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POPULATION MODEL BASED ON INDIVIDUAL DYNAMICAL CELLS

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Abstract. Traditional population dynamics models, explaining separate aspects of observed ecological phenomena, are well understood mathematically, but their extension to a wider class of phenomena is difficult. Artificial life models represent another extreme, capable of simulating almost every biological phenomenon, but not accessible to mathematical analysis. A population model having a scope between the two extremes – but flexible, extensible, and within reach of mathematical analysis – is introduced in this paper. The model is based on piece-wise linear dynamical models of individual organisms. Parameter ranges in which the model meets natural ecological requirements is explored through analysis and simulations.

Key words: population model, piece-wise linear, parameter tuning.

1. Introduction. Ecological systems can be so varied and complex so that it is not surprising that there is no single general theory for the behavior of such systems. What is perhaps surprising is that there is no fully satisfactory theory for even simple ecological systems, for example, a population consisting of several kinds of organisms living in a compact space or time varying environment.

The simplest (and oldest) theories attempt to describe ecological systems in terms of a small number of aggregate variables, such as the total number of individuals or the biomass of the population. The time development of these variables is then described by a set of ordinary differential or difference equations. An example of this approach for a single species is provided by the logistic equation:

$$\frac{dN}{dt} = bN(t)\left(1 - \frac{N(t)}{K}\right), \tag{1}$$

where $N(t)$ – the total number of organisms, b, K – model parameters, the equation being introduced to clarify the notion of system carrying capacity. Another example, for a system consisting of two species, is provided by the Lotka-Volterra equations

$$\begin{cases} \frac{dN_1}{dt} = N_1(t)\left(c_{10} + c_{11}N_1(t) + c_{12}N_2(t)\right), \\ \frac{dN_2}{dt} = N_2(t)\left(c_{20} + c_{21}N_1(t) + c_{22}N_2(t)\right), \end{cases} \tag{2}$$

where $N_1(t)$, $N_2(t)$ – the number of organisms for the two species; c_{10}, c_{11}, c_{12}, c_{20}, c_{21}, c_{22} – model parameters, and provides a simple model which may show oscillatory behavior (see Murray, 1994; Hofbauer and Sigmund, 1990).

More complex population models introduce distributions over age, space, and sometimes other variables. An age distribution may be used to more fully reflect the influence of death and reproduction processes in the population, while organism dispersal may be represented by introducing a spatial distribution. Distributed cases often are modeled by partial differential equations, of which the Fisher equation is a typical example:

$$\frac{\partial N(t,x)}{\partial t} = b \cdot N(t,x)\left(1 - \frac{N(t,x)}{K}\right) + D\frac{\partial^2 N(t,x)}{\partial x^2}, \tag{3}$$

where $N(t,x)$ – population density at time t and space position x; b, K – model growth parameters, D – diffusion coefficient.

One additional property of traditional models can be explicitly mentioned: they usually attempt to explain only one ecological phenomenon at a time. For this reason the traditional models cannot be readily extended beyond the specific ecological phenomena they were designed to describe.

The limited scope of the traditional, analytic population models creates a need for ecological models which are more flexible and possibly more realistic. To some extent this need is met by purely computational models, often called "artificial life" models. Artificial life models can describe complicated biological, ecological and evolutionary phenomena, without regard for analytical tractability, and have been used to model such processes as reactions of enzymes, the coexistence of several species, species evolution (see Banzhaf, 1995; Bedau, 1995; Langton, 1989; Lindgren and Nordahl, 1994; Yager, 1994). The models are usually rule-based and expressed in the form of computer programs. If true values for the required parameters and inputs are available then such programs indeed can provide output which matches observed results well. However the programs are not accessible to mathematical analysis and transformations, so that they are really no easier to understand than the experimental data themselves.

In this paper we will introduce a population model, constructed to be more general and more extensible than the traditional mathematical models, but yet more amenable to analysis than the computer program based artificial life models. Analytical methods will be applied to define parameter ranges, where the proposed model satisfies important ecological requirements. In the next section we describe the model itself, and in the following sections we present some preliminary explorations of the properties of this model.

2. Model description. The population model is constructed by combining models of individual organisms within an encompassing environment with which each organism interacts. Each organism is considered to be an open system, and is modeled as a dynamical system. The environment is also modeled as a dynamical system through which the organisms can influence each other.

As organisms in this version of the model reproduce by division into two equal parts, we will refer to them, for picturesqueness, as cells. A cell is described as a dynamic object whose state development is governed by piecewise linear equations of motion and whose total parameter, state, and input specification is given by a list which determines the cell properties:

$$l(t) = \{\boldsymbol{x}(t), \boldsymbol{A}, \boldsymbol{B}, \boldsymbol{H}, L_D, L_N, u(t)\}, \tag{4}$$

where $\boldsymbol{x} = \begin{pmatrix} x_g \\ x_f \end{pmatrix}$ – cell state vector with x_g – genotypic state, x_f – phenotypic state; $\boldsymbol{A} = \begin{pmatrix} a_{gg} & a_{gf} \\ a_{fg} & a_{ff} \end{pmatrix}$, $\boldsymbol{B} = \begin{pmatrix} 0 \\ b \end{pmatrix}$, $\boldsymbol{H} = \begin{pmatrix} h_g \\ h_f \end{pmatrix}$, L_D, L_N – cell dynamics parameters, $u(t) > 0$ – environmental input.

Specification of cell properties:

1. Growth

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{A}\boldsymbol{x}(t) + \boldsymbol{B}u(t) + \boldsymbol{H} \tag{5}$$

valid, when $L_D/2 \leqslant x_g(t) < L_D$, $x_f(t) > L_N$.

2. Division

$$x(t+\varepsilon) = x(t)/2, \quad \varepsilon \to 0 \tag{6}$$

valid, when $x_g(t) = L_D$.

3. Death

$$x(t+\varepsilon) = 0, \quad \varepsilon \to 0 \tag{7}$$

valid, when $x_f(t) = L_N$.

The segmentation of the cell state space implied by this cell model, with possible cell trajectories, is illustrated in Fig. 1. The cell growth region is a rectangular patch, bounded by lines in state space at $x_g = L_D/2$, $x_g = L_D$ and $x_f = L_N$. The division and death regions $x_g = L_D$, $x_f = L_N$ are degenerate patches, since in this model these processes occur at the growth patch boundaries.

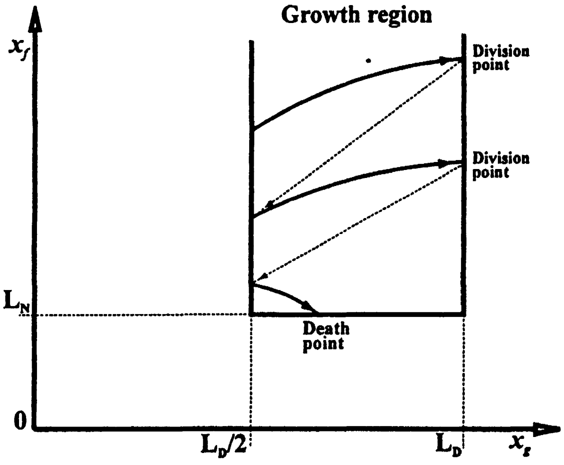

Fig. 1. Regions of the cell state space with possible trajectories in the growth region.

By specification (6), cell life is defined to begin on the line $x_g = L_D/2$. A cell is allowed to divide on reaching $x_g = L_D$, or to die upon reaching $x_f = L_N$. It is not possible for a cell to leave the growth region through $x_g = L_D/2$, this constraint being achieved by selecting appropriate parameter values for the $\boldsymbol{A}, \boldsymbol{B}, \boldsymbol{H}, L_D, L_N$ combinations.

It is worth noting that the genotypic dynamics in the cell model is independent of environmental input $u(t)$. This causes the steady points of the linear growth equation (5) to lie on a straight line in state space.

A linear dynamics for cell growth is convenient for preserving analyzability of the model. In this paper the cell model with one linear growth patch, as described by (4), and an extension of (4), including two linear patches in the growth region, will be examined.

A population was modeled as a set of cells, developing as a result of individual cell growth, duplication, and extinction processes in the simulated environment:

$$\boldsymbol{P}(t) = \left\{N(t), \boldsymbol{l}^1(t), \boldsymbol{l}^2(t), \dots, \boldsymbol{l}^{N(t)}(t), \boldsymbol{E}(t)\right\}, \tag{8}$$

where $N(t)$ – number of cells in population, $\boldsymbol{l}^i(t),\ i = 1, \dots, N(t)$ – individual cells, as defined by (4), $\boldsymbol{E}(t)$ – environment, which will be defined below.

Specification of population properties:

1. Cell duplication

$$\begin{cases} \boldsymbol{l}^i(t) \to \left\{\boldsymbol{l}^i(t+\varepsilon), \boldsymbol{l}^{N(t)+1}(t+\varepsilon)\right\}, & \\ N(t+\varepsilon) = N(t) + 1, & \varepsilon \to 0 \end{cases} \tag{9}$$

valid, when $x_g^i(t) = L_D$ in $\boldsymbol{l}^i,\ i \in \{1, 2, \dots, N(t)\}$.

2. Cell extinction

$$\begin{cases} \boldsymbol{l}^j(t) \to \varnothing, & \\ N(t+\varepsilon) = N(t) - 1, & \varepsilon \to 0 \end{cases} \tag{10}$$

valid, when $x_f^j(t) = L_N$ in $\boldsymbol{l}^j,\ j \in \{1, 2, \dots, N(t)\}$.

The environment was modeled by a global dynamics and by the distribution of overall resources to individual cells, with total cell number in the population as the only input:

$$\boldsymbol{E}(t) = \left\{U(t), N(t), u^1(t), u^2(t), \dots, u^{N(t)}(t)\right\}, \tag{11}$$

where $U(t) > 0$ – overall environmental resource flux, $N(t)$ – the total number of cells in the population (8), $u^i(t)$ – amount of resources allocated to the cell $\boldsymbol{l}^i(t)$ from (8).

The environment is characterized in the form

$$u^i(t) = F_i\left(U(t), N(t)\right), \quad i = 1, 2, \ldots, N(t), \tag{12}$$

where F may be deterministic or stochastic. $u^i(t)$ should satisfy the balance equations indicated below, as appropriate for the deterministic and stochastic cases:

1. Deterministic case

$$\sum_{i=1}^{N(t)} u^i(t) = U(t); \tag{13}$$

2. Stochastic case

$$\mathrm{E}\left[u^i(t)\right] = \frac{U(t)}{N(t)}, \tag{14}$$

where E – expectation.

We have used an equal division of environmental resources for (12) in the deterministic case:

$$u^i(t) = \frac{U(t)}{N(t)}, \quad i = 1, 2, \ldots, N(t), \tag{15}$$

and $u^i(t)$ from uniform distribution with average (15) for the stochastic case. The global environmental resources were kept steady $U(t) \equiv U$. Resources were redistributed to cells after every division or death event. Further in this paper we will investigate the resultant populations, with different parameter values, for one and two linear growth patch cases. We will analyze whether these populations satisfy natural ecological requirements in some parameter range.

3. Objectives for the model analysis. In the preceding sections we have defined the form of the model. The following model analysis will be applied for tuning the set of parameters $\{\boldsymbol{A}, \boldsymbol{B}, \boldsymbol{H}, L_D, L_N\}$ so as to satisfy the biological requirements for individual cells, the ecological requirements for the whole population, and to meet the model constraints.

Some biological properties of a cell, such as the need for environmental resources if growth is to occur, eventual reproduction by division, and death are already incorporated in the very form of the model. More specifically, the requirement that a cell both be able to divide and die with input $u(t) > 0$ will be satisfied by parameter tuning.

The main ecological requirements to be achieved by parameter tuning concern population stability: 1) the population size should be limited by environmental resources in any environment; 2) the population should persist in some environment.

A model constraint, to be met by parameter tuning, prevents a cell from leaving the growth region through the boundary $x_g = L_D/2$. This could be ascribed to biological requirements, if the genotypic state were interpreted as reflecting the process of duplication of genetic material of a cell.

4. Analysis of the diagonal matrix A case

4.1. Mathematical specification. The diagonal growth matrix $A = \begin{pmatrix} a_{gg} & 0 \\ 0 & a_{ff} \end{pmatrix}$ case is the simplest one to analyze. In this case the steady state points of a cell fall on the line $x_g = -h_g/a_{gg}$, which is parallel to the cell division line. The duration of a generation is independent of the cell input $u(t)$. Cell motion in the phenotypic direction is independent of the genotypic state and vice versa. All cells in a population are synchronized in the genotypic direction.

Solutions for the cell growth equations (5) in diagonal case, if $u(t) \equiv u_s$, are exponentials in time:

$$\begin{cases} x_g(t) = e^{a_{gg}t}x_g(0) + \frac{h_g}{a_{gg}}\left(e^{a_{gg}t} - 1\right), \\ x_f(t) = e^{a_{ff}t}x_f(0) + \frac{1}{a_{ff}}\left(e^{a_{ff}t} - 1\right)(h_f + bu_s). \end{cases} \tag{16}$$

Monotonicity of the solutions facilitates meeting the model constraint which requires an increasing genotypic state in the growth region. The required direction is achieved by placing the steady point line to the right of the growth region in the stable case ($a_{gg} < 0$; $h_g > -L_D a_{gg}$) and placing it to the left of the growth region in the unstable case ($a_{gg} > 0$; $h_g > -L_D a_{gg}/2$). $b > 0$ is needed in both cases to keep phenotypic solutions higher with a bigger input u_s.

As the genotypic state is dependent neither on the phenotypic state nor on the environment, the impact of the genotypic equation reduces to providing a clock, measuring duration of a generation t_g:

$$t_g = \frac{1}{a_{gg}} \ln\left(\frac{2(a_{gg}L_D + h_g)}{a_{gg}L_D + 2h_g}\right). \tag{17}$$

t_g can be given any desired value, by selecting appropriate parameters a_{gg} and h_g, whatever the genotypic dynamics, stable or unstable. Given t_g, the solution of equations (5) inside the growth patch reduces to a one-dimensional problem, with only two qualitatively different cases: stable ($a_{ff} < 0$) and unstable ($a_{ff} > 0$) phenotypic dynamics.

4.2. Requirements for cell division and death. We want to discover if a subspace in parameter space $\{\boldsymbol{A}, \boldsymbol{B}, \boldsymbol{H}, L_N, L_D\}$ exists where a cell is able to both divide and die with an environmental input $u_s > 0$. We will investigate the limit between division and death ranges in u_s. If the limit turns out to be positive, then both cases should be possible.

Various initial conditions for the phenotypic state $x_f(0) \in]1, \infty[$ and different death scenarios are possible for a cell in the model. We must pick one initial condition and one death scenario to define the single limit in u_s. Let us take the greatest phenotypic state, predicting death of the cell. This is $x_f = 2L_N$, if reached at the end of generation ($t = t_g$): such cell will die after division. It is reasonable to take the same initial condition, $x_f(0) = 2L_N$, as we want the condition not to force the outcome. We will investigate

$$x_f(t_g)\Big|_{x_f(0)=2L_N} = 2L_N, \tag{18}$$

as the limit between the phenotypic solutions driving a cell towards division, and those driving the cell towards death.

In the monotonic case the derivative at the beginning point of the solution will represent its end point being lower or higher. Analyzing the derivative

$$\frac{dx_f}{dt}\Big|_{t=0,\, x_f(0)=2L_N} = a_{ff}2L_N + bu_s + h_f, \tag{19}$$

condition (18) can be changed to:

$$\frac{dx_f}{dt}\Big|_{t=0,\, x_f(0)=2L_N} = 0. \tag{20}$$

Equations (19), (20) give an equation for the limit between division and death ranges in u_s, which will be denoted by U_L,

$$a_{ff}2L_N + bU_L + h_f = 0, \tag{21}$$

with the solution:

$$U_L = \frac{1}{b}(-a_{ff}2L_N - h_f). \tag{22}$$

It is evident from (22), that by selecting an appropriate h_f we can place U_L at any desired point, including $U_L > 0$, whatever a_{ff} and L_N. Both stable and unstable phenotypic dynamics cases, with appropriate h_f, fulfill the requirement for division and death of a single cell.

4.3. Requirement for limitation of population size. If a cell parameter set $\{A, B, H, L_D, L_N\}$ is tuned so that both division and death are possible with a positive u_s, we can expect to create a population limited by environmental resources. Let us analyze the limiting requirement in the case of equal division of overall environmental resources (15). In this case population tends towards a single phenotypic state.

As generation length t_g is constant, we can derive an expression for the phenotypic state of a cell at the end of generation:

$$x_f(t_g) = e^{a_{ff}t_g}x_f(0) + \frac{1}{a_{ff}}\left(e^{a_{ff}t_g} - 1\right)(h_f + b\cdot u_s). \tag{23}$$

Similarly, we can derive a difference equation for the transition of the whole concentrated population for each generation. In the case of such concentration the state of a single cell, together with the number of cells, represents the state of the whole population. We will incorporate the cell number as a divisor of overall resources, when evaluating the input of the observed cell.

Let us take the initial population consisting of a single cell, given overall environmental resources U. Let us define constants:

$$C_1 = e^{a_{ff}t_g}, \qquad C_2 = \frac{1}{a_{ff}}\left(e^{a_{ff}t_g} - 1\right) \tag{24}$$

to simplify notation. Then generation transition difference equation will be:

$$x_f(n) = \frac{C_1}{2}x_f(n-1) + \frac{C_2}{2}\left(h_f + b\frac{U}{2^{n-1}}\right), \tag{25}$$

where n – number of a generation.

Eq. 25 incorporates the fact that phenotypic state is divided by two and number of cells doubles at the end of each generation. Solution for (25), taken with $x_f(0) = x_{f0}$ is:

$$x_f(n) = \left(\frac{C_1}{2}\right)^n x_{f0} + \frac{C_2}{2}\sum_{i=1}^{n}\left(\frac{C_1}{2}\right)^{n-i}\left(h_f + b\cdot U\cdot(1/2)^{i-1}\right). \tag{26}$$

Stability of solution (26) implies limitation of population size, and is determined by the constant $C_1/2$. In the stable single cell dynamics case, we have $C_1/2 \in]0, 1/2[$. Consequently, solution (26) is stable and the population is limited. In the unstable single cell dynamics case we have $C_1/2 \in]1/2, \infty[$, and consequently solution (26) can be both stable when $C_1 < 2$, and unstable when $C_1 > 2$. The population can be limited or unlimited, correspondingly. The factor which makes the population limited, though single cell dynamics is unstable, is division by two of the cell state at the end of each generation.

Computer experiments have shown that in the stable cell dynamics case the maximum number of cells in the population is not sensitive to initial conditions. In the unstable case with $C_1 < 2$, though the maximum number of cells is limited, the population is sensitive to initial conditions. Great sensitivity of the population size to initial conditions could be true in the case of several interacting populations, yet for an isolated population it does not appear to be biologically meaningful. Consequently we assert that the population model based on stable cells would be more realistic than the one based on unstable cells with $C_1 < 2$, though the requirement on limitation by environmental resources is fulfilled in both cases.

4.4. Requirement for population persistence. Equal division of resources gives a concentrated population, which dies out after the resource limit is reached. If we want to keep the model population persistent, we must prevent it from becoming concentrated. Concentration of cells in the model may be disturbed in two ways: by unequal distribution of resources to individual cells or by unequal cell division. We will investigate the case of unequal distribution of resources and analyze how the cell parameters influence the degree of dispersal.

For analysis of dispersal at least two cells are required. Let us take the generation transition equations for two cells:

$$\begin{aligned} x_f^1(t_g) &= e^{a_{ff}t_g} x_{f0}^1 + \frac{1}{a_{ff}} \left(e^{a_{ff}t_g} - 1\right)\left(h_f + b \cdot u_s^1\right), \\ x_f^2(t_g) &= e^{a_{ff}t_g} x_{f0}^2 + \frac{1}{a_{ff}} \left(e^{a_{ff}t_g} - 1\right)\left(h_f + b \cdot u_s^2\right), \end{aligned} \tag{27}$$

where x_{f0}^1, x_{f0}^2 – initial conditions for the two cells.

By subtraction of (27) equations, we obtain an expression for the distance between the cells at the end of a generation:

$$\Delta x_f(t_g) = e^{a_{ff}t_g}\Delta x_{f0} + \frac{b}{a_{ff}}\left(e^{a_{ff}t_g} - 1\right)\cdot\Delta u_s, \tag{28}$$

where $\Delta x_f = x_f^2 - x_f^1$, $\Delta x_{f0} = x_{f0}^2 - x_{f0}^1$, $\Delta u_s = u_s^2 - u_s^1$.

The distance between cells at the end of a generation is expressed by the sum of two components, the first involving a difference in the initial conditions Δx_{f0}, and the second involving a difference in environmental inputs Δu_s. Dependence on initial conditions is qualitatively different for stable and unstable cases. The weight coefficient of Δx_{f0} is $e^{a_{ff}t_g} < 1$ in a stable cell dynamics case and it is $e^{a_{ff}t_g} > 1$ in the unstable case, which means contraction and expansion of the initial difference, respectively. Weight coefficient of Δu_s is $\frac{b}{a_{ff}}(e^{a_{ff}t_g} - 1) > 0$, whatever a_{ff}. There is no qualitative difference between the impact of Δu_s in the stable and the unstable cases, though the weight coefficient is always bigger for the unstable case.

The change of distance between two cells throughout several generations is rather interesting. Let us form a generation transition difference equation for Δx_f. We will use definitions (24) and allow the environmental inputs to change only on the change of generations. The difference equations for Δx_f will be:

$$\Delta x_f(n) = \frac{C_1}{2}\Delta x_f(n-1) + \frac{C_2 b}{2}\Delta u_s(n), \tag{29}$$

with the solution:

$$\Delta x_f(n) = \left(\frac{C_1}{2}\right)^n \Delta x_{f0} + \frac{C_2 b}{2}\sum_{i=1}^{n}\left(\frac{C_1}{2}\right)^{n-i}\Delta u_s(i). \tag{30}$$

Solution (30) holds until death of any of the observed cells happens. Stability of $\Delta x_f(n)$ is determined by $C_1/2$, the same constant which defines the stability of $x_f(n)$ itself. Different cells would converge throughout generations when $C_1 < 2$, and diverge when $C_1 > 2$. As we are seeking cell dispersal, we prefer the divergent case here. On the other hand, if an initial difference between cells fades, the difference in inputs Δu_s may still preserve the cells from concentration.

If we did not encounter cell death, the population would simply expand with time. As we want to hold the population steady and persistent, on the average half of the cells should die every generation. We cannot model the process of cell divergence in population, involving death, with only two cells. Let us interpret the two observed cells in another way, as if they represented the margins of an overall cell distribution. In the next generation we will pick marginal cells for observation again. If we encounter death of half of the cells (those with the lower phenotypic states) in each generation, then the distance between marginal cells should be reduced four times at the end of each generation instead of the two times as in (29). An approximate description of the divergence process for marginal cells will be:

$$\Delta x_f(n) = \frac{C_1}{4}\Delta x_f(n-1) + \frac{C_2 b}{4}\Delta u_s(n), \tag{31}$$

with the solution:

$$\Delta x_f(n) = \left(\frac{C_1}{4}\right)^n \Delta x_{f0} + \frac{C_2 b}{4}\sum_{i=1}^{n}\left(\frac{C_1}{4}\right)^{n-i} \Delta u_s(i). \tag{32}$$

Stability of the solution depends on the coefficient $C_1/4$. We need approximately $C_1 > 4$ to have a population with cells' phenotypic states divergent on initial distribution. This requirement cannot be reconciled with that of $C_1 < 2$ needed for the limitation of population size. It is impossible to have both a divergence of the initial distribution and a resource limited population at the same time.

A possible alternative way to produce a persistent population is to produce cell divergence by having sufficient variability of the environmental inputs. Computer experiments showed that a persistent and resource limited population is possible in the stable cell dynamics case, when the distribution of environmental resources given to individual cells is sufficiently wide. For example, a uniform distribution of individual cell inputs in the range $[0, 2U/N(t)]$ proved to be sufficient to preserve a population for a long time. Such a distribution is probably much wider than the supposed fluctuations in a natural environment. Consequently, a population model with one linear growth patch is not entirely satisfactory.

4.5. The case of two growth patches. We have shown above that a population consisting of cells, each described by a single growth patch, whether stable or unstable, does not show the sort of behavior that is desired. Combining two patches promises to give better results. If we put an unstable patch with $C_1 > 4$ below, and a stable patch above some limit $x_f = L_S$, a population limited by environmental resources and having good dispersal characteristics can be attained. The lower unstable patch would be responsible for producing cell dispersal. The upper stable patch would be responsible for maintaining the limitation by environmental resources. For the upper patch to perform its function, a limit $L_S \leqslant 2L_N$ is required. An example of a combination of stable and unstable patches, with possible trajectories for two different values of input u_s, is given in Fig. 2.

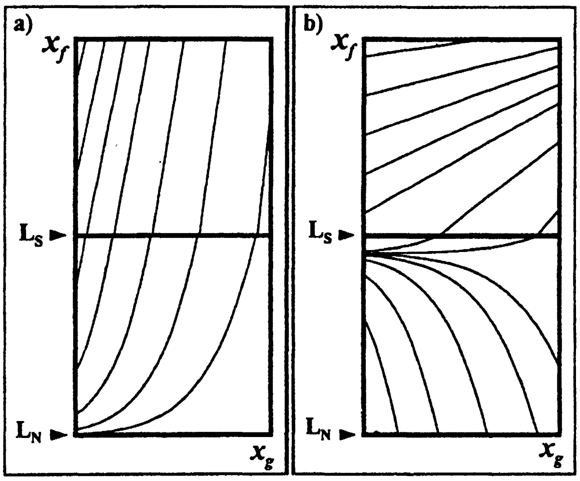

Fig. 2. Combination of stable patch above and unstable patch below, with trajectories for two different environmental inputs: a) $u_s = 12$; b) $u_s = 3$. Parameter values for both, a) and b): $a_{gg} = -1.0$, $a_{gf} = a_{fg} = 0$, $a_{ff} = -1.1$, $b = 1$, $h_g = 3.0$, $h_f = 0.5$ for the stable patch; $a_{gg} = 1.0$, $a_{gf} = a_{fg} = 0$, $a_{ff} = 10$, $b = 1$, $h_g = 0.5$, $h_f = -22$ for the unstable patch.

Computer experiments have showed validity of the two patch model. An unstable patch with $C_1 \geqslant 10$ was found to provide sufficient distribution of cell phenotypic states for the population to persist. The difference from the approximate relation $C_1 > 4$ found above is probably due to the contraction arising in the upper stable patch.

An exact analysis of the diagonal case helped to determine a successful form for the model, with two linear patches for cell growth dynamics being introduced to satisfy both ecological and model behavior constraints. The conclusions of this analysis can be extended to more complicated cases, which are not so easy to analyze.

5. Extensions to more complex cases

5.1. Lower triangular matrix A case. Above we have explicitly analyzed the diagonal growth matrix case. Another case for which an exact analysis is possible, is that of a cell whose dynamics is given by the lower triangular matrix $A = \begin{pmatrix} a_{gg} & 0 \\ a_{fg} & a_{ff} \end{pmatrix}$. In this case the genotypic state x_g is independent of the environment. Consequently, the steady point line $x_g = -h_g/a_{gg}$ is parallel to the cell division line, and the duration of a generation t_g is fixed. Genotypic solutions of $x_g(t)$ are montonic. Parameter sets defining the direction of increasing genotypic state are distinguished as in the diagonal case.

On the other hand, phenotypic solutions $x_f(t)$ for the lower triangular case are not monotonic, which complicates the analysis. Generation transition difference equations are more involved than in the diagonal case, but they suggest the same conclusions. In the lower triangular case persistent and limited populations can be obtained with one stable growth patch, if environmental fluctuations are sufficiently large. The same characteristics of a population can be achieved under minor environmental fluctuations in the case of two linear patches, the upper being stable and the lower being unstable. Inconsistency with ecological reality, that generation length is independent of environmental input and that genotypic synchronization of cells occurs, is the same as in the diagonal case.

5.2. The general matrix case. Analysis of the general case, with the cell growth matrix $A = \begin{pmatrix} a_{gg} & a_{gf} \\ a_{fg} & a_{ff} \end{pmatrix}$, $a_{gf} \neq 0$ is much more complicated than in the diagonal or lower triangular cases. We do not consider separately the upper triangular case, because it is almost as hard as the general case.

The time development of the genotypic state x_g in this general case is dependent on the environmental input $u(t)$. Generation length t_g is no longer fixed. The population is no longer synchronized in genotypic direction. The steady point line,

$$x_f = -\frac{1}{a_{gf}}\left(a_{gg}x_g + h_g\right), \tag{33}$$

is no longer parallel to the cell division line. We must take care that the line (33) does not cross the growth region, else the cell may fall on the stable point inside growth region (which is not biologically realistic) or may leave the growth region through $x_g = L_D/2$ in the unstable case (which is not defined in the model). In this general case, the genotypic solution $x_g(t)$ is not necessarily monotonic, so we must take care that the cells do not to leave the growth region through the boundary $x_g = L_D/2$, even when the steady point line is outside the growth region. Though not often seen in practice, these cases are not easy to distinguish analytically.

Solutions of the growth Eq. 5 in the general case can be most compactly expressed in the matrix exponential notation:

$$\boldsymbol{x}(t) = e^{\boldsymbol{A}t} \cdot \boldsymbol{x}(0) + \boldsymbol{A}^{-1} \left(e^{\boldsymbol{A}t} - I \right) \left(\boldsymbol{B} \cdot u_s + \boldsymbol{H} \right). \tag{34}$$

An exact analysis of population growth in the general case is complicated by transcendental equations, which result from (34), when we attempt to obtain the length of generation t_g, required for analysis. One of the possible approaches for approximate analysis is linearization of the solution (34):

$$\boldsymbol{x}(t) = (I + \boldsymbol{A}t) \cdot \boldsymbol{x}(0) + \boldsymbol{B} \cdot u_s t + \boldsymbol{H}t. \tag{35}$$

Considerable errors can be introduced by approximation (35), because exponential solutions are not very appropriate functions for linearization. Also linearization can hide nonmonotonicity of solutions, which may be significant in some cases. Investigation of approximate methods for the general case analysis is an important direction for future work.

Though the general case analysis proved to be complicated, computer experiments have shown that the conclusions obtained from the diagonal case analysis can be extended to the general case. A persistent and limited population in the case of one stable growth patch can be obtained only under considerable environmental fluctuations. In the case of two growth patches, stable in the upper region and unstable in the lower region, realistic population behavior can be obtained under minor environmental fluctuations. A time series of the number of cells in the model population with two linear growth patches is given in Fig. 3. Desynchronization of the population after four generations can be observed in the figure.

The advantage of the proposed population model lies in the possibility to relate analytically to some extent the properties of populations to the characteristics of individual organisms. Additionally the model can be extended for investigation of evolutionary phenomena.

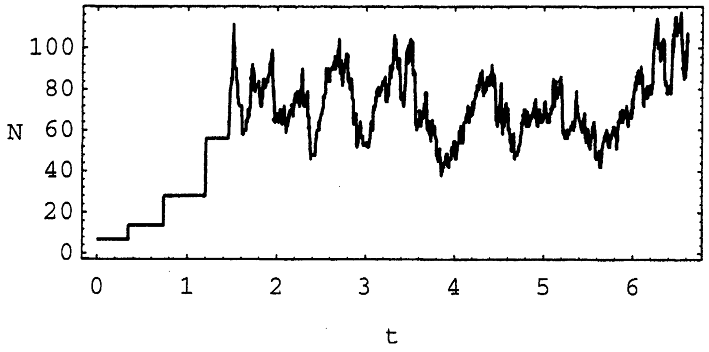

Fig. 3. Time series of the number of cells in model population, with two linear growth patches. Parameter values: $a_{gg} = -1.0$, $a_{gf} = 0.3$, $a_{fg} = -0.5$, $a_{ff} = -1.1$, $b = 1.0$, $h_g = 3.0$, $h_f = 0.5$ for the stable patch; $a_{gg} = 4.0$, $a_{gf} = 3.0$, $a_{fg} = 0$, $a_{ff} = 40$, $b = 1$, $h_g = 0.5$, $h_f = -42$ for the unstable patch; $L_D = 2$, $L_N = 1$, $L_S = 2$, $U = 100$. Individual cell inputs are selected from uniform distribution over the range $[U/N - 0.01U/N; U/N + 0.01U/N]$.

6. Conclusions. In the paper we have introduced a population model based on individual piece-wise linear cells. The model in certain cases proved to be accessible to exact analysis. It proved possible to define the parameter range where persistent and resource limited populations could be obtained. Cell growth dynamics parameters proved to play an important role in determining the characteristics of the whole population. Cells with one unstable linear growth patch produced inappropriate population behavior. Cells with one stable linear growth patch were capable of forming a population with the required characteristics, if environmental fluctuations were significant. Cells with two growth patches, one unstable, the other stable, proved to be capable of producing a persistent, and bounded population in an environment with minor fluctuations in accord with usual ecological expectations. Experience with the model suggests that it can be extended to encompass evolutionary phenomena involving several kinds of populations, where even very modest analytical results should be rewarding.

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VIDINE LĄSTELIŲ DINAMIKA PAGRĮSTAS POPULIACIJOS MODELIS

Minija TAMOŠIŪNAITĖ ir J. Rimas VAIŠNYS

Tradiciniai populiacinės dinamikos modeliai aiškina pavienius ekologinių reiškinių bruožus. Šie modeliai yra gerai išanalizuoti matematiškai, bet jų neįmanoma lengvai pritaikyti naujų reiškinių tyrimui. Dirbtinės gyvybės (artificial life) modeliai, iš kitos pusės, gali pamėgdžioti beveik visus biologinius reiškinius, deja, šių modelių dažniausiai neįmanoma naudingai išanalizuoti. Straipsnyje pateiktas bandymas sukurti populiacijos modelį, kuris būtų tarp dviejų kraštutinumų – pakankamai lankstus ir kažkiek analizuojamas. Kuriamas modelis yra pagrįstas atskirais organizmais, kurių kiekvienas turi nuosavą, dalimis tiesinę dinamiką. Parametrų poerdviui, kuriame modelis patenkintų ekologinius reikalavimus, rasti naudojami analiziniai metodai ir kompiuterinis modeliavimas.