Working Paper

Limit Cycles in Slow-Fast Forest-Pest Models

S. Muratori and S. Rinaldi

WP-90-38
July 1990

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FOREWORD

Some of the most exciting current work in the environmental sciences involves simplified but analytically tractable versions of a few basic equations. IIASA's Environment Program has developed such an approach in its analysis of forest systems. A number of previous papers (WP-87-70, and WP-87-92) have demonstrated the progress that has been made. In this new work some of the ideas contained in those papers have been further developed.

In particular a simple aged-structure forest model is considered to prove that a forest can exhibit periodic behaviour even in the case the insect pest is adapted only to mature trees. The insect pest assumed to have a very fast dynamics with respect to trees and the analysis is carried out through singular perturbation arguments. The method is based only upon simple geometric characteristics of the equilibrium manifolds of the fast, intermediate and slow variables of the system and allows one to derive explicit conditions on the parameters that guarantee the existence of a limit cycle in the extreme case of very fast-very slow dynamics.

Bo R. Döös
Leader
Environment Program

LIMIT CYCLES IN SLOW-FAST FOREST-PEST MODELS

S. Muratori and S. Rinaldi

1. INTRODUCTION

In a recent paper, Antonovsky *et al.* (1990) have presented two simple age-structured forest models in which the insect pest attacks either young or old trees. The analysis of their three-dimensional models, mainly based on the existence of eteroclinic and Hopf bifurcations, shows that a stable limit cycle can exist for suitable values of the parameters if the insect pest feeds upon young trees. On the contrary, if the insect pest is adapted only to old trees, then periodic oscillations cannot occur. This means that age-dependent predation has a very sharp and strategic role in determining forest dynamics.
Although we believe that stability of ecosystems may be (as pointed out by Hasting 1983, 1984) sensitive to age-dependent predation, we also believe that the result of Antonovsky *et al.* (1990) is definitely too crude. Indeed, the result is in contrast with the conclusions that Ludwig *et al.* (1978) have obtained with a somehow similar three-dimensional forest model in which foliage and wood were considered as state variables. Moreover, and this is possibly more important, the conclusion of Antonovsky *et al.* (1990) is also in contrast with the evidence in the data of the forest they analyze, namely the balsam fir forest of Eastern North America which has experienced periodic outbreaks of spruce budworms although such a pest is mainly feeding on the foliage of adult trees. We suspect that this is due to the oversimplified dynamics of the insect pest (constant mortality and linear functional response). For this reason we present in this paper a modified model in which we assume that insect pest is subjected to predation and intraspecific competition and has a saturating functional response (i.e. limited gut capacity) (see Holling, 1965). Our model can therefore be viewed as the most natural extension of classical prey-predator models (May, 1981) to the case of age-structured predators.

In contrast with the result pointed out by Antonovsky *et al.* (1990), our model can display limit cycles for suitable values of the parameters even if the insect pest attacks only old trees. This shows that there are no structural discrepancies between even and non-even-aged forests provided the insect pest is modelled with some realism. Of course, this does not overshadow the neat contribution of Antonovsky *et al.* (1990) which has the merit of proving that in the case of extremely simple predation mechanisms the stability of the model is dominated by the way age structure is incorporated.

From a methodological point of view, our analysis is quite interesting because it is based on a very simple but rather effective geometrical technique (Muratori and Rinaldi, 1990a) that can be applied to detect limit cycles in dynamical systems with slow-fast dynamics. Such a method is of great potential in the analysis of ecological systems when different populations can be hierarchically ordered from the point of view of their time responses. The method, used for decades to analyze relaxation oscillations in second order systems (see Guckenheimer and Holmes, 1983), has been extended and successfully applied to three-dimensional prey-predator systems by Muratori and Rinaldi (1989a, 1990b) and is applied here under the assumption (certainly satisfied to a good extent) that old trees have slow dynamics and insect pests have fast dynamics. The method proceeds as follows. First the dynamics of the fast component of the system is studied and the existence of multiple equilibria and catastrophic bifurcations is ascertained. Then, it is shown that for suitable values of the parameters the equilibrium manifold of the slow variable separates the above bifurcations. This separation condition allows us to prove, through singular perturbation analysis, that a limit cycle exists and that it is composed by the alternate concatenation of two slow and two fast transitions. This has interesting biological interpretations and is in agreement with the data on balsam fir forests.

2. DESCRIPTION OF THE MODEL

The model we consider is the following

$$\dot{x} = a_1 y - a_2 x - a_3 \frac{x}{a_4 + x} z \tag{1a}$$

$$\varepsilon \dot{y} = a_5 x - [a_6 (x - a_7)^2 + a_8] y - a_1 y \tag{1b}$$

$$\varepsilon \delta \dot{z} = (-a_9 - a_{10} z - \frac{a_{11}}{a_{12} + z} + a_{13} \frac{x}{a_4 + x}) z \tag{1c}$$

where x and y are densities of old and young trees, z is the insect pest density, a_i, $i = 1, \dots 13$, are positive constant parameters and ε and δ are small positive parameters. The biological interpretation of the parameters is the following.

a_1 is the aging rate (namely the rate at which young trees become mature (old)).

a_2 is the natural death rate of old trees.

a_3 is the maximum harvest rate of old trees per unit of insect pest.

a_4 is the half saturation constant for the insect pest (namely the prey density at which the functional response $a_3 x/(a_4 + x)$ of the predator is half maximal).

a_5 is the fertility rate of mature (old) trees.

a_6, a_7 and a_8 are parameters that specify the mortality rate of young trees (a unimodal function of old tree density).

a_9 is the basic mortality rate of the insect pest.

$a_{10}z$ is the surplus of mortality rate of the insect pest due to intraspecific competition.

a_{11} and a_{12} are parameters that specify the surplus of mortality rate of the insect pest due to predation ($a_{11}z/(a_{12}+z)$ is the functional response of the predators of the insect pest).

a_{13} is a conversion factor proportional to the efficiency of the insect pest (i.e. the number of newly born predators for each unit of captured prey).

On the contrary, ε and δ are two small dimensionless positive parameters which hierarchically scale the dynamics of the three components of the system. Thus, the growth of mature trees is slower than the growth of young trees, and the insect pest has, in comparison, a very fast dynamics. The second assumption is obviously satisfied while the first might be doubtful, in particular because it is often difficult to rigorously distinguish between old and young trees. Nevertheless, the analysis we develop shows that the limit cycles of model (1) are composed only by very fast and very slow transitions so that the assumption that old and young trees have a differentiated dynamics does not play any substantial role.

Equations (1a, b) are structurally similar to those used by Antonovsky *et al.* (1990) to model old and young trees (notice that x and y are interchanged). Nevertheless, the forest-insect interaction is different, because it is modelled by a saturating functional response, while in Antonovsky *et al.* (1990) a linear functional response is used. This means that in our model the insect pest has a finite growth rate per capita ($\dot{z}/z$) even in the most favorable case of infinitely abundant resource ($x \rightarrow \infty$). The second difference is that our predator has a density dependent mortality due to intraspecific competition and predation by insectivores. For suitable values of the parameters a_{10}, a_{11} and a_{12} the mortality of the pest can be decreasing and then increasing with density. Very often these nonlinearities are disregarded because they play an important role only at extremely low and at extremely high densities. But this is exactly what happens in periodically infested forests where the insect is either almost absent or present at very high numbers.

3. SINGULAR PERTURBATION ANALYSIS AND LIMIT CYCLES

Let us rewrite model (1) in the form

$$\dot{x} = f(x, y, z, a) \tag{2a}$$

$$\varepsilon \dot{y} = g(x, y, a) \tag{2b}$$

$$\varepsilon \delta \dot{z} = h(x, z, a) \tag{2c}$$

where a is the vector of constant parameters, and notice that g and h depend only upon two of the three state variables. For small values of ε and δ the solution of (2) for given initial conditions can be approximately found by means of singular perturbation analysis (see Hoppensteadt, 1974).

First, the slow (x) and intermediate (y) variables are frozen at their initial values $x(0)$ and $y(0)$, and the evolution of the fast component of the system is determined by solving the "fast system"

$$\dot{z}(t) = h(x(0), z(t), a)$$

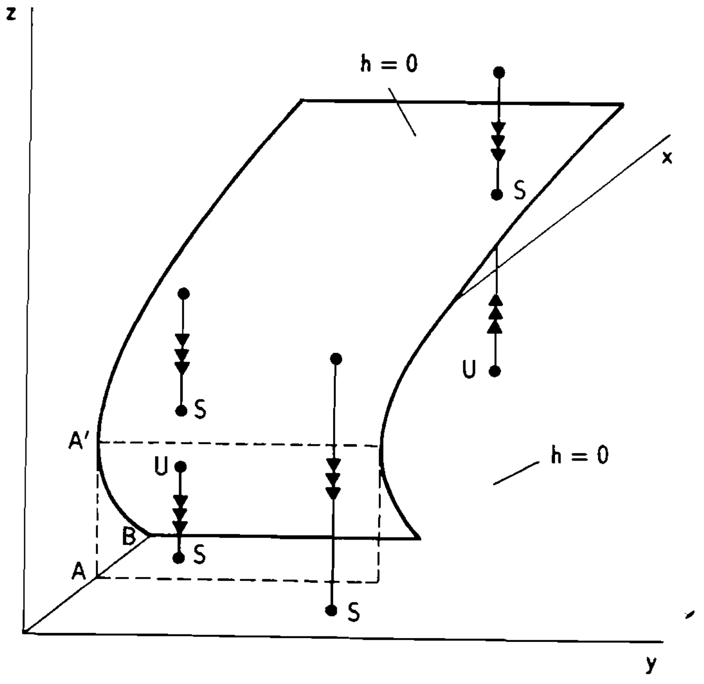

Figure 1. The equilibrium manifold $h = 0$ of the fast variable and the fast transients (triple arrow).

Thus, $z(t)$ tends asymptotically to one of the stable equilibria of the fast system (in general, characterized by $\partial h/\partial z < 0$). Figure 1 shows the geometry of the equilibrium manifold $h = 0$ of the fast system and its trajectories for suitable values of the parameters. The points denoted by

S are stable ($\partial h/\partial z < 0$) while those denoted by U are unstable ($\partial h/\partial z > 0$). For low values of $x(0)$, $\bar{z} = 0$ is the unique and stable equilibrium, i.e. when the density of the old trees is below a certain threshold (point A in Figure 1), the insect pest very quickly goes extinct. On the contrary, for intermediate values of $x(0)$ (segment AB in Figure 1) there are three equilibria, two of which are stable. In this case $z(t)$ approaches very quickly a positive equilibrium if its initial value is sufficiently high, and goes to zero otherwise. Finally, if $x(0)$ is large, $z(t)$ tends to a positive equilibrium in any case.

Once the state of the system has reached (actually approached) the fast manifold $h = 0$, the time scale of the evolution changes and the variable with intermediate dynamics, namely y, becomes of interest. This is equivalent of saying that one can consider the "intermediate system"

$$\dot{y}(t) = g(x(0), y(t)a),$$

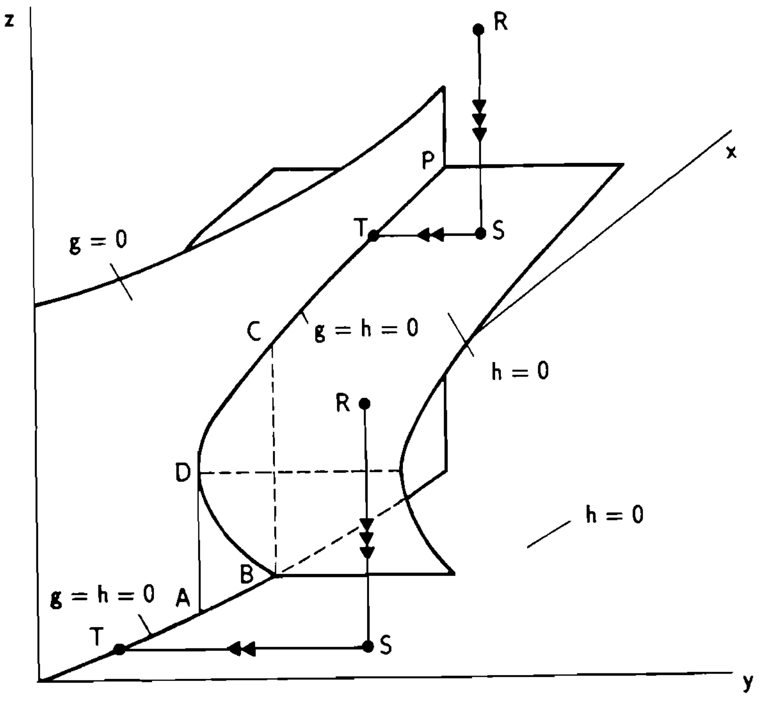

Figure 2. The fast ($h = 0$) and intermediate ($g = 0$) manifolds and the corresponding fast (triple arrow) and intermediate (double arrow) transients.

determine its solution with initial condition $y(0)$, and then concatenate the corresponding trajectory with the one previously found by analyzing the fast system. (Notice that in the most general case in which g depends upon all state variables one has to integrate the equation $\dot{y} = g$ with the constraint $h = 0$, that is to say that the intermediate variable drives the fast one). As before, the variable $y(t)$ tends to a stable point of its equilibrium manifold $g = 0$. Figure 2 shows such a manifold in the case of equation (1b) for a suitable value of the parameter vector a. The trajectories start from a stable point S of the fast manifold and tend toward a stable point T of the intermediate manifold. The result is that after two transients, the first at high speed and the second at intermediate speed, the state of the system has reached either line $0B$ (absence of insect pest) or line DP (presence of insect pest).

At this point a slow transient governed by the dynamics of the old trees develops. Such a transient is obviously described by equation (2a) subject to the constraints

$$g(x,y,a) = h(x,z,a) = 0$$

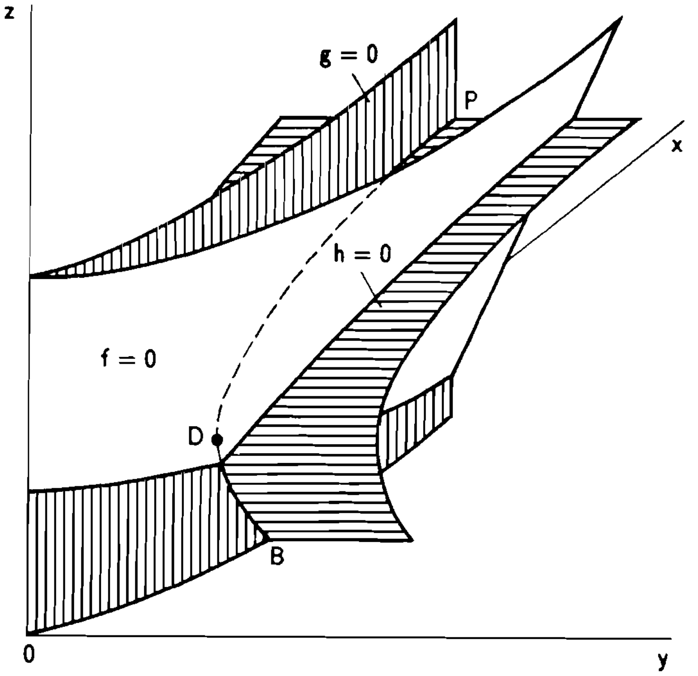

Figure 3. The three manifolds $f = 0$, $g = 0$, and $h = 0$. The slow manifold $f = 0$ separates line $0B$ from line PD.

Therefore the trajectory coincides either with line $0B$ or with line DP of Figure 2 where insect pests and young trees smoothly vary at the same speed than old trees do. In order to detect in which direction the state of the system moves along these lines one has simply to look at the sign of $\dot{x}$, namely of f. Thus, let us assume that for suitable values of the parameters the slow manifold $f = 0$ separates line $0B$ from line DP as sketched in Figure 3 and that f is positive below the manifold and negative above it. Under this condition the system moves toward point D along line PD (see Figure 4) and when D is reached we have a saddle-node bifurcation of the fast system : the variable z at point D is not at a stable equilibrium anymore and a catastrophic transition from D to A (extinction of the insect pest) takes place at a very high speed as shown in Figure 4. Once the system is in A, a slow motion develops from A toward B because f is positive along line $0B$. Thus, old (and young) trees slowly grow until point B in Figure 4 is reached. But this point corresponds to the threshold at which the trivial equilibrium of the fast system becomes unstable. Again we have a bifurcation and a catastrophic high speed transient brings the state of the system back on line PD (point C of the figure). Thus, a cycle $ABCD$ has been closed.

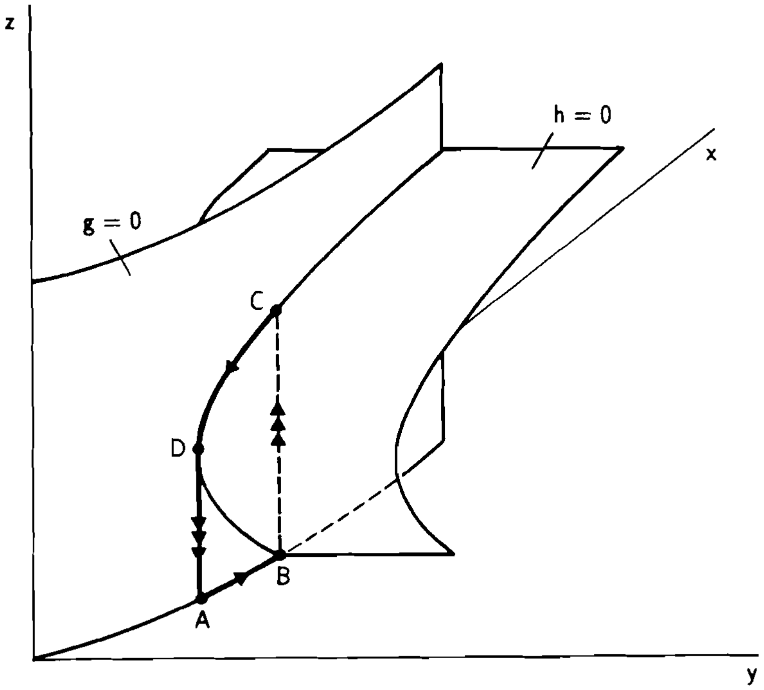

Figure 4. The cycle $ABCD$. Transitions AB and CD are slow while transitions DA and BC are fast.

Comment 1

Let us now interpret the cycle we have found starting from point A. In the absence (actually endhemic presence) of the insect pest the old (and young) trees grow slowly (the transition from A to B takes from 20 - 30 years in balsam fir forests of Eastern North America) until they reach a biomass (point B) at which the mechanisms that keep the pest under control are overcome. Thus, the insect pest population becomes unstable and a demographic explosion of the insect pest occurs (transition BC). For a long period to follow (6 - 15 years in the above mentioned forest) the insect density is high in stands of mature trees and the biomass of trees slowly decays. As a consequence the insect pest population also decreases smoothly and finally reaches a density (point D) at which its mortality mechanisms destabilise it, so that the pest population collapses to zero, thus closing the cycle.

Comment 2

This comment has to do with some technicalities of singular perturbation analysis (Hoppensteadt, 1974). Usually the singular perturbation argument is presented with reference to the case in which the fast system has a unique stable equilibrium $\bar{z}(x,y)$ for each frozen value of (x,y). This condition implies that for a finite t and an initial condition (x,y,z) with z in the domain of attraction of $\bar{z}(x,y)$ of the fast system, the solution of system (1) can be approximated by a fast transition from (x,y,z) to $(x,y,\bar{z})$ followed by a trajectory with intermediate speed along the equilibrium manifold $h=0$ and, finally, by a slow-motion trajectory along the manifold $g=h=0$. Moreover, if the slow-motion system is uniformly stable, then the above approximation also holds in the limit for $t \to \infty$. In the present case, in which we are interested in the asymptotic behavior of the solution, the fast-time system has two stable equilibria, but the slow-motion system cannot evolve indefinitely on one of the two equilibrium manifolds but must recursively commute from one to the other. Therefore, since the system remains on each manifold only for a finite interval of time, the approximation guaranteed by the standard singular perturbation conditions holds also asymptotically. The formal proof of this fact is not given because it is long and trivial, and because this argument has already been discussed and extensively used in the literature (see, for example, Guckenheimer and Holmes (1983) pp. 68-69 for the analysis of a similar case and May (1977) and Muratori and Rinaldi (1989a, 1990b) for applications in predator-prey systems). The conclusion is that, strictly speaking, we do not prove the existence of a limit cycle, but the existence of stable solutions that lie in an ε-tube around the closed line $ABCD$. Nevertheless, in the following we will take the liberty to say that a limit cycle exists because for our aims the two situations are practically and conceptually indistinguishable.

Comment 3

The geometry of the three manifolds $f=0$, $g=0$, and $h=0$ can be analyzed and explicit inequalities on the parameters a_i can be found that guarantee the existence of the catastrophic bifurcations of the fast variable and the satisfaction of the separation condition required by the method (actually only the line segments AB and CD must be separated by the manifold $f=0$ in order to guarantee the existence of a cycle). The detailed analysis is reported in the Appendix and the result is the following.

Existence of a limit cycle. If ε and δ are sufficiently small and

$$a_{13} > a_9 + \frac{a_{11}}{a_{12}} \tag{3}$$

$$a_{10} < \frac{a_{11}}{a_{12}^2} \tag{4}$$

$$a_2 < \Psi(a_1, a_4, a_5, \ldots, a_{13}) \tag{5}$$

$$a_3 > \chi(a_1, a_2, a_4, a_5, \ldots, a_{13}) \tag{6}$$

where

$$\Psi = a_1 \min \{\frac{y_A}{x_A}, \frac{y_B}{x_B}\} \tag{7}$$

$$\chi = \frac{a_1}{\sqrt{\frac{a_{11}}{a_{10}}} - a_{12}} (a_4 + x_A)(\frac{y_B}{x_A} - \frac{a_2}{a_1}) \tag{8}$$

and

$$x_A = a_4 \frac{a_9 + 2\sqrt{a_{10}a_{11}} - a_{10}a_{12}}{a_{13} - a_9 - 2\sqrt{a_{10}a_{11}} + a_{10}a_{12}} \tag{9}$$

$$y_A = \frac{a_5 x_A}{a_1 + a_6(x_A - a_7)^2 + a_8} \tag{10}$$

$$x_B = a_4 \frac{a_9 + \frac{a_{11}}{a_{12}}}{a_{13} - a_9 - \frac{a_{11}}{a_{12}}} \tag{11}$$

$$y_B = \frac{a_5 x_B}{a_1 + a_6(x_B - a_7)^2 + a_8} \tag{12}$$

a limit cycle exists for system (1). □

It is worthwhile noticing that conditions (3), (4) as well as Ψ, do not depend upon a_2, so that (5) can always be satisfied. Similarly, (3), (4), (5) and χ do not depend upon a_3 so that (6) can be easily satisfied. Conditions (3-12) are therefore very useful to construct sets of parameter values that guarantee the existence of a limit cycle. For example, if we fix a priori

$$a_1 = a_4 = a_5 = a_6 = a_7 = a_8 = a_9 = a_{10} = a_{12} = 1$$

then (4) is satisfied if

$$a_{11} = 2$$

so that (3) is satisfied if

$$a_{13} = 5.$$

Thus, computing Ψ, a value of a_2 that satisfies (5) can be found, for example

$$a_2 = 0.4$$

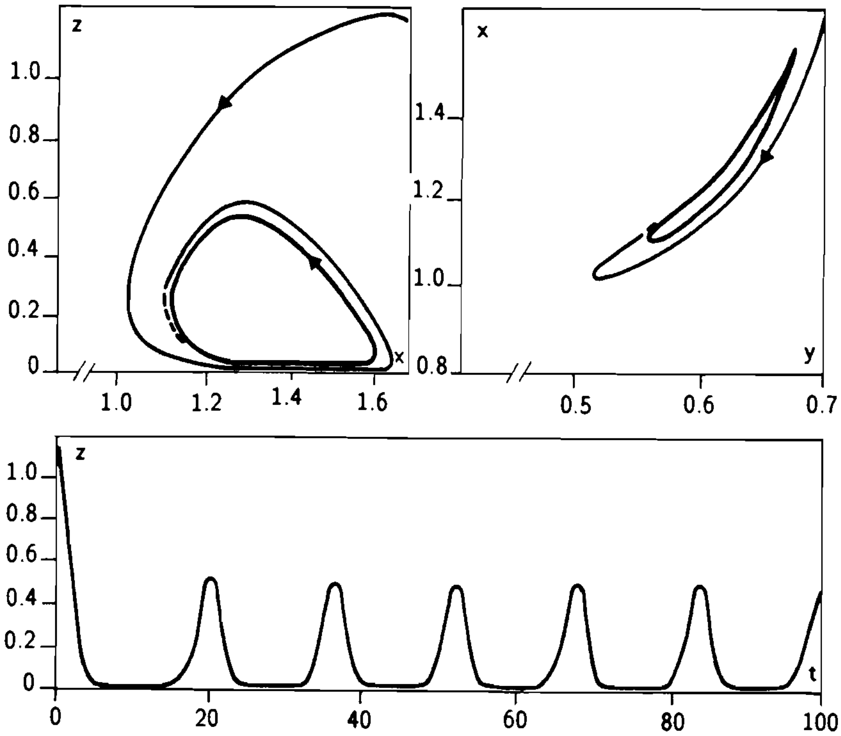

Figure 5. Example of limit cycle. All parameters are equal to 1 with the exception of $a_2 = 0.4$, $a_{11} = 2$, $a_{13} = 5$, $\varepsilon = \delta = 0.5$.

Finally, be means of (8) one can compute χ and give to a_3 a sufficiently high value ($a_3 = 1$ in the present case) in order to satisfy (6). Thus, with a few simulation trials one can find values for ε and δ such that the system oscillates, as shown in Figure 5 for $\varepsilon = \delta = 0.5$.

Comment 4

The conditions we have pointed out for the existence of a limit cycle unfortunately require that the two time-scale parameters ε and δ are small. This could be a rather unpleasant requirement. In fact,, if the limit cycle of a system satisfying conditions (3-12) would exist only for extremely small values of ε and δ, our result would only be a futile curiosity because the typical time-scale of old trees growth is the decade while demographic explosions of pest insects can take place in a few months. In order to prove that our result is sound, we should therefore show that conditions

(3-12) imply that a cycle exists also for values of the product $\varepsilon\delta$ ranging in the interval 0.01 - 0.05. Moreover, we should also show that the cycle can exist for relatively high values of ε since, as already pointed out, the assumption that old and young trees have a strongly differentiated dynamics is certainly not acceptable.

A formal proof of these properties would require to analyze the mechanisms by which the limit cycle eventually shrinks and disappears when ε and δ increase. An analysis of this type is easy to be performed for the classical two-dimensional predator-prey model with saturating functional response since the conditions on the parameters a_i that one obtains by means of the singular perturbation method (Muratori and Rinaldi, 1989a) coincide with the necessary and sufficient conditions for the existence (and actually uniqueness) of the cycle. This means that in such a case the time scale factor ε is completely irrelevant.

For third order predator-prey systems an analysis of this kind has only been performed by means of extensive simulations. In particular, in the one prey-two predators system considered by Hsu *et al.* (1978), the time scale parameter seems to be uninfluencial for the existence of the limit cycle (Muratori and Rinaldi, 1989a), while for a three-dimensional food chain system Muratori and Rinaldi (1990b) have proved that for increasing values of ε the cycle disappears through a Hopf bifurcation. This is not a surprise, since Hopf bifurcations are quite frequent in predator-prey models of any type (see, for instance, Butler and Waltman (1981) and Muratori and Rinaldi (1989b, c, d)).

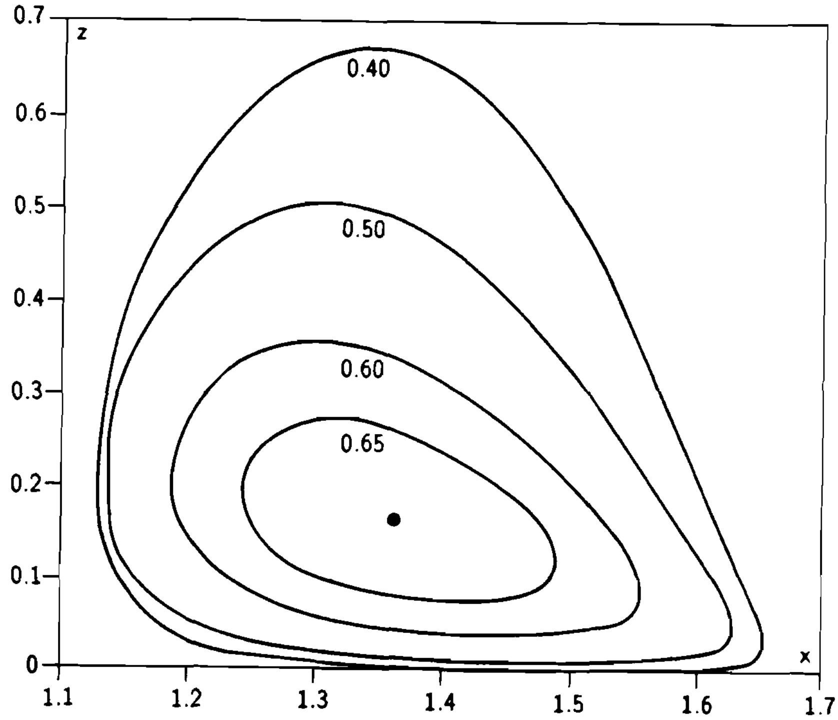

Figure 6. Family of limit cycles for different values of $\varepsilon = \delta$. Parameters a_i are as in Figure 5.

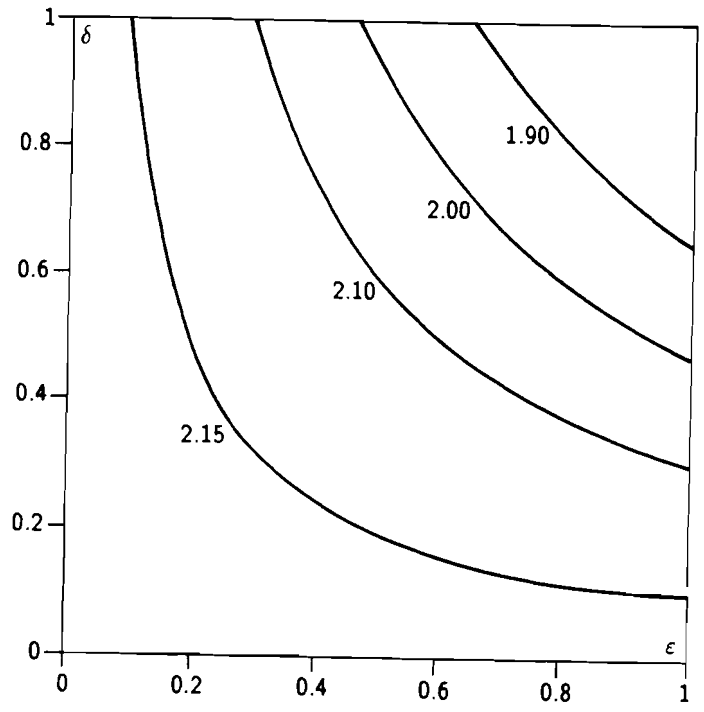

Figure 7. Families of parameter values that give rise to Hopf bifurcations in system (1). The value identifying each curve is that a_{11}. All other parameters are as in Figure 5.

In the present case, the simulations have clearly indicated that limit cycles are sensitive to ε and δ and that they disappear through a Hopf bifurcation when these parameters increase. Figure 6 reports a typical example: the projection on the (x, z) plane of the cycle of system (1) for the numerical values of the parameters indicated above (see also caption of Figure 5) and for four different values of $\varepsilon = \delta$. The Hopf bifurcation is obtained for $\varepsilon = \delta = 0.68$ so that cycles exist in this system for $\varepsilon\delta < 0.46$, a very satisfactory result. Moreover, the numerical analysis of the Hopf bifurcations has produced the graphs of Figure 7 where on each curve we have reported the numerical value of a_{11} (the value $a_{11} = 2$ is the one used for producing Figures 5 and 6). All values of ε and δ below a curve associated to a particular value of a_{11} guarantee the existence of the limit cycle for that value of a_{11}. From the figure one can immediately check that the condition that $\varepsilon\delta$ is in the range 0.01 - 0.05 is definitely satisfied. Moreover, the curves of Figure 7 are (or are very similar to) hyperbola $\varepsilon\delta =$ const. This means that the value of ε is actually irrelevant and that the only important parameter is $\varepsilon\delta$ which is the time scale factor of insect pest with respect to old trees.

4. CONCLUDING REMARKS

In this paper we have proved that age-structured forest-pest models can exhibit limit cycles even when the insect pest is adapted only to old trees. This is in contrast with the recent findings of Antonovsky *et al.* (1990), but it is in agreement with the evidence in the data on balsam fir forests of Eastern North America which have experienced periodic outbreaks of spruce budworms. Our model and analysis have a number of common features with the study of Ludwig *et al.* (1978): the insect pest has a density dependent mortality and is kept under control by insectivores (birds in the case of spruce budworms) and the growth of trees is assumed to be much slower than that of the insect pest. On the contrary, the structure of our model is much more similar to that of Antonovsky *et al.* (1990) because we use young and old trees as state variables as opposed to foliage and wood as done by Ludwig *et al.* (1978).

The method of analysis is purely geometric and based on singular perturbation arguments. It is an extension of a known method used to study relaxation oscillations in second order systems and has already been applied by the authors to detect limit cycles in predator-prey models (Muratori and Rinaldi, 1989a, 1990b). The method allows one to determine explicit conditions on the parameters (see (3-12)) that guarantee the existence of a limit cycle in the case the insect pest has an infinitely faster dynamics than that of the trees. Nevertheless, extensive simulation has proved that the limit cycle is preserved under reasonable perturbations of the time scaling factors.

An interesting feature of our analysis, which perfectly fits with the observations on balsam fir forests, is that the limit cycle is composed by two slow and two fast alternate transitions. When insect pests are only endhemically present in the forest, old and young trees grow slowly for a long period until they reach a biomass at which the mechanisms that keep the pest under control are overcome. Thus, in a very short time, we have an insect outbreak, followed by a second long period during which tree biomass slowly decays. As a consequence, pest population also decreases smoothly until it reaches a density at which its mortality mechanisms destabilise it. Then, the pest population very quickly collapses to zero.

Finally, it is worthwhile noticing that conditions (3-12) can be given interesting biological interpretations. Inequality (3), for example, says that the efficiency a_{13} of the insect pest must by high as it is usually the case in second-order oscillatory prey-predator models with saturating functional response. Condition (4), on the contrary, says that at low insect density z the surplus $a_{10}z$ of mortality due to intraspecific competition must be smaller than the decrease of mortality $a_{11}z/a_{12}^2$ due to predation by birds, a condition which is often satisfied in practice and gives rise to multiple stable equilbria in the insect-pest dynamics. Therefore, the analysis carried out in this paper proves, once more, that the saturating functional response of the predators (insect pests and birds) is a key feature for the existence of limit cycles in complex communities.

APPENDIX

Aim of this Appendix is to prove that inequalities (3), (4), (5) and (6) in the text guarantee that the geometry of the manifolds $f = 0$, $g = 0$, and $h = 0$ is like in Figures 1 - 4.

Manifold $h = 0$.

Let us first prove that (3) and (4) imply that the manifold $h = 0$ is like in Figures 1-4. For this, let us first considier the non-trivial part of the manifold $h = 0$ (see (1c)), i.e.

$$a_9 + a_{10}z + \frac{a_{11}}{a_{12} + z} = a_{13}\frac{x}{a_4 + x} \tag{13}$$

Equation (13) defines a surface $x = \varphi(z)$ parallel to the y axis that intersects the (x, y) plane at (see also (11))

$$x_B = \varphi(0) = \frac{a_9 + \dfrac{a_{11}}{a_{12}}}{a_{13} - a_9 - \dfrac{a_{11}}{a_{12}}} a_4$$

Therefore, condition (3) implies $x_B > 0$ as in Figure 1. On the other hand, letting $x = \varphi(z)$ in (13) and derivating with respect to z one obtains

$$a_{10} - \frac{a_{11}}{(a_{12} + z)^2} = a_{13}\frac{a_4}{(a_4 + x)^2}\frac{d\varphi}{dx}$$

so that condition (4) implies $d\varphi/dx < 0$ for $z = 0$. Thus, the manifold $h = 0$ is shaped as in Figure 1, i.e. the function $x = \varphi(z)$ has a minimum at point A'. The coordinate of this point is therefore given by

$$z_{A'} = \sqrt{\frac{a_{11}}{a_{10}}} - a_{12} \tag{14}$$

while its x coordinate is (see also (9))

$$x_{A'} = x_A = \varphi(z_{A'}) = a_4\frac{a_9 + 2\sqrt{a_{10}a_{11}} - a_{10}a_{12}}{a_{13} - a_9 - 2\sqrt{a_{10}a_{11}} + a_{10}a_{12}}$$

Manifold $g = 0$.

The manifold $g = 0$ is a surface parallel to the z axis given by (see (1b))

$$y = \frac{a_5 x}{a_1 + a_6(x - a_7)^2 + a_8} \tag{15}$$

Thus, $y > 0$ for $x > 0$ and $\partial y/\partial x > 0$ for $x = 0$ so that the manifold is like in Figure 2-4. Moreover, $\partial g/\partial y < 0$ for all positive values of x and of the parameters, so that the equilibria of the "intermediate system" ((2b)) with x frozen) are always stable.

The intersection of the manifold $g = 0$ with the manifold $h = 0$ (see line $BDCP$ of Figure 2) is therefore characterized by values of y_A and y_B as in (10) and (12).

Manifold $f = 0$.

The manifold $f = 0$ is given by (see (1a))

$$y = \rho(x,z) = \frac{a_2}{a_1}x + \frac{a_3}{a_1}\frac{x}{a_4 + x}z$$

Since $\rho(x,z)$ is increasing with x and z, and y increases from D to C along line DP of Figure 2, the manifold $y = \rho(x,z)$ is certainly below the line segment CD of Figure 2 if

$$\rho(x_D, z_D) > y_C. \tag{16}$$

But $y_C = y_B$, $x_D = x_A$, and $z_D = z_{A'}$, so that from (12), (9), and (14) it follows that (16) is equivalent to (6) and (8).

On the other hand, we can prove that (5) and (7) imply that the manifold $f = 0$ is above the line segment AB of Figure 2. In fact, the ratio y/x along line $0B$ is given by (see (15))

$$\frac{y}{x} = \frac{a_5}{a_1 + a_6(x - a_7)^2 + a_8} \tag{17}$$

and is therefore a unimodal function of x with maximum at $x = a_7$. But the intersection of the manifold $f = 0$ with the (x,y) plane is given by the straight line

$$y = \rho(x,0) = \frac{a_2}{a_1}x \tag{18}$$

so that (5) and (7) imply that the straight line (18) in the plane (x,y) is below the two points (x_A, y_A), (x_B, y_B) and hence below the line segment AB because of the above unimodality property.

Thus, the manifold $y = \rho(x,z)$ separates the line segment AB from the line segment CD.

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