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Non-linear sensitivity analysis as a tool for explaining population dynamics in a life-system conceptual framework

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Abstract

Life-system analysis is the examination of interacting ecological processes affecting population dynamics. The major problem in application of life-system analysis is in developing methods for analysis of ecological processes. I use a non-linear sensitivity analysis of simulation models to evaluate the role of individual ecological processes and their interactions in population dynamics. The method is applied to the problem of population stability. Coefficients of m - and v -stability characterize stability of the mean and variance of population density, respectively. Contributions of ecological processes and their interactions to m - and v -stability are represented by non-linear sensitivity coefficients. The second application is the analysis of common pine sawfly (*Diprion pini* L.) population dynamics in Russia. Process interactions are shown to be important in outbreak patterns of this pest.

Keywords: Population dynamics; Population stability; Sensitivity analysis

1. Introduction

The life-system was defined by Clark (1964) and Geier (1964) as a population together with its effective environment, i.e., all components of the ecosystem which have significant direct or indirect effects on the population. A life-system is thus that part of an ecosystem which affects the dynamics of the particular population. The major facet of the life-system paradigm is that population dynamics result from complex interactions of ecological processes, and the role of each process depends upon other processes in the system (Clark et al., 1967). A life-system approach to population dynamics has considerable advantage over the traditional theoretical approach based on analytical modeling. Analytical models usually describe one, but seldom two or more ecological processes. As a result, they inadequately represent biological reality because the dynamics of natural populations are governed by numerous interacting ecological processes. In the best case they can be applied to

some laboratory populations in extremely simple environments. The more biological information that is available, the more difficult it is to apply analytical models to the population. Thus, population ecology theory does not stimulate field and experimental work.

One major problem in the application of the life-system approach is in measuring interactions among ecological processes. For example, the introduction of a parasitoid may result in reduction of host pest density. This effect can be measured by a coefficient $q = K/N$, where K is the carrying capacity for the host and N is the equilibrium host density after introduction of the parasitoid (Beddington et al., 1978). Other natural enemies (pathogens, predators) present in the system will also affect the value of q . The question is then, how to measure the effects of other life-system components on the host–parasite interactions.

In this paper I propose to measure interactions between ecological processes using non-linear sensitivity analysis of simulation models. Traditional linear sensitivity analysis is the estimation of sensitivity coefficients which are defined as the ratio of the model response, ΔR_i , to parameter change, ΔP_j , or as a derivative $\partial R_i / \partial P_j$ (Tomovic, 1963; Kaye and Ball, 1979). In simple models they can often be estimated analytically, but as ecological models become more realistic and hence, more complex, sensitivity coefficients can be found more efficiently using numerical methods. A linear sensitivity coefficient represents a linear relationship between a model parameter and a model response, and thus, I call this approach a linear sensitivity analysis. To study interactions between model components, it is necessary to know how a sensitivity coefficient changes in response to changes in other parameters. The result can be expressed by a non-linear sensitivity coefficient such as $\partial^2 R_i / (\partial P_j \cdot \partial P_k)$, where R_i is the model response and P_j and P_k are parameters.

Interactions between model components are explicitly defined by the programmer. However, they are defined in structural but not in functional terms, and thus, a model developer cannot predict the dynamic features of the model. Therefore, measuring process interactions is not tautological. For example, parasitism and starvation each reduces the density of an insect population. The order of these ecological processes in an insect life cycle is a structural feature of the life-system which can be used in model development. If parasitism occurs earlier in the life cycle than competition for food (e.g., in the egg stage), then an increase in parasitism will reduce the mortality due to starvation because at lower density, competition will be less. If parasitism occurs after food consumption (e.g., in the pupal stage), then the outcome of these process interactions will be different: parasitism will have no effect on starvation in the same generation, but starvation can increase parasitism because a reduction in the number of hosts can increase the probability of being parasitized. Interactions among ecological processes depend on the structure of the life system which is assumed to be accurately represented in the model. Thus, non-linear sensitivity analysis of the model allows one to predict what interactions can be expected in nature.

In natural systems it is difficult, or some times impossible, to change the flow of ecological processes. Therefore, the analysis of interactions can be done more effectively using simulation models. Here I do not consider the problem of model

validation but assume that the model is valid which means that: (1) the structure of the model represents biological reality with desired accuracy (all important ecological processes are included, and equations correspond to current knowledge of these processes in this particular or similar life-systems); (2) model behavior reflects reality (as represented by independent data) with desired accuracy. At initial steps of model validation the accuracy may be low. However, if a model gives an economically or ecologically important result, then further calibration and validation tests should be performed to increase model accuracy.

Sensitivity analysis can be applied to both quantitative and qualitative model parameters. Here I consider only qualitative parameter changes; in particular, ecological processes are turned on and off and the effects of individual processes and their interactions on some characteristics of population dynamics are studied.

2. General description of the method

Some terms should be clarified before explanation of the method. An ecological process is a set of similar ecological events (Sharov, 1992). Examples are reproduction, development, growth, migration and death of organisms due to some particular cause. Insect death in larval and pupal stages due to the same predator are considered as different processes because their rates (mortality) may be different and may depend on different factors. Similarly, larval death due to predators and parasites are different ecological processes.

Each process has a specific rate (fecundity is the rate of reproduction, mortality is the rate of death, etc.) which depends on different factors (temperature, humidity, population density, density of predators etc.). Process rates are usually measured by the number of ecological events per unit of time per individual (Sharov, 1992).

Biological interpretation of a model is important for designing model analysis. The correspondence between model components (variables, equations) and elements of the life system (factors, processes) must be known first. One model may have several interpretations. For example, the logistic model has at least two interpretations: resource limited and equilibrium interpretation (Pollard, 1981). In the first case, population density is regulated by resource-dependent fecundity, while in the second case, it is regulated by density-dependent mortality. In this case, model interpretation should be selected prior to analysis.

A host–parasitoid model developed by May et al. (1981) will be used to illustrate non-linear sensitivity analysis. Two processes are considered in this model: parasitism and host competition. Parasitism is measured by the proportion of parasitized hosts, A , which is a function of parasitoid density P_t in generation t :

$$A(P_t) = 1 - \exp(-a \cdot P_t), \quad (1)$$

where a is the area of discovery. Competition is measured by the rate of population growth (without parasitism), B , which is a function of host density N_t in generation t :

$$B(N_t) = \exp[r \cdot (1 - (N_t/K))], \quad (2)$$

where r is the intrinsic rate of host population increase and K is the carrying

capacity of the host environment. Competition follows parasitism in the host life cycle, and thus only unparasitized hosts are involved in competition. The full model is represented by a system of equations:

$$\begin{aligned} N_{t+1} &= N_t \cdot (1 - A(P_t)) \cdot B[N_t \cdot (1 - A(P_t))] \\ P_{t+1} &= N_t \cdot A(P_t) \end{aligned} \quad (3)$$

This is not a full simulation model because it does not represent all processes in a real host–parasitoid system, but it can be used as a simple example to illustrate methods which can be applied to more complicated simulation models.

The next step is to analyze the effect of ecological processes on some population characteristic. For example, one can examine the effect of parasitism and competition on the equilibrium host density. The effect of a process can be evaluated by comparing results from simulations with this process included or excluded from the model.

Two methods of ecological process exclusion from the model can be used. The first is the complete exclusion of a process. For example, if parasitism is excluded from the model of May et al. (1981), then A is a constant and is equal to zero. When competition is completely excluded, then the rate of host population growth B should be replaced by a constant equal to the maximum population growth rate: $B = \exp(r)$.

The second method is to exclude the regulative role of a process. In this case the rate of the process should be a constant and equal to the equilibrium (or average) rate of this process. For example, if N^* and P^* are equilibrium host and parasitoid densities in Eq. 3, then $A = 1 - \exp(-a \cdot P^*)$ and $B = \exp[r \cdot (1 - (N^*/K))]$. When the process rate is set to a constant, the process becomes density-independent and has no regulative role.

Ecological processes are excluded from the model in different combinations (Table 1) and some characteristic of population dynamics (e.g., equilibrium or av-

Table 1
Non-linear sensitivity analysis of a simulation model (a hypothetical example)

Ecological processes ^a			Characteristic of population dynamics y	Contribution of ecological processes into characteristic y
x_1	x_2	x_3		
0	0	0	0.0	$b_0 = 0.0$
1	0	0	0.3	$b_1 = 0.3$
0	1	0	0.7	$b_2 = 0.7$
1	1	0	0.5	$b_{12} = -0.5$
0	0	1	1.2	$b_3 = 1.2$
1	0	1	1.7	$b_{13} = 0.2$
0	1	1	1.3	$b_{23} = -0.6$
1	1	1	1.4	$b_{123} = 0.1$

^a Each row corresponds to a certain modification of the model with some processes being included and the other being excluded: $x_i = 1$ if the i th process is included into the model, and $x_i = 0$ if this process is not included; the table is organized as a full factorial design.

erage population density, or standard deviation of population density) is measured. The contribution of individual processes and process interactions to the population characteristic y can be measured by sensitivity coefficients b_i and $b_{i\dots j}$, respectively, in equation:

$$y = b_0 + b_1x_1 + b_2x_2 + b_{12}x_1x_2 + b_3x_3 + \dots, \quad (4)$$

where x_i is a dummy variable: $x_i = 1$ if the i th ecological process is included in the model, and $x_i = 0$ if this process is excluded. Coefficient b_i represents the contribution of the i th process to population characteristic y , and b_{ij} represents the contribution of the interaction between the i th and the j th processes. In simple deterministic models (like Eqs. 1–3), there is only one y value for each combination of included ecological processes, and thus coefficients b_i and $b_{i\dots j}$ are found using the system of linear equations (4). For more complex models these coefficients are estimated using standard multiple regression methods, generating the data for regression from results of numerous independent simulations to complete replication within the designed analysis.

This kind of sensitivity analysis is non-linear because the terms in Eq. 4 which correspond to process interactions are of second or higher order. By interactions we mean that the effect of one process on population characteristic y can be modified by another process. This method has the advantage over standard linear sensitivity analysis that it can evaluate the role of process interaction in complex life-systems where analytic methods for estimating interaction rates are impossible or extremely difficult. Eq. 4 is a regression analysis of simulation results. Combining simulation and regression, it is possible to find a biological interpretation (mechanism) for each regression coefficient, in contrast to regression analysis of empirical data where regression coefficients represent only correlation.

3. Analysis of population stability

In this section, non-linear sensitivity analysis is applied to the problem of population stability. First, characteristics of population stability should be selected. Qualitative indications of stability can be obtained but ecologists often need quantitative information which indicate the degree of stability or the time required to return to a prescribed state. May (1973) suggested a quantitative criterion of stability = $-\max(\text{Re}(i))$, where $\text{Re}(i)$ are the real parts of characteristic roots of a linearized model at the equilibrium point. This criterion indicates the rate of convergence of trajectories to the steady state in deterministic models. But in stochastic models as well as in real populations one cannot observe the convergence rate of population trajectories to the steady state because environmental fluctuations will cause the trajectory to meander in the neighborhood of an otherwise stable equilibrium point. The magnitude of environmental fluctuations relative to the convergence rate can cause an otherwise stable system to be unstable. That is one reason why this criterion is often difficult to interpret biologically.

I use a stochastic approach to measure population stability: the response of the mean and variance of log-transformed population density to a change in the mean

and variance of input factors is evaluated, where means and variances are estimated from time series. For example, we can compare mean density in two populations one of which is managed and the other is unmanaged. Management is an input factor which has a non-zero mean value for the first population and a zero mean value for the second one.

Two characteristics of population stability will be used: *m*- and *v*-stability (for simplicity I avoid generalized definitions which can be found in Sharov (1986a, 1992)). *M*-stability (*MS*) is a measure of the difficulty of affecting a change in mean population density through a change in survival and/or mortality. It is estimated in two steps. First, we obtain an estimate of the sensitivity of the average log population density to a change in log survival ($\partial \overline{\ln N} / \partial \overline{\ln s}$), where *N* is population density, *s* is survival due to the independent “disturbing factor”, and $\overline{\ln N}$ and $\overline{\ln s}$ are mean log-transformed values of *N* and *s*, respectively (averaged in a time-series). The second step is to take a reciprocal of sensitivity, because stability and sensitivity are opposite characteristics:

$$MS = (\partial \overline{\ln N} / \partial \overline{\ln s})^{-1}. \quad (5)$$

Negative log-transformed survival is a measure of mortality which is called a *k*-value (Varley and Gradwell, 1960). The magnitude of *m*-stability shows how much additional mortality (increase in *k*-value) must be applied to the population to decrease its mean log-transformed density by 1. Success of pest population suppression depends on *m*-stability: the mean density of populations with high *m*-stability will be suppressed less than the mean density of populations with low *m*-stability for the same decrease in survival associated with pesticide application.

V-stability (*VS*) is a measure of the difficulty of affecting a change in variance of population density through a change in variance of survival (or mortality):

$$VS = (\partial \sigma_{\ln N}^2 / \partial \sigma_{\ln s}^2)^{-1}, \quad (6)$$

where $\sigma_{\ln N}^2$ and $\sigma_{\ln s}^2$ are variances of log-transformed values of population density *N*, and survival *s* due to the disturbing factor. If there is only one disturbing factor and population density is close to equilibrium, then *v*-stability is equal to:

$$VS = \sigma_{\ln s}^2 / \sigma_{\ln N}^2. \quad (7)$$

As *VS* increases, fluctuations in population density decrease in a given environment.

In order to measure *MS* and *VS* in the model of May et al. (1981), it is necessary to add host survival *s_t* due to disturbing factors (random perturbations) in generation *t* to Eq. 3. Now the host population dynamics are described by the equation:

$$N_{t+1} = N_t \cdot (1 - A(P_t)) \cdot B[N_t \cdot (1 - A(P_t))] \cdot s_t. \quad (8)$$

Using the following parameters in the model: *a* = 0.1, *r* = 2 and *K* = 50; and assuming that survival *s_t* due to disturbing factors is stochastic with mean 0.2817 (it was selected so that $\ln N = 2.5$) and very small variance (when the variance from

disturbing factors is small, the model can be linearized near the equilibrium and the coefficients of m - and v -stability are independent from the variance).

MS and VS were estimated: (1) with neither parasitism nor competition being fixed, (2) with competition fixed at the equilibrium rate, (3) with parasitism fixed at the equilibrium rate, and (4) with both processes having fixed rates. Coefficients of m -stability in these four cases are 1.775, 2.146, 0.324, and 0.0, respectively. As a result, (4) has the form:

$$MS = 2.146x_1 + 0.324x_2 - 0.695x_1x_2, \quad (9)$$

where -0.695 is the difference: $1.775 - 0.324 - 2.146$. Here $b_0 = 0$ because in the absence of both density-dependent processes $MS = 0$. The equation VS was obtained in the same way:

$$VS = -0.484x_1 + 0.543x_2 + 0.262x_1x_2. \quad (10)$$

Parasitism has the greatest contribution to MS (2.146) and host competition has the greatest contribution VS (0.543). Parasitism destabilizes the dynamics of host population because its contribution to VS is negative (-0.484). The interaction of two processes has a negative effect on MS (-0.695).

4. Analysis of the life-system of the common pine sawfly

The common pine sawfly (*Diprion pini* L.) is a serious pest of Scotch pine in the steppe zone of Russia. It overwinters as an eonymph (pre-pupa) in the cocoon in the litter. There are two waves of flight of overwintered sawflies: in the first half of May and in the end of July–beginning of August, the second wave being much greater than the first. More than half of eonymphs remain in a prolonged diapause for the whole year. The progeny of sawflies, emerging in spring, reach the adult stage at the end of July, synchronously with the second wave of overwintered sawflies.

The dynamics of sawfly populations was investigated with a simulation model (Sharov, 1986b). The model was based on original life-table and experimental data obtained in the Rostov region (Sharov and Safonkin, 1982; Sharov, 1983, 1987) and data from the literature. The model simulates interaction of the sawfly with two guilds of parasitoids developing in eggs and eonymphs, respectively, and with the host plant. Diapause mechanisms and sawfly mortality due to predation and diseases are also considered. Weather is characterized by the mean air temperature in May–September.

Simulation results were compared with the records of population outbreaks in the Rostov region in 1956–1983. These records were not used for estimation of model parameters. The model predicted 5 out of 6 real outbreaks (Sharov, 1986b). Thus, the model was considered to be sufficiently valid on the qualitative level. Unfortunately, no quantitative long-term data are available.

Population dynamics of the common pine sawfly in the Rostov region is pulse eruptive according to the classification of Isaev et al. (1984) and Berryman (1987). I consider 4 periods of an outbreak: (1) stability (between outbreaks); (2) growth

(the first year after drought); (3) collapse (the second year after drought); and (4) depression (the year after collapse). Each period was described by a specific population characteristic and the contribution of ecological processes to these characteristics were estimated using (4). MS and VS values were used in the analysis of the period of stability. Use of these values in the analysis of global dynamics would give less details. I analyzed the role of: (1) egg-parasitoids, (2) parasitoids of eonymphs, (3) food shortage, (4) sawfly diapause termination in the first wave, (5) sawfly diapause termination in the second wave, and (6) diseases and unidentified causes of death. The method of estimation of 95% confidence intervals is described by Sharov (1992). The period of stability was simulated assuming that the average summer temperature in the model was constant and equal to the mean temperature in non-drought years. Population density was measured at the larval stage.

M -stability is relatively high ($MS = 0.7$) and depends on the regulative role of both guilds of parasitoids (Table 2). V -stability is low ($VS = 0.3$) and is supported mainly by parasitoids of eonymphs. Low v -stability indicates that the life-system is sensitive to fluctuations of input factors (such as drought).

An outbreak was simulated by increasing temperature for one year (drought simulation). Sensitivity analysis of the outbreak growth period was conducted on a measure of population growth: $y_3 = \ln(N_o/N_s)$, where N_s is population density in the previous period of stability and N_o is the maximum outbreak density. Population density is measured on the larval stage in September. When $x_i = 0$ in Eq. 4 then the i th process rate was fixed at the level peculiar to the period of stability. The decrease in sawfly mortality due to diseases and unidentified causes after the drought has the greatest contribution ($b_6 = 0.55$) to the population growth y_3 (Table 2). This mortality is apparently related to physiological state of host trees. Mass reactivation of diapausing sawflies in the second wave is also important ($b_4 = 0.35$). Reactivation is induced by increased temperature (Sharov and Safonkin, 1982).

The sum of regression coefficients for single processes (1.05) is less than half the sum of coefficients for process interactions (2.32). In the absence of interactions, population density increases during an outbreak only 3 times ($e^{1.05}$), while in the presence of interactions it increases 30 times ($e^{1.05+2.32}$). This indicates the importance of process interactions in sawfly population growth at the beginning of an outbreak. The interaction of egg parasitism with mortality due to diseases and unidentified causes ($b_{16} = 0.46$), and with diapause termination in the second wave ($b_{14} = 0.32$), are the most important. They suggest that initial population growth due to processes 4 and 6 is amplified by escape from egg-parasitoids. An outbreak is unlikely without this interaction.

Sensitivity analysis of outbreak collapse was conducted using a rate of population density decrease: $y_4 = \ln(N_o/N_c)$, where N_o is the maximum outbreak density and N_c is the population density after collapse. When $x_i = 0$ in Eq. 4, the rate of the i th process in the period of collapse was fixed at a level peculiar to the period of stability. Food shortage ($b_3 = 1.61$) is the main cause of population collapse (Table 2). The sum of regression coefficients for process interactions (2.03) is greater than the sum of coefficients for individual processes (1.91), suggesting a slightly greater importance of process interactions than individual processes in

Table 2

Contribution of ecological processes in the life-system of the common pine sawfly (coefficients $b_i, b_{i\dots j}, \dots$ in (4) with confidence intervals, $P = 0.05$) to the quantitative characteristics of population dynamics y_k (from Sharov, 1992)

Process number (combination of numbers- interaction of processes) ^a <i>I</i> or <i>I, \dots, j</i>	b_i or $b_{i\dots j}$ for y_k ^b			
	$y_1 = MS$	$y_2 = VS$	$y_3 = \ln(N_o/N_s)$	$y_4 = \ln(N_o/N_c)$
1	2	3	4	5
- [intercept in (4)]	0	0	0	0.62 ± 0.15
1	0.51 ± 0.17	0.20 ± 0.20	0	-0.83 ± 0.38
2	0.41 ± 0.11	0.68 ± 0.09	0	0.68 ± 0.26
1, 2	-0.22 ± 0.10	-0.59 ± 0.10	0	0.54 ± 0.35
3	-0.01 ± 0.01	-0.02 ± 0.01	0	1.61 ± 0.50
1, 3	0.01 ± 0.01	0.02 ± 0.01	0	1.75 ± 0.52
2, 3	0.01 ± 0.01	0.02 ± 0.01	0	-0.15 ± 0.20
1, 2, 3	-0.01 ± 0.01	-0.02 ± 0.01	0	0.51 ± 0.52
4	0	0	0.35 ± 0.12	0.45 ± 0.15
1, 4	0	0.01 ± 0.01	0.32 ± 0.11	0.12 ± 0.16
2, 4	0	0	0.05 ± 0.03	-0.34 ± 0.15
1, 2, 4	0	0	0.05 ± 0.03	-0.28 ± 0.16
3, 4	0.01 ± 0.01	0.02 ± 0.01	0	-0.36 ± 0.11
1, 3, 4	-0.01 ± 0.01	-0.02 ± 0.01	0	-0.35 ± 0.19
2, 3, 4	-0.01 ± 0.01	-0.02 ± 0.01	0	0.26 ± 0.12
1, 2, 3, 4	0.01 ± 0.01	0.02 ± 0.01	0	0.33 ± 0.26
5	0	0	0.15 ± 0.09	0
1, 5	0	0	0.37 ± 0.27	0
4, 5	0	0	0.13 ± 0.04	0
1, 4, 5	0	0	0.17 ± 0.12	0
6	0	0	0.55 ± 0.15	0
1, 6	0	0	0.46 ± 0.15	0
4, 6	0	0	0.24 ± 0.07	0
1, 4, 6	0	0	0.13 ± 0.12	0
5, 6	0	0	0.20 ± 0.05	0
1, 5, 6	0	0	0.29 ± 0.16	0
4, 5, 6	0	0	-0.05 ± 0.02	0
1, 4, 5, 6	0	0	-0.22 ± 0.07	0
Sum of other coefficients in (4)	0	0	0.18 ± 0.14	0
Total	0.70 ± 0.12	0.30 ± 0.19	3.37 ± 0.45	-4.56 ± 1.08

^a 1 = egg death due to parasitism; 2 = eonymph death due to parasitism; 3 = larvae death due to food shortage; 4 = diapause termination of overwintered sawflies in the first wave; 5 = diapause termination of overwintered sawflies in the second wave; and 6 = sawfly death due to diseases and unidentified causes.

^b *MS* and *VS* are coefficients of *m*- and *v*-stability of the sawfly population between outbreaks (input factor – larval log-transformed survival in September); N_s is sawfly density in the period of stability; N_o is maximum outbreak density; N_c is density after population collapse (all densities are considered on the larval stage in September).

this period of an outbreak. The interaction of egg parasitoids with food shortage ($b_{13} = 1.75$) is the most important. This interaction can be explained as follows. Parasitism is low in growing host populations because of the one-generation delay in the growth of parasite populations. When food shortages stop the sawfly population growth, parasitoids have time to increase their relative numbers to levels that are sufficient to destroy the host population.

5. Discussion

To study the role of ecological processes and their interactions in population dynamics I propose a non-linear sensitivity analysis of simulation models. I consider traditional statistical analysis of life tables as only the first step towards the explanation of population dynamics. The second step is the construction of a simulation model using all available information (life tables, results of laboratory and field experiments). The third step is the estimation of integral quantitative characteristics of population dynamics such as m -stability and v -stability and the analysis of ecological process contributions to these variables. Application of this method to a model of the common pine sawfly population dynamics suggests that outbreaks of the pest are caused mainly by process interactions and not by individual processes.

My current work with the Gypsy Moth Life-System Model supports the same conclusion. This model describes interactions of gypsy moth (*Lymantria dispar* L.) population in Northeastern USA with stand and with natural enemies (Sheehan, 1989). Complete sensitivity analysis of this model is still to be done, but preliminary results indicate significant process interactions in the life-system. For example, in resistant stands (beech), simulated gypsy moth population densities are low and regulated by predators, especially small mammals. If small mammals are excluded from the life-system then gypsy moth densities increase, but large outbreaks are prevented by the carabid beetle *Calosoma sycophanta* L. After exclusion of *C. sycophanta* the pest has considerable outbreaks which collapse due to viral epizootics and parasites. Lastly, if the virus and parasites are excluded from the system, outbreaks collapse due to starvation. This example illustrates that the role of each ecological process in population dynamics depends on the presence of other processes.

The life-system approach is a powerful methodology for the analysis of process interactions within an ecosystem, and non-linear sensitivity analysis can be used for quantitative assessment of these interactions. This approach can integrate biological observations and experimental data in order to analyze dynamics of natural populations driven by a complex interaction of numerous ecological processes. It can be considered as a system approach in population ecology (Sharov, 1992).

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References

- Beddington, J.R., Free, C.A. and Lawton, J.H. (1978) Modelling biological control: on the characteristics of successful natural enemies. *Nature*, 273: 573–579.
- Berryman, A.A. (1987) The theory and classification of outbreaks. In: P. Barbosa and J.C. Schultz (Editors), *Insect Outbreaks*. Academic Press, New York, N.Y., pp. 3–30.
- Clark, L.R. (1964) The population dynamics of *Cardiospina albitextura* (Psyllidae). *Aust. J. Zool.*, 12: 362–380.
- Clark, L.R., Geier, P.W., Hughes, R.D. and Morris, R.F. (1967) *The Ecology of Insect Populations*. Methuen, London, 232 pp.
- Geier, P.W. (1964) Population dynamics of codling moth *Cydia pomonella* (L.) (Tortricidae), in the Australia Capital territory. *Aust. J. Zool.*, 12: 381–416.
- Isaev, A.S., Khlebopros, R.G., Nedorezov, L.V., Kondakov, Y.P. and Kiselev, V.V. (1984) *Population Dynamics of Forest Insects*. Nauka, Novosibirsk, 224 pp. (in Russian).
- Kaye, S.V. and Ball, S.J. (1979) Systems analysis of a coupled compartment model for radionuclide transfer in a tropical environment. In: H.H. Shugart and R.V. O'Neill (Editors), *Systems Ecology*. Dowden, Hutchinson & Ross, Stroudsburg, Pa., pp. 31–39.
- May, R.M. (1973) Stability in randomly fluctuating versus deterministic environments. *Am. Nat.*, 107: 621–650.
- May, R.M., Hassell, M.P., Anderson, R.M. and Tonkyn, D.W. (1981) Density dependence in host-parasitoid models. *J. Anim. Ecol.*, 50: 855–865.
- Pollard, E. (1981) Resource limited and equilibrium models of populations. *Oecologia*, 49: 377–378.
- Sharov, A.A. (1983) Parasitoid complex of the common pine sawfly (*Diprion pini* L.) in Rostov region. *Entomol. Obozr.*, 62: 302–313 (in Russian).
- Sharov, A.A. (1986a) Population buffer ability and homeostasis and their role in population dynamics. *Zh. Obshch. Biol.*, 47: 183–192 (in Russian).
- Sharov, A.A. (1986b) A simulation model of the common pine sawfly (*Diprion pini* L.) in Rostov region. Deposited manuscript N7104-B86, Moscow, 20 pp. (in Russian).
- Sharov, A.A. (1987) On the role of parasitoids and diseases in population dynamics of common pine sawfly *Diprion pini* L. (Hymenoptera, Diprionidae) in Rostov region. *Zool. Zh.*, 66: 66–74 (in Russian).
- Sharov, A.A. (1992) The life-system approach: a system paradigm in population ecology. *Oikos*, 63: 485–494.
- Sharov, A.A. and Safonkin, A.F. (1982) Spontaneous and inductive processes in reactivation of common pine sawfly *Diprion pini* (Hymenoptera, Diprionidae). *Zool. Zh.*, 61: 1171–1179 (in Russian).
- Sheehan, K.A. (1989) Models for the population dynamics of *Lymantria dispar*. In: W.E. Wallner and K.A. McManus (Technical Coordinators), *Proceedings, Lymantriidae: A Comparison of Features of New and Old World Tussock Moths*, 26 June–1 July 1986, at New Haven, Conn. Gen. Tech. Rep. NE-123, USDA For. Serv., NE For. Exp. Sta., Radnor, Pa., pp. 533–547.
- Tomovic, R. (1963) *Sensitivity Analysis of Dynamic Systems*. McGraw-Hill, New York, N.Y.
- Varley, G.C. and Gradwell, G.R. (1960) Key factors in population studies. *J. An. Ecol.*, 29: 399–401.