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### **Potential Turing instability and application to plant-insect models**

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# Potential Turing Instability and Application to Plant-insect Models

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## Abstract

We show in this paper that the analysis of diffusion-induced instability in spatially extended models can be performed by separating local dynamics from diffusion. This is possible not only in the case studied by Turing, namely models with two interacting variables, but also in the general case of three or more variables. The advantage of this decomposition, based on the notion of potential Turing instability, is illustrated through the analysis of two spatially extended plant-insect models.

*Key words:* Turing instability, diffusion-induced instability, prey-predator models, spatial pattern, plant-insect models.

# 1 Introduction

Spatially extended models can be described, under the assumption of diffusive dispersal, by a PDE of the form

$$\frac{\partial x}{\partial t} = f(x) + \varepsilon D \nabla^2 x \quad (1)$$

where  $x \in \mathbb{R}^n$  is the  $n$ -dimensional state vector depending upon time and space in a given domain of  $\mathbb{R}^2$ ,  $\varepsilon > 0$  is diffusion and  $D = \text{diag}(d_1, d_2, \dots, d_n)$  is a diagonal matrix, here called *dispersal profile*, characterized by  $0 \leq d_i \leq 1$ , and  $\sum_{i=1}^n d_i = 1$ . Typically, in order to have a well posed problem, zero-flux or periodic boundary conditions are also imposed.

Model (1) can be naturally transformed, through standard space discretization, into an equivalent model with  $N$  patches, described by one ODE for each patch  $i$ , namely

$$\dot{x}^{(i)} = f(x^{(i)}) + \varepsilon \sum_{j=\mathcal{S}_i} D(x^{(j)} - x^{(i)}) \quad (2)$$

where  $\mathcal{S}_i$  is the set of patches directly coupled to patch  $i$ .

A homogeneous and stationary solution  $\bar{x}$  of (1), characterized by  $f(\bar{x}) = 0$ , can be stable in absence of diffusion (i.e. for  $\varepsilon = 0$ ) but unstable for suitable pairs  $(\varepsilon, D)$ . This somehow counterintuitive phenomenon, first investigated by Turing in a celebrated paper [41], is known as diffusion-induced instability, but is also called Turing instability. Model (1) is actually a parameterized family of models depending not only upon diffusion  $\varepsilon$  and dispersal profile  $D$ , but also upon parameters  $p$  influencing the function  $f$ . In many applications it is therefore of interest to determine the so-called Turing set, namely all the triplets  $(p, \varepsilon, D)$  for which the equilibrium  $\bar{x}$  is unstable in (1) but stable in the system

$$\dot{x} = f(x, p). \quad (3)$$

However, quite frequently, one is mainly interested in finding the set of parameters for which Turing instability is possible for at least one pair  $(\varepsilon, D)$ . This set, which is nothing but the

projection of the Turing set onto the subspace of parameters, is here called set of *potential Turing instability*, or, more shortly, *potential Turing set*. The interest for potential Turing instability is not only motivated by physical reasons, but also because the potential Turing set can be determined quite easily.

The original Turing analysis considers the effect of small perturbations with wavenumber  $\sqrt{\varepsilon}$  imposed upon  $\bar{x}$  in the Fourier expansion of the solution of (1). The key result is that diffusion induced instability is equivalent to the instability of the matrix

$$C(p, \varepsilon, D) = A(p) - \varepsilon D \quad (4)$$

where  $A(p)$  is the Jacobian of (3) at the equilibrium  $\bar{x}$ , i.e.

$$A(p) = \left[ \frac{\partial f}{\partial x} \right]_{\bar{x}(p)}.$$

The same conclusion is obtained straightforwardly by studying the stability of  $\bar{x}$  in model (2) with the well known *Master Stability Function* approach ([34, 22]). If the dispersal profile  $D$  is perfectly balanced, i.e. if  $D$  is proportional to the identity matrix, the spectrum of  $C$  in (4) is simply the spectrum of  $A$  shifted to the left of an amount  $\varepsilon/n$ . This is why the dispersion profile must be unbalanced in order to have Turing instabilities.

In the case  $n = 2$

$$\text{tr}[C] = \text{tr}[A] - \varepsilon \quad \det[C] = \det[A] - \varepsilon (d_1 a_{22} + d_2 a_{11})$$

with  $\text{tr}[A] < 0$  and  $\det[A] > 0$ . Since  $\text{tr}[C]$  is always negative,  $C$  is unstable if and only if  $\det[C]$  is negative, i.e.

$$\varepsilon (d_1 a_{22}(p) + d_2 a_{11}(p)) > \det[A(p)]. \quad (5)$$

Inequality (5) can be satisfied if and only if one of the two diagonal elements of  $A$ , say  $a_{ii}$ , is positive (in which case, the other diagonal element  $a_{jj}$  is negative, since  $\text{tr}[A] < 0$ ). In

particular, if  $a_{ii} > 0$  (i.e., if  $i$  is a so-called *activator*, while  $j$  is an *inhibitor*) the simplest (extreme) solution of (5) is

$$d_i = 0, \quad d_j = 1 \quad \varepsilon > \frac{1}{a_{ii}} \det[A].$$

By continuity, less extreme dispersal profiles will also satisfy (5). Thus, in conclusion, in the case  $n = 2$  a parameter  $p$  is in the set of potential Turing instability if and only if the system contains an activator for that value of  $p$ . Moreover, this potential instability is realized if the activator does not disperse or disperses much less than the inhibitor.

Turing result can be extended to the case  $n > 2$  provided the notion of activator is generalized as follows [38]: a stable  $n$ -dimensional linear system

$$\dot{z} = Az \tag{6}$$

is said to contain a  $m$ -dimensional activator ( $m < n$ ) if an unstable  $m \times m$  submatrix with the same indices of rows and columns can be extracted from the matrix  $A$ . The linear system associated to this submatrix is called activator and has, by definition, at least one eigenvalue with positive real part. Then, it is possible to prove [38] that a stable hyperbolic equilibrium  $\bar{x}$  of (3), i.e. an equilibrium that has a stable Jacobian matrix  $A$ , is potentially unstable in (1) if and only if  $A$  contains an activator. But what is even more interesting, is that if an activator exists, it is always possible to determine a sufficiently high diffusion  $\varepsilon$  and a sufficiently unbalanced dispersal profile  $D$  that destabilize the homogeneous and stationary solution  $\bar{x}$  in (1). This implies that the analysis of Turing instability can actually be performed in two steps, by separating the role of local dynamics from that of diffusion, namely

- (i) determine if system (6) contains an activator;
- (ii) if an activator exists, determine (if needed) the diffusion  $\varepsilon$  and the dispersal profile  $D$

realizing Turing instability.

This decomposition, which has never been systematically exploited in the literature, greatly simplifies the analysis, in particular when the identification of the factors promoting or inhibiting diffusion-induced instabilities is the problem of major concern. In the next section we discuss some of the advantages of this decomposition, keeping the simple case  $n = 2$  separated from the case  $n > 2$ , while in the third section we show the power of the decomposition by studying in some detail Turing instabilities in two plant-insect models.

## 2 Potential Turing instability

We assume in this section to be interested in the influence that some parameters  $p$  characterizing the function  $f$  of model (1) have on diffusion-induced instability. More precisely we want to determine the set of potential Turing instability. Thus, we can follow the approach outlined in the previous section and perform only the first step (i) of the analysis, namely find out for which parameter values the linearized system (6) contains an activator.

### The case $n = 2$

In this case, the existence of an activator, is equivalent to the satisfaction of the following three inequalities

$$\operatorname{tr}[A] = a_{11} + a_{22} < 0 \tag{7}$$

$$\det[A] = a_{11}a_{22} - a_{12}a_{21} > 0 \tag{8}$$

$$\operatorname{tur}[A] \triangleq a_{11}a_{22} < 0 \tag{9}$$

where (7) and (8) guarantee the stability of the equilibrium  $\bar{x}$  in (3), while (9) guarantees that either  $a_{11}$  or  $a_{22}$  are positive, i.e. that an activator exists.

In any two-dimensional parameter space the boundary of the potential Turing set is composed of curves where one of the three functions  $\operatorname{tr}[A]$ ,  $\det[A]$ ,  $\operatorname{tur}[A]$  changes sign.

Curves delimiting the potential Turing set can therefore be Hopf bifurcation curves (where  $\text{tr}[A] = 0$ ), transcritical or saddle-node bifurcation curves (where  $\det[A] = 0$ ) and so-called Turing bifurcation [19] curves (where  $\text{tur}[A] = 0$ ).

In simple models, the potential Turing set can be determined analytically, as in the three examples concerning prey-predator models reported in Fig. 1. In Fig. 1.a, which refers to the first study of diffusion induced instabilities in ecology [39], the potential Turing set coincides with the entire set of stable equilibria. This is because in the prey-predator model considered by Segel and Jackson the prey is strictly cooperative, i.e. it has a per-capita growth rate ( $\dot{x}_1/x_1$ ) increasing with prey density and this is sufficient to imply  $a_{11} > 0$ , i.e. that the prey is an activator. By contrast, in Fig. 1.b, that refers to the Rosenzweig-MacArthur model [36], the potential Turing set is empty (as noticed in [1]), because in that model  $\dot{x}_2/x_2$  is independent upon  $x_2$ , so that  $a_{22} = 0$ , which prevents the existence of an activator. Finally, in Fig. 1.c, which refers to a ratio-dependent prey-predator model [3], the potential Turing set is a proper subset of the region of stable equilibria, as already ascertained [42, 43] through the computation of the entire Turing set in the space  $(p, \varepsilon, D)$ .

When the potential Turing set can not be determined analytically, it can be produced numerically by determining the signs of  $\text{tr}[A]$ ,  $\det[A]$  and  $\text{tur}[A]$  at all points of a grid in parameter space. More effectively, the boundary of the potential Turing set can be computed automatically and with high accuracy through standard continuation techniques [12, 11, 24]. For this, the detection of codimension-2 points [25] is strategically important because various bifurcation curves delimiting the potential Turing set merge from those points. The most interesting of such codimension-2 bifurcations is the Turing-Hopf (TH) bifurcation [6], where

$$\text{tr}[A] = \text{tur}[A] = 0.$$

The existence of a TH point can be easily ascertained from the matrix  $A$ , which must have  $a_{11} = a_{22} = 0$ , or, equivalently, from the geometry of the two null-isoclines  $\dot{x}_1 = 0$  and  $\dot{x}_2 = 0$



which must be, respectively, horizontal and vertical at their intersection point  $\bar{x}$ , as sketched in Fig. 2. The existence of a TH bifurcation point is the key feature for identifying potential Turing instability in the simplest model considered in the next section.

### The case $n > 2$

For determining the set of potential Turing instability of a system with  $n > 2$  one should detect the values of the parameter  $p$  for which the matrix  $A(p)$  is stable and contains an activator. This is not always easy to accomplish, in particular if the analysis must be carried out analytically. For this reason, we suggest here a simple rule, that can be applied through inspection of the signs of the diagonal elements of the Jacobian matrix. In general, this rule allows one to determine only a subregion of the potential Turing set. The rule, based on the fact that a square matrix with positive trace is unstable, is the following: if the Jacobian matrix  $A(p)$  is stable and the sum of  $m (< n)$  of its diagonal elements is positive, then  $p$  is a point of the potential Turing set (because  $A(p)$  contains a  $m$ -dimensional activator).

This rule is very simple but often quite effective. For example, in tritrophic food chain models with logistic prey and Holling type II predator and super-predator described by [20]

$$\begin{cases} \dot{x}_1 = rx_1 \left(1 - \frac{x_1}{K}\right) - \frac{a_1 x_1 x_2}{1 + a_1 h_1 x_1}, \\ \dot{x}_2 = e_1 \frac{a_1 x_1 x_2}{1 + a_1 h_1 x_1} - m_1 x_2 - \frac{a_2 x_2 x_3}{1 + a_2 h_2 x_2}, \\ \dot{x}_3 = e_2 \frac{a_2 x_2 x_3}{1 + a_2 h_2 x_2} - m_2 x_3, \end{cases}$$

where  $r$  and  $K$  are net growth rate and carrying capacity of the prey and  $a_i, h_i, m_i, e_i$ ,  $i = 1, 2$ , are attack rate, handling time, mortality rate, and efficiency of predator and super-predator, respectively, the Jacobian matrix  $A(p)$  associated with any stable positive equilibrium  $\bar{x}(p)$  has always  $a_{11} < 0$ ,  $a_{22} > 0$  and  $a_{33} = 0$ . Thus the system has two activators, namely the predator, which is a one-dimensional activator, and the pair (predator, super-predator), which is a two-dimensional activator. A first pair  $(\varepsilon, D)$  that destabilizes  $\bar{x}$  is,

therefore, characterized by a sufficiently high diffusion  $\varepsilon$  and by  $d_2 = 0$ , or, by continuity, by

$$d_2 \ll \min(d_1, d_3) \tag{10}$$

while another destabilizing pair  $(\varepsilon, D)$  is characterized by  $d_2 = d_3 = 0$  or, more realistically, by

$$d_1 \gg \max(d_2, d_3). \tag{11}$$

Food chains where conditions (10) or (11) are satisfied are not many but certainly exist. For example, tritrophic food chains composed of insects, spiders and birds, satisfy condition (10) because in general, spiders disperse much less than insects and birds (even when spiders colonize habitats through long-distance aerial dispersal [14, 15]).

### 3 Application to plant-insect models

We study in this section the problem of diffusion-induced instability in two different plant-insect models, with  $n$  equal to 2 and 3, respectively, in order to show the power of the notion of potential Turing instability. The problem is of interest per se, because plant-insect interactions have been recognized to be the source of many intriguing spatio-temporal phenomena such as recurrent insect outbreaks, synchronization, and travelling waves in forest [28, 27, 23].

The models proposed in the literature for studying plant-insect interactions are many and involve, in general, segments of the food chain starting with the plant, continuing with the insect and ending with insectivores or with parasitoids and their pathogens. 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 [17], but more often with only two variables namely wood and foliage [29], adult and young trees [2, 35], foliage and maternal effect [16], foliage and energy [40]. In the most extreme cases

the vegetational compartment has been described with a single variable, say biomass of the plant [7, 32] 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 [5]. 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. All these simple models could a priori be considered as equally good candidates for studying diffusion-induced instability. However, if we are interested in deriving a formal theory, we are forced to avoid numerical analysis and use very simple models that can be studied analytically. Since, in practice, only second order models, i.e., models with only two variables (plant and insect), enjoy this property, our first 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 described in [32] because it has been shown to mimic rather well the behavior of more complex models [17]. The model is

$$\begin{cases} \dot{x}_1 = rx_1 \left(1 - \frac{x_1}{K}\right) - \frac{a_2 x_1}{1 + a_2 h_2 x_1} x_2, \\ \dot{x}_2 = e_2 \frac{a_2 x_1}{1 + a_2 h_2 x_1} x_2 - m_2 x_2 - c_2 x_2^2 - \frac{a_3 x_2}{1 + a_3 h_3 x_2 + a'_3 h'_3 V} x_3, \end{cases} \quad (12)$$

where  $x_1$  and  $x_2$  are plant and insect biomasses,  $r$  and  $K$  are net growth rate and carrying capacity of the plant,  $a_2$  and  $h_2$  are insect attack rate and handling time,  $e_2$  is the plant/insect conversion factor,  $m_2$  is basic insect mortality,  $c_2$  is insect intraspecific competition,  $x_3$  is biomass of insect enemies (assumed constant),  $a_3(a'_3)$  and  $h_3(h'_3)$  are attack rates and handling times of insect enemies, while  $V$  is the density of alternative preys.

For  $c_2 = x_3 = 0$ , model (12) is the standard Rosenzweig-MacArthur model [36] that can not have Turing instability (see Fig. 1.b). By contrast, if all demographic parameters of the model are positive, Turing instability is possible. In fact, the prey non-trivial isocline  $x_2 = \varphi(x_1)$  is a parabola, with a maximum that can be arbitrarily placed in the state space  $(x_1, x_2)$  by varying, for example, the two parameters  $r$  and  $K$  in (12). The predator non-trivial isocline written in the form  $x_1 = \psi(x_2)$  is more complex, but can be shown to have

a minimum with respect to  $x_2$  in the positive quadrant if  $x_3$  is sufficiently large. Thus, for suitable combinations of the parameters, the two isoclines of model (12) intersect as in Fig. 2. This means that a TH codimension-2 bifurcation point generically exists in any two dimensional parameter space. As pointed out in the previous section, this implies the existence of Turing instabilities, because two Turing bifurcation curves merge from the TH point. In the specific case, the potential Turing set can be obtained by determining, through continuation, the Hopf and Turing bifurcation curves merging from the TH point. The result is shown in Fig. 3 for the parameter setting indicated in the caption. It is worth noticing that only in one of the two subregions of the potential Turing set (namely the gray region delimited by  $a_{11} = 0$ , in which the activator is the plant) the diffusion-induced instability can be realized, while in the other this is certainly not possible, since it would require that plants disperse more than insects.

The consequence of the above findings is the existence of stationary spatial patterns when the parameters are in the subregion of the potential Turing set where the activator is the plant. An example of the spatial distribution of the vegetational biomass obtained after transient is shown in Fig. 4 which has been produced by solving numerically on a unitary square eqs.(1,12) with  $d_1 = 10^{-5}$ ,  $d_2 = 1 - 10^{-5}$ ,  $\varepsilon = 1.5$  starting from random initial conditions. In agreement with previous studies predicting that spatial patterns can arise even within homogeneous habitats (see, for example, [10, 21, 33, 9, 30, 1, 6, 42, 43]), Fig.4 points out the formation of vegetational patches that look very much like those observed in the field (see Fig.5). The transients toward stationary solutions or toward more complex solutions are also interesting and reveal the existence of various kinds of waves. However, these waves are not strictly related with Turing instability, because they have been observed also in systems where Turing instability is not possible [18, 31] as well as in systems with more complex dispersal mechanisms [26, 37, 4, 8].

As a second example of application of the notion of potential Turing instability in spatially extended systems, we now consider a model with  $n = 3$ . The model is the most natural

extension of the previous one, obtained by adding to it a third equation describing the dynamics of the insect enemy, namely

$$\begin{cases} \dot{x}_1 = rx_1 \left(1 - \frac{x_1}{K}\right) - \frac{a_2 x_1}{1 + a_2 h_2 x_1} x_2, \\ \dot{x}_2 = e_2 \frac{a_2 x_1}{1 + a_2 h_2 x_1} x_2 - m_2 x_2 - c_2 x_2^2 - \frac{a_3 x_2}{1 + a_3 h_3 x_2 + a'_3 h'_3 V} x_3 \\ \dot{x}_3 = \frac{e_3 a_3 x_2 + e'_3 a'_3 V}{1 + a_3 h_3 x_2 + a'_3 h'_3 V} x_3 - m_3 x_3 - c_3 x_3^2, \end{cases} \quad (13)$$

In order to show that model (13) can have Turing instabilities for suitable values of its parameters, let us first reconsider model (12) that has already been proved to have  $a_{11} > 0$  and  $a_{22} < 0$  at the positive equilibrium  $\bar{x} = (\bar{x}_1, \bar{x}_2)$  corresponding to suitable values of its parameters, including the value, say  $\bar{x}_3 > 0$ , of the insect enemy. Then, consider the third equation in (13) and remark that it can be satisfied with  $x_3 = \bar{x}_3$  and  $\dot{x}_3 = 0$  provided

$$c_3 = \frac{1}{\bar{x}_3} \left( \frac{e_3 a_3 \bar{x}_2 + e'_3 a'_3 V}{1 + a_3 h_3 \bar{x}_2 + a'_3 h'_3 V} - m_3 \right)$$

Thus, for suitably small values of  $e_3$ ,  $e'_3$  and  $m_3$  (that do not affect model (12)) model (13) has a stable positive equilibrium  $\bar{x} = (\bar{x}_1, \bar{x}_2, \bar{x}_3)$  and  $a_{11} > 0$ ,  $a_{22} < 0$  and  $a_{33} = -c_3 \bar{x}_3 < 0$ . This means that the plant is an activator and, Turing instability is obtained if the plants disperse much less than the insects and their enemies, a condition that is very often satisfied. Figure 6 shows spatial patterns obtained after transient with model (1,13) which favorably compare with those reported in Fig.5.

## 4 Concluding remarks

We have shown in this paper that diffusion-induced instability in spatially extended models can be studied by separating local dynamics from diffusion. This decomposition is possible thanks to the notion of potential Turing instability, which has been illustrated through the analysis of two spatially extended plant-insect models. Potential Turing sets can be

easily produced through continuation, in particular when special codimension-2 bifurcation points, like the Turing-Hopf point, have already been detected.

The extension of the approach to other kinds of models where dispersal is active instead of diffusive [4,26,nuovaRef] would certainly be relevant for studying ecological systems. In the same context, it would also be interesting to identify, through the systematic analysis of the most standard prey-predator models, which are the mechanisms (e.g. competition, cooperation, harvesting, cannibalism, ...) that promote the emergence of spatial patterns in homogeneous environments.

## References

- [1] D. ALONSO, F. BARTUMEUS, J. CATALAN, *Mutual interference between predators can give rise to Turing spatial patterns*, Ecology 83 , pp. 28-34, 2002.
- [2] M.Y. ANTONOVSKY, R.A. FLEMING, YU.A. KUZNETSOV, W.C. CLARK, *Forest - pest interaction dynamics: The simplest mathematical models*, Theoretical Population Biology 37, 343-367, 1990.
- [3] R. ARDITI, L. R. GINZBURG, *Coupling in predator-prey dynamics: Ratio-dependence*, Journal of Theoretical Biology, 139 (3), 311-326, 1989.
- [4] R. ARDITI, Y. TYUTYUNOV, A. MORGULIS, ET AL., *Directed movement of predators and the emergence of density-dependence in predator-prey models*, Theoretical Population Biology, 59(3), 207-221, 2001.
- [5] W. BALTENSWEILER, A. FISCHLIN, *The larch budmoth in the Alps*, in *Dynamics of Forest Insect Populations: Patterns, Causes, Implications*, (Berryman, A.A., ed.), 331-351, Plenum Press, 1988.

- [6] M. BAURMANN, T. GROSS, U. FEUDEL, *Instabilities in spatially extended predator-prey systems: Spatio-temporal patterns in the neighborhood of Turing-Hopf bifurcations*, Journal of Theoretical Biology, 245(2), 220-229, 2007.
- [7] A.A. BERRYMAN, N.C. STENSETH, A.S. ISAEV, *Natural regulation of herbivorous forest insect populations*, Oecologia 71, 174-184, 1987.
- [8] A. CHAKRABORTY, M. SINGH, D. LUCY, P. RIDLAND, *A numerical study of the formation of spatial patterns in twospotted spider mites*, Mathematical and Computer Modelling, 49, 1905-1919, 2009.
- [9] H. COMINS, M. HASSELL, *Persistence of multispecies host-parasitoid interactions in spatially distributed models with local dispersal*, Journal of Theoretical Biology, 183(1), 19-28, 1996.
- [10] D. H. DEUTSCHMANN ET AL., Patch Dynamics, in S. A. Levin, T. M. Powell, J. H. Steel, Eds. Springer-Verlag, 184-209, 1993.
- [11] E. J. DOEDEL, ET AL., AUTO97: *Continuation and Bifurcation Software for Ordinary Differential Equations (with HomCont)*, Concordia University, Montreal, Canada, [ftp.cs.concordia.ca/pub/doedel/auto](http://ftp.cs.concordia.ca/pub/doedel/auto), 1997.
- [12] A. DHOOGHE, W. GOVAERTS, AND YU. A. KUZNETSOV: MATCONT: *A MATLAB package for numerical bifurcation analysis of ODEs*, ACM Transaction Mathematical Software, 29, 141-164, 2003.
- [13] A. DHOOGHE, W. GOVAERTS, YU. A. KUZNETSOV ET AL., CL\_MATCONT: *A continuation toolbox in MATLAB*, in Proceedings of the 2003 ACM Symposium on Applied Computing, Melbourne, FL, 161-166, 2003.
- [14] W.J. EHMANN, *Spider habitat selection - an experimental field-test of the role of substrate diameter*, Journal of Arachnology, 22(1), 77-81, 1994.

- [15] W.J. EHMANN, *Organization of spider assemblages on shrubs - an assessment of the role of dispersal mode in colonization*, American Midland Naturalist, 131(2), 301-310, 1994.
- [16] L.R. GINZBURG, D.E. TANEYHILL, *Population cycles of forest Lepidoptera-a maternal effect hypothesis*, Journal of Animal Ecology 63, 79-92, 1994.
- [17] A. GRAGNANI, M. GATTO, S. RINALDI, *Acidic deposition, plant pests, and the fate of forest ecosystems*, Theoretical Population Biology 54, 257-269, 1998.
- [18] W. GURNEY, A. VEITCH, I. CRUICKSHANK AND G. MCGEACHIN, *Circles and spirals: Population persistence in a spatially explicit predator-prey model*, Ecology, 79(7), 2516-2530, 1998.
- [19] A. HAGBERG, E. MERON, *Pattern formation in non-gradient reaction-diffusion systems: the effects of front bifurcations*, Nonlinearity, 7, 805-835, 1994.
- [20] A. HASTINGS, T. POWELL, *Chaos in a 3-species food-chain*, Ecology, 72(3), 896-903, 1991.
- [21] E. HOLMES, M. LEWIS, J. BANKS, R. VEIT, *Partial-differential equations in ecology - spatial interactions and population-dynamics*, Ecology, 75(1), 17-29, 1994.
- [22] V. JANSEN, A. LLOYD, *Local stability analysis of spatially homogeneous solutions of multi-patch systems*, Journal of Mathematical Biology, 41(3), 232-252, 2000.
- [23] D. JOHNSON, O. BJORNSTAD, A. LIEBHOLD, *Landscape geometry and travelling waves in the larch budmoth*, Ecology Letters, 7(10), 967-974, 2004.
- [24] YU. A. KUZNETSOV AND V. V. LEVITIN, *CONTENT: A Multiplatform Environment for Analyzing Dynamical Systems*, Dynamical Systems Laboratory, Centrum voor Wiskunde en Informatica, Amsterdam, ftp.cwi.nl/pub/CONTENT, 1997.



- [25] YU. A. KUZNETSOV, *Elements of Applied Bifurcation Theory*, 3rd ed., Springer-Verlag, New York, 2004.
- [26] Z. LI, M. GAO, C. HUI, X. HAN AND H. SHI, *Impact of predator pursuit and prey evasion on synchrony and spatial patterns in metapopulation*, *Ecological Modelling*, 185(2-4), 245-254, 2005.
- [27] A. LIEBHOLD, J. ELKINTON, D. WILLIAMS AND R.M. MUZIKA, *What causes outbreaks of the gypsy moth in North America?*, *Population Ecology*, 42(3), 257-266, 2000.
- [28] A. LIEBHOLD, N. KAMATA, *Introduction - Are population cycles and spatial synchrony a universal characteristic of forest insect populations?*, *Population Ecology*, 42(3), 205-209, 2000.
- [29] D. LUDWIG, D.D. JONES, C.S. HOLLING, *Qualitative analysis of insect outbreak systems: the spruce budworm and forest*, *Journal of Animal Ecology* 47,315-322, 1978.
- [30] J. MARON, S. HARRISON, *Spatial pattern formation in an insect host-parasitoid system*, *Science*, 278, 1997.
- [31] A. MEDVINSKY, S. PETROVSKII, I. TIKHONOVA, H. MALCHOW AND B.L. LI, *Spatiotemporal complexity of plankton and fish dynamics*, *Siam Review*, 44(3), 311-370, 2002.
- [32] S. MURATORI, S. RINALDI, *Catastrophic bifurcations in a second-order dynamical system with application to acid rain and forest collapse*, *Applied Mathematical Modelling* 13, 674-681, 1989.
- [33] M. NEUBERT, M. KOT, M. A. LEWIS, *Dispersal and pattern-formation in a discrete-time predator-prey model*, *Theoretical Population Biology*, 48(7), 1995.
- [34] L. M. PECORA, T. L. CARROLL, *Master stability functions for synchronized coupled systems*, *Physical Review Letters*, 80, 2109-2112, 1998.

- [35] S. RINALDI, S. MURATORI, *Limit cycles in slow-fast forest pest models*, Theoretical Population Biology 41, 26-43, 1992.
- [36] M. P. ROSENZWEIG, R. H. MACARTHUR, *Graphic representation and stability conditions of predator-prey interaction*, The American Naturalist, 97, 209-223, 1963.
- [37] A. DE ROOS, E. MCCAULEY, W. WILSON, *Pattern formation and the spatial scale of interaction between predators and their prey*, Theoretical Population Biology, 53(2), 108-130, 1998.
- [38] R. SATNOIANU, M. MENZINGER, PK. MAINI, *Turing instabilities in general systems*, Journal of Mathematical Biology, 41(6), 493-512, 2000.
- [39] L. SEGEL, J. JACKSON, *Dissipative structure - explanation and an ecological example*, Journal of Theoretical Biology, 37(3), 545-559, 1972.
- [40] S.H. STROGATZ, *Nonlinear Dynamics and Chaos*, Addison Wesley, Reading, MA, 1994.
- [41] A. TURING, *The chemical basis of morphogenesis*, Philosophical Transactions B, 237(641), 37-72, 1952.
- [42] W. WANG, Q. X. LIU, Z. JIN, *Spatiotemporal complexity of a ratio-dependent predator-prey system*, Physical Review E, 75(5), 051903, 2007.
- [43] L. ZHANG, W. WANG, Y. XUE, *Spatiotemporal complexity of a predator-prey system with constant harvest rate*, Chaos, Solitons & Fractals, 41(1), 38-46, 2009.

# Figure captions

## Figure 1

Examples of potential Turing sets (gray regions) for three different prey-predator models: (a) Segel-Jackson model [39]; (b) Rosenzweig-MacArthur model [36]; (c) Arditi-Ginzburg model [3]. In the black regions there is no stable positive equilibrium, while in the other regions such an equilibrium exists.

## Figure 2

Prey and predator null-isoclines at a TH codimension-2 bifurcation point:  $\dot{x}_1 = 0$  is maximum with respect to  $x_1$ , while  $\dot{x}_2 = 0$  is minimum with respect to  $x_2$ .

## Figure 3

Bifurcation diagram in the parameter plane  $(c_2, a_2)$  of model (12). In the black regions there is no stable positive equilibrium, while in the other regions such an equilibrium exists. The positive stable equilibrium can not be diffusively unstable in the white regions (where  $a_{11} < 0, a_{22} < 0$ ), while it can in the gray regions (potential Turing sets). In the gray region delimited by the curve  $a_{11} = 0$  the activator is the plant, so that Turing instability can be obtained since insects disperse much more than plants. The parameter values are  $r = 1.3$ ,  $K = 10$ ,  $h_2 = 2/3$ ,  $e_2 = 0.6$ ,  $m_2 = 0.3$ ,  $a_3 = 1$ ,  $h_3 = 2.5$ ,  $a'_3 = 1$ ,  $h'_3 = 1$ ,  $V = 3$  and  $x_3 = 1$ .

## Figure 4

Plant density at equilibrium in a spatial domain of model (1,12): The figure has been obtained by integrating eqs. (1,12) using finite difference spatial discretization and forward Euler time integration for the parameter values reported in the caption of Fig. 3 and for  $a_2 = 0.86$  and  $c_2 = 0.08$ .

**Figure ??**

Vegetational patches observed at extremely different scales : (a) Ticchiolatura della rosa, attaccata da “Marsonnina rosae” (b) pini silvestri deperiti sui versanti della Valtellina attaccati da bostrico.

**Figure 6**

Plant density at equilibrium in a spatial domain of model (1,13): The parameter values are as in Fig. 3 and  $e'_3 = 1$ ,  $m_3 = 1$ ,  $c_3 = 0.8$ ,  $d_1 = 10^{-5}$ ,  $d_2/d_3 = 0.5$  and  $\varepsilon = 0.5$ .

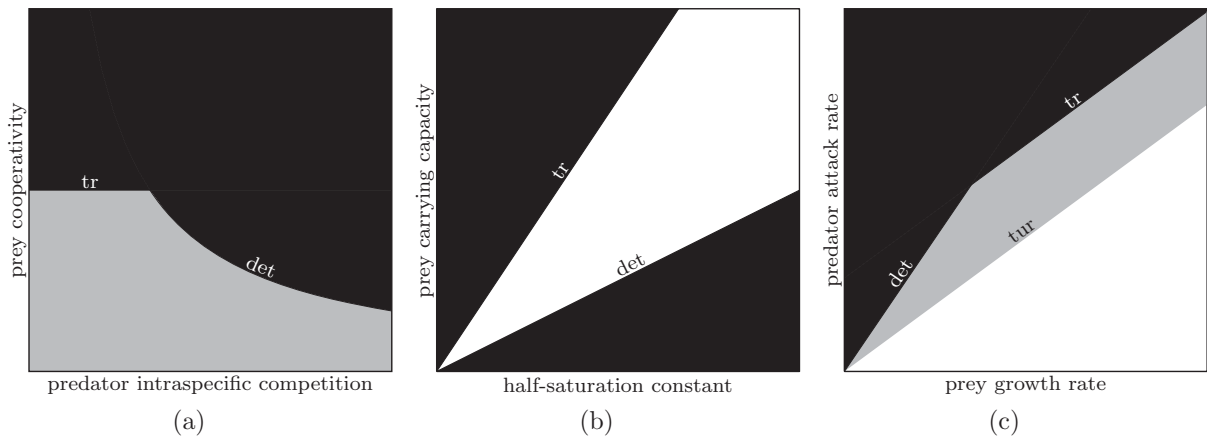


Figure 1

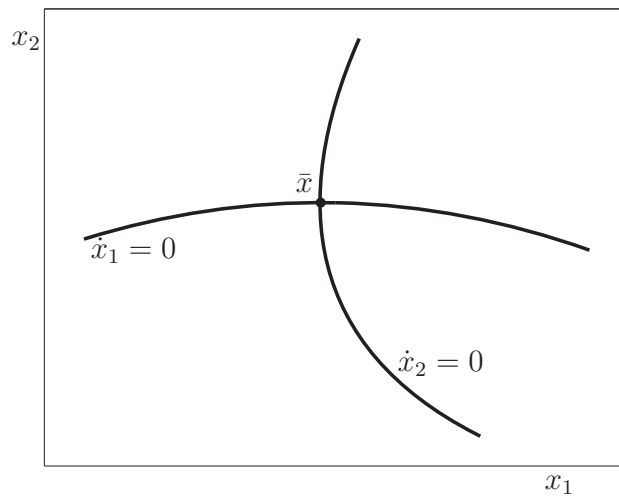


Figure 2

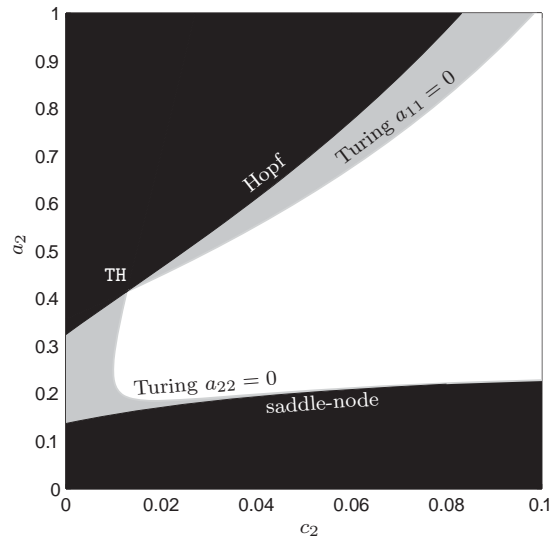


Figure 3

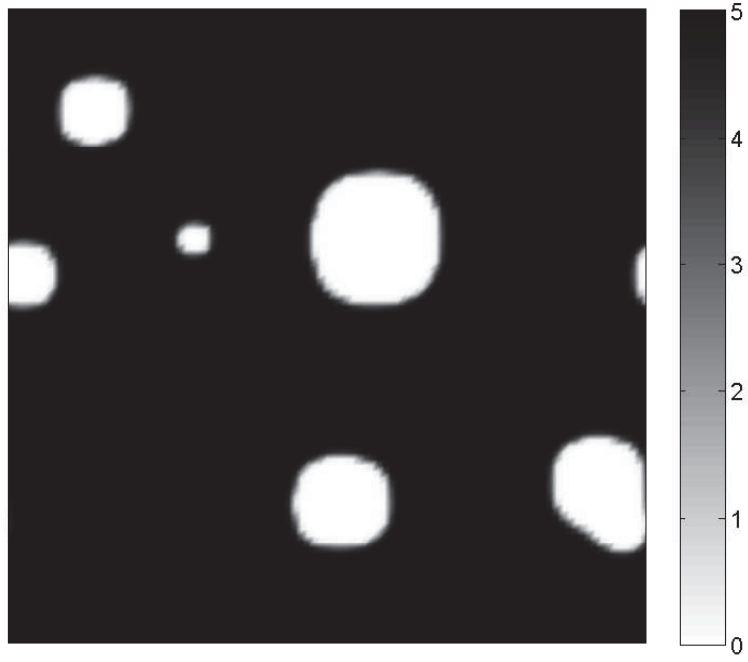


Figure 4





(a)



(b)

**Figure 5**

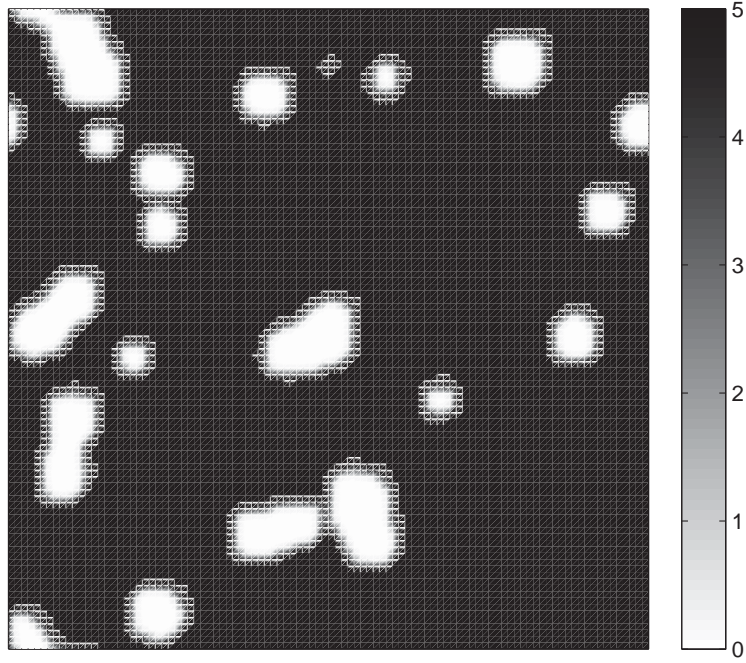


Figure 6