



HAL
open science

Dynamique spatio-temporelle et identification des diffusions non linéaires

Naamat Ali

► **To cite this version:**

Naamat Ali. Dynamique spatio-temporelle et identification des diffusions non linéaires. Mathématiques générales [math.GM]. Université de La Rochelle, 2013. Français. NNT : 2013LAROS403 . tel-01066085

HAL Id: tel-01066085

<https://theses.hal.science/tel-01066085>

Submitted on 19 Sep 2014

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



UNIVERSITÉ DE LA ROCHELLE

THÈSE

pour l'obtention du Grade de

DOCTEUR de l'Université de La Rochelle

École Doctorale: **Sciences et Ingénierie pour l'Information (S2I)**

Laboratoire: **Mathématiques: Images et Applications**

Mention: **Mathématiques et Applications**

présentée par:

Naamat ALI¹

Dynamique spatio-temporelle et Identification des diffusions non linéaires

Soutenue le 11 Juillet 2013
devant la commission d'Examen

Jury

Mostafa Adimy	Directeur de recherche INRIA	Rapporteur
Samir Adly	Professeur, Université de Limoges	Examineur
Abdallah El Hamidi	MCF, Université de La Rochelle	Directeur de thèse
Mustapha Jazar	Professeur, Université Libanaise	Directeur de thèse
Mokhtar Kirane	Professeur, Université de La Rochelle	Examineur
Jean-Christophe Poggiale	Professeur, Université de Marseille	Rapporteur
Arnaud Rougirel	MCF, Université de Poitiers	Examineur

1. N'hésitez pas à m'envoyer vos remarques à: naamat_ali@hotmail.com

A mes parents

A Imad

Remerciements

Mes premiers remerciements s'adressent à mes directeurs de thèse Abdallah El Hamidi et Mustapha Jazar. Merci pour votre gentillesse, votre disponibilité, vos conseils, votre rigueur scientifique et votre aide très précieuse tant au niveau personnel que professionnel. M. El Hamidi, merci particulièrement pour l'accueil chaleureux dès mes premières minutes en France. Vous m'avez initié à la simulation numérique, et vous m'avez également poussé pour obtenir des résultats. M. Jazar, c'était un très grand honneur d'avoir travaillé sous votre direction pendant le stage de master et durant le doctorat. Je vous remercie aussi pour votre soutien moral sans faille et votre optimisme.

Mes respectueux remerciements s'adressent aux rapporteurs de cette thèse, M. Mostafa Adimy, directeur de recherche à l' INRIA, et M. Jean-Christophe Poggiale, Professeur à l'Université de Marseille, pour avoir consacré du temps et de l'énergie à la lecture de mon manuscrit et pour l'intérêt qu'ils ont porté à mon travail. J'associe à ces remerciements les membres du jury : M. Samir Adly, M. Mokhtar Kirane et M. Arnaud Rougirel pour avoir accepté d'examiner mon travail et contribué aux discussions lors de la soutenance.

J'adresse en particulier de sincères remerciements à M. Kirane pour son soutien, ses conseils ; ses remarques et suggestions m'ont été très utiles, ainsi que les échanges enrichissants qui ont accompagné nos conversations.

J'exprime ma gratitude à M. Michel Berthier, Directeur du Laboratoire de Mathématiques Images et Applications de l'Université de La Rochelle pour m'avoir accueillie dans son laboratoire. Je remercie aussi Isabelle Hirsh et Jennifer De la corté Gomez pour leur aide efficace dans les démarches administratives à l'Université de La Rochelle.

Un immense merci à mes amies, Marwa et Samar, deux amies très spéciales, qui m'ont énormément soutenu dès le début, peu importe les différents endroits où nous étions tous.

Mes dernières remerciements s'adressent à ma famille qui m'ont toujours ap-

porté leur soutien sans faille et encouragé à poursuivre mes études jusqu'à l'obtention du doctorat, et en particulier à celle qui est toujours présente, à ma mère Halima, ta présence, ton dévouement, tes encouragements, et tes prières m'ont accompagné tout le long de mes études, il m'est impossible de trouver des mots pour dire à quel point je suis fière de toi, et à quel point je t'aime, merci tout simplement d'être...*ma mère*. Merci aussi à mes frères et mes sœurs et en particulier ma petite sœur Nour, d'être toujours à mes côtés, par son amour, par son soutien, malgré les milliers de kilomètres qui nous séparent.

Enfin, je termine par remercier la personne qui est toujours présent : Imad. Ta tendresse m'a toujours portée, ton écoute, tes conseils et surtout ton amour qui m'a été essentiel durant ces années. Pour tout cela et pour ces années passionnantes, du fond du coeur : Merci et je remercie Dieu de t'avoir connue. Ces quelques mots ne suffisent pas à exprimer ma gratitude pour toi.

Table des matières

Remerciements	v
Table des matières	vii
Table des figures	xi
Liste des tableaux	xv
Notations et abréviations	xvii
1 Introduction et présentation des travaux	1
1.1 Contexte général et scientifique	2
1.2 Dynamique temporelle	3
1.2.1 Formulation générale	3
1.2.2 Le modèle “proie-prédateur ”	5
1.3 Dynamique spatio-temporelle	9
1.3.1 Formulation générale	10
1.3.2 Instabilité de Turing	13
1.4 Plan de la thèse	13
1.5 Résumé des chapitres 2 à 6	14
1.5.1 Chapitre 2 : Diffusions couplées non-linéaires dans des systèmes de compétition	14
1.5.2 Chapitre 3 : Un modèle d’EDP de plantes clonales en compétition avec diffusions non-linéaires	16
1.5.3 Chapitre 4 : Identification de paramètres dans les systèmes des diffusions couplées non-linéaires via les données IBM	17
1.5.4 Chapitre 5 : Dynamique globale du modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin	17
1.5.5 Chapitre 6 : Dynamiques spatio-temporelles d’un modèle proie-prédateur de type Leslie-Gower modifié et avec une fonction de réponse de type Crowley-Martin	20
2 On nonlinear coupled diffusions in competition systems	21
Présentation du chapitre	22
Abstract	22
2.1 Introduction	22
2.2 Local and global existence results	24

2.2.1	Definitions and notations	25
2.3	Competition systems and diffusion driven instability	29
2.4	Simplified competition model for clonal plants	31
2.4.1	Lotka-Volterra nonlinear coupled diffusion model	31
2.4.2	Numerical Simulation of a Benchmark Problem	35
3	A PDE model of clonal plant competition with nonlinear diffusion	43
	Présentation du chapitre	44
	Abstract	44
3.1	Introduction	44
3.2	A general PDE Model	46
3.3	Simplified Competition model for clonal plants	49
3.3.1	Lotka-Volterra-nonlinear diffusion model	49
3.3.2	Numerical Simulation of a Benchmark Problem	52
3.4	Discussion	57
4	Nonlinear identification in cross-diffusion competition systems	63
	Présentation du chapitre	64
	Abstract	64
4.1	Introduction	64
4.2	Local existence and positively invariant sets	65
4.3	Study of the inverse problem	70
4.3.1	Regularity results of solutions with respect to the parameters	71
4.3.2	Computation of the gradient of J_0	80
4.4	Numerical simulations	84
5	Global dynamics of a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses	89
	Présentation du chapitre	90
	Abstract	90
5.1	Introduction	90
5.2	Boundedness of the model and existence of a positively invariant attracting set	94
5.3	Equilibria and their local stability analysis	95
5.3.1	Conditions for the existence of a unique positive equilibrium	95
5.3.2	Local stability and Hopf bifurcation	97
5.4	Permanence	99
5.5	Limit cycle	100
5.5.1	Existence of periodic orbits	100
5.5.2	Non-existence of a periodic orbit	100
5.6	Global stability	102
5.7	Numerical simulations	106

5.8 Discussion and conclusions	109
Appendix : First Lyapunov Coefficient	114
6 Spatio-temporal dynamics of a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses	115
Présentation du chapitre	116
Abstract	116
6.1 Introduction	116
6.2 Global existence of solutions	119
6.3 Dissipation and persistence	121
6.4 Steady states and their local stability	124
6.4.1 Local stability of the steady states	125
6.5 Global stability	130
6.6 Hopf bifurcation	133
6.7 Turing instability	134
6.8 Periodic Solutions	135
6.9 Conclusions	138
7 Rappels et notions générales	141
7.1 Cadre fonctionnel et notions générales	142
7.1.1 Espaces fonctionnels	142
7.1.2 Formules et inégalités principales	144
7.1.3 Lemme de Gronwall	146
7.1.4 Règle des signes de Descartes	146
7.1.5 Triplet de Gelfand	147
7.1.6 Théorème de Minty-Browder	147
7.2 Systèmes dynamiques	147
7.2.1 Définitions et généralités	148
7.2.2 Bifurcations des systèmes dynamiques	151
7.3 Systèmes de réaction-diffusion	152
7.3.1 Régions invariantes	153
7.3.2 Fonctionnelle de Lyapunov	153
7.3.3 Sous-solutions et sur-solutions du problème elliptique associé	153
Conclusions et perspectives	155
Glossaire	159
Liste des travaux	161
Bibliographie	163
Index	173

TABLE DES MATIÈRES

Table des figures

2.1	Top-left : Case (i), top-right : Case (ii), bottom-left : Case (iii) and bottom-right : Case (vi).	33
2.2	Two species system with quasi uniform diffusion : $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 100$. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval (0.1, 0.5), is indicated by dots ‘.’. . .	36
2.3	Two species system with strong exclusive diffusion $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 0.1$. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval (0.1, 0.5), is indicated by dots ‘.’. . .	37
2.4	First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 100$, but both species have quasi uniform diffusion. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval (0.1, 0.5), is indicated by dots ‘.’.	38
2.5	First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 0.1$, but both species have strong exclusive diffusion. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval (0.1, 0.5), is indicated by dots ‘.’.	39
2.6	Space distribution of ramets for Phalanx.	40
2.7	Space distribution of ramets for Guerilla.	41
3.1	Two species system with quasi uniform diffusion : $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 100$. First species (respt. the second species) is marked by black label (respt. red label). Density above 0.5 is indicated by circles ‘o’, density in the interval (0.1, 0.5) is indicated by dots ‘.’.	54

3.2	Two species system with strong exclusive diffusion $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 0.1$. First species (respt. the second species) is marked by black label (respt. red label). Density above 0.5 is indicated by circles ‘o’, density in the interval (0.1, 0.5) is indicated by dots ‘.’	54
3.3	First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 100$, but both species have quasi uniform diffusion. First species (respt. the second species) is marked by black label (respt. red label). Density above 0.5 is indicated by circles ‘o’, density in the interval (0.1, 0.5) is indicated by dots ‘.’	55
3.4	First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 100$, but both species have quasi uniform diffusion. First species (respt. the second species) is marked by black label (respt. red label). Density above 0.5 is indicated by circles ‘o’, density in the interval (0.1, 0.5) is indicated by dots ‘.’	55
3.5	Space distribution of ramets for Phalanx.	56
3.6	Space distribution of ramets for Guerilla.	56
4.1	Profile of the observation u_{obs} at $t = 1$.	86
4.2	” – .” Dashed-dotted curve : diffusion curve to be identified. ” – ” dashed curve : initial diffusion curve. Continuous line : the computed curve.	87
4.3	” – .” Dashed-dotted curve : diffusion curve to be identified. ” – ” dashed curve : initial diffusion curve. Continuous line : the computed curve.	87
4.4	” – .” Dashed-dotted curve : diffusion curve to be identified. ” – ” dashed curve : initial diffusion curve. Continuous line : the computed curve.	88
4.5	Profile of the cost functional J .	88
5.1	Isoclines graph for the system (5.5) for parametric values; (a) $B < 1$ and A, C, D, E are positive parameters; (b) $B > 1$ and A, C, D, E are positive parameters. Here u_1 is the positive root of the polynomial $1 - B(1 - u)(1 + Au)$.	102
5.2	The phase portrait of the system (5.5) when $A = 2, B = 0.1, C = 0.6, D = 0.3$, and $E = 0.2$. The positive equilibrium $E^*(0.17613, 1.2538)$ is a global attractor.	106
5.3	The phase portrait of system (5.5) when $A = 0.1, B = 0.1, C = 1, D = 0.57$ and $E = 1.5$. The prey-extinction equilibrium $E_2(0, E/D)$ of system (5.5) is a global attractor.	107
5.4	The phase portrait of system (5.5) when $A = 2, B = 0.1, C = 0.02, D = 0.3$ and $E = 0.2$. The positive equilibrium $E^*(0.17613, 1.2538)$ is unstable and (5.5) has a nonconstant periodic solution surrounding E^* .	107

5.5	Graph trajectory of prey $u(t)$ of system (5.5). Here $A = 2, B = 0.1, D = 0.3, E = 0.2$ and $C = 0.02, 0.038486, 0.6$, respectively. . .	108
5.6	Graph trajectory of predator $v(t)$ of system (5.5). Here $A = 2, B = 0.1, D = 0.3, E = 0.2$ and $C = 0.02, 0.038486, 0.6$, respectively. . .	108
5.7	Stable limit cycle around the positive equilibrium $E^*(0.17613, 1.2538)$ of the system (5.5) when $A = 2, B = 0.1, C = 0.038486, D = 0.3$ and $E = 0.2$	109
5.8	Phase portrait of system (5.5). Positive equilibrium $E^*(0.30527, 1.6842)$ is globally asymptotically stable. Here $A = 2, B = 0.3, C = 0.02, D = 0.3$ and $E = 0.2$	110
5.9	Graph trajectory of prey $u(t)$ of system (5.5). Here $A = 2, C = 0.02, D = 0.3, E = 0.2$ and $B = 0.1, 0.171113, 0.3$ respectively. . . .	111
5.10	Graph trajectory of predator $v(t)$ of system (5.5). Here $A = 2, C = 0.02, D = 0.3, E = 0.2$ and $B = 0.1, 0.171113, 0.3$ respectively. . . .	111
5.11	Stable limit cycle around the positive equilibrium $E^*(0.21695, 1.3898)$ of the system (5.5) when $A = 2, B = 0.171113, C = 0.02, D = 0.3$ and $E = 0.2$	112

Liste des tableaux

1.1	Synthèse de différentes formulations de la réponse fonctionnelle du prédateur. Les paramètres a, b et c sont positifs.	8
1.2	Synthèse de différentes formulations de la réponse numérique du prédateur. Les paramètres d, e, f, g et h sont positifs.	9

Notations et abréviations

Notations

Symbole	Description	Page ²
\mathbb{R} :	Corps des réels	10
$\overline{\mathbb{R}}$ =	$\mathbb{R} \cup \{\infty\}$	25
\mathbb{R}_+ =	Ensemble des nombre réels positifs	26
\mathbb{R}^N	\mathbb{R} -Espace euclidien de dimension N	10
Ω	Ouvert borné de \mathbb{R}^N	10
\mathbf{n}	Vecteur normal unitaire orienté vers l'extérieur du Ω	14
$L^p(\Omega)$	Espace de Lebesgue	10
$L(\Omega, \rho)$	Espace de fonction de Banach	25
$C^1(X; \mathbb{R})$	Fonctions C^1 -différentiables de X dans \mathbb{R}	26
$C_c^\infty(\Omega)$	Fonctions C^∞ -différentiables à support compact	25

Abréviations

EDO	Équations différentielles ordinaires
EDP	Équations aux dérivées partielles
PDE	Partial differential equations
IBM	Individual based models

2. page de première apparition

Chapitre 1

Introduction et présentation des travaux

Sommaire

1.1	Contexte général et scientifique	2
1.2	Dynamique temporelle	3
1.2.1	Formulation générale	3
1.2.2	Le modèle “proie-prédateur ”	5
1.3	Dynamique spatio-temporelle	9
1.3.1	Formulation générale	10
1.3.2	Instabilité de Turing	13
1.4	Plan de la thèse	13
1.5	Résumé des chapitres 2 à 6	14
1.5.1	Chapitre 2 : Diffusions couplées non-linéaires dans des systèmes de compétition	14
1.5.2	Chapitre 3 : Un modèle d’EDP de plantes clonales en compétition avec diffusions non-linéaires	16
1.5.3	Chapitre 4 : Identification de paramètres dans les systèmes des diffusions couplées non-linéaires via les données IBM	17
1.5.4	Chapitre 5 : Dynamique globale du modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin	17
1.5.5	Chapitre 6 : Dynamiques spatio-temporelles d’un modèle proie-prédateur de type Leslie-Gower modifié et avec une fonction de réponse de type Crowley-Martin	20

1.1 Contexte général et scientifique

La modélisation mathématique consiste à utiliser les mathématiques pour décrire, expliquer ou prévoir un comportement ou des phénomènes dans le monde réel. Cette modélisation peut être particulièrement utile pour approfondir des questions ou tester des idées dans des systèmes complexes. Un modèle mathématique est une abstraction d'un système physique utilisant un langage précis pour décrire le comportement du système.

Apparu au cours du XIX^{ème} siècle, le premier exemple de modélisation mathématique moderne inspiré d'une problématique épidémiologique, est utilisé par Daniel Bernoulli sur l'amélioration de l'espérance de vie.

Le XX^{ème} siècle a été marqué par le développement de la modélisation mathématique des phénomènes issus de : la physique, chimie, biologie, écologie, épidémiologie, économie, Sciences de l'ingénieur : aérodynamique, calcul des structures, électromagnétisme, énergie, automatique, signal, finance, sciences sociales....

Modéliser, c'est convertir un problème concret issu du monde réel en termes de nature mathématique. C'est transformer un besoin, plus ou moins bien exprimé, en équations, en essayant de rendre compte de toutes les contraintes. Historiquement, la modélisation mathématique a été en grande partie réalisée sur la base d'équations différentielles, les équations différentielles ordinaires modélisent une grande famille de phénomènes qui se manifestent dans plusieurs domaines.

L'écologie décrit les relations entre les organismes, et entre ces derniers et leur environnement, déterminant ainsi des aspects tels que l'abondance des espèces, des compositions d'une communauté biologique qui représente un groupe d'organismes en espace et en temps.

Les systèmes de réaction-diffusion tenant compte des phénomènes de diffusions croisées sont pertinents dans la modélisation de nombreux phénomènes, dans des disciplines variées (cinétique chimique, dynamique des populations...). De nombreux problèmes mathématiques concernant ces systèmes sont toujours ouverts. En particulier les problèmes inverses concernant l'identifiabilité des termes de diffusions non linéaires dans les cas scalaires ou les diffusions croisées dans le cas des systèmes. Concernant l'identification, le point crucial dans ce type de problèmes est le fait que la diffusion non-linéaire que l'on cherche à identifier est définie sur un ensemble qui dépend de la solution du problème, qui dépend elle-même de la diffusion recherchée. D'autre part, les énergies que l'on définit à partir d'observations spatio-temporelles et que l'on cherche à minimiser font intervenir des gradients (pour les méthodes de descente) qui sont compliqués à caractériser au sens fort. En effet, à notre connaissance seule une caractérisation de ces gradients au sens faible (au sens des distributions) figurent dans la littérature, on peut citer

par exemple le travail de G. Chavent et P. Lemonnier [23]. Pour cette raison, nous pensons que notre travail est le premier dans cette direction à donner une caractérisation du gradient dans un problème d'identification de diffusion non-linéaire, via la fameuse formule de co-aire de Federer.

Nous présentons dans ce document les résultats obtenus au cours de cette thèse sous la direction de Abdallah El Hamidi et Mustapha Jazar. Le travail suivant se décompose selon trois axes mathématiques autour des équations différentielles ordinaires (EDO) et des équations aux dérivées partielles (EDP) :

- L'étude de modèles de dynamique des populations : modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin .
- L'étude de modèles mathématiques basés sur les systèmes de réaction-diffusion non-linéaires. Un premier modèle qui permet la coexistence entre deux plantes, ces deux types de plantes sont en compétition spatiale dans un milieu saturé. L'autre modèle est de type proie-prédateur avec diffusion classique, dont la dynamique locale est de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin , et la dynamique spatiale est représentée par des termes de diffusion.
- L'identification des paramètres dans les systèmes paraboliques avec de diffusions non-linéaires.

1.2 Dynamique temporelle

La dynamique temporelle d'une population peut se décrire simplement en terme de variation de l'effectif de la population pendant un temps donné, en fonction de paramètres tels que l'effectif au temps t , les taux de natalité (fécondité, viabilité...), de mortalité, le sex-ratio...

1.2.1 Formulation générale

Le but de ce paragraphe est de montrer comment on obtient les équations modélisant la dynamique temporelle des populations, c'est à dire l'évolution des espèces (ou des entités) qui interagissent entre elles.

Le cadre général est celui des modèles continus, en temps continu, déterministes, autonomes, construits à partir de systèmes d'équations différentielles ordinaires.

On considère une communauté de plusieurs populations (deux par la suite), décrite à tout instant par le vecteur $u(t)$ dont les composantes représentent la densité de différentes populations étudiées ; la dynamique de l'évolution de u est

une fonction qui dépend explicitement de u à l'instant considéré, soit :

$$\frac{du(t)}{dt} = f(u(t)).$$

Dans le cas d'un modèle prenant en compte une communauté de m espèces, on considère donc $u = (u_1, \dots, u_m)$. La fonction d'évolution de la dynamique f est définie pour chaque espèce d'un terme de dynamique de la communauté sera définie pour chaque espèce comme une somme de terme de croissance intrinsèque et d'un terme d'interaction avec les autres espèces (ces différentes interactions soient couplées ou bien découplées), ce que l'on écrit comme suit :

$$\frac{du_i}{dt} = g_i(u_i) + h_i(u), \quad i = 1, \dots, m.$$

Le choix de la fonction d'interaction $h_i(u)$ reflète le type d'interaction considéré. Dans le paragraphe suivant, nous définissons les différents types d'interactions entre les individus des populations.

Interactions entre populations

Les populations ne vivent pas isolées et sont donc en perpétuelles interactions entre elles. Lorsque les espèces interagissent, la dynamique de chaque espèce est affectée par ces interactions. Il y a principalement trois types d'interactions (voir par exemple Murray [85]) :

- (i) *Mutualisme ou symbiose* : Lorsque les interactions entre espèces entraînent une augmentation du taux de croissance ou de reproduction de chaque population et chaque espèce tire profit de ces interactions. Les relations plantes/bactéries au niveau de la rhizosphère proposent de nombreux exemples de mutualisme.
- (ii) *Prédation ou parasitisme* : Lorsque le taux de croissance d'une ou de plusieurs espèces décroît tandis que le taux de croissance des autres espèces croît, on dit qu'on est en présence d'un système proie-prédateur. Par exemple, les protozoaires ciliés type paramécie sont des prédateurs des bactéries.
- (iii) *Compétition* : Lorsque les espèces interagissent et que cette interaction entraîne la décroissance du taux de reproduction ou du taux de croissance de chaque espèce. Par exemple, deux prédateurs d'espèces différentes mais chassant les mêmes proies sur le même territoire.

Parmi ces interactions certaines sont bénéfiques pour tous les espèces - c'est le cas du mutualisme - ou négatives comme dans le cas de compétition - ou positives pour des espèces et négatives pour les autres, c'est le cas de prédation.

Dans cette thèse, nous considérons des modèles avec des interactions de type compétition et prédation. Nous allons examiner en détail ci-dessous le modèle "proie-prédateur".

1.2.2 Le modèle “proie-prédateur ”

Le système proie-prédateur a été imaginé par Volterra (1925) pour modéliser l'évolution des sardines et des requins dans la mer Adriatique. Depuis le modèle de Lotka-Volterra, de nombreuses études ont contribué à exprimer de différents manières les taux de croissance des populations et leurs interactions.

Un système proie-prédateur, est un système permettant de prévoir l'évolution du nombre de proies et de prédateurs en fonction du temps. L'étude des systèmes proie-prédateur est utile car elle permet d'éviter l'extinction de certaines espèces et donc de préserver la biodiversité.

Dans ce paragraphe, nous considérons la famille des modèles proie-prédateur s'écrivant comme un système de 2 équations différentielles ordinaires.

Soit la formulation très générale d'un système proie-prédateur (Yodzis [122]) :

$$\begin{cases} \frac{du}{dt} = f(u) - vF(u, v), \\ \frac{dv}{dt} = vG(u, v), \end{cases} \quad (1.1)$$

où $u(t)$ et $v(t)$ désignent respectivement les densités de proies et de prédateurs à l'instant t .

Dans un tel système généralisé, trois fonctions sont à spécifier :

- $f(u)$: le taux de croissance de la population de proies en l'absence de prédateurs,
- $F(u, v)$: la réponse fonctionnelle du prédateur, i.e. le nombre de proies consommées par unité de temps par un prédateur,
- $G(u, v)$: la réponse numérique du prédateur décrivant la production de prédateurs, i.e. le taux de conversion de la proie en prédateur.

Les formes particulières choisies pour ces trois fonctions contiennent une quantité importante d'informations biologiques et sont déterminantes pour la dynamique du système étudié.

Taux de croissance de la population de proies

Une des premières description de la croissance d'une population a été introduite par Malthus (1798) quand il énonça que toute espèce a une capacité de croissance pouvant excéder une valeur moyenne observée. Cette capacité de croissance est dite croissance exponentielle ou géométrique ou malthusienne : une population augmente exponentiellement tant que ses ressources ne sont pas limitantes. En désignant par $u(t)$ l'abondance de la population au temps t , cette croissance peut être décrite par l'équation différentielle

$$f(u) = ru(t),$$

où r est le taux de croissance. Mais, l'hypothèse de croissance malthusienne de la population de proies est une hypothèse non réaliste du modèle de Lotka-Volterra. Les modèles subséquents prédateur-proie font plutôt l'hypothèse d'une croissance logistique densité-dépendante (Verhulst [102]) :

$$f(u) = ru \left(1 - \frac{u}{K}\right),$$

où $K > 0$ représente la capacité d'accueil (ou de charge) de l'habitat par rapport à la proie.

Différentes formulations de la réponse fonctionnelle

La relation entre l'effectif des proies et le taux de consommation de la nourriture pour un individu prédateur (taux de consommation de proies) a été appelé réponse fonctionnelle du prédateur (Solomon 1949). Le taux de consommation de proies dépend de deux facteurs : le taux d'attaque et le temps de manipulation des proies.

Dans ce paragraphe, nous présentons les différentes formulations de la réponse fonctionnelle du prédateur utilisées dans la littérature (Tableau 1.1).

La réponse fonctionnelle de type I est la relation linéaire du modèle de Lotka-Volterra, dans laquelle le nombre de proies capturées augmente linéairement avec l'accroissement de ces dernières. A la fin des années cinquante, Holling élaborera deux nouvelles réponses fonctionnelles pour la prédation visant également à transcrire une certaine satiété du prédateur vis-à-vis de ses proies : la fonction de Holling type II et la fonction de Holling type III. Cette formulation suppose que le prédateur divise son temps en deux sortes d'activités : la recherche de sa proie et sa capture qui comprend le temps mis pour la chasser, la tuer, la dévorer et la digérer.

Les modèles comportant ce type de réponse fonctionnelle qui ne dépend que de la densité de proies sont qualifiés de proie-dépendante (prey-dependent). En plus, ce type de réponses fonctionnelles correspond à la situation "laissez-faire" introduite par Caughley et Lawton [22] lorsqu'il n'y a pas d'interférence entre les prédateurs dans leurs activités d'alimentation. D'autres biologistes (Arditi et Ginzburg [8], Arditi, Ginzburg et Akçakaya [10], Akçakava [3], etc...) ont suggéré une classe de réponses fonctionnelles qui tiennent compte des densités de proies et de prédateurs, particulièrement quand les prédateurs doivent rechercher la nourriture (et doit donc partager ou concurrencer pour la nourriture).

Hassel et Varley (1969) sont les premiers qui ont considéré un modèle proie-prédateur tenant compte de l'interférence entre les prédateurs, leur fonction de réponse implique que le taux d'attaque décroît lorsque le prédateur v augmente et que pour une densité donnée de proies u , plus le nombre de prédateurs est élevé, plus le taux de consommation F par prédateur est faible (Tableau 1.1). Cette formulation très générale de réponse fonctionnelle avec interférence permet son application à un grand nombre de systèmes proie-prédateur. Ensuite,

Arditi et Ginzburg (1989) ont proposé la dépendance prédatrice, en modélisant la réponse fonctionnelle comme fonction d'un seul argument, cet argument étant toutefois le rapport ($\frac{u}{v}$) entre l'abondance des proies et celle des prédateurs. Leur fonction de réponse implique que le taux de consommation décroît proportionnellement avec l'abondance des prédateurs. Les modèles comportant ce type de réponse fonctionnelle sont qualifiés de ratio-dépendant. Cependant les formulations de Hassel-Varley et ratio-dépendant rendent le comportement du système pathologique : lorsque $v \rightarrow 0$, le taux d'attaque $a \rightarrow \infty$.

En outre, la réponse fonctionnelle de Beddington-DeAngelis (1975) permet de s'affranchir de cette limite d'application en supposant que le prédateur répartit le temps non seulement pour la recherche des proies, mais aussi à s'engager dans des rencontres avec d'autres prédateurs. La formulation de Beddington-DeAngelis est représentée par :

$$F(u, v) = \frac{au}{1 + bu + c(v - 1)},$$

où a (unité : 1/temps), b (unité : 1/proie), et c (unité : 1/prédateur) sont des constantes positives, a représente le taux de capture de la proie, b est le temps de manipulation, et c représente l'amplitude de l'interférence entre les prédateurs. Si $c = 0$, la réponse fonctionnelle de type Beddington-DeAngelis à une réponse fonctionnelle de type Holling II. L'hypothèse sous-jacente de la réponse fonctionnelle de Beddington-DeAngelis est que l'interférence et la manipulation sont des activités exclusives.

Crowley et Martin (1989) ont proposé une fonction de réponse qui permet l'interférence entre les prédateurs engagés dans la manipulation ou la recherche à un instant donné. Cette réponse fonctionnelle est donnée par :

$$F(u, v) = \frac{au}{1 + bu + c(v - 1) + bcu(v - 1)},$$

$(v - 1)$ est remplacé par v lorsque l'interférence des prédateurs est modélisée comme une variable continue. La réponse fonctionnelle de Crowley-Martin est dérivée de Beddington-DeAngelis en ajoutant un terme supplémentaire au dénominateur. La différence fondamentale entre ces deux réponses fonctionnelles est que la réponse fonctionnelle de type Beddington-DeAngelis suggère que les effets des interférences entre les prédateurs deviennent négligeables lorsque la densité des proies est forte. Alors que la réponse fonctionnelle de type Crowley-Martin estime que les effets d'interférence entre les prédateurs sur le taux d'alimentation restent importants sur toutes les densités des proies.

Hypothèses	Réponse fonctionnelle	Références
Pas d'interactions entre les prédateurs (laissez-faire)	$F = bu$	Lotka-Volterra type I 1925
	$F = \frac{au}{1+bu}$	Holling type II 1959
	$F = \frac{au^2}{1+bu^2}$	Holling type III 1959
Interférence entre les prédateurs	$F = \frac{u}{u+vm}$	Hassel et Varley 1969
	$F = \frac{au}{1+bu+cv}$	Beddington et DeAngelis 1975
	$F = \frac{au}{1+bu+cv+bcuv}$	Crowley et Martin 1989
Interférence et ratio-dépendance	$F = \frac{au}{u+v}$	Arditi et Ginzburg 1989

TABLE 1.1 – Synthèse de différentes formulations de la réponse fonctionnelle du prédateur. Les paramètres a, b et c sont positifs.

Différentes formulations de la réponse numérique du prédateur

La réponse numérique la plus courante correspondant aux systèmes “laissez-faire” (Tableau 1.2) représente un équilibre entre les gains de la population prédatrice (terme $eF(u)$ proportionnel à la quantité de proies consommées par prédateur), et ses pertes (terme $-d$).

Il existe une plus grande variété de modèles lorsqu’une interférence entre les prédateurs est prise en compte. L’effet de l’interférence peut porter sur le taux de consommation de chaque prédateur (i.e. la réponse fonctionnelle) ou sur le taux de croissance de la population de prédateurs (Tableau 1.2).

De structure très différente, la réponse numérique de Leslie (1948) repose sur l’idée que la population prédatrice croît de manière logistique, avec une capacité d’accueil hv proportionnelle à l’abondance de proies. Dans le système (1.1), la formulation donnée par Leslie et discutée par Leslie et Gower en 1960 et par Pielou en 1969 est

$$\frac{dv}{dt} = g \left(1 - \frac{v}{hu} \right) v.$$

Dans cette équation, la croissance du prédateur est logistique avec C la constante conventionnelle, qui mesure le niveau d’équilibre dû aux ressources de l’environnement, est proportionnelle aux ressources disponibles, c.à.d, à l’abondance des proies, $C = hu$. Le facteur h représente la conversion des proies en prédateurs. La

quantité $\frac{v}{hu}$ de cette équation est appelée le terme de Leslie-Gower. Il mesure la perte dans la population des prédateurs due à une pénurie (rapporté à la quantité $\frac{v}{u}$ de sa nourriture préférée. En cas de pénurie grave est sévère, il peut s'orienter vers d'autres ressources. Ceci affectera sa croissance qui sera très limitée par le fait que sa nourriture préférée ou de base est la proie u . Cette situation peut être prise en compte en ajoutant une constante positive k au dénominateur, ainsi cette équation dévient

$$\frac{dv}{dt} = g \left(1 - \frac{v}{k + hu} \right) v.$$

Le terme $\frac{v}{k+hu}$ est appelée terme modifié de Leslie-Gower et $g \left(1 - \frac{v}{k+hu} \right)$ est la réponse numérique modifiée de Leslie-Gower.

Hypothèses	Réponse numérique
laissez-faire	$G = -d + eF(u)$
Intéférence entre les prédateurs sur le taux de consommation	$G = -d + eF(u, v)$
Interférence entre les prédateurs sur le taux de croissance	$G = -d + eF(u) - fu^s$
Réponse numérique de Leslie	$G = g \left(1 - \frac{v}{hu} \right)$
Réponse numérique modifiée de Leslie-Gower	$G = g \left(1 - \frac{v}{k+hu} \right)$

TABLE 1.2 – Synthèse de différentes formulations de la réponse numérique du prédateur. Les paramètres d, e, f, g et h sont positifs.

1.3 Dynamique spatio-temporelle

Dans la section précédente, nous nous sommes intéressés à l'évolution temporelle des populations, mais lorsque la densité des populations devient trop élevée, que les ressources deviennent insuffisantes et que l'habitat est détérioré, les individus ont tendance à se disperser. La dispersion peut être passive ou active ; elle est passive dans le cas des espèces dont les capacités de déplacement autonome sont nulles ou limitées. Elle peut être active, dans le cas des individus qui se déplacent par leurs propres moyens. La dispersion des espèces d'une population peut être liée :

- à la recherche de la nourriture,

- à une recherche d’extension territoriale,
- au besoin de se déplacer vers un endroit mieux adapté qui maximise le taux de croissance et minimise la probabilité d’extinction de cette population.

Dans cette thèse, nous avons choisi le modèle de type réaction-diffusion pour décrire le déplacement des espèces qui ont tendance à augmenter leur mouvement en présence d’autres espèces.

1.3.1 Formulation générale

Le but de ce paragraphe est de montrer comment on obtient les équations modélisant la dynamique spatio-temporelle des populations, c’est à dire l’évolution d’espèces (ou d’entités) qui interagissent entre elles et se déplacent spatialement de façon aléatoire, en utilisant les lois de la conservation de la masse et les lois phénoménologiques de la diffusion.

Ces équations interviennent dans des domaines très variés comme la dynamique des populations [39, 62, 99, 100, 102], l’épidémiologie [19, 68] et l’écologie [5, 63, 66, 96].

Supposons que les individus résident dans une région Ω , qui est un domaine ouvert de l’espace euclidien \mathbb{R}^n , avec $n \geq 1$. En particulier nous serons intéressés par le cas $n = 2$, bien que le formalisme présenté ici s’applique à toute dimension de l’espace.

La variable mathématique que nous considérons ici est le vecteur des fonctions : $u(x, t) = (u_1(x, t), \dots, u_m(x, t))$, où t est le temps et $x \in \Omega$, dont les composantes représentent les densités (concentrations, densités de population, températures, etc.). Pour un domaine quelconque B de Ω , il est clair que la quantité totale de la population u dans B , au temps t est $\int_B u(x, t) dx$. Soit $J = (J_1, \dots, J_m)$ (resp. J_i , $i = 1, \dots, m$) le vecteur densité de flux qui contrôle la perte ou l’augmentation de u (resp. de u_i , $i = 1, \dots, m$), à travers ∂B , la frontière de B , et le terme de réaction $f = (f_1, \dots, f_m)$ correspond au taux de croissance de la population, il permet de modéliser les interactions entre les individus et les caractéristiques de l’habitat ou du milieu.

En général, les fonctions J et f peuvent dépendre de l’espace x , de temps t , de densité de population u , ainsi de ∇u_j , qui représente le mouvement (diffusion) de u_j , où pour chaque $i \in \{1, \dots, m\}$, j peut varier de 1 à m .

La loi de conservation de la masse s’exprime alors par le fait que le taux de variation temporelle de la quantité u contenue dans le domaine B est égale au flux total à travers ∂B et la quantité totale de réaction (naissance, mortalité) de u dans le domaine B :

$$\frac{d}{dt} \int_B u_i(x, t) dx = - \int_{\partial B} J_i(x, t) \cdot \mathbf{n}(x) d\sigma + \int_B f_i(x, t, u(x, t)) dx, \quad i = 1, \dots, m. \quad (1.2)$$

où \mathbf{n} est le vecteur unitaire normal extérieur à ∂B . Mais d'après le théorème de Stokes,

$$\int_{\partial B} J_i(x, t) \cdot \mathbf{n}(x) d\sigma = \int_B \operatorname{div}(J_i(x, t)) dx,$$

par suite, on a

$$\frac{d}{dt} \int_B u_i(x, t) dx = - \int_B \operatorname{div}(J_i(x, t)) dx + \int_B f_i(x, t, u(x, t)) dx. \quad (1.3)$$

Puisque le choix du domaine B est arbitraire, on peut choisir $B = B(y, R)$, une boule centrée en tout point fixé y de Ω , de rayon $R > 0$, suffisamment petit. En divisant (1.3) par $|B(y, R)|$, la mesure de Lebesgue de B , on obtient

$$\frac{1}{|B(y, R)|} \int_{B(y, R)} [(u_i)_t + \operatorname{div}(J_i) - f_i] dx = 0. \quad (1.4)$$

Par passage à la limite, lorsque R tend vers zéro, on obtient

$$(u_i)_t + \operatorname{div}(J_i) = f_i, \quad (1.5)$$

dans Ω , pour tout $1 \leq i \leq m$. L'éq. (1.5) est l'éq. de conservation de la masse encore appelée équation de continuité.

Le flux J_i de l'espèce u_i se définit grâce aux lois phénoménologiques de la diffusion (loi de Fick, loi de Fourier, loi d'Hom, ect). Dans de nombreuses situations, il est de la forme

$$J_i = - \sum_{j=1}^m [D_{ij}(x, t, u) \nabla u_j + \alpha_{ij}(x, t, u) u_j], \quad (1.6)$$

où D_{ij} et α_{ij} sont des fonctions connues à valeurs réelles pour tout $1 \leq i, j \leq m$. La première somme dans (1.6) est le terme de diffusion de u_i , et les termes $\alpha_{ij} u_j$ décrivent les déviations dans la direction du champ de vecteur α_{ij} , proportionnelles à la concentration de l'espèce u_j .

On va supposer dans la suite que α_{ij} sont des fonctions nulles, par suite $J_i = - \sum_{j=1}^m D_{ij}(x, t, u) \nabla u_j$.

En substituant cette dernière expression du flux dans l'équation (1.5), il vient

$$(u_i)_t - \sum_{j=1}^m \operatorname{div}(D_{ij}(x, t, u) \nabla u_j) = f_i(x, t, u(x, t)), \quad (1.7)$$

ce qui se réécrit

$$(u_i)_t - \operatorname{div}(D_{ii}(x, t, u) \nabla u_i) - \sum_{j, j \neq i}^m \operatorname{div}(D_{ij}(x, t, u) \nabla u_j) = f_i(x, t, u(x, t)),$$

où les termes D_{ii} sont les coefficients d'auto-diffusion (self-diffusion coefficients) et les termes $(D_{ij})_{j,j \neq i}$ sont les coefficients de diffusion croisée (cross-diffusion coefficients). Ces termes de diffusion croisée relient le gradient des espèces $(u_j)_{1 \leq j \leq m}$ avec le flux de l'espèce u_i . Biologiquement, les espèces u_i ont tendance à être attirés (resp. repoussés) par les espèces u_j , si $D_{ij}(x, t, u) > 0$, (resp. si $D_{ij}(x, t, u) < 0$).

En général, le système d'équations (1.7) est appelé "système de diffusions croisées". Ici $\sum_{j=1}^m \text{div}(D_{ij}(x, t, u) \nabla u_j)$ est le terme de diffusion qui décrit les mouvements des individus de l'espèce u_i , et $f_i(x, t, u)$ est le terme de réaction qui décrit la naissance/mort ou la réaction se produisant à l'intérieur de l'habitat.

Lorsque les coefficients D_{ii} sont des constantes positives pour tout $1 \leq i \leq m$, et $D_{ij} = 0$, pour tout $1 \leq j \leq m$, alors (1.7) est un système de réaction-diffusion

$$(u)_t - D\Delta u = f, \quad (1.8)$$

où D est une matrice diagonale d'ordre m .

Modèle de réaction-diffusion avec diffusions croisées

Afin de mieux comprendre la signification de diffusions croisées, on donne le modèle de Lotka-Volterra avec des diffusions croisées introduit en (1979) par Shigezada, Kawasaki et Teramoto dans [105],

$$\begin{cases} \frac{\partial u}{\partial t} - \Delta[u(d_1 + \alpha_{11}u + \alpha_{12}v)] = u(a_1 - b_1u - c_1v), & \text{dans } \Omega \times]0, +\infty[, \\ \frac{\partial v}{\partial t} - \Delta[v(d_2 + \alpha_{21}u + \alpha_{22}v)] = v(a_2 - b_2v - c_2u), & \text{dans } \Omega \times]0, +\infty[, \end{cases} \quad (1.9)$$

où Ω est un domaine borné de \mathbb{R}^n , $n \geq 1$, u et v représentent les densités de deux espèces en compétition, Les conditions aux limites sont de type Neumann homogènes. les coefficients d_i et α_{ij} , ainsi que les coefficients a_i , b_i et c_i sont supposés des constantes positives. Les expressions $\alpha_{12}\Delta(uv)$ et $\alpha_{21}\Delta(uv)$ sont les coefficients de diffusions croisées, et $\alpha_{11}\Delta(u^2)$ et $\alpha_{22}\Delta(v^2)$ décrivent l'auto-diffusion pour les espèces u et v respectivement.

Dans ce qui suit, on présente un type d'instabilité qui conduit à des comportements asymptotiques (des solutions) non homogènes (avec motifs spatiaux ou "patterns").

1.3.2 Instabilité de Turing

Turing (1952) a été le premier à mettre en évidence que l'interaction de deux substances chimiques de vitesses de diffusion différentes pouvait conduire à la formation de structures auto-organisées.

Le modèle proposé par Turing est un exemple typique de système réaction-diffusion. Turing explique la formation de structures, appelées aujourd'hui des structures de Turing, par la conjonction de réactions locales et de la diffusion moléculaire.

L'objectif dans ce paragraphe est de mettre en évidence le phénomène d'instabilité de Turing, c'est à dire le fait que dans le cas des systèmes, un équilibre stable de l'équation différentielle de réaction (sans espace, sans diffusion) peut devenir instable lorsqu'on ajoute de l'espace et de la diffusion en espace. Considérons le système de réaction-diffusion dans le cas de deux espèces, de concentrations u et v respectivement :

$$\begin{cases} \frac{\partial u}{\partial t} = D_u \Delta u + f(u, v), \\ \frac{\partial v}{\partial t} = D_v \Delta v + g(u, v), \end{cases} \quad (1.10)$$

où les fonctions f et g sont en général non-linéaires et la stabilité de système (1.10) au voisinage d'une solution homogène stationnaire (u^*, v^*) , définie par $f(u^*, v^*) = g(u^*, v^*) = 0$, peut être étudiée en linéarisant le système et en écrivant les relations de dispersion associées.

Théorème 1.3.1. *Une analyse linéaire montre que les conditions nécessaires pour donner les motifs de Turing sont*

$$f_1 + g_2 > 0$$

$$f_1 g_2 - f_2 g_1 > 0,$$

$$D_u f_1 + D_v g_2 > 0,$$

où f_1 et f_2 (resp. g_1 et g_2) sont les dérivées de f (resp. de g) par rapport à u et v respectivement.

1.4 Plan de la thèse

Cette thèse est constituée de 7 chapitres, chaque chapitre est indépendant des autres et utilise ses propres notations. Le premier et le dernier chapitre sont rédigés en français, tandis que les autres chapitres sont rédigés en anglais. Le chapitre 1 présente une introduction à la modélisation dynamique temporelle et

spatio-temporelle, et un résumé en français des travaux présentés dans les autres chapitres de thèse. Le chapitre 2 décrit un travail, intitulé *On nonlinear coupled diffusions in competition systems*, que j'ai effectué en début de thèse, et qui a été publié dans le Journal of Nonlinear Analysis : Real World Applications. Dans le chapitre 3, je présente un travail intitulé *A PDE model of clonal plant competition with nonlinear diffusion*, et qui a été accepté dans le Journal of Ecological Modelling. Le chapitre 4 est consacré à l'identification des diffusions croisées dans un modèle de réaction-diffusion non linéaires. Dans le chapitre 5, nous considérons un modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin, ce travail est accepté pour publication dans le Journal of Applied Mathematic and Computing. Ensuite, dans le chapitre 6, nous considérons le modèle proie-prédateur proposé dans le chapitre 5 en tenant en compte la dimension spatiale et la diffusion. Enfin, dans le chapitre 7, nous présentons les notions de base et les outils mathématiques utilisés dans les chapitres précédents.

1.5 Résumé des chapitres 2 à 6

1.5.1 Chapitre 2 : Diffusions couplées non-linéaires dans des systèmes de compétition

On s'intéresse dans ce chapitre à une classe de systèmes de réaction-diffusion modélisant la croissance des plantes en compétition spatiale dans un milieu saturé.

$$\left\{ \begin{array}{ll} u_t - \operatorname{div}(\mu_1(u, v)\nabla u) = f(u, v) & \text{dans } \Omega \times]0, +\infty[, \\ v_t - \operatorname{div}(\mu_2(u, v)\nabla v) = g(u, v) & \text{dans } \Omega \times]0, +\infty[, \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 & \text{sur } \partial\Omega \times [0, +\infty[, \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x) & \text{sur } \Omega, \end{array} \right. \quad (1.11)$$

où Ω est un domaine borné de \mathbb{R}^N , $N \geq 2$, à frontière régulière et \mathbf{n} est le vecteur unitaire normal dirigé vers l'extérieur de $\partial\Omega$.

(H1) μ_1, μ_2 appartiennent à $C^{2-}(D)$.

(H2) f, g continûment différentiables sur D et $f(0, v) \geq 0, g(u, 0) \geq 0$, pour tout $u, v \geq 0$.

(H3) $(u_0, v_0) \in C^{1-}(\overline{\Omega}, D)$.

On commence par un résultat d'existence globale en adaptant un résultat dû à Kouachi [71].

Théorème 1.5.1. (existence globale) Supposons que les hypothèses (H1)-(H3) sont vérifiées et

– Il existe $m \geq 1$ tel que

$$|f(u, v)|, |g(u, v)| \leq C_2(u + v + 1)^m, \text{ pour tout } u, v > 0, \quad (1.12)$$

– Il existe un entier $p > \frac{Nm}{2}$ tel que, pour chaque $u, v \geq 0$, on a

$$K^{2i-1}f(u, v) + g(u, v) \leq C_1(u + v + 1), \quad i = 1, \dots, p, \quad (1.13)$$

où C_1 et C_2 sont deux constantes positives et K est une constante arbitraire satisfaisant

$$K \geq \frac{\overline{\mu}_1(1 + \varepsilon_1) + \overline{\mu}_2(1 + \varepsilon_2)}{2\sqrt{\mu_1 \mu_2 \varepsilon_1 \varepsilon_2}}.$$

Alors toute solution (u, v) de (1.11) avec conditions initiales (u_0, v_0) dans $\mathbf{L}^\infty(\Omega)$ sont définies pour tout $t > 0$.

Dans le cas particulier où les termes de réaction sont de type logistique-compétition, nous montrons que le problème d'instabilité ne peut pas avoir lieu lorsque les coefficients de diffusion sont positifs.

Considérons le système suivant :

$$\begin{cases} u'_t = f(u, v), & t \geq 0, \\ v'_t = g(u, v), & t \geq 0, \end{cases} \quad (1.14)$$

où f et g sont des fonctions satisfaisant

$$\frac{\partial f}{\partial v} \leq 0 \quad \text{et} \quad \frac{\partial g}{\partial u} \leq 0, \quad (1.15)$$

$$f(0, v) \geq 0 \quad \text{et} \quad g(u, 0) \geq 0 \quad \text{pour tout } u \geq 0, v \geq 0. \quad (1.16)$$

Alors on a le résultat suivant :

Théorème 1.5.2. Soient μ_1 et μ_2 deux fonctions positives, de classe C^1 sur $[0, +\infty[\times [0, +\infty[$. Soient f et g deux fonctions de classe C^1 sur $[0, +\infty[\times [0, +\infty[$ satisfaisant les conditions de compétition (1.15) et la condition de positivité (1.16). Soit (u^*, v^*) un état d'équilibre linéairement stable de (1.11) tel que $\mu_i(u^*, v^*) > 0$. Alors (u^*, v^*) possède la même stabilité linéaire du système (1.14). Ainsi, la présence des diffusions dans (1.11) n'a pas d'influence sur la stabilité linéaire de (u^*, v^*) . En particulier, l'instabilité de Turing n'a pas lieu.

Nous terminons ce chapitre par des simulations numériques du modèle de Lotka-Volterra avec des diffusions couplées suivant

$$\left\{ \begin{array}{l} u_t - \operatorname{div}(\mu_1(u, v)\nabla u) = u(\alpha_1 - \beta_1 u - \gamma_1 v) \text{ sur }]0, +\infty[\times \Omega \\ v_t - \operatorname{div}(\mu_2(u, v)\nabla v) = v(\alpha_2 - \beta_2 v - \gamma_2 u) \text{ sur }]0, +\infty[\times \Omega \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 \text{ dans } \partial\Omega \times [0, +\infty[, \\ u(0, x) = u_0(x), \quad v(0, x) = v_0(x) \text{ sur } \Omega \end{array} \right. \quad (1.17)$$

1.5.2 Chapitre 3 : Un modèle d'EDP de plantes clonales en compétition avec diffusions non-linéaires

Dans ce chapitre, nous avons présenté dans quelle mesure un modèle EDP simplifié de compétition spatio-temporelle pourrait constituer un modèle de substitution à un modèle d'agent de type individu-centré (Individual Based Models ou IBM en abrégé). En effet, le modèle EDP peut apporter une grande variété de résultats au niveau macroscopique tel le comportement asymptotique et la structure spatiale avec des algorithmes faciles à implémenter et peu gourmand en temps de calcul. Contrairement aux modèles d'agent (microscopique de nature) qui sont trop complexes lorsque plusieurs espèces sont en jeu et requièrent du calcul intensifs.

Nous avons motivé le type de diffusion croisées qu'il faudrait considérer dans les modèles EDP de compétition pour avoir les structures spatiales observées dans les simulations IBM d'une part. D'autre part, nous avons essayé de trouver des analogies entre les termes sources et les termes de diffusions croisées respectivement d'une part avec l'accès aux ressources et à la lumière d'autre part.

Le système modèle que nous avons considéré est le suivant :

$$\left\{ \begin{array}{ll} u_t - \operatorname{div}(\mu_1(u, v)\nabla u) = f(u, v) & \text{dans } \Omega \times]0, +\infty[, \\ v_t - \operatorname{div}(\mu_2(u, v)\nabla v) = g(u, v) & \text{dans } \Omega \times]0, +\infty[, \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 & \text{sur } \partial\Omega \times [0, +\infty[, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0 & \text{dans } \Omega. \end{array} \right. \quad (1.18)$$

Lorsque, par exemple, $\mu_1(u, v)$ est nulle pour $v > \eta > 0$, alors l'espèce v empêche l'espèce u de diffuser aux endroits où v est suffisamment présente.

1.5.3 Chapitre 4 : Identification de paramètres dans les systèmes des diffusions couplées non-linéaires via les données IBM

Dans ce chapitre, on considère l'un des points centraux de cette thèse qu'est le problème d'identification des termes de diffusions croisées. Le problème d'identification se fait à partir d'observations spatio-temporelles. Pour cela, on construit une fonctionnelle d'énergie appropriée à minimiser dont le minimiseur est le vecteur dont les composantes sont les fonctions diffusions croisées recherchées. La difficulté dans ce type de problèmes de minimisation est le fait que le gradient de la diffusion (recherchée) dépend de la solution du système non-linéaire qui dépend elle-même de cette diffusion.

Nous avons considéré un système général :

$$\left\{ \begin{array}{l} u_t - \operatorname{div}(\mu_1(x, t, u, v, \nabla u)) = u f_1(x, t, u, v) := f(x, t, u, v) \text{ dans } \Omega \times]0, T], \\ v_t - \operatorname{div}(\mu_2(x, t, u, v, \nabla v)) = v g_1(x, t, u, v) := g(x, t, u, v) \text{ dans } \Omega \times]0, T], \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 \text{ sur } \partial\Omega \times]0, T], \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x) \text{ dans } \Omega, \end{array} \right. \quad (1.19)$$

où les termes μ_i , $i = 1, 2$, satisfont les conditions classiques de Leray-Lions. Les fonctions f_1 et f_2 intervenant dans les termes sources sont supposées lipschitziennes.

Grâce à la théorie développée par Minty et Browder, nous montrons l'existence de solutions dans $L^\infty(0, T; L^2(\Omega)) \cap L^2(0, T; H^1(\Omega))$.

Nous avons introduit ensuite une énergie à partir d'observations spatio-temporelles. Comme l'identification requiert le calcul du gradient de cette énergie, alors la différentiabilité de la solution du système par rapport aux diffusions. Nous avons explicité le gradient de cette énergie grâce à la formule de co-aire . A notre connaissance, cette caractérisation est une contribution nouvelle. Nous terminons ce chapitre par des simulations numériques basées sur l'optimisation via les méthodes de type quasi-Newton.

1.5.4 Chapitre 5 : Dynamique globale du modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin

Dans ce chapitre, nous proposons et étudions un modèle proie-prédateur qui résulte d'une combinaison du modèle modifié de Leslie-Gower avec une réponse fonctionnelle de type Crowley-Martin . Le modèle mathématique associé est le

suivant

$$\begin{cases} \frac{du}{dt} = a_1 u \left(1 - \frac{u}{K}\right) - \frac{buv}{(1+cu)(1+dv)}, \\ \frac{dv}{dt} = v \left(a_2 - \frac{ev}{u+f}\right), \end{cases} \quad (1.20)$$

avec $u(0) \geq 0$ et $v(0) \geq 0$, u et v représentent respectivement la densité de proies et de prédateurs à l'instant t ; a_1, a_2, b, c, d, e, f et K sont les paramètres du modèle supposés strictement positifs.

Ces paramètres sont définis de la manière suivante : Le terme a_1 (resp. a_2) est le taux de croissance de la proie u (resp. de prédateur v), K représente la capacité d'accueil du milieu, $\frac{a_1}{k}$ mesure la mortalité due à la compétition entre les individus de l'espèce u . Les réels b, c et d sont les paramètres saturants de la réponse fonctionnelle de type Crowley-Martin, e est la valeur maximale que le taux de réduction par individu v peut atteindre, f mesure la protection dont la prédateur bénéficie grâce à l'environnement.

Il s'agit ici d'un modèle proie-prédateur car le terme d'interaction dans l'équation de la proie $\frac{buv}{(1+cu)(1+dv)}$ agit négativement sur la dynamique des proies, tandis que le terme d'interaction dans l'équation de prédateur $\frac{ev}{u+f}$ est favorable aux prédateurs : leur capacité limite augmente avec la densité de proie. En l'absence de prédateurs, la dynamique des proies suit un modèle logisitique.

Nous nous intéressons particulièrement à la bornitude des solutions, nous étudions ensuite l'analyse qualitative des solutions, la stabilité locale des équilibres, les bifurcations locales. En plus, nous étudions également la permanence, l'existence et la non-existence de cycles limites. En outre, des simulations numériques sont présentées pour illustrer les résultats théoriques.

Afin d'étudier le modèle (1.20), nous réduisons le nombre de paramètres en introduisant le changement de variables suivant :

$$A = cK, \quad B = \frac{da_1}{b}, \quad C = \frac{a_2}{a_1}, \quad D = \frac{ea_1}{Kba_2}, \quad E = \frac{f}{K}.$$

Le problème (1.20) s'écrit alors

$$\begin{cases} \frac{du}{dt} = u \left(1 - u - \frac{v}{(1+Au)(1+Bv)}\right) =: F_1(u, v), \\ \frac{dv}{dt} = Cv \left(1 - \frac{Dv}{u+E}\right) =: F_2(u, v). \end{cases} \quad (1.21)$$

Résultats : Bornitude des solutions, Existence des équilibres, stabilité asymptotique locale, permanence, Existence et non-existence de cycles limites, stabilité globale.

Théorème 1.5.3. *Soit \mathcal{A} l'ensemble défini par*

$$\mathcal{A} = \left\{ (u, v) \in \mathbb{R}_+^2 : 0 \leq u \leq 1, 0 \leq v \leq \frac{1+E}{D} \right\},$$

Alors,

- (a) \mathcal{A} est positivement invariant,
- (b) Toute solution du problème (1.20) dont la condition initiale est dans $\mathbb{R}^+ \times \mathbb{R}^+$, converge vers \mathcal{A} .

Théorème 1.5.4. *(Permanence) Si $E < EB + D$, alors le système (1.20) est permanent.*

Théorème 1.5.5. *(non-existence de cycle limite) Supposons que l'hypothèses suivante soit satisfaite,*

$$A(1 - C) < 1, \tag{1.22}$$

alors le système (1.20) n'a pas de cycles limites.

Théorème 1.5.6. *(Stabilité globale) L'unique équilibre positif du système (1.20) est globalement asymptotiquement stable si*

$$\frac{Av^*}{(1 + Au^*)(1 + Bv^*)} < \frac{E + 2}{E + 1}, \tag{1.23}$$

et l'une des deux conditions suivantes est satisfaite

$$4D^2 \leq \frac{2E + 1}{E(3E + 1)} \quad \text{et} \quad \frac{1}{E} \left(1 - \frac{1}{4D^2E} \right) \geq Q \tag{1.24}$$

ou

$$4D^2 > \frac{2E + 1}{E(3E + 1)} \quad \text{et} \quad \frac{1}{(E + 1)} \left(1 - \frac{1}{4D^2(E + 1)} \right) \geq Q. \tag{1.25}$$

Théorème 1.5.7. *Si $E > EB + D$ et la condition suivante est satisfaite*

$$\frac{(1 + A)(D + B(1 + E))}{E} < D < \frac{E}{E + 1}, \tag{1.26}$$

alors l'équilibre de l'extinction de proies $E_2(0, E/D)$ de système (1.23) est globalement asymptotiquement stable .

Nous terminons le chapitre par des simulations numériques pour illustrer les résultats théoriques obtenus.

1.5.5 Chapitre 6 : Dynamiques spatio-temporelles d'un modèle proie-prédateur de type Leslie-Gower modifié et avec une fonction de réponse de type Crowley-Martin

Nous présentons dans ce chapitre un modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin, qui prend en compte l'évolution de la distribution spatiale des deux populations.

$$\left\{ \begin{array}{l} \frac{\partial u}{\partial t} = D_1 \Delta u + a_1 u \left(1 - \frac{u}{K} \right) - \frac{bv}{1 + cu + dv + cduv} \quad x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} = D_2 \Delta v + v \left(a_2 - \frac{ev}{u + f} \right) \quad x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, \quad x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, \quad x \in \Omega, \end{array} \right. \quad (1.27)$$

où $u(x, t)$ et $v(x, t)$ représentent respectivement la densité de proies et de prédateurs à l'instant t et à la position x , Δ étant l'opérateur Laplacien. D_1 et D_2 sont respectivement les coefficients de diffusion des proies et des prédateurs. Les termes a_1, a_2, b, c, d, e, f et K sont des paramètres du modèle (1.20). Ils jouent le même rôle décrit dans le modèle (1.20) et ils sont supposés positifs.

On s'intéresse particulièrement à l'existence globale des solutions, la dissipation et la persistance uniforme du système; et on étudie la stabilité des états d'équilibre. Nous démontrons aussi l'existence et l'unicité des orbites périodiques. De même, les bifurcations de Hopf et l'instabilité de Turing survenant dans ce modèle sont étudiées.

* - * - * - * - * - * - *

Chapitre 2

On nonlinear coupled diffusions in competition systems

Sommaire

| | |
|---|-----------|
| Présentation du chapitre | 22 |
| Abstract | 22 |
| 2.1 Introduction | 22 |
| 2.2 Local and global existence results | 24 |
| 2.2.1 Definitions and notations | 25 |
| 2.3 Competition systems and diffusion driven instability | 29 |
| 2.4 Simplified competition model for clonal plants | 31 |
| 2.4.1 Lotka-Volterra nonlinear coupled diffusion model . . . | 31 |
| 2.4.2 Numerical Simulation of a Benchmark Problem | 35 |

Le travail présenté dans ce chapitre est issu d'une collaboration avec Abdallah El Hamidi et Marc Garbey. Nous nous intéressons aux modèles de réaction-diffusion avec des diffusions couplées non-linéaires modélisant la croissance de deux types de plantes en compétition spatiale dans un milieu saturé. Nous démontrons, dans ce contexte, que la diffusion standard ne peut pas conduire à la formation des motifs. Ce travail a fait l'objet d'un article publié dans le journal *Nonlinear Analysis : Real World Applications*.

Abstract

A class of reaction-diffusion systems modeling plant growth with spatial competition in saturated media is presented. We show, in this context, that standard diffusion can not lead to patterns formation (Diffusion Driven Instability of Turing). Degenerated nonlinear coupled diffusions inducing free boundaries and exclusive spatial diffusions are proposed. Local and global existence results are proved for smooth approximations of the degenerated nonlinear diffusions systems which give rise to long-time pattern formations. Numerical simulations of a competition model with degenerate/non degenerate nonlinear coupled diffusions are performed and we carry out the effect of the these diffusions on patterns formation and on the change of basins of attraction.

Keywords : Nonlinear diffusion, Competition, Turing instability, Pattern formation, Lyapunov.

2.1 Introduction

The role of spatial heterogeneities and dispersal for chemical reacting species or biological interacting populations in the linear or nonlinear regime has been the subject of a sizeable literature (see e.g. the reference books of Aris [11], Cussler [28] and Okubo [90]).

In particular cross-diffusion in modeling interactions among different species has attracted special attentions. Apart the above quoted books, one can cite [39, 62, 99, 100, 102] in physical-chemistry, [19, 68] in epidemics, [5, 63, 66, 96] in ecology, population dynamics or biology and [21] in economics.

Before announcing our main results, let us dwell for a while on the modeling part [35]. Consider, for example, two substances (species, chemicals, etc.) that are activating or inhibiting each other according to some law of reaction and diffusing in a spatial domain by Fick's law but the diffusion of one of the substances is influenced also by the other one and vice versa. The density of the two substances at time t and place x are denoted by $u(x, t)$ and $v(x, t)$ respectively.

On one hand, the substance u flows from places where its density is high towards places where the density is low. On the other hand, v has an attracting

or repelling effect on u , so that u flows towards high, resp. low density places of v . In this situation the flow vector of u is given by

$$J_u = -d_{11}(u, v)\nabla u - d_{12}(u, v)\nabla v,$$

where $d_{11}(u, v) > 0$ and $d_{12}(u, v) \leq 0$, resp. ≥ 0 according as v attracts, resp repels u .

Similarly, the flow of v is given by

$$J_v = -d_{21}(u, v)\nabla u - d_{22}(u, v)\nabla v,$$

where $d_{22}(u, v) > 0$ and $d_{21}(u, v) \leq 0$, resp. ≥ 0 according as u attracts, resp repels v . Then a macroscopic continuous model describing this interaction is given by the reaction-diffusion system

$$\begin{cases} u_t - \operatorname{div}(d_{11}(u, v)\nabla u + d_{12}(u, v)\nabla v) &= f(u, v), \\ v_t - \operatorname{div}(d_{21}(u, v)\nabla u + d_{22}(u, v)\nabla v) &= g(u, v), \end{cases} \quad (2.1)$$

where $f(u, v)$ and $g(u, v)$ are the reaction terms.

A well-known model describing the competition between two ecological species is the special case

$$\begin{cases} u_t - d_{11}\Delta u &= u(\alpha_1 - \beta_1 u - \gamma_1 v), \\ v_t - d_{22}\Delta v &= v(\alpha_2 - \beta_2 v - \gamma_2 u), \end{cases} \quad (2.2)$$

where d_{ii} denote the diffusion rates, α_i the intrinsic growth rates, β_i the intra-specific competition rates and γ_i the inter-specific competition rates of u and v , $1 \leq i \leq 2$. A brief description of this system is given in Section 4 when the parameters are all constants. In this case, if the two species u and v are (ecologically) strongly competing, that is

$$\frac{\beta_1}{\gamma_2} < \frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2},$$

the competitive exclusion principle between the u and v occurs [69, 85]. More precisely, any nonnegative solution (u, v) converges to either $(\alpha_1/\beta_1, 0)$ or $(0, \alpha_2/\beta_2)$. However, observations in natural fields show that strongly competing species can coexist. In [105], the authors show that this phenomenon can be assigned to the repulsive effect between competing species. In the same vein, we propose a model of nonlinear coupled diffusion which give rise to coexistence of two strongly competing species and thus to pattern formation.

2.2 Local and global existence results

This section is devoted to local and global existence results to the nonlinear coupled diffusion problem

$$\left\{ \begin{array}{ll} u_t - \operatorname{div}(\mu_1(u, v)\nabla u) = f(u, v) & \text{in } \Omega \times]0, +\infty[, \\ v_t - \operatorname{div}(\mu_2(u, v)\nabla v) = g(u, v) & \text{in } \Omega \times]0, +\infty[, \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 & \text{on } \partial\Omega \times [0, +\infty[, \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x) & \text{in } \Omega, \end{array} \right. \quad (2.3)$$

where Ω is a bounded domain in \mathbb{R}^N , $N \geq 2$, with smooth boundary and \mathbf{n} is the unit outward pointing normal on $\partial\Omega$.

In our context, $u(x, t) \geq 0$ and $v(x, t) \geq 0$ stand for the biomass of the two species at $x \in \Omega$ and $t \geq 0$. The reaction terms $f(u, v)$ and $g(u, v)$ account for the interaction between species (intraspecific and interspecific interactions). The medium is supposed to be homogeneous, that is, there is no explicit dependence on the space variables and the system is autonomous. In [41], the authors consider that when populations behave so as to avoid crowding it is reasonable to assume that the diffusion terms μ_1 and μ_2 are increasing functions of the population densities u and v respectively. On the other hand, since the diffusion of u is penalized where v is positive, and *vice versa*, it is reasonable to assume also that the diffusion terms μ_1 and μ_2 are strongly decreasing in v and u respectively. Notice that these generalized diffusion terms are more realistic since they allow *finite speed propagation* in space unlike constant diffusions which led to the standard Laplacian operator and its well known *infinite speed propagation* [115]. The assumptions on the diffusions μ_1 and μ_2 , on the source terms f , g and the initial data u_0 , v_0 will be specified later.

Theoretically, the dependence of μ_1 in v (resp. μ_2 in u) is such that u (resp. v) can not diffuse wherever $v > 0$ (resp. $u > 0$). Then μ_1 and μ_2 have to behave as the following

$$\begin{aligned} \mu_1(u(x), v(x)) &= \varphi_1(u(x)) \times \mathbf{1}_{\Omega \setminus \operatorname{supp}(v)}(x), \\ \mu_2(u(x), v(x)) &= \varphi_2(v(x)) \times \mathbf{1}_{\Omega \setminus \operatorname{supp}(u)}(x), \end{aligned}$$

for every $x \in \Omega$, where φ_1 and φ_2 are positive, increasing and smooth functions on $[0, +\infty[$. The set $\operatorname{supp}(u)$ is the closure of $\{x \in \Omega : u(x) \neq 0\}$ and for every subset ω of Ω :

$$\mathbf{1}_\omega(x) = \begin{cases} 1 & \text{if } x \in \omega, \\ 0 & \text{if } x \notin \omega. \end{cases} \quad (2.4)$$

This kind of diffusion terms leads to very complicated mathematical free boundary models which not reflect the weak *miscibility* between plant populations. Then,

we introduce smooth approximations, to these free boundary problems, which allow a small miscibility between u and v :

$$\mu_1(u, v) = \varphi_1(u)T_\eta(v), \quad \mu_2(u, v) = \varphi_2(v)T_\eta(u), \quad (2.5)$$

where T_η is an approximation of the standard truncation function defined by

$$T_\eta(s) = \begin{cases} \exp\left(\frac{s^2}{s^2 - \eta^2}\right) & \text{if } 0 \leq s < \eta \\ 0 & \text{if } s \geq \eta \end{cases} \quad (2.6)$$

for some $\eta > 0$ sufficiently small. This means that if the biomass u satisfies $u \geq \eta$, then the diffusion coefficient $\mu_2(u, v)$ vanishes and vice versa.

To show local existence of a classical solution, we will use some results due to H. Amann [6]. For the reader's convenience, we will recall some definitions and notations used in [6].

2.2.1 Definitions and notations

Let $(X, \|\cdot\|_X)$ and $(E, \|\cdot\|_E)$ be two Banach spaces and $u \in \mathcal{F}(X, E)$, the set of all functions from X to E .

Definition 2.2.1. *The function $u : X \rightarrow E$ is ρ -uniform Hölder continuous, where $0 < \rho \leq 1$, if*

$$\|u\|_{\rho, X} = \sup_{x \neq y} \frac{\|u(x) - u(y)\|_E}{\|x - y\|_X^\rho} < \infty.$$

Definition 2.2.2. *The function u is ρ -Hölder continuous if every point in X has a neighborhood $Y \subset X$ such that the restriction $u|_Y$ is ρ -uniform Hölder continuous. We pose*

$$\mathcal{C}^\rho(X, E) = \{u \in \mathcal{F}(X, E) : u \text{ is } \rho\text{-Hölder continuous}\}, \quad 0 < \rho < 1$$

and $\mathcal{C}^0(X, E) = \mathcal{C}(X, E)$ is the set of all continuous functions from X to E . A 1-Hölder continuous function is called Lipschitz continuous and we set

$$\mathcal{C}^{1-}(X, E) = \{u \in \mathcal{F}(X, E) : u \text{ is Lipschitz continuous}\}. \quad (2.7)$$

At this stage, we define Hölder continuous spaces for $\rho > 1$:

Definition 2.2.3. *Let $s > 1$.*

– *If $s \in]1, +\infty[\setminus \mathbb{N}$ then $\mathcal{C}^s(X, E)$ is the space defined by :*

$$\mathcal{C}^s(X, E) = \{u \in \mathcal{F}(X, E) : \partial^{[s]}u \text{ is } (s - [s])\text{-Hölder continuous and } \partial^\alpha u \text{ are Lipschitz continuous } \forall \alpha = 0, \dots, [s] - 1\}.$$

- If $s \in]1, +\infty[\cap \mathbb{N}$ then $\mathcal{C}^{s-}(X, E)$ is defined by

$$\mathcal{C}^{s-}(X, E) = \{u \in E^X : \partial^\alpha u \text{ sont Lipschitz continues } \forall \alpha = 0, \dots, s-1\}. \quad (2.8)$$

Consider the open subset D of $[0, +\infty[\times [0, +\infty[$ given by $D = [0, \eta[\times [0, \eta[$. It is clear that under our assumptions on μ_1 and μ_2 , for every $(u, v) \in D$, one has

$$\mu_1(u, v) > 0 \text{ and } \mu_2(u, v) > 0,$$

Then System (2.3) is normally elliptic in the sense of [6]. Next, we will do the following assumptions on the data :

(H1) μ_1, μ_2 belong to $C^{2-}(D)$.

(H2) f, g are continuously differentiable on D and $f(0, v) \geq 0, g(u, 0) \geq 0$, for every $u, v \geq 0$.

(H3) $(u_0, v_0) \in C^{1-}(\overline{\Omega}, D)$.

Notice that the hypothesis (H2) allows the positivity of solutions to (2.3) on their interval of existence [107]. Therefore, we have the following local existence result :

Theorem 2.2.4 ([6] pages 85 and 88). *There exists $t_{max} > 0$ such that Problem (2.3) has a unique solution $u, v \in C^{2,1}([0, t_{max}[\times \overline{\Omega}, D) \cap C([0, t_{max}[\times \overline{\Omega}, D)$. In particular, $u \geq 0$ and $v \geq 0$ on $[0, t_{max}[\times \overline{\Omega}$.*

Notice that the previous result guarantees local existence as the diffusion operators are normally elliptic, that is, $(u, v) \in D$. Therefore, our local existence result concerns only "small" data (which is not restrictive) but also only small solutions (which is restrictive) ; this is due to the strong degeneracy of the diffusion operators (diffusion operators have compact supports in \mathbb{R}^2).

We will encounter the same difficulty for global existence in the degenerate coupled diffusion case, then we will regularize the diffusion operators by *small* positives parameters. More precisely, we will assume that :

$$(H4) \begin{cases} \mu_1(u, v) = \varphi_1(u) T_{\eta_1}^{\varepsilon_1}(v), & \text{with } T_{\eta_1}^{\varepsilon_1}(v) := T_{\eta_1}(v) + \varepsilon_1, \\ \mu_2(u, v) = \varphi_2(v) T_{\eta_2}^{\varepsilon_2}(u), & \text{with } T_{\eta_2}^{\varepsilon_2}(u) := T_{\eta_2}(u) + \varepsilon_2, \\ \varphi_i(s) \in [\underline{\mu}_i, \overline{\mu}_i], & i = 1, 2, \text{ for every } s \geq 0, \end{cases}$$

where $\eta_i, \varepsilon_i, \underline{\mu}_i$ and $\overline{\mu}_i, i = 1, 2$, are given positive parameters. In this situation the restrictive condition (H3) can be weakened as (u_0, v_0) in $L^\infty(\Omega) \times L^\infty(\Omega)$. At this stage, we can state and show the following

Theorem 2.2.5. (global existence) *Assume that hypotheses (H1)-(H2) hold true and*

– There is $m \geq 1$ such that

$$|f(u, v)|, |g(u, v)| \leq C_2(u + v + 1)^m, \quad \text{for every } u, v > 0, \quad (2.9)$$

– there is an integer $p > \frac{Nm}{2}$ such that, for every $u, v \geq 0$, one has

$$K^{2i-1}f(u, v) + g(u, v) \leq C_1(u + v + 1), \quad i = 1, \dots, p, \quad (2.10)$$

where C_1 and C_2 are two positive constants and K is an arbitrary constant satisfying

$$K \geq \frac{\overline{\mu}_1(1 + \varepsilon_1) + \overline{\mu}_2(1 + \varepsilon_2)}{2\sqrt{\underline{\mu}_1 \underline{\mu}_2 \varepsilon_1 \varepsilon_2}}.$$

Then every solution (u, v) of (2.3) with initial data (u_0, v_0) in $L^\infty(\Omega)$ are defined for every $t > 0$.

Proof. The proof is inspired from a result due to S. Kouachi [71].

Let $(u(\cdot, t), (v(\cdot, t)))$, $t > 0$, be a solution of (2.3) and let

$$L(t) = \int_{\Omega} H_p(u(t, x), (v(t, x))) dx, \quad (2.11)$$

where

$$H_p(u, v) = \sum_{i=0}^p C_p^i K^{i^2} u^i v^{p-i}.$$

The function L is then uniformly bounded on every interval of the form $[0, t^*]$, with $t^* < t_{max}$. Indeed, we have

$$\begin{aligned} L'(t) &= \int_{\Omega} \left[\sum_{i=1}^p i C_p^i K^{i^2} u^{i-1} v^{p-i} \frac{\partial u}{\partial t} \right] dx + \int_{\Omega} \left[\sum_{i=1}^p (p-i) C_p^i K^{i^2} u^i v^{p-i-1} \frac{\partial v}{\partial t} \right] dx \\ &= \int_{\Omega} \sum_{i=1}^p \left(i C_p^i K^{i^2} u^{i-1} v^{p-i} \operatorname{div}(\mu_1 \nabla u) \right) dx \\ &+ \int_{\Omega} \sum_{i=1}^p \left((p-i+1) C_p^{i-1} K^{(i-1)^2} u^{i-1} v^{p-i} \operatorname{div}(\mu_2 \nabla v) \right) dx \\ &+ \int_{\Omega} \sum_{i=1}^p \left(i C_p^i K^{i^2} u^{i-1} v^{p-i} f(u, v) \right) dx \\ &+ \int_{\Omega} \sum_{i=1}^p \left((p-i+1) C_p^{i-1} K^{(i-1)^2} u^{i-1} v^{p-i} g(u, v) \right) dx \\ &= I + J. \end{aligned}$$

where I is the sum of the two first terms and J is the sum of the two last ones.

Using Green's formula we get :

$$I = - \int_{\Omega} [\mathcal{A}(u, v) |\nabla u|^2 + \mathcal{B}(u, v) \nabla u \cdot \nabla v + \mathcal{C}(u, v) |\nabla v|^2] dx,$$

where

$$\mathcal{A} = p(p-1)\mu_1(u, v) \sum_{j=0}^{p-2} C_{p-2}^j K^{(j+2)^2} u^j v^{p-j-2},$$

$$\mathcal{B} = p(p-1)(\mu_1(u, v) + \mu_2(u, v)) \sum_{j=0}^{p-2} C_{p-2}^j K^{(j+2)^2} u^j v^{p-j-2},$$

and

$$\mathcal{C} = p(p-1)\mu_2(u, v) \sum_{j=0}^{p-2} C_{p-2}^j K^{j^2} u^j v^{p-j-2}.$$

On the other hand, using the identity $iC_p^i = pC_{p-1}^{i-1}$, for every $i = 1, \dots, p$, we can rewrite :

$$\begin{aligned} \mathcal{A} &= \mu_1(u, v) \sum_{i=2}^p i(i-1)C_p^i K^{i^2} u^{i-2} v^{p-i}, \\ \mathcal{B} &= \mu_1(u, v) \sum_{i=1}^{p-1} i(p-i)C_p^i K^{i^2} u^{i-1} v^{p-i-1} \\ &\quad + \mu_2(u, v) \sum_{i=2}^p (i-1)(p-i+1)C_p^{i-1} K^{(i-1)^2} u^{i-2} v^{p-i}, \end{aligned}$$

and

$$\mathcal{C} = p(p-1)\mu_2(u, v) \sum_{j=0}^{p-2} C_{p-2}^j K^{j^2} u^j v^{p-j-2}.$$

Therefore, it holds

$$I = -p(p-1) \sum_{j=0}^{p-2} C_{p-2}^j \int_{\Omega} u^j v^{p-j-2} \mathcal{D}_j(u, v) dx,$$

where

$$\begin{aligned} \mathcal{D}_j(u, v) &:= \mu_1(u, v)K^{(j+1)^2} |\nabla u|^2 + (\mu_1(u, v) + \mu_2(u, v))K^{(j+1)^2} \nabla u \cdot \nabla v \\ &\quad + \mu_2(u, v)K^{j^2} |\nabla v|^2, \end{aligned}$$

for every $j \in \{0, 1, \dots, p-2\}$. Using the fact that

$$K \geq \frac{\overline{\mu_1}(1 + \varepsilon_1) + \overline{\mu_2}(1 + \varepsilon_2)}{2\sqrt{\underline{\mu_1}\underline{\mu_2}\varepsilon_1\varepsilon_2}}$$

and the Cauchy-Schwarz inequality, we conclude that $I \leq 0$. Now, applying assumptions (2.9) and (2.10), we obtain the differential inequality

$$L'(t) \leq c_3 L(t) + c_4 L^{(p-1)/p}(t).$$

Integrating the last inequality, we obtain that L is uniformly bounded on $[0, t^*]$. Using again the inequality (2.10), it follows that every solution of (2.3), with initial data (u_0, v_0) in $[L^\infty(\Omega)]^2$, belongs to $L^\infty(0, T^*; [L^p(\Omega)]^2)$. Combining this with (2.9), we conclude that any solution (u, v) of (2.3) with initial data (u_0, v_0) in $[L^\infty(\Omega)]^2$ is in fact global, which achieves the proof. \square

In the following section, we focus our study on diffusion driven instability in saturated competition systems.

2.3 Competition systems and diffusion driven instability

Let us consider the reaction-diffusion competition system (2.3) in the competition case, then we assume in the sequel the *competition conditions* :

$$\frac{\partial f}{\partial v} \leq 0 \quad \text{and} \quad \frac{\partial g}{\partial u} \leq 0. \quad (2.12)$$

We also assume the standard condition which preserves the nonnegativity of the solutions u and v

$$f(0, v) \geq 0 \quad \text{and} \quad g(u, 0) \geq 0, \quad \text{for any } u \geq 0, v \geq 0. \quad (2.13)$$

In the following result, we show that *diffusion driven instability* (*Turing instability*) can not occur. In particular, the presence of nonlinear diffusions has no impact on the linear stability of homogeneous steady state solutions of (2.3).

Before stating this result, we introduce the temporal dynamical system associated to (2.3)

$$\begin{cases} u'(t) = f(u, v), & t \geq 0, \\ v'(t) = g(u, v), & t \geq 0. \end{cases} \quad (2.14)$$

Then the homogeneous steady state solutions of (2.3) are the steady state solutions of (2.14).

Theorem 2.3.1. *Let μ_1, μ_2 be any two nonnegative and C^1 functions on $[0, +\infty[\times [0, +\infty[$. Let f and g be two C^1 functions on $[0, +\infty[\times [0, +\infty[$ satisfying the competition conditions (2.12) and the nonnegativity condition (2.13). Let (u^*, v^*) be a linearly stable steady state of (2.14) such that $\mu_i(u^*, v^*) > 0$. Then (u^*, v^*) has the same linear stability nature for the system (2.3). That is, the presence of diffusions in (2.3) has no effect on the linear stability of (2.14). In particular, diffusion driven instability can not hold true.*

Proof. Since $\mu_i(u^*, v^*) \neq 0$, $i = 1, 2$, the linearized system of (2.3) at $\mathbf{s}^* \equiv (u^*, v^*)$ is given by

$$\begin{cases} \mathbf{w}_t = D(\mathbf{s}^*)\Delta\mathbf{w} + J(\mathbf{s}^*)\mathbf{w}, & (x, t) \in \Omega \times]0, +\infty[\\ \nabla\mathbf{w} \cdot \mathbf{n} = 0, & (x, t) \in \partial\Omega \times [0, +\infty[\end{cases} \quad (2.15)$$

where the diffusion and Jacobian matrices at \mathbf{s}^* are given respectively by

$$D(\mathbf{s}^*) = \begin{pmatrix} \mu_1(\mathbf{s}^*) & 0 \\ 0 & \mu_2(\mathbf{s}^*) \end{pmatrix} \quad \text{and} \quad J(\mathbf{s}^*) = \begin{pmatrix} \frac{\partial f}{\partial u}(\mathbf{s}^*) & \frac{\partial f}{\partial v}(\mathbf{s}^*) \\ \frac{\partial g}{\partial u}(\mathbf{s}^*) & \frac{\partial g}{\partial v}(\mathbf{s}^*) \end{pmatrix}. \quad (2.16)$$

To solve this linear system in \mathbf{w} , we consider a general separable solution given by

$$\mathbf{w}(x, t) = A(t)\mathbf{p}(x),$$

where $A(t)$ is a scalar function of time t . After substitution of the expression $\mathbf{w}(x, t) = A(t)\mathbf{p}(x)$ in (2.15) we deduce that

$$A(t) = A_0 e^{\lambda t},$$

for some real numbers λ and A_0 . The vectorial function \mathbf{p} is a solution of the linear eigenvalue problem

$$\begin{cases} D(\mathbf{s}^*)\Delta\mathbf{p} + J(\mathbf{s}^*)\mathbf{p} = \lambda\mathbf{p}, & \text{in } \Omega, \\ \nabla\mathbf{w} \cdot \mathbf{n} = 0, & \text{on } \partial\Omega. \end{cases}$$

Let $(\varphi_k)_{k \geq 1}$ be the complete orthonormal family in $L^2(\Omega)$ of the eigenfunctions of the Laplacian with Neumann homogeneous boundary conditions, and $(\sigma_k)_{k \geq 1}$ the corresponding eigenvalues respectively. Hence, the general solution of (2.15) is given by

$$\mathbf{w}(x, t) = \sum_{k \geq 1} A_0(\sigma_k) e^{\lambda(\sigma_k)t} \varphi_k(x),$$

where, for every $k \geq 1$, $A_0(\sigma_k)$ is a real number and $\lambda(\sigma_k)$ is a complex number satisfying the condition

$$\det[-\sigma_k D(\mathbf{s}^*) + J(\mathbf{s}^*) - \lambda I_2] = 0,$$

and I_2 is the identity matrix of size two. This can be rewritten as

$$\det \begin{pmatrix} \frac{\partial f}{\partial u}(\mathbf{s}^*) - \mu_1(\mathbf{s}^*)\sigma_k - \lambda & \frac{\partial f}{\partial v}(\mathbf{s}^*) \\ \frac{\partial g}{\partial u}(\mathbf{s}^*) & \frac{\partial g}{\partial v}(\mathbf{s}^*) - \mu_2(\mathbf{s}^*)\sigma_k - \lambda \end{pmatrix} = 0.$$

Recall here that the linear stability of \mathbf{s}^* implies :

$$\text{tr}(J(\mathbf{s}^*)) = \frac{\partial f}{\partial u}(\mathbf{s}^*) + \frac{\partial g}{\partial v}(\mathbf{s}^*) < 0, \quad (2.17)$$

$$\det(J(\mathbf{s}^*)) = \frac{\partial f}{\partial u}(\mathbf{s}^*) \frac{\partial g}{\partial v}(\mathbf{s}^*) - \frac{\partial f}{\partial v}(\mathbf{s}^*) \frac{\partial g}{\partial u}(\mathbf{s}^*) > 0. \quad (2.18)$$

For the steady state \mathbf{s}^* to be unstable to spatial diffusions, the following necessary condition

$$\det [J(\mathbf{s}^*) - \sigma_k D(\mathbf{s}^*)] < 0$$

has to occur, for some $k \geq 1$. That is,

$$\exists k \geq 1 : P_2(\sigma_k) < 0,$$

where $P_2(\sigma_k)$ is the quadratic polynomial in σ_k given by

$$P_2(\sigma_k) := \mu_1(\mathbf{s}^*)\mu_2(\mathbf{s}^*)\sigma_k^2 - \left(\mu_1(\mathbf{s}^*)\frac{\partial g}{\partial v}(\mathbf{s}^*) + \mu_2(\mathbf{s}^*)\frac{\partial f}{\partial u}(\mathbf{s}^*) \right) \sigma_k + \det(J(\mathbf{s}^*)).$$

Then the inequality on the discriminant :

$$\left(\mu_1(\mathbf{s}^*)\frac{\partial f}{\partial u}(\mathbf{s}^*) + \mu_2(\mathbf{s}^*)\frac{\partial g}{\partial v}(\mathbf{s}^*) \right)^2 - 4\mu_1(\mathbf{s}^*)\mu_2(\mathbf{s}^*)\det(J(\mathbf{s}^*)) > 0 \quad (2.19)$$

must hold true. In this situation, the lower root of P_2 has to be positive, since all eigenvalues σ_k , $k \geq 1$, are positive, except $\sigma_1 = 0$ (Neumann homogeneous boundary condition). Then, one must have

$$\mu_1(\mathbf{s}^*)\frac{\partial g}{\partial v}(\mathbf{s}^*) + \mu_2(\mathbf{s}^*)\frac{\partial f}{\partial u}(\mathbf{s}^*) > 0, \quad (2.20)$$

but this last condition is impossible. Indeed, (2.12) implies that

$$\frac{\partial f}{\partial v}(\mathbf{s}^*)\frac{\partial g}{\partial u}(\mathbf{s}^*) \geq 0,$$

on one hand, and (2.18) implies that $\frac{\partial f}{\partial u}(\mathbf{s}^*)$ and $\frac{\partial g}{\partial v}(\mathbf{s}^*)$ must have the same sign which is negative, due to (2.17). This ends the proof. \square

2.4 Simplified competition model for clonal plants

2.4.1 Lotka-Volterra nonlinear coupled diffusion model

In this section, we will study a simple reaction-diffusion system which models plant growth with spatial competition. We limit ourselves to saturated systems with respect to nitrates :

$$\left\{ \begin{array}{ll} u_t - \operatorname{div}(\mu_1(u, v)\nabla u) = u(\alpha_1 - \beta_1 u - \gamma_1 v) & \text{in }]0, +\infty[\times \Omega \\ v_t - \operatorname{div}(\mu_2(u, v)\nabla v) = v(\alpha_2 - \beta_2 v - \gamma_2 u) & \text{in }]0, +\infty[\times \Omega \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 & \text{on } \partial\Omega \times [0, +\infty[, \\ u(0, x) = u_0(x), \quad v(0, x) = v_0(x) & \text{in } \Omega \end{array} \right. \quad (2.21)$$

where $\alpha_1 > 0$, denotes the growth rate of the biomass u ; $\alpha_1/\beta_1 > 0$ is the carrying capacity of biomass u in the absence of v and $\gamma_2 > 0$ is the competition rate of u . The positive constants $\alpha_2 > 0$, $\beta_2 > 0$ and $\gamma_1 > 0$ are defined in the same way. Let us recall some classical results concerning the dynamical system :

$$\begin{cases} u'(t) = u(t)(\alpha_1 - \beta_1 u(t) - \gamma_1 v(t)), & t > 0, \\ v'(t) = v(t)(\alpha_2 - \beta_2 v(t) - \gamma_2 u(t)), & t > 0, \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{cases} \quad (2.22)$$

where the solutions of interest have to be nonnegative. System (2.22) has 4 equilibrium points :

$$\begin{aligned} (u_1, v_1) &= (0, 0), \\ (u_2, v_2) &= \left(\frac{\alpha_1}{\beta_1}, 0 \right), \\ (u_3, v_3) &= \left(0, \frac{\alpha_2}{\beta_2} \right), \\ (u_4, v_4) &= \left(\frac{\alpha_2 \gamma_1 - \alpha_1 \beta_2}{\gamma_1 \gamma_2 - \beta_1 \beta_2}, \frac{\alpha_1 \gamma_2 - \alpha_2 \beta_1}{\gamma_1 \gamma_2 - \beta_1 \beta_2} \right). \end{aligned}$$

We can distinguish 4 situations, see Fig. 2.1 :

(i) $\frac{\gamma_1}{\beta_2} < \frac{\alpha_1}{\alpha_2} < \frac{\beta_1}{\gamma_2}$

(ii) $\frac{\beta_1}{\gamma_2} < \frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2}$

(iii) $\frac{\alpha_1}{\alpha_2} > \frac{\beta_1}{\gamma_2}$ and $\frac{\alpha_1}{\alpha_2} > \frac{\gamma_1}{\beta_2}$

(iv) $\frac{\alpha_1}{\alpha_2} < \frac{\beta_1}{\gamma_2}$ and $\frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2}$.

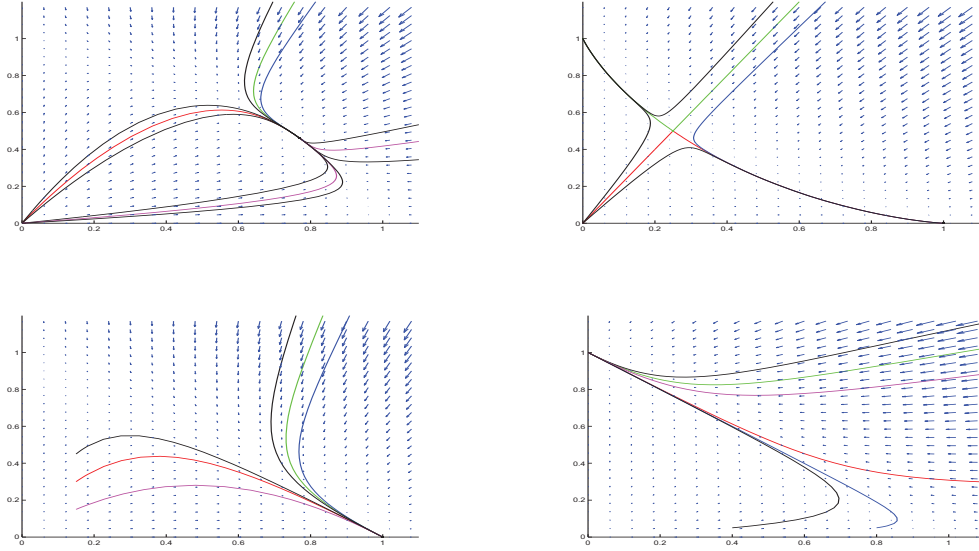


FIGURE 2.1 – Top-left : Case (i), top-right : Case (ii), bottom-left : Case (iii) and bottom-right : Case (vi).

Notice that in all cases, the steady point $(0, 0)$ is linearly unstable. Let us describe the (linear) nature of the other steady states. In case (i), (u_2, v_2) and (u_3, v_3) are saddle points and (u_4, v_4) is asymptotically stable. In case (ii), (u_2, v_2) and (u_3, v_3) are stable and (u_4, v_4) is a saddle point. In this case, the line of equation

$$v = \frac{\alpha_1 \gamma_2 - \alpha_2 \beta_1}{\alpha_2 \gamma_1 - \alpha_1 \beta_2} u$$

in the plane (u, v) is a separatrix, which divides the quadrant $[0, +\infty[\times [0, +\infty[$ into the basins of attraction of (u_2, v_2) and (u_3, v_3) respectively.

In case (iii), the steady point $(u_4, v_4) \notin [0, +\infty[\times [0, +\infty[$ and its nature has no effect on the steady states (u_2, v_2) and (u_3, v_3) which are stable and saddle-point respectively. In case (iv), the same situation occurs but the nature of (u_2, v_2) and (u_3, v_3) is reversed. These four situations are described in Fig. 2.1, where we fixed $\alpha_1 = \alpha_2 = \beta_1 = \beta_2 = 1$.

Let us conclude with the following special situation for the dynamical system

$$\begin{cases} u'(t) = \eta_1 u(t)(1 - \beta u(t) - \gamma v(t)), & t > 0, \\ v'(t) = \eta_2 v(t)(1 - \beta u(t) - \gamma v(t)), & t > 0, \\ u(0) = u_0 > 0, & v(0) = v_0 > 0. \end{cases} \quad (2.23)$$

This degenerated case, $\frac{\gamma_1}{\beta_2} = \frac{\alpha_1}{\alpha_2} = \frac{\beta_1}{\gamma_2} = \frac{\eta_1}{\eta_2}$, implies that each species has the same intra-specific and inter-specific competition performance. However, one species may grow faster at a faster time scale than the other. It follows that

$$\eta_2 \frac{u'(t)}{u(t)} = \eta_1 \frac{v'(t)}{v(t)}, \text{ for every } t > 0$$

and hence

$$\left[\frac{u(t)}{u_0} \right]^{\eta_2} = \left[\frac{v(t)}{v_0} \right]^{\eta_1}, \text{ for every } t > 0.$$

On the one hand, the system (2.23) admits the linear set of steady states

$$\beta u + \gamma v = 1, \quad u \geq 0, \quad v \geq 0, \quad (2.24)$$

that ends with the two critical points of each equation separately

$$u = \frac{1}{\beta}, \text{ when } v = 0,$$

or

$$v = \frac{1}{\gamma}, \text{ when } u = 0.$$

We observe that the initial condition (u_0, v_0) can be set such each steady solution of this set (2.24) can be reached.

On the contrary, if the two species differ by their nutrient requirement in the same proportion as we have seen before, i.e

$$\begin{cases} u'(t) = \eta_1 u(t)(\alpha_1 - \beta u(t) - \gamma v(t)), & t > 0, \\ v'(t) = \eta_2 v(t)(\alpha_2 - \beta u(t) - \gamma v(t)), & t > 0, \\ u(0) = u_0 > 0, & v(0) = v_0 > 0, \end{cases} \quad (2.25)$$

with

$$\alpha_1 \neq \alpha_2,$$

the species that gets the poorest environment support for its specific needs, gets wiped out by the other one.

We are going now to exercise with numerical simulations the influence of the spatial competition with respect to nonlinear coupled diffusions on the competition mechanism driven by the Lotka-Volterra system (2.22) .

2.4.2 Numerical Simulation of a Benchmark Problem

We consider the following benchmark situation with nonlinear coupled diffusions :

$$\begin{cases} u_t - \varepsilon_1 \operatorname{div}(\Phi(v)\nabla u) = u(\alpha_1 - \beta_1 u - \gamma_1 v), & (x, y) \in \Omega, t > 0, \\ v_t - \varepsilon_2 \operatorname{div}(\Phi(u)\nabla v) = v(\alpha_2 - \beta_2 v - \gamma_2 u), & (x, y) \in \Omega, t > 0, \end{cases} \quad (2.26)$$

with homogeneous Neumann boundary conditions on $\partial\Omega$,

$$\nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 \text{ on } [0, +\infty[\times \partial\Omega.$$

The nonlinear cross diffusion coefficient is the smooth function $0 \leq \Phi \leq 1$:

$$\Phi(s) = \begin{cases} \exp\left(\frac{s^2}{s^2 - \eta^2}\right) & \text{if } 0 \leq s < \eta \\ 0 & \text{if } s \geq \eta \end{cases}$$

We set up the parameters of the Lotka-Volterra system such that the second species v has a competitive advantage on the first species. The system a unique stable critical point

$$\left(u = 0, v = \frac{\alpha_2}{\beta_2} > 0 \right)$$

with

$$\alpha_1 = 1, \alpha_2 = 1.3, \beta_1 = 1.2, \beta_2 = 0.8, \gamma_1 = 3., \gamma_2 = 1.1.$$

We test out the influence of the competitive advantage of motility by comparing the result for $\varepsilon_1 = \varepsilon_2$ with the result for $\varepsilon_1 \gg \varepsilon_2$. Similarly, we test the competitive advantage of space exclusion that corresponds to $\eta \ll 1$ by comparing to the situation with quasi uniform diffusion $\eta \gg 1$. Fig. 2.1 shows the four possible combinations of these parameter setting.

The initial condition for the benchmark problem is a collection of well separated sharp bell functions

$$\exp\left[-\frac{\operatorname{dist}((x, y), M_j)}{\nu}\right],$$

that play the role of initial "seeds of population density", centered on a set of points M_j - see Figs. 2.2 to 2.5 at $T = 0$. We use a similar number of "seeds" for both species.

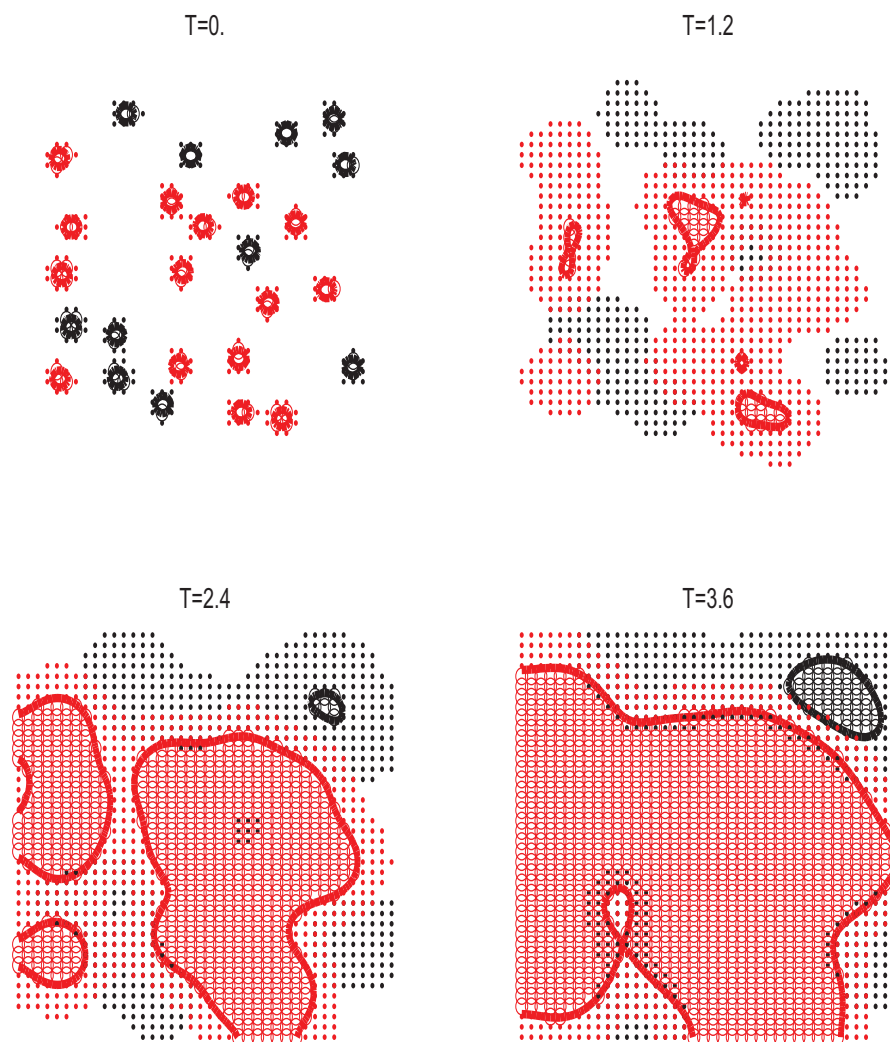


FIGURE 2.2 – Two species system with quasi uniform diffusion : $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 100$. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval $(0.1, 0.5)$, is indicated by dots ‘.’.

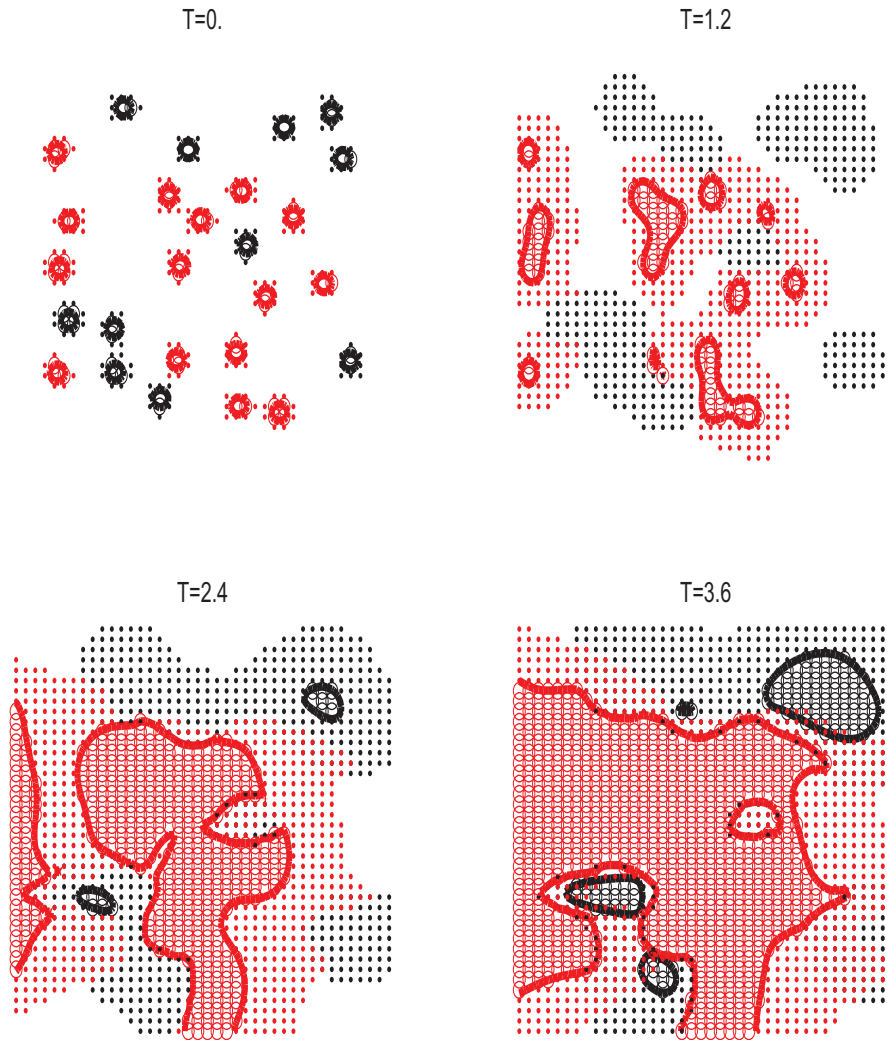


FIGURE 2.3 – Two species system with strong exclusive diffusion $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 0.1$. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval $(0.1, 0.5)$, is indicated by dots ‘.’.

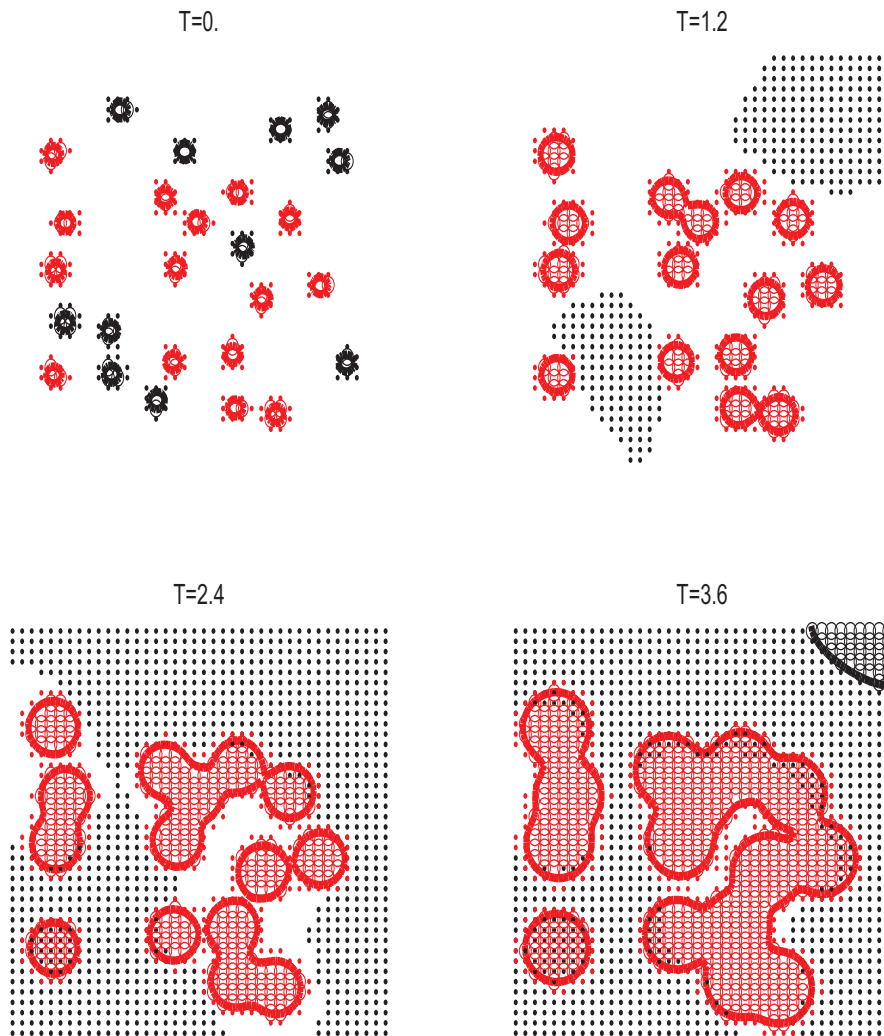


FIGURE 2.4 – First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 100$, but both species have quasi uniform diffusion. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval (0.1, 0.5), is indicated by dots ‘.’.

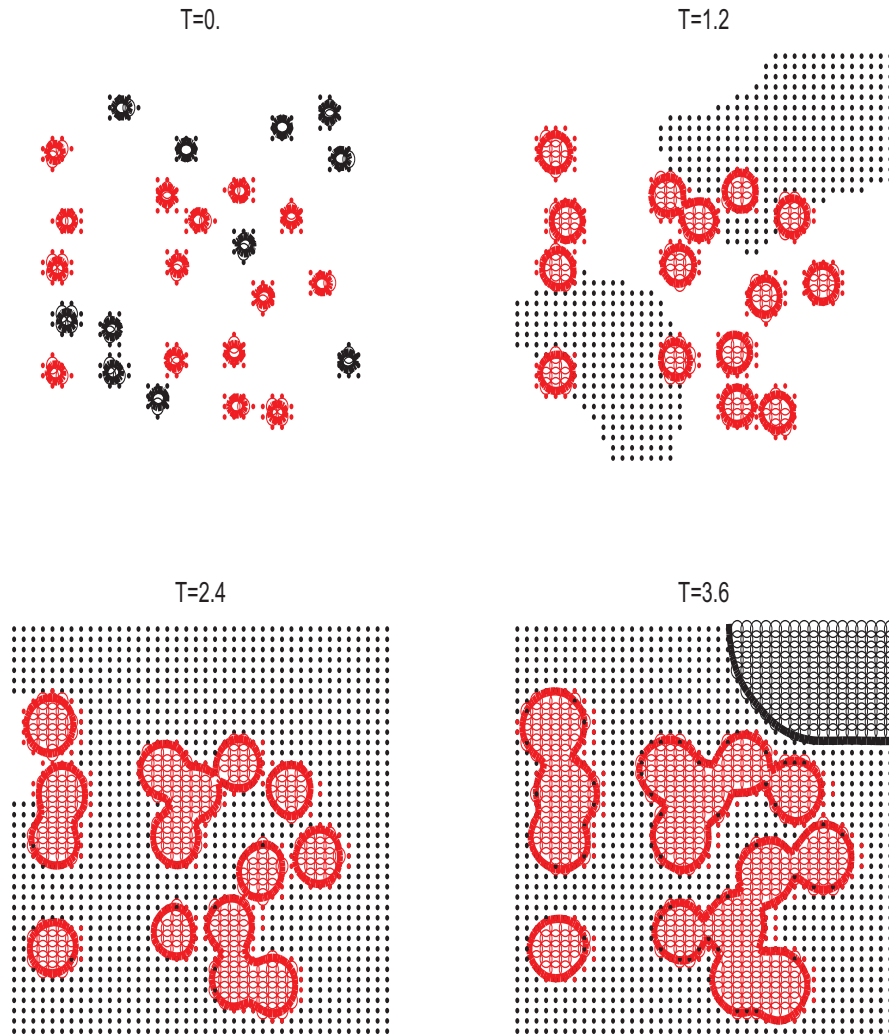


FIGURE 2.5 – First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 0.1$, but both species have strong exclusive diffusion. Black label (resp. red label) : space invaded by the first species (resp. the second species). The area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval $(0.1, 0.5)$, is indicated by dots ‘.’.

The numerical implementation is straightforward. We use a regular Cartesian grid with a second order finite volume approximation in space and a second order Crank-Nicolson implicit time stepping.

When we run the simulation, we observe at early time the diffusion process that represents plant colonization. After some time, we start to see some interaction with narrow fronts layers where both species compete. This boundary layer that separates the species is more or less diffused depending on how small is the ν value.

In these figures, we use the following convention : the space invaded by the first species (resp. the second species) is marked by black label (resp. red label). The simulation exhibits then a nice pattern formation for each species.

In the figures, the area where density is above 0.5 is indicated by circles ‘o’, while the area with lower concentration, in the interval (0.1, 0.5), is indicated by dots ‘.’. This helps to visualize the area where the second species is strongly dominant, i.e red circle zone, the area where the first species diffuses everywhere, black dot area, and the overlapping zone where competition occurs. These patterns are somewhat similar to the spatial distribution of ramets in a Phalanx-Guerrilla system emerging from the simulation of prairies with the agent based model [84]. Figs. 2.6 and 2.7 give a snapshot of one of these agent based simulations between population of Phalanx and Guerilla : we start from an equal number of roots for each plant.

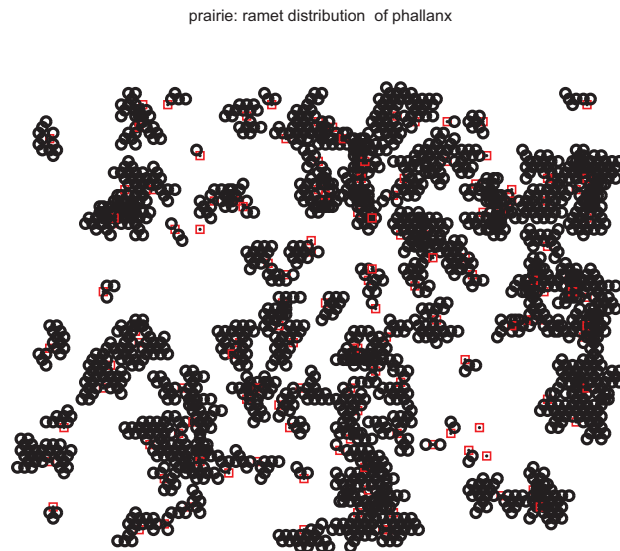


FIGURE 2.6 – Space distribution of ramets for Phalanx.



FIGURE 2.7 – Space distribution of ramets for Guerilla.

We assume a small probability that clones dies but asexual reproduction is implemented which allows the clonal plant to survive through its youngest shoot. In agent based simulation, we let the system evolve for several thousand steps, which may represent several seasons. Figs. 2.6 and 2.7 illustrate the emergence of spatial pattern formation where phalanx are clustered in space, while Guerilla are distributed with sparsity everywhere. The prairie is actually the superposition of both distributions of ramets, since there is no space sharing of the cellular automata cells at the ramet location.

The next step in this work would be to calibrate the simplified PDE model to best fit the agent based simulation using the identification of parameters and inverse problems techniques. However, this is not an easy task from the mathematical point of view, and it will be the purpose of a future publication.

Let us report on the simulation result of our simplified Lotka-Volterra- nonlinear cross-diffusion model.

As expected, with uniform spatial diffusion, i.e $\eta \gg 1$, the most competitive species wipe out the other one that goes to extinction.

This process might be slowed down if the less competitive species is space dominant, i.e diffuse the fastest ($\varepsilon_1 \gg \varepsilon_2$).

With strong exclusive cross diffusion, i.e $\eta \ll 1$, the less competitive species can survive much better in the transient. However, as time goes to infinity, the most competitive species will eventually take over because of the small diffusivity at the interface between species. As $\eta \rightarrow 0$, this process takes longer and longer time. It is clear that for $\eta = 0$, the less competitive species will always survive,

and perhaps get most of the field thanks to its initial fast space invasion. This implies that degenerate nonlinear diffusions can modify the linear stability of homogeneous steady states and their basins of attraction.

* - * - * - * - * - * - * - * - *

Chapitre 3

A PDE model of clonal plant competition with nonlinear diffusion

Sommaire

| | |
|---|-----------|
| Présentation du chapitre | 44 |
| Abstract | 44 |
| 3.1 Introduction | 44 |
| 3.2 A general PDE Model | 46 |
| 3.3 Simplified Competition model for clonal plants | 49 |
| 3.3.1 Lotka-Volterra-nonlinear diffusion model | 49 |
| 3.3.2 Numerical Simulation of a Benchmark Problem | 52 |
| 3.4 Discussion | 57 |

Le travail présenté dans ce chapitre a été effectué en collaboration avec Abdallah El Hamidi et Marc Garbey. Le but principal était de déterminer dans quelle mesure un modèle EDP simplifié de compétition spatio-temporelle pourrait constituer un modèle de substitution à un modèle d'agent de type individu-centré (Individual Based Models ou IBM en abrégé). Ce travail a fait l'objet d'un article publié dans le journal *Ecological Modelling*.

Abstract

We present a spatial competition model for clonal plant growth that combines two different mechanisms of competition. The first one is described by the standard underlying Kolmogorov Model for two interacting populations. A second competition mechanism, more specific to clonal plant growth, expresses the motility of each species and their capacity to resist to competitor's space intrusion. This model leads to a degenerated nonlinear reaction-diffusion system in which the diffusion coefficient of each species vanishes wherever the other species is beyond a certain biomass value.

Indeed, we show that pattern forming instability cannot occur in general competition systems if the exclusion ability of both species is small even if the diffusions are degenerated. The effect of diffusion degeneracy on patterns formation is carried out. Numerical simulations of this two level competition model are performed when the reaction terms are given by the competitive Lotka-Volterra equations. We, finally, discuss the potential of such nonlinear reaction-diffusion systems to be a surrogate model for phalanx-guerilla species competition.

Keywords : Clonal plant, Reaction-diffusion, Partial differential equation, Spatial-temporal pattern formation, Cross diffusion, Spatial competition.

3.1 Introduction

The dynamic of clonal plant population is a fascinating area of research (Van Groenendael and de Kroon [114]). Agent based models with explicit representation of plant individual have been the main modeling tool both for understanding mechanism and predicting spatial-temporal behavior (Oborny et al. [87], submitted). On the other hand PDE based model provide information at the macroscopic level, i.e does not represent explicitly plants individual, but rather represent a density of plants. PDE models are interesting tools to extract global indicators on competition such as speed of propagation or space and time scale for dynamic. Up to our knowledge there have been no PDE model specifically designed to model clonal plants. There is, however, a vast literature on PDE modeling of the dynamic of population in general.

The role of spatial heterogeneities and dispersal for chemically reacting species or biologically interacting populations, in the linear or nonlinear regime, has been the subject of a sizeable literature, see e.g. the classical books (Aris [11], Cussler [28]).

In particular, cross diffusion in modelling interactions among different species has attracted special attentions. Apart from the above quoted books, one can cite [39, 62, 99, 100, 102] in physical-chemistry, [19, 68] in epidemics, [5, 63, 66, 96] in ecology, population dynamics or biology and [21] in economics.

Clonality in plant corresponds to vegetative multiplication (Bell [15]). A clonal individual is composed of genetically identical and potentially autonomous descendants (ramets), generally linked altogether by connective stems. At first approximation, a clone can be modeled as a two dimensional tree structure more or less compact that grows from the initial ramet by branch elongations and branching. This tree structure supports resource sharing (Jónsdóttir and Watson [61], Stuefer et al., [108]) and storage for the clone (Suzuki and Stuefer [111], Suzuki and Hutchings [110]). A connection between ramets might be broken. In that case, the clone splits : two new tree structures are formed. The main tradeoff controlling horizontal growth of plant is linked with spatial colonization and resistance to competitors. These two opposite strategies are represented by clonal plants classified as *phalanx* and *guerilla* species according to Lovett-Doust [80]. Guerilla are plants that invest resources to build distant connections in order to explore and conquest space rapidly. Their architecture is characterized by long connections between ramets which can be easily intruded by competitors. Conversely, phalanx plants are compact and produce dense clouds of ramets to extract all resources on site. Thanks to this compact structure phalanx plants resist to competition, but has limited ability to invade space.

This ensemble of properties gives a very peculiar nature to space invasion by clonal plants where the plant architecture and the competition for space are strongly coupled.

The objective of this paper is to present a spatial competition model for clonal plant growth that combines two different mechanisms of competition. One is described by the standard underlying Kolmogorov Model for two interacting populations (Brauer and Castillo-Chevez [18] Cushing [27]). A second competition mechanism more specific to clonal plant growth, is expressed by adding coupling nonlinear diffusion terms, such as the motility of each species, and their capacity to exclude the other from its territory. In Kolmogorov systems, an important topic is whether every orbit starting in the interior of the first quadrant of the phase plane (*i.e.* the population densities are strictly positive) remains persistent. Following Czárán & Bartha [29] and Czárán [30], the main assumptions in the PDE model are :

(i) populations are large enough for stochastic effects not to be taken into account. In particular if one of the species has very low density, the PDE model

may become irrelevant.

(ii) individuals are identical in their population dynamical attributes.

The PDE models attempt to give a phenomenological description than can reproduce spatiotemporal patterns observed in nature.

Most models of clonal plant communities are agent based models (Grimm and Railback [40]) that take into account explicitly the plant architecture.

The question we address in this paper is the construction of a PDE model that reproduces some of the phenomenology on space competition that is typical of agent base simulations such as :

(i) no space sharing between ramets and therefore, the density of different populations has small overlaps,

(ii) space invasion has finite speed,

(iii) species with low motility have the tendency to cluster, while species with high motility disperse rather uniformly.

We will present a general PDE model for plant competition with nonlinear diffusion and examine its mathematical properties. We show in particular that, in competition systems with small spatial exclusion ability, the nonlinear diffusions do not impact the stability of the equilibrium points of the dynamical system. However, these nonlinear diffusions may modify the linear stability of these points if the considered species have strong spatial exclusion ability. We will use this model to describe the competition between two populations of clonal plants and analyze and/or compute pattern formation.

3.2 A general PDE Model

The spatial competition model for plant growth combines two different mechanisms, one described by the standard underlying Kolmogorov model for two interacting populations (Brauer and Castillo-Chevez [18], Cushing [27])

$$\begin{cases} u'(t) = u(t)F(u(t), v(t)), & t > 0, \\ v'(t) = v(t)G(u(t), v(t)), & t > 0, \\ u(0) = u_0 > 0, & v(0) = v_0 > 0, \end{cases} \quad (3.1)$$

with another competition mechanism more adapted to clonal plant growth that expresses, by adding coupling nonlinear diffusion terms, the motility of each species, and their capacity to exclude the other from its territory.

Let us denote $(u(x, t), v(x, t))$ the time dependent spatial density of each population. The system of Partial Differential Equations (PDE) model writes :

$$\begin{cases} u_t - \operatorname{div}(\varepsilon_1 \mu_1(u, v) \nabla u) = u F(u, v), \\ v_t - \operatorname{div}(\varepsilon_2 \mu_2(u, v) \nabla v) = v G(u, v). \end{cases} \quad (3.2)$$

The diffusion coefficients $(\varepsilon_1, \varepsilon_2)$ are linked to the motility of each species. Let us suppose that species u would disappear in the long run in the competition mechanism with v driven by the underlying dynamical system (3.1). If species u has the ability to exclude strongly species v from its territory, which corresponds to $\mu_2(u, v) = 0$ if $u > 0$ and $\mu_2(0, v) > 0$, then wherever $u(x, 0)$ is positive, species u will survive.

The so called community matrix associated to the Kolmogorov system

$$\begin{pmatrix} \frac{\partial F}{\partial u} & \frac{\partial F}{\partial v} \\ \frac{\partial G}{\partial u} & \frac{\partial G}{\partial v} \end{pmatrix},$$

describes, mathematically, the aggressive rate of a species versus the other in the dynamical system.

In Gurtin and MacCamy [41], the authors consider that when populations behave so as to avoid crowding it is reasonable to assume that the diffusion terms μ_1 and μ_2 are increasing functions of the population densities u and v respectively. On the other hand, since the diffusion of u is penalized where v is positive, and *vice versa*, it is reasonable to assume also that the diffusion terms μ_1 and μ_2 are strongly decreasing in v and u respectively. In space these generalized diffusion terms are more realistic since they allow *finite speed propagation* in space. This is in contrast to constant diffusion which leads to the standard Laplacian operator and its well known *infinite speed propagation* ([?]). The assumptions on the diffusions μ_1 and μ_2 , on the source terms F, G and the initial data u_0, v_0 will be specified later.

Theoretically, the dependence of μ_1 in v (resp. μ_2 in u) is such that u (resp. v) cannot diffuse in spatial positions where $v > 0$ (resp. $u > 0$). Then, μ_1 and μ_2 have to behave as the following

$$\begin{aligned} \mu_1(u(x), v(x)) &= \varphi_1(u(x)) \times \mathbf{1}_{\Omega \setminus \text{supp}(v)}(x), \\ \mu_2(u(x), v(x)) &= \varphi_2(v(x)) \times \mathbf{1}_{\Omega \setminus \text{supp}(u)}(x), \end{aligned}$$

for every $x \in \Omega$, where φ_1 and φ_2 are positive, increasing and smooth functions on $[0, +\infty[$. The set $\text{supp}(u)$ is the closure of $\{x \in \Omega : u(x) \neq 0\}$ and for every subset ω of Ω :

$$\mathbf{1}_\omega(x) = \begin{cases} 1 & \text{if } x \in \omega, \\ 0 & \text{if } x \notin \omega. \end{cases} \quad (3.3)$$

This kind of diffusion terms leads to very complicated mathematical free boundary models which do not reflect the possible *miscibility* between the two plant populations. Then, we introduce parameters η_1 and η_2 which may reflect the ability rate of a species to exclude the other one, that is :

$$\mu_1(u, v) = \varphi_1(u)T_{\eta_1}(v), \quad \mu_2(u, v) = \varphi_2(v)T_{\eta_2}(u), \quad (3.4)$$

where T_η is an approximation of the standard truncation function defined by

$$T_\eta(s) = \begin{cases} \exp\left(\frac{\eta^2}{s^2 - \eta^2}\right) & \text{if } 0 \leq s < \eta, \\ 0 & \text{if } s \geq \eta. \end{cases} \quad (3.5)$$

This means that if the biomass u satisfies $u \geq \eta_2$, then the diffusion coefficient $\mu_2(u, v)$ vanishes and vice versa.

In the companion paper [46], we have shown local and global existence results of classical solutions to System

$$\begin{cases} u_t - \operatorname{div}(\mu_1(u, v)\nabla u) = f(u, v) & \text{in } \Omega \times]0, +\infty[, \\ v_t - \operatorname{div}(\mu_2(u, v)\nabla v) = g(u, v) & \text{in } \Omega \times]0, +\infty[, \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 & \text{on } \partial\Omega \times [0, +\infty[, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0 & \text{in } \Omega, \end{cases} \quad (3.6)$$

- For local existence, we used the theory developed by (Amann [6]) for semi-linear reaction-diffusion systems.
- For global existence, we constructed an explicit Lyapunov functional for System (3.6), inspired by the work of (Kouachi [71]).

Let us, now, present the competition systems and the absence of diffusion driven instability. Let us consider the reaction-diffusion competition system (3.6) in the competition case, then, we assume in the sequel the *competition conditions* :

$$\frac{\partial f}{\partial v} \leq 0 \quad \text{and} \quad \frac{\partial g}{\partial u} \leq 0. \quad (3.7)$$

We, also, assume the standard condition which preserves the nonnegativity of the solutions u and v

$$f(0, v) \geq 0 \quad \text{and} \quad g(u, 0) \geq 0, \quad \text{for any } u \geq 0, v \geq 0. \quad (3.8)$$

In the following result, we show that *diffusion driven instability*, (or *Turing instability*), cannot occur. In particular, the presence of diffusion cannot change the linear stability of homogeneous steady state solutions of (3.6).

Before stating this result, we introduce the temporal dynamical system associated to (3.6)

$$\begin{cases} u'(t) = f(u, v), \quad t \geq 0, \\ v'(t) = g(u, v), \quad t \geq 0. \end{cases} \quad (3.9)$$

Then, the homogeneous steady state solutions of (3.6) are the steady state solutions of (3.9).

Theorem 3.2.1. *Let μ_1, μ_2 be any two nonnegative and C^1 functions on $[0, +\infty[\times [0, +\infty[$. Let f and g be two C^1 functions on $[0, +\infty[\times [0, +\infty[$ satisfying the competition conditions (3.7) and the nonnegativity condition (3.8). Let (u^*, v^*) be a linearly stable steady state of (3.9) such that $\mu_i(u^*, v^*) > 0$. Then, (u^*, v^*) has the same linear stability nature for the system (3.6). That is, the presence of diffusions in (3.6) has no effect on the linear stability of (3.9). In particular, diffusion driven instability cannot hold true.*

Remark 3.2.2. *Consider the system (3.6) with $\mu_i(u, v)$ given by (3.4). If $\eta_1 \gg 1$ and $\eta_2 \gg 1$, since u and v are bounded then, $\mu_i(u, v) > 0$ for every $u \geq 0$ and $v \geq 0$ for $i = 1, 2$. In particular, $\mu_i(u^*, v^*) > 0$ for every equilibrium solutions. In this situation, the system behaves as in the non degenerated systems, that is, the solutions tend asymptotically to a equilibrium solution of the dynamical system.*

We are going, now, to consider a special case for plant competition using the standard Lotka-Volterra-Gause competition model described in the introduction.

3.3 Simplified Competition model for clonal plants

In this section, we will study a simple reaction-diffusion system which models plant growth with spatial competition. Its aim is to give an illustration of Theorem 3.2.1 on a well known competitive system.

3.3.1 Lotka-Volterra-nonlinear diffusion model

We consider the following system of PDE equations :

$$\begin{cases} u_t - \operatorname{div}(\mu_1(u, v)\nabla u) = u(\alpha_1 - \beta_1 u - \gamma_1 v) & \text{in }]0, +\infty[\times \Omega \\ v_t - \operatorname{div}(\mu_2(u, v)\nabla v) = v(\alpha_2 - \beta_2 v - \gamma_2 u) & \text{in }]0, +\infty[\times \Omega \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 & \text{on } [0, +\infty[\times \partial\Omega \\ u(0, x) = u_0(x), \quad v(0, x) = v_0(x) & \text{in } \Omega \end{cases} \quad (3.10)$$

where $\alpha_1 > 0$ denotes the growth rate of the biomass u , $\alpha_1/\beta_1 > 0$ is the carrying capacity of biomass u in the absence of v and $\gamma_2 > 0$ is the competition rate of u . The positive constants $\alpha_2 > 0$, $\beta_2 > 0$ and $\gamma_1 > 0$ are defined in the same way.

It is well known that if μ_1 and μ_2 are two positive constants then every solution

of (3.10) converges to a equilibrium point of the associated dynamical system :

$$\begin{cases} u'(t) = u(t)(\alpha_1 - \beta_1 u(t) - \gamma_1 v(t)), & t > 0, \\ v'(t) = v(t)(\alpha_2 - \beta_2 v(t) - \gamma_2 u(t)), & t > 0, \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{cases} \quad (3.11)$$

System (3.11) has 4 equilibrium points :

$$\begin{aligned} (u_1, v_1) &= (0, 0) \\ (u_2, v_2) &= \left(\frac{\alpha_1}{\beta_1}, 0 \right), \\ (u_3, v_3) &= \left(0, \frac{\alpha_2}{\beta_2} \right), \\ (u_4, v_4) &= \left(\frac{\alpha_2 \gamma_1 - \alpha_1 \beta_2}{\gamma_1 \gamma_2 - \beta_1 \beta_2}, \frac{\alpha_1 \gamma_2 - \alpha_2 \beta_1}{\gamma_1 \gamma_2 - \beta_1 \beta_2} \right). \end{aligned}$$

We can distinguish 4 situations :

- (i) $\frac{\gamma_1}{\beta_2} < \frac{\alpha_1}{\alpha_2} < \frac{\beta_1}{\gamma_2}$
- (ii) $\frac{\beta_1}{\gamma_2} < \frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2}$
- (iii) $\frac{\alpha_1}{\alpha_2} > \frac{\beta_1}{\gamma_2}$ and $\frac{\alpha_1}{\alpha_2} > \frac{\gamma_1}{\beta_2}$
- (iv) $\frac{\alpha_1}{\alpha_2} < \frac{\beta_1}{\gamma_2}$ and $\frac{\alpha_1}{\alpha_2} < \frac{\gamma_1}{\beta_2}$

Notice that in all cases, the steady point $(0, 0)$ is linearly unstable. Let us describe the (linear) nature of the other steady states. In case (i), (u_2, v_2) and (u_3, v_3) are saddle points and (u_4, v_4) is asymptotically stable. In case (ii), (u_2, v_2) and (u_3, v_3) are stable and (u_4, v_4) is a saddle point. In this case, the line of equation

$$v = \frac{\alpha_1 \gamma_2 - \alpha_2 \beta_1}{\alpha_2 \gamma_1 - \alpha_1 \beta_2} u$$

in the plane (u, v) is a separatrix, which divides the quadrant $[0, +\infty[\times [0, +\infty[$ into the basins of attraction of (u_2, v_2) and (u_3, v_3) respectively.

In case (iii), the steady point $(u_4, v_4) \notin [0, +\infty[\times [0, +\infty[$ and its nature has no effect on the steady states (u_2, v_2) and (u_3, v_3) which are, respectively, stable and saddle-point. In case (iv), the same situation occurs but the nature of (u_2, v_2) and (u_3, v_3) is reversed.

Let us conclude with the following special situation for the dynamical system

$$\begin{cases} u'(t) = \eta_1 u(t)(1 - \beta u(t) - \gamma v(t)), & t > 0, \\ v'(t) = \eta_2 v(t)(1 - \beta u(t) - \gamma v(t)), & t > 0, \\ u(0) = u_0 > 0, & v(0) = v_0 > 0, \end{cases} \quad (3.12)$$

This degenerated case, $\frac{\gamma_1}{\beta_2} = \frac{\alpha_1}{\alpha_2} = \frac{\beta_1}{\gamma_2} = \frac{\eta_1}{\eta_2}$, implies that each species has the same intra-specific and inter-specific competition performance, however, one species may grow faster at a faster time scale than the other. It follows that

$$\eta_2 \frac{u'(t)}{u(t)} = \eta_1 \frac{v'(t)}{v(t)}, \text{ for every } t > 0$$

and hence

$$\left[\frac{u(t)}{u_0} \right]^{\eta_2} = \left[\frac{v(t)}{v_0} \right]^{\eta_1}, \text{ for every } t > 0.$$

On the other hand, the system (3.12) admits the linear set of steady states

$$\beta u + \gamma v = 1, \quad u \geq 0, \quad v \geq 0, \quad (3.13)$$

that ends with the two equilibrium points of each equation separately

$$u = \frac{1}{\beta}, \text{ when } v = 0,$$

or

$$v = \frac{1}{\gamma}, \text{ when } u = 0.$$

We observe that the initial condition (u_0, v_0) can be set such as each steady solution of this set (3.13) can be reached.

On the contrary, if the two species differ by their nutrient requirement in the same proportion as we have seen before, i.e.

$$\begin{cases} u'(t) = \eta_1 u(t)(\alpha_1 - \beta u(t) - \gamma v(t)), & t > 0, \\ v'(t) = \eta_2 v(t)(\alpha_2 - \beta u(t) - \gamma v(t)), & t > 0, \\ u(0) = u_0 > 0, & v(0) = v_0 > 0, \end{cases} \quad (3.14)$$

with

$$\alpha_1 \neq \alpha_2,$$

the species that gets the poorest environment support for its specific needs, gets wiped out by the other one.

We are going, now, to exercise with numerical simulations, the influence of the spatial competition with respect to nonlinear diffusions on the competition mechanism driven by the Lotka-Volterra system (3.11) .

3.3.2 Numerical Simulation of a Benchmark Problem

We consider the following Benchmark case :

$$\begin{cases} u_t - \operatorname{div}(\varepsilon_1 \Phi(v) \nabla u) = u (\alpha_1 - \beta_1 u - \gamma_1 v), & (x, y) \in \Omega, t > 0, \\ v_t - \operatorname{div}(\varepsilon_2 \Phi(u) \nabla v) = v (\alpha_2 - \beta_2 v - \gamma_2 u), & (x, y) \in \Omega, t > 0, \end{cases} \quad (3.15)$$

with homogeneous Neumann boundary conditions on $\partial\Omega$,

$$\nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 \quad \text{on } [0, +\infty[\times \partial\Omega.$$

The nonlinear diffusion coefficient is the smooth function

$$\Phi(s) = C \exp\left(\frac{\eta^2}{s^2 - \eta^2}\right), \text{ if } 0 \leq s < \eta \quad \text{and} \quad \Phi(s) = 0, \text{ if } s \geq \eta > 0.$$

We set $C = \exp(1)$ and $0 \leq \Phi(s) \leq 1$.

Let's set up the parameters of the Lotka-Volterra system such that the second species v has a competitive advantage on the first species, i.e unique stable equilibrium point

$$\left(u = 0, v = \frac{\alpha_2}{\beta_2} > 0\right)$$

with

$$\alpha_1 = 1, \alpha_2 = 1.3, \beta_1 = 1.2, \beta_2 = 0.8, \gamma_1 = 3., \gamma_2 = 1.1.$$

We test out the influence of the competitive advantage of motility by comparing the result for $\varepsilon_1 = \varepsilon_2$ with the result for $\varepsilon_1 \gg \varepsilon_2$.

Similarly, we test the competitive advantage of space exclusion that corresponds to $\eta \ll 1$ by comparing to the situation with quasi uniform diffusion $\eta \gg 1$. Figs 3.1 to 3.4 show the four possible combinations of these parameters settings.

The initial condition for the Benchmark problem is a collection of well separated sharp bell function

$$\exp\left[-\frac{\operatorname{dist}((x, y), M_j)}{\nu}\right],$$

that plays the role of initial "density of plant populations", centered on a set of points M_j - see Figs. 3.1 to 3.4 at $T = 0$. We use similar initial densities for both species.

The numerical implementation is straightforward. We use a regular Cartesian grid with a second order finite volume approximation in space and a second order Crank-Nicolson implicit time stepping.

When we run the simulation, we observe, at early time, the diffusion process

that represents plant colonization. After some time, we start to see some interaction with narrow front layers where both species compete. This boundary layer that separates the species, is more or less diffused depending on how small is the ν value.

In these figures, we use the following convention : the space invaded by the first species (respt. the second species) is marked by black label (respt. red label). The simulation exhibit then nice pattern formation for each species.

In the figures, area where density is above 0.5, is indicated by circles 'o', while the area with lower concentration in the interval (0.1, 0.5) is indicated by dots '.'. This helps to visualize area where the first species is strongly dominant, i.e red circle zone, areas where the second species diffuses every where, i.e. black dot point area, and overlapping zone where competition occurs. These patterns are, somewhat, similar to the spatial distribution of ramets in a phalanx-guerilla species system emerging from the simulation of prairies with the agent base model of Mony [84].

Figs. 3.5 and 3.6 give a snap shot of one of these agent based simulations between populations of phalanx and guerilla plants : we start from an equal number of roots for each plant. We assume a small probability that clones die but asexual reproduction is implemented which let the clonal plant surviving through its youngest shoot. In agent based simulations, we let the system evolve for several thousand steps, which may represent several seasons. Figs. 3.5 and 3.6 illustrate the emergence of pattern spatial formations such as the clustering in space of phalanx plants, while guerilla plants are distributed with sparsity everywhere. The prairie is, actually, the superposition of both distribution of ramets, since there is no space sharing of the cellular automata cells at the ramet location.

The next step, in this work, would be to calibrate the PDE simplified model to best fit the agent based simulation using the assimilation technique of Le Dimet [75] for example. However, this is not an easy task from the mathematical point of view, since it requires investigations about regularity of solutions to degenerated nonlinear reaction-diffusion systems with respect to the parameters to be assimilated. These investigations will be the purpose of a future publication.

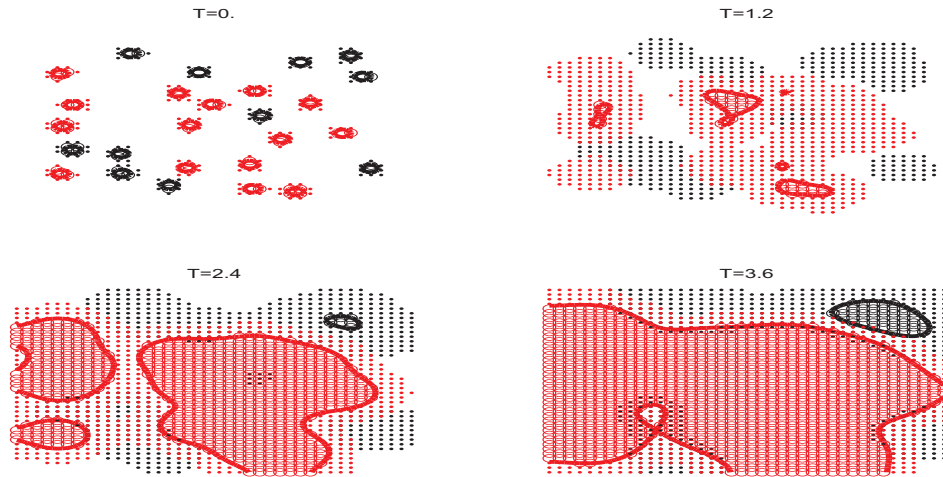


FIGURE 3.1 – Two species system with quasi uniform diffusion : $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 100$. First species (respt. the second species) is marked by black label (respt. red label). Density above 0.5 is indicated by circles ‘o’, density in the interval (0.1, 0.5) is indicated by dots ‘.’.

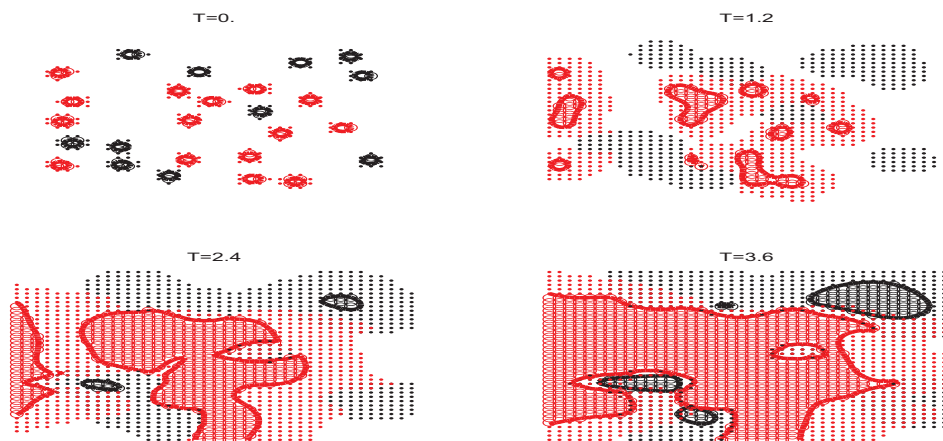


FIGURE 3.2 – Two species system with strong exclusive diffusion $\varepsilon_1 = \varepsilon_2 = 0.001$, $\eta = 0.1$. First species (respt. the second species) is marked by black label (respt. red label). Density above 0.5 is indicated by circles ‘o’, density in the interval (0.1, 0.5) is indicated by dots ‘.’

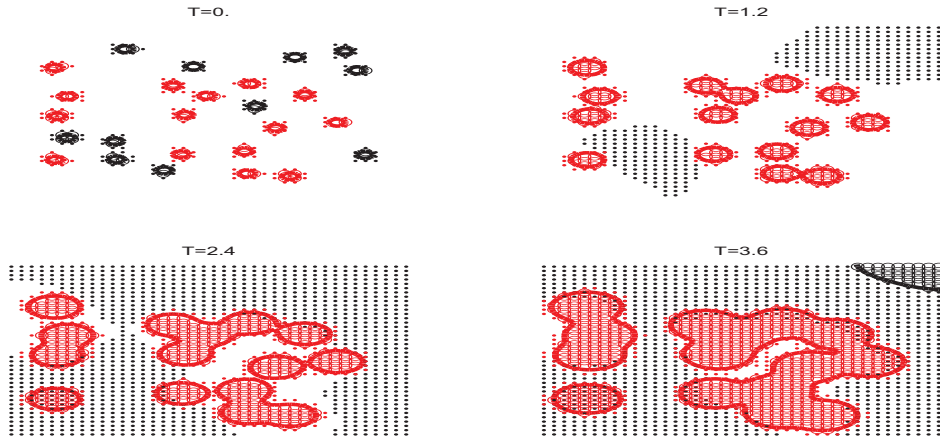


FIGURE 3.3 – First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 100$, but both species have quasi uniform diffusion. First species (respt. the second species) is marked by black label (respt. the red label). Density above 0.5 is indicated by circles ‘o’, density in the interval $(0.1, 0.5)$ is indicated by dots ‘.’

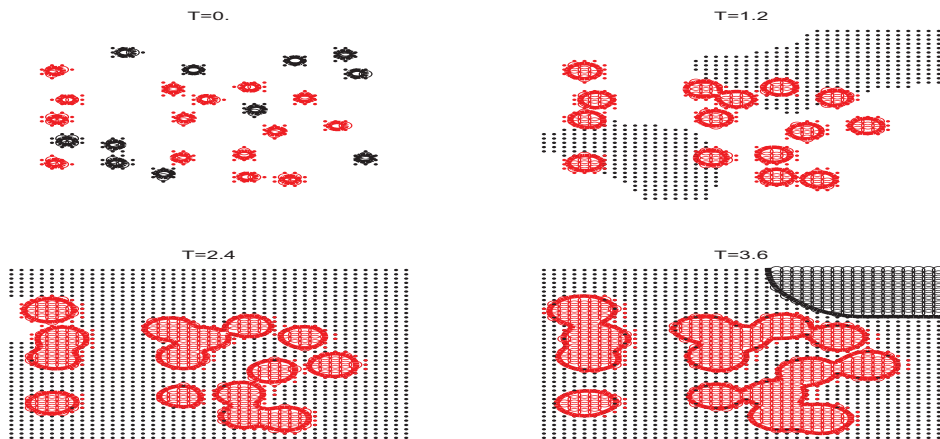


FIGURE 3.4 – First species has dominant motility $\varepsilon_1 = 0.1 \gg \varepsilon_2 = 0.0001$, $\eta = 100$, but both species have quasi uniform diffusion. First species (respt. the second species) is marked by black label (respt. the red label). Density above 0.5 is indicated by circles ‘o’, density in the interval $(0.1, 0.5)$ is indicated by dots ‘.’

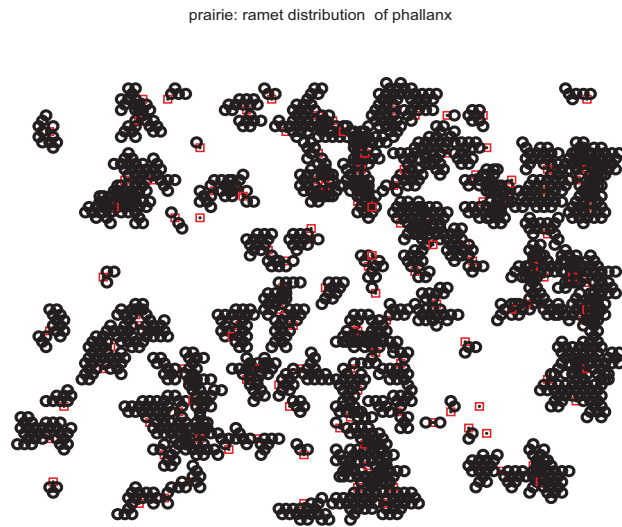


FIGURE 3.5 – Space distribution of ramets for Phallanx.

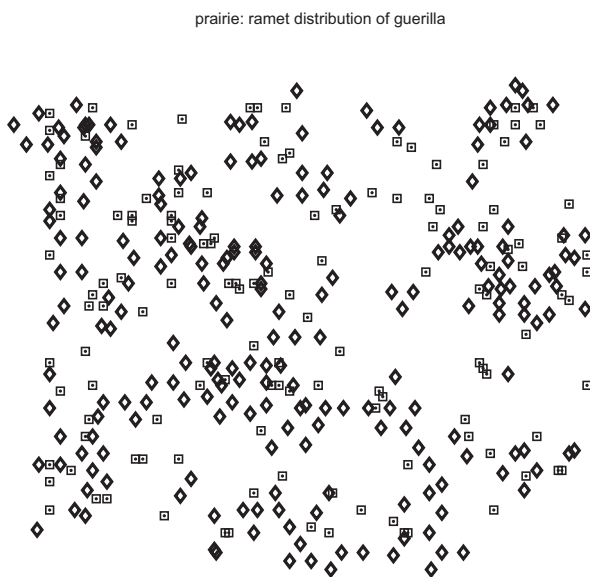


FIGURE 3.6 – Space distribution of ramets for Guerilla.

Let us report on the simulation result of our simplified Lotka-Volterra- nonlinear diffusion model.

As expected, with uniform spatial diffusion, i.e $\eta \gg 1$, the most competitive species wipes out the other one that goes to extinction. Indeed, in Figs. 3.1 and 3.3, the nonlinear diffusion coefficients is positive, i.e $\mu_i(u_k, v_k) > 0$, $i = 1, 2$ and $k = 1, \dots, 4$, where (u_k, v_k) denotes the equilibrium points of (3.17). In particular,

the unique stable equilibrium point (u_3, v_3) for (3.17) remains stable for (3.16). In Fig. 3.1, we see clearly the convergence of the solution to the equilibrium point (u_3, v_3) .

This process might be slowed down if the less competitive species is space dominant, i.e. diffuses the fastest ($\varepsilon_1 \gg \varepsilon_2$).

However, for strong exclusive diffusions, i.e. $\eta \ll 1$, we have $\mu_1(u_3, v_3) = 0$. In this case, Theorem 3.2.1 is not applicable and we cannot predict the stability of (u_3, v_3) from Theorem 3.2.1.

In this situation, we expect that the less competitive species can survive much better in the transient. However, as time goes to infinity, it seems that the most competitive species will, eventually, take over. As $\eta \rightarrow 0$, this process takes longer and longer time.

Eventually, for $\eta = 0$, the less competitive species will, always, survive, and perhaps gets most of the field, thanks to its initial fast space invasion. In particular, the linear stability of equilibria is completely modified by this strong degeneracy.

3.4 Discussion

We are going to, successively, discuss the modeling approach, its validation, and the concept of surrogate model for ecology engineering.

Density of Population's Modelling

The new reaction-diffusion model was designed to reproduce some of the phenomenology on space competition observed in the field and that are illustrated by agent based simulations.

The first level of competition between plants is described by a standard Kolmogorov model that can apply to many different population models.

The second level of competition is focused on spatial competitions and is more specific to clonal plant. We have introduced a new mechanism in the model by adding a nonlinear diffusion that takes into account both the motility characteristic of the plant and its capacity to exclude other species in space.

We provided a general PDE model with proof of global and local existences and analyzed the mechanism of stability and instability. It was shown mathematically that the additional competition mechanism, described by the nonlinear diffusion, cannot change the equilibrium points of the Kolmogorov model. The nonlinear source terms in the Lotka-Volterra dynamical system stays the primary mechanism of competition.

Our new model, illustrated by the Benchmark problem of Section 3.3.2, seems to demonstrate that it can capture some of the emerging properties observed in spatial colonization with guerilla-phalanx species systems.

It should be noticed that our model can be readily generalized to clonal plant communities with multiple species :

$$W_t - \operatorname{div}(\mu(W)) = F(W),$$

where W is a vector of the density function for each species. We conjecture that the equilibrium points of the dynamical system $W_t = F(W)$, will not be affected by the nonlinear diffusion term either. Besides nonlinear diffusion, as opposed to uniform constant diffusion, will allow to obtain spatial pattern formation.

There are many ways, indeed, to improve the realism of our PDE model. For example, a digital map of the terrain Ω , may provide spatial heterogeneities that can be directly translated into the diffusion matrix. This might be also an interesting way to test the PDE model for heterogeneous patching (Oborny, 1994 ; Oborny et al., 2000 ; Pacala and Tilman, 1994).

Of course, the scale of the patching has to be larger than the scale of the clonal plant, for the PDE model to operate. This may limit, severely, the interest of the PDE model to address any interesting theoretical questions on the effect of small heterogeneities in the environment.

Another interesting question that we are currently investigating, is to add the so called "aging term" in the model. Let us consider, for example, a single species logistic model :

$$\frac{dM}{dt} = \alpha (\kappa - M(t)) M(t). \quad (3.16)$$

Adding the effect of aging, thanks to the delay term $-\lambda \frac{M(t)}{M_{max}} M(t - T)$,

$$\frac{dM}{dt} = \alpha (\kappa - M(t)) M(t) - \lambda \frac{M(t)}{M_{max}} M(t - T). \quad (3.17)$$

not only changes the dynamic of the model, but also adds interesting phenomena such as overshooting above the so called "maximum capacity" κ during the transient.

This aging term may turn out to be essential in another aspect of the competition between clonal plants depending on if its life cycle is seasonable or not.

An interesting third kind of extension of our model would be to add, in the model, a feedback mechanism with the environment. We can take into account the complex coupling with ground flow that may, definitively, influence the supplies of nutrient, and/or add external perturbations such as grazing.

Link to Agent Based Modelling

Most models of clonal plant communities are agent based models (Grimm and Railback, 2005) that take into account, explicitly, the plant architecture. In this bottom up modeling approach, all the basic rules on plant growth are

implemented at the level of the ramet, stolon, and finally clonal plant itself. These rules describe the plant architecture growth rules and metabolic functions. Rules for intra and interspecific competition are directly expressed at the ramet level. Such model involves a large number of parameters that need to be carefully calibrated.

In addition, agent based models are rather computationally intensive applications, that have at least a linear growth of arithmetic complexity that depends on the number of ramets. Agent based computational models are essential to analyze the emerging mechanism of competition between plants. However, there are not practical, in the field as engineering application tools. One may just need to predict at the macro scale if there is coexistence between species or which plant survives. The speed of invasion of one species versus the other would be a key prediction factor.

PDEs as opposed to agent base model, do not describe the plant community at the ramet level nor require the hourly time scale. PDE models rather estimate the local density of plants and are focussing on local average (macroscopic) approximation. The PDE model may start from an underlying dynamical system, here we have chosen the Kolmogorov model, that expresses the competition, for example the competition for nutrient resources. The clonal Plant motion, thanks to growth and asexual reproduction, is taken into account by a diffusion term. In this modeling approach, the mathematical theory of traveling waves for reaction diffusion systems (Smoller, [107]) may provide a velocity of propagation of a species. These data may serve as global indicator of an ecosystem dynamic. Besides PDE models involve, in general, fewer parameters and are less computationally intensive than an agent based model. In principle, a PDE model can run on a PC in a matter of minutes and can companion ecology engineering with a simple graphic user interface showing patterns of population.

To summarize, agent based models are the perfect tool to investigate ecology theoretical questions but may not be computer efficient in engineering. Vice versa PDE models may not be good enough to elucidate how a clonal plant community functions but might be a computationally efficient tool as a surrogate model, once properly calibrated.

Our point of view would be to reconnect both approaches with standard assimilation techniques designed for PDEs (Le Dimet [75]) and use the PDE model as a surrogate model for coarse engineering prediction.

We would like, however, to discuss what seems a fundamental conceptual limitation of our approach.

Let us consider the same Benchmark problem of Section 3.3.2 and add periodic spatial disturbance as follows : At periodic time $t = k T, T > 0, k$ positive integer, a part of the domain Ω is wiped out from its vegetation in a disk of random position $C(M, R)$ of center M and radius $R > 0$ inside the domain Ω :

$$U(x, y, k T) \equiv 0 \text{ and } V(x, y, k T) \equiv 0, \forall (x, y) \in C(M, R).$$

For $\eta \ll 1$, and $\epsilon_1 \gg \epsilon_2$, the less competitive species is going to have much better chances to survive, thanks to these periodic perturbations, than the strongest one. We can even mathematically prove that for η_1 and ϵ_2 asymptotically small enough, the strongest species will go for extinction, while the weakest will always survive. This is an interesting situation that correlates with the theoretical conjecture that states that, in the absence of external perturbation, Guerilla plants are led to extinction by phalanx plants, while, with periodic perturbations of the environment, guerilla species get a strategic advantage to survive. While it is somehow satisfying to have a PDE model that supports this theory, we get absolutely no conceptual insight from our PDE model on why this conjecture should be true or not. It seems, in this situation, that an agent based model is at a better position to answer such a theoretical question.

Model validation

In engineering, computing (Roache, 1998) "verification" is the process of determining whether or not a code is "solving the equation right", while "validation" is the process of whether or not the code is solving "the right equation". Verification of the numerical code for our PDE model is, somehow, a much easier task than for an agent based model. The process of verification is mathematically well defined, while validation is, somehow, an ad hoc principle to the specific domain of science under consideration.

Validation of a model needs experimental data. It is a serious difficulty to get experimental data on clonal plant species with precisely two species only and an accurate control of environmental conditions. In addition this experimental data should be spatially explicit. We can speculate that systematic imaging of prairies with a pixel accuracy of the order of a centimeter, may provide, in some particular situations, a map of plant densities. This is the kind of data that one would need to validate a PDE model with spatially accurate competition. Unfortunately, we have not been able to access such data so far.

We propose alternatively to validate the PDE model against a realistic agent based simulation. This strategy has two advantages.

First, we can get as many spatial information as we want from an agent based simulation, provided that one has access to enough computing time. Second, comparing a PDE model to an agent based model, would be an elegant way to extract systematically global information on the dynamic of an ecological system that may have some inherent theoretical value. If our model is properly "fitted" to an agent based model of a phalanx-guerilla species system, we should be able to retrieve the two by two community matrix. Similarly we may found the coefficient of diffusion for each species ϵ_1 and ϵ_2 , as well as the coefficient of "permeability" η that is characteristic of the size of the layer where species densities can overlap.

Perhaps, this would be a way to classify quantitatively clonal species produced out of agent based simulation.

The difficulty of fitting a nonlinear PDE model to an agent based model through numerical simulations should not be underestimated. This problem might be rigorously formulated with a variational formulation approach as in (Le Dimet [75]). However, there should be, first, an agreement on what should be the fitness function, and what should be the mathematical formulation to filter out the noise from the data set.

As a matter of fact, agent based simulations are stochastic methods of Monte Carlo type. We observe, in general, a significant level of noise on agent based simulation data. We feel, however, that this is an interesting challenge that should result into new families of compact surrogate models based on PDE that can be used in the field with, perhaps, some engineering practical values.

* - * - * - * - * - * - * - * - *

Chapitre 4

Nonlinear identification in cross-diffusion competition systems

Sommaire

| | |
|---|----|
| Présentation du chapitre | 64 |
| Abstract | 64 |
| 4.1 Introduction | 64 |
| 4.2 Local existence and positively invariant sets | 65 |
| 4.3 Study of the inverse problem | 70 |
| 4.3.1 Regularity results of solutions with respect to the pa-
rameters | 71 |
| 4.3.2 Computation of the gradient of J_0 | 80 |
| 4.4 Numerical simulations | 84 |

Ce travail effectué en collaboration avec Abdallah El Hamidi, constitue l'un des points centraux de cette thèse qui est le problème d'identification des termes de diffusions croisées. Le problème d'identification se fait à partir d'observations spatio-temporelles. Pour cela, on construit une fonctionnelle d'énergie appropriée à minimiser dont le minimiseur est le vecteur dont les composantes sont les fonctions diffusions croisées recherchées. Ce manuscrit sera soumis prochainement pour publication.

Abstract

In nonlinear diffusion identification problems, the gradient of the cost functional energy is given usually in weak (distributional) sense. In the present manuscript we characterize this type of gradients in the classical sense via the Federer's coarea formula. Our identification method is applied to a nonlinear reaction-diffusion competition system. Numerical simulations are performed to a reaction-diffusion equation with logistic source term whose nonlinear diffusion is identified via quasi-Newton type methods.

Keywords : Cross-diffusion, Competition, Nonlinear identification, Coarea formula, Minty-Browder.

4.1 Introduction

This manuscript deals with identification of cross-diffusion in reaction-diffusion competition systems. Evolution partial differential equations with cross-diffusion have been the subject of a sizeable literature [35, 78, 82, 83, 105]. Indeed, consider for example, two species that are activating or inhibiting each other according to some law of reaction and diffusing in a spatial domain by Fick's law but the diffusion of one of the substances is influenced also by the other one and conversely. The density of the two substances at time t and place x are denoted by $u(x, t)$ and $v(x, t)$ respectively. On one hand, the substance u flows from places where its density is high towards places where the density is low. On the other hand, v has an attracting or repulsing effect on u , so that u flows towards high, resp. low density places of v . In this situation the flow vector of u is given by

$$J_u = -d_{11}(u, v)\nabla u - d_{12}(u, v)\nabla v,$$

where $d_{11}(u, v) > 0$ and $d_{12}(u, v) \leq 0$, resp. ≥ 0 according as v attracts, resp. repulses u . Analogous behavior occurs for the flow vector J_v . Then a macroscopic continuous model (in the autonomous and spatial homogeneous case) describing

this interaction is given by the reaction-diffusion system

$$\begin{cases} u_t - \operatorname{div}(d_{11}(u, v)\nabla u + d_{12}(u, v)\nabla v) = f(u, v), \\ v_t - \operatorname{div}(d_{21}(u, v)\nabla u + d_{22}(u, v)\nabla v) = g(u, v), \end{cases} \quad (4.1)$$

where $f(u, v)$ and $g(u, v)$ are the reaction terms.

In [41], the authors consider that when populations behave so as to avoid crowding it is reasonable to assume that the diffusion terms μ_1 and μ_2 are increasing functions of the population densities u and v respectively. On the other hand, since the diffusion of u is penalized where v is positive, and *vice versa*, it is reasonable to assume also that the diffusion terms μ_1 and μ_2 are decreasing in v and u respectively.

In the present manuscript, we consider a system of nonlinear reaction-diffusion equations with cross-diffusion terms. We show how to deal with the identification of the nonlinear diffusion terms, from measure data in time/space, and give an accurate computation of the gradient of cost functional. Finally, numerical simulations describing the theoretical results are performed.

4.2 Local existence and positively invariant sets

Consider the reaction diffusion Kolmogorov system

$$\begin{cases} u_t - \operatorname{div}(\mu_1(x, t, u, v, \nabla u)) = u f_1(x, t, u, v) := f(x, t, u, v) \text{ in } \Omega \times]0, T], \\ v_t - \operatorname{div}(\mu_2(x, t, u, v, \nabla v)) = v g_1(x, t, u, v) := g(x, t, u, v) \text{ in } \Omega \times]0, T], \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 \text{ on } \partial\Omega \times]0, T], \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x) \text{ in } \Omega, \end{cases} \quad (4.2)$$

where T is a given positive real number and the operators $-\operatorname{div}(\mu_1(x, t, u, v, \nabla u))$ and $-\operatorname{div}(\mu_2(x, t, u, v, \nabla v))$ satisfy the Leray-Lions assumptions :

- (i) $\mu_i(x, t, r, s, \xi) : \Omega \times \mathbb{R}^{N+3} \rightarrow \mathbb{R}^N$ is measurable in (x, t) , for every $(r, s, \xi) \in \mathbb{R}^{N+2}$ and continuous in (r, s, ξ) for almost every $(x, t) \in \Omega \times \mathbb{R}$.
- (ii) There is a real number $\mu_* > 0$ such that for almost every $(x, t) \in \Omega \times \mathbb{R}$ and for every $(r, s, \xi) \in \mathbb{R}^{N+2}$, one has

$$\mu_i(x, t, r, s, \xi) \cdot \xi \geq \mu_* |\xi|_{\mathbb{R}^N}^2$$

- (iii) for every $(r, s, \xi, \eta) \in \mathbb{R}^{2N+2}$ and for almost every $(x, t) \in \Omega \times \mathbb{R}$ it holds

$$[\mu_i(x, t, r, s, \xi) - \mu_i(x, t, r, s, \eta)] \cdot (\xi - \eta) > 0, \text{ for } \xi \neq \eta \in \mathbb{R}^N$$

(iv) There exists $\theta(x, t) \in L^2(Q_T)$ and a real number $\mu^* > 0$ such that for almost every $(x, t) \in \Omega \times \mathbb{R}$ and for every $(r, s, \xi) \in \mathbb{R}^{N+2}$:

$$|\mu_i(x, t, r, s, \xi)| \leq \mu^* \times \{\theta(x, t) + |r| + |s| + |\xi|_{\mathbb{R}^N}\}.$$

Notice that these assumptions are standard for the study of nonlinear operators with divergential form. As usually, a weak solution of System (4.2) is a pair of functions (u, v) defined on Q_T satisfying :

$$u, v \in L^2(]0, T[, H^1(\Omega)) \text{ and } u_t, v_t \in L^2(]0, T[, H^1(\Omega)')$$

and for every φ and ψ in $H^1(\Omega)$ and almost every $t \in [0, T]$:

$$\langle u_t(t), \varphi \rangle_{H^1(\Omega)', H^1(\Omega)} + \int_{\Omega} \mu_1(x, t, u, v, \nabla u) \cdot \nabla \varphi(x) dx = \int_{\Omega} f(x, t, u, v) \varphi(x) dx,$$

$$\langle v_t(t), \psi \rangle_{H^1(\Omega)', H^1(\Omega)} + \int_{\Omega} \mu_2(x, t, u, v, \nabla v) \cdot \nabla \psi(x) dx = \int_{\Omega} g(x, t, u, v) \psi(x) dx,$$

$$u(0) = u_0 \text{ and } v(0) = v_0.$$

In what follows, we show a local existence result to System (4.2) and that its solutions remain in an adequate bounded set as long as the initial data belong to this set. The proof is based on *a priori* classical estimates and the positively invariant set is a consequence of the Kolmogorov nature of the system.

Lemma 4.2.1. *If*

(H₁) $u_0 \geq 0$ and $v_0 \geq 0$ are in $L^\infty(\Omega)$,

(H₂) $\exists M \geq 0 : \forall (x, t, u, v) \in \Omega \times [0, T] \times [0, +\infty[\times [0, +\infty[$ one has

$$f_1(x, t, u, v) \leq M \text{ and } g_1(x, t, u, v) \leq M,$$

(H₃) *The functions f_1 and g_1 are Lipschitzian in u and v .*

Then System (4.2) admits a unique nonnegative solution satisfying :

$$u, v \in L^\infty(]0, T[, L^2(\Omega)) \cap L^2(]0, T[, H^1(\Omega)) \text{ and } u_t, v_t \in L^2(]0, T[, H^1(\Omega)').$$

Proof. The proof is divided into two step :

Existence.

Let (u^0, v^0) the initial condition, satisfying the hypothesis (H₁). We will construct a sequence $(u^n, v^n)_{n \geq 1}$ which is uniformly bounded in $L^\infty(Q_T) \cap L^2(]0, T[, H^1(\Omega))$ such that (u_t^n, v_t^n) is uniformly bounded in $L^2(]0, T[, H^1(\Omega)')$. Indeed, for every

$n \in \mathbb{N}$, consider the linear iterative system

$$\left\{ \begin{array}{l} u_t - \operatorname{div}(\mu_1(x, t, u^n, v^n, \nabla u)) = u f_1(x, t, u^n, v^n) \text{ in } \Omega \times]0, T], \\ v_t - \operatorname{div}(\mu_2(x, t, u^n, v^n, \nabla v)) = v g_1(x, t, u^n, v^n) \text{ in } \Omega \times]0, T], \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 \text{ on } \partial\Omega \times]0, T], \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x) \text{ in } \Omega, \end{array} \right. \quad (4.3)$$

whose solution is denoted by (u^{n+1}, v^{n+1}) . Using the fact that the RHS of System (4.3) is Lipschitz, the classical theory implies that $u^{n+1}, v^{n+1} \in L^\infty(Q_T) \cap L^2(]0, T[, H^1(\Omega))$ and $u_t^{n+1}, v_t^{n+1} \in L^2(]0, T[, H^1(\Omega)')$. Moreover, multiplying the first equation of (4.3) by the function $[u^{n+1}]^-$ where $w^- := \max\{-w, 0\}$ and integrate on Ω , it follows that for every $t \in [0, T]$:

$$\left\| [u^{n+1}(t)]^- \right\|_{L^2(\Omega)}^2 \leq M \left\| [u^{n+1}(0)]^- \right\|_{L^2(\Omega)}^2 = 0.$$

Then $u^{n+1}(t) \geq 0$ *a.e.* in Ω , for every $t \in [0, T]$, that is $u^{n+1} \geq 0$ in Q_T . Similarly, multiplying the first equation of (4.3) by the function u^{n+1} and integrating on Ω , it follows that the sequences $(u^n)_n$ and $(v^n)_n$ are uniformly bounded in $L^\infty(]0, T[, L^2(\Omega))$. On the other hand, using the ellipticity of the divergence terms in the system, one concludes that $(u^n)_n$ and $(v^n)_n$ are also uniformly bounded in $L^2(]0, T[, H^1(\Omega))$.

Finally, the function $u_t^{n+1}(t)$, seen as an element of $H^1(\Omega)'$, satisfies :

$$\begin{aligned} \langle u_t^{n+1}(t), \varphi \rangle_{H^1(\Omega)', H^1(\Omega)} &= - \int_{\Omega} \mu_1(x, t, u^n, v^n, \nabla u^{n+1}) \cdot \nabla \varphi \, dx \\ &\quad + \int_{\Omega} u^{n+1} \varphi f_1(x, t, u^n, v^n) \, dx. \end{aligned}$$

Then

$$\|u_t^{n+1}(t)\|_{H^1(\Omega)'} \leq c \|u^{n+1}(t)\|_{H^1(\Omega)}$$

and hence $(u_t^n)_{n \geq 1}$ is uniformly bounded in $L^2(]0, T[, H^1(\Omega)')$. We conclude, up to a subsequence, that

$$\left\{ \begin{array}{llll} (u^n, v^n) & \rightharpoonup & (u, v) & \text{in } L^2(]0, T[, H^1(\Omega)) \quad \text{weak,} \\ (u_t^n, v_t^n) & \rightharpoonup & (u_t, v_t) & \text{in } L^2(]0, T[, H^1(\Omega)') \quad \text{weak,} \\ (u^n, v^n) & \rightarrow & (u, v) & \text{in } L^2(Q_T) \text{ and a. e. in } Q_T \quad \text{strong,} \\ - \operatorname{div}(\mu_1(x, t, u^n, v^n, \nabla u^{n+1})) & \rightharpoonup & \chi_1 & \text{in } L^2(]0, T[, H^1(\Omega)') \quad \text{weak,} \\ - \operatorname{div}(\mu_2(x, t, u^n, v^n, \nabla v^{n+1})) & \rightharpoonup & \chi_2 & \text{in } L^2(]0, T[, H^1(\Omega)') \quad \text{weak,} \end{array} \right.$$

Since u and v belong then to $C([0, T], L^2(\Omega))$, it follows that

$$u(0) = u_0, v(0) = v_0, u^n(T) \longrightarrow u(T) \text{ and } v^n(T) \longrightarrow v(T), \text{ in } L^2(\Omega) \text{ weak.}$$

It remains to show that

$$\begin{aligned} \chi_1 &= -\operatorname{div}(\mu_1(x, t, u, v, \nabla u)), \\ \chi_2 &= -\operatorname{div}(\mu_2(x, t, u, v, \nabla v)), \end{aligned}$$

via the monotony method of Minty-Browder.

Indeed, on one hand, we have, in $L^2(]0, T[, H^1(\Omega)')$,

$$\begin{aligned} u_t + \chi_1 &= f(x, t, u, v), \\ v_t + \chi_2 &= g(x, t, u, v). \end{aligned}$$

On the other hand, let us denote $\mu_i(\xi(t)) := \mu_i(x, t, u^n(t), v^n(t), \xi(t))$, for $i = 1, 2$, then for every $w \in L^2(]0, T[, H^1(\Omega))$:

$$\begin{aligned} A_n &= \int_0^T \langle \mu_1(\nabla u^{n+1}(t)) - \mu_1(\nabla w(t)), u^{n+1}(t) - w(t) \rangle_{L^2(\Omega)} dt \geq 0, \\ B_n &= \int_0^T \langle \mu_2(\nabla v^{n+1}(t)) - \mu_2(\nabla w(t)), v^{n+1}(t) - w(t) \rangle_{L^2(\Omega)} dt \geq 0. \end{aligned}$$

Using the fact that

$$\begin{aligned} \int_0^T \langle \mu_1(\nabla u^{n+1}(t)), u^{n+1}(t) \rangle_{L^2(\Omega)} dt &= \int_0^T \langle u^{n+1}(t) f_1(t), u^{n+1}(t) \rangle_{L^2(\Omega)} dt \\ &\quad + \frac{1}{2} \left(\|u_0\|_{L^2(\Omega)}^2 - \|u^{n+1}(T)\|_{L^2(\Omega)}^2 \right) \\ \int_0^T \langle \mu_2(\nabla v^{n+1}(t)), v^{n+1}(t) \rangle_{L^2(\Omega)} dt &= \int_0^T \langle v^{n+1}(t) g_1(t), v^{n+1}(t) \rangle_{L^2(\Omega)} dt \\ &\quad + \frac{1}{2} \left(\|v_0\|_{L^2(\Omega)}^2 - \|v^{n+1}(T)\|_{L^2(\Omega)}^2 \right) \\ \liminf \|u^{n+1}(T)\|_{L^2(\Omega)} &\geq \|u(T)\|_{L^2(\Omega)} \\ \liminf \|v^{n+1}(T)\|_{L^2(\Omega)} &\geq \|v(T)\|_{L^2(\Omega)} \end{aligned}$$

it follows that

$$\begin{aligned} 0 \leq \limsup A_n &\leq \int_0^T \langle u(t) f_1(t), u(t) \rangle_{L^2(\Omega)} dt + \frac{1}{2} \left(\|u_0\|_{L^2(\Omega)}^2 - \|u(T)\|_{L^2(\Omega)}^2 \right) \\ &\quad - \int_0^T \langle \chi_1, w(t) \rangle_{H^1(\Omega)', H^1(\Omega)} dt - \int_0^T \langle \mu_1(\nabla w(t)), u(t) - w(t) \rangle_{L^2(\Omega)} dt \\ &= \int_0^T \langle \chi_1 + \operatorname{div}(\mu_1(\nabla w(t))), u(t) - w(t) \rangle_{H^1(\Omega)', H^1(\Omega)} dt. \end{aligned}$$

Now, we chose $w = u + \lambda\varphi$, with $\varphi \in L^2(]0, T[, H^1(\Omega))$ and $\lambda > 0$. Then

$$\int_0^T \langle \chi_1 + \operatorname{div}(\mu_1(\nabla u(t) + \lambda\varphi(t))), \varphi(t) \rangle_{H^1(\Omega)', H^1(\Omega)} dt \leq 0,$$

$$\forall \varphi \in L^2(]0, T[, H^1(\Omega)).$$

The continuity of $\mu_1(x, t, r, s, \xi)$ w.r.t to r, s and ξ implies the continuity of the map $u \mapsto \operatorname{div}(\mu_1(x, t, u, v, \nabla u))$ from $H^1(\Omega)$ to $H^1(\Omega)'$ and consequently the continuity of the function $\lambda \mapsto \langle \chi_1 + \operatorname{div}(\mu_1(\nabla u(t) + \lambda\varphi(t))), \varphi(t) \rangle_{H^1(\Omega)', H^1(\Omega)}$.

Therefore, using the fact that $(u^n, v^n) \rightarrow (u, v)$ in $L^2(Q_T)$ and *a. e.* in Q_T strong, and passing to the limit $\lambda \rightarrow 0^+$, we obtain :

$$\int_0^T \langle \chi_1 + \operatorname{div}(\mu_1(x, t, u, v, \nabla u(t))), \varphi(t) \rangle_{H^1(\Omega)', H^1(\Omega)} \geq 0, \quad \forall \varphi \in L^2(]0, T[, H^1(\Omega)),$$

which leads to

$$\chi_1 = -\operatorname{div}(\mu_1(x, t, u, v, \nabla u)).$$

Similar arguments give

$$\chi_2 = -\operatorname{div}(\mu_2(x, t, u, v, \nabla v)),$$

which achieves the claim.

Uniqueness.

Let (u_1, v_1) and (u_2, v_2) be two solutions of (4.2) on Q_T and set $\delta u = u_2 - u_1$ and $\delta v = v_2 - v_1$. Using the property (iii) of the diffusions $\mu_i, i = 1, 2$:

$$[\mu_i(x, t, u_2, v_2, \nabla u_2) - \mu_i(x, t, u_1, v_1, \nabla u_1)] \cdot (\nabla \delta u) \geq 0,$$

we get :

$$\begin{aligned} \frac{d}{dt} \|\delta u(t)\|_{L^2(\Omega)}^2 &\leq L_{f_1} \int_{\Omega} |u_1| |\delta u(t)| (|\delta u(t)| + |\delta v(t)|) dx \\ &\quad + \int_{\Omega} [\delta u(t)]^2 f_1(x, t, u_2(t), v_2(t)) dx \\ &\leq C_1 \left(\|\delta u(t)\|_{L^2(\Omega)}^2 + \|\delta v(t)\|_{L^2(\Omega)}^2 \right), \end{aligned}$$

where L_{f_1} is the maximum of the two Lipschitz constants of f_1 with respect to u and v . Similar arguments imply that

$$\frac{d}{dt} \left(\|\delta u(t)\|_{L^2(\Omega)}^2 + \|\delta v(t)\|_{L^2(\Omega)}^2 \right) \leq C_2 \left(\|\delta u(t)\|_{L^2(\Omega)}^2 + \|\delta v(t)\|_{L^2(\Omega)}^2 \right).$$

The Gronwall Lemma leads to $\|\delta u(t)\|_{L^2(\Omega)} = \|\delta v(t)\|_{L^2(\Omega)} = 0$, for almost every $t \in [0, T]$, which ends the proof. \square

4.3 Study of the inverse problem

In this section, we confine ourself to the competition model [?]

$$\begin{cases} u_t - \operatorname{div}(\mu_1(v)\nabla u) = f(\mathbf{a}, u, v) \text{ in } \Omega \times]0, T], \\ v_t - \operatorname{div}(\mu_2(u)\nabla v) = g(\mathbf{b}, u, v) \text{ in } \Omega \times]0, T], \\ \nabla u \cdot \mathbf{n} = \nabla v \cdot \mathbf{n} = 0 \text{ on } \partial\Omega \times]0, T], \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x) \text{ in } \Omega, \end{cases} \quad (4.4)$$

where \mathbf{a} and \mathbf{b} are unknown vectors of real parameters, μ_1 and μ_2 are unknown smooth diffusion functions.

In our applications, the functions f and g have the form : $f(u, v, \mathbf{a}) = uf_1(u, v, \mathbf{a})$ and $g(u, v, \mathbf{b}) = vg_1(u, v, \mathbf{b})$, where

$$\begin{aligned} f_1(u, v, \mathbf{a}) &= \alpha_1 - \beta_1 u - \gamma_1 v, \\ g_1(u, v, \mathbf{b}) &= \alpha_2 - \beta_2 v - \gamma_2 u, \\ \mu_1(x, t, u, v, \nabla u) &:= \mu_1(v)\nabla u, \\ \mu_2(x, t, u, v, \nabla v) &:= \mu_2(u)\nabla v, \end{aligned}$$

and $\mathbf{a} := (\alpha_1, \beta_1, \gamma_1)$ and $\mathbf{b} := (\alpha_2, \beta_2, \gamma_2)$. Thus all the hypotheses of Lemma 4.2.1 are clearly satisfied except the condition (iii), in the Leray-Lions properties. This point will be studied in the future.

The purpose of what follows is the identification of the nonlinear diffusion functions μ_1, μ_2 , the intrinsic growth rates α_i , the intra-specific competition rates β_i and the inter-specific competition rates γ_i of the species u and v respectively, $i = 1, 2$. The identification process is based on the *observations* $(u_{\text{obs}}, v_{\text{obs}})$ given in all Q_T .

Consider

$$\mathcal{N} = \{\mu \in \mathcal{C}^2(\mathbb{R}) : \mu, \mu' \text{ and } \mu'' \text{ are bounded}\}.$$

The space of diffusion coefficients is defined as :

$$\mathcal{M} = \{\mu \in \mathcal{N} : 0 < \underline{\mu} \leq \mu \leq \bar{\mu}\}.$$

and the admissible set for the vectors $\mathbf{a} := (\alpha_1, \beta_1, \gamma_1)$ and $\mathbf{b} := (\alpha_2, \beta_2, \gamma_2)$ is

$$\mathcal{A} = [\underline{\alpha}, \bar{\alpha}] \times [\underline{\beta}, \bar{\beta}] \times [\underline{\gamma}, \bar{\gamma}] \subset \mathbb{R}^3,$$

where $\underline{\mu}, \bar{\mu}, \underline{\alpha}, \bar{\alpha}, \underline{\beta}, \bar{\beta}, \underline{\gamma}$ and $\bar{\gamma}$ are given positive constants.

Suppose now that System (4.4), admits a solution

$$u, v \in L^\infty(]0, T[, L^2(\Omega)) \cap L^2(]0, T[; H^1(\Omega)).$$

If $0 \leq u_0(x) \leq \frac{\alpha_1}{\beta_1}$ in Ω , then multiplying the first equation of System (4.4) by u^- and by $(\alpha_1 - \beta_1 u)^+$ respectively, integrating over Ω and using similar arguments as in Lemma 4.2.1, we show easily that

$$0 \leq u(x, t) \leq \frac{\alpha_1}{\beta_1} \text{ in } Q_T,$$

where $Q_T :=]0, T[\times \Omega$, the *parabolic cylinder*. In the same way, we obtain :

$$0 \leq v_0(x) \leq \frac{\alpha_2}{\beta_2} \text{ in } \Omega \implies 0 \leq v(x, t) \leq \frac{\alpha_2}{\beta_2} \text{ in } Q_T.$$

In particular, u, v belong to $L^2(Q_T)$. In what follows, we will assume that

$$0 \leq u_0(x) \leq \frac{\alpha_1}{\beta_1} \quad \text{and} \quad 0 \leq v_0(x) \leq \frac{\alpha_2}{\beta_2} \text{ in } \Omega.$$

Consider the cost functional

$$J_0(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) = \frac{1}{2} \int_{Q_T} \{ |u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - u_{\text{obs}}|^2 + |v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - v_{\text{obs}}|^2 \} dx dt.$$

which is well defined. Notice that the question of the existence of minimizers to J_0 is very intricate in the case of systems with cross diffusions. Indeed, on one hand, one can not write the terms $\text{div}(\mu_1(v)\nabla u)$ and $\text{div}(\mu_2(u)\nabla v)$ as Laplacians of smooth functions of u and v as in the scalar case. On the other hand, if we regularize the functional J_0 , we have to show additional regularity results of ∇u and ∇v with respect to the parameters μ_1 and μ_2 .

In order to use gradient type methods, we need to compute the gradient of the cost functional J_0 with respect to its parameters. To do this, we show first that the solution (u, v) of (4.4) depends in a differentiable way with respect to these parameters. This point is the purpose of the next subsection. Throughout what follows, the letter c (or c_1, c_2 , etc \dots) denotes a positive constant which may vary from line to line but is independent of the terms which will take part in any limit process.

4.3.1 Regularity results of solutions with respect to the parameters

In this part, we will show that the solution (u, v) of the system (4.4) is Gâteaux-differentiable with respect to the functional parameters μ_i and the vectors of real parameters \mathbf{a} and \mathbf{b} , for every source terms $f(u, v, \mathbf{a})$ and $g(u, v, \mathbf{b})$ of class C^2 .

For this, we will do the following assumption :

$$(H) \quad |\nabla u(\cdot, t)| \in L^\infty(\Omega) \quad \text{and} \quad |\nabla v(\cdot, t)| \in L^\infty(\Omega), \quad \text{for almost every } t \in [0, T].$$

1.Continuity of the application : $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \rightarrow (u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}), v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}))$.

Lemma 4.3.1. *The application $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \rightarrow (u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}), v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}))$ is continuous from $(\mathcal{M}, \|\cdot\|_\infty)^2 \times \mathbb{R}^6$ to $L^\infty(0, T; L^2(\Omega)) \cap L^2(0, T; H^1(\Omega))$.*

Proof. Let $(\mu_1, \mu_2) \in \mathcal{M}$ and $(d\mu_1, d\mu_2) \in \mathcal{N}$ such that $(\mu_1 + d\mu_1, \mu_2 + d\mu_2) \in \mathcal{M}$ and $(d\mathbf{a}, d\mathbf{b}) \in \mathbb{R}^3 \times \mathbb{R}^3$. We set

$$\tilde{\mu}_1 = \mu_1 + d\mu_1, \quad \tilde{\mu}_2 = \mu_2 + d\mu_2$$

and then

$$\tilde{u} = u + w_1 \quad \tilde{v} = v + w_2,$$

where (u, v) and (\tilde{u}, \tilde{v}) are the solutions of (4.4) for $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b})$ and $(\tilde{\mu}_1, \tilde{\mu}_2, \mathbf{a} + d\mathbf{a}, \mathbf{b} + d\mathbf{b})$ respectively. The system satisfied by (\tilde{u}, \tilde{v}) is

$$\left\{ \begin{array}{l} \tilde{u}_t - \operatorname{div}(\tilde{\mu}_1(\tilde{v})\nabla\tilde{u}) = f(\mathbf{a} + d\mathbf{a}, \tilde{u}, \tilde{v}) \text{ in } \Omega \times]0, T], \\ \tilde{v}_t - \operatorname{div}(\tilde{\mu}_2(\tilde{u})\nabla\tilde{v}) = g(\mathbf{b} + d\mathbf{b}, \tilde{u}, \tilde{v}) \text{ in } \Omega \times]0, T], \\ \nabla\tilde{u} \cdot \mathbf{n} = \nabla\tilde{v} \cdot \mathbf{n} = 0 \text{ on } \partial\Omega \times]0, T], \\ \tilde{u}(x, 0) = u_0(x), \quad \tilde{v}(x, 0) = v_0(x) \text{ in } \Omega, \end{array} \right. \quad (4.5)$$

It follows that the system satisfied by (w_1, w_2) is

$$\left\{ \begin{array}{l} (w_1)_t - \operatorname{div}(\tilde{\mu}_1(\tilde{v})\nabla\tilde{u}) + \operatorname{div}(\mu_1(v)\nabla u) = f(\mathbf{a} + d\mathbf{a}, \tilde{u}, \tilde{v}) - f(\mathbf{a}, u, v) \text{ in } \Omega \times]0, T], \\ (w_2)_t - \operatorname{div}(\tilde{\mu}_2(\tilde{u})\nabla\tilde{v}) + \operatorname{div}(\mu_2(u)\nabla v) = g(\mathbf{b} + d\mathbf{b}, \tilde{u}, \tilde{v}) - g(\mathbf{b}, u, v) \text{ in } \Omega \times]0, T], \\ \nabla w_1 \cdot \mathbf{n} = \nabla w_2 \cdot \mathbf{n} = 0 \text{ on } \partial\Omega \times]0, T], \\ w_1(x, 0) = 0, \quad w_2(x, 0) = 0 \text{ in } \Omega, \end{array} \right. \quad (4.6)$$

Applying the Taylor-Young formula

$$f(\mathbf{a} + d\mathbf{a}, \tilde{u}, \tilde{v}) - f(\mathbf{a}, u, v) = \nabla f(\mathbf{a} + \theta_1 d\mathbf{a}, u + \theta_1 w_1, v + \theta_1 w_2) \cdot (d\mathbf{a}, w_1, w_2)$$

$$g(\mathbf{b} + d\mathbf{b}, \tilde{u}, \tilde{v}) - g(\mathbf{b}, u, v) = \nabla g(\mathbf{b} + \theta_2 d\mathbf{b}, u + \theta_2 w_1, v + \theta_2 w_2) \cdot (d\mathbf{b}, w_1, w_2)$$

and the fact that

$$\tilde{\mu}_1(\tilde{v})\nabla\tilde{u} - \mu_1(v)\nabla u = \mu_1(\tilde{v})\nabla w_1 + \mu_1'(v + \theta_3 w_2)w_2\nabla u + d\mu_1(\tilde{v})\nabla u$$

$$\tilde{\mu}_2(\tilde{u})\nabla\tilde{v} - \mu_2(u)\nabla v = \mu_2(\tilde{u})\nabla w_2 + \mu_2'(u + \theta_4 w_1)w_1\nabla v + d\mu_2(\tilde{u})\nabla v$$

the first equation of (4.6) can be thus rewritten

$$(w_1)_t - \operatorname{div}(\mu_1(\tilde{v})\nabla w_1) = \operatorname{div}((\mu_1'(v + \theta_1 w_3)w_2 + d\mu_1(\tilde{v}))\nabla u) + \nabla f((\mathbf{a}, u, v) + \theta_1(d\mathbf{a}, w_1, w_2)) \cdot (d\mathbf{a}, w_1, w_2). \quad (4.7)$$

Multiplying (4.7) by w_1 and integrating in time and space, we get

$$\begin{aligned} \frac{1}{2}\|w_1(t)\|_2^2 + \mu_* \int_{Q_t} |\nabla w_1|^2 dx ds &\leq \int_{Q_t} |d\mu_1(\tilde{v}) + (\mu_1'(v + \theta_3 w_2)w_2)| \times |\nabla u| \times |\nabla w_1| dx ds \\ &+ \int_{Q_t} |d\mathbf{a}| w_1 \frac{\partial f}{\partial \mathbf{a}}((\mathbf{a}, u, v) + \theta_1(d\mathbf{a}, w_1, w_2)) dx ds \\ &+ \int_{Q_t} w_1^2 \frac{\partial f}{\partial u}((\mathbf{a}, u, v) + \theta_1(d\mathbf{a}, w_1, w_2)) dx ds \\ &+ \int_{Q_t} w_1 w_2 \frac{\partial f}{\partial v}((\mathbf{a}, u, v) + \theta_1(d\mathbf{a}, w_1, w_2)) dx ds, \end{aligned}$$

where $Q_t = \Omega \times [0, t]$, for every $t \in [0, T]$. That is :

$$\begin{aligned} \frac{1}{2}\|w_1(t)\|_2^2 + \mu_* \int_{Q_t} |\nabla w_1|^2 dx ds &\leq c_1 \|d\mu_1\|_\infty^2 + c_2 \int_0^t \|w_2(s)\|_2^2 ds \\ &+ \frac{\mu_*}{2} \int_{Q_t} |\nabla w_1|^2 dx ds \\ &+ c_3 \left(|d\mathbf{a}|^2 + \int_0^t \|w_1(s)\|_2^2 ds + \int_0^t \|w_1(s)\|_2^2 ds \right) \\ &+ c_4 \left(\int_0^t \|w_1(s)\|_2^2 ds + \int_0^t \|w_2(s)\|_2^2 ds \right) \quad (4.8) \end{aligned}$$

Therefore, we get

$$\frac{1}{2}\|w_1(t)\|_2^2 + \frac{\mu_*}{2} \int_{Q_t} |\nabla w_1|^2 dx ds \leq c \|d\mu_1\|_\infty^2 + c |d\mathbf{a}|^2 + c \int_0^t (\|w_1(s)\|_2^2 + \|w_2(s)\|_2^2) ds. \quad (4.9)$$

Similarly, one has

$$\frac{1}{2}\|w_2(t)\|_2^2 + \frac{\mu_*}{2} \int_{Q_t} |\nabla w_2|^2 dx ds \leq c \|d\mu_2\|_\infty^2 + c |d\mathbf{b}|^2 + c \int_0^t (\|w_1(s)\|_2^2 + \|w_2(s)\|_2^2) ds. \quad (4.10)$$

Summing the last two inequalities, it follows

$$\begin{aligned} \frac{1}{2} (\|w_1(t)\|_2^2 + \|w_2(t)\|_2^2) + \frac{\mu_*}{2} \int_0^t (\|\nabla w_1\|^2 + \|\nabla w_2\|^2) &\leq c \int_0^t (\|w_1(s)\|_2^2 + \|w_2(s)\|_2^2) ds \\ &+ c (\|d\mu_1\|_\infty^2 + \|d\mu_2\|_\infty^2 + c |d\mathbf{a}|^2 + c |d\mathbf{b}|^2) \quad (4.11) \end{aligned}$$

and the Gronwall's lemma gives

$$\|w_1(t)\|_2^2 + \|w_2(t)\|_2^2 \leq c (\|d\mu_1\|_\infty^2 + c\|d\mu_2\|_\infty^2 + c|d\mathbf{a}|^2 + c|d\mathbf{b}|^2).$$

Hence, the two estimates

$$\|(w_1(t), w_2(t))\|_{L^\infty(0,T,L^2)} \leq c(\|d\mu_1\|_\infty + c\|d\mu_2\|_\infty + c|d\mathbf{a}| + c|d\mathbf{b}|), \quad (4.12)$$

$$\|(w_1(t), w_2(t))\|_{L^2(0,T,H^1)} \leq c(\|d\mu_1\|_\infty + c\|d\mu_2\|_\infty + c|d\mathbf{a}| + c|d\mathbf{b}|) \quad (4.13)$$

which give the continuity of the map $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \mapsto (u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}), v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}))$ from $(\mathcal{M}, \|\cdot\|_\infty)^2 \times \mathbb{R}^6$ to $L^\infty(0, T; L^2(\Omega)) \cap L^2(0, T; H^1(\Omega))$.

Notice in passing that since the right hand size $(f, g) \in L^\infty(Q_T) \times L^\infty(Q_T)$ and $(u_0, v_0) \in L^\infty(\Omega) \times L^\infty(\Omega)$, then the solution (u, v) of (4.4) satisfies

$$(u, v) \in L^\infty(Q_T) \times L^\infty(Q_T)$$

and consequently, the solution (w_1, w_2) of (4.6) satisfies

$$(w_1, w_2) \in L^\infty(Q_T) \times L^\infty(Q_T) \quad \text{et} \quad \|(w_1(t), w_2(t))\|_{L^\infty(Q)} \leq c. \quad (4.14)$$

Also, substituting (4.14) in (4.11) it follows

$$\|(\nabla w_1(t), \nabla w_2(t))\|_{L^\infty(0,T,L^2)} \leq c(\|d\mu_1\|_\infty + c\|d\mu_2\|_\infty + c|d\mathbf{a}| + c|d\mathbf{b}|), \quad (4.15)$$

and thus

$$\|(\nabla w_1(t), \nabla w_2(t))\|_{L^2(Q_T)} \leq c(\|d\mu_1\|_\infty + c\|d\mu_2\|_\infty + c|d\mathbf{a}| + c|d\mathbf{b}|). \quad (4.16)$$

We present another continuity result which will be useful hereinafter.

Corollary 4.3.2. *The application $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \rightarrow (u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}), v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}))$ is continuous from $(\mathcal{M}, \|\cdot\|_\infty)^2 \times \mathbb{R}^6$ to $L^p(Q_T)$, for every $p \geq 2$.*

Moreover, if $N \leq 3$ then this continuity result can be more specified as

$$\|(w_1, w_2)\|_{L^p(Q_T)} \leq \begin{cases} c(\|(d\mu_1, d\mu_2)\|_\infty + \|(d\mathbf{a}, d\mathbf{b})\|_{\mathbb{R}^6}) & \text{if } 2 \leq p \leq \frac{10}{3}, \\ c(\|(d\mu_1, d\mu_2)\|_\infty + \|(d\mathbf{a}, d\mathbf{b})\|_{\mathbb{R}^6})^{\frac{10}{3p}} & \text{if } \frac{10}{3} \leq p < +\infty. \end{cases} \quad (4.17)$$

Proof. The first claim follows easily from the estimates (4.12) and (4.14). For the second claim, the continuous embedding $H^1(\Omega) \subset L^6(\Omega)$ implies that

$$\|(w_1, w_2)\|_{L^2(0,T,L^6(\Omega))} \leq c(\|(d\mu_1, d\mu_2)\|_\infty + \|(d\mathbf{a}, d\mathbf{b})\|_{\mathbb{R}^6}).$$

On the other hand, applying the interpolation between the spaces $L^2(0, T; L^6(\Omega))$ and $L^\infty(0, T; L^2(\Omega))$, that is

$$L^{\frac{10}{3}}(Q_T) = [L^2(0, T; L^6(\Omega)), L^\infty(0, T; L^2(\Omega))]_{\frac{2}{5}},$$

we get

$$\|(w_1, w_2)\|_{L^{\frac{10}{3}}(Q_T)} \leq c (\|(d\mu_1, d\mu_2)\|_\infty + \|(d\mathbf{a}, d\mathbf{b})\|_{\mathbb{R}^6}),$$

which gives the first estimate of (4.17).

Now, for every $p \geq \frac{10}{3}$, applying again the interpolation between the spaces $L^{10/3}(Q_T)$ and $L^\infty(Q_T)$

$$L^p(\Omega) = \left[L^\infty(Q_T), L^{\frac{10}{3}}(Q_T) \right]_{\frac{10}{3p}},$$

we obtain

$$\begin{aligned} \|(w_1, w_2)\|_{L^p(Q_T)} &\leq \|(w_1, w_2)\|_{L^\infty(Q_T)}^{1-\frac{10}{3p}} \times \|(w_1, w_2)\|_{L^{\frac{10}{3}}(Q_T)}^{\frac{10}{3p}} \\ &\leq c (\|(d\mu_1, d\mu_2)\|_\infty + \|(d\mathbf{a}, d\mathbf{b})\|_{\mathbb{R}^6})^{\frac{10}{3p}}. \end{aligned}$$

which achieves the pr.

2. Differentiability of the application : $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \rightarrow (u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}), v((\mu_1, \mu_2, \mathbf{a}, \mathbf{b}))).$

Lemma 4.3.3. *The application $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \rightarrow (u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}), v((\mu_1, \mu_2, \mathbf{a}, \mathbf{b})))$ is Gâteaux differentiable from $(\mathcal{M}, \|\cdot\|_\infty)^2 \times \mathbb{R}^6$ to $L^2(Q_T)$.*

Proof. From System (4.6), one has

$$(w_1)_t - \operatorname{div}(\tilde{\mu}_1(\tilde{v})\nabla\tilde{u}) + \operatorname{div}(\mu_1(v)\nabla u) = f(\mathbf{a} + d\mathbf{a}, \tilde{u}, \tilde{v}) - f(\mathbf{a}, u, v)$$

with

$$\tilde{\mu}_1(\tilde{v}) = \mu_1(v) + d\mu_1(v) + \tilde{\mu}'_1(v)w_2 + \int_0^1 (1-\xi)\tilde{\mu}''_1(v + \xi w_2)w_2^2 d\xi,$$

$$f(\mathbf{a} + d\mathbf{a}, \tilde{u}, \tilde{v}) = f(\mathbf{a}, u, v) + \nabla f(\mathbf{a}, u, v) \cdot (d\mathbf{a}, w_1, w_2) + \int_0^1 (1-\xi)Q_1(\xi) d\xi$$

and

$$Q_1(\xi) = \nabla^2 f(\mathbf{a} + \xi d\mathbf{a}, u + \xi w_1, v + \xi w_2) \cdot ((d\mathbf{a}, w_1, w_2), (d\mathbf{a}, w_1, w_2)).$$

Then

$$(w_1)_t = L_1 + R_1,$$

where

$$\begin{aligned} L_1 &= \operatorname{div}(\mu_1(v)\nabla w_1) + \operatorname{div}(d\mu_1(v)\nabla\tilde{u}) + \operatorname{div}(\tilde{\mu}'_1(v)w_2\nabla\tilde{u}) \\ &\quad + \nabla f(\mathbf{a}, u, v) \cdot (d\mathbf{a}, w_1, w_2), \end{aligned}$$

$$R_1 = \operatorname{div}\left(\int_0^1 (1-\xi)\tilde{\mu}''_1(v + \xi w_2)w_2^2\nabla\tilde{u} d\xi\right) + \int_0^1 (1-\xi)Q_1(\xi) d\xi.$$

In the same manner, one gets

$$(w_2)_t = L_2 + R_2,$$

with appropriate terms L_2 and R_2 .

Let us decompose (w_1, w_2) as the following : $w_1 = z_1 + h_1$, $w_2 = z_2 + h_2$, where (z_1, z_2) is the solution of the linear system in $(d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b})$:

$$\left\{ \begin{array}{l} (z_1)_t - \operatorname{div}(\mu_1(v)\nabla z_1) - \operatorname{div}(\mu_1'(v)z_2\nabla u) \operatorname{div}(d\mu_1(v)\nabla u) + \nabla f(\mathbf{a}, u, v) \cdot (d\mathbf{a}, z_1, z_2) \text{ in } Q_T \\ (z_2)_t - \operatorname{div}(\mu_2(u)\nabla z_2) - \operatorname{div}(\mu_2'(u)z_1\nabla v) = \operatorname{div}(d\mu_2(u)\nabla v) + \nabla g(\mathbf{b}, u, v) \cdot (d\mathbf{b}, z_1, z_2) \text{ in } Q_T \\ \nabla z_1 \cdot n = \nabla z_2 \cdot n = 0 \quad \text{sur } \Gamma \times]0, T[\\ z(x, 0) = 0, \quad z_2(x, 0) = 0 \quad \text{dans } \Omega \end{array} \right. \quad (4.18)$$

Then (h_1, h_2) satisfies the system

$$\begin{aligned} (h_1)_t - \operatorname{div}(\mu_1(v)\nabla h_1) &= \operatorname{div}(\mu_1'(v)h_2\nabla u) + \operatorname{div}(d\mu_1(v)\nabla w_1) + \operatorname{div}(\tilde{\mu}_1'(v)w_2\nabla w_1) \\ &+ \operatorname{div}((d\mu_1)'(v)w_2\nabla u) + \nabla f(\mathbf{a}, u, v) \cdot (0, h_1, h_2) + R_1 \end{aligned}$$

$$\begin{aligned} (h_2)_t - \operatorname{div}(\mu_2(u)\nabla h_2) &= \operatorname{div}(\mu_2'(u)h_1\nabla v) + \operatorname{div}(d\mu_2(u)\nabla w_2) + \operatorname{div}(\tilde{\mu}_2'(u)w_1\nabla w_2) \\ &+ \operatorname{div}((d\mu_2)'(u)w_1\nabla v) + \nabla g(\mathbf{b}, u, v) \cdot (0, h_1, h_2) + R_2 \end{aligned} \quad (4.19)$$

Multiplying Equation (4.19) by h_1 and integrating with respect to space and

time, we get

$$\begin{aligned}
 \frac{1}{2}\|h_1(t)\|_2^2 + \int_0^t \int_{\Omega} \mu_1(v) |\nabla h_1|^2 dx ds &= \int_0^t \int_{\Omega} \mu_1'(v) h_2 \nabla u \cdot \nabla h_1 dx ds \\
 &+ \int_0^t \int_{\Omega} d\mu_1(v) \nabla w_1 \cdot \nabla h_1 dx ds \\
 &+ \int_0^t \int_{\Omega} \tilde{\mu}_1'(v) w_2 \nabla w_1 \cdot \nabla h_1 dx ds \\
 &+ \int_0^t \int_{\Omega} (d\mu_1)'(v) w_2 \nabla u \cdot \nabla h_1 dx ds \\
 &+ \int_0^t \int_{\Omega} \nabla f(\mathbf{a}, u, v) \cdot (0, h_1, h_2) h_1 dx ds. \\
 &+ \int_0^t \int_{\Omega} \int_0^1 (1-\xi) \tilde{\mu}_1''(v + \xi w_2) w_2^2 \nabla \tilde{u} \cdot \nabla h_1 d\xi dx ds \\
 &+ \int_0^t \int_{\Omega} \int_0^1 (1-\xi) Q_1(\xi) h_1 d\xi dx ds
 \end{aligned}$$

Using the inequalities, for ε sufficiently small and positive parameter :

- $$\begin{aligned}
 \bullet \int_0^t \int_{\Omega} \mu_1'(v) h_2 \nabla u \cdot \nabla h_1 dx ds &\leq c \|\nabla u\|_{L^\infty(Q_T)} \int_0^t \int_{\Omega} |h_2| \times |\nabla h_1| dx ds \\
 &\leq c_1(\varepsilon) \int_0^t \|h_2(t)\|_2^2 ds + \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds
 \end{aligned}$$
- $$\begin{aligned}
 \bullet \int_0^t \int_{\Omega} d\mu_1(v) \nabla w_1 \cdot \nabla h_1 dx ds &\leq \int_0^t \int_{\Omega} |d\mu_1(v)|^2 |\nabla w_1|^2 dx ds + \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 &\leq c_1(\varepsilon) \|d\mu_1\|_\infty^2 \int_0^t \int_{\Omega} |\nabla w_1|^2 dx ds \\
 &\quad + \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 &\leq c_1(\varepsilon) \|d\mu_1\|_\infty^2 \|\nabla w_1\|_{L^\infty(0,T,L^2(\Omega))}^2 \\
 &\quad + \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 &\leq c_1(\varepsilon) \|d\mu_1\|_\infty^2 (\|d\mu_1\|_\infty + \|d\mu_2\|_\infty + |d\mathbf{a}| + |d\mathbf{b}|)^2 \\
 &\quad + \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 &\leq c_1(\varepsilon) (\|d\mu_1\|_\infty + \|d\mu_2\|_\infty + |d\mathbf{a}| + |d\mathbf{b}|)^4 \\
 &\quad + \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds
 \end{aligned}$$

$$\begin{aligned}
 \bullet \int_0^t \int_{\Omega} \tilde{\mu}'_1(v) w_2 \nabla w_1 \cdot \nabla h_1 dx ds &\leq c \int_0^t \int_{\Omega} w_2 (\nabla w_1)^{2/5} (\nabla w_1)^{3/5} \nabla h_1 dx ds \\
 &\leq c_1(\varepsilon) \int_0^t \int_{\Omega} w_2^2 |\nabla w_1|^{4/5} dx ds \\
 &+ \varepsilon c_2 \int_0^t \int_{\Omega} |\nabla w_1|^{6/5} |\nabla h_1|^2 dx ds \\
 &\leq c_1(\varepsilon) \|w_2\|_{L^{10/3}(Q_T)}^2 \|\nabla w_1\|_{L^2(Q_T)}^{4/5} \\
 &+ \varepsilon c_2 \|\nabla w_1\|_{L^\infty(Q_T)}^{6/5} \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 &\leq c_1(\varepsilon) (\|d\mu_1\|_\infty + c\|d\mu_2\|_\infty + c|\mathbf{da}| + c|\mathbf{db}|)^{2+\frac{4}{5}} \\
 &+ \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 \\
 \bullet \int_0^t \int_{\Omega} (d\mu_1)'(v) w_2 \nabla u \cdot \nabla h_1 dx ds &\leq \|(d\mu_1)'\|_\infty \|\nabla u\|_{L^\infty(Q_T)} \int_0^t \int_{\Omega} w_2 |\nabla h_1| dx ds \\
 &\leq c_1(\varepsilon) \|(d\mu_1)'\|_\infty (\|d\mu_1\|_\infty + \|d\mu_2\|_\infty + |\mathbf{da}| + |\mathbf{db}|)^2 \\
 &+ \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 \\
 \bullet \int_0^t \int_{\Omega} \nabla f(\mathbf{a}, u, v) \cdot (0, h_1, h_2) h_1 dx ds &\leq c_1(\varepsilon) \int_0^t \|h_1(t)\|_2^2 ds + \varepsilon c_2 \int_0^t \|h_2(t)\|_2^2 ds, \\
 \\
 \bullet \int_0^t \int_{\Omega} \int_0^1 (1-\xi) \tilde{\mu}''_1(v + \xi w_2) w_2^2 \nabla \tilde{u} \cdot \nabla h_1 d\xi dx ds &\leq c_1(\varepsilon) \int_0^t \int_{\Omega} w_2^4 dx ds \\
 &+ \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 &= c_1(\varepsilon) \|w_2\|_{L^4(Q_T)}^4 \\
 &+ \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds \\
 &\leq c_1(\varepsilon) (\|d\mu_1\|_\infty + \|d\mu_2\|_\infty + |\mathbf{da}| + |\mathbf{db}|)^{10/3} \\
 &+ \varepsilon c_2 \int_0^t \|\nabla h_1(t)\|_2^2 ds.
 \end{aligned}$$

Using the fact that $|d\mathbf{a}|^4 \leq c|d\mathbf{a}|^{10/3}$ and $|d\mathbf{b}|^4 \leq c|d\mathbf{b}|^{10/3}$, the same argument as before shows that

$$\begin{aligned} \int_0^t \int_{\Omega} \int_0^1 (1-\xi)Q_1(\xi) h_1 d\xi dx ds &\leq c_1(\|d\mu_1\|_{\infty} + \|d\mu_2\|_{\infty} + |d\mathbf{a}| + |d\mathbf{b}|)^{10/3} \\ &+ c_3(\varepsilon)\|(d\mu_1)'\|_{\infty} (\|d\mu_1\|_{\infty} + \|d\mu_2\|_{\infty} + |d\mathbf{a}| + |d\mathbf{b}|)^2. \end{aligned}$$

Therefore the following estimate :

$$\begin{aligned} \frac{1}{2}\|h_1(t)\|_2^2 &\leq c_1(\varepsilon) \int_0^t (\|h_1\|_2^2 + \|h_2\|_2^2) ds \\ &+ c_2(\varepsilon)(\|d\mu_1\|_{\infty} + c\|d\mu_2\|_{\infty} + c|d\mathbf{a}| + c|d\mathbf{b}|)^{\min(4,14/5,10/3)} \\ &+ c_3(\varepsilon)\|(d\mu_1)'\|_{\infty} (\|d\mu_1\|_{\infty} + \|d\mu_2\|_{\infty} + |d\mathbf{a}| + |d\mathbf{b}|)^2. \end{aligned} \quad (4.20)$$

Similar computations concerning h_2 imply the following estimate

$$\begin{aligned} \frac{1}{2}\|h_2(t)\|_2^2 &\leq c_1(\varepsilon) \int_0^t (\|h_1\|_2^2 + \|h_2\|_2^2) ds \\ &+ c_2(\varepsilon)(\|d\mu_1\|_{\infty} + c\|d\mu_2\|_{\infty} + c|d\mathbf{a}| + c|d\mathbf{b}|)^{\min(4,14/5,10/3)} \\ &+ c_3(\varepsilon)\|(d\mu_2)'\|_{\infty} (\|d\mu_1\|_{\infty} + \|d\mu_2\|_{\infty} + |d\mathbf{a}| + |d\mathbf{b}|)^2, \end{aligned} \quad (4.21)$$

and hence

$$\begin{aligned} \frac{1}{2}(\|h_1(t)\|_2^2 + \|h_2(t)\|_2^2) &\leq c_1(\varepsilon) \int_0^t (\|h_1\|_2^2 + \|h_2\|_2^2) ds \\ &+ c_2(\varepsilon)(\|d\mu_1\|_{\infty} + c\|d\mu_2\|_{\infty} + c|d\mathbf{a}| + c|d\mathbf{b}|)^{10/3} \\ &+ c_3(\varepsilon) (\|(d\mu_1)'\|_{\infty} + \|(d\mu_2)'\|_{\infty}) (\|d\mu_1\|_{\infty} + \|d\mu_2\|_{\infty} + |d\mathbf{a}| + |d\mathbf{b}|)^2. \end{aligned}$$

The Gâteaux differentiability follows easily, via Gronwall's lemma, by setting $d\mu_1 = \delta \nu_1$, $d\mu_2 = \delta \nu_2$, $d\mathbf{a} = \delta \alpha$ and $d\mathbf{b} = \delta \beta$, where ν_1 and ν_2 are arbitrary (but fixed) functions in \mathcal{N} . The parameters α and β are arbitrary (but fixed) real numbers and δ is a sufficiently small parameter (intended to converge towards 0).

Remark 4.3.4. *To obtain Fréchet differentiability instead of Gâteaux differentiability, the norm on \mathcal{M} has to be modified as*

$$\|\mu\|_{1,\infty} := \|\mu\|_{\infty} + \|\mu'\|_{\infty}.$$

4.3.2 Computation of the gradient of J_0

To provide a minimization numerical algorithm, we will compute the gradient of J . We start by the computation of the gradient of J_0 . We showed before that J_0 is Gâteaux-differentiable.

Let $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \in \mathcal{M}^2 \times \mathcal{A}^2$ and $(d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b}) \in [\mathcal{C}^2(\mathbb{R})]^2 \times [\mathbb{R}^3]^2$. Then

$$\begin{aligned} J'_0(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \cdot (d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b}) &= \int_{Q_T} (u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - u_{\text{obs}}) \times z_1(d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b}) \, dx \, dt \\ &+ \int_{Q_T} (v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - v_{\text{obs}}) \times z_2(d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b}) \, dx \, dt, \end{aligned}$$

where (z_1, z_2) is the solution of the linear system :

$$\left\{ \begin{array}{l} (z_1)_t - \text{div}(\mu_1(v)\nabla z_1) - \text{div}(\mu_1(v)z_2\nabla u) = \text{div}(d\mu_1(v)\nabla u) + \nabla f(\mathbf{a}, u, v) \cdot (d\mathbf{a}, z_1, z_2) \text{ in } Q_T, \\ (z_2)_t - \text{div}(\mu_2(u)\nabla z_2) - \text{div}(\mu_2(u)z_1\nabla v) = \text{div}(d\mu_2(u)\nabla v) + \nabla g(\mathbf{b}, u, v) \cdot (d\mathbf{b}, z_1, z_2) \text{ in } Q_T, \\ \nabla z_1 \cdot \mathbf{n} = \nabla z_2 \cdot \mathbf{n} = 0 \text{ on } \partial\Omega \times [0, +\infty[, \\ z_1(x, 0) = 0, \quad z_2(x, 0) = 0 \text{ in } \Omega, \end{array} \right. \quad (4.22)$$

whose solution (z_1, z_2) is linear in $(d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b})$. To express the derivative of J_0 in a more convenient way, we introduce the dual system

$$\left\{ \begin{array}{l} -p_t - \text{div}(\mu_1(v)\nabla p) - \mu_2(u)\nabla v \cdot \nabla q - \frac{\partial f}{\partial u} p - \frac{\partial g}{\partial u} q = u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - u_{\text{obs}} \text{ in } Q_T, \\ -q_t - \text{div}(\mu_2(u)\nabla q) - \mu_1(v)\nabla u \cdot \nabla p - \frac{\partial g}{\partial v} q - \frac{\partial f}{\partial v} p = v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - v_{\text{obs}} \text{ in } Q_T, \\ \nabla p \cdot \mathbf{n} = \nabla q \cdot \mathbf{n} = 0 \text{ on } \partial\Omega \times]0, +\infty[, \\ p(x, T) = 0, \quad q(x, T) = 0 \text{ in } \Omega. \end{array} \right. \quad (4.23)$$

Then, we can rewrite

$$\begin{aligned} J'_0(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \cdot (d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b}) &= \int_{Q_T} (d\mu_1(v(x, t))\nabla u \cdot \nabla p + d\mu_2(u(x, t))\nabla v \cdot \nabla q) \, dx \, dt \\ &+ \int_{Q_T} (p \nabla_{\mathbf{a}} f(\mathbf{a}, u, v) \, d\mathbf{a} + q \nabla_{\mathbf{b}} g(\mathbf{b}, u, v) \, d\mathbf{b}) \, dx \, dt, \end{aligned}$$

where $\nabla_{\mathbf{a}}$ (resp. $\nabla_{\mathbf{b}}$) denotes the gradient with respect to the vector \mathbf{a} (resp. to the vector $\nabla_{\mathbf{b}}$).

In order to express the term $\int_{Q_T} (d\mu_1(v(x, t))\nabla u \cdot \nabla p + d\mu_2(u(x, t))\nabla v \cdot \nabla q) \, dx \, dt$ as a scalar product between $(d\mu_1, d\mu_2)$ and an adequate pair of functions in $L^2(Q_T) \times$

$L^2(Q_T)$, we introduce the functions

$$\begin{aligned} F(\ell) &:= \int_{\{v \geq \ell\}} \nabla u(x, t) \cdot \nabla p(x, t) \, dx \, dt, \quad \ell \in [v_{\min}, v_{\max}] \subset \left[0, \frac{\alpha_2}{\beta_2}\right] \\ G(\ell) &:= \int_{\{u \geq \ell\}} \nabla v(x, t) \cdot \nabla q(x, t) \, dx \, dt, \quad \ell \in [u_{\min}, u_{\max}] \subset \left[0, \frac{\alpha_1}{\beta_1}\right], \end{aligned} \quad (4.24)$$

where $\{u \geq \ell\}$, u_{\min} and u_{\max} (similarly for v) are defined by

$$\begin{aligned} \{u \geq \ell\} &= \{(x, t) \in Q_T : u(x, t) \geq \ell\}, \\ u_{\min} &= \sup \{\ell \in \mathbb{R} : u(x, t) \geq \ell, \text{ a. e. in } Q_T\}, \\ u_{\max} &= \inf \{\ell \in \mathbb{R} : u(x, t) \leq \ell, \text{ a. e. in } Q_T\}. \end{aligned}$$

It is interesting to point here some properties of F and G that not arise in the scalar case.

Lemma 4.3.5. *The functions F and G are bounded, continuous and satisfy*

$$\begin{aligned} \int_{Q_T} d\mu_1(v(x, t)) \nabla u(x, t) \cdot \nabla p(x, t) \, dx \, dt &= d\mu_1(0)F(0) + \int_0^{\frac{\alpha_2}{\beta_2}} d\mu'_1(s)F(s) \, ds, \\ \int_{Q_T} d\mu_2(u(x, t)) \nabla v(x, t) \cdot \nabla q(x, t) \, dx \, dt &= d\mu_2(0)G(0) + \int_0^{\frac{\alpha_1}{\beta_1}} d\mu'_2(s)G(s) \, ds. \end{aligned}$$

Moreover, if F and G are differentiable, it holds

$$\begin{aligned} J'_0(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) \cdot (d\mu_1, d\mu_2, d\mathbf{a}, d\mathbf{b}) &= -\langle d\mu_1, F' \rangle_{L^2(0, \frac{\alpha_2}{\beta_2})} - \langle d\mu_2, G' \rangle_{L^2(0, \frac{\alpha_1}{\beta_1})} \\ &\quad + \langle d\mathbf{a}, X \rangle_{\mathbb{R}^3} + \langle d\mathbf{b}, Y \rangle_{\mathbb{R}^3}, \end{aligned}$$

where

$$X = \int_{Q_T} p \nabla_{\mathbf{a}} f(\mathbf{a}, u, v) \, dx \, dt \quad \text{and} \quad Y = \int_{Q_T} q \nabla_{\mathbf{b}} g(\mathbf{b}, u, v) \, dx \, dt. \quad (4.25)$$

Proof. Since $(\nabla u, \nabla p) \in L^2(Q_T) \times L^2(Q_T)$ it follows that $\nabla u \cdot \nabla p \in L^1(Q_T)$ and then $F \in L^\infty(\mathbb{R})$. We claim that F and G are continuous. Indeed, let O be an open subdomain of Q_T such that $\text{meas}(O) > 0$. Due to the Kolmogorov nature of System (4.2), the assertion

$$\begin{cases} u \text{ is constant in } O \\ u \neq 0 \text{ in } O \end{cases} \implies v \text{ is constant in } O,$$

holds true, and *vice versa*. Hence, we get

$$\int_{\{v=\ell\}} \nabla u(x, t) \cdot \nabla p(x, t) \, dx \, dt = 0, \quad \forall \ell \in [v_{\min}, v_{\max}] \setminus \{0\},$$

$$\int_{\{u=\ell\}} \nabla v(x, t) \cdot \nabla q(x, t) dx dt = 0, \quad \forall \ell \in [u_{\min}, u_{\max}] \setminus \{0\}.$$

Therefore, for every $\ell \in [v_{\min}, v_{\max}] \setminus \{0\}$, the Lebesgue theorem implies that

$$\lim_{\varepsilon \rightarrow 0} (F(\ell + \varepsilon) - F(\ell)) = \pm \int_{\{v=\ell\}} \nabla u(x, t) \cdot \nabla p(x, t) dx dt = 0,$$

that is the continuity of F on $[v_{\min}, v_{\max}] \setminus \{0\}$. The same arguments give the continuity of G on $[u_{\min}, u_{\max}] \setminus \{0\}$.

Moreover, since $v_{\min} \leq v(x, t) \leq v_{\max}$ for every $(x, t) \in Q_T$, it follows that $F(\ell) = \int_{Q_T} \nabla u(x, t) \cdot \nabla p(x, t) dx dt = C^{\text{st}}$ for every $\ell \leq v_{\min}$ and $F(\ell) = 0$ for every $\ell \geq v_{\max}$. In the same way, one has $G(\ell) = \int_{Q_T} \nabla v(x, t) \cdot \nabla q(x, t) dx dt = C^{\text{st}}$ for every $\ell \leq u_{\min}$ and $G(\ell) = 0$ for every $\ell \geq u_{\max}$. At this stage, for every positive integer N , consider the discretization $\ell_i = i \times h$, where $0 \leq i \leq N$ and $h_N = \frac{v_{\max} - v_{\min}}{N}$, of the interval $[v_{\min}, v_{\max}]$. It follows that

$$\begin{aligned} \int_{Q_T} d\mu_1(v(x, t)) \nabla u \cdot \nabla p dx dt &= \sum_{i=0}^{N-1} \int_{\ell_i \leq v \leq \ell_{i+1}} d\mu_1(v(x, t)) \nabla u \cdot \nabla p dx dt \\ &= \sum_{i=0}^{N-1} d\mu_1(\ell_i) \int_{\ell_i \leq v \leq \ell_{i+1}} \nabla u \cdot \nabla p dx dt + \mathcal{R}_N, \end{aligned}$$

where

$$\mathcal{R}_N = \sum_{i=0}^{N-1} \int_{\ell_i \leq v \leq \ell_{i+1}} (v(x, t) - \ell_i) d\mu_1'(\xi_i) \nabla u \cdot \nabla p dx dt, \quad \xi_i \in]\ell_i, \ell_{i+1}[.$$

Then

$$\begin{aligned} |\mathcal{R}_N| &\leq C^{\text{st}} h_N \sum_{i=0}^{N-1} \int_{\ell_i \leq v \leq \ell_{i+1}} |\nabla u \cdot \nabla p| dx dt \\ &= C^{\text{st}} h_N \int_{Q_T} |\nabla u \cdot \nabla p| dx dt = C^{\text{st}} h_N \|\nabla u \cdot \nabla p\|_{L^1(Q_T)}. \end{aligned}$$

Consequently, we get $\lim_{N \rightarrow +\infty} \mathcal{R}_N = 0$ and

$$\begin{aligned}
 \int_{Q_T} d\mu_1(v(x, t)) \nabla u \cdot \nabla p \, dx \, dt &= \lim_{N \rightarrow +\infty} \sum_{i=0}^{N-1} d\mu_1(\ell_i) \int_{\ell_i \leq v \leq \ell_{i+1}} \nabla u \cdot \nabla p \, dx \, dt \\
 &= \lim_{N \rightarrow +\infty} \sum_{i=0}^{N-1} d\mu_1(\ell_i) (F(\ell_i) - F(\ell_{i+1})) \\
 &= d\mu_1(0)F(0) + \lim_{N \rightarrow +\infty} \sum_{i=1}^N (d\mu_1(\ell_i) - d\mu_1(\ell_{i-1})) F(\ell_i) \\
 &= d\mu_1(0)F(0) + \lim_{N \rightarrow +\infty} \sum_{i=1}^N \frac{d\mu_1(\ell_i) - d\mu_1(\ell_{i-1})}{h_N} F(\ell_i) \times h_N \\
 &= d\mu_1(0)F(0) + \int_{v_{\min}}^{v_{\max}} d\mu_1'(s) F(s) \, ds.
 \end{aligned}$$

Finally, if F is differentiable, we get

$$\int_{Q_T} d\mu_1(v(x, t)) \nabla u \cdot \nabla p \, dx \, dt = - \int_{v_{\min}}^{v_{\max}} d\mu_1(s) F'(s) \, ds = - \langle d\mu_1, F' \rangle_{L^2(v_{\min}, v_{\max})},$$

which achieves the proof.

Remark 4.3.6. *The previous lemma gives the gradient of J_0 in the special case where F and G are differentiable, that is :*

$$\nabla J_0(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) = (-F', -G', X, Y) \in L^2(v_{\min}, v_{\max}) \times L^2(u_{\min}, u_{\max}) \times \mathbb{R}^3 \times \mathbb{R}^3. \quad (4.26)$$

In the following lemma, we characterize the derivative, when it exists, of the functions F and G , via the coarea formula of Federer [36].

Lemma 4.3.7. *If the function*

$$\frac{\nabla u \cdot \nabla p}{|\nabla_{x,t} v|} \in W^{1,\infty}(Q_T)$$

then the function F is differentiable and

$$F'(\ell) = \int_{\{v=\ell\}} \frac{\nabla u \cdot \nabla p}{|\nabla_{x,t} v|} \, d\sigma(x, t), \quad (4.27)$$

where $d\sigma$ is the hypersurface measure in Q_T and $\nabla_{x,t} v$ denotes the spatiotemporal gradient of v .

Proof. Since

$$\frac{\nabla u \cdot \nabla p}{|\nabla_{x,t} v|} \in W^{1,\infty}(Q_T)$$

then the function $\frac{\nabla u \cdot \nabla p}{|\nabla_{x,t} v|}$ is Lipschitz on Q_T . Applying the coarea formula [7, 36], we get

$$F(\ell) = \int_{\ell}^{v_{\max}} \left(\int_{\{v=s\}} \frac{\nabla u \cdot \nabla p}{|\nabla_{x,t} v|} d\sigma \right) ds.$$

Then, F is differentiable and

$$F'(\ell) = - \int_{\{v=\ell\}} \frac{\nabla u \cdot \nabla p}{|\nabla_{x,t} v|} d\sigma.$$

Notice that a similar result is obtained for the differentiability of G if the assumption

$$\frac{\nabla v \cdot \nabla q}{|\nabla_{x,t} u|} \in W^{1,\infty}(Q_T)$$

is satisfied, that is :

$$G'(\ell) = \int_{\{u=\ell\}} \frac{\nabla v \cdot \nabla q}{|\nabla_{x,t} u|} d\sigma, \quad (4.28)$$

4.4 Numerical simulations

In this section, we will present the method followed to implement the identification problem and some obtained simulations. Recall that we dispose of observations $(u_{\text{obs}}, v_{\text{obs}})$ on the parabolic cylinder Q_T . The identification of the parameters $(\mu_1, \mu_2, \mathbf{a}, \mathbf{b})$ is performed via the minimization of the energy functional

$$J_0(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) = \frac{1}{2} \int_{Q_T} \{ |u(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - u_{\text{obs}}|^2 + |v(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) - v_{\text{obs}}|^2 \} dx dt. \quad (4.29)$$

subject to the regularization

$$J_1(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) = \frac{\lambda}{2} \left[\int_{m_1}^{M_1} |\mu_1'(s)|^2 ds + \int_{m_2}^{M_2} |\mu_2'(s)|^2 ds \right] + \frac{\delta}{2} (|\mathbf{a}|^2 + |\mathbf{b}|^2), \quad (4.30)$$

where λ and δ are regularization parameters, $m_1 = \min_{(x,t) \in Q_T} v(x,t)$, $M_1 = \max_{(x,t) \in Q_T} v(x,t)$, $m_2 = \min_{(x,t) \in Q_T} u(x,t)$ and $M_2 = \max_{(x,t) \in Q_T} u(x,t)$. We set

$$J(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) = J_0(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}) + J_1(\mu_1, \mu_2, \mathbf{a}, \mathbf{b}). \quad (4.31)$$

We perform the minimization process using the well-known LBFGS quasi-Newton method. Notice that this method requires the value of the energy and the its gradient and computes an approximation of the Hessian matrix at the iterates in a clever numerical way.

The computation of the gradient of J_0 is given by the formulas (4.26,4.27,4.28). The gradient of the quadratic functional is straightforward.

To simplify the presentation, we will confine ourselves to the scalar problem

$$\begin{cases} u_t - \operatorname{div}(\mu(u)\nabla u) = u(\alpha - \beta u) & \text{in } \Omega \times]0, T], \\ \nabla u \cdot \mathbf{n} = 0 & \text{on } \partial\Omega \times]0, T], \\ u(x, 0) = u_0(x) & \text{in } \Omega, \end{cases} \quad (4.32)$$

The crucial point in the identification process is the *nonlinear* term $\mu(u)$, so we will assume that the scalar parameters α and β are known. The cost functional becomes thus :

$$J_0(\mu) = \frac{1}{2} \int_{Q_T} |u(\mu) - u_{\text{obs}}|^2 dx dt. \quad (4.33)$$

The analogous formulas to (4.26) and (4.27) can be easily rewritten as :

$$\nabla J_0(\mu) = -F' \in L^2(u_{\min}, u_{\max}) \quad (4.34)$$

and

$$F'(\ell) = \int_{\{u=\ell\}} \frac{\nabla u \cdot \nabla p}{|\nabla_{x,t} u|} d\sigma(x, t), \quad (4.35)$$

where

$$\begin{cases} -p_t - \operatorname{div}(\mu(u)\nabla p) = (\alpha - 2\beta u)p + u(\mu) - u_{\text{obs}} & \text{in } Q_T, \\ \nabla p \cdot \mathbf{n} = 0 & \text{on } \partial\Omega \times]0, +\infty[, \\ p(x, T) = 0 & \text{in } \Omega. \end{cases} \quad (4.36)$$

One of the major difficulty to identify the diffusion function μ is the fact that it is defined on the interval $\left[\min_{(x,t) \in Q_T} u(x, t), \max_{(x,t) \in Q_T} u(x, t) \right]$ which depends itself on μ .

To overcome this difficulty, we start by the interval $\left[\min_{(x,t) \in Q_T} u_{\text{obs}}(x, t), \max_{(x,t) \in Q_T} u_{\text{obs}}(x, t) \right]$ as domain of μ and $u_{\text{obs}}(x, 0)$ as initial condition. We use few descent gradient method in μ to find an invariant interval $\left[\min_{(x,t) \in Q_T} u(x, t), \max_{(x,t) \in Q_T} u(x, t) \right]$ as domain for all all iterates of μ . Once, this domain is fixed, we use a quasi-Newton method to compute the minimizer of the energy J .

On the other hand, the identification problem is ill-posed for the values $m := \min_{(x,t) \in Q_T} u(x, t)$ and $M := \max_{(x,t) \in Q_T} u(x, t)$ since the ∇u vanishes at m et M . The idea

is to identify the diffusion function μ on the interval $\left[\min_{(x,t) \in Q_T} u(x, t) + \varepsilon, \max_{(x,t) \in Q_T} u(x, t) - \varepsilon \right]$,

for $\varepsilon > 0$ sufficiently small, to avoid the weak values of ∇u .

The domain $\Omega =]-1, 1[\times]-1, 1[$ and $T = 1$. The initial condition is $u_0(x) = \frac{1}{10} e^{(1-x^2)^2} e^{(1-y^2)^2}$.

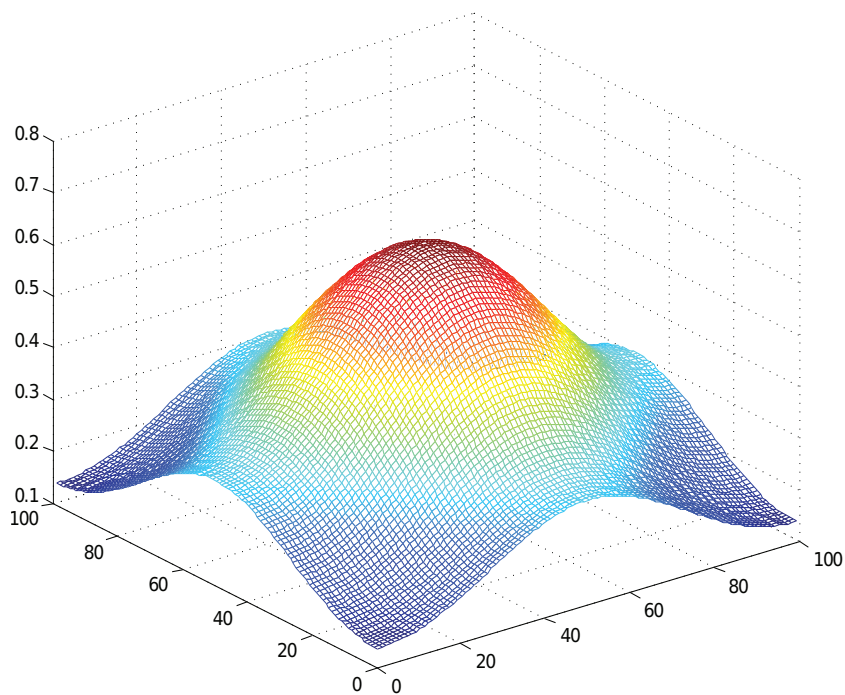


FIGURE 4.1 – Profile of the observation u_{obs} at $t = 1$.

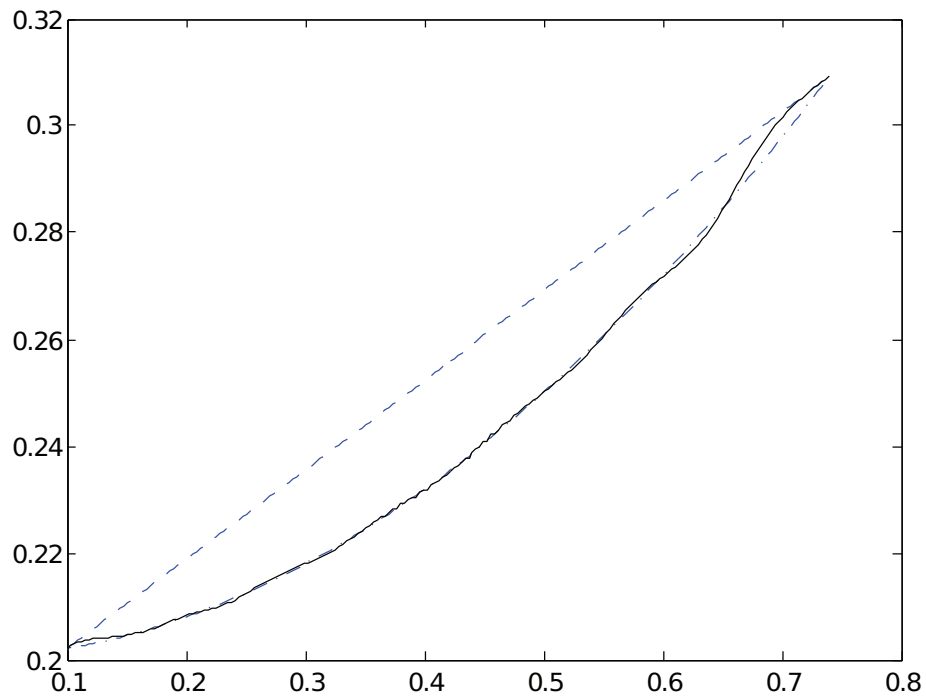


FIGURE 4.2 – “-.” Dashed-dotted curve : diffusion curve to be identified. “-” dashed curve : initial diffusion curve. Continuous line : the computed curve.

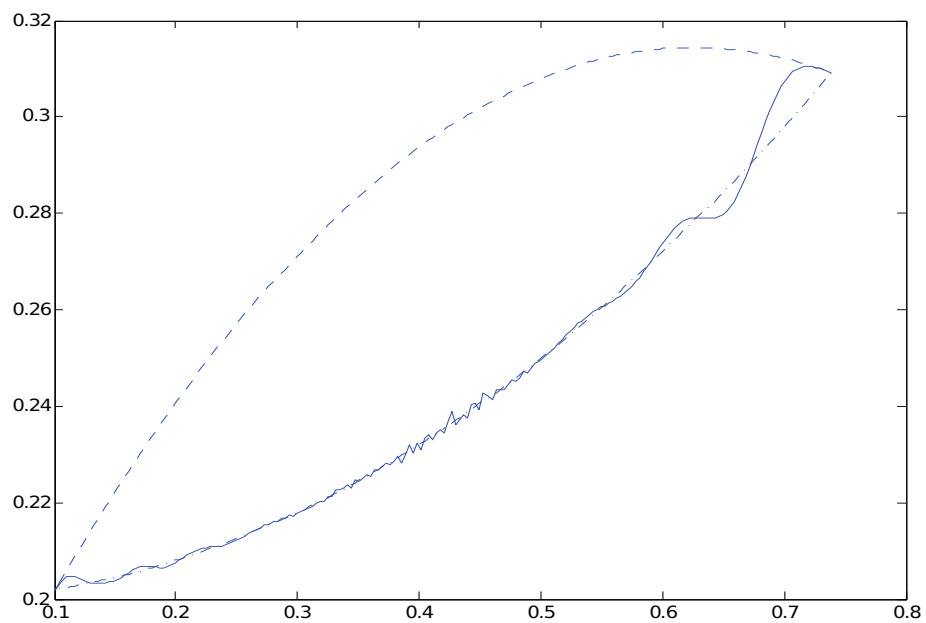


FIGURE 4.3 – “-.” Dashed-dotted curve : diffusion curve to be identified. “-” dashed curve : initial diffusion curve. Continuous line : the computed curve.

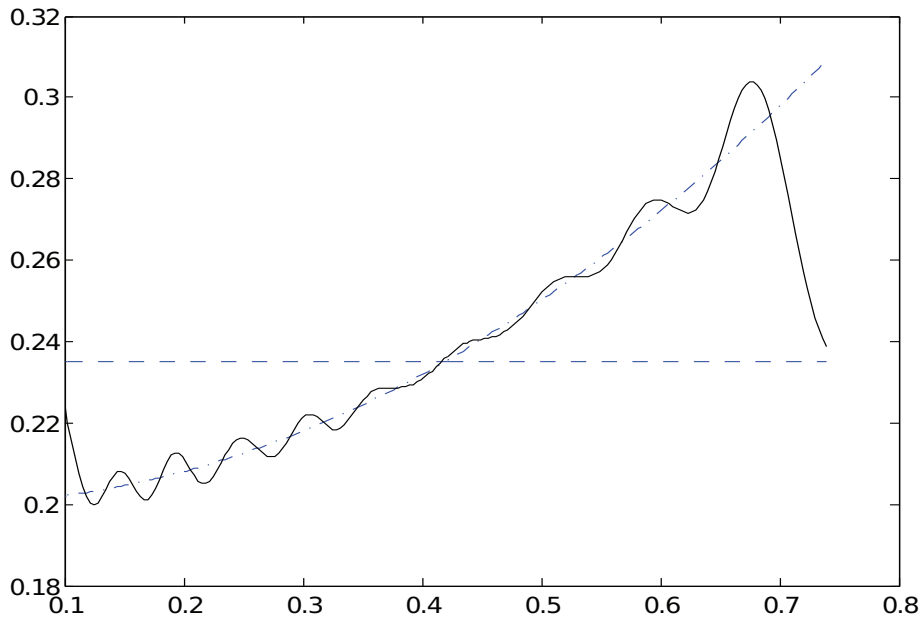


FIGURE 4.4 – ” - .” Dashed-dotted curve : diffusion curve to be identified. ” - ” dashed curve : initial diffusion curve. Continuous line : the computed curve.

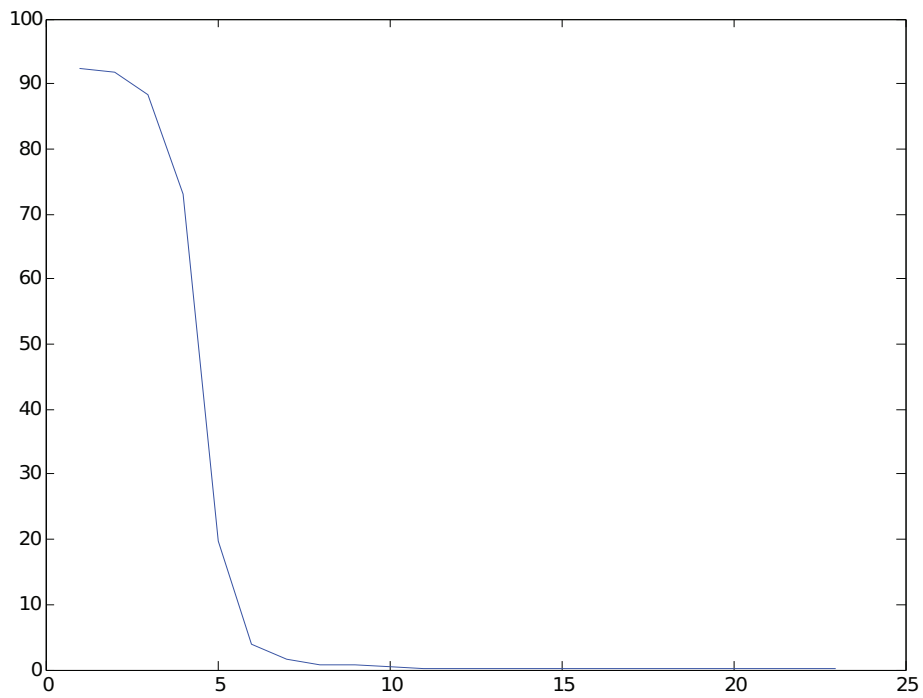


FIGURE 4.5 – Profile of the cost functional J .

* - * - * - * - * - * - *

Chapitre 5

Global dynamics of a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses

Sommaire

| | |
|---|-----|
| Présentation du chapitre | 90 |
| Abstract | 90 |
| 5.1 Introduction | 90 |
| 5.2 Boundedness of the model and existence of a positively invariant attracting set | 94 |
| 5.3 Equilibria and their local stability analysis | 95 |
| 5.3.1 Conditions for the existence of a unique positive equilibrium | 95 |
| 5.3.2 Local stability and Hopf bifurcation | 97 |
| 5.4 Permanence | 99 |
| 5.5 Limit cycle | 100 |
| 5.5.1 Existence of periodic orbits | 100 |
| 5.5.2 Non-existence of a periodic orbit | 100 |
| 5.6 Global stability | 102 |
| 5.7 Numerical simulations | 106 |
| 5.8 Discussion and conclusions | 109 |
| Appendix : First Lyapunov Coefficient | 114 |

Ce chapitre, coécrit avec Mustapha Jazar, a fait l'objet d'un article publié dans le *Journal of Applied Mathematic and Computing*. Le travail présenté concerne l'étude de la dynamique globale d'un modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin. On s'intéresse particulièrement à la bornitude et à la stabilité des solutions et on étudie l'extinction, la permanence, l'existence et la non-existence de cycles limites. De même, les bifurcations de Hopf survenant dans ce modèle sont étudiées. En outre, des simulations numériques sont présentées pour illustrer les résultats théoriques.

Abstract

In this paper, we study a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses. We show the existence of a bounded positive invariant and attracting set. The possibility of existence and uniqueness of positive equilibrium are considered. The asymptotic behavior of the positive equilibrium and the existence of Hopf-bifurcation of nonconstant periodic solutions surrounding the interior equilibrium are considered. The existence and non-existence of periodic solutions are established under suitable conditions. The permanence conditions are also established. We obtained sufficient conditions to ensure the global stability of the unique positive equilibrium, by using suitable Lyapunov functions, LaSalle invariance principle and Dulac's criterion. We obtained also sufficient conditions for the global stability of the prey-extinction equilibrium when the unique positive equilibrium is not feasible. Finally, numerical simulations are presented to illustrate the analytical results.

Keywords : Predator-prey model, Crowley-Martin functional response, Permanence, Limit cycles, Global stability.

AMS Classification : 34D23, 92D25.

5.1 Introduction

Based on the principles of “mass conservation” and “decomposition of the dynamics of a population into birth and death processes”, we write a canonical form of a predator-prey model as (see for instance [1, 8]).

$$\left\{ \begin{array}{l} \frac{du}{dt} = ug(u) - vP(u, v), \\ \frac{dv}{dt} = \varepsilon vP(u, v) - \mu(v)v, \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0, \end{array} \right. \quad (5.1)$$

where $u(t)$ and $v(t)$ represent the population densities of prey and predator at time t , respectively, $g(u)$ is the growth rate of prey, $\mu(v)$ is the mortality rate of predator, ε is the conversion efficiency ($0 < \varepsilon < 1$). The function $P(u, v)$ is the consumption rate of prey by a predator or the functional response of the predator. In most cases, the prey is always assumed to grow logistically, i.e., $g(u) = r(1 - u/K)$, where r and K are the intrinsic growth rate and the carrying capacity of prey respectively. The predator mortality μ is assumed to be a positive constant. Therefore, the system becomes

$$\left\{ \begin{array}{l} \frac{du}{dt} = ru \left(1 - \frac{u}{K}\right) - vP(u, v), \\ \frac{dv}{dt} = \varepsilon vP(u, v) - \mu v, \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0. \end{array} \right. \quad (5.2)$$

Lotka and Volterra (1925) were the first to propose a functional response with $P(u, v) = mu$. After that several models with several variations for P as function of prey only, or as function of prey and predator were studied (see for instance [64, Appendix A]) for different types of functional responses can be found in the literature. All these studies depend on the classical types of functional responses, such as Holling types [37, 38, 60, 92, 109], ratio-dependent type [8, 9, 16, 34, 56, 65, 73, 121], Beddington-DeAngelis type [20, 34, 52, 58, 59], Hassell-Varley type [55, 120], Ivlev type [70, 94], Watt type [116, 118] and so on.

Predator-prey models that do not follow the “mass conservation” principle are not considered as the models (5.1). Leslie and Gower (1960) were the first who introduced this type of model [76]. After that May (1973), Holling (1975), Berryman (1992), Turchin and Hanski (1995) proposed other types of these predator-prey models. Recently, there has been a growing interest in the study of mathematical models incorporating a modified version of Leslie-Gower functional response [12] with Holling-type II [51]. This model can be written as follows

$$\begin{cases} \frac{du}{dt} = r_1 u \left(1 - \frac{u}{K}\right) - \frac{auv}{b+u}, \\ \frac{dv}{dt} = r_2 v \left(1 - \frac{v}{u+c}\right), \\ u(0) = u_0 > 0, \quad v(0) = v_0 > 0. \end{cases} \quad (5.3)$$

where r_1, r_2, a, b, c and K are all positive constants and $u(t), v(t)$ represent the population densities at time t . The Holling type II functional response $P(u) = \frac{a}{b+u}$ in (5.3) is classified as one of prey-dependent functional response, it assumes that predators do not interfere with one another's activities; thus competition among predators for food occurs only via the depletion of prey. However, Crowley and Martin (1989) proposed in [26] a functional response that can accommodate interference among predators, it is similar to the well-known Beddington-DeAngelis functional response but has an additional term in the first right term equation modeling mutual interference among predators term. The Crowley-Martin type functional response is used for data sets that indicate feeding rate that is affected by predator density. It is assumed that predator-feeding rate decreases by higher predator density even when prey density is high, and therefore the effects of predator interference in feeding rate remain important all the time whether an individual predator is handling or searching for a prey at a given instant of time. It can be generated by a number of natural mechanisms and because it admits rich but biologically reasonable dynamics [26], it is worthy for us to further study the Crowley-Martin. The per capita feeding rate in this formulation is given by

$$P(u, v) = \frac{mu}{1 + Au + Bv + ABuv}.$$

Here m, A and B are positive parameters that describe the effects of capture rate handling time and the magnitude of interference among predators, respectively, on the feeding rate. One can refer to [98, 104, 112, 113, 123, 127] for related works.

Therefore, it is interesting and important to consider and study a predator-prey model which incorporates a modified version of the Leslie-Gower scheme with Crowley-Martin functional response. Namely

$$\begin{cases} \frac{du}{dt} = a_1 u \left(1 - \frac{u}{K}\right) - \frac{buv}{(1+cu)(1+dv)}, \\ \frac{dv}{dt} = v \left(a_2 - \frac{ev}{u+f}\right), \end{cases} \quad (5.4)$$

where u and v represent the population densities at time t ; a_1, a_2, b, c, d, e, f and K are model parameters assuming only positive values and are defined as

follows : a_1 and K are the intrinsic growth rate and the carrying capacity of prey population u , respectively. The constants b, c and d are the saturating Crowley-Martin type functional response parameters, in which c measures the magnitude of interference among prey. Further, a_2 describes the growth rate of predator v ; e is the maximum value which per capita reduction rate of v can attain, f measure the extent to which environment provides protection to predator v .

The model system (5.4) has 8 parameters in all, which make mathematical analysis complex. In order to avoid such difficulties we reduce the number of parameters by non-dimensionlizing the model system. The model is rendered dimensionless using the following change of variables and parameters :

$$u \rightarrow Ku, \quad v \rightarrow \frac{a_1}{b}v, \quad t \rightarrow \frac{t}{a_1}.$$

With the scaling, system (5.4) takes the form

$$\begin{cases} \frac{du}{dt} = u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) =: F_1(u, v), \\ \frac{dv}{dt} = Cv \left(1 - \frac{Dv}{u + E} \right) =: F_2(u, v), \end{cases} \quad (5.5)$$

where

$$A = cK, \quad B = \frac{da_1}{b}, \quad C = \frac{a_2}{a_1}, \quad D = \frac{ea_1}{Kba_2}, \quad E = \frac{f}{K}.$$

We denote by $F = (F_1, F_2)$ and by $R(u, v) = (1 + Au)(1 + Bv)$.

Clearly, the dimensionless system (5.5) has five parameters in all. The system (5.5) needs to be analyzed with the following initial conditions :

$$u_0 > 0, \quad v_0 > 0.$$

We denote by

$$\mathbb{R}_+^2 := \{(u, v) \in \mathbb{R}^2, u \geq 0, v \geq 0\},$$

and

$$\text{Int}(\mathbb{R}_+^2) := \{(u, v) \in \mathbb{R}^2, u > 0, v > 0\}.$$

Standard and simple arguments [43, 48] show existence and uniqueness of solutions of the system (5.5).

The rest of this article is organized as follows. In Section 5.2, we show boundedness of solutions and existence of a positively invariant and attracting set. In Section 5.3, the existence and the local stability of equilibria of the system (5.5) are studied. In section 5.4, the permanence of the system (5.5) is investigated. In Section 5.5, we establish the existence and nonexistence of periodic solutions of the system (5.5). Global stability of the positive equilibrium and the prey-extinction equilibrium, when the unique positive equilibrium does not exist, is discussed in Section 5.6. In Section 5.7, the numerical simulations are presented to illustrate the results.

5.2 Boundedness of the model and existence of a positively invariant attracting set

It is important to show positivity and boundedness of solutions for the system (5.5) as they represent populations. Positivity implies that populations survive and boundedness may be interpreted as a natural restriction to growth as a consequence of limited resources. In this section, we will show that all solutions starting in $\text{Int}(\mathbb{R}_+^2)$ remain bounded and positive.

Obviously, using Cauchy-Lipschitz theorem, and as the u -axis and the v -axis are orbits, the positive quadrant $\text{Int}(\mathbb{R}_+^2)$ is positively invariant.

Definition 5.2.1. A solution $(u(t), v(t))$ of system (5.5) is said to be ultimately bounded with respect to \mathbb{R}_+^2 , if there exists a compact region $\mathcal{A} \in \mathbb{R}_+^2$ and a finite time T ($T = T(t_0, u_0, v_0)$) such that, for any $(t_0, u_0, v_0) \in \mathbb{R}_+ \times \mathbb{R}_+^2$, $(u(t, t_0, u_0, v_0), v(t, t_0, u_0, v_0)) \in \mathcal{A}$ for all $t > T$.

Theorem 5.2.2. Let \mathcal{A} be the set defined by

$$\mathcal{A} = \left\{ (u, v) \in \mathbb{R}_+^2 : 0 \leq u \leq 1, 0 \leq v \leq \frac{1+E}{D} \right\}.$$

Then,

- (a) \mathcal{A} is positively invariant,
- (b) all solutions of (5.5) starting in \mathbb{R}_+^2 are bounded with respect to \mathbb{R}_+^2 and enter the attracting set \mathcal{A} .

This, in particular, means that system (5.5) is dissipative.

Proof.

- (a) Letting $(u_0, v_0) \in \mathcal{A}$, we will show that $(u(t), v(t)) \in \mathcal{A}$ for all $t \geq 0$. As $u(t) > 0$ and $v(t) > 0$ for all t , it remains to show that for all $t \geq 0$, $u(t) \leq 1$ and $v(t) \leq \frac{1+E}{D}$.
 - (a₁) We first prove that $u(t) \leq 1$, for all $t \geq 0$. Since $u > 0$ and $v > 0$ in $\text{Int}(\mathbb{R}_+^2)$, every solution $(u(t), v(t))$ of (5.5), which starts in $\text{Int}(\mathbb{R}_+^2)$, satisfies the differential inequality $\frac{du}{dt} \leq u(1-u)$. Thus $u(t) \leq x(t)$, where $x(t)$ is the solution of $\frac{dx}{dt} = x(1-x)$, $x(0) = u_0$. As $x(0) \leq 1$, then $x(t) \leq 1$, for all t . Then $u(t) \leq 1$ for all t .
 - (a₂) As $0 < v_0 \leq \frac{1+E}{D}$ and $0 < u_0 \leq 1$, we can prove similarly that $v(t) \leq \frac{1+E}{D}$ for all t .
- (b) all solutions of (5.5) starting in \mathbb{R}_+^2 are ultimately bounded with respect to \mathbb{R}_+^2 and enter the attracting set \mathcal{A} .

(b₁) Let $u_0 > 1$ and $t_0 = \max \{t < T_{\max} \text{ s.t. } u(s) > 1, \forall s \in (0, t)\}$. Then $u'(t) < 0, \forall t \in (0, t_0)$.

Assume by contradiction that $t_0 = T_{\max}$ and set $\alpha = \lim_{t \rightarrow T_{\max}} u(t) \geq 1$.

Firstly, assume that $\alpha > 1$, then $u'(t) \leq u(1 - \alpha)$, hence $u(t) \leq e^{(1-\alpha)t}u_0$.

Therefore, $T_{\max} = +\infty$ and $\lim_{t \rightarrow +\infty} u(t) = 0$, which is a contradiction.

Hence $t_0 < T_{\max}$.

Assume now that $\alpha = \lim_{t \rightarrow T_{\max}} u(t) = 1$. Then $u(t_0) = 1$ and $u'(t_0) = -\frac{v(t_0)}{R(1, v(t_0))} < 0$.

Therefore, $t_0 < T_{\max}$, and then $u(t) < 1$ for $t \in (t_0, t_0 + \varepsilon)$ for some $\varepsilon > 0$, and hence by (a₁), for all $t > t_0$.

(b₂) Similarly, we can prove that if $v_0 > \frac{1+E}{D}$, there exists $t_1 < T_{\max}$, such that $v(t) < \frac{1+E}{D}$, for all $t > t_1$.

As a conclusion, we showed the existence of a time $t_2 = \max(t_0, t_1)$ such that $(u(t), v(t)) \in \mathcal{A}$ for all $t \geq t_2$.

This completes the proof and we also conclude that system (5.5) is dissipative in \mathbb{R}_+^2 . \square

5.3 Equilibria and their local stability analysis

In this section, we discuss mainly the existence and the linearized stability of the unique positive equilibrium of (5.5), and the existence of Hopf bifurcation of nonconstant periodic solutions surrounding the interior equilibrium in (5.5).

5.3.1 Conditions for the existence of a unique positive equilibrium

System (5.5) has always three boundary equilibria $E_0(0, 0)$, $E_1(1, 0)$ and $E_2(0, \frac{E}{D})$. Since we are dealing with populations, we are interested in studying the uniqueness of positive equilibrium $E^* = (u^*, v^*)$, i.e. $u^* > 0$ and $v^* > 0$. A direct calculation shows that we have a unique positive equilibrium E^* if and only if the following cubic equation

$$ABu^3 + (B + AD - AB + ABE)u^2 + (D - B - AD + EB - ABE + 1)u + E - D - EB = 0 \quad (5.6)$$

has a unique positive root u^* . In fact, by applying the rule signs of Descartes, (5.6) has a unique positive root, if

$$E < EB + D \quad (5.7)$$

and any of the following three conditions is satisfied

$$B + AD + ABE > AB, \quad D + EB + 1 > B + AD + ABE \quad (5.8)$$

$$B + AD + ABE > AB, \quad D + EB + 1 < B + AD + ABE \quad (5.9)$$

$$B + AD + ABE < AB, \quad D + EB + 1 < B + AD + ABE. \quad (5.10)$$

Hence the positive equilibrium E^* of system (5.5) is (u^*, v^*) , where $v^* = \frac{E+u^*}{D}$, and in this case, using Cardan's formula, u^* is given by

$$u^* = \sqrt[3]{-\frac{q}{2} + \sqrt{\left(\frac{q}{2}\right)^2 + \left(\frac{p}{3}\right)^3}} + \sqrt[3]{-\frac{q}{2} - \sqrt{\left(\frac{q}{2}\right)^2 + \left(\frac{p}{3}\right)^3}} - \frac{c_1}{3}$$

where

$$c_1 = (B - AB + AD + ABE)/AB,$$

$$c_2 = (D - B - AD + EB - ABE + 1)/AB,$$

$$c_3 = (E - D - EB)/AB,$$

$$p = c_2 - \frac{c_1^2}{3} \quad \text{and}$$

$$q = \frac{c_1}{27}(2c_1^2 - 9c_2) + c_3.$$

Remark 5.3.1. *We will use the following condition (5.11) :*

$$B + AD + ABE < AB, \quad D + EB + 1 > B + AD + ABE. \quad (5.11)$$

Case 1. *If (5.7) is satisfied and any of the assumptions (5.8) or (5.9) or (5.10) is satisfied, then system (5.5) has a unique positive equilibrium E^* in the first quadrant.*

Case 2. *If (5.8) is satisfied and $E > EB + D$, then system (5.5) has no positive equilibrium in the first quadrant.*

Case 3. *If $E > EB + D$ and any of the assumptions (5.9) or (5.10) or (5.11) is satisfied, then system (5.5) has either two positive equilibria or no positive equilibrium in the first quadrant.*

Case 4. *If (5.7) and (5.11) are satisfied, then system (5.5) has either one positive equilibrium or three positive equilibria in the first quadrant.*

In the rest of this article, we always assume that at least one of the three conditions (5.8), (5.9) or (5.10) is satisfied.

5.3.2 Local stability and Hopf bifurcation

Now, we will begin analyzing the geometric properties of the equilibria of system (5.5).

By Remark 5.3.1, it is obvious that the system (5.5) has always three boundary equilibria E_0, E_1 and E_2 ; the unique positive equilibrium E^* exists if and only if $E < EB + D$.

To investigate the local stability of the equilibria E_0, E_1, E_2 and E^* whenever it exists, we have to look to the Jacobian matrix for the system of equations (5.5). This is given at any point $E(u, v)$ by

$$J(E) = \begin{pmatrix} 1 - 2u - \frac{v}{(1 + Au)^2(1 + Bv)} & -\frac{u}{(1 + Au)(1 + Bv)^2} \\ \frac{CDv^2}{(E + u)^2} & C - \frac{2CDv}{E + u} \end{pmatrix}. \quad (5.12)$$

The stability of the equilibrium point will be determined by the nature of the eigenvalues of the Jacobian matrix evaluated at the corresponding equilibrium point. Clearly, E_0 is unstable, E_1 is a saddle point, and if $E > EB + D$, E_2 is locally asymptotically stable; while if $E < EB + D$, E_2 is a saddle point.

Thus, we can conclude that E_0 is unstable, E_1 is a saddle point, and if in addition $E > EB + D$, then E_2 is locally asymptotically stable and there is not an unique positive equilibrium in the first quadrant. If $E < EB + D$, then E_2 is unstable and system (5.5) has a unique positive equilibrium E^* in the first quadrant; the stability of E^* is discussed in the following.

Now, we assume that $E < EB + D$, the Jacobian matrix of system (5.5) at E^* takes the form

$$J(E^*) = \begin{pmatrix} C^* & \frac{-u^*}{(1 + Au^*)(1 + Bv^*)^2} \\ \frac{C}{D} & -C \end{pmatrix} \quad (5.13)$$

where $C^* \stackrel{\text{def}}{=} u^* \left(\frac{Av^*}{(1 + Au^*)^2(1 + Bv^*)} - 1 \right)$.

We have

$$\text{tr}(J(E^*)) = C^* - C$$

and

$$\det(J(E^*)) = -CC^* + \frac{C}{D(1 + Au^*)(1 + Bv^*)^2}.$$

Thus, we have the following propositions

Proposition 5.3.2. *If the condition (5.7) and the following two conditions are satisfied*

$$Av^*(1 + Bv^*) - R(u^*, v^*)^2 < \frac{1 + Au^*}{D}, \quad (5.14)$$

$$C > C^*, \quad (5.15)$$

then the positive equilibrium E^* is locally asymptotically stable.

Proposition 5.3.3. *If the condition (5.7) and the following condition is satisfied*

$$Av^*(1 + Bv^*) - R(u^*, v^*)^2 > \frac{1 + Au^*}{D}, \quad (5.16)$$

then the positive equilibrium E^* is a saddle point.

Proposition 5.3.4. *If the conditions (5.7), (5.14) hold true, and*

$$C < C^*, \quad (5.17)$$

then the positive equilibrium E^* is locally asymptotically unstable.

We now present the conditions for the existence of a Hopf-bifurcation small amplitude periodic solution.

Lemma 5.3.5. *Assume that $C = C^*$ and conditions (5.7) and (5.14) of Proposition 5.3.2 hold true, then the system (5.5) exhibits Hopf-bifurcation near E^* .*

Proof. Since the conditions (5.7) and (5.14) hold true, it is clear from Proposition 5.3.2 and 5.3.4 that E^* changes its nature from locally asymptotically stable to unstable as the parameter C passes through its critical value $C = C^*$ from higher to lower. For $C = C^*$, we have $\text{tr}(J(E^*)) = 0$ and hence the roots of the characteristic equation become purely imaginary and they are conjugate to each other. Also we have

$$\frac{d}{dC}[\text{tr}J]_{C=C^*} = u^* \left(\frac{Av^*}{(1 + Au^*)^2(1 + Bv^*)} - 1 \right) - 1 = C^* - 1 \neq 0. \quad (5.18)$$

Hence by the Andronov-Hopf bifurcation theorem (Theorem 3.1, [81]), system (5.5) enters into a Hopf-type small amplitude periodic oscillations at the parameter $C = C^*$ near the positive equilibrium E^* . \square

The above Lemma establishes the existence of a small amplitude periodic solution near the interior equilibrium point E^* . Furthermore, according to Poincaré-Andronov theorem, the stability of the Hopf-bifurcating periodic solution depends on the sign of first Lyapunov coefficient ℓ_1 at the critical parametric value $C = C^*$. These solutions are stable limit cycles if $\ell_1 < 0$ and unstable for $\ell_1 > 0$. Details of the calculation of the Lyapunov coefficient are provided in the Appendix.

5.4 Permanence

In this section, we present the permanence of the system, that is, uniform persistence plus dissipativity. Firstly, we give some definitions.

Definition 5.4.1. *System (5.5) is said to be permanent if there are positive constants M_1 and M_2 such that each positive solution $(u(t), v(t))$ of system (5.5) with initial conditions $(u_0, v_0) \in \text{Int}(\mathbb{R}_+^2)$ satisfies*

$$0 < M_1 \leq \liminf_{t \rightarrow +\infty} u(t) \leq \limsup_{t \rightarrow +\infty} u(t) \leq M_2,$$

$$0 < M_1 \leq \liminf_{t \rightarrow +\infty} v(t) \leq \limsup_{t \rightarrow +\infty} v(t) \leq M_2.$$

Suppose that Y is a complete metric space with $Y = Y_0 \cup \partial Y_0$ for an open set Y_0 . We will typically choose Y_0 to be the positive cone in \mathbb{R}^2 . For the following definitions and theorem, one can see [20].

Definition 5.4.2. *A flow or semi-flow on Y under which Y_0 and ∂Y_0 are forward invariant is said to be permanent if it is dissipative and if there is a number $\epsilon > 0$ such that any trajectory with initial data in Y_0 will be bounded away from ∂Y_0 by a distance greater than ϵ for t sufficiently large.*

Let $\omega(\partial Y_0) \in \partial Y_0$ denote the union of the sets $\omega(u)$ for $u \in \partial Y_0$.

Definition 5.4.3. *The set $\omega(\partial Y_0)$ is said to be isolated if it has a covering $M = \cup_{k=1}^N M_k$ of pairwise disjoint sets M_k which are isolated and invariant with respect to the flow or the semi flow both on ∂Y_0 and on $Y = Y_0 \cup \partial Y_0$, (M is called an isolated covering). The set $\omega(\partial Y_0)$ is said to be acyclic if there exists an isolated covering $M = \cup_{k=1}^N M_k$ such that no subset of M_k is a cycle.*

Theorem 5.4.4. *(Theorem 4.2, [45]) Suppose that a semi-flow on Y leaves both Y_0 and ∂Y_0 forward invariant, maps bounded sets in Y to pre-compact set for $t > 0$, and it is dissipative. If in addition*

- (i) $\omega(\partial Y_0)$ is isolated and acyclic,
- (ii) $W^s(M_k) \cap Y_0 = \emptyset$ for all k , where $\cup_{k=1}^N M_k$ is the isolated covering used in the definition of acyclicity of ∂Y_0 , (W^s denotes the stable manifold),

then the semi-flow is permanent.

Theorem 5.4.5. *Let us assume that the condition (5.7) holds true, namely*

$$E < EB + D,$$

then, system (5.5) is permanent.

Proof. If we take Y_0 to be the positive quadrant, then $\omega(\partial Y_0)$ consists of the equilibria $(0, 0)$, $(1, 0)$ and $(0, E/D)$.

The positive u -axis, except the origin, is the stable manifold of the saddle point $(1, 0)$.

Similarly, the positive v -axis, except the origin, is the stable manifold of the saddle point $(0, E/D)$.

Since, by Theorem 5.2.2, every orbit starting in $\text{Int}(\mathbb{R}_+^2)$ enters the attracting set $\mathcal{A} = [0, 1] \times [0, \frac{1+E}{D}]$, and as $(0, 0)$ is unstable, the phase plane implies that $\omega(\partial Y_0)$ is isolated and acyclic. Thus Theorem 5.4.4 implies permanence of system (5.5). \square

5.5 Limit cycle

In this section, we will provide some sufficient conditions for the existence and non-existence of periodic orbits of system (5.5) (See for instance [57]).

5.5.1 Existence of periodic orbits

Theorem 5.5.1. *Under the hypothesis (5.7), assume in addition either (5.16) or [(5.14) and (5.17)] are satisfied, then system (5.5) has at least one limit cycle.*

Proof. Since $\mathring{\mathcal{A}}$ is positively invariant, by (5.16) or [(5.14) and (5.17)], E^* is unstable. Thus Poincaré-Bendixon theory implies the existence of a limit cycle in \mathcal{A} turning around E^* . \square

5.5.2 Non-existence of a periodic orbit

In view of Theorem 5.5.1, for the non-existence of periodic orbit, we will look in the region where the parameters A, B, C, D and E satisfy the conditions

$$Av^*(1 + Bv^*) - R(u^*, v^*)^2 = \frac{1 + Au^*}{D},$$

or

$$Av^*(1 + Bv^*) - R(u^*, v^*)^2 < \frac{1 + Au^*}{D} \quad \text{and} \quad C \geq C^*.$$

Now, to prove that the system has no limit cycle, we will use Dulac's criterion, see [42].

Theorem 5.5.2. *(Dulac's criterion [42]) Let $D \subset \mathbb{R}^2$ be a simply connected open set and $H(u, v)$ be a real-valued \mathcal{C}^1 function in D .*

If the function $\text{div}(HF)$ is of constant sign and not identically zero on D , then the system $\frac{dU}{dt} = F(U)$, where $U = (u, v)$, has no periodic orbit lying entirely in the region D .

Theorem 5.5.3. *If $A(1 - C) < 1$, then the system (5.5) has no periodic orbit.*

Proof. Let $H(u, v) = \frac{1+Au}{Auv^2}$, $u > 0$, $v > 0$. We have

$$\begin{aligned} \operatorname{div}(HF) &= P(u, v) \left[1 - 2u - C - \frac{(1-u)}{1+Au} \right] \\ &= \frac{H(u, v)}{1+Au} [-2Au^2 + u(A(1-C) - 1) - C]. \end{aligned}$$

Since the solutions of the system (1.6) are ultimately bounded and enter the set \mathcal{A} , we restrict the study for this set. It is obvious that, if $A(1 - C) < 1$, then $\operatorname{div}(HF) < 0$. By Dulac's criterion, we conclude that system (5.5) has no periodic orbit under this assumption. \square

In the following, we will use another criteria to deny the existence of periodic orbit (see Lemma 3.1 of [43]).

Theorem 5.5.4. *If $A \leq B + \frac{D}{E+1}$, then the system (5.5) has no nontrivial periodic orbit in \mathbb{R}_+^2 .*

Proof. Let $\Gamma(t) = (u(t), v(t))$ be a nontrivial periodic orbit of system (5.5) with period $T > 0$. We will show that

$$\Delta = \int_0^T \operatorname{tr}(J(u(t), v(t))) dt < 0. \quad (5.19)$$

As $\operatorname{tr}(J(u(t), v(t))) = \frac{\partial F_1}{\partial u} + \frac{\partial F_2}{\partial v} = f + u \frac{\partial f}{\partial u} + g + v \frac{\partial g}{\partial v} = f + u \frac{\partial f}{\partial u} + g + v \frac{\partial g}{\partial v} = \frac{u'}{u} + \frac{v'}{v} + u \frac{\partial f}{\partial u} + v \frac{\partial g}{\partial v}$, where $F_1(u, v) = uf(u, v)$ and $F_2(u, v) = vg(u, v)$, and by periodicity,

$$\int_0^T \frac{u'(t)}{u(t)} dt = \int_0^T \frac{v'(t)}{v(t)} dt = 0.$$

So we have

$$\Delta = \int_0^T \left[u \left(-1 + \frac{Av}{(1+Au)^2(1+Bv)} \right) - \frac{CDv}{u+E} \right] dt. \quad (5.20)$$

As $A \leq B + \frac{D}{E+1}$, then $Av \leq Bv + \frac{Dv}{E+1} \leq Bv + 1$, since $v \leq \frac{1+E}{D}$. Then $Av \leq 1 + Bv \leq (1+Au)^2(1+Bv)$. Hence $\Delta < 0$.

Therefore, using Lemma 3.1 of [43], every such orbit is asymptotically stable. A contradiction since an asymptotically stable critical point mandates at least one periodic orbit being unstable. Thus there are no periodic orbits. \square

5.6 Global stability

In the case where system (5.5) has a unique positive equilibrium E^* , we will prove in this section the global asymptotic stability of the unique positive equilibrium E^* by using three methods. The first is the method of limit cycle stability analysis. The second method is based on Dulac criterion and Poincaré-Bendixon theorem. For the third method, we construct a Lyapunov function and establish the global stability by LaSalle's invariance principle.

In order to study the global stability of the positive equilibrium E^* , we will assume that hypotheses of Proposition 5.3.2 are satisfied.

Firstly, we will study the global stability by using the analysis of the phase plane, the Dulac criterion, and the Poincaré-Bendixon theorem.

Phase plane analysis

For the system (5.5), the isocline for u is given by the v -axis and the straight line $Dv = E + u$, the isocline for v is given by the u -axis and the curve $v = \frac{(1-u)(1+Au)}{1-B(1-u)(1+Au)}$.

Two cases occur :

- If $B < 1$, then the phase plane looks like figure 5.1-a).
- If $B > 1$, then the phase plane looks like figure 5.1-b).

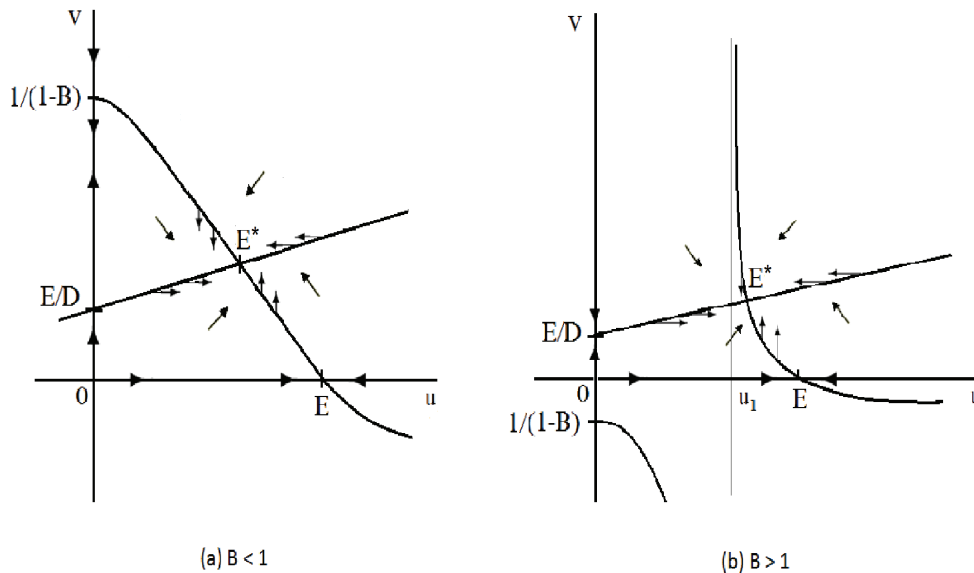


FIGURE 5.1 – Isoclines graph for the system (5.5) for parametric values ; (a) $B < 1$ and A, C, D, E are positive parameters ; (b) $B > 1$ and A, C, D, E are positive parameters. Here u_1 is the positive root of the polynomial $1 - B(1 - u)(1 + Au)$.

Corollary 5.6.1. *If (5.14) and (5.15) are satisfied and one of the following conditions is satisfied*

$$A(1 - C) < 1, \quad (5.21)$$

or

$$A \leq B + \frac{D}{E + 1}, \quad (5.22)$$

then the positive equilibrium E^* is globally asymptotically stable in the first quadrant.

Proof. Since $(0, 0)$ and $(0, E/D)$ are unstable and $(1, 0)$ is saddle point, the corollary follows immediately from the phase plane analysis, Theorems 5.5.3, 5.5.4 and Poincaré-Bendixon theorem. \square

Remark 5.6.2. *Notice that, if $A \leq B$, then (5.14), (5.15) and (5.21) are satisfied. In other words, if $A \leq B$, then for a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses, the local and global stability of E^* coincide.*

Now, using the Lyapunov method, we will prove that, under some assumptions, the positive equilibrium E^* is globally asymptotically stable.

In the following theorem we set

$$Q := \frac{Av^*}{E(1 + Au^*)} + \frac{1}{4(1 + Bv^*)^2} - \frac{1}{2(1 + A)(1 + E)(D + B(1 + E))(1 + Bv^*)}.$$

Theorem 5.6.3. *Suppose that the positive equilibrium E^* is locally asymptotically stable. Then it is globally asymptotically stable if*

$$\frac{Av^*}{(1 + Au^*)(1 + Bv^*)} < \frac{E + 2}{E + 1}, \quad (5.23)$$

and any of the two following conditions is satisfied

$$4D^2 \leq \frac{2E + 1}{E(3E + 1)} \quad \text{and} \quad \frac{1}{E} \left(1 - \frac{1}{4D^2E} \right) \geq Q \quad (5.24)$$

or

$$4D^2 > \frac{2E + 1}{E(3E + 1)} \quad \text{and} \quad \frac{1}{(E + 1)} \left(1 - \frac{1}{4D^2(E + 1)} \right) \geq Q. \quad (5.25)$$

Proof. The proof is based on a positive definite Lyapunov function. Let $(u(t), v(t))$ be any solution of system (5.5). Define $V(u, v) = V_1(u, v) + V_2(u, v)$, where

$$V_1(u, v) = u - u^* - u^* \ln \left(\frac{u}{u^*} \right) \quad \text{and} \quad V_2(u, v) = \frac{1}{CD} \left(v - v^* - v^* \ln \left(\frac{v}{v^*} \right) \right).$$

This function is defined and continuous on $\text{Int}(\mathbb{R}_+^2)$. It can be easily verified that the function $V(u, v)$ is zero at the equilibrium (u^*, v^*) and is positive for all other positive values of u and v , and thus, $E^*(u^*, v^*)$ is the global minimum of V .

Since solutions of system (5.5) are ultimately bounded and enter the set \mathcal{A} , we restrict the study for this set. Using the relation between u^* and v^* , a direct calculation implies that

$$\frac{dV_1}{dt} = (u - u^*) \left(-(u - u^*) + \frac{Av^*(1 + Bv)(u - u^*) - (1 + Au^*)(v - v^*)}{(1 + Au)(1 + Bv)(1 + Au^*)(1 + Bv^*)} \right),$$

and

$$\frac{dV_2}{dt} = (v - v^*) \left(-\frac{(v - v^*)}{E + u} + \frac{(u - u^*)}{D(E + u)} \right).$$

Therefore,

$$\begin{aligned} \frac{dV}{dt} &= \left(-1 + \frac{Av^*}{(1 + Au)(1 + Au^*)(1 + Bv^*)} \right) (u - u^*)^2 \\ &+ \left(\frac{-1}{(1 + Au)(1 + Bv)(1 + Bv^*)} + \frac{1}{D(E + u)} \right) (u - u^*)(v - v^*) \\ &- \frac{1}{E + u} (v - v^*)^2. \end{aligned}$$

This can be written as

$$\frac{dV}{dt} = -(u - u^*, v - v^*) \begin{pmatrix} k(u, v) & \ell(u, v) \\ \ell(u, v) & m(u, v) \end{pmatrix} \begin{pmatrix} u - u^* \\ v - v^* \end{pmatrix}, \quad (5.26)$$

where

$$\begin{aligned} k(u, v) &= 1 - \frac{Av^*}{(1 + Au)(1 + Au^*)(1 + Bv^*)}, \\ \ell(u, v) &= \frac{1}{2} \left(\frac{1}{(1 + Au)(1 + Bv)(1 + Bv^*)} - \frac{1}{D(E + u)} \right) \end{aligned}$$

and

$$m(u, v) = \frac{1}{E + u}.$$

From (5.26), it is obvious that $\frac{dV}{dt} < 0$ if and only if the matrix above is positive definite, which is equivalent to $k(u, v) + m(u, v) > 0$ and $\varphi(u, v) = m(u, v)k(u, v) - \ell^2(u, v) > 0$, where

$$\begin{aligned} \varphi(u, v) &= \frac{1}{E + u} - \frac{Av^*}{(1 + Au)(1 + Au^*)(1 + Bv^*)(E + u)} \\ &- \frac{1}{4(1 + Au)^2(1 + Bv)^2(1 + Bv^*)^2} \\ &+ \frac{1}{2} \frac{1}{D(1 + Au)(1 + Bv)(1 + Bv^*)(E + u)} - \frac{1}{4} \frac{1}{D^2(E + u)^2}. \end{aligned}$$

$k(u, v) + m(u, v) > 0$ is guaranteed by (5.23) and $\varphi(u, v) > 0$ using (5.24) or (5.25). Consequently, except at E^* , V is decreasing along all trajectories in the first quadrant. Thus E^* is globally asymptotically stable. \square

Now we consider the case where there is no positive equilibrium, we will prove the global asymptotic stability of the prey-extinction equilibrium $E_2(0, E/D)$ by constructing a suitable Lyapunov function and using LaSalle's invariance principle .

Theorem 5.6.4. *If $E > EB + D$ and the following condition is satisfied*

$$\frac{(1+A)(D+B(1+E))}{E} < D < \frac{E}{E+1}, \quad (5.27)$$

then the prey-extinction equilibrium $E_2(0, E/D)$ of system (5.5) is globally asymptotically stable.

Proof. Since $E > EB + D$ then system (5.5) has no unique positive equilibrium. The proof is based on a positive definite Lyapunov function. Let $(u(t), v(t))$ be any solution of system (5.5). Define

$$V_0(u, v) = u + \frac{1}{C} \left(v - v^0 - v^0 \ln \left(\frac{v}{v^0} \right) \right)$$

where $v^0 = E/D$. Since the solutions of the system (5.5) are ultimately bounded and enter the set \mathcal{A} , we restrict the study for this set. The time derivative of the functional V_0 along trajectories of the system (5.5) is given by

$$\frac{dV_0}{dt} = u \left(1 - u - \frac{v}{(1+Au)(1+Bv)} \right) + (v - v^0) \left(1 - \frac{Dv}{E+u} \right). \quad (5.28)$$

Substituting $E = Dv^0$ into (5.28), it follows that

$$\begin{aligned} \frac{dV_0}{dt} &= u \left(1 - u - \frac{v}{(1+Au)(1+Bv)} \right) - \frac{u(v^0 - v)}{Dv^0 + u} - (v - v^0)^2 \frac{D}{Dv^0 + u} \\ &= u \left(1 - u - \frac{v}{(1+Au)(1+Bv)} - \frac{v^0}{Dv^0 + u} + \frac{v}{Dv^0 + u} \right) \\ &\quad - (v - v^0)^2 \frac{D}{Dv^0 + u}. \end{aligned}$$

Hence, if (5.27) is satisfied, $V_0'(t) \leq 0$ and except at E_2 , V is decreasing along all trajectories in the first quadrant. Thus E_2 is globally asymptotically stable. \square

5.7 Numerical simulations

In this section, we present some numerical simulations to verify our theoretical results proved in the previous sections by using Matlab programming.

- (1) **Global stability of the unique positive equilibrium :** Let $A = 2, B = 0.1, C = 0.6, D = 0.3, E = 0.2$. Using Corollary 5.6.1, the unique positive equilibrium $E^* = (0.17613, 1.2538)$ is globally asymptotically stable. Numerical simulation illustrate this conclusion (see Fig. 5.2).
- (2) **Global stability of the prey-extinction equilibrium :** Let $A = 0.1, B = 0.1, C = 1, D = 0.57$, and $E = 1.5$. Using Theorem 5.6.4, the prey-extinction equilibrium $E_2(0, E/D)$ of system (5.5) is globally asymptotically stable. Numerical simulation illustrate this conclusion (see Fig. 5.3).
- (3) **Periodic orbit :** Let $A = 2, B = 0.1, C = 0.02, D = 0.3, E = 0.2$. Using Proposition 5.3.3, the unique positive equilibrium $E^* = (0.17613, 1.2538)$ is unstable. Numerical simulation show that system (5.5) admits a periodic solution (see Fig. 5.4).
- (4) **Hopf bifurcation :** From Figs. 5.2 and 5.4, and from Lemma 5.3.5, we can see that if we select the parameter C as a bifurcation parameter, Hopf bifurcation will occur (see Fig. 5.5 and 5.6). Here, we take, $A = 2, B = 0.1, D = 0.3, E = 0.2$ and $C = 0.02, 0.038486, 0.6$ respectively.

Moreover, the calculation of the first Lyapunov coefficient at the parametric value $C = 0.038486$ show that the Hopf-bifurcating periodic solution is stable and all other trajectories around the limit cycle ultimately approach it (see Fig. 5.7).

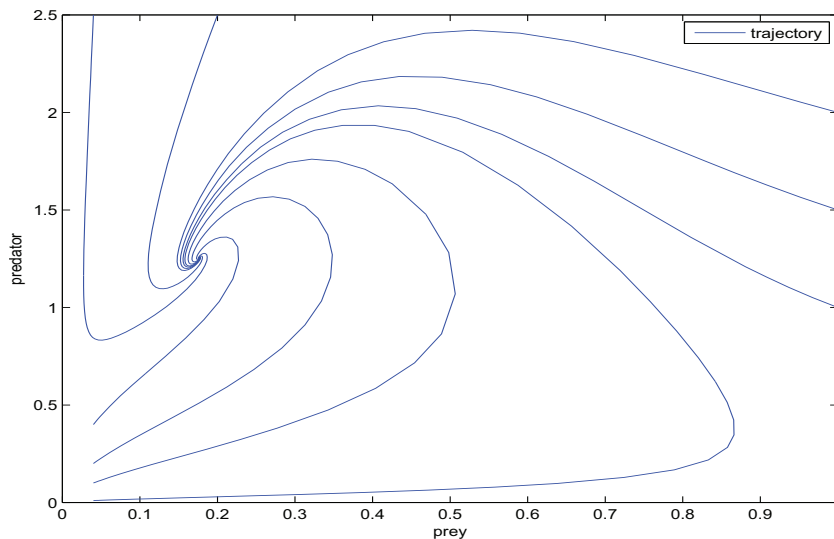


FIGURE 5.2 – The phase portrait of the system (5.5) when $A = 2, B = 0.1, C = 0.6, D = 0.3$, and $E = 0.2$. The positive equilibrium $E^*(0.17613, 1.2538)$ is a global attractor.

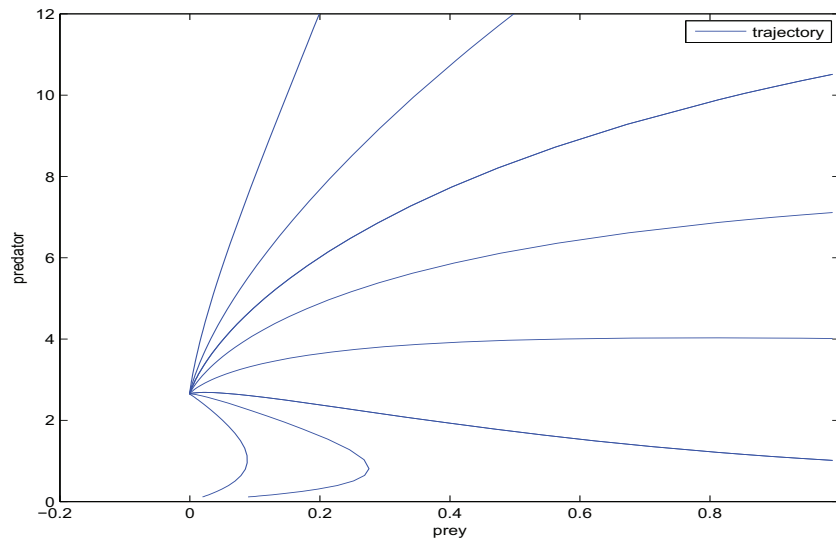


FIGURE 5.3 – The phase portrait of system (5.5) when $A = 0.1, B = 0.1, C = 1, D = 0.57$ and $E = 1.5$. The prey-extinction equilibrium $E_2(0, E/D)$ of system (5.5) is a global attractor.

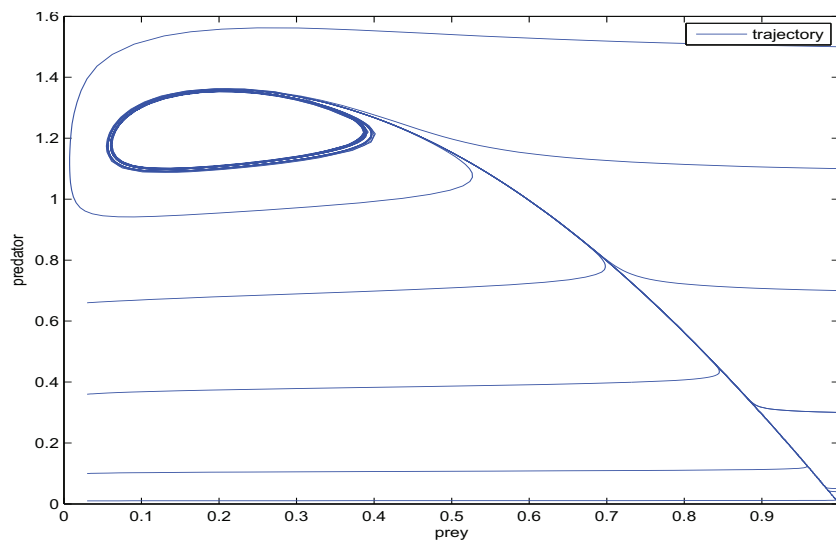


FIGURE 5.4 – The phase portrait of system (5.5) when $A = 2, B = 0.1, C = 0.02, D = 0.3$ and $E = 0.2$. The positive equilibrium $E^*(0.17613, 1.2538)$ is unstable and (5.5) has a nonconstant periodic solution surrounding E^* .

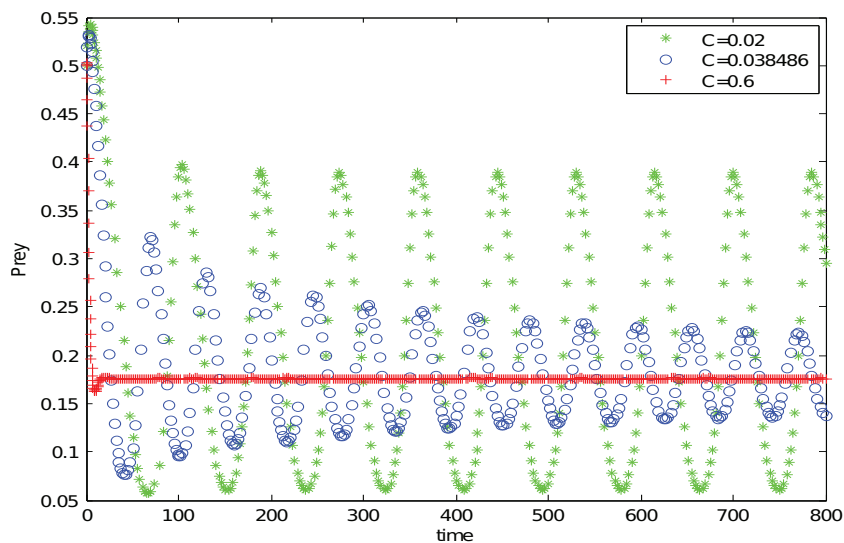


FIGURE 5.5 – Graph trajectory of prey $u(t)$ of system (5.5). Here $A = 2$, $B = 0.1$, $D = 0.3$, $E = 0.2$ and $C = 0.02, 0.038486, 0.6$, respectively.

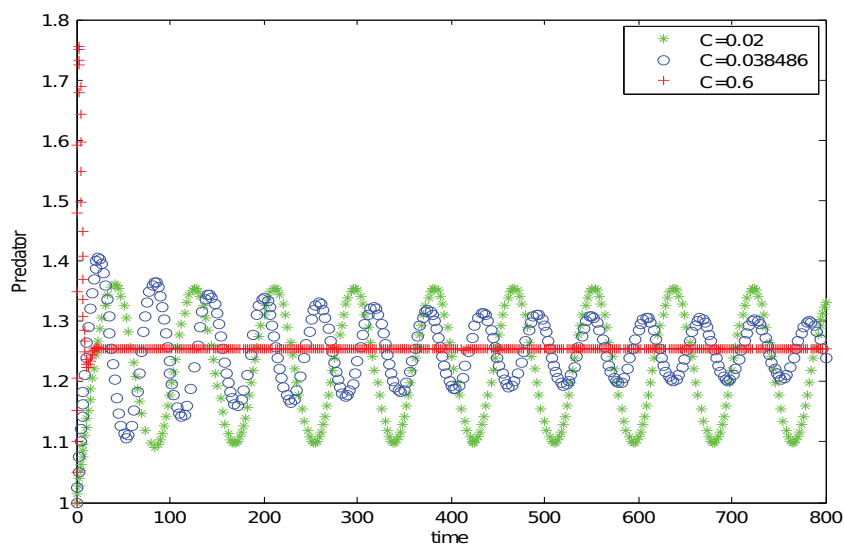


FIGURE 5.6 – Graph trajectory of predator $v(t)$ of system (5.5). Here $A = 2$, $B = 0.1$, $D = 0.3$, $E = 0.2$ and $C = 0.02, 0.038486, 0.6$, respectively.

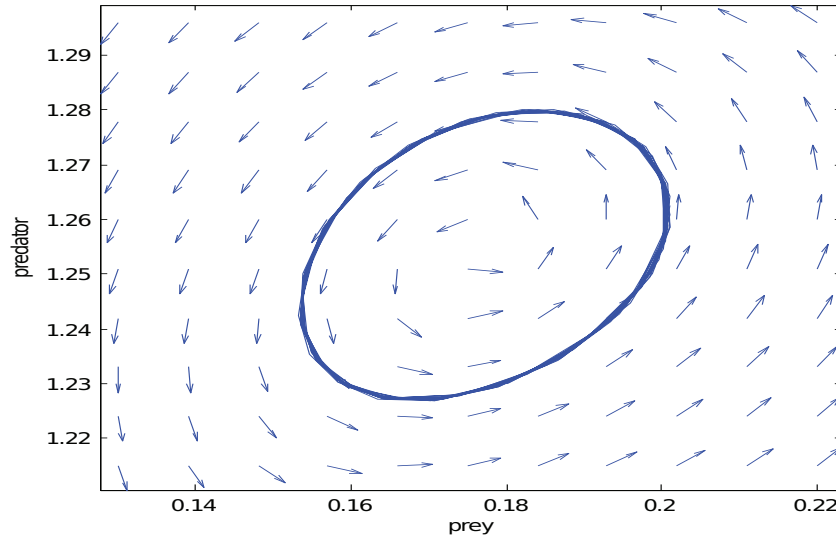


FIGURE 5.7 – Stable limit cycle around the positive equilibrium $E^*(0.17613, 1.2538)$ of the system (5.5) when $A = 2$, $B = 0.1$, $C = 0.038486$, $D = 0.3$ and $E = 0.2$.

5.8 Discussion and conclusions

In this paper, a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses is proposed and investigated. We show that the modified Leslie-Gower predator-prey model with Crowley-Martin functional responses has much richer boundary dynamics which includes the possibilities of extinction, permanence, stable or unstable equilibria and limit cycle. These results have important biological implications and indicate different results of the interaction of the predator-prey system (5.5).

- (i) As $t \rightarrow \infty$, if the trajectory tends to the boundary (extinction) equilibrium $(0, E/D)$, then it expresses the extinction of the prey population and the predator population converges to the balance density E/D .
- (ii) A balance behavior is obtained where the trajectory tends to the unique positive equilibrium E^* as $t \rightarrow \infty$.

Recall that $A = cK$, $B = d\frac{a_1}{b}$, $C = \frac{a_2}{a_1}$, $D = \frac{ea_1}{Kba_2}$, and $E = \frac{f}{K}$.

The conclusion of this paper is the importance of the two parameters d , the degree of predator interference, and C the ratio of the birth rates of the predator and the prey.

Firstly, we discuss the importance of the degree of predator interference d .

Theorem 5.4.5 shows that the permanence for the modified Leslie-Gower predator-prey model with Crowley-Martin functional responses depends on $B = d\frac{a_1}{b}$. This shows that B will affect the survival of all populations of the system in future time.

Furthermore, B plays a role of Hopf-bifurcation parameter. Figs. 5.4 and 5.8 show such Hopf-bifurcation when E^* changes its nature from unstable to locally asymptotically stable as the parameter B passes through its critical value $B = B^*$ from lower to higher. This is the case, for instance, for $A = 2, C = 0.02, D = 0.3, E = 0.2$ and select $B = 0.1, 0.171113, 0.3$ respectively (see Figs. 5.9 and 5.10).

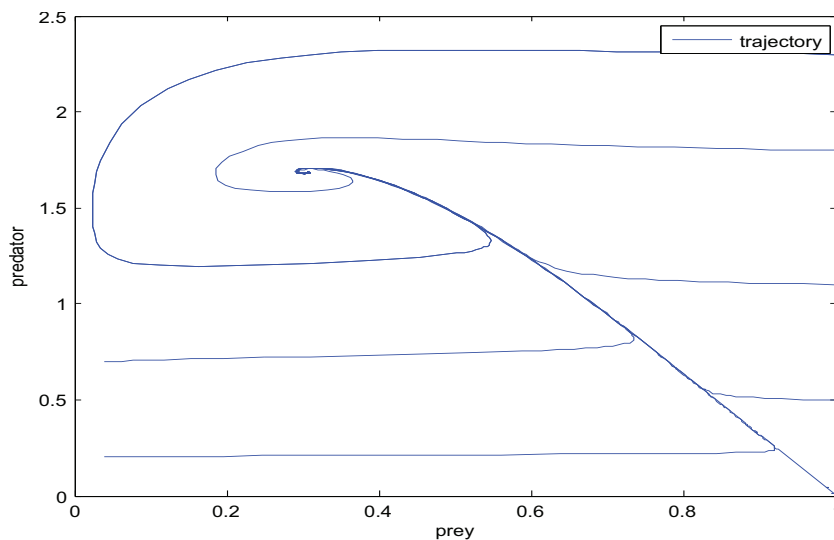


FIGURE 5.8 – Phase portrait of system (5.5). Positive equilibrium $E^*(0.30527, 1.6842)$ is globally asymptotically stable. Here $A = 2, B = 0.3, C = 0.02, D = 0.3$ and $E = 0.2$.

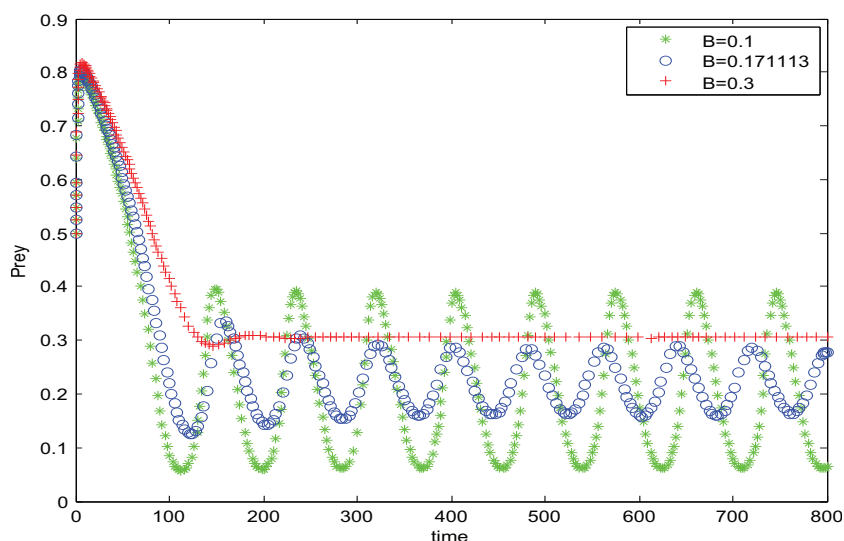


FIGURE 5.9 – Graph trajectory of prey $u(t)$ of system (5.5). Here $A = 2$, $C = 0.02$, $D = 0.3$, $E = 0.2$ and $B = 0.1, 0.171113, 0.3$ respectively.

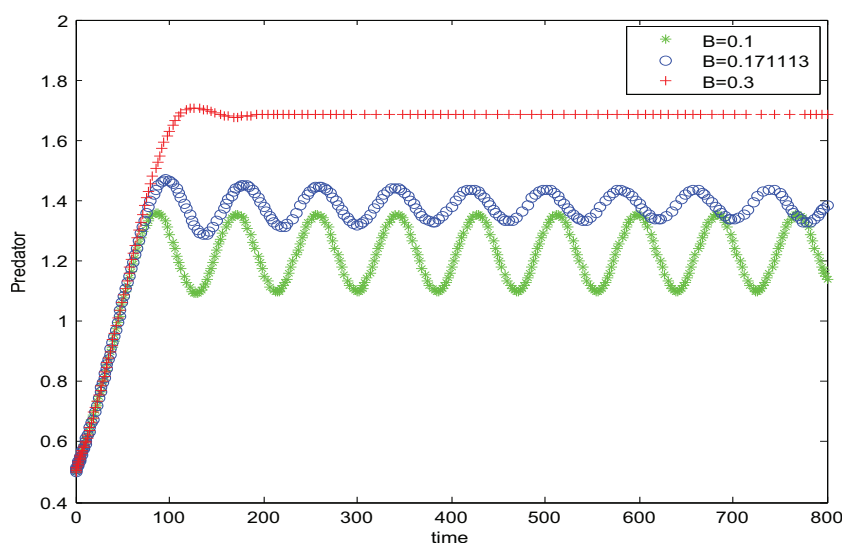


FIGURE 5.10 – Graph trajectory of predator $v(t)$ of system (5.5). Here $A = 2$, $C = 0.02$, $D = 0.3$, $E = 0.2$ and $B = 0.1, 0.171113, 0.3$ respectively.

Moreover, the calculation of the first Lyapunov coefficient at the parametric value $B = 0.171113$ shows that the Hopf-bifurcating periodic solution is stable and all other trajectories around the limit cycle ultimately approach it (see Fig. 5.11). The biological implication of this limit cycle is that the predator coexists with the prey, exhibiting oscillatory balance behavior.

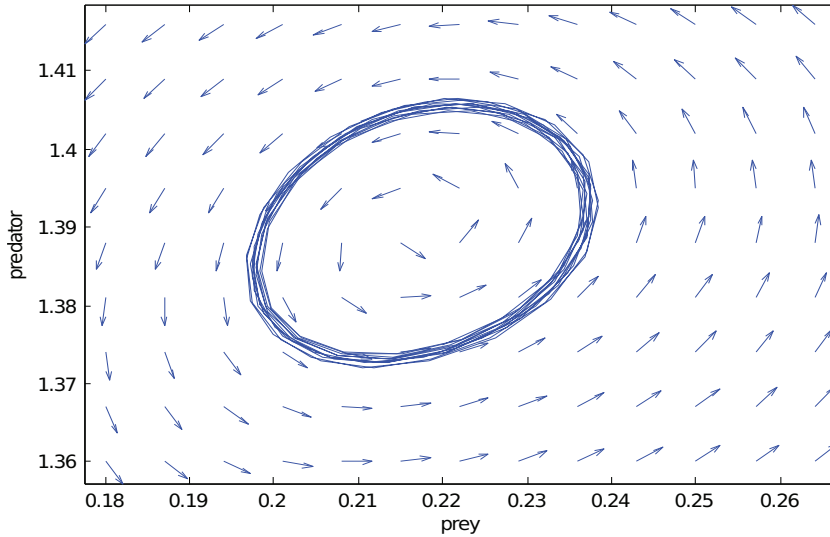


FIGURE 5.11 – Stable limit cycle around the positive equilibrium $E^*(0.21695, 1.3898)$ of the system (5.5) when $A = 2, B = 0.171113, C = 0.02, D = 0.3$ and $E = 0.2$.

Lastly, when $B = 0$, system (5.5) becomes :

$$\begin{cases} \frac{du}{dt} = u \left(1 - u - \frac{v}{1 + Au} \right), \\ \frac{dv}{dt} = Cv \left(1 - \frac{Dv}{u + E} \right), \end{cases} \quad (5.29)$$

which is a modified Leslie-Gower predator-prey model with Holling type II. In [13], Alaoui and Okiye have studied the global asymptotic behavior of positive solutions of the system (5.29).

In the following, we shall discuss the importance of parameter C . Section 5.3 shows that the stability of the unique positive equilibrium E^* depends on C with respect to C^* , this is also suggests a Hopf-bifurcation behavior.

Moreover, Section 5.5 shows that the existence of a periodic orbits or not depends on C .

Finally, There are still many interesting and challenging mathematical questions that need to be studied for system (5.5). For example, we are unable to show

that system (5.5) has a unique positive limit cycle, when E^* exists and is unstable. This is known to be true for system (5.1) where $P(u, v)$ is a Crowley-Martin functional responses (see [72]). Also, we will study the predator-prey model (5.1) where $P(u, v)$ is a Crowley-Martin functional responses and compare between the two predator-prey models with Crowley-Martin functional response for future research.

* - * - * - * - * - * - *

Appendix : First Lyapunov Coefficient

As mentioned in Section 5.3, the sign of the first Lyapunov coefficient ℓ_1 evaluated at the fixed point \mathbf{u}^* and Hopf-bifurcation parameter λ^* determines the criticality of the Hopf-bifurcation. In the following, we present the expressions for calculating $\ell_1|_{(\mathbf{u}^*, \lambda^*)}$ as introduced in [74].

Consider the 2-dimensional dynamical system

$$\dot{\mathbf{u}} = F(\mathbf{u}, \lambda), \quad (5.30)$$

where $\mathbf{u} = (u, v)$ and $\lambda \in \mathbb{R}$. Let $A_0 = D_{\mathbf{u}}F|_{(\mathbf{u}^*, \lambda^*)}$, where $\mathbf{u}^* = (u^*, v^*)$ is a steady state for the system (5.30) and λ^* is a Hopf-bifurcation parameter. A_0 has two purely imaginary complex conjugate eigenvalues, given by $\pm i\omega_0$, where $\omega_0 > 0$. Define T_1, T_2 and T_3 as follows

$$\begin{aligned} T_1 &= \langle \mathbf{p}, \mathfrak{C}(\mathbf{q}, \mathbf{q}, \bar{\mathbf{q}}) \rangle, \\ T_2 &= \langle \mathbf{p}, \mathfrak{B}(\bar{\mathbf{q}}, (2i\omega_0 - A_0)^{-1}\mathfrak{B}(\mathbf{q}, \mathbf{q})) \rangle, \\ T_3 &= -2 \langle \mathbf{p}, \mathfrak{B}(\mathbf{q}, A_0^{-1}\mathfrak{B}(\mathbf{q}, \bar{\mathbf{q}})) \rangle. \end{aligned}$$

Here $\langle \mathbf{r}, \mathbf{s} \rangle = \bar{\mathbf{r}} \cdot \mathbf{s}$ is the complex inner product between two complex vector, and \mathbf{p} and \mathbf{q} are respectivel the normalized eigenvector and adjoint-eigenvector of A_0 satisfying $A_0\mathbf{q} = i\omega_0\mathbf{q}$, $A_0^T\mathbf{p} = -i\omega_0\mathbf{p}$, and normalization $\langle \mathbf{p}, \mathbf{q} \rangle = 1$, \mathfrak{B} and \mathfrak{C} are high dimensional tensors given by

$$\mathfrak{B}(\mathbf{r}, \mathbf{s}) = \begin{bmatrix} \mathfrak{B}_1(\mathbf{r}, \mathbf{s}) \\ \mathfrak{B}_2(\mathbf{r}, \mathbf{s}) \\ \vdots \\ \mathfrak{B}_N(\mathbf{r}, \mathbf{s}) \end{bmatrix}, \quad \mathfrak{B}_i(\mathbf{r}, \mathbf{s}) = \sum_{k,l} \frac{\partial^2 f_i}{\partial x_k \partial x_l} \Big|_{\mathbf{u}=\mathbf{u}^*} r_k s_l, \quad (5.31)$$

$$\mathfrak{C}(\mathbf{r}, \mathbf{s}, \mathbf{t}) = \begin{bmatrix} \mathfrak{C}_1(\mathbf{r}, \mathbf{s}, \mathbf{t}) \\ \mathfrak{C}_2(\mathbf{r}, \mathbf{s}, \mathbf{t}) \\ \vdots \\ \mathfrak{C}_N(\mathbf{r}, \mathbf{s}, \mathbf{t}) \end{bmatrix}, \quad \mathfrak{C}_i(\mathbf{r}, \mathbf{s}, \mathbf{t}) = \sum_{k,l,m} \frac{\partial^3 f_i}{\partial x_k \partial x_l \partial x_m} \Big|_{\mathbf{u}=\mathbf{u}^*} r_k s_l t_m. \quad (5.32)$$

Thus, the first Lyapunov coefficient $\ell_1|_{(\mathbf{u}^*, \lambda^*)}$ can then be defined by Kuznetsov [74]

$$\ell_1|_{(\mathbf{u}^*, \lambda^*)} = \frac{1}{2\omega_0} \text{Re}(T_1 + T_2 + T_3).$$

* - * - * - * - * - * - *

Chapitre 6

Spatio-temporal dynamics of a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses

Sommaire

| | |
|---|-----|
| Présentation du chapitre | 116 |
| Abstract | 116 |
| 6.1 Introduction | 116 |
| 6.2 Global existence of solutions | 119 |
| 6.3 Dissipation and persistence | 121 |
| 6.4 Steady states and their local stability | 124 |
| 6.4.1 Local stability of the steady states | 125 |
| 6.5 Global stability | 130 |
| 6.6 Hopf bifurcation | 133 |
| 6.7 Turing instability | 134 |
| 6.8 Periodic Solutions | 135 |
| 6.9 Conclusions | 138 |

Nous présentons dans ce chapitre un modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin, qui prend en compte l'évolution de la distribution spatiale de deux populations. On s'intéresse particulièrement à l'existence globale des solutions, la dissipation et la persistance uniforme du système; et on étudie la stabilité des états d'équilibres. Nous démontrons aussi l'existence et l'unicité des orbites périodiques. De même, les bifurcations de Hopf et l'instabilité de Turing survenant dans ce modèle sont étudiées.

Abstract

In this manuscript, we consider a predator-prey model given by a reaction-diffusion system with homogeneous Neumann boundary conditions. This model incorporates Crowley-Martin and modified Leslie-Gower type functional responses. The qualitative properties, including the global attractor, dissipation and persistence property, and the local stability of non-negative constant steady states are studied. In particular, we obtained sufficient conditions to ensure the global stability of the unique constant positive steady state and the global stability of the prey-extinction equilibrium when the unique positive constant steady state is not feasible, by using a Lyapunov function. Furthermore, we derive the conditions for Hopf bifurcations and Turing instability. The existence of a unique globally stable periodic solutions is also presented.

Keywords : Predator-prey model, Crowley-Martin functional response, Persistence, Stability, Hopf bifurcation, Turing instability, Periodic solutions, Steady-state.

6.1 Introduction

The study of spatio-temporal dynamics of interacting populations in ecological systems becomes an important and interesting problem in theoretical ecology [37]. The main goal of this study is to determine the causes and consequences of the distribution of species in time and space. An important type of interaction that affects population dynamics of all species is predation.

Recently, there has been an increasing interest in studying spatial predator-prey models [79, 101, 117, 123, 125]. In such cases, spatio-temporal dynamics of an ecological system is represented by a system of coupled nonlinear reaction-diffusion equations.

In this paper, we study the following predator-prey model with Crowley-Martin functional responses and modified Leslie-Gower functional responses, and

reaction diffusion :

$$\begin{cases} \frac{\partial u}{\partial t} = D_1 \Delta u + a_1 u \left(1 - \frac{u}{K}\right) - \frac{bv}{1 + cu + dv + cdv} & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} = D_2 \Delta v + v \left(a_2 - \frac{ev}{u + f}\right) & x \in \Omega, t > 0, \end{cases} \quad (6.1)$$

where u and v represent the population densities at time t ; a_1, a_2, b, c, d, e, f and K are model parameters assuming only positive values and are defined as follows : a_1 and K are the intrinsic growth rate and the carrying capacity of prey population u respectively. The constants b, c and d are the saturating Crowley-Martin type functional response parameters, in which c measures the magnitude of interference among prey. Further, a_2 describes the growth rate of predator v ; e is the maximum value which per capita reduction rate of v can attain, f measures the extent to which environment provides protection to predator v . The diffusion coefficients are denoted by D_1 and D_2 , respectively.

The (non spatial) kinetic model or the ODE model corresponding to system (6.1) was introduced as the predator-prey model with modified Leslie-Gower and Crowley-Martin functional responses, by Ali and Jazar [4],

$$\begin{cases} \frac{\partial u}{\partial t} = a_1 u \left(1 - \frac{u}{K}\right) - \frac{bv}{1 + cu + dv + cdv}, \\ \frac{\partial v}{\partial t} = v \left(a_2 - \frac{ev}{u + f}\right), \end{cases} \quad (6.2)$$

with $u(0) \geq 0$ and $v(0) \geq 0$.

In [4], the authors showed that the predator-prey model with Crowley-Martin functional responses has much richer boundary dynamics which includes the possibilities of extinction, permanence, stable or unstable equilibria and limit cycle. These results have important biological implications and indicate different results of the interaction of the predator-prey system.

The aim purpose of this manuscript is to study the predator-prey model with diffusion (6.1) and show the effects of the diffusion on the dynamic of the kinetic model (6.2).

The model system (6.1) has 10 parameters overall, which makes mathematical analysis fairly complex. In order to avoid such difficulties we reduce the number of parameters by non-dimensionalizing the model system. The model is rendered dimensionless using the following variables and parameters :

$$t \rightarrow \frac{t}{a_1}, \quad x \rightarrow x \left(\frac{a_1}{KD_1}\right)^{\frac{1}{2}}, \quad u \rightarrow Ku, \quad v \rightarrow \frac{a_1}{b}v.$$

With the scaling, system (6.1) takes the form

$$\begin{cases} \frac{\partial u}{\partial t} = \Delta u + u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} = \delta \Delta v + Cv \left(1 - \frac{Dv}{u + E} \right), & x \in \Omega, t > 0, \end{cases} \quad (6.3)$$

where

$$A = cK, \quad B = \frac{da_1}{b}, \quad C = \frac{a_2}{a_1}, \quad D = \frac{ea_1}{Kba_2}, \quad E = \frac{f}{K}, \quad \text{and} \quad \delta = \frac{D_2}{D_1}.$$

Similarly, with the scaling, system (6.2) takes the form

$$\begin{cases} \frac{du}{dt} = u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) =: F_1(u, v), \\ \frac{dv}{dt} = Cv \left(1 - \frac{Dv}{u + E} \right) =: F_2(u, v). \end{cases} \quad (6.4)$$

We denote by $R(u, v) = (1 + Au)(1 + Bv)$.

Assume that prey and predator are confined to a bounded domain Ω in \mathbb{R}^n , ($n \geq 1$), with a smooth boundary. In this manuscript, we consider the following reaction-diffusion system

$$\begin{cases} \frac{\partial u}{\partial t} = \Delta u + u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) & x \in \Omega, t > 0, \\ \frac{\partial v}{\partial t} = \delta \Delta v + Cv \left(1 - \frac{Dv}{u + E} \right), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (6.5)$$

where \mathbf{n} is the outward unit normal vector of the boundary $\partial\Omega$ and the zero-flux boundary conditions mean that model (6.5) is self-contained and has no population flux across the boundary $\partial\Omega$. The initial data $u_0(x)$ and $v_0(x)$ are continuous functions on $\bar{\Omega}$.

The rest of this manuscript is organized as follows. In Section 6.2, we prove the existence and boundedness of the global solution of the system. In Section 5.3, the permanence of the system (5.5) is investigated. Moreover, we establish the local stability of the non-negative constant steady-states, by using the linearization method and analyzing the corresponding characteristic equations in Section

refsec6 4. In Section 6.5, we obtained sufficient conditions to ensure the global stability of the unique constant positive steady state and the global stability of the prey-extinction equilibrium when the unique positive constant steady state is not feasible, by using a Lyapunov function. Furthermore, in Sections 6.6 and 6.7, we derive the conditions for Hopf bifurcations and Turing instability. The existence of a unique globally stable periodic solutions is also presented in Section 6.8.

6.2 Global existence of solutions

In this section, we establish the global existence and uniqueness of classical solutions by proving that for any time T , $\|u(\cdot, t)\|_{L^\infty}$ and $\|v(\cdot, t)\|_{L^\infty}$ are bounded for $0 \leq t < T$.

We first introduce the following comparison theorem and a basic lemma, that are needed throughout the manuscript.

Theorem 6.2.1. (*[86]*) *Suppose that vector functions $u(x, t) = (u_1(x, t), \dots, u_m(x, t))$ and $v(x, t) = (v_1(x, t), \dots, v_m(x, t))$, $m \geq 1$ satisfy the following conditions :*

(C₁) *u and v are of class C^2 in x ; $x \in \Omega$ and of class C^1 in $(x, t) \in \Omega \times [0, \infty)$, where $\Omega \subset \mathbb{R}^n$ is a bounded domain with smooth boundary;*

(C₂) *$u_t - \mu \Delta u - g(x, t; u) \leq v_t - \mu \Delta v - g(x, t; v)$, where $(x, t) \in \Omega \times [0, \infty)$, $\mu = (\mu_1, \dots, \mu_m) > 0$ (inequalities between vectors are satisfied coordinate-wise), vector functions $g(x, t; u) = (g_1(x, t; u), \dots, g_m(x, t; u))$ is continuously differentiable and quasi-monotonically with respect to*

$$\frac{\partial g_i(x, t; u)}{\partial u_j} \geq 0, \quad u = (u_1, \dots, u_m), \quad i, j = 1, \dots, m, \quad i \neq j;$$

(C₃) $\frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0$, $(x, t) \in \partial\Omega \times [0, \infty)$.

Then $u(x, t) \leq v(x, t)$ for $(x, t) \in \bar{\Omega} \times [0, \infty)$.

Lemma 6.2.2. *Consider the semilinear parabolic problem*

$$\left\{ \begin{array}{ll} \alpha_1 \frac{\partial w}{\partial t} - \alpha_2 \Delta w = w(\alpha_3 - \alpha_4 w) & x \in \Omega, t > 0, \\ \frac{\partial w}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ w(x, 0) = w_0(x) \geq 0, & x \in \Omega, \end{array} \right. \quad (6.6)$$

where α_i ($i = 1, 2, 3, 4$) are positive constants. It is well known that there is unique positive solution $w(x, t)$ of (6.12), satisfying $w(x, t) \rightarrow \frac{\alpha_3}{\alpha_4}$, as $t \rightarrow \infty$ uniformly in x .

Theorem 6.2.3. *Assume that Ω is a bounded domain in $\mathbb{R}^n, n \leq 3$, with a boundary $\partial\Omega$ of class $C^{2+\nu}, \nu > 0$. Let (u_0, v_0) be a nonnegative initial data in $L^\infty(\Omega)$, such that,*

$$u_0(x) \leq 1 \quad \text{and} \quad v_0(x) \leq \frac{1+E}{D}. \quad (6.7)$$

Then, there exists a unique nonnegative classical solution of the spatial predator-prey model (6.5) for all $(x, t) \in \Omega \times [0, \infty)$.

Proof. The local existence of solutions is based on the well-known semigroup theory. After noting that F_1 and F_2 are continuously differentiable and from the assumptions on the initial data, it follows immediately from Proposition 1 in [53] that system (6.5) has a unique classical solution (u, v) , for $(x, t) \in \Omega \times [0, T_{\max})$. moreover, if $T_{\max} < \infty$ then

$$\lim_{t \rightarrow T_{\max}} \sup_{x \in \Omega} \{|u(x, t)| + |v(x, t)|\} = \infty. \quad (6.8)$$

To prove the nonnegativity of solutions, observe that the fonctions F_1 and F_2 satisfy

$$F_1(0, v) \geq 0 \quad \text{and} \quad F_2(u, 0) \geq 0, \quad \text{for all } u \geq 0, v \geq 0, \quad (6.9)$$

and by assumption the initial data $(u_0(x), v_0(x))$ are in $[0, \infty)^2$ for all $x \in \Omega$. Thus, by a maximum principle [107], the solution $u(x, t), v(x, t)$ lies in $[0, \infty)^2$ for all $x \in \Omega$ and for all $t > 0$. In other words, $[0, \infty)^2$ is positively invariant for the system (6.5).

In order to obtain the global existence and uniqueness of classical solutions from local existence and uniqueness, it sufficies to show that for any time T , $\|u(\cdot, t)\|_{L^\infty}$ and $\|v(\cdot, t)\|_{L^\infty}$ are bounded for $0 \leq t < T$.

Let $u_1(t) = \frac{u_{01}}{u_{01} + (1-u_{01})e^{-t}}$ be the solution of the initial value problem,

$$\begin{cases} \frac{\partial u_1}{\partial t} = u_1(1 - u_1), & t > 0, \\ u_1(0) = u_{01} \leq 1. \end{cases}$$

By using inequality

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} - \Delta u - u(1 - u) \leq 0 = \frac{\partial u_1(x, t)}{\partial t} - \Delta u_1 - u_1(1 - u_1), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial u_1}{\partial \mathbf{n}} = 0, \\ u(0, x) = u_0(x) \leq u_{01} \equiv \max_{\bar{\Omega}} u_0(x). \end{cases}$$

Applying Theorem 6.3.3, we conclude that $u(x, t) \leq u(x, t) \leq 1$. Therefore $u(x, t) \leq 1$ for all $0 \leq t \leq T$ and $x \in \Omega$.

Similarly, as $v_0(x) \leq \frac{1+E}{D}$ and $u(x, t) \leq 1$ for all $0 \leq t \leq T$ and $x \in \Omega$, we conclude that $v(x, t) \leq \frac{1+E}{D}$ for all $0 \leq t \leq T$.

This is complete the proof and we also conclude that the domain $[0, 1) \times [0, \frac{1+E}{D})$ is a positively invariant region for global solutions of system (6.5). \square

6.3 Dissipation and persistence

In this section, we study the dissipation and the uniform persistence of (6.5) by the standard comparison. From the view point of biology, persistence means that the two species of prey and predator will always coexist at any time and any location of the habitat domain, no matter what their diffusion coefficients are, under certain conditions on parameters.

We first introduce some definitions.

Definition 6.3.1. *The system (6.5) is said to be dissipative if for any nonnegative initial data $(u_0(x), v_0(x))$ with $u_0(x) \not\equiv 0$, $v_0(x) \not\equiv 0$, there exists a positive constant $\xi = \xi(u_0, v_0)$ such that the solution the solution $(u(x, t), v(x, t))$ of (6.5) satisfies*

$$\limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} u(., t) \leq \xi, \quad \limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} v(., t) \leq \xi.$$

Definition 6.3.2. *The system (6.5) is said to be uniformly persistent if for any nonnegative initial data $(u_0(x), v_0(x))$ with $u_0(x) \not\equiv 0$, $v_0(x) \not\equiv 0$, there exists a positive constant $\eta = \eta(u_0, v_0)$ such that the solution the solution $(u(x, t), v(x, t))$ of (6.5) satisfies*

$$\liminf_{t \rightarrow \infty} \min_{\bar{\Omega}} u(., t) \geq \eta, \quad \liminf_{t \rightarrow \infty} \min_{\bar{\Omega}} v(., t) \geq \eta.$$

Theorem 6.3.3. *Any solution (u, v) of (6.5) satisfies :*

$$\limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} u(., t) \leq 1, \quad \limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} v(., t) \leq \frac{1+E}{D}. \quad (6.10)$$

Proof. Assume that (u, v) is any solution of (6.5) with $u_0(x) \geq 0$, $v_0(x) \geq 0$ and $u_0(x) \not\equiv 0$, $v_0(x) \not\equiv 0$. Since $u_0(x) \not\equiv 0$, we have $u(., t) \geq 0$ for all $t \geq 0$ and $v(., t) > 0$ for all $t \geq 0$. The first element u satisfies :

$$\left\{ \begin{array}{ll} \frac{\partial u}{\partial t} - \Delta u \leq u(1-u), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \mathbf{n}} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{array} \right.$$

Consider the following initial value problem of ordinary differential equation :

$$\left\{ \begin{array}{l} \frac{\partial y}{\partial t} = y(1-y), \quad t > 0, \\ y(0) = \max_{\bar{\Omega}} u_0(\cdot) > 0. \end{array} \right.$$

Since $\lim_{t \rightarrow \infty} y(t) \leq 1$, thus the first inequality of (6.10) is followed by the standard comparison principle.

As a result, for any $\varepsilon > 0$, there exists $T > 0$, such that $u(x, t) \leq 1 + \varepsilon$ for all $x \in \Omega$ and $t \geq T$. it follows then that v satisfies :

$$\left\{ \begin{array}{ll} \frac{\partial v}{\partial t} - \delta \Delta v \leq v \left(C - \frac{CDv}{1 + \varepsilon + E} \right) & x \in \bar{\Omega}, t \geq T, \\ \frac{\partial v}{\partial \mathbf{n}} = 0, & x \in \partial\bar{\Omega}, t > T, \\ v(x, T) \geq 0, & x \in \bar{\Omega}. \end{array} \right.$$

Consider now the following initial value problem of ordinary differential equation :

$$\left\{ \begin{array}{l} \frac{\partial z}{\partial t} = z \left(C - \frac{CDz}{1 + \varepsilon + E} \right), \quad t > T, \\ z(T) = \max_{\bar{\Omega}} v_0(\cdot) > 0. \end{array} \right.$$

Since $\lim_{t \rightarrow +\infty} z(t) \leq \frac{1 + \varepsilon + E}{D}$, we have

$$\limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} v(\cdot, t) \leq \frac{1 + \varepsilon + E}{D}.$$

Let $\varepsilon \rightarrow 0$, we can get

$$\limsup_{t \rightarrow \infty} \max_{\bar{\Omega}} v(\cdot, t) \leq \frac{1 + E}{D}.$$

this ends the proof. \square

The above theorem implies that for any $\varepsilon > 0$, the rectangle $[0, 1 + \varepsilon) \times [0, \frac{1+E+\varepsilon}{D})$ is a global attractor of the model (6.5) in \mathbb{R}_+^2

Theorem 6.3.4. *If $B > 1$, then the system (6.5) is uniformly persistent.*

Proof. Suppose that (u, v) is the solution of (6.5) with $u_0(x) \geq 0$, $v_0(x) \geq 0$ and $u_0(x) \not\equiv 0$, $v_0(x) \not\equiv 0$. Since $u_0(x) \not\equiv 0$, we have $u(\cdot, t) \geq 0$ for all $t \geq 0$ and $v(\cdot, t) > 0$ for all $t > 0$. By the first equation of (6.5), we have

$$\begin{cases} \frac{\partial u}{\partial t} - \Delta u \geq u \left(1 - u - \frac{1}{B} \right), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \mathbf{n}} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Since $\frac{1}{B} < 1$, then

$$\liminf_{t \rightarrow \infty} \min_{\bar{\Omega}} u(\cdot, t) \geq 1 - \frac{1}{B} \triangleq \eta$$

by Lemma 6.2.2 and a comparison principle. Thus, for any $\epsilon > 0$ with $0 < \epsilon < 1 - \frac{1}{B}$, there exists $T > 0$ such that $u(x, t) \geq 1 - \frac{1}{B} - \epsilon$ in $\bar{\Omega} \times [T, \infty)$.

As a result, v satisfies

$$\begin{cases} \frac{\partial v}{\partial t} - \delta \Delta v \geq v \left(C - \frac{CDv}{1 - 1/B - \epsilon + E} \right), & x \in \bar{\Omega}, t \geq T, \\ \frac{\partial v}{\partial \mathbf{n}} = 0, & x \in \partial\bar{\Omega}, t > T, \\ v(x, T) \geq 0, & x \in \bar{\Omega}. \end{cases} \quad (6.11)$$

Consider now the following initial value problem of ordinary differential equation :

$$\begin{cases} \frac{\partial z}{\partial t} = z \left(C - \frac{CDz}{1 - 1/B - \epsilon + E} \right), & t > T, \\ z(T) = \min_{\bar{\Omega}} v(\cdot, T) > 0. \end{cases}$$

The comparison argument shows that

$$\liminf_{t \rightarrow \infty} \min_{\bar{\Omega}} v(\cdot, t) \geq \frac{1}{D} \left(1 - \frac{1}{B} + E \right)$$

by the continuity as $\epsilon \rightarrow 0$. The proof is complete. \square

Remark 6.3.5. *System (6.5) is said to be permanent if it is uniformly persistence and dissipative, that is, if for any nonnegative initial data $(u_0(x), v_0(x))$ with $u_0(x) \not\equiv 0, v_0(x) \not\equiv 0$, there exist positive constants $\eta = \eta(u_0, v_0)$ and $\xi = \xi(u_0, v_0)$ such that the solution the solution $(u(x, t), v(x, t))$ of (6.5) satisfies*

$$0 < \eta \leq \liminf_{t \rightarrow +\infty} u(t) \leq \limsup_{t \rightarrow +\infty} u(t) \leq \xi,$$

$$0 < \eta \leq \liminf_{t \rightarrow +\infty} v(t) \leq \limsup_{t \rightarrow +\infty} v(t) \leq \xi.$$

6.4 Steady states and their local stability

In this section we study the local stability of the non-negative constant steady states solutions of system (6.5).

The steady states $(u(x), v(x))$ of system (6.5) satisfy

$$\begin{cases} \Delta u + u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) = 0, & x \in \Omega, \\ \delta \Delta v + Cv \left(1 - \frac{Dv}{u + E} \right) = 0, & x \in \Omega, \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0, & x \in \partial\Omega. \end{cases} \quad (6.12)$$

From analysis above and from [4], it is easily seen that system (6.5) has the following non-negative constant solutions :

- (i) $E_0 = (0, 0)$, which corresponds to extinction of both the prey and predator.
- (ii) $E_1 = (1, 0)$, which corresponds to extinction of the predator.
- (iii) $E_2 = (0, E/D)$, which corresponds to extinction of the prey.

Moreover, system (6.5) has a unique positive constant steady-state solution $E^* = (u^*, v^*)$ (i.e., $u^* > 0, v^* > 0$), which corresponds to coexistence of prey and predator, if

$$E < EB + D, \quad (6.13)$$

and any of the following three conditions is satisfied,

$$B + AD + ABE > AB, \quad D + EB + 1 > B + AD + ABE \quad (6.14)$$

$$B + AD + ABE > AB, \quad D + EB + 1 < B + AD + ABE \quad (6.15)$$

$$B + AD + ABE < AB, \quad D + EB + 1 < B + AD + ABE. \quad (6.16)$$

Hence the positive constant steady state E^* of system (6.5) is (u^*, v^*) , where (u^*, v^*) is the unique positive solution of

$$\begin{cases} u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) = 0, \\ Cv \left(1 - \frac{Dv}{u + E} \right) = 0. \end{cases} \quad (6.17)$$

Furthermore, system (6.5) has a non-constant positive steady states $E_3 = (u(x), v(x))$, where $u(x)$ and $v(x)$ are two positive functions whose existence is proved in Theorem 6.3.3.

In the rest of this article, we always assume that at least one of the three conditions (6.14), (6.34) and (6.16) is satisfied.

6.4.1 Local stability of the steady states

In this subsection, we investigate the linear stability of the above equilibria $(E_i)_{i=0,1,2}$ and E^* of system (6.5), It is well-known that the stability question for an equilibrium E is answered by considering the corresponding eigenvalue problem for the linearized operator around E . For this purpose, we need introduce some notations.

Let $0 = \mu_0 < \mu_1 < \mu_2 < \dots$ be the eigenvalues of the operator $-\Delta$ in Ω with the homogeneous Neumann boundary condition, $S(\mu_j)$ be the space of the eigenfunctions corresponding to μ_j in $C^1(\bar{\Omega})$ for $j = 0, 1, 2, \dots$; $\{\varphi_{jl}; l = 1, \dots, \dim[S(\mu_j)]\}$ be an orthonormal basis of $S(\mu_j)$, and $\mathbf{X}_{jl} = \{\mathbf{c}\varphi_{jl} : \mathbf{c} \in \mathbb{R}^2\}$. Define

$$\mathbf{X} := \left\{ (u, v)^T \in [C^1(\bar{\Omega})]^2 : \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0 \text{ on } \partial\Omega \right\},$$

and consider the decomposition $\mathbf{X} = \bigoplus_{j=0}^{\infty} \mathbf{X}_j$, where $\mathbf{X}_j = \bigoplus_{l=1}^{\dim[S(\mu_j)]} \mathbf{X}_{jl}$ is the eigenspace corresponding to μ_j .

Now, we can state the result of this section as follows

Theorem 6.4.1. *We have the following results :*

- (i) $E_0 = (0, 0)$ is unstable.
- (ii) $E_1 = (1, 0)$ is unstable.
- (iii) If $E > EB + D$, then $E_2 = (0, E/D)$ is locally asymptotically stable; while $E < EB + D$, E_2 is unstable.

(iv) If $E < EB + D$, and the following condition is satisfied

$$Av^*(1 + Bv^*) - R(u^*, v^*)^2 < \frac{1 + Au^*}{D}, \quad (6.18)$$

then the unique positive constant steady state E^* of (6.5) is locally asymptotically stable if either one of the following two conditions holds

$$C > \max\{C^*, \delta C^*\}, \quad (6.19)$$

or

$$C > C^*, \quad (6.20)$$

and

$$\mu_1 > \left\{0, C^* - \frac{C}{\delta}\right\}, \quad (6.21)$$

where μ_1 is the first eigenvalue subject to the zero-flux boundary conditions, and $C^* \stackrel{\text{def}}{=} u^* \left(\frac{Av^*}{(1+Au^*)^2(1+Bv^*)} - 1 \right)$.

Furthermore, if either $C < C^*$ or the following condition is satisfied

$$Av^*(1 + Bv^*) - R(u^*, v^*)^2 > \frac{1 + Au^*}{D}, \quad (6.22)$$

then E^* is unstable.

Proof. The linearization of (6.5) at a constant solution $E_c = (u_c, v_c)$ can be expressed by

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = L \begin{pmatrix} u \\ v \end{pmatrix} := D \begin{pmatrix} \Delta u \\ \Delta v \end{pmatrix} + J(u_c, v_c) \begin{pmatrix} u \\ v \end{pmatrix}, \quad (6.23)$$

where

$$D = \begin{pmatrix} 1 & 0 \\ 0 & \delta \end{pmatrix}, \quad J(u_c, v_c) = \begin{pmatrix} J_1(u_c, v_c) & J_2(u_c, v_c) \\ J_3(u_c, v_c) & J_4(u_c, v_c) \end{pmatrix}$$

and

$$J_1(u_c, v_c) = 1 - 2u_c - \frac{v_c}{(1 + Au_c)^2(1 + Bv_c)}, \quad J_2(u_c, v_c) = -\frac{u_c}{(1 + Au_c)(1 + Bv_c)^2},$$

$$J_3(u_c, v_c) = \frac{CDv_c^2}{(E + u_c)^2}, \quad J_4(u_c, v_c) = C - \frac{2CDv_c}{E + u_c}.$$

From [49], it is known that if all the eigenvalues of the operator L have negative real parts, then $E_c = (u_c, v_c)$ is locally asymptotically stable; if there is an eigenvalue with a positive real part, then $E_c = (u_c, v_c)$ is unstable; if all the eigenvalues have non-positive real parts, while some eigenvalues have zero real part, then the

stability of $E_c = (u_c, v_c)$ cannot be determined by the linearization.

For each $j \in \{0, 1, 2, \dots\}$, \mathbf{X}_j is invariant under the operator L , and λ is an eigenvalue of L if and only if λ is an eigenvalue of the matrix $A_j := -\mu_j D + J(u_c, v_c)$ for some $j \geq 0$.

So, the local stability is reduced to consider the characteristic equation

$$\det(\lambda I - A_j) = \lambda^2 - \lambda \cdot \text{Tr}(A_j) + \det(A_j) = 0, \quad (6.24)$$

where

$$\begin{aligned} \text{Tr}(A_j) &= -(1 + \delta)\mu_j + J_1(u_c, v_c) + J_4(u_c, v_c) \\ \det(A_j) &= \delta\mu_j^2 - (\delta J_1(u_c, v_c) + J_4(u_c, v_c))\mu_j + \det(J(u_c, v_c)). \end{aligned}$$

By direct calculation, the real parts of the eigenvalues of the matrix A_0 at any constant point $E_c(u_c, v_c)$ are defined by

$$\begin{aligned} \text{Re}\lambda_0^- &= \frac{1}{2}[J_1(u_c, v_c) + J_4(u_c, v_c) - \sqrt{(J_1(u_c, v_c) + J_4(u_c, v_c))^2 - 4\det(J(u_c, v_c))}], \\ \text{Re}\lambda_0^+ &= \frac{1}{2}[J_1(u_c, v_c) + J_4(u_c, v_c) + \sqrt{(J_1(u_c, v_c) + J_4(u_c, v_c))^2 - 4\det(J(u_c, v_c))}]. \end{aligned}$$

We also have

$$\begin{aligned} \text{Re}\lambda_j^- &= \frac{1}{2}[\text{Tr}(A_j) - \sqrt{(\text{Tr}(A_j))^2 - 4\det(A_j)}], \\ \text{Re}\lambda_j^+ &= \frac{1}{2}[\text{Tr}(A_j) + \sqrt{(\text{Tr}(A_j))^2 - 4\det(A_j)}], \end{aligned}$$

where $\text{Re}\lambda_j^-$ and $\text{Re}\lambda_j^+$ are the real parts of the eigenvalues of the matrix A_j at any constant point $E_c(u_c, v_c)$.

(i) For $E_0 = (0, 0)$, $J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & C \end{pmatrix}$, and

$$\begin{aligned} \text{Re}\lambda_0^- &= \begin{cases} C & C < 1 \\ 1 & C > 1 \end{cases} \\ \text{Re}\lambda_0^+ &= \begin{cases} 1 & C < 1 \\ C & C > 1. \end{cases} \end{aligned}$$

Thus, the two eigenvalues λ_0^+ and λ_0^- of A_0 have positive real parts. Hence, the spectrum $\sigma(L) \cap \{\text{Re}\lambda > 0\} \neq \emptyset$ and therefore E_0 is unstable.

(ii) For $E_1 = (1, 0)$, $J(1, 0) = \begin{pmatrix} -1 & -(1+A) \\ 0 & C \end{pmatrix}$, and

$$\begin{aligned} \text{Re}\lambda_0^- &= -1, \\ \text{Re}\lambda_0^+ &= C. \end{aligned}$$

Thus, one of the eigenvalue of the matrix J_0 has positive real part. Hence, the spectrum $\sigma(L) \cap \{\text{Re}\lambda > 0\} \neq \emptyset$ and therefore E_1 is unstable.

(iii) For $E_2 = (0, \frac{E}{D})$, $J(0, \frac{E}{D}) = \begin{pmatrix} 1 - \frac{E}{EB+D} & 0 \\ \frac{C}{D} & -C \end{pmatrix}$, and

$$\text{Tr}(A_j) = -(1 + \delta)\mu_j + 1 - \frac{E}{EB + D} - C$$

$$\det(A_j) = \delta\mu_j^2 - \left(\delta \left(1 - \frac{E}{EB + D} \right) - C \right) \mu_j - C \left(1 - \frac{E}{EB + D} \right).$$

Firstly, if $E < EB + D$, then

$$\text{Re}\lambda_0^- = -C < 0$$

$$\text{Re}\lambda_0^+ = 1 - \frac{E}{EB + D} > 0.$$

Thus, one of the eigenvalue of the matrix A_0 has positive real part. Hence, the spectrum $\sigma(L) \cap \{\text{Re}\lambda > 0\} \neq \emptyset$ and therefore $E_1(0, \frac{E}{D})$ is unstable.

Now, we assume that $E > EB + D$, then $\det(A_j) > 0$ and $\text{Tr}(A_j) < 0$, for all $j \geq 0$. Therefore, the two eigenvalues λ_j^+ and λ_j^- of A_j have negative real parts. Note that $\lambda_0^\pm < 0$. For any $j \geq 1$, the following holds :

Case 1 : If $(\text{Tr}(A_j))^2 - 4\det(A_j) \leq 0$, then

$$\text{Re}\lambda_j^\pm = \frac{1}{2}\text{Tr}(A_j) < -\frac{1}{2} \left[\frac{E}{EB + D} - 1 + C \right] < 0,$$

Case 2 : If $(\text{Tr}(A_j))^2 - 4\det(A_j) > 0$, then

$$\text{Re}\lambda_j^- = \frac{1}{2} \left\{ \text{Tr}(A_j) - \sqrt{(\text{Tr}(A_j))^2 - 4\det(A_j)} \right\} \leq \frac{1}{2}\text{Tr}(A_j) < -\frac{C}{2} < 0,$$

$$\begin{aligned} \text{Re}\lambda_j^+ &= \frac{1}{2} \left\{ \text{Tr}(A_j) + \sqrt{(\text{Tr}(A_j))^2 - 4\det(A_j)} \right\} \\ &= \frac{2\det(A_j)}{\text{Tr}(A_j) - \sqrt{(\text{Tr}(A_j))^2 - 4\det(A_j)}} \\ &\leq \frac{\det(A_j)}{\text{Tr}(A_j)} \\ &< -\frac{\delta\mu_j^2}{(1 + \delta)\mu_j + \left(C - 1 + \frac{E}{EB+D}\right)\mu_j} \\ &< \begin{cases} -\frac{\delta}{(1+\delta)+(C-1+\frac{E}{EB+D})} < -\alpha < 0, & \mu_j > 1, \\ -\frac{\delta\mu_1}{(1+\delta)+(C-1+\frac{E}{EB+D})} < -\alpha < 0, & \mu_j \leq 1, \end{cases} \end{aligned}$$

for some α which is independent of j .

This shows that there exists a positive constant α , which is independent on j , such that for all j , $\operatorname{Re}\lambda_j^\pm < -\alpha$, $\forall j \geq 1$. Consequently, the spectrum of L lies in $\{\operatorname{Re}\lambda < -\alpha\}$ (since the spectrum of L consists of eigenvalues), and therefore $(0, \frac{E}{D})$ is locally asymptotically stable.

$$(iv) \text{ For } E^* = (u^*, v^*), J(u^*, v^*) = \begin{pmatrix} C^* & \frac{-u^*}{(1 + Au^*)(1 + Bv^*)^2} \\ \frac{C}{D} & -C \end{pmatrix},$$

and

$$\operatorname{Tr}(A_j) = -(1 + \delta)\mu_j + C^* - C$$

$$\det(A_j) = \delta\mu_j^2 - (\delta C^* - C)\mu_j - CC^* + \frac{C}{D(1 + Au^*)(1 + Bv^*)^2}.$$

Since the conditions (6.18) and either (6.19) or [(6.20) and (6.21)] are satisfied, then $\operatorname{Tr}(A_j) < 0$ and $\det(J(u^*, v^*)) > 0$, for all $j \geq 0$. Moreover, recall that if $\mu_1 > \max\{0, C^* - \frac{C}{\delta}\}$, we conclude that

$$\begin{aligned} \det(A_j) &= \mu_j(\delta\mu_j - (\delta C^* - C)) + \det(J(u^*, v^*)) \\ &> \mu_1(\delta\mu_1 - (\delta C^* - C)) + \det(J(u^*, v^*)) \\ &> 0 \end{aligned}$$

for all $j \geq 0$.

Similarly, if $C > \max\{C^*, \delta C^*\}$, then $\det(A_j) > 0$, for all $j \geq 0$.

Therefore, the two eigenvalues λ_j^+ and λ_j^- of the matrix A_j have negative real parts. Note that $\lambda_0^\pm < 0$. For any $j \geq 1$, we prove by using an argument similar as (iii), that there exists $\alpha > 0$ such that

$$\operatorname{Re}\lambda_j^- = -\alpha < 0,$$

$$\operatorname{Re}\lambda_j^+ = -\alpha < 0.$$

Consequently, the spectrum of L lies in $\{\operatorname{Re}\lambda < -\alpha\}$ (since the spectrum of L consists of eigenvalues), and therefore $E^*(u^*, v^*)$ is locally asymptotically stable.

Furthermore, if either $C < C^*$, or the condition (6.22) is satisfied, then

$$\operatorname{Re}\lambda_0^+ = \frac{1}{2} \left\{ C^* - C + \sqrt{(C^* - C)^2 - 4 \left(\frac{C}{D(1 + Au^*)(1 + Bv^*)^2} - CC^* \right)} \right\} > 0.$$

Thus, one of the eigenvalue of the matrix A_0 has positive real part. Hence, the spectrum $\sigma(L) \cap \{\operatorname{Re}\lambda > 0\} \neq \emptyset$ and therefore $E^*(u^*, v^*)$ is unstable. \square

6.5 Global stability

Biologically, the statement of the global stability of the unique positive constant steady state E^* means that : however quickly or slowly the two species diffuse, they will be spatially homogeneously distributed as times goes to infinity. Otherwise, the global stability of the prey extinction equilibrium $(0, E/D)$ means that : however quickly or slowly the two species diffuse, the prey population will go extinct and the predator population converges to the balance density E/D as times goes to infinity. In this section, we prove the global asymptotic stability of the unique positive constant steady state E^* of system (6.5), then we will prove the global stability of the prey-extinction equilibrium $E_2(0, E/D)$ when the unique positive constant steady state E^* does not exist.

Theorem 6.5.1. *Suppose that the unique positive constant steady state solution E^* is locally asymptotically stable. Then it is a globally asymptotically stable if*

$$B > 1 \quad \text{and} \quad \frac{1}{1+E} - \frac{1}{2} - \frac{A}{B} - \frac{1}{2D(E+\eta)} > 0, \quad (6.25)$$

where η is defined in Theorem 6.3.4.

Proof. Let $(u(x, t), v(x, t))$ be the solution of (6.5). To prove our statement, it suffices to construct a Lyapunov function. For this purpose, adapting the Lyapunov function in [4], we define

$$V(u, v) = u - u^* - u^* \ln \left(\frac{u}{u^*} \right) + \frac{1}{CD} \left(v - v^* - v^* \ln \left(\frac{v}{v^*} \right) \right),$$

and

$$W(u, v) = \int_{\Omega} V(u(x, t), v(x, t)) dx.$$

Since $W(u, v)$ is positive for all (u, v) in the positive quadrant, except for E^* , for which $W(u^*, v^*) = 0$, we only show that $\frac{dW}{dt} < 0$ to prove that W is a Lyapunov function.

By simple computations, the orbital derivative of W , along the flow of of system (6.5) is

$$\begin{aligned} \frac{dW}{dt} &= \int_{\Omega} \{V_u(u(x, t), v(x, t))u_t + V_v(u(x, t), v(x, t))v_t\} dx \\ &= \int_{\Omega} \left\{ \frac{u - u^*}{u} \Delta u + \frac{\delta}{CD} \frac{v - v^*}{v} \Delta v \right\} dx \\ &\quad + \int_{\Omega} (u - u^*) \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) dx \\ &\quad + \int_{\Omega} \frac{(v - v^*)}{D} \left(1 - \frac{Dv}{E + u} \right) dx \\ &= I_1(t) + I_2(t). \end{aligned}$$

where

$$I_1(t) = \int_{\Omega} \left\{ \frac{u - u^*}{u} \Delta u + \frac{\delta}{CD} \frac{v - v^*}{v} \Delta v \right\} dx,$$

and

$$I_2(t) = \int_{\Omega} \left\{ (u - u^*) \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) + \frac{(v - v^*)}{D} \left(1 - \frac{Dv}{E + u} \right) \right\} dx.$$

Due to the Neumann boundary condition, it is evident that

$$I_1(t) = - \int_{\Omega} \left\{ \frac{u^*}{u^2} |\nabla u|^2 + \frac{\delta}{CD} \frac{v^*}{v^2} |\nabla v|^2 \right\} dx \leq 0.$$

Further,

$$\begin{aligned} I_2(t) &= \int_{\Omega} \left\{ (u - u^*) \left[-(u - u^*) + \frac{Av^*(1 + Bv)(u - u^*) - (1 + Au^*)(v - v^*)}{(1 + Au)(1 + Bv)(1 + Au^*)(1 + Bv^*)} \right] \right. \\ &\quad \left. + (v - v^*) \left[\frac{(u - u^*)}{D(E + u)} - \frac{(v - v^*)}{E + u} \right] \right\} dx \\ &= \int_{\Omega} \left\{ -(u - u^*)^2 + \frac{Av^*(u - u^*)^2}{(1 + Au)(1 + Au^*)(1 + Bv^*)} \right. \\ &\quad \left. - \frac{(u - u^*)(v - v^*)}{(1 + Au)(1 + Bv)(1 + Bv^*)} + \frac{(u - u^*)(v - v^*)}{D(E + u)} - \frac{(v - v^*)^2}{E + u} \right\} dx \\ &\leq \int_{\Omega} \left\{ -(u - u^*)^2 + \frac{A}{B}(u - u^*)^2 + (u - u^*)(v - v^*) + \frac{(u - u^*)(v - v^*)}{D(E + u)} \right. \\ &\quad \left. - \frac{(v - v^*)^2}{E + u} \right\} dx. \end{aligned}$$

Using the inequality $a^2 + b^2 \geq 2ab$ and by Theorem 6.3.4, we derive for $t > T$ that

$$\begin{aligned} I_2(t) &\leq \int_{\Omega} \left\{ -(u - u^*)^2 + \frac{A}{B}(u - u^*)^2 + \frac{(u - u^*)^2 + (v - v^*)^2}{2} \right. \\ &\quad \left. + \frac{1}{D(E + \eta)} \frac{(u - u^*)^2 + (v - v^*)^2}{2} - \frac{1}{E + 1} (v - v^*)^2 \right\} dx \\ &\leq \int_{\Omega} \left\{ - \left(1 - \frac{A}{B} - \frac{1}{2} - \frac{1}{2D(E + \eta)} \right) (u - u^*)^2 \right. \\ &\quad \left. - \left(\frac{1}{E + 1} - \frac{1}{2} - \frac{1}{2D(E + \eta)} \right) (v - v^*)^2 \right\} dx. \end{aligned}$$

Under the assumption (6.25), we have $I_2(t) \leq 0$, and thus $\frac{dW(t)}{dt} = I_1(t) + I_2(t) \leq 0$. Therefore, the function W satisfies Lyapunov's asymptotic stability theorem, and

E^* is globally asymptotically stable.

Now we consider the case when the system (6.5) does not have any constant positive steady state. We will prove the global asymptotic stability of the prey-extinction equilibrium $E_2(0, E/D)$ by constructing a suitable Lyapunov function.

Theorem 6.5.2. *If $E > EB + D$ and the following condition is satisfied*

$$\frac{(1+A)(D+B(1+E))}{E} < D < \frac{E}{E+1}, \quad (6.26)$$

then the prey-extinction equilibrium $E_2(0, E/D)$ of system (5.5) is globally asymptotically stable. \square

Proof. Since $E > EB + D$ then system (5.5) does not have any positive constant steady state. The proof is based on a positive definite Lyapunov function. Define

$$V_0(u, v) = u + \frac{1}{C} \left(v - v^0 - v^0 \ln \left(\frac{v}{v^0} \right) \right),$$

and

$$W_0(u, v) = \int_{\Omega} V_0(u(x, t), v(x, t)) dx,$$

where $v^0 = E/D$. The time derivative of the functional W_0 along trajectories of the system (5.5) is given by

$$\begin{aligned} \frac{dW_0}{dt} &= \int_{\Omega} \left\{ \Delta u + \frac{\delta}{C} \frac{v - v^0}{v} \Delta v \right\} dx + \int_{\Omega} u \left(1 - u - \frac{v}{(1+Au)(1+Bv)} \right) dx \\ &\quad + \int_{\Omega} (v - v^0) \left(1 - \frac{Dv}{E+u} \right) dx \\ &= I_1(t) + I_2(t). \end{aligned}$$

where

$$I_1(t) = \int_{\Omega} \left\{ \Delta u + \frac{\delta}{C} \frac{v - v^0}{v} \Delta v \right\} dx,$$

and

$$I_2(t) = \int_{\Omega} u \left(1 - u - \frac{v}{(1+Au)(1+Bv)} \right) dx + \int_{\Omega} (v - v^0) \left(1 - \frac{Dv}{E+u} \right) dx.$$

Due to the Neumann boundary condition, it is evident that

$$I_1(t) = -\frac{\delta}{C} \int_{\Omega} \left\{ \frac{v^0}{v^2} |\nabla v|^2 \right\} dx \leq 0.$$

Further, substituting $E = Dv^0$ into I_2 , it follows that

$$\begin{aligned} I_2 &= \int_{\Omega} \left\{ u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} \right) - \frac{u(v^0 - v)}{Dv^0 + u} - (v - v^0)^2 \frac{D}{Dv^0 + u} \right\} dx \\ &= \int_{\Omega} \left\{ u \left(1 - u - \frac{v}{(1 + Au)(1 + Bv)} - \frac{v^0}{Dv^0 + u} + \frac{v}{Dv^0 + u} \right) \right. \\ &\quad \left. - (v - v^0)^2 \frac{D}{Dv^0 + u} \right\} dx. \end{aligned}$$

Hence, if (6.26) is satisfied, then $\frac{dW_0(t)}{dt} \leq 0$. Therefore, the function W_0 satisfies Lyapunov's asymptotic stability theorem, and E_2 is globally asymptotically stable. \square

6.6 Hopf bifurcation

In this section, we derive the conditions under which a family of periodic solutions bifurcate from the positive constant steady state solution $E^* = (u^*, v^*)$ of system (6.5), then we study the direction of these Hopf bifurcations and stability of bifurcated periodic solutions arising through Hopf bifurcations.

Theorem 6.6.1. *Assume that $C = C^*$ and conditions (6.18) and (6.21) of Theorem 6.4.1 hold true, then the system (6.5) undergoes a Hopf bifurcations at E^* .*

Proof. Since the conditions (6.18) and (6.21) hold true, it is clear from Theorem 6.4.1 that E^* change its nature from locally asymptotically stable to unstable as the parameter C passes through its critical value $C = C^*$ from higher to lower. For Hopf bifurcation to occur at the positive constant steady state E^* , the matrix $A_j = -\mu_j + J(u^*, v^*)$ must have a pure imaginary, conjugate pair of eigenvalues, i.e. $\text{Tr}(A_j) \equiv 0$

Suppose that $i\omega$ is a pure imaginary root of (6.24). Substituting $i\omega$ into (6.24), we have

$$-\omega^2 - \lambda \cdot \text{Tr}(A_j) + \det(A_j) = 0. \quad (6.27)$$

Separating the real and imaginary parts of the above equation, one can get

$$\omega^2 = \det(A_j) > 0, \quad \text{Tr}(A_j) = -(1 + \delta)\mu_j + J_1(u^*, v^*) + J_4(u^*, v^*) = 0.$$

Let

$$C_k = -(1 + \delta)\mu_j + C^*, \quad (j \in \mathbb{N}). \quad (6.28)$$

Then, the only value of C at which the homogeneous Hopf bifurcation occurs is $C = C_0 = C^*$. Near C^* , substituting $\lambda = p_1 + iq_1$ into (6.24) and separating the real and imaginary parts, one can get that

$$p_1^2 - q_1^2 - p_1 \text{Tr}(A_j) + \det(A_j) = 0, \quad (6.29)$$

$$2p_1q_1 - q_1\text{Tr}(A_j) = 0. \quad (6.30)$$

Differentiating two sides of (6.30) with respect to C , we get

$$\text{sgn} \left[\frac{dp_1}{dC} \right]_{C=C^*} = -\frac{1}{2} \neq 0.$$

Therefore the transversality condition holds. According to the hopf bifurcation theorem [24], system (6.5) enters into a Hopf-type small amplitude periodic oscillations at the parameter $C = C^*$ near the positive constant steady state E^* . \square

The above Theorem establishes the existence of a small amplitude periodic solution near the interior equilibrium point E^* .

6.7 Turing instability

In this section, we will investigate the effect of the diffusion and derive conditions for the Turing instability (diffusion-driven instability) with respect to the positive constant steady state $E^* = (u^*, v^*)$ of model (6.5).

Definition 6.7.1. *We say that the positive constant steady state $E^* = (u^*, v^*)$ of model (6.5) is Turing instability if it is an asymptotically stable equilibrium of the kinetic model (6.5), but is unstable with respect to solutions of spatial model (6.5) (see [90]). The parametric space which satisfies the Turing conditions is referred to as “Turing space”.*

An equilibrium E^* of model (6.5) is Turing instability means that there are solutions of (6.5) that have initial values $(u(x, 0), v(x, 0))$ arbitrarily closed to (u^*, v^*) (in the supremum norm) but do not tend to (u^*, v^*) as t tends to ∞ .

According to the Definition 6.7.1, Turing instability occurs when the condition either $\text{Tr}(A_j) < 0$ or $\det(A_j) > 0$ is violated, where

$$\text{Tr}(A_j) = -(1 + \delta)\mu_j + J_1(u^*, v^*) + J_4(u^*, v^*)$$

$$\det(A_j) = \delta\mu_j^2 - (\delta J_1(u^*, v^*) + J_4(u^*, v^*))\mu_j + \det(J(u^*, v^*)).$$

Now, the conditions for the positive equilibrium $E^* = (u^*, v^*)$ to be stable for the ODE are given by

$$\text{Tr}(J(E^*)) = J_1(u^*, v^*) + J_4(u^*, v^*) < 0,$$

and

$$\det(J(E^*)) = J_1(u^*, v^*)J_4(u^*, v^*) - J_2(u^*, v^*)J_3(u^*, v^*) > 0.$$

Hence, $\text{Tr}(A_j) < 0$, and the matrix A_j has an eigenvalue with a negative real part, and the other eigenvalue must be a positive real one, and only the violation

of condition $\det(A_j) > 0$ gives rise to diffusive instability. A necessary condition for the Turing instability of model (6.5) is given by

$$\delta J_1(u^*, v^*) + J_4(u^*, v^*) > 0. \quad (6.31)$$

Otherwise, $\det(A_j) > 0$ for all eigenvalues μ_j of the operator Δ , since $\det(J(u^*, v^*)) > 0$. For the Turing instability, we must have $\det(A_j) < 0$ for some μ_j . And we notice that $\det(A_j)$ achieves its minimum

$$\min_{\mu_j} \det(A_j) = \frac{4\delta \det(A_j) - (\delta J_1(u^*, v^*) + J_4(u^*, v^*))^2}{4\delta}$$

at the critical value $\mu^* > 0$ when

$$\mu^* = \frac{\delta C^* - C}{2\delta}.$$

However, the inequality $\min_{\mu_j} \det(A_j) < 0$ is necessary but not sufficient for the Turing instability in the bounded domain Ω . The possible eigenvalues μ_j are discrete. In this case, $\det(A_j) = 0$ has two positive roots k_1 and k_2

$$k_1 = \frac{\delta C^* - C - \sqrt{(\delta C^* - C)^2 - 4\delta \det(J(u^*, v^*))}}{2\delta},$$

$$k_2 = \frac{\delta C^* - C + \sqrt{(\delta C^* - C)^2 - 4\delta \det(J(u^*, v^*))}}{2\delta},$$

so if we can find some μ_j such that $k_1 < \mu_j < k_2$, then, $\det(A_j) < 0$, and the positive constant steady state $E^* = (u^*, v^*)$ of model (6.5) is unstable.

Summarizing the previous analysis and calculations, we have the following results.

Theorem 6.7.2. *If the conditions (6.18), (6.19) are satisfied, then the positive constant steady state $E^* = (u^*, v^*)$ of model (6.5) is a Turing instability if $0 < k_1 < \mu_j < k_2$ for some μ_j , and the following hypotheses hold :*

- (i) $\delta C^* - C > 0$;
- (ii) $\delta C^* - C > 2\sqrt{\delta \det(J(u^*, v^*))}$.

6.8 Periodic Solutions

In this section we study the existence and uniqueness of ω -periodic solutions of the system (6.5), we prove also the global asymptotic stability of these ω -periodic solutions.

Theorem 6.8.1. *Assume that system (6.5) is permanent, that is, there exist positive constants η and ξ such that an arbitrary solution of the system (6.5) with non-negative initial functions not identically equal to zero satisfies the condition*

$$(u(x, t), v(x, t)) \in \{(u, v) : \eta \leq u(x, t) \leq \xi, \eta \leq v(x, t) \leq \xi\} \quad (6.32)$$

starting with a certain moment of time. Moreover

$$\lambda_M(W) < 0, \quad (6.33)$$

where λ_M is the maximal eigenvalue of the matrix

$$W = \begin{bmatrix} 2 \left(1 - 2\eta - \frac{\eta}{(1 + A\xi)^2(1 + B\xi)} \right) & \frac{\eta}{(1 + A\eta)(1 + B\eta)^2} + \frac{\eta^2}{(E + \xi)^2} \\ \frac{\eta}{(1 + A\eta)(1 + B\eta)^2} + \frac{\eta^2}{(E + \xi)^2} & 2C \left(1 - \frac{2ED\eta + 2\eta^2}{(E + \xi)^2} \right) \end{bmatrix}.$$

Then, the system has a unique globally asymptotically stable strictly positive ω -periodic solution.

Proof. Let $(u_1(x, t), v_1(x, t))$ and $(u_2(x, t), v_2(x, t))$ be two solutions of system (6.5) bounded by constants ξ and η for below and above. Consider the function

$$U(t) = \int_{\Omega} [(u_1(x, t) - u_2(x, t))^2 + (v_1(x, t) - v_2(x, t))^2] dx, \quad (6.34)$$

one has

$$\begin{aligned} \frac{dU(t)}{dt} &= 2 \int_{\Omega} (u_1 - u_2) \left(\frac{\partial u_1}{\partial t} - \frac{\partial u_2}{\partial t} \right) dx + 2 \int_{\Omega} (v_1 - v_2) \left(\frac{\partial v_1}{\partial t} - \frac{\partial v_2}{\partial t} \right) dx \\ &= 2 \int_{\Omega} (u_1 - u_2) \Delta(u_1 - u_2) dx + 2\delta \int_{\Omega} (v_1 - v_2) \Delta(v_1 - v_2) dx \\ &\quad + 2 \int_{\Omega} (u_1 - u_2) \left[\left(u_1(1 - u_1) - \frac{u_1 v_1}{1 + Au_1(1 + Bv_1)} \right) \right. \\ &\quad \quad \left. + \left(u_2(1 - u_2) - \frac{u_2 v_2}{1 + Au_2(1 + Bv_2)} \right) \right] dx \\ &\quad + 2 \int_{\Omega} (v_1 - v_2) \left[\left(Cv_1 - \frac{CDv_1^2}{E + u_1} \right) - \left(Cv_2 - \frac{CDv_2^2}{E + u_2} \right) \right] dx \\ &:= I_1 + I_2 + I_3 + I_4. \end{aligned} \quad (6.35)$$

Due to the Neumann boundary condition, it is evident that

$$\begin{aligned} I_1 + I_2 &= -2 \int_{\Omega} \nabla^2(u_1 - u_2) dx - 2\delta \int_{\Omega} \nabla^2(v_1 - v_2) dx \\ &\leq -2 \int_{\Omega} |\nabla(u_1 - u_2)|^2 dx - 2\delta \int_{\Omega} |\nabla(v_1 - v_2)|^2 dx \leq 0. \end{aligned}$$

For the third and the fourth term in (6.35), we have

$$\begin{aligned}
 I_3 + I_4 &= 2 \int_{\Omega} (u_1 - u_2)^2 \left[1 - (u_1 + u_2) - \frac{Bv_1v_2}{(1 + Au_1)(1 + Bv_1)(1 + Au_2)(1 + Bv_2)} \right] dx \\
 &\quad + 2C \int_{\Omega} (v_1 - v_2)^2 \left[1 - \frac{ED(v_1 + v_2)}{(E + u_1)(E + u_2)} \right] dx \\
 &\quad - 2 \int_{\Omega} (u_1 - u_2)(v_1 - v_2) \left[\frac{Au_1u_2}{(1 + Au_1)(1 + Bv_1)(1 + Au_2)(1 + Bv_2)} \right] \\
 &\quad - 2 \int_{\Omega} (u_1 - u_2) \left[\frac{u_1v_1 - u_2v_2}{(1 + Au_1)(1 + Bv_1)(1 + Au_2)(1 + Bv_2)} \right] dx \\
 &\quad - 2 \int_{\Omega} (v_1 - v_2) \left[\frac{u_1v_1^2 - u_2v_2^2}{(E + u_1)(E + u_2)} \right] dx.
 \end{aligned}$$

Note that $u_1v_1 - u_2v_2 = u_1(v_1 - v_2) + v_2(u_1 - u_2)$ and $u_1v_1^2 - u_2v_2^2 = (v_1 - v_2)(u_1v_1 + u_2v_2) - v_1v_2(u_1 - u_2)$, thus

$$\begin{aligned}
 I_3 + I_4 &= 2 \int_{\Omega} (u_1 - u_2)^2 \left[1 - (u_1 + u_2) - \frac{v_2}{(1 + Au_1)(1 + Au_2)(1 + Bv_2)} \right] dx \\
 &\quad + 2C \int_{\Omega} (v_1 - v_2)^2 \left[1 - \frac{ED(v_1 + v_2) + (u_1v_1 + u_2v_2)}{(E + u_1)(E + u_2)} \right] dx \\
 &\quad - 2 \int_{\Omega} (u_1 - u_2)(v_1 - v_2) \left[\frac{u_1}{(1 + Au_1)(1 + Bv_1)(1 + Bv_2)} \right. \\
 &\quad \quad \quad \left. + \frac{v_1v_2}{(E + u_1)(E + u_2)} \right].
 \end{aligned}$$

Using $\eta \leq u_i \leq 1$ and $\eta \leq v_i \leq \frac{1+E}{D}$, for $i = 1, 2$, we get

$$\begin{aligned}
 I_3 + I_4 &\leq 2 \int_{\Omega} (u_1 - u_2)^2 \left[1 - 2\eta - \frac{\eta}{(1 + A\xi)^2(1 + B\xi)} \right] dx \\
 &\quad + 2 \int_{\Omega} (u_1 - u_2)(v_1 - v_2) \left[\frac{\eta}{(1 + A\eta)(1 + B\eta)^2} + \frac{\eta^2}{(E + \xi)^2} \right] dx \\
 &\quad + 2 \int_{\Omega} (v_1 - v_2)^2 \left[1 - \frac{2ED\eta + 2\eta^2}{(E + \xi)^2} \right] dx \\
 &\leq \lambda_M(W) \int_{\Omega} [(u_1 - u_2)^2 + (v_1 - v_2)^2] dx.
 \end{aligned}$$

By (6.34), one has

$$U(t) \leq U(0)e^{\lambda_M(W)t} \rightarrow 0 \quad \text{as } t \rightarrow \infty.$$

Thus, we have proved that $\|u_1(x, t) - u_2(x, t)\|_2 \rightarrow 0$ and $\|v_1(x, t) - v_2(x, t)\|_2 \rightarrow 0$ as $t \rightarrow \infty$, where $\|\cdot\|_2$ is the norm of the space of the space $L^2(\Omega)$. Note that by, solutions of system (6.5) are bounded in the space $C^{1+\nu}(\bar{\Omega}, \mathbb{R}^2)$, where $0 < \nu < 2\ell - 1 - n/p$ and $1/2 + n/(2p) < \ell < 1$. Therefore,

$$\limsup_{t \rightarrow \infty} \sup_{x \in \bar{\Omega}} |u_1(x, t) - u_2(x, t)| = 0, \quad \limsup_{t \rightarrow \infty} \sup_{x \in \bar{\Omega}} |v_1(x, t) - v_2(x, t)| = 0. \quad (6.36)$$

Consider the sequence $(u(k\omega, x, u_0, v_0), v(k\omega, x, u_0, v_0)) = w(k\omega, w_0)$, $k \in \mathbb{N}$, where ω is positive. Then $\{w(k\omega, w_0), k \in \mathbb{N}\}$ is compact in the space $C(\bar{\Omega}) \times C(\bar{\Omega})$. Let \bar{w} be a limit point of this sequence, then $w(\omega, \bar{w}) = \bar{w}$. Indeed, it follows, from $w(k\omega, w(k_n\omega, w_0)) = w(k_n\omega, w(\omega, w_0))$ and $w(k_n\omega, w(\omega, w_0)) - w(k_n\omega, w_0) \rightarrow 0$ as $k_n \rightarrow \infty$, that

$$\begin{aligned} \|w(\omega, \bar{w}) - \bar{w}\|_C &\leq \|w(\omega, \bar{w}) - w(\omega, w(k_n\omega, w_0))\|_C \\ &\quad + \|w(\omega, w(k_n\omega, w_0)) - w(k_n\omega, w_0)\|_C + \|w(k_n\omega, w_0) - \bar{w}\|_C \\ &\rightarrow \infty \quad \text{as } n \rightarrow \infty. \end{aligned}$$

Next, we claim the sequence $\{w(k\omega, w_0) : k \in \mathbb{N}\}$ has a unique limit point. On the contrary, there are two limit points $\tilde{w} = \lim_{n \rightarrow \infty} w(k_n\omega, w_0)$. Then, by (6.36) and $\tilde{w} = \lim_{n \rightarrow \infty} w(k_n\omega, \tilde{w})$, one has

$$\|\bar{w} - \tilde{w}\|_C \leq \|\bar{w} - w(k_n\omega, w_0)\|_C + \|w(k_n\omega, w_0) - \tilde{w}\|_C \rightarrow 0 \quad \text{as } n \rightarrow \infty.$$

Thus, $\bar{w} = \tilde{w}$. The solution $(u(x, t, \bar{u}, \bar{v}), v(x, t, \bar{u}, \bar{v}))$ is the unique periodic solutions of system (6.5). By (6.36), it is asymptotically stable. \square

6.9 Conclusions

In this manuscript, we have considered a spatio-temporel predator-prey model with modified Leslie-Gower and Crowley-Martin functional responses given by two coupled reaction-diffusion equations with homogeneous Neumann boundary conditions. We established the local stability of the non-negative steady-states. The global asymptotic stability of the unique constant positive steady state and the global stability of the prey-extinction equilibrium when the unique positive constant steady state is not feasible, by considering a Lyapunov function. Ecologically, this means :

- (i) As $t \rightarrow \infty$, if the trajectory tends to boundary (extinction) equilibrium $(0, E/D)$, then it expresses the extinction of the prey population and the predator population converges to the balance density E/D .
- (ii) A balance behavior is obtained where the trajectory tend to the unique positive constant steady-state E^* as $t \rightarrow \infty$.

Furthermore, we derived the conditions for the Hopf bifurcation and Turing instability, we showed that C plays a role of Hopf-bifurcation parameter. The existence of a unique globally stable periodic solutions is also presented.

* - * - * - * - * - * - *

Chapitre 7

Rappels et notions générales

Sommaire

| | | |
|------------|---|------------|
| 7.1 | Cadre fonctionnel et notions générales | 142 |
| 7.1.1 | Espaces fonctionnels | 142 |
| 7.1.2 | Formules et inégalités principales | 144 |
| 7.1.3 | Lemme de Gronwall | 146 |
| 7.1.4 | Règle des signes de Descartes | 146 |
| 7.1.5 | Triplet de Gelfand | 147 |
| 7.1.6 | Théorème de Minty-Browder | 147 |
| 7.2 | Systèmes dynamiques | 147 |
| 7.2.1 | Définitions et généralités | 148 |
| 7.2.2 | Bifurcations des systèmes dynamiques | 151 |
| 7.3 | Systèmes de réaction-diffusion | 152 |
| 7.3.1 | Régions invariantes | 153 |
| 7.3.2 | Fonctionnelle de Lyapunov | 153 |
| 7.3.3 | Sous-solutions et sur-solutions du problème elliptique
associé | 153 |

Dans ce chapitre nous exposons les notions de base et les outils mathématiques utilisés dans les chapitres précédents. Les concepts que nous rappelons ici sont classiques. Nous les introduisons ici dans le but de rendre plus facile, pour un écologiste ou un biologiste ou un autre chercheur, la lecture des autres chapitres.

Ce chapitre est constitué de trois sections indépendantes les unes des autres, il est organisé comme suit : dans la Section 7.1, nous présentons les espaces fonctionnels, ainsi que les formules et les différents types d'inégalités utilisés dans cette thèse. La Section 7.2 a pour objet de rappeler les notions de base et quelques résultats classiques sur les systèmes dynamiques d'équations différentielles ordinaires. Ensuite, dans la Section 7.3, nous énonçons quelques résultats classiques sur les systèmes réaction-diffusion.

7.1 Cadre fonctionnel et notions générales

7.1.1 Espaces fonctionnels

Nous reprenons ici certains énoncés de le livre Brézis [17], pour une présentation plus complète des espaces de Sobolov, on pourra voir Adams [2]. Par la suite, Ω désigne un ouvert borné régulier de \mathbb{R}^N , X et E sont deux espaces de Banach et $T > 0$.

Espaces de Lebesgue : Pour $1 \leq p < \infty$, l'espace de Lebesgue $L^p(\Omega)$ est l'espace de fonctions u (ou plus exactement des classes d'équivalence de fonctions, au sens de l'égalité presque partout) mesurables sur Ω telles que

$$\int_{\Omega} |u|^p dx < \infty,$$

muni de la norme (parfois notée $\|\cdot\|_p$)

$$\|u\|_{L^p(\Omega)} = \left(\int_{\Omega} |u|^p dx \right)^{\frac{1}{p}},$$

et pour $p = \infty$, on désigne par $L^\infty(\Omega)$ l'espace de fonctions u mesurables telle que

$$|u| \leq C \quad \text{p.p (presque partout) sur } \Omega,$$

où C est une constante positive. $L^\infty(\Omega)$ est muni de la norme (parfois notée $\|\cdot\|_\infty$)

$$\|u\|_{L^\infty(\Omega)} = \sup_{x \in \Omega} |u(x)| = \inf\{C, |u| \leq C \text{ p.p sur } \Omega\}.$$

Espaces de Sobolev : Pour $m \in \mathbb{N}^*$ et $1 \leq p < \infty$, l'espace de Sobolev $W^{m,p}(\Omega)$ est défini par :

$$W^{m,p}(\Omega) = \{u \in L^p(\Omega) : D^\alpha u \in L^p(\Omega) \text{ pour tout multi-indice } \alpha, |\alpha| \leq m\},$$

muni, pour $1 \leq p < \infty$, de la norme (parfois notée $\|\cdot\|_{m,p}$)

$$\|u\|_{W^{m,p}(\Omega)} = \left(\sum_{|\alpha| \leq m} \|D^\alpha u\|_{L^p(\Omega)}^p \right)^{\frac{1}{p}},$$

et pour $p = \infty$

$$\|u\|_{W^{m,\infty}(\Omega)} = \sum_{|\alpha| \leq m} \sup_{\Omega} \|D^\alpha u\|,$$

où dans cette définition la dérivée partielle D^α est étendue au sens des distributions.

Dans le cas $p = 2$, pour désigner l'espace de Sobolev $W^{m,2}(\Omega)$, on utilise une notation spéciale : $W^{m,2}(\Omega) = H^m(\Omega)$, où $H^m(\Omega)$ est un espace de Hilbert muni de la norme

$$\|u\|_{H^m(\Omega)} = \left(\sum_{|\alpha| \leq m} \|D^\alpha u\|_{L^2(\Omega)}^2 \right)^{\frac{1}{2}}.$$

Espaces de Sobolev vectoriels : Pour $1 \leq p < \infty$, l'espace de Lebesgue vectoriels $L^p(0, T, X)$ est l'espace de fonctions u (ou plus exactement des classes d'équivalence de fonctions, au sens de l'égalité presque partout) mesurables sur $[0, T]$ et à valeurs dans X telle que

$$\int_0^T \|u\|_X^p dt < \infty,$$

muni de la norme

$$\|u\|_{L^p(0,T,X)} = \left(\int_0^T \|u\|_X^p dt \right)^{\frac{1}{p}},$$

et pour $p = \infty$, on note

$$L^\infty(0, T, X) = \left\{ u : [0, T] \rightarrow X \text{ mesurable ; } \sup_{t \in (0,T)} \text{ess } \|u\|_X < \infty \right\},$$

muni de la norme

$$\|u\|_{L^\infty(0,T,X)}^p = \sup_{t \in (0,T)} \text{ess } \|u\|_X^p.$$

Naturellement on a : $L^p(0, T, L^p(\Omega)) = L^p((0, T) \times \Omega)$, $1 \leq p < \infty$.

Espaces de Hölder : Pour $0 < \rho < 1$, l'espace des fonctions uniformément ρ -Hölderiennes $\mathcal{C}^\rho(X, E)$ est l'espace de fonctions u de X à valeurs dans E telle que

$$\sup_{x \neq y} \frac{\|u(x) - u(y)\|_E}{\|x - y\|_X^\rho} < \infty,$$

muni de la norme

$$\|u\|_{\rho, X} = \sup_{x \neq y} \frac{\|u(x) - u(y)\|_E}{\|x - y\|_X^\rho}.$$

et pour $\rho = 0$

$\mathcal{C}^0(X, E) = \mathcal{C}(X, E)$, où $\mathcal{C}(X, E)$ est l'ensemble des fonctions continues de X dans E .

7.1.2 Formules et inégalités principales

Dans cette partie, nous introduisons quelques notions de base apparaissant tout au long de mon étude.

Formule de Green

Soit Ω un ouvert borné de frontière régulière $\partial\Omega$ et $\mathbf{n}(x)$ la normale extérieure au point x . Soient u une fonction de $H^2(\Omega)$ et v une fonction de $H^1(\Omega)$. Alors la formule de Green s'écrit :

$$\int_{\Omega} (\Delta u)v \, dx = - \int_{\Omega} \nabla u \cdot \nabla v \, dx + \int_{\partial\Omega} \frac{\partial u}{\partial \mathbf{n}} v \, d\sigma.$$

Formule de Co-aire

Soit $u : \mathbb{R}^N \rightarrow \mathbb{R}$, ($N \geq 2$) une fonction Lipschitzienne et supposons que pour $r \in \mathbb{R}$ p.p., l'ensemble de niveau

$$\{x \in \mathbb{R}^N : u(x) = r\}$$

est une hypersurface lisse de dimension $N - 1$ dans \mathbb{R}^N . Supposons encore que $f : \mathbb{R}^N \rightarrow \mathbb{R}$ est continue et dérivable. Alors

$$\int_{\mathbb{R}^N} f |\nabla u| \, dx = \int_{\mathbb{R}} \left(\int_{\{u=r\}} f \, ds \right) dr.$$

Inégalité de Poincaré

Soit Ω est un ouvert borné de \mathbb{R}^N et $u \in W_0^{1,p}(\Omega) = \{u : u \in W^{1,p}(\Omega); u|_{\partial\Omega} = 0\}$, $1 \leq p < N$. Alors il existe une constante $C > 0$ telle que

$$\|u\|_{L^q(\Omega)} \leq C \|\nabla u\|_{L^p(\Omega)}, \quad q \in \left[1, \frac{np}{n-p}\right]$$

pour une certaine constante C dépendant seulement de p, n, q et Ω .

Inégalité de Young

Soit $1 < p, q < \infty$, $\frac{1}{p} + \frac{1}{q} = 1$. Alors pour tout a et b deux réels positifs, la formule de Young s'écrit

$$ab \leq \frac{a^p}{p} + \frac{b^q}{q}$$

Inégalité de Young avec ϵ

Soit $1 < p, q < \infty$, $\frac{1}{p} + \frac{1}{q} = 1$. Alors pour tout a et b deux réels positifs, la formule de Young avec ϵ s'écrit

$$ab \leq \epsilon a^p + C(\epsilon)b^q \quad \text{pour} \quad C(\epsilon) = (\epsilon)^{-q/p}q^{-1}.$$

Inégalités de Hölder

Soit $1 \leq p, q \leq \infty$, $\frac{1}{p} + \frac{1}{q} = 1$. Alors, si $u \in L^p(\Omega)$, $v \in L^q(\Omega)$, on a $u \cdot v \in L^1(\Omega)$ et l'inégalité de Hölder s'écrit :

$$\|u \cdot v\|_{L^1(\Omega)} \leq \|u\|_{L^p(\Omega)} \|v\|_{L^q(\Omega)}.$$

Inégalité de Minkowski

Soit $1 \leq p < \infty$ et $u, v \in L^p(\Omega)$. Alors

$$\|u + v\|_{L^p(\Omega)} \leq \|u\|_{L^p(\Omega)} + \|v\|_{L^p(\Omega)}.$$

Inégalité d'inclusion

Si de plus $|\Omega| < \infty$ et $u \in L^q(\Omega)$, alors $u \in L^p(\Omega)$ et

$$\|u\|_{L^p(\Omega)} \leq |\Omega|^{1/p-1/q} \|u\|_{L^q(\Omega)}.$$

En particulier

$$L^q(\Omega) \subset L^p(\Omega), \quad \forall 1 \leq p \leq q < \infty.$$

Inégalité d'interpolation des espaces de Lebesgue

Si $u \in L^p(\Omega) \cap L^q(\Omega)$, avec $1 \leq p, q \leq \infty$, alors $u \in L^r(\Omega)$, pour tout $r \in [p, q]$ et on a l'inégalité d'interpolation

$$\|u\|_{L^r(\Omega)} \leq \|u\|_{L^p(\Omega)}^\alpha \|u\|_{L^q(\Omega)}^{1-\alpha} \quad \text{où} \quad \frac{1}{r} = \frac{\alpha}{p} + \frac{1-\alpha}{q}$$

pour un certain $0 \leq \alpha \leq 1$.

Inégalité d'interpolation des espaces de Sobolev vectoriels

Soient $p_1, p_2, q_1, q_2 \in [1, +\infty]$, $\lambda \in [0, 1]$, et $u \in L^{p_1}(0, T, L^{q_1}(\Omega)) \cap L^{p_2}(0, T, L^{q_2}(\Omega))$. Alors pour tout p et q vérifiant $\frac{1}{p} = \frac{\lambda}{p_1} + \frac{1-\lambda}{p_2}$ et $\frac{1}{q} = \frac{\lambda}{q_1} + \frac{1-\lambda}{q_2}$, on a

$$\|u\|_{L^p(0, T, L^q(\Omega))} \leq \|u\|_{L^{p_1}(0, T, L^{q_1}(\Omega))}^\lambda \|u\|_{L^{p_2}(0, T, L^{q_2}(\Omega))}^{1-\lambda}$$

7.1.3 Lemme de Gronwall

Inégalité de Gronwall (forme intégrale)

Soient $[a, b] \subset \mathbb{R}$ et φ, ψ et u trois fonctions continues de $[a, b]$ sur \mathbb{R} telle que φ est positive sur $[a, b]$ et

$$u(t) \leq \varphi(t) + \int_a^t \psi(s)u(s) ds \quad \forall t \in [a, b],$$

alors

$$u(t) \leq \varphi(t) + \int_a^t \varphi(s)\psi(s)e^{\int_s^t \psi(\tau)d\tau} ds \quad \forall t \in [a, b],$$

Il s'agit du lemme de Gronwall dans les cas particulier où φ est constante égale à C , on a donc pour tout $t \in [a, b]$

$$u(t) \leq Ce^{\int_a^t \psi(s)ds}.$$

où φ et ψ sont de fonctions constante égales à une constante C et K respectivement, on a donc pour tout $t \in [a, b]$

$$u(t) \leq Ce^{K(a-b)}.$$

Inégalité de Gronwall (forme différentielle)

Soient u une fonction de $[a, b]$ à valeurs dans \mathbb{R}^N de classe C^1 vérifiant

$$\exists \alpha > 0, \beta \geq 0, \forall t \in [a, b], \quad \|u'(t)\| \leq \beta + \alpha \|u(t)\|,$$

Alors,

$$\forall t \in [a, b], \quad \|u(t)\| \leq \|u(a)\|e^{\alpha(t-a)} + \frac{\beta}{\alpha} (e^{\alpha(t-a)} - 1).$$

7.1.4 Règle des signes de Descartes

Soit $p(x) = a_0x^{b_0} + a_1x^{b_1} + \dots + a_nx^{b_n}$ un polynôme à coefficients réels non nuls a_i , où les coefficients b_i sont des entiers satisfaisant $0 \leq b_0 < b_1 < b_2 < \dots < b_n$. Alors le nombre des racines positives de $p(x)$ (comptées avec leur multiplicité) est soit égal au nombre de changements de signes de la suite de coefficients (a_0, \dots, a_n) ou inférieur au nombre de variations par un entier positif pair. Le nombre des racines négatives de $p(x)$ (comptée avec leur multiplicité) est soit égal au nombre de changements des signes de coefficients de $p(-x)$ ou ou inférieur au nombre de variations par un entier positif pair.

7.1.5 Triplet de Gelfand

Soit H un espace de Hilbert séparable et V est un sous-espace dense dans H . Supposons que V est muni d'une structure de Banach réflexif et séparable. L'espace V est identifié avec son dual V^* (c'est l'espace pivot). De plus, les injections ci-dessous sont supposées continues et denses :

$$V \subseteq H \subseteq V^*.$$

Un tel triplet $V \subseteq H \subseteq V^*$ est appelé « triplet de Gelfand ». Les normes sur H, V et V^* sont notées respectivement $|\cdot|, \|\cdot\|$ et $\|\cdot\|_*$. Le produit scalaire sur H est noté $(\cdot, \cdot)_H$ et le crochet de dualité entre les espaces V^* et V est $\langle \cdot, \cdot \rangle_{V^* \times V}$.

7.1.6 Théorème de Minty-Browder

Soit V un espace de Banach réflexif séparable et V^* son dual. Soit $A : V \rightarrow V^*$ un opérateur non linéaire vérifiant

- A est borné,
- A est hémi-continu, i.e. l'application

$$t \mapsto \langle A(u + tv), w \rangle \text{ est continue de } \mathbb{R} \text{ dans } \mathbb{R} \quad \forall u, v, w \in V,$$

- A est monotone, i.e. $\langle A(u) - A(v), u - v \rangle \geq 0 \quad \forall u, v \in V$,
- A est coercif, i.e. $\frac{\langle A(u), u \rangle}{\|u\|_X} \rightarrow \infty$ lorsque $\|u\|_V \rightarrow \infty$.

Alors A est surjectif, i.e. $\forall f \in V^*$, il existe $u \in V$ tel que $A(u) \ni f$. Si de plus, A est strictement monotone, alors u est unique.

7.2 Systèmes dynamiques

Dans cette section, nous rappelons quelques concepts classiques de la théorie des systèmes dynamiques. Nous renvoyons aux ouvrages [45, 48, 50, 106] pour plus des détails.

Un système dynamique est un système qui évolue par rapport à un paramètre donné. Par exemple, le temps est un paramètre souvent utilisé. L'étude de l'évolution d'un système nécessite donc la connaissance de son état initial, et de sa loi d'évolution. Lorsque la loi d'évolution du système dynamique ne dépend pas explicitement du temps, le système est dit autonome, il est non autonome si sa loi d'évolution dépend explicitement du temps.

Un système dynamique peut être également

- à temps continu : si sa loi d'évolution est régie par des équations différentielles,
- à temps discret : si sa loi d'évolution est régie par des équations aux différences finies ou à temps discret [67, 103].

Dans toute la suite, nous considérons un système dynamique autonome à temps continu dont l'évolution obéit à des lois qu'on peut exprimer de la manière suivante

$$\frac{du}{dt} = F(u), \quad (7.1)$$

où $F = (u) : \Omega \rightarrow \mathbb{R}^n$ est une application supposée localement Lipschitzienne sur Ω un ouvert de \mathbb{R}^n et $u = (u_1, \dots, u_n)$ est la liste des variables d'état. La fonction $F = (f_1, \dots, f_n)$ est appelée champs de vecteurs, car à chaque u , elle attribue un vecteur $F(u)$. L'équation $u'(t) = F(u(t))$, où $u' = \frac{du}{dt}$, représente un système de n équations différentielles ordinaires :

$$u'_i = f_i(u_1, \dots, u_n), \quad i = 1, \dots, n, \quad \text{où } u'_i = du_i/dt.$$

Connaissant l'état initial du système $u(0) := u_0 \in \Omega$, on peut donc prédire son évolution future en tout instant. Un tel système est parfaitement déterministe.

D'après le théorème de Cauchy-Lipschitz, il existe une solution maximale unique $u \in \mathcal{C}([0, T], \mathbb{R}^n)$ de (7.1) pour $t < T$, vérifiant la condition initiale $u(0) = u_0$.

7.2.1 Définitions et généralités

Théorème 7.2.1. (*Existence globale*)

Soit u la solution maximale de (7.1) définie pour $t < T$. Si u est bornée sur $[0, T)$, alors $T = \infty$.

Definition 7.2.2. (*Flot*)

La correspondance $\Phi_t : u_0 \rightarrow u(t)$ qui associe à une donnée initiale u_0 la valeur de la solution maximale $u(t)$ au temps t , qui correspond à cette donnée initiale, est appelée le flot au temps t du champ de vecteurs F . Le flot du système dynamique est la famille d'application qui associe à (t, u) la solution maximale $u(t)$ au temps t qui correspond à la donnée initiale u_0 définie par :

$$\begin{aligned} \Phi : \mathbb{R} \times \Omega &\rightarrow \mathbb{R}^n \\ (t, u_0) &\rightarrow \Phi(t, u) := \Phi_t(u_0) = u(t) \end{aligned}$$

et qui vérifie :

- (i) $\frac{d}{dt} \Phi_t(x) = F(\Phi_t(x))$,
- (ii) $\Phi_0 = Id$,
- (iii) $\Phi_{t+s} = \Phi_t \Phi_s$.

Definition 7.2.3. (*Trajectoire, Orbite périodique*)

Soit u un point de Ω .

- On appelle trajectoire ou orbite (resp. trajectoire positive, resp. trajectoire négative) d'un point u de Ω l'ensemble $\Gamma_u = \{\Phi_t(u), t \in \mathbb{R}\}$ (resp. $\Gamma_u^+ = \{\Phi_t(u), t \in \mathbb{R}_+\}$, resp. $\Gamma_u^- = \{\Phi_t(u), t \in \mathbb{R}_-\}$).
- Une orbite périodique de période T est une trajectoire fermée Γ_u qui n'est pas un point fixe et qui est telle que $\forall v \in \Gamma_u, \Phi_T(v) = v$. On dit alors que T est une période de l'orbite périodique considérée.

Le théorème de Cauchy-Lipschitz entraîne le résultat suivant :

Corollaire 7.2.4. Deux trajectoires distinctes sont disjointes.

Definition 7.2.5. (Point d'équilibre)

On appelle point d'équilibre, ou point fixe, ou point stationnaire, ou point critique, ou point singulier du système dynamique (7.1), tout point u_e qui vérifie $\frac{du}{dt}|_{u_e} = 0$ (la variation au cours du temps des variables au point u_e est nulle). Les points d'équilibre de (7.1) vérifient donc l'équation suivante

$$F(u_e) = 0.$$

Definition 7.2.6. (Stabilité d'un point d'équilibre)

Soit u_e un point d'équilibre du système (7.1).

On dit que u_e est un point d'équilibre stable pour (7.1) ssi

$$\forall \epsilon > 0, \exists \delta > 0, \|u_0 - u_e\| < \delta \Rightarrow \forall t > 0, \|u(t) - u_e\| < \epsilon.$$

De plus, s'il existe δ_0 tel que $0 < \delta_0 < \delta$ et

$$\|u_0 - u_e\| < \delta_0 \Rightarrow \lim_{t \rightarrow \infty} \|u(t) - u_e\| = 0,$$

alors le point u_e est asymptotiquement stable.

Un équilibre qui n'est pas stable est dit instable.

Definition 7.2.7. (Bassin d'attraction d'un point d'équilibre)

Soit u_e un point d'équilibre stable du système (7.1).

On appelle bassin d'attraction de u_e l'ensemble B des conditions initiales u_0 telle que la solution $\Phi_t(u_0)$ converge vers u_e quand t tend vers l'infini.

$$B = \left\{ u_0 \in \Omega : \lim_{t \rightarrow \infty} \Phi_t(u_0) \rightarrow u_e \right\}.$$

Definition 7.2.8. (Ensemble invariant)

un sous-ensemble K de Ω est dit invariant relativement à (7.1) si toute solution u de (7.1) ayant une condition initiale u_0 appartenant à K vérifie $u(t) \in K$ pur tout t réel, c'est à dire

$$K = \{u : u_0 \in K \Rightarrow u(t) \in K, \forall t \in \mathbb{R}\}.$$

On dira que l'ensemble K est positivement (resp. négativement) invariant si cette propriété est vraie pour $t > 0$ (resp. $t < 0$).

L'ensemble invariant le plus simple possible est un point d'équilibre. Ensuite viennent les orbites périodiques.

Definition 7.2.9. (Ensemble limite, cycle limite)

Soit u un point de Ω .

- On appelle point ω -limite (resp. α -limite) d'une trajectoire Γ_u un point v tel qu'il existe une suite $(t_n)_{n \in \mathbb{N}}$ de \mathbb{R}_+ (resp. de \mathbb{R}_-) tendant vers $+\infty$ (resp. $-\infty$) telle que $v = \lim_{n \rightarrow \infty} \Phi_{t_n}(u)$.
- L'ensemble des points ω -limites de Γ_u est l'ensemble ω -limite de Γ_u , noté $\omega(\Gamma_u)$ (même définition avec α à la place de ω).
- Une orbite périodique est appelée un cycle limite s'il existe deux points de \mathbb{R}^n , l'un à l'intérieur de Γ et l'autre à l'extérieur tels que les ensembles ω - ou α - limite des orbites de ces points soit l'orbite périodique Γ elle-même. Autrement dit, on appelle cycle limite une orbite périodique qui est isolée dans l'ensembles des orbites périodiques.

Definition 7.2.10. (Dissipativité du système dynamique)

un système dynamique est dit dissipatif s'il existe un compact K tel que pour toute condition initiale, la solution issue de cette condition initiale rentre dans ce compact et n'en ressort plus. En d'autres termes, si on désigne par $\Phi_t(u_0)$ l'unique solution au temps t issue de u_0 ,

$$\exists K \text{ compact}; \forall t > 0, \Phi_t(u_0) \in K.$$

Definition 7.2.11. (Fonction de Lyapunov)

Soit u_e un équilibre du système (7.1). On appelle fonction de Lyapunov pour F en u_e , une fonction V définie sur \mathbb{R}^n ou sur un ensemble invariant par F vérifiant :

- (i) $V(u) > 0$ sauf en u_e , où elle vaut $V(u_e) = 0$.
- (ii) V est différentiable à dérivées continues et $\dot{V} \leq 0$.
- (iii) V est radialement non borné.

La théorie de Lyapunov joue un rôle très important dans l'étude théorique de la stabilité des systèmes non linéaires.

Théorème 7.2.12. (Principe d'invariance de LaSalle)

Soient Ω un sous-ensemble de \mathbb{R}^n ; supposons que Ω est un ouvert positivement invariant pour le système (7.1). Soit $V : \Omega \rightarrow \mathbb{R}$ une fonction de classe C^1 pour le système (7.1) telle que

1. $\dot{V} \leq 0$ sur Ω ;

2. soient $E = \{u \in \Omega : \dot{V}(u) = 0\}$ et L le plus grand ensemble invariant par F et contenu dans E .

Alors, toute solution bornée de (7.1) commençant dans Ω converge vers l'ensemble L lorsque t tend vers l'infini.

On suppose dans les théorèmes suivants que $n = 2$, et on considère le système dynamique planaire dans \mathbb{R}^2 suivant :

$$\begin{cases} u'_1 = f_1(u_1, u_2) \\ u'_2 = f_2(u_1, u_2) \end{cases} \quad (7.2)$$

Théorème 7.2.13. (Théorème de Poincaré-Bendixon)

Soit u un point de Ω . Si l'orbite positive $\Gamma^+(u)$ de u est bornée, alors une des assertions suivantes est vraie :

- (i) L'ensemble ω -limite $\omega(u)$ est réduit à u_e , qui est point d'équilibre du système (7.2), de plus la solution $\Phi_t(u)$ vérifie $\Phi_t(u) \rightarrow u_e$ quand t tend vers l'infini.
- (ii) $\omega(u)$ est une orbite périodique Γ et soit on a $\Gamma^+(u) = \omega(u) = \Gamma$, soit l'orbite $\Gamma^+(u)$ décrit une spirale qui tend vers Γ lorsque t tend vers l'infini.
- (iii) $\omega(u)$ est constitué des points d'équilibre du système (7.2) et des orbites dont les ensembles α - et ω -limite sont des points d'équilibre.

Théorème 7.2.14. (Critère de Dulac)

Soit D un ouvert simplement connexe de \mathbb{R}^2 et B est une fonction à valeurs réelles de classe C^1 définie sur D . Si $\text{div}(BF) = \frac{\partial(Bf_1)}{\partial u_1} + \frac{\partial(Bf_2)}{\partial u_2}$ est de signe constant et non identiquement nulle sur D , alors (7.2) n'admet pas de cycle limite entièrement contenu dans D .

7.2.2 Bifurcations des systèmes dynamiques

Une bifurcation dans un système dynamique est une modification de la nature de ses points stationnaires ou de ses cycles limites (stabilité ou instabilité d'une ou plusieurs solutions suivant les conditions initiales) due au changement de la valeur d'un paramètre du système, le paramètre de bifurcation. L'analyse de bifurcation d'un système dynamique $\frac{du}{dt} = F(u, a)$ en fonction du paramètre de bifurcation a consiste à étudier le comportement asymptotique des solutions $u(t)$ pour $t \rightarrow \pm\infty$, solutions stationnaires, cycles limites ou explosion.

Différents types de bifurcations peuvent avoir lieu dans le cas de systèmes en dimension 2 : bifurcation noeud-col (ou saddle node), bifurcation fourche (ou Pitchfork), bifurcation verticale, bifurcation homocline, bifurcation de Hopf, bifurcation de Bogdanov-Takens.

Nous rappelons dans la suite de cette sous-section le théorème de Poincaré-Andronov-Hopf qui donne les conditions nécessaires d'existence d'une bifurcation

de Hopf , qui correspond au passage abrupt d'un point fixe à un cycle sous l'effet de la variation d'un paramètre.

Théorème 7.2.15. (*Théorème de Poincaré-Andronov-Hopf*)

Soit le système à deux équations différentielles ordinaires

$$\begin{cases} u_1' = f_1(u_1, u_2, a) \\ u_2' = f_2(u_1, u_2, a) \end{cases} \quad (7.3)$$

où $a \in \mathbb{R}$. Soit (u_1^*, u_2^*) un point d'équilibre du système (7.3) pour tout a .

Si la matrice jacobienne du système en (u_1^*, u_2^*) admet deux valeurs propres imaginaires conjuguées, $\lambda_{1,2}(a) = \alpha(a) \pm i\omega(a)$ et s'il existe un certain $a = a_c$, tel que

1. $\alpha(a_c) = 0$ et $\omega(a_c) \neq 0$ condition de non dégénérescence,

2. $\left. \frac{d\alpha(a)}{da} \right|_{a=a_c} \neq 0$ condition de transversalité.

Alors une bifurcation de Hopf survient lorsque la valeur du paramètre de bifurcation a passe a_c et une famille d'orbites périodiques ayant une période approximativement égale à $2\pi/\omega(a_c)$ bifurque du point d'équilibre (u_1^*, u_2^*) ; le point $((u_1^*, u_2^*), a_c)$ est un point de bifurcation de Hopf. En outre, la stabilité des ces solutions périodiques dépend du signe du premier coefficient de Lyapunov ℓ_1 . Ces solutions sont stable si $\ell_1 < 0$ et instable pour $\ell_1 > 0$. On peut se référer à l'appendice du Chapitre 5.

Remarque 7.2.16. Le théorème de Poincaré-Andronov-Hopf (aussi connu sous le nom de théorème d'Andronov-Hopf) n'est pas valable que dans le plan. En 1942, Hopf [54] a généralisé le résultat et il a prouvé que ce théorème est aussi applicable en dimension supérieure à deux.

7.3 Systèmes de réaction-diffusion

L'objectif de cette section est de présenter quelques résultats principales sur les équations d'évolution de type "réaction-diffusion" qui interviennent dans des domaines variés. Ces équations (ou systèmes) de réaction-diffusion s'écrivent sous la forme :

$$\begin{cases} \frac{\partial u}{\partial t}(x, t) - \Delta u(x, t) = F(u(x, t)), & \text{sur } \Omega \times]0, +\infty[, \\ u(x, 0) = u_0(x), & \text{sur } \Omega, \end{cases} \quad (7.4)$$

où Ω est un ouvert borné de \mathbb{R}^N de frontière régulière; $u = (u_1, \dots, u_n)$ est une fonction vectorielle à valeurs dans \mathbb{R}^N , qui dans les applications visées, correspond à un n -vecteurs de concentrations d'espèces chimiques, de températures, de

densités, de populations, ect. Δ est le laplacien en la variable $x = (x_1, \dots, x_n)$, D est une matrice carrée d'ordre n définie positive et diagonalisable appelée matrice de diffusion et $F = (f_1, \dots, f_n) : \mathbb{R}^n \rightarrow \mathbb{R}^n$ est une fonction non-linéaire, appelée terme de réaction qui est le résultat de toutes les interactions entre les composantes de u . On ajoutera une condition aux limites $\partial\Omega$ de manière à ce que le problème (7.4) soit bien posé.

7.3.1 Régions invariantes

Definition 7.3.1. *Un sous ensemble fermé $\Sigma \subset \mathbb{R}^N$ est appelé une région invariante pour le système (7.4), si toute solution $u(x, t)$ ayant ses valeurs initiales $u_0(x)$ dans Σ , reste dans Σ pour tout $(x, t) \in \Omega \times [0, T_{\max})$.*

7.3.2 Fonctionnelle de Lyapunov

Definition 7.3.2. *On appelle fonctionnelle de Lyapunov associée au système (7.4), toute fonction*

$$L : [0, +\infty) \rightarrow [0, +\infty),$$

telle que

$$\frac{d}{dt}L(u(\cdot, t)) \leq 0,$$

pour tout $t > 0$ et toute solution $u(\cdot, t) = (u_1(\cdot, t), \dots, u_n(\cdot, t))$ du système (7.4).

7.3.3 Sous-solutions et sur-solutions du problème elliptique associé

Nous considérons dans ce paragraphe le système (7.4) sur le domaine Ω , avec des conditions aux bords de type Neumann homogènes :

$$\begin{cases} \frac{\partial u}{\partial t}(x, t) - \Delta u(x, t) - F(u(x, t)) = 0, & \text{sur } \Omega \times]0, +\infty[, \\ \frac{\partial \tilde{u}}{\partial \mathbf{n}} = 0 & \text{sur } \partial\Omega \times]0, +\infty[. \end{cases} \quad (7.5)$$

Definition 7.3.3. *On dit qu'une fonction $\tilde{u} : (0, T] \times \Omega \rightarrow \mathbb{R}$ est une sur-solution de (7.5) si elle vérifie le système suivante :*

$$\begin{cases} \frac{\partial u}{\partial t}(x, t) - \Delta u(x, t) - F(u(x, t)) \leq 0, & \text{sur } \Omega \times]0, +\infty[, \\ \frac{\partial \tilde{u}}{\partial \mathbf{n}} \leq 0 & \text{sur } \partial\Omega \times]0, +\infty[. \end{cases} \quad (7.6)$$

De la même façon, la fonction $\hat{u} : (0, T] \times \Omega \rightarrow \mathbb{R}$ est une sous-solution de (7.5) si elle satisfait les inégalités inverses de (7.6) .

* - * - * - * - * - * - *

Conclusions et perspectives

Conclusions

Dans cette thèse nous nous sommes intéressés à l'étude des systèmes d'équations différentielles ordinaires, et ceux aux dérivées partielles paraboliques issus de modèles de dynamique des populations (en particulier de dynamique de plantes) et de la biologie. L'objectif principal est de faire l'analyse mathématique, la simulation numérique ainsi que l'identification des diffusions croisées dans les modèles considérés.

Dans la première partie de cette thèse, nous présentons un système de réaction-diffusion modélisant la croissance de plantes en compétition. Nous étudions dans un premier temps l'existence locale et globale de solutions, et nous démontrons ensuite que la diffusion standard ne peut pas conduire à la formation des motifs. Des simulations numériques du modèle avec coefficients de diffusions couplées dégénérés/ non dégénérés sont aussi effectuées.

Dans un deuxième travail, nous avons démontré dans quelle mesure un modèle EDP simplifié de compétition spatio-temporelle pourrait constituer un modèle de substitution à un modèle d'agent de type individu-centré (Individual Based Models ou IBM en abrégé). Nous avons spécifié le type de diffusion croisées qu'il faudrait considérer dans les modèles EDP de compétition pour avoir les structures spatiales observées dans les simulations IBM d'une part. En outre, nous avons essayé de trouver des analogies entre les termes sources et les termes de diffusions croisées, respectivement, avec l'accès aux ressources d'une part et à la lumière d'autre part.

L'un des résultats principaux de cette thèse est la méthode d'identification des termes de diffusions croisées. Ce problème d'identification se fait à partir d'observations spatio-temporelles. Pour cela, on construit une fonctionnelle d'énergie appropriée à minimiser dont le minimiseur est le vecteur dont les composantes sont les fonctions diffusions croisées recherchées. Lors de l'étude de ce type de problèmes de minimisation, une principale difficulté rencontrée est le fait que le gradient de la diffusion (recherchée) dépend de la solution du système non-linéaire qui dépend elle-même de cette diffusion.

Grâce à la théorie développée par Minty et Browder, nous montrons l'exis-

tence de solutions, nous avons introduit ensuite une énergie à partir d'observations spatio-temporelles. Comme l'identification requiert le calcul du gradient de cette énergie, alors il est nécessaire de démontrer la différentiabilité de la solution du système par rapport aux diffusions. Nous avons explicité le gradient de cette énergie grâce à la formule de co-aire. A notre connaissance, cette caractérisation est une contribution nouvelle. Des simulations numériques basées sur l'optimisation via les méthodes de type quasi-Newton ont été illustrées.

Dans la deuxième partie de la thèse, nous proposons un modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin. L'originalité de ce travail réside dans l'utilisation d'une fonction de réponse qui n'est pas classique et qui est rarement utilisée dans la littérature : fonction de réponse de type Crowley-Martin.

Dans un premier temps, la dynamique temporelle globale du modèle considéré a été étudiée. Nous avons démontré que ce type de modèle possède une dynamique très riche qui inclut les possibilités d'extinction, permanence, des équilibres stables ou instables et cycle limite. Ces résultats ont des implications biologiques importantes et indiquent différents résultats de l'interaction entre les proies et les prédateurs. Des simulations numériques ont été réalisées pour illustrer les résultats analytiques obtenus.

En outre, nous avons introduit la dimension spatiale dans le modèle dynamique considéré. C'est un type de modèle spatio-temporel couramment utilisé en écologie ou en biologie. Nous avons effectué une analyse théorique complète de la dynamique spatio-temporelle du modèle.

Perspectives

Les perspectives de notre recherche sont multiples :

Modèles de compétition avec de coefficients de diffusions fortement dégénérées

Dans cette thèse nous avons évité l'étude des diffusions fortement dégénérées vue la complexité des problèmes correspondants et le peu des résultats théoriques existants dans la littérature. Considérons le système suivant comme un simple exemple pour illustrer cette difficulté

$$\begin{cases} u_t - \operatorname{div}(\mu_1(v)\nabla u) = f(u, v), \\ v_t - \operatorname{div}(\mu_2(u)\nabla v) = g(u, v), \\ + \text{C.L} + \text{C.I}, \end{cases}$$

avec

$$\begin{cases} \mu_1(v) = 0 & \text{pour } v \geq u^* \\ \mu_2(u) = 0 & \text{pour } u \geq v^* \end{cases}$$

où u^* et v^* sont des constantes strictement positives.

L'existence de solutions de tels systèmes n'est pas facilement démontrable sachant que les estimations sur $|\nabla u|$ et $|\nabla v|$ n'ont plus lieu sur Ω en entier.

Nous nous donnons comme objectifs :

- L'étude théorique de tels systèmes de compétition.
- l'étude des problèmes inverses correspondants.

Étude de sensibilité

Dans l'étude du modèle de réaction-diffusion avec des coefficients de diffusions non dégénérés, dans le Chapitre 4, nous avons étudié le problème d'identification de diffusions croisées sans tenir compte de la présence de bruit. Il serait intéressant, d'approfondir ce résultat grâce à une étude de sensibilité de notre méthode de minimisation (données IBM).

Motifs spatio-temporel dans le système de proie-prédateur avec diffusion

Dans le Chapitre 6, Nous avons étudié les bifurcations de Hopf et l'instabilité de Turing survenant dans le modèle du proie-prédateur avec diffusion. Il serait important dans la suite de valider ces connaissances théoriques par des simulations numériques afin d'inférer les motifs spatio-temporels du modèle.

* - * - * - * - * - * - *

Glossaire

Écologie : science des interactions entre un "être vivant" (êtres humains, plantes, animaux) et son environnement.

Dynamique d'une population : discipline qui étudie les effets des forces antagonistes (reproduction, croissance et immigration d'une part, mortalités et émigration d'autre part) et les facteurs écologiques qui les déterminent, non en terme de bilan énergétique mais en terme de biomasse et de structures démographiques.

Plantes clonales : (clonal plant) les plantes clonales sont des organismes qui exploitent une ressource répartie de manière hétérogène dans leur environnement (eau, nutriments, lumière). Elles exploitent leur environnement en fixant des ramets séparées par des inter-nœuds.

Coexistence : maintien à long terme de plusieurs entités (espèces) partageant une même ressource spatiale, énergétique ou informationnelle (NB : ce partage n'implique pas nécessairement compétition).

Compétition interspécifique : compétition entre individus d'espèces différentes, par opposition à la compétition intra-spécifique.

Compétition intraspécifique : interaction entre individus d'une même espèce, mettant en jeu une ressource limitante (énergie, temps, espace) et dont les effets directs sur le succès reproducteur d'un individu sont négatifs.

Dispersion : en écologie ou en biologie, la dispersion désigne de manière générale tous les processus par lesquels des êtres vivants, se séparant géographiquement d'une population d'origine, colonisent (ou recolonisent) un nouveau territoire.

Modèle individu-centré : (individual-based model ou IBM dans la terminologie anglo-saxonne) modèle utilisé en écologie qui se fonde sur une représentation explicite de l'ensemble des individus du système, par opposition aux modèles dynamiques.

Liste des travaux

Articles publiés

- ▶ On nonlinear coupled diffusions in competition systems, *Nonlinear Anal. : Real World Appl.* 13(3), 1306–1318, 2012, avec A. El Hamidi et M. Garbey. [Chapitre 2].
- ▶ A PDE model of clonal plant competition with nonlinear diffusion, *Ecological Modelling* 234, 83–92, 2012, avec A. El Hamidi et M. Garbey. [Chapitre 3].
- ▶ Global dynamics of a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses, *Journal of Applied Mathematic and Computing*, avec M. Jazar. [Chapitre 5].

Travaux en cours

- ▶ Nonlinear identification in cross-diffusion competition systems, avec A. El Hamidi. (à soumettre prochainement) [Chapitre 4].
- ▶ Spatio-temporel dynamics of a modified Leslie-Gower predator-prey model with Crowley-Martin, avec M. Jazar. [Chapitre 6].

* - * - * - * - * - * - *

Bibliographie

- [1] P.A. Abrams, *The nature of predation : prey dependent, ratio-dependent or neither*, Trends Ecol. Evol., 15 (2000), 337–341.
- [2] R. Adams, *Sobolev spaces*, vol. 65, Academic press, 1975.
- [3] H.R. Akçakaya, *Population cycles of mammals : evidence for a ratio-dependent predation hypothesis*, Ecological Monographs 62 : (1992) 119–142.
- [4] N. Ali, M. Jazar, *Global dynamics of a modified Leslie-Gower predator-prey model with Crowley-Martin functional responses*. Journal of Applied Mathematic and Computing. (2013), 1–23.
- [5] S. Aly, M. Farkas, *Competition in patchy environment with cross diffusion*, Nonlinear Analysis : Real World Applications, 5 (2004), 589 – 595.
- [6] H. Amann, *Nonhomogeneous linear and quasilinear elliptic and parabolic boundary value problems*. Function Spaces, Differential Operators and Nonlinear Analysis. H.J. Schmeisser, H. Triebel (editors), Teubner, Stuttgart, Leipzig. (1993), 9 –126.
- [7] L. Ambrosio, N. Fusco, D. Pallara, *Functions of bounded variation and free discontinuity problems*, Oxford Mathematical Monographs. Oxford University Press, 2000.
- [8] R. Arditi, L.R. Ginzburg, *Coupling in predator-prey dynamics : ratio-dependence*, J. Theoretical Biology 139 (1989), 311–326.
- [9] R. Arditi, H. Saiah, *Empirical evidence of the role of heterogeneity in ratio-dependent consumption*, Ecology 73 (1992), 1544–1551.
- [10] R. Arditi, L.R. Ginzburg, H.R. Akçakaya, *Variation in plankton densities among lakes : a case for ratio-dependent predation models*, The American Naturalist 138 : (1991)1287–1296.
- [11] R. Aris, *The mathematical theory of diffusion and reaction in permeable catalysts. Vol. I : The theory of the steady state*. Oxford University Press. XVI, (1975).
- [12] M.A. Aziz-Alaoui, *Study of a Leslie-Gower type tritrophic population model*, Chaos Solitons and Fractals 14 (8) (2002), 1275–1293.

- [13] M.A. Aziz-Alaoui, M. Daher Okiye, *Boundeness and global stability for a predator-prey model with modified Leslie-Gower and Holling-type II schemes*, Appl. Math. Lett. 16 (2003), 1069–1075.
- [14] E. Bassiri, R. Bryant, M. George, K. Yerion, *A finite difference method for modeling the formation of animal coat patterns*, Nonlinear Analysis : Real World Applications, 10 (2009), 1730 – 1737.
- [15] A. D. Bell *Dynamic morphology : a contribution to plant population ecology*, in : Dirzo R & Sarukhán J (eds) Perspectives in Plant Population Ecology, Sinauer, Sunderland, Massachusetts, (1984) 48-65.
- [16] F. Berezovskaya, G. Karev, R. Arditi, *Parametric analysis of the ratio-dependent predator-prey model*, J. Math. Biol. 43 (2001), 221–246.
- [17] H. Brezis, *Analyse fonctionnelle. Théorie et applications*, Masson, 1993.
- [18] F. Brauer, C. Castillo-Chavez C, *Mathematical Models in Population Biology and Epidemiology*. Springer Verlag, Texts in applied mathematics (2000).
- [19] S.N. Busenberg, C.C. Travis, *Epidemic models with spatial spread due to population migration*, J. Math. Biol. 16 (1983), 181 – 198.
- [20] R.S Cantrell, C. Cosner, *On the dynamics of predator-prey models with the Beddington-DeAngelis functional response*, J. Math. Anal. Appl., 257 (2001), 206–222.
- [21] V. Capasso, A. Di Liddo, L. Maddalena : *Asymptotic behaviour of a nonlinear model for the geographical diffusion of innovations*, Dyn. Syst. Appl. (2) 3 (1994), 207 – 219.
- [22] G. Caughley, P. H. Lawton, *Plant-herbivore systems. In : Theoretical ecology*, , May RM. (ed.), Blackwell Scientific, Oxford, Angleterre : (1976) 132-166.
- [23] G. Chavent, P. Lemmonier, *Identification de la non linéarité d'une équation parabolique quasilinéaire*, Applied Mathematics and Optimization 1, 2 (1974), 121–162.
- [24] S. N. Chow, J.K. Smale, *Methods of bifurcation theory*, Springer, New York (1982).
- [25] Y.S. Choi, R. Lui, Y. Yamada, *Existence of global solutions for the Shigesada-Kawasaki-Teramoto model with strongly coupled cross-diffusion*. Discrete Contin. Dyn. Syst. 10 (2004), 719 – 730.
- [26] P. H. Crowley, E. K. Martin, *Functional responses and interference within and between year classes of a dragonfly population*, Journal of the North American Benthological Society 8 (1989), 211–221.
- [27] J. M. Cushing, *An Introduction to Structured Population Dynamics*. CBMS-NSF Regional Conf. Series in Appl. Math. 71, SIAM, Philadelphia (1998).
- [28] E.L. Cussler, *Multicomponent Diffusion*, Chemical Engineering Monographs, Elsevier Scientific Publishing Company, Amsterdam, (3) (1976).

-
- [29] T. Czárán, S. Bartha, Spatiotemporal Dynamic Models of Plant Populations and Communities. TREE vol. 7, no. 2 (1992).
- [30] T. Czárán, Spatiotemporal modelling of population and community dynamics. Population and Community Biology Series 21(1998).
- [31] H. de Kroon, J. van Groenendael, *The Ecology and Evolution of Clonal Plants* Backhuys Publishers, Leiden (1997).
- [32] L. C. Evans, *Partial differential equations*, vol 19 of graduate studies in Mathematics. Proceedings of the American Mathematical Society, 1998.
- [33] M. Fan, Q. Wang, X.F. Zou, *Dynamics of a nonautonomous ratio-dependent predator-prey system*, Proc. Roy. Soc. Edinburgh Sect. A 133 (2003), 97–118.
- [34] M. Fan, Y. Wang, *Dynamics of a nonautonomous predator-prey system with the Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 295 (2004), 15–39.
- [35] M. Farkas, *Comparison of different ways of modeling cross-diffusion*, Differential Equations Dynam. Systems 2 (1999), 121 – 138.
- [36] H. Federer, *Geometric measure theory*, Springer, 1969.
- [37] H. I. Freedman, *Deterministic mathematical models in population ecology*, Marcel Dekker, New York (1980).
- [38] P. Gaie, H. Zhang, *Qualitative analysis of a prey-predator system with Holling I functional response*, J. Jilin Univ. Sci. 44, no. 3 (2006), 373–376.
- [39] P.L. Garcia-Ybarra, P. Calvin, *Cross transport effects in premixed flames*, Progress in Astronautics and Aeronautics, The American Institute of Aeronautics and Astronautics, New York, 76 (1981), 463 – 481.
- [40] G. Grimm, S. F. Railback, *Individual-based Modeling and Ecology*. Princeton series in theoretical and computational biology, ed. S.A. Levin, Princeton Univ. Press 428 (2005).
- [41] M.E. Gurtin, R.C. MacCamy, *On the diffusion of biological population*. Math. Biosci. 33 (1977), 35-49.
- [42] J.K. Hale, H. Kocak, *Dynamics and bifurcations*, Springer-Verlag, New York, (1991).
- [43] J. K Hale, *Ordinary differential equations*, New York, Wiley-Interscience, New York, (1969).
- [44] J.K. Hale, M. McCracken, *Ordinary Differential Equations*, Wiley, New York, 1969.
- [45] J. K Hale, P. Waltman, *Persistence in infinite-dimensional systems*, SIAM J Math. Analysis, 20 (2) (1989), 388–395.
- [46] El Hamidi, A., Garbey, M., Ali, N *On nonlinear coupled diffusions in competition systems*, Nonlinear Analysis : Real World Applications, 13 (3) (2012), 1306 – 1318.

- [47] El Hamidi, A., Garbey, M., Ali, N *A PDE model of clonal plant competition with nonlinear diffusion*, Ecological Modeling 234, (2012), 83–92.
- [48] P. Hartman, *Ordinary Differential Equations*, Wiley, New York, 1964.
- [49] D. Henry, *Geometric Theory of Semilinear Parabolic Equations*, Lecture Notes in Math., vol. 840, Springer-Verlag, Berlin/New York, (1981).
- [50] M. Hirsch, H. Smale, *Differential Equations, Dynamical Systems and Linear Algebra*, Academic Press, New York (1974).
- [51] C. S. Holling, *Some characteristics of simple types of predation and parasitism*, The Canadian Entomologist 91 (7) (1966), 385–398.
- [52] C.S. Holling, *On the dynamics of predator-prey systems with Beddington-Deangelis functional response*, J. Assian-Eur. J. Math, 4 (2011), 35–48.
- [53] S. L. Hollis, R. H. Martin, M. pierre, *Global existence and boundedness in reaction-diffusion systems*, SIAM J. Math. Anal. 18, 744-761, (1987).
- [54] E. Hopf, *Abzweigung einer periodischen Lösung von einer stationären Lösung eines Differentialsystems*, Berichten der Mathematisch-Physischen Klasse der Sächsischen Akademie der Wissenschaften zu Leipzig, XCIV, 1-22 (1942). An English translation, with comments, is included as Section 5 in [?].
- [55] S. B. Hsu, T. W. Hwang, Y. Kuang, *Global dynamics of a predator prey model with Hassell-Varley type functional response*, Contino Dynam. Syst. Series B, 10(4) (2005), 857–875.
- [56] S. B. Hsu, T. W. Hwang, Y. Kuang, *Global analysis of the Michaelis-Menten-type ratio-dependent predator-prey system*, J. Math. Biol., 42 (2001), 489–506.
- [57] J. Huentutripay, M. Jazar and L. Véron, *A dynamical system approach to the construction of singular solutions of some degenerate elliptic equations*, J. Differential Equations 195 (1), (2003), 175–193.
- [58] T.W. Hwang, *Global analysis of the predator-prey system with Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 281, (2003) 395–401.
- [59] T.W. Hwang, *Uniqueness of limit cycles of the predator-prey system with Beddington-DeAngelis functional response*, J. Math. Anal. Appl. 290 (2004), 113–122.
- [60] J. Hwang, D. Xiao, *Analyses of bifurcations and stability in a predator-prey system with Holling Type-IV functional response*, Acta Mathematicae Applicatae Sinica, English Series 20 (2004), 167–178.
- [61] S. I. Jónsdóttir, M. A. Watson, *Extensive physiological integration : an adaptive trait in resource limited environments ?* In : de Kroon, H., van Groenendael, J. (Eds), *The ecology and evolution of clonal growth in plants*. Backhuys Publishers, Leiden, pp. (1997) 109-136.

-
- [62] J. Jorné, *Negative ionic cross-diffusion coefficients in electrolytic solutions*, J. Theor. Biol. 55 (1975), 529 – 532.
- [63] J. Jorné, *The Diffusive Lotka-Volterra Oscillating System*, J. Theor. Biol. 65 (1977), 133 – 139.
- [64] C. Jost, *Comparaison qualitative et quantitative de modèles proie-prédateur à des données chronologiques en écologie*, Springer, New York, (1998).
- [65] C. Jost, O. Arini, R. Arditi, *About deterministic extinction in ratio-dependent predator-prey models*, Bulletin of Mathematical Biology, vol. 61, no. 1 (1999), 19–32.
- [66] E.F. Keller, L. A. Segel, *Initiation of slime mold aggregation viewed as an instability*, J. Theor. Biol. 26 (1970), 399 – 415.
- [67] M. P. Kennedy, *Basic concepts of nonlinear dynamics and chaos*, Tutorials (IEEE), 289–313, (1994).
- [68] M. Kirane, S. Kouachi : *Asymptotic behaviour for a system describing epidemics with migration and spatial spread of infection*, Dyn. Syst. Appl. 2 (1993), 121 – 130.
- [69] K. Kishimoto, H. Weinberger, *The spatial homogeneity of stable equilibria of some reaction-diffusion systems on convex domains*. J. Differential Equations 58 (1985), 15 – 21.
- [70] R. E. Kooij, A. Zegeling, *A predator-prey model with Ivlev's functional response*, J. Math. Anal. Appl., 198 : (1996), 473–489.
- [71] S. Kouachi, *Existence of Global solutions to reaction-diffusion systems via a Lyapunov functional*. Elect. J. Diff. Equ. 68 (2001), 1 – 10.
- [72] Y. Kuang, H. I. Freedman *Uniqueness of limit cycles in Gause-type predator-prey systems*, Math. Biosci. 8810 (4) (1988), 67–84.
- [73] Y. Kuang, E. Beretta, *Global qualitative analysis of a ratio-dependent predator-prey system*, J. Math. Biol. 36 (1998), 389–406.
- [74] Y. A. Kuznetov, *Elements of applied bifurcation theory (2nd Ed)*, Biometrica 47 (1960), 219–234.
- [75] Le Dimet F.X, Shutyayev V and Gejadze I. (2006) On optimal solution error in variational data assimilation : theoretical aspects. Russian Journal of Numerical Analysis and Mathematical Modelling 21 : 139-152.
- [76] P. H. Leslie, J. C. Crowley, *The properties of a stochastic model for the predator-prey type of interaction between two species*, Biometrica 47 (1960), 219–234.
- [77] Y.W. Qi, H. A. Levine, *The critical exponent of degenerate parabolic systems*, Z. Angew. Math. Phys. (2) 44 (1993), 249 – 265.
- [78] M. Iida, M. Mimura, H. Ninomiya, *Diffusion, cross-diffusion and competitive interaction*. J. Math. Biol. 53 (2006), 617 – 641.

- [79] Y. Lou and W.-M. Ni, *Diffusion, self-diffusion and cross-diffusion*, J. Differential Equations, 131 (1996), 79-131.
- [80] L. Lovett-Doust, Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. J. Ecol. 69 : 743-755 (1981).
- [81] J. Marsden, M. McCracken, *The Hopf bifurcation and its applications*, New York, Springer, (1976).
- [82] H. Matano, M. Mimura, *Pattern formation in competition-diffusion systems in nonconvex domains*, Publ. Res. Inst. Math. Sci. 19 (1983), 1049 – 1079.
- [83] M. Mimura, K. Kawasaki, *Spatial segregation in competitive interaction-diffusion equations*. J. Math. Biol. 9 (1980), 49 – 64.
- [84] C. Mony, M. Garbey, M. Smaoui, M. L. Benot, *Large Scale Parameter Study of an Individual Based Model of Clonal Plant with Volunteer Computing*, Ecological Modelling, in press.
- [85] J.D. Murray, *Mathematical biology*. Springer-Verlag, 1993.
- [86] H. Nie, J. Wu, *Coexistence of an unstirred chemostat model with Beddington-DeAngelis functional response and inhibitor*, Nonlinear Analysis : Real World Applications, 11 (2010), 1312 – 1322.
- [87] B. Oborny, *Growth Rules in Clonal Plants and Environmental Predictability – A Simulation Study*, The Journal of Ecology 2 (1994), 341 – 351.
- [88] Oborny B, Czárán T and Kun A. (2001) Exploration and Exploitation of Resource Patches by Clonal Growth : a Spatial Mode on the Effect of Transport Between Modules. Ecological Modelling 141 : 151-169.
- [89] B. Oborny B, C. Mony, T. Herben, From Virtual Plant to Real communities : A Review of Modeling Clonal Growth. Ecology Modeling. This special issue (submitted).
- [90] A. Okubo, *Diffusion and Ecological Problems : Mathematical Models*, Springer Verlag (1991), 169 – 184.
- [91] S. W. Pacala, D. Tilman, Limiting Similarity in Mechanistic and Spatial Models of Plant Competition in Heterogeneous Environments. American naturalist 143 :(1994) 222-257.
- [92] R. Peng, M. Wang, *Positive steady states of the Holling-Tanner prey-predator model with diffusion*, Proc. Roy. Soc. Edinburgh A, 135 (2005), 149–164.
- [93] Y.W. Qi, H. A. Levine, *The critical exponent of degenerate parabolic systems*, Z. Angew. Math. Phys. (2) 44 (1993), 249 – 265.
- [94] T. Quilin, *A Predator-prey System with Ivlev's Functional Response*, Journal of Beihua University (Natural Science), 3(5) (2002), 381–384.
- [95] Roache P.J. (1998) Verification and Validation in Computational Science and Engineering. Hermosa publisher, Albuquerque, New Mexico.

-
- [96] G. Rosen, *Effect of diffusion on the stability of the equilibrium in multi-species ecological systems*, Bull. Math. Biol. 39 (1977), 373 – 383.
- [97] J. Savchik, B. Chang, H. Rabits, *Application of moments to the general linear multicomponents reaction-diffusion equations*, J. Phys. Chem. 87 (1983), 1990 – 1997.
- [98] M. Balabane, M. Jazar and Ph. Souplet, *Oscillatory blow-up in nonlinear second order ODE's : the critical case*, Discrete Contin. Dyn. Syst. 9 (3) (2003), 577–584.
- [99] H.L. Toor, *Solution of the linearized equations of multicomponent mass transfer : I*, A. I. Ch. E. Journal, 10 (1964), 448 – 455.
- [100] H.L. Toor, *Solution of the linearized equations of multicomponent mass transfer : II. matrix methods*, A. I. Ch. E. Journal, 10 (1964), 460 – 465.
- [101] P.Y.H. Pang and M. Wang, *Qualitative analysis of a ratio-dependent predator-prey system with diffusion*, Proc. Roy. Soc. Edinburgh A, 133(4) (2003), 919- 942.
- [102] J. Savchik, B. Chang, H. Rabits, *Application of moments to the general linear multicomponents reaction-diffusion equations*, J. Phys. Chem. 87 (1983), 1990 – 1997.
- [103] A. Serbanescu, *Dynamical systems - Applications in Communications*, Ed. ATM, 2004.
- [104] X. Shi, X. Zhou, X. Song, *Analysis of a stage-structured predator-prey model with Crowley-Martin function*, Korean society for computational and applied mathematics (2010), 461–472.
- [105] N. Shigesada, K. Kawasaki, E. Teramoto, *Spatial segregation of interacting species*. J. Theoret. Biol. 79 (1979), 83 – 99.
- [106] S. Smale, *Differentiable dynamical systems*, Bull. Amer. Math. Soc. 73 747–817 (1967).
- [107] J. Smoller, *Shock waves and reaction-diffusion equations*. Springer-Verlag, New York (1983).
- [108] Stuefer J.F., Gómez S and van Mólken T (2004) Clonal integration beyond resource sharing : implications for defence signalling and disease transmission in clonal plant networks. Evolutionary Ecology, 18 : 647-667
- [109] J. Sugie, R. Kohno, R. Miyazaki, *On a predator-prey system of Holling type*, Proc. Amer. Math. Soc. 125, no. 7 (1997), 2041–2050.
- [110] Suzuki JI and Hutchings MJ (1997) Interactions between shoots in clonal plants and the effect of stored resources on the structure of shoot populations. In : de Kroon H and van Groenendael J (eds) The ecology and evolution of clonal plants. Backhuys Publishers, Leiden, pp 311-329.

- [111] Suzuki JI and Stuefer J (1999) On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biology*, 14 : 11-17.
- [112] R.K. Upadhyay, R.K. Naji, *Dynamics of a three species food chain model with Crowley-Martin type functional response*, *Chaos Soliton. Fract.*, 42 (2009), 1337–1346.
- [113] R.K. Upadhyay, S.N. Raw, V. Rai, *Dynamical complexities in a tri-trophic hybrid food chain model with Holling type II and Crowley-Martin functional responses*, *Nonlinear Analysis : Modelling and Control*, 15 (2010), 366–375.
- [114] van Groenendael, J. and de Kroon, H. (1990, eds.) *Clonal Growth in Plants : Regulation and Function*, SPB Academic Publishing, The Hague.
- [115] J. L. Vazquez, *The Porous Medium Equation : Mathematical Theory*. Oxford Mathematical Monographs. Oxford University Press (2006).
- [116] X. Wang, *Dynamics of a predator-prey system with Watt-type functional response*, Master-Thesis. Northeast Normal University : Changchun Jilin, China ; 2005.
- [117] M. Wang, *Stationary patterns for a prey-predator model with prey-dependent and ratio-dependent functional responses and diffusion*, *Physica D : Nonlinear Phenomena*, 196 (2004), 172-192.
- [118] X. Wang, W. Wang, X. Lin, *Chaotic behavior of a Watt-type predator-prey system with impulsive control strategy*, *Chaos Solitons. Fract* ; 37 (2008), 706–718.
- [119] S. Wiggins, *Introduction to applied nonlinear dynamical systems and chaos*, volume 2 of Texts in Applied Mathematics. Springer-Verlag, New York, 1990.
- [120] R. Wu, L. Lin, *Permanence and global attractivity of discrete predator-prey system with Hassell-Varley type functional response*, *Discrete Dyn. Nat. Soc* (2009), 1–17.
- [121] D. Xiao, S. Ruan, *Global dynamics of a ratio-dependent predator-prey system* *J. Math. Biol.* 43 (2001), 268–290.
- [122] P. Hartman, *Predator-prey theory and management of multispecies fisheries*, *Ecol. Appl.* 4. 51 (1994).
- [123] X. Zhou, J. Cui, *Global stability of the viral dynamics with Crowley-Martin functional response*, *Bull. Korean Math. Soc* 48 (2011), 555–574.
- [124] W. Zhou, *Positive solutions for a diffusive Bazykin model in spatially hetero- geneous environment*, *Nonlinear Analysis : Theory, Methods and Applications*, 73 (2010), 922-932.
- [125] S. Zheng, *A Reaction-Diffusion System of a Competitor- Competitor-Mutualist* *J. Math. Anal. Appl.*, 124 (1987), 254-280.
- [126] K. Zhuang, Z. Wen, *Analysis for a food chain model with Crowley-Martin functional response and time delay*, *World academy of Science, Engineering and Technology* 61(2010), 562–565.

- [127] K. Zhuang, Z. Wen, *Analysis for a food chain model with Crowley-Martin functional response and time delay*, World academy of Science, Engineering and Technology 61(2010), 562–565.

Index

- Bifurcation de Hopf (Hopf bifurcation),
90, 95, 98, 116, 119, 133, 151,
152
- Critère de Dulac, 151
- Crowley-Martin, 3, 7, 14, 17, 18, 20, 89,
90, 92, 93, 103, 109, 110, 113,
115–117, 138
- Formule de Co-aire (Co-area formula),
3, 17, 64, 83
- Lyapunov, 90, 98, 102, 103, 105, 106,
111, 116, 119, 130–133, 150, 152,
153
- Minty-Browder, 17, 64, 68
- Principe d’invariance de LaSalle (LaSalle’s invariance principle), 90, 102,
105, 150
- Proie-prédateur (predator-prey), 3–6, 14,
17, 18, 20, 89–92, 103, 109, 110,
112, 113, 156
- Règle des signes de Descartes (Rule sign
of Descartes), 95, 146
- Théorème de Poincaré-Bendixon, 151
- Triplet de Gelfand, 147

Dynamique spatio-temporelle et Identification des diffusions non linéaires

Résumé Cette thèse est consacrée à l'étude des systèmes d'équations différentielles ordinaires, et ceux aux dérivées partielles paraboliques issus de modèles de dynamique des populations et de la biologie. L'objectif principal est de faire l'analyse mathématique, la simulation numérique ainsi que l'identification des diffusions croisées dans les modèles construits. Nous présentons d'abord un système de réaction-diffusion modélisant la croissance de plantes en compétition spatiale dans un milieu saturé. Nous effectuons par la suite l'étude théorique et numérique de tels systèmes, ainsi que l'étude des problèmes d'identification des termes de diffusions croisées. Ensuite, nous proposons un modèle proie-prédateur de type Leslie-Gower modifié avec une fonction de réponse de type Crowley-Martin. Nous étudions dans un premier temps la dynamique temporelle globale du modèle considéré, et nous présentons des simulations numériques pour illustrer les résultats théoriques. En outre, nous introduisons la dimension spatiale dans le modèle dynamique considéré, et nous effectuons une analyse théorique complète de la dynamique spatio-temporelle du modèle.

Mot-clefs : Modèle de compétition, Proie-prédateur, Diffusions croisées, Identification, Instabilité de Turing, Minty-Browder, Simulations numériques.

Spatio-temporal dynamics and Identification of nonlinear diffusions

Abstract This thesis is devoted to the study of ordinary differential systems, and systems of nonlinear parabolic PDEs resulting from models of population dynamics and biology. The main objective is to perform mathematical analysis, numerical simulations, and identification of cross-diffusion in built models. We first present a reaction-diffusion system that models the spatial competition of plants in a saturated environment. We then perform a theoretical and a numerical study of such systems, and handle the identification of cross-diffusion problem. Secondly, we propose a modified Leslie-Gower-type predator-prey model with a Crowley-Martin type functional response. Within this context, we study the global temporal dynamics of the considered model, and present numerical simulations as illustration of the theoretical results. Finally, we introduce the spatial dimension in the previous dynamical model, and perform a comprehensive theoretical analysis of the spatio-temporal model.

Keywords : Competition model, Predator-prey, Nonlinear diffusion, Identification, Turing instability, Minty-Browder, Numerical simulations.

MIA

Laboratoire Mathématiques, Images et
Applications, Av. Michel Crépeau
17042 LA ROCHELLE

