

Mathematical analysis on the effect of
temporally changing environment on the
structure of an ecosystem

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Abstract

After a reminder of four very used models in Mathematical ecology, we breach into two different topics. In chapter 2, we study the phenomenon of apparent competition on a 1 predator species - N prey species system. We prove the conditions for the survival of the prey species or predator species, with the existence of a unique globally asymptotically stable steady state in any case. In chapter 3, we study the diffusion of a species, first alone, then in a system competing for resources with a motionless species. We use Neumann bordering conditions, but we prove that there is a similarity between this system and a system of one species diffusing with Dirichlet bordering condition. Indeed, here in some cases the motionless species acts as a "death zone" for the diffusing species. Finally by looking at the ratio of the size of the motionless species' habitat and the total size of the patch, we also show the existence of a critical ratio size under which the diffusing species can survive whatever the total size of the patch is.

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Chapter 1

Introduction

1.1 Mathematical modeling in ecology

The very first step when modeling a population dynamic is to lay down the biological assumptions we make about the situation. Those assumptions will then be transformed into the language of mathematics.

For all the models that will be presented in this paper, we will neglect the effects of stochastic events. If we suppose the population to be large enough, this assumption is a reasonable one.

Furthermore, we will assume that we *isolated* our population, and no migration (immigration nor emigration) occurs.

Finally, we will assume there are *no distinctions* between individuals of a same species.

Though those assumptions are never exactly satisfied in field situations, they are reasonable enough to allow for models that give a good description of the data while being simple enough to be analyzed through a mathematical lens.

1.2 A first model : exponential growth (Malthus Model, 1798)

The easiest way to model a population is to consider that the environment it is in is not affected by the population. Meaning, the resources and life conditions stay the same, however big the population becomes. We call such

an environment *invariant*.

The growth of a species in such an environment boils down to a *conservation equation*. If we call β the growth rate per individual, μ the death rate per individual, and $N(t)$ the population of the species at time t , then we have the model called Malthus model :

$$\frac{dN}{dt} = \text{births} - \text{deaths} = \beta N - \mu N \quad (1.1)$$

with β and μ positive constants, and $N(0) = N_0 > 0$. Then :

$$N(t) = N_0 e^{(\beta - \mu)t} \quad (1.2)$$

If $\beta > \mu$, the species grows exponentially. If $\mu > \beta$, then it decays until extinction.

This model can be applied, for example, at the beginning of the growth of a species, when it invades a new habitat. Or to the growth of a bacteria in a Petri dish with enough nutrient that it can be viewed as invariant for the duration of the observation.

Though, the assumption of an invariant habitat is not really realistic in a lot of other situations.

1.3 A more realistic model : logistic growth (Verhulst model, 1838)

As stated by Verhulst a long time ago, "the growth of a population is limited by the space available and the fertility of its fields" [13]. This cannot be expressed with the previous model, based on the idea of an invariant habitat. With this new assumption, if the population exceeds some threshold level, the habitat cannot support its growth. More precisely, the higher a population number, the less its growth rate. This leads to the new model :

$$\frac{dN}{dt} = rN - \phi(N) \quad (1.3)$$

The easiest function for ϕ will be a power function, simplest of all being the square function $\phi(N) = aN^2$. The new equation given by Verhulst is then

$$\frac{dN}{dt} = (r - aN)N \quad (1.4)$$

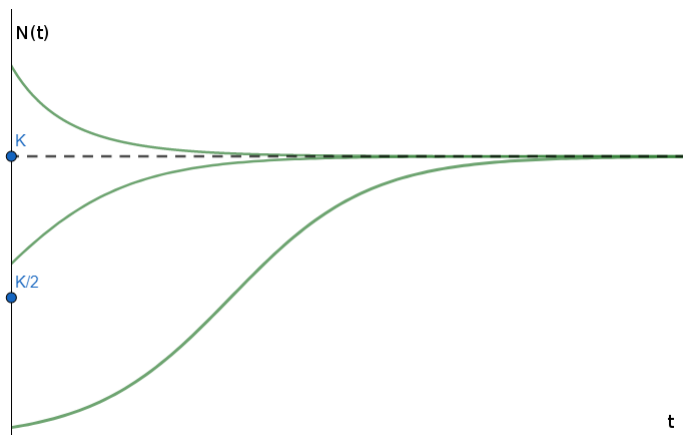


Figure 1.1: Logistic population growth

frequently written as

$$\frac{dN}{dt} = r \left(1 - \frac{N}{K} \right) N \quad (1.5)$$

to put forward K , called the *carrying capacity*, representing the limit of the population size in the model.

In this case, we can obtain an analytical solution for N by a separation of variables :

$$N(t) = K \frac{N_0}{N_0 + (K - N_0)e^{-rt}} \rightarrow K \text{ as } t \rightarrow +\infty \quad (1.6)$$

The graph of $N(t)$ is shown in Figure 1.1 depending on the value N_0 . When $N_0 < K/2$, the curve is a sigmoid (it presents an inflection point), as the function N is a logistic function. This gives the other name of this model: the *logistic growth model*.

1.4 A model of an interaction between a prey species and its predator species

To model the interaction between one species (the prey) being eaten by another (the predator), we make the following assumptions :

- The prey species undergoes a Malthusian growth in the absence of predation with a rate $r > 0$.
- The predator species would go extinct in the absence of prey with a rate $-\delta < 0$.
- We assume the response to predation will follow a *mass action law*.

We then obtain the Lotka-Volterra model for predation :

$$\begin{cases} \frac{dH}{dt} = rH(t) - aH(t)P(t) \\ \frac{dP}{dt} = -\delta P(t) + \gamma aH(t)P(t) \end{cases} \quad (1.7)$$

where a is the *predation rate*, with aHP the number of preys consumed by predator in the time unit, and γ is the *energy conversion rate*, meaning the per capita number of new predators for each prey consumed.

From the system(1.7) we get the equations

$$H(t) = H(0)e^{\int_0^t (r - aP(s)) ds}, \quad P(t) = P(0)e^{\int_0^t (-\delta + \gamma aH(s)) ds} \quad (1.8)$$

and since we take $H(0) \geq 0, P(0) \geq 0$, then $H(t) \geq 0, P(t) \geq 0, \forall t \geq 0$.

From the Cauchy-Lipschitz theorem, and since the system(1.7) is autonomous, the trajectories of the solutions in the phase plane cannot cross each other. Furthermore, we notice that the function

$$F(H, P) = \delta \ln(H) + r \ln(P) - \gamma aH - aP \quad (1.9)$$

is such that $dF/dt = 0$; F is called a *first integral* of the system(1.7). Thus, the trajectories of the solutions follow the curves given by $F = \text{constant}$. And since

$$\lim_{H+P \rightarrow \infty} (\delta \ln(H) + r \ln(P) - \gamma aH - aP) = -\infty \quad (1.10)$$

the solutions of the system(1.7) are bounded. Furthermore, the trajectories in the phase plane are closed, as illustrated in Figure(1.2). It means that the solutions are periodic, as we can see in Figure(1.3).

For an ecological interpretation, when the predator species grows in size, it means they will eat more, implying the decay of the prey species. On the other hand, when the number of prey is low, the predators have less to eat, and it's their turn to decay, leading to the growth of the prey species. It is then natural to find periodic solutions with a phase shift.

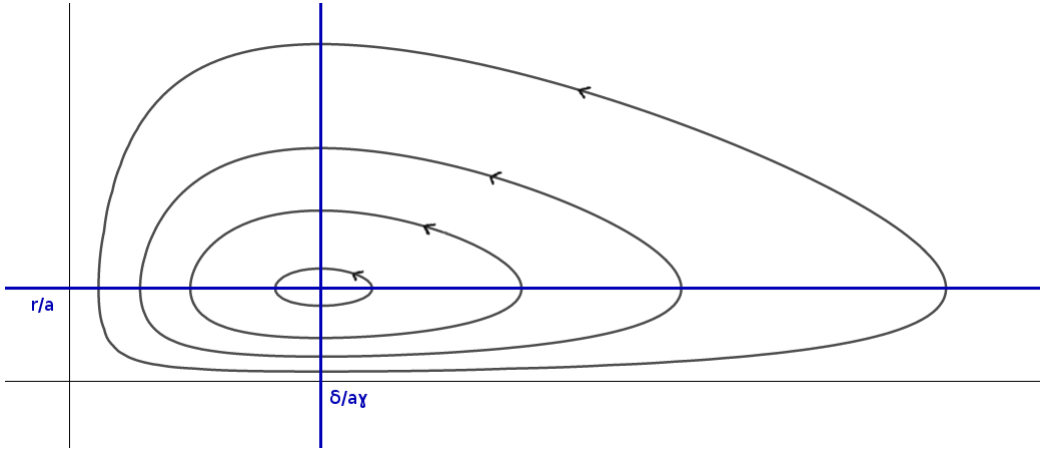


Figure 1.2: Phase plane (H, P) of the Lotka-Volterra prey-predator model.

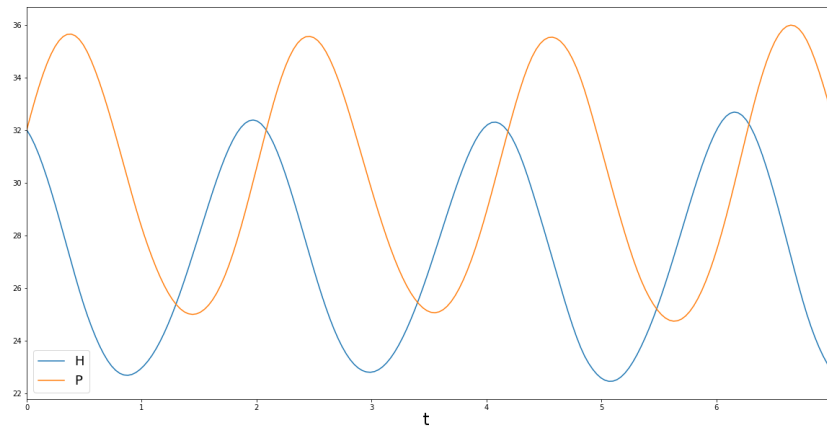


Figure 1.3: Solutions of the Lotka-Volterra prey-predator model, with $r = 3$; $a = 0.1$; $\delta = 3$; $\gamma = 1.1$.

1.5 A model of an interaction between two species competing for natural resources

Finally we will present the Lotka-Volterra model for describing the interaction of two prey species competing for natural resources. We consider that in the absence of competitor, the species would follow a logistic growth. The model is the following ;

$$\begin{cases} \frac{\partial N_1}{\partial t} = (r_1 - \gamma_{11}N_1 - \gamma_{12}N_2)N_1 = f_1(N_1, N_2) \\ \frac{\partial N_2}{\partial t} = (r_2 - \gamma_{21}N_1 - \gamma_{22}N_2)N_2 = f_2(N_1, N_2) \end{cases} \quad (1.11)$$

where $r_1 > 0$, $r_2 > 0$ are the intrinsic growth of each species, $\gamma_{11} > 0$, $\gamma_{22} > 0$ describe the effect of logistic growth, and $\gamma_{12} > 0$, $\gamma_{21} > 0$ describe the effect of the competition on the species.

The *steady states* are given by the equations

$$\begin{cases} 0 = (r_1 - \gamma_{11}N_1 - \gamma_{12}N_2)N_1 \\ 0 = (r_2 - \gamma_{21}N_1 - \gamma_{22}N_2)N_2 \end{cases} \quad (1.12)$$

which give the following possibilities

$$\begin{aligned} (N_1^*, N_2^*) &= (0, 0), \text{ or } \left(\frac{r_1}{\gamma_{11}}, 0\right), \text{ or } \left(0, \frac{r_2}{\gamma_{22}}\right) \\ &\text{or } \left(\frac{r_1\gamma_{22} - r_2\gamma_{12}}{\gamma_{11}\gamma_{22} - \gamma_{21}\gamma_{12}}, \frac{r_2\gamma_{11} - r_1\gamma_{21}}{\gamma_{11}\gamma_{22} - \gamma_{21}\gamma_{12}}\right) \end{aligned}$$

For the *stability* of those steady states, we study the eigenvalues of the community matrix :

$$\begin{aligned} &\begin{pmatrix} \frac{\partial f_1}{\partial N_1} & \frac{\partial f_1}{\partial N_2} \\ \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \end{pmatrix}_{(N_1^*, N_2^*)} \\ = &\begin{pmatrix} r_1 - 2\gamma_{11}N_1 - \gamma_{12}N_2 & -\gamma_{12}N_1 \\ -\gamma_{21}N_2 & r_2 - \gamma_{21}N_1 - 2\gamma_{22}N_2 \end{pmatrix}_{(N_1^*, N_2^*)} \end{aligned} \quad (1.13)$$

- For $(0, 0)$ the eigenvalues are $\lambda_1 = r_1$, $\lambda_2 = r_2$, so it's always unstable.
- For $(r_1/\gamma_{11}, 0)$, the eigenvalues are $\lambda_1 = -r_1$, $\lambda_2 = r_2 - \gamma_{21}r_1/\gamma_{11}$, so it's stable when $\gamma_{21}/\gamma_{11} > r_2/r_1$.

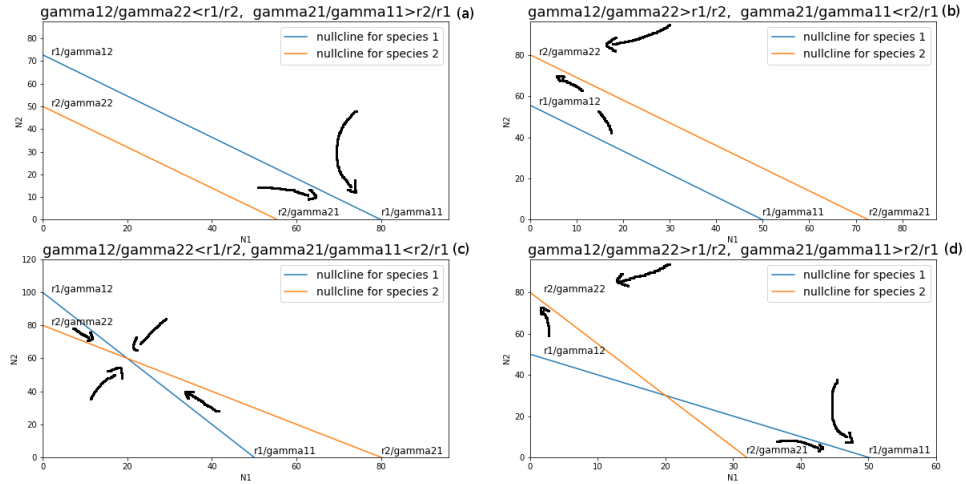


Figure 1.4: Stability of a two species with interspecific competition system depending on the parameters.

- For $(0, r_2/\gamma_{22})$, the eigenvalues are $\lambda_1 = r_1 - \gamma_{12}r_2/\gamma_{22}$, $\lambda_2 = r_2$, so it's stable when $\gamma_{12}/\gamma_{22} > r_1/r_2$.
- For the coexistence equilibrium, it is stable when $\gamma_{12}/\gamma_{22} < r_1/r_2$ and $\gamma_{21}/\gamma_{11} < r_2/r_1$.

The Figure(1.4) sums up the results. We observe that in the case (d), there is a case of *bistability*. The final state of the system depends on the initial values.

Chapter 2

Number of prey species that can coexist with a shared predator

2.1 Modeling the Apparent competition effect

2.1.1 Apparent competition

The competition we talked about in the previous chapter are direct effects. But there are also indirect effect. The *apparent competition*, as described by Holt [5], is such an effect. It is the negative effect the prey species have on one another *through* the existence of a shared predator. It is also called the competition for enemy-free space [7]. A schematic representing its working is given in Figure 2.1.

2.1.2 Hypothesis

In this chapter, we are interested in knowing how many prey species could coexist when sharing a predator, and what kind of species are the most likely to survive.

To answer this question, we model the situation following those assumptions :

- The interactions between species follow a Lotka-Voltera model.

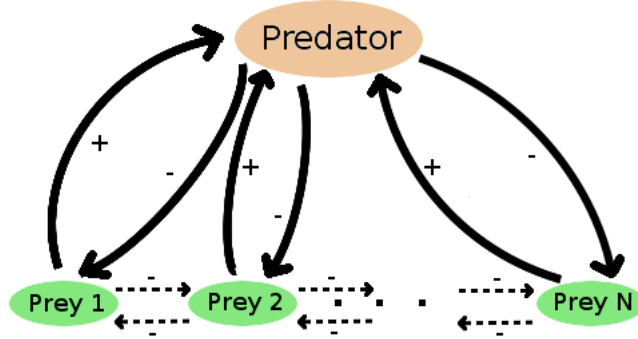


Figure 2.1: The + symbol indicates a positive effect on the species at the end of the arrow, the - a negative effect. The plain arrows illustrate direct effect, the dotted arrows indicate the apparent competition effect.

- The growth of every prey species is limited by their environment natural capacity (logistic growth).
- There are no direct competition for food or space between the prey species (no interspecific competition)
- No intraspecific density effect (logistic effect) is assumed for the predator.

2.1.3 Model

$$\begin{cases} \frac{dP}{dt} = -\delta P + \sum_{i=1}^n c_i b_i H_i P \\ \frac{dH_i}{dt} = (r_i - \beta_i H_i) H_i - b_i H_i P \quad (i = 1, 2, \dots, n), \end{cases} \quad (2.1)$$

with P the population size of the predators, $\delta > 0$ their natural death rate, H_i the population size of the preys i , $r_i > 0$ their intrinsic growth rate, $c_i > 0$ the energy conversion rate of the predation for preys i , $b_i > 0$ the predation rate for preys i and $\beta_i > 0$ the coefficient of the intraspecific density effect on preys i .

Without loss of generality, we assume the following order of the numbering for preys:

$$\frac{r_1}{b_1} \geq \frac{r_2}{b_2} \geq \dots \geq \frac{r_n}{b_n}. \quad (2.2)$$

2.2 Equilibria and their stability

2.2.1 Domain of study

The solution for $P(t)$ in the system (2.1) being :

$$P(t) = P(t_0) \exp \left[-\delta t + \sum_{i=1}^n c_i b_i \int_{t_0}^t H_i(\tau) d\tau \right] \quad (2.3)$$

then $P(0) = 0 \iff P(t) = 0 \forall t > 0$ and $P(0) > 0 \iff P(t) > 0 \forall t > 0$.

With the initial data

$$(P(t_0), H_1(t_0), \dots, H_{i-1}(t_0), 0, H_{i+1}(t_0), \dots, H_n(t_0)), P(t_0) \geq 0$$

we have a Cauchy problem.

$$(P(t), H_1(t), \dots, H_{i-1}(t), 0, H_{i+1}(t), \dots, H_n(t)), \forall t > t_0$$

is a solution of this Cauchy problem, and this maximal solution is then unique (Cauchy-Lipschitz Theorem). As we are in an autonomous system, it means that if $H_i(0) > 0$, then $H_i(t) > 0, \forall t > 0$. This being true for any $1 \leq i \leq n$.

Finally, if $H_i(t) \geq \frac{r_i}{\beta_i}$ and $P(t) > 0$, then $\frac{dH_i}{dt} < 0$. As we have

$$y'(t) = (r_i - \beta_i y)y \implies \lim_{t \rightarrow \infty} y(t) = \frac{r_i}{\beta_i}$$

and here $P(t \rightarrow \infty) > 0$, then :

$$\lim_{t \rightarrow \infty} H_i(t) < \frac{r_i}{\beta_i}$$

Meaning that there exists a t_1 where $H_i(t_1) = \frac{r_i}{\beta_i}$. Furthermore, since

$$\left. \frac{dH_i}{dt} \right|_{H_i \geq \frac{r_i}{\beta_i}} \leq -b_i \frac{r_i}{\beta_i} P < 0 \text{ if } P > 0$$

then $P(t) > 0 \iff H_i(t) < \frac{r_i}{\beta_i}$.

On the other hand if $P = 0$ then $H_i \rightarrow \frac{r_i}{\beta_i}$, and we can approximate that there also exists a time t_2 where $H_i(t_2) = \frac{r_i}{\beta_i}$.

Then, without loss of generality, we can assume that we will work in the domain $0 < H_i(t) \leq \frac{r_i}{\beta_i}, \forall t > 0, \forall 1 \leq i \leq n$ and $P(t) \geq 0, \forall t > 0$.

2.2.2 Conditions for Predator's extinction

Theorem 1. *The steady state with the predator's extinction for the system (2.1)*

$$(P, H_1, H_2, \dots, H_n) = \left(0, \frac{r_1}{\beta_1}, \frac{r_2}{\beta_2}, \dots, \frac{r_n}{\beta_n}\right) \quad (2.4)$$

is stable if and only if :

$$\delta \geq R_n := \sum_{i=1}^n \frac{c_i b_i^2 r_i}{\beta_i b_i} \quad (2.5)$$

Furthermore, it is then globally asymptotically stable.

Proof.

$$\frac{dP}{dt} = \left(-\delta + \sum_{i=1}^n c_i b_i H_i\right) P \leq \left(-\delta + \sum_{i=1}^n \frac{c_i b_i^2 r_i}{\beta_i b_i}\right) P = (-\delta + R_n)P$$

If $\delta > R_n$, then

$$0 \leq P(t) \leq P(0)e^{(-\delta+R_n)t} \xrightarrow[t \rightarrow \infty]{} 0,$$

and then $P(t) \xrightarrow[t \rightarrow \infty]{} 0$.

If $\delta = R_n$, then

$$\frac{dP}{dt} = \left(-R_n + \sum_{i=1}^n c_i b_i H_i\right) P = \sum_{i=1}^n c_i b_i \left(-\frac{r_i}{\beta_i} + H_i\right) P < 0$$

and $P(t) \xrightarrow[t \rightarrow \infty]{} 0$.

On the other hand, if we suppose $P(t) \xrightarrow[t \rightarrow \infty]{} 0$, then $H_i(t) \xrightarrow[t \rightarrow \infty]{} \frac{r_i}{\beta_i}$, $\forall 1 \leq i \leq n$. And from the logistic model, we can also say that for any $k > 0$, $(0, \frac{r_1}{\beta_1}, \dots, \frac{r_k}{\beta_k}, 0, \dots, 0)$ is unstable. A local stability analysis of $(0, \frac{r_1}{\beta_1}, \dots, \frac{r_n}{\beta_n})$ gives the necessary condition $-\delta + R_n \leq 0$, and the previous arguments allow to say this is then a condition for global asymptotic stability. \square

This theorem is illustrated on the Figure (2.2).

Since R_n increases with n , it means that the more prey species available to be preyed upon, the higher are the chances of the predator to survive. On the other hand, we see here that the most relevant prey species to the predator survival are those with a high $c_i b_i r_i / \beta_i$

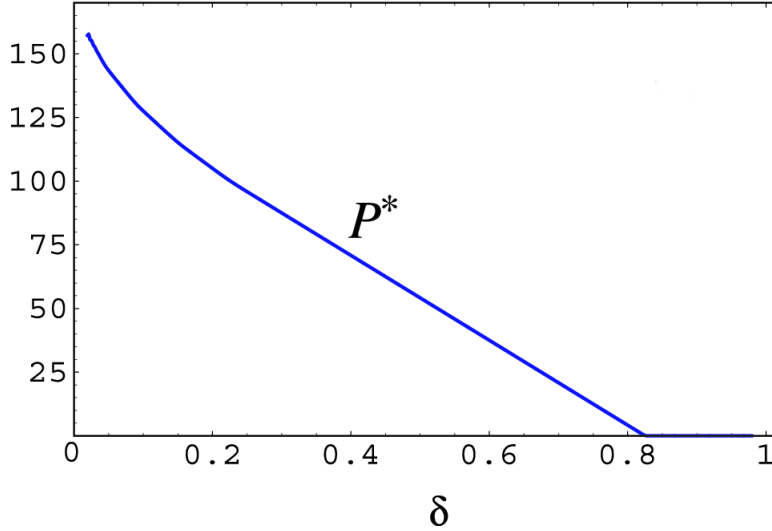


Figure 2.2: Evolution of the equilibrium size of the predator population depending on the parameter delta. $c_i = 0.1$; $r_1 = 0.1$; $r_2 = 0.115$; $r_3 = 0.13$; $r_4 = 0.145$; $r_5 = 0.16$; $r_6 = 0.175$; $b_i = 0.001$; $\beta_i = 0.0001$; $1 \leq i \leq 6$

2.2.3 Conditions for prey species' extinction

As seen in Figure (2.3), the number of prey surviving after some time depends on the condition of the system. We will now try to understand those conditions. Let's then study the steady state E_k^* for (2.1) :

$$E_k^* = (P_{[k]}^*, H_{[k],1}^*, H_{[k],2}^*, \dots, H_{[k],k}^*, \underbrace{0, \dots, 0}_{n-k}) \quad (2.6)$$

$$H_{[k],i}^* > 0 \text{ for } 1 \leq i \leq k, \text{ and } P_{[k]}^* > 0 \quad (2.7)$$

From (2.1) this steady state E_k^* can be uniquely given by

$$H_{[k],i}^* = \frac{r_i - b_i P_{[k]}^*}{\beta_i}; \quad P_{[k]}^* = \frac{R_k - \delta}{B_k} \quad (2.8)$$

where

$$R_k := \sum_{i=1}^k \frac{c_i b_i^2 r_i}{\beta_i b_i}; \quad B_k := \sum_{i=1}^k \frac{c_i b_i^2}{\beta_i} \quad (2.9)$$

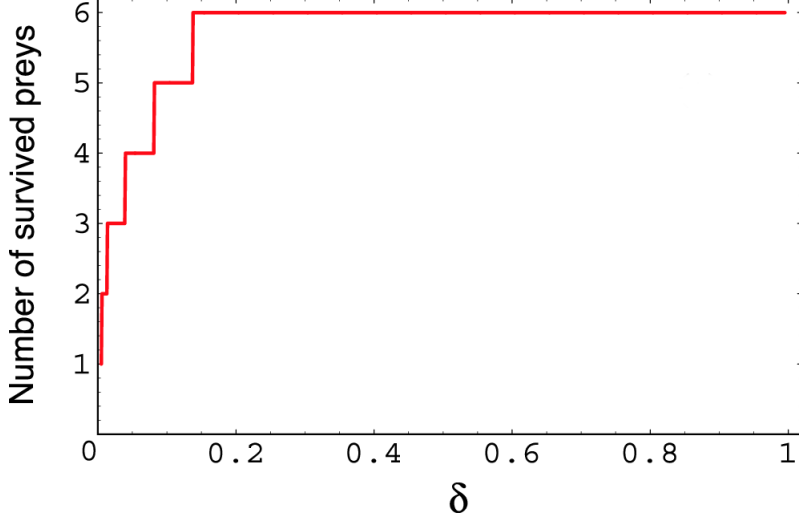


Figure 2.3: Evolution of the number of prey species depending on the parameter delta. $c_i = 0.1$; $r_1 = 0.1$; $r_2 = 0.115$; $r_3 = 0.13$; $r_4 = 0.145$; $r_5 = 0.16$; $r_6 = 0.175$; $b_i = 0.001$; $\beta_i = 0.0001$; $1 \leq i \leq 6$

From (2.7) and (2.8), we can find the following condition for the existence of the equilibrium E_k^* :

$$R_k - \frac{r_i}{b_i} B_k < \delta < R_k, \quad \forall 1 \leq i \leq k \quad (2.10)$$

And from (2.2), this condition is equivalent to

$$R_k - \frac{r_k}{b_k} B_k < \delta < R_k \quad (2.11)$$

For the convenience of the mathematical arguments in the following part, we show here the following lemma :

Lemma 1. *The sequence $\{R_k - (r_k/b_k)B_k\}$, $1 \leq k \leq n$ is non-negative and non-decreasing.*

Indeed, from (2.2) and (2.9), we have

$$R_{\ell+1} - \frac{r_{\ell+1}}{b_{\ell+1}} B_{\ell+1} - \left(R_{\ell} - \frac{r_{\ell}}{b_{\ell}} B_{\ell} \right) = \left(\frac{r_{\ell}}{b_{\ell}} - \frac{r_{\ell+1}}{b_{\ell+1}} \right) \sum_{i=1}^{\ell} \frac{c_i b_i^2}{\beta_i} \geq 0$$

and $R_1 - \frac{r_1}{b_1}B_1 = 0$ from the definition (2.9). This proves the lemma.

Now we define a specific index of prey species \bar{s} by :

$$\bar{s} := \max\{\ell \in [1, n] \mid \frac{r_\ell}{b_\ell} > P_{[\ell]}^*\} = \max\{\ell \in [1, n] \mid \delta > R_\ell - \frac{r_\ell}{b_\ell}B_\ell\} \quad (2.12)$$

From (2.8) and (2.9), we note that

$$P_{[1]}^* = \frac{R_1 - \delta}{B_1} = \frac{r_1}{b_1} - \frac{\delta\beta_1}{c_1b_1^2} < \frac{r_1}{b_1} \quad (2.13)$$

which proves that \bar{s} always exists. Then we note that

$$\frac{r_j}{b_j} \leq P_{[j]}^* := \frac{R_j - \delta}{B_j}, \quad \text{that is} \quad \delta \leq R_j - \frac{r_j}{b_j}B_j \quad \forall j > \bar{s} \quad (2.14)$$

because of lemma (1). We can then prove the following two theorems concerning the existence and stability of the steady state

$$E_{\bar{s}}^* = (P_{[\bar{s}]}^*, H_{[\bar{s}],1}^*, H_{[\bar{s}],2}^*, \dots, H_{[\bar{s}],\bar{s}}^*, 0, \dots, 0) :$$

Theorem 2. *The steady state $E_{\bar{s}}^*$ with $\bar{s} < n$ exists and is globally asymptotically stable if and only if*

$$R_{\bar{s}} - \frac{r_{\bar{s}}}{b_{\bar{s}}}B_{\bar{s}} < \delta \leq R_{\bar{s}+1} - \frac{r_{\bar{s}+1}}{b_{\bar{s}+1}}B_{\bar{s}+1} \quad (2.15)$$

Theorem 3. *The steady state E_n^* exists and is globally asymptotically stable if and only if*

$$R_n - \frac{r_n}{b_n}B_n < \delta < R_n \quad (2.16)$$

Proof. First we consider the existence of the steady state $E_{\bar{s}}^*$. When $\bar{s} < n$, from (2.14), we have (2.15). On the other hand, from the definition (2.9) we can easily find that

$$R_{k+1} - \frac{r_{k+1}}{b_{k+1}}B_{k+1} = R_k - \frac{r_{k+1}}{b_{k+1}}B_k \quad \forall 1 \leq k \leq n \quad (2.17)$$

Therefore we have

$$\delta \leq R_{\bar{s}+1} - \frac{r_{\bar{s}+1}}{b_{\bar{s}+1}}B_{\bar{s}+1} = R_{\bar{s}} - \frac{r_{\bar{s}+1}}{b_{\bar{s}+1}}B_{\bar{s}} < R_{\bar{s}} \quad \text{for } \bar{s} < n \quad (2.18)$$

Hence, when the condition (2.15) is satisfied, the condition (2.11) for the existence of the steady state $E_{\bar{s}}^*$ with $\bar{s} < n$ holds. When $\bar{s} = n$, the condition (2.16) is the condition (2.11) with $\bar{s} = n$ for the existence of the steady state E_n^* .

Next, let's consider the stability of this steady state. For the case of $\bar{s} < n$, we define the function

$$\begin{aligned} V_{\bar{s}}(t) &:= P_{[\bar{s}]}^* \left\{ \frac{P(t)}{P_{[\bar{s}]}^*} - 1 - \log \frac{P(t)}{P_{[\bar{s}]}^*} \right\} \\ &\quad + \sum_{i=1}^{\bar{s}} c_i H_{[\bar{s}],i}^* \left\{ \frac{H_i(t)}{H_{[\bar{s}],i}^*} - 1 - \log \frac{H_i(t)}{H_{[\bar{s}],i}^*} \right\} + \sum_{i=\bar{s}+1}^n c_i H_i(t) \end{aligned} \quad (2.19)$$

This function is continuously differentiable (on the study domain), radially unbounded and positive definite for any $(P, H_1, \dots, H_n) \neq E_{\bar{s}}^*$. Furthermore,

$$\begin{aligned} \frac{dV_{\bar{s}}(t)}{dt} &= - \sum_{i=1}^{\bar{s}} c_i \beta_i \{H_i(t) - H_{[\bar{s}],i}^*\}^2 \\ &\quad + \sum_{i=\bar{s}+1}^n c_i H_i(t) \{r_i - \beta_i H_i(t) - b_i P_{[\bar{s}]}^*\} \end{aligned} \quad (2.20)$$

From the definition of \bar{s} by (2.12),

$$\begin{aligned} r_i - \beta_i H_i(t) - b_i P_{[\bar{s}]}^* &< r_i - \beta_i H_i(t) - b_i \frac{r_{\bar{s}}}{b_{\bar{s}}} \\ &= -\beta_i H_i(t) - b_i \left(\frac{r_{\bar{s}}}{b_{\bar{s}}} - \frac{r_i}{b_i} \right) < 0 \end{aligned} \quad (2.21)$$

for any $i > \bar{s}$ and any $t > 0$. Thus from this, we can say that

$$\begin{cases} \dot{V}_{\bar{s}}(P, H_1, \dots, H_n) \leq 0, & (P, H_1, \dots, H_n) \in \Omega =]0, +\infty[^{\bar{s}+1} \times [0, +\infty[^{n-\bar{s}} \\ \dot{V}_{\bar{s}}(\mathbf{X}) = 0 \iff \mathbf{X} = (P, H_{[\bar{s}],1}^*, \dots, H_{[\bar{s}],\bar{s}}^*, 0, \dots, 0), & \forall P > 0 \end{cases} \quad (2.22)$$

Then, the *LaSalle Invariance Theorem* states that :

$$\begin{aligned} \forall \mathbf{Y}_0 = (P(0), H_1(0), \dots, H_n(0)) \in \Omega =]0, +\infty[^{\bar{s}+1} \times [0, +\infty[^{n-\bar{s}}, \\ \omega(\mathbf{Y}_0) \subset \{\mathbf{X} \mid \dot{V}(\mathbf{X}) = 0\} = \{(P, H_{[\bar{s}],1}^*, \dots, H_{[\bar{s}],\bar{s}}^*, 0, \dots, 0) \mid P > 0\} \end{aligned}$$

where $\omega(\mathbf{Y}_0)$ is the limit set of the solution of our system starting at the point \mathbf{Y}_0 .

Since our solution must still obey the system (2.1) while belonging to this limit set, then

$$\lim_{t \rightarrow +\infty} P(t) = P_{[\bar{s}]}^* \quad (2.23)$$

This concludes the proof of the global asymptotic stability of $E_{\bar{s}}^*$, and the arguments at the beginning of the proof combined with this prove the Theorem 2.

For the case of $\bar{s} = n$, let's consider the continuously differentiable (on the study domain) and radially unbounded function

$$\begin{aligned} V_n(t) &:= P_{[n]}^* \left\{ \frac{P(t)}{P_{[n]}^*} - 1 - \log \frac{P(t)}{P_{[n]}^*} \right\} \\ &+ \sum_{i=1}^n c_i H_{[n],i}^* \left\{ \frac{H_i(t)}{H_{[n],i}^*} - 1 - \log \frac{H_i(t)}{H_{[n],i}^*} \right\} \end{aligned} \quad (2.24)$$

As before, this function is continuously differentiable (on the study domain), radially unbounded and positive definite for any $(P, H_1, \dots, H_n) \neq E_n^*$. Furthermore,

$$\frac{dV_n(t)}{dt} = - \sum_{i=1}^n c_i \beta_i \{ H_i(t) - H_{[n],i}^* \}^2 \leq 0 \quad (2.25)$$

With the same arguments as previously, with $\Omega =]0, +\infty[^{n+1}$ and applying the *LaSalle's Invariance Theorem*, we can also conclude in this case that E_n^* is globally asymptotically stable, which in turn finishes the proof of the Theorem 3. \square

If we look more specifically at the steady state with only one prey species surviving, E_1^* , we have the following corollary from Theorem 2 :

Corollary 1. *The steady state E_1^* exists and is globally asymptotically stable if and only if*

$$0 < \delta \leq R_2 - \frac{r_2}{b_2} B_2 = R_1 \quad (2.26)$$

This comes from the fact that $R_1 - (r_1/b_1)B_1 = 0$ from the definition (2.9).

Finally, from Theorem 1, 2, 3 and Corollary 2, we get the principal theorem :

Theorem 4. *The system (2.1) always has a globally asymptotically stable steady state.*

As for the proof of this theorem, it is easily seen since the conditions for the existence and global stability of the steady states given by (2.5), (2.15), (2.16), (2.26) are complementary, and the union of those conditions for all equilibria covers all parameter regions from Lemma 1. As a consequence, we do not need to consider any periodic or chaotic stationary solution for (2.1), because such a solution is not approachable from almost any initial condition even if it exists. Furthermore, it also gives this last corollary :

Corollary 2. *For the system (2.1), any equilibrium with the persistent predator other than the type of E_k^* -defined by (2.6)- is always unstable even if it exists.*

2.2.4 Which prey species can coexist with a shared predator ?

This analysis shows that the prey species with the most risk to be eliminated are the ones with the lowest r_i/b_i in this model.

Another result shown here is, if all the species have the same ratio r/b , then theoretically there can be an unlimited number of them cohabiting. More realistically, it means that if the ratio r_i/b_i are close from one another, then more species can coexist with a shared predator.

On the other hand, if one or two species have a high ratio r_i/b_i , then it is much more likely for fewer species to be able to coexist. Indeed, in the second case, the species with a high r_i/b_i ratio will create a strong apparent competition on the other species, leading them to extinction. Those results are shown on the figures (2.4) and (2.5).

This phenomenon was already empirically stated in [5] and [10] : a high species diversity exists under the condition that the value of r/b is similar for all prey species.

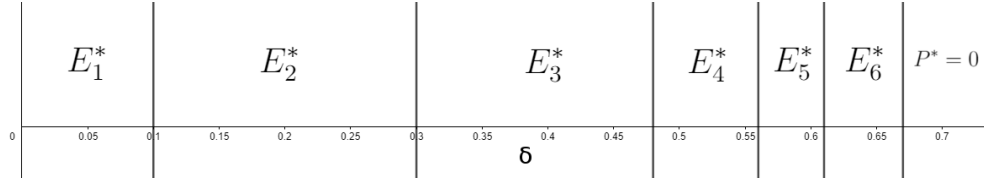


Figure 2.4: Bifurcation diagram depending on the parameter delta, for 6 species with ratio r_i/b_i far from one another. $r_1 = 0.3$; $r_2 = 0.2$; $r_3 = 0.1$; $r_4 = 0.04$; $r_5 = 0.02$; $r_6 = 0.01$; $b_i = 0.001$; $c_i = 0.1$; $\beta_i = 0.0001$; $1 \leq i \leq 6$

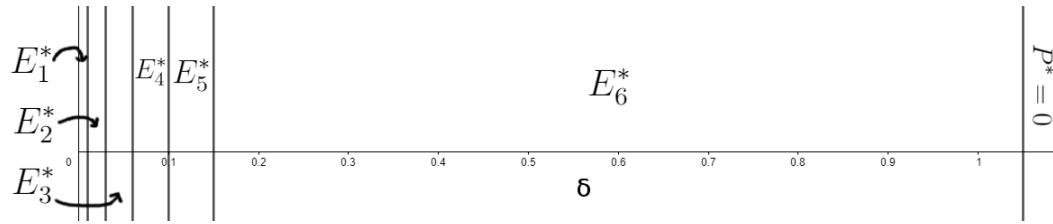


Figure 2.5: Bifurcation diagram depending on the parameter delta, for 6 species with ratio r_i/b_i close from one another. $r_1 = 0.2$; $r_2 = 0.19$; $r_3 = 0.18$; $r_4 = 0.17$; $r_5 = 0.16$; $r_6 = 0.15$; $b_i = 0.001$; $c_i = 0.1$; $\beta_i = 0.0001$; $1 \leq i \leq 6$

Chapter 3

Spatial movement

In all our previous work, we considered the species as spatially-homogeneous. It gives good result to understand some situations, but it is obviously wrong for studying others, for example the spread of a population. To solve that problem, Skellam introduced the diffusion in the ecological model, and successfully applied it to the data of Ulbrich [12] to explain the speed of spreading of a muskrat population [11], see Figure (3.1).

In this chapter, we will ask ourselves how is the diffusion phenomenon affecting the previously known results of prey interactions. More precisely, how is it affecting the survival of a species living by itself, or the competition between two prey species.

3.1 One species diffusing in a finite space

3.1.1 Modeling the spatial spread

We now consider a spatial region $\Omega \in \mathbb{R}^d$, $d \leq 3$. Then, the description of the local density of the population is given by

$$N(\mathbf{x}, t), \quad \mathbf{x} \in \Omega, t \geq 0$$

To formulate our model, we will follow the conservation principle. There are two terms that regulate our population density :

- $\mathbf{J}(\mathbf{x}, t)$, the **population flux**, represents what comes into or goes out

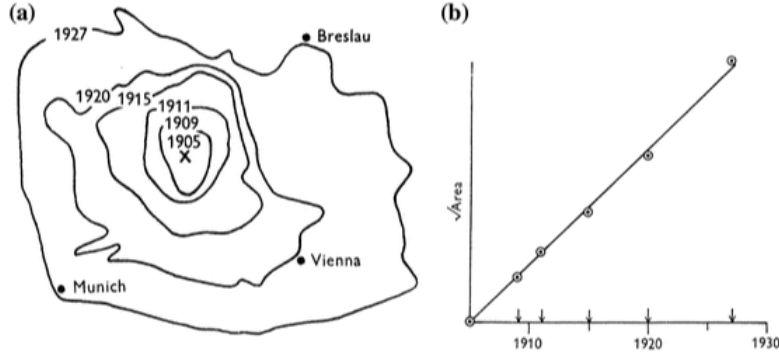


Figure 3.1: (a) Muskrat spread in Europe. (b) Square root of the area expansion depending on years. It increases linearly, as predicted by Skellam.

off our spatial boundary. It is a vector field such as :

$$\mathbf{J}(\mathbf{x}, t) \cdot \mathbf{n}_\sigma(\mathbf{x}) d\sigma dt = \text{number of individuals crossing the infinitesimal surface } d\sigma \text{ at } \mathbf{x} \text{ per unit time at time } t \text{ in the direction } \mathbf{n}_\sigma(\mathbf{x}).$$

where $\mathbf{n}_\sigma(\mathbf{x})$ is the normal to $d\sigma$.

- $f(\mathbf{x}, t)$, the **total growth rate**, represents the population local births and deaths at \mathbf{x} at time t .

Based on the conservation equation, we obtain

$$\frac{d}{dt} \int_V N(\mathbf{x}, t) d\mathbf{x} = \int_{\partial V} \mathbf{J}(\mathbf{x}, t) \cdot \mathbf{n}_\sigma(\mathbf{x}) d\sigma + \int_V f(\mathbf{x}, t) d\mathbf{x}$$

and by using the divergence theorem, we obtain

$$\frac{dN(\mathbf{x}, t)}{dt} = -\nabla \cdot \mathbf{J}(\mathbf{x}, t) + f(\mathbf{x}, t) \tag{3.1}$$

Depending on what motivates the movement, there are different ways to model a spatial spreading of a population in a model..

- The Advection : it's a transport of substance due to the motion of a fluid. For examples, a fish in a stream, or a pollen in the wind.

- The Diffusion : it arises from a Random Walk, and induces a movement from a region of higher concentration to a region of lower concentration.

We will only focus on the diffusion case. With the hypothesis that dx^2/dt is constant and that there is an equal probability to go in any direction, the model for $\mathbf{J}(\mathbf{x}, t)$ is given by *Fick Law* (which is the result of a simple Taylor-expansion) :

$$\mathbf{J}(\mathbf{x}, t) = -D\nabla N(\mathbf{x}, t) \quad (3.2)$$

With $D \geq 0$ the diffusion coefficient, representing the speed at which the species spreads.

As for $f(\mathbf{x}, t)$, we will use the usual models we studied previously, depending on the situation (logistic growth, prey-predator, ...)

Finally, we must implement *boundary conditions* to describe what happens at the border of the habitat. Among all the possibilities, there are two in particular that are more frequently used :

- The Dirichlet condition : used in case of an extremely inhospitable border.

$$N(\mathbf{x}, t) = 0, \quad \forall t \geq 0, \quad \forall \mathbf{x} \in \partial\Omega \quad (3.3)$$

- The Neumann conditions : used in case of a completely closed habitat.

$$\mathbf{J}(\mathbf{x}, t) \cdot \mathbf{n}(\mathbf{x}) = 0, \quad \forall t \geq 0, \quad \forall \mathbf{x} \in \partial\Omega \quad (3.4)$$

3.1.2 The model and steady states with diffusion and Dirichlet conditions

For the simplicity of all the models to come, we will now consider them in one dimensional spaces, unless specified otherwise. We consider a finite space, $x \in [0, L]$.

We assume that the species follows a logistic growth, and diffuses according to Fick Law. This is called the *Fisher equation*. Furthermore, we use Dirichlet conditions for boundary conditions :

$$\frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} + r \left(1 - \frac{N}{K}\right) N \quad (3.5)$$

$$N(0, t) = N(L, t) = 0 \quad \forall t \geq 0 \quad (3.6)$$

To find the steady states of (3.5), we study

$$0 = D \frac{\partial^2 N}{\partial x^2} + r \left(1 - \frac{N}{K}\right) N \quad (3.7)$$

When taking the diffusion into account, there are two kinds of Steady states. The *homogeneous steady states*, solutions that are independent of both time and space, and the *non-homogeneous steady states*, solutions that are independent of time only.

For the homogeneous steady states, $\partial^2 N / \partial x^2 = 0$ and the two steady states possible would be $N(x) = 0$ and $N(x) = K$, $\forall x \in [0, L]$, as in the logistic model. However, here $N(0) = N(L) = 0$, so $N(x) = K$ is impossible.

To find the non-homogeneous steady state, we will introduce $V(x) = \frac{dN(x)}{dx}$ to create a system of first order differential equations :

$$\begin{cases} \frac{dN}{dx} = V(x) \\ \frac{dV}{dx} = -\frac{r}{D} \left(1 - \frac{N(x)}{K}\right) N(x) \end{cases} \quad (3.8)$$

This will make it much easier to proceed.

If we then take the function

$$F(N, V) = V^2 + \frac{r}{D} N^2 \left(1 - \frac{2N}{3K}\right) \quad (3.9)$$

then we notice that $\frac{d}{dx} F(N(x), V(x)) = 0$. F is then a first integral of the system (3.5), which leads to :

$$\left(\frac{dN}{dx}\right)^2 + \frac{r}{D} N(x)^2 \left(1 - \frac{2N(x)}{3K}\right) = c \quad (3.10)$$

with c a real number given by $F(N(0), V(0)) = V_0^2$

Finally we obtain the relation describing our steady states with an implicit function

$$\int_0^{N^*} \frac{dy}{\sqrt{c - \frac{r}{D} y^2 \left(1 - \frac{2y}{3K}\right)}} = x \quad (3.11)$$

Finding a direct relation describing N^* cannot be achieved through this equation (3.11) ; but it will allow us to find another very important value.

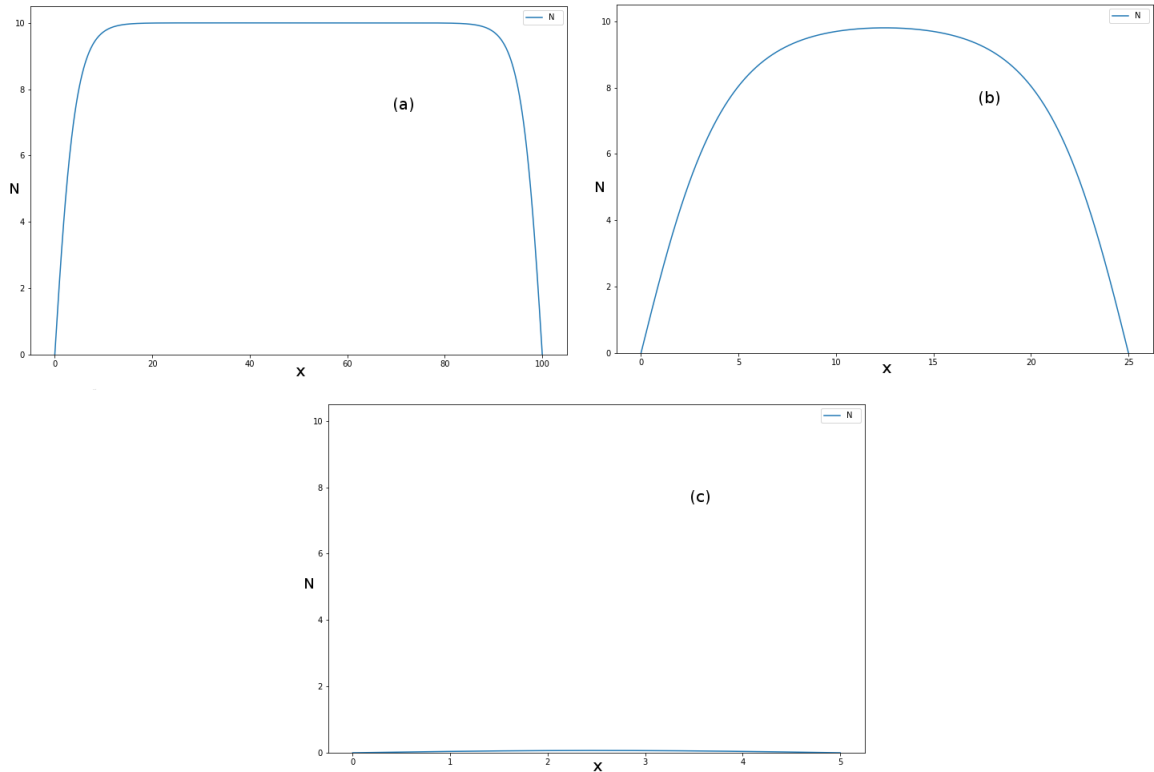


Figure 3.2: Spatial allocation of the population with $t > 100$, with $r = 0.5$; $D = 3$; $K = 10$ in the three cases. For (a) $L = 100$; for (b) $L = 25$; for (c) $L = 5$.

3.1.3 Critical patch size

A numerical analysis of this model gives the Figure (3.1.3), picturing the spatial allocation of the population after a very long time. We see on this figure that the total size of the space has a direct impact on the survival of the species. It is said that the model (3.5) with Dirichlet condition has a *critical patch size*, under which the species cannot survive. Let's find out its value.

The system (3.5) describes a species with no competitor, no predator, but dying when getting closer to the border. Then it is symmetric, with the maximum of population reached in $x = \frac{L}{2}$. This maximum cannot be greater

than K . Let's call this maximum N_M . We have

$$N(0) = 0, \quad N\left(\frac{L}{2}\right) = N_M, \quad c = F\left(N\left(\frac{L}{2}\right), 0\right) = \frac{r}{D}N_M^2\left(1 - \frac{2N_M}{3K}\right) \quad (3.12)$$

Then

$$2 \int_0^{N_M} \frac{dy}{\sqrt{\frac{r}{D}N_M^2\left(1 - \frac{2N_M}{3K}\right) - \frac{r}{D}y^2\left(1 - \frac{2y}{3K}\right)}} = L$$

and if we change the variables for $z = N_M y$, we obtain

$$2\sqrt{\frac{D}{r}} \int_0^1 \frac{dz}{\sqrt{1-z}\sqrt{1+z - \frac{2N_M}{3K}(1+z+z^2)}} = L \quad (3.13)$$

Then the minimum size possible for the species to survive is given by the limit $N_M \rightarrow 0$:

$$2\sqrt{\frac{D}{r}} \int_0^1 \frac{dz}{\sqrt{1-z^2}} = L$$

This antiderivative is given by arcsin. All in all, we find a critical patch size of value

$$L_M = \pi\sqrt{\frac{D}{r}} \quad (3.14)$$

For a species to survive while diffusing with Dirichlet bordering conditions, the space it lives in needs to be greater than L_M .

3.1.4 Stability of Steady states

Since the species is unable to survive in case $L_M < \pi\sqrt{D/r}$, then $N^* = 0$ is globally asymptotically stable within this condition.

For the study of the stability of the non-homogeneous steady states, we look at $n(x, t) = N(x, t) - N^*(x)$ with $|n(x, t)| \ll 1$ and $n(0, t) = n(M, t) = 0$. With a Taylor expansion on (3.5) we get the relation

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + r\left(1 - 2\frac{N^*}{K}\right)n \quad (3.15)$$

We will study this equation with the method of separation of variables : let's take $n(x, t) = f(t)g(x)$. It gives us

$$\begin{cases} f'(t) & = \lambda f(t) & (a) \\ Dg''(x) + g(x) \cdot r \left(1 - \frac{2N^*(x)}{K}\right) & = \lambda g(x) & (b) \end{cases} \quad (3.16)$$

This is a regular Sturm-Liouville problem, which implies :

- There exist solutions, all associated to a discrete set of eigenvalues $\lambda_1 > \lambda_2 \geq \dots \geq \lambda_k \geq \dots$
- These solutions make an orthogonal basis of the solution space
- The solution g_n associated to λ_n has exactly $n - 1$ zeros in $[0, M]$, $\forall n \geq 1$

The second point tell us that all solutions of the system will be of the form

$$n(t, x) = \sum_{n=1}^{\infty} c_n e^{\lambda_n t} g_n(x) \quad (3.17)$$

$$= e^{\lambda_1 t} \left(c_1 g_1(x) + \sum_{n=2}^{\infty} c_n e^{(\lambda_n - \lambda_1)t} g_n(x) \right) \quad (3.18)$$

To know the stability of the $N^*(x)$, we only need to know the sign of λ_1 . When multiplying by $N^*(x)$ and doing an integration by parts on (3.16.b) we obtain :

$$\begin{aligned} - \int_0^M g_1'(x) N^{*'}(x) dx + \frac{r}{D} \int_0^M \left(g_1(x) N^*(x) - 2g_1(x) \frac{(N^*(x))^2}{K} \right) dx & (3.19) \\ & = \frac{\lambda_1}{D} \int_0^M g_1(x) N^*(x) dx \end{aligned}$$

And by multiplying (3.7) by $g_1(x)$, and doing an integration by parts, we obtain :

$$- \int_0^M g_1'(x) N^{*'}(x) dx + \frac{r}{D} \int_0^M \left(g_1(x) N^*(x) - g_1(x) \frac{N^*(x)^2}{K} \right) dx = 0 \quad (3.20)$$

By adding (3.19) and (3.20) we obtain :

$$\lambda_1 = \frac{-r \int_0^M g_1(x) \frac{N^*(x)^2}{K} dx}{\int_0^M g_1(x) N^*(x) dx} \quad (3.21)$$

Since $N^*(x) > 0 \forall x \in]0, M[$ when $L_M > \pi\sqrt{D/r}$ and g_1 has no zero (so its sign is constant) then $\lambda_1 < 0$. We conclude that the non-homogeneous steady state $N^*(x)$ is stable when $L_M > \pi\sqrt{D/r}$.

3.1.5 The model and steady states with diffusion and Neumann conditions

In the same space as before, $x \in [0, L]$, we will now impose *Neumann bordering conditions*, also called *no-flux bordering conditions*

$$\frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} + r \left(1 - \frac{N}{K}\right) N r \quad (3.22)$$

$$\frac{\partial N}{\partial x} \Big|_{x=0} = \frac{\partial N}{\partial x} \Big|_{x=L} = 0 \quad \forall t \geq 0 \quad (3.23)$$

In this case, both homogeneous states $N^* = 0$ and $N^* = K$ are possible. On the other hand, when we draw the phase plane base on the first integral (3.9), we obtain Figure (3.3). A non-homogeneous solution would link two points on the U-axis, but such a trajectory doesn't exist. Hence, there are no non-homogeneous steady state with Neumann conditions.

From the same system (3.16) as in the Dirichlet case, we obtain the result for the λ_1 as in (3.21), but here since we are only concerned with N^* constant, we have :

$$\lambda_1 = -r \frac{N^*}{K} \quad (3.24)$$

So the steady states $N^* = 0$ is unstable, and the steady states $N^* = K$ is stable.

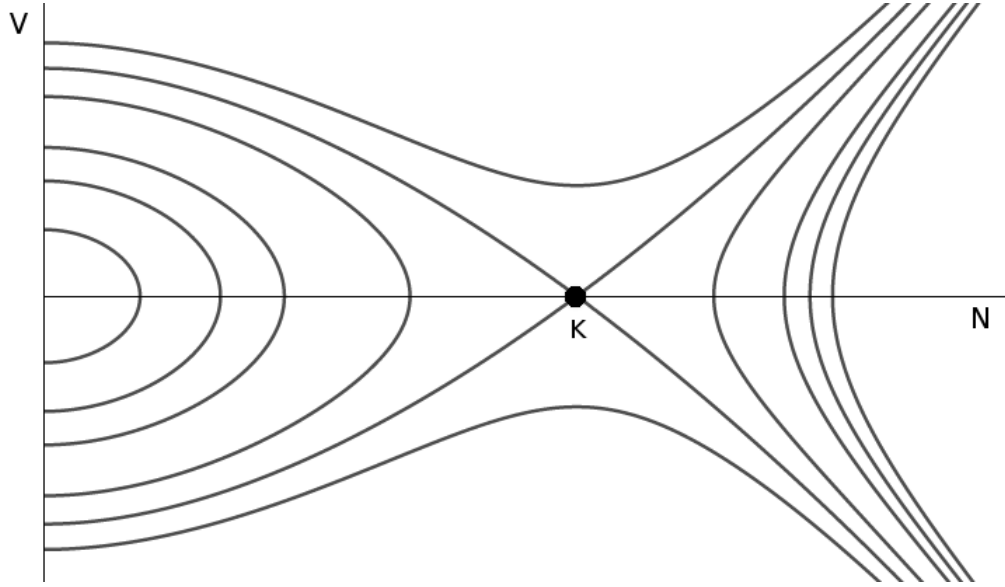


Figure 3.3: Trajectories for the system (3.22) in the phase plane (V, N)

3.2 Some general results for a 2 species competition-diffusion model with Neumann boundary conditions

3.2.1 General settings

The generalized system we work on for now is the following :

$$\begin{cases} \frac{\partial N_1}{\partial t} = D_1 \Delta N_1 + f(N_1, N_2) & (x \in \Omega, t > 0) \\ \frac{\partial N_2}{\partial t} = D_2 \Delta N_2 + g(N_1, N_2) & (x \in \Omega, t > 0) \end{cases} \quad (3.25)$$

where D_1 and D_2 are positive constants, f and g are smooth mappings of \mathbb{R}^2 into \mathbb{R} , and Ω is a bounded domain in \mathbb{R}^n with smooth boundary $\partial\Omega$. We impose Neumann boundary conditions :

$$\frac{\partial N_1}{\partial n} = \frac{\partial N_2}{\partial n} = 0 \quad (3.26)$$

where $\frac{\partial}{\partial n}$ denotes the outer normal derivative on $\partial\Omega$. Finally the initial conditions are given by the continuous functions N_{1_0} and N_{2_0} :

$$N_1(x, 0) = N_{1_0}(x), \quad N_2(x, 0) = N_{2_0}(x) \quad (x \in \Omega) \quad (3.27)$$

With the addition of the conditions :

$$\frac{\partial f}{\partial N_2}(N_1, N_2) \leq 0, \quad \frac{\partial g}{\partial N_1}(N_1, N_2) \leq 0 \quad (3.28)$$

this system is a general competition diffusion system.

3.2.2 Convergence of solutions

Then, according to Kishimoto and Weinberger [6] we have the following results:

Theorem 5. *Any non constant (i.e. spatially non-homogeneous) equilibrium solution of this competition-diffusion system is unstable if Ω is any bounded convex domain.*

Furthermore, according to Hirsch [4] we also have :

Theorem 6. *For this system, any periodic solution, if existing, is unstable.*

So all in all, we conclude :

Theorem 7. *The phenomenon of pattern formation never occurs if Ω is bounded and convex; more precisely, almost all the bounded solutions converge to some constant (i.e., spatially-homogeneous) equilibrium solutions as $t \rightarrow +\infty$*

See also for those results Matamo and Mimura [3].

3.2.3 Meaning of such a study

According to the results from before, if we want to have any kind of pattern formation, we must take a non convex domain. In 2 dimensions, it is possible, as demonstrated by the Figure(3.4).

According to the results from before, and knowing that an interval in \mathbb{R} is necessarily bounded and convex, we can have no pattern formation in a 1 dimensional setup, whatever the parameters taken. If we want to study the pattern formation in a 1 dimensional setup, it is therefore necessary to study a patchy system, or to modify the model.

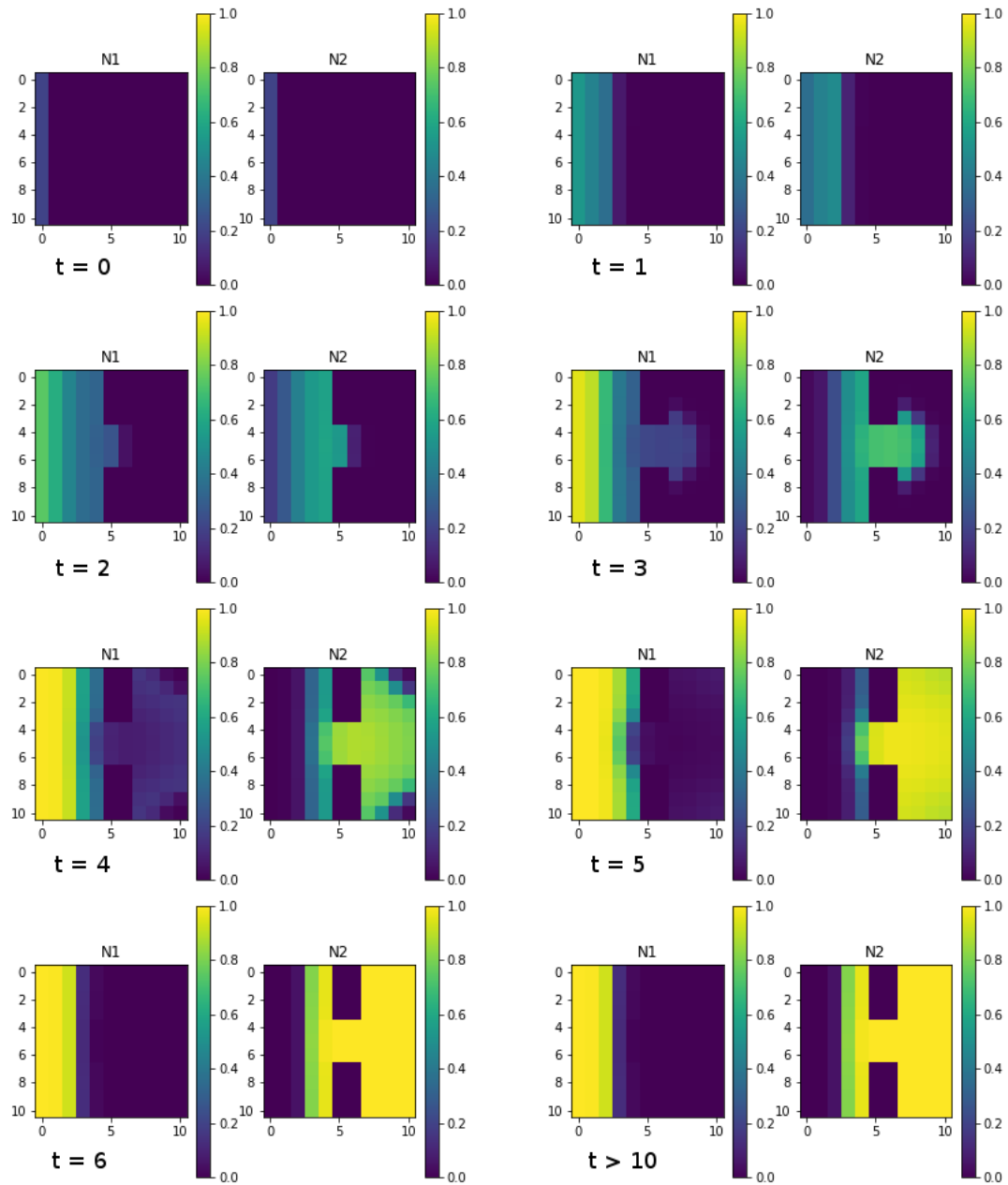


Figure 3.4: Diffusion of two species starting from the same point in a non-convex environment, with a Lotka-Volterra interspecific competition model. We can observe the formation of a naturally occurring pattern. $r_1, K_1, a_{12}, D_1 = 1, 1, 1.2, 0.3$; $r_2, K_2, a_{21}, D_2 = 1.1, 1, 1.3, 1.5$.

3.3 2 prey species competition with one of them diffusing

3.3.1 Model

Here, we are considering that one of the species is moving and the other is not. This can be seen as an approximation of a case where one of the species is diffusing much faster than the other.

$$\begin{cases} \frac{\partial N_1}{\partial t} = \begin{cases} (r_1 - \gamma_{11}N_1 - \gamma_{12}N_2)N_1 & x \in [0, l] \\ 0 & x \in (l, L] \end{cases} \\ \frac{\partial N_2}{\partial t} = (r_2 - \gamma_{21}N_1 - \gamma_{22}N_2)N_2 + D_2 \frac{\partial^2 N_2}{\partial x^2} & x \in [0, L] \end{cases} \quad (3.29)$$

To reduce the number of relevant parameters in this model, we will express it in non dimensional terms. Let's take $U = \frac{\gamma_{11}}{r_1}N_1$, $V = \frac{\gamma_{22}}{r_2}N_2$, $\hat{t} = r_2t$, $\hat{x} = \frac{x}{L}$, $d = \frac{l}{L}$, $R = \frac{r_1}{r_2}$, $a = \frac{\gamma_{12}}{\gamma_{22}}$, $b = \frac{\gamma_{21}}{\gamma_{11}}$, $c = \frac{1}{L}\sqrt{\frac{D_2}{r_2}}$:

$$\begin{cases} \frac{\partial U}{\partial t} = \begin{cases} R(1 - U - \frac{a}{R}V)U & x \in [0, d] \\ 0 & x \in (d, 1] \end{cases} \\ \frac{\partial V}{\partial t} = (1 - RbU - V)V + c^2 \frac{\partial^2 V}{\partial x^2} & x \in [0, 1] \end{cases} \quad (3.30)$$

With initial conditions :

$$\begin{cases} U(x, 0) = \begin{cases} 1 & x \in [0, d] \\ 0 & x \in (d, 1] \end{cases} \\ V(x, 0) = \begin{cases} 0 & x \in [0, d] \\ 1 & x \in (d, 1] \end{cases} \end{cases} \quad (3.31)$$

We will study it under Neumann bordering conditions :

$$\left. \frac{\partial V}{\partial x} \right|_{x=0} = \left. \frac{\partial V}{\partial x} \right|_{x=1} = 0 \quad (3.32)$$

Finally, we force our solutions to be smooth enough :

$$\lim_{x \rightarrow d^-} V(x, t) = \lim_{x \rightarrow d^+} V(x, t) \quad \forall t > 0 \quad (3.33)$$

$$\lim_{x \rightarrow d^+} \frac{\partial V}{\partial x} = \lim_{x \rightarrow d^+} \frac{\partial V}{\partial x} \quad \forall t > 0 \quad (3.34)$$

3.3.2 Conditions for the diffusing species to survive

In order to know the conditions for our diffusing species to survive, we are looking at the Stability of $(U(x, 0), 0)$. More precisely, we are looking for the condition when this Steady State is unstable. We then look at the small oscillations around it.

$$U = U(x, 0) + u(x, t), \quad |u(x, t)| \ll 1 \quad (3.35)$$

$$V = v(x, t), \quad v(x, t) > 0, v(x, t) \ll 1 \quad (3.36)$$

After introducing those oscillation in the system (3.29) and linearizing, we obtain

$$\begin{cases} \frac{\partial u}{\partial t} = \begin{cases} -RU - av & x \in [0, d] \\ 0 & x \in (d, 1] \end{cases} \\ \frac{\partial v}{\partial t} = \begin{cases} (1 - Rb)v + c^2 \frac{\partial^2 v}{\partial x^2} & x \in [0, d] \\ v + c^2 \frac{\partial^2 v}{\partial x^2} & x \in (d, 1] \end{cases} \end{cases} \quad (3.37)$$

Since $\partial u / \partial t \leq 0 \forall x \in [0, 1], \forall t > 0$, then the stability conditions come from the study of $\partial v / \partial t$.

If we take a look at $v(x, t)$, it's in the form

$$\frac{\partial v}{\partial t} = q(x)v + c^2 \frac{\partial^2 v}{\partial x^2} \quad \text{with } q \in L^\infty([0, 1])$$

It's then a Sturm-Liouville equation, and there exists a set of eigenvalues λ_n such that

$$v(x, t) = \sum_{n=1}^{\infty} c_n e^{\lambda_n t} g_n(x)$$

with g_n the eigenfunctions verifying :

$$\begin{cases} c^2 g''(x) + (q(x) - \lambda)g(x) = 0 \\ g'(0) = g'(1) = 0 \end{cases} \quad (3.38)$$

To solve that we separate (3.38) in two systems :

$$\begin{cases} c^2 g''_-(x) + (1 - Rb - \lambda)g_-(x) = 0 & x \in [0, d] \\ g'_-(0) = 0 \end{cases} \quad (3.39)$$

and

$$\begin{cases} c^2 g_+''(x) + (1 - \lambda)g_+(x) = 0 & x \in [d, 1] \\ g_+'(1) = 0 \end{cases} \quad (3.40)$$

Sols of (3.39) :

$$\begin{cases} \lambda > 1 - Rb & \rightarrow g_-(x) = A \cosh\left(x \frac{\sqrt{Rb + \lambda - 1}}{c}\right) \\ \lambda = 1 - Rb & \rightarrow g_-(x) = A \\ \lambda < 1 - Rb & \rightarrow g_-(x) = A \cos\left(x \frac{\sqrt{1 - Rb - \lambda}}{c}\right) \end{cases} \quad (3.41)$$

Sols of (3.40) :

$$\begin{cases} \lambda > 1 & \rightarrow g_+(x) = A \cosh\left((1 - x) \frac{\sqrt{\lambda - 1}}{c}\right) \\ \lambda = 1 & \rightarrow g_+(x) = A \\ \lambda < 1 & \rightarrow g_+(x) = A \cos\left((1 - x) \frac{\sqrt{1 - \lambda}}{c}\right) \end{cases} \quad (3.42)$$

Finally, to respect the smoothness of the solutions, we need :

$$g_-(d-) = g_+(d+) \quad (3.43)$$

$$g_-'(d-) = g_+'(d+) \quad (3.44)$$

We are looking for solutions with $\lambda > 0$. If there are, then the Steady States is unstable.

The case where $\lambda \geq 1$

First, when $\lambda \geq 1$, (3.43) and (3.44) give :

$$\begin{aligned} A \cosh\left(d \frac{\sqrt{Rb + \lambda - 1}}{c}\right) &= \cosh\left((1 - d) \frac{\sqrt{\lambda - 1}}{c}\right) \\ A \frac{\sqrt{Rb + \lambda - 1}}{c} \sinh\left(d \frac{\sqrt{Rb + \lambda - 1}}{c}\right) &= -\frac{\sqrt{\lambda - 1}}{c} \sinh\left((1 - d) \frac{\sqrt{\lambda - 1}}{c}\right) \end{aligned}$$

Then

$$\begin{aligned} \frac{\sqrt{Rb + \lambda - 1}}{c} \tanh\left(d \frac{\sqrt{Rb + \lambda - 1}}{c}\right) & \\ &= -\frac{\sqrt{\lambda - 1}}{c} \tanh\left((1 - d) \frac{\sqrt{\lambda - 1}}{c}\right) \end{aligned} \quad (3.45)$$

The functions $f : x \rightarrow x \tanh(ax)$ is positive on \mathbb{R}^+ for $a \in]0, 1[$, so this equality is impossible. There are no solutions with $\lambda \geq 1$.



Figure 3.5: $f(\lambda)$ in blue, $g(\lambda)$ in red. $Rb < 1$

The case where $1 - Rb < \lambda < 1$

Now, if $1 - Rb < \lambda < 1$, (3.43) and (3.44) give:

$$A \cosh\left(d \frac{\sqrt{Rb + \lambda - 1}}{c}\right) = \cos\left((1-d) \frac{\sqrt{1-\lambda}}{c}\right)$$

$$A \frac{\sqrt{Rb + \lambda - 1}}{c} \sinh\left(d \frac{\sqrt{Rb + \lambda - 1}}{c}\right) = -\frac{\sqrt{1-\lambda}}{c} \sinh\left(-(1-d) \frac{\sqrt{1-\lambda}}{c}\right)$$

Then

$$\frac{\sqrt{Rb + \lambda - 1}}{c} \tanh\left(d \frac{\sqrt{Rb + \lambda - 1}}{c}\right) = \frac{\sqrt{1-\lambda}}{c} \tan\left((1-d) \frac{\sqrt{1-\lambda}}{c}\right) \quad (3.46)$$

Let's call :

$$g(\lambda) = \frac{\sqrt{Rb + \lambda - 1}}{c} \tanh\left(d \frac{\sqrt{Rb + \lambda - 1}}{c}\right) \quad (3.47)$$

$$f(\lambda) = \frac{\sqrt{1-\lambda}}{c} \tan\left((1-d) \frac{\sqrt{1-\lambda}}{c}\right) \quad (3.48)$$

Figure 3.5 is when $Rb < 1$. In this case, as seen on the Figure, there is necessarily an intersection between both curves. Meaning, if $Rb < 1$, there exists a $\lambda_n > 0$ and a g_n associated. Then the steady states is *unstable*.

Now, if $Rb > 1$. Figure 3.6 shows when the asymptote is greater than $x = 0$. Then there is an intersection between both curves in the positive

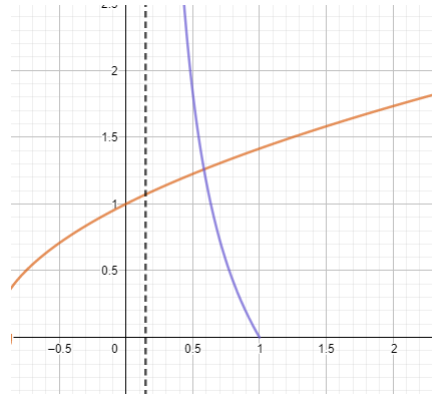


Figure 3.6: $f(\lambda)$ in blue, $g(\lambda)$ in red. $Rb > 1$. Asymptote greater than 0

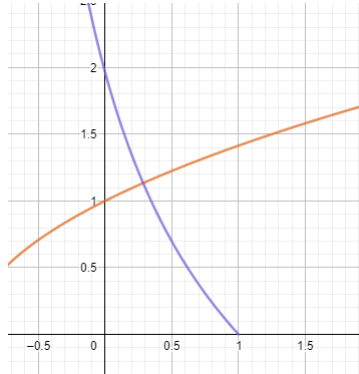


Figure 3.7: $f(\lambda)$ in blue, $g(\lambda)$ in red. $Rb > 1$. Asymptote lesser than 0. $f(0) > g(0)$

interval for lambda. Meaning that, if $Rb > 1$ and $d < 1 - \frac{\pi c}{2}$, then the steady states is *unstable*.

Finally, if $Rb > 1$ and $d > 1 - \frac{\pi c}{2}$. Then, as seen in Figure 3.7 and Figure 3.8, the existence of an intersection in the positive values for λ depends on if $f(0) > g(0)$ is true. In other words, in those conditions, the steady states is unstable if :

$$\tan\left(\frac{1-d}{c}\right) > \sqrt{Rb-1} \tanh\left(d\frac{\sqrt{Rb-1}}{c}\right) \quad (3.49)$$

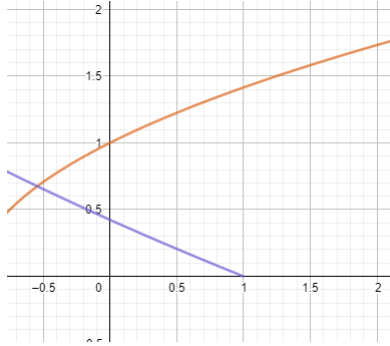


Figure 3.8: $f(\lambda)$ in blue, $g(\lambda)$ in red. $Rb > 1$. Asymptote lesser than 0. $f(0) < g(0)$

Summary

By rewriting the conditions with the initial variables, we obtained that the conditions for the instability of the steady states are :

- $Rb < 1 \iff \frac{\gamma_{21}}{\gamma_{11}} < \frac{r_2}{r_1}$
- $\frac{\gamma_{21}}{\gamma_{11}} > \frac{r_2}{r_1}$ and $l < L - \frac{\pi}{2} \sqrt{\frac{D_2}{r_2}}$
- $\frac{\gamma_{21}}{\gamma_{11}} > \frac{r_2}{r_1}$, $l > L - \frac{\pi}{2} \sqrt{\frac{D_2}{r_2}}$,
 $\tan\left(\left(L - l\right)\sqrt{\frac{r_2}{D_2}}\right) > \sqrt{\frac{r_1\gamma_{21}}{r_2\gamma_{11}} - 1} \tanh\left(l\sqrt{\frac{r_2}{D_2}}\sqrt{\frac{r_1\gamma_{21}}{r_2\gamma_{11}} - 1}\right)$

3.3.3 Comparison with a non diffusion system of two species with interspecific competition

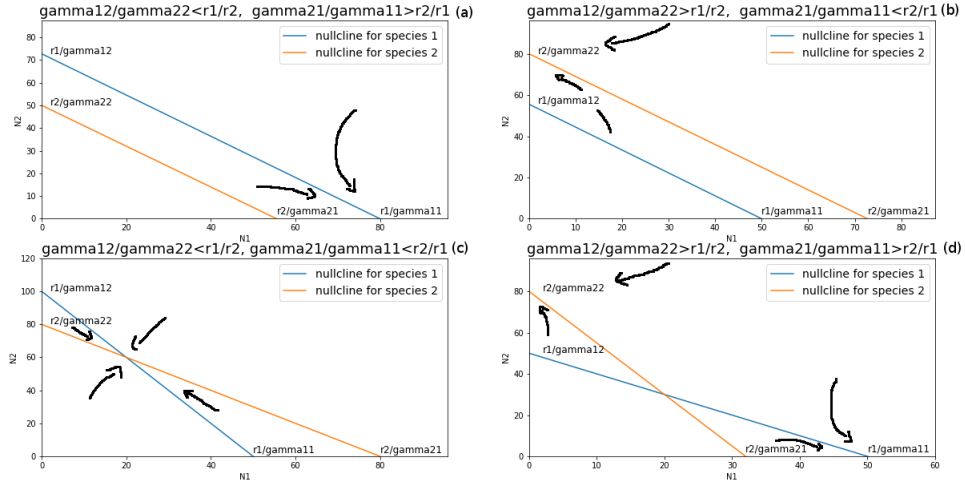


Figure 3.9: phase plane of a two species with interspecific competition system depending on the parameters. (b) and (c) have the second condition equivalent to $Rb < 1$

As we can see in Figure 3.9, in a non-diffusion system, $\frac{\gamma_{21}}{\gamma_{11}} < \frac{r_2}{r_1} \iff$ the Steady State $(\frac{r_1}{\gamma_{11}}, O)$ is locally unstable. That coincides perfectly with the first condition we found for our diffusion system.

On the other hand, the local stability of $(\frac{r_1}{\gamma_{11}}, O)$ is assured in the non-diffusion system case, but *not* in our system. Indeed, there are added conditions coming from the diffusion of the second species that allows it to survive in a wider range of cases. Which makes sense, since the only contact both species have comes from the diffusion of the second one.

What is interesting is that, in case we have :

$$\frac{\gamma_{21}}{\gamma_{11}} > \frac{r_2}{r_1} \quad , \quad l > L - \frac{\pi}{2} \sqrt{\frac{D_2}{r_2}}$$

$$\tan \left((L - l) \sqrt{\frac{r_2}{D_2}} \right) < \sqrt{\left(\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1 \right)} \tanh \left(l \sqrt{\frac{r_2}{D_2}} \sqrt{\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1} \right)$$

Then the species diffusing cannot survive. It is effectively killed by its own diffusion. This is the same phenomenon as the critical patch size in case

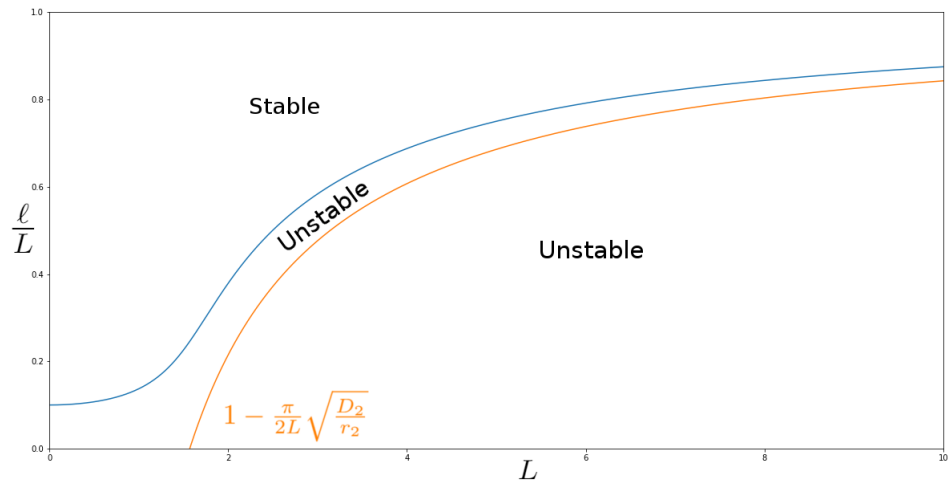


Figure 3.10: Bifurcation diagram of the steady state depending on l/L and L . Comparison with the critical patch size coming from Dirichlet bordering conditions.

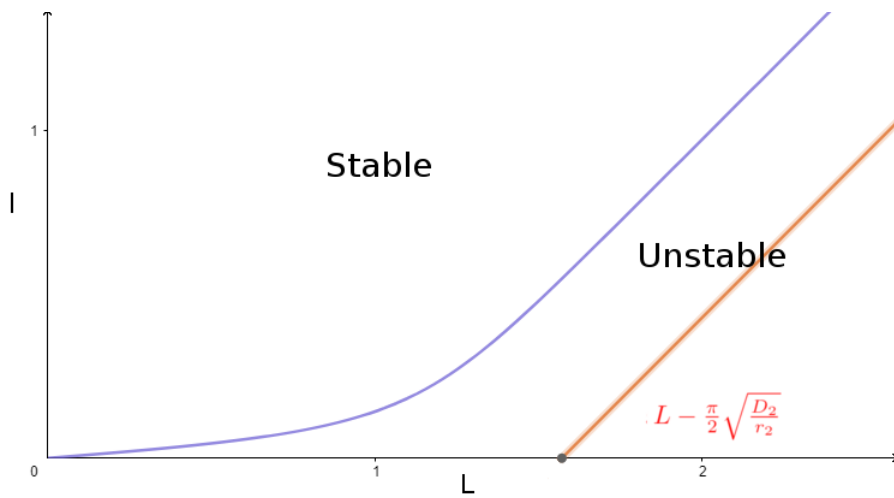


Figure 3.11: Bifurcation diagram of the steady state depending on l and L . Comparison with the critical patch size coming from Dirichlet bordering conditions.

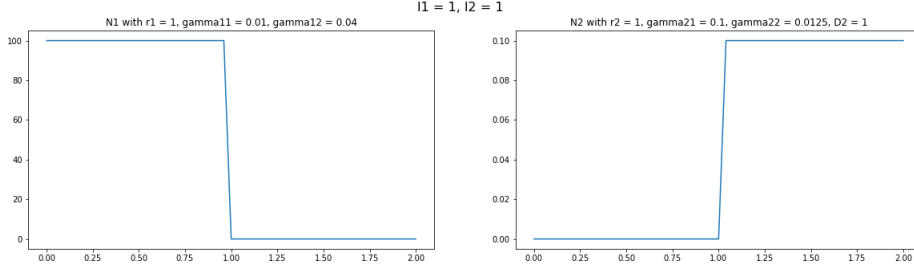


Figure 3.12: Initial State for the numerical analysis

of Dirichlet bordering conditions, but there is a difference that appears due to the death coming from a species competition. This difference is clearly visible in the Figure(3.10) and (3.11). We also see the existence of a critical ratio size for the ratio l/L . With $c \rightarrow \infty$ since $L \rightarrow 0$ and $l/L = d \in]0, 1[$, and since the boundary is given by the equation

$$1 - d = c * \arctan \left(\sqrt{Rb - 1} \tanh \left(d \frac{\sqrt{Rb - 1}}{c} \right) \right) \quad (3.50)$$

then a linearization of \tanh and artanh gives us that this critical ratio size is

$$\left(\frac{\ell}{L} \right)_M = \frac{1}{Rb} = \frac{r_2 \gamma_{11}}{r_1 \gamma_{21}} \quad (3.51)$$

3.3.4 Numerical confirmation

For the test, the parameter values are $r_1 = 1, r_2 = 1, \gamma_{11} = 0.01, \gamma_{12} = 0.04, \gamma_{21} = 0.1, \gamma_{22} = 0.0125, D_2 = 1$. Which means that the condition $\frac{r_2}{r_1} < \frac{\gamma_{21}}{\gamma_{11}}$ is here always assumed to be true.

The initial state is one very close from the Steady State $(\frac{r_1}{\gamma_{11}}, 0)$, to simulate a small perturbation of it, as shown in Figure 3.12

The first verification is on the instability of the Steady State whenever the condition $L - l < \frac{\pi}{2} \sqrt{\frac{D_2}{r_2}}$ is met. As seen in the Figure 3.13, where the condition is not met, the steady states is stable. Whereas, in Figure 3.14, where the condition is met, the instability is clear.

As for the last condition, when we take $L - l < \frac{\pi}{2} \sqrt{\frac{D_2}{r_2}}$ as true, then the

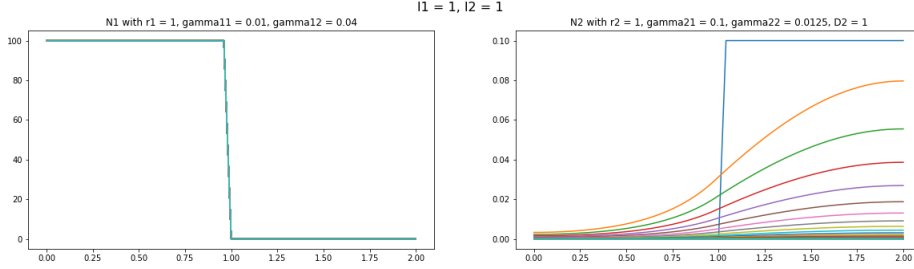


Figure 3.13: $L - l < \frac{\pi}{2} \sqrt{\frac{D_2}{r_2}}$

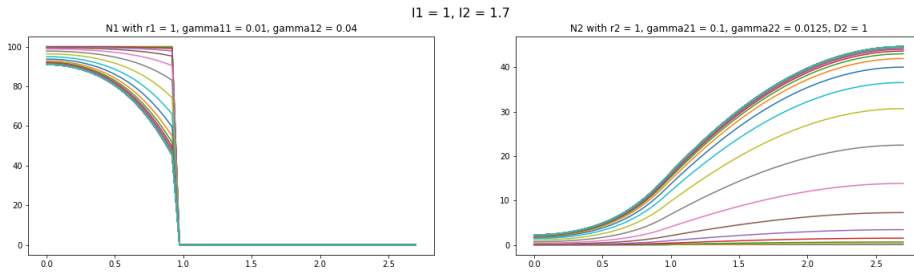


Figure 3.14: $L - l > \frac{\pi}{2} \sqrt{\frac{D_2}{r_2}}$

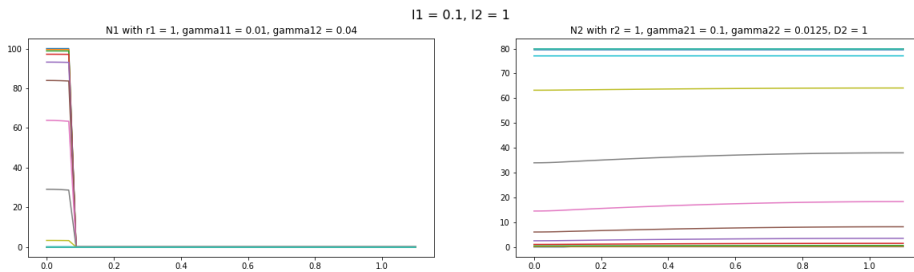


Figure 3.15: $\tan \left((L - l) \sqrt{\frac{r_2}{D_2}} \right) < \sqrt{\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1} \tanh \left(l \sqrt{\frac{r_2}{D_2}} \sqrt{\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1} \right)$

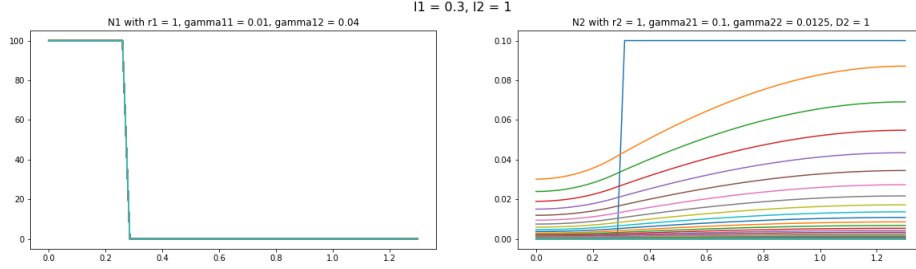


Figure 3.16: $\tan \left((L - l) \sqrt{\frac{r_2}{D_2}} \right) > \sqrt{\left(\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1 \right)} \tanh \left(l \sqrt{\frac{r_2}{D_2}} \sqrt{\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1} \right)$

last condition for instability is

$$\tan \left((L - l) \sqrt{\frac{r_2}{D_2}} \right) < \sqrt{\left(\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1 \right)} \tanh \left(l \sqrt{\frac{r_2}{D_2}} \sqrt{\frac{r_1 \gamma_{21}}{r_2 \gamma_{11}} - 1} \right)$$

With the value taken here, and with taking $L - l = 1$, this conditions gives that the instability is true if and only if :

$$l < \frac{1}{3} \operatorname{artanh} \left(\frac{\tan(1)}{3} \right) \approx 0.2$$

The numerical results seen in the Figures 3.15 and 3.16 concur with this condition.

3.3.5 Ecological meaning

It is interesting to compare the stability of this "extinction of the diffusing species" equilibrium with the length and ratio of the habitat, because this length is modified by the destruction of said habitat for example. Nowadays the human activities have modified a lot of the natural habitat of species, and we can see from our results that the smaller the L , the more difficult it is for a diffusing species to invade it. Indeed, if another species is already established in the area, occupying most of the territory (high ℓ/L ratio), whether the territory itself is big enough will have a huge impact on the success of invasion by another species.

On the other hand if it is only ℓ that shrinks, for example because of a policy that extends the area of hunting, or a chemical contamination of part of the area, then we might suddenly cross the border of this bifurcation diagram.

In this case, either coexistence happen, or we might see the extinction of the motionless species, which would be a drastic hysteresis effect.

3.3.6 Bistability of the system

When taking the system(3.29), and studying the small oscillation around the steady state $(0, \frac{r_2}{\gamma_{22}})$:

$$U = u(x, t), \quad u(x, t) > 0, u(x, t) \ll 1 \quad (3.52)$$

$$V = \frac{r_2}{\gamma_{22}} + v(x, t), \quad |v(x, t)| \ll 1 \quad (3.53)$$

we obtain after linearization

$$\begin{cases} \frac{\partial u}{\partial t} = \begin{cases} Ru(1 - \frac{a}{R}) & x \in [0, d] \\ 0 & x \in (d, 1] \end{cases} \\ \frac{\partial v}{\partial t} = \begin{cases} -(Rbu + v) + \frac{\partial^2 v}{\partial x^2} & x \in [0, d] \\ -v + \frac{\partial^2 v}{\partial x^2} & x \in (d, 1] \end{cases} \end{cases} \quad (3.54)$$

If our motionless species disappears, meaning a $(0, -)$ steady state, then nothing prevent the diffusive species to diffuse and fill the whole space, reaching its carrying capacity r_2/γ_{22} . So we only need to study $\frac{\partial u}{\partial t}$. Then :

$$(R < a \iff) \frac{r_1}{r_2} < \frac{\gamma_{12}}{\gamma_{22}} \iff (0, \frac{r_2}{\gamma_{22}}) \text{ is locally stable} \quad (3.55)$$

In other words, the stability that we found before was a case of *Bistability*.

If we take the same conditions as Figure 3.16, but with the starting values of both species at their carrying capacity, then we obtain Figure 3.17, which illustrates the bistability.

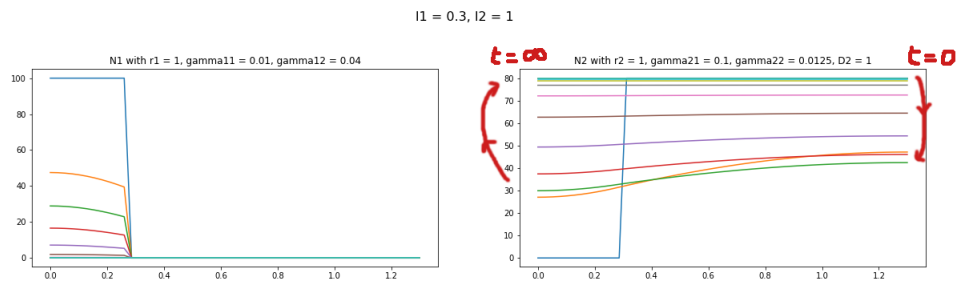


Figure 3.17: $\tan\left((L-l)\sqrt{\frac{r_2}{D_2}}\right) > \sqrt{\left(\frac{r_1\gamma_{21}}{r_2\gamma_{11}} - 1\right)} \tanh\left(l\sqrt{\frac{r_2}{D_2}}\sqrt{\frac{r_1\gamma_{21}}{r_2\gamma_{11}} - 1}\right)$.
 Initial values of both species are at their respective carrying capacity.

Chapter 4

Conclusions

Through this paper, we have explored two different aspect of the Mathematical ecology field. The first brought us to analyze the relationship engendered by the existence of a generalist predator among an indefinite number of preys. The apparent competition exerted between the prey species through this common predator is a non negligible threat to some endangered species, as was shown by DeCesare et all[8] for the Sierra Nevada bighorn sheep or the Vancouver Island marmot. Indeed, if some new prey species with a higher r/b is introduced in the natural habitat, or the change in environment brings a modification of the ratio r/b to a much higher value from an already present species, then they will feed the predator much more. This in turn will let the population of the predator grows, and all the species will be subject to more frequent attacks, not only the changed one. As we shown in our analysis, this may bring the condition of the steady states into a range where some species will disappear.

On the other hand, it also means we may be able to control this phenomenon to help an endanger species to survive. As shown by Serrouya et all [9], an important decrease in the principal prey may be an important conservation strategy for the other preys. Another interesting aspect is the possibility of biological pest control thanks to the apparent competition. For example, this effect has been observed by Karban et all [1], and Hanna et all [2], with the Pacific mites, a very damaging herbivorous to grapevines. The introduction of another economically unimportant mites species, sharing the same predator as the Pacific mites, effectively reduced the population of this harmful mite species.

We have to remember though, we considered that the prey species have

no direct competition between themselves. It would be an interesting point to compare the results from this model to a result where we would add an interspecific competition. It might be possible to know what effect these two kinds of competition (apparent competition and interspecific competition) have on one another.

The second aspect we explored was the diffusion of a species, and how taking into consideration the spatial aspect would change our logistic model and interspecific competition model. As there are quite some mathematical difficulties added by taking into account this new space variable, the model we ended up studying was of a competition with only one of the two species. Though it stays interesting and relevant. Indeed, because of the global warming or human activities, many species are forced to flee their habitat and invade new ones . In this situation, they will be confronted to already implanted species.

Bibliography

- [1] R. Karban D. Hougén-Eitzmann G. English-Loeb. “Predator-mediated apparent competition between two herbivores that feed on grapevines”. In: *Oecologia* 97 (1994), pp. 508–511. DOI: <https://doi.org/10.1007/BF00325889>.
- [2] R. Hanna L. T. Wilson F. G. Zalom D. L. Flaherty. “Effects of predation and competition on the population dynamics of *Tetranychus pacificus* on grapevines”. In: *Journal of Applied Ecology* 34 (1997), pp. 878–888. DOI: <https://www.jstor.org/stable/2405279>.
- [3] M. Mimura H. Matano. “Pattern Formation in Competition-Diffusion Systems in Nonconvex Domains”. In: *Publications of the Research Institute for Mathematical Sciences* 19 (1983), pp. 1049–1079. DOI: <https://doi.org/10.2977/prims/1195182020>.
- [4] M. W. Hirsch. “Differential equations and convergence almost everywhere in strongly monotone semiflows”. In: *Contemporary Mathematics* 17 (1983). DOI: <http://dx.doi.org/10.1090/conm/017/706104>.
- [5] R. D. Holt. “Predation, apparent competition, and the structure of prey communities”. In: *Theoretical Population Biology* 12 (1977), pp. 197–229. DOI: [https://doi.org/10.1016/0040-5809\(77\)90042-9](https://doi.org/10.1016/0040-5809(77)90042-9).
- [6] H.F. Weinberger K. Kishimoto. “The spatial homogeneity of stable equilibria of some reaction-diffusion systems on convex domains”. In: *Journal of Differential Equations* 58 (1985), pp. 15–21. DOI: [https://doi.org/10.1016/0022-0396\(85\)90020-8](https://doi.org/10.1016/0022-0396(85)90020-8).
- [7] J. H. Lawton M. J. Jeffries. “Enemy free space and the structure of ecological communities”. In: *Biological Journal of the Linnean Society* 23 (1984), pp. 269–286. DOI: <https://doi.org/10.1111/j.1095-8312.1984.tb00145.x>.

- [8] N. J. DeCesare M. Hebblewhite H. S. Robinson M. Musiani. “Endangered, apparently: the role of apparent competition in endangered species conservation”. In: *Animal Conservation* 13 (2010), pp. 353–362. DOI: <https://doi.org/10.1111/j.1469-1795.2009.00328.x>.
- [9] R. Serrouya B. N. McLellan H. van Oort G. Mowat S. Boutin. “Experimental moose reduction lowers wolf density and stops decline of endangered caribou”. In: *PeerJ* 5:e3736 (2017). DOI: <https://doi.org/10.7717/peerj.3736>.
- [10] M. B. Bonsall R. D. Holt. “Apparent Competition”. In: *Annual Review of Ecology, Evolution and Systematics* 48 (2017), pp. 447–471. DOI: <https://doi.org/10.1146/annurev-ecolsys-110316-022628>.
- [11] J. G. Skellam. “Random Dispersal in Theoretical Populations”. In: *Biometrika* 38 (1951), pp. 196–218. DOI: <https://doi.org/10.1093/biomet/38.1-2.196>.
- [12] J. Ulbrich. *Die Bisamratte : Lebensweise, Gang ihrer Ausbreitung in Europa, wirtschaftliche Bedeutung und Bekämpfung*. Dresden: Heinrich, 1930.
- [13] P. F. Verhulst. “Notice sur la loi que la populations suit dans son accroissement”. In: *Correspondence Mathématique et Physique* 10 (1838), pp. 113–121. DOI: https://doi.org/10.1007/978-3-642-81046-6_37.