**International Institute for
Applied Systems Analysis
www.iiasa.ac.at**

Recurrent and synchronous insect pest outbreaks in forests

Rinaldi, S.

IIASA Interim Report
2012

Interim Report　　　　　　　　　　**IR-12-059**

Recurrent and synchronous insect pest outbreaks in forests

Sergio Rinaldi (rinaldi@iiasa.ac.at)

Approved by

Ulf Dieckmann
Director, Evolution and Ecology Program

February 2015

RECURRENT AND SYNCHRONOUS INSECT PEST OUTBREAKS IN FORESTS

Sergio Rinaldi[a,*]

[a]*DEI, Politecnico di Milano, Via Ponzio 34/5,20133 Milano, Italy
ph. -39-02-23993563 fax.-39-02-23993412*

[*]EEP, International Institute for Applied Systems Analysis, Laxenburg, Austria
Email address: `rinaldi@elet.polimi.it` (Sergio Rinaldi)

Abstract

The simplest model of plant-insect interactions available in the literature is used to discuss periodicity and synchrony of insect outbreaks in forests. The novelty of the paper is that we present through various formulas and a circular graph a comprehensive theory and show that many, if not all, properties of insect outbreaks pointed out in the past by looking at specific data sets could have been predicted from our theory. In line with the tradition of classical ecology all results are derived without resorting to computer simulation.

Keywords: Outbreaks, Synchronization, Insect, Forest, Cycles

1. Introduction

Observed and documented insect outbreaks are certainly a few hundreds (more than 120, with the first one occurring in 1932, are reported in Myers (1998)). They differ for the species involved, for the spatial extension and for the characteristics of the environment in which they occur. Some outbreaks are impressive and involve variations of insect density from 1 to 10000 (or more), like in the case of larch budmoth (*Zeiraphera diniana*) in the Oberengadin Valley (Baltensweiler, 1989). Sometimes the outbreaks are triggered by the occurrence of quite peculiar random exogenous factors (Berryman, 1996; Jones et al., 1998; Myers, 1998; Liebhold et al., 2000; Selas et al., 2004; Johnson et al., 2005) in areas with susceptible forest stands and then eventually propagate to other areas ("epicentre hypotheses" Hardy et al. (1983)), giving rise to recurrent mosaics of infestation. By contrast , in other cases, the outbreaks are due to endogenous density-dependent mechanisms and are therefore periodic or almost periodic. The very regular cycle of larch budmoth in the Oberengadin Valley (Baltensweiler, 1989) is the best known example of periodic infestation regime. The estimated periodicities vary from 8-12 yr for larch budmoth,*Zeiraphera diniana*, (Baltensweiler, 1989), western tent caterpillars, *Malacosoma californicum pluviale*, (Myers, 1990), and gypsy moth, *Lymantria dispar*, (Johnson et al., 2005), to 30-35 yr for spruce budworm, *Choristoneura fumiferana*, (Williams and Liebhold, 2000).

The impacts of introductions and removals of insects on outbreaks (see Berryman (1996) for a review) have been studied through field experiments by various authors. The results are not very impressive but point out that an introduction (removal) of insects, performed when the forest is scarcely populated, accelerates (delays) the next outbreak.

After the investigations of recurrent insect pest outbreaks in many forests around the world, the attention has shifted toward outbreak synchronization (Barbour, 1990; Myers, 1988; Hawkins and Holyoak, 1998; Liebhold and A. Kamata, 2000; Williams and Liebhold, 2000; Peltonen et al., 2002; Selas et al., 2004; Raimondo et al., 2004; Johnson et al., 2005) and, more recently, toward waves of outbreaks over large areas (Williams and Liebhold, 2000; Bjorstad et al., 2002; Johnson et al., 2004; Tenow et al., 2007). On the basis of the available information it seems that synchronization is ubiquitous, in particular when outbreaks are of remarkable intensity, *i.e.*, when they concern those insects that are called pests.

The scientific debate has been mainly concentrated on the causes of synchronization which, in agreement with the general theory, can be the presence of suitable environmental shocks perturbing in unison the various sites of a spatially extended forest (Moran effect) or insect dispersal among neighboring sites. The presence of both mechanisms has been ascertained from the available data. The Moran effect is obviously essential in all cases in which the outbreaks are exogenously triggered, but dispersal is present in the cases that can be described with the epicenter hypotheses. The conclusion of this debate (see, for instance, Williams and Liebhold (2000), for spruce budworm, and Johnson et al. (2005) for gypsy moth) is that the two mechanisms are usually copresent but have different roles: spatially correlated weather anomalies (detectable up to one or more thousands kilometers) can facilitate insect synchronization at continental scale, while dispersal can produce east-west or north-south synchronization patterns.

The aim of this paper is quite ambitious, namely show how the characteristics of insect outbreaks can be derived through the analysis of a simple analytically tractable model. Since the structure of the selected model fits with the characteristics of a specific class of forests (logistic vegetational growth, saturating functional response of the insects, intraspecific competition among insects, and saturating functional response of generalist insect enemies), the obtained results are, in principle, only guaranteed for that class. However, as we will see, the results are in very good agreement with all field data reported in the literature on triggered insect outbreaks and their synchrony.

2. Minimal models

The method of investigation followed in this paper needs that the bifurcation analysis of the model has been already accomplished, a task that usually requires an entire paper. In order to avoid this part and focus immediately on synchronization, the model used in the paper is selected among the very few for which the bifurcations

are already known. This means that the model can certainly not describe the details of insect outbreaks in all kind of forests of the world, but can allow one to perform, for the very first time, a complete theoretical analysis of the synchronization of insect outbreaks in a specific class of forests.

The models proposed in the literature for studying insect pest outbreaks in forests are many and involve, in general, segments of the food chain starting with the tree, continuing with the insect and ending with insectivores or with parasitoids and their pathogens (Berryman et al., 1987; Berryman, 1996). In order to emphasize the role of diversified time scales we focus here on tree-insect interactions taking however into account, in a naive way (we admit), insect enemies (small mammals, birds, and/or parasitoids). There are a number of models of this sort with a more or less detailed description of the vegetational and insect compartments. The vegetational compartment has been described with five variables, namely organic carbon and nitrogen contained in the foliage and in the soil and inorganic nitrogen contained in the soil in Gragnani et al. (1998), but more often with only two variables namely wood and foliage (Ludwig et al., 1978; Ledder, 2007), adult and young trees (Antonovsky et al., 1990; Muratori and Rinaldi, 1992), foliage and maternal effect (Ginzburg and Taneyhill, 1994), foliage and energy (Strogatz, 1994). In the most extreme cases the vegetational compartment has been described with a single variable, say biomass of the host tree species (Berryman et al., 1987; Muratori and Rinaldi, 1989) or with foliage quality, because it has been noticed that heavy defoliation can cause marked changes in the quality of new foliage in the following years (Baltensweiler and Fischlin, 1988). Similar considerations hold for the insect which should, for example, be described by four variables (eggs, larvae, pupae, and adults) in the case one likes to include in the model strategic details on the interactions with insect enemies. In principle, all these simple models could a priori be considered as equally good candidates for studying recurrent and synchronous insect pest outbreaks in forests. However, if we are interested in deriving a formal theory that explains the main properties of insect outbreaks, we are forced to avoid numerical analysis and use very simple models that can be studied analytically. Since, in practice, only models with two variables (tree and insect), enjoy this remarkable property, our choice is limited to the three models in which the vegetational compartment is described with a single variable. Among these three we have selected the model by Muratori and Rinaldi (1989) because it has been shown to mimic rather well the behaviour of more complex models (Gragnani et al., 1998) and its bifurcations are already known. The

model is

$$\dot{x} = rx\left(1 - \frac{x}{K}\right) - a\frac{x}{b+x}y \tag{1}$$

$$\dot{y} = c^*\frac{x}{b+x}y - d^*y - e^*y^2 - z^*\frac{y}{f+y} \tag{2}$$

where x and y are trees and insects, r and K are net growth rate and carrying capacity of the trees, a is maximum insect consumption rate, b is half-saturation constant of insect functional response, c^* is the tree\insect conversion factor, d^* is basic insect mortality, e^* is insect intraspecific competition, z^* is predation pressure of insect enemies (assumed constant) and f is the half-saturation constant of their functional response, *i.e*, the density of the insects at which the damages produced by their enemies is half maximum. For $z^* = 0$, i.e. in the absence of insect enemies, the model degenerates into the prey-predator model first studied by Bazykin (1998). The parameters with a star in eq. (2) are assumed to be large and can therefore be written as

$$c^* = \frac{c}{\varepsilon} \quad d^* = \frac{d}{\varepsilon} \quad e^* = \frac{e}{\varepsilon} \quad z^* = \frac{z}{\varepsilon}$$

with ε positive and small, so that model (1,2) can be given the standard form of slow-fast systems (Muratori and Rinaldi, 1992; Rinaldi and Scheffer, 2000)

$$\dot{x} = xf(x,y) \tag{3}$$

$$\varepsilon\dot{y} = yg(x,y) \tag{4}$$

with

$$f(x,y) = r(1 - \frac{x}{K}) - a\frac{y}{b+x} \qquad g(x,y) = \frac{cx}{b+x} - d - ey - \frac{z}{f+y} \tag{5}$$

When tree and insect densities are generic, *i.e*, when (x,y) is not too close to the trivial insect isocline $y = 0$ or to the non-trivial insect isocline $g(x,y) = 0$, then the rate of change of the insect population is very high because $|\dot{y}| = y|g(x,y)|/\varepsilon$. In other words, the insect density varies quickly when the state of the system is far from the insect isoclines and slowly in the opposite case, namely when the system evolves along the insect isoclines.

In the Concluding Remarks, the possibility of relaxing some of the biological assumptions supporting model (3–5) is discussed. In particular, in line with Turchin (2003), the cases of generalist (i.e. constant) insect enemies with type III functional response and of specialist insect enemies are considered in some detail.

3. Endogenously vs exogenously generated outbreaks

In this section we show that model (3–5) suggests that insect outbreaks can be endogenously generated in some forests, while in other forests they can only be triggered by exogenous factors.

Model (3–5) can have many different modes of behavior depending upon the values of the parameters (the interested reader can find all details in Muratori and Rinaldi (1989)). However, only two of these modes are relevant for our discussion. They correspond to the two slightly different geometries of the non-trivial tree and insect isoclines qualitatively sketched in Fig. 1. In the following we will say that a forest is of type A if its isoclines are as in Fig. 1-(a) and of type B when its isoclines are as in Fib. 1-(b). The non-trivial tree isocline $f = 0$ is a parabola that intersects the x axis at the tree carrying capacity K,while the insect isocline $g = 0$ is a more complex curve that intersects the x axis at point

$$x_0 = b\frac{df + z}{cf - df - z} \tag{6}$$

and tends for very high tree density to a high insect density $\bar{y}$ satisfying the equation

$$c - d - e\bar{y} - \frac{z}{f + \bar{y}} = 0 \tag{7}$$

Notice that $x_0 < K$ in forest of type A, while $x_0 > K$ in forests of type B. From (6) it follows that a forest of type A can become of type B if the pressure z exerted on
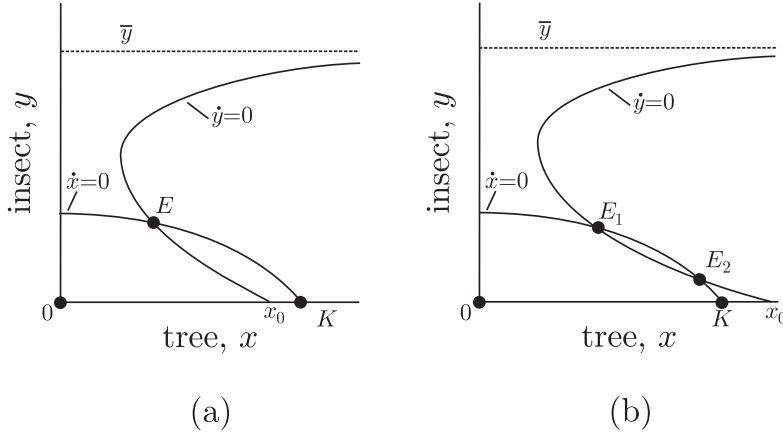

Figure 1: Non-trivial tree and insect isoclines of model (3-5): (a) type A forest characterized by $x_0 < K$ and by a single non-trivial equilibrium; (b) type B forest characterized by $x_0 > K$ and by two non-trivial equilibria.
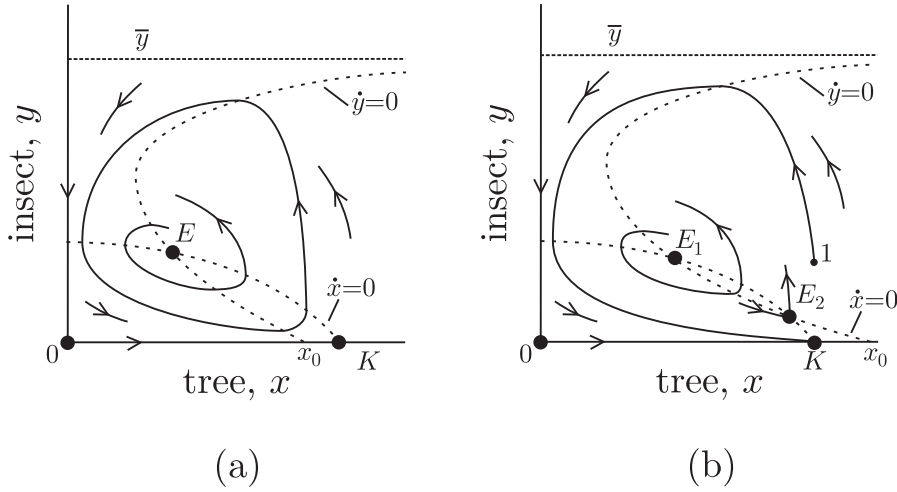
Figure 2: State portraits of model (3-5): (a) type A forests have endogenously generated periodic insect outbreaks; (b) type B forests have no insects at equilibrium but can have triggered insect outbreaks (see trajectory starting from point 1).

the insects by their enemies increases, while from eq. (7) it follows (through a little bit of algebra) that the same perturbation would lower the highest insect density $\bar{y}$ if $z/f < (c-d)$, *i.e*, if insects can invade the forest when tree density is very high.

Using standard arguments of the theory of dynamical systems (Strogatz, 1994) one can prove that in a forest of type A (see Fig. 1-(a)) the equilibrium $(K, 0)$ is a saddle, while the equilibrium point E (intersection of the two non-trivial isoclines) is unstable and surrounded by a limit cycle, so that the state portrait is, qualitatively speaking, like in Fig. 2-(a). By contrast, in a forest of type B there is no cycle (provided x_0 is not too close to K) and the two positive equilibria E_1 and E_2 are an unstable focus and a saddle, respectively, while the trivial equilibrium $(K, 0)$ is stable, so that the state portrait is like in Fig. 2-(b).

The most striking feature of Fig. 2 is that the long term behavior of the model is radically different in the two forests. In fact, in a forest of type A the attractor is a limit cycle along which the insect population has periodic outbreaks, while in a forest of type B the attractor is an equilibrium (point $(K, 0)$) characterized by the absence of insects. Thus, in forests of type A recurrent insect outbreaks are endogenously generated and hence guaranteed like in the case of budworm (Williams and Liebhold, 2000), while in forest of type B insect outbreaks can only be generated by strategic exogenous factors. In fact, if in a forest of type B trees are at their carrying capacity (or close to it) and insects are practically absent, an injection of a mass of insects, due

to migration from a nearby infested forest site, can perturb the state of the system from the equilibrium $(K, 0)$ to point 1 of Fig. 2-(b), thus triggering an insect outbreak as first noticed in Berryman et al. (1987). This is, in principle, an isolated outbreak since after a long transient the system returns to the equilibrium $(K, 0)$. This does not mean, however, that there cannot be in the future new insect migrations from infested forests or other perturbations that trigger new outbreaks like, most likely, in the case of gypsy moth (Johnson et al., 2005). The time intervals separating these exogenously generated outbreaks can be quite variable but not shorter than the time needed by the forest to come back to the equilibrium $(K, 0)$ after a perturbation.

Many exogenous factors observed in the field have been considered as potential instigators of insect outbreaks. Interestingly, all of them find a theoretical support in Fig. 2. Assume, in fact, that a forest of type B is at equilibrium (or not too far from it) and imagine that a change occurs in the forest and that this change can be interpreted as an increase of parameter c or as a decrease of one of the parameters b, d, z in eq. (6). If the perturbation is sufficiently strong it follows from (6) that $x_0 < K$ after the perturbation so that the forest of type B has been transformed by the perturbation into a forest of type A. This means that after the perturbation the insect population increases along a trajectory of Fig. 2-(a) starting close to point $(K, 0)$. Thus, insects increase and if they become sufficiently abundant (while trees are still close to their carrying capacity) the outbreak becomes inevitable even if after sometime the perturbation ceases and the forest becomes again of type B. The mechanisms reported in the literature as possible causes of triggered insect outbreaks are many. Here is a list in which the corresponding parameter perturbation is an increase of parameter c or a decrease of one of the parameters b, d, z in eq. (6).

- *Unusual Springs* (Myers, 1998). Particular weather conditions in Spring enhance synchronization of egg hatch and leaf development, thus giving rise to an increase in fertility. This means that the parameter c increases

- *Sunspot troughs* (Myers, 1998; Selas et al., 2004; Johnson et al., 2005). In a period of low sunspot activity, surface ultraviolet B radiation is high so that the production of protective phenolics increases at the expense of production of chemicals for herbivore resistance so that the half-saturation constant b decreases

- *Acidic deposition* (Gragnani et al., 1998). Acid rain can damage leaves which can then be more easily attacked by insects. This means that the half-saturation constant b decreases.

- *Windfall events* (Okland and Bjornstad, 2003). Large windfall events can drastically favour the survival of the bark beetle in spruce forests. This means that the death rate d decreases.

- *Interruption of the use of pesticides* (Myers, 1988). The interruption of the use of pesticides reduces insect mortality d.

- *Failure of mast abundance* (Jones et al., 1998; Liebhold et al., 2000; Johnson et al., 2005). Failure of mast abundance implies a surplus of death rate of small mammals during the winter. This can be interpreted as a decrease of z.

- *Phathogen-parasitoids interactions* (Berryman, 1996). An increase of pathogens can reduce the density and efficiency of parasitoids, *i.e*, the parameter z.

4. Effects of introductions and removals of insects

The aim of this section is to identify from model (3–5) the possible effects of introductions of insects due to migrations from nearby infested forests and of removals of insects due to spreading of pesticides.

Let us start with the case in which the introduction or removal occurs when insects are scarce and assume that the forest is of type A. In such a case, the trajectories are very dense close to the x axis and evolve smoothly to the right, as sketched in Fig. 3. In other words, trees grow slowly and are basically unaffected by insects which are very scarce. However, when tree density passes the threshold x_0, the insect population starts growing at the rate given by (4), *i.e.*, $\dot{y} = (y/\varepsilon)g(x, y)$. This means that until y remains small (*i.e.*, order ε or smaller) insect growth remains under control, but when y finally becomes larger than ε then $\dot{y}$ becomes quickly very large, *i.e*, there is an insect outbreak.

Figure 3 says that introductions of insects occurring when trees are at densities $x_{in} < x_0$ (see points $0'$ and $0''$ in Fig. 3-(a)) are followed by a long phase of low density of insects which is finally interrupted by an outbreak occurring when trees are at a density $x_{out} > x_0$ (see points $4'$ and $4''$ in Fig. 3-(a)). The input-output function

$$x_{out} = \psi(x_{in}) \tag{8}$$

shown in Fig. 3-(b) is derived in Appendix Appendix A under the assumption of very diversified insect and vegetational growths.

Figure 3 points out an obvious but interesting consequence of insect introductions. Assume that the system evolves along the trajectory $0'$ $1'$ $2'$... but that at point $2'$
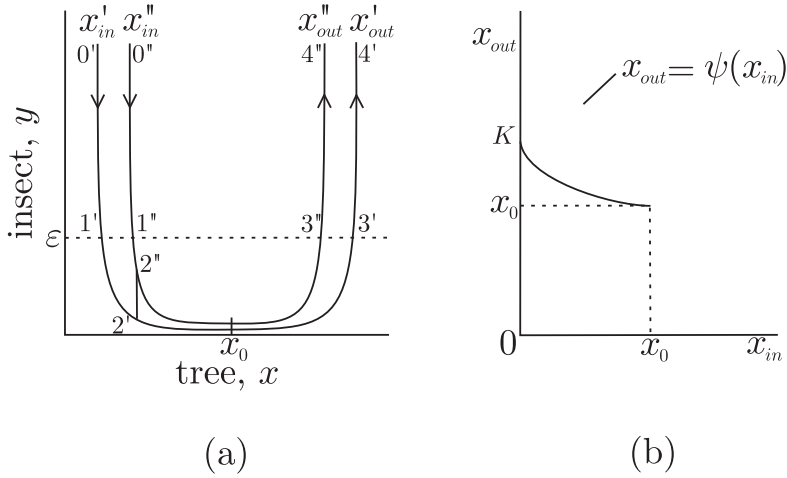
Figure 3: Type A forests: (a) evolution when insects are almost absent; (b) the input-output function $x_{out} = \psi(x_{in})$ derived in Appendix A.

a mass of insects is suddenly introduced. This corresponds to an instantaneous jump from point $2'$ to point $2''$ in the system state which then evolves along the trajectory $2''$ $3''$ $4''$... Thus, the final result is that the insect outbreak is accelerated because it occurs when trees reach the density x''_{out} which is lower than x'_{out}. This phenomenon has been observed (Auer et al., 1981) in the French Alps. Indeed, after the introduction of 35000 larch budmoth (*Zeiraphera diniana*) pupae in an area of 650 ha where the population had declined 2yr previously, the insect outbreak began 1 yr earlier than in control areas (however, similar attempts to cause premature outbreaks of western tent caterpillar (*Malacosoma californicum pluviale*), by introducing eggs into two islands, were not so successful (Myers, 1990).

The effect of an insect removal can also be deduced from Fig. 3. One has only to imagine to evolve along the trajectory starting from point $0''$ and to remove part of the insects at point $2''$, thus switching to point $2'$. The consequence is a delay in the insect outbreak which occurs when trees reach the density x'_{out} which is higher than x'''_{out}. Also this phenomenon has been observed by Auer and coworkers.

Let us now assume that the introduction or removal of insects occurs when insects are very abundant. Thus, y is very high in (4) so that $\dot{y}$ is also very high, unless y is very close to the insect non-trivial isocline $g(x, y) = 0$. This means that the system slowly evolves along the isocline $g = 0$ and that deviations from it due to introductions or removals of insects are very quickly compensated and have no consequences on the future behavior of the forest. Also this robustness to introductions and removals of insects has been observed in the field (Auer et al., 1981; Myers,

1990).

5. Synchronization of outbreaks

We show in this section that model (3–5) implies that synchronization is practically guaranteed when outbreaks are of remarkable intensity.

We first analyze forests of type *A, i.e.*, forests with endogenously generated outbreaks. Moreover, in order to simplify the discussion, we start with the case of a forest composed of two identical but separated sites. If the sites are not coupled through insect dispersal, then they behave on the same limit cycle but remain out-of-phase. In other words, the insect outbreaks in the two sites are always separated by τ units of time. As far as dispersal is concerned, we can say that insect dispersal varies noticeably with the species (den Boer, 1990) but at least for some of them it is really remarkable. Greenbank et al. (1980) report, for example, that spruce budworm, *Choristoneura fumiferana*, is a strong disperser: females frequently emigrate in mass flights in which they are carried by wind currents at about 40 km/hr and typical night flights may carry moths hundreds of kilometers. It is therefore justified to assume that migration is a blinking process (Belykh et al., 2004), *i.e.*, that migration episodes are due to rare and short particular meteorological conditions which, however, occur relatively frequently during each outbreak cycle (which has a period of the order of decades). The assumption of blinking dispersal not only is realistic in many cases, but, as shown in the following, it allows one to discuss synchronization very effectively.

In order to find an explicit condition for synchronization we imagine, once more, that the insect compartment is much faster than the vegetational one. When $\varepsilon \to 0$ the limit cycle of Fig. 2-(a) tends to the so called singular limit cycle, which is identified by the isoclines (Rinaldi and Scheffer, 2000). The singular limit cycle is shown in Fig. 4 and is composed of two slow and two fast phases:

  i A slow transition from A to B during which trees and insects decay at a comparable speed; this shows that insects decline before food shortage becomes an important factor, as observed long ago for blackheaded budworm (Morris, 1959; Miller, 1966)

 ii A fast transition from B to C during which the insect population collapses to zero (in practice, insect densities fall to very low values if ε is small) while tree abundance remains constant;

iii A slow transition from C to D during which insects are absent (almost absent if $\varepsilon > 0$) and trees grow logistically ($y = 0$ in (1));

iv A fast transition from D to A corresponding to an outbreak of the insect popu-
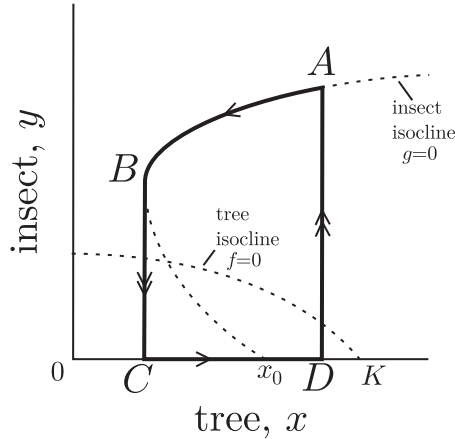lation.

Figure 4: The singular limit cycle ABCD of model (3-5) in the case of a type A forest (double
arrows indicate fast evolution).

While the singular limit cycle ABCD can be very easily derived from the model,
available field observations do not allow its full identification . There are various
reasons for this. First, one must keep in mind that the singular limit cycle is only an
approximation of the real cycle since insect dynamics are not infinitely faster than
vegetational dynamics. Second, data on vegetation are rarely available because the
variations of tree density along the cycle are often quite limited and therefore hardly
observable. Moreover, the insect density at point B is a few order of magnitude lower
than that at point A (typically in the sketch of Fig. 4 insect density is in logarithmic
scale) and the minimum insect density along the real cycle is small but not zero.
Thus, it is very difficult, if not impossible, to separate, using the data concerning
insect decline, the slow phase AB from the fast phase BC of the singular limit cycle.
This is why in the literature, the insect cycle is often divided only in three phases:
decline (AC in Fig. 4), absence (CD in Fig. 4), and outbreak (DA in Fig. 4).
Typically, the decline phase AC is shorter than the absence phase (for example 2-3
years against 6-8 years) but longer than the outbreak phase.

The $x-$coordinate of point B (and hence of point C), *i.e.*, the minimum tree
biomass x_{min} along the cycle, can be easily computed by writing the insect isocline
$g = 0$ in the form $x = x(y)$ and then by minimizing $x(y)$ with respect to y, thus

obtaining

$$x_{min} = b\frac{d + 2\sqrt{ez} - ef}{c - d - 2\sqrt{ez} + ef} \tag{9}$$

By contrast, the maximum tree biomass x_{max} along the cycle, *i.e.*, the coordinate of point D, can be obtained using the method described in the previous section. In fact, when trees grow in the absence of insects, point C where $x_{min} = x$ can be considered as a point of introduction of insects, while D is the point of the corresponding outbreak, so that (see eq.(8))

$$x_{max} = \psi(x_{min})$$

Let us then consider the effect of dispersal. If both sites are in the slow phase *(iii)*, migration can not be significant because the sites practically do not contain insects. On the other hand, if both sites are in the slow phase *(i)*, migration can be relevant but cannot have consequences since (see previous section) the introduction or removal of insects in a densely populated forest is immediately compensated. Thus, the only migrations that matter are those that transfer insects from a densely populated site to an empty site. In order to determine if these migrations can synchronize the outbreaks we restrict our attention to so-called local synchronization by assuming that the two sites are only slightly out-of-phase.

Assume then that both sites are in the slow phase *(i)* and delayed of τ units of time with τ small, as shown in panel 1 of Fig. 5. Then, follow the evolution of the two sites by looking clockwise at the 10 panels of Fig. 5 where the states of the two sites are identified with two different small circles. In the second and third panels the leading site is at the point where tree density is minimum, but in panel 2 there are still insects in the forest while in panel 3 the site is empty. Therefore the transition from panel 2 to panel 3 corresponds to the crash of the insects in the leading site. In the limit case $\varepsilon \to 0$, such a transition is instantaneous while in the field it is obviously soft. The same kind of transition is described by panels 5 and 6 for the other site. When the leading site is empty and the other not (panel 4) there are from time to time relevant injections of insects in the leading site due to migration episodes generated by special meteorological conditions. As we have seen in the previous section, each one of these introductions of insects accelerates the next outbreak in the leading site. If migration episodes are relatively frequent we can assume that the last introduction in the leading site occurs just before the insect crash in the other forest site, see panel 5. This determines uniquely the next outbreak of the leading site. In fact if x^* is the tree density of the leading site in panel 5 then $\psi^* = \psi(x^*)$ will be tree density at the outbreak as shown in panels 8 and 9 which indeed describe such an outbreak. Up to panel 9 the delay between the two sites is still τ . However, shortly after the leading site has become densely
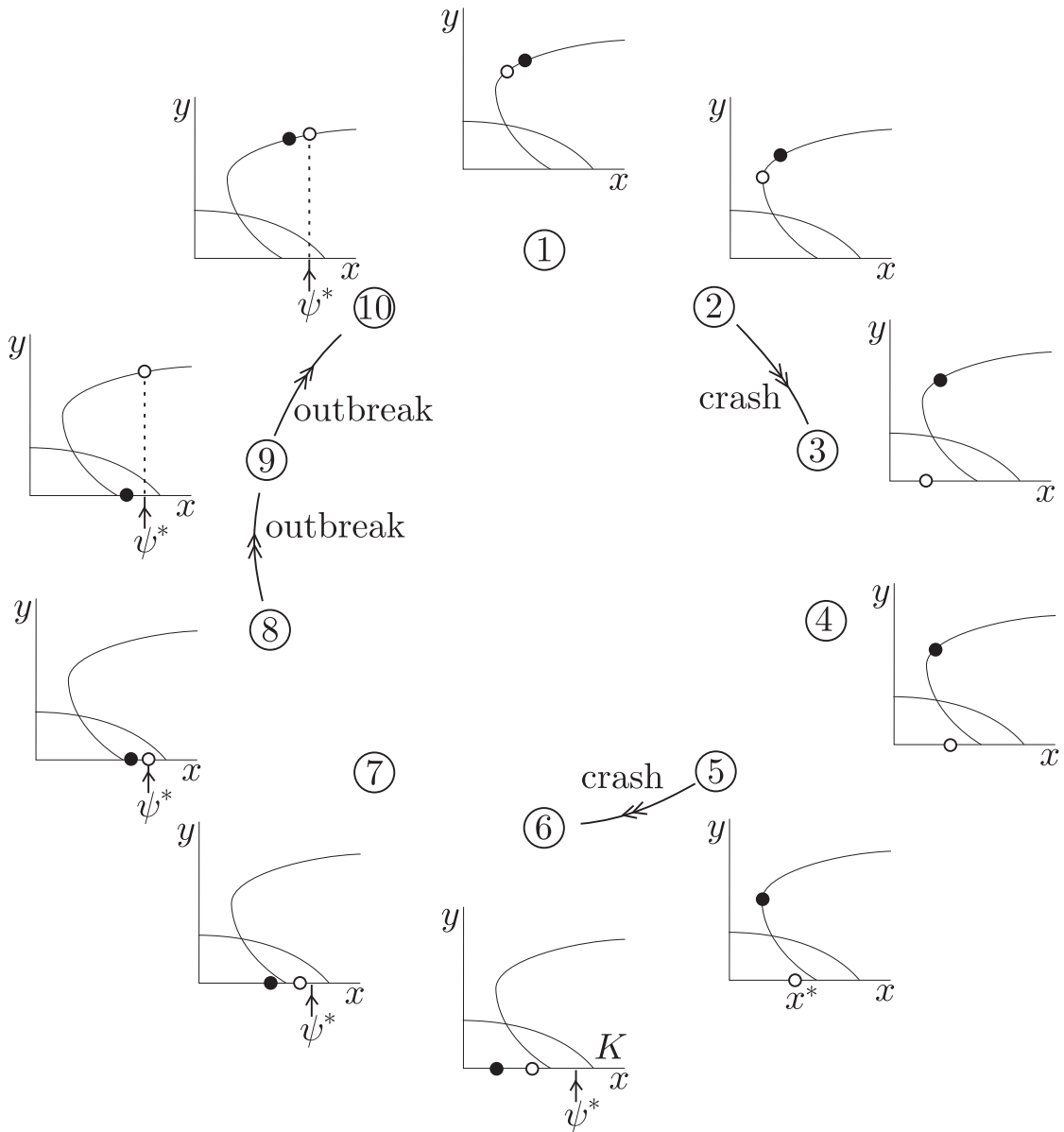
Figure 5: Circular cartoon. Synchronization of two identical sites (of a type A forest) connected through blinking dispersal. The states of the two sites are identified with two different small circles. The outbreak 9-10 is triggered by a transfer of insects from a densely populated site to an empty site. Notice that in panels 1 and 10 the leading sites are different.

populated of insects (panel 9) there is a transfer of insects to the empty site and this introduction, as explained in the previous section, immediately triggers an outbreak (see panel 10) because, τ being small, the tree density in the empty site of panel 9 is above the threshold x_0. The final result is that the two sites are again in the slow phase *(i)* but the delay between them is now $\tau' \neq \tau$ because there has been a triggered outbreak (notice that the delayed site is now the leading site).

Synchronization is therefore guaranteed if $\tau' < \tau$ and this condition is satisfied (see eq.(1)) if the tree decay rate just after an outbreak $(a\hat{y}/(b+\hat{x}) - r(1 - \hat{x}/K))$ is greater than the growth rate just before the outbreak $(r(1 - \hat{x}/K))$, *i.e.*,if

$$\frac{a\hat{y}}{b + \hat{x}} > 2r(1 - \frac{\hat{x}}{K}) \tag{10}$$

where $\hat{x}$ and $\hat{y}$ are insect and tree densities after the outbreak. In Appendix Appendix B it is shown that the synchronization condition (10) is satisfied when the insect is a so-called pest, i.e. when the outbreaks are violent. Finally, it is important to remark that the result we have obtained for two site forests, obviously holds true also for longer chains of forest sites, provided special meteorological conditions favoring insect migrations between pairs of contiguous sites are not extremely rare.

We have therefore shown that model (3–5) supports the conjecture mentioned at the beginning of this section, namely that greater are the outbreaks stronger is synchronization. We must recall, however, that our analysis has been limited up to now to chains of forest sites with endogenously generated outbreaks (type A forests). We must therefore still analyze the synchronization of spatially extended forests containing sites of type B in which the outbreaks can be triggered only by exogenous factors.

The simplest case is that of two nearby forest sites, one of type A and one of type B. In such a case, site a has periodic outbreaks while in site b insects are absent if there is no coupling. However, if special meteorological conditions favor migration, relevant masses of insects will be transferred from time to time from the densely populated site of type A to the empty site of type B in which sooner or later an outbreak will occur. Obviously, the same argument can be applied to chains of forest sites which will therefore synchronize provided there is one site of type A. In other words, a (master) site of type A with endogenously generated outbreaks, triggers outbreaks in the other (slave) sites of type B which therefore synchronize. Since the real outbreaks do not develop instaneously, as in our slow-fast model, there will be a certain delay between outbreaks at contiguous sites, giving rise to traveling waves of outbreaks, as those observed, for example, in Tenow et al. (2007).

The last case that we still need to analyze is that of a chain of forest sites exclusively of type B in which outbreaks do not occur spontaneously. As we have seen in

the third section, there is a long list of possible exogenous causes capable of triggering insect outbreaks in such forests. If the outbreak is triggered in one of the sites then insect migrations from that site have high chances to trigger outbreaks also in the contiguous empty sites, which in turn will trigger outbreaks in other contiguous sites, and so on. This means that there is the possibility that a single exogenously triggered outbreak entrains a synchronous outbreak in all sites. But if migrations are not sufficiently strong it might be that the entrainment does not concern all sites of the forest but only a few of them. Of course, after a sufficiently long period of time all sites return to the equilibrium $(K, 0)$ characterized by absence of insects and trees at carrying capacity, so that the conditions are settled for another exogenously triggered outbreak in one or more sites. This simple discussion supports the idea that spatially extended forests of type B where outbreaks do not spontaneously occur, might have synchronous recurrent insect outbreaks triggered from time to time at a specific (but different) site and then propagating to a number of neighborhood sites. This kind of synchronization, however, is weaker than the previous ones because it is neither periodic nor global. However, it fits with a fascinating characteristic of many recurrent outbreaks, namely the tendency of geographically separated populations of a species to remain in synchrony even when not all populations necessarily reach high densities in each cycle (Myers, 1988, 1998).

6. Concluding remarks

The simplest available model for the interactions of trees, insects and their enemies shows that there are two types of forests: type A where insect outbreaks are periodic and endogenously generated, and type B where outbreaks are triggered by exogenous factors and are, in general, recurrent but aperiodic. The condition specifying the type of the forest is easy to interpret and is in full agreement with a number of studies in which various phenomena triggering insect outbreaks have been identified. The observed consequences of introductions and removals of insects are also well predicted by the model. But, even more surprisingly, the model allows one to derive a simple and explicit condition for the synchronization of outbreaks in spatially extended forests. This condition is in general satisfied when the insect is a so-called pest, *i.e.*, when the outbreaks are violent. In the case of extended forests of type B the model also predicts the possibility of travelling waves of insect outbreaks.

The conclusion of this study is that the most important characteristics of insect outbreaks in forests (endogenous vs. exogenous, periodic vs. aperiodic, synchronous vs. asynchronous) seem to be the direct consequence of four basic features of the "tree-insect-insectivore" food chain, namely logistic vegetational growth, saturating

functional response of insect, intraspecific competition among insects, and saturating functional response of insect enemies.

While the method of analysis, combining very effectively the assumptions of slow-fast dynamics and blinking dispersal, is very general and has a promising potential, the specific results obtained on insect outbreaks in forests are of more limited value because they have been derived using a very simple model (Muratori and Rinaldi, 1989). In particular, in this model the insect enemies have a type II functional response and are assumed to be generalist (i.e. constant) while a more standard assumption (Turchin, 2003) would be to consider them either as generalists with a type III functional response or as specialists with a type II functional response.

Thus, there are two major extensions that should be considered for making the theory of insect outbreaks in forest more complete. The first, is to consider constant predators with type III functional response because this is a quite reasonable assumption although in some cases (e.g. birds and small mammals) generalist predators continue to encounter insects even when they are very rare and are therefore characterized by a type II functional response (Turchin, 2003). This first extension would require to perform the bifurcation analysis of a model similar to (1,2) but with type III functional response, which to our knowledge is not available. Then, after the bifurcation analysis has been performed, one could apply the methodology described in this paper, namely slow-fast analysis and blinking dispersal for deriving trough the circular cartoon the conditions for synchronization. In principle, this first extension should be possible with a reasonable effort.

By contrast, the extension to the case of a specialist predator is certainly more problematic. It requires to add to model (1,2) a third differential equation describing the dynamics of the specialist predator. This would transform the model into a genuine tritrophic food chain model (Hastings and Powell, 1991) that can have very complex behaviors (including chaos) for suitable values of its parameters (Kuznetsov et al., 2001). Of course the analysis simplifies if each population evolves at radically different speeds. Although there are a number of contributions along this line (Muratori, 1991; Rinaldi and Muratori, 1992; Muratori and Rinaldi, 1992; De Feo and Rinaldi, 1998; Mehidi, 2001; Deng, 2001, 2004; Brons and Kaasen, 2010) none of them fits with the present case. Moreover, the slow fast analysis can become quite sophisticated if the phenomenon known as "canard explosion" is involved (Deng, 2004; Brons and Kaasen, 2010). Thus it can be that this extension is difficult, if not impossible. We can however attenuate this negative conclusion through the following argument. Let us imagine that the extra differential equation for z contains a non negative parameter p through which we could control the variability of the dynamics of insect enemies. Then, for $p = 0$ the enemies would become constant and

the conclusions obtained in this paper would be valid. But, by continuity, the same conclusion would remain valid also for p small, i.e. for enemies that slightly vary over time. Then, for larger values of p the results could either continue to be valid or brake. But understanding in which case we are would require detailed simulations because it might easily be that the ridge separating the two cases strongly depends upon a lot of details. Thus, the conclusion is that the present analysis makes sense also for forests with specialist enemies, although it does not guarantee that in those forests synchronization of the insect outbreaks occurs exactly in the form discussed in the paper.

Other interesting extensions of the work presented in this study refer to the methodological aspect, in particular to the combined use of slow-fast analysis and blinking dispersal. Indeed the mix of this two ideas has produced the circular cartoon (described in Fig. 5) which is a powerful and transparent method of analysis of synchronization in spatially distributed ecosystems. The use of the circular cartoon is certainly not limited to the discussion (performed in this paper) of complete synchrony. For example, the cartoon could be used to derive (as suggested by one of the reviewers) explicit estimates of the blinking frequency that guarantee synchronization or to detect conditions under which two forest sites synchronize in antiphase.

References

Antonovsky, M., Fleming, R., Kuznetsov, Y. A., Clark, W., 1990. Forest - pest interaction dynamics: The simplest mathematical models. Theoretical Population Biology 37, 343–367.

Auer, C., Roques, A., Goussard, F., Charles, P., 1981. Effets de l'accroissement provoque du niveau de population de la tordeuse meleze Zeiraphera diniana Guenee (Lep., Tortricidae) au cours de la phase de regression dans un massif forestier du Brianconnais. Z.Angew. Entomol. 92, 286–303.

Baltensweiler, W., 1989. The folivore guild on larch (larix decidua) in the Alps, in forest insect guilds: Patterns of interaction with host trees. Tech. Rep. NE-153, US Forest Service, Dordrecht, The Netherlands.

Baltensweiler, W., Fischlin, A., 1988. The larch budmoth in the Alps. In: Berryman, A. (Ed.), Dynamics of Forest Insect Populations: Patterns, Causes, Implications. Plenum Press, Dordrecht, The Netherlands, pp. 331–351.

Barbour, D., 1990. Synchronous fluctuations in spatially separated populations of

cyclic forest insects. In: Watt, A., Leather, S., Unter, M., , Kidd, N. (Eds.), Population Dynamics of Forest Insects. Intercept Press, Andover, pp. 339–346.

Bazykin, A., 1998. Nonlinear Dynamics of Interacting Populations. World Scientific.

Belykh, V., Belykh, I., Hasler, M., 2004. Connection graph stability method for syncronized chaotic systems. Physica D 195, 159–187.

Berryman, A., 1996. What causes population cycles of forest Lepidoptera? Trends in Ecology & Evolution 11, 28–32.

Berryman, A., Stenseth, N., Isaev, A., 1987. Natural regulation of herbivorous forest insect populations. Oecologia 71, 174–184.

Bjorstad, O., Peltonen, M., Liebhold, A., Baltensweiler, W., 2002. Waves of larch budmoth outbreaks in the European Alps. Science 298, 1020–1023.

Brons, M., Kaasen, R., 2010. Canards and mixed-mode oscillations in a forest pest model. Theoretical Population Biology 77(4), 238–242.

De Feo, O., Rinaldi, S., 1998. Singular homoclinic bifurcations in tritrophic food chains. Mathematical Biosciences 148, 7–20.

Deng, B., 2001. Food chain chaos due to junction-fold point. Chaos 11, 514–525.

Deng, B., 2004. Food chain chaos with canard explosions. Chaos 14, 1083–1092.

Ginzburg, L., Taneyhill, D., 1994. Population cycles of forest Lepidoptera: a maternal effect hypothesis. Journal of Animal Ecology 63, 79–92.

Gragnani, A., Gatto, M., Rinaldi, S., 1998. Acidic deposition, plant pests, and the fate of forest ecosystems. Theoretical Population Biology 54, 257–269.

Greenbank, D., Schaefer, G., Rainey, F., 1980. Spruce budworm moth flight and dispersal: New understanding from canopy observations, radar, and aircraft. Memoirs of the Entomological Society of Canada 110, 1–49.

Hardy, Y., Lafond, A., Hamel, L., 1983. The epidemiology of the current spruce budworm outbreak in Quebec. Forest Science 29, 715–725.

Hastings, A., Powell, T., 1991. Chaos in a three species food chain. Ecology 72, 896–903.

Hawkins, B., Holyoak, M., 1998. Transcontinental crashes of insect populations? The American Naturalist 152, 480–484.

Johnson, D., Bjornstad, O., Liebhold, A., 2004. Landscape geometry and traveling waves in the larch budmoth. Ecology Letters 7, 967–974.

Johnson, D., Liebhold, A., Bjornstad, O., McManus, M., 2005. Circumpolar variation in periodicity and synchrony among gypsy moth populations. Journal of Animal Ecology 74, 882–892.

Jones, C., Ostfeld, R., Richard, M., Schauber, E., Wolff, J., 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279, 1023–1026.

Kuznetsov, Y., De Feo, O., Rinaldi, S., 2001. Belyakov homoclinic bifurcations in a tritrophic food chain model. SIAM Journal of Applied Mathematics 62, 462–487.

Ledder, G., 2007. Forest defoliation scenarios. Mathematical Biosciences and Engineering 4, 1–14.

Liebhold, A. Kamata, N., 2000. Are population cycles and spatial synchrony a universal characteristic of forest insect populations? Population Ecology 42, 205–209.

Liebhold, A., Elkinton, J., Williams, D., Muzika, R., 2000. What causes outbreaks of the gypsy moth in North America? Population Ecology 42, 257–266.

Ludwig, D., Jones, D., Holling, C., 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. Journal of Animal Ecology 47, 315–322.

Mehidi, N., 2001. A prey-predator-superpredator system. Journal of Biological Systems 9(3), 187–199.

Miller, C., 1966. The black-headed budworm in Eastern Canada. Canadian Entomologist 98, 592–613.

Morris, R., 1959. Single factor analysis in population dynamics. Ecology 40, 580–588.

Muratori, S., 1991. An application of the separation principle for detecting slow-fast limit-cycles in a 3-dimensional system. Applied Mathematics and Computation 43(1), 1–18.

Muratori, S., Rinaldi, S., 1989. Catastrophic bifurcations in a second-order dynamical system with application to acid rain and forest collapse. Applied Mathematical Modelling 13, 674–681.

Muratori, S., Rinaldi, S., 1992. Slow fast limit-cycles in predator prey models. Ecological Modelling 61(3-4), 287–308.

Myers, J., 1988. Can a general hypothesis explain population cycles in forest Lepidoptera? Advances in Ecological Research 18, 179–242.

Myers, J., 1990. Population cycles of western tent caterpillars: experimental introductions and synchrony of fluctuations. Ecology 71, 986–995.

Myers, J., 1998. Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. Ecology 79, 1111–1117.

Okland, B., Bjornstad, O., 2003. Synchrony and geographical variation of the spruce bark beetle (Ips typographus) during a non-epidemic period. Population Ecology 45, 213–219.

Peltonen, M., Liebhold, A., Bjornstad, O., Williams, D., 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83, 3120–3129.

Raimondo, S., Turcani, M., Patoeka, J., Liebhold, A., 2004. Interspecific synchrony among foliage-feeding forest Lepidoptera species and the potential role of generalist predators as synchronizing agents. Oikos 107, 462–470.

Rinaldi, S., Muratori, S., 1992. Limit cycles in slow-fast forest pest models. Theoretical Population Biology 41, 26–43.

Rinaldi, S., Scheffer, M., 2000. Geometric analysis of ecological models with slow and fast processes. Ecosystems 3, 507–521.

Selas, V., Hogstad, A., Kobro, S., Rafoss, T., 2004. Can sunspot activity and ultraviolet-B radiation explain cyclic outbreaks of forest moth pest species? Series B: Biological Sciences 271, 1897–1901.

Strogatz, S., 1994. Nonlinear Dynamics and Chaos. Addison Wesley, Reading, MA.

Tenow, O., Nilssen, A., Bylund, H., Hogstad, O., 2007. Waves and synchrony in Epirrita autumnata/Operophtera brumata outbreaks. I. Lagged synchrony: regionally, locally and among species. Journal of Animal Ecology 76, 258–268.

Turchin, P., 2003. Complex Population Dynamics: A Theoretical/Empirical Synthesis. Princeton University Press.

Williams, D., Liebhold, A., 2000. Spatial synchrony of spruce budworm outbreaks in Eastern North America. Ecology 81, 2753–2766.

Appendix A.

In this Appendix we derive the input-output function (8) reported in Fig. 3 by assuming that the insect growth is extremely high with respect to tree growth (*i.e.*, ε is very small). First, write eqs. (3,4) in the form

$$dt \quad = \quad \frac{dx}{xf(x,y)} \tag{A.1}$$

$$\varepsilon\frac{dy}{y} \quad = \quad g(x,y)dt. \tag{A.2}$$

Then integrate along the trajectory (see Fig. 3a from point (x_{in},ε) to point (x_{out},ε), and finally let $\varepsilon \to 0$, by substituting y with 0, thus obtaining

$$\int\limits_{x_{in}}^{x_{out}} \frac{g(x,0)}{xf(x,0)}dx = 0 \tag{A.3}$$

In general, eq. (A.3) cannot be solved analytically with respect to x_{out} so that the input-output function (8) cannot be derived in closed form. Equation (A.3) must therefore be solved numerically if one wants to derive the input-output function ψ. A typical graph of the function ψ is reported in Fig. 3b. Once x_{in} and x_{out} are known, the time $T_{i/o}$ separating the introduction of insects from their outbreak can be computed by integrating eq. (A.1) from x_{in} to x_{out} with $y = 0$, *i.e.*,

$$T_{i/o=} \int\limits_{x_{in}}^{x_{out}} \frac{1}{xf(x,0)}dx \tag{A.4}$$

Although eqs.(A.3,A.4) are very useful because they completely specify the consequences of insect introductions it is worth to remember that they are only approximate relationships since they virtually hold only for ε very small.

Appendix B.

Since after an outbreak the sites are close to point A in Fig. 4 and point A is, in turn, almost on the asymptote $y = \bar{y}$ of the tree isocline $g = 0$, we can approximate $\hat{x}$ in (10) with the maximum tree density x_{max} along the singular cycle and y_{max} with the insect density $\bar{y}$, thus obtaining the following compact synchronization condition

$$a\frac{\bar{y}}{b + x_{max}} > 2r(1 - \frac{x_{max}}{K}). \tag{B.1}$$

When using condition (B.1) we should take into account that $\bar{y}$ depends upon the parameters c, d, e, f and z (see eq.(7)) and that $x_{max} = \psi(x_{min})$ with x_{min} given by (9). However, condition (B.1) is already sufficient for our purposes. In fact, in many cases $\bar{y}$ is very high and x_{max} is close to tree carrying capacity K, so that condition (B.1) is obviously satisfied, in particular if the growth rate of the trees (r) is low. Another interesting remark is that condition (B.1) predicts stronger synchronization (*i.e.*, higher compressions from τ to τ') in forests with lower pressure of insectivores and/or parasitoids on insects because a decrease of z implies an increase of $\bar{y}$, while x_{max} varies only a little because it remains bounded between x_0 and K which, anyway, are not too different.