Factors promoting or inhibiting Turing instability in spatially extended prey-predator systems

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Abstract

The emergence of inhomogeneities in the distributions of the abundances of spatially extended prey-predator systems is investigated. The method of analysis, based on the notion of diffusive (Turing) instability, is systematically applied to nine different models obtained by introducing an extra-factor into the standard Rosenzweig-MacArthur prey-predator model. The analysis confirms that the standard model is critical in the context of Turing instability, and that the introduction of any small amount of the extra-factor can easily promote or inhibit the emergence of spatial patterns.

Key words: prey-predator model, spatial pattern, Turing instability, diffusive instability, dispersal.
1 Introduction

As is well known, plant and animal populations are not uniformly distributed in the environment but are packed in patches that remain fixed or move over time (spatio-temporal patterns). The most obvious reasons for patchiness are the occurrence of local perturbations (e.g. the sudden discharge of a chemical species at a specific point) and the presence of permanent spatial inhomogeneities in the environment (e.g. better exposition to sun of one of the river banks). A much more subtle reason for patchiness in ecology has been pointed out long ago by Segel and coauthors [9, 16] who used the idea of diffusive instability and the results obtained by Turing [18] to show that simple prey-predator interactions can be responsible of patchiness even in perfectly homogeneous environments. However, the prey-predator models used by Segel are rather special and not very convincing, in particular in the context of plankton dynamics [9]. Most likely, the reason for this is that more standard models, like the Rosenzweig-MacArthur model [12], are not appropriate for proving the existence of diffusive instability. In fact, as recognized later [1], the Rosenzweig-MacArthur model is ‘critical’ in the context of Turing’s theory. More precisely, the two biological mechanisms taken into account in the Rosenzweig-MacArthur model, namely logistic growth of the prey and saturating functional response of the predator, do not imply the emergence of diffusive instability, unless, as shown in this paper, a small amount (actually any small amount) of a suitable extra-mechanism is also included in the model. Since the Rosenzweig-MacArthur model is one of the most popular prey-predator models in ecology, the identification of the extra-mechanisms that must be added to it to obtain a model supporting pattern formation, is an interesting problem.

After recalling the basic Turing results and the interpretation given to them by Satnoianu et al.[15] and by the authors [7], we show how the problem can be solved with almost no effort. The result of the analysis is that all elementary mechanisms not taken into account in the Rosenzweig-MacArthur model can be partitioned in three classes:
(i) Mechanisms, like predator cooperation or exploitation, promoting diffusive instability if predator disperse much less than prey.

(ii) Mechanisms, like predator interference, intraspecific competition and stocking, always inhibiting diffusive instability.

(iii) Mechanisms, like prey harvesting or stocking, with absolutely no influence on diffusive instability.

2 Conditions for diffusive (Turing) instability

Spatially extended prey-predator systems can be described, under the assumption of diffusive dispersal, by a PDE of the form

\[
\begin{align*}
\frac{\partial x}{\partial t} &= f(x, y, p)x + d_x \nabla^2 x \\
\frac{\partial y}{\partial t} &= g(x, y, p)y + d_y \nabla^2 y
\end{align*}
\]

where \(x\) and \(y\) are prey and predator abundances depending upon time and space in a given domain of \(\mathbb{R}^2\), \(f\) and \(g\) are per-capita growth rates depending upon demographic parameters \(p\), and \(d_x\) and \(d_y\) are the non-negative dispersal coefficients of the two populations. Typically, in order to have a well posed problem, zero-flux or periodic boundary conditions are also imposed.

A positive, homogeneous and stationary solution \((\bar{x}, \bar{y})\) of (1) (characterized by \(f = g = 0\)) can be stable in absence of diffusion (i.e. for \(d_x = d_y = 0\)) but unstable for suitable pairs \((d_x, d_y)\). In other words, an equilibrium \((\bar{x}, \bar{y})\) can be stable in lumped prey-predator model

\[
\begin{align*}
\frac{\partial x}{\partial t} &= f(x, y, p)x \\
\frac{\partial y}{\partial t} &= g(x, y, p)y
\end{align*}
\]
but unstable in its spatially extended version (1). This somehow counterintuitive phenomenon, first investigated by Turing in a celebrated paper [18], is known as diffusion-induced instability, but is also called Turing instability.

The original Turing analysis considers the effect of small perturbations imposed on \((\bar{x}, \bar{y})\) in the Fourier expansion of the solution of (1) and the key result [15] is that diffusion induced instability is equivalent to the instability of the matrix

\[
C = A(p) - D
\]  

(3)

where \(A(p)\) is the Jacobian of (2) at the equilibrium \((\bar{x}, \bar{y})\), i.e.

\[
A(p) = \begin{bmatrix}
\bar{x} \frac{\partial f}{\partial x} & \bar{x} \frac{\partial f}{\partial y} \\
\bar{y} \frac{\partial g}{\partial x} & \bar{y} \frac{\partial g}{\partial y}
\end{bmatrix}
\]

and \(D\) is the diagonal matrix with \(d_x\) and \(d_y\) as diagonal elements. If \(d_x = d_y\), i.e. if \(D\) is proportional to the identity matrix, the spectrum of \(C\) in (3) is simply the spectrum of \(A\) shifted to the left; so that \(C\) can not be unstable if \(A\) is stable. This is why the dispersion coefficients must be unbalanced in order to have Turing instability.

As shown in [15, 7], the problem of finding triples \((p, d_x, d_y)\) for which \((\bar{x}, \bar{y})\) is stable in (2) but is unstable in (1) can be solved in two steps, namely:

(i) find values of \(p\) for which one diagonal element of the Jacobian matrix \(A\) is positive.

Notice that if \(a_{ii} > 0\) (i.e. if \(i\) is the so-called activator) then \(a_{jj} < 0\) since \(tr(A) < 0.\)

(ii) determine (if needed) the dispersal coefficients \((d_x, d_y)\) realizing Turing instability by imposing that \(C\) is unstable. This is possible if the activator disperses much less than the other population (inhibitor).

This decomposition, which has never been systematically exploited in the literature (see [5, 3, 19, 20, 2, 8, 4, 13, 6, 10, 11, 14, 17]), greatly simplifies the analysis, in particular when
the identification of the factors promoting or inhibiting diffusion-induced instability is the problem of concern.

3 Criticality of the Rosenzweig-Mac Arthur model

One of the most standard prey-predator models [12] is composed of a logistic prey and a type II predator and is therefore described by

\[
\begin{align*}
\frac{\partial x}{\partial t} &= \left[ r \left(1 - \frac{x}{K}\right) - \frac{a y}{1 + ahx}\right] x \\
\frac{\partial y}{\partial t} &= \left[e\frac{ax}{1 + ahx} - d\right] y
\end{align*}
\] (4)

where \( r \) and \( K \) are prey net growth rate and carrying capacity and \( a, h, e \) and \( d \) are predator attack rate, handling time, efficiency and death rate, respectively. Model (4) is of the form (2) and has a positive stable equilibrium \((\bar{x}, \bar{y})\) for suitable values of its parameters. Since the per-capita growth rate \( g \) does not depend on predator density, the second diagonal element of the Jacobian \( A \) in (3) is zero, i.e. \( a_{22}=0 \) for all parameter values, while \( a_{11} < 0 \) since \( tr(A) < 0 \) at a stable equilibrium. This means that Turing condition \((a_{11}a_{22} < 0)\) can not be satisfied in model (4), although it is almost satisfied since \( a_{11}a_{22} = 0 \). In other words, model (4) is critical in the context of Turing instability.

4 Small factors can trigger Turing instability

The addition to model (4) of any small amount \( p \) of an extra demographic factor slightly modifies the equilibrium \((\bar{x}, \bar{y})\) as well as the elements \( a_{11} \) and \( a_{22} \) of the matrix \( A \). Hence, by continuity, the equilibrium \((\bar{x}, \bar{y})\) remains positive and stable and \( a_{11} \) remains negative. By contrast, \( a_{22} \) might become positive, thus indicating that the \( p \)-factor promotes Turing instability, i.e. pattern formation, if predator disperse much less than prey. The conclusion is that the factors promoting Turing instability can be simply identified by looking at the
We now consider nine independent factors that are not taken into account in model (4) but can be easily added to it by modifying the predator per capita growth rate. Table 1 reports the nine factors, the functions \( g(x, y, p) \) and the signs of \( \frac{\partial g}{\partial y} \). Of course \( g(x, y, 0) \) is the Rosenzweig-MacArthur predator growth rate in all cases.

For the first three factors, \( \frac{\partial g}{\partial y} \) is positive for all parameter values, so that one can conclude that even the existence of a small amount of predator harvesting, of a generalist superpredator, and of predator cooperation guarantees the emergence of spatial pattern if predator dispersal is sufficiently lower than prey dispersal. Of course, strictly speaking, this conclusion is valid only for the particular functional form used in Table 1 for modelling the \( p \)-factor. However, in this specific case, the conclusion should be rather robust since the functions \( g \) in Table 1 are the most standard ones, namely, predator harvesting, rate saturating with predator density, generalist superpredator with type II functional response characterized by an attack rate \( a' \) and a handling time \( h' \) for the predator population \( y \) and

\[
\begin{array}{|c|c|c|}
\hline
\text{Factor } p & \text{predator per-capita growth rate } g(x, y, p) & \text{Sign of } \frac{\partial g}{\partial y} \\
\hline
1. \text{ predator harvesting} & \frac{a y}{1 + a h x} - d - \frac{p}{1 + a' h' y} & + \\
2. \text{ generalist superpredator} & \frac{a y}{1 + a h x} - d - \frac{1}{1 + a' h' y + a'' h'' w} & + \\
3. \text{ predator cooperation} & \frac{a (1 + p y) y}{1 + a (1 + p y) h x} - d & + \\
4. \text{ predator interference} & \frac{a y}{1 + a h x + p y} - d & - \\
5. \text{ predator intraspecific competition} & \frac{a y}{1 + a h x} - d - p y & - \\
6. \text{ predator stocking} & \frac{a y}{1 + a h x} - d + \frac{p}{y} & - \\
7. \text{ prey harvesting} & \frac{a y}{1 + a h x} - d & 0 \\
8. \text{ prey stocking} & \frac{a y}{1 + a h x} - d & 0 \\
9. \text{ prey cooperation} & \frac{a (1 - p x) y}{1 + a (1 - p x) h x} - d & 0 \\
\hline
\end{array}
\]

\textbf{Table 1}: Nine independent factors \( p \) not taken into account in the Rosenzweig-MacArthur model (4) (first column) and the predator per-capita growth rate \( g(x, y, p) \) that should be used in model (2) to take these factors into account (second column). The sign of \( \frac{\partial g}{\partial y} \) (third column) allows one to identify if the factor \( p \) promotes (+) or inhibits (-) diffusive instability.
by an attack rate $a''$ and a handling time $h''$ for an extra source of food $W$ [8], predator cooperation positively impacting on predator attack rate.

By contrast, factors 4-6 in Table 1, i.e. predator interference [4], predator intraspecific competition and constant predator stocking, inhibit pattern formation since $\partial g/\partial y$ is negative for all parameter values. It is worth noticing that the growth rate $g$ used for the fourth factor, coincides with that proposed by Ruxton [13] for modelling the effect of prey refuges, so that also antipredator behaviour inhibits pattern formation.

Finally, the last three factors, dealing with prey characteristics, do not have any impact on Turing instability because they do not introduce a dependence of the per-capita growth rate $g$ upon predator density.

5 Concluding remarks

We have shown in this paper how the emergence of spatial pattern in prey-predator systems can effectively be discussed by using the theory developed long ago by Turing. In particular, we have confirmed that the standard Rosenzweig-Mac Arthur prey-predator model is critical in the context of Turing theory, so that the addition of any small amount of an extra-factor not considered in that model can easily promote or inhibit pattern formation. The analysis is almost trivial since it requires only to find out if after the introduction of the extra-factor the predator per capita growth rate increases or decreases with predator density. Thus, in many cases, the analysis can be performed on purely intuitive grounds.

The nine factors we have considered (see Table 1) are only a few out of many so that some extra-effort would be justified to produce a richer catalog. However, it might be that a factor missing in our list is actually equivalent to one present in the list (like antipredator behaviour due to prey refuges which is equivalent to predator interference). But even in the case that a new factor is really different from those we have considered in Table 1, it should not be difficult to detect its potential impact on pattern formation if the analysis is carried
out along the lines indicated above.

As a final remark, we like to stress that in this paper we have studied models obtained by slightly perturbing the Rosenzweig-MacArthur model with a stable equilibrium. This implies that the equilibrium of our model is also stable if the newly introduced extra-factor is small and that the prey remains a so-called inhibitor. This means that in the case the extra-factor promotes diffusive instability, the activator is the predator and spatial patterns really emerge if predator disperse much less than prey. This is not in conflict with studies in which spatial patterns have been detected in cases where prey disperse less than predator, like plant insect communities [7]; indeed, in those cases the model is quite different and the equilibrium which is stable in the lumped model and unstable in the spatially extended model has the prey as activator.

References


