For the models (2) presented, there is a problem of exact parameter values for : $h, s, \varepsilon_0, D_1, D_2$. These values are to be derived from measurements and their precise estimation presents great difficulties.

The parameter estimation problem usually has no unique solution. Particularly if the number of observations is small, different parameter combinations of equal significance are feasible. Therefore, predictions have to be used with care.

A sensitivity study yields reasonable intervals for the parameters and gives some insight into the uncertainty of results. From the formal (mathematical) point of view, problems which arise are related to the theory of guaranteed estimates (Kurzhanski, 1977, 1988), the viability theory (Aubin and Cellina, 1984; Aubin and Eckland, 1984), stochastic and nondifferentiable optimization (Ermoliev, 1933; Ermoliev and Wets, 1988). IIASA has made a significant contribution to the understanding of these problems.

A rather general approach to the estimation and identification of model parameters may be based on the application of optimization techniques.

VI. Conclusions

In this paper, a variety of models are considered from the temporal dynamics type to the diffusion-reaction type.

The purpose of this work was to discover what could be learned by considering different types of insect feeding and mortality in temporal models. The main objective was to discover what could be learned by fitting these models with spatial heterogeneity and therefore diffusion and advection terms.

We can see that the species dispersion patterns should not be ignored. Consideration of spatial effects allows a better understanding of the spatio-temporal behavior of forest-insect systems and the study of immigration and emigration processes.

Some points on the further development of the models being developed in this paper are as follows:

1. The study of model coefficients as functions of specie densities (density-dependent coefficients). In this paper a constant-coefficient version of the models is considered.
2. The investigation and solution of 2D and 3D problems.

   Here, an efficient ADI-type method for the solution of the diffusion problems may be used (Ermoliev and Wets, forthcoming).
3. The study of a general "directed movement" mechanism such as seed convection or attractive phenomena in population dispersal models.
4. The application and development of parameter estimation techniques for estimating the coefficients, boundary and initial data associated with parabolic distributed models.

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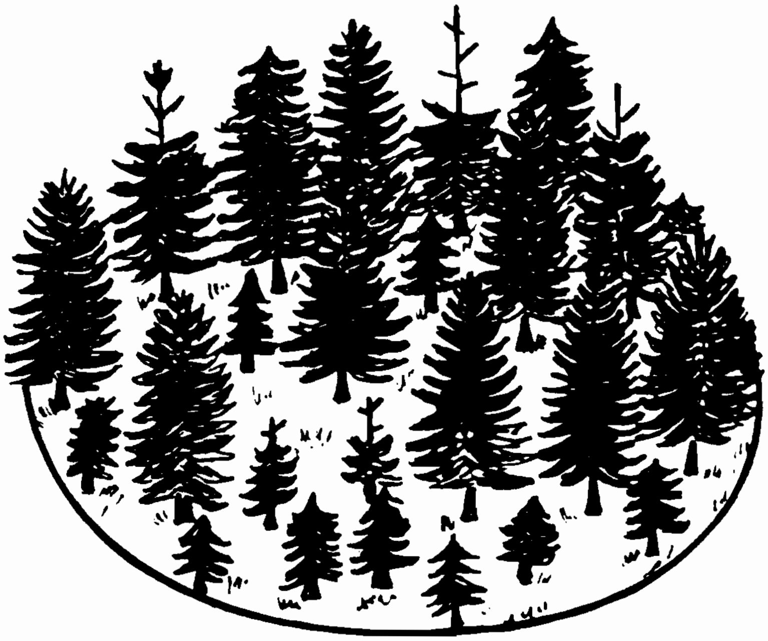


Figure 1: Schematic representation of two-age forest model

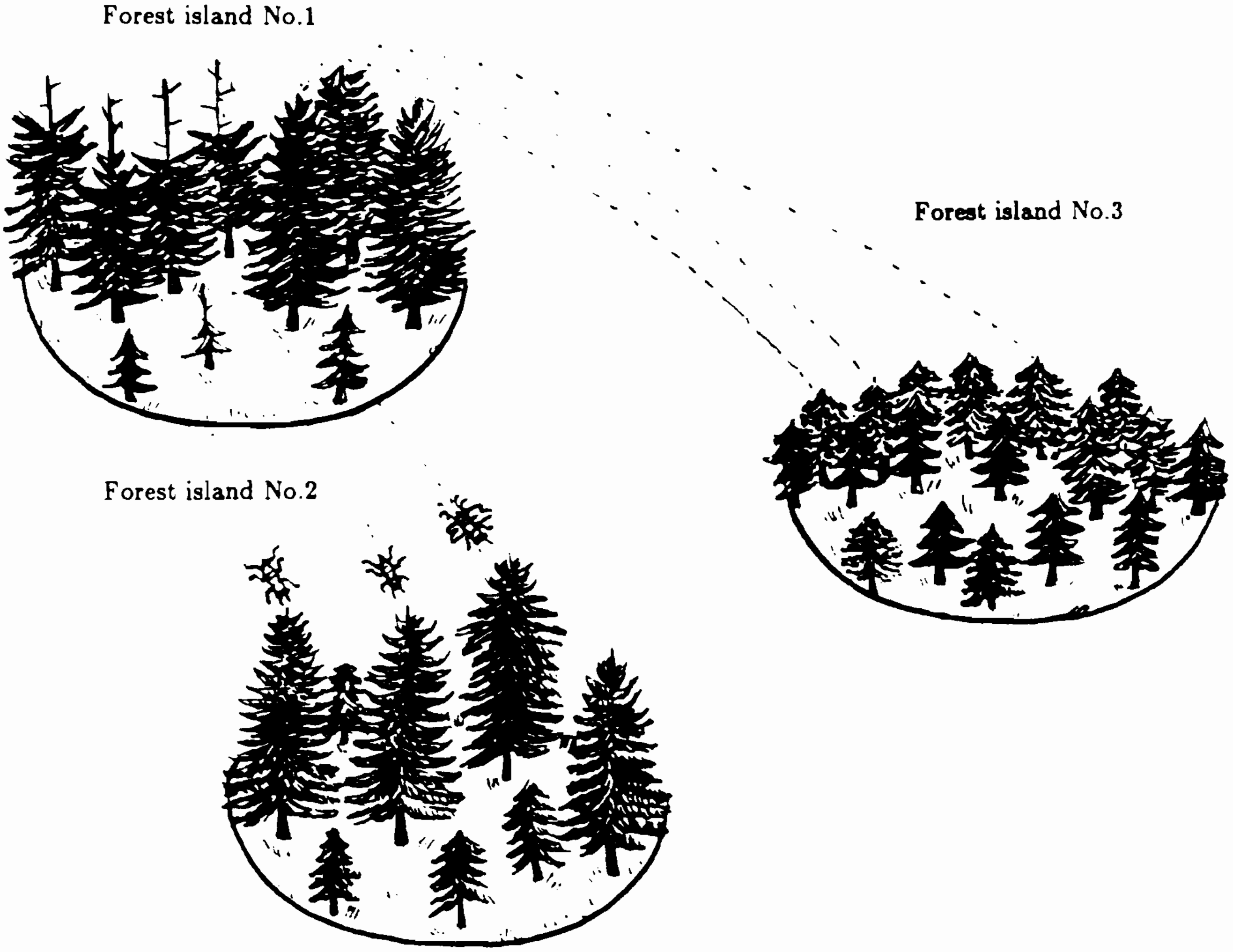


Figure 2 Schematic representation of "seed rain" and insect migration.

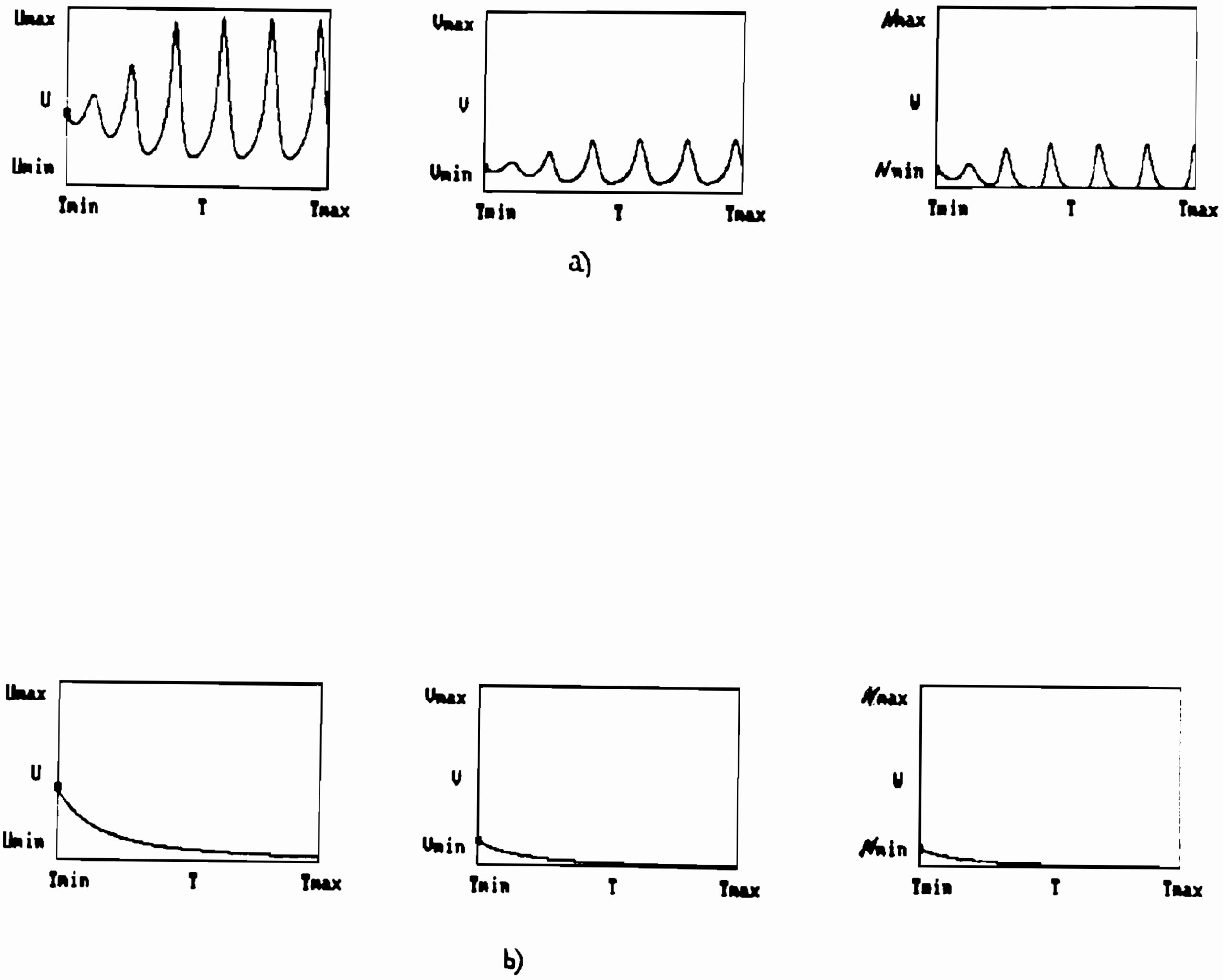
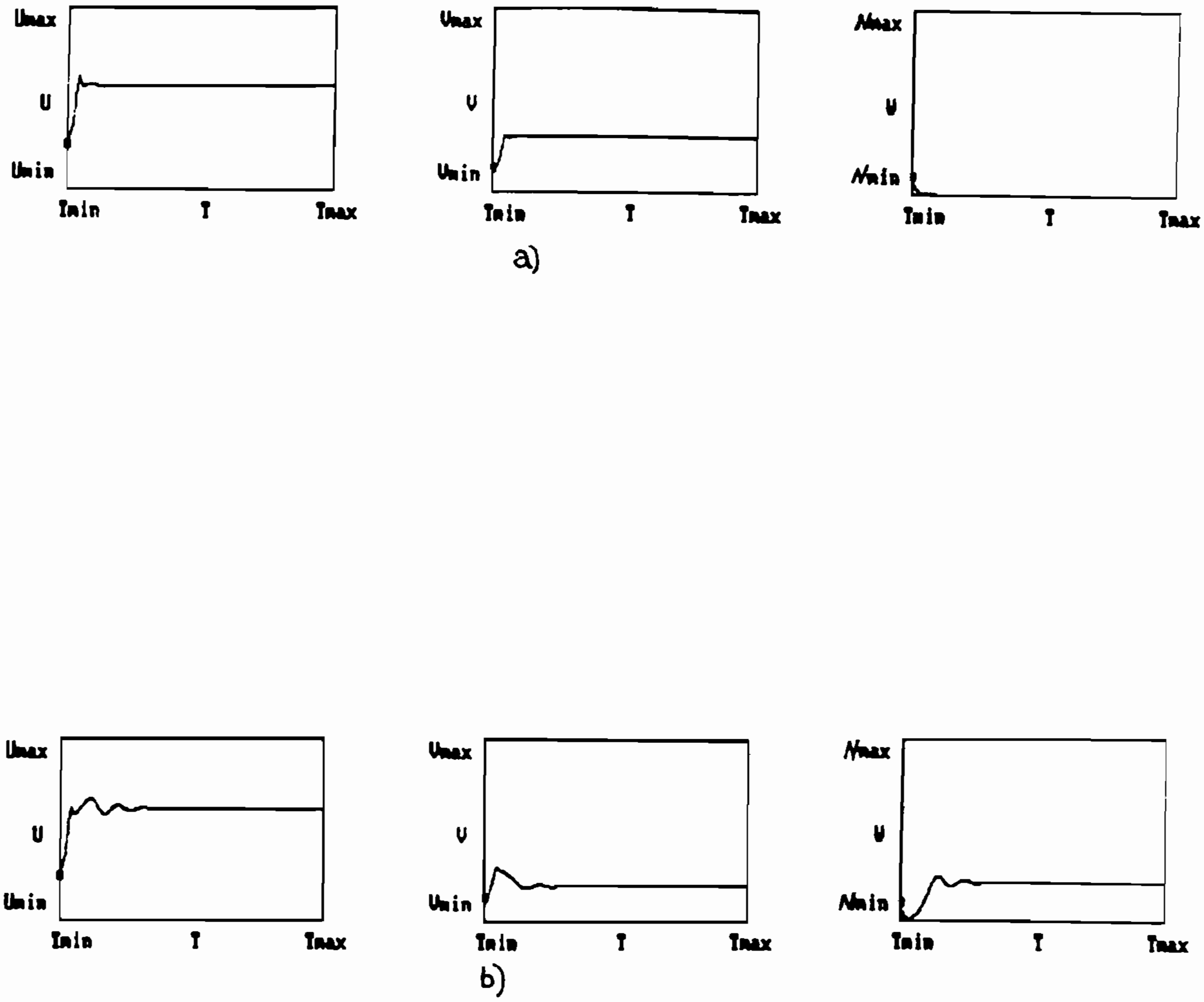


Figure 3: $\rho = 6$, $s = 1$, $h = 3$, $\varepsilon_0 = 2$, $b = 1$, $c = 1$, $\alpha = 1$, $\sigma = 0.5$:
a) Model A (basic model when $\alpha = 1$); b) model B.



a)

b)

Figure 4: $\rho = 6$, $s = 1$, $h = 3$, $\varepsilon_0 = 2$, $b = 1$, $c = 1$, $\alpha = 1$, $\sigma = 0.5$:
a) model A; b) model C.

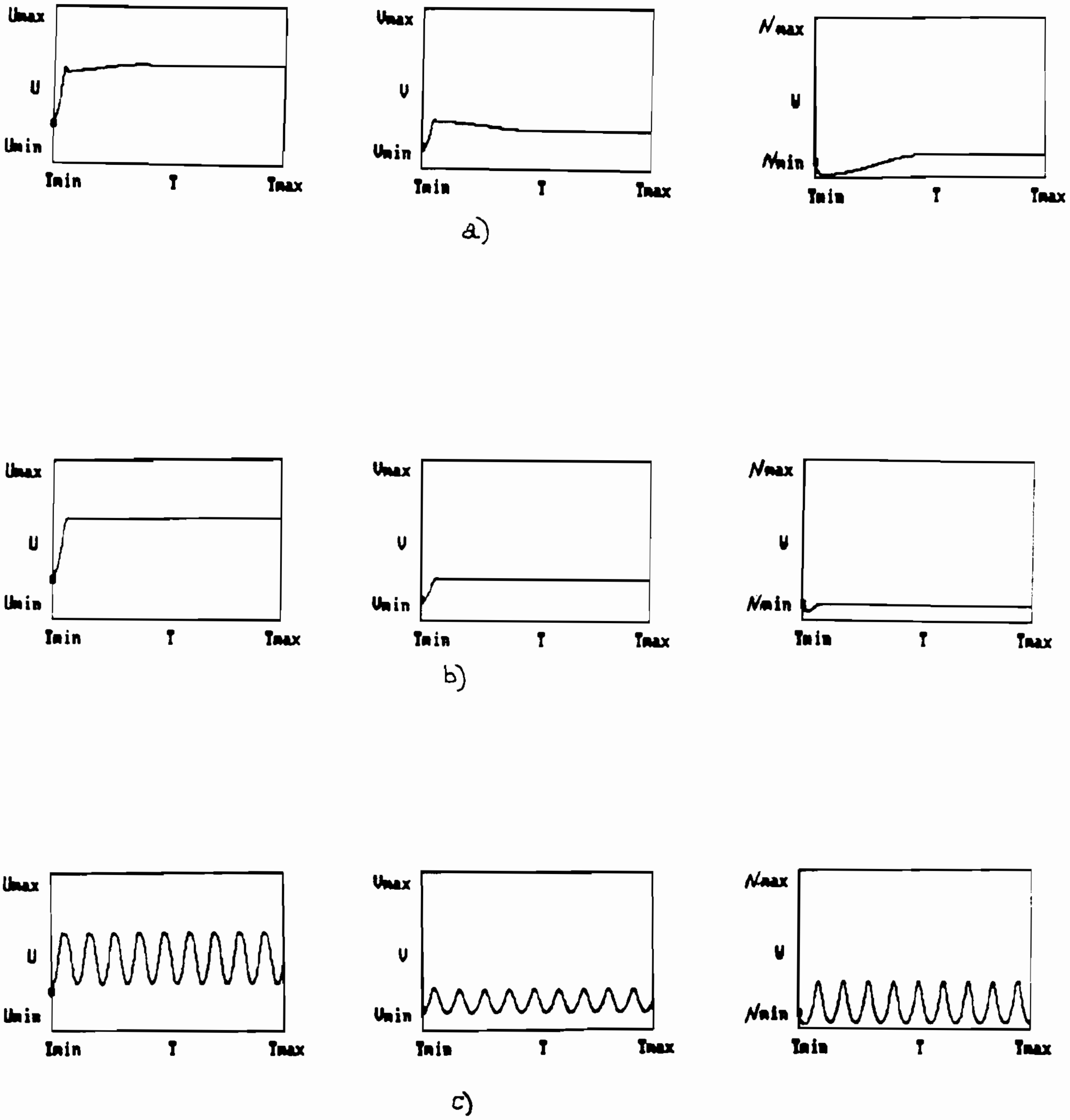


Figure 5: $\rho = 6$, $s = 1$, $h = 3$, $\varepsilon_0 = 2$, $b = 1$, $c = 1$, $\alpha = 0.2$, $\sigma = 0.5$:
a) model A; b) model B; c)model C.

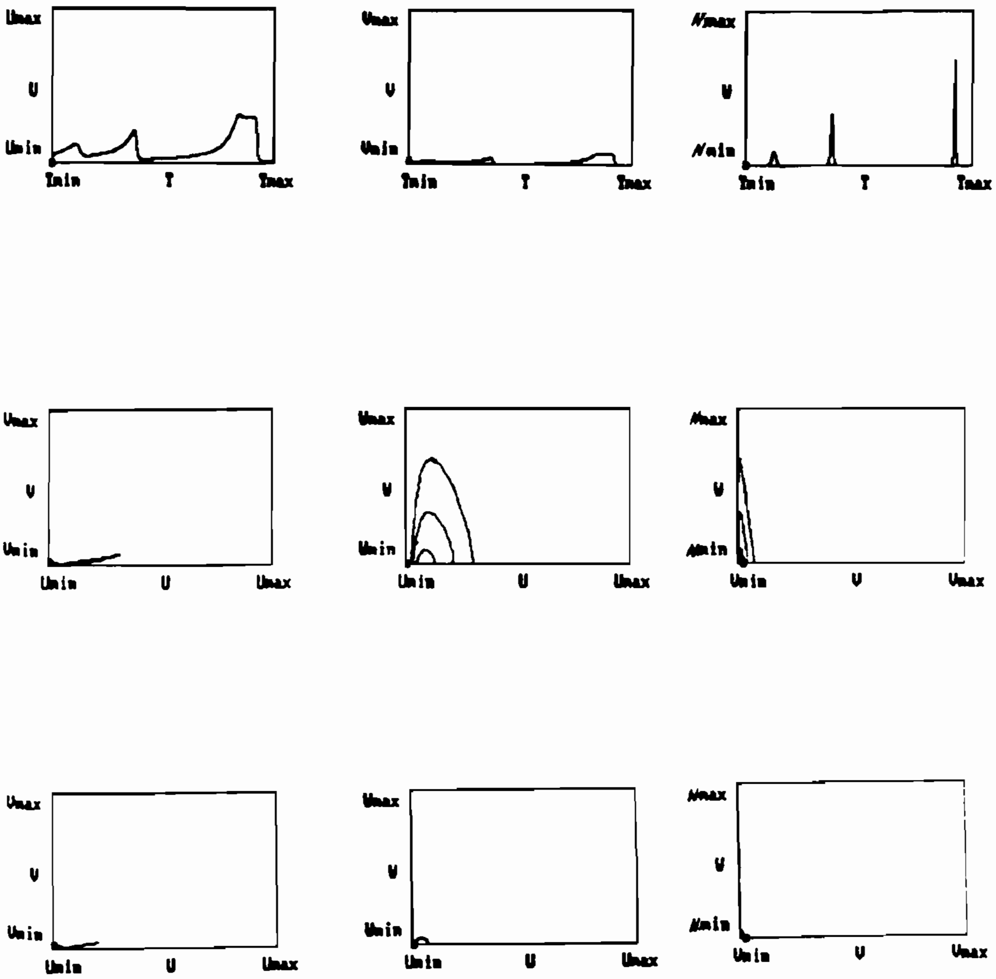
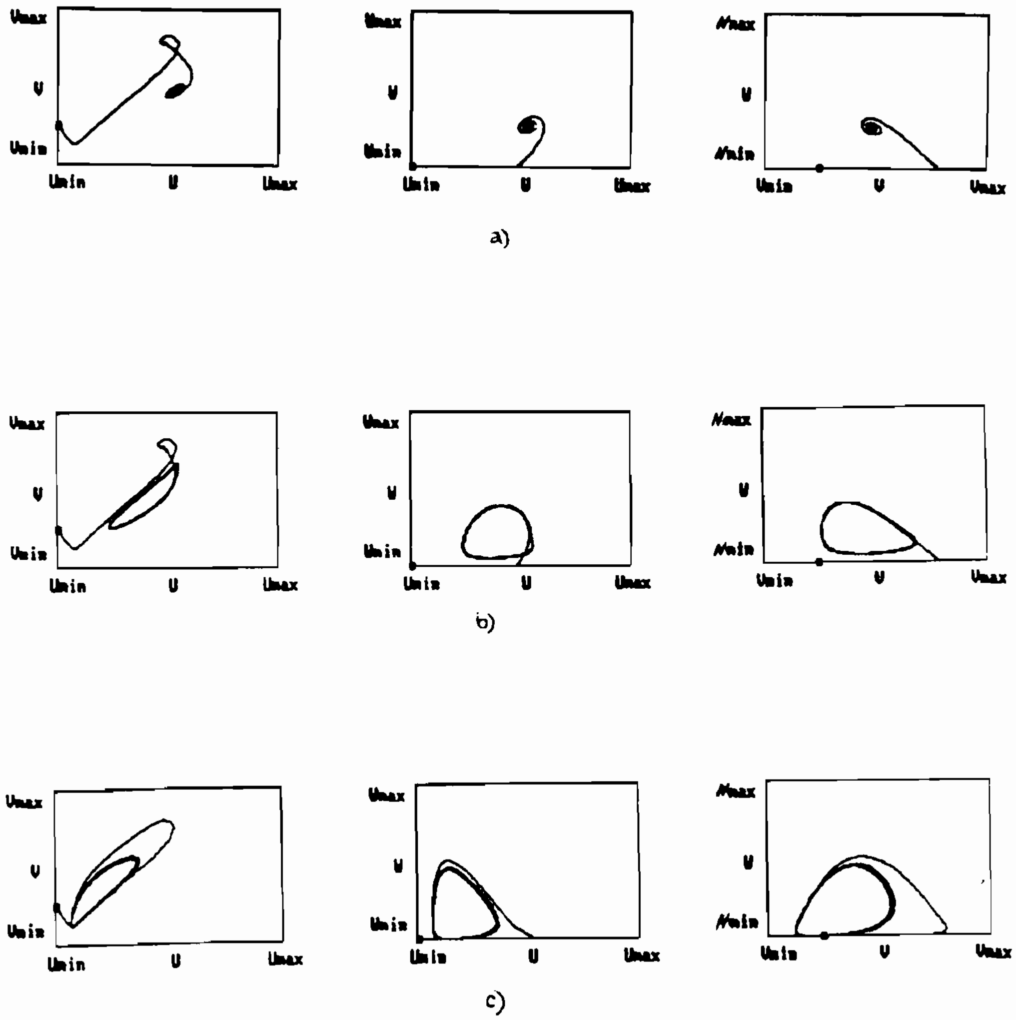


Figure 6: $\rho = 6$, $s = 2$, $h = 2$, $\varepsilon_0 = 2$, $b = 8$, $c = 8$, $\sigma = 0.5$, $\alpha = 0.3$:
a) model C; b) model A.

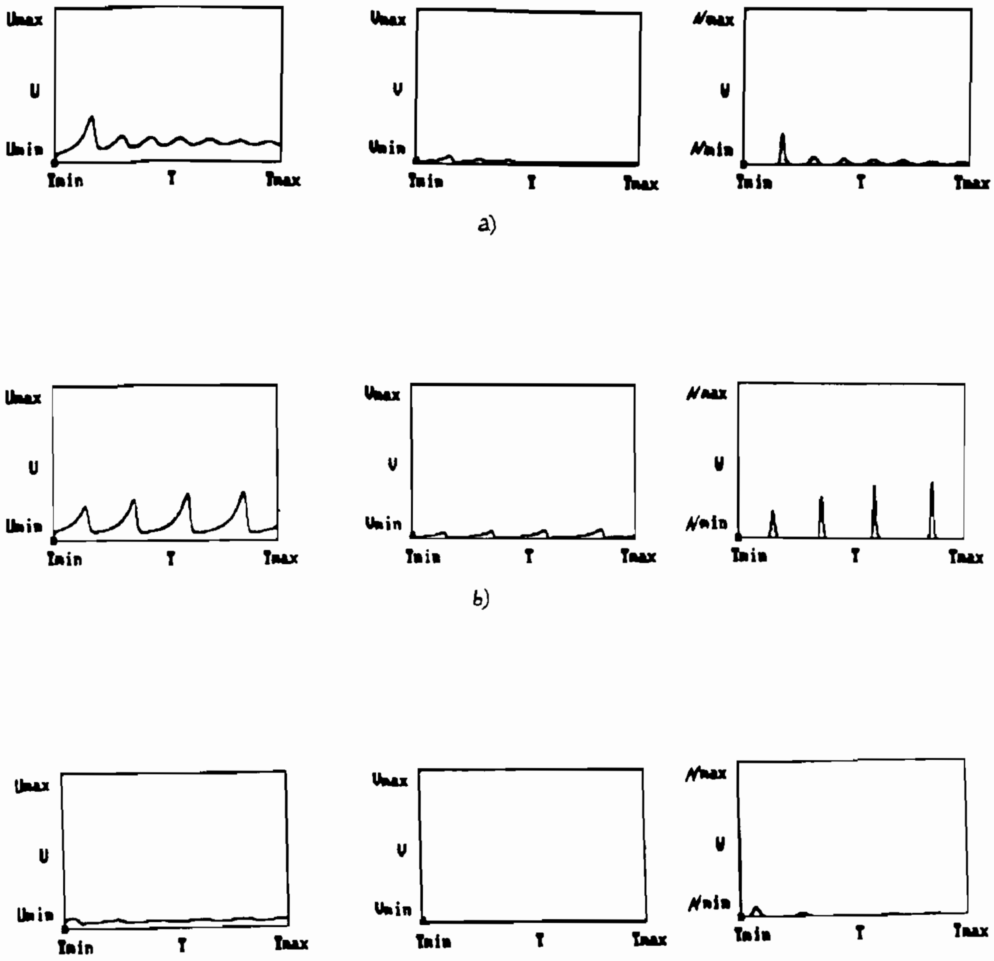


a)

b)

c)

Figure 7: $\rho = 7$, $s = 1$, $h = 3$, $\varepsilon_0 = 2$, $b = 1$, $c = 1$, $\sigma = 0.5$:
a) $\alpha = 0.1$ - stable focus; b) $\alpha = 0.2$ - stable cycle; c) $\alpha = 1$.



a)

b)

c)

Figure 8: $p = 6$, $s = 2$, $h = 2$, $\varepsilon_0 = 2$, $b = 8$, $c = 8$, $\alpha = 0.5$:
a) $\alpha = 0$; b) $\alpha = 0.1$; c) $\alpha = 1$.

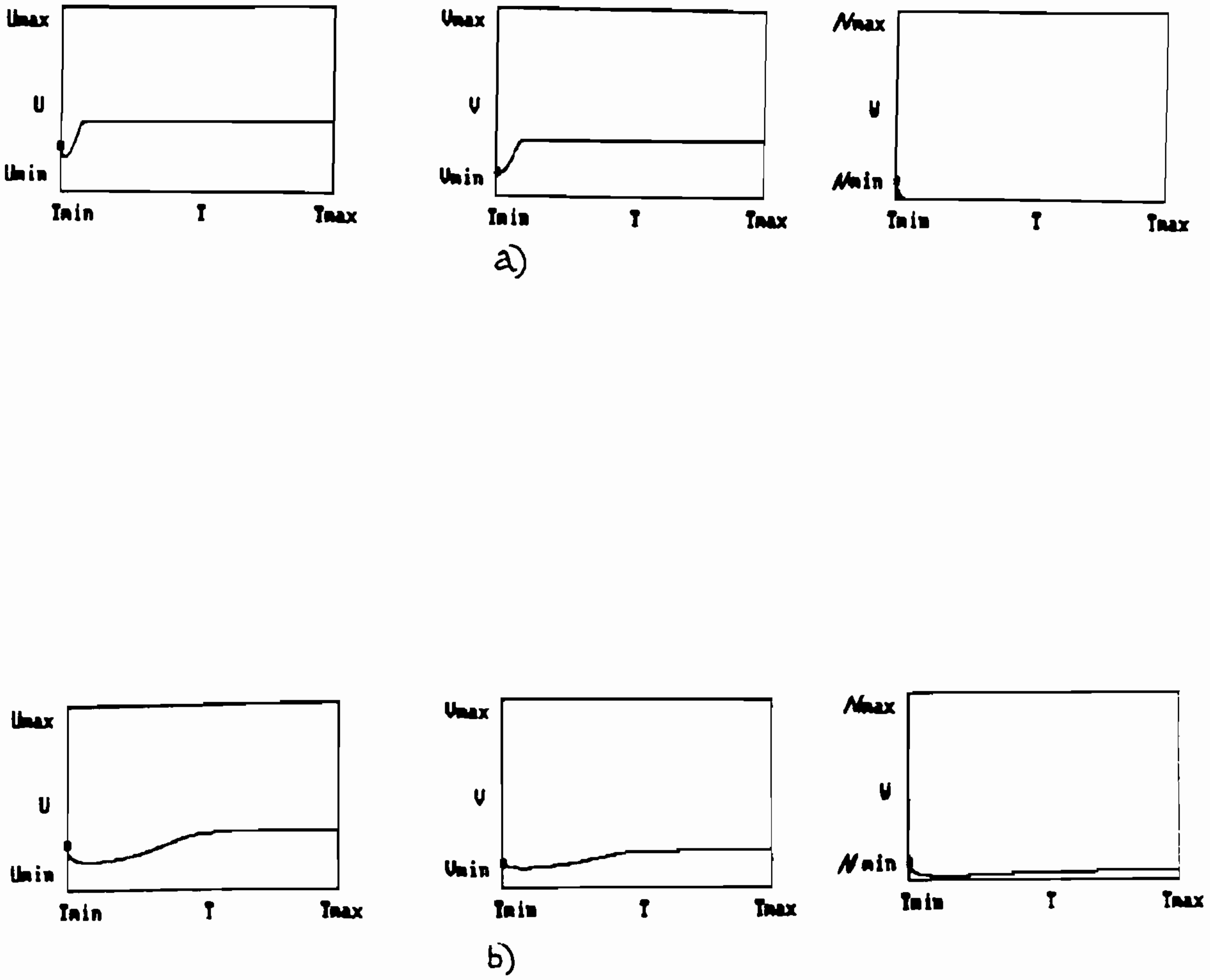


Figure 9: $\rho = 10$, $s = 4$, $h = 2$, $\varepsilon_0 = 2$, $b = 1$, $c = 1$, $\alpha = 0$, $\sigma = 0.5$:
a) model A (basic model when $\alpha = 1$); b) model B.

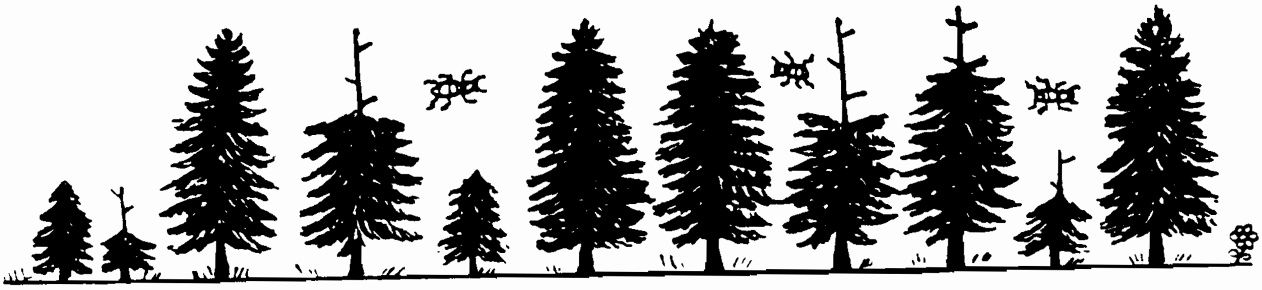


Figure 10: Schematic representation of one-dimensional model

Appendices

Appendix A: Finite Difference Approximation

In this section the difference schemes which have been employed for systems (1) and (3) are briefly commented on.

1. For system (1) define the uniform (for simplicity) time grid

$$\omega_\tau = (t_{n+1} = t_n + \tau,\ n = 0,1,\ldots,N, t_0 = 0) \tag{A.1}$$

and consider respective abstract grid functions $u(t_n)$, $v(t_n)$, $N(t_n)$, etc.

We shall use the abbreviated notations

$$g = g^n = g(x, t_n),\ \bar{g} = g^{n+1/2} = g(x, t_{n+1/2}),$$
$$\hat{g} = g^{n+1} = g(x, t_{n+1}). \tag{A.2}$$

Replace in (1) the derivatives in t by the difference in relations and obtain difference equations:

$$\frac{\hat{u} - u}{\tau} = \sigma \hat{f}_1 + (1 - \sigma) f_1,$$

$$\frac{\hat{v} - v}{\tau} = \sigma \hat{f}_2 + (1 - \sigma) f_2, \tag{A.3}$$

$$\frac{\hat{N} - N}{\tau} = \sigma \hat{f}_3 + (1 - \sigma) f_3,$$

where

$$f_1 = f_1(u, v, N) = \rho v - (v - 1)^2 u - su - \alpha u N,$$
$$f_2 = f_2(u, v, N) = u - hv - (1 - \alpha) vN,$$
$$f_3 = f_3(u, v, N) = -\varepsilon N + \alpha buN + (1 - \alpha) cvN,$$

$\sigma \in [0,1]$ is a difference scheme's parameter. The case when $\sigma = 0$ corresponds to the implicit scheme, $\sigma > 0$ - to the explicit scheme (of second order approximation when $\sigma = 0.5$), $\sigma = 1$ - to the completely explicit scheme. For the solution of the system of nonlinear algebraic equations (A.3), Newton's method and the algorithm background substitution are applied.

Consider system (3). Replace the derivatives in t by difference relations. Equations (3) can be split into two steps as

$$\text{Step 1:}\quad \begin{cases} \dfrac{\bar{u}-u}{\tau} = \sigma\bar{f}_1 + (1-\sigma)f_1, \\ \dfrac{\bar{v}-v}{\tau} = \sigma\bar{f}_2 + (1-\sigma)f_2, \\ \dfrac{\bar{N}-N}{\tau} = \sigma\bar{f}_3+(1-\sigma)f_3, \end{cases} \tag{A.4}$$

$$\text{Step 2:}\quad \begin{cases} \dfrac{\hat{N}-\bar{N}}{\tau} = \sigma\dfrac{\partial}{\partial x}\left[\bar{D}_2\dfrac{\partial\hat{N}}{\partial x}\right] + (1-\sigma)\dfrac{\partial}{\partial x}\left[D_2\dfrac{\partial\bar{N}}{\partial x}\right], \\ \hat{u}=\bar{u}\ , \\ \hat{v}=\bar{v}\ . \end{cases} \tag{A.5}$$

For approximation of systems (A.4) and (A.5) a finite difference method is used. The theory of finite elements may also be applied.

Appendix B: Software Support

The software allows interactive exploration of the models described in this paper. The software includes plotting routines for described models. It can be run on an IBM-PC/AT.

The main characteristics of interactive model are the following.

I. In interactive regime it is possible to define:

1. domain's boundary (L);
2. initial conditions in four forms and their combination:

$u(\rho,0) = u_0(x)$, $v(\rho,0) = v_0(x)$, $N(x,0) = N_0(x)$;

3. additional initial conditions:

   $ud(x)$, $vd(x)$, $wd(x)$;

4. two types of boundary conditions for $x=0$ and $x=L$;

5. minimum and maximum initial values of functions: u, v, N;

6. birth rate ρ; coefficients b, c;

7. type of function $z(u, v, N)$ representation;

8. death rates: s, h, z_0 ;

9. coefficient α;

10. constant D_0 for diffusivity

    $\left[D_2 = D_0 f(u, v, N)\right]$;

11. maximum number of iterations and maximum value

    of calculations error;

12. number of time steps and time step τ;

13. scheme's coefficient σ;

II. Results of calculations can be represented in the following forms:

a). as plots of functions $u(t), v(t), N(t)$ or in the phase space - for system (1);

b). as plots of functions $u(x), v(x), N(x)$ for system (3);

III. Where plots are made it is possible to change minimum and maximum values of functions: u, v, N if it is necessary.

IV. For plots, printing program Pizzas is used.