

Short Communication

Basic properties of ELP-model

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Description of ELP-model

Various species of forest insects have one-year generations, and during winter time individuals stay in pupae phase (for example, pine looper moth *Bupalus piniarius* L.; Klomp, 1966; Isaev et al., 1984, 2001; Nedorezov, 1986, 2012; Kendall et al., 2005; Nedorezov, Utyupin, 2011 and others). For description of population dynamics for these species models of isolated population dynamics can be used (Kostitzin, 1937; Pielou, 1977; Nedorezov, 1986, 1997, 2012) but series problems can appear if we want to take into account an information which contains several coupled time series (like in the case with pine looper: time series on pupae, larvae, and eggs were collected by H. Klomp in one and the same location). In considering situation special models which contain several variables, must be created (see, for example, Costantino et al., 1997; Dennis et al., 2001; Desharnais et al., 2001; Nedorezov, Nekljudova, 2000).

Let P_k be a number of pupae at year number k . Respectively, B_k is a number of butterflies, L_k is a number of larvae, E_k is a number of eggs. Relation between B_{k+1} and P_k is determined by the following equation:

$$B_{k+1} = \mu_1 P_k. \quad (1)$$

In (1) μ_1 , $0 \leq \mu_1 \leq 1$, is quota of survived pupae during the winter period. Amount of this quota depends on weather conditions but now we'll assume that these conditions are constant. It also depends on food conditions for larvae: in indirect way it can be described as dependence on L_k : $\mu_1 = \mu_1(L_k)$. Increasing of number of larvae leads to decreasing of food conditions for them and, respectively, to decrease of amount of μ_1 . Asymptotically μ_1 goes to zero:

$$\mu_1(\infty) = 0, \quad \frac{d\mu_1}{dL_k} < 0. \quad (2)$$

Below the following function will be used:

$$\mu_1 = \frac{g_1}{1 + g_2 L_k^{g_3}}. \quad (3)$$

It is obvious that function (3) corresponds to conditions (2). All parameters g_j are non-negative constants and $0 \leq g_1 \leq 1$.

Relation between variables E_{k+1} and B_{k+1} can be described with the following equation:

$$E_{k+1} = CB_{k+1}. \quad (4)$$

In (4) C is productivity of butterflies. Below it will be assumed that productivity depends on L_k , $C = C(L_k)$. This function decreases with increase of number of larvae, and asymptotically it goes to zero:

$$C(\infty) = 0, \quad \frac{dC}{dL_k} < 0. \quad (5)$$

Simple function which satisfies conditions (5), can be presented in the form:

$$C = \frac{c_1}{1 + c_2 L_k^{c_3}}. \quad (6)$$

All parameters c_j are non-negative constants. Taking into account that number of butterflies is real *invisible* variable (amount of this variable is rather difficult to determine in field conditions), it can be deleted from model. Combining of equations (1) and (4) we get

$$E_{k+1} = C\mu_1 P_k. \quad (7)$$

In (7) functions in right-hand side satisfy to conditions (2) and (5), and in simple cases can be presented in forms (3) and (6).

Let μ_2 be a quota of eggs successfully transformed into larvae, $0 \leq \mu_2 \leq 1$. Below we'll assume that $\mu_2 = const$ (but in general case it is naturally to assume that amount of this quota depends on weather conditions). Thus, we have the following equation:

$$L_{k+1} = \mu_2 E_{k+1}. \quad (8)$$

The final equation is analog of Moran – Ricker model:

$$P_{k+1} = L_{k+1} e^{-\alpha L_{k+1}}. \quad (9)$$

In (9) parameter α corresponds to influence of self-regulative mechanisms on larvae's surviving, and expression $Exp\{-\alpha L_{k+1}\}$ is equal to quota of larvae successfully transformed into pupae. Combining equations (7), (8), and (9) we obtain ELP-model of insect population dynamics. This model has eight non-negative parameters. Initial values of model variables are additional parameters which must be determined at a process of model parameter estimations.

Transformation of ELP-model

If we want to estimate model parameters and have three coupled time series (like for pine looper moth; Klomp, 1966) we have to use ELP-model (7)-(9) as it is. But in current publication we want to describe basic properties of ELP-model. In this occasion we can transform model, and present it as one equation for description of number of larvae dynamics:

$$L_{k+1} = \frac{c_1 g_1 L_k e^{-\alpha L_k}}{(1 + c_2 L_k^{c_3})(1 + g_2 L_k^{g_3})}. \quad (10)$$

Let's note, if we want to estimate model (10) parameters using one time series on larvae dynamics it will be possible to estimate value of product $c_1 g_1$, and there are no possibilities to estimate values of these parameters separately. Moreover, taking into account a certain symmetry for expressions $1 + c_2 L_k^{c_3}$ and $1 + g_2 L_k^{g_3}$ in (10) obtaining of final results will not allow us saying what kind of estimations have relation to productivity of butterflies and what kind of estimations have relation to surviving of pupae during the winter time.

Properties of model (10)

1. For all non-negative initial values of variable solutions of model are non-negative and bounded. It follows from the following inequalities:

$$L_{k+1} = \frac{c_1 g_1 L_k e^{-\alpha L_k}}{(1 + c_2 L_k^{c_3})(1 + g_2 L_k^{g_3})} \leq c_1 g_1 L_k e^{-\alpha L_k} \leq \frac{c_1 g_1}{\alpha e^1}.$$

2. For all values of model parameters origin is stationary state. If product $c_1 g_1 < 1$ origin is global stable equilibrium of model. If inverse inequality $c_1 g_1 > 1$ is truthful origin is unstable stationary state. Thus, $c_1 g_1 = 1$ is cylindrical bifurcation surface in space of model parameters.

3. If inequality $c_1 g_1 > 1$ is truthful non-trivial stationary state exists in phase space. Coordinate of this stationary state can be found as solution of algebraic equation

$$(1 + c_2 L_k^{c_3})(1 + g_2 L_k^{g_3}) = c_1 g_1 e^{-\alpha L_k}.$$

In left-hand side of this equation there is monotonic increasing function, and monotonic decreasing function is in right-hand side of equation.

4. In Fig. 1 bifurcation diagram is presented. This diagram was obtained for following values of model parameters: $\alpha = 1$, $c_2 = 1$, $c_3 = 1$, $g_2 = 1$, $g_3 = 1$. For every fixed values of product $c_1 g_1$ ordinate line contains coordinates of asymptotically stable attractors.

As we can see on this figure 1, if $c_1 g_1 < 1$ origin is global stable equilibrium: population eliminates for all initial values of population size. Intersection of bifurcation value $c_1 g_1 = 1$ leads

to appearance of non-trivial stationary state; at that values origin is unstable equilibrium. On the interval [8,12] non-trivial stationary state loses its stability and in phase space global stable 2cycle appears.

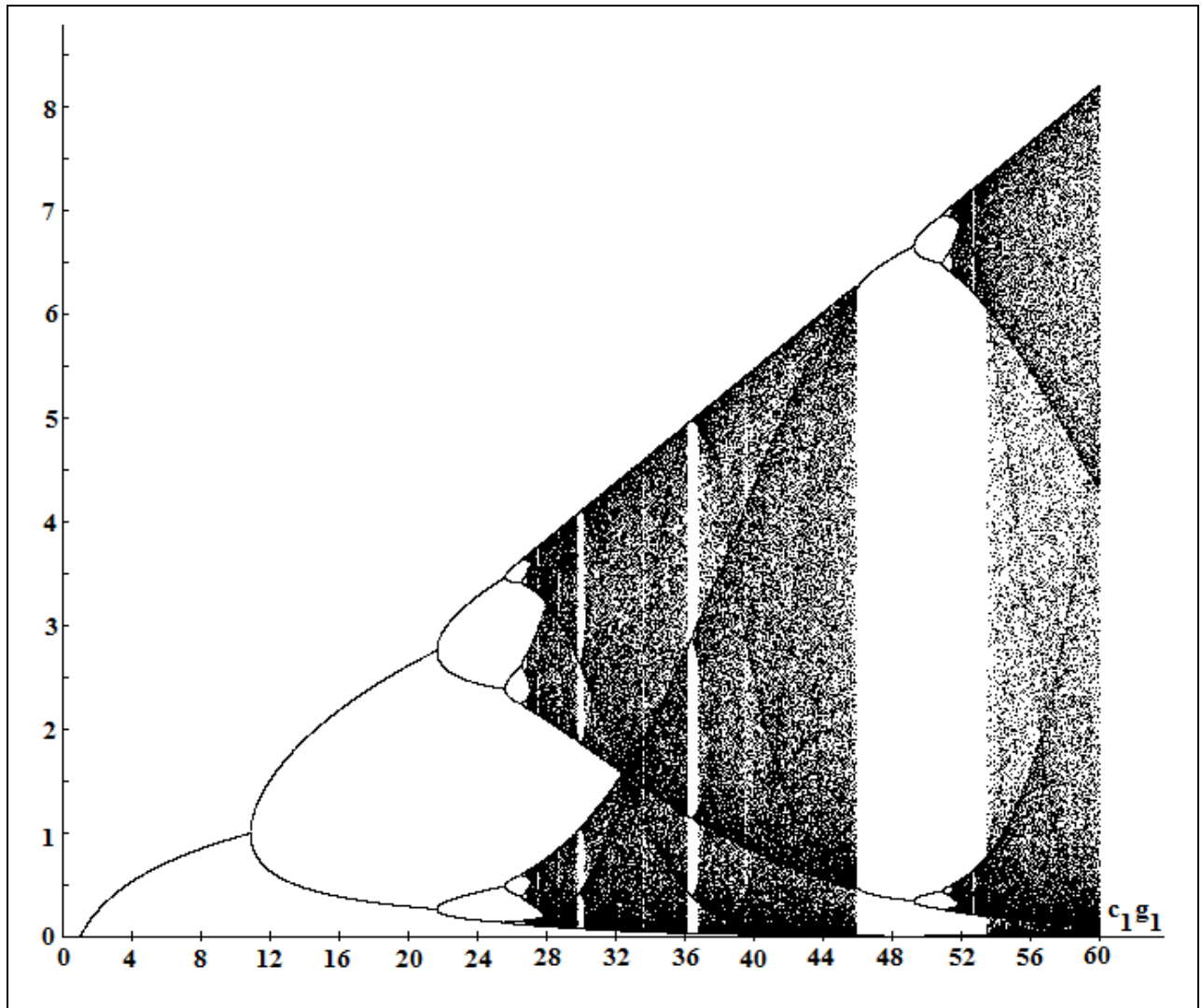


Fig. 1. Bifurcation diagram: $\alpha = 1, c_2 = 1, c_3 = 1, g_2 = 1, g_3 = 1$.

On the interval [20,24] 2-cycle loses its stability and stable 4-cycle appears in phase space. In other words, in Fig. 1 we can observe standard process of doubling of cycles and appearance in phase space various cyclic and chaotic dynamic regimes. It allows concluding that model (1) contains very rich set of dynamic regimes.

If parameter $c_3 = 10$ (values of all other parameters are the same) bifurcation diagram has other form (Fig. 2). Note that parameter c_3 plays a role of modifier of productivity of butterflies: bigger value of this parameter leads to faster decreasing of productivity with respect

to population size. Similar role is observed for parameter g_3 , and results observed for first parameter will be observed for the second one.

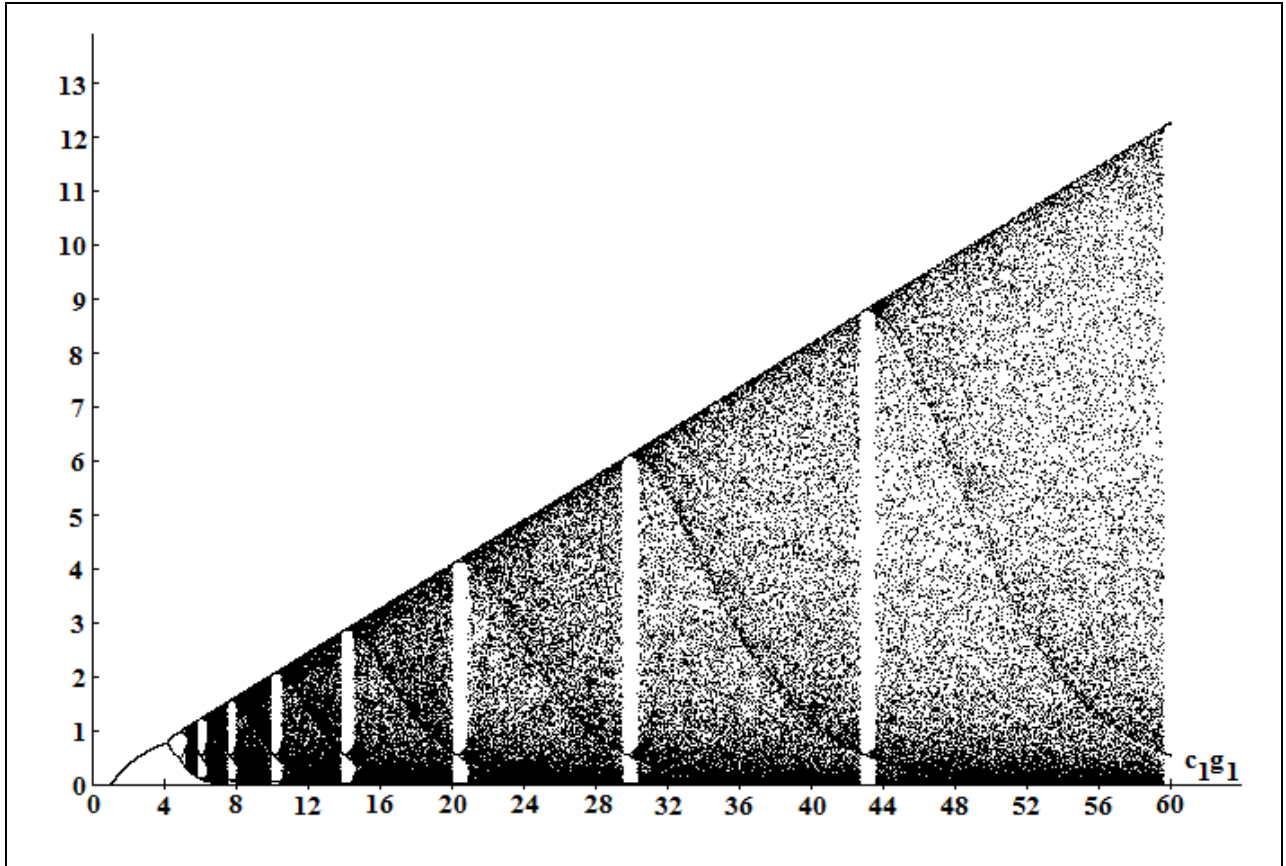


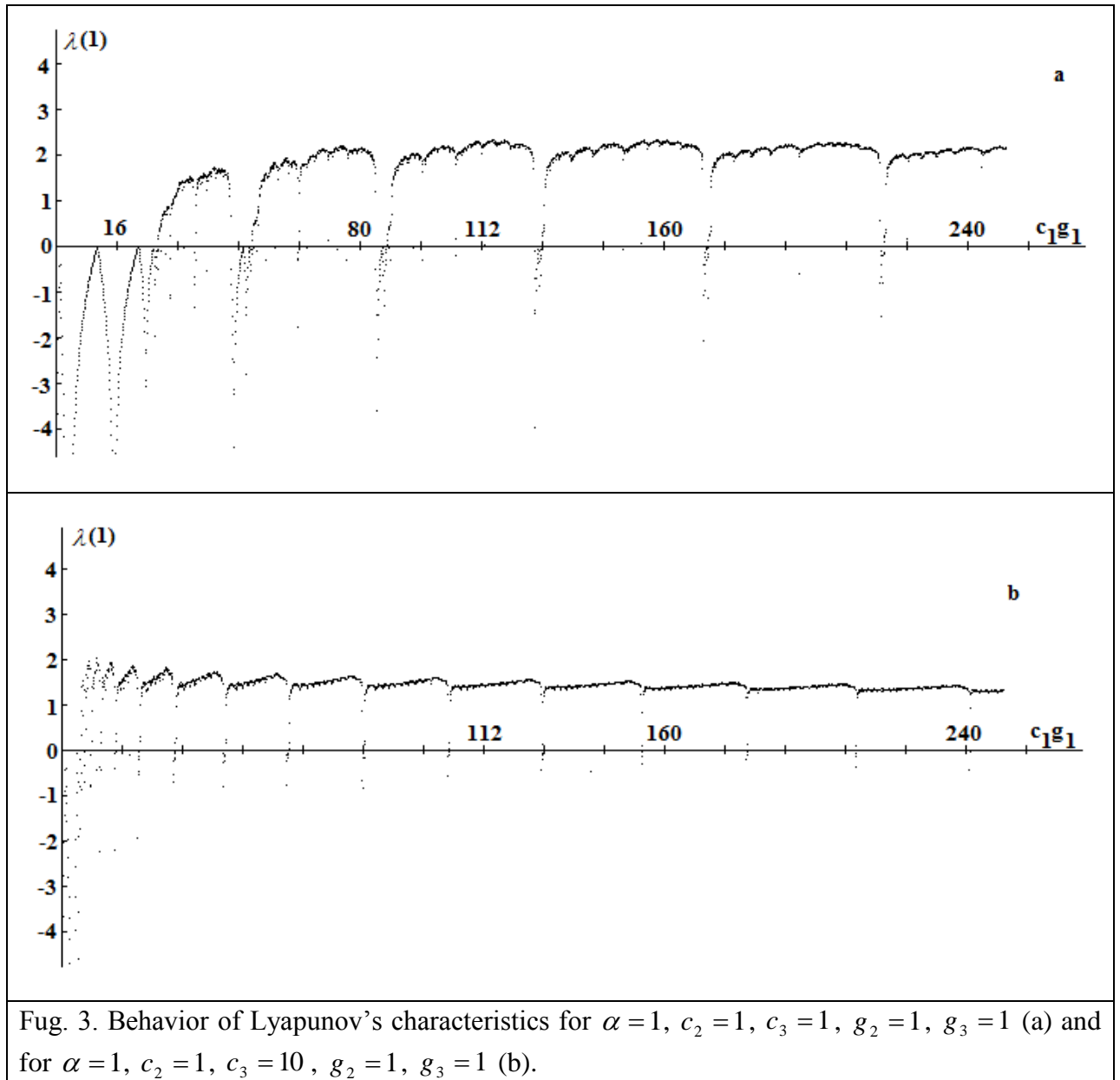
Fig. 2. Bifurcation diagram: $\alpha = 1, c_2 = 1, c_3 = 10, g_2 = 1, g_3 = 1$.

First of all, in the second case (Fig. 2) non-trivial equilibrium loses its stability faster than in the first case (Fig. 1): it is observed about 4. The second, productivity decreases faster but coordinates of stable attractors are bigger than in the first case. And, the third, there are no big windows (intervals of changing of product c_1g_1 when rather simple dynamic regime is realized in model) like in first case.

5. In Figure 3 there are two variants of behavior of Lyapunov's characteristics corresponding to situations presented in Fig. 1 and 2:

$$\lambda(x_0) = \lim_{n \rightarrow \infty} \frac{1}{n} \sum_{i=0}^{n-1} \ln \left| \frac{df}{dx}(x_i) \right|. \quad (11)$$

In (11) f is the function in right-hand side of equation (1). Sequence $x_0, x_1, x_2 \dots$ is trajectory of model (10) which is generated for fixed values of model parameters and initial population size x_0 .



As we can see in these pictures, exponential divergence of trajectories of model (10) in the second case (Fig. 3b) is observed for smaller values of product c_1g_1 than it is observed in the first case (Fig. 3a). It allows create a hypothesis about influence of dependence of productivity and quota of survived individuals on food conditions for larvae. We can also see that windows in the second case are not so wide like in the first case.

6. On Figure 4 domains where conditions of Diamond theorem (Diamond, 1976) are truthful (red points) are presented on the plane (c_1g_1, α) . Parameters of model corresponding to Figure 4a are the same like for Fig. 1 and 3a; in the second case (Fig. 4b) parameters are the same like for Fig. 2 and 3b. As we can see in Fig. 4, structures of domains of red points are qualitatively different.

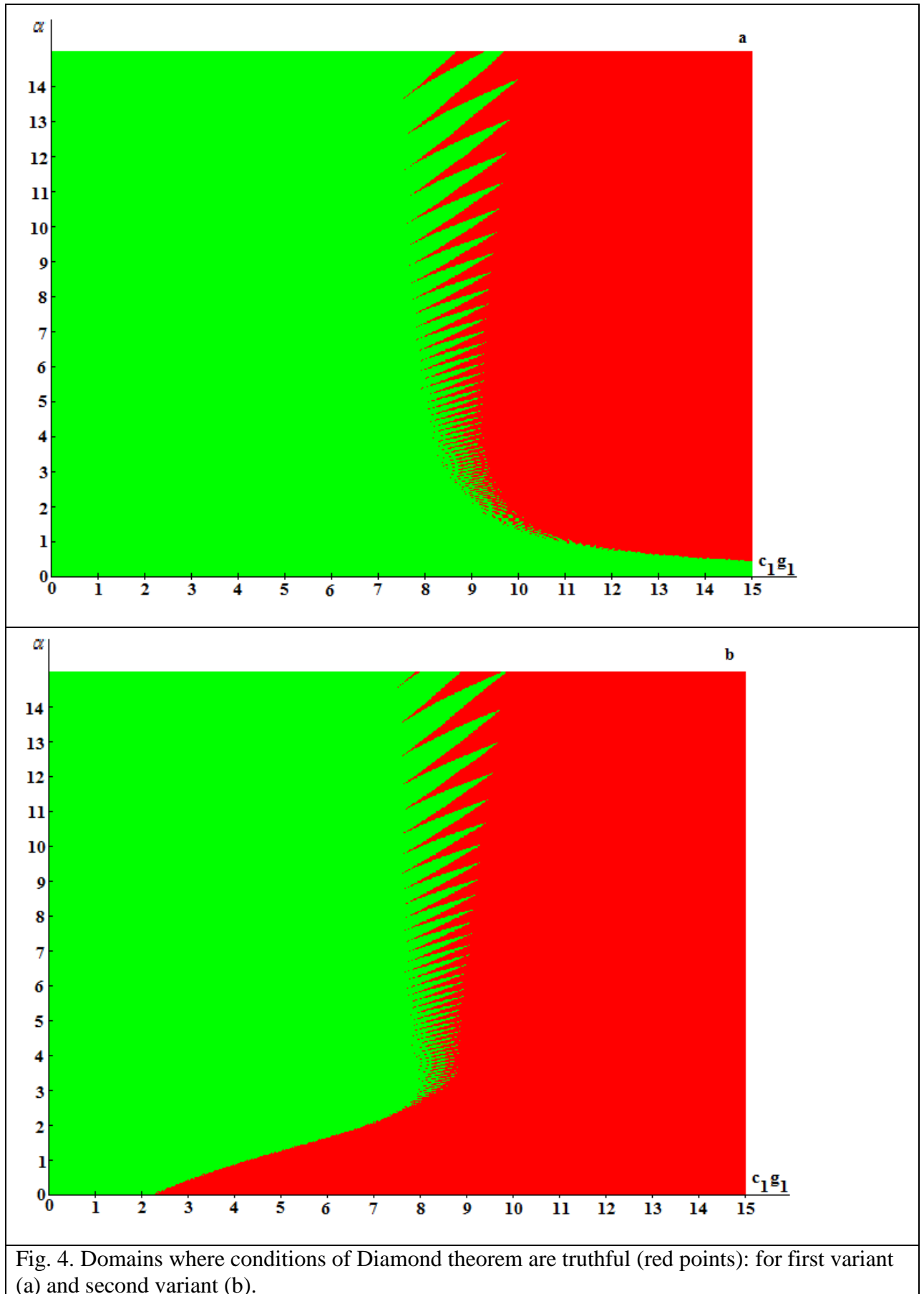


Fig. 4. Domains where conditions of Diamond theorem are truthful (red points): for first variant (a) and second variant (b).

Comparison of sets in Fig. 4 allows conclusion that specificity of dependence of butterfly's productivity and/or coefficient of surviving of individuals during the winter can be a reason of appearance of chaotic changing of population size.

Conclusion

Analysis of ELP-model shows that it contains very rich set of dynamic regimes including cyclic regimes of all lengths and chaotic dynamic regimes. At the same time it does not contain regimes with several stationary states in phase space – it can lead to appearance of problems in application of this model for description of outbreak species.

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