POPULATION DYNAMICS MODELS ON THE SPECIES PERSISTENCE IN THE NATIVE HABITAT WITH THE INVASION OF ALIEN SPECIES

外来種侵入下の固有生息地における種存続性に関する個体群動態モデル

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by

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Summary

In the face of ongoing loss of biodiversity and habitat transformations, understanding the complex dynamics governing species survival and competition is critical. This study investigates the interplay of habitat characteristics, such as size and fragmentation, and the invasion of alien species in native habitats. We use mathematical modeling and analysis to tackle the topic, with each chapter addressing a distinct aspect of the issue.

We first explore a two patches model of species invasion and competition, highlighting the role of migration rates in determining species survival. We continue onto investigating the impact of habitat size on the success of alien species invasion and survival of native species. Finally, we examine the effect of habitat fragmentation on the persistence of native species.

Our results reveal that high immigration rates for the alien species can negatively affect the native species while also increasing the chances of the alien species extinction. Smaller habitats can enhance the prevention of invasion by alien species, particularly when faced with a well-established native species. Additionally, under certain conditions, habitat fragmentation may be beneficial for the survival of native species.

These findings challenge traditional models and offer nuanced insights into the complex dynamics of species competition and survival, with implications for both theoretical ecology and practical conservation efforts. This study provides a stepping stone toward a deeper understanding of species interactions and the effects of habitat transformations, advocating for future research that incorporates other environmental factors.

Table of Contents

Chapter 1

Introduction

In today's world, we face a very high rate of species extinction, so high that more and more scientists are talking about the Sixth Mass Extinction (Barnosky et al. [6]). Although the scope of the contribution from human actions is still under debate, most scientists agree that we contributed (Cowie et al. [11]). Arguably, degradation and loss of natural habitats are the leading causes of species extinction (Tilman et al. [72]), for example, through climate change (Thomas et al. [71]), urbanization (McKinney [47]), or forest fire (Turner et al. [74]).

Among all its consequences, the degradation of habitats also forces the relocation of some species, and there has been a global increase in sightings of invading species recently (Seebens et al. [59]). Without talking about degradation, simply the changes in a habitat can open it up to invasion by previously unsuitable species (Sittaro et al. [66]). This invasion, in turn, may endanger native species, which were a priori not affected by the changes in their habitat.

That is why it is becoming increasingly important for conservation biology to understand the conditions under which native species can persist in the case of such an invasion, and mathematical models are an essential tool to help with that. By better understanding the dynamics of these complex ecological systems, we could inform the development of conservation and management strategies aimed at mitigating the impacts of species invasion and protecting the biodiversity and ecosystem services provided by natural habitats (Courchamp et al. [10])

There are plenty of different ways that have been used to model the interaction between species (Abrams [1]; Seno [62]). Even when considering spatially uniform habitat and species density, the different relationships between species give many different models. There are, for example, the prey-predator relationship (Volterra [79]; Gilpin [26]; Nisbet and Gurney [50]), the competition relationship (Volterra [78]; MacArthur [43]; Freedman and Waltman [23]), or the shared predation relationship, also called apparent competition (Holt [30]; Holt and Bonsall [32]; Seno, Schneider and Kimura [63]).

While those models highlight essential phenomena, like the periodicity of the density of actors in a prey-predator system or the possible extinction of one species in a competition system, it is difficult to conceive an invasion with the alien species already present in the native species' habitat. Those models could be used for the direct introduction of a new species in a habitat, for example, for resource enrichment purposes (Marshall [7]) or pest control (Karban [38]). However, ignoring the spatial effect limits them for describing an invasion. As Simon Levin [42] stated, "The distribution of a species over its range of habitats is a fundamental and inseparable aspect of its interaction with its environment, and no complete study of population dynamics can afford to ignore it".

It is typically only possible to incorporate some spatial and local factors required for an accurate mathematical representation of species interaction. Even if such a model were possible, it would be challenging to analyze it thoroughly. A common simplification to account for spatial effects is to use discrete patches separated by areas where the species of interest cannot thrive but where movement is allowed for one or more focal species. Let us note, however, that this simplification does not necessarily imply a considerable loss in realism since many organisms occupy habitats that naturally occur as discrete units. Take, for example, the plankton of small ponds or sparsely scattered plants like algae or trees (Vance [76]). Numerous theoretical investigations have been conducted to explore the impact of patchy environments on the persistence, stability, and spatial patterns of populations (Zeigler [82]; DeAngelis et al. [13]; Kawasaki and Teramoto [39]; Allen [4]; Seno [60]). The metacommunity concept developed through the study of those models is also a valuable framework for understanding ecological communities at multiple scales (May [46]; Travis and Post [73]; Mouquet and Loreau [48]; Leibodl et al. [41])

Another way to model the spatial effect, perhaps more rigorous though technically more challenging to analyze, is to consider a continuous space. Fisher [20] and Skellam [67] pioneered this modeling method, which has since received much attention from the mathematical biology community (Kierstead and Slobodkin [40]; Levin [42]; Okubo [52]; Pao [55]; Allen [3]; Iida et al. [36], Hilhorst, Salin, Schneider and Gao [28]). It has also been combined with the idea of multiple patches with different resources (Pacala and Roughgarden [54]; Takeuchi [70]; Seno [61]; Namba and Hashimoto [49]). Those analyses bring into light how space-related phenomena, such as the size of the habitat or the speed of the populations, impact the competition effect and counterbalance it on occasion (Holmes et al. [29]).

The research presented here aims to develop, analyze, and discuss reasonable mathematical modeling of a competitive interaction between a native species and an invading species, looking at how different spatial effects affect the outcome of the invasion. Using ordinary or partial differential equations, we will base our models on a population dynamics approach. We will analyze the models mathematically and perform numerical simulations to illustrate our results. We will also interpret the results we obtained in ecological terms to be understandable to most.

After this introduction, the second chapter will establish some crucial concepts in mathematical biology for a single species growth. The new research we present begins in the third chapter. We will consider a two patches model, one patch being the original habitat for a native species, the other being the original habitat for the invader species, also called alien species. The alien species will be free to move between both patches and compete with the native species for resources in the habitat of the native species. We discuss how the migration allowing the invasion to take place influences both species' persistence. The fourth chapter considers again two different areas representing the original habitat of each species, and two species competing for resources, but in a continuous space setting. It will allow us to discuss more specifically the influence of the size of the habitats on the invasion success and the persistence of the species. Finally, the fifth chapter will return to considering a patchy system, and we will discuss the influence of habitat fragmentation on an exploitative competition dynamics between native and alien species.

Chapter 2

Relevance of habitat size to a single species persistence

2.1 Mathematical models for single species population dynamics

The first step in modeling a population dynamic is to describe the biological assumptions we make about the situation. We then transform these assumptions into a mathematical model.

In all of the models we present in this paper, we consider populations large enough to neglect the effects of stochastic events safely.

Finally, we assume that all individuals of the same species are identical.

Those assumptions are only somewhat satisfied in field situations. However, 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.

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

The growth of a species in such an environment boils down to a conservation equation. Let us take 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 the Malthus model:

$$\frac{dN}{dt} = \text{birth} - \text{death} = \beta N - \mu N.$$

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

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

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

This model can be applied when there are few individuals of a species, when it invades a new habitat, for example. Another application is the growth of bacteria in a Petri dish with so many nutrients that the amount of nutrients is considered invariant for the duration of the observation.

However, assuming an invariant habitat is only realistic in some situations.

As Verhulst [77] said long ago, "The growth of a population is limited by the space available and the fertility of its fields". Those ideas are not expressed in 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 the population number, the lower its growth rate. It leads to the new model given by

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

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

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

frequently written as

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

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

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

$$N(t) = \frac{K}{1 + (K/N_0 - 1)e^{-rt}} \quad \to K \quad as \quad t \to \infty.$$

We show the graph of $N(t)$ in Figure 2.1 depending on the value N_0. When $N_0 < K/2$, we obtain the so called logistic curve, or sigmoid. This curve gives the other name for this model: the logistic growth model.

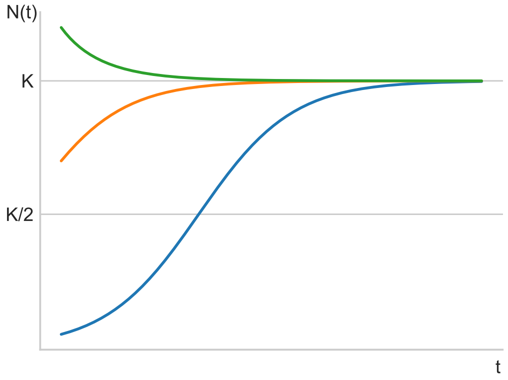


Figure 2.1: Population growth following a logistic equation. For any initial value $N(0) > 0$, the population density monotonically converges to a carrying capacity K. The growth follows a sigmoid curve for an initial value under $K/2$.

2.2 Modeling of population dispersal in space

In the previous model, we considered the species as spatially homogeneous. It is enough to understand some situations, but it sometimes needs improvement, for example, in studying the spread of a population. To solve this problem, Skellam [67] introduced diffusion in the ecological model and successfully applied it to Ulbrich data [75] to explain the speed of spreading of a muskrat population. In this section, we will see how the diffusion phenomenon affects the survival of a species that lives by itself.

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 follow the conservation principle. Two terms regulate our population density:

- $\mathbf{J}(\mathbf{x}, \mathrm{t})$, the **population flux**, represents what comes into or goes out of our spatial boundary. It is a vector field such that

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

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

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

Based on the conservation equation, we obtain

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

and by using the divergence theorem, it becomes

$$\frac{dN(\mathbf{x}, t)}{dt} \quad = \quad -\nabla \mathbf{J}(\mathbf{x}, t) + f(\mathbf{x}, t).$$

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

- Advection: It is the transport of substances due to the motion of a fluid. For example, a fish in a stream or pollen in the wind.
- Diffusion: It arises from a random walk and induces a movement from a higher concentration region to a lower concentration region.

We will focus only 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)

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

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

As for $f(\mathbf{x}, t)$, it is a growth model dependent on the situation (logistic growth, prey-predator, ...).

Finally, we must implement boundary conditions to describe what happens at the habitat border. Two, in particular, are most commonly seen among all the possibilities.

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

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

- The Neumann condition is used in case of a completely closed habitat:

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

2.3 Critical habitat size

2.3.1 Habitat with absorbing boundary

Stationary solution

For the simplicity of all the models to come, we now consider them in one dimensional space. 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 leads us to an equation called the Fisher equation (Fisher [20]).

In this section, we consider an isolated habitat with absorbing boundary (Dirichlet boundary condition). Then our model is given as follows:

$$\begin{aligned} \frac{\partial N}{\partial t} &= D\frac{\partial^2 N}{\partial x^2} + r\left(1 - \frac{N}{K}\right) N, \qquad (2.1) \\ N(0,t) &= N(L,t) \;=\; 0, \quad \forall t \geq 0. \end{aligned}$$

To find the stationary solution $N^*(x)$ of this model, we study

$$0 = D\frac{d^2 N^*}{dx^2} + r\left(1 - \frac{N^*}{K}\right) N^*. \qquad (2.2)$$

When we consider diffusion, there are two kinds of stationary solutions. The homogeneous stationary solutions are solutions that are independent of both time and space, and the non-homogeneous stationary solutions are solutions that are independent of time only.

For homogeneous stationary solutions, $d^2N^*/dx^2 = 0$, and the two possible stationary solutions would be $N^*(x) \equiv 0$ and $N^*(x) \equiv K$, as in the logistic growth model. However, here $N(0) = N(L) = 0$, so $N(x) \equiv K$ is impossible.

To find the non-homogeneous stationary solution, we introduce $V^*(x) = dN^*(x)/dx$ to create a system of first-order differential equations:

$$\begin{cases} \dfrac{dN^*(x)}{dx} = V^*(x); \\[2ex] \dfrac{dV^*(x)}{dx} = -\dfrac{r}{D}\left(1 - \dfrac{N^*(x)}{K}\right) N^*(x). \end{cases}$$

This makes it much easier to proceed. If we take the function

$$F(N^*, V^*) = V^{*2} + \frac{r}{D}N^{*2}\left(1 - \frac{2N^*}{3K}\right), \qquad (2.3)$$

we notice that $\frac{d}{dx}F(N^*(x),V^*(x))=0$. F is then a first integral of the system (2.1), which leads to

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

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

Finally, we obtain the relation describing our stationary solution with an implicit function

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

Finding a direct relation describing N^* cannot be achieved through this equation, but it can give us other information.

Relation to habitat size L

The system (2.1) describes a species that does not have a competitor or predator but that dies when it approaches the border. Then it is symmetric, with the maximum population reached in $x=L/2$. This maximum cannot exceed K. Let us call this maximum N_M. We have

$$N(0)=0, \qquad N\left(L/2\right)=N_M, \qquad \text{and} \quad \left.\frac{dN}{dx}\right|_{x=L/2}=0$$

so

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

Then

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

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

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

Then the minimum size possible for the species to survive is given by taking the limit $N_M\to 0$. It leads to

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

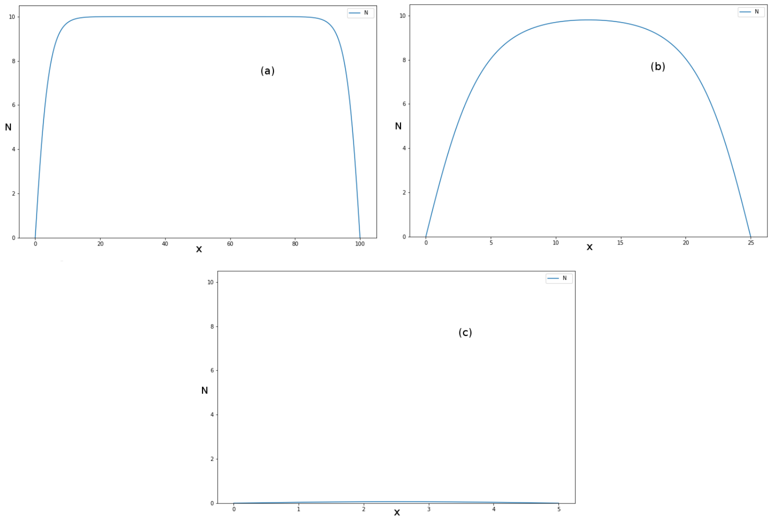


Figure 2.2: Spatial allocation of the population, with $r = 0.5; D = 3; K = 10$ in the three cases. For (a) $L = 100$; for (b) $L = 25$; for (c) $L = 5$.

This antiderivative is given by Arcsin. All in all, we found a critical habitat size, also commonly called critical patch size, of value

$$L_M = \pi\sqrt{\frac{D}{r}}.$$

For a species to survive while diffusing with Dirichlet boundary condition, the habitat size must be greater than L_M.

A numerical analysis of this model gives the Figure (2.2), picturing the spatial allocation of the population at the stationary solution depending on the total habitat size L.

Stability of the stationary solution

Since the species cannot survive in the case $L_M < \pi\sqrt{D/r}$, $N^* = 0$ is globally asymptotically stable under this condition.

For the study of the stability of the non-homogeneous stationary solutions, we look at $n(x,t) = N(x,t) - N^*(x)$ with $|n(x,t)| \ll 1$ and $n(0,t) = n(L,t) = 0$. With a Taylor expansion on (2.1) we get the relation

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

We study this equation with the method of separation of variables: let us take $n(x,t) = f(t)g(x)$. It gives

$$\begin{aligned} f'(t) &= \lambda f(t); & (2.4)\\ Dg''(x) + g(x)\cdot r\left(1 - \frac{2N^*(x)}{K}\right) &= \lambda g(x). & (2.5)\end{aligned}$$

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

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

The second point tells us that all solutions of the system are of the form

$$\begin{aligned} n(t,x) &= \sum_{n=1}^{\infty} c_n e^{\lambda_n t} g_n(x)\\ &= e^{\lambda_1 t}\left(c_1 g_1(x) + \sum_{n=2}^{\infty} c_n e^{(\lambda_n - \lambda_1)t} g_n(x)\right).\end{aligned}$$

To know the stability of $N^*(x)$, we only need to know the sign of λ_1. When multiplying by $N^*(x)$ and performing an integration by parts on (2.5) we obtain

$$\begin{aligned} -\int_0^L g_1'(x) N^{*\prime}(x)dx + \frac{r}{D}\int_0^L \left(g_1(x)N^*(x) - 2g_1(x)\frac{(N^*(x))^2}{K}\right)dx \\ = \frac{\lambda_1}{D}\int_0^L g_1(x)N^*(x)dx. \quad (2.6)\end{aligned}$$

By multiplying (2.2) by $g_1(x)$, and performing an integration by parts, we also obtain

$$-\int_0^L g_1'(x)N^{*\prime}(x)dx + \frac{r}{D}\int_0^L \left(g_1(x)N^*(x) - g_1(x)\frac{(N^*(x))^2}{K}\right)dx = 0. \quad (2.7)$$

Finally, subtracting (2.6) and (2.7) gives us

$$\lambda_1 = \frac{-r\int_0^L g_1(x)\frac{(N^*(x))^2}{K}dx}{\int_0^L g_1(x)N^*(x)dx}. \quad (2.8)$$

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

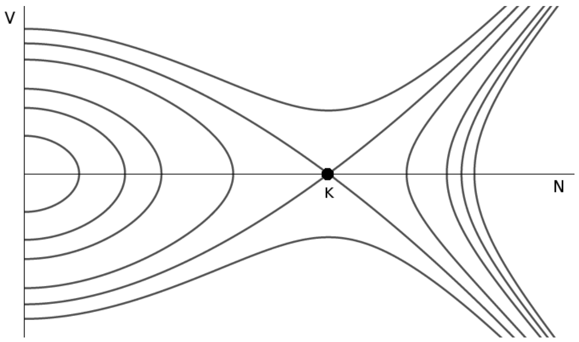


Figure 2.3: Trajectories for the system (2.9) in the phase plane (N, V)

2.3.2 Habitat with reflecting boundary

In the same space as before, $x \in [0, L]$, we now impose reflecting boundary, that is, Neumann boundary condition, also called no-flux boundary condition:

$$\begin{aligned} \frac{\partial N}{\partial t} &= D\frac{\partial^2 N}{\partial x^2} + r\left(1 - \frac{N}{K}\right)N, \\ \left.\frac{\partial N}{\partial x}\right|_{x=0} &= \left.\frac{\partial N}{\partial x}\right|_{x=L} = 0, \quad \forall t \geq 0. \end{aligned} \tag{2.9}$$

In this case, homogeneous stationary solutions $N^* = 0$ and $N^* = K$ are possible. On the other hand, when we draw the phase plane based on the first integral (2.3), we obtain Figure (2.3). A non-homogeneous solution of the Neumann boundary problem would link two points on the N-axis (since $V(x) = N'(x)$), but such a trajectory does not exist. Hence, there are no non-homogeneous stationary solutions with Neumann condition.

From the same system (2.5) as in the Dirichlet case, we obtain the result for the λ_1 as in (2.8), but here since we are only concerned with N^* constant, we have

$$\lambda_1 = -r\frac{N^*}{K}.$$

So the stationary solution $N^* \equiv 0$ is unstable, and the stationary solution $N^* \equiv K$ is stable.

2.3.3 Habitat with absorbing and reflecting boundaries

Let us take a space half as large as previously, $x \in [0, L/2]$. We have a Dirichlet boundary condition on the left side, whereas, on the right side, we have a Neumann boundary condition.

$$\begin{aligned}\frac{\partial N}{\partial t} &= D\frac{\partial^2 N}{\partial x^2} + r\left(1-\frac{N}{K}\right)N, \\ N(0) &= \left.\frac{\partial N}{\partial x}\right|_{x=L/2} = 0, \quad \forall t \geq 0.\end{aligned} \tag{2.10}$$

In this model, the only homogeneous stationary solution possible is $N^*(x) \equiv 0$, and a non-homogeneous one is possible.

By taking the space half as large, we have the Neumann condition at the same spatial coordinate as the peak of our function in the previous model (with only Dirichlet boundary condition). The analysis is then identical, and we can prove that in this condition, we also have a critical habitat size of the same value as before, $L_M = \pi\sqrt{D/r}$, and the stability conditions are the same.

To sum up this result, in a space of size S with one Dirichlet boundary and one Neumann boundary, the critical habitat size is

$$S_M = \frac{\pi}{2}\sqrt{\frac{D}{r}}$$

and the non-homogeneous stationary solution $N^*(x)$ is stable when $S > 0.5\pi\sqrt{D/r}$.

Chapter 3

Competition dynamics model with an alien invasion

3.1 Lotka-Volterra two species competition model

We first present the Lotka-Volterra model for describing the interaction of two prey species competing for natural resources. It is considered one (if not the) fundamental mathematical model for describing competing species. In this model, the species follow a logistic growth when no competitors exist. The model is

$$\begin{cases} \dfrac{dN_1}{dt} & = & r_1\left(1-\dfrac{N_1}{K_1}-c_{12}\dfrac{N_2}{K_1}\right)N_1 & = & F_1(N_1,N_2); \\ \\ \dfrac{dN_2}{dt} & = & r_2\left(1-c_{21}\dfrac{N_1}{K_2}-\dfrac{N_2}{K_2}\right)N_2 & = & F_2(N_1,N_2), \end{cases} \tag{3.1}$$

where $r_1 > 0$, $r_2 > 0$ are the intrinsic growth of each species, $K_1 > 0$, $K_2 > 0$ are the carrying capacity of the respective species, and $c_{12} > 0$, $c_{21} > 0$ describe the negative effect of the competition between the species, called interspecific competition.

The equilibria of this model are given by the equations

$$\begin{cases} 0 & = & r_1\left(1-\dfrac{N_1^*}{K_1}-c_{12}\dfrac{N_2^*}{K_1}\right)N_1^*; \\ \\ 0 & = & r_2\left(1-c_{21}\dfrac{N_1^*}{K_2}-\dfrac{N_2^*}{K_2}\right)N_2^*, \end{cases}$$

which give the following possibilities for (N_1^*, N_2^*):

$$(0,0); \quad (K_1, 0); \quad (0, K_2); \quad \left(\frac{K_1 - c_{12}K_2}{1 - c_{12}c_{21}}, \frac{K_2 - c_{21}K_1}{1 - c_{12}c_{21}}\right).$$

The first is the extinction of both species, the second and third are the competition exclusion equilibria, and the last is the coexistence equilibrium. This last equilibrium exists if and only if

$$\begin{gathered} \frac{K_1}{K_2} > c_{12} \quad \text{and} \quad \frac{K_2}{K_1} > c_{21}, \\ \text{or} \\ \frac{K_1}{K_2} < c_{12} \quad \text{and} \quad \frac{K_2}{K_1} < c_{21}. \end{gathered}$$

For the stability of those equilibria, we study the eigenvalues of the Jacobian matrix:

$$\begin{aligned} &\begin{pmatrix} \dfrac{\partial F_1}{\partial N_1} & \dfrac{\partial F_1}{\partial N_2} \\ \\ \dfrac{\partial F_2}{\partial N_1} & \dfrac{\partial F_2}{\partial N_2} \end{pmatrix}_{(N_1^*, N_2^*)} \\ = \quad &\begin{pmatrix} r_1\left(1 - 2\dfrac{N_1}{K_1} - c_{12}\dfrac{N_2}{K_1}\right) & -r_1 c_{12}\dfrac{N_1}{K_1} \\ -r_2 c_{21}\dfrac{N_2}{K_2} & r_2\left(1 - c_{21}\dfrac{N_1}{K_2} - 2\dfrac{N_2}{K_2}\right) \end{pmatrix}_{(N_1^*, N_2^*)}. \end{aligned}$$

- For $(N_1^*, N_2^*) = (0,0)$ the eigenvalues are $\lambda_1 = r_1, \lambda_2 = r_2$, so this equilibrium is always unstable.
- For $(N_1^*, N_2^*) = (K_1, 0)$, the eigenvalues are $\lambda_1 = -r_1$, $\lambda_2 = r_2(1 - c_{21}K_1/K_2)$, so this equilibrium is stable when $c_{21} > K_2/K_1$.
- For $(N_1^*, N_2^*) = (0, K_2)$, the eigenvalues are $\lambda_1 = r_1(1 - c_{12}K_2/K_1)$, $\lambda_2 = -r_2$, so it is stable when $c_{12} > K_1/K_2$.
- For the coexistence equilibrium, it is stable when $c_{21} < K_2/K_1$ and $c_{12} < K_1/K_2$.

Figure 3.1 summarizes the results. We observe that in case (d), there is a case of bistability: two equilibrium points are locally stable, and the initial values of the system determine its final state.

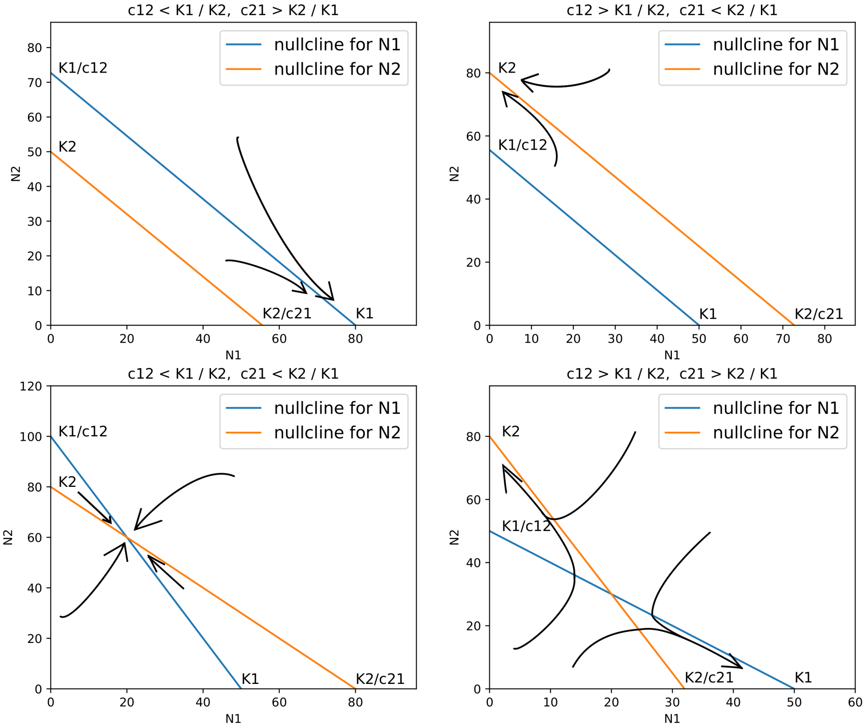


Figure 3.1: Phase space configuration according to the stability of equilibria for a Lotka-Volterra two species competition model. The result of the competition depends on the conditions for the parameters.

3.2 A model with habitats for native and alien species

We seek to model an alien species that invades a native habitat already inhabited, creating a competition for resources between both species. For this first model, we consider a two-species competitive system with two patches. Invasive species usually have strong dispersal ability (Elliott and Cornell [15]); we can mention for example the red imported fire ant in California (Jetter et al. [37]) or the giant bamboo in Japan (Suzuki [68]; Okutomi et al. [53]). We consider here that the alien species dispersal ability are far superior to the species inhabiting the native habitat. We approximate this situation by saying that the native species is not capable of migration between the patches, and hence can only exist in one of the two patches. We want to know under which conditions the different species can persist.

3.2.1 Assumptions

To model the situation we are considering, we make the following assumptions.

- There are two patches and two species. Species 1, called the native species, lives in patch 1, the native habitat. Species 2, called alien species, live in both patches, and patch 2 is a source for the alien species.
- Both species follow a logistic growth if left alone.
- The environment in both patches is not necessarily the same.
- The alien species can move between patches, while the native species cannot.
- A competition for resources occurs in patch 1, the native habitat.

We show a schema of the two patches system in Figure 3.2.

3.2.2 Population dynamics model

To transform our assumptions into a valid mathematical model, we use the following variables and parameters

$N(t)$: Population size of native species in patch 1 at time t;

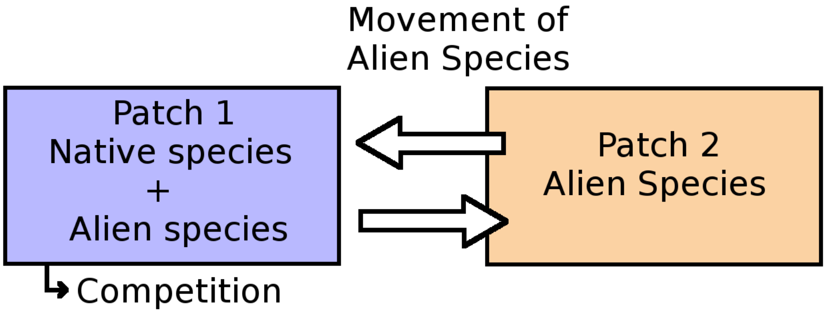


Figure 3.2: Illustration of the two patches model with invasion from a competing alien species.

$A_i(t)$: Population size of alien species in patch i at time t;

r_N: Intrinsic growth rate of native species at patch 1;

r_{Ai}: Intrinsic growth rate of alien species at patch i;

K_N: Carrying capacity for the native species in patch 1 when the alien species is absent;

K_{Ai}: Carrying capacity for the alien species in patch i when the native species is absent;

c_{12}: Coefficient of the competition effect from the alien species on the native species in patch 1;

c_{21}: Coefficient of the competition effect from the native species on the alien species in patch 2;

m_{ij}: Migration rate of the alien species from patch j to patch i.

We finally construct the following population dynamics model, representing our situation:

$$\begin{cases} \dfrac{dN}{dt} &= r_N\left(1-\dfrac{N}{K_N}-\dfrac{c_{12}A_1}{K_N}\right)N; \\ \dfrac{dA_1}{dt} &= r_{A1}\left(1-\dfrac{c_{21}N}{K_{A1}}-\dfrac{A_1}{K_{A1}}\right)A_1+m_{12}A_2-m_{21}A_1; \\ \dfrac{dA_2}{dt} &= r_{A2}\left(1-\dfrac{A_2}{K_{A2}}\right)A_2-m_{12}A_2+m_{21}A_1. \end{cases}$$

As the appropriate initial condition for this modeling, we have

$$(N(0), A_1(0), A_2(0)) \quad = \quad (K_N, 0, K_{A2})$$

which is the equilibrium the populations reach in their respective area before the invasion begins.

3.2.3 Non-dimensionalized system

We apply the following transformation of variables and parameters

$$\tau = r_N t; \quad x_1 = \frac{N}{K_N}; \quad x_{2i} = \frac{A_i}{K_{Ai}}; \quad \rho_{2i} = \frac{r_{Ai}}{r_N};$$
$$\alpha_{ij} = \frac{m_{ij}}{r_N}; \quad \kappa = \frac{K_{A1}}{K_{A2}}; \quad \gamma_{12} = \frac{K_{A1}}{K_N} c_{12}; \quad \gamma_{21} = \frac{K_N}{K_{A1}} c_{21},$$

for our model, and we obtain the non-dimensionalized system

$$\begin{cases} \dfrac{dx_1}{dt} & = \quad (1 - x_1 - \gamma_{12} x_{21}) x_1; \\[2ex] \dfrac{dx_{21}}{dt} & = \quad \rho_{21}(1 - \gamma_{21} x_1 - x_{21}) x_{21} + \frac{1}{\kappa} \alpha_{12} x_{22} - \alpha_{21} x_{21}; \\[2ex] \dfrac{dx_{22}}{dt} & = \quad \rho_{22}(1 - x_{22}) x_{22} - \alpha_{12} x_{22} + \kappa \alpha_{21} x_{21}, \end{cases} \tag{3.2}$$

with the initial condition

$$(x_1(0), x_{21}(0), x_{22}(0)) \quad = \quad (1, 0, 1).$$

3.2.4 Well-posedness and boundedness

(3.2) is an autonomous system with a continuously differentiable function in terms of (x_1, x_{21}, x_{22}), so according to the Cauchy-Lipschitz theorem, it is globally well-posed. We also prove it is bounded.

Proposition 1. *Boundedness of the system*
Let us take

$$M \quad = \quad \max\left(1 + \frac{\kappa\alpha_{21} - \alpha_{12}}{\rho_{22}}, 1 + \frac{\alpha_{12} - \kappa\alpha_{21}}{\kappa\rho_{21}}\right).$$

Then for any

$$\big(x_1(0), x_{21}(0), x_{22}(0)\big) \in [0,1]^3 \times [0, M[\times [0, M[,$$

we have for all $t > 0$*,*

$$\big(x_1(t), x_{21}(t), x_{22}(t)\big) \in [0,1] \times [0, M[\times [0, M[.$$

In other words, the system is bounded.

Being assured that we are studying a proper model, we can start trying to find the different equilibria to which this model can lead.

3.3 Feasible equilibrium for the competition dynamics

To find the equilibria, we need to solve the system

$$\begin{cases} 0 &= (1 - x_1^* - \gamma_{12} x_{21}^*) x_1^*; \\ \\ 0 &= \rho_{21}(1 - \gamma_{21} x_1^* - x_{21}^*) x_{21}^* + \frac{1}{\kappa}\alpha_{12} x_{22}^* - \alpha_{21} x_{21}^*; \\ \\ 0 &= \rho_{22}(1 - x_{22}^*) x_{22}^* - \alpha_{12} x_{22}^* + \kappa \alpha_{21} x_{21}^*; \end{cases}$$

Proposition 2. *Exclusion equilibria*
For any given parameters, the following equilibria always exist:

$$(0,0,0), \qquad (1,0,0), \qquad (0, x_{21}^*, x_{22}^*).$$

Proposition 3. *Coexistence equilibria*
We may have one or two coexistence equilibria $(x_1^*, x_{21}^*, x_{22}^*)$ *with* x_1^*, x_{21}^* *and* $x_{22}^* > 0$.

Figure 3.3 illustrates the number of existing coexistence equilibria depending on the parameters. We can first notice that in the case of the competition effect being simultaneously low, respectively simultaneously high, at least one coexistence equilibrium exists. This existence is similar to a standard Lotka-Volterra competition model with those conditions. Let us note, however, that those conditions also lead to the instability of the coexistence equilibrium and a bistability case in the standard model.

In our system, in case of a high competition effect affecting the native species — high γ_{12} — but a low competition effect affecting the alien species — low γ_{21} — there is no coexistence equilibrium. This is once again the same as the Lotka-Volterra competition model. Based on this comparison, we can postulate that the native species go extinct in this case, though a stability analysis is needed for confirmation.

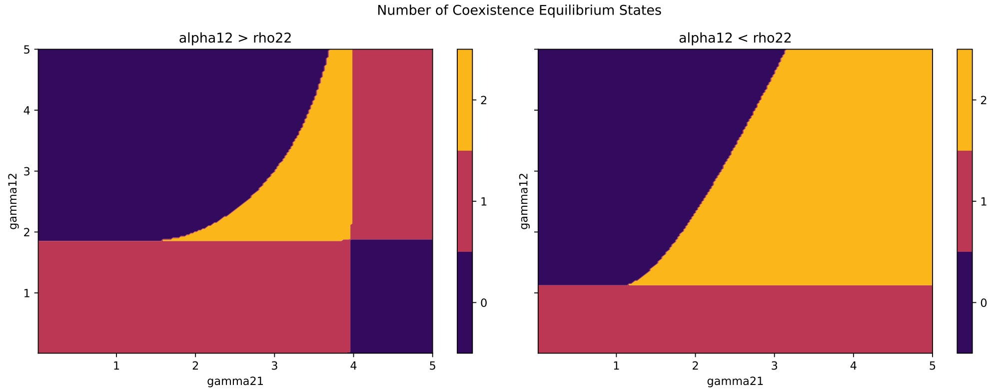


Figure 3.3: In both cases, $\kappa = 2$. For the left side graph, $\alpha_{12} = 2$, $\rho_{22} = 1$, $\alpha_{21} = 3$ and $\rho_{21} = 1$. For the right side graph, $\alpha_{12} = 1$, $\rho_{22} = 2$, $\alpha_{21} = 1$ and $\rho_{21} = 3$.

On the other hand, in the opposite case — low γ_{12} and high γ_{21} — where we would expect the alien species to go extinct, a coexistence equilibrium exists as long as $\alpha_{12} < \rho_{22}$. Changing those non-dimensionalized parameters back to the original ones, we get the condition $m_{12} < r_{A2}$. So if the migration rate of the alien species leaving its source patch is lower than its intrinsic growth rate in the same patch, a coexistence equilibrium exists, which hints at the survival of the alien species. Figure 3.4 shows an example of this situation. To better understand this condition, we should consider the opposite case: $m_{12} > r_{A2}$. This condition means that the alien species leaves its source patch faster than it grows in it. Since, in addition, it is outcompeted in the native habitat, it leads to an unsustainable situation, explaining the non-existence of a coexistence equilibrium.

3.4 Condition for the extinction of alien species

The Jacobian matrix of this system is

$$J = \begin{pmatrix} 1 - 2x_1^* - \gamma_{12}x_{21}^* & -\gamma_{12}x_1^* & 0 \\ -\rho_{21}\gamma_{21}x_{21}^* & \rho_{21}(1 - \gamma_{21}x_1^* - 2x_{21}^*) - \alpha_{21} & \dfrac{\alpha_{12}}{\kappa} \\ 0 & \kappa\alpha_{21} & \rho_{22}(1 - 2x_{22}^*) - \alpha_{12} \end{pmatrix}.$$

It is a matrix tridiagonal and sign-symmetric, so all eigenvalues are real (see for example Mitchell and Wilkinson [81]).

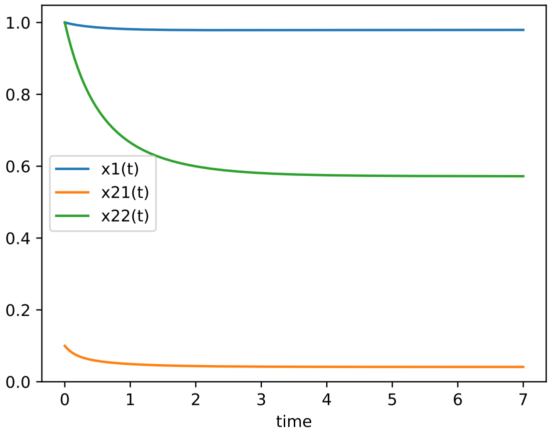


Figure 3.4: Existence of coexistence equilibrium even with low γ_{12} and high γ_{21} if $\alpha_{12} < \rho_{22}$. Here $\alpha_{12} = 1$, $\rho_{22} = 2$, $\gamma_{12} = 0.5$, $\gamma_{21} = 3$ $\alpha_{21} = 1$, $\rho_{21} = 3$, and $\kappa = 2$. We used $(1, 0.1, 1)$ as initial conditions.

For the equilibrium $(0, 0, 0)$ the matrix becomes

$$J_{(0,0,0)} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & \rho_{21} - \alpha_{21} & \dfrac{\alpha_{12}}{\kappa} \\ 0 & \kappa\alpha_{21} & \rho_{22} - \alpha_{12} \end{pmatrix}.$$

By block matrices, one eigenvalue is 1, so this equilibrium is always unstable. There is always a least one species in our system.

Proposition 4. *$J_{(1,0,0)}$ has a positive eigenvalue if and only if*

$$\begin{aligned} & \gamma_{21} < 1 + \frac{\rho_{22}}{\rho_{21}} - \frac{\alpha_{21} + \alpha_{12}}{\rho_{21}}, \\ \text{or} \quad & (\gamma_{21} - 1)\left(\frac{\alpha_{12}}{\rho_{22}} - 1\right) < \frac{\alpha_{21}}{\rho_{21}}. \end{aligned}$$

In particular, if $\gamma_{21} < 1$ or $\alpha_{12} < \rho_{22}$, those conditions are fulfilled.

Figure 3.5 show the local stability of this equilibrium, while Figure 3.6 shows that it is not a global stability.

In a standard Lotka-Volterra system, the equilibrium point of alien extinction is unstable if and only if $\gamma_{21} < 1$, which indicates that the alien species is not significantly affected by the competition effect. We also find this characteristic in the system we are studying now with an added migration. However, here, it is only a sufficient condition: the matrix $J_{(1,0,0)}$ can

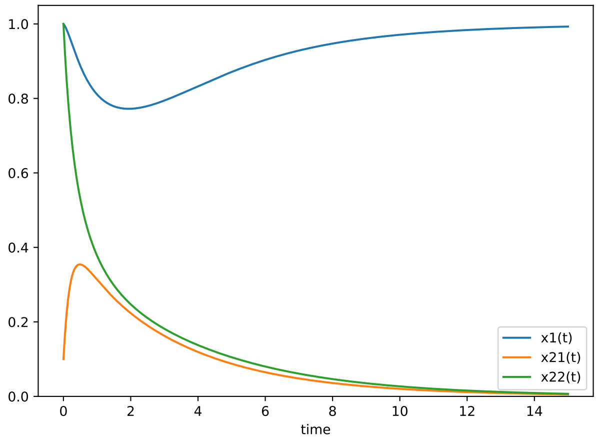


Figure 3.5: Illustration of the local stability of $(1,0,0)$. Parameters $\gamma_{12} = 1, \gamma_{21} = 3, \alpha_{12} = 2, \alpha_{21} = 1, \rho_{21} = \rho_{22} = 1, \kappa = 1$ and initial values of the system are $(1, 0.1, 1)$

have positive eigenvalues even with $\gamma_{21} > 1$. Indeed, since the alien species also lives in a patch free of competition, it is easier for the species to survive than in the system without diffusion.

Another characteristic that guarantees the survival of the alien species is if $\alpha_{12} < \rho_{22}$; rewritten with the original parameters, it means $m_{12} < r_{A2}$. If the rate at which the alien species leave its source patch is lower than the intrinsic growth rate in the same patch, the alien species does not go extinct in this patch. By extension, it does not go extinct in the whole system.

3.5 Condition for the persistence of native species

Proposition 5. *$J_{(0,x^*_{21},x^*_{22})}$ has a positive eigenvalue if and only if the following condition is satisfied:*

$$1 - \frac{\alpha_{21}}{\rho_{21}} < \frac{1}{\gamma_{12}} \quad \text{and} \quad f_0(1/\gamma_{12}) > h_0(1/\gamma_{12}),$$

where

$$\begin{aligned} f_0(x) &:= \frac{\kappa}{\alpha_{12}} x\Big(\alpha_{21} - \rho_{21}(1-x)\Big); \\ h_0(x) &:= 1 + \frac{\alpha_{12}}{\rho_{22}}\left(\frac{\alpha_{21}}{\alpha_{21} - \rho_{21}(1-x)} - 1\right). \end{aligned}$$

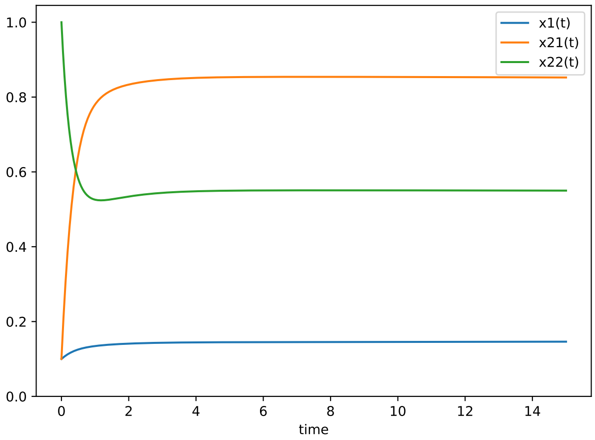


Figure 3.6: The stability of $(1, 0, 0)$ is only local and not global, as shown in this numerical computation. Parameters $\gamma_{12} = 1, \gamma_{21} = 3, \alpha_{12} = 2, \alpha_{21} = 1, \rho_{21} = \rho_{22} = 1, \kappa = 1$ and initial values of the system are $(0.05, 0.01, 1)$

Figure 3.7 gives an illustration of those conditions, and Figure 3.8 is a numerical computation of the system in a stable case (on the left) and unstable case (on the right).

Note that the condition $1 - \alpha_{21}/\rho_{21} < 1/\gamma_{12}$ is automatically true if $\alpha_{21} > \rho_{21}$ or $\gamma_{12} < 1$. For comparison once again with a Lotka-Volterra model without migration, the equilibrium point of the extinction of native species is unstable if and only if $\gamma_{12} < 1$, so when the species is not very affected by the competition effect. It is also a sufficient condition in our system for the survival of the native species; however, it is not necessary. It is easier for the native species to survive in this model than in a system without diffusion.

Another possibility that is sufficient to ensure the survival of native species is if $\alpha_{21} > \rho_{21}$. With the original parameters, it means $m_{21} > r_{A1}$. If the alien species leaves the native habitat faster than it can grow in this same patch, the native species can survive, even when outcompeted. Indeed, in this case, there would never be enough alien species individuals in the native habitat to endanger the native species.

Let us notice from Figure 3.7 that the higher α_{12}, the lower γ_{12} needs to be to assure the stability of the native species extinction equilibrium. In other words, the higher the migration rate of the alien species into the native habitat, the lower the competition effect needs to be for the native species extinction equilibrium to be stable.

Finally, for low α_{12}, the equilibrium $(0, x^*_{21}, x^*_{22})$ is unstable even for some

$\gamma_{12} > 1$, while for high α_{12}, it is stable even for some $\gamma_{12} < 1$. 1 is the cut-off point for stability in a standard Lotka-Volterra system.

Proposition 6. *$J_{(0,x_{21}^*,x_{22}^*)}$ has a positive eigenvalue for all $\alpha_{12} > 0$ and $\alpha_{21} > 0$ if and only if*

$$\gamma_{12} < \gamma_{12,lim} \quad := \quad 2\kappa \frac{\rho_{21}}{\rho_{22}} \left(-1 + \sqrt{1 + \frac{\rho_{22}}{\kappa \rho_{21}}} \right).$$

$J_{(0,x_{21}^*,x_{22}^*)}$ has a positive eigenvalue for all $\alpha_{21} > 0$ if and only if $\gamma_{12} < \gamma_{12,lim}$, or

$$\begin{aligned} &\alpha_{12} < \frac{\rho_{22}}{2} \text{ and} \\ &\gamma_{12} < \kappa \frac{\rho_{22}\rho_{21}}{2\alpha_{12}(\rho_{22} - \alpha_{12})} \left(-1 + \sqrt{1 + 4\frac{\alpha_{12}}{\kappa\rho_{21}} \left(1 - \frac{\alpha_{12}}{\rho_{22}} \right)} \right). \end{aligned}$$

It is notable that for a low enough γ_{12}, then whatever the migration rate of the alien species, the native species can persist. The limit until this is true depends positively on the ratio r_{A1}/r_{A2} (respectively K_{A1}/K_{A2}), so the higher r_{A1}/r_{A2} (resp K_{A1}/K_{A2}), the higher $\gamma_{12,lim}$. In essence, a high ratio r_{A1}/r_{A2} means that its original patch has less to contribute to the growth of alien species than the native habitat, and so migration plays a less important role than what happens in the native habitat itself.

Furthermore, if the immigration rate into the native habitat m_{12} is small enough — more precisely, if $m_{12} < r_{A2}/2$ — then there is a small parameters' window in which the return rate m_{21} will not affect the survival of the native species. We can conclude from this that at a low immigration rate relative to the growth in the alien species source patch, the immigration rate parameter is much more important to consider for the survival of the native species than the return rate.

3.6 Dependence of the terminal state on the initial condition

If we regroup the condition we gave for the stability of both equilibria, we obtain

$$\begin{aligned} \gamma_{21} &> 1 + \frac{\rho_{22}}{\rho_{21}} - \frac{\alpha_{21} + \alpha_{12}}{\rho_{21}} \\ \text{and} \qquad (\gamma_{21} - 1)\left(\frac{\alpha_{12}}{\rho_{22}} - 1 \right) &> \frac{\alpha_{21}}{\rho_{21}} \\ \text{and} \quad \left(1 - \frac{\alpha_{21}}{\rho_{21}} > \frac{1}{\gamma_{12}} \right. &\left. \text{ or } f_0(1/\gamma_{12}) < h_0(1/\gamma_{12}) \right) \end{aligned}$$

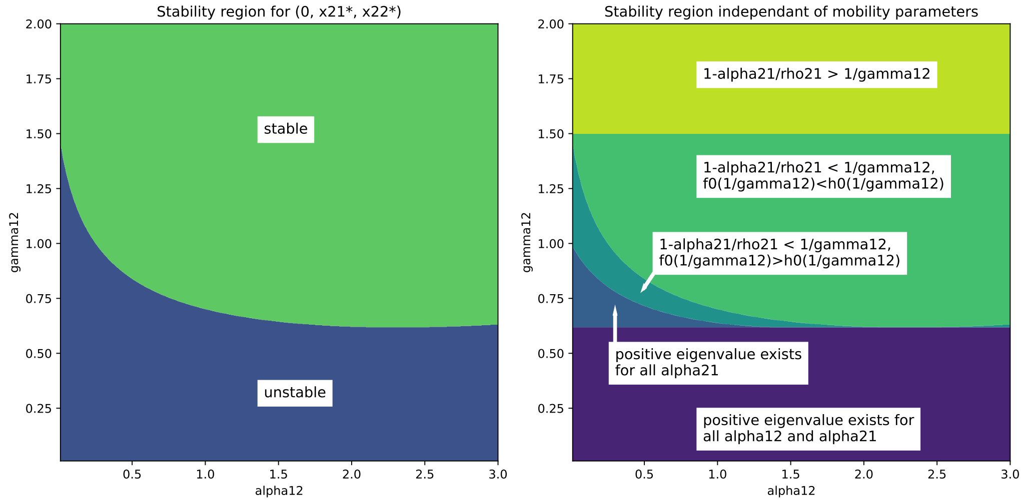


Figure 3.7: Conditions for the stability of $(0, x_{21}^*, x_{22}^*)$. $\kappa = 0.5$, $\alpha_{21} = 0.5$, $\rho_{22} = 3$. On the left is the illustration of the proposition 5 while on the right is the illustration of the proposition 6.

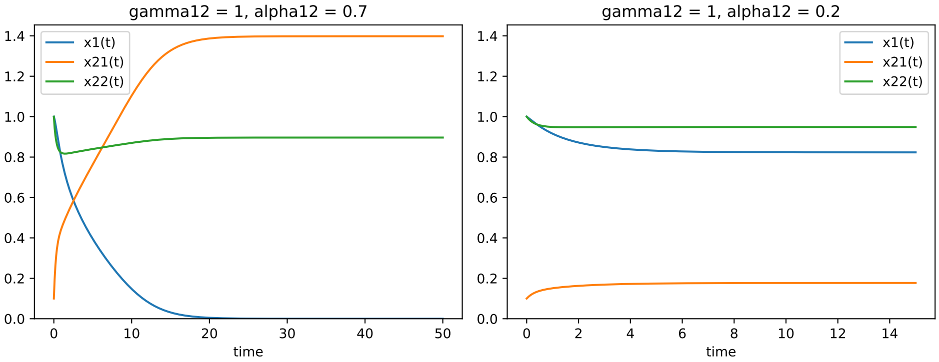


Figure 3.8: Illustration of the local stability of $(0, x_{21}^*, x_{22}^*)$ on the left, and instability on the right. For both graphs, parameters are $\gamma_{12} = 1, \gamma_{21} = 3, \alpha_{21} = 0.5, \rho_{21} = 1, \rho_{22} = 3, \kappa = 0.5$, and initial values of the system are $(1, 0.01, 1)$. For the graph on the left $\alpha_{12} = 0.5$, while on the right $\alpha_{12} = 0.1$.

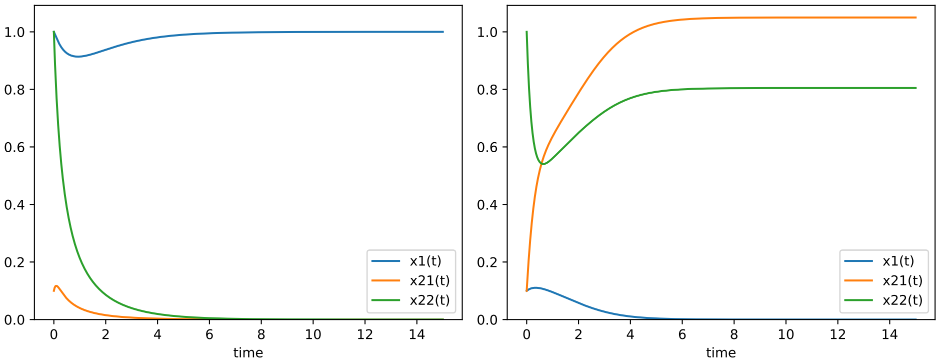


Figure 3.9: Illustration of the bistability phenomenon in this model. For the left side graph, $\gamma_{21} = 2$, $\gamma_{12} = 4$, $\alpha_{12} = 3$, $\rho_{22} = 2$, $\alpha_{21} = 1$, $\rho_{21} = 3$, and $\kappa = 2$. Initial parameter on the left graph are $(1, 0.1, 1)$ while on the right they are $(0.1, 0.1, 1)$.

Then we are in a bistable case. In particular, we need to have at least (but it is not sufficient)

$$\gamma_{21} > 1, \quad \gamma_{12} > 1, \quad \alpha_{12} > \rho_{22}, \quad \alpha_{21} < \rho_{22}.$$

In other words, suppose that the competition effects strongly affect both the native species and the alien species. Furthermore, suppose that the alien species leave its original habitat faster than it grows in it. Finally, suppose that the alien species leaves the native habitat slower than it grows in it. Then, both species cannot coexist, but either has a chance of surviving, depending on their initial conditions. Figure 3.9 gives an example of this situation.

3.7 Discussion

In this chapter, we explored the characteristics of a two patches model representing the invasion of a native habitat by an alien species and the competition for resources. Studying a patchy model for this invasion allows us to focus on a more nuanced result derived from the spatial effect (DeAngelis and Yurek [12]) compared to a standard Lotka-Volterra model. Similar models have been studied previously, for example, with a symmetrical migration rate (Ruiz-Herrera and Torres [57]) or considering a sink instead of a source patch, with (Wang et al. [80]) and without competition (Holt [31]; Arditi et al. [5]). Some of those results were shown in a laboratory (Zhang et al. [84];

Zhang et al. [83]). However, to the best of our knowledge, research has yet to be done on the case we presented, modeling an invasion.

These topics of research can help policymakers and land managers make rational decision about the creation of ecological corridors. While it was shown that corridors are usually beneficial for species conservation (Gaines et al. [24]; Gilbert-Norton et al. [25]), it is not always true and they can also promote the spreading of an invasive species (Simberloff et al. [65]; Resasco et al. [56]), thus causing more harm than good. An understanding of the characteristics of the species using those corridors mitigates the risks of constructing detrimental ones.

In this chapter we showed that, as in the Lotka-Voltera competition model, we have the possibility for the alien species to go extinct, for the native species to go extinct, or for both species to coexist. In a specific range of parameters, we also showed that the initial conditions play a role in the extinction of one of the two species. The difference in our model is that the migration rates, non-existent in the Lotka-Voltera competition model, play a significant role in determining the outcome.

We showed that the immigration rate of the alien species into the native habitat negatively impacts the survival chances of the native species. However, it is a double-edged sword since a high immigration rate is also needed for the alien species to get extinct. More specifically, a high immigration rate and the competition effect strongly affecting the alien species make the outcome either a bistable case or an exclusion of the alien species.

Furthermore, we showed that even if the immigration rate of the alien species negatively impacts the survival of the native species, it cannot guarantee its extinction. On the other hand, a high enough competition effect affecting the native species will ensure, at the very least, a bistability effect or even the extinction of the native species. A low one will guarantee the native species' persistence, independently of all migration rates.

Finally, in our model, it is easier for the native species to survive when the alien species has a low immigration rate compared to the Lotka-Volterra competition model. On the other hand, when the alien species has a high immigration rate, it is harder for the native species to survive than in the Lotka-Volterra competition model.

Chapter 4

Habitat size and competition dynamics

4.1 A model with population dispersal in space

As in the previous chapter, we again seek to model an alien species invading a native habitat already inhabited, creating a competition for resources between both species. The alien species is considered to have a much stronger dispersal ability than the native species again. However here, we consider a two-species competitive system in a continuous space, notably in order to study the impact of the size of the space itself on the species survival.

4.1.1 Assumptions

To model the situation we are considering, we make the following assumptions.

- The native species only exists in a part of the total space, the native habitat. The alien species can exist everywhere.
- Only the alien species is diffusing. The native species cannot spread, or its spread is slow enough compared to the alien species that we consider it nonexistent.
- Both species follow a logistic growth if left alone.
- We consider the environment homogeneous.
- A competition for resources takes place in the native habitat.
- We consider the environment to be isolated.

4.1.2 Population dynamics model

To transform our assumptions into a valid mathematical model, we use the following variables and parameters

$N(x,t)$: Population size of native species at position x and time t;

$A(x,t)$: Population size of alien species at position x and time t;

r_N: Intrinsic growth rate of native species;

r_A: Intrinsic growth rate of alien species;

K_N: Carrying capacity for the native species;

K_A: Carrying capacity for the alien species;

c_{12}: Coefficient of the competition effect from the alien species on the native species;

c_{21}: Coefficient of the competition effect from the native species on the alien species;

D_A: Diffusion coefficient of the alien species.

L: Total length of the habitat.

l: Length of the habitat containing the native species.

We finally construct the following population dynamics model:

$$\left\{\begin{array}{lll} \dfrac{\partial N}{\partial t} & = & \left\{\begin{array}{ll} r_N\left(1-\dfrac{N}{K_N}-c_{12}\dfrac{A}{K_N}\right)N, & x\in[0,l]; \\ \\ \qquad 0, & x\in(l,L]; \end{array}\right. \\ \\ \dfrac{\partial A}{\partial t} & = & r_A\left(1-c_{21}\dfrac{N}{K_A}-\dfrac{A}{K_A}\right)A+D_A\dfrac{\partial^2 A}{\partial x^2}, \quad x\in[0,L]. \end{array}\right. \tag{4.1}$$

Since we consider the isolated environment, we adopt the no-flux (Neumann) boundary conditions

$$\left.\frac{\partial A}{\partial x}\right|_{x=0} = \left.\frac{\partial A}{\partial x}\right|_{x=L} = 0.$$

4.1.3 Non-dimensionalized system

To reduce the number of relevant parameters in this model, we express it in non-dimensionalized terms. Applying the following transformations:

$$U = \frac{N}{K_N}; \quad V = \frac{A}{K_A}; \quad \hat{t} = r_A t; \quad \hat{x} = \frac{x}{L}; \quad d = \frac{l}{L};$$
$$R = \frac{r_N}{r_A}; \quad a = c_{12}\frac{K_A}{K_N}\frac{r_N}{r_A}; \quad b = c_{21}\frac{K_N}{K_A}\frac{r_A}{r_N}; \quad c = \frac{1}{L}\sqrt{\frac{D_A}{r_A}},$$

we obtain

$$\begin{cases} \dfrac{\partial U}{\partial \hat{t}} = \begin{cases} R(1 - U - \dfrac{a}{R}V)U, & \hat{x} \in [0,d]; \\ 0, & \hat{x} \in (d,1]; \end{cases} \\ \dfrac{\partial V}{\partial \hat{t}} = (1 - RbU - V)V + c^2\dfrac{\partial^2 V}{\partial \hat{x}^2}, \quad \hat{x} \in [0,1]. \end{cases} \tag{4.2}$$

We omit the hat symbol from here on for readability. The non-dimensionalized Neumann boundaries conditions become:

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

We take initial conditions appropriate for the invasion situation we are considering:

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

$$V(x,0) = \begin{cases} 0, & x \in [0,d]; \\ V_0, & x \in (d,1], \end{cases}$$

with $V_0 \in]0,1]$. Figure 4.1 illustrates the initial conditions. Finally, we force our solutions to be smooth enough by imposing

$$\lim_{x\to d-} V(x,t) = \lim_{x\to d+} V(x,t), \quad \forall t > 0;$$
$$\lim_{x\to d+} \frac{\partial V}{\partial x} = \lim_{x\to d+} \frac{\partial V}{\partial x}, \quad \forall t > 0.$$

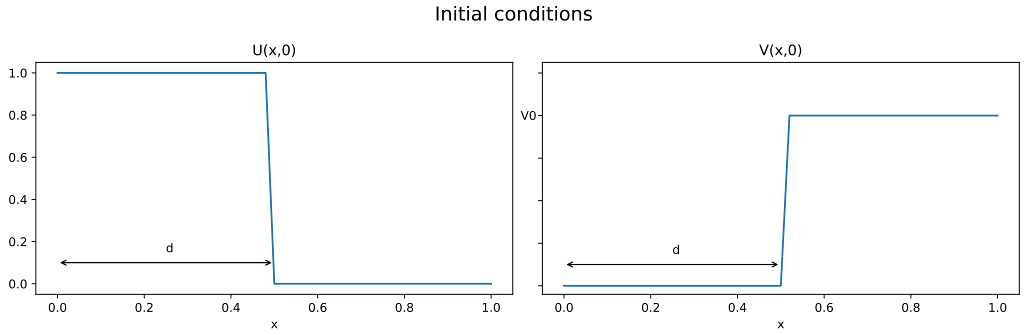


Figure 4.1: Initial conditions illustrations.

4.2 Condition for the invasion success of alien species

4.2.1 Stability of the alien species extinction stationary solution

For the stationary solutions with $V(x) = 0$, the only possibilities are $(0, 0)$ or $(U(x, 0), 0)$. We study their respective stability.

Homogeneous stationary solution $(0, 0)$

To study the perturbations around the homogeneous stationary solution $(0, 0)$, we define the functions $u(x, t)$ and $v(x, t)$. Those functions only take small values:

$$\begin{aligned} U &= u(x,t) \ , \quad 0 \le u(x,t) \ll 1, \\ V &= v(x,t) \ , \quad 0 \le v(x,t) \ll 1, \end{aligned}$$

U and V are the non-dimensionalized representation of population densities and, as such, are non-negative. We still consider that there is no native species in the area $(d, 1]$, so we add the following restrictions on $u(x, t)$:

$$u(x,t) = 0 \text{ for } x \in (d, 1].$$

We obtain after linearization

$$\frac{\partial u}{\partial t} = \begin{cases} Ru, & x \in [0,d]; \\ 0, & x \in (d,1]; \end{cases}$$

$$\frac{\partial v}{\partial t} = v + c^2 \frac{\partial^2 v}{\partial x^2}, \quad x \in [0,1].$$

$\partial u/\partial t > 0$ for $x \in [0,d]$ so this stationary solution is always unstable.

Stationary solution $(U(x,0),0)$

We now look at the perturbations around the stationary solution $(U(x,0),0)$. For the same reason as previously, we introduce $u(x,t)$ and $v(x,t)$ the functions representing the perturbations such that

$$\begin{aligned} U &= U(x,0) + u(x,t), \quad |u(x,t)| \ll 1 \text{ for } x \in (0,d], \\ & \qquad\qquad\qquad\qquad\quad u(x,t) = 0 \text{ for } x \in (d,1]; \\ V &= v(x,t), \quad 0 < v(x,t) \ll 1. \end{aligned}$$

After introducing these functions in the system (4.1) and linearizing, we obtain

$$\frac{\partial u}{\partial t} = \begin{cases} -Ru - av, & x \in [0,d]; \\ 0, & x \in (d,1]; \end{cases}$$

$$\frac{\partial v}{\partial t} = \begin{cases} (1-Rb)v + c^2 \dfrac{\partial^2 v}{\partial x^2}, & x \in [0,d]; \\ v + c^2 \dfrac{\partial^2 v}{\partial x^2}, & x \in (d,1]. \end{cases} \tag{4.3}$$

Notice that the stability of v is independent of u, so we start by studying $\partial v/\partial t$. Rewriting $v(x,t)$, it's in the form

$$\frac{\partial v}{\partial t} = q(x)v + c^2 \frac{\partial^2 v}{\partial x^2}, \quad \text{with} \quad q = \begin{cases} 1 - Rb & x \in [0,d] \\ 1 & x \in (d,1] \end{cases} \quad \text{and } q \in L^\infty([0,1]).$$

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

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

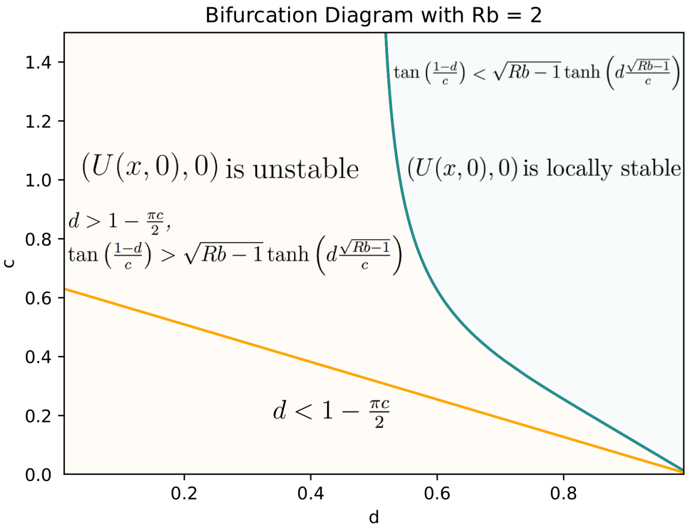


Figure 4.2: Last two conditions of Proposition 7 with $Rb = 2$.

with g_n the eigenfunctions verifying

$$\left\{\begin{array}{lcl} c^2 g''(x) + (q(x) - \lambda)g(x) & = & 0; \\ \\ g'(0) \;=\; g'(1) & = & 0. \end{array}\right.$$

Proposition 7. *For* $v(x,t) = \sum_{n=1}^{\infty} c_n e^{\lambda_n t} g_n(x)$ *solving the system (4.3), there is no* $k \geq 1$ *such that* $\lambda_k > 0$ *if and only if*

$$1 > d > \frac{1}{bR}, \quad d > 1 - \frac{\pi c}{2} \text{ and } \tan\left(\frac{1-d}{c}\right) < \sqrt{Rb-1}\tanh\left(d\frac{\sqrt{Rb-1}}{c}\right).$$

Figure 4.2 illustrates the last two conditions. When those conditions are achieved, then for a t big enough, we have

$$\frac{\partial u}{\partial t} \simeq \begin{cases} -Ru, & x \in [0,d]; \\ 0, & x \in (d,1]. \end{cases}$$

Because of the special case $\lambda = 0$, this conditions is not sufficient for the asymptotic stability of $(U(x,0),0)$ and the survival of the alien species. It is however a necessary conditions for it. We have a numerical illustration of this phenomenon in Figure 4.3.

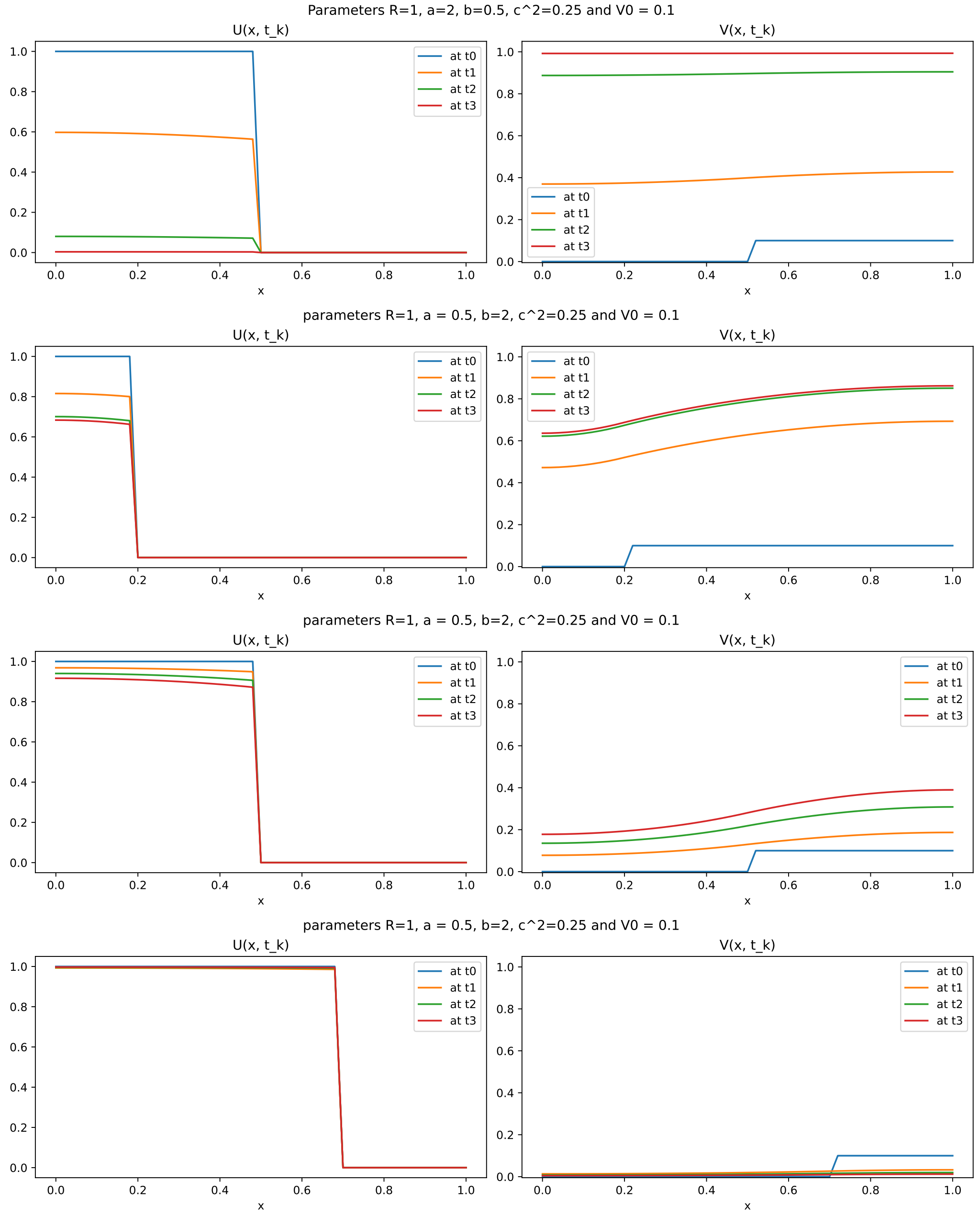


Figure 4.3: Illustration of the conditions for the alien persistence. On the first line, we have $Rb < 1$. On the second line, we have $Rb > 1$and $d > 1 - \frac{\pi c}{2}$. On the thirds line we have $Rb > 1$, $d > 1 - \frac{\pi c}{2}$ and $\tan\left(\frac{1-d}{c}\right) > \sqrt{Rb-1}\tanh\left(d\frac{\sqrt{Rb-1}}{c}\right)$. The last line is such that $Rb > 1$, $d > 1 - \frac{\pi c}{2}$, $\tan\left(\frac{1-d}{c}\right) < \sqrt{Rb-1}\tanh\left(d\frac{\sqrt{Rb-1}}{c}\right)$, and the stationary solution $(U(x,0),0)$ is locally stable.

4.2.2 Parameter dependence of the invasion success

By rewriting the conditions with the initial parameters and calling $l_A = L - l$ the portion of the space where only the alien species lives, we obtain that the conditions for the alien persistence are

- $c_{21} < \dfrac{K_A}{K_N}$,
- or $\dfrac{l}{L} < \dfrac{1}{c_{21}} \dfrac{K_A}{K_N}$,
- or $l_A > \frac{\pi}{2}\sqrt{\frac{D_2}{r_2}}$,
- or $\tan\left(l_A\sqrt{\frac{r_A}{D_A}}\right) > \sqrt{c_{21}\frac{K_N}{K_A} - 1}\tanh\left(l\sqrt{\frac{r_A}{D_A}}\sqrt{c_{21}\frac{K_N}{K_A} - 1}\right)$.

In a standard Lotka-Volterra system without diffusion, the homogeneous stationary solution $(K_N, 0)$ is unstable if and only if $c_{21} < K_A/K_N$. In other words, if the effect of the competition on the alien species is lower than the carrying capacity ratio, then the alien species cannot go extinct.

However, not fulfilling these conditions does not mean the alien species goes extinct. In our model, the alien species does not live only in the same space as the native species but also has its own space, which is free from competition. Even if the competition affects it strongly, it can survive by relying on this space, given that it is big enough to counterbalance the death in the shared space. The second condition gives us a critical ratio for the area with competition. It will survive if enough of the area is free from competition for the alien species.

While the second condition gives us a reference for the ratio of the area essential for the alien species' survival, the third condition gives a reference for the actual length of the alien habitat necessary (relative to the alien species spreading rate). If we consider the extreme case of the competition effect, such that the alien species would immediately die in the shared space, we can compare the delimiting position of the shared space to a Dirichlet boundary. The third condition here is similar to what we found in chapter 2, section 2.3.3 when analyzing the critical patch size of a space with a Neumann boundary on one side and a Dirichlet boundary on the other. The alien species can survive if the alien-only space is larger than what is needed for this extreme case.

Finally, the last condition shows that this situation is, in fact, not equivalent to the extreme case just mentioned. The alien species need a less extensive competition-free space to survive. This last condition depends on

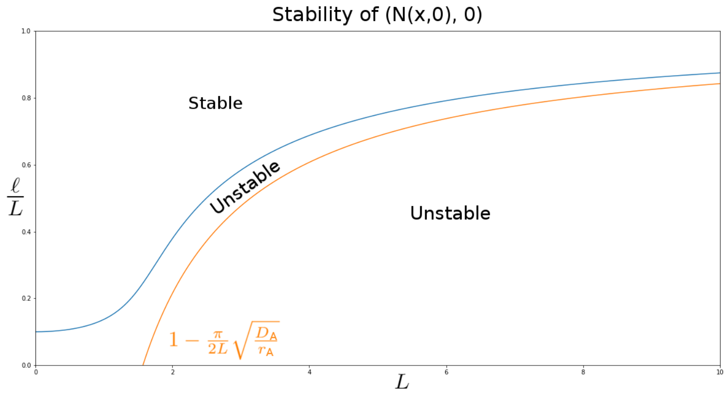


Figure 4.4: Bifurcation diagram of the alien species extinction stationary solution, depending on l/L and L with $c_{21} > K_A/K_N$. Comparison with the third condition for stability, akin to a critical patch size for the diffusing species. $D_A/r_A = 1$, $c_{21} = 2$, $K_A/K_N = 1/5$.

the space's size and the strength of the competition effect applied to the alien species.

From another point of view, rather than the size, it depends on the speed of diffusion of the alien species. Moreover, despite this result being mellower than a Dirichlet boundary model, as explained, it is still possible for the alien species to get extinct if it diffuses too fast for the growth in its personal space to counterbalance the death coming from the competition.

Figure (4.4) illustrates the bifurcation diagram depending on the space parameters. We can again see the critical ratio exhibited previously that allows the alien species to persist independently of its diffusion rate and the area's total size. Rewritten, this ratio is

$$\frac{l}{L} < \frac{1}{c_{21}}\frac{K_A}{K_N} \quad \Longrightarrow \quad \text{alien species survives}$$

and is one of the main differences compared to the Neumann and Dirichlet boundaries model. Note that when $c_{21} < K_A/K_N$, the alien species survives.

This ratio means that if the habitat of native species occupies an area less than a certain percent of the total size, the alien species can always survive, even when highly outcompeted.

4.3 Condition for the persistence of native species

Finding the stationary solution associated with $U = 0$ in the system(4.2) comes back to finding the solutions for

$$\big(1 - V(x)\big)V(x) + c^2V''(x) \;=\; 0, \quad x \in [0,1]$$

$$V''(0) \;=\; V''(1) \;=\; 0$$

This is the problem of finding the stationary solutions of the Fisher equation (Fisher [20]). The homogeneous functions

$$V(x) = 0 \quad \text{and} \quad V(x) = 1$$

are obvious solutions, and since we have Neumann boundary conditions, those are the only possible solutions (see Iannelli and Pugliese [35] chapter 5 for example). We already showed the instability of the homogeneous stationary solution $(0,0)$. We now study the stability of $(0,1)$.

To study the perturbations around the homogeneous stationary solution $(0,1)$ we again introduce the functions $u(x,t)$ and $v(x,t)$ such that

$$U \;=\; u(x,t), \quad |u(x,t)| \ll 1;$$

$$V \;=\; 1 + v(x,t), \quad |v(x,t)| \ll 1.$$

U represents a population density, and we consider that there is no native species in the area $(d,1]$, so we add the following restrictions on $u(x,t)$:

$$u(x,t) \geq 0 \text{ for } x \in [0,d], \quad u(x,t) = 0 \text{ for } x \in (d,1].$$

After linearization, we obtain

$$\frac{\partial u}{\partial t} \;=\; \begin{cases} Ru(1-\frac{a}{R}), & x \in [0,d]; \\ 0, & x \in (d,1]; \end{cases}$$

$$\frac{\partial v}{\partial t} \;=\; \begin{cases} -(Rbu + v) + c^2\dfrac{\partial^2 v}{\partial x^2}, & x \in [0,d]; \\ -v + c^2\dfrac{\partial^2 v}{\partial x^2}, & x \in (d,1]. \end{cases} \quad .$$

$\partial u/\partial t < 0$ for $x \in [0, d]$ if and only if $R < a$. In case we do have $R < a$, then for large enough time we have $u(x, t) \to 0$ and then

$$\begin{aligned} \frac{\partial v}{\partial t} &\simeq -v + c^2\frac{\partial^2 v}{\partial x^2}; \\ \left.\frac{\partial v}{\partial x}\right|_{x=0} &= \left.\frac{\partial v}{\partial x}\right|_{x=1} = 0. \end{aligned}$$

These functions follow a Skellam model (Skellam [67]). A classical method of separation of variables gives us

$$v(x, t) = g(x)f(t)$$

then we get

$$\frac{f'(t)}{f(t)} = -1 + \frac{g''(x)}{g(x)} = -\lambda \in \mathbb{R},$$

so

$$f(t) = Ce^{-\lambda t}$$

and

$$\begin{cases} g''(x) = (1 - \lambda)g(x); \\ g'(0) = g'(1) = 0. \end{cases}$$

If $\lambda \leq 1$, there are no non-zero solutions to this boundary value problem. Then through the superposition principle, the Fourier series solution of the problem is given by

$$v(x, t) = e^{-\lambda_k t}\sum_{n\geq 1} c_n g_n(x)$$

with c_n the Fourier coefficients depending on the initial values of the problem, $\lambda_n > 1$ for all $n \geq 1$, and g_n are bounded. We can conclude that at any $x \in [0, 1]$, $\lim_{t\to\infty} v(x, t) = 0$ then. All in all, we have the following results:

If $R > a$ then $(0, 1)$ is unstable;
If $R < a$ then $(0, 1)$ is stable.

See Figure 4.5

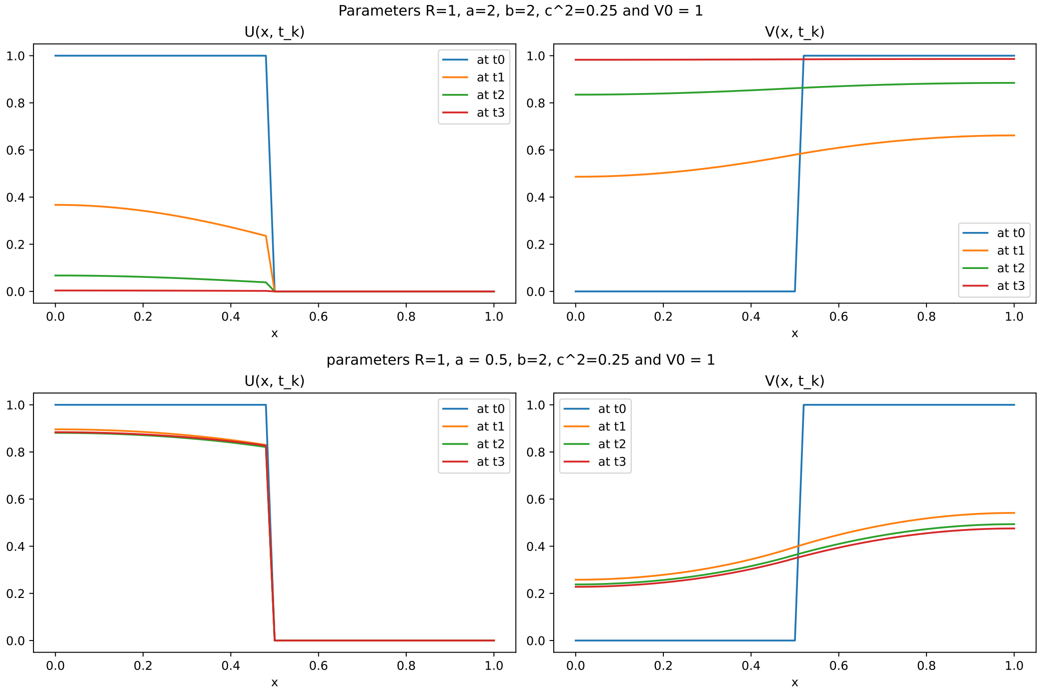


Figure 4.5: Illustration of the persistence condition for the native species.

We can rewrite this condition with the original parameters, which gives us the following results:

$$\begin{aligned}
&\text{If } c_{12} < \frac{K_N}{K_A} \quad \text{then} \quad (0, K_A) \text{ is unstable ;}\\
&\text{If } c_{12} > \frac{K_N}{K_A} \quad \text{then} \quad (0, K_A) \text{ is stable.}
\end{aligned}$$

So to say, the survival of the native species depends on the effect of the competition applied to them, as well as both species' theoretical maximum density in the environment (carrying capacity). If the effect of the competition on the native species is lower than the carrying capacity ratio, then the native species cannot go extinct. Interestingly, those are the same stability conditions as the standard Lotka-Volterra system

$$\left\{\begin{array}{rcl}
\dfrac{dN}{dt} & = & r_N\left(1 - \dfrac{N}{K_N} - c_{12}\dfrac{A}{K_N}\right)N;\\[2ex]
\dfrac{dA}{dt} & = & r_A\left(1 - c_{21}\dfrac{N}{K_A} - \dfrac{A}{K_A}\right)A.
\end{array}\right.$$

From this first approach, the diffusion of the alien species does not seem

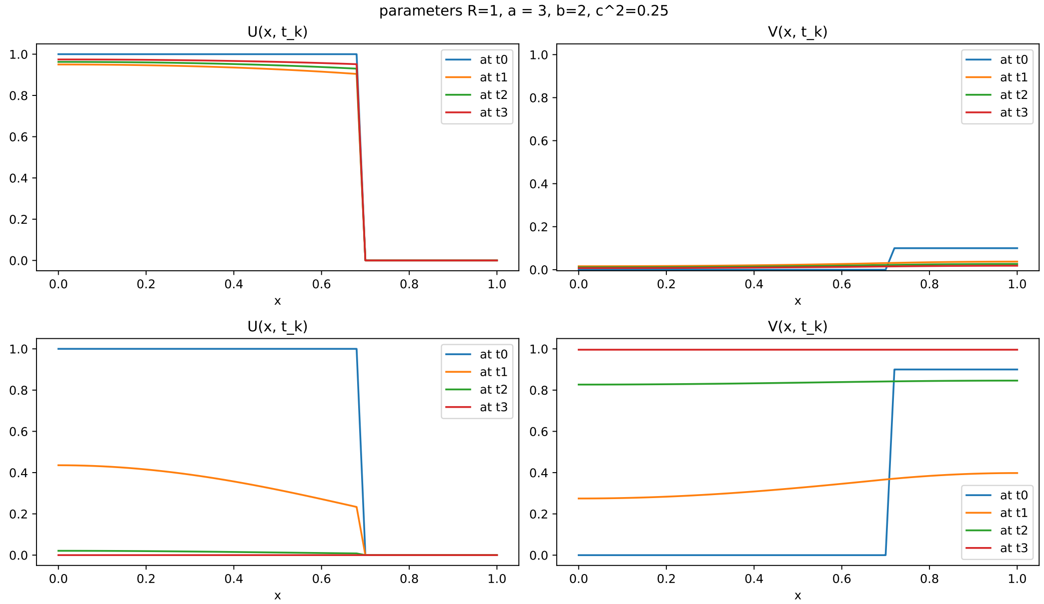


Figure 4.6: Illustration of the possibility of bistability of the system. We have the same parameters on both lines, however the initial conditions differ. $V_0 = 0.1$ on the first line, and the native species persists in the end, whereas $V_0 = 0.9$ on the second line, and the native species goes extinct.

to change the conditions of survival of the native species. However, in the standard Lotka-Volterra system, when the former condition is not achieved — when $(0, K_A)$ is stable — we can have either a single stability case or a bistability case.

4.4 Bistable situation

It is perfectly possible to have the local stability conditions for $(0, 1)$ and $(U(x, 0), 0)$ to be fulfilled at the same time. More precisely, when the following conditions are true:

$$a > R, \quad d > \frac{1}{Rb}, \quad d > 1 - \frac{\pi c}{2}$$
$$\text{and} \quad \tan\left(\frac{1-d}{c}\right) < \sqrt{Rb-1}\tanh\left(d\frac{\sqrt{Rb-1}}{c}\right)$$

we are in a bistability case, where the system's final state depends on the initial conditions. See an example in Figure 4.6.

Translated into the original parameters, we get the bistability conditions

$$c_{12} > \frac{K_N}{K_A}, \quad \frac{l}{L} > \frac{1}{c_{21}} \frac{K_A}{K_N}, \quad l_A < \frac{\pi}{2}\sqrt{\frac{D_2}{r_2}}$$

$$\text{and} \quad \tan\left(l_A\sqrt{\frac{r_A}{D_A}}\right) < \sqrt{c_{21}\frac{K_N}{K_A} - 1}\tanh\left(l\sqrt{\frac{r_A}{D_A}}\sqrt{c_{21}\frac{K_N}{K_A} - 1}\right)$$

This means that even if the native species is heavily affected by the competition for resources, the invasion can still fail as long as it occupies most of the space available to the alien species.

4.5 Discussion

In this chapter, we explored the characteristics of a model of a native species facing an invasion by an alien species in continuous space. More precisely, we focused on the conditions for the persistence of these species. The addition of diffusion to a standard model has already been extensively studied, be it in a resource competition model in a single patch (Pao [55]; Iida et al. [36]) or with multiple patches (Pacala and Roughgarden [54]; Takeuchi [69]). The asymmetrical modeling of a spreading and a motionless species was studied by Seno (Seno [61]), but in a prey-predator setting instead of our resource competition model.

Despite these works and much more, we have yet to achieve a complete understanding of the effect of diffusion, and the topic remains interesting and more relevant than ever. For example, due to global warming or human activities, many species are forced to flee their habitat and migrate. They might then become invasive species. (Seebens et al. [59]). ”The best way to avoid the harm that invasive species can cause is to prevent them from [invading]. We use several ways to predict species at risk of becoming invasive.” (U.S. Department of the Interior, [51]). As Shigesada and Kawasaki explained ([64]), predicting that is one of the main goals of the mathematical models, along with which habitats are at risks of being invaded and the impact on the native biota. Those risk assessment have become ”the frontline in the prevention of biological invasions” (Hulme [34]).

Another application of these theories is biological pest control. Through modeling, it was theorized that it is possible to stop the spread of some pest species (diffusing species) by creating a spatial barrier of sterile pest males of the same species (motionless species). An example of a successful attempt is the one done in the USA on the border with Mexico to stop the seasonal invasion of screwworms (Marsula and Wissel [44]).

The total habitat space is a critical aspect to consider in regard to the possibility of survival for an invading species, because this space is easily reduced, for example, by the destruction of said habitat. Human activities have modified many of the natural habitats of species through logging, farming, and, most importantly, urbanization (Marzluff and Ewing [45]), and this impact will continue to grow (Alig et al. [2]). Our analysis shows that if another species is already established in the area, occupying most of the territory, whether the territory itself is large enough has a significant effect on the success of an invasion. Interestingly, it reveals that if the competition severely affects the alien species, the smaller the total habitat, the higher the chance the invasion will fail. If the goal is to preserve both species to conserve biodiversity, then a larger habitat is preferable. However, a smaller habitat could help prevent invasion if the alien species is undesirable.

On the other hand, if it is only the size of the habitat that hosts the native species that shrinks, for example, due to a change in a hunting policy (Benitez-Lopez [8]), or chemical contamination of part of the area affecting a native plant species (Devatha et al. [14]), then a failed invasion can suddenly become a successful one. In this case, either coexistence happens, or more drastically, but still conceivable, the native species would go extinct.

Finally, the critical ratio that we found for the size of the area with a competition tells us that if the native species occupy a small part of the total area, the alien species cannot get extinct from this invasion, however high the species spreading rate is and the competition effect they are affected by. Then at best, a stationary solution with the coexistence of both species would occur, and at worst, the native species would become extinct.

Chapter 5

Habitat fragmentation and species persistence

5.1 Modeling of habitat fragmentation

Habitat fragmentation could be a threat to biodiversity. Understanding the ecological dynamics in a fragmented habitat is crucial, for example, for the conservation of a species inhabiting there. Here we consider the influence of habitat fragmentation on competition population dynamics, which is not yet well understood by the mathematical biology community (Fahrig [17]). We based our modeling on the one proposed by Robert H. MacArthur for the competition for a resource (MacArthur [43]).

5.1.1 Introduction of resource dynamics model

We assume that there is a resource R in the native habitat, and we consider that this resource grows until it reaches a limit depending on its characteristics and environment, governed by

$$\frac{dR}{dt} \;=\; D(R(t)),$$

with $D(0) > 0$, $D'(R) < 0$ and $\lim\limits_{R\to+\infty} D(R) < 0$. Here we choose a logistic equation for the growth model of the resource.

$$D(R) \;=\; \lambda R - \gamma R^2,$$

with $\lambda > 0$ the growth of the resource, and $\gamma > 0$ its decay. From this, we know that the saturation value of the resource is

$$R_0^* \;:=\; \lim_{t\to+\infty} R(t) \;=\; \frac{\lambda}{\gamma}.$$

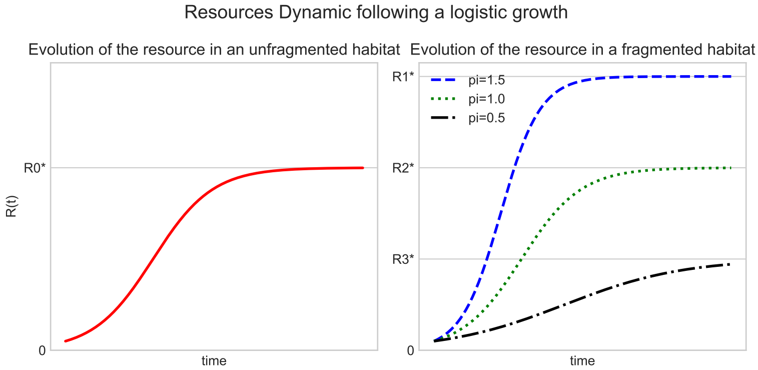


Figure 5.1: Numerical example of the resource dynamics growing without consumption. $\lambda = 1$ and $\gamma = 0.5$

We suppose that the habitat fragmentation affects the resource availability in each patch of the habitat. To model this effect, we introduce p_i, the fragmentation effect on the resource for each patch $i \in \mathbb{N}$. Furthermore, we assume that the growth of the resource in each patch is independent of the other patches. Then

$$D_i(R_i) \quad = \quad p_i \lambda R_i - \gamma R_i^2.$$

This $p_i > 0$ is a general term in our model that contains all the phenomena resulting from the fragmentation that affects the growth of the resource. The saturation value of the resource in each patch is then

$$R_i^* \quad := \quad \lim_{t \to +\infty} R_i(t) \quad = \quad p_i R_0^*.$$

We give a numerical example of the evolution of this resource in Figure 5.1.

Let us call $P_n := \sum_{i=1}^{n} p_i$. Hence the parameter P_n represents the influence of habitat fragmentation on the whole space. Furthermore, p_i/P_n is the effect of the fragmentation on patch i, relative to the total effect in the system. A higher ratio in patch i means a more beneficial effect of the fragmentation in this patch than in the other patch.

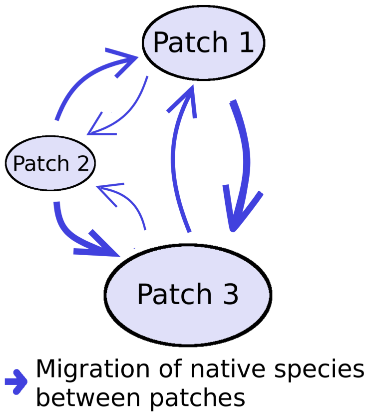


Figure 5.2: Illustration of the movement between patches for the native species. A bigger patch represents a higher fragmentation effect p_i, and a bigger arrow represents a higher migration rate towards the patch.

5.2 A population dynamics model under the habitat fragmentation

5.2.1 Population dynamics of native species

We now consider that a native species uses the previous resource. We will assume a simple consumption method, that is, if the native species encounter the resources, it consumes it. Then in each patch of the habitat, the resource growth follows the model:

$$\frac{dR_i}{dt} = D_i\big(R_i(t)\big) - \beta N_i(t) R_i(t),$$

with N_i the native species' density in the patch i, and β the consumption efficiency of the resource by the native species.

For the native species, we assume that it needs at least a certain amount of the resource to survive. Its growth rate is given by $\big(-\alpha R^c + \alpha R_i(t)\big)$, with R^c the aforementioned critical resource value under which the native species would not reproduce, and α the coefficient for the conversion of the resource for the native species.

We also consider that the native species can move between the different patches of the native habitat. For simplification purpose, we consider that the emigration rate depends entirely on the species, not on the characteristics of the patch. Then for any patch i, the native species leaves the patch at a rate m. Furthermore, we consider that there is no death occurring during the migrations, so the total amount of emigrants and immigrants balance each other. Finally, for the immigration, we ignore the geography of the patches. Instead, we consider that what influence the immigration rate is the attractivity in terms of the resource of the patch. If a patch contains more of the resource, more individuals migrate in it. See Figure 5.2 for an illustration. Then the immigration rate in the patch k is given by mp_k/P_n. For the growth of the native species in a given patch i we obtain in the end

$$\frac{dN_i}{dt} \;=\; \alpha\big(-R^c + R_i(t)\big)N_i - mN_i + \frac{p_i}{P_n}\sum_{j=1}^{n} mN_j.$$

By considering that the change of the resource is much faster than the species populations change (using the Quasi-Steady-States Approximation, in short QSSA), we obtain

$$\begin{aligned} \frac{dR_i}{dt} &\approx 0 \\ \Longleftrightarrow \quad R_i &\approx p_i\frac{\lambda}{\gamma} - \frac{\beta}{\gamma}N_i. \end{aligned}$$

Hence the native species' growth model becomes

$$\frac{dN_i}{dt} \;=\; \alpha\left(-R^c + p_i\frac{\lambda}{\gamma} - \frac{\beta}{\gamma}N_i\right)N_i - mN_i + \frac{p_i}{P_n}\sum_{j=1}^{n} mN_j.$$

Finally, by performing the following change of variables and parameters:

$$\tilde{t} := \frac{\alpha\lambda}{\gamma}t; \quad x_i := \frac{\beta}{\lambda}N_i; \quad \sigma := \frac{\gamma}{\lambda}R^c; \quad \eta := \frac{\gamma}{\lambda}\frac{m}{\alpha},$$

we obtain the non-dimensionalized model (renaming $\tilde{t}$ as t for convenience)

$$\frac{dx_i}{dt} \;=\; (p_i - \sigma - x_i)\,x_i - \eta x_i + \frac{p_i}{P_n}\eta\sum_{j=1}^{n} x_j. \tag{5.1}$$

We call *hard fragmentation* the case where the species do not migrate between the different patches, that is, $m = 0$ ($\eta = 0$ in the non-dimensionalized model). On the other hand, we call *soft fragmentation* whenever there are migrations between patches, that is, $m > 0$ ($\eta > 0$ in the non-dimensionalized model).

5.2.2 Competition dynamics model with an alien invasion

Let us now consider an invading species that make use of the same resource as the native species. Then the growth of the resource is given by

$$\frac{dR_i}{dt} \;=\; D_i\big(R_i(t)\big) - \beta_N N_i R_i - \beta_A A_i R_i,$$

with N_i (resp A_i) the native (resp alien) species in patch i, and β_N (resp β_A) the consumption efficiency of the resource by the native (resp alien) species.

The native species follow the same assumption as previously. We use the subscript (or superscript) $_N$ to refer to the parameters pertaining to the native species, giving the model

$$\frac{dN_i}{dt} \;=\; \alpha_N\big(-R_N^c + R_i(t)\big)N_i - m_N N_i + \frac{p_i}{P_n} m_N \sum_j N_j.$$

The alien species can also migrate between patches, and we make the same assumptions for it as we did for the native species. In addition to the migrations inside the native habitat, the alien species also migrate to and from its source patch outside the native habitat. Figure 5.3 shows the migrations considered. To simplify the analysis, we assume that the aliens original habitat's density is big enough compared to what leaves and enters it. Then we can assume that the alien's source patch density is constant. The model we obtain for the alien species is

$$\frac{dA_i}{dt} \;=\; \alpha_A\big(-R_A^c + R_i(t)\big)A_i \underbrace{-m_A A_i + \frac{p_i}{P_n} m_A \sum_j A_j}_{\text{Inside of native habitat}} \underbrace{-m_0 A_i + \frac{p_i}{P_n} M_0 A_0}_{\substack{\text{Between original habitat}\\ \text{and native habitat}}}.$$

We use the subscript (or superscript) $_A$ to refer to the parameters concerning the alien species. m_0 is the alien return rate to their source patch, and M_0 is the alien immigration rate from their source patch. A_0 is the alien density in their source patch, which we consider constant.

This time too, we can simplify the model by using the QSSA:

$$\begin{aligned} \frac{dR_i}{dt} &\approx 0 \\ \iff \quad R_i(t) &\approx p_i\frac{\lambda}{\gamma} - \frac{\beta_N}{\gamma}N_i(t) - \frac{\beta_A}{\gamma}A_i(t). \end{aligned}$$

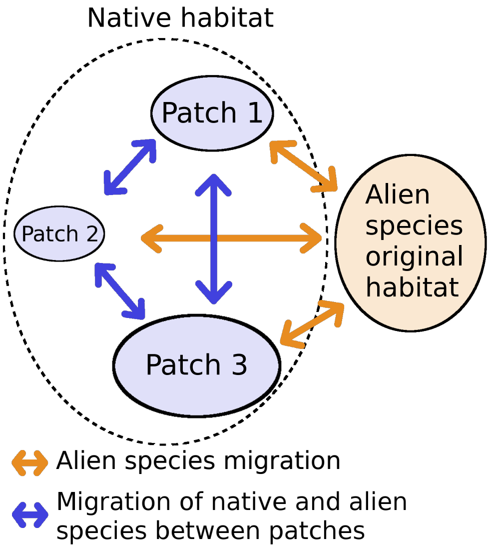


Figure 5.3: Illustration of the movement between patches for the native and alien species

Then the model becomes

$$\begin{cases} \dfrac{dN_i}{dt} &= \alpha_N \left(-R_N^c + p_i \dfrac{\lambda}{\gamma} - \dfrac{\beta_N}{\gamma} N_i - \dfrac{\beta_A}{\gamma} A_i \right) N_i - m_N N_i + \dfrac{p_i}{P_n} m_N \displaystyle\sum_j N_j; \\ \\ \dfrac{dA_i}{dt} &= \alpha_A \left(-R_A^c + p_i \dfrac{\lambda}{\gamma} - \dfrac{\beta_N}{\gamma} N_i - \dfrac{\beta_A}{\gamma} A_i \right) A_i - m_A A_i + \dfrac{p_i}{P_n} m_A \displaystyle\sum_j A_j \\ & \quad - m_0 A_i + \dfrac{p_i}{P_n} M_0 A_0. \end{cases}$$

Finally, by performing the following change of variables and parameters:

$$\tilde{t} := \alpha_N \frac{\lambda}{\gamma} t; \quad x_i := \frac{\beta_N}{\lambda} N_i; \quad y_i := \frac{\beta_A}{\lambda} A_i; \quad \sigma_N := \frac{\gamma}{\lambda} R_N^c; \quad \sigma_A := \frac{\gamma}{\lambda} R_A^c;$$

$$\omega := \frac{\alpha_A}{\alpha_N}; \quad \eta_N := \frac{\gamma}{\lambda} \frac{m_N}{\alpha_N}; \quad \eta_0 := \frac{\gamma}{\lambda} \frac{m_0}{\alpha_A}; \quad \eta_A := \frac{\gamma}{\lambda} \frac{m_A}{\alpha_A}; \quad \zeta := \frac{\gamma}{\lambda} \frac{\beta_A}{\lambda} \frac{M_0}{\alpha_A} A_0,$$

we obtain the non-dimensionalized model

$$\begin{cases} \dfrac{dx_i}{d\tilde{t}} &= (p_i - \sigma_N - x_i - y_i)\, x_i - \eta_N x_i + \dfrac{p_i}{P_n} \eta_N \displaystyle\sum_j x_j; \\ \\ \dfrac{dy_i}{d\tilde{t}} &= \omega \left[(p_i - \sigma_A - x_i - y_i)\, y_i - \eta_A y_i + \dfrac{p_i}{P_n} \eta_A \displaystyle\sum_j y_j - \eta_0 y_i + p_i \dfrac{\zeta}{P_n}. \right] \end{cases} \tag{5.2}$$

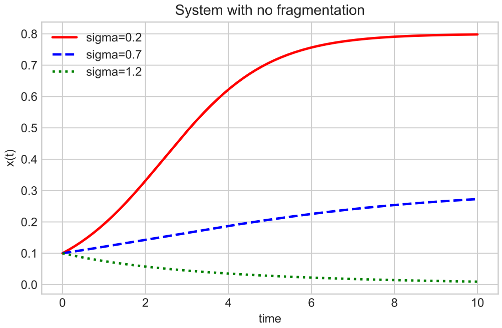


Figure 5.4: Numerical example of the dynamics for the native species in an unfragmented habitat with $P_1 = 1$. The native species survives if and only if $\sigma < P_1$

5.3 Condition for the persistence of native species

5.3.1 In the unfragmented habitat

As a standard for comparison, we first analyze when the habitat is cohesive. It is a special case of our model with no migrations ($m = 0$) and no fragmentation effect ($n = 1, p_1 = P_1$). When translated to their non-dimensionalized counterpart, the model (5.1) becomes

$$\frac{dx}{dt} = (P_1 - \sigma - x)\, x.$$

The equilibria here are 0 and $P_1 - \sigma$. The latter exists (here, it means that it is non-negative) and is different from 0 if and only if $\sigma < P_1$ and is then stable. The equilibrium point 0 is stable if and only if the other equilibrium does not exist. See Figure 5.4 for a numerical example.

In the unfragmented habitat and without competition, the native species survives if and only if the resource is sufficiently abundant to satisfy the native species minimal needs: $R_0^* > R^c$. Since no other parameters influence the species survival in this case than its own intrinsic growth, this is the result we were expecting.

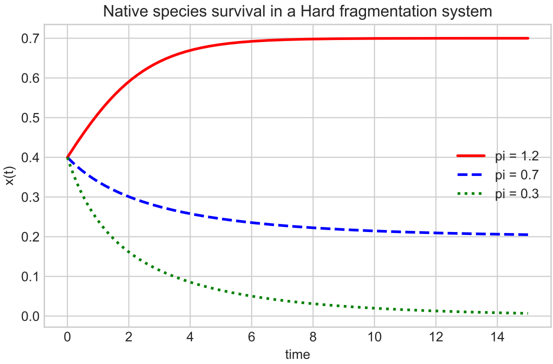


Figure 5.5: Numerical example of the Hard Fragmentation with $\sigma = 0.5$. In each patch i, the native species survives when $p_i > \sigma$

5.3.2 Under a hard fragmentation

If we consider a fragmented native habitat, but no migration between the different patches, for each patch i, the model (5.1) becomes

$$\frac{dx_i}{dt} = (p_i - \sigma - x_i)\, x_i.$$

So in each patch, the equilibrium points are 0 and $p_i - \sigma$. The latter exists and is different from 0 if and only if $p_i > \sigma$ and is then stable. The equilibrium point 0 is stable if and only if the other equilibrium does not exist. See a numerical example of this system in Figure 5.5

The species globally survives means it survives in at least one patch. That is true if and only if $\max_i(p_i) > \sigma$. In other words, the native species globally survives if and only if $\max_i(R_i^*) > R^c$. Since every patch is isolated, this result means that we need at least one patch with more of the resource than the critical amount needed for the reproduction of native species.

The model without fragmentation is mathematically equivalent to a single patch with $p_1 = P_1$. So the native species survival chances are better in a hard fragmented habitat than in an unfragmented habitat if and only if there exists a patch i such that $p_i > P_1$. It means that if the fragmentation increases the density of the resource in a patch, then it is possible for the fragmentation to help the native species persist in the habitat.

5.3.3 Under a soft fragmentation

In case there are migrations between patches, we want to know the stability of the equilibrium $(0, ..., 0)$ for the model (5.1). Let us call $J_{(0,0,...,0)}$ the

Jacobian matrix of this equilibrium.

Lemma 8. *For $J_{(0,0,...,0)}$ the Jacobian matrix of the equilibrium $(0,0,...,0)$, we have its characteristic polynomial*

$$Q(X) \;=\; \prod_{i}^{n}\left(p_i-(\sigma+\eta)-X\right)+\eta\sum_{i}^{n}\frac{p_i}{P_n}\prod_{j\neq i}^{n}\left(p_j-(\sigma+\eta)-X\right).$$

With the order of our fragmentation coefficients such that $0<p_1\leq p_2\leq ...\leq p_n$, the polynomial Q has exactly one root in $\left]p_k-(\sigma+\eta),p_{k+1}-(\sigma+\eta)\right[$ for $1\leq k\leq n-1$, and exactly one root in $\left]p_n-(\sigma+\eta),+\infty\right[$. If there exist some indices i and j in$[|1,n|]$ such that $p_i=...=p_{i+j}$ with $i+j\leq n$, then $p_i-(\sigma+\eta)$ is a root of Q, with multiplicity j.

According to this result, the largest root of Q is in the interval $\left]p_k-(\sigma+\eta),+\infty\right[$, where $k=\arg\max\limits_{i\in[|1,n|]}p_i$. To know if the equilibrium is unstable, we need to know if there is at least one positive eigenvalue for the Jacobian matrix. In other words, whether the biggest root of Q is positive.

Lemma 9. *The biggest root of Q is positive if and only if*

$$\max_{i\in[|1,n|]}p_i-(\sigma_N+\eta_n)\geq 0,\quad\text{or}$$

$$\max_{i\in[|1,n|]}p_i-(\sigma_N+\eta_n)<0\ \text{ and }\ \eta\sum_{l}^{n}\frac{p_l/P_n}{\sigma+\eta-p_l}>1.$$

This last lemma completely describes the stability of $(0,...,0)$. However, to expose the different phenomena happening, we rewrite it in the following proposition:

Proposition 10. *All eigenvalues of $J_{(0,...,0)}$ are real. Let's call μ its biggest eigenvalue, then we have the following cases:*

- *If $\max\limits_{i\in[|1,n|]}p_i<\sigma$ then $\mu<0$ so $(0,...,0)$ is stable.*
- *If $\min\limits_{i\in[|1,n|]}p_i>\sigma$ then $\mu>0$ so $(0,...,0)$ is unstable.*
- *If $\max\limits_{i\in[|1,n|]}p_i\geq\sigma+\eta$ then $\mu>0$ so $(0,...,0)$ is unstable.*
- *If $\min\limits_{i\in[|1,n|]}p_i<\sigma<\max\limits_{i\in[|1,n|]}p_i<\sigma+\eta$ then*

$$\mu>0\iff\sum_{l}^{n}\frac{p_l}{\sigma+\eta-p_l}>\frac{P_n}{\eta}.$$

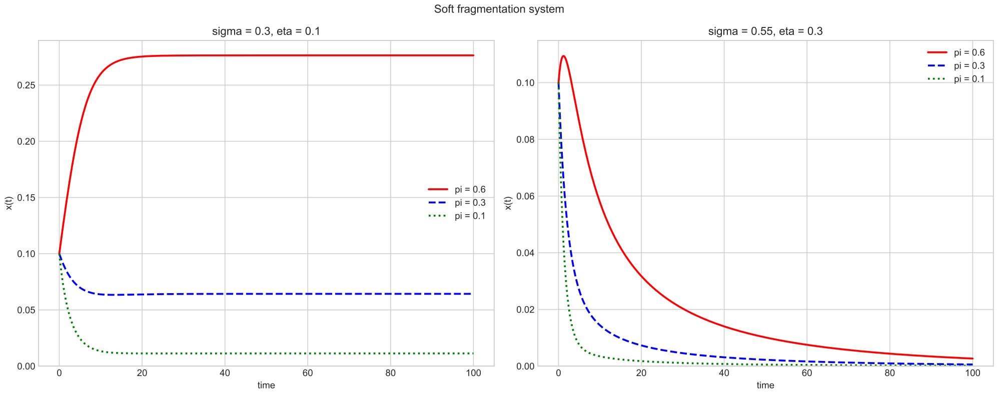


Figure 5.6: Numerical example of the Soft Fragmentation. On the left side, the native species survives in every patch since $\max_{i\in[|1,n|]} p_i \geq \sigma+\eta$. On the right side, $\min_i p_i < \sigma < \max_i p_i < \sigma + \eta$. Since $\frac{\eta}{P_n}\sum_l^n \frac{p_l}{\sigma+\eta-p_l} \approx 0.92 < 1$ then $(0,...,0)$ is stable.

Figure 5.6 illustrates this result's third and last cases. Rewriting the first two results of this proposition, we obtain that

$$\begin{aligned}
\max_{i\in[|1,n|]} R_i^* &< R^c \implies (0,...,0) \text{ is stable;}\\
\min_{i\in[|1,n|]} R_i^* &> R^c \implies (0,...,0) \text{ is unstable.}
\end{aligned}$$

So if there is no patch with enough of the resource to allow the species to reproduce, it cannot survive. On the other hand, if all patches have enough of the resource to allow the species to reproduce, then it survives. The third condition can be rewritten as

$$\max_{i\in[|1,n|]} \alpha R_i^* - \alpha R^c \geq m \implies (0,...,0) \text{ is unstable.}$$

$\alpha R_i^* - \alpha R^c$ is the growth rate of the native species in the patch i. That means that if we have (at least) one patch where the growth rate of the species is greater than the migration out of the patch, then this patch acts as an inexhaustible source patch for the species, and the native species persists. Alternatively, from the point of view of resources, if there are enough of the resource in at least one patch to sustain enough birth to more than compensate for the emigration outside of the patch, then the native species survive.

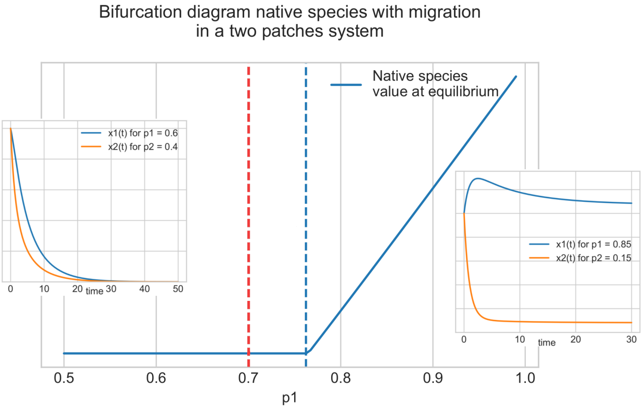


Figure 5.7: Bifurcation diagram depending on p_i in a soft fragmented, two patches system with no invaders. In this diagram, $p_1 + p_2 = 1$. The blue dashes are the condition $\sum_l^n \frac{p_l}{\sigma+\eta-p_l} = P_n/\eta$. The red dashes are the persistence condition if it was a hard fragmentation. Other parameters are $\sigma = 0.7$, $\eta = 0.5$.

Finally, the last condition with the original parameters is

$$\text{If } \min_{i\in[|1,n|]} R_i^* < R^c < \max_{i\in[|1,n|]} R_i^* < R^c + \frac{m}{\alpha}, \text{ then}$$

$$\mu > 0 \iff \sum_l^n m \frac{p_l/P_n}{\alpha(R^c - R_l^*) + m} > 1$$

If some but not all the patches are self-sustainable, and we do not have a real source patch, then we look at sum of the contribution of all patches. Since with the given conditions, for any patch p_i we have $\alpha(R^c - R_l^*) + m > 0$, then

$$m\frac{p_i/P_n}{\alpha(R^c - R_i^*) + m} > \frac{p_i}{P_n} \iff R_i^* > R^c.$$

When there is sufficient resources in a patch — $R_i^* > R^c$ — then the patches contribute more to the global system than it takes, and vice versa. This contribution is measured by the inequality on the left side.

According to this proposition, added mobility makes it more difficult for species to survive globally than the hard fragmentation case. Figure 5.7 gives the bifurcation diagram in a two patches system. The blue dashes represent a more stringent condition on p_1 than the red dashes. Indeed, in the hard fragmentation case, at least one patch having enough of the resource is enough for the species to survive. This is a necessary but not sufficient condition to ensure survival once we add mobility between patches.

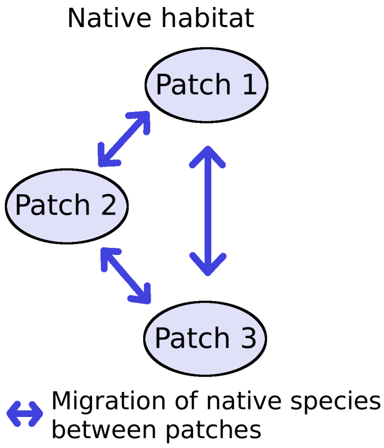


Figure 5.8: Illustration of a habitat with equivalent divisions of patches

Let us also note that in this system, it is more important for the persistence of the native species to have more than enough of the resource in one or a few patches, than to have an average amount of resource in every patches.

5.3.4 A specific habitat fragmentation: Even division

In order to understand the effect of the number of patches in the system, we will study a simplified model, where the fragmentation effect in all the patches is the same. Then all patches have the same amount of the resource. See Figure 5.8 for an illustration of the simplified model. In mathematical terms, for all i, $p_i = P_n/n$, with $P_n \in \mathbb{R}^+$. Then we obtain the stability of the native species extinction through the study of

$$\begin{aligned} Q(X) &= \left(\frac{P_n}{n} - (\sigma+\eta) - X\right)^n + \eta\left(\frac{P_n}{n} - (\sigma+\eta) - X\right)^{n-1} \\ &= \left(\frac{P_n}{n} - \sigma - X\right)\left(\frac{P_n}{n} - \sigma - \eta - X\right)^{n-1}. \end{aligned}$$

We have for eigenvalues

$$\frac{P_n}{n} - \sigma - \eta \quad \text{and} \quad \frac{P_n}{n} - \sigma.$$

$P_n/n - \sigma - \eta > 0 \implies P_n/n > \sigma$ so we can focus on the condition $P_n/n - \sigma > 0$ to study the stability of the equilibrium $(0, ...0)$.

If $n < P_n/\sigma$ then the equilibrium $(0, ...0)$ is unstable.

In other words, if $n < P_n R_0^*/R^c$, the native species survives. On the other hand, if $n > P_n R_0^*/R^c$ then $(0,...0)$ is stable and the native species goes extinct.

Let us notice that the condition here is the same as $\max_i(R_i^*) > R^c$ since

$$\max_{i\in[|1,n|]} R_i^* = \frac{P_n}{n} R_0^*.$$

We found that the survival condition in this special case is the same as in the hard fragmentation case.

When P_n does not increase with the fragmentation

In this case, the result we obtained, that is, the native species goes extinct when $n > P_n/\sigma$, tells us that fragmentation is detrimental to the survival of the native species, and the more patches we have, the greater the risk of species extinction.

When P_n increases with the fragmentation

Suppose that P_n increases with the number of patches in the system. Depending on the rate of increase, fragmentation can have either a beneficial effect, a detrimental effect, or the native species may even need a fragmented area to survive at all. Figure 5.9 illustrates the possible cases.

5.4 Tolerance of the native species for an alien invasion

5.4.1 Alien invasion in unfragmented habitat

Once again, we start by analyzing when the habitat is cohesive. In this case, the model (5.2) becomes

$$\begin{cases} \dfrac{dx}{dt} &= (P_1 - \sigma_N - x - y)\,x; \\ \\ \dfrac{dy}{dt} &= \omega\Big[\,(P_1 - \sigma_A - x - y)\,y - \eta_0 y + \zeta\Big]. \end{cases}$$

Since we want to know the persistence of the native species, we study the existence and stability of the native species' extinction equilibrium.

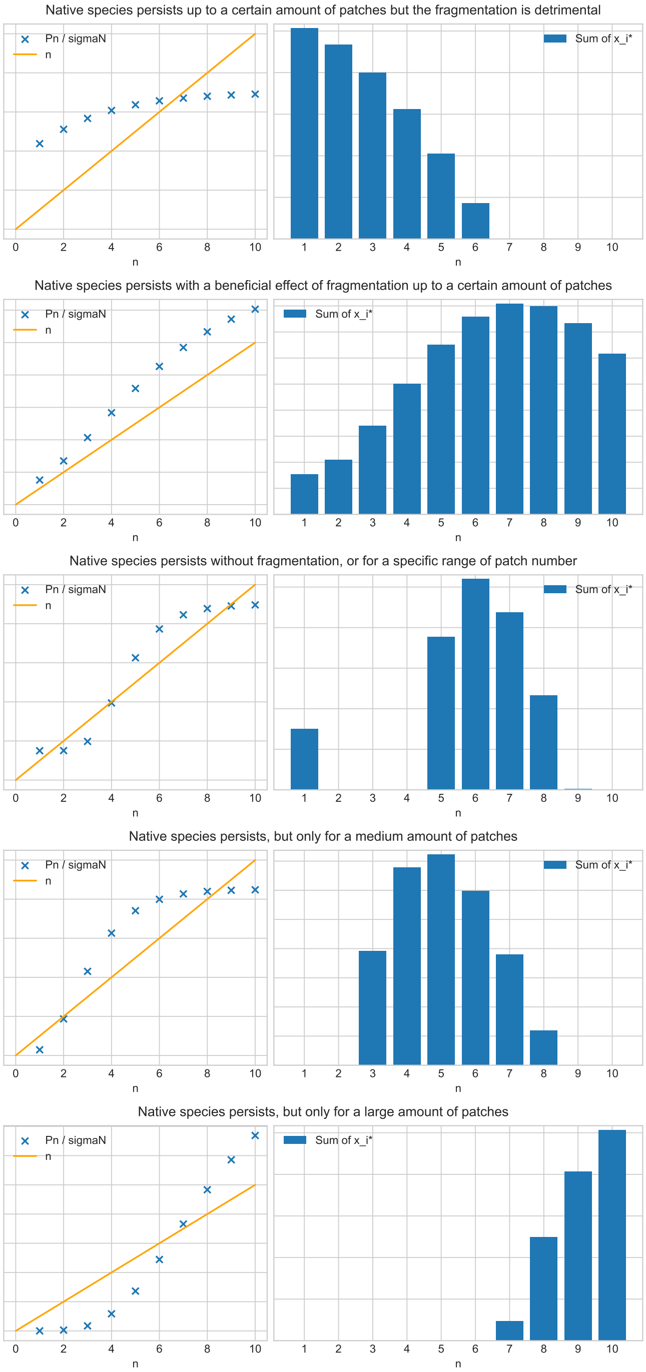


Figure 5.9: Effect of the habitat fragmentation into an equivalent number of patches on the total population size of the native species. On the left graph is given the value of P_n depending on the number of patches. The native species survives when the blue cross is above the orange line. On the right, the sum of x_i. The native species survives for a given amount of patches n when this sum is not 0.

Proposition 11. *The equilibrium* $(0, y^*)$ *exists and is uniquely defined. Furthermore, its stability entirely depends on the eigenvalue* $\mu := P_1 - \sigma_N - y^*$*.*

$$\mu > 0 \iff \sigma_N < P_1 \quad \text{and} \quad \zeta < (P_1 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N).$$

If $\mu > 0$*, then the equilibrium* $(0, y^*)$ *is unstable.*

Rewriting the condition with the original parameters, we obtain that the native species survives if

$$P_1 R_0^* > R_N^c \quad \text{and} \quad A_0 M_0 \frac{\beta_A}{\gamma} < \alpha_A \Big(P_1 R_0^* - R_N^c \Big) \left(R_A^c - R_N^c + \frac{m_0}{\alpha_A} \right).$$

$P_1 R_0^*$ is the density of resources in the unfragmented habitat. The first inequality tells us that the habitat needs to contain at least enough resource to sustain the native species in order for it to survive.

For the second inequality to be true, we need to have at least $R_N^c < R_A^c + m_0/\alpha_A$. That is instantly true if the minimum amount of the resource the alien species needs for reproduction is higher than what the native species needs. We can consider this the case where the alien is less adapted to the resource than the native species. It is also true if the return rate of the alien species to its original habitat is high enough, which prevents it from consuming too much of the habitat resource.

The term $A_0 M_0 \beta_A / \gamma$ represents the consumption of the resource made by the alien species newly immigrated into the native habitat. If it is too high, for example, in case of a strong immigration rate, the native species goes extinct.

The stability diagram originating from the second condition is represented in Figure 5.10. Note that the first condition is for the native species to survive without competition.

5.4.2 Alien invasion in the habitat with a hard fragmentation

In the Hard fragmentation case, the model (5.2) becomes

$$\begin{cases} \dfrac{dx_i}{d\tilde{t}} &= (p_i - \sigma_N - x_i - y_i)\, x_i; \\[2ex] \dfrac{dy_i}{d\tilde{t}} &= \omega \Big[(p_i - \sigma_A - x_i - y_i)\, y_i - \eta_0 y_i + p_i \dfrac{\zeta}{P_n} \Big]. \end{cases}$$

With this type of fragmentation, since the patches are not directly linked, we only need to study the situation in one patch for a given $i \in [|1, n|]$. Since,

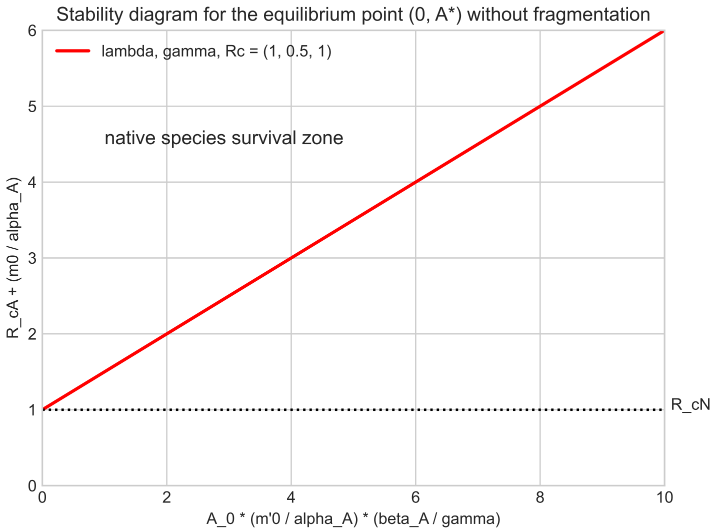


Figure 5.10: Stability diagram for the equilibrium point $(0, A^*)$ without fragmentation. On the x-axis is $A_0 \dfrac{M_0}{\alpha_A} \dfrac{\beta_A}{\gamma}$, and on the y-axis is $R^c_A + \dfrac{m_0}{\alpha_A}$. The native species survives in the parameter space above the red line.

once again, we are interested in the survival of the native species, we look at the existence and stability of the native species' extinction equilibrium. Then we have the following two results.

Proposition 12. *For any given patch i, the equilibrium $(0, y^*_i)$ in this patch exists and is uniquely defined. The stability of this equilibrium depends only on the eigenvalue $\mu_i := p_i - \sigma_N - y^*_i$:*

$$\mu_i > 0 \quad \Longleftrightarrow \quad \begin{aligned} \zeta &< P_n(\sigma_A + \eta_0 - \sigma_N) \quad \text{and} \\ p_i &> \sigma_N \frac{\sigma_A + \eta_0 - \sigma_N}{\sigma_A + \eta_0 - \sigma_N - \zeta/P_n}. \end{aligned}$$

Figure 5.11 illustrates this proposition.

In this proposition, the first inequality rewritten gives $M_0 A_0 \beta_A/\gamma < P_n R^*_0\big(\alpha_A(R^c_A - R^c_N) + m_0\big)$. That tells us that for the native species to survive, the total amount of the resource consumed in the whole system by the incoming alien migration must be smaller than the amount of the resource left behind as by the dead and returning alien species individuals. We can also note that this inequality is instantly wrong when $R^c_N < R^c_A + m_0/\alpha_A$, which is a condition we already had in the above unfragmented habitat case.

For the second inequality, it gives us a condition on the patch i itself. If p_i verifies these conditions, it implies $p_i > \sigma_N$. We notice that if we consider a

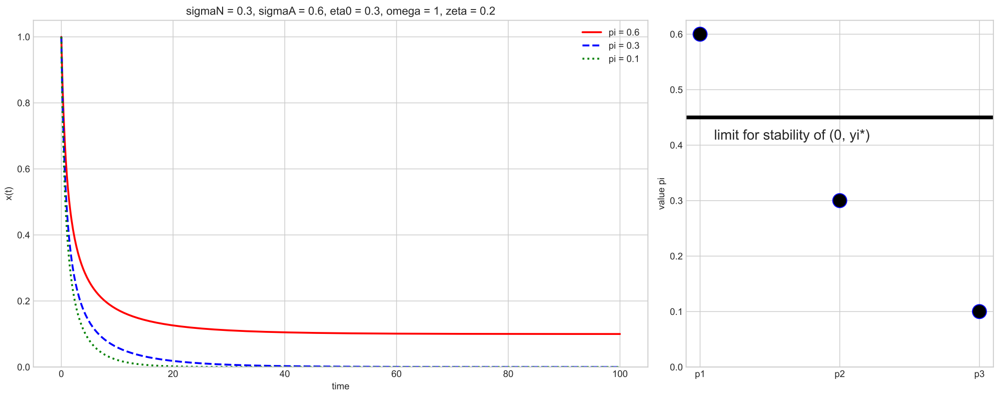


Figure 5.11: Numerical example of the Hard Fragmentation with invaders case. The second graph illustrates the limit over which the native species survives. The parameters are $\sigma_N = 0.3, \sigma_A = 0.6, \eta_0 = 0.3, \omega = 1, \zeta = 0.2$

system with a single patch (no fragmentation effect), then $n = 1$ and $p_1 = P_1$, and the second inequality becomes

$$\begin{aligned} 1 &> \sigma_N \frac{\sigma_A + \eta_0 - \sigma_N}{P_1(\sigma_A + \eta_0 - \sigma_N) - \zeta} \\ \iff \quad \zeta &< (P_1 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N). \end{aligned}$$

We found the same conditions as in the previous case without fragmentation.

Let us also remark that

$$\lim_{\zeta \to 0} \sigma_N \frac{\sigma_A + \eta_0 - \sigma_N}{\sigma_A + \eta_0 - \sigma_N - \zeta / P_n} \quad = \quad \sigma_N.$$

So when $\zeta \to 0$, we obtain as the survival condition in patch i that $\sigma_A + \eta_0 - \sigma_N > 0$ and $p_i > \sigma_N$, which is a similar result to the case of hard fragmentation without alien invasion. Although we are in the case of a hard fragmentation here, there is still an indirect connection between all patches through the incoming Alien migration, present in the non-dimensionalized parameter ζ, since this migration depends on the fraction of the total resource present in each patch. It is only when there is no incoming migration that there is complete independence of all patches.

On the other hand, the higher the incoming immigration, the higher ζ and the higher p_i must be above σ_N to ensure the survival of the native species. In other words, with high immigration, the amount of the resource in the patch need to be well above the value of the native species' critical resource for the native species to survive.

In summary, for native species to survive in a given patch i in a hard fragmentation case, they need three conditions.

- The alien species is not very well adapted to the resource present.
- The resource consumed by the incoming migration in the whole system is sustainable
- The patch i itself needs to have enough resource to sustain the native species after taking into consideration the consumption from the alien species.

In case the alien species consumes more of the resource than the habitat can sustain, it does not threaten its survival since its original habitat is inexhaustible. On the other hand, the native species will suffer the consequences and goes extinct.

In case one patch in the system changes we want to know how the stability of the native species extinction equilibrium behaves. For that, we obtain the following propositions.

Proposition 13. *For any given patch i, when looking at y_i^* as a function of p_i, $y_i^*(p_i)$ increases strictly monotonically, starting from 0 for $p_i = 0$.*

Since this $y_i^*(p_i)$ is the equilibrium for the alien species in patch i without native species, it is natural that an increase in the resource leads to an increase in the final number of alien individuals.

Proposition 14. *We show the mostly monotonous behavior of $\mu_i(p_i)$.*

- *If $\zeta < (\sigma_A + \eta_0) \sum_{j \neq i} p_j$ then $\mu_i(p_i)$ is strictly monotonically increasing.*
- *If $\zeta > (\sigma_A + \eta_0) \sum_{j \neq i} p_j$ then there exists a unique $\hat{p}_i$ such that $\mu_i(p_i)$ strictly decreases monotonically for $p_i \in [0, \hat{p}_i[$ then strictly increases monotonically for $p_i \in]\hat{p}_i, +\infty[$. Furthermore, $\mu_i(p_i) < 0$ for all $p_i \leq \hat{p}_i$.*

The first inequality can be rewritten

$$\frac{\beta_A}{\gamma} M_0 A_0 < (\alpha_A R_A^c + m_0) R_0^* \sum_{j \neq i} p_j$$

and stands for a situation when the resource consumed by the totality of incoming aliens does not reach the amount of resource not consumed by returning individuals and unborn individuals (due to high demand for the resource to birth the new generation, for example) in all patches but the one we want to enrich. In other words, there is enough total resource left by the alien species when accounting for the other patch to satisfy all the incoming alien individuals. In this way, the resource goes to help the native species and, straightforwardly, increase its chances of survival.

On the other hand, if the total amount of the resource in the whole system is insufficient for the incoming aliens, then adding of the resource in our patch goes primarily to help the incoming alien. So, before helping the native species survive, it makes the native species' extinction equilibrium even more stable.

Finally, suppose that we have $0 < p_i \leq P_1$, with P_1 the amount of the resource in an unfragmented system, such that $\mu_i(p_i) > 0$. Then according to this proposition, $\mu_i(P_1) > 0$. In other words, if there exists an index i with $p_i \leq P_1$ such that the equilibrium point $(0, A_i^*)$ is unstable in this patch model, then with the same parameters, $(0, A^*)$ is also unstable in the one patch model. An example would be to have $P_n \leq P_1$ for example, then $p_i < P_1 \forall i$. So if for all i, $p_i < P_1$, then the native species survives in a fragmented environment implies that it also survives in an unfragmented environment. Then the fragmentation effect is not beneficial for the native species persistence.

5.4.3 Alien invasion in the habitat with a soft fragmentation

As we did previously, we now study the existence and stability of the native species extinction equilibrium to determine the native species persistence in this case too.

Proposition 15. *The equilibrium* $(0, y_1^*, 0, y_2^*, ..., 0, y_n^*)$ *exists and is uniquely defined.*

We cannot study only one patch to determine the stability of this equilibrium this time since all patches are explicitly linked through the migration process.

Lemma 16. *The eigenvalues of* $J_{(0,y_1^*,0,y_2^*,...,0,y_n^*)}$ *are the roots of the polynomial*

$\Phi(X) \times \Psi(X)$, with

$$\begin{aligned}
\Phi(X) &:= \prod_{i=1}^{n} \Big(p_i - (\sigma_N + \eta_N) - y_i^* - X\Big) \\
&\quad + \eta_N \sum_{i=1}^{n} \frac{p_i}{P_n} \prod_{j \neq i}^{n} \Big(p_j - (\sigma_N + \eta_N) - y_j^* - X\Big); \\
\Psi(X) &:= \prod_{i=1}^{n} \Big(\omega\big[p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*\big] - X\Big) \\
&\quad + \omega\eta_A \sum_{i=1}^{n} \frac{p_i}{P_n} \prod_{j \neq i}^{n} \Big(\omega\big[p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*\big] - X\Big).
\end{aligned}$$

All the roots of Ψ are real negative. All the roots of Φ are real. With the order of our fragmentation coefficients such that $0 < p_1 - y_1^* \leq p_2 - y_2^* \leq \ldots \leq p_n - y_n^*$, then Φ has exactly one root in $\big]p_k - (\sigma_N + \eta_N) - y_k^*, p_{k+1} - (\sigma_N + \eta_N) - y_{k+1}^*\big[$ for $1 \leq k \leq n-1$, and exactly one root in $\big]p_n - (\sigma_N + \eta_N) - y_n^*, +\infty\big[$. If there exists some indices i and j in$[|1,n|]$ such that $p_i = \ldots = p_{i+j}$ with $i + j \leq n$, then $p_i - (\sigma_N + \eta)_N - y_i$ is a root of Φ, with multiplicity j.

The biggest root of Φ is positive if and only if

$$\max_{i \in [|1,n|]} (p_i - (\sigma_N + \eta_n) - y_i^*) \geq 0, \quad \text{or}$$

$$\max_{i \in [|1,n|]} (p_i - (\sigma_N + \eta_n) - y_i^*) < 0 \ \text{ and } \eta_N \sum_{l}^{n} \frac{p_l / P_n}{pl - (\sigma_N + \eta_N) - y_l^*} < -1.$$

As we did before in the soft fragmentation without competition, we can show with this lemma that we only need to focus on finding the sign of one eigenvalue and give an equivalence for it. However, here those conditions involve the equilibrium value of the alien species y_i^* in addition to the parameters. We look for a way to explain the stability conditions without this y_i^*. The next lemma tells us more about the patch involved in finding this sign.

Lemma 17. *For $i \neq k$ we have*

$$p_i > p_k \iff y_i^* > y_k^*.$$

Furthermore, we have the relation

$$\zeta > P_n(\sigma_A + \eta_0) \iff \exists i,\ y_i^* > p_i \iff \forall i,\ y_i^* > p_i \iff \sum_{l=1}^{n} y_l^* > \sum_{l=1}^{n} p_l,$$

with the equality case, given that all $p_i \neq 0$,

$$\zeta = P_n(\sigma_A + \eta_0) \iff \exists i,\ y_i^* = p_i \iff \forall i,\ y_i^* = p_i \iff \sum_{l=1}^{n} y_l^* = \sum_{l=1}^{n} p_l.$$

We also have that

$$\text{if } \zeta < P_n(\sigma_A + \eta_0) \text{ and } p_i > p_k, \text{ then } p_i - y_i^* > p_k - y_k^* \text{ and } \frac{y_i^*}{p_i} > \frac{y_k^*}{p_k},$$
$$\text{if } \zeta > P_n(\sigma_A + \eta_0) \text{ and } p_i > p_k, \text{ then } p_i - y_i^* < p_k - y_k^* \text{ and } \frac{y_i^*}{p_i} < \frac{y_k^*}{p_k}.$$

This lemma notably tells us that if $\zeta \geq P_n(\sigma_A + \eta_0)$, then $p_i - (\sigma_N + \eta_N) - y_i^* < 0$ for all i. On the other hand, if $\zeta < P_n(\sigma_A + \eta_0)$ then $\max_{i \in [|1,n|]} (p_i - (\sigma_N + \eta_n) - y_i^*) = p_k - (\sigma_N + \eta_n) - y_k^*$, where k is such that $p_k = \max_{i \in [|1,n|]} p_i$, and we need to look at the patch with the highest amount of the resource to get information on the sign of the largest eigenvalue.

For the next part, what happens when p_i increases. For example, we can once again consider the case of enriching the resource in one patch. We show in Figure 5.12 a numerical illustration of a bifurcation diagram depending on the value of one p_i. The following proposition tells us more about the evolution of y_i when p_i changes.

Proposition 18. *Let us suppose that the parameter* p_k *changes. The direction of change of the equilibrium points* y_k^* *and* y_i^**, with* $i \neq k$*, is given by*

$$\frac{\partial y_k^*}{\partial p_k} > 0, \qquad \frac{\partial y_i^*}{\partial p_k} < 0, \qquad \sum_{l=1}^{n} \frac{\partial y_l^*}{\partial p_k} > 0$$
$$\zeta \leq P_n(\sigma_A + \eta_0) \implies \frac{\partial y_k^*}{\partial p_k} < 1.$$

This proposition is illustrated in the figure 5.13. The first result intuitively tells us that with more of the resource in a patch, the final number of alien species individuals increases in the same patch. We could think that, due to migration, the number of alien individuals increases in all patches. However, in our model, the more of the resource in a given patch, the more both species migrate towards this patch in particular, and the less they go to the other patches. This means that the final number of alien individuals in the other patches decreases.

From there, we can categorize in which conditions we can have $p_k - (\sigma_N + \eta_N) - y_k^* > 0$

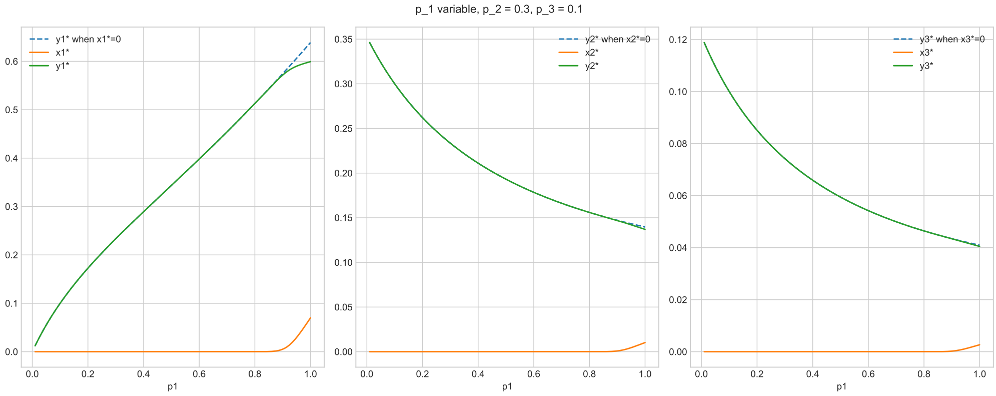


Figure 5.12: Illustration of the change of the equilibrium in a three patches system with the change of the parameter p_1. The parameters are $\sigma_N = 0.3, \eta_N = 0.2, \sigma_A = 0.6, \eta_A = 0.1, \eta_0 = 0.2, \omega = 1, \zeta = 0.4$

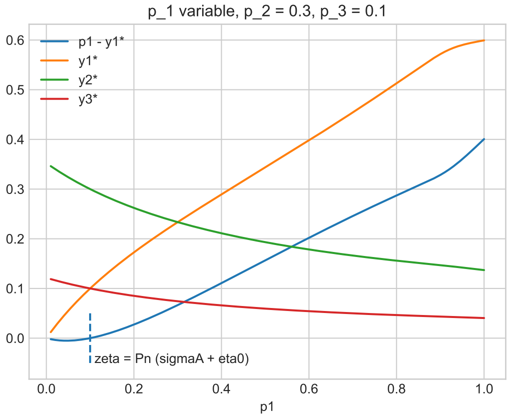


Figure 5.13: Illustration of Lemma 18, in a three patches system. The parameters here are $\sigma_N = 0.3, \eta_N = 0.2, \sigma_A = 0.6, \eta_A = 0.1, \eta_0 = 0.2, \omega = 1, \zeta = 0.4$

Proposition 19. *For any k, there exists a unique $p_k^* \in \mathbb{R}^+$ such that $p_k^* - (\sigma_N + \eta_N) - y_k^*(p_k^*) = 0$ if and only if $\sigma_N + \eta_N < \sigma_A + \eta_A$. If p_k^* exists, then $p_k^* > (\sigma_N + \eta_N)$, and for $0 < p_k < p_k^*$ we have $p_k - (\sigma_N + \eta_N) - y_k^* < 0$ while for $p_k > p_k^*$ we have $p_k - (\sigma_N + \eta_N) - y_k^* > 0$. If it does not exist, then for all $p_k > 0$ we have $p_k - (\sigma_N + \eta_N) - y_k^* < 0$.*

With this proposition, we give the condition for the change in sign of $p_k - (\sigma_N + \eta_N) - y_k^*$, which is related to the stability of our equilibrium point of interest. If there were no invaders, we had the possibility of having a patch that alone guarantees the survival of the native species in all other patches if this one patch was such that $p_i > (\sigma_N + \eta_N)$. This proposition gives us the necessary conditions on the migration rate and critical amount of the resource to have the same possibility in the event of an invasion. The added information is that even if those conditions are met, the allocation of the resource in the super patch needs to be more important than what was needed without invaders, since we need $p_i > p_i^* > (\sigma_N + \eta_N)$.

Finally, we combine everything up to this point in the following Proposition.

Proposition 20. *If $\zeta \geq P_n(\sigma_A + \eta_0)$, $\sigma_N > \sigma_A + \eta_0$ or $\sigma_N > \max\limits_{0\leq i\leq n} p_i$ then the equilibrium $(0, y_1^*, 0, y_2^*, ..., 0, y_n^*)$ is locally stable.*

Let us call $p_k := \max\limits_{0\leq i\leq n} p_i$. If

$$\begin{aligned} \sigma_N + \eta_N &< P_n, \quad \sigma_N + \eta_N < \sigma_A + \eta_0 \\ \text{and } \zeta &< \Big(P_n - (\sigma_N + \eta_N)\Big)\Big(\sigma_A + \eta_0 - (\sigma_N + \eta_N)\Big), \end{aligned}$$

then there exists a $P_n > \tilde{p} > \sigma_N + \eta_N$ such that for all $p_k > \tilde{p}$, $(0, y_1^*, 0, y_2^*, ..., 0, y_n^*)$ is unstable.

The stability of the native species' extinction equilibrium does not guarantee the extinction of native species (it could be a bistable case), but there is a high chance that it happens, as shown in Figure 5.14.

We first find here three conditions for the extinction of the native species, that we already encountered in the previous analysis, if not precisely in the same form. The first inequality $\zeta \geq P_n(\sigma_A + \eta_0)$ is about the incoming migration of the alien species and the amount of the resource it consumes in the native habitat. If this amount is too high, it drives the native species to extinction. The second $\sigma_N > \sigma_A + \eta_A$ represents a higher adaptation of the native species to the present resource than the alien species, with the return rate of the alien species also taken into account. We already had the third inequality $\max_i p_i < \sigma_N$ in the soft fragmentation system without invaders.

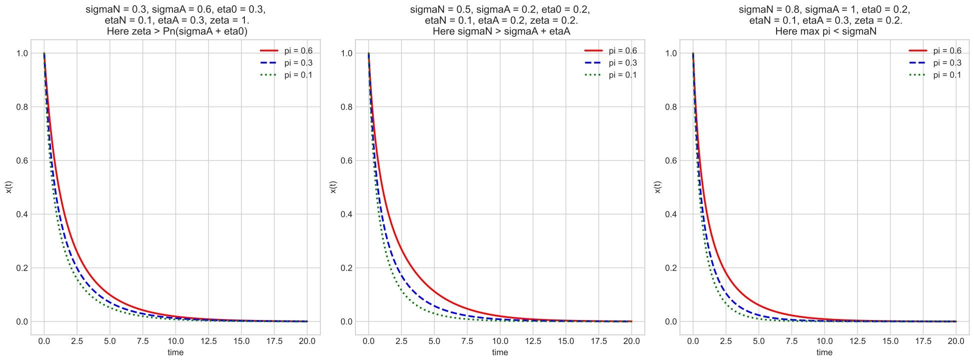


Figure 5.14: Illustration of the three conditions of Proposition 20 for the stability of $(0, y_1^*, 0, y_2^*, ..., 0, y_n^*)$

If none of the patches produces sufficient resources to go above the critical amount needed by the native species, then it cannot survive. Taking into account a system in which native species were already present and thriving before the invasion, we would assume that $\max\limits_{0 \leq i \leq n} p_i > \sigma_N$.

Finally, the last thing this Proposition tells us is that we can have a native species source patch in the native habitat if some conditions are achieved:

- The system has enough total resources to support the native species.
- The native needs less of the resource to reproduce than the alien species after discounting what the individuals leaving the patch (and therefore not contributing to the reproduction) consumed.
- The newly incoming alien individuals do not consume too much of the resource.

Only then can we have a patch with enough of the resource to sustain enough births to more than compensate for the emigration outside of the patch, even after accounting for the competition.

The numerical simulations in Figure 5.15 illustrate the possibility of a native species source patch. On the left side of Figure 5.15, the incoming migration is not low enough, and the native species' extinction equilibrium is stable. On the right side, $\zeta < \Big(P_n - (\sigma_N + \eta_N)\Big)\Big(\sigma_A + \eta_0 - (\sigma_N + \eta_N)\Big)$, and the patch with the most amount of the resource is sufficient to support the persistence of native species in the whole system. Note that the conditions we obtained are sufficient conditions, not an equivalence.

This final result concludes our present analysis of the general system. In the following parts, we look in more detail at two particular cases, a two

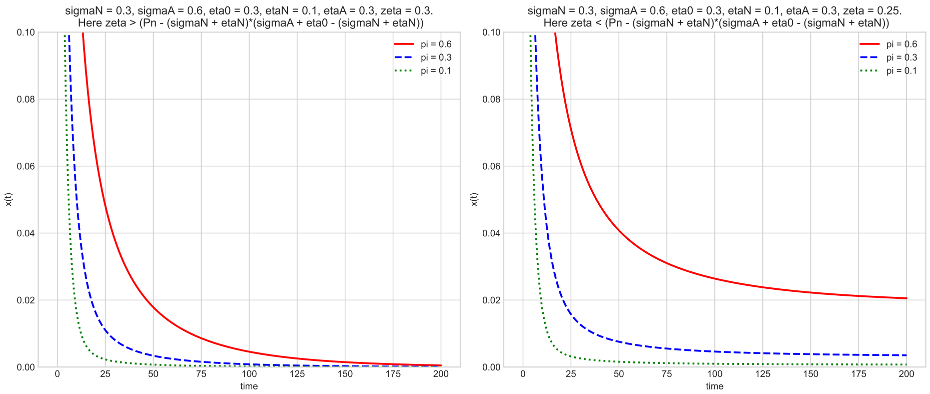


Figure 5.15: Illustration of the numerical simulation for the Proposition 20. On the left, $\zeta > \Big(P_n - (\sigma_N + \eta_N)\Big)\Big(\sigma_A + \eta_0 - (\sigma_N + \eta_N)\Big)$ and $(0, y_1^*, 0, y_2^*, ..., 0, y_n^*)$ is locally stable.

patch cases and an equivalent patch division case.

5.4.4 A simple case: Soft habitat fragmentation into two patches

In an $n > 2$ patches system, if P_n is fixed, the change of one p_k makes all the other p_i change. Depending on the distribution of the change, it is possible to have a different result. A two patches case does not present this dilemma due to the direct relation between p_1 and p_2. We now study the system

$$\begin{cases} (p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*)\, y_1^* + \dfrac{p_1}{P_2}\Big(\zeta + \eta_A(y_1^* + y_2^*)\Big) & = \quad 0; \\ \\ (P_2 - p_1 - (\sigma_A + \eta_0 + \eta_A) - y_2^*)\, y_2^* + \dfrac{P_2 - p_1}{P_2}\Big(\zeta + \eta_A(y_1^* + y_2^*)\Big) & = \quad 0. \end{cases}$$

Note that this system is symmetric around $p_1 = P_2/2$. A numerical simulation of the equilibrium value depending on p_1 can be found in Figure 5.16 for $P_2 = 1$. We can see the symmetry of the system reflected in the graph. Figure 5.17 shows the influence of the value of P_2.

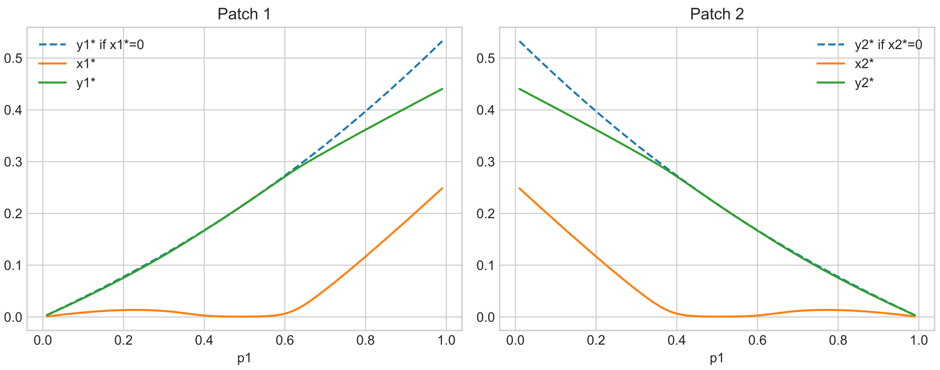


Figure 5.16: Illustration of the change of the equilibrium with the change of the parameter $p_1 \in]0, P_2[$ with $P_2 = 1$. The other parameters here are $\sigma_N = 0.3, \eta_N = 0.2, \sigma_A = 1, \eta_A = 0.2, \eta_0 = 0.2, \omega = 1, \zeta = 0.4$

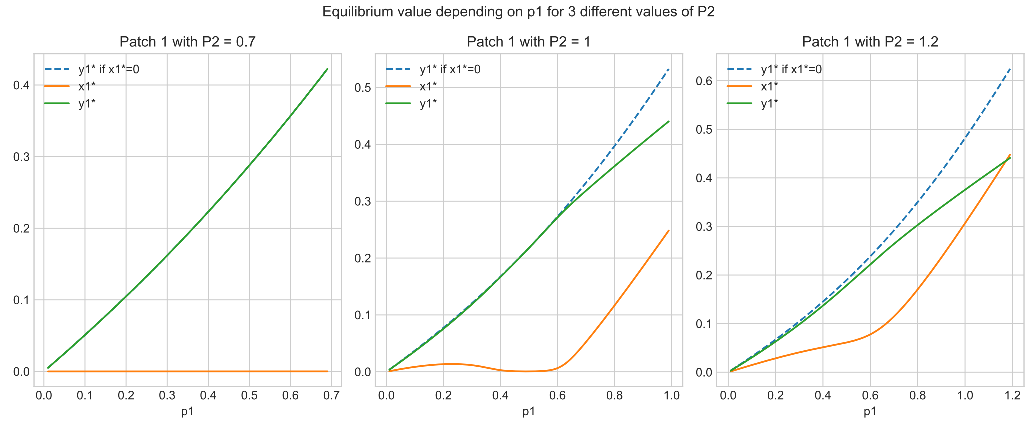


Figure 5.17: Illustration of the change of the equilibrium with the change of the parameter $p_1 \in]0, P_2[$. The second patch is not shown due to its symmetry with the first patch. The parameters here are $\sigma_N = 0.3, \eta_N = 0.2, \sigma_A = 1, \eta_A = 0.2, \eta_0 = 0.2, \omega = 1, \zeta = 0.4$

Proposition 21.

$$\begin{aligned}
&\text{The Jacobian matrix of the equilibrium } \big(0, y_1^*(P_2/2), 0, y_2^*(P_2/2)\big) \\
&\ \text{has only negative eigenvalues} \\
\iff\ & \sigma_N \ > \ \frac{P_2}{2} \quad \text{or} \quad \sigma_N \ > \sigma_A + \eta_0 \\
&\text{or} \quad \zeta \ > \ \left(\frac{P_2}{2} - \sigma_N\right)(\sigma_A + \eta_0 - \sigma_N),
\end{aligned}$$

and

$$\begin{aligned}
&\text{The Jacobian matrix of the equilibrium } \big(0, y_1^*(p_1), 0, y_2^*(p_1)\big) \\
&\ \text{for } p_1 \simeq P_2 \text{ has only negative eigenvalues} \\
\iff\ & \sigma_N \ > \ P_2 \quad \text{or} \quad \sigma_N \ > \sigma_A + \eta_0 \\
&\text{or} \quad \zeta \ > \ (P_2 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N).
\end{aligned}$$

Finally, if the following conditions are true:

$$\begin{aligned}
&\sigma_N + \eta_N \ < \ \frac{P_2}{2} \ \text{ and} \\
&0 \ < \ \zeta \ < \ \Big(P_2 - 2(\sigma_N + \eta_N)\Big)\Big(\sigma_A + \eta_0 - (\sigma_N + \eta_N)\Big),
\end{aligned}$$

then for any $p_1 \in]0, P_2[$*,* $\big(0, y_1^*(p_1), 0, y_2^*(p_1)\big)$ *is unstable.*

Note that the conditions for local stability of the equilibrium $(0, y_1^*)$ in the system with only one patch (no fragmentation) that we analyzed in Proposition 11 are the same as those found here for the limit when $p_1 \to P_2$.

We obtained the stability conditions for an even division and an extreme division. We know from the previous general Proposition that if

$$\sigma_N + \eta_N \ < \ P_2 \ \text{ and } \ 0 \ < \ \zeta \ < \ \Big(P_2 - (\sigma_N + \eta_N)\Big)\Big(\sigma_A + \eta_0 - (\sigma_N + \eta_N)\Big),$$

then there exists a division that allows the native species to survive. In this special case, we can go further and give a more strict condition on the immigration rate, to obtain a sufficient condition for the persistence of the native species independently of the division considered.

Note that from the numerical illustrations in Figure 5.17, it seems that the best division for the native species persistence is the extreme division $p_1e \simeq P_2$ (res $p_2 \simeq P_2$). We computed the system's stability for $P_2 = 1$ and showed the result in Figure 5.18. The function's maximum is reached in $p_1 = P2/2$, for an even division. Its minimum is reached for $p_1 \simeq 0$

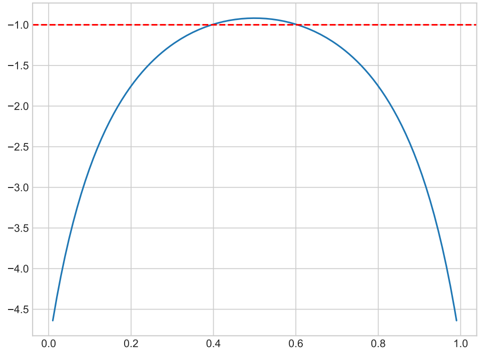


Figure 5.18: Illustration of the stability function for the system depending on $p_1 \in]0, P_2[$ with $P_2 = 1$. The native species' extinction equilibrium is stable if and only if the function is above -1. The parameters here are $\sigma_N = 0.3, \eta_N = 0.2, \sigma_A = 1, \eta_A = 0.2, \eta_0 = 0.2, \omega = 1, \zeta = 0.4$

or $P_1 \simeq P_2$, so for an extreme division. Based on these observations, we postulate two properties.

$$\begin{aligned} & \text{There exists a division allowing the native species to survive} \\ \iff \quad & \text{The Jacobian matrix of the equilibrium } \big(0, y_1^*(p_1), 0, y_2^*(p_1)\big) \\ & \text{ for } p_1 \simeq P_2 \text{ has a positive eigenvalue} \\ \iff \quad & \sigma_N \ < \ P_2 \quad \text{and} \quad \zeta \ < \ (P_2 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N) \end{aligned}$$

and

$$\begin{aligned} & \text{The native species survives for all divisions} \\ \iff \quad & \text{The Jacobian matrix of the equilibrium } \big(0, y_1^*(P_2/2), 0, y_2^*(P_2/2)\big) \\ & \text{ has a positive eigenvalue} \\ \iff \quad & \sigma_N \ < \ \frac{P_2}{2} \quad \text{and} \quad \zeta \ < \ \left(\frac{P_2}{2} - \sigma_N\right)(\sigma_A + \eta_0 - \sigma_N). \end{aligned}$$

However, those results have yet to be proven.

5.4.5 A specific habitat fragmentation: Even division

We consider the problem of equivalent patch division, with the same resource distribution in all patches, so $\forall i \ p_i = P_n/n$, $P_n \in \mathbb{R}^+$. See Figure 5.19. Then by the symmetry of the problem, we also have $\forall i \ y_i^* = y_n^*$, and we obtain the following proposition.

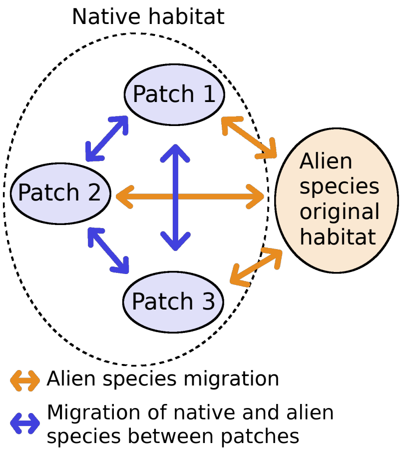


Figure 5.19: Illustration of the movement between patches for the native and alien species in a native habitat with equivalent resource distribution among patches.

Proposition 22. *If* $\forall i,\ p_i = P_n/n$*, then*

$$\begin{aligned} y_n^* &< \frac{P_n}{n} - \sigma_N \quad \implies \quad (0, y_1^*, ..., 0, y_n^*) \text{ is unstable;} \\ y_n^* &> \frac{P_n}{n} - \sigma_N \quad \implies \quad (0, y_1^*, ..., 0, y_n^*) \text{ is stable,} \end{aligned}$$

and

$$\begin{aligned} & y_n^* < \frac{P_n}{n} - \sigma_N \\ \iff \quad & 0 < \zeta < P_n(\sigma_A + \eta_0 - \sigma_N) \ \text{ and } \ n < \frac{P_n}{\sigma_N} - \frac{\zeta}{\sigma_N(\sigma_A + \eta_0 - \sigma_N)}. \end{aligned}$$

Note that this is a stronger condition than $n < P_n/\sigma_N$, which was the condition for the native species' survival in the special case of soft fragmentation with an even division case and no invaders.

When P_n does not increase with the fragmentation

In this case, we have the same results as in the even division case without competition: fragmentation is detrimental to the survival of the native species, and the more patches we have, the greater the species' risk of extinction.

When P_n increases with the fragmentation

In addition to the effects we found for an increasing P_n in the case without competition, the fragmentation can also help or hinder the native species regarding the competition it is submitted to. Figures 5.20 and 5.21 illustrate the possible cases.

As we can see, with this model, it is possible for the species to survive the competition solely due to habitat fragmentation, for example, in the third and fourth lines of Figure 5.20. However, we cannot just conclude that fragmentation is beneficial in some cases and detrimental in others. The same fourth line as mentioned above and the first line of Figure 5.21 show examples where only a medium amount of fragmentation allows the species to survive the competition. In those cases, a very fragmented habitat is as bad for the persistence of the native species as an unfragmented one.

5.5 Discussion

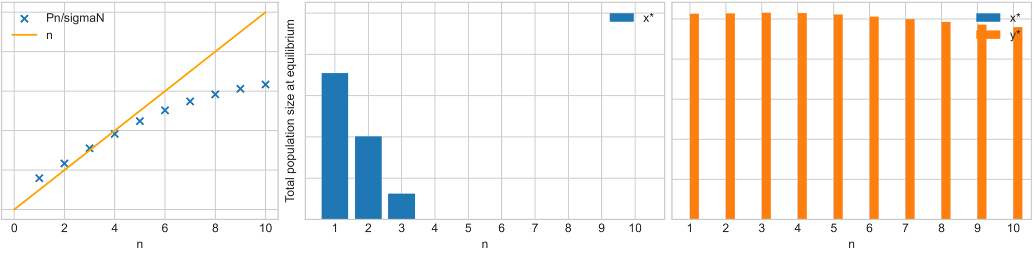
Habitat fragmentation, the separation of space into multiple patches, is often associated with loss of habitat, and by association, loss of resources, while it does not have to be. For a single species, theoretical frameworks exist to explain the effects of fragmentation and spatial configuration (Hanski and Ovaskainen [27]). These frameworks generally conclude to the detrimental effect of fragmentation, even without habitat loss.

For multiple interacting species, there is more debate on the effect of fragmentation (Fahrig et al. [19]). Some authors conclude that there is generally a detrimental effect on biodiversity richness (Ewers and Didham [16]), arguing that small patches have little biodiversity value. Other authors concluded that this is generally beneficial. Fahrig emitted the assumption that the number of species in a given patch increases with the total habitat area surrounding the plot (Fahrig [18]). Other authors also showed that in a competitive community, the total amount of habitat area could dictate the effect of fragmentation: nonexistent, beneficial, or detrimental (Rybicki et al. [58]).

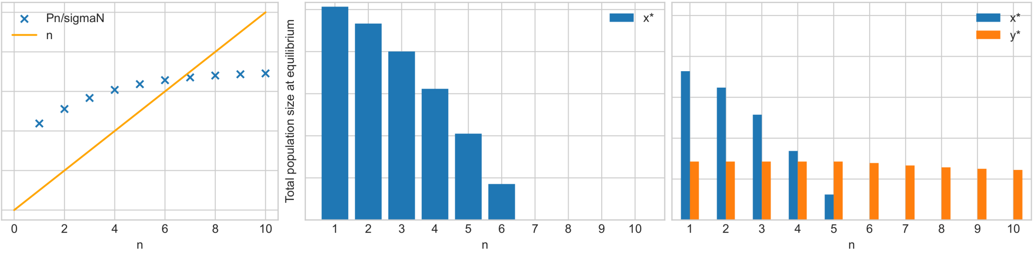
However, to the best of our knowledge, there is still a lack of mathematical models studying the effect of habitat fragmentation. The models we presented in this chapter consider foremost the use of a resource, without any assumption on what this resource is.

In concordance with the theory that small habitats have less ecological value than large ones, we showed in this research that one patch with a high concentration of resources is more relevant for the persistence of the native species than a lesser concentration in more patches. In fact, a patch with enough of the resource can single-handedly support the survival of the native species in the system. This is true whether the native species can migrate between patches or not, and is still valid in the event of a competition for the resource with an alien species, under the condition that the native species is

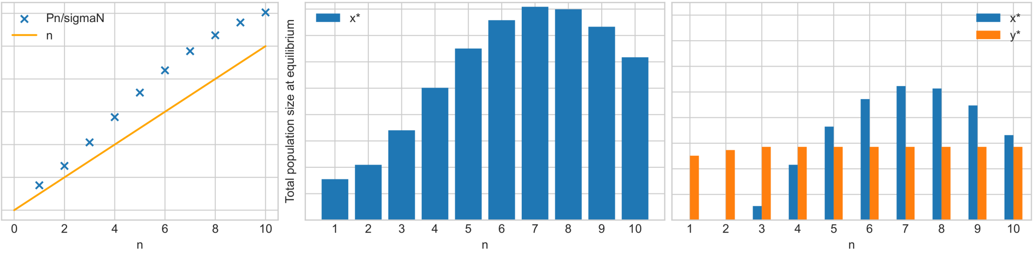
Detrimental effect of fragmentation on native species without competition, becomes extinct with competition



Detrimental effect of fragmentation on native species with and without competition



Native species persists without competition, survives with competition only with fragmentation



Native species persists without fragmentation, or for a specific range of patch number; it persists with competition only for a medium amount of patches

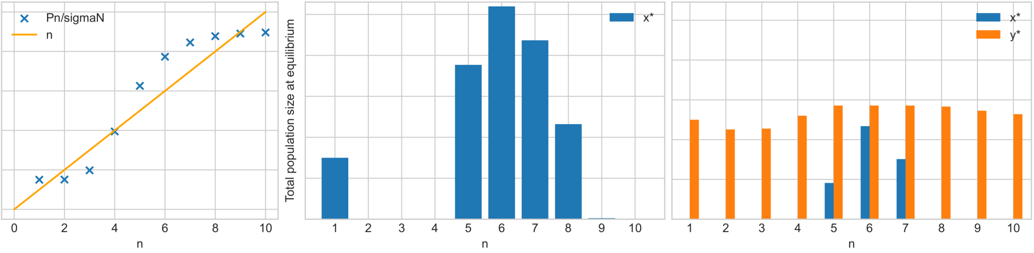
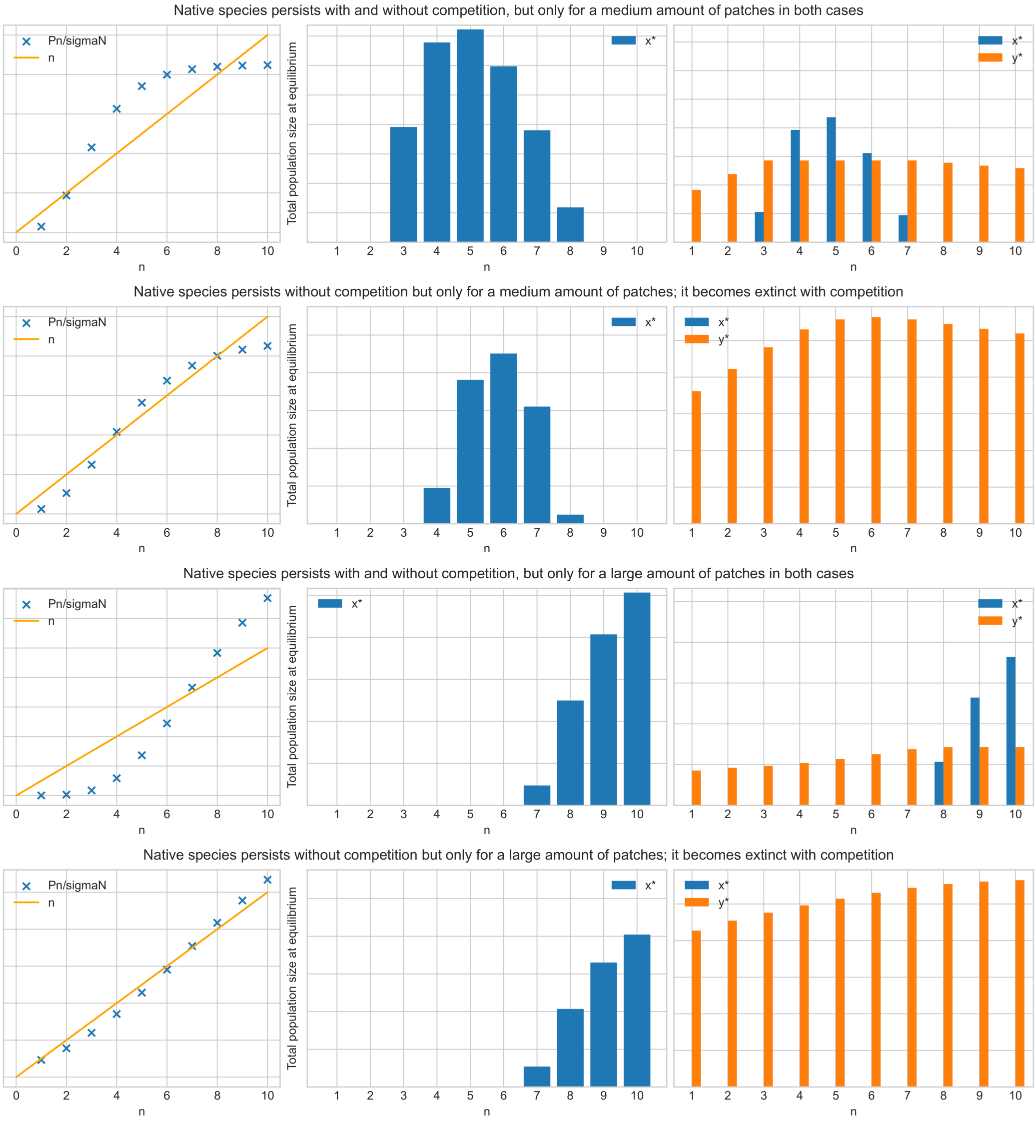


Figure 5.20: Effect of the native habitat fragmentation into an equivalent number of patches on the total population size of the native species with and without a competing species invading — part 1.


Native species persists with and without competition, but only for a medium amount of patches in both cases

Native species persists without competition but only for a medium amount of patches; it becomes extinct with competition

Native species persists with and without competition, but only for a large amount of patches in both cases

Native species persists without competition but only for a large amount of patches; it becomes extinct with competition

Figure 5.21: Effect of the native habitat fragmentation into an equivalent number of patches on the total population size of the native species with and without a competing species invading — part 2.

better adapted to the resource at hand and that the resource in the whole habitat can support the added consumption from the incoming migration.

However, we also showed that if fragmenting a habitat increases the total amount of resources in the system, then in opposition to common knowledge, fragmentation can be beneficial to the persistence of the native species. It can even allow the native species to survive where it would have gone extinct in an unfragmented habitat. This can happen if a small habitat hosts a higher density of the resource. Then multiple small habitats will be host to a higher amount of resources than a unique big one. As for how this higher concentration is achieved, we can consider a resource more abundant on the edge of a habitat. Edges are known to be richer in resources and species than adjacent habitats; alien plant species (Brothers and Spingarn [9]; Fraver [22]), colonizing plant (Fox et al. [21]) or weedy plant species (Honnay et al. [33]) for example tend to become more common near the boundaries of a forest.

With this work, we propose a possible explanation to the positive fragmentation effect empirically observed sometimes (Fahrig [17]). We hope it will inspire more research on the reason for this beneficial effect, which could change the way conservation habitat are designed.

Chapter 6

Conclusion

In this dissertation, we explored the dynamics involving alien and native species within shared habitats. Throughout the chapters, we studied the various factors influencing their interactions and the consequences of their competition.

Chapter 3 focused on a two-patch model representing an invasion of a native habitat by an alien species and ensuing competition for resources. The traditional Lotka-Volterra competition model was our starting point, however, we augmented it to encapsulate the spatial effect and the role of migration rates. We established that like the Lotka-Volterra model, our model also allowed for the extinction of the alien species, native species, or the coexistence of both. However, the addition of migration rates provided new perspectives, elucidating that a high immigration rate of the alien species into the native habitat negatively impacts the survival chances of the native species, while on the other hand causing the alien own potential extinction under specific conditions. This analysis also showed that if the competition effect on the native species is high enough or low enough, then the result of the competition is independent of the migration rates.

Chapter 4 shifted focus to the role of habitat size in the failure or success of the invasion . The analysis revealed that a smaller total habitat increases the chance of a failed invasion if the alien species faces substantial competition. Interestingly, we found that if the size of the shared habitat decreases, then an initially unsuccessful invasion could suddenly succeed, which could then lead to coexistence or, more drastically, extinction of the native species.

Chapter 5 delved into the contentious topic of habitat fragmentation and its impact on native species. Building on existing frameworks, we presented models that argued against the commonly held belief that fragmentation is invariably detrimental. Our findings suggested that the existence of a patch with sufficient resource availability is relevant for the persistence of the native species in the whole system. Importantly, we also exposed that if habitat fragmentation increases the total resource pool, it can benefit the native species, allowing survival where extinction would have otherwise been certain in an unfragmented habitat. These findings challenge traditional assumptions and shed light on the sometimes empirically observed positive fragmentation effect.

Through the study made in these chapters, we obtained a deeper understanding of the complexities inherent in species competition, invasion, and survival within shared habitats. The different models presented provide mathematical bases to describe phenomena observed in ecological systems, contributing to the understanding of invasion dynamics and the consequences of changes to habitats.

Our findings further expose the delicate balance of ecological systems and the intricate dynamics at play within shared habitats. Understanding these nuances is paramount in the context of growing pressures on habitats and species. By modeling these complexities, we can help guide strategies for conservation and management, offering valuable insights into the potential repercussions of specific actions.

The mathematical models and insights generated in this thesis provide a building block for future research, particularly on the influence of fragmentation and the positive outcomes that can emerge. However, it is important to bear in mind the limitations of mathematical models. While these models offer valuable insights, they simplify real-world complexities. Each model's parameters are abstractions, and there is an inherent risk in translating these results directly to real-world scenarios. As we move forward, we may consider integrating additional factors into our models, such as species-specific traits or geographical factors.

This dissertation underscores the significance of mathematical biology in elucidating complex ecological interactions. By bridging mathematics and ecology, we can unravel intricate dynamics, make sense of past ecological events, and anticipate future changes, thus aiding in safeguarding biodiversity and ensuring the health of our ecosystems. The knowledge gained here paves the way for more integrated research, lending momentum to the quest for a deeper comprehension of our natural world.

Appendices

Appendix A

Supplements for Chapter 3

A.1 Proof of Proposition 1

Proof of Proposition 1.

The solutions form a family of curves that do not cross each other. In other words, for any given point in the solution space (x_1, x_{21}, x_{22}), there is a unique trajectory associated to this point.

Now, let us consider the case of $x_1 = 0$. Since

$$\left.\frac{dx_1}{dt}\right|_{x_1=0} = 0,$$

the solution will stay in the solution plane (x_{21}, x_{22}). Since the system

$$\begin{cases} \dfrac{dx_{21}}{dt} & = & \rho_{21}(1 - x_{21})x_{21} + \dfrac{1}{\kappa}\alpha_{12}x_{22} - \alpha_{21}x_{21}; \\ \\ \dfrac{dx_{22}}{dt} & = & \rho_{22}(1 - x_{22})x_{22} - \alpha_{12}x_{22} + \kappa\alpha_{21}x_{21}, \end{cases}$$

with the initial condition

$$(x_{21}(0), x_{22}(0)),$$

is also a well-posed autonomous system, any value $(0, x_{21}, x_{22})$ is associated with a unique trajectory in the solution space (x_{21}, x_{22}). So, if there exists a t for which $x_1(t) = 0$, then for all $t \in \mathbb{R}$, $x_1(t) = 0$. Or, in other words, for any initial value $x_1(0) > 0$, then for all $t > 0$, $x_1(t) > 0$.

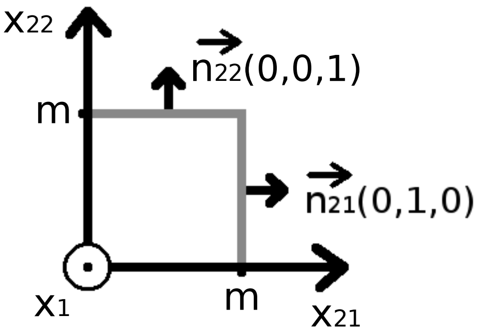


Figure A.1: The planes we consider to bound the values of (x_{21}, x_{22}), forming a square in the coordinates system (x_{21}, x_{22}).

For x_{21} and x_{22}, we have

$$\begin{aligned} \left.\frac{dx_{21}}{dt}\right|_{x_{21}=0} &= \frac{1}{\kappa}\alpha_{12}x_{22} &\geq& \quad 0 &\iff& \quad x_{22} \geq 0; \\ \left.\frac{dx_{22}}{dt}\right|_{x_{22}=0} &= \kappa\alpha_{21}x_{21} &\geq& \quad 0 &\iff& \quad x_{21} \geq 0. \end{aligned}$$

So as long as the initial values $(x_{21}(0), x_{22}(0)) \in (\mathbb{R}^+)^2$, then for all $t > 0$, $(x_{21}(t), x_{22}(t)) \in (\mathbb{R}^+)^2$. Indeed, this is also true if $(x_{21}(0), x_{22}(0)) = (0,0)$ since then for all $t > 0$, $(x_{21}(t), x_{22}(t)) = (0,0)$. We will only consider the case of non-negative initial values from this point on.

For $x_1 \geq 1$, we have

$$\left.\frac{dx_1}{dt}\right|_{x_1 \geq 1} \quad \leq \quad -\gamma_{12}x_{21} \;\leq\; 0,$$

so for all $t > 0$, if $x_1(0) \leq 1$, then $x_1(t) \leq 1$.

Finally let us take

$$m \quad = \quad \max\left(1 + \frac{\kappa\alpha_{21} - \alpha_{12}}{\rho_{22}}, 1 + \frac{\alpha_{12} - \kappa\alpha_{21}}{\kappa\rho_{21}}\right) + \epsilon, \quad \epsilon > 0.$$

We will study the sign of

$$\begin{aligned} \left.\left(\frac{dx_1}{dt}, \frac{dx_{21}}{dt}, \frac{dx_{22}}{dt}\right)\right|_{(x_1,x_{21},m)} \cdot \vec{n}_{22} &= \left.\frac{dx_{22}}{dt}\right|_{x_{22}=m} \quad \text{for} \quad x_{21} \leq m; \\ \left.\left(\frac{dx_1}{dt}, \frac{dx_{21}}{dt}, \frac{dx_{22}}{dt}\right)\right|_{(x_1,m,x_{22})} \cdot \vec{n}_{21} &= \left.\frac{dx_{21}}{dt}\right|_{x_{21}=m} \quad \text{for} \quad x_{22} \leq m. \end{aligned}$$

If $\frac{\kappa\alpha_{21}-\alpha_{12}}{\rho_{22}} > \frac{\alpha_{12}-\kappa\alpha_{21}}{\kappa\rho_{21}}$

Then

$$m = 1 + \frac{\kappa\alpha_{21} - \alpha_{12}}{\rho_{22}} + \epsilon.$$

We obtain

$$\begin{aligned} \left.\frac{dx_{22}}{dt}\right|_{x_{22}=m} &= \rho_{22}(1-m)m - \alpha_{12}m + \kappa\alpha_{21}x_{21} \\ &= -\kappa\alpha_{21}m - \epsilon\rho_{22}m + \kappa\alpha_{21}x_{21} \\ (\text{ since } x_{21} \leq m) \quad &< 0 \end{aligned}$$

and

$$\begin{aligned} \left.\frac{dx_{21}}{dt}\right|_{x_{21}=m} &= \rho_{21}(1-\gamma_{21}x_1 - m)m + \frac{1}{\kappa}\alpha_{12}x_{22} - \alpha_{21}m \\ (\text{ since } x_1 \geq 0) \quad &\leq \rho_{21}(1-m)m + \frac{1}{\kappa}\alpha_{12}x_{22} - \alpha_{21}m \\ (\text{ since } x_{22} \leq m) \quad &\leq m\rho_{21}\left(-\frac{\kappa\alpha_{21}-\alpha_{12}}{\rho_{22}} + \frac{\alpha_{12}-\kappa\alpha_{21}}{\kappa\rho_{21}} - \epsilon\right) \\ (\text{by hypothesis on parameters}) \quad &< 0. \end{aligned}$$

If $\frac{\alpha_{12}-\kappa\alpha_{21}}{\kappa\rho_{21}} \geq \frac{\kappa\alpha_{21}-\alpha_{12}}{\rho_{22}}$

Then

$$m = 1 + \frac{\alpha_{12} - \kappa\alpha_{21}}{\kappa\rho_{21}} + \varepsilon.$$

In this case we obtain

$$\begin{aligned} \left.\frac{dx_{22}}{dt}\right|_{x_{22}=m} &= \rho_{22}(1-m)m - \alpha_{12}m + \kappa\alpha_{21}x_{21} \\ (\text{ since } x_{21} \leq m) \quad &\leq m\rho_{22}\left(-\frac{\alpha_{12}-\kappa\alpha_{21}}{\kappa\rho_{21}} + \frac{\kappa\alpha_{21}-\alpha_{12}}{\rho_{22}} - \epsilon\right) \\ &< 0 \end{aligned}$$

and

$$\begin{aligned} \left.\frac{dx_{21}}{dt}\right|_{x_{21}=m} &= \rho_{21}(1-\gamma_{21}x_1 - m)m + \frac{1}{\kappa}\alpha_{12}x_{22} - \alpha_{21}m \\ &\leq \rho_{21}(1-m)m + \frac{1}{\kappa}\alpha_{12}m - \alpha_{21}m \\ &= -\epsilon m\rho_{21} \\ &< 0. \end{aligned}$$

All in all, we just proved that as long as we start with $\big(x_1(0), x_{21}(0), x_{22}(0)\big) \in \mathbb{R}^{+*} \times [0,m] \times [0,m]$, our system is bounded. Since it is true for any $\varepsilon > 0$, we also see that if $\big(x_1(0), x_{21}(0), x_{22}(0)\big) \in \mathbb{R}^{+*} \times [0,M[\times[0,M[$ with

$$M = \max\left(1 + \frac{\kappa\alpha_{21} - \alpha_{12}}{\rho_{22}}, 1 + \frac{\alpha_{12} - \kappa\alpha_{21}}{\kappa\rho_{21}}\right)$$

. □

A.2 Proof of Proposition 2

Proof of Proposition 2.

$$\begin{cases} 0 = (1 - x_1^* - \gamma_{12}x_{21}^*)x_1^*; \\ 0 = \rho_{21}(1 - \gamma_{21}x_1^* - x_{21}^*)x_{21}^* + \frac{1}{\kappa}\alpha_{12}x_{22}^* - \alpha_{21}x_{21}^*; \\ 0 = \rho_{22}(1 - x_{22}^*)x_{22}^* - \alpha_{12}x_{22}^* + \kappa\alpha_{21}x_{21}^* \end{cases}$$

and combining the last two equations, we can isolate x_{22}^*:

$$x_{22}^* = 1 + \frac{\alpha_{12}}{\rho_{22}}\left(\frac{\alpha_{21}}{\alpha_{21} - \rho_{21}(1 - \gamma_{21}x_1^* - x_{21}^*)} - 1\right).$$

First of all, based on the second and third equations, we have

$$x_{22}^* = 0 \iff x_{21}^* = 0.$$

So we will only work with x_{21}^* and $x_{22}^* > 0$. Also, for x_1^*, we find

$$\begin{aligned} 0 &= (1 - x_1^* - \gamma_{12}x_{21}^*)x_1^* \\ \iff x_1^* &= 0 \quad \text{or} \quad x_1^* = 1 - \gamma_{12}x_{21}^*. \end{aligned}$$

In this proof we suppose $x_1^* = 0$. Then the system is

$$\begin{cases} 0 = \rho_{21}(1 - x_{21}^*)x_{21}^* + \frac{1}{\kappa}\alpha_{12}x_{22}^* - \alpha_{21}x_{21}^*; \\ 0 = \rho_{22}(1 - x_{22}^*)x_{22}^* - \alpha_{12}x_{22}^* + \kappa\alpha_{21}x_{21}^* \end{cases}$$

Let us define

$$\begin{aligned} f_0(x) &:= \frac{\kappa}{\alpha_{12}}x\Big(\alpha_{21} - \rho_{21}(1 - x)\Big); \\ h_0(x) &:= 1 + \frac{\alpha_{12}}{\rho_{22}}\left(\frac{\alpha_{21}}{\alpha_{21} - \rho_{21}(1 - x)} - 1\right). \end{aligned}$$

x is a solution of the previous system if and only if $x > 0$, and $f_0(x) = h_0(x) > 0$. In this case, $x_{21}^* = x$ and $x_{22}^* = f_0(x) = h_0(x)$.

The study of these two functions shows that $h_0(x)$ is a hyperbole, with a vertical asymptote at $x = 1 - \alpha_{21}/\rho_{21}$. For $x > 1 - \alpha_{21}/\rho_{21}$, it is strictly monotonically decreasing. Furthermore, independently of the parameters, we have $h_0(1) = 1$.

$f_0(x)$ is a parabola, with 0 and $1 - \alpha_{21}/\rho_{21}$ for its roots, and a minimum reached in $x = 0.5(1 - \alpha_{21}/\rho_{21})$.

- If $\frac{\alpha_{21}}{\rho_{21}} > 1$

  In this condition, both the minimum of the parabola f_0, as well as the vertical asymptote are before (or on) 0. And since $f_0(0) = 0$, f_0 increases strictly monotonically on $\mathbb{R}^+$, is positive and tends toward infinity. Then, according to the intermediate value theorem, f_0 and h_0 cross each other for one and only one value of $x > 0$ in the positive quadrant. See Figure A.2.

  Hence, in this case, there exists a unique equilibrium $(0, x_{21}^*, x_{22}^*)$.

- If $\frac{\alpha_{21}}{\rho_{21}} < 1$

  In this condition, if $0 \leq x < 1 - \alpha_{21}/\rho_{21}$, we are in between the two roots of f_0, so $f_0(x) \leq 0$. And for $x = 1 - \alpha_{21}/\rho_{21}$, there cannot be a crossing since h_0 is not defined at its vertical asymptote.

  For $x > 1 - \alpha_{21}/\rho_{21}$, the same arguments as before can be used to invoke the intermediate value theorem, which guarantees the existence of a unique value $x > 1 - \alpha_{21}/\rho_{21}$ such that $f_0(x) = h_0(x)$. See Figure A.3.

So in both cases, we have the existence of a unique equilibrium $(0, x_{21}^*, x_{22}^*)$. Furthermore, we then have $x_{21}^* > 1 - \alpha_{21}/\rho_{21}$.

$\square$

A.3 Proof of Proposition 3

Proof of Proposition 3.

Let us take $x_1^* = 1 - \gamma_{12} x_{21}^*$. Since x_1^* cannot be negative, this defines a limit on the equilibrium point x_{21}^*:

$$\text{if } x_1^* \neq 0, \text{ then } x_{21}^* < \frac{1}{\gamma_{12}}.$$

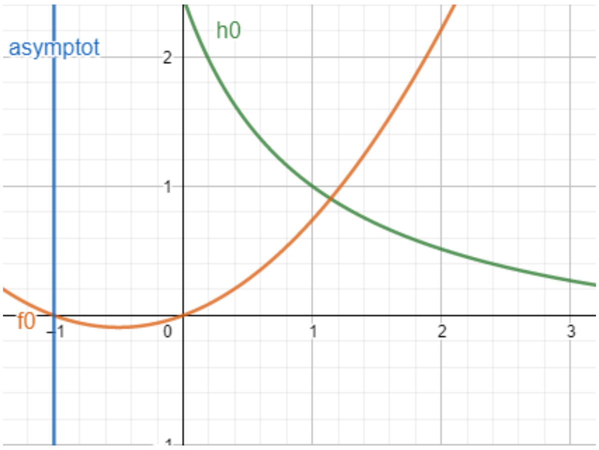


Figure A.2: Case with $x_1^* = 0, \ \frac{\alpha_{21}}{\rho_{21}} > 1$

Figure A.3: Case with $x_1^* = 0, \ \frac{\alpha_{21}}{\rho_{21}} < 1$

We will call in this case the coexistence equilibrium $(x^*_{1,co}, x^*_{21,co}, x^*_{22,co})$. The system is then

$$\begin{cases} 0 &= \rho_{21}\big(1-\gamma_{21}(1-\gamma_{12}x^*_{21,co}) - x^*_{21,co}\big)x^*_{21,co} + \dfrac{1}{\kappa}\alpha_{12}x^*_{22,co,co} - \alpha_{21}x^*_{21,co}; \\ \\ 0 &= \rho_{22}(1-x^*_{22,co})x^*_{22,co} - \alpha_{12}x^*_{22,co} + \kappa\alpha_{21}x^*_{21,co} \end{cases}$$

and let us define

$$\begin{aligned} f_1(x) &:= \frac{\kappa}{\alpha_{12}}x\Big(\alpha_{21} - \rho_{21}(1-\gamma_{21} - x(1-\gamma_{12}\gamma_{21}))\Big); \\ h_1(x) &:= 1 + \frac{\alpha_{12}}{\rho_{22}}\left(\frac{\alpha_{21}}{\alpha_{21} - \rho_{21}(1-\gamma_{21} - x(1-\gamma_{12}\gamma_{21}))} - 1\right). \end{aligned}$$

The above system is satisfied if and only if there exists $0 < x < 1/\gamma_{12}$ such that $f_1(x) = h_1(x) > 0$. Then $x^*_{21,co} = x$ and $x^*_{22} = f_1(x) = h_1(x)$.

h_1 has a vertical asymptote at abscissa

$$A := \frac{1 - \alpha_{21}/\rho_{21} - \gamma_{21}}{1 - \gamma_{12}\gamma_{21}},$$

a horizontal asymptote of equation

$$y = 1 - \frac{\alpha_{12}}{\rho_{22}}$$

and

$$\begin{aligned} h_1'(x) &= \frac{\alpha_{12}\alpha_{21}(\gamma_{12}\gamma_{21} - 1)}{\rho_{21}\rho_{22}\Big(\alpha_{21} - \rho_{21}(1-\gamma_{21} - x(1-\gamma_{12}\gamma_{21}))\Big)^2}, \\ \text{so } h_1'(x) &< 0 \iff 1 - \gamma_{12}\gamma_{21} > 0 \end{aligned}$$

1. First, suppose $\alpha_{12} < \rho_{22}$. All the following cases are illustrated in Figure A.4.

   (a) Let us also suppose that $f_1(1/\gamma_{12}) > h_1(1/\gamma_{12})$ and $\dfrac{\rho_{21} - \alpha_{21}}{\rho_{21}} < \dfrac{1}{\gamma_{12}}$ If $1 - \gamma_{12}\gamma_{21} > 0$, then $A < 1/\gamma_{21}$. Furthermore, f_1 is a concave parabola, going from 0 to $+\infty$ for $x \in [A, +\infty[$, and h_1 is a decreasing hyperbola, going from $+\infty$ to $1 - \alpha_{12}\rho_{22} > 0$, so the intermediate value theorem tells us that there is a unique crossing for those two functions. Since $f_1(1/\gamma_{12}) > h_1(1/\gamma_{12})$ the crossing is at an abscissa $x < 1/\gamma_{12}$.

   If $1-\gamma_{12}\gamma_{21}<0$ then $A>1/\gamma_{21}>0$. Furthermore, h_1 increases monotonically with a horizontal asymptote in $1-\alpha_{12}\rho_{22}>0$ so $h_1(0)>0$. And since $f_1(0)=0$ and $f_1(1/\gamma_{12})>h_1(1/\gamma_{12})$, we have a unique crossing for $0<x<1/\gamma_{12}$.

   In both cases, we have a unique crossing for $0<x<1/\gamma_{12}$.

   (b) Let us suppose that $f_1(1/\gamma_{12})<h_1(1/\gamma_{12})$ and $\dfrac{\rho_{21}-\alpha_{21}}{\rho_{21}}<\dfrac{1}{\gamma_{12}}$

   If $1-\gamma_{12}\gamma_{21}>0$ then $A<1/\gamma_{21}$. The same arguments as before tell us that there is a unique crossing in the positive area, but it is for $x>1/\gamma_{12}$. So, there is 0 crossing in the positive area for $0<x<1/\gamma_{12}$.

   If $1-\gamma_{12}\gamma_{21}<0$ then $A>1/\gamma_{21}>0$. f_1 is a concave parabola and can cross h_1. However, if it does, it has to recross it in the interval $0<x<1/\gamma_{12}$ since $f_1(1/\gamma_{12})>h_1(1/\gamma_{12})$. There can be 0 or 2 crossings for $0<x<1/\gamma_{12}$.

   Here in both cases, there are 0 or 2 crossings.

   (c) Let us finally suppose that $\dfrac{\rho_{21}-\alpha_{21}}{\rho_{21}}>\dfrac{1}{\gamma_{12}}$

   If $1-\gamma_{12}\gamma_{21}>0$ then $A>1/\gamma_{21}$ and $f_1(x)\leq 0$ for $x\in[0,A]$ so there is 0 crossing in the positive area for $0<x<1/\gamma_{12}$.

   If $1-\gamma_{12}\gamma_{21}<0$ then $A<1/\gamma_{21}$. h_1 increases from $h_1(0)>0$ to $+\infty$ in $x=A$, and f_1 is a concave parabola. There are 0 or 2 crossings for those two functions in the positive area between $0<x<1/\gamma_{12}$.

   Here too, in both cases, there are 0 or 2 crossings

To sum up the case $\alpha_{12}<\rho_{22}$, if $f_1(1/\gamma_{12})>h_1(1/\gamma_{12})$ and $\dfrac{\rho_{21}-\alpha_{21}}{\rho_{21}}<\dfrac{1}{\gamma_{12}}$ then there is a unique co-existence equilibrium. Otherwise, there are either none or 2 of them.

2. Now suppose $\alpha_{12}>\rho_{22}$

   (a) Let us also suppose that $f_1(1/\gamma_{12})>h_1(1/\gamma_{12})$ and $\dfrac{\rho_{21}-\alpha_{21}}{\rho_{21}}<\dfrac{1}{\gamma_{12}}$.

   If $1-\gamma_{12}\gamma_{21}>0$ then $A<1/\gamma_{21}$. If $h_1(0)<0$ then there is no crossing for $0<x<1/\gamma_{12}$. If $h_1(0)>0$, then since $f_1(1/\gamma_{12})>h_1(1/\gamma_{12})$ we have a unique crossing for $0<x<1/\gamma_{12}$.

   If $1-\gamma_{12}\gamma_{21}<0$ then $A>1/\gamma_{21}$. Since $f_1(1/\gamma_{12})>h_1(1/\gamma_{12})$ there is a crossing for $x>1/\gamma_{12}$, which we do not consider. The other is in the positive area if and only if $h_1(0)>0$.

In both cases, if $h_0(0) > 0$, then there is 1 crossing, otherwise there is none.

(b) Let us suppose that $f_1(1/\gamma_{12}) < h_1(1/\gamma_{12})$ and $\dfrac{\rho_{21} - \alpha_{21}}{\rho_{21}} < \dfrac{1}{\gamma_{12}}$.

If $1 - \gamma_{12}\gamma_{21} > 0$ then $A < 1/\gamma_{21}$ and h_1 is decreasing, so since $f_1(1/\gamma_{12}) < h_1(1/\gamma_{12})$ they can never cross for $0 < x < 1/\gamma_{12}$.

If $1 - \gamma_{12}\gamma_{21} < 0$ then $A > 1/\gamma_{21}$ and there can be crossings. However, since $f_1(1/\gamma_{12}) < h_1(1/\gamma_{12})$, if $h_1(0) > 0$, there can be only 0 or 2 crossings in the positive area. If $h_1(0) < 0$, there is necessarily one unique crossing in the positive area for $0 < x < 1/\gamma_{12}$.

In both cases, if $h_1(0) > 0$ then there is 1 crossing, otherwise there are 2 or 0.

(c) Let us finally suppose that $\dfrac{\rho_{21} - \alpha_{21}}{\rho_{21}} > \dfrac{1}{\gamma_{12}}$

If $1 - \gamma_{12}\gamma_{21} > 0$ then $A > 1/\gamma_{21}$ and $f_1(x) \leq 0$ for $x \in [0, A]$ so there is 0 crossing in the positive area for $0 < x < 1/\gamma_{12}$.

If $1 - \gamma_{12}\gamma_{21} < 0$ then $A < 1/\gamma_{21}$. h_1 increases from $h_1(0) > 0$ to $+\infty$ in $x = A$, and f_1 is a concave parabola. If $h_1(0) > 0$, there are 0 or 2 crossings for those two functions in the positive area between $0 < x < 1/\gamma_{12}$. If $h_1(0) < 0$ there is necessarily a unique crossing in the positive area for $0 < x < 1/\gamma_{12}$. In both cases, if $h_1(0) > 0$ then there is 1 crossing; otherwise, there are 2 or 0.

To sum up this case, we have:

- If $h_1(0) > 0$, $f_1(1/\gamma_{12}) > h_1(1/\gamma_{12})$, $\dfrac{\rho_{21} - \alpha_{21}}{\rho_{21}} < \dfrac{1}{\gamma_{12}}$ then there is one co-existence equilibrium.
- If $h_1(0) < 0$, $f_1(1/\gamma_{12}) > h_1(1/\gamma_{12})$, $\dfrac{\rho_{21} - \alpha_{21}}{\rho_{21}} < \dfrac{1}{\gamma_{12}}$ then there is no co-existence equilibrium.
- If $h_1(0) > 0$ and $\left\{ f_1(1/\gamma_{12}) < h_1(1/\gamma_{12}) \text{ or } \dfrac{\rho_{21} - \alpha_{21}}{\rho_{21}} > \dfrac{1}{\gamma_{12}} \right\}$ then there is one co-existence equilibrium.
- If $h_1(0) < 0$ and $\left\{ f_1(1/\gamma_{12}) < h_1(1/\gamma_{12}) \text{ or } \dfrac{\rho_{21} - \alpha_{21}}{\rho_{21}} > \dfrac{1}{\gamma_{12}} \right\}$ then there is either 0 or 2 co-existence equilibrium.

$\square$

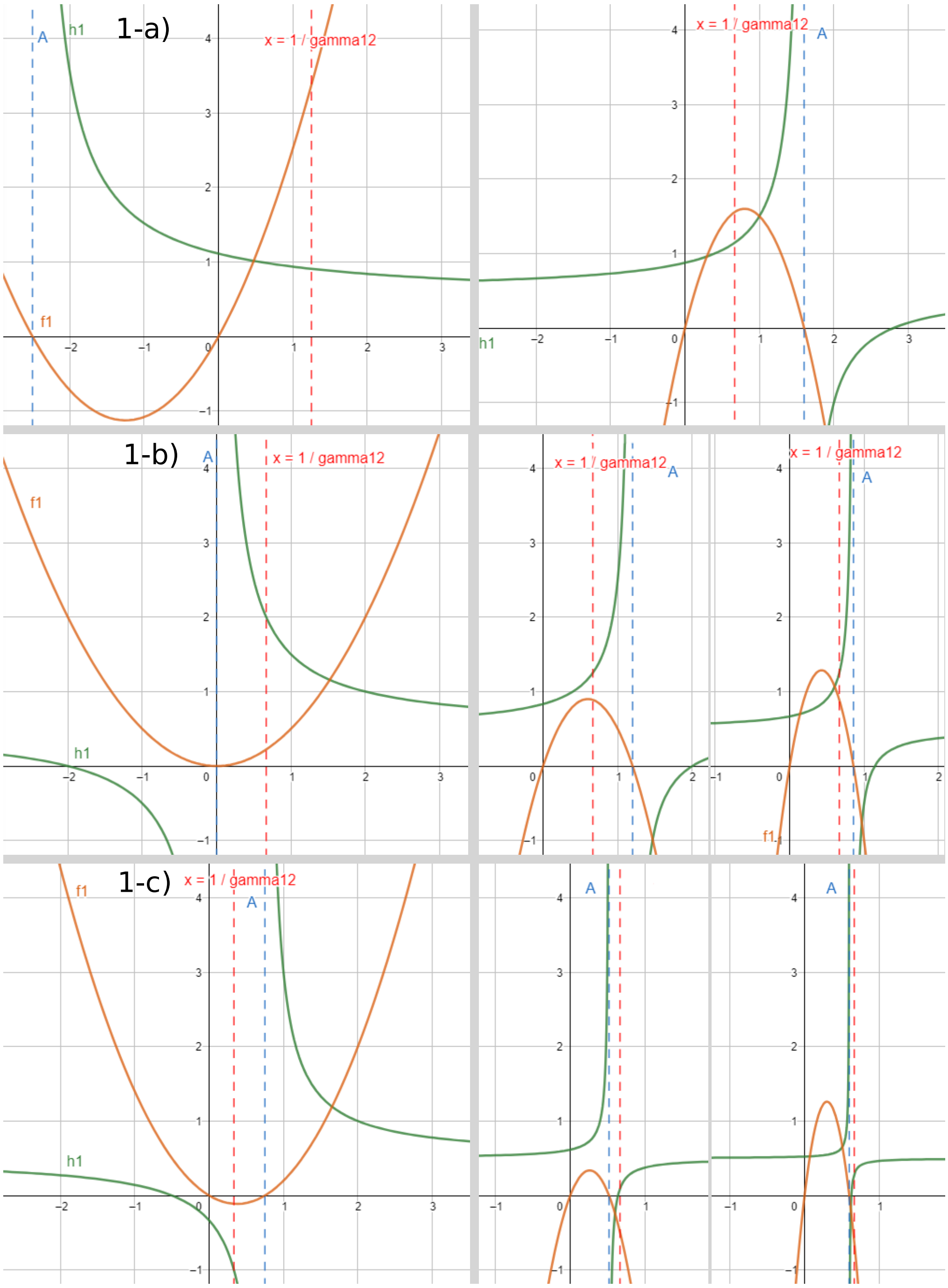


Figure A.4: On the left are the cases when $1 - \gamma_{12}\gamma_{21} > 0$, opposite on the right column. For all pictures, $\alpha_{12} = 1$, $\rho_{22} = 2$.

A.4 Proof of Proposition 4

Proof of Proposition 4.

For the equilibrium $(1,0,0)$:

$$J_{(1,0,0)} = \begin{pmatrix} -1 & -\gamma_{12} & 0 \\ 0 & \rho_{21}(1-\gamma_{21})-\alpha_{21} & \dfrac{\alpha_{12}}{\kappa} \\ 0 & \kappa\alpha_{21} & \rho_{22}-\alpha_{12} \end{pmatrix}.$$

$J_{(1,0,0)}$ is triangular by block. Reminder: with $\lambda(A)$ the spectrum of a matrix A, if A is block (upper/lower) triangular:

$$A = \begin{pmatrix} B_{11} & B_{12} \\ 0 & B_{22} \end{pmatrix},$$

then

$$\lambda(A) = \lambda(B_{11}) \cup \lambda(B_{22}).$$

So

$$\begin{aligned} \begin{vmatrix} \rho_{21}(1-\gamma_{21})-\alpha_{21}-\lambda & \dfrac{\alpha_{12}}{\kappa} \\ \kappa\alpha_{21} & \rho_{22}-\alpha_{12}-\lambda \end{vmatrix} &= 0 \\ \iff \lambda^2 - \big(\rho_{21}(1-\gamma_{21}) + \rho_{22} - \alpha_{21} - \alpha_{12}\big)\lambda & \\ +\rho_{21}(1-\gamma_{21})(\rho_{22}-\alpha_{12}) - \alpha_{21}\rho_{22} &= 0. \end{aligned}$$

We already know that λ_1, λ_2 can only be real, so $\Delta \geq 0$. If I write $b = -(\rho_{21}(1-\gamma_{21}) + \rho_{22} - \alpha_{21} - \alpha_{12})$ and $c = \rho_{21}(1-\gamma_{21})(\rho_{22}-\alpha_{12}) - \alpha_{21}\rho_{22}$ then eigenvalues are of the form

$$\lambda_i = \frac{-b \pm \sqrt{b^2-4ac}}{2}$$

and a positive eigenvalue exist if and only if $b < 0$ or $c < 0$, with

$$\begin{aligned} b < 0 \quad &\iff \quad \gamma_{21} < 1 - \frac{\alpha_{21}+\alpha_{12}-\rho_{22}}{\rho_{21}}; \\ c < 0 \quad &\iff \quad (1-\gamma_{21})\left(1 - \frac{\alpha_{12}}{\rho_{22}}\right) < \frac{\alpha_{21}}{\rho_{21}}. \end{aligned}$$

With condition $c < 0$, it is obvious that if only one of the two case:

$$\begin{aligned} \gamma_{21} &< 1; \\ \alpha_{12} &< \rho_{22}, \end{aligned}$$

is fulfilled then we have a positive eigenvalue. Let us see what happens if the two are fulfilled at the same time. $\alpha_{12} < \rho_{22}$ so

$$c < 0 \quad \Longleftrightarrow \quad \gamma_{21} > 1 - \frac{\alpha_{21}}{\rho_{21}} \frac{\rho_{22}}{\rho_{22} - \alpha_{12}}.$$

If $b \geq 0$ and $c \geq 0$, then

$$1 - \frac{\alpha_{21}}{\rho_{21}} \frac{\rho_{22}}{\rho_{22} - \alpha_{12}} \geq \gamma_{21} \geq 1 - \frac{\alpha_{21} + \alpha_{12} - \rho_{22}}{\rho_{21}}$$

However,

$$1 - \frac{\alpha_{21}}{\rho_{21}} \frac{\rho_{22}}{\rho_{22} - \alpha_{12}} \geq 1 - \frac{\alpha_{21} + \alpha_{12} - \rho_{22}}{\rho_{21}} \quad \Longleftrightarrow \quad -(\alpha_{12} - \rho_{22})^2 > \alpha_{12}\alpha_{21},$$

so it is not possible to have $b > 0$ and $c > 0$ in this case, which concludes the proof. □

A.5 Proof of Proposition 5

Proof of Proposition 5.

For the equilibrium $(0, x_{21}^*, x_{22}^*)$, the defining system of x_{21}^* and x_{22}^* is

$$\begin{cases} 0 &= \rho_{21}(1 - x_{21}^*)x_{21}^* + \frac{1}{\kappa}\alpha_{12}x_{22}^* - \alpha_{21}x_{21}^*; \\ \\ 0 &= \rho_{22}(1 - x_{22}^*)x_{22}^* - \alpha_{12}x_{22}^* + \kappa\alpha_{21}x_{21}^*. \end{cases}$$

As seen in the Proof of Proposition 2, we have in this case:

$$x_{21}^* \quad > \quad \max(0, 1 - \alpha_{21}/\rho_{21}).$$

The Jacobian matrix is

$$J_{(0,x_{21}^*,x_{22}^*)} \quad = \quad \begin{pmatrix} 1 - \gamma_{12}x_{21}^* & 0 & 0 \\ -\rho_{21}\gamma_{21}x_{21}^* & \rho_{21}(1 - 2x_{21}^*) - \alpha_{21} & \frac{\alpha_{12}}{\kappa} \\ 0 & \kappa\alpha_{21} & \rho_{22}(1 - 2x_{22}^*) - \alpha_{12} \end{pmatrix}.$$

$1 - \gamma_{12}x_{21}^*$ is an eigenvalue for this equilibrium. If $x_{21}^* < 1/\gamma_{12}$, then this eigenvalue is positive.

Conditions for $x_{21}^* < 1/\gamma_{12}$

Reminder: we find x_{21}^* and x_{22}^* when these two functions cross in the positive quadrant:

$$\begin{aligned} f_0(x) &= \frac{\kappa}{\alpha_{12}} x\Big(\alpha_{21} - \rho_{21}(1 - x)\Big); \\ h_0(x) &= 1 + \frac{\alpha_{12}}{\rho_{22}} \left(\frac{\alpha_{21}}{\alpha_{21} - \rho_{21}(1 - x)} - 1\right). \end{aligned}$$

Then $x^*_{21} = x$ is the intersection abscissa, and $x^*_{22} = f_0(x) = h_0(x)$. Furthermore, $h_0(x)$ is a hyperbola, with a vertical asymptote at $x = 1 - \alpha_{21}/\rho_{21}$. Then

$$x^*_{21} < \frac{1}{\gamma_{12}} \iff 1 - \frac{\alpha_{21}}{\rho_{21}} < \frac{1}{\gamma_{12}} \text{ and } f_0(1/\gamma_{12}) > h_0(1/\gamma_{12}).$$

Rest of the eigenvalues

$$\begin{aligned}
&\begin{vmatrix} \rho_{21}(1-2x^*_{21}) - \alpha_{21} - \lambda & \dfrac{\alpha_{12}}{\kappa} \\ \kappa\alpha_{21} & \rho_{22}(1-2x^*_{22}) - \alpha_{12} - \lambda \end{vmatrix} = 0 \\
\iff \quad & \lambda^2 - \lambda\Big(\rho_{21}(1-2x^*_{21}) + \rho_{22}(1-2x^*_{22}) - (\alpha_{21}+\alpha_{12})\Big) \\
& +\big(\rho_{21}(1-2x^*_{21}) - \alpha_{21}\big)\big(\rho_{22}(1-2x^*_{22}) - \alpha_{12}\big) - \alpha_{21}\alpha_{12} = 0
\end{aligned}$$

and we know that the eigenvalues are real, so $\Delta \geq 0$. Calling

$$\begin{aligned}
b &:= -\Big(\rho_{21}(1-2x^*_{21}) + \rho_{22}(1-2x^*_{22}) - (\alpha_{21}+\alpha_{12})\Big); \\
c &:= \big(\rho_{21}(1-2x^*_{21}) - \alpha_{21}\big)\big(\rho_{22}(1-2x^*_{22}) - \alpha_{12}\big) - \alpha_{21}\alpha_{12},
\end{aligned}$$

then the eigenvalues are of the form

$$\lambda_i = \frac{-b \pm \sqrt{b^2 - 4ac}}{2}$$

and at least one is positive if and only if $b < 0$ or $c < 0$. However,

$$\begin{aligned}
\rho_{21}(1 - x^*_{21}) &= \alpha_{21} - \frac{1}{\kappa}\alpha_{12}\frac{x^*_{22}}{x^*_{21}}; \\
\rho_{22}(1 - x^*_{22}) &= \alpha_{12} - \kappa\alpha_{21}\frac{x^*_{21}}{x^*_{22}},
\end{aligned}$$

so

$$b = \left(\frac{1}{\kappa}\alpha_{12}\frac{x^*_{22}}{x^*_{21}} + \kappa\alpha_{21}\frac{x^*_{21}}{x^*_{22}}\right) + (\rho_{21}x^*_{21} + \rho_{22}x^*_{22}) > 0$$

and

$$\begin{aligned}
c &= \alpha_{12}\alpha_{21}\left(\frac{1}{\kappa}\frac{\alpha_{12}}{\alpha_{21}}\frac{x^*_{22}}{x^*_{21}} + \frac{\rho_{21}}{\alpha_{21}}x^*_{21}\right)\left(\kappa\frac{\alpha_{21}}{\alpha_{12}}\frac{x^*_{21}}{x^*_{22}} + \frac{\rho_{22}}{\alpha_{12}}x^*_{22}\right) - \alpha_{12}\alpha_{21} \\
&= \frac{1}{\kappa}\alpha_{12}\rho_{22}\frac{{x^*_{22}}^2}{x^*_{21}} + \kappa\alpha_{21}\rho_{21}\frac{{x^*_{21}}^2}{x^*_{22}} + \rho_{22}\rho_{21}x^*_{21}x^*_{22} \\
&> 0.
\end{aligned}$$

And since the 2 eigenvalues from this block matrix are both always negatives, it concludes the proof. □

A.6 Proof of Proposition 6

Proof of Proposition 6.

If we suppose $1 - \alpha_{21}/\rho_{21} < 1/\gamma_{12}$, then

$$\begin{aligned}
& f_0(1/\gamma_{12}) > h_0(1/\gamma_{12}) \\
\iff \quad & \frac{\kappa}{\alpha_{12}} \frac{\rho_{21}}{\gamma_{12}} \left(\frac{\alpha_{21}}{\rho_{21}} - \left(1 - \frac{1}{\gamma_{12}}\right)\right)^2 \\
& > \frac{\alpha_{21}}{\rho_{21}} - \left(1 - \frac{1}{\gamma_{12}}\right) + \frac{\alpha_{12}}{\rho_{22}} \left(1 - \frac{1}{\gamma_{12}}\right) \\
\iff \quad & \alpha_{21}^2 - \left(2\rho_{21}\left(1 - \frac{1}{\gamma_{12}}\right) + \frac{\alpha_{12}\gamma_{12}}{\kappa}\right)\alpha_{21} \\
& + \rho_{21}\left(1 - \frac{1}{\gamma_{12}}\right)\left(\frac{\alpha_{12}\gamma_{12}}{\kappa}\left(1 - \frac{\alpha_{12}}{\rho_{22}}\right) + \rho_{21}\left(1 - \frac{1}{\gamma_{12}}\right)\right) > 0.
\end{aligned}$$

For this second order polynomial (in terms of α_{21}) we have a discriminant Δ given by

$$\Delta \quad = \quad \left(\frac{\alpha_{12}\gamma_{12}}{\kappa}\right)^2 \left(1 + 4\frac{\kappa}{\gamma_{12}}\frac{\rho_{21}}{\rho_{22}}\left(1 - \frac{1}{\gamma_{12}}\right)\right).$$

Since $\gamma_{12} > 0$,

$$\Delta < 0 \quad \iff \quad \gamma_{12} < 2\kappa\frac{\rho_{21}}{\rho_{22}}\left(-1 + \sqrt{1 + \frac{\rho_{22}}{\kappa\rho_{21}}}\right).$$

Furthermore we have

$$\gamma_{12} < 2\kappa\frac{\rho_{21}}{\rho_{22}}\left(-1 + \sqrt{1 + \frac{\rho_{22}}{\kappa\rho_{21}}}\right) \quad \iff \quad \frac{1}{\gamma_{12}} > \frac{1}{2}\left(\sqrt{1 + \frac{\rho_{22}}{\kappa\rho_{21}}} + 1\right).$$

Since

$$\frac{1}{2}\left(\sqrt{1 + \frac{\rho_{22}}{\kappa\rho_{21}}} + 1\right) \; > \; 1 \; > \; 1 - \frac{\alpha_{21}}{\rho_{21}}$$

we have in the end, knowing that $\Delta < 0$ means that the previous polynomial equation is positive for any value of α_{21}:

$$\begin{aligned}
& \gamma_{12} < 2\kappa\frac{\rho_{21}}{\rho_{22}}\left(-1 + \sqrt{1 + \frac{\rho_{22}}{\kappa\rho_{21}}}\right) \\
\implies \quad & \frac{1}{\gamma_{12}} > 1 - \frac{\alpha_{21}}{\rho_{21}} \text{ and } f_0(1/\gamma_{12}) > h_0(1/\gamma_{12}) \\
\iff \quad & x_{21}^* < \frac{1}{\gamma_{12}}.
\end{aligned}$$

Suppose now that $\gamma_{12} \geq 2\kappa\frac{\rho_{21}}{\rho_{22}}\left(-1+\sqrt{1+\frac{\rho_{22}}{\kappa\rho_{21}}}\right)$, so $\Delta \geq 0$. From the previous second-order polynomial, let us call

$$\begin{aligned} b &:= -\left(2\rho_{21}\left(1-\frac{1}{\gamma_{12}}\right)+\frac{\alpha_{12}\gamma_{12}}{\kappa}\right); \\ c &:= \rho_{21}\left(1-\frac{1}{\gamma_{12}}\right)\left(\frac{\alpha_{12}\gamma_{12}}{\kappa}\left(1-\frac{\alpha_{12}}{\rho_{22}}\right)+\rho_{21}\left(1-\frac{1}{\gamma_{12}}\right)\right). \end{aligned}$$

There exist roots, since $\Delta \geq 0$. However, those roots could be negative, and in this case, the inequality $f_0\left(1/\gamma_{12}\right) > h_0\left(1/\gamma_{12}\right)$ is always true, independently of the value of α_{21}. Since for the two roots we always have $(-b+\sqrt{b^2-4ac})/2a > (-b-\sqrt{b^2-4ac})/2a$, they are both negative if and only if $(-b+\sqrt{b^2-4ac})/2a < 0$, which means

$$\text{Both roots are negative} \quad \Longleftrightarrow \quad b > 0 \text{ and } c > 0.$$

Here, $\gamma_{12} > 0$, so we have:

$$b > 0 \quad \Longleftrightarrow \quad \gamma_{12} < \kappa\frac{\rho_{21}}{\alpha_{12}}\left(-1+\sqrt{1+2\frac{\alpha_{12}}{\kappa\rho_{21}}}\right).$$

Let us define the function

$$\varphi(x) \;:=\; \kappa x\left(-1+\sqrt{1+\frac{2}{\kappa x}}\right).$$

This function increases monotonically on $\mathbb{R}^+$, so

$$\varphi(2\rho_{21}/\rho_{22}) \leq \gamma_{12} < \varphi(\rho_{21}/\alpha_{12}) \quad \Longrightarrow \quad \alpha_{12} < \frac{\rho_{22}}{2}.$$

In other words, if $\alpha_{12} > \rho_{22}/2$, then it is not possible to have $\Delta \geq 0$ and $b > 0$. Since we assumed the former, it means that in this case $b < 0$, and the stability of the equilibrium will depend on the value of α_{21}.

Then,

$$\begin{aligned} & \Delta \geq 0 \text{ and } b > 0 \\ \Longleftrightarrow\quad & \alpha_{12} < \frac{\rho_{22}}{2} \text{ and} \\ & 2\kappa\frac{\rho_{21}}{\rho_{22}}\left(-1+\sqrt{1+\frac{\rho_{22}}{\kappa\rho_{21}}}\right) \leq \gamma_{12} < \kappa\frac{\rho_{21}}{\alpha_{12}}\left(-1+\sqrt{1+2\frac{\alpha_{12}}{\kappa\rho_{21}}}\right). \end{aligned}$$

Let us also note that for any κ, α_{12} and ρ_{21}, $\kappa\frac{\rho_{21}}{\alpha_{12}}\left(-1+\sqrt{1+2\frac{\alpha_{12}}{\kappa\rho_{21}}}\right) < 1$. Meaning that $b > 0 \implies \gamma_{12} < 1$, and then $1 - 1/\gamma_{12} < 0$.

Supposing $\Delta > 0$ and $b > 0$, let us look for the conditions that give $c > 0$. With those suppositions we have

$$\begin{aligned} c > 0 \quad &\iff \quad 1 - \frac{\alpha_{12}}{\rho_{22}} + \frac{\kappa}{\alpha_{12}} \frac{\rho_{21}}{\gamma_{12}} \left(1 - \frac{1}{\gamma_{12}} \right) < 0 \\ &\iff \quad p(\gamma_{12}) := \left(1 - \frac{\alpha_{12}}{\rho_{22}} \right) \gamma_{12}^2 + \frac{\kappa}{\alpha_{12}} \rho_{21} \gamma_{12} - \frac{\kappa}{\alpha_{12}} \rho_{21} < 0. \end{aligned}$$

Let us note that $\alpha_{12} < \rho_{22}/2$ so $1 - \alpha_{12}/\rho_{22} > 1/2$ and p is a convex parabola, with $p(0) < 0$. Then

$$p(\gamma_{12}) < 0 \quad \iff \quad \gamma_{12} < \kappa \frac{\rho_{22}\rho_{21}}{2\alpha_{12}(\rho_{22} - \alpha_{12})} \left(-1 + \sqrt{1 + 4 \frac{\alpha_{12}}{\kappa\rho_{21}} \left(1 - \frac{\alpha_{12}}{\rho_{22}} \right)} \right).$$

Note that the right side of this inequation is $\varphi(\frac{\rho_{22}\rho_{21}}{2\alpha_{12}(\rho_{22}-\alpha_{12})})$, and we have

$$\begin{aligned} & \alpha_{12} < \frac{\rho_{22}}{2} \\ \iff \quad & \frac{\rho_{22}\rho_{21}}{2\alpha_{12}(\rho_{22} - \alpha_{12})} < \frac{\rho_{21}}{\alpha_{12}} \\ \iff \quad & \kappa \frac{\rho_{22}\rho_{21}}{2\alpha_{12}(\rho_{22} - \alpha_{12})} \left(-1 + \sqrt{1 + 4 \frac{\alpha_{12}}{\kappa\rho_{21}} \left(1 - \frac{\alpha_{12}}{\rho_{22}} \right)} \right) \\ & \quad < \kappa \frac{\rho_{21}}{\alpha_{12}} \left(-1 + \sqrt{1 + 2 \frac{\alpha_{12}}{\kappa\rho_{21}}} \right). \end{aligned}$$

This also means that $\gamma_{12} < 1$ when those conditions are achieved, so $1 - \alpha_{21}/\rho_{21} < 1/\gamma_{12}$. Finally we obtain

$$\begin{aligned} & 1 - \frac{\alpha_{21}}{\rho_{21}} < \frac{1}{\gamma_{12}} \text{ and } f_0(1/\gamma_{12}) > h_0(1/\gamma_{12}) \text{ true for all } \alpha_{21} > 0 \\ \iff \quad & \Delta < 0 \text{ or } \Big(\Delta \geq 0 \ \text{ and } \ b > 0 \ \text{ and } \ c > 0 \Big) \\ \iff \quad & \gamma_{12} < 2\kappa \frac{\rho_{21}}{\rho_{22}} \left(-1 + \sqrt{1 + \frac{\rho_{22}}{\kappa\rho_{21}}} \right) \text{ or} \\ & \Bigg(\alpha_{12} < \frac{\rho_{22}}{2} \ \text{ and} \\ & \gamma_{12} < \kappa \frac{\rho_{22}\rho_{21}}{2\alpha_{12}(\rho_{22} - \alpha_{12})} \left(-1 + \sqrt{1 + 4 \frac{\alpha_{12}}{\kappa\rho_{21}} \left(-1 - \frac{\alpha_{12}}{\rho_{22}} \right)} \right) \Bigg) \end{aligned}$$

which concludes the proof. □

Appendix B

Proof of Proposition 7 in Chapter 4

Proof of Proposition 7.

We try to find eigenfunctions verifying

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

To solve that we separate the system in two:

$$\begin{cases} c^2 g_-''(x) + (1-Rb-\lambda)g_-(x) \;=\; 0, \quad x \in [0,d]; \\ \\ g_-'(0) \;=\; 0, \end{cases} \tag{B.1}$$

and

$$\begin{cases} c^2 g_+''(x) + (1-\lambda)g_+(x) \;=\; 0, \qquad x \in [d,1]; \\ \\ g_+'(1) \;=\; 0. \end{cases} \tag{B.2}$$

The solutions of (B.1) are given by:

$$\begin{cases} \text{If } \lambda > 1-Rb \quad \text{then} \quad g_-(x) = A\cosh\left(x\dfrac{\sqrt{Rb+\lambda-1}}{c}\right); \\ \text{If } \lambda = 1-Rb \quad \text{then} \quad g_-(x) = A; \\ \text{If } \lambda < 1-Rb \quad \text{then} \quad g_-(x) = A\cos\left(x\dfrac{\sqrt{1-Rb-\lambda}}{c}\right), \end{cases}$$

while the solutions of (B.2) are given by:

$$\begin{cases} \text{If } \lambda > 1 \quad \text{then} \quad g_+(x) = A\cosh\left((1-x)\dfrac{\sqrt{\lambda-1}}{c}\right); \\ \text{If } \lambda = 1 \quad \text{then} \quad g_+(x) = A; \\ \text{If } \lambda < 1 \quad \text{then} \quad g_+(x) = A\cos\left((1-x)\dfrac{\sqrt{1-\lambda}}{c}\right). \end{cases}$$

Finally, to respect the smoothness of the solutions, we had imposed:

$$g_-(d-) = g_+(d+) \tag{B.3}$$

$$g'_-(d-) = g'_+(d+) \tag{B.4}$$

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

If $\lambda \geq 1$

First, when $\lambda \geq 1$, (B.3) and (B.4) 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

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

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

If $1 - Rb < \lambda < 1$

Now, if $1 - Rb < \lambda < 1$, (B.3) and (B.4) give:

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

Then

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

Let us call:

$$\begin{aligned} h(\lambda) &:= \frac{\sqrt{Rb+\lambda-1}}{c}\tanh\left(d\frac{\sqrt{Rb+\lambda-1}}{c}\right); \\ f(\lambda) &:= \frac{\sqrt{1-\lambda}}{c}\tan\left((1-d)\frac{\sqrt{1-\lambda}}{c}\right). \end{aligned}$$

Then the rightmost vertical asymptote of f is at the abscissa

$$\lambda_m \;=\; 1-\left(\frac{c}{1-d}\frac{\pi}{2}\right)^2$$

and for $\lambda_m < \lambda < 1$, $f(\lambda)$ decreases monotonically from $+\infty$ to 0. Furthermore, $h(1-Rb) = 0$, and h increases monotonically for $1-Rb < \lambda < 1$, going from 0 to $h(1) > 0$. According to those and the continuity of the two functions, there is always at least one λ such that $f(\lambda) = h(\lambda)$. We need to find out when this crossing is in the positive quadrant.

First of all, if $Rb < 1$ then $h(\lambda)$ only exists in the positive quadrant, and the crossing is also in it. See Figure B.1, case a). Meaning, if $Rb < 1$, there exist a $\lambda_n > 0$ and a g_n associated.

Suppose now $Rb > 1$. The vertical asymptote mentioned above is in the positive quadrant if and only if $d < 1 - \frac{\pi c}{2}$. Then there is an intersection between both curves in the positive quadrant. See Figure B.1 case b). That is, if $Rb > 1$ and $d < 1 - \frac{\pi c}{2}$, then there also exist a positive λ_n and an associated g_n.

Finally, if $Rb > 1$ and $d > 1 - \frac{\pi c}{2}$. Then, as seen in Figure B.1 case c) and d), the existence of an intersection in the positive values for λ depends on whether $f(0) > h(0)$ is true. In other words, with these conditions, there exists a positive λ_n if and only if

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

Returning the statement, we obtain that there does not exist any $k \geq 1$ such that $\lambda_k > 0$ if and only if

$$b > \frac{1}{R}, \quad d > 1 - \frac{\pi c}{2}, \text{ and } \tan\left(\frac{1-d}{c}\right) < \sqrt{Rb-1}\tanh\left(d\frac{\sqrt{Rb-1}}{c}\right).$$

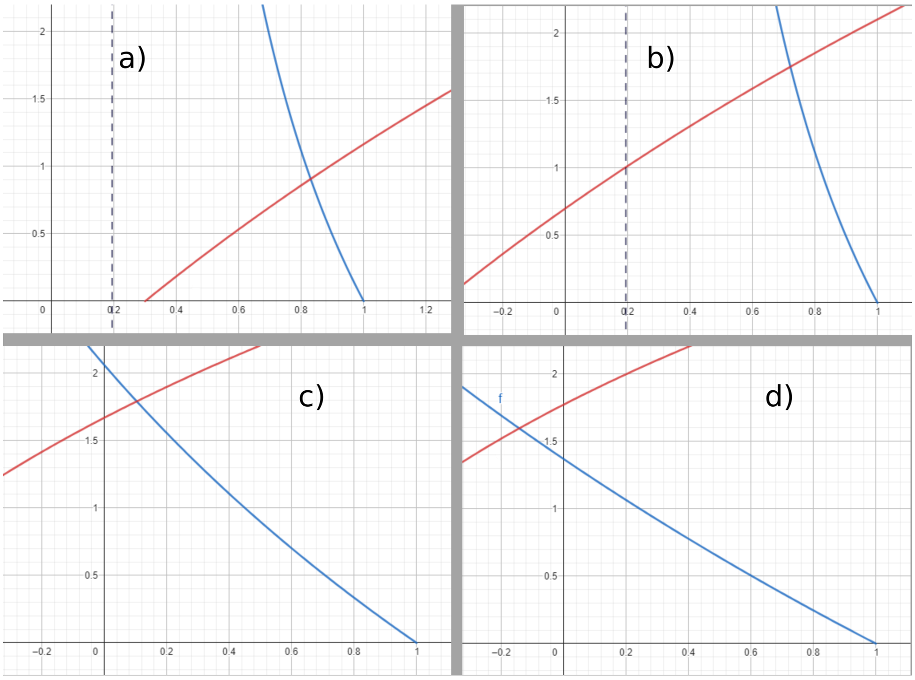


Figure B.1: $f(\lambda)$ in blue, $h(\lambda)$ in red. For a) we have $Rb < 1$. For b) we have $Rb > 1$ and vertical asymptote after 0. For c) we have $Rb > 1$, the vertical asymptote before 0, and $f(0) > h(0)$. Finally, for d) we have $Rb > 1$, the vertical asymptote before 0, and $f(0) < h(0)$

Since the equation

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

has a vertical asymptote that we can find by a linearization of both sides when $c \to +\infty$:

$$\frac{1-d}{c} \quad \underset{c\to\infty}{\simeq} \quad \big(Rb-1\big)\frac{d}{c}$$

So the curve given by this equation has a vertical asymptote at $d = 1/Rb$. Then

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

and since $d < 1$, that encompasses the first condition we had, $b > 1/R$.

$\square$

Appendix C

Supplements for Chapter 5

C.1 Proof of Lemma 8

Proof of Lemma 8.

Let us first notice that

$$\begin{aligned}
J_{(x_1,\ldots,x_n)} &= \begin{pmatrix} D_1(x_1) & \eta p_1/P_n & \ldots & \eta p_1/P_n \\ \eta p_2/P_n & D_2(x_2) & \ldots & \eta p_2/P_n \\ \ldots & \ldots & \ldots & \ldots \\ \eta p_n/P_n & \eta p_n/P_n & \ldots & D_n(x_n) \end{pmatrix} \\
&= \mathrm{Diag}\left(D_i(x_i) - \eta \frac{p_i}{P_n}\right) + \begin{pmatrix} \eta p_1/P_n & \ldots & \eta p_1/P_n \\ \eta p_2/P_n & \ldots & \eta p_2/P_n \\ \ldots & \ldots & \ldots \\ \eta p_n/P_n & \ldots & \eta p_n/P_n \end{pmatrix} \\
&= \mathrm{Diag}\left(D_i(x_i) - \eta \frac{p_i}{P_n}\right) + \begin{pmatrix} \eta p_1/P_n \\ \eta p_2/P_n \\ \ldots \\ \eta p_n/P_n \end{pmatrix} \begin{pmatrix} 1 \\ 1 \\ \ldots \\ 1 \end{pmatrix}^T .
\end{aligned}$$

So

$$\begin{aligned}
Q(X) &= \det(J_{(0,0,\ldots,0)} - XI_n) \\
&= \det\left(\mathrm{Diag}\big(p_i - (\sigma+\eta) - X\big) + \begin{pmatrix} \eta p_1/P_n \\ \eta p_2/P_n \\ \ldots \\ \eta p_n/P_n \end{pmatrix} \begin{pmatrix} 1 \\ 1 \\ \ldots \\ 1 \end{pmatrix}^T \right).
\end{aligned}$$

A reminder of the matrix determinant lemma:

Lemma. *Suppose A is an invertible square matrix and u, v are column vectors. Then*

$$\det(A + \boldsymbol{u}\boldsymbol{v}^T) \;=\; (1 + \boldsymbol{v}^T A^{-1}\boldsymbol{u}) \det(A).$$

A direct application of this lemma gives us that for any $X \neq p_i - (\sigma + \eta)$,

$$\begin{aligned} Q(X) &= \left[1 + \sum_i^n \frac{\eta p_i / P_n}{p_i - (\sigma+\eta) - X}\right] \prod_i^n (p_i - (\sigma+\eta) - X) \;\text{ if } X \neq p_i - (\sigma+\eta) \\ &= \prod_i^n (p_i - (\sigma+\eta) - X) + \eta \sum_i^n \frac{p_i}{P_n} \prod_{j\neq i}^n (p_j - (\sigma+\eta) - X)\,. \end{aligned}$$

By continuity arguments for a polynomial, we can say that this last expression is valid even for $X = p_i - (\sigma + \eta)$, for all $i \in [|1, n|]$.

Let us now find the roots of Q. To do that, we order the p_i such that $p_1 \leq p_2 \leq \ldots \leq p_n$.

- First, we suppose that no p_i are equal. In other words, we suppose $p_1 < p_2 < \ldots < p_n$. This means that we have $p_1 - (\sigma + \eta) < p_2 - (\sigma + \eta) < \ldots < p_n - (\sigma + \eta)$.

Let us take $X = p_k - (\sigma + \eta)$, for a given $k \in [|1, n|]$. Then

$$\begin{aligned} Q\big(p_k - (\sigma+\eta)\big) &= \eta \frac{p_k}{P_n} \prod_{j\neq k}^n (p_j - p_k) \\ &= \eta \frac{p_k}{P_n} \prod_{1\leq j<k} \overbrace{(p_j - p_k)}^{<0} \prod_{k<j\leq n} \overbrace{(p_j - p_k)}^{>0}. \end{aligned}$$

From this we deduce that

$$\operatorname{sgn}\Big(Q(p_k - (\sigma+\eta))\Big) \;=\; (-1)^{(k-1)}.$$

Since $\operatorname{sgn}\big(Q(p_k - (\sigma+\eta))\big) = -\operatorname{sgn}\big(Q(p_{k+1} - (\sigma+\eta))\big)$, and because of the continuity of the polynomial function $Q(X)$, we know that there exists at least one root of Q in $\big]p_k - (\sigma+\eta), p_{k+1} - (\sigma+\eta)\big[$, for any $k \in [|1, n-1|]$.

Furthermore, we have that

$$Q(X) \underset{X\to\pm\infty}{\sim} (-1)^n X^n \quad \text{and} \quad \operatorname{sgn}\Big(Q(p_n - (\sigma+\eta))\Big) = (-1)^{(n-1)}.$$

- If there exists $q \in \mathbb{N}$ such that $n = 2q$ (if n is even), then

$$\begin{cases} \lim\limits_{X \to +\infty} Q(X) & = \quad +\infty; \\ \operatorname{sgn}\Big(Q(p_n - (\sigma + \eta))\Big) & = \quad -1. \end{cases}$$

  So there exists at least one root of Q in $\big]p_n - (\sigma + \eta), +\infty\big[$

- On the other hand, if there exists $q \in \mathbb{N}$ such that $n = 2q + 1$ (if n is odd), then

$$\begin{cases} \lim\limits_{X \to +\infty} Q(X) & = \quad -\infty; \\ \operatorname{sgn}\Big(Q(p_n - (\sigma + \eta))\Big) & = \quad 1. \end{cases}$$

  And there also exists at least one root of Q in $\big]p_n - (\sigma + \eta), +\infty\big[$.

Since Q is a polynomial of degree n, it has exactly n roots. With the previous analysis, we found exactly n roots of Q, so we can say that Q has exactly one root in each interval $\big]p_k - (\sigma + \eta), p_{k+1} - (\sigma + \eta)\big[$, for all $k \in [|1, n-1|]$, and one root in $\big]p_n - (\sigma + \eta), +\infty\big[$.

- Let us now suppose that some p_i are equal. In other words, let us suppose $p_i = p_{i+1} = ... = p_{i+j}$, with $i, j \in [|1, n|], i + j \leq n$. This means we have $p_i - (\sigma + \eta) = p_{i+1} - (\sigma + \eta) = ... = p_{i+j} - (\sigma + \eta)$.

Let us take $X = p_k - (\sigma + \eta)$, for a given $k \in [|1, n|]$. Then

- Case 1: if $k < i$,

$$\begin{aligned} Q(p_k - (\sigma + \eta)) \quad &= \quad \eta \frac{p_k}{P_n} \prod_{1 \leq l < k} \overbrace{(p_l - p_k)}^{<0} \prod_{k < l < i} \overbrace{(p_l - p_k)}^{>0} \\ &\quad \times \overbrace{(p_i - p_k)}^{>0}{}^{(j+1)} \times \prod_{i+j < l \leq n} \overbrace{(p_l - p_k)}^{>0}; \\ \operatorname{sgn}\Big(Q(p_k - (\sigma + \eta))\Big) \quad &= \quad (-1)^{(k-1)}. \end{aligned}$$

  So there exists at least one root of Q in each interval $\big]p_k - (\sigma + \eta), p_{k+1} - (\sigma + \eta)\big[$, for $1 \leq k \leq i - 2$, which gives us at least $i - 2$ roots.

- Case 2: if $i \leq k \leq i+j$,

$$\begin{aligned} Q(p_k-(\sigma+\eta)) &= \eta\frac{p_k}{P_n}\prod_{1\leq l<i}\overbrace{(p_l-p_k)}^{<0} \times \overbrace{(p_i-p_k)}^{=0}{}^{j} \times \prod_{i+j<l\leq n}\overbrace{(p_l-p_k)}^{>0} \\ &= 0. \end{aligned}$$

- Case 3: if $i+j<k$,

$$\begin{aligned} Q(p_k-(\sigma+\eta)) &= \eta\frac{p_k}{P_n}\prod_{1\leq l<i}\overbrace{(p_l-p_k)}^{<0} \times \overbrace{(p_i-p_k)}^{<0}{}^{(j+1)} \\ &\quad \times \prod_{i+j<l<k}\overbrace{(p_l-p_k)}^{<0}\prod_{k<l\leq n}\overbrace{(p_l-p_k)}^{>0}; \\ \operatorname{sgn}\Big(Q(p_k-(\sigma+\eta))\Big) &= (-1)^{(k-1)}. \end{aligned}$$

  So there exists at least one root of Q in each interval $\big]p_k-(\sigma+\eta), p_{k+1}-(\sigma+\eta)\big[$, for $i+j+1 \leq k \leq n-1$, which gives us at least $n-(i+j+1)$ roots.

From case 2, we see that $p_i-(\sigma+\eta)$ is a root of Q. Furthermore, if some p_i are equal, we can rewrite $Q(X)$ as:

$$\begin{aligned} Q(X) = & \prod_{1\leq l<i}(p_l-(\sigma+\eta)-X) \times (p_i-(\sigma+\eta)-X)^{(j+1)} \\ & \quad \times \prod_{i+j<l\leq n}(p_l-(\sigma+\eta)-X) \\ & +\eta\sum_{1<l<i}\frac{p_l}{P_n}\prod_{\substack{1\leq h<i \\ h\neq l}}(p_h-(\sigma+\eta)-X) \times (p_i-(\sigma+\eta)-X)^{(j+1)} \\ & \quad \times \prod_{i+j<h\leq n}(p_h-(\sigma+\eta)-X) \\ & +\eta\frac{p_i}{P_n}\sum_{i\leq l\leq i+j}\prod_{1\leq h<i}(p_h-(\sigma+\eta)-X) \times \big(p_i-(\sigma+\eta)-X\big)^{j} \\ & \quad \times \prod_{i+j<h\leq n}(p_h-(\sigma+\eta)-X) \\ & +\eta\sum_{1<l<i}\frac{p_l}{P_n}\prod_{1\leq h<i}(p_h-(\sigma+\eta)-X) \times (p_i-(\sigma+\eta)-X)^{(j+1)} \\ & \quad \times \prod_{\substack{i+j<h\leq n \\ h\neq l}}(p_h-(\sigma+\eta)-X). \end{aligned}$$

This writing easily shows us that the root $p_i - (\sigma + \eta)$ is of multiplicity j.

In addition, we can also see that when taking $X = p_i - (\sigma + \eta) + \epsilon$ we obtain

$$\begin{aligned}
& Q(p_i - (\sigma + \eta) + \epsilon) \\
\underset{\epsilon \to 0}{\sim} \quad & \eta \frac{p_i}{P_n} \sum_{i \leq l \leq i+j} \Bigg[\prod_{1 \leq h < i} (p_h - (\sigma + \eta) - p_i + (\sigma + \eta) - \epsilon) \\
& \qquad \times \big(- \epsilon \big)^j \times \prod_{i+j < h \leq n} (p_h - (\sigma + \eta) - p_i + (\sigma + \eta) - \epsilon) \Bigg] \\
= \quad & \eta \frac{p_i}{P_n} (j+1) \big(- \epsilon \big)^j \prod_{1 \leq h < i} \big(p_h - p_i - \epsilon \big) \prod_{i+j < h \leq n} \big(p_h - p_i - \epsilon \big).
\end{aligned}$$

For ϵ small enough, we can also say that $p_h - p_i - \epsilon < 0$ for $1 \leq h < i$ and $p_h - p_i - \epsilon > 0$ for $i + j < h \leq n$. So we obtain that

$$\begin{aligned}
\operatorname{sgn} \left(\lim_{\substack{\epsilon \to 0 \\ \epsilon < 0}} Q(p_i - (\sigma + \eta) + \epsilon) \right) &= (-1)^{(i-1)}; \\
\operatorname{sgn} \left(\lim_{\substack{\epsilon \to 0 \\ \epsilon > 0}} Q(p_i - (\sigma + \eta) + \epsilon) \right) &= (-1)^{(j+i-1)} \\
&= \operatorname{sgn} \left(\lim_{\substack{\epsilon \to 0 \\ \epsilon > 0}} Q(p_{i+j} - (\sigma + \eta) + \epsilon) \right).
\end{aligned}$$

Since $\operatorname{sgn}\Big(Q(p_{i-1} - (\sigma + \eta)) \Big) = (-1)^{(i-2)}$ from the case 1, (respectively $\operatorname{sgn}\Big(Q(p_{i+j+1} - (\sigma + \eta)) \Big) = (-1)^{(i+j)}$ from the case 3), we find that there is at least one root of Q in $\big] p_{i-1} - (\sigma + \eta), p_i - (\sigma + \eta) \big[$ (respectively, in $\big] p_{i+j} - (\sigma + \eta), p_{i+j+1} - (\sigma + \eta) \big[$).

And finally, for the same reason as previously (case with no equality between p_i), there exists at least one root of Q in $\big] p_n - (\sigma + \eta), +\infty \big[$.

Taking into account the multiplicity of the root $p_i - (\sigma + \eta)$, we found at least n roots, and since Q is a polynomial of degree n, we can conclude that each of these intervals contains exactly one root.

□

C.2 Proof of Lemma 9

Proof of Proof of Lemma 9.

We suppose $\max\limits_{i\in[|1,n|]} p_i - (\sigma+\eta) < 0$. So $p_i - (\sigma+\eta) < 0$ for all i. We also have:

$$\begin{aligned} Q(0) &= \prod_i^n (p_i - (\sigma+\eta)) + \eta \sum_{i=1}^n \frac{p_i}{P_n} \prod_{j\neq i}^n (p_j - (\sigma+\eta)) \\ &= \prod_i^n \underbrace{\Big(p_i - (\sigma+\eta)\Big)}_{<0} \left[1 + \sum_l^n \frac{\eta p_l/P_n}{p_l - (\sigma+\eta)}\right]. \end{aligned}$$

So

$$\begin{aligned} & \operatorname{sgn}\big(Q(0)\big) = (-1)^{n+1} = (-1)^{n-1} = \operatorname{sgn}\left(Q\left(\max_{i\in[|1,n|]} p_i - (\sigma+\eta)\right)\right) \\ \iff \quad & \sum_l^n \frac{\eta p_l/P_n}{p_l - (\sigma+\eta)} < -1, \end{aligned}$$

and

$$\begin{aligned} & \operatorname{sgn}\big(Q(0)\big) = \operatorname{sgn}\left(Q\left(\max_{i\in[|1,n|]} p_i - (\sigma+\eta)\right)\right) \\ \iff \quad & \text{there is no root in } \Big]\max_{i\in[|1,n|]} p_i - (\sigma+\eta),\ 0\Big[\\ \iff \quad & \text{the biggest root of } Q \text{ is positive.} \end{aligned}$$

□

C.3 Proof of Proposition 10

Proof of Proposition 10.

Due to the previous lemmas, it is trivial to see that if $\max\limits_{i\in[|1,n|]} p_i - (\sigma+\eta) > 0$ then the biggest root of Q, which is also the biggest eigenvalue of $J_{(0,\ldots,0)}$ is positive. Suppose now that $\max\limits_{i\in[|1,n|]} p_i - (\sigma+\eta) < 0$.

- First, we suppose $\max\limits_{i\in[|1,n|]} p_i - \sigma < 0$.

Then for all l, we have $\sigma + \eta - p_l > \eta$, meaning

$$\forall\, l,\ \frac{p_l/P_n}{\sigma+\eta-p_l} \quad < \quad \frac{p_l/P_n}{\eta}$$

and

$$\eta \sum_{l=1}^{n} \frac{p_l/P_n}{\sigma + \eta - p_l} \;<\; 1.$$

So the biggest eigenvalue of $J_{(0,\ldots,0)}$ is negative, and the equilibrium $(0, \ldots, 0)$ is stable.

- On the other hand, let us assume $\min i \in [|1, n|] p_i - \sigma > 0$.

Then for all l, we have $\sigma + \eta - p_l < \eta$, meaning

$$\forall\, l,\ \frac{p_l/P_n}{\sigma + \eta - p_l} > \frac{p_l/P_n}{\eta}$$

and

$$\eta \sum_{l=1}^{n} \frac{p_l/P_n}{\sigma + \eta - p_l} > 1.$$

So the biggest eigenvalue of $J_{(0,\ldots,0)}$ is positive, and the equilibrium $(0, \ldots, 0)$ is unstable. □

C.4 Proof of Proposition 11

Proof of Proposition 11.

The Jacobian of the system is

$$J_{(x_i^*, y_i^*)} \;=\; \begin{pmatrix} P_1 - \sigma_N - 2x^* - y^* & -x^* \\ & \\ -\omega y^* & \omega\big[P_1 - (\sigma_A + \eta_0) - x^* - 2y^*\big] \end{pmatrix}.$$

Furthermore, when $x^* = 0$, we have the equation

$$-y^{*2} + \Big(P_1 - (\sigma_A + \eta_0)\Big) y^* + \zeta \;=\; 0. \tag{C.1}$$

Finding the y^* satisfying this equation comes back to finding the roots of a concave parabola in term of y^*. Since this parabola reaches $\zeta \geq 0$ for $y^* = 0$, there is always a unique positive solution.

For the stability of the then uniquely defined equilibrium $(0, y^*)$, we look at the Jacobian matrix

$$J_{(0,y^*)} \;=\; \begin{pmatrix} P_1 - \sigma_N - y^* & 0 \\ & \\ -\omega y^* & \omega\big[P_1 - (\sigma_A + \eta_0) - 2y^*\big] \end{pmatrix}.$$

Eigenvalues are on the diagonal, and for the bottom right value, by using equation(C.1), we can say (since we consider $y^* \neq 0$):

$$\omega\big[P_1 - (\sigma_A + \eta_0) - 2y^*\big] \;=\; -\omega\left[\frac{\zeta}{y^*} + y^*\right] \;<\; 0 \text{ always.}$$

So instability of the equilibrium can only come from

$$\mu \;:=\; P_1 - \sigma_N - y^*.$$

Let us note that

$$\mu \;>\; 0 \quad\Longleftrightarrow\quad y^* \;<\; P_1 - \sigma_N \;=:\; X.$$

To characterize this equation, we look again at the parabola defining y^*, which is the equation (C.1). $y^* < X$ is equivalent to X being on the right side of the positive root of this parabola. To do so is the same as the two following conditions. X is positive; and we want the parabola to be negative at axis X.

The former gives us

$$X > 0 \quad\Longleftrightarrow\quad \sigma_N < P_1$$

As for the latter, it gives us:

$$\begin{aligned} & -(P_1 - \sigma_N)^2 + \Big(P_1 - (\sigma_A + \eta_0)\Big)(P_1 - \sigma_N) + \zeta \;<\; 0 \\ \Longleftrightarrow\quad & \zeta \;<\; (P_1 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N). \end{aligned}$$

All in all, we have that

$$\mu \;>\; 0 \quad\Longleftrightarrow\quad \sigma_N \;<\; P_1 \;\text{ and }\; \zeta < (P_1 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N)$$

□

C.5 Proof of Proposition 12

Proof of Proposition 12.

We prove the existence and unicity of $(0, y_i^*)$ in the same way as before. For a hard fragmentation with invaders, the Jacobian of the system in any given patch i is

$$J_{(x_i^*, y_i^*)} \;=\; \begin{pmatrix} p_i - \sigma_N - 2x_i^* - y_i^* & -x_i^* \\ -\omega y_i^* & \omega\big[p_i - (\sigma_A + \eta_0) - x_i^* - 2y_i^*\big] \end{pmatrix}.$$

Furthermore, when $x_i^* = 0$, we have the equation

$$-y_i^{*2} + \Big(p_i - (\sigma_A + \eta_0)\Big) y_i^* + p_i \frac{\zeta}{P_n} \;=\; 0. \tag{C.2}$$

Since this parabola reaches $p_i\zeta/P_n \geq 0$ for $y_i^* = 0$, then there is always a unique positive solution.

For the stability of the then uniquely defined equilibrium $(0, y_i^*)$, we look at the Jacobian matrix:

$$J_{(0,y_i^*)} \;=\; \begin{pmatrix} p_i - \sigma_N - y_i^* & 0 \\ & \\ -\omega y_i^* & \omega\big[p_i - (\sigma_A + \eta_0) - 2y_i^*\big] \end{pmatrix}.$$

Eigenvalues are on the diagonal, and for the bottom right value, by using equation (C.2), we can say (since we consider $y_i^* \neq 0$) that

$$\omega\big[p_i - (\sigma_A + \eta_0) - 2y_i^*\big] \;=\; \omega\left[-\frac{p_i\zeta}{P_n y_i^*} - y_i^*\right] \;<\; 0 \text{ always.}$$

So instability of the equilibrium can only come from

$$\mu_i \;:=\; p_i - \sigma_N - y_i^*.$$

The same analysis as for the Proof of Proposition 11 gives us the same first condition for $X_i = p_i - \sigma_N$:

$$X_i > 0 \quad\Longleftrightarrow\quad p_i > \sigma_N,$$

and we have this time

$$\mu_i > 0 \quad\Longleftrightarrow\quad p_i > \sigma_N \quad \text{and} \quad p_i\frac{\zeta}{P_n} < (p_i - \sigma_N)(\sigma_A + \eta_0 - \sigma_N).$$

We can see from this result that if $\sigma_A + \eta_0 - \sigma_N < 0$ then $\mu_i < 0$. Also,

$$\begin{aligned} & p_i\frac{\zeta}{P_n} \;<\; (p_i - \sigma_N)(\sigma_A + \eta_0 - \sigma_N) \\ \Longleftrightarrow\quad & p_i(\sigma_A + \eta_0 - \sigma_N - \frac{\zeta}{P_n}) \;>\; \sigma_N(\sigma_A + \eta_0 - \sigma_N). \end{aligned}$$

□

C.6 Proof of Proposition 13

Proof of Proposition 13.

Let us look at y_i^* as a function of p_i. From the equation (C.2) we obtain that for $p_i = 0$ we have:

$$-\big(y_i^*(0)\big)^2 - (\sigma_A + \eta_0) y_i^*(0) = 0$$

$$\iff \quad \left\{ \begin{array}{lcl} y_i^*(0) & = & 0, \\ \text{or} & & \\ y_i^*(0) & = & -(\sigma_A + \eta_0) \ < 0 \text{ , impossible in our case.} \end{array} \right.$$

So $y_i^*(0) = 0$.

By differentiating depending on p_i the equation (C.2), we obtain:

$$(y_i^*)'(p_i)\big[-2y_i^*(p_i) + p_i - (\sigma_A + \eta_0)\big] \quad = \quad -\zeta \, \frac{P_n(p_i) - p_i}{P_n(p_i)^2} - y_i^*(p_i). \quad \text{(C.3)}$$

Knowing that

$$(y_i^*)'(p_i) = 0 \quad \Longrightarrow \quad \zeta \frac{P_n(p_i) - p_i}{P_n(p_i)^2} = -y_i^*(p_i),$$

$$\text{impossible since } y_i^*(p_i) \geq 0,\ \zeta > 0,\ \frac{P_n(p_i) - p_i}{P_n(p_i)^2} > 0$$

so $(y_i^*)'(pi)$ is always of the same sign, and

$$(y_i^*)'(0) \quad = \quad \frac{\zeta}{(\sigma_A + \eta_0) \sum_{j \neq i} p_j} > 0.$$

So, for all p_i, $(y_i^*)'(p_i) > 0$. Then $y_i^*(p_i)$ increases strictly monotonically, starting from 0 for $p_i = 0$. □

C.7 Proof of Proposition 14

Proof of Proposition 14.

For the growth of $\mu_i(p_i)$ we have

$$\mu_i(p_i) \quad = \quad p_i - \sigma_N - y_i^*(p_i),$$

so

$$\mu_i'(p_i) = 1 - (y_i^*)'(p_i) = 0 \quad \iff \quad (y_i^*)'(p_i) = 1.$$

Let us first suppose that there exists $\hat{p}_i > 0$ such that $(y_i^*)'(\hat{p}_i) = 1$. By replacing $(y_i^*)'(\hat{p}_i) = 1$ in (C.3), we obtain

$$\hat{p}_i - (\sigma_A + \eta_0) \;=\; y_i^*(\hat{p}_i) - \zeta\, \frac{P_n(\hat{p}_i) - \hat{p}_i}{P_n(\hat{p}_i)^2}.$$

Combining with (C.2) we obtain

$$y_i^*(\hat{p}_i) \;=\; \frac{\hat{p}_i P_n(\hat{p}_i)}{P_n(\hat{p}_i) - \hat{p}_i}$$

which, when inserted back into the previous equation gives us

$$\begin{aligned} P_n(\hat{p}_i)^2\big(\hat{p}_i - (\sigma_A + \eta_0)\big) \;&=\; \frac{\hat{p}_i P_n(\hat{p}_i)^3}{P_n(\hat{p}_i) - \hat{p}_i} - \zeta\big(P_n(\hat{p}_i) - \hat{p}_i\big) \\ \iff \quad f(\hat{p}_i) \;:=\; -\left(\hat{p}_i + \sum_{j\neq i} p_j\right)^2 &\left(\sigma_A + \eta_0 + \frac{\hat{p}_i^{\,2}}{\sum_{j\neq i} p_j}\right) + \zeta \sum_{j\neq i} p_j \;=\; 0. \end{aligned}$$

If we now assume that there exists $p_i > 0$ such that $f(\hat{p}_i) = 0$, then equation (C.2) becomes:

$$-y_i^*(\hat{p}_i)^2 + y_i^*(\hat{p}_i)\left(\frac{\hat{p}_i P_n(\hat{p}_i)}{P_n(\hat{p}_i) - \hat{p}_i} - \zeta \frac{P_n(\hat{p}_i) - \hat{p}_i}{P_n(\hat{p}_i)^2}\right) + \zeta \frac{\hat{p}_i}{P_n(\hat{p}_i)} \;=\; 0,$$

and with the relation between roots and coefficient we obtain $y_i^*(\hat{p}_i) = \dfrac{\hat{p}_i P_n(\hat{p}_i)}{P_n(\hat{p}_i) - \hat{p}_i}$. Furthermore, equation (C.3) becomes

$$(y_i^*)'(\hat{p}_i)\left(\frac{\hat{p}_i P_n(\hat{p}_i)}{P_n(\hat{p}_i) - \hat{p}_i} - y_i^*(\hat{p}_i)\right) - \Big((y_i^*)'(\hat{p}_i) - 1\Big)\left(\zeta \frac{P_n(\hat{p}_i) - \hat{p}_i}{P_n(\hat{p}_i)^2} + y_i^*(\hat{p}_i)\right) \;=\; 0.$$

After replacing y_i^* by the value we found, we obtain:

$$\Big((y_i^*)'(\hat{p}_i) - 1\Big)\underbrace{\left(\zeta \frac{P_n(\hat{p}_i) - \hat{p}_i}{P_n(\hat{p}_i)^2} + \frac{\hat{p}_i P_n(\hat{p}_i)}{P_n(\hat{p}_i) - \hat{p}_i}\right)}_{>0} \;=\; 0,$$

so $(y_i^*)'(\hat{p}_i) = 1$. All in all,

$$(y_i^*)'(\hat{p}_i) = 1 \iff f(\hat{p}_i) = 0$$

For the behavior of the function $f(p_i)$, we have that

$$f'(p_i) = -2\left(p_i + \sum_{j\neq i} p_j\right)^2 \left(\sigma_A + \eta_0 + 2\frac{p_i^2}{\sum_{j\neq i} p_j} + p_i\right), < 0 \quad \forall p_i > 0,$$

and

$$f(0) = \left(\zeta - (\sigma_A + \eta_0) \sum_{j \neq i} p_j\right) \sum_{j \neq i} p_j.$$

Since $f(p_i)$ is strictly monotonically decreasing, there exists a $\hat{p}_i > 0$ such that $f(\hat{p}_i) = 0$ if and only if $f(0) > 0$. If it exists, it is unique.

To sum up:

1) If $\zeta < (\sigma_A + \eta_0) \sum_{j \neq i} p_j$ then there is no $\hat{p}_i > 0$ such that $(y_i^*)'(\hat{p}_i) = 1$.

2) If $\zeta > (\sigma_A + \eta_0) \sum_{j \neq i} p_j$ then there is exactly one $\hat{p}_i > 0$ such that $(y_i^*)'(\hat{p}_i) = 1$.

We also have

$$\begin{array}{rcl} \mu_i(0) & = & -\sigma_N < 0; \\ \mu_i'(0) & = & \dfrac{(\sigma_A + \eta_0) \sum_{j \neq i} p_j - \zeta}{(\sigma_A + \eta_0) \sum_{j \neq i} p_j}. \end{array}$$

So in the first case, $\mu_i'(0) > 0$ and $\mu_i'(p_i) > 0 \, \forall p_i \leq 0$. In the second case $\mu_i'(0) < 0$, so the local extremum that exists can only be a local minimum. All in all, we have:

- If $\zeta < (\sigma_A + \eta_0) \sum_{j \neq i} p_j$ then $\mu_i(p_i)$ strictly increases monotonically.
- If $\zeta > (\sigma_A + \eta_0) \sum_{j \neq i} p_j$ then there exists a $\hat{p}_i$ such that $\mu_i(p_i)$ strictly increases monotonically for all $p_i > \hat{p}_i$, and $\mu_i(p_i) < 0$ for all $p_i < \hat{p}_i$.

□

C.8 Proof of Proposition 15

Proof of Proposition 15.

We are looking for the equilibrium $(0, y_1^*, 0, y_2^*, ..., 0, y_n^*)$ in the system:

$$\left\{ \begin{array}{rcl} \dfrac{dx_i}{d\tilde{t}} & = & (p_i - \sigma_N - x_i - y_i)\, x_i - \eta_N x_i + \dfrac{p_i}{P_n} \eta_N \displaystyle\sum_j x_j; \\ \dfrac{dy_i}{d\tilde{t}} & = & \omega \left[(p_i - \sigma_A - x_i - y_i)\, y_i - \eta_0 y_i + \zeta \dfrac{p_i}{P_n} - \eta_A y_i + \dfrac{p_i}{P_n} \eta_A \displaystyle\sum_j y_j \right]. \end{array} \right.$$

When $x_i^* = 0 \; \forall i$, we have:

$$-y_i^{*2} + y_i^* \left[p_i \left(1 + \frac{\eta_A}{P_n} \right) - (\sigma_A + \eta_0 + \eta_A) \right] + \frac{p_i}{P_n} \left(\eta_A \sum_{j \neq i} y_j^* + \zeta \right) = 0.$$

This is a concave parabola in term of y_i^*, positive at the origin, so a positive solution for y_i^* exists.

Suppose that there are $(0, y_1^*, 0, y_2^*, ..., 0, y_n^*)$ and $(0, \bar{y}_1^*, 0, \bar{y}_2^*, ..., 0, \bar{y}_n^*)$. By definition we have

$$\begin{aligned} \big(p_l - (\sigma_A + \eta_0 + \eta_A) - y_l^*\big) y_l^* + \zeta \frac{p_l}{P_n} + \frac{p_l}{P_n} \eta_A \sum_j y_j^* &= 0; \\ \big(p_l - (\sigma_A + \eta_0 + \eta_A) - \bar{y}_l^*\big) \bar{y}_l^* + \zeta \frac{p_l}{P_n} + \frac{p_l}{P_n} \eta_A \sum_j \bar{y}_j^* &= 0, \end{aligned}$$

which gives us

$$\big(p_l - (\sigma_A + \eta_0 + \eta_A) - (y_l^* + \bar{y}_l^*)\big)(y_l^* - \bar{y}_l^*) + \frac{p_l}{P_n} \eta_A \sum_j (y_j^* - \bar{y}_l^*) = 0.$$

Since

$$\big(p_l - (\sigma_A + \eta_0 - \eta_A) - y_l^*\big) y_l^* = -\zeta \frac{p_l}{P_n} - \frac{p_l}{P_n} \eta_A \sum_j y_j^* < 0,$$

then

$$\big(p_l - (\sigma_A + \eta_0 + \eta_A) - (\bar{y}_l^* + y_l^*)\big) < \big(p_l - (\sigma_A + \eta_0 + \eta_A) - y_l^*\big) < 0, \; \forall l.$$

Furthermore

$$\forall l, \; \underbrace{\big(p_l - (\sigma_A + \eta_0 + \eta_A) - (y_l^* + \bar{y}_l^*)\big)}_{<0} (y_l^* - \bar{y}_l^*) = -\frac{p_l}{P_n} \eta_A \sum_j (y_j^* - \bar{y}_l^*),$$

which gives us

$$\forall l, \; \mathrm{sgn}(y_l^* - \bar{y}_l^*) = (-1) \times \mathrm{sgn} \left(\sum_j (y_j^* - \bar{y}_l^*) \right).$$

However, the sign of $\sum_j (y_j^* - \bar{y}_l^*)$ does not depend on l, so the sign of $(y_j^* - \bar{y}_l^*)$ is the same for all l. The only possibility to solve this equation is $y_j^* = \bar{y}_l^*, \forall l$. This proves the unicity of the solution. □

C.9 Proof of Lemma 16

Proof of Lemma 16.

Let us call $D_i(x_i^*, y_i^*)$ the 2 by 2 matrix

$$\begin{pmatrix} p_i(1+\eta_N/P_n) - (\sigma_N+\eta_N) & -x_i^* \\ -2x_i^* - y_i^* & \\ & \\ -\omega y_i^* & \omega\Big[p_i(1+\eta_A/P_n) - (\sigma_A+\eta_0+\eta_A) \\ & -x_i^* - 2y_i^*\Big] \end{pmatrix}$$

and

$$M_i \quad := \quad \begin{pmatrix} p_i\eta_N/P_n & 0 \\ 0 & \omega p_i \eta_A/P_n \end{pmatrix}.$$

Then we have

$$J_{(x_1^*,y_1^*,\dots,x_n^*,y_n^*)} \quad = \quad \begin{pmatrix} D_1(x_1^*,y_1^*) & M_1 & M_1 & \dots & M_1 \\ M_2 & D_2(x_2^*,y_2^*) & M_2 & \dots & M_2 \\ \dots & \dots & \dots & \dots & M_2 \\ M_n & M_n & M_n & \dots & D_n(x_n^*,y_n^*) \end{pmatrix},$$

which is a $2n \times 2n$ matrix. It can be rewritten

$$\begin{aligned} J_{(x_1^*,y_1^*,\dots,x_n^*,y_n^*)} \quad &= \quad \mathrm{Diag}\left(D_i(x_i^*,y_i^*) - M_i\right) + \begin{pmatrix} M_1 & \dots & M_1 \\ M_2 & \dots & M_2 \\ \dots & \dots & \dots \\ M_n & \dots & M_n \end{pmatrix} \\ &= \quad \mathrm{Diag}\left(D_i(x_i^*,y_i^*) - M_i\right) + \begin{pmatrix} M_1 \\ M_2 \\ \dots \\ M_n \end{pmatrix} \begin{pmatrix} I_2 \\ I_2 \\ \dots \\ I_2 \end{pmatrix}^T, \quad \text{with } I_2 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}. \end{aligned}$$

We are studying the stability of $(0, y_1^*, \dots, 0, y_n^*)$, so we will look at $J_{(0,y_1^*,\dots,0,y_n^*)}$. Let us call

$$\begin{aligned} B(X) \quad &:= \quad \det(J_{(0,y_1^*,\dots,0,y_n^*)} - X \times I_{2n}) \\ &= \quad \det\left[\mathrm{Diag}\Big(D_i(0,y_i^*) - M_i - X * I_2\Big) + \begin{pmatrix} M_1 \\ M_2 \\ \dots \\ M_n \end{pmatrix} \begin{pmatrix} I_2 \\ I_2 \\ \dots \\ I_2 \end{pmatrix}^T\right]. \end{aligned}$$

$\mathrm{Diag}\Big(D_i(0,y_i^*) - M_i - X\times I_2\Big)$ is lower triangular so its eigenvalues are on its diagonal, and it is non-invertible if and only if at least one of them is 0. Let us then call Λ the set:

$$\Big\{p_i - (\sigma_N+\eta_N) - y_i^*, i\in[|1,n|]\Big\} \cup \Big\{\omega\left[p_i - (\sigma_A+\eta_0+\eta_A) - 2y_i^*\right], i\in[|1,n|]\Big\}.$$

We take $X\in\mathbb{R}\backslash\Lambda$. This way, $\mathrm{Diag}\Big(D_i(0,y_i^*) - M_i - X\times I_2\Big)$ is invertible, and a generalized version of the lemma C.1 (Matrix determinant lemma) gives us that

$$\begin{aligned} B(X) &= \det\left[I_2 + \begin{pmatrix} I_2\\ I_2\\ ...\\ I_2\end{pmatrix}^T \Big(\mathrm{Diag}\Big(D_i(0,y_i^*) - M_i - X\times I_2\Big)\Big)^{-1}\begin{pmatrix} M_1\\ M_2\\ ...\\ M_n\end{pmatrix}\right] \\ &\quad\times\det\Big(\mathrm{Diag}\Big(D_i(0,y_i^*) - M_i - X\times I_2\Big)\Big). \end{aligned}$$

Since

$$\begin{aligned} &\Big(D_i(0,y_i^*) - M_i - X\times I_2\Big)^{-1} M_i \\ =& \begin{pmatrix} \dfrac{p_i\eta_N/P_n}{p_i - (\sigma_N+\eta_N) - y_i^* - X} & 0 \\ ... & \dfrac{\omega p_i\eta_A/P_n}{\omega\big[p_i - (\sigma_A+\eta_0+\eta_A) - 2y_i^*\big] - X}\end{pmatrix}, \end{aligned}$$

then

$$I_2 + \begin{pmatrix} I_2\\ I_2\\ ...\\ I_2\end{pmatrix}^T \Big(\mathrm{Diag}\Big(D_i(0,y_i^*) - M_i - X\times I_2\Big)\Big)^{-1}\begin{pmatrix} M_1\\ M_2\\ ...\\ M_n\end{pmatrix}$$

is equal to

$$\begin{pmatrix} 1+\displaystyle\sum_{i=1}^n \frac{p_i\eta_N/P_n}{p_i - (\sigma_N+\eta_N) - y_i^* - X} & 0 \\ ... & 1+\displaystyle\sum_{i=1}^n \frac{\omega p_i\eta_A/P_n}{\omega\big[p_i - (\sigma_A+\eta_0+\eta_A) - 2y_i^*\big] - X}\end{pmatrix}.$$

So for $X \in \mathbf{R}\backslash\Lambda$ we have

$$\begin{aligned}
B(X) &= \left(1+\sum_{i=1}^{n}\frac{p_i\eta_N/P_n}{p_i-(\sigma_N+\eta_N)-y_i^*-X}\right)\\
&\quad\times\left(1+\sum_{i=1}^{n}\frac{\omega p_i\eta_A/P_n}{\omega\big[p_i-(\sigma_A+\eta_0+\eta_A)-2y_i^*\big]-X}\right)\\
&\quad\times\prod_{i=1}^{n}\Big(p_i-(\sigma_N+\eta_N)-y_i^*-X\Big)\Big(\omega\big[p_i-(\sigma_A+\eta_0+\eta_A)-2y_i^*\big]-X\Big)\\
&= \Phi(X)\times\Psi(X).
\end{aligned}$$

By continuity of a polynomial, and since Λ is a discrete space, this result stands true for $X \in \mathbb{R}$.

Let us now first order the indices such that $p_1-y_1^* \leq p_2-y_2^* \leq \dots \leq p_n-y_n^*$. A similar analysis as the proof of the lemma 8, but taking $X = p_k-(\sigma_N+\eta_N)-y_k^*$, for a given $k \in [|1,n|]$, gives us a similar result for $\Phi(X)$. Φ has exactly one root in each interval $\big]p_k-(\sigma_N+\eta_N)-y_k^*, p_{k+1}-(\sigma_N+\eta_N)-y_{k+1}^*\big[$, for $1 \leq k \leq n-1$, and exactly one root in $\big]p_n-(\sigma_N+\eta_N)-y_n^*, +\infty\big[$. Those are all the roots of Φ. If there exist some indices $i, j\ in[|1,n|], i+j \leq n$ such that $p_i-y_i^* = \dots = p_{i+j}-y_{i+j}$, then $p_i-(\sigma_N+\eta_N)-y_i$ is a root of Φ, of multiplicity j.

Furthermore, if we suppose that there are two indices l, h such that $p_l = p_h$, the corresponding y_l^* and y_h^* are respectively given by

$$\begin{aligned}
\left(p_l-(\sigma_A+\eta_0+\eta_A)-y_l^*\right)y_l^*+\frac{p_l}{P_n}\left(\zeta+\eta_A\sum_j y_j^*\right) &= 0;\\
\left(p_h-(\sigma_A+\eta_0+\eta_A)-y_h^*\right)y_h^*+\frac{p_h}{P_n}\left(\zeta+\eta_A\sum_j y_j^*\right) &= 0.
\end{aligned}$$

We can easily see that $p_l = p_h \iff y_l^* = y_h^*$ (equivalence coming from uniqueness of y_l^* and y_h^*). So, we can rewrite the last part: If there exist some indices $i, j\ in[|1,n|], i+j \leq n$ such that $p_i = \dots = p_{i+j}$, then $p_i-(\sigma_N+\eta_N)-y_i$ is a root of Φ, of multiplicity j.

Once again a similar analysis for Ψ, this time supposing that the indices are such that $p_1-2y_1^* \leq p_2-2y_2^* \leq \dots \leq p_n-2y_n^*$, and taking $X = p_k-(\sigma_A+\eta_A+\eta_0)-2y_k^*$, for a given $k \in [|1,n|]$ gives us the following result. Ψ has exactly one root in each interval $\big]p_k-(\sigma_A+\eta_A+\eta_0)-2y_k^*, p_{k+1}-(\sigma_A+\eta_A+\eta_0)-2y_{k+1}^*\big[$, for $1 \leq k \leq n-1$, and exactly one root in $\big]p_n-(\sigma_A+\eta_A+\eta_0)-2y_n^*, +\infty\big[$. Those are all the roots of Ψ. Suppose that there exist some indices $i, j \ in[|1,n|], i+j \leq n$ such that $p_i = ... = p_{i+j}$, then $p_i - (\sigma_A + \eta_A + \eta_0) - 2y_i$ is a root of Ψ, of multiplicity j. However, here we can further notice that

$$\begin{aligned}\Psi(0) &= \omega^n \left(\prod_{i=1}^{n} \Big(p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^* \Big) \right. \\ &\quad \left. + \eta_A \sum_{i=1}^{n} \frac{p_i}{P_n} \prod_{j \neq i}^{n} \Big(p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^* \Big) \right),\end{aligned}$$

and

$$\begin{aligned}(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*) &= -\frac{p_i}{y_i^* P_n} \left(\zeta + \eta_A \sum_l y_l^* \right) \quad \text{(exists since } y_i^* \neq 0 \, \forall i) \\ &< 0 \quad (\text{since } p_i > 0 \, \forall i, \ \zeta > 0),\end{aligned}$$

so

$$\begin{aligned}\Psi(0) &= \omega^n \prod_{i=1}^{n} \Big(\underbrace{p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*}_{<0} \Big) \\ &\quad \times \left(1 + \eta_A \sum_{j=1}^{n} \frac{p_j / P_n}{p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*} \right).\end{aligned}$$

Furthermore,

$$\begin{aligned}\sum_{j=1}^{n} \frac{p_j / P_n}{p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*} &= \sum_{j=1}^{n} \frac{-y_j^*}{\zeta + \eta_A \sum_l y_l^* + y_j^{*2} P_n / p_j} \\ &> \sum_{j=1}^{n} \frac{-y_j^*}{\eta_A \sum_l y_l^*} = -\frac{1}{\eta_A},\end{aligned}$$

so

$$1 + \eta_A \sum_{j=1}^{n} \frac{p_j / P_n}{p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*} > 0,$$

and

$$\operatorname{sgn}\Big(\Psi(0)\Big) = (-1)^n.$$

Since we also have that

$$\operatorname{sgn}\Big(\Psi\big(p_n - (\sigma_A + \eta_A + \eta_0) - 2y_n^*\big)\Big) = (-1)^{n-1}$$

then the biggest root of Ψ is actually in the interval $]p_n - (\sigma_A + \eta_A + \eta_0) - 2y_n^*, \ 0[$ and all the roots of Ψ are real and negative. □

C.10 Proof of Lemma 17

Proof of Lemma 17. Let us call

$$f_i(X) \quad := \quad -X^2 + X\left(p_i - (\sigma_A + \eta_0 + \eta_A)\right) + \frac{p_i}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right), \quad \text{defined on } \mathbb{R}_+.$$

Then

$$f_i(X) - f_k(X) \quad = \quad (p_i - p_k)\left(X + \frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right)\right),$$

so

$$\forall X \geq 0,\ \operatorname{sgn}\big(f_i(X) - f_k(X)\big) \quad = \quad \operatorname{sgn}(p_i - p_k).$$

Since f_i is part of a concave parabola with $f_i(0) > 0$, $f_i(X) = 0 \iff X = y_i^*$.

If $p_i > p_k$, then $f_i(y_k^*) > f_k(y_k^*) = 0$ and since f_i is part of a concave parabola with $f_i(0) > 0$, it means that f_i has not yet reached its 0. So $y_i^* > y_k^*$. If $y_i^* > y_k^*$, then $f_i(y_i^*) = 0$ and $f_i(y_i^*) < f_i(y_k^*)$. Since $f_k(y_k^*) = 0 = f_i(y_i^*)$, we have $f_k(y_k^*) < f_i(y_k^*)$, so $p_i > p_k$. All in all,

$$p_i > p_k \quad \iff \quad y_i^* > y_k^*.$$

Furthermore,

$$\begin{aligned} y_i^* > p_i \quad &\iff \quad f_i(p_i) > 0 \\ &\iff \quad \zeta + \eta_A \sum_l y_l^* > P_n(\sigma_A + \eta_0 + \eta_A). \end{aligned}$$

However, this last conditions does not depend on the index i, and as such

$$\zeta + \eta_A \sum_l y_l^* > P_n(\sigma_A + \eta_0 + \eta_A) \iff \exists i,\ y_i^* > p_i \iff \forall i,\ y_i^* > p_i.$$

To that, we can add one more: suppose $\forall i,\ y_i^* > p_i$ then $\sum y_i^* > \sum p_i$. Suppose $\sum y_i^* > \sum p_i$. Then $y_i^* < p_i$ for all i is impossible, and $\exists i,\ y_i^* > p_i$, so $\forall i,\ y_i^* > p_i$. Then we can write

$$\exists i,\ y_i^* > p_i \iff \forall i,\ y_i^* > p_i \iff \sum_{l=1}^n y_l^* > \sum_{l=1}^n p_l.$$

The same work gives us

$$\begin{aligned} y_i^* = p_i &\iff f_i(p_i) = 0 \\ \text{(since } p_i = y_i^* > 0) &\iff \zeta + \eta_A \sum_l y_l^* = P_n(\sigma_A + \eta_0 + \eta_A), \end{aligned}$$

and

$$\zeta + \eta_A \sum_l y_l^* = P_n(\sigma_A + \eta_0 + \eta_A) \iff \sum_{l=1}^n y_l^* = \sum_{l=1}^n p_l.$$

All in all we have the equality case:

$$\zeta = P_n(\sigma_A + \eta_0) \iff \exists i,\ y_i^* = p_i \iff \forall i,\ y_i^* = p_i \iff \sum_{l=1}^n y_l^* = \sum_{l=1}^n p_l.$$

Suppose now that there exists an i such that $p_i < y_i^*$. Then it is true for all i, and

$$-\frac{p_i}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right) = \left(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*\right) y_i^* \quad < \quad -(\sigma_A + \eta_0 + \eta_A) y_i^*.$$

Taking the sum we obtain

$$\left(\zeta + \eta_A \sum_l y_l^*\right) \quad > \quad (\sigma_A + \eta_0 + \eta_A) \sum_l y_l^*,$$

and since $P_n < \sum_i y_i^*$,

$$\zeta \quad > \quad (\sigma_A + \eta_0 +) P_n.$$

Suppose now that $\zeta > (\sigma_A + \eta_0) P_n$. Then since

$$\sum_l (p_l - (\sigma_A + \eta_0) - y_l^*) y_l^* = -\zeta$$

we have

$$\begin{aligned} & \sum_l (p_l - y_l^*) y_l^* - (\sigma_A + \eta_0) \sum_l y_l^* \quad < \quad -(\sigma_A + \eta_0) P_n \\ \iff & \sum_l (p_l - y_l^*) y_l^* + (\sigma_A + \eta_0) \left(P_n - \sum_l y_l^*\right) \quad < \quad 0. \end{aligned}$$

Either $P_n < \sum_l y_l^*$, or $\sum_l (p_l - y_l^*) y_l^* < 0$, meaning in both cases that there exists an index i such that $p_i < y_i^*$.

Finally, let us prove that if $\zeta < P_n(\sigma_A + \eta_0)$ then $p_i > p_k \implies p_i - y_i^* > p_k - y_k^*$. We have $\zeta < P_n(\sigma_A + \eta_0)$ and we suppose $p_i > p_k$. From the defining equations of y_i^* we have that for any i, k,

$$\begin{aligned}\Big(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*\Big)\frac{y_i^*}{p_i} &= -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right) \\ &= \Big(p_k - (\sigma_A + \eta_0 + \eta_A) - y_k^*\Big)\frac{y_k^*}{p_k},\end{aligned}$$

and since $p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^* < 0$ (same with k), we have

$$\begin{aligned} & p_i - y_i^* > p_k - y_k^* \\ \iff & p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^* > p_k - (\sigma_A + \eta_0 + \eta_A) - y_k^* \\ \iff & \frac{y_i^*}{p_i} > \frac{y_k^*}{p_k}.\end{aligned}$$

Let us suppose $p_i - y_i^* < p_k - y_k^*$. Since $\zeta < P_n(\sigma_A + \eta_0)$, then $p_i - y_i^* > 0$, $p_k - y_k^* > 0$, so

$$(p_i - y_i^*) y_k^* \quad < \quad (p_k - y_k) y_k^*.$$

Since $p_i > p_k$, we have furthermore $y_i^* > y_k^*$ and

$$(p_i - y_i^*) y_k^* \quad < \quad (p_k - y_k) y_k^* \quad < \quad (p_k - y_k) y_i^*,$$

so

$$p_i y_k^* - y_i^* y_k^* \;\; < \;\; p_k y_i^* - y_k y_i^*.$$

It means that

$$\frac{y_i^*}{p_i} \; > \; \frac{y_k^*}{p_k},$$

which is not compatible with our assumption $p_i - y_i^* < p_k - y_k^*$. This assumption is then wrong, so in the end we have $p_i - y_i^* > p_k - y_k^*$ (the equality case is not possible with $\zeta < Pn(\sigma_A + \eta_0)$).

Let us note that the same arguments apply for $\zeta > P_n(\sigma_A + \eta_0)$, which gives the results with an opposite inequality. $\square$

C.11 Proof of Proposition 18

Proof of Proposition 18.

We call

$$\partial_k y_i^* \quad := \quad \frac{\partial y_i^*}{\partial p_k}.$$

For all i we have

$$\left(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*\right)\frac{y_i^*}{p_i} \quad = \quad -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right),$$

and for $i > 1$

$$\begin{aligned} &\partial_1 y_i^*(p_1)\Big(p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*\Big)\frac{1}{p_i} \\ = \quad & \frac{1}{P_n^2}\left(\zeta + \eta_A \sum_l y_l^*(p_1)\right) - \frac{1}{P_n}\eta_A \sum_l \partial_1 y_l^*(p_1), \end{aligned}$$

while for the index 1 we have

$$\begin{aligned} &\partial_1 y_1^*\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*\Big) + y_1^* \\ = \quad & -\frac{P_n - p_1}{P_n^2}\left(\zeta + \eta_A \sum_l y_l^*\right) - \frac{p_1}{P_n}\eta_A \sum_l \partial_1 y_l^*. \end{aligned}$$

Since the right side of the first equation is actually independent of i, we also have for $j \neq i$

$$\left(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*\right)\frac{y_i^*}{p_i} \quad = \quad \left(p_j - (\sigma_A + \eta_0 + \eta_A) - y_j^*\right)\frac{y_j^*}{p_j}.$$

Let us consider that the equilibrium depends (arbitrarily) on p_1, and see their variations when deriving. For $j \neq i$ and $j, i \neq 1$ we have

$$\begin{aligned} &\partial_1 y_i^*(p_1)\underbrace{\Big(p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*\Big)}_{<0}\frac{1}{p_i} \\ = \quad & \partial_1 y_j^*(p_1)\underbrace{\Big(p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*\Big)}_{<0}\frac{1}{p_j}. \end{aligned}$$

So for $j \neq i$ and $j, i \neq 1$, we have that for all p_1,

$$\operatorname{sgn}\left(\partial_1 y_i^*(p_1)\right) \quad = \quad \operatorname{sgn}\left(\partial_1 y_j^*(p_1)\right).$$

Let us suppose that there exists a $\tilde{p_1}$ such that $\partial_1 y_i(\tilde{p_1}) = 0$, with $i > 1$. Then, according to the previous result, for all $l > 1$, $\partial_1 y_l(\tilde{p_1}) = 0$, and in particular $\sum_{l>1} \partial_1 y_l(\tilde{p_1}) = 0$. Then, the defining equation for $\partial_1 y_i(\tilde{p_1})$ gives us

$$\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*(\tilde{p_1})\right) \;=\; \eta_A \partial_1 \sum_l y_l^*(\tilde{p_1}) \;=\; \eta_A \partial_1 y_1(\tilde{p_1}),$$

and the equation of the sum gives us

$$\partial_1 y_1(\tilde{p_1})\Big(\tilde{p_1} - (\sigma_A + \eta_0) - 2y_1^*(\tilde{p_1})\Big) \;=\; -y_1^*(\tilde{p_1}).$$

From that we obtain

$$\tilde{p_1}\eta_A \;=\; \Big(\tilde{p_1} - (\sigma_A + \eta_0) - 2y_1^*(\tilde{p_1})\Big)\Big(\tilde{p_1} - (\sigma_A + \eta_0 + \eta_A) - y_1^*(\tilde{p_1})\Big),$$

which is equivalent to

$$\begin{aligned} &2y_1^*(\tilde{p_1})^2 + y_1^*(\tilde{p_1})\Big(3(\sigma_A + \eta_0 + \eta_A - \tilde{p_1}) - \eta_A\Big) \\ &+\tilde{p_1}\Big(\tilde{p_1} - 2(\sigma_A + \eta_0 + \eta_A)\Big) + (\sigma_A + \eta_0)(\sigma_A + \eta_0 + \eta_A) \;=\; 0. \end{aligned}$$

If the polynomial

$$\begin{aligned} P(X) \;:=\; & 2X^2 + X\Big(3(\sigma_A + \eta_0 + \eta_A - \tilde{p_1}) - \eta_A\Big) \\ & +\tilde{p_1}\Big(\tilde{p_1} - 2(\sigma_A + \eta_0 + \eta_A)\Big) + (\sigma_A + \eta_0)(\sigma_A + \eta_0 + \eta_A) \end{aligned}$$

has no real root, or positive roots, then $\tilde{p_1}$ does not exist. Let us be in the case where it has, and let us suppose that $y_1^*(\tilde{p_1})$ is the root of $P(X)$. Then $y_1^*(\tilde{p_1})$ verifying that this root equation is independent of any p_i, with $i > 1$. This $y_1^*(\tilde{p_1})$ still also verifies

$$\left(\tilde{p_1} - (\sigma_A + \eta_0 + \eta_A) - y_1^*(\tilde{p_1})\right)\frac{y_1^*(\tilde{p_1})}{\tilde{p_1}} \;=\; -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*(\tilde{p_1})\right)$$

and so the right-hand side of the equation is also independent from any p_i, with $i > 1$. It has the same value even for $p_i \to 0$, for all $i > 1$, meaning

$$-\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*(\tilde{p_1})\right) \;=\; -\frac{1}{\tilde{p_1}}\Big(\zeta + \eta_A y_1^*(\tilde{p_1})\Big).$$

However, we also have, for $i > 1$

$$(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*(\tilde{p_1}))\,\frac{y_i^*(\tilde{p_1})}{p_i} \;=\; -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*(\tilde{p_1})\right) \;=\; C(\tilde{p_1}),$$

so

$$\begin{aligned} 2y_i^*(\tilde{p_1}) &= p_i - (\sigma_A + \eta_0 + \eta_A) + \sqrt{\big(p_i - (\sigma_A + \eta_0 + \eta_A)\big)^2 - 4C(\tilde{p_1})p_i} \\ &> 2\big(p_i - (\sigma_A + \eta_0 + \eta_A)\big), \end{aligned}$$

and when $p_i \to \infty$, $y_i^*(\tilde{p_1}) \to \infty$. So, for $i > 1$ we have that

$$-\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*(\tilde{p_1})\right) \underset{p_i \to \infty}{\to} -\infty.$$

This is not possible according to our previous result. Therefore, $y_1^*(\tilde{p_1})$ is not a root of $P(X)$. Then, it means that there does not exist a $\tilde{p_1}$ such that $\partial_1 y_i(\tilde{p_1}) = 0$ for $i > 1$. Or, in other words, for all $i > 1$, $\partial_1 y_i(p_1)$ is never null, so it is always the same sign.

Furthermore, we have the relations, for all $j \neq 1$ and for all $p_1 > 0$

$$\begin{aligned} & \partial_1 y_1^*(p_1)\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*(p_1)\Big)\frac{1}{p_1} \\ & \quad + \frac{y_1^*(p_1)}{p_1} + \frac{1}{p_1 P_n}\left(\zeta + \eta_A \sum_l y_l^*(p_1)\right) \\ = \; & \partial_1 y_j^*(p_1)\Big(p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*(p_1)\Big)\frac{1}{p_j}, \end{aligned}$$

so for all $j \neq 1$ and for all $p_1 > 0$

$$\begin{aligned} & \partial_1 y_1^*(p_1)\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*(p_1)\Big)\frac{1}{p_1} \\ & \quad < \partial_1 y_j^*(p_1)\Big(p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*(p_1)\Big)\frac{1}{p_j} \\ \iff \quad & \partial_1 y_1^*(p_1) \; > \; \partial_1 y_j^*(p_1)\,\frac{p_1}{p_j}\,\frac{p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*(p_1)}{p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*(p_1)}. \end{aligned}$$

From this relation, we always have that if $\partial_1 y_2^* \geq 0$, then $\partial_1 y_1^* > 0$; and if $\partial_1 y_1^* \leq 0$, then $\partial_1 y_2^* < 0$.

Since also

$$\sum_l \partial_1 y_l^*(p_1)\Big(p_l - (\sigma_A + \eta_0) - 2y_l^*(p_1)\Big) \;=\; -y_1^*(p_1)$$

when $p_1 \to 0$, we have

$$\partial_1 y_1^*(0^+)\Big(-(\sigma_A+\eta_0)\Big) + \sum_{l>1} \partial_1 y_l^*(0^+)\Big(p_l - (\sigma_A+\eta_0) - 2y_l^*(0^+)\Big) \quad = \quad 0.$$

Then

$$\begin{aligned} & \partial_1 y_1^*(0^+)(\sigma_A+\eta_0) - \eta_A \sum_{l>1} \partial_1 y_l^*(0^+) \\ = \quad & \sum_{l>1} \partial_1 y_l^*(0^+)\Big(p_l - (\sigma_A+\eta_0+\eta_A) - 2y_l^*(0^+)\Big). \end{aligned}$$

The defining equation of $\partial_1 y_l^*$ gives us

$$\begin{aligned} & \partial_1 y_l^*(0^+)\Big(p_l - (\sigma_A+\eta_0+\eta_A) - 2y_l^*(0^+)\Big) \\ = \quad & \frac{p_l}{P_n^2}\left(\zeta + \eta_A \sum_l y_l^*(0^+)\right) - \frac{p_l}{P_n}\eta_A \sum_l \partial_1 y_l^*(0^+), \end{aligned}$$

so

$$\begin{aligned} & \sum_{l>1} \partial_1 y_l^*(0^+)\Big(p_l - (\sigma_A+\eta_0+\eta_A) - 2y_l^*(0^+)\Big) \\ = \quad & \frac{P_n - p_1}{P_n^2}\left(\zeta + \eta_A \sum_l y_l^*(0^+)\right) - \frac{P_n - p_1}{P_n}\eta_A \sum_l \partial_1 y_l^*(0^+). \end{aligned}$$

This means, since $p_1 \to 0$ and with the previous equation, that

$$\begin{aligned} & \partial_1 y_1^*(0^+)(\sigma_A+\eta_0) - \eta_A \sum_{l>1} \partial_1 y_l^*(0^+) \\ = \quad & \frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*(0^+)\right) - \eta_A \sum_{l>1} \partial_1 y_l^*(0^+) - \eta_A \partial_1 y_1^*(0^+) \end{aligned}$$

and since

$$(-(\sigma_A+\eta_0+\eta_A))\,\frac{y_1^*(p_1)}{p_1} \quad = \quad -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*(0^+)\right),$$

we obtain

$$\lim_{p_1 \to 0} \partial_1 y_1^*(p_1) \quad = \quad \lim_{p_1 \to 0} \frac{y_1^*(p_1)}{p_1}.$$

Also, since we have

$$\begin{aligned}
&\partial_1 y_1^*(p_1)\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*\Big)\frac{1}{p_1} \\
&\quad + \frac{y_1^*(p_1)}{p_1} \; + \; \frac{1}{p_1 P_n}\left(\zeta + \eta_A \sum_l y_l^*(p_1)\right) \\
= \;\; & \partial_1 y_j^*(p_1)\Big(p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*\Big)\frac{1}{p_j},
\end{aligned}$$

which we can rewrite

$$\begin{aligned}
&\partial_1 y_1^*(p_1)\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*\Big)\frac{1}{p_1} \\
&\quad + \frac{y_1^*(p_1)}{p_1} \; - \; \frac{1}{p_1}\frac{y_1^*}{p_1}\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*\Big) \\
= \;\; & \partial_1 y_j^*(p_1)\Big(p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*\Big)\frac{1}{p_j},
\end{aligned}$$

then for $p_1 \to 0$, we have that

$$\lim_{p_1 \to 0} \partial_1 y_j^*(p_1)\Big(p_j - (\sigma_A + \eta_0 + \eta_A) - 2y_j^*\Big)\frac{1}{p_j} \;\; = \;\; \lim_{p_1 \to 0} \frac{y_1^*(p_1)}{p_1}.$$

So $\lim\limits_{p_1 \to 0} \partial_1 y_j^*(p_1) < 0$, and in the end we obtain

$$\text{For all } i > 1, \text{ for all } p_1 > 0, \; \partial_1 y_i(p_1) < 0.$$

According to the above result, $0 < y_i^*(p_1) < y_i^*(0)$ for all $i > 1$ and $p_1 > 0$. Suppose that $y_1^*(p_1)$ does not tend towards infinity when p_1 does. We would have that

$$\left(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*(p_1)\right)\frac{y_1^*(p_1)}{p_1} \;\; = \;\; -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right),$$

so

$$p_1 \frac{y_1^*(p_1)}{p_1} \;\; \underset{p_1 \to \infty}{=} \;\; -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right).$$

This is not possible since $y_1^*(p_1)$. So

$$\lim_{p_1 \to +\infty} y_1(p_1) \;\; = \;\; +\infty.$$

Taking the sum, we have then

$$\Big(p_1 - (\sigma_A + \eta_0) - y_1^*(p_1)\Big)y_1^*(p_1) + \sum_{l>1}\Big(p_l - (\sigma_A + \eta_0) - y_l^*(p_1)\Big)y_l^*(p_1) = -\zeta.$$

Since for all p_1, $i > 1$,

$$0 > \Big(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*(p_1)\Big)\frac{y_i^*(p_1)}{p_i} > \Big(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*(0)\Big)\frac{y_i^*(0)}{p_i},$$

then it means that

$$\Big(p_1 - (\sigma_A + \eta_0) - y_1^*(p_1)\Big) \underset{p_1\to\infty}{\to} 0.$$

Since also for $i > 1$

$$\begin{aligned} & (p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*(p_1))\,\frac{y_i^*(p_1)}{p_i} \\ = \;& -\frac{1}{P_n}\left(\zeta + \eta_A\sum_l y_l^*\right) \quad \underset{p_1\to\infty}{\simeq} -\eta_A\frac{y_1^*(p_1)}{p_1} \underset{p_1\to\infty}{\to} -\eta_A, \end{aligned}$$

then

$$\lim_{p_1\to\infty} y_i^*(p_1) = \frac{1}{2}\left(p_i - (\sigma_A + \eta_0 + \eta_A) + \sqrt{\Big(p_i - (\sigma_A + \eta_0 + \eta_A)\Big)^2 + 4\eta_A p_i}\right)$$

and so, for all p_1, for any parameter, since $\partial_1 y_i^*(p_1) < 0$, we have that

$$\Big(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*(p_1)\Big)y_i^*(p_1) \quad < \quad -\eta_A p_i$$

and

$$y_i^*(p_1) \quad > \quad \frac{1}{2}\left(p_i - (\sigma_A + \eta_0 + \eta_A) + \sqrt{\Big(p_i - (\sigma_A + \eta_0 + \eta_A)\Big)^2 + 4\eta_A p_i}\right).$$

Furthermore,

$$\begin{aligned} & \Big(p_i - (\sigma_A + \eta_0 + \eta_A)\Big)^2 + 4\eta_A p_i \\ = \;& \Big(p_i - (\sigma_A + \eta_0)\Big)^2 + \eta_A^2 + 2\eta_A(p_i + \sigma_A + \eta_0) \\ > \;& \Big(p_i - (\sigma_A + \eta_0)\Big)^2 + \eta_A^2 + 2\eta_A\Big(p_i - (\sigma_A + \eta_0)\Big) \\ = \;& \Big(p_i - (\sigma_A + \eta_0) + \eta_A\Big)^2, \end{aligned}$$

which means that, for all p_1, for all $i > 1$,

$$p_i - (\sigma_A + \eta_0) - y_i^*(p_1) \;<\; 0.$$

Since the choice of p_1 as a variable is entirely subjective, doing the same analysis again with p_2 would gives us that the previous result is also true in patch 1. So we have in the end

$$\text{for all } i,\; p_i - (\sigma_A + \eta_0) - y_i^* \;<\; 0.$$

Knowing in addition that for all p_1,

$$\sum_l \partial_1 y_l^*(p_1)\Big(p_l - (\sigma_A + \eta_0) - 2y_l^*(p_1)\Big) \;=\; -y_1^*(p_1),$$

then there needs to be a i such that $\partial_1 y_i^*(p_1) > 0$. However, for all $k > 1$ we know that $\partial_1 y_k^*(p_1) < 0$. Which means in the end that for all p_1,

$$\partial_1 y_1^*(p_1) \;>\; 0.$$

From the value of $\lim\limits_{p_1 \to \infty} y_i^*(p_1)$, we also obtain that

$$\begin{aligned}\lim_{p_1 \to \infty} \Big(p_l - (\sigma_A + \eta_0) - 2y_l^*(p_1)\Big) \;&=\; \eta_A - \sqrt{\Big(p_l - (\sigma_A + \eta_0 + \eta_A)\Big)^2 + 4\eta_A p_l} \\ &<\; 0,\end{aligned}$$

with $l > 1$. Since we also showed that

$$\Big(p_1 - (\sigma_A + \eta_0) - y_1^*(p_1)\Big) \underset{p_1 \to \infty}{\to} 0.$$

then $y_1^*(p_1) \underset{p_1 \to \infty}{\sim} p_1$ and $\partial_1 y_1^*(p_1) \underset{p_1 \to \infty}{\to} 1$. So

$$\lim_{p_1 \to \infty} \Big(\partial_1 y_1^*(p_1)\Big(p_1 - (\sigma_A + \eta_0) - 2y_1^*(p_1)\Big)\Big) \;=\; -\lim_{p_1 \to \infty} y_1^*(p_1).$$

Then from

$$\sum_l \partial_1 y_l^*(p_1)\Big(p_l - (\sigma_A + \eta_0) - 2y_l^*(p_1)\Big) \;=\; -y_1^*(p_1),$$

we obtain that

$$\lim_{p_1 \to \infty} \left(\sum_{l>1} \partial_1 y_l^*(p_1)\Big(\underbrace{p_l - (\sigma_A + \eta_0) - 2y_l^*(p_1)}_{<0}\Big)\right) \;=\; 0.$$

With that, we can conclude that $\lim_{p_1\to\infty} \partial_1 y_l^*(p_1) = 0$ for $l > 1$. So

$$\lim_{p_1\to\infty} \sum_l \partial_1 y_l^*(p_1) = 1$$

Furthermore, suppose that there exists a p_1 such that $\sum_l \partial_1 y_l^*(p_1) = 0$. Then the defining equation of $\partial_1 y_1^*$ becomes

$$\underbrace{\partial_1 y_1^*(p_1)}_{>0} \underbrace{\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*\Big)\frac{1}{p_1}}_{<0} \;=\; \underbrace{\frac{1}{P_n^2}\left(\zeta + \eta_A \sum_l y_l^*(p_1)\right)}_{>0}.$$

This is impossible, and so there there exists no such p_1. From this and the limit we found, we can conclude that for all $p_1 > 0$,

$$\partial_1 \sum_l y_l^*(p_1) > 0$$

Let us finally show that $\zeta < P_n(\sigma_A + \eta_0) \implies \partial_1 y_1^*(p_1) < 1$. If $\partial_1 y_1^*(p_1) = 1$ then the definitions of ∂y_1^* gives

$$\begin{aligned} & P_n\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*\Big) + \frac{P_n - p_1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right) + p_1\eta_A \\ = \;\; & -p_1\eta_A\partial_1 \sum_{l>1} y_l^*. \end{aligned}$$

Furthermore,

$$-(P_n - p_1)\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*\Big)\frac{y_1^*}{p_1} \;=\; \frac{P_n - p_1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right),$$

so

$$\begin{aligned} & (P_n - p_1 + p_1)\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*\Big) \\ & \quad -(P_n - p_1)\Big(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*\Big)\frac{y_1^*}{p_1} + p_1\eta_A \\ = \;\; & -p_1\eta_A\partial_1 \sum_{l>1} y_l^*. \end{aligned}$$

It means that

$$\begin{aligned} & p_1\Big(p_1-(\sigma_A+\eta_0+\eta_A)-y_1^*\Big) \\ & \quad +(P_n-p_1)\Big(p_1-(\sigma_A+\eta_0+\eta_A)-y_1^*\Big)\left(1-\frac{y_1^*}{p_1}\right)+p_1\eta_A \\ = & \; -p_1\eta_A\partial_1\sum_{l>1}y_l^*. \end{aligned}$$

From the previous results, we know that

$$\Big(p_1-(\sigma_A+\eta_0+\eta_A)-y_1^*\Big) \;<\; -\eta_A\frac{p_1}{y_1^*},$$

so

$$\begin{aligned} \underbrace{-p_1\eta_A\sum_{l>1}\partial_1 y_l^*}_{>0} \;<\; & p_1\eta_A\left(1-\frac{p_1}{y_1^*}\right) \\ & +\underbrace{(P_n-p_1)\Big(p_1-(\sigma_A+\eta_0+\eta_A)-y_1^*\Big)}_{<0}\left(1-\frac{y_1^*}{p_1}\right). \end{aligned}$$

If $p_1 \geq y_1^*$, then the right hand side is non positive, which is not possible. Hence, if $p_1 \geq y_1^*$, then $\partial_1 y_1^*(p_1) \neq 1$. Or, we know that $\lim\limits_{p_1\to\infty} p_1-y_1^* = \sigma_A+\eta_0$, so $\lim\limits_{p_1\to\infty}\partial_1 y_1^* = 1$. Furthermore, for all p_1, $p_1-y_1^* < \sigma_A+\eta_0$, so this limit is reached by $f_1(p_1) := p_1-y_1^*(p_1)$ which increases monotonically when $p_1 \geq y_1^*$, since we just showed that we could not have $\partial_1 f_1 = 0$ with this condition. Finally, we know that $p_1 > y_1 \iff \zeta < P_n(\sigma_A+\eta_0)$, which concludes the proof.

□

C.12 Proof of Proposition 19

Proof of Proposition 19.

Suppose first that $\zeta \geq \sum_{l>1} p_l(\sigma_A+\eta_0)$. Then there exists a $\tilde{p_1} \geq 0$ such that $\zeta = \left(\sum_{l>1} p_l + \tilde{p_1}\right)(\sigma_A+\eta_0)$ and for $p_1 \in [0, \tilde{p_1}[$ we have $\zeta > P_n(\sigma_A+\eta_0)$. Then $\forall\, i,\ p_i \leq y_i^*$, and so $p_i-(\sigma_N+\eta_N)-y_i^* < 0$. On the other hand, for $p_1 \in]\tilde{p_1}, \infty[$ we have $\zeta < P_n(\sigma_A+\eta_0)$. We know through the previous proposition 18 that $\partial_1 y_1^*(p_1) < 1$, so $f_1(p_1) := p_1 - y_1^*(p_1)$ is increasing monotonically on $]\tilde{p_1}, \infty[$. We also have $y_1^*(\tilde{p_1}) = \tilde{p_1}$ so $f(\tilde{p_1}) = 0$. Finally, we also have proved in the previous lemma that

$$\lim_{p_1 \to +\infty} (p_1 - y_1^*(p_1)) = (\sigma_A + \eta_0).$$

It means that for all $p_1 \in]\tilde{p_1}, \infty[$, we have $p_1 - y_1^*(p_1^*) < (\sigma_A + \eta_0)$. It also means that there exists a unique $p_1^* > \tilde{p_1}$ such that $p_1^* - y_1^*(p_1^*) = \sigma_N + \eta_N$ if and only if $\sigma_N + \eta_N < \sigma_A + \eta_0$.

If we now assume that $\zeta < \sum_{l>1} p_l(\sigma_A + \eta_0)$, then $\zeta < P_n(\sigma_A + \eta_0)$ and a similar process as before tell us that there exists a unique $p_1^* > 0$ such that $p_1^* - y_1^*(p_1^*) = \sigma_N + \eta_N$ if and only if $\sigma_N + \eta_N < \sigma_A + \eta_0$.

All in all we have

$$\sigma_N + \eta_N < \sigma_A + \eta_0 \quad \Longleftrightarrow \quad \exists!\ p_1^* > 0 \text{ such that } p_1^* - y_1^*(p_1^*) = \sigma_N + \eta_N.$$

With this condition, for all $p_1 > p_1^*$ then $p_1 - (\sigma_N + \eta_N) - y_1(p_1) > 0$. Note that it necessarily implies that $\zeta < P_n(\sigma_A + \eta_0)$.

Since the choice of p_1 was arbitrary all along and nothing was assumed about p_1, this is also true for any other patch i. □

C.13 Proof of Proposition 20

Proof of Proposition 20.

From the previous proof, we have that if $\zeta \geq P_n(\sigma_A + \eta_0)$ or $\sigma_N + \eta_N > \sigma_A + \eta_0$, then for all p_k we have $p_k - (\sigma_N + \eta_N) - y_k^* < 0$.

Furthermore, if $\zeta \geq P_n(\sigma_A + \eta_0)$, then for all i, $p_i \leq y_i^*$ and we have

$$\frac{\eta_N p_i / P_n}{p_i - (\sigma_N + \eta_N) - y_i^*} \quad \geq \quad -\frac{\eta_N p_i / P_n}{(\sigma_N + \eta_N)},$$

so

$$\sum_{l=1}^{n} \frac{\eta_N p_l / P_n}{p_l - (\sigma_N + \eta_N) - y_l^*} \quad \geq \quad -\frac{\eta_N}{(\sigma_N + \eta_N)} \quad > \quad -1$$

which means that the largest eigenvalue is negative.

If $\sigma_N > \sigma_A + \eta_0$, then $\sigma_N + \eta_N > \sigma_A + \eta_0$. Furthermore, since we always have $p_i - y_i < \sigma_A + \eta_0$ then $p_i - y_i < \sigma_N$ so

$$\frac{\eta_N p_i / P_n}{p_i - (\sigma_N + \eta_N) - y_i^*} \quad > \quad -\frac{p_i}{P_n},$$

and

$$\sum_{l=1}^{n} \frac{\eta_N p_l / P_n}{p_l - (\sigma_N + \eta_N) - y_l^*} \quad > \quad -1$$

which means that the largest eigenvalue is negative.

If $\max_i p_i < \sigma_N$, then for all index l we have

$$p_l - (\sigma_N + \eta_N) - y_l^* < -\eta_N - y_l^* < -\eta_N,$$

so

$$\frac{\eta_N p_l / P_n}{p_l - (\sigma_N + \eta_N) - y_l^*} \quad > \quad -\frac{p_l}{P_n}$$

and

$$\sum_{l=1}^{n} \frac{\eta_N p_l / P_n}{p_l - (\sigma_N + \eta_N) - y_l^*} \quad > \quad -1.$$

Let's suppose that P_n is fixed in the system, and that when p_1 increase, there is a decrease for all the others p_i, $i > 1$. We then have

$$\frac{dp_i}{dp_1} \; < \; 0, \quad \text{and} \quad \sum_{l=2}^{n} \frac{dp_l}{dp_1} = -1$$

We will write d_1 from here on to denote the derivative by p_1 operation.

$$\begin{aligned} d_1 y_1^* &= \sum_{l=1}^{n} \frac{\partial y_1^*}{\partial p_l} \frac{dp_l}{dp_1} \\ &= \frac{\partial y_1^*}{\partial p_1} - \sum_{l=2}^{n} \frac{\partial y_1^*}{\partial p_l} \left| \frac{dp_l}{dp_1} \right| \end{aligned}$$

From the lemma 18, for all $l > 1$, $\partial_l y_1^* < 0$, and we obtain that $d_1 y_1^* > 0$. Let's consider

$$\begin{aligned} d_1 \sum_{k=2}^{n} y_k^* &= \sum_{k=2}^{n} \sum_{l=1}^{n} \frac{\partial y_k^*}{\partial p_l} \frac{dp_l}{dp_1} \\ &= \sum_{k=2}^{n} \frac{\partial y_k^*}{\partial p_1} + \sum_{k=2}^{n} \sum_{l=2}^{n} \frac{\partial y_k^*}{\partial p_l} \frac{dp_l}{dp_1} \\ &= \sum_{k=2}^{n} \frac{\partial y_k^*}{\partial p_1} - \sum_{l=2}^{n} \left| \frac{dp_l}{dp_1} \right| \sum_{k=2}^{n} \frac{\partial y_k^*}{\partial p_l} \end{aligned}$$

From the lemma 18 we also know that $\displaystyle\sum_{k=1}^{n} \frac{\partial y_k^*}{\partial p_l} > 0$, and since $l > 1$, for $k = 1$ we have $\partial_l y_k^* < 0$ so $\displaystyle\sum_{k=2}^{n} \frac{\partial y_k^*}{\partial p_l} > 0$. Then

$$\begin{aligned} d_1 \sum_{k=2}^{n} y_k^* &= \overbrace{\sum_{k=2}^{n} \frac{\partial y_k^*}{\partial p_1}}^{<0} - \sum_{l=2}^{n} \overbrace{\left|\frac{dp_l}{dp_1}\right| \sum_{k=2}^{n} \frac{\partial y_k^*}{\partial p_l}}^{>0} \\ &< 0 \end{aligned}$$

By symmetry of the system, for $i, k \neq 1$, then

$$\text{sign } d_1 y_i^* = \text{sign } d_1 y_k^*,$$

and this tells us that for all $i > 1$, $d_1 y_i^* < 0$.

Let us now suppose that when p_1 increases, there is a uniform decrease for all the others p_i, $i > 1$. We then have

$$d_1 p_i = -\frac{1}{n-1}.$$

The system for the change of y_i^* when p_1 changes is then

$$\left\{ \begin{aligned} (p_1 - (\sigma_A + \eta_0 + \eta_A) - 2y_1^*)\, d_1 y_1^* \; + \; y_1^* \; &+ \; \frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right) \\ &+ \; \frac{p_1}{P_n} \eta_A \sum_l d_1 y_l^* \; = \; 0; \\ (p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*)\, d_1 y_i^* \; - \; \frac{y_i^*}{n-1} \; &- \; \frac{1}{P_n(n-1)}\left(\zeta + \eta_A \sum_l y_l^*\right) \\ &+ \; \frac{p_i}{P_n} \eta_A \sum_l d_1 y_l^* \; = \; 0, \end{aligned} \right.$$

with the sum being

$$\sum_l (p_l - (\sigma_A + \eta_0) - 2y_l^*)\, d_1 y_l^* + y_1^* - \frac{1}{n-1} \sum_{l>1} y_l^* \; = \; 0.$$

If we suppose $d_1 y_1^* = 1$ we have

$$\begin{cases} p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^* + \dfrac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right) \\ \qquad + \dfrac{p_1}{P_n}\eta_A + \dfrac{p_1}{P_n}\eta_A \sum_{l>1} d_1 y_l^* = 0; \\ \\ (p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*)\, d_1 y_i^* - \dfrac{y_i^*}{n-1} - \dfrac{1}{P_n(n-1)}\left(\zeta + \eta_A \sum_l y_l^*\right) \\ \qquad + \dfrac{p_i}{P_n}\eta_A + \dfrac{p_i}{P_n}\eta_A \sum_{l>1} d_1 y_l^* = 0. \end{cases}$$

For all i we have

$$(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*)\, \frac{y_i^*}{p_i} = -\frac{1}{P_n}\left(\zeta + \eta_A \sum_l y_l^*\right)$$

so

$$\begin{aligned} & \frac{P_n}{p_1}\big(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*\big)\left(1 - \frac{y_1^*}{p_1}\right) \\ = \; & \frac{P_n}{p_i}\Bigg(\big(p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*\big) d_1 y_i^* \\ & \qquad - \frac{y_i^*}{n-1}\left(\frac{1}{p_i}\big(p_i - (\sigma_A + \eta_0 + \eta_A) - y_i^*\big) - 1\right)\Bigg) \end{aligned}$$

We only consider the case $\zeta < P_n(\sigma_A + \eta_0)$, so $y_1^* < p_1$ and $\big(p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*\big)\left(1 - \frac{y_1^*}{p_1}\right) < 0$. Then, the right hand side of the previous equation gives us

$$\frac{P_n}{p_i}\left(\underbrace{\big(p_i - (\sigma_A + \eta_0 + \eta_A) - 2y_i^*\big) d_1 y_i^*}_{>0} + \frac{y_i^*}{n-1}\frac{\sigma_A + \eta_0 + \eta_A + y_i^*}{p_i}\right) > 0.$$

This is not possible, so there is no $p_1 \in]0, P_n[$ such that $d_1 y_1^* = 1$.

Finally, a similar proof as in the lemma 18 tells us that

$$\lim_{p_1 \to 0} d_1 y_1^*(p_1) = \lim_{p_1 \to 0} \frac{y_1(p_1)}{p_1} < 1,$$

and then for all $p_1 \in]0, P_n[, d_1 y_1 < 1$. That also means the function $f_1(p_1) = p_1 - y_1^*$ increases monotonically (and is positive since $f(0) = 0$), and reaches its maximum when $p_1 \to P_n$. The monotonicity of the function is fully dependent on how the p_i changes withe the changes of p_1. However, since f_1 reaches its unique maximum for the unique point $(p_1, p_2, ..., p_n) \to (P_n, 0, ..., 0)$. Even if it is not reached monotonically, the $(P_n, 0, ..., 0)$ will always be the unique maximum of f.

Let us consider this situation. $p_1 \simeq P_n$, and for all $i > 1$, $p_i << 1$. A study of this system gives us that

$$(P_n - (\sigma_A + \eta_0) - y_1^*)y_1^* + \zeta \simeq 0$$

so we obtain

$$y_1^* \simeq \frac{1}{2}\left(P_n - (\sigma_A + \eta_0) + \sqrt{\big(P_n - (\sigma_A + \eta_0)\big)^2 + 4\zeta}\right).$$

If $p_1 - y_1^* > \sigma_N + \eta_N$ then this equilibrium is unstable, and we know that

$$\begin{aligned} & p_1 - y_1^* > \sigma_N + \eta_N \\ \iff \quad & \sigma_N + \eta_N < \sigma_A + \eta_0 \text{ and } \zeta < \Big(P_n - (\sigma_N + \eta_N)\Big)\Big(\sigma_A + \eta_0 - (\sigma_N + \eta_N)\Big). \end{aligned}$$

Furthermore, if for $p_1 \simeq P_n$ we have $p_1 - y_1^* > \sigma_N + \eta_N$, and since this maximum is unique, it means that for all distribution for the p_i, there exists a unique $P_n > \tilde{p_1} > \sigma_N + \eta_N$ such that for all $p_1 > \tilde{p_1}$ we have $p_1 - y_1^* > \sigma_N + \eta_N$.

□

C.14 Proof of Proposition 21

Proof of Proposition 21.

Two patches scenario, with P_n fixed, so $p_2 = P_2 - p_1$. The study we study is

$$\begin{cases} (p_1 - (\sigma_A + \eta_0 + \eta_A) - y_1^*)\, y_1^* + \dfrac{p_1}{P_2}\Big(\zeta + \eta_A(y_1^* + y_2^*)\Big) & = 0; \\ \\ (P_2 - p_1 - (\sigma_A + \eta_0 + \eta_A) - y_2^*)\, y_2^* + \dfrac{P_2 - p_1}{P_2}\Big(\zeta + \eta_A(y_1^* + y_2^*)\Big) & = 0, \end{cases}$$

and the sum is

$$(p_1 - (\sigma_A + \eta_0) - y_1^*)\, y_1^* + (P_2 - p_1 - (\sigma_A + \eta_0) - y_2^*)\, y_2^* = -\zeta.$$

We will always suppose $\zeta < P_2(\sigma_A + \eta_0)$ in this proof, except explicitly stated otherwise. If $p_1 \to P_2$, then we obtain from the second equation that

$$(-(\sigma_A + \eta_0 + \eta_A) - y_2^*)y_2^* \quad \to \quad 0,$$

so $y_2 \to 0$, and

$$y_1^{*2} - \Big(p_1 - (\sigma_A + \eta_0)\Big)y_1^* - \zeta \quad \simeq \quad \eta_A y_2^*,$$

so

$$y_1^* \quad \to \quad \frac{1}{2}\left(P_2 - (\sigma_A + \eta_0) + \sqrt{\big(P_2 - (\sigma_A + \eta_0)\big)^2 + 4\zeta}\right).$$

Then

$$\begin{aligned} & P_2 - (\sigma_N + \eta_N) - y_1^* \quad < \quad 0 \\ \Longleftrightarrow \quad & 2(\sigma_N + \eta_N) \quad > \quad P_2 + (\sigma_A + \eta_0) - \sqrt{\big(P_2 - (\sigma_A + \eta_0)\big)^2 + 4\zeta} \ (\ > 0\ ). \end{aligned}$$

Furthermore,

$$\frac{\eta_N p_1/P_2}{p_1 - (\sigma_N + \eta_N) - y_1^*} + \frac{\eta_N p_2/P_2}{p_2 - (\sigma_N + \eta_N) - y_2^*} \quad \simeq \quad \frac{\eta_N}{P_2 - (\sigma_N + \eta_N) - y_1^*}$$

and if $P_2 - (\sigma_N + \eta_N) - y_1^* < 0$, we have

$$\begin{aligned} & \frac{\eta_N}{P_2 - (\sigma_N + \eta_N) - y_1^*} \quad > \quad -1 \\ \Longleftrightarrow \quad & 2\sigma_N \quad > \quad P_2 + \sigma_A + \eta_0 - \sqrt{\big(P_2 - (\sigma_A + \eta_0)\big)^2 + 4\zeta} \\ \Longleftrightarrow \quad & \sigma_N \ > \ P_2 \quad \text{or} \quad \sigma_N \ > \sigma_A + \eta_0 \quad \text{or} \quad \zeta \ > \ (P_2 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N). \end{aligned}$$

In the end, when $p_2 << p_1$ we obtained two results.

If $\sigma_N \ > \ P_2$ or $\sigma_N \ > \sigma_A + \eta_0$ or $\zeta \ > \ (P_2 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N)$,
then $(0, y_1^*, 0, y_2^*)$ is locally stable.
If $\sigma_N \ < \ P_2$ and $0 \ < \ \zeta \ < \ (P_2 - \sigma_N)(\sigma_A + \eta_0 - \sigma_N)$
then $(0, y_1^*, 0, y_2^*)$ is unstable.

On the other hand, if $p_1 = p_2 = P_2/2$, then by symmetry $y_1^* = y_2^*$ and

$$\left(\frac{P_2}{2} - (\sigma_A + \eta_0) - y_1^*\right) y_1^* \quad = \quad -\frac{\zeta}{2},$$

so

$$y_1^* = \frac{1}{2}\left(\frac{P_2}{2} - (\sigma_A + \eta_0) + \sqrt{\left(\frac{P_2}{2} - (\sigma_A + \eta_0)\right)^2 + 2\zeta}\right).$$

Then

$$\begin{aligned}
& \frac{P_2}{2} - (\sigma_N + \eta_N) - y_1^* \ > \ 0 \\
\iff \quad & 2(\sigma_N + \eta_N) \ < \ \frac{P_2}{2} + (\sigma_A + \eta_0) - \sqrt{\left(\frac{P_2}{2} - (\sigma_A + \eta_0)\right)^2 + 2\zeta} \ (> 0\ ) \\
\iff \quad & \sigma_N + \eta_N \ < \ \frac{P_2}{2} \\
& \quad \text{and } \ 0 \ < \ \zeta \ < \ \Big(P_2 - 2(\sigma_N + \eta_N)\Big)\Big(\sigma_A + \eta_0 - (\sigma_N + \eta_N)\Big).
\end{aligned}$$

Furthermore,

$$\frac{\eta_N p_1/P_2}{p_1 - (\sigma_N + \eta_N) - y_1^*} + \frac{\eta_N p_2/P_2}{p_2 - (\sigma_N + \eta_N) - y_2^*} \quad = \quad \frac{\eta_N}{P_2/2 - (\sigma_N + \eta_N) - y_1^*}$$

and if $P_2/2 - (\sigma_N + \eta_N) - y_1^* < 0$, we have

$$\begin{aligned}
& \frac{\eta_N}{P_2/2 - (\sigma_N + \eta_N) - y_1^*} \quad > \quad -1 \\
\iff \quad & 2\sigma_N \quad > \quad \frac{P_2}{2} + \sigma_A + \eta_0 - \sqrt{\left(\frac{P_2}{2} - (\sigma_A + \eta_0)\right)^2 + 2\zeta} \\
\iff \quad & \sigma_N \ > \ \frac{P_2}{2} \quad \text{or} \quad \sigma_N \ > \sigma_A + \eta_0 \quad \text{or} \quad \zeta \ > \ \left(\frac{P_2}{2} - \sigma_N\right)(\sigma_A + \eta_0 - \sigma_N).
\end{aligned}$$

In the end, when $p_1 = p_2 = P_2/2$,

$$\begin{aligned}
& \text{If } \ \sigma_N \ > \ \frac{P_2}{2} \quad \text{or} \quad \sigma_N \ > \sigma_A + \eta_0 \quad \text{or} \quad \zeta \ > \ \left(\frac{P_2}{2} - \sigma_N\right)(\sigma_A + \eta_0 - \sigma_N) \\
& \qquad \text{then } \Big(0, y_1^*(P_2/2), 0, y_2^*(P_2/2)\Big) \text{ is locally stable.} \\
& \text{If } \ \sigma_N \ < \ \frac{P_2}{2} \quad \text{and} \quad 0 \ < \ \zeta \ < \ \left(\frac{P_2}{2} - \sigma_N\right)(\sigma_A + \eta_0 - \sigma_N) \\
& \qquad \text{then } \Big(0, y_1^*(P_2/2), 0, y_2^*(P_2/2)\Big) \text{ is unstable.}
\end{aligned}$$

Also, let us notice that

$$\begin{aligned}
&\frac{P_2}{2}+\sigma_A+\eta_0-\sqrt{\left(\frac{P_2}{2}-(\sigma_A+\eta_0)\right)^2+2\zeta} \\
&\quad< \ P_2+\sigma_A+\eta_0-\sqrt{\big(P_2-(\sigma_A+\eta_0)\big)^2+4\zeta} \\
\iff &\quad \zeta<P_2(\sigma_A+\eta_0)
\end{aligned}$$

The above proof for the Proposition 20 tells us here too that $y_1^*(p_1)$ is monotonically increasing, and $y_2^*(p_1)$ is monotonically decreasing when $p_1+p_2=P_2$ is fixed. We also have that for $\zeta<P_2(\sigma_A+\eta_0)$, then $dy_1^*<1$ for all $p_1\in]0,P_2[$

That means that $p_1-y_1^*$ increases monotonically, and if $P_2/2-(\sigma_N+\eta_N)-y_1^*>0$ then the equilibrium $(0,y_1^*,0,y_2^*)$ is unstable for all $p_1\geq P_2$ or $p_2\geq P_2$, so by symmetry of the system, for all $p_1\in]0,P_2[$. □

C.15 Proof of Proposition 22

Proof of Proposition 22.

In case of $p_i=P_n/n\ \forall i$ we can rewrite the polynomials:

$$\begin{aligned}
\Phi(X) &= \left(\frac{P_n}{n}-(\sigma_N+\eta_N)-y_n^*-X\right)^{n-1}\left(\frac{P_n}{n}-\sigma_N-y_n^*-X\right); \\
\Psi(X) &= \left(\omega\left[\frac{P_n}{n}-(\sigma_A+\eta_0+\eta_A)-2y_n^*\right]-X\right)^{n-1} \\
&\qquad\times\left(\omega\left[\frac{P_n}{n}-(\sigma_A+\eta_0)-2y_n^*\right]-X\right).
\end{aligned}$$

However we know that all the roots of Ψ are negative already, we need only to look at Φ. The biggest root of Φ is $P_n/n-\sigma_N-y_n^*$, so in this special case we have:

$$\begin{aligned}
y_n^*<\frac{P_n}{n}-\sigma_N &\implies (0,y_1^*,...,0,y_n^*)\text{ is unstable;} \\
y_n^*>\frac{P_n}{n}-\sigma_N &\implies (0,y_1^*,...,0,y_n^*)\text{ is stable.}
\end{aligned}$$

First of all, if $n>P_n/\sigma_N$ then $(0,y_1^*,...,0,y_n^*)$ is stable. Let us suppose $n<P_n/\sigma_N$ or in other words $P_n/n>\sigma_N$. From the definition of y_n^* we obtain (concave parabola in y_n^*):

$$y_n^*<\frac{P_n}{n}-\sigma_N \iff \Big(\sigma_N-(\sigma_A+\eta_0)\Big)\left(\frac{P_n}{n}-\sigma_N\right)+\frac{\zeta}{n}<0.$$

If $\sigma_N > \sigma_A + \eta_0$, then $y_n^* > P_n/n - \sigma_N$. Let us suppose now also that $\sigma_A + \eta_0 > \sigma_N$. Then

$$y_n^* < \frac{P_n}{n} - \sigma_N \quad \Longleftrightarrow \quad \frac{1}{n}\bigg(P_n\Big(\sigma_A + \eta_0 - \sigma_N\Big) - \zeta\bigg) > \sigma_N\Big(\sigma_A + \eta_0 - \sigma_N\Big).$$

If $\zeta > P_n\big(\sigma_A + \eta_0 - \sigma_N\big)$, then $y_n^* > P_n/n - \sigma_N$. Let us suppose now also that $0 < \zeta < P_n\big(\sigma_A + \eta_0 - \sigma_N\big)$. We have in the end

$$\begin{aligned} \frac{1}{n} &> \sigma_N \frac{\sigma_A + \eta_0 - \sigma_N}{P_n(\sigma_A + \eta_0 - \sigma_N) - \zeta} \\ \Longleftrightarrow n &< \frac{P_n}{\sigma_N}\frac{\sigma_A + \eta_0 - \sigma_N - \zeta/P_n}{\sigma_A + \eta_0 - \sigma_N}. \end{aligned}$$

□

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