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# Système dynamique stochastique de certains modèles proies-prédateurs et applications.

Safia Slimani

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# THÈSE EN CO - TUTELLE INTERNATIONALE

Pour obtenir le diplôme de doctorat

Spécialité Mathématiques Appliquées

Préparée au sein de l'Université de Rouen Normandie  
et de l'Université Badji Mokhtar-Annaba

## Systeme dynamique stochastique de certains modèles proies- prédateurs et applications

Présentée et soutenue par  
**Safia SLIMANI**

Thèse soutenue publiquement le 10 décembre 2018  
devant le jury composé de

M. Hacène BOUTABIA	Professeur, Université Badji Mokhtar-Annaba	Président du jury
M. Khaled KHALDI	Professeur, Université M'Hamed Bougara Boumerdès	Rapporteur
M. Pierre MAGAL	Professeur, Université de Bordeaux	Rapporteur
Mme. Sabrina BADI	Maître de conférences, Université 08 mai 1945 Guelma	Invitée
Mme. Michèle THIEULLEN	Maître de conférences, Université Pierre et Marie Curie-Paris 6	Examineur

### Thèse dirigée par

M. Paul RAYNAUD DE FITTE  
M. Azzedine BENCHETTAH

Université de Rouen Normandie  
Université Badji Mokhtar-Annaba





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# Résumé

Ce travail est consacré à l'étude de la dynamique d'un système proie-prédateur de type Leslie-Gower défini par un système d'équations différentielles ordinaires (EDO) ou équations différentielles stochastiques (EDS), ou par des systèmes couplés d'EDO ou d'EDS. L'objectif principal est de faire l'analyse mathématique et la simulation numérique des modèles construits. Cette thèse est divisée en deux parties : La première partie est consacrée à un système proie-prédateur où les proies utilisent un refuge, le modèle est donné par un système d'équations différentielles ordinaires ou d'équations différentielles stochastiques. Le but de cette partie est d'étudier d'impact du refuge ainsi que la perturbation stochastique sur le comportement des solutions du système. Dans la deuxième partie, Nous considérons un système proie-prédateur couplé en réseau. Il s'agit d'étudier comment des couplages plus ou moins forts entre plusieurs systèmes affectent l'existence et la position des points d'équilibre, et la stabilité de ces systèmes.

**Mots Clés :** Proie-prédateur, Bifurcation de Hopf, Stabilité, Terme refuge, Systèmes couplés, Perturbation stochastique.



# Abstract

This work is devoted to the study of the dynamics of a predator-prey system of Leslie-Gower type defined by a system of ordinary differential equations (EDO) or stochastic differential equations (EDS), or by coupled systems of EDO or EDS. The main objective is to do mathematical analysis and numerical simulation of the models built. This thesis is divided into two parts : The first part is dedicated to a predator-prey system where the prey uses a refuge, the model is given by a system of ordinary differential equations or stochastic differential equations. The purpose of this part is to study the impact of the refuge as well as the stochastic perturbation on the behavior of the solutions of the system. In the second part, we consider a networked predator-prey system. We show that symmetric couplings speed up the convergence to a stationary distribution.

**Key Words :** Predator-prey, Hopf bifurcation, Stability, Refuge term, Coupled systems, Stochastic perturbation.





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# Chapitre 1

## Introduction

### 1.1 Introduction générale

La relation dynamique entre les proies et les prédateurs a longtemps été et continuera d'être l'un des sujets dominants de l'écologie mathématique en raison de son existence et de son importance universelles. Un système dynamique proie-prédateur peut généralement être écrit comme suit

$$\begin{cases} \dot{X} = F_X(X) - \phi_X(X, Y)Y, \\ \dot{Y} = G_Y(X)Y, \end{cases} \quad (1.1)$$

où  $X, Y$  représentent les densités de population de proies et de prédateurs respectivement. La fonction  $F_X(X)$  représente la croissance des proies,  $G_Y(X)Y$  est la variation du prédateur en fonction de la variation du proie à laquelle est soustraite sa mortalité naturelle et  $\phi_X(X, Y)Y$  est la réponse fonctionnelle du prédateur à la densité des proies. Il existe trois types de modèles proie-prédateur en fonction de l'expression de la réponse fonctionnelle  $\phi_X(X, Y)Y$  :

- Le modèle dit *proie-dépendant* lorsque la réponse fonctionnelle dépend seulement de la densité de proie, c'est à dire  $\phi_X(X, Y) = \phi_X(X)$ . La population de prédateurs a seulement un effet indirect sur l'élimination des proies comme le terme  $\phi_X(X)$ . En plus, ce type de modèle correspond à la situation nommée "laissez-faire" lorsqu'il n'y a pas d'interférence entre les prédateurs dans leurs activités d'alimentation.
- Le modèle dit *ratio-dépendant* lorsque la réponse fonctionnelle s'écrit sous la forme  $\phi_X(X, Y) = \phi_X(X)Y$ .
- Le modèle dit *densité-dépendant* (ou *prédateur-dépendant*) si la réponse fonctionnelle dépend à la fois de  $X$  et  $Y$ .

La réponse fonctionnelle la plus simple a été proposée par Lotka (1925) et Volterra (1926). Il s'agit d'une relation linéaire entre le taux de consommation du prédateur et la densité de la proie, qu'on retrouve dans leur modèle de prédation :

$$\phi_X(X, Y) = \lambda_X X, \quad (1.2)$$

avec  $\lambda_X$  le taux d'attaque de la proie principale par le prédateur. Ce terme implique que la prédation augmente ou diminue proportionnellement avec le taux de rencontre entre le prédateur et la proie. C'est le cas dans la nature de certaines espèces comme les araignées.

Holling est l'un des fondateurs de la notion de réponse fonctionnelle. Selon les densités et les caractéristiques des proies et du prédateur, il a défini trois principaux types de réponse fonctionnelle qui ont gardé son nom.

**Holling de type I (Fig. 1.1) :** En (1959), Holling a considéré que le prédateur peut rechercher aléatoirement ses proies et que le temps de recherche est négligeable et le taux de recherche est alors constant quelle que soit la densité de proies. Le nombre de proies tuées est de ce fait proportionnel à leur densité. Si le prédateur ne peut plus ingérer davantage d'individus, un niveau de saturation peut être atteint :

$$\phi_{X_I}(X) = \begin{cases} \lambda X & \forall X < \bar{X}, \\ \lambda \bar{X} & \forall X \geq \bar{X}. \end{cases} \quad (1.3)$$

**Holling de type II (Fig. 1.1) :** La réponse fonctionnelle de Type Holling II décrit une situation dans laquelle le nombre des proies consommées par les prédateurs augmente rapidement lorsque la densité des proies augmente, mais après diminue avec une nouvelle augmentation de la densité des proies. Ce phénomène est représenté par une expression de la forme :

$$\phi_{X_{II}}(X) = \frac{\lambda_X X}{1 + h_X X}, \quad (1.4)$$

où  $\lambda_X > 0$  est l'efficacité maximale de prédation (c'est-à-dire le taux de croissance maximal de prédateur) et  $h_X > 0$  est la constante de demi-saturation. Cette fonction a été utilisée pour la première fois en 1913 par Michaelis et Menten [41], dans l'étude des réactions enzymatiques. Ensuite la dynamique de la réponse de type II a été étudiée par Holling (1959), il a utilisé cette fonction comme réponse fonctionnelle dans le cas des prédateurs vertébrés et invertébrés.

**Holling de type III (Fig. 1.1) :** La réponse fonctionnelle de Type Holling III est une réponse fonctionnelle dans laquelle le taux d'attaque du prédateur augmente lorsque le nombre des proies est faible, puis ralentit lorsque le prédateur atteint la satiété. La réponse fonctionnelle de ces espèces peut être représentée par :

$$\phi_{X_{III}}(X) = \frac{\lambda_X X^2}{1 + h_X X^2}, \quad (1.5)$$

où  $\lambda_X$  et  $h_X$  jouent le même rôle que  $\lambda_X$  et  $h_X$  de la réponse fonctionnelle de type II.

Ces différents types de réponse fonctionnelle ont une importance toute particulière dans la dynamique des modèles proies-prédateurs. En particulier, la limitation du prédateur par son temps de recherche et de consommation de ses proies peut fortement modifier le comportement qualitatif des solutions. Nous nous en tiendrons au deuxième type et nous étudions un modèle qui résulte d'une combinaison du modèle de Leslie et Gower avec une réponse fonctionnelle de Holling de type II.

Le modèle proie-prédateur de Leslie-Gower a été introduit en 1948 par Leslie [44]. Dans ce modèle, la capacité de soutien que l'environnement offre aux prédateurs est proportionnelle

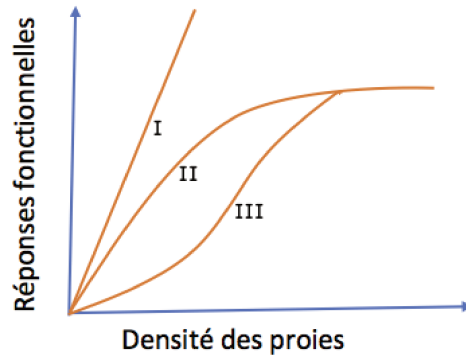


FIGURE 1.1 – Les trois réponses fonctionnelles de Holling

au nombre de proies et à la dynamique des prédateurs. Ce modèle a été discuté par Leslie et Gower en 1960 et par Pielou en 1969. Le modèle proie-prédateur de Leslie-Gower s'écrit sous la forme suivante :

$$\begin{cases} \frac{dX}{dt} = r_1 X \left(1 - \frac{X}{K}\right) - aXY, \\ \frac{dY}{dt} = r_2 Y \left(1 - \frac{Y}{\rho X}\right), \end{cases} \quad (1.6)$$

où  $r_1$  et  $r_2$  sont les taux de croissance des proies (repec. des prédateurs) et  $\rho$  représente la conversion des proies en prédateurs. Dans la deuxième équation, la quantité  $\frac{Y}{\rho X}$  est appelée le terme de Leslie-Gower, il mesure la perte dans la population des prédateurs due à un manque de sa nourriture préférée.

Nous nous intéressons particulièrement dans cette thèse, aux modèles de type proie-prédateur, nous étudions un modèle avec une réponse fonctionnelle de Holling type II avec une modification de Leslie-Gower en incorporant un terme refuge qui modélise la probabilité pour une perte des proies de se réfugier dans une zone où le prédateur ne peut les atteindre.

La dynamique du système proie-prédateur avec la réponse fonctionnelle Holling de type II a été étudiée dans [12, 65].

La dynamique de la population est obligatoirement affectée par le bruit aléatoire de l'environnement qui est une composante importante dans un écosystème. Mais les modèles déterministes supposent que les paramètres du système sont tous déterministes indépendamment des fluctuations environnementales. Par conséquent, ils ont quelques limites dans la modélisation mathématique des systèmes écologiques.

May [62] a souligné le fait qu'en raison de la fluctuation de l'environnement, les taux de natalité, la capacité de charge, les coefficients de compétition et d'autres paramètres impliqués dans le système modèle présentent des fluctuations aléatoires plus ou moins importantes. Par conséquent, la distribution de la population à l'équilibre fluctue de manière aléatoire autour de certaines valeurs moyennes.



Par conséquent, de nombreux auteurs introduisent une perturbation stochastique dans des modèles déterministes pour révéler l'effet de la variabilité environnementale sur les dynamiques de la population en écologie mathématique. Levin [46] a d'abord considéré un système autonome proie-prédateur de Lotka-Volterra à deux espèces et montré que la dispersion pouvait déstabiliser le système. Par ailleurs, Freedman et Waltman [23] et Arnold, Horsthemke et Stucki [6] ont également considéré le modèle de Lotka-Volterra avec des perturbations aléatoires.

## 1.2 Présentation du travail

Cette thèse se divise en trois chapitres. Nous détaillons ici le contenu de chacun d'entre eux.

Dans le premier chapitre, nous rappelons des notions essentielles utilisées pour l'étude des systèmes dynamiques déterministes et stochastiques.

Dans le second chapitre, nous étudions une version modifiée d'un système proie-prédateur avec la réponse fonctionnelle modifiée de Leslie-Gower et Holling de type II étudié par M.A. Aziz-Alaoui et M. Daher-Okiye. La modification consiste à incorporer un refuge pour les proies, et complique considérablement la dynamique du système, et nous étudions également une perturbation stochastique du système. Pour le cas déterministe, le modèle est donné par un système de deux équations différentielles ordinaires qui décrivent les interactions entre les proies et les prédateurs. Nous montrons que les solutions du système sont bornées. Nous étudions l'existence et la positivité des points d'équilibres du système associé. Ensuite, nous analysons la stabilité locale des points d'équilibres positifs et les conditions suffisantes pour l'existence d'un point d'équilibre globalement asymptotiquement stable. Par ailleurs, nous donnons des conditions nécessaires suffisantes et parfois suffisantes pour l'absence de cycles limites. Ainsi nous montrons numériquement l'existence d'un cycle limite autour de trois points d'équilibres.

Dans la deuxième partie, nous considérons le même modèle avec une perturbation stochastique, nous montrons l'existence et l'unicité de la solution globale positive. Ensuite, nous comparons les dynamiques du système avec des modèles simples afin de voir le comportement des solutions. Par ailleurs, nous montrons sous certaines conditions l'existence et l'unicité d'une distribution stationnaire. Nous finalisons ce chapitre par des simulations numériques pour illustrer nos résultats. Les résultats de ce travail font l'objet d'un article soumis pour publication [74].

Le dernier chapitre est consacré à l'étude d'un système proie-prédateur stochastique avec réponse fonctionnelle modifiée de Leslie-Gower et Holling de type II, où les proies se dispersent entre  $n$  "patches" (zones) avec des échanges de populations entre ces zones. Nous montrons l'existence et l'unicité ainsi que la bornitude de la solution. De plus, nous obtenons des conditions suffisantes pour l'existence d'une distribution stationnaire ergodique. Enfin, nous illustrons nos conclusions par la simulation numérique. Ce dernier travail est une version corrigée

de l'article publié dans le journal **Gazi University Journal of Science**, volume 2018, sous le titre *Dynamics of a stochastic predator-prey coupled system with modified Leslie-Gower and Holling type II schemes* [73].



# Chapitre 2

## Généralités sur les équations différentielles ordinaires et les équations différentielles stochastiques

Dans ce chapitre, Nous rappelons quelques définitions et résultats nécessaires utilisés pour l'étude des systèmes dynamiques déterministes et stochastiques.

### 2.1 Systèmes déterministes

#### 2.1.1 Définitions

— Un *semi-flot* sur  $R^n$  est une application  $U : R^+ \times R^n \longrightarrow R^n$ , telle que

i)  $U(0, x) = x$ ,

ii)  $U(t + s, x) = U(t, U(s, x))$  pour  $t, s \in R^+$ ,  $x \in R^n$ .

Il est dit *continu* (resp. *différentiable* si  $U$  est continu (resp. différentiable) pour tout  $t$ , *linéaire* si  $U$  est de la forme

$$U(t, x) = A(t)x,$$

où  $A(t) : \mathbf{R}^n \longrightarrow \mathbf{R}^n$  est une application linéaire, et *autonome* s'il ne dépend pas explicitement du temps.

— Les fonctions  $U(x, \cdot)$ , pour tout  $x \in \mathbf{R}^n$ , sont appelées orbites du semi-flot.

— Considérons le système différentiel autonome dans  $\mathbf{R}^n$  :

$$\begin{cases} \frac{dx}{dt} = f(x(t)), \\ x(0) = x_0 \end{cases} \quad (2.1)$$

où  $f$  est une fonction continue. La solution  $\phi(t, x_0) = \phi_t(x_0)$  de (2.1) est un semi-flot différentiable.

#### 2.1.2 Points d'équilibre et linéarisation

**Définition 2.1.** On appelle point d'équilibre (ou critique ou stationnaire) du système (2.1) tout point  $x^* \in R^n$  tel que :  $f(x^*) = 0$ .

**Définition 2.2.** *Un point critique  $x^*$  est dit hyperbolique si aucune des valeurs propres de la matrice jacobienne  $Df(x^*)$  n'a de partie réelle nulle.*

### Linéarisation

On considère le système linéaire associé à (2.1) :

$$\begin{cases} \dot{x} = Ax(t), \\ x(0) = 0 \end{cases} \quad (2.2)$$

où  $A = Df(x^*)$  est la matrice jacobienne de  $f$  au point  $x^*$ , i.e.,

$$A = \left( \frac{\partial f_i}{\partial x_j}(x^*) \right)_{1 \leq i, j \leq n}. \quad (2.3)$$

Pour tout point initial  $x_0 \in \mathbf{R}^n$ , le système (2.2) a une unique solution donnée par  $x(t) = e^{At}x_0$ , elle est définie pour  $t \in \mathbf{R}$ .

En général, l'étude locale du système non linéaire (2.1) est équivalente à celle, plus simple, du système linéarisé (2.2) grâce au Théorème de Hartman-Grobman, voir par exemple [68] :

**Théorème 2.1.** *(Hartman-Grobman) Soient  $E$  un sous-ensemble de  $\mathbf{R}^n$  contenant l'origine,  $f \in C^1(E)$  et  $\phi_t$  le flot du système non linéaire (2.1). On suppose que  $f(0) = 0$  et que la matrice  $A = Df(0)$  n'a aucune valeur propre de partie réelle nulle. Alors, il existe un homéomorphisme  $H : U \rightarrow V$ , où  $U$  et  $V$  sont deux ouverts de  $\mathbf{R}^n$  contenant l'origine, tel que pour tout  $x_0 \in U$  et  $t \in I_0 \subset \mathbf{R}$  on ait*

$$H \circ \phi_t(x_0) = e^{At}H(x_0).$$

### Nature des points critiques

Nous allons restreindre l'étude de la nature des points critiques au cas où l'espace d'état est de dimension deux. Considérons le système (2.2), où  $A$  est une matrice d'ordre 2, inversible ( $\det A \neq 0$ ). L'équation caractéristique associée au système (2.2) est donnée par :

$$\lambda^2 - \text{trace } A\lambda + \det A = 0, \quad (2.4)$$

alors les valeurs propres de cette équation sont, dans  $\mathbf{C}$ ,

$$\lambda_{1,2} = \frac{\text{trace } A \pm \sqrt{(\text{trace } A)^2 - 4 \det A}}{2}. \quad (2.5)$$

Suivant la nature des valeurs propres, nous avons les résultats suivants :

— **Si les deux valeurs propres  $\lambda_1$  et  $\lambda_2$  sont réelles distinctes**

Le système (2.2) se transforme en  $\dot{Y} = JY$ , avec  $Y = (Y_1, Y_2)$  et

$$J = \begin{pmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{pmatrix}. \quad (2.6)$$

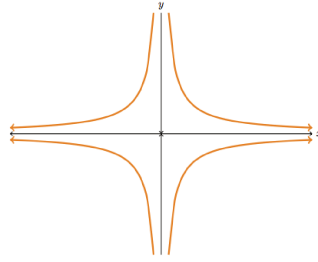


FIGURE 2.1 – Point selle

1. Si  $\lambda_1 > 0$  et  $\lambda_2 < 0$ , alors  $\lim_{t \rightarrow \infty} Y_1 = \infty$ , et  $\lim_{t \rightarrow \infty} Y_2 = 0$ , donc le point critique  $x = x_0$  est un point selle qui est toujours instable.
2. Si  $\lambda_1$  et  $\lambda_2$  sont réelles de même signe on a deux cas :
  - (a) Si  $\lambda_1 < \lambda_2 < 0$ , alors  $\lim_{t \rightarrow \infty} Y_1 = 0$  et  $\lim_{t \rightarrow \infty} Y_2 = 0$ , le point critique  $x = x_0$  est un noeud stable.

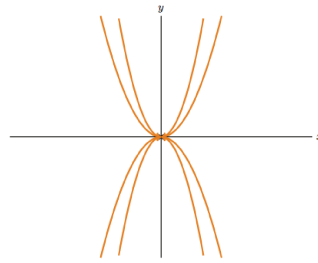


FIGURE 2.2 – Noeud stable

- (b) Si  $0 < \lambda_1 < \lambda_2$ , alors  $\lim_{t \rightarrow \infty} Y_1 = +\infty$  et  $\lim_{t \rightarrow \infty} Y_2 = +\infty$ , le point critique  $x = x_0$  est un noeud instable.

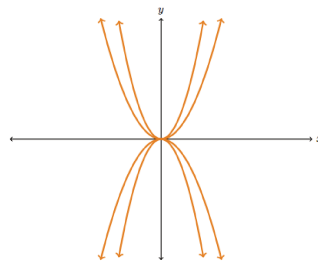
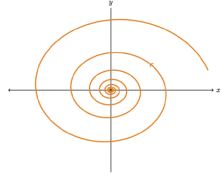


FIGURE 2.3 – Noeud instable

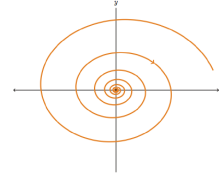
— Si les deux valeurs propres sont complexes conjuguées  $\lambda_{1,2} = \alpha \pm i\beta$ , la matrice  $J$  s'écrit

$$J = \begin{pmatrix} \alpha & -\beta \\ \beta & \alpha \end{pmatrix}. \quad (2.7)$$

1. Si  $\beta \neq 0$ , alors le point critique  $x = x_0$  est un foyer. Il est stable si  $Re(\lambda_{1,2}) < 0$  et il est instable si  $\alpha > 0$ .



Foyer stable



Foyer instable

2. Si  $\lambda_1$  et  $\lambda_2$  sont imaginaires pures, alors le point critique  $x = x_0$  est un centre, il est stable mais pas asymptotiquement stable.

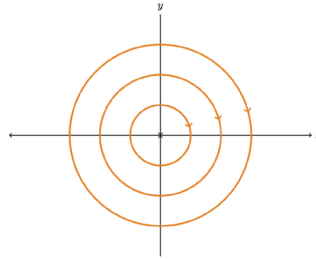


FIGURE 2.4 – Centre

### 2.1.3 Orbites périodiques et cycles limites

**Définition 2.3.** On appelle solution périodique toute solution  $x = \Phi(t)$  de l'équation (2.1) telle qu'il existe un nombre  $T$  vérifiant  $\Phi(t + T) = \Phi(t)$ ,  $\forall t \geq 0$ .

Ainsi, une solution périodique du système (2.1) correspond à une orbite (une courbe) fermée dans l'espace des phases.

**Théorème 2.2.** (Poincaré-Bendixson) Soit le système

$$\begin{cases} \dot{x} = f(x, y) \\ \dot{y} = g(x, y), \end{cases} \quad (2.8)$$

où les fonctions  $f$  et  $g$  sont de classe  $C^1$ . Soit  $(x(t), y(t))_{t \geq 0}$  une solution maximale de (2.8). S'il existe un compact  $K$  du plan tel que  $(x(t), y(t)) \in K$ ,  $\forall t \geq 0$ , alors  $(x(t), y(t))$  converge lorsque  $t \rightarrow +\infty$  soit vers un point critique, soit vers une orbite périodique de (2.8).

### 2.1.4 Stabilité de Lyapunov

**Théorème 2.3.** [68, Theorem 3 page 131] (Fonction de Lyapunov) Soit  $x^* \in N \subset \mathbf{R}^n$  un point d'équilibre du système (2.1). On suppose que  $f$  est de classe  $C^1$  et qu'il existe une fonction  $V : N \rightarrow \mathbf{R}$ , de classe  $C^1$  telle que :

- $V(x^*) = 0$ ,
- $V(x) > 0, \forall x \in N / \{x^*\}$ ,
- $\dot{V}(x) \leq 0, \forall x \in N$ .

Alors  $x^*$  est stable, c'est à dire que, pour tout  $\varepsilon > 0$ , il existe  $\eta > 0$  tel que, si  $\|x(0) - x^*\| < \eta$ , alors, pour tout  $t \geq 0$ ,  $\|x(t) - x^*\| < \varepsilon$ .

### 2.1.5 Bifurcations

Une bifurcation (locale ou globale) d'un système dynamique est une modification (locale ou globale) de son comportement qualitatif ( nature de ses points stationnaires, existence des cycles limites) due au changement de la valeur d'un paramètre (qui peut être multidimensionnel) du système, le paramètre de bifurcation. Dans le cas de systèmes en dimension 2, nous observons plusieurs types de bifurcations : bifurcation noeud-col (ou saddle node), bifurcation fourche (ou Pitchfork), bifurcation verticale, bifurcation de Hopf, etc... Dans la théorie des bifurcations, une bifurcation de Hopf (parfois aussi appelé Poincaré-Andronov-Hopf [14]), est une bifurcation locale dans laquelle un point fixe d'un système dynamique perd sa stabilité lorsqu'une paire de valeurs propres complexes conjuguées de la linéarisation autour du point fixe franchissent l'axe imaginaire du plan complexe. Considérons le système suivant :

$$\begin{cases} \frac{du}{dt} = f(u, v, \beta) = f_\beta(u, v), \\ \frac{dv}{dt} = g(u, v, \beta) = g_\beta(u, v), \end{cases} \quad (2.9)$$

qui dépend d'un paramètre scalaire  $\beta \in \mathbf{R}$ . Soit  $(u^*, v^*)$  un point d'équilibre du système (2.9) pour tout  $\beta$ . Le théorème suivant nous donne les conditions nécessaires pour l'apparition d'une bifurcation de Hopf.

**Théorème 2.4.** (Théorème de Poincaré-Andronov-Hopf)[79, 32]. Supposons que  $f$  soit de classe  $C^5$  et que la matrice jacobienne du système (2.9) en  $(u^*, v^*)$  admette deux valeurs propres imaginaires conjuguées,  $\lambda_{1,2}(\beta) = \eta(\beta) \pm i\alpha(\beta)$  et qu'il existe un certain  $\beta = \beta_c$ , tel que

- $\eta(\beta_c) = 0$  et  $\alpha(\beta_c) \neq 0$ , (condition de non dégénérescence).
- $\frac{d\eta(\beta)}{dt} |_{\beta=\beta_c} \neq 0$ , (condition de transversalité : les valeurs propres traversent l'axe imaginaire avec une vitesse non nulle).

Alors une bifurcation de Hopf se produit lorsque la valeur du paramètre de bifurcation  $\beta$  passe  $\beta_c$  et une famille d'orbites périodiques ayant une période approximativement égale à  $2\pi$  bifurque du point d'équilibre  $(u^*, v^*)$ ; le point  $((u^*, v^*), \beta_c)$  est un point de bifurcation de Hopf.



## 2.2 Systèmes stochastiques

Nous donnons quelques éléments de base pour éclairer la partie stochastique de la thèse. Le lecteur pourra se reporter, par exemple, à [67, Chapitres 2 à 5] ou à [39, Chapitres 1 à 4] pour une présentation plus complète.

### 2.2.1 Processus stochastiques

Dans toute la suite, on supposera donné un espace probabilisé  $(\Omega, \mathcal{F}, P)$ , et une filtration  $(\mathcal{F}_t)_{t \geq 0}$ , c'est à dire une famille de sous-tribu de  $\mathcal{F}$  telle que  $s \leq t \Rightarrow \mathcal{F}_s \subset \mathcal{F}_t$  pour tous  $s, t \geq 0$ .

**Définition 2.4.** *Un processus stochastique à valeurs dans  $\mathbf{R}^d$  est une famille de variables aléatoires*

$$X = \{X_t, 0 \leq t < +\infty\} = (X_t)_{t \geq 0},$$

définie sur  $(\Omega, \mathcal{F})$  à valeurs dans  $\mathbf{R}^d$ . La fonction  $t \mapsto X_t(\omega)$  est une trajectoire du processus  $X$  associée à  $\omega$ . Il est dit adapté à la filtration si pour tout  $t$ ,  $X_t$  est  $\mathcal{F}_t$ -mesurable.

**Définition 2.5.** *Un processus stochastique  $(W(t), t \geq 0)$  défini sur  $(\Omega, \mathcal{F}, (\mathcal{F}_t), P)$  à valeurs dans  $\mathbf{R}^d$ , à trajectoires continues, est appelé mouvement brownien standard (ou processus de Wiener) sur  $\mathbf{R}^d$  si*

- (i)  $W(0) = 0$ ,
- (ii) Pour tous  $t, s \geq 0$ ,  $W(t+s) - W(t)$  est indépendant de  $\mathcal{F}_t$ ,
- (iii) Pour tout  $t, s \geq 0$ , la variable  $W(t+s) - W(t)$  suit une loi normale  $\mathcal{N}(0_{\mathbf{R}^d}, s\text{Id}_{\mathbf{R}^d})$ .

### 2.2.2 Intégrale stochastique

**Définition 2.6.** *On appelle processus prévisible élémentaire  $X = (X_t)_{0 \leq t \leq T}$  tout processus de la forme*

$$X_t = H_0 \mathbf{1}_0(t) + \sum_{i=1}^p H_i \mathbf{1}_{]t_{i-1}, t_i]}(t), \tag{2.10}$$

où  $0 = t_0 < t_1 < \dots < t_p < +\infty$ ,  $H_0$  est  $\mathcal{F}_0$ -mesurable et bornée et, pour  $i = 1, \dots, p$ ,  $H_i$  est une variable aléatoire  $\mathcal{F}_{t_{i-1}}$ -mesurable et bornée de  $\mathbf{R}^d$ .

Pour définir l'intégrale stochastique multidimensionnelle, nous devons considérer des processus stochastiques à valeurs dans des espaces d'applications linéaires. On identifiera l'espace des applications linéaires de  $\mathbf{R}^d$  dans  $\mathbf{R}^n$  à l'espace des matrices à  $n$  lignes et  $d$  colonnes, noté  $\mathcal{M}_{n \times d}$ . Cet espace étant isomorphe à  $\mathbf{R}^{nd}$ , les définitions précédentes s'appliquent aux processus à valeurs dans  $\mathcal{M}_{n \times d}$ . On identifie bien sûr  $\mathcal{M}_{1 \times 1}$  à  $\mathbf{R}$ .

Soit  $W$  un mouvement brownien standard sur  $\mathbf{R}^d$ , et soit  $X$  un processus prévisible élémentaire à valeurs dans  $\mathcal{M}_{n \times d}$ , défini comme dans (2.10) :

$$X_t = H_0 \mathbf{1}_0(t) + \sum_{i=1}^p H_i \mathbf{1}_{]t_{i-1}, t_i]}(t),$$

où les  $H_i$ , ( $0 \leq i \leq p$ ) sont à valeurs dans  $\mathcal{M}_{n \times d}$ . On définit l'intégrale stochastique de  $X$  par rapport à  $W$  comme le processus à valeurs dans  $\mathbf{R}^n$  :

$$\int_0^t X_s dW_s = \sum_{i=1}^p H_i (W_{t \wedge t_{i+1}} - W_{t_i}), \quad t \geq 0.$$

Soit  $X = (X_t)$  un processus stochastique adapté à valeurs dans  $\mathcal{M}_{n \times d}$  tel que

$$\int_0^t \|X_s\|^2 ds < \infty \text{ p.s. } \forall t \geq 0.$$

(où  $\|\cdot\|^2$  est la norme euclidienne sur  $\mathbf{R}^{nd}$ ). On peut trouver une suite  $X^{(n)}$  de processus prévisibles élémentaires telle que

$$\int_0^t \|X_s^{(n)} - X_s\|^2 ds \longrightarrow 0 \text{ en probabilité } \forall t \geq 0.$$

De plus, pour tout  $t \geq 0$ , les intégrales stochastiques  $\int_0^t X^{(n)} dW_s$  convergent en probabilité vers une limite, qui ne dépend pas de la suite approximante  $(X^{(n)})$ . On définit  $\int_0^t X_s dW_s$  comme étant cette limite.

### 2.2.3 Formule d'Itô multidimensionnelle

**Définition 2.7.** On dit que  $(X_t)_{t \geq 0}$  est un processus d'Itô s'il est de la forme  $X_t = (X_t^i)_{1 \leq i \leq n}$  avec, pour  $1 \leq i \leq n$  :

$$X_t^i = X_0^i + \int_0^t a_s^i ds + \sum_{j=1}^d \int_0^t b_s^{ij} dW_s^j, \quad (2.11)$$

où

- $a_t^i$  et les  $(b_t^{ij})$  sont adaptés à  $\mathcal{F}_t$ ,  $a \in \mathbf{R}^d$ ,  $a = (a^i)$  à valeurs dans  $\mathbf{R}^n$  et  $b = (b_{ij})$  à valeurs dans  $\mathcal{M}_{n \times d}$
- $\int_0^t |a_s^i| ds < +\infty \forall t \geq 0 \mathbf{P} - \text{p.s.}, 1 \leq i \leq n$
- $\int_0^t |b_s^j|^2 ds < +\infty \forall t \geq 0 \mathbf{P} - \text{p.s.}, 1 \leq i \leq n, (1 \leq j \leq d).$

On utilise la notation différentielle

$$dX_t = a_t dt + b_t dW_t$$

**Théorème 2.5.** (Formule d'Itô) Soit  $X(t) \in \mathbf{R}^n$  un processus d'Itô, défini en (2.11).

Si  $f(t, x_1, \dots, x_d)$  est une fonction continue sur  $[0, +\infty[ \times \mathbf{R}^n$  admettant les dérivées partielles continues  $\frac{\partial f}{\partial t}, \frac{\partial f}{\partial x_i}, \frac{\partial^2 f}{\partial x_i \partial x_j}$ ,  $i, j = 1, \dots, d$ . Alors, le processus  $F_t = f(t, X(t))$  satisfait l'équation (en notation différentielle)

$$\begin{aligned} dF_t = & \left( \frac{\partial f}{\partial t}(t, X(t)) + \sum_{i=1}^d \frac{\partial f}{\partial x_i}(t, X(t)) a_i(t) \right. \\ & \left. + \frac{1}{2} \sum_{k=1}^n \sum_{i,j=1}^d \frac{\partial^2 f}{\partial x_i \partial x_j}(t, X(t)) b_{ik}(t) b_{jk}(t) \right) dt \\ & + \sum_{k=1}^n \sum_{i=1}^d \frac{\partial f}{\partial x_i} b_{ik}(t) dW_k(t). \end{aligned}$$

### 2.2.4 Equations différentielles stochastiques

Le concept d'équation différentielle stochastique (EDS) généralise celui d'équation différentielle ordinaire aux processus stochastiques. À partir de la théorie de l'intégration stochastique, on construit la théorie des EDS qui sont utilisées dans différentes branches des sciences où l'on a besoin d'un modèle de la forme

$$\frac{dX(t)}{dt} = a(t, X(t)) + v(t), \quad (2.12)$$

où  $v(t)$  est l'effet de perturbation. Dans le cas où l'effet de perturbation est irrégulier, c'est à dire, lorsque les phénomènes sont soumis à des excitations stochastiques de type

$$v(t) = b(t, X(t)) \frac{dW(t)}{dt},$$

où  $(W(t), t \in [0, T])$  est un mouvement brownien, l'équation (2.12) devient

$$\frac{dX(t)}{dt} = a(t, X(t)) + b(t, X(t)) \frac{dW(t)}{dt}, \quad t \in [0, T]. \quad (2.13)$$

C'est une équation différentielle ordinaire perturbée par une perturbation aléatoire

$$b(t, X(t)) \frac{dW(t)}{dt}$$

où  $\frac{dW(t)}{dt}$  est une dérivée formelle par rapport au temps du mouvement brownien  $W$  sur  $\mathbf{R}^d$ . Pour donner un sens à  $\frac{dW(t)}{dt}$ , on écrit l'équation (2.12) sous la forme (en notation différentielle)

$$dX(t) = a(t, X(t))dt + b(t, X(t))dW(t), \quad t \in [0, T]. \quad (2.14)$$

Soient  $a : [0, \infty[ \times \mathbf{R}^n \rightarrow \mathbf{R}^n$  et  $b : [0, \infty[ \times \mathbf{R}^n \rightarrow \mathcal{M}_{n \times d}$  et supposons que les  $a_i, b_{ij}$ ,  $i = 1, \dots, n, j = 1, \dots, d$  sont mesurables en  $(t, x)$  avec,  $W$  est un mouvement brownien en dimension

$t$  défini sur l'espace probabilisé filtré  $(\Omega, \mathcal{F}, \mathcal{F}_t, \mathbf{P})$ . Si  $X(t)$  est un processus stochastique tel que

$$X(t) = x_0 + \int_0^t a(s, X(s))ds + \int_0^t b(s, X(s))dW(s), \quad t \in [0, \infty[, \quad (2.15)$$

où  $x_0 \in \mathbf{R}^n$  est fixé. alors on dit que  $X(t)$  vérifie le système de Cauchy

$$\begin{cases} dX(t) = a(t, X(t))dt + b(t, X(t))dW(t), & t \in [0, \infty[, \\ X(0) = x_0, & \mathbf{P}\text{-p.s.} \end{cases} \quad (2.16)$$

La première équation de (2.16) (c'est à dire l'équation (2.14)) s'appelle une *équation différentielle stochastique*.

**Définition 2.8.** *Le système (2.16) est dit uniformément persistant s'il existe  $\varepsilon > 0$  tel que*

$$\liminf_{t \rightarrow \infty} X(t) \geq \varepsilon$$

Concernant l'existence et l'unicité de la solution, on a les résultats suivants.

**Théorème 2.6.** *(Théorème d'existence et d'unicité globales [24]) Supposons que pour tous  $t \geq 0$ ,  $x, y \in \mathbf{R}^n$ ,*

- 1)  $a(t, x)$  et  $b(t, x)$  sont mesurables dans  $[0, T] \times \mathbf{R}^n$  à valeurs dans  $\mathbf{R}^n$  et  $\mathcal{M}_{n \times d}$  respectivement
- 2)  $|a(t, x) - a(t, y)| \leq k_1|x - y|$ ,  $|b(t, x) - b(t, y)| \leq k_1|x - y|$ ,
- 3)  $|a(t, x)| \leq k_1(1 + |x|)$ ,  $|b(t, x)| \leq k_2(1 + |x|)$ , ( $k_1$  et  $k_2$  deux constantes quelconques).

Alors il existe une solution unique globale (définie sur  $\mathbf{R}^+$ ) du système (2.16), et cette solution est un processus d'Itô.

Notons que l'unicité est comprise au sens des trajectoires  $\mathbf{P}$  - p.s., c'est à dire, si  $\xi_1(t)$  et  $\xi_2(t)$  sont deux solutions, alors  $\mathbf{P}\{\xi_1(t) = \xi_2(t), t \in [0, T]\} = 1$ .

**Théorème 2.7.** *(Théorème de comparaison global [22, Theorem 1])*

*Soient les équations différentielles*

$$\begin{aligned} dX_j(t) &= a_j(t, X(t))dt + \sum_{k=1}^r \sigma_{jk}(t, X_j(t))dW_k(t) \\ dY_j(t) &= b_j(t, Y(t))dt + \sum_{k=1}^r \sigma_{jk}(t, Y_j(t))dW_k(t) \end{aligned}$$

où  $j = 1, \dots, d$ , supposons que :

A.1  $X(0) \leq Y(0)$

A.2 Les fonctions  $a_j$ ,  $b_j$  et  $\sigma_{jk}$  sont continues par rapport aux deux variables, et elles sont lipschitziennes par rapport à la deuxième variable, uniformément par rapport à la première pour tous  $j \in 1, \dots, d$  et  $k \in 1, \dots, r$ .

A.3 Pour tout  $t \geq 0$ ,  $a_j(t, x) \leq b_j(t, y)$  si  $x_i \leq y_i$  et  $x_j = y_j$ .

Alors, on a

$$\mathbf{P}\{X(t) \leq Y(t) : t \geq 0\} = 1.$$

### 2.2.5 Temps d'arrêt, localisation

**Définition 2.9.** On appelle temps d'arrêt par rapport à la filtration  $(\mathcal{F}_t)_{t \geq 0}$  une variable aléatoire  $\tau$  à valeurs dans  $\mathbf{R}^+ \cup +\infty$  telle que, pour tout  $t \geq 0$  :

$$\{\tau \leq t\} \in \mathcal{F}_t.$$

L'utilisation d'une suite croissante  $(\tau_n)$  de temps d'arrêt telle que  $\lim_{n \rightarrow \infty} \tau_n = +\infty$  p.s. permet de donner des versions locales de certains théorèmes :

**Théorème 2.8. Théorème d'existence et d'unicité locales** Supposons que

- 1)  $a(t, x)$  et  $b(t, x)$  sont mesurables dans  $[0, T] \times \mathbf{R}^n$ ,
- 2)  $|a(t, x) - a(t, y)| \leq k_1|x - y|$ ,  $|b(t, x) - b(t, y)| \leq k_1|x - y|$ ,

Alors il existe un temps d'arrêt maximal  $\tau_e$  et une solution unique du système (2.16) définie sur un intervalle stochastique  $\llbracket 0, \tau_e \rrbracket = \{(\omega, t) \in \Omega \times \mathbf{R}^+ / 0 \leq t \leq \tau_e\}$  où  $\tau_e = \sup_N \tau_N$ .

Le temps d'arrêt  $\tau_e$  est appelé *temps d'explosion*.

**Théorème 2.9. Théorème de comparaison local**

Soient les équations différentielles

$$\begin{aligned} dX_j(t) &= a_j(t, X(t))dt + \sum_{k=1}^r \sigma_{jk}(t, X_j(t))dW_k(t) \\ dY_j(t) &= b_j(t, Y(t))dt + \sum_{k=1}^r \sigma_{jk}(t, Y_j(t))dW_k(t) \end{aligned}$$

où  $j = 1, \dots, d$ , supposons que :

A.1  $X(0) \leq Y(0)$

A.2 Les fonctions  $a_j$ ,  $b_j$  et  $\sigma_{jk}$  sont continues par rapport aux deux variables, et elles sont localement lipschitziennes par rapport à la deuxième variable, uniformément par rapport à la première pour tous  $j \in 1, \dots, d$  et  $k \in 1, \dots, r$ ,  $t \geq 0$  et  $x, y \in \mathbf{R}^n$

A.3 Pour tout  $t \geq 0$ ,  $a_j(t, x) \leq b_j(t, y)$  si  $x_i \leq y_i$  et  $x_j = y_j$ .

Alors, on a

$$\mathbf{P}\{X(t) \leq Y(t) : t \geq 0\} = 1.$$

Nous donnons seulement la démonstration du Théorème (2.9), celle du Théorème (2.8) s'obtient par des arguments similaires.

**Démonstration du Théorème (2.9)**

Soit  $X$  solution de

$$dX_t = b(t, X_t)dt + \sigma(t, X_t)dW_t, \quad (2.17)$$

où les applications  $b(t, \cdot)$  et  $\sigma(t, \cdot)$  sont localement lipschitziennes uniformément par rapport à  $t$ , et soit  $X^N$  vérifiant

$$dX_t^N = b^N(t, X_t)dt + \sigma^N(t, X_t)dW_t, \quad (2.18)$$

où  $b^N(t, X_t) = b(t, \alpha_N(X_t)X_t)$  et  $\sigma^N(t, X_t) = \sigma(t, \alpha_N(X_t)X_t)$  avec

$$\alpha_N(X) = \begin{cases} 1 & \text{si } \|X\| \leq N \\ \frac{N}{\|X\|} & \text{si } \|X\| > N. \end{cases}$$

**Etape 1** Montrons que pour chaque  $N$ ,  $b^N$  et  $\sigma^N$  vérifient les hypothèses globales du théorème de comparaison.

Pour tout  $x$ , il existe  $R_x > 0$  et  $K_x > 0$ , tels que  $b(t, \cdot)$  est  $K_x$ -lipschitzienne, uniformément sur la boule  $B(x, R_x)$ , pour tout  $t$ . Soit  $N > 0$ , on a  $B(0, N) \subset \cup_{x \in B(0, N)} B(x, R_x)$ , avec  $R_x > 0$  pour tout  $x$ . Par compacité, on obtient  $B(0, N) \subset \cup_{i=1}^n B(x_i, R_{x_i})$ , donc  $b(t, \cdot)$  est  $K = \vee_{i=1}^n k_{x_i}$ -lipschitzienne sur  $B(0, N)$ . On en déduit que  $b^N(t, \cdot)$  est  $K$ -lipschitzienne, pour tout  $t$ . De même  $\sigma^N$  est lipschitzienne par rapport à la deuxième variable, uniformément par rapport à la première variable.

**Etape 2** On définit le temps d'arrêt  $\tau_N = \inf\{t < \tau_e; \|X\| > N\}$ ,  $N > 0$ , où  $\tau_e$  est le temps d'explosion. Montrons que  $\lim_{N \rightarrow \infty} \tau_N = \tau_e$ .

La suite  $(\tau_N)$  est croissante, donc  $\tau = \lim_{N \rightarrow \infty} \tau_N = \sup_N \tau_N \leq \tau_e$ .

Pour  $\omega$  fixé dans  $\Omega$ , pour chaque  $N$ , il existe  $t_N \in [\tau_N(\omega), \tau_N(\omega) + \frac{1}{N}]$  tel que  $|X_{t_N}(\omega)| > N$ . On a  $\lim_{N \rightarrow \infty} |X_{t_N}(\omega)| = +\infty$ , donc  $\lim_{N \rightarrow \infty} t_N(\omega) \geq \tau_e(\omega)$ , or  $\lim_{N \rightarrow \infty} t_N(\omega) = \tau(\omega)$ . Donc  $\tau(\omega) = \tau_e(\omega)$  pour tout  $\omega$ .

**Etape 3** Montrons que, pour chaque  $N$ ,  $X = X^N$ ,  $Y = Y^N$  sur l'intervalle stochastique  $[[0, \tau_N]]$ .

Soient  $X$  et  $X^N$  deux solutions des équations (2.17) et (2.18) respectivement. Pour tout  $t \geq 0$ , on a

$$\begin{aligned} X_{t \wedge \tau_N} - X_{t \wedge \tau_N}^N &= \int_0^{t \wedge \tau_N} (b(s, X_s) - b^N(s, X_s^N))dt + \int_0^{t \wedge \tau_N} (\sigma(s, X_s) - \sigma^N(s, X_s^N))dW_s \\ \|X_{t \wedge \tau_N} - X_{t \wedge \tau_N}^N\|^2 &= \left\| \int_0^{t \wedge \tau_N} (b(s, X_s) - b^N(s, X_s^N))dt + \int_0^{t \wedge \tau_N} (\sigma(s, X_s) - \sigma^N(s, X_s^N))dW_s \right\|^2 \\ &\leq 4 \int_0^{t \wedge \tau_N} \|b(s, X_s) - b^N(s, X_s^N)\|^2 ds + 4 \int_0^{t \wedge \tau_N} \|\sigma(s, X_s) - \sigma^N(s, X_s^N)\|^2 dW_s \\ &= 4 \int_0^{t \wedge \tau_N} \|b^N(s, X_s) - b^N(s, X_s^N)\|^2 ds + 4 \int_0^{t \wedge \tau_N} \|\sigma^N(s, X_s) - \sigma^N(s, X_s^N)\|^2 dW_s \\ \mathbf{E}\|X_{t \wedge \tau_N} - X_{t \wedge \tau_N}^N\|^2 &\leq 4(T+1)K^2 \int_0^t \mathbf{E}\|X_{s \wedge \tau_N} - X_{s \wedge \tau_N}^N\|^2 ds. \end{aligned}$$

D'après l'inégalité de Gronwall, on trouve

$$\mathbf{E}\|X_{t \wedge \tau_N} - X_{t \wedge \tau_N}^N\|^2 \leq 0.$$

Donc, pour tout  $N > 0$ ,  $X = X^N$  sur  $[[0, \tau_N]]$ . De même  $Y = Y^N$  sur  $[[0, \tau_N]]$ .

**Etape 4** Il suffit d'appliquer le théorème de comparaison global (2.7) à  $X^N$  et  $Y^N$  et faire converger  $N$  vers  $\infty$ .

### 2.2.6 Simulation par la méthode de Milstein

Soit le processus stochastique  $X = \{X_t, t \geq 0\}$  de la forme

$$X_t = x_0 + \int_0^t a(X_s)ds + \int_0^t b(X_s)dW_s \quad (2.19)$$

Pour simuler numériquement les solutions de l'équation (2.19), on peut discrétiser l'équation (2.19) par le schéma de Milstein. Dans le cas multidimensionnel général, la  $k$ -ème coordonnée de  $X$  dans le schéma de Milstein a la forme

$$X_{n+1}^k = X_n^k + a^k(t_{i+1} - t_i) + b^k(W_{i+1} - W_i) + \frac{1}{2} \left( \sum_{l=1}^d b^l \frac{\partial b^k}{\partial x^l} \right) ((W_{i+1} - W_i)^2 - (t_{i+1} - t_i))$$

On dit qu'une solution numérique  $X^n$  converge fortement vers  $X$  solution de (2.19) à l'ordre  $\gamma > 0$  s'il existe une constante  $c > 0$  telle que

$$\mathbf{E}\|X_T(\omega) - X_T^n(\omega)\| \leq c\delta_n^\gamma \text{ pour } \delta_n \leq \delta_0,$$

où  $\delta_n = \max_{i=1, \dots, n} t_i - t_{i-1}$ . Le schéma de Milstein converge fortement à l'ordre 1.0. Le lecteur pourra se reporter, à [39] pour une présentation plus complète et la démonstration de ce résultat.

# Chapitre 3

## Dynamics of a stochastically perturbed prey-predator system with modified Leslie-Gower and Holling type II schemes incorporating a prey refuge

### 3.1 Introduction

We study a two-dimensional prey-predator system with modified Leslie-Gower and Holling type II functional responses. This system is a generalization of the system investigated in the papers by M.A. Aziz-Alaoui and M. Daher-Okiye [7, 19].

Aziz-Alaoui and Daher-Okiye's model has been studied and generalized in numerous papers : models with spatial diffusion term [12, 80, 2, 1], with time delay [65, 82, 81], with stochastic perturbations [55, 54, 59, 52], or incorporataing a refuge for the prey [13], to cite but a few.

A novelty of the present paper is that we add a refuge in a way which is different from [13], since the density of prey in our refuge is not proportional to the total density of prey. This kind of refuge entails a qualitatively different behavior of the solutions, even for a small refuge, contrarily to the type of refuge investigated in [13]. Let us emphasize that, even in the case without refuge, our study provides new results.

In the first and main part of the paper (Section 3.2), we study the system of [7, 19] with refuge, but without stochastic perturbation :

$$\begin{cases} \dot{\mathbf{x}} = \mathbf{x}(\rho_1 - \beta\mathbf{x}) - \frac{\alpha_1\mathbf{y}(\mathbf{x} - \mu)_+}{\kappa_1 + (\mathbf{x} - \mu)_+}, \\ \dot{\mathbf{y}} = \mathbf{y} \left( \rho_2 - \frac{\alpha_2\mathbf{y}}{\kappa_2 + (\mathbf{x} - \mu)_+} \right). \end{cases} \quad (3.1)$$

In this system,

- $\mathbf{x} \geq 0$  is the density of prey,
- $\mathbf{y} \geq 0$  is the density of predator,
- $\mu \geq 0$  models a refuge for the prey, i.e, the quantity  $(\mathbf{x} - \mu)_+ := \max(0, \mathbf{x} - \mu)$  is the density of prey which is accessible to the predator,
- $\rho_1 > 0$  (resp.  $\rho_2 > 0$ ) is the growth rate of prey (resp. of predator),



- $\beta > 0$  measures the strength of competition among individuals of the prey species,
- $\alpha_1 > 0$  (resp.  $\alpha_2 > 0$ ) is the rate of reduction of preys (resp. of predators)
- $\kappa_1 > 0$  (resp.  $\kappa_2 > 0$ ) measures the extent to which the environment provides protection to the prey (resp. to the predator).

When the predator is absent, the density of prey  $\mathbf{x}$  satisfies a logistic equation and converges to  $\frac{\rho_1}{\beta}$ , so we assume that

$$0 \leq \mu < \frac{\rho_1}{\beta}.$$

The last term in the right hand side of the first equation of (3.1), which expresses the loss of prey population due to the predation, is a modified Holling type II functional response, where the modification consists in the introduction of the refuge  $\mu$ . The predation rate of the predators decreases when they are driven to satiety, so that the consumption rate of preys decreases when the density of prey increases.

Similarly, if its favorite prey is absent (or hidden in the refuge), the predator has a logistic dynamic, which means that it survives with other prey species, but with limited growth. The last term in the right hand side of the second equation, of (3.1) is a modified Leslie-Gower functional response, see [45, 69]. Here, the modification lies in the addition of the constant  $\kappa_2$ , as in [7, 19], as well as in the introduction of the refuge  $\mu$ . It models the loss of predator population when the prey becomes less available, due its rarity and to the presence of the refuge.

Setting, for  $i = 1, 2$ ,

$$\begin{aligned} x(t) &= \frac{\beta}{\rho_1} \mathbf{x} \left( \frac{t}{\rho_1} \right), \quad y(t) = \frac{\beta}{\rho_1} \mathbf{y} \left( \frac{t}{\rho_1} \right), \\ m &= \frac{\mu\beta}{\rho_1}, \quad a = \frac{\alpha_1\rho_2}{\alpha_2\rho_1}, \quad k_i = \frac{\kappa_i\beta}{\rho_1}, \quad b = \frac{\rho_2}{\rho_1}, \end{aligned}$$

we get the simpler equivalent system

$$\begin{cases} \dot{x} = x(1-x) - \frac{ay(x-m)_+}{k_1 + (x-m)_+}, \\ \dot{y} = by \left( 1 - \frac{y}{k_2 + (x-m)_+} \right), \end{cases} \tag{3.2}$$

where  $0 \leq m < 1$ , all other parameters are positive, and  $(x, y)$  takes its values in the quadrant  $\mathbf{R}_+ \times \mathbf{R}_+$ .

In this first part, we study the dynamics of Equation 3.2, which is complicated by the refuge parameter  $m$ . However, even in the case when  $m = 0$ , we provide some new results. We first show the persistence and the existence of a compact attracting set. Then, we study in detail the equilibrium points (there can be 3 distinct non trivial such points when  $m > 0$ ) and their local stability. We also give sufficient conditions for the existence of a globally asymptotically stable equilibrium, and we give some sufficient conditions for the absence of periodic orbits. A stable limit cycle may surround several limit points, as we show numerically.

In a second part (Section 3.3), we study the stochastically perturbed system

$$\begin{cases} dx(t) = \left( x(t)(1 - x(t)) - \frac{ay(t)(x(t) - m)_+}{k_1 + (x(t) - m)_+} \right) dt + \sigma_1 x(t) dw_1(t), \\ dy(t) = by(t) \left( 1 - \frac{y(t)}{k_2 + (x(t) - m)_+} \right) dt + \sigma_2 y(t) dw_2(t), \end{cases} \quad (3.3)$$

where  $w = (w_1, w_2)$  is a standard Brownian motion defined on the filtered probability space  $(\Omega, \mathcal{F}, (\mathcal{F}_t), \mathbb{P})$ , and  $\sigma_1$  and  $\sigma_2$  are constant real numbers. This perturbation represents the environmental fluctuations. There are many ways to model the randomness of the environment, for example using random parameters in Equation (3.2). Since the right hand side of Equation (3.2) depends nonlinearly on many parameters, the approach using Itô stochastic differential equations with Gaussian centered noise models in a simpler way the fuzzyness of the solutions around their mean values. The choice of a multiplicative noise in this context is classical, see [62], and it has the great advantage over additive noise that solutions starting in the quadrant  $]0, +\infty[ \times ]0, +\infty[$  remain in it. Furthermore, the independence of the Brownian motions  $w_1$  and  $w_2$  reflects the independence of the parameters in both equations of (3.2).

Another possible choice of stochastic perturbation would be to center the noise on an equilibrium point of the deterministic system, as in [8]. But we shall see in Theorem 3.2 that the system (3.2) may have three distinct equilibrium points. Furthermore, as in the case of additive noise, this type of noise would allow the solutions to have excursions outside the quadrant  $]0, +\infty[ \times ]0, +\infty[$ , which of course would be unrealistic.

We show in Section 3.3 the existence and uniqueness of the global positive solution with any initial positive value of the stochastic system (3.3), and we show that, when the diffusion coefficients  $\sigma_1 > 0$  and  $\sigma_2 > 0$  are small, the solutions to (3.3) converge to a unique ergodic stationary distribution, whereas, when they are large, the system (3.3) goes asymptotically to extinction. Small values of  $\sigma_1$  and  $\sigma_2$  are more interesting for ecological modeling, because they make solutions of (3.3) closer to the prey-predator dynamics. The effect of such a small or moderate perturbation is the disparition of all equilibrium points of the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , replaced by a unique equilibrium, the stationary ergodic distribution, which is an attractor.

The last part of the paper is Section 3.4, where we make numerical simulation to illustrate our results.

## 3.2 Dynamics of the deterministic system

In this section, we study the dynamics of (3.2).

Throughout, we denote by  $\mathbf{v}$  the vector field associated with (3.2), and

$$\mathbf{v} = v_1 \frac{\partial}{\partial x} + v_2 \frac{\partial}{\partial y},$$

so that (3.2) reduces to  $(\dot{x} = v_1 \text{ and } \dot{y} = v_2)$ .

The right hand side of (3.2) is locally Lipschitz, thus, for any initial condition, (3.2) has a unique solution defined on a maximal time interval.

Furthermore, the axes are invariant manifolds of (3.2) :

— If  $x(0) = 0$ , then  $x(t) = 0$  for every  $t$ , and  $\dot{y} = by(1 - y/k_2)$  yields

$$y(t) = \frac{y(0)k_2}{k_2 + y(0)(e^{bt} - 1)},$$

thus  $\lim_{t \rightarrow +\infty} y(t) = k_2$  if  $y(0) > 0$ .

— If  $y(0) = 0$ , then  $y(t) = 0$  for every  $t$ , and  $\dot{x} = x(1 - x)$  yields

$$x(t) = \frac{x(0)}{1 + x(0)(e^t - 1)},$$

thus  $\lim_{t \rightarrow +\infty} x(t) = 1$  if  $x(0) > 0$ .

From the uniqueness theorem for ODEs, we deduce that the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  is stable, thus there is no extinction of any species in finite time.

### 3.2.1 Persistence and compact attracting set

The next result shows that there is no explosion of the system (3.2). It also shows a qualitative difference brought by the refuge : when  $m = 0$ , the density of prey may converge to 0, whereas, when  $m > 0$ , the system (3.2) is always uniformly persistent.

Let

$$\mathcal{A} = \{(x, y) \in \mathbf{R}^2; m \leq x \leq 1, k_2 \leq y < L\},$$

where  $L = 1 + k_2 - m$ .

**Théorème 3.1.** (a) *The set  $\mathcal{A}$  is positively invariant for (3.2). Furthermore, if the initial condition  $(x(0), y(0))$  is in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , we have*

$$\begin{cases} m \leq \liminf_{t \rightarrow +\infty} x(t) \leq \limsup_{t \rightarrow +\infty} x(t) \leq 1, \\ k_2 \leq \liminf_{t \rightarrow +\infty} y(t) \leq \limsup_{t \rightarrow +\infty} y(t) \leq L. \end{cases} \quad (3.4)$$

(b) *In the case when  $m > 0$ , for any initial condition  $(x(0), y(0))$  in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , the solution  $(x(t), y(t))$  enters  $\mathcal{A}$  in finite time. In particular, the system (3.2) is uniformly persistent.*

(c) *In the case when  $m = 0$ , for any  $\epsilon > 0$  such that  $k_2 - \epsilon > 0$ , the compact set  $[0, 1] \times [k_2 - \epsilon, L]$  is positively invariant, and, for any initial condition  $(x(0), y(0))$  in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , the solution  $(x(t), y(t))$  enters  $[0, 1] \times [k_2 - \epsilon, L]$  in finite time. Furthermore :*

(i) If  $aL < k_1$ , the system (3.2) is uniformly persistent. More precisely, if  $(x(0), y(0)) \in ]0, +\infty[ \times ]0, +\infty[$ , we have

$$\liminf_{t \rightarrow +\infty} x(t) \geq \frac{k_1 - aL}{k_1}. \quad (3.5)$$

(ii) If  $ak_2 < k_1 \leq aL$ , the system (3.2) is uniformly weakly persistent. More precisely, if  $(x(0), y(0)) \in ]0, +\infty[ \times ]0, +\infty[$ , we have

$$\limsup_{t \rightarrow +\infty} x(t) \geq \min \left( \frac{k_1}{a} - k_2, \frac{1 - k_1 - a + \sqrt{(1 - k_1 - a)^2 + 4(k_1 - ak_2)}}{2} \right). \quad (3.6)$$

(iii) If  $k_1 = ak_2$ , then :

— If  $1 - k_1 - a > 0$ , the system (3.2) is uniformly weakly persistent. More precisely, if  $(x(0), y(0)) \in ]0, +\infty[ \times ]0, +\infty[$ , we have

$$\limsup_{t \rightarrow +\infty} x(t) \geq 1 - k_1 - a. \quad (3.7)$$

— If  $1 - k_1 - a \leq 0$ , the point  $E_2 = (0, k_2)$  is globally attracting, thus the prey becomes extinct asymptotically for any initial condition in  $]0, +\infty[ \times ]0, +\infty[$ .

(iv) If  $k_1 < ak_2$ , the point  $E_2 = (0, k_2)$  is globally attracting, thus the prey becomes extinct in infinite time for any initial condition in  $]0, +\infty[ \times ]0, +\infty[$ .

**Remark 3.1.** A more general sufficient condition of global attractivity of  $E_2$  is provided by Theorem 3.3 (see Remark 3.5).

**Proof.** [Proof of Theorem 3.1] (a) When  $m = 0$ , the first inequality in (3.4) is trivial. In the case when  $m > 0$ , we need to prove that  $\liminf x(t) \geq m$ , provided that  $x(0) > 0$ . Actually we have a better result, since, if  $x(0) \leq m$ , then  $x$  coincides with the solution to the logistic equation  $\dot{x} = x(1 - x)$  as long as  $x$  does not reach the value  $m$ , that is,

$$x(t) = \frac{e^t x(0)}{1 + x(0)(e^t - 1)}.$$

If  $x(0) > 0$ , this function converges to 1, thus there exists  $t_m > 0$  such that

$$t \geq t_m \Rightarrow x(t) \geq m. \quad (3.8)$$

Note that, when  $m > 0$ , if  $x(t) = m$ , we have  $\dot{x}(t) = m(1 - m) > 0$ . Thus

$$\left( x(0) \geq m \right) \Rightarrow \left( x(t) \geq m, \forall t \geq 0 \right), \quad (3.9)$$

which implies the first inequality in (3.4). Now, from the first equation of (3.2), we have

$$\dot{x} \leq x(1 - x),$$

which implies that, for every  $t \geq 0$ ,

$$x(t) \leq \frac{x(0)e^t}{1 + x(0)(e^t - 1)}. \quad (3.10)$$

In particular, we have

$$\limsup_{t \rightarrow +\infty} x(t) \leq 1 \text{ and } \left( x(0) \leq 1 \Rightarrow x(t) \leq 1, \forall t \geq 0 \right). \quad (3.11)$$

This implies that, for any  $\epsilon > 0$ , and for  $t$  large enough (depending on  $x(0)$ ), we have  $x(t) \leq 1 + \epsilon$ . We deduce that, for any  $\epsilon > 0$ , and for  $t$  large enough, we have

$$by \left( 1 - \frac{y}{k_2} \right) \leq \dot{y}(t) \leq by \left( 1 - \frac{y}{k_2 + 1 + \epsilon - m} \right) = by \left( 1 - \frac{y}{L + \epsilon} \right), \quad (3.12)$$

which implies that, for  $t$  large enough, say,  $t \geq t_0$ ,

$$\frac{y(0)k_2e^{bt}}{k_2 + y(0)(e^{bt} - 1)} \leq y(t) \leq \frac{y(t_0)(L + \epsilon)e^{b(t-t_0)}}{L + \epsilon + y(t_0)(e^{b(t-t_0)} - 1)}. \quad (3.13)$$

Of course, if  $x(0) \leq 1$ , we can drop  $\epsilon$  in (3.12) and (3.13). Thus, we have

$$\left( x(0) \leq 1 \text{ and } k_2 \leq y(0) \leq L \right) \Rightarrow \left( k_2 \leq y(t) \leq L, \forall t \geq 0 \right). \quad (3.14)$$

We deduce from (3.9), (3.11), and (3.14) that  $\mathcal{A}$  is positively invariant.

As  $\epsilon$  is arbitrary in (3.13), we have also, when  $y(0) > 0$ ,

$$k_2 \leq \liminf_{t \rightarrow +\infty} y(t) \leq \limsup_{t \rightarrow +\infty} y(t) \leq L. \quad (3.15)$$

From (3.8), (3.11), and (3.15), we deduce (3.4).

(b) We have already seen that  $x(t) \geq m$  for  $t$  large enough, let us now check that  $x(t) \leq 1$  for  $t$  large enough. Since  $\mathcal{A}$  is positively invariant, we only need to prove this for  $x(0) > 1$ . Let  $\epsilon > 0$  such that  $k_2 - \epsilon > 0$ . Let  $\delta > 0$  such that  $\delta + m < 1$  and such that

$$(x \geq 1 - \delta) \Rightarrow x(1 - x) < \frac{a(k_2 - \epsilon)(1 - m)}{1 + \epsilon - m}. \quad (3.16)$$

From the first inequality in (3.15), we have  $y(t) \geq k_2 - \epsilon$  for  $t$  large enough, say  $t \geq t_0$ . From (3.11), we can take  $t_0$  large enough such that, for  $t \geq t_0$ , we have also  $x(t) \leq 1 + \epsilon$ . Using (3.16), we deduce, for  $t \geq t_0$  and  $x(t) \geq 1 - \delta$ ,

$$\begin{aligned} \dot{x}(t) &\leq x(t)(1 - x(t)) - \frac{a(k_2 - \epsilon)(1 - \delta - m)}{1 + \epsilon - m} \\ &\leq -\frac{a\delta(k_2 - \epsilon)}{1 + \epsilon - m}. \end{aligned}$$

Thus  $x$  decreases with speed less than  $-\frac{a\delta(k_2 - \epsilon)}{1 + \epsilon - m} < 0$ . Thus  $x(t) \leq 1 - \delta$  for  $t$  large enough.

We can now repeat the reasoning of (3.12) and (3.13), replacing  $\epsilon$  by  $-\delta$ , which yields that  $\limsup y(t) \leq L - \delta$ . In particular,  $y(t) < L$  for  $t$  large enough.

To prove that  $y(t) > k_2$  for  $t$  large enough, let us first sharpen the result of (3.8). This is where we use that  $m > 0$ . Let  $\delta > 0$ , with  $m + \delta < 1$ . If  $|x - m| < \delta$ , we have

$$|x(1-x) - m(1-m)| = |(x-m)(1-(x+m))| \leq |x-m| < \delta.$$

From (3.15), we deduce that, for any  $\epsilon > 0$ , and  $t$  large enough, depending on  $\epsilon$ , we have

$$y(t) \leq L + \epsilon \text{ and } x(t) \geq m,$$

from which we deduce

$$\dot{x} \geq x(1-x) - \frac{a(L+\epsilon)\delta}{k_1} \geq D := m(1-m) - \delta - \frac{a(L+\epsilon)\delta}{k_1}.$$

(we do not write  $t$  here for the sake of simplicity). For  $\delta$  small enough, we have  $D > 0$ . Thus, if  $m > 0$ , we can find  $\delta > 0$  small enough (depending on  $m$ ), such that, when  $x(t)$  is in the interval  $[m, m + \delta]$ , it reaches the value  $m + \delta$  in finite time (at most  $D\delta$ ), and then it stays in  $[m + \delta, 1]$ . Using (3.8), we deduce that there exists  $t_{m+\delta} > 0$  such that

$$t \geq t_{m+\delta} \Rightarrow x(t) \geq m + \delta. \quad (3.17)$$

Using (3.17) in (3.2), we obtain, for  $t \geq t_{m+\delta}$ ,

$$\dot{y} \geq by \left(1 - \frac{y}{k_2 + \delta}\right),$$

which yields, if  $y(0) > 0$ ,

$$y(t) \geq \frac{y(t_{m+\delta})(k_2 + \delta)e^{b(t-t_{m+\delta})}}{k_2 + \delta + y(t_{m+\delta})(e^{b(t-t_{m+\delta})} - 1)}.$$

This proves that

$$\liminf_{t \rightarrow +\infty} y(t) \geq k_2 + \delta,$$

and that  $y > k_2$  for  $t$  large enough.

(c) Assume now that  $m = 0$ . Since the first part of the proof of (b) is valid for all  $m \geq 0$ , we have already proved that  $x(t) < 1$  and  $y(t) < L$  for  $t$  large enough. Let  $\epsilon > 0$  such that  $k_2 - \epsilon > 0$ . For  $y < k_2$ , we have  $\dot{y} > 0$ , thus  $[0, 1] \times [k_2 - \epsilon, L]$  is positively invariant. Furthermore, for any initial condition  $(x(0), y(0)) \in ]0, +\infty[ \times ]0, +\infty[$ , since  $\liminf y(t) \geq k_2$ , we have  $y(t) > k_2 - \epsilon$  for  $t$  large enough, thus  $(x(t), y(t))$  enters  $[0, 1] \times [k_2 - \epsilon, L]$  in finite time.

(ci) Assume that  $aL < k_1$ , and let  $\epsilon > 0$  such that  $a(L + \epsilon) < k_1$ . Let  $K_\epsilon = \frac{k_1 - a(L + \epsilon)}{k_1}$ . By the second inequality in (3.15), we have, for  $t$  large enough

$$\dot{x} \geq x(1-x) - \frac{ax(L+\epsilon)}{k_1} = K_\epsilon x \left(1 - \frac{x}{K_\epsilon}\right). \quad (3.18)$$

Thus  $\liminf x(t) \geq K_\epsilon$ . As  $\epsilon$  is arbitrary, this proves (3.5). From (3.5) and the first inequality in (3.15), we deduce that (3.2) is uniformly persistent.

(cii) Assume now that  $ak_2 < k_1 \leq aL$ . Observe first that, if  $\limsup x(t) < l$  for some  $l > 0$ , then, for  $t$  large enough, we have  $x(t) < l$ , thus  $\dot{y}(t) < by(1 - y/(k_2 + l))$ . We deduce that

$$\limsup_{t \rightarrow \infty} x(t) < l \Rightarrow \limsup_{t \rightarrow \infty} y(t) < k_2 + l. \quad (3.19)$$

Let us now rewrite the first equation of (3.2) as

$$\dot{x} = x \left( 1 - x - \frac{ay}{k_1 + x} \right) = \frac{x}{k_1 + x} \left( -(x - 1)(x + k_1) - ay \right),$$

that is,

$$\dot{x} = \frac{ax}{k_1 + x} \left( U(x) - y \right) \quad (3.20)$$

where  $U(x) = (-1/a)(x - 1)(x + k_1)$ . Since  $ak_2 < k_1$ , the point  $E_2$  lies below the parabola  $y = U(x)$ , thus in the neighborhood of  $E_2$ , for  $x > 0$ , we have  $\dot{x} > 0$ .

By (3.19), if  $\limsup x(t) < l$  for some  $l > 0$ , then for  $t$  large enough, the point  $(x(t), y(t))$  remains in the rectangle  $\mathcal{R} = [0, l] \times [0, k_2 + l]$ . But if, furthermore,  $l$  is small enough such that  $\mathcal{R}$  lies entirely below the parabola  $y = U(x)$ , then, when  $(x(t), y(t)) \in \mathcal{R}$ , we have  $\dot{x}(t) > 0$ , which entails that  $x(t)$  is eventually greater than  $l$ , a contradiction. This shows that, for  $l > 0$  small enough, we have necessarily

$$\limsup_{t \rightarrow \infty} x(t) \geq l.$$

Let us now calculate the largest value of  $l$  such that  $(x, y) \in \mathcal{R}$  implies  $y < U(x)$ , that is, the largest  $l$  such that

$$\min_{x \in [0, l]} U(x) \geq k_2 + l.$$

From the concavity of  $U$ , the minimum of  $U$  on the interval  $[0, l]$  is attained at 0 or  $l$ . Thus the optimal value of  $l$  is the minimum of  $U(0) - k_2 = \frac{k_1}{a} - k_2$  and the positive solution to  $U(x) - k_2 = x$ , which is

$$\frac{1 - k_1 - a + \sqrt{(1 - k_1 - a)^2 + 4(k_1 - ak_2)}}{2}.$$

This proves (3.6).

(ciii) Assume that  $k_1 = ak_2$ . With the change of variable  $\tilde{y} = y - k_2$ , the system (3.2) becomes

$$\begin{cases} \dot{x} = \frac{ax}{k_1 + x} \left( V(x) - \tilde{y} \right), \\ \dot{\tilde{y}} = b \frac{\tilde{y} + k_2}{x + k_2} (x - \tilde{y}), \end{cases}$$

where  $V(x) = \frac{1}{a}((1 - k_1)x - x^2)$ . The second equation shows that  $\dot{\tilde{y}} > 0$  when  $\tilde{y} < x$ , and  $\dot{\tilde{y}} < 0$  when  $\tilde{y} > x$ . The first equation shows that  $\dot{x} > 0$  when  $(x, \tilde{y})$  is above the parabola  $\tilde{y} = V(x)$ , and  $\dot{x} < 0$  when  $(x, \tilde{y})$  is below the parabola  $\tilde{y} = V(x)$ .

• Assume that  $1 - k_1 - a > 0$ , that is,  $V'(0) = (1 - k_1)/a > 1$ . Then, the parabola  $\tilde{y} = V(x)$  is above the line  $\tilde{y} = x$  for all  $x$  in the interval  $]0, l[$ , where  $l$  is the non-zero solution to  $V(x) = x$ , that is,

$$l = 1 - k_1 - a.$$

Let us show that  $\limsup x(t) \geq l$ . Assume the contrary, that is,  $\limsup x(t) < \delta$  for some  $\delta < l$ . For  $t$  large enough, say,  $t \geq t_\delta$ , we have  $x(t) < \delta$ . Let us first prove that  $|\tilde{y}(t)| < \delta$  for  $t$  large enough. If  $\tilde{y}(t_\delta) < \delta$ , we have, for all  $t \geq t_\delta$ , as long as  $\tilde{y}(t) < \delta$ ,

$$\dot{\tilde{y}}(t) < b \frac{l + k_2}{k_2} (\delta - \tilde{y}(t)).$$

Since the constant function  $\tilde{y} = \delta$  is a solution to  $\dot{\tilde{y}} = b \frac{l + k_2}{k_2} (\delta - \tilde{y})$ , we deduce that  $\tilde{y}(t)$  remains in  $[-k_2, \delta]$  for all  $t \geq t_\delta$ . Furthermore, if  $\tilde{y}(t) < -\delta$ , for  $t \geq t_\delta$ , we have  $\dot{\tilde{y}}(t) > 0$ , thus

$$\dot{\tilde{y}}(t) > b \frac{\tilde{y}(t_\delta) + k_2}{k_2 + \delta} (-\tilde{y}(t)).$$

Thus

$$\tilde{y}(t) \geq y(t_\delta) \exp\left(-b \frac{\tilde{y}(t_\delta) + k_2}{k_2 + \delta} (t - t_\delta)\right),$$

which proves that  $\tilde{y}(t)$  enters  $] - \delta, \delta[$  in finite time. Similarly, if  $\tilde{y}(t_\delta) > \delta$ , then, for all  $t \geq t_\delta$  such that  $\tilde{y}(s) > \delta$  for all  $s \in [t_\delta, t]$ , we have

$$\dot{\tilde{y}}(t) < b \frac{\tilde{y}(t_\delta) + k_2}{k_2} (\delta - \tilde{y}(t)),$$

thus

$$\tilde{y}(t) < \delta + (\tilde{y}(t_\delta) - \delta) \exp\left(-b \frac{\tilde{y}(t_\delta) + k_2}{k_2} (t - t_\delta)\right),$$

which proves that  $\tilde{y}(t) < \delta$  after a finite time.

We have proved that, for  $t$  large enough,  $(x(t), \tilde{y}(t))$  stays in the box  $[0, \delta[\times] - \delta, \delta[$ . Since  $V(x) > x$  for all  $x \in ]0, l[$ , we deduce that, for  $t$  large enough, we have

$$\dot{x}(t) > x(t) \frac{V(\delta) - \delta}{k_1 + \delta},$$

which shows that  $x(t) > \delta$  for  $t$  large enough, a contradiction. This proves (3.7).

• Assume that  $1 - k_1 - a \leq 0$ , that is,  $V'(0) = (1 - k_1)/a \leq 1$ . Then, the portion of the parabola  $\tilde{y} = V(x)$  which lies in  $]0, +\infty[\times] - k_2, +\infty[$ , is below the line  $\tilde{y} = x$ . This means that, for any  $\epsilon > 0$  such that  $k_2 - \epsilon > 0$ , the system (3.2) has no other equilibrium point than  $E_2$  in the positively invariant attracting compact set  $[0, 1] \times [k_2 - \epsilon, L]$ . Since there cannot be any periodic orbit around  $E_2$  (because  $E_2$  is on the boundary of  $[0, 1] \times [k_2 - \epsilon, L]$ ), this entails that  $E_2$  is attracting for all initial conditions in  $[0, 1] \times [k_2 - \epsilon, L]$ , thus for all initial conditions in  $]0, +\infty[\times]0, +\infty[$ .

(civ) If  $k_1 < ak_2$ , we can use exactly the same arguments as in the case when  $k_1 = ak_2$  with  $1 - k_1 - a \leq 0$ .  $\square$



### 3.2.2 Local study of equilibrium points

#### Trivial critical points

The right hand side of (3.2) has continuous partial derivatives in the first quadrant  $\mathbf{R}_+ \times \mathbf{R}_+$ , except on the line  $x = m$  if  $m > 0$ . The Jacobian matrix of the right hand side of (3.2) (for  $x \neq m$  if  $m > 0$ ), is

$$\mathcal{J}(x, y) = \begin{pmatrix} 1 - 2x - \frac{ayk_1}{(k_1+(x-m)_+)^2} \mathbf{1}_{x \geq m} & \frac{-a(x-m)_+}{k_1+(x-m)_+} \\ \frac{by^2}{(k_2+(x-m)_+)^2} \mathbf{1}_{x \geq m} & b - \frac{2by}{k_2+(x-m)_+} \end{pmatrix}, \quad (3.21)$$

where  $\mathbf{1}_{x \geq m} = 1$  if  $x \geq m$  and  $\mathbf{1}_{x \geq m} = 0$  if  $x < m$ .

We start with a result on the obvious critical points of (3.2) which lie on the axes.

**Proposition 3.2.** *The system (3.2) has three trivial critical points on the axes :*

- $E_0 = (0, 0)$ , which is an hyperbolic unstable node,
  - $E_1 = (1, 0)$ , which is an hyperbolic saddle point whose stable manifold is the  $x$  axis, and with an unstable manifold which is tangent to the line  $(b+1)(x-1) + \frac{a(1-m)}{k_1+1-m}y = 0$ ,
  - $E_2 = (0, k_2)$ , which is
    - an hyperbolic saddle point whose stable manifold is the  $y$  axis, with an unstable manifold which is tangent to the line  $bx + \left(b+1 - \frac{ak_2}{k_1} \mathbf{1}_{m=0}\right)(y-k_2) = 0$  if  $m > 0$  or if  $ak_2 < k_1$ , where  $\mathbf{1}_{m=0} = 1$  if  $m = 0$  and  $\mathbf{1}_{m=0} = 0$  otherwise,
    - an hyperbolic stable node if  $m = 0$  with  $ak_2 > k_1$ ,
    - a semi-hyperbolic point if  $m = 0$  and  $ak_2 = k_1$ , which is
      - an attracting topological node if  $1 - k_1 - a \leq 0$ ,
      - a topological saddle point if  $1 - k_1 - a > 0$ . In this case, the  $y$  axis is the stable manifold, and there is a center manifold which is tangent to the line  $y - k_2 = x$ .
- (Compare with the case (c) of Theorem 3.1).

**Proof.** The nature of  $E_0$ ,  $E_1$ , and  $E_2$ , is obvious since

$$\mathcal{J}(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & b \end{pmatrix}, \quad \mathcal{J}(1, 0) = \begin{pmatrix} -1 & \frac{-a(1-m)}{k_1+1-m} \\ 0 & b \end{pmatrix}, \quad \mathcal{J}(0, k_2) = \begin{pmatrix} 1 - \frac{ak_2}{k_1} \mathbf{1}_{m=0} & 0 \\ b & -b \end{pmatrix}.$$

The results on stable and unstable manifolds of hyperbolic saddles are straightforward. In the case when  $E_2$  is semi-hyperbolic, since it is either a topological node or a topological saddle (see [21, Theorem 2.19]), the nature of  $E_2$  follows from Part (ciii) of Theorem 3.1. In the topological saddle case, that is, when  $m = 0$  with  $ak_2 = k_1$  and  $1 - k_1 - a > 0$ , the eigen values of  $\mathcal{J}(0, k_2)$  are  $-b$  and  $1$ , with corresponding eigenvectors  $(0, 1)$  and  $(1, 1)$ . Clearly, the  $y$  axis is the stable manifold. The change of variables

$$X = x, \quad Y = (y - k_2) - x$$

yields the normal form

$$\begin{aligned}\dot{X} = \dot{x} &= \frac{X}{X+k_1} \left( (1-k_1)X - X^2 - a(X+Y) \right) \\ &= \frac{X}{X+k_1} \left( (1-k_1-a)X - X^2 - aY \right), \\ \dot{Y} = \dot{x} - \dot{y} &= \dot{x} - b \frac{X+Y+k_2}{X+k_2} (-Y) = \dot{X} - b \left( 1 + \frac{Y}{X+k_2} \right) Y \\ &= -bY + \dot{X} - b \frac{Y^2}{X+k_2}.\end{aligned}$$

We can thus write

$$\begin{aligned}\dot{X} &= A(X, Y), \\ \dot{Y} &= -bY + B(X, Y),\end{aligned}\tag{3.22}$$

where  $A$  and  $B$  are analytic and their jacobian matrix at  $(0,0)$  is 0. In the neighborhood of  $(0,0)$ , the equation  $0 = -bY + B(X, Y)$  has the unique solution  $Y = \mathbf{f}(X)$ , where

$$\mathbf{f}(X) = \frac{k_2 a}{b k_2} X + O(X),$$

and  $\mathbf{g}(X) = A(X, \mathbf{f}(X))$  has the form

$$\mathbf{g}(X) = \frac{X^2}{k_2} \left( 1 + k_1 - a - \frac{a^2 k_2}{b k_1} \right) + O(X).$$

From [21, Theorem 2.19], we deduce that there exists an unstable center manifold which is infinitely tangent to the line  $Y = 0$ .  $\square$

### Counting and localizing equilibrium points

Let us now look for critical points outside the axes, i.e., critical points  $E = (x, y)$  with  $x > 0$  and  $y > 0$ . From the results of Section 3.2.1, such points are necessarily in  $\mathcal{A}$ , in particular they satisfy  $x \geq m$ . We have, obviously :

**Lemma 3.3.** *The set of equilibrium points of (3.2) which lie in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  consists of the intersection points of the curves*

$$x(1-x)(k_1+x-m) = a(k_2+x-m)(x-m),\tag{3.23}$$

$$k_2+x-m = y.\tag{3.24}$$

Furthermore, these points lie in  $\mathcal{A}$ .

We shall see that, when  $m > 0$ , the system (3.2) has always at least one equilibrium point in  $]0, +\infty[ \times ]0, +\infty[$ , whereas, for  $m = 0$ , some condition is necessary for the existence of such a point.

• When  $m > 0$ , the solutions to (3.23) lie at the abscissa of the intersection of the parabola  $z = P(x) := a(k_2 + x - m)(x - m)$  and of the third degree curve  $z = Q(x) := x(1 - x)(k_1 + x - m)$ . We have  $P(m) - Q(m) = -Q(m) = -k_1m(1 - m) < 0$  and, for  $x > 1$ , we have  $P(x) < 0$  and  $Q(x) > 0$ , thus  $P(x) - Q(x) > 0$ . This implies that the curves of  $P$  and  $Q$  have at least one intersection whose abscissa is greater than  $m$ , and that the abscissa of any such intersection lies necessarily in the interval  $]m, 1[$ . The change of variable  $X = x - m$  leads to

$$R(X) := P(x) - Q(x) = X^3 + \alpha_2 X^2 + \alpha_1 X + \alpha_0, \quad (3.25)$$

with

$$\alpha_2 = a + k_1 - 1 + 2m, \quad \alpha_1 = m^2 + m(2k_1 - 1) + ak_2 - k_1, \quad \alpha_0 = -k_1m(1 - m). \quad (3.26)$$

By Routh's scheme (see [26]), the number  $\mathbf{p}$  of roots of (3.25) with positive real part, counted with multiplicities, is equal to the number of changes of sign of the sequence

$$V := \left(1, \alpha_2, \alpha_1 - \frac{\alpha_0}{\alpha_2}, \alpha_0\right), \quad (3.27)$$

provided that all terms of  $V$  are non zero. Thus  $\mathbf{p} = 3$  when

$$\alpha_2 < 0 \text{ and } \alpha_1 \alpha_2 < \alpha_0, \quad (3.28)$$

and, in all other cases,  $\mathbf{p} = 1$ . When  $\mathbf{p} = 1$ , we know that the number  $\mathbf{n}$  of real positive roots of  $R$  is exactly 1. When  $\mathbf{p} = 3$ , we have either  $\mathbf{n} = 1$  if  $R$  has two complex conjugate roots, or  $\mathbf{n} = 3$ . So, we need to examine when all roots of  $R$  are real numbers. A very simple method to do that for cubic polynomials is described by Tong [76] : a necessary and sufficient condition for  $R$  to have three distinct real roots is that  $R$  has a local maximum and a local minimum, and that these extrema have opposite signs. The abscissa of these extrema are the roots of the derivative  $R'(X) = 3X^2 + 2\alpha_2 X + \alpha_1$ , thus  $R$  has three distinct real roots if, and only if, the following conditions are simultaneously satisfied :

- (i) The discriminant  $\Delta_{R'}$  of  $R'$  is positive,
- (ii)  $R(\underline{x})R(\bar{x}) < 0$ , where  $\underline{x}$  and  $\bar{x}$  are the distinct roots of  $R'$ .

If  $R(\underline{x})R(\bar{x}) = 0$  with  $\Delta_{R'} > 0$ , the polynomial  $R$  still has three real roots, two of which coincide and differ from the third one. If  $R(\underline{x})R(\bar{x}) = 0$  with  $\Delta_{R'} = 0$ , it has a real root with multiplicity 3, which is  $\underline{x} = \bar{x}$ , and if  $\Delta_{R'} = 0$  with  $R(\underline{x})R(\bar{x}) \neq 0$ , it has only one real root. Fortunately, all radicals disappear in the calculation of  $R(\underline{x})R(\bar{x})$  :

$$R(\underline{x})R(\bar{x}) = \frac{1}{27} (4\alpha_2^3 \alpha_0 - \alpha_2^2 \alpha_1^2 + 4\alpha_1^3 - 18\alpha_2 \alpha_1 \alpha_0 + 27\alpha_0^2).$$

In particular, Conditions (i) and (ii) can be summarized as

$$\alpha_2^2 - 3\alpha_1 > 0 \text{ and } 4\alpha_2^3 \alpha_0 - \alpha_2^2 \alpha_1^2 + 4\alpha_1^3 - 18\alpha_2 \alpha_1 \alpha_0 + 27\alpha_0^2 < 0. \quad (3.29)$$

Let us now examine what happens when one term of the sequence  $V$  in (3.27) is zero. We skip temporarily the case  $\alpha_0 = 0$ , which is equivalent to  $m = 0$ .

— If  $\alpha_2\alpha_1 = \alpha_0$ , we have

$$R(X) = (X + \alpha_2)(X^2 + \alpha_1),$$

and  $\alpha_2$  and  $\alpha_1$  have opposite signs, because  $\alpha_0 < 0$ . Thus, in that case,  $R$  has a unique positive root, which is  $\sqrt{-\alpha_1}$  if  $\alpha_2 > 0$ , and  $-\alpha_2$  if  $\alpha_2 < 0$ .

— If  $\alpha_2 = 0$ , the derivative of  $R$  becomes  $R'(X) = 3X^2 + \alpha_1$ . If  $\alpha_1 > 0$ ,  $R$  is increasing on  $] -\infty, \infty[$ , thus it has only one (necessarily positive) real root. If  $\alpha_1 = 0$ , we have  $R(X) = X^3 + \alpha_0$ , thus  $R$  has only one real root, which is  $\sqrt[3]{-\alpha_0} > 0$ . If  $\alpha_1 < 0$ ,  $R$  is decreasing in the interval  $[-\sqrt{-\alpha_1}, \sqrt{-\alpha_1}]$ , and increasing in  $[\sqrt{-\alpha_1}, +\infty[$ . Since  $R(0) < 0$ ,  $R$  has only one positive root. Thus, in that case too,  $R$  has a unique positive root.

From the preceding discussion, we deduce the following theorem :

**Théorème 3.2.** *Assume that  $m > 0$ . With the notations of (3.26), the number  $\mathbf{n}$  of distinct equilibrium points of the system (3.2) which lie in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  is*

(a)  $\mathbf{n} = 3$  if  $\left( \alpha_2 < 0, \alpha_1\alpha_2 < \alpha_0, \alpha_2^2 - 3\alpha_1 > 0, \text{ and } 4\alpha_2^3\alpha_0 - \alpha_2^2\alpha_1^2 + 4\alpha_1^3 - 18\alpha_2\alpha_1\alpha_0 + 27\alpha_0^2 < 0 \right)$ ,

(b)  $\mathbf{n} = 2$  if  $\left( \alpha_2 < 0, \alpha_1\alpha_2 < \alpha_0, \alpha_2^2 - 3\alpha_1 > 0 \text{ and } 4\alpha_2^3\alpha_0 - \alpha_2^2\alpha_1^2 + 4\alpha_1^3 - 18\alpha_2\alpha_1\alpha_0 + 27\alpha_0^2 = 0 \right)$ ,

(c)  $\mathbf{n} = 1$  in all other cases, i.e., if  $\left( \alpha_2 \geq 0 \text{ or } \alpha_1\alpha_2 \geq \alpha_0 \text{ or } \alpha_2^2 - 3\alpha_1 \leq 0 \text{ or } 4\alpha_2^3\alpha_0 - \alpha_2^2\alpha_1^2 + 4\alpha_1^3 - 18\alpha_2\alpha_1\alpha_0 + 27\alpha_0^2 > 0 \right)$ .

**Remark 3.4.** *Numerical computations show that all cases considered in Theorem 3.2 are nonempty. See Figure 3.1 for an example of positive numbers  $(a, k_1, k_2, m)$  satisfying (3.28) and (3.29).*

• When  $m = 0$ , the system (3.2) is exactly the system studied by M.A. Aziz-Alaoui and M. Daher-Okiye [7, 19]. As  $x$  is assumed to be positive, (3.23) is equivalent to the quadratic equation

$$(1 - x)(k_1 + x) = a(k_2 + x), \quad (3.30)$$

which can be written

$$x^2 + \alpha_2x + \alpha_1 = 0,$$

where  $\alpha_2 = a + k_1 - 1$  and  $\alpha_1 = ak_2 - k_1$  as in (3.26). The associated discriminant is

$$\Delta = \alpha_2^2 - 4\alpha_1 = (a + k_1 - 1)^2 - 4ak_2 + 4k_1, \quad (3.31)$$

thus a sufficient and necessary condition for the existence of solutions to (3.30) in  $\mathbf{R}$  is  $\Delta \geq 0$ , i.e.,  $k_2$  must not be too large :

$$4ak_2 \leq (1 - k_1 - a)^2 + 4k_1. \quad (3.32)$$

Since the sum of the solutions to (3.30) is  $-\alpha_2$  and their product is  $\alpha_1$ , we deduce the following result :

**Théorème 3.3.** *Assume that  $m = 0$ . With the notations of (3.26), the number  $\mathbf{n}$  of distinct equilibrium points of the system (3.2) which lie in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  is*

(a)  $\mathbf{n} = 2$  if  $\Delta > 0$  and  $\alpha_1 > 0$  and  $\alpha_2 < 0$ , i.e., if

$$4ak_2 < (1 - k_1 - a)^2 + 4k_1 \text{ and } ak_2 > k_1 \text{ and } 1 - k_1 - a > 0. \quad (3.33)$$

(b)  $\mathbf{n} = 1$  if  $\left( \Delta > 0 \text{ and } \left( \alpha_1 < 0 \text{ or } (\alpha_1 = 0 \text{ and } \alpha_2 < 0) \right) \right)$ , or  $\left( \Delta = 0 \text{ and } \alpha_2 < 0 \right)$  i.e., if

$$\left( \left( 4ak_2 < (1 - k_1 - a)^2 + 4k_1 \right) \text{ and } \left( ak_2 < k_1 \text{ or } (ak_2 = k_1 \text{ and } 1 - k_1 - a > 0) \right) \right),$$

or  $\left( 4ak_2 = (1 - k_1 - a)^2 + 4k_1 \text{ and } 1 - k_1 - a > 0 \right),$

(c)  $\mathbf{n} = 0$  if  $\Delta < 0$ , or if  $\left( \alpha_1 \geq 0 \text{ and } \alpha_2 \geq 0 \right)$ , i.e., if

$$\left( 4ak_2 > (1 - k_1 - a)^2 + 4k_1 \right) \text{ or } \left( ak_2 \geq k_1 \text{ and } 1 - k_1 - a \leq 0 \right).$$

**Remark 3.5.** *If  $m = 0$  and  $\mathbf{n} = 0$ , the point  $E_2$  is the only equilibrium point in the compact positively invariant attracting set  $[0, 1] \times [k_2 - \epsilon, L]$ , for any  $\epsilon > 0$  such that  $k_2 - \epsilon > 0$ , thus  $E_2$  is globally attractive, because there is no cycle around  $E_2$  (since  $E_2$  is on the boundary of  $[0, 1] \times [k_2 - \epsilon, L]$ ). This gives a more general condition of global attractivity of  $E_2$  than the result given in Parts (ciii) and (civ) of Theorem 3.1.*

**Remark 3.6.** *Since the roots of the polynomial  $R$  defined by (3.25) depend continuously on its coefficients, Theorem 3.3 expresses the limiting localization of the equilibrium points of (3.2) when  $m$  goes to 0. In particular, the case (a) of Theorem 3.3 is the limiting case of (a) in Theorem 3.2. Indeed, it is easy to check that Condition (3.33), with  $m = 0$ , is a limit case of (3.28) and (3.29). This means that, in the case (a) of Theorem 3.2, when  $m$  goes to 0, one of the equilibrium points in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  goes to  $E_2$  and leaves the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ . (Note that, when  $m = 0$ , the equilibrium point  $E_2 = (0, k_2)$  is in  $\mathcal{A}$ .)*

**Remark 3.7.** *When  $k_1 = k_2 := k$ , since  $x > m$ , Equation (3.23) is equivalent to  $x(1 - x) = a(x - m)$ , i.e.,*

$$x^2 + x(a - 1) - am,$$

thus it has at most one positive solution. In that case, the coordinates of the unique non trivial equilibrium point  $E^*$  can be explicitated in a simple way, and we have

$$E^* = \left( \frac{1 - a + \sqrt{(1 - a)^2 + 4am}}{2}, k + x^* - m \right).$$

If  $a \geq 1$ , the point  $E^*$  converges to  $E_2$  when  $m$  goes to 0. If  $a > 1$ , it converges to  $(1 - a, 1 - a + k)$ .

### Local stability

Let  $E^* = (x^*, y^*)$  be an equilibrium point of (3.2) in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ . Since  $E^*$  is necessarily in  $\mathcal{A}$ , we get, using (3.21) and (3.24),

$$\mathcal{J}(x^*, y^*) = \begin{pmatrix} 1 - 2x^* - \frac{ay^*k_1}{(k_1 + x^* - m)^2} & \frac{-a(x^* - m)}{k_1 + x^* - m} \\ b & -b \end{pmatrix}. \quad (3.34)$$

The characteristic polynomial of  $\mathcal{J}(x^*, y^*)$  is

$$\chi(\lambda) = \lambda^2 + s\lambda + p,$$

where

$$s = -\text{trace}(\mathcal{J}(x^*, y^*)) = -1 + 2x^* + \frac{ay^*k_1}{(k_1 + x^* - m)^2} + b, \quad (3.35)$$

$$p = \det(\mathcal{J}(x^*, y^*)) = b \left( -1 + 2x^* + \frac{ay^*k_1}{(k_1 + x^* - m)^2} + \frac{a(x^* - m)}{k_1 + x^* - m} \right). \quad (3.36)$$

The roots of  $\chi$  are real if, and only if,  $\Delta_\chi \geq 0$ , where

$$\Delta_\chi = s^2 - 4p = \left( -1 + 2x^* + \frac{ay^*k_1}{(k_1 + x^* - m)^2} - b \right)^2 - 4b \frac{a(x^* - m)}{k_1 + x^* - m}.$$

The point  $E^*$  is non-hyperbolic if one of the roots of  $\chi$  is zero (that is, if  $p = 0$ ), or if  $\chi$  has two conjugate purely imaginary roots (that is, if  $s = 0$  with  $p > 0$ ). If only one root of  $\chi$  is zero, that is, if  $p = 0$  with  $s \neq 0$ , the point  $E^*$  is semi-hyperbolic.

**a- Hyperbolic equilibria** When  $E^*$  is hyperbolic, we get, using the Routh-Hurwitz criterion, that  $E^*$  is

- a saddle point if  $p < 0$ ,
- an unstable node if  $s < 0$  and  $p > 0$  with  $\Delta_\chi > 0$ ,
- an unstable focus if  $s < 0$  and  $p > 0$  with  $\Delta_\chi < 0$ ,
- an unstable degenerated node if  $s < 0$  and  $p > 0$  with  $\Delta_\chi = 0$ ,
- a stable node if  $s > 0$  and  $p > 0$  with  $\Delta_\chi > 0$ ,
- a stable degenerated node if  $s > 0$  and  $p > 0$  with  $\Delta_\chi = 0$ ,
- a stable focus if  $s > 0$  and  $p > 0$  with  $\Delta_\chi < 0$ .

**Remark 3.8.** *An obvious sufficient condition for any equilibrium point  $E^* \in \mathcal{A}$  to be stable hyperbolic is  $m \geq 1/2$ , since  $x^* > m$ . This condition can be slightly improved, as we shall see in the study of global stability (see Theorem 3.5).*

**Application of the Poincaré index theorem** When  $E^*$  is an hyperbolic equilibrium, its index is either 1 (if it is a node or focus) or  $-1$  (if it is a saddle). Let  $\mathbf{n}$  be the number of distinct equilibrium points, which we denote by  $E_1^*, \dots, E_n^*$ , and let  $I_1, \dots, I_n$  their respective topological indices. As we shall see in the proof of the next theorem, by a generalized version of the Poincaré index theorem, we have  $I_1 + \dots + I_n = 1$ . When all equilibrium points are hyperbolic, this allows us to count the number of nodes or foci and of saddles.

**Théorème 3.4.** *Assume that all equilibrium points of the system (3.2) which lie in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  (equivalently, in the interior of  $\mathcal{A}$ ) are hyperbolic, and let  $\mathbf{n}$  be their number.*

1. *Assume that  $m > 0$ . Then  $\mathbf{n}$  is equal to 3 or 1.*
  - *If  $\mathbf{n} = 1$ , the unique equilibrium point in the interior of  $\mathcal{A}$  is a node or a focus.*
  - *If  $\mathbf{n} = 3$ , the system (3.2) has one saddle point and two nodes or foci in the interior of  $\mathcal{A}$ .*
2. *Assume now that  $m = 0$ . Then  $\mathbf{n}$  is equal to 2, 1, or 0.*
  - *If  $\mathbf{n} = 2$ , one equilibrium point is a node or focus, and the other is a saddle.*
  - *If  $\mathbf{n} = 1$ , the unique equilibrium point in the interior of  $\mathcal{A}$  is a node or a focus.*

**Proof.** Let  $N$  (respectively  $S$ ) denote the number of nodes or foci (respectively of saddles) among the hyperbolic singular points which lie in  $\mathcal{A}$ .

1. Assume that  $m > 0$ . By Theorem 3.1, the vector field  $\mathbf{v} = v_1 \frac{\partial}{\partial x} + v_2 \frac{\partial}{\partial y}$  generated by (3.2) is directed inward along the boundary of  $\mathcal{A}$ . By continuity of  $\mathbf{v}$ , we can round the corners of  $\mathcal{A}$  and define a compact domain  $\mathcal{A}' \subset \mathcal{A}$  with smooth boundary which contains all critical points of  $\mathcal{A}$ , and such that  $\mathbf{v}$  is directed inward along the boundary of  $\mathcal{A}'$ . Applying a generalized version of the Poincaré index theorem (see e.g. [53, 29, 71]) to  $\mathbf{v}$  in  $\mathcal{A}'$ , we get  $N - S = 1$ . Since  $1 \leq N + S \leq 3$ , the only possibilities are  $(N = 1 \text{ and } S = 0)$  or  $(N = 2 \text{ and } S = 1)$ .

2. Assume now that  $m = 0$ . We use the same reasoning as for  $m > 0$ , but with a different domain. Instead of  $\mathcal{A}$ , we consider the domain

$$\mathcal{B} = [-\epsilon, 1] \times [k_2 - \epsilon, L]$$

for a small  $\epsilon > 0$ . Thus  $\mathcal{B}$  contains  $E_2$ .

• With the notations of (3.20), if  $ak_2 > k_1$ , we have  $y > U(x)$  for  $x = 0$  and for all  $y \in [k_2, L]$ . We have

$$v_1 = \frac{ax}{k_1 + x} (U(x) - y).$$

By continuity of  $\mathbf{v}$ , we can choose  $\epsilon > 0$ , with  $\epsilon < k_1$ , such that the inequality  $y > U(x)$  remains true on the rectangle  $[-\epsilon, 0] \times [k_2 - \epsilon, L]$ . We then have  $v_1 > 0$  on the segment  $\{-\epsilon\} \times [k_2 - \epsilon, L]$ . Since  $v_2 > 0$  for  $y = k_2 - \epsilon$  and  $v_2 < 0$  for  $y = L$ , the field  $\mathbf{v}$  is directed inward along the boundary of  $\mathcal{B}$ . Again, by rounding the corners, we can modify  $\mathcal{B}$  into a compact domain  $\mathcal{B}'$  with smooth boundary which contains the same critical points as  $\mathcal{B}$  and such that  $\mathbf{v}$  is directed inward along the boundary of  $\mathcal{B}'$ . By the Poincaré Index Theorem, we have  $N' - S' = 1$ , where  $N'$  (respectively  $S'$ ) is the number of nodes or foci (respectively of saddles) in the interior of  $\mathcal{B}'$ . If we have chosen  $\epsilon$  small enough, the singularities of  $\mathbf{v}$  in  $\mathcal{B}'$  are those which are in the interior of  $\mathcal{A}$ , with the addition of the point  $E_2$ , which is a node by Proposition 3.2. Thus  $N = N' - 1$  and  $S = S'$  which entails  $N - S = 0$ . Thus, taking into account Theorem 3.3, we have  $N = S = 1$  (if  $\mathbf{n} = 2$ ), or  $N = S = 0$  (if  $\mathbf{n} = 0$ ).

- If  $ak_2 < k_1$ ,  $E_2$  is a saddle point, thus, constructing  $\mathcal{B}$  and  $\mathcal{B}'$  as precedingly, we have now  $S = S' - 1$  and  $N = N'$ . Furthermore, the vector field  $\mathbf{v}$  is no more outward directed along the whole boundary of  $\mathcal{B}'$ . We use Pugh's algorithm [71] to compute  $N' - S'$  : taking  $\epsilon$  small enough such that the vector field  $\mathbf{v}$  does not vanish on  $\partial\mathcal{B}'$ , we have

$$N' - S' = \chi(\mathcal{B}') - \chi(\partial\mathcal{B}') + \chi(R_-^1) - \chi(\partial R_-^1) + \chi(R_-^2) - \chi(\partial R_-^2), \quad (3.37)$$

where  $\chi$  denotes the Euler characteristic,  $R_-^1$  is the part of the boundary of  $\mathcal{B}'$  where  $\mathbf{v}$  is directed outward, and  $R_-^2$  is the part of  $\partial R_-^1$  where  $\mathbf{v}$  points to the exterior of  $R_-^1$ . Since  $k_2 < k_1/a$ , we see that the parabola  $y = U(x)$  crosses the line  $\{x = -\epsilon; y > k_2\}$  at some point  $(-\epsilon, r)$ , so that the part of the boundary of  $\mathcal{B}$  where  $\mathbf{v}$  points outward is the segment  $\{-\epsilon\} \times [k_2 - \epsilon, \min(r, L)]$ . Thus, for small  $\epsilon$ ,  $R_-^1$  is an arc whose extremities are tangency points. Observe also that, since  $v_1 < 0$  for  $x < 0$  and  $v_2 < 0$  for  $y > k_2 + x > 0$ , the field  $\mathbf{v}$  points toward the interior of  $R_-^1$  at those tangency points, thus  $R_-^2$  is empty. Formula (3.37) becomes

$$\Sigma(\mathbf{v}) = 1 - 0 + 1 - 2 + 0 - 0 = 0,$$

that is,  $N - S = N' - (S' - 1) = 1$ . Since, by Theorem 3.3, we have  $N + S = 1$ , we deduce that  $N = 1$  and  $S = 0$ .  $\square$

**b. Semi hyperbolic equilibria** This is when  $p = 0$  and  $s \neq 0$ . The set of parameters such that  $p = 0$  is nonempty. Indeed, the values  $a = 0,5$ ,  $b = 0,01$ ,  $m = 0,001$ ,  $k_2 = 0,25$ ,  $k_1 = 0,08$  lead to  $p = -0.1003032464$  with  $\alpha_2 = 0.044161 > 0$  and  $a = 0,5$ ,  $b = 0,01$ ,  $m = 0,001$ ,  $k_2 = 0,25$ ,  $k_1 = 0,112$  lead to  $p = 0.002422466814$  with  $\alpha_2 = 0.012225 > 0$ . Since  $\alpha_2$  is a linear function of  $k_1$ , this shows that  $\alpha_2 > 0$  for  $a = 0,5$ ,  $b = 0,01$ ,  $m = 0,001$ ,  $k_2 = 0,25$  and  $0,08 \leq k_1 \leq 0,112$ . Thus, by Theorem 3.2, for all these values, the number  $\mathbf{n}$  of equilibrium points remains equal to 1. By the intermediate value theorem, we deduce that there exists a value  $k_1$ , with  $0,08 \leq k_1 \leq 0,112$ , such that, for  $a = 0,5$ ,  $b = 0,01$ ,  $m = 0,001$ ,  $k_2 = 0,25$ , the unique equilibrium point satisfies  $p = 0$ .



From (3.35), (3.36) and (3.26), it is obvious that we can chose  $b$  such that  $s \neq 0$  without changing  $p = 0$  nor the coefficients  $\alpha_0, \alpha_1, \alpha_2$ .

For  $p = 0$ , the Jacobian matrix  $\mathcal{J}(x^*, y^*)$  is

$$\mathcal{J}(x^*, y^*) = \begin{pmatrix} a\rho & -a\rho \\ b & -b \end{pmatrix}.$$

The change of variables

$$\mathbf{u} = \frac{a\rho Y - bX}{a\rho - b}, \quad \mathbf{v} = \frac{X - Y}{a\rho - b}$$

yields

$$\begin{aligned} v_1 = & a\rho(a\rho - b)\mathbf{v} + a^2\rho \frac{k_1(y^*a\rho - b\kappa) - \rho\kappa^3}{\kappa^3}\mathbf{v}^2 - \frac{ak_1(\kappa - y^*) + \kappa^3}{\kappa^3}\mathbf{u}^2 \\ & - a \frac{k_1\kappa(b + a\rho) + \rho(2\kappa^3 - y^*k_1a)}{\kappa^3}\mathbf{v}\mathbf{u} + a^3k_1\rho^2 \frac{b\kappa - y^*a\rho}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{v}^3 \\ & - ak_1 \frac{y^* - \kappa}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{u}^3 + ak_1 \frac{b\kappa + 2a\rho\kappa - 3y^*a\rho}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{u}^2\mathbf{v} + a^2k_1\rho \frac{2b\kappa + a\rho\kappa - 3y^*a\rho}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{v}^2\mathbf{u}, \\ v_2 = & b(\rho a - b)\mathbf{v} + b \frac{-b^2 + 2b\rho a - \rho^2 a^2}{\mathbf{u} + \rho a\mathbf{v} + y^*}\mathbf{v}^2. \end{aligned}$$

The coordinates of  $\mathbf{v}$  are, in the basis  $(\frac{\partial}{\partial \mathbf{u}}, \frac{\partial}{\partial \mathbf{v}})$ ,

$$\begin{aligned} \dot{\mathbf{u}} = & \frac{1}{a\rho - b}(a\rho\dot{Y} - b\dot{X}) = \frac{1}{a\rho - b}(a\rho v_2 - b v_1) \\ = & \frac{b}{b - \rho a} \left( -\frac{(-k_1y^*a + \kappa^3 + ak_1)\mathbf{u}^2}{\kappa^2} + \frac{ak_1(\kappa - y^*)}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{u}^3 + \frac{a\rho(-\kappa^3\rho a + y^*k_1a^2\rho - \kappa ak_1b)}{\kappa^3}\mathbf{v}^2 \right. \\ & + \frac{a^3k_1\rho^2(\kappa b - y^*a\rho)}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{v}^3 - \frac{a\kappa(k_1b + ak_1\rho + 2\kappa^2\rho) - 2y^*k_1a^2\rho}{\kappa^3}\mathbf{v}\mathbf{u} - \rho a \frac{-b^2 + 2b\rho a - \rho^2 a^2}{\mathbf{u} + \rho a\mathbf{v} + y^*}\mathbf{v}^2 \\ & \left. + \frac{ak_1(b\kappa + 2a\kappa\rho - 3y^*a\rho)}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{u}^2\mathbf{v} + \frac{a^2k_1\rho(2b\kappa + a\kappa\rho - 3y^*a\rho)}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{v}^2\mathbf{u} \right), \\ \dot{\mathbf{v}} = & -\frac{1}{a\rho - b}(\dot{X} - \dot{Y}) = \frac{1}{a\rho - b}(v_1 - v_2) \\ = & (a\rho - b)\mathbf{v} + \frac{1}{b - \rho a} \left( a^2\rho \frac{k_1b\kappa + \rho\kappa^3 - y^*k_1a\rho}{\kappa^3}\mathbf{v}^2 + \frac{ak_1\kappa - k_1y^*a + \kappa^3}{\kappa^3}\mathbf{u}^2 \right. \\ & + a \frac{k_1b\kappa + ak_1\rho\kappa + 2\rho\kappa^3 - 2y^*k_1a\rho}{\kappa^3}\mathbf{u}\mathbf{v} + k_1a^3\rho^2 \frac{y^*a\rho - b\kappa}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{v}^3 + ak_1 \frac{y^* - \kappa}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{u}^3 \\ & \left. + b \frac{(a\rho - b)^2}{\mathbf{u} + \rho a\mathbf{v} + y^*}\mathbf{v}^2 + ak_1 \frac{3y^*a\rho - \kappa(b + 2a\rho)}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{u}^2\mathbf{v} + k_1a^2\rho \frac{3y^*a\rho - a\rho\kappa - 2b\kappa}{\kappa^3(\kappa + \mathbf{u} + \rho a\mathbf{v})}\mathbf{v}^2\mathbf{u} \right). \end{aligned}$$

We can thus write

$$\begin{aligned} \dot{\mathbf{u}} &= A(\mathbf{u}, \mathbf{v}), \\ \dot{\mathbf{v}} &= \lambda\mathbf{v} + B(\mathbf{u}, \mathbf{v}), \end{aligned} \tag{3.38}$$

where  $A$  and  $B$  are analytic and their jacobian matrix at  $(0, 0)$  is 0 and  $\lambda > 0$ . It is not easy to determine  $\mathbf{v} = f(\mathbf{u})$  the solution to the equation  $\lambda \mathbf{v} + B(\mathbf{u}, \mathbf{v}) = 0$  in a neighborhood of the point  $(0, 0)$ , for that we use implicit function theorem. We find :

**Case 1 :** If  $\kappa^3 - ky^*a + ak_1\kappa \neq 0$ , we have

$$f(\mathbf{u}) = -\frac{\kappa^3 - ky^*a + ak_1\kappa}{\kappa^3(b + \rho^2a^2 - \rho ab)}\mathbf{u}^2,$$

and  $g(\mathbf{u}) = A(\mathbf{u}, f(\mathbf{u}))$  has the form

$$g(\mathbf{u}) = \frac{b}{b - a\rho} \left( \frac{\kappa^3 - ky^*a + ak_1\kappa}{\kappa^3} \right) \mathbf{u}^2.$$

We apply [21, Theorem 2.19] to System (3.38). Since the power of  $\mathbf{u}$  in  $f(\mathbf{u})$  is even, we deduce from Part (iii) of [21, Theorem 2.19] :

**Lemma 3.9.** *If  $E^*$  is a semi-hyperbolic equilibrium of (3.2) in the positive quadrant  $]0, +\infty[ \times ]0, +\infty[$ , and if  $\kappa^3 - ky^*a + ak_1\kappa \neq 0$ , then  $E^*$  is a saddle-node, that is, its phase portrait is the union of one parabolic and two hyperbolic sectors. In this case, the index of  $E^*$  is 0.*

**Case 2 :** if  $\kappa^3 - ky^*a + ak_1\kappa = 0$ , we have

$$f(\mathbf{u}) = \frac{ak_1(\kappa - y^*)}{\kappa^4(a\rho - b)^2}\mathbf{u}^3,$$

and  $g(\mathbf{u}) = A(\mathbf{u}, f(\mathbf{u}))$  has the form

$$g(\mathbf{u}) = \frac{bak_1(\kappa - y^*)}{\kappa^4(a\rho - b)^2}\mathbf{u}^3.$$

Again, we apply [21, Theorem 2.19] to System (3.38). Since the power of  $\mathbf{u}$  in  $f(\mathbf{u})$  is odd, we look at the coefficient of  $\mathbf{u}^3$  and we have two possibilities :

**P1 :** If  $k_1 > k_2$ , we deduce from Part (ii) of [21, Theorem 2.19] :

**Lemma 3.10.** *If  $E^*$  is a semi-hyperbolic equilibrium of (3.2) in the positive quadrant  $]0, +\infty[ \times ]0, +\infty[$ , and if  $\kappa^3 - ky^*a + ak_1\kappa = 0$  with  $k_1 > k_2$ , then  $E^*$  is a unstable node. In this case, the index of  $E^*$  is 1.*

**P2 :** If  $k_1 < k_2$ , we deduce from Part (i) of [21, Theorem 2.19] :

**Lemma 3.11.** *If  $E^*$  is a semi-hyperbolic equilibrium of (3.2) in the positive quadrant  $]0, +\infty[ \times ]0, +\infty[$ , and if  $\kappa^3 - ky^*a + ak_1\kappa = 0$  with  $k_1 < k_2$ , then  $E^*$  is a saddle. In this case, the index of  $E^*$  is -1.*

**Remark 3.12.** *From Theorem 3.4, when the system (3.2) has one equilibrium point, this point cannot be a saddle.*

**Hopf bifurcation** When  $\Delta_\chi < 0$ , the roots of  $\chi$  are  $\frac{-s \pm i\sqrt{4p-s^2}}{2}$ . The values of  $x^*$ ,  $y^*$  and  $p$  do not depend on the parameter  $b$ , whereas  $s$  is an affine function of  $b$ , so that the eigenvalues of  $\chi$  cross the imaginary axis at speed  $-1/2$  when  $b$  passes through the value

$$b_0 = 1 - 2x^* + \frac{ay^*k_1}{\kappa^2}.$$

Let us check the genericity condition for Hopf bifurcations. We use the condition of Guckenheimer and Holmes [30, Formula (3.4.11)]. Let us denote

$$\dot{\mathbf{u}} = \mathcal{V}_1(\mathbf{u}, \mathbf{v}), \quad \dot{\mathbf{v}} = \mathcal{V}_2(\mathbf{u}, \mathbf{v}),$$

and  $\mathcal{V}_{1\mathbf{u}\mathbf{v}} = \frac{\partial \mathcal{V}_1}{\partial \mathbf{u} \partial \mathbf{v}}$ , etc. We have

$$\begin{aligned} \lambda &= \mathcal{V}_{1\mathbf{u}\mathbf{u}\mathbf{u}} + \mathcal{V}_{1\mathbf{u}\mathbf{v}\mathbf{v}} + \mathcal{V}_{2\mathbf{u}\mathbf{u}\mathbf{v}} + \mathcal{V}_{2\mathbf{v}\mathbf{v}\mathbf{v}} \\ &+ \frac{1}{\delta} (\mathcal{V}_{1\mathbf{u}\mathbf{v}}(\mathcal{V}_{1\mathbf{u}\mathbf{u}} + \mathcal{V}_{1\mathbf{v}\mathbf{v}}) - \mathcal{V}_{2\mathbf{u}\mathbf{v}}(\mathcal{V}_{2\mathbf{u}\mathbf{u}} + \mathcal{V}_{2\mathbf{v}\mathbf{v}}) - \mathcal{V}_{1\mathbf{u}\mathbf{u}}\mathcal{V}_{2\mathbf{u}\mathbf{u}} + \mathcal{V}_{1\mathbf{v}\mathbf{v}}\mathcal{V}_{2\mathbf{v}\mathbf{v}}) \\ &= ak_1\kappa^3(-2y^* + \kappa)b_0^2 + \kappa(2c\kappa^5 + 2k_1y^*a\kappa^3 - \kappa^3ck_1a + 3\kappa ck_1y^{*2}a + \kappa a^2k_1^2y^* - 2a^2k_1^2y^{*2})b_0 \\ &- 2c(c - y^*)\kappa^6 + ak_1\kappa^4cy^* + 2acy^*k_1(-2y^* + c)\kappa^3 - 3\kappa^2k_1y^{*2}ac^2 - a^2k_1^2\kappa cy^{*2} + 2k_1^2y^{*3}a^2c. \end{aligned}$$

If  $\lambda < 0$ , then the periodic solutions are stable limit cycles, while if  $\lambda > 0$ , the periodic solutions are repelling. See Figure 3.3 for a numerical exemple.

**c- Non-elementary equilibria** Let us rewrite the vector field  $\mathbf{v} = v_1 \frac{\partial}{\partial x} + v_2 \frac{\partial}{\partial y}$  associated with (3.2) in the neighborhood of an equilibrium point  $E^* = (x^*, y^*) \in \mathcal{A}$ . Let  $X = x - x^*$  and  $Y = y - y^*$ . Since  $E^*$  is a critical point of  $\mathbf{v}$ , we have

$$\begin{aligned} v_1 &= x(1-x) - \frac{ay(x-m)}{k_1 + (x-m)} \\ &= (X+x^*)(1-x^*-X) - \frac{a(Y+y^*)(X+x^*-m)}{X+x^*+k_1-m} \\ &= x^*(1-x^*) + X(1-2x^*-X) - \frac{ay^*(x^*-m)}{X+x^*+k_1-m} - \frac{a(Y(X+x^*-m) + Xy^*)}{X+x^*+k_1-m} \\ &= x^*(1-x^*) - \frac{ay^*(x^*-m)}{x^*+k_1-m} + X(1-2x^*-X) \\ &\quad + \frac{ay^*(x^*-m)}{x^*+k_1-m} - \frac{ay^*(x^*-m)}{X+x^*+k_1-m} - \frac{a(Y(X+x^*-m) + Xy^*)}{X+x^*+k_1-m} \\ &= X(1-2x^*-X) + \frac{ay^*(x^*-m)}{x^*+k_1-m} - \frac{ay^*(x^*-m)}{X+x^*+k_1-m} - \frac{a(Y(X+x^*-m) + Xy^*)}{X+x^*+k_1-m} \\ &= X(1-2x^*-X) + ay^*(x^*-m) \left( \frac{1}{x^*+k_1-m} - \frac{1}{X+x^*+k_1-m} \right) \\ &\quad - \frac{a(Y(X+x^*-m) + Xy^*)}{X+x^*+k_1-m} \end{aligned}$$

$$= X(1 - 2x^* - X) + \frac{ay^*(x^* - m)X}{(x^* + k_1 - m)(X + x^* + k_1 - m)} - \frac{a(Y(X + x^* - m) + Xy^*)}{X + x^* + k_1 - m}.$$

For simplification, we denote

$$\kappa = x^* + k_1 - m, \quad \rho = \frac{x^* - m}{x^* + k_1 - m}, \quad (3.39)$$

thus

$$v_1 = X(1 - 2x^* - X) + \frac{a(Xy^*(\rho - 1) - Y(x^* - m) - YX)}{X + \kappa}.$$

Using the equality

$$\frac{1}{x + K} = \frac{1}{K} \left( 1 - \frac{x}{K} + \cdots + (-1)^n \frac{x^n}{K^n} + (-1)^{n+1} \frac{x^{n+1}}{K^n(x + K)} \right), \quad n \geq 1,$$

we get

$$\begin{aligned} v_1 &= X(1 - 2x^* - X) \\ &\quad + \frac{a}{\kappa} \left( 1 - \frac{X}{\kappa} + \frac{X^2}{\kappa(X + \kappa)} \right) (Xy^*(\rho - 1) - Y(x^* - m) - YX) \\ &= X(1 - 2x^* - X) \\ &\quad + \frac{a}{\kappa} (Xy^*(\rho - 1) - Y(x^* - m) - YX) \\ &\quad - \frac{aX}{\kappa^2} (Xy^*(\rho - 1) - Y(x^* - m) - YX) \\ &\quad + \frac{aX^2}{\kappa^2(X + \kappa)} (Xy^*(\rho - 1) - Y(x^* - m) - YX) \\ &= X \left( 1 - 2x^* + \frac{a}{\kappa} y^*(\rho - 1) \right) - Y \frac{a}{\kappa} (x^* - m) \\ &\quad - X^2 \left( 1 + \frac{a}{\kappa^2} y^*(\rho - 1) \right) + XY \left( -\frac{a}{\kappa} + \frac{a}{\kappa^2} (x^* - m) \right) \\ &\quad + \frac{aX^2Y}{\kappa^2} + \frac{aX^2}{\kappa^2(X + \kappa)} (Xy^*(\rho - 1) - Y(x^* - m + X)) \\ &= X \left( 1 - 2x^* - \frac{ay^*k_1}{\kappa^2} \right) - Y a \rho - X^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} \right) - XY \frac{ak_1}{\kappa^2} \\ &\quad - X^3 \frac{ay^*k_1}{\kappa^3(X + \kappa)} + X^2Y \frac{a}{\kappa^2} \left( 1 - \frac{x^* - m + X}{X + \kappa} \right) \\ &= X \left( 1 - 2x^* - \frac{ay^*k_1}{\kappa^2} \right) - Y a \rho - X^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} \right) - XY \frac{ak_1}{\kappa^2} \\ &\quad - X^3 \frac{ay^*k_1}{\kappa^3(X + \kappa)} + X^2Y \frac{ak_1}{\kappa^2(X + \kappa)}. \end{aligned} \quad (3.40)$$

Since  $y^* = x^* + k_2 - m$ , we have also

$$v_2 = b(Y + y^*) \left( 1 - \frac{Y + y^*}{k_2 + x - m} \right) = b(Y + y^*) \left( 1 - \frac{Y + y^*}{X + y^*} \right)$$

$$\begin{aligned}
 &= b(X - Y) \frac{Y + y^*}{X + y^*} \\
 &= b(X - Y) \left( 1 - (X - Y) \frac{1}{X + y^*} \right) \\
 &= b(X - Y) - \frac{b}{y^*} (X - Y)^2 \left( 1 - \frac{X}{X + y^*} \right). \tag{3.41}
 \end{aligned}$$

This shows in particular that the linear part of  $\mathbf{v}$  is never zero. Thus the only non-hyperbolic cases are the nilpotent case and the case when  $E^*$  is a center for the linear part of  $\mathbf{v}$ . Let us now investigate these cases :

### c<sub>1</sub>. Nilpotent case

This is when  $p = 0 = s$ . From the discussion at the beginning of Case b, it is clear that this case is nonempty.

In this case, the Jacobian matrix  $\mathcal{J}(x^*, y^*)$  is

$$\mathcal{J}(x^*, y^*) = \begin{pmatrix} b & -b \\ b & -b \end{pmatrix}.$$

With the preceding notations, we thus have

$$v_1 = b(X - Y) - X^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} \right) - XY \frac{ak_1}{\kappa^2} - X^3 \frac{ay^*k_1}{\kappa^3(X + \kappa)} + X^2Y \frac{ak_1}{\kappa^2(X + \kappa)}.$$

The change of variables

$$\mathbf{u} = X, \quad \mathbf{v} = Y - X$$

yields

$$\begin{aligned}
 v_1 &= -\mathbf{v}b - \mathbf{u}^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} \right) - \mathbf{u}(\mathbf{u} + \mathbf{v}) \frac{ak_1}{\kappa^2} - \mathbf{u}^3 \frac{ay^*k_1}{\kappa^3(\mathbf{u} + \kappa)} + \mathbf{u}^2(\mathbf{u} + \mathbf{v}) \frac{ak_1}{\kappa^2(\mathbf{u} + \kappa)} \\
 &= -\mathbf{v}b - \mathbf{u}^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) - \mathbf{u}\mathbf{v} \frac{ak_1}{\kappa^2} \\
 &\quad + \mathbf{u}^3 \frac{ak_1}{\kappa^2(\mathbf{u} + \kappa)} \left( -\frac{y^*}{\kappa} + 1 \right) + \mathbf{u}^2\mathbf{v} \frac{ak_1^2}{\kappa^2(\mathbf{u} + \kappa)}, \\
 v_2 &= -\mathbf{v}b - \mathbf{v}^2 \frac{b}{y^*} \left( 1 - \frac{\mathbf{u}}{\mathbf{u} + y^*} \right).
 \end{aligned}$$

The coordinates of  $\mathbf{v}$  are, in the basis  $(\frac{\partial}{\partial \mathbf{u}}, \frac{\partial}{\partial \mathbf{v}})$ ,

$$\begin{aligned}
 \dot{\mathbf{u}} &= \dot{X} = v_1, \\
 \dot{\mathbf{v}} &= \dot{Y} - \dot{X} = v_2 - v_1 \\
 &= -\mathbf{v}b - \mathbf{v}^2 \frac{b}{y^*} \left( 1 - \frac{\mathbf{u}}{\mathbf{u} + y^*} \right) + \mathbf{v}b + \mathbf{u}^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) + \mathbf{u}\mathbf{v} \frac{ak_1}{\kappa^2}
 \end{aligned}$$

$$\begin{aligned}
& -u^3 \frac{ak_1}{\kappa^2(u+\kappa)} \left( -\frac{y^*}{\kappa} + 1 \right) - u^2 v \frac{ak_1^2}{\kappa^2(u+\kappa)} \\
& = u^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) + uv \frac{ak_1}{\kappa^2} - v^2 \frac{b}{y^*} + u^3 \frac{ak_1}{\kappa^2(u+\kappa)} \left( \frac{y^*}{\kappa} - 1 \right) \\
& \quad - u^2 v \frac{ak_1^2}{\kappa^2(u+\kappa)} + uv^2 \frac{b}{y^*(u+y^*)}.
\end{aligned}$$

We can thus write

$$\begin{aligned}
\dot{u} &= -vb + A(u, v), \\
\dot{v} &= B(u, v),
\end{aligned} \tag{3.42}$$

where  $A$  and  $B$  are analytic and their jacobian matrix at  $(0,0)$  is 0. In the neighborhood of  $(0,0)$ , the equation  $0 = -vb + A(u, v)$  has the unique solution  $v = f(u)$ , where

$$\begin{aligned}
f(u) &= \frac{-u^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) - u^3 \frac{ak_1}{\kappa^2(u+\kappa)} \left( \frac{y^*}{\kappa} - k_1 \right)}{b + u \frac{ak_1}{\kappa^2} - u^2 \frac{ak_1^2}{\kappa^2(u+\kappa)}} \\
&= -\frac{1}{b} \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) u^2 + \frac{ak_1 (-k_1 y^* a + \kappa^3 + ak_1 \kappa + b \kappa^2 - y^* \kappa b)}{b^2 \kappa^5} u^3 + O(u^4).
\end{aligned}$$

Let  $F(u) = B(u, f(u))$ . Since  $A(u, f(u)) = bf(u)$  and  $B(u, v)$  has the form

$$B(u, v) = vb - A(u, v) - vb - v^2 \frac{b}{y^*} \left( 1 - \frac{u}{u+y^*} \right),$$

we have

$$\begin{aligned}
F(u) &= -bf(u) - f^2(u) \frac{b}{y^*} \left( 1 - \frac{u}{u+y^*} \right) \\
&= \frac{(-k_1 y^* a \kappa b - k_1^2 y^* a^2 + \kappa^3 a k_1 + a k_1 \kappa^2 b + a^2 k_1^2 \kappa) u^3}{\kappa^5 b^2} \\
&\quad + \frac{(b \kappa^2 k_1 y^* a - \kappa^5 b - b \kappa^3 a k_1) u^2}{\kappa^5 b^2} + o(u^3).
\end{aligned}$$

Let also  $G(u) = (\partial A / \partial u + \partial B / \partial v)(u, f(u))$ . We have

$$\begin{aligned}
\partial A / \partial u &= -v \frac{ak_1}{\kappa^2} - 2u \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) + 2uv \frac{ak_1}{\kappa^2(u+\kappa)} \\
&\quad + 3u^2 \frac{ak_1}{\kappa^2(u+\kappa)} \left( -\frac{y^*}{\kappa} + 1 \right) - u^3 \frac{ak_1}{\kappa^2(u+\kappa)^2} \left( -\frac{y^*}{\kappa} + 1 \right) - u^2 v \frac{ak_1}{\kappa^2(u+\kappa)^2}, \\
\partial B / \partial v &= -2v \frac{b}{y^*} \left( 1 - \frac{u}{u+y^*} \right) + u \frac{ak_1}{\kappa^2} - u^2 \frac{ak_1}{\kappa^2}.
\end{aligned}$$

Replacing  $v$  by  $f(u)$  yields

$$\begin{aligned}
G(u) &= u \left[ -2 \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) + \frac{ak_1}{\kappa^2} \right] \\
&\quad + u^2 \left[ \frac{1}{b} \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) \frac{ak_1}{\kappa^2} + 3 \frac{ak_1}{\kappa^3} \left( -\frac{y^*}{\kappa} + k_1 \right) \right] + o(u^2).
\end{aligned}$$

**Case 1 :** If  $1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \neq 0$ , then

$$F(\mathbf{u}) = u^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) + o(u^2),$$

and

$$G(\mathbf{u}) = u \left[ -2 \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) + \frac{ak_1}{\kappa^2} \right] \\ + u^2 \left[ \frac{1}{b} \left( 1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \right) \frac{ak_1}{\kappa^2} + 3 \frac{ak_1}{\kappa^3} \left( -\frac{y^*}{\kappa} + k_1 \right) \right] + o(u^2).$$

We can now apply [21, Theorem 3.5] to system (3.42). Since the coefficient of  $u^2$  in  $F(\mathbf{u})$  is nonzero, we deduce from Part (4)-(i1) of [21, Theorem 3.5] :

**Lemma 3.13.** *If  $E^*$  is a nilpotent equilibrium of (3.2) in the positive quadrant  $]0, +\infty[ \times ]0, +\infty[$ , and if  $1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} \neq 0$ , then  $E^*$  is a cusp, that is, its phase portrait consists of two hyperbolic sectors and two separatrices. In this case, the index of  $E^*$  is 0.*

**Case 2 :** if  $1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} = 0$ , then

$$f(\mathbf{u}) = \frac{ak_1(-k_1y^*a + \kappa^3 + ak_1\kappa + b\kappa^2 - y^*\kappa b)}{b^2\kappa^5} u^3 + O(u^4) \\ = -\frac{1}{b\kappa} u^3 + O(u^3), \\ F(\mathbf{u}) = \frac{1}{\kappa} u^3 + o(u^3),$$

and

$$G(\mathbf{u}) = u \left( \frac{ak_1}{\kappa^2} \right) + u^2 \left[ 3 \frac{ak_1}{\kappa^3} \left( -\frac{y^*}{\kappa} + k_1 \right) \right] + o(u^2).$$

Again, we apply [21, Theorem 3.5] to System (3.42). Since the coefficient of  $u^3$  in  $F(\mathbf{u})$  is positive, we deduce from Part (4)-(ii) of [21, Theorem 3.5] :

**Lemma 3.14.** *If  $E^*$  is a nilpotent equilibrium of (3.2) in the positive quadrant  $]0, +\infty[ \times ]0, +\infty[$ , and if  $1 - \frac{ay^*k_1}{\kappa^3} + \frac{ak_1}{\kappa^2} = 0$ , then  $E^*$  is a saddle point. In this case, the index of  $E^*$  is -1.*

### **c<sub>2</sub>. The case of a center of the linearized vector field**

The point  $E^*$  is a center of the linear part of  $\mathbf{v}$  if the Jacobian  $\mathcal{J}(x^*, y^*)$  has purely imaginary eigenvalues  $\pm i\sqrt{p}$ , that is, when  $p > 0$  and  $s = 0$ . Again, this case is nonempty. Let us denote

$$b_0 = 1 - 2x^* + \frac{ay^*k_1}{\kappa^2}. \tag{3.43}$$

With the notations of (3.39), we have  $p > 0$  and  $s = 0$  if, and only if,

$$b = b_0 < a\rho. \tag{3.44}$$

Note that  $x^*$ ,  $y^*$ , as well as  $b_0$ ,  $a$ ,  $\rho$ , and the sign of  $p$  do not depend on the parameter  $b$ , and that  $s = b - b_0$ . Let us fix all parameters except  $b$ , and assume that  $\Delta_\chi < 0$ , that is, the eigenvalues of  $\mathcal{J}(x^*, y^*)$  are

$$\frac{-s \pm i\sqrt{4p - s^2}}{2}.$$

These eigenvalues cross the imaginary axis at speed  $-1/2$  when  $b$  passes through the value  $b_0$ . Let us denote  $c = a\rho$ . By (3.40) and (3.41), we have

$$\begin{aligned} v_1 &= Xb_0 - Yc - X^2 \left(1 - \frac{ay^*k_1}{\kappa^3}\right) - XY \frac{ak_1}{\kappa^2} - X^3 \frac{ay^*k_1}{\kappa^3(X + \kappa)} + X^2Y \frac{ak_1}{\kappa^2}, \\ v_2 &= (X - Y)b - \frac{b}{y^*}(X - Y)^2 \left(1 - \frac{X}{X + y^*}\right). \end{aligned}$$

Let us denote by  $(\mathbf{i}, \mathbf{j})$  the standard basis of  $\mathbf{R}^2$ . In this basis, the matrix of the linear part  $\varphi$  of  $(X, Y) \mapsto (v_1, v_2)$  is

$$A(b) = \begin{pmatrix} b_0 & -c \\ b & -b \end{pmatrix}.$$

Let

$$\begin{aligned} \delta &= \sqrt{\det A(b_0)} = \sqrt{b_0(c - b_0)}, & \gamma &= \frac{c - b_0}{\delta} = \sqrt{\frac{c - b_0}{b_0}}, \\ \mathbf{u} &= \mathbf{i} + \mathbf{j}, & \mathbf{v} &= \frac{1}{\delta}\varphi(\mathbf{u}) = -\gamma\mathbf{i}. \end{aligned}$$

The matrix of  $\varphi$  in the basis  $(\mathbf{u}, \mathbf{v})$  is

$$\tilde{A}(b) = \begin{pmatrix} 0 & -\frac{b}{b_0}\delta \\ \delta & b_0 - b \end{pmatrix}.$$

The coordinates  $(\mathbf{u}, \mathbf{v})$  in the basis  $(\mathbf{u}, \mathbf{v})$  satisfy  $\mathbf{u} = Y$ ,  $\mathbf{v} = \frac{1}{\gamma}(Y - X)$ ,  $X = \mathbf{u} - \mathbf{v}\gamma$ ,  $Y = \mathbf{u}$ . The coordinates of  $\mathbf{v}$  in the basis  $(\frac{\partial}{\partial \mathbf{u}}, \frac{\partial}{\partial \mathbf{v}})$  are

$$\begin{aligned} \dot{\mathbf{u}} &= v_2 = -b\gamma\mathbf{v} + \frac{b}{y^*}\gamma^2\mathbf{v}^2 \left(1 - \frac{\mathbf{u} - \mathbf{v}\gamma}{\mathbf{u} - \mathbf{v}\gamma + y^*}\right), \\ \dot{\mathbf{v}} &= \frac{1}{\gamma}(v_2 - v_1) \\ &= -b\mathbf{v} + \frac{b}{y^*}\gamma\mathbf{v}^2 \left(1 - \frac{\mathbf{u} - \mathbf{v}\gamma}{\mathbf{u} - \mathbf{v}\gamma + y^*}\right) \\ &\quad - \frac{1}{\gamma} \left[ (\mathbf{u} - \mathbf{v}\gamma)b_0 - \mathbf{u}c - (\mathbf{u} - \mathbf{v}\gamma)^2 \left(1 - \frac{ay^*k_1}{\kappa^3}\right) - \mathbf{u}(\mathbf{u} - \mathbf{v}\gamma) \frac{ak_1}{\kappa^2} \right. \\ &\quad \left. - (\mathbf{u} - \mathbf{v}\gamma)^3 \frac{ay^*k_1}{\kappa^3(\mathbf{u} - \mathbf{v}\gamma + \kappa)} + \mathbf{u}(\mathbf{u} - \mathbf{v}\gamma)^2 \frac{ak_1}{\kappa^2} \right]. \end{aligned}$$



In particular, for  $b = b_0$ ,

$$\begin{aligned} \dot{u} &= -\delta v + \frac{c - b_0}{y^*} v^2 \left( 1 - \frac{u - v\gamma}{u - v\gamma + y^*} \right), \\ \dot{v} &= \delta u + \frac{c - b_0}{y^*} v^2 \left( 1 - \frac{u - v\gamma}{u - v\gamma + y^*} \right) \\ &\quad + \frac{1}{\gamma} \left[ (u - v\gamma)^2 \left( 1 - \frac{ay^*k_1}{\kappa^3} \right) + u(u - v\gamma) \frac{ak_1}{\kappa^2} \right. \\ &\quad \left. + (u - v\gamma)^3 \frac{ay^*k_1}{\kappa^3(u - v\gamma + \kappa)} - u(u - v\gamma)^2 \frac{ak_1}{\kappa^2} \right]. \end{aligned}$$

### 3.2.3 Existence of a globally asymptotically stable equilibrium point

When  $m = 0$ , in the case (c) of Theorem 3.3, we have seen that (3.2) has no cycle, because the compact set delimited by a cycle would contain a critical point, see [11, Theorem V.3.8]. As the compact set  $\mathcal{A}$  is positively invariant and contains all equilibrium points of the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , all trajectories starting in the quadrant  $\mathbf{R}_+ \times \mathbf{R}_+$  converge to  $E_1$  or  $E_2$  ( $E_0$  is excluded because it is an unstable node). On the  $x$  axis, we have  $\dot{y} = 0$  and  $x$  satisfies the logistic equation  $\dot{x} = x(1 - x)$ , thus, for  $x(0) > 0$ ,  $x(t)$  converges to 1, i.e.,  $(x(t), y(t))$  converges to  $E_1$ . On the other hand, for  $0 < y < k_2 + x$ , we have  $\dot{y} > 0$ , thus, if  $y(0) > 0$ ,  $(x(t), y(t))$  cannot converge to  $E_1$ , it converges necessarily to  $E_2$ .

**Théorème 3.5.** *A sufficient condition for the existence of a globally asymptotically stable equilibrium point  $E^* = (x^*, y^*)$  in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  (equivalently, in the interior of  $\mathcal{A}$ ) is that*

$$\left( 2m + k_1 \geq 1 \right) \text{ and } \left( m > 0 \right) \text{ or } \left( 4ak_2 \leq (1 - k_1 - a)^2 + 4k_1 \right). \quad (3.45)$$

**Proof.** Let  $E^* = (x^*, y^*) \in \mathcal{A}$  be an equilibrium point in the interior of  $\mathcal{A}$ . Let us denote

$$\rho(x) = \frac{a(x - m)}{k_1 + x - m},$$

and let us set

$$V(x, y) = \int_{x^*}^x \frac{u - x^*}{(k_2 + u - m)\rho(u)} du + \frac{1}{b} \int_{y^*}^y \frac{v - y^*}{v} dv.$$

Then, using (3.23) and (3.24), we have

$$\begin{aligned} \dot{V} &= \frac{x - x^*}{(k_2 + x - m)\rho(x)} \dot{x} + \frac{1}{b} \frac{y - y^*}{y} \dot{y} \\ &= \frac{x - x^*}{k_2 + x - m} \left( \frac{x(1 - x)}{\rho(x)} - \frac{a(x - m)}{k_1 + x - m} \frac{1}{\rho(x)} y \right) + \frac{1}{b} (y - y^*) b \left( 1 - \frac{y}{k_2 + x - m} \right) \\ &= \frac{x - x^*}{a(k_2 + x - m)} \left( \frac{x(1 - x)(k_1 + x - m)}{x - m} - y^* \right) - \frac{(x - x^*)(y - y^*)}{k_2 + x - m} \end{aligned}$$

$$\begin{aligned}
& + (y - y^*) \left( \frac{y^*}{k_2 + x^* - m} - \frac{y}{k_2 + x - m} \right) \\
& = \frac{x - x^*}{a(k_2 + x - m)} \left( \frac{x(1-x)(k_1 + x - m)}{x - m} - \frac{x^*(1-x^*)(k_1 + x^* - m)}{x^* - m} \right) \\
& \quad - \frac{(x - x^*)(y - y^*)}{k_2 + x - m} \\
& \quad + (y - y^*) \frac{y^*(k_2 + x - m) - y(k_2 + x^* - m)}{(k_2 + x^* - m)(k_2 + x - m)}.
\end{aligned}$$

Let us denote  $\mathbf{g}(x) = x(1-x)(k_1 + x - m)/(x - m)$ . Then

$$\begin{aligned}
\dot{V} & = \frac{x - x^*}{a(k_2 + x - m)} (\mathbf{g}(x) - \mathbf{g}(x^*)) - \frac{(x - x^*)(y - y^*)}{k_2 + x - m} \\
& \quad + (y - y^*) \frac{(y^* - y)(k_2 - m) + y^*x - yx^*}{(k_2 + x^* - m)(k_2 + x - m)} \\
& = \frac{x - x^*}{a(k_2 + x - m)} (\mathbf{g}(x) - \mathbf{g}(x^*)) - \frac{(x - x^*)(y - y^*)}{k_2 + x - m} \\
& \quad + \frac{y - y^*}{y^*} \frac{(y^* - y)(x^* + k_2 - m) + y^*(x - x^*)}{k_2 + x - m} \\
& = \frac{x - x^*}{a(k_2 + x - m)} (\mathbf{g}(x) - \mathbf{g}(x^*)) + \frac{y - y^*}{y^*} \frac{(y^* - y)(x^* + k_2 - m)}{k_2 + x - m} \\
& = \frac{1}{k_2 + x - m} \left( \frac{x - x^*}{a} (\mathbf{g}(x) - \mathbf{g}(x^*)) - (y - y^*)^2 \right).
\end{aligned}$$

For  $x \geq m$ , a sufficient condition for  $\dot{V}$  to be negative when  $(x, y) \neq (x^*, y^*)$  is that  $\mathbf{g}$  be nonincreasing. Let us make the change of variable  $X = x - m$ . We have

$$\mathbf{g}(x) = \frac{(X + m)(1 - X - m)(X + k_1)}{X},$$

which leads to

$$\mathbf{g}'(x) = \frac{-2X^3 + (1 - 2m - k_1)X^2 - k_1(m - m^2)}{X^2}.$$

Thus, if  $2m + k_1 \geq 1$ ,  $\mathbf{g}'(X)$  remains negative for  $X > 0$ , i.e., for  $x > m$ . Thus, for  $x > m$ , under the assumption (3.45),  $\dot{V}$  is negative.

We have seen that the first part of (3.45) implies that the equilibrium point  $E^*$ , if it exists, is globally asymptotically stable. Note that Condition (3.45) is independent of the coordinates of  $E^*$ , and the global stability implies that the equilibrium point  $E^*$ , if it exists, is unique.

The second part of (3.45) is a necessary and sufficient condition for the existence of such an equilibrium point.

When  $m > 0$ , we already know that there exists at least one equilibrium point in  $\mathcal{A}$ . Actually, Condition (3.45) implies that the coefficient  $\alpha_2 = a + k_1 - 1 + 2m$  of (3.26) is positive. Thus, when  $m > 0$ , (3.45) is a particular case of (c) in Theorem 3.2.

When  $m = 0$ , by Theorem 3.3-(c), since  $\alpha_2 > 0$ , there exists an equilibrium point in the interior of  $\mathcal{A}$  if, and only if, (3.32) is satisfied.  $\square$

### 3.2.4 Cycles

Let us investigate the existence of periodic orbits of (3.2). By Theorem 3.1 such orbits can take place only in  $\mathcal{A}$ .

#### Refuge free case ( $m = 0$ )

This case has been studied by M.A. Aziz-Alaoui and M. Daher-Okiye [19], but we add some new results.

**Lemma 3.15.** *In the cases (c) and (a) of Theorem 3.3, that is, when (3.2) has 0 or 2 equilibrium points in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , the system (3.2) has no limit cycle. On the other hand, in the case (b) of Theorem 3.3, that is, when (3.2) has 1 equilibrium point in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , if furthermore  $s < 0$  and  $p > 0$ , the system (3.2) has at least one limit cycle.*

**Proof.** In the case (c), the only equilibrium points of (3.2) in  $\mathbf{R}_+ \times \mathbf{R}_+$  are the trivial points  $E_0$ ,  $E_1$ , and  $E_2$ , on the axes. Thus (3.2) has no cycle, because the compact set delimited by a cycle would contain a critical point, see [11, Theorem V.3.8].

In the case (a), if there was a cycle inside  $\mathcal{A}$ , we could apply the Poincaré-Hopf Index Theorem to the compact manifold whose boundary is delineated by this cycle (see [57] for a version of this theorem when the vector field is tangent to the boundary). Denoting  $N$  the number of nodes or foci and  $S$  the number of saddles in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ , we would have  $N - S = 1$ . But Theorem 3.4 shows that  $N - S = 0$ , a contradiction.

In the case (b), if  $s < 0$  and  $p > 0$ , the system (3.2) has an unstable equilibrium point. From Theorem 3.1 and Poincaré-Bendixson Theorem, there exists at least one limit cycle around this equilibrium.  $\square$

Note that the conditions of Lemma 3.15 do not involve the value of  $b$ . Using Bendixson-Dulac criterion, M.A. Aziz-Alaoui and M. Daher-Okiye obtain another criterion :

**Lemma 3.16.** *[19, Theorem 7] if  $b + k_1 \geq 1$ , then the system (3.2) has no limit cycle.*

#### Case with refuge ( $m > 0$ )

By Theorem 3.5, if Condition (3.45) is satisfied, there can be no periodic orbits.

Let us now give some sufficient conditions for the absence of periodic orbits, using Bendixson-Dulac criterion. Let us denote by  $f(x, y)$  and  $g(x, y)$  the coordinates of the vector field in (3.2). For a Dulac function, we choose

$$D(x, y) = x + k_1 - m.$$

Let us look for conditions that ensure that  $\frac{\partial(fD)}{\partial x} + \frac{\partial(gD)}{\partial y} < 0$  in  $\mathcal{A}$ . We have

$$\frac{\partial(fD)}{\partial x}(x, y) = -3x^2 + 2(1 - k_1 + m)x + k_1 - m - ay,$$

$$\frac{\partial(gD)}{\partial y}(x, y) = \frac{b(x + k_1 - m)(x + k_2 - m - 2y)}{x + k_2 - m}.$$

For  $(x, y) \in \mathcal{A}$ , we have

$$\frac{\partial(fD)}{\partial x}(x, y) < -3m^2 + 2(1 - k_1 + m)x + k_1 - m - ak_2.$$

Since the maximum of  $-3m^2 + m$  is  $1/12$  and the maximum of  $-m^2 + m$  is  $1/4$ , we deduce :

$$\begin{aligned} 1 - k_1 + m > 0 &\Rightarrow \frac{\partial(fD)}{\partial x}(x, y) < -3m^2 + m - k_1 - ak_2 + 2 \\ &\leq 2 + \frac{1}{12} - k_1 - ak_2, \\ 1 - k_1 + m < 0 &\Rightarrow \frac{\partial(fD)}{\partial x}(x, y) < -m^2 + m(1 - 2k_1) - k_1 - ak_2 \\ &< -m^2 - m - k_1 - ak_2 < 0. \end{aligned}$$

In particular, a condition that ensures that  $\frac{\partial(fD)}{\partial x} < 0$  in  $\mathcal{A}$  is

$$(k_1 > 1 + m) \text{ or } (ak_2 + k_1 > 2 + \frac{1}{12}). \quad (3.46)$$

On the other hand, for  $(x, y) \in \mathcal{A}$ ,  $\frac{\partial(gD)}{\partial y}(x, y)$  has the same sign as  $x + k_2 - m - 2y$ , and we have  $x + k_2 - m - 2y < 1 - m - k_2$ . Thus a sufficient condition for  $\frac{\partial(gD)}{\partial x} < 0$  in  $\mathcal{A}$  is

$$k_2 > 1 - m. \quad (3.47)$$

The same technique does not provide any sufficient condition for  $\frac{\partial(fD)}{\partial x} + \frac{\partial(gD)}{\partial y} > 0$  in  $\mathcal{A}$ . So, our next result concerning the absence of cycles is :

**Lemma 3.17.** *A sufficient condition for (3.2) to have no periodic solution is*

$$\left( k_2 > 1 - m \right) \text{ and } \left( (k_1 > 1 + m) \text{ or } (ak_2 + k_1 > 2 + \frac{1}{12}) \right).$$

Now, we consider the existence of limit cycles which are not occurring from a Hopf bifurcation. The special configuration of the existence of a limit cycle enclosing three equilibrium points is numerically investigated. In particular, when the system parameters satisfy  $a = 0.5, k_1 = 0.08, k_2 = 0.2, b = 0.1, m = 0.0025$ , then three hyperbolic equilibrium points exist, namely,  $E_1^* = (0.0222589; 0.2197589)$ ,  $E_2^* = (0.0299525; 0.2274525)$ ,  $E_3^* = (0.3702886; 0.5677886)$ . They define respectively a stable focus, a saddle point and an unstable focus. Accordingly to the Poincaré index theorem, the sum of the corresponding indexes is equal to 1.

The numerical simulations show that there exists a limit cycle, which is hyperbolic and stable, see Figure 3.1.

### 3.3 Stochastic model

We now study the dynamics of the system (3.3), with initial conditions  $x_0 > 0$  and  $y_0 > 0$ . In the case when  $m = 0$  and  $k_1 = k_2$ , the persistence and boundedness of solutions have been investigated in by Ji, Jiang and Shi in [37]. A similar model has been studied by Fu, Jiang, Shi, Hayat and Alsaedi in [25].

#### 3.3.1 Existence and uniqueness of the positive global solution

**Théorème 3.6.** *For any initial condition  $(x_0, y_0) \in \mathbb{R}_+^2$ , the system (3.3) admits a unique solution  $(x(t), y(t))$ , defined for all  $t \geq 0$  a.s. and this solution remains in  $]0, +\infty[ \times ]0, +\infty[$ . Furthermore, if  $(x_0, y_0) \in ]0, +\infty[ \times ]0, +\infty[$ , this solution remains in  $]0, +\infty[ \times ]0, +\infty[$ , whereas, if  $(x_0, y_0)$  belongs to one of the axis  $\mathbf{R}_+ \times \{0\}$  or  $\{0\} \times \mathbf{R}_+$ , it remains on this axis.*

**Proof.** Since the coefficients of (3.3) are locally Lipschitz, uniqueness of the solution until explosion time is guaranteed for any initial condition.

Let us now prove global existence of the solution.

The case when  $(x_0, y_0) \in (\mathbf{R}_+ \times \{0\}) \cup (\{0\} \times \mathbf{R}_+)$  is trivial because both equations in (3.3) become independent, for example if  $y_0 = 0$  with  $x_0 \neq 0$ , we have  $y(t) = 0$  for all  $t \geq 0$ , and  $x$  is a solution to the stochastic logistic equation

$$dx(t) = x(t)(1 - x(t))dt + \sigma_1 x(t)dw_1(t)$$

which is well known (see Section 3.3.2), thus  $x(t)$  is defined for every  $t \geq 0$ .

Assume now that  $x_0 > 0$  and  $y_0 > 0$ . Since the coordinate axes are stable by (3.3), we deduce, applying locally the comparison theorem for SDEs (see [22, Theorem 1], this theorem is given for globally Lipschitz coefficients), that the solution to (3.3) remains in  $]0, +\infty[ \times ]0, +\infty[$  until its explosion time.

Let  $\tau_e$  be the explosion time of the solution to (3.3). To show that  $\tau_e = \infty$ , we adapt the proof of [20]. Let  $k_0 > 0$  be large enough, such that  $(x_0, y_0) \in [\frac{1}{k_0}, k_0] \times [\frac{1}{k_0}, k_0]$ . For each integer  $k \geq k_0$  we define the stopping time

$$\tau_k = \inf \left\{ t \in [0, \tau_e) : x \notin \left(\frac{1}{k}, k\right) \text{ or } y \notin \left(\frac{1}{k}, k\right) \right\}.$$

The sequence  $(\tau_k)$  is increasing as  $k \rightarrow \infty$ . Set  $\tau_\infty = \lim_{k \rightarrow \infty} \tau_k$ , whence  $\tau_\infty \leq \tau_e$ , (in fact, as  $(x(t), y(t)) > 0$  a.s., we have  $\tau_\infty = \tau_e$ ). It suffices to prove that  $\tau_\infty = \infty$  a.s.. Assume that this statement is false, then there exist  $T > 0$  and  $\varepsilon \in ]0, 1[$  such that  $\mathbb{P}(\{\tau_\infty \leq T\}) > \varepsilon$ . Since  $(\tau_k)$  is increasing we have

$$\mathbb{P}(\{\tau_k \leq T\}) > \varepsilon.$$

Now, we consider the positive definite function  $V : ]0, +\infty[ \times ]0, +\infty[ \rightarrow ]0, +\infty[ \times ]0, +\infty[$  given by

$$V(x, y) = (x + 1 - \log x) + (y + 1 - \log y).$$

Applying Itô's formula, we get

$$dV(x, y) = \left[ (x-1) \left( 1 - x - \frac{ay(x-m)}{k_1 + x - m} \right) + \frac{\sigma_1^2}{2} + b(y-1) \left( 1 - \frac{y}{k_2 + x - m} \right) + \frac{\sigma_2^2}{2} \right] dt + \sigma_1(x-1)dW_1 + \sigma_2(y-1)dW_2.$$

The positivity of  $x(t)$  and  $y(t)$  implies

$$\begin{aligned} dV(x, y) &\leq \left( 2x + ay + \frac{\sigma_1^2 + \sigma_2^2}{2} + by + \frac{y}{k_2} \right) dt + \sigma_1(x-1)dW_1 + \sigma_2(y-1)dW_2 \\ &\leq \left( 2x + \left( a + b + \frac{1}{k_2} \right) y + \frac{\sigma_1^2 + \sigma_2^2}{2} \right) dt + \sigma_1(x-1)dW_1 + \sigma_2(y-1)dW_2. \end{aligned}$$

Denote  $c_1 = a + b + \frac{1}{k_2}$ ,  $c_2 = \frac{\sigma_1^2 + \sigma_2^2}{2}$ . Using [20, lemma 4.1], we can write

$$\begin{aligned} 2x + c_1 y &\leq 4(x+1 - \log x) + 2c_1(y+1 - \log y) \\ &\leq c_3 V(x, y), \text{ where } c_3 = \max(4, 2c_1). \end{aligned}$$

Hence

$$\begin{aligned} dV(x, y) &\leq (c_2 + c_3 V(x, y)) dt + \sigma_1(x-1)dW_1 + \sigma_2(y-1)dW_2 \\ &\leq c_4(1 + V(x, y)) dt + \sigma_1(x-1)dW_1 + \sigma_2(y-1)dW_2, \text{ where } c_4 = \max(c_2, c_3). \end{aligned}$$

Integrating both sides from 0 to  $\tau_k \wedge T$ , and taking expectations, we get

$$\mathbb{E} V(x(\tau_k \wedge T), y(\tau_k \wedge T)) \leq V(x_0, y_0) + c_4 T + c_4 \int_0^T \mathbb{E} V(x(\tau_k \wedge t), y(\tau_k \wedge t)) dt.$$

By Gronwall's inequality, this yields

$$\mathbb{E} V(x(\tau_k \wedge T), y(\tau_k \wedge T)) \leq c_5, \quad (3.48)$$

where  $c_5$  is the finite constant given by

$$c_5 = (V(x_0, y_0) + c_4 T) e^{c_4 T}. \quad (3.49)$$

Let  $\Omega_k = \{\tau_k \leq T\}$ . We have  $\mathbb{P}(\Omega_k) \geq \varepsilon$ , and for all  $\omega \in \Omega_k$ , there exists at least one element of  $x(\tau_k, \omega), y(\tau_k, \omega)$  which is equal either to  $k$  or to  $\frac{1}{k}$ , hence

$$V(x(\tau_k), y(\tau_k)) \geq (k+1 - \log k) \wedge \left( \frac{1}{k} + 1 + \log k \right).$$

Therefore, by (3.48),

$$c_5 \geq \mathbb{E}[1_{\Omega_k}(\omega) V(x(\tau_k, \omega), y(\tau_k, \omega))] \geq \varepsilon \left[ (k+1 - \log k) \wedge \left( \frac{1}{k} + 1 + \log k \right) \right],$$

where  $1_{\Omega_k}$  is the indicator function of  $\Omega_k$ . Letting  $k \rightarrow \infty$ , we get  $c_5 = \infty$ , which contradicts (3.49). So we must have  $\tau_\infty = \infty$  a.s.  $\square$

**Remark 3.18.** *An alternative proof of non explosion in finite time can be obtained by using the comparison theorem, since  $0 \leq x(t) \leq z_1(t)$  and  $0 \leq y(t) \leq z_2(t)$  a.s. for every  $t \geq 0$ , where  $z_1$  and  $z_2$  are geometric Brownian motions, with*

$$dz_1(t) = z_1(t)dt + \sigma_1 z_1(t)dW_1(t) \text{ and } dz_2(t) = bz_2(t)dt + \sigma_2 z_2(t)dW_2(t).$$

### 3.3.2 Comparison results

In this section, we compare the dynamics of (3.3) with some simpler models, in view of applications to the long time behaviour of the solutions to (3.3).

Applying locally the comparison theorem for SDEs (see [22, Theorem 1], this theorem is given for globally Lipschitz coefficients), we have, for every  $t \geq 0$ ,

$$0 \leq x(t) \leq u(t) \text{ a.s.} \tag{3.50}$$

where  $u$  is the solution to the stochastic logistic equation (also called stochastic Verhulst equation) with initial condition  $x_0$  :

$$du(t) = u(t)(1 - u(t))dt + \sigma_1 u(t)dw_1(t), \quad u(0) = x_0. \tag{3.51}$$

The process  $u$  is well known and can be written explicitly, see [39, page 125] :

$$u(t) = \frac{e^{\left(1 - \frac{\sigma_1^2}{2}\right)t + \sigma_1 w_1(t)}}{\frac{1}{x_0} + \int_0^t e^{\left(1 - \frac{\sigma_1^2}{2}\right)s + \sigma_1 w_1(s)} ds}.$$

By [50, Lemma 2.2],  $u$  is uniformly bounded in  $L^p$  for every  $p > 0$ . Thus, by (3.50), for every  $p > 0$ , there exists a constant  $K_p$  such that

$$\sup_{t \geq 0} \mathbb{E}(x(t)^p) < K_p. \tag{3.52}$$

Using again the comparison theorem, we get, for every  $t \geq 0$ ,

$$0 \leq y(t) \leq v(t), \tag{3.53}$$

where  $v$  is the solution to

$$dv(t) = bv(t) \left(1 - \frac{v(t)}{k_2 + u(t)}\right) dt + \sigma_2 v(t)dw_2(t), \quad v(0) = y_0, \tag{3.54}$$

which can be explicitated with the help of  $u$  :

$$v(t) = \frac{e^{\left(b - \frac{\sigma_2^2}{2}\right)t + \sigma_2 w_2(t)}}{\frac{1}{y_0} + b \int_0^t \frac{1}{k_2 + u(s)} e^{\left(b - \frac{\sigma_2^2}{2}\right)s + \sigma_2 w_2(s)} ds}. \tag{3.55}$$

Similarly, we have, for every  $t \geq 0$ ,

$$0 \leq \check{u}(t) \leq x(t) \text{ a.s.}, \tag{3.56}$$

$$0 \leq \check{v}(t) \leq y(t) \text{ a.s.}, \tag{3.57}$$

with

$$d\check{u}(t) = \left(\check{u}(t)(1 - \check{u}(t)) - a\check{v}(t)\right)dt + \sigma_1 \check{u}(t)dw_1(t), \quad \check{u}(0) = x_0, \tag{3.58}$$

$$d\check{v}(t) = b\check{v}(t) \left(1 - \frac{\check{v}(t)}{k_2}\right) dt + \sigma_2 \check{v}(t) dw_2(t), \quad \check{v}(0) = y_0. \quad (3.59)$$

Note that  $\check{u}$  is defined with the help of the process  $v$  defined by (3.54).

The following property of stochastic logistic processes will be useful :

**Lemma 3.19.** ([50, Theorem 3.2 and Theorem 4.1]) *The process  $u$  converges a.s. to 0 if  $\sigma_1^2 \geq 2$ , whereas it converges to a nondegenerate stationary distribution if  $\sigma_1^2 < 2$ .*

*Similarly,  $\check{v}$  converges a.s. to 0 if  $\sigma_2^2 \geq 2b$ , whereas it converges to a nondegenerate stationary distribution if  $\sigma_2^2 < 2$ .*

**Remark 3.20.** *The global existence and uniqueness of  $(u, v, \check{u}, \check{v})$  can be obtained via the same methods as in Section 3.3.1, see in particular Remark 3.18.*

### 3.3.3 Extinction

We show that, when the noise is large, the system (3.3) goes almost surely (but in infinite time) to extinction.

**Théorème 3.7.** *Assume that  $\sigma_1^2 \geq 2$ . Then  $\lim_{t \rightarrow \infty} x(t) = 0$  a.s. If moreover  $\sigma_2^2 \geq 2b$ , then  $\lim_{t \rightarrow \infty} y(t) = 0$  a.s.*

**Proof.** If  $\sigma_1^2 \geq 2$ , we deduce from (3.51) and Lemma 3.19 that  $x(t)$  converges to 0 a.s.

Assume moreover that  $\sigma_2^2 \geq 2b$ . From (3.55), the random variable  $v : \Omega \rightarrow C(\mathbf{R}_+; \mathbf{R}_+)$  is a function of two independent random variables,  $w_2$  and  $u$  (the latter is a function of  $w_1$ ). For a fixed  $u \in C(\mathbf{R}_+; \mathbf{R}_+)$  such that  $\lim_{t \rightarrow \infty} u(t) = 0$ , we have

$$\lim_{t \rightarrow \infty} (v(t) - \check{v}(t)) = 0, \quad (3.60)$$

where  $\check{v}$  is defined by (3.58). Thus, since  $u(t)$  goes to 0 a.s., Equation 3.60 is satisfied a.s. Since, by Lemma 3.19,  $\check{v}(t)$  converges a.s. to 0 if  $\sigma_2^2 \geq 2b$ , we deduce that  $\lim_{t \rightarrow \infty} v(t) = 0$  a.s., and the result follows from (3.53).  $\square$

**Remark 3.21.** *Since  $\check{v}(t) \leq y(t) \leq v(t)$ , we can deduce also from (3.60) that, if  $\sigma_1^2 \geq 2$  with  $0 < \sigma_2^2 < 2b$ , then  $x(t)$  converges a.s. to 0 while  $y(t)$  converges to a nondegenerate stationary distribution.*

### 3.3.4 Existence of a stationary distribution

In this section, we assume that  $m > 0$ . The existence of a stationary distribution is proved for a similar (but different) system without refuge in [25].



**Théorème 3.8.** *Assume that  $0 < \sigma_1^2 < 2$  and  $0 < \sigma_2^2 < 2b$ , with  $m > 0$ . Then the system (3.3) has a unique stationary distribution  $\mu$  on  $]0, +\infty[ \times ]0, +\infty[$ . Moreover, the system (3.3) is ergodic and its transition probability  $P((x, y), t, \cdot)$  satisfies*

$$P((x_0, y_0), t, \varphi) \rightarrow \mu(\varphi) \text{ when } t \rightarrow \infty$$

for each  $(x_0, y_0) \in ]0, +\infty[ \times ]0, +\infty[$  and each bounded continuous function  $\varphi : ]0, +\infty[ \times ]0, +\infty[ \rightarrow \mathbf{R}$ .

**Remark 3.22.** *Theorem 3.8 shows that, contrarily to the deterministic case, when  $\min\{\sigma_1, \sigma_2\} > 0$ , there is only one equilibrium for the system (3.3) in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$ .*

*Note also that, when  $\min\{\sigma_1, \sigma_2\} > 0$ , there is no invariant closed subset in the open quadrant  $]0, +\infty[ \times ]0, +\infty[$  for the system (3.3). Indeed, since the noise in (3.3) acts in all directions, the viability conditions of [18] are satisfied for no closed convex subset of  $]0, +\infty[ \times ]0, +\infty[$ .*

*In particular, there is no equilibrium point for (3.3), thus the limit stationary distribution is nondegenerate.*

**Remark 3.23.** *The ecologically less interesting case when  $(x, y)$  stays in one of the coordinate axes has similar features, since, by [50, Theorem 3.2], the stochastic logistic equation admits a unique invariant ergodic distribution when the diffusion coefficient is positive but not too large.*

Our proof of Theorem 3.8 is based on the following well known result :

**Lemma 3.24.** *Consider the equation*

$$dX(t) = f(X(t)) dt + g(X(t)) dW(t) \tag{3.61}$$

where  $f : \mathbf{R}^d \rightarrow \mathbf{R}^d$  and  $g : \mathbf{R}^d \rightarrow \mathbf{R}^{m \times d}$  are locally Lipschitz functions with locally sublinear growth, and  $W$  is a standard Brownian motion on  $\mathbf{R}^m$ . Denote by  $A(x)$  the  $m \times m$  matrix  $g(x)g(x)^T$ . Assume that  $]0, +\infty[^d$  is invariant by (3.61) and that there exists a bounded open subset  $U$  of  $]0, +\infty[^d$  such that the following conditions are satisfied :

- (B.1) *In a neighborhood of  $U$ , the smallest eigenvalue of  $A(x)$  is bounded away from 0,*
- (B.2) *If  $x \in \mathbf{R}^d \setminus U$ , the expectation of the hitting time  $\tau^U$  at which the solution to (3.61) starting from  $x$  reaches the set  $U$  is finite, and  $\sup_{x \in K} \mathbf{E}^x \tau^U < \infty$  for every compact subset  $K$  of  $]0, +\infty[^d$ .*

Then (3.61) has a unique stationary distribution  $\mu$  on  $]0, +\infty[^d$ . Moreover, (3.61) is ergodic, its transition probability  $P(x, t, \cdot)$  satisfies

$$P(x, t, \varphi) \rightarrow \mu(\varphi) \text{ when } t \rightarrow \infty \tag{3.62}$$

for each  $x \in \mathbf{R}^d$  and each bounded continuous  $\varphi : ]0, +\infty[^d \rightarrow \mathbf{R}$ .

The existence of the stationary distribution comes from [38, Theorem 4.1], its uniqueness from [38, Corollary 4.4], the ergodicity from [38, Theorem 4.2], and (3.62) comes from [38, Theorem 4.3]. Section 4.8 of [38] contains remarks that allow the restriction to an positively invariant domain such as  $]0, +\infty[^d$ .

To prove Condition (B.2), we establish some preliminary results using the systems (3.51)-(3.54) and (3.58)-(3.59) of Section 3.3.2. Let us first set some notations : For  $r, R, x_0, y_0 > 0$ , we denote

$$\begin{aligned}\tau_1^{(R)}(x_0) &= \inf\{t \geq 0; u(t) < R\}, \\ \tau_2^{(R)}(x_0, y_0) &= \inf\{t \geq 0; v(t) < R\}, \\ \check{\tau}_1^{(r)}(x_0) &= \inf\{t \geq 0; x(t) > r\}, \\ \check{\tau}_2^{(r)}(y_0) &= \inf\{t \geq 0; \check{v}(t) > r\},\end{aligned}$$

where  $\inf \emptyset = +\infty$ ,  $u$ ,  $v$ , and  $\check{v}$  are the solutions to (3.51), (3.54), and (3.59) respectively, and  $x$  is the first component of the solution to (3.3) starting from  $(x_0, y_0)$ . Note that, since  $v$  depends on  $u$ , the hitting time  $\tau_2^{(R)}$  depends on  $(x_0, y_0)$ .

Since (3.51) and (3.59) are stochastic logistic equations, the proof of [50, Theorem 3.2] shows the following :

**Lemma 3.25.** *Assume that  $0 < \sigma_1^2 < 2$ . There exists  $R_1 > 0$  sufficiently large such that  $\mathbb{E}\left(\tau_1^{(R_1)}(x_0)\right)$  is finite and uniformly bounded on compact subsets of  $[R_1, +\infty[$ .*

*Assume that  $0 < \sigma_2^2 < 2b$ . There exists  $r_2 > 0$  sufficiently small such that  $\mathbb{E}\left(\check{\tau}_2^{(r_2)}(y_0)\right)$  is finite and uniformly bounded on compact subsets of  $]0, r_2]$ .*

Note that the proof of [50, Theorem 3.2] provides a two-sided version of Lemma 3.25 (that is, each of the processes  $u$  and  $\check{v}$  hits an interval of the form  $]r, R[$  in finite time), but we only need the one-sided version stated here.

**Lemma 3.26.** *Assume that  $0 < \sigma_1^2 < 2$ . There exists  $r_1$  sufficiently small such that  $\mathbb{E}(\check{\tau}_1^{(r_1)}(y_0))$  is finite and uniformly bounded on compact subsets of  $]0, r_1]$ .*

**Proof.** We use the fact that, when  $x < m$ ,  $x$  coincides with a process  $z$  solution to the stochastic logistic equation

$$dz(t) = z(1 - z)dt + \sigma_1 z dw_1(t).$$

The proof of [50, Theorem 3.2] provides a number  $r > 0$  such that the expectation of the hitting time of  $]r, +\infty[$  by  $z$  is finite and uniformly bounded on each compact subset of  $]0, r]$ . Then, we only need to take  $r_1 = \min\{r, m\}$ .  $\square$

**Lemma 3.27.** *There exists  $R_2$  sufficiently large such that  $\mathbb{E}(\tau_2^{((R_2))}(x_0, y_0))$  is finite and uniformly bounded on compact subsets of  $]0, +\infty[ \times [R_2, +\infty[$ .*

**Proof.** Let us set, for  $u, v > 0$ ,

$$V(u, v) = \frac{1}{u} + u + \frac{1}{v} + \log(v).$$

We have  $V(u, v) \geq V(1, 1) > 0$ . Let  $L$  be the infinitesimal operator (or Dynkin operator) of the system (3.51)-(3.54). We have

$$\begin{aligned} LV(u, v) &= u(1-u) \left(1 - \frac{1}{u^2}\right) + \frac{\sigma_1^2}{u} \\ &\quad + bv \left(1 - \frac{v}{k_2 + u}\right) \left(-\frac{1}{v^2} + \frac{1}{v}\right) + \frac{\sigma_2^2}{2} \left(\frac{2}{v} - 1\right) \\ &= -\frac{1+u}{u} \left((u-1)^2 - \sigma_1^2\right) - \sigma_1^2 \\ &\quad + b \frac{v-1}{v} \frac{k_2 + u - v}{k_2 + u} + \frac{\sigma_2^2}{2} \frac{2-v}{v}. \end{aligned}$$

Let  $\rho \geq 1$  such that

$$u > \rho \Rightarrow (u-1)^2 - \sigma_1^2 > bu.$$

For  $u > \rho$  and  $v > \max\{4, 1/(b + \sigma_1^2)\}$ , we get  $(2-v)/v \leq -1/2$  and

$$LV(u, v) \leq -\frac{1+u}{u} bu - \sigma_1^2 + b - \frac{\sigma_2^2}{4} = -bu - \sigma_1^2 - \frac{\sigma_2^2}{4} \leq -\frac{b + \sigma_1^2}{b + \sigma_1^2} - \frac{\sigma_2^2}{4} < -1.$$

On the other hand, there exists a number  $K \geq 0$  such that

$$u \leq \rho \Rightarrow (u-1)^2 - \sigma_1^2 \leq K.$$

For  $u \leq \rho$  and  $v \geq \max\{4, (1+2/b)(k_2 + \rho)\}$ , we have  $(v-1)/v \geq 3/4$  and  $(k_2 + \rho - v)/(k_2 + \rho) \leq -2/b$ , thus

$$\begin{aligned} LV(u, v) &\leq -\frac{1+\rho}{\rho} K - \sigma_1^2 + b \frac{v-1}{v} \frac{k_2 + \rho - v}{k_2 + \rho} - \frac{\sigma_2^2}{4} \\ &\leq -\frac{1+\rho}{\rho} K - \sigma_1^2 + b \times \frac{3}{4} \times \frac{-2}{b} - \frac{\sigma_2^2}{4} \\ &< -1. \end{aligned}$$

Let  $R_2 = \max\{4, 1/(b + \sigma_1^2), (1 + 2/b)(k_2 + \rho)\}$ . For every  $y_0 > R_2$  and every  $x_0 > 0$ , we have  $LV(u, v) < -1$ . Denote for simplicity  $\tau = \tau_2^{(R_2)}(x_0, y_0)$ . We have

$$\begin{aligned} 0 &\leq \mathbb{E}^{(x_0, y_0)} V(u(\tau), v(\tau)) \\ &= V(x_0, y_0) + \mathbb{E}^{(x_0, y_0)} \int_0^\tau LV(u(s), v(s)) ds \leq V(x_0, y_0) - \mathbb{E}(\tau), \end{aligned}$$

which proves that  $\mathbb{E}(\tau) \leq V(x_0, y_0) < \infty$ .  $\square$

**Proof.** [Proof of Theorem 3.8] Condition (B.1) of Lemma 3.24 is trivially satisfied.

To prove Condition (B.2), with the notations of Lemma (3.25) to (3.27), taking into account the inequalities (3.50), (3.53), and (3.57), we only need to take  $r$  and  $R$  such that  $0 < r < R$ ,  $r \leq \min\{r_1, r_2\}$ ,  $R \geq \max\{R_1, R_2\}$ , and  $U = ]r, R[ \times ]r, R[$ .  $\square$

## 3.4 Numerical simulations and figures

All simulations and pictures of this section are obtained using Scilab.

### 3.4.1 Deterministic system

We numerically simulate solutions to System (3.2). Using the Euler scheme, we consider the following discretized system :

$$\begin{aligned} x_{k+1} &= x_k + \left[ x_k(1 - x_k) - \frac{ay_k(x_k - m)}{k_1 + x_k - m} \right] h, \\ y_{k+1} &= y_k + by_k \left[ 1 - \frac{y_k}{k_2 + x_k - m} \right] h. \end{aligned} \tag{3.63}$$

Simulations are shown in Figure 3.1 to 3.3.

### 3.4.2 Stochastically perturbed system

We numerically simulate the solution to System (3.3). Using the Milstein scheme (see [39]), we consider the discretized system

$$\begin{aligned} x_{k+1} &= x_k + \left[ x_k(1 - x_k - \frac{ay_k}{k_1 + x_k - m}) \right] h + \sigma_1 x_k \sqrt{h} \xi_k^2 + \frac{1}{2} \sigma_1^2 x_k (h \xi_k^2 - h), \\ y_{k+1} &= y_k + by_k \left[ 1 - \frac{y}{k_2 + x} \right] h + \sigma_2 y_k \sqrt{h} \xi_k^2 + \frac{1}{2} \sigma_2^2 y_k (h \xi_k^2 - h), \end{aligned} \tag{3.64}$$

where  $(\xi_k)$  is an i.i.d. sequence of normalized centred Gaussian variables.

Simulations of the stochastically perturbed case are shown in Figure 3.4. These simulations show the permanence of the system (3.3).

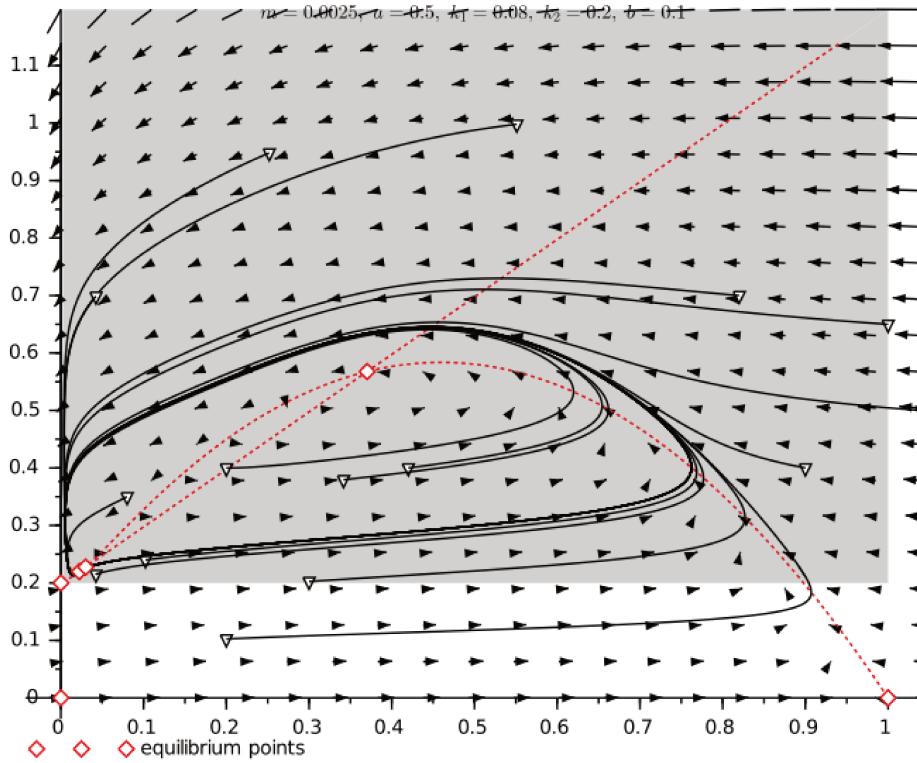


FIGURE 3.1 – A phase portrait of (3.2) with three equilibrium points and a cycle in the interior of  $\mathcal{A}$ . The dashed lines are isoclines  $y = \frac{x(1-x)(k_1+x-m)}{a(x-m)}$  and  $y = k_2 + x - m$ . The grey region is the positively invariant attracting domain  $\mathcal{A}$ .

$m = 0.0025$ ,  $a = 0.5$ ,  $k_1 = 0.08$ ,  $k_2 = 0.2$ ,  $b = 0.1$ .

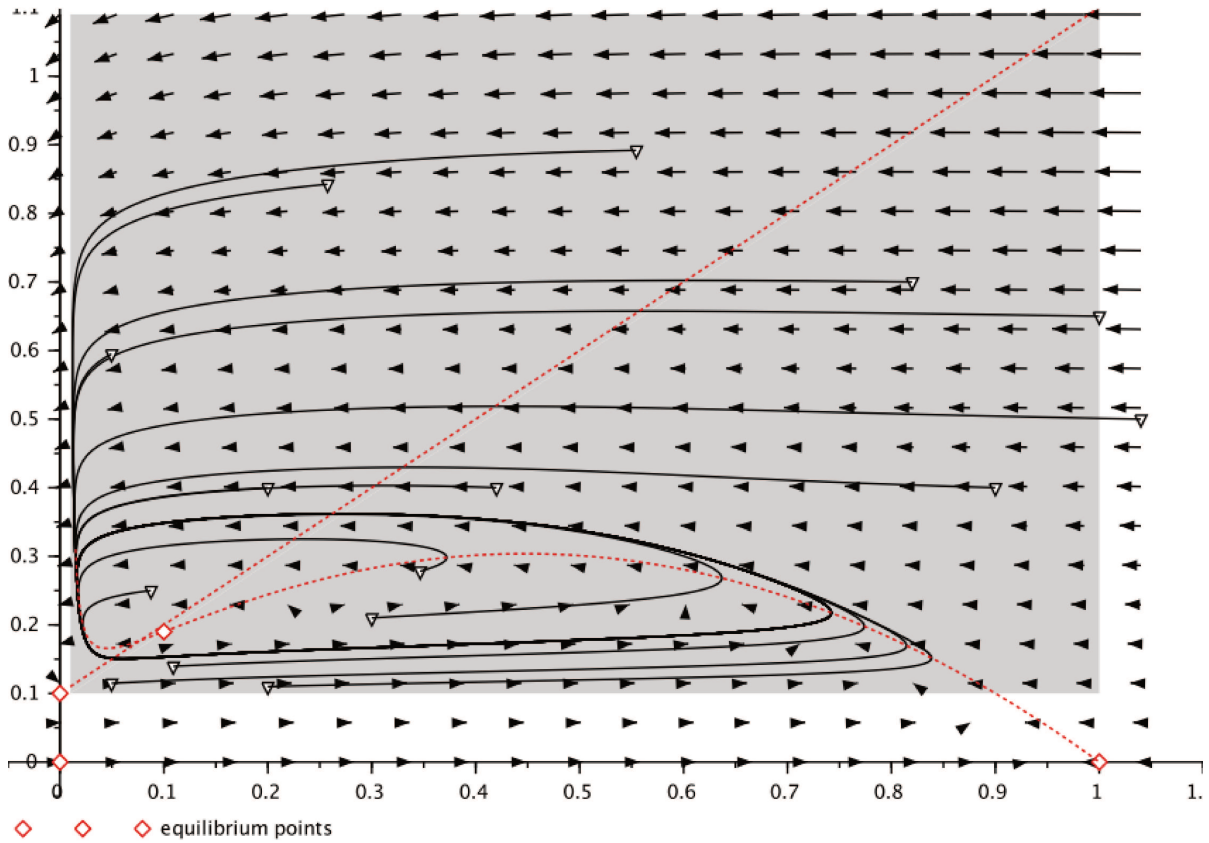
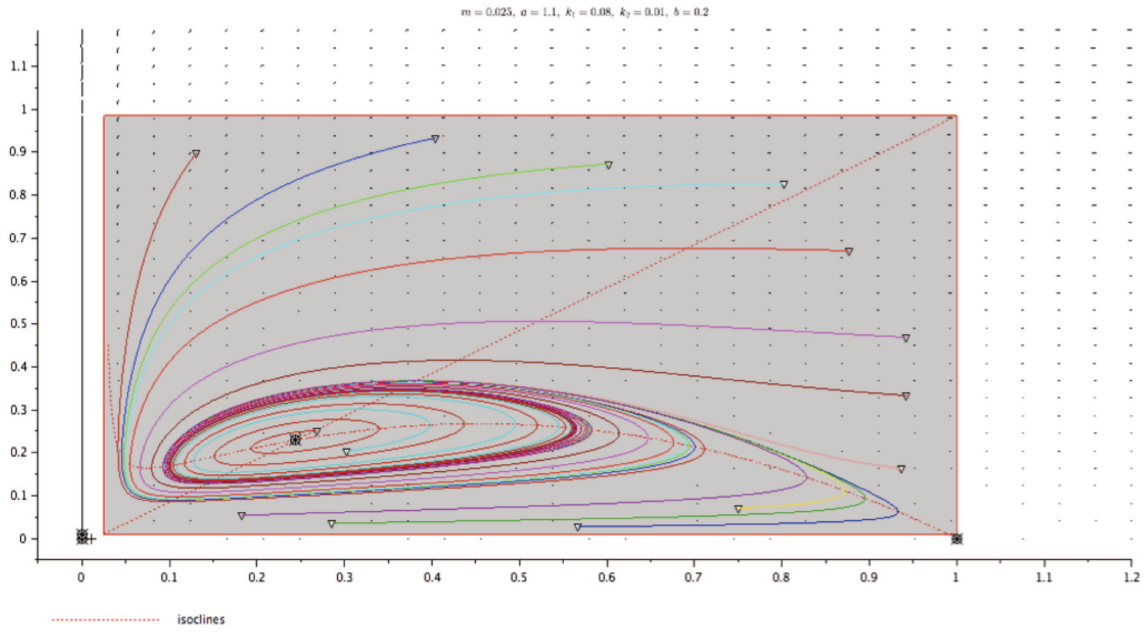
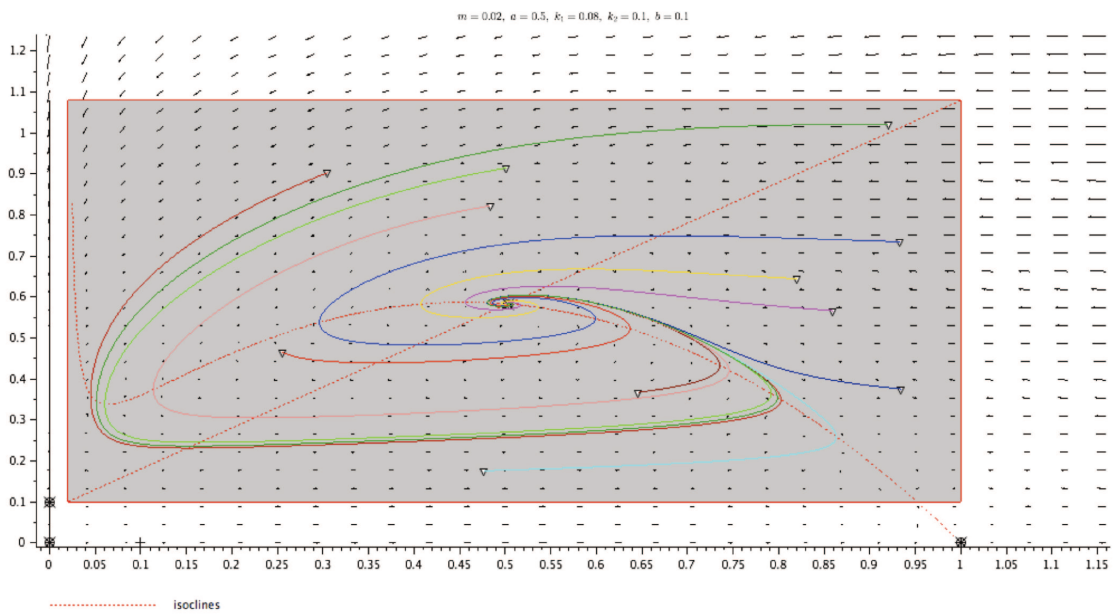


FIGURE 3.2 – A phase portrait of (3.2) with an unstable equilibrium and a stable limit cycle.  $m = 0.01$ ,  $a = 1$ ,  $k_1 = 0.1$ ,  $k_2 = 0.1$ ,  $b = 0.05$ .



(a)  $\lambda < 0$  (semi hyperbolic case) :  $m = 0.0025, a = 1.1, k_1 = 0.08, k_2 = 0.01, b = 0.2$ .



(b)  $\lambda > 0$  (semi hyperbolic case) :  $m = 0.002, a = 0.5, k_1 = 0.08, k_2 = 0.1, b = 0.1$ .

FIGURE 3.3 – Hopf bifurcation of the system (3.2).

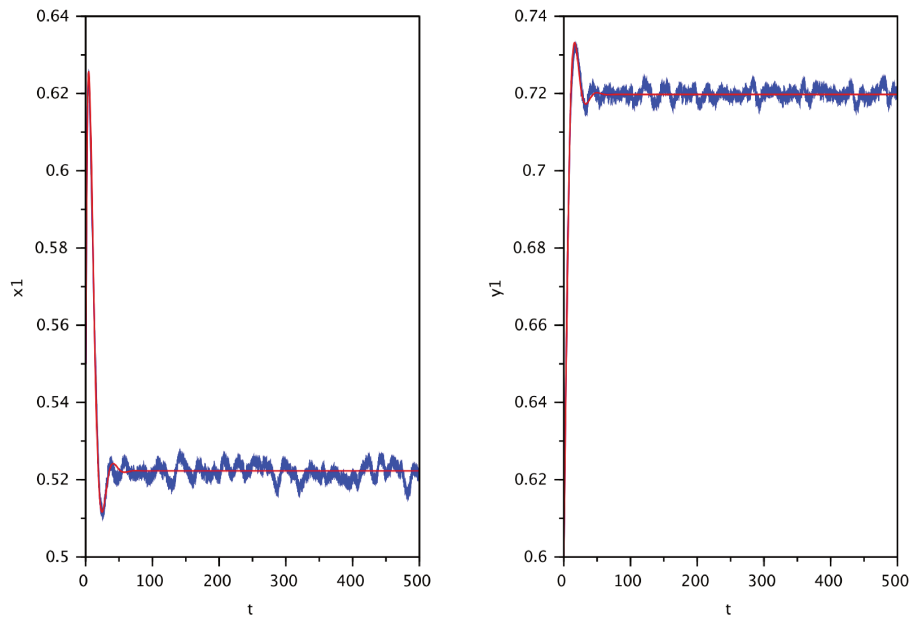
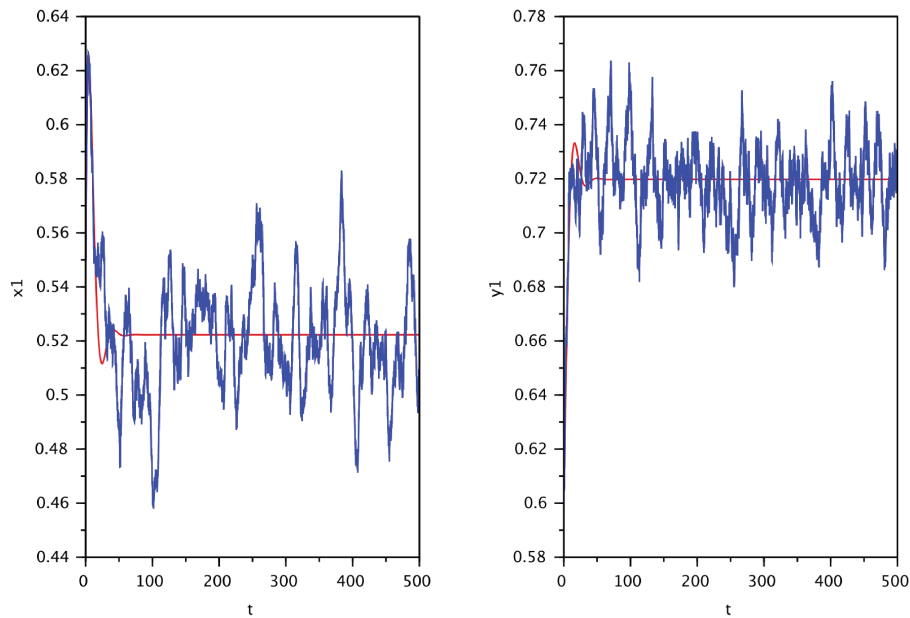
(a)  $\sigma_1 = 0.01, \sigma_2 = 0.01$ (b)  $\sigma_1 = 0.3, \sigma_2 = 0.2$ 

FIGURE 3.4 – Solutions to the stochastic system (3.3) and the corresponding deterministic system, represented respectively by the blue line and the red line.

$a = 0.4$ ,  $k_1 = 0.08$ ,  $k_2 = 0.2$ ,  $b = 0.1$ ,  $m = 0.0025$ , the initial value  $(x(0), y(0)) = (0.55, 0.6)$ , and the time step  $h = 0.01$ . The deterministic model has a globally stable equilibrium point  $(x^*, y^*) = (0.55, 0.75)$ .





# Chapitre 4

## Dynamics of a stochastic predator-prey coupled system with modified Leslie-Gower and Holling type II schemes

### 4.1 Introduction

We consider an autonomous predator-prey model with modified Leslie-Gower and Holling type II functional response in which preys and predators disperse among  $n$  patches. As, the effect of dispersion on the species survival plays an important role in the study of dynamic biology and ecology, the analysis of mathematical models of populations dispersing among patches in a heterogeneous environment has been the subject of several recent papers[84, 85].

In this paper, we are interested in a predator-prey model with modified Leslie-Gower and Holling type II functional response studied incorporating a prey refuge, studied in the previous chapter. The key method used in this paper is the analysis of Lyapunov functions [61].

### 4.2 Deterministic coupled system

We consider the system :

$$\begin{cases} dx_i(t) = \left( x_i(t)(1 - x_i(t)) - \frac{a_i y_i(t)(x_i(t) - m_i)_+}{k_{1i} + (x_i(t) - m_i)_+} + \sum_{j=1}^n c_{ij}(x_j(t) - x_i(t)) \right) dt \\ dy_i(t) = \left( b_i y_i(t) \left( 1 - \frac{y_i(t)}{k_{2i} + (x_i(t) - m_i)_+} \right) + \sum_{j=1}^n d_{ij}(y_j(t) - y_i(t)) \right) dt, \end{cases} \quad (4.1)$$

with the initial conditions

$$x_i(0) = x_{0i}, \quad y_i(0) = y_{0i},$$

where,  $x_i, y_i$  denote respectively the densities of preys and predators on the patch  $i$  and, for all  $i, j \in \{1, \dots, n\}$ ,  $a_i, k_{1i}, k_{2i}, m_i$  and  $b_i$  are nonnegative constants, as in [7]. The constants  $c_{ij} = c_{ji}$ , and  $d_{ij} = d_{ji}$  correspond to the dispersal rates from patch  $j$  to  $i$ .

In the sequel, we denote

$$x_0 = (x_{01}, \dots, x_{0n}), \quad y_0 = (y_{01}, \dots, y_{0n}), \quad z_0 = ((x_{01}, y_{01}), \dots, (x_{0n}, y_{0n})).$$

For any sequence  $(f_i)_{1 \leq i \leq n}$ , we deduce

$$\bar{f} = \max_{1 \leq i \leq n} f_i, \quad \underline{f} = \min_{1 \leq i \leq n} f_i,$$

We suppose that

$$\underline{m} > 0, \quad \bar{m} < 1, \quad \underline{k}_2 > 0.$$

### 4.2.1 Persistence and attractor invariant set

**Theorem 4.1.** *Let*

$$\mathcal{A} = ([\underline{m}, 1] \times [k_2, 1 + \bar{k}_2 - \underline{m}])^n.$$

*The set  $\mathcal{A}$  is invariant and an attractor for the system (4.1).*

**Corollary 4.2.** *The system (4.1) is uniformly persistent :*

$$\begin{cases} \liminf_{t \rightarrow +\infty} \underline{x} \geq \underline{m} > 0 \\ \liminf_{t \rightarrow +\infty} \underline{y} \geq \underline{k}_2 > 0. \end{cases} \quad (4.2)$$

To proof of Theorem 4.1 uses the next lemma, whose proof is straightforward.

**Lemma 4.3.** *The functions  $\underline{x}$  and  $\bar{x}$  have right and left derivatives  $\dot{\underline{x}}^d$  and  $\dot{\bar{x}}^g$  at every point, with*

$$\begin{aligned} \dot{\underline{x}}^d(t) &= \min(\dot{x}_i(t) : x_i(t) = \underline{x}(t)), \quad \dot{\bar{x}}^d(t) = \max(\dot{x}_i(t) : x_i(t) = \bar{x}(t)) \\ \dot{\underline{x}}^g(t) &= \max(\dot{x}_i(t) : x_i(t) = \underline{x}(t)), \quad \dot{\bar{x}}^g(t) = \max(\dot{x}_i(t) : x_i(t) = \bar{x}(t)). \end{aligned}$$

**Proof of Theorem 4.1.** For any  $t$ , there is (at least) an integer  $i = i(t)$  such that

$$\underline{x}(t) = x_i(t) \text{ et } \dot{\underline{x}}^d(t) = \dot{x}_i(t).$$

We have

$$\begin{aligned} \dot{\underline{x}}^d(t) &= x_i(t)(1 - x_i(t)) - \frac{a_i y_i(t)(x_i(t) - m_i)_+}{k_{1i} + (x_i(t) - m_i)_+} + \sum_{j=1}^n c_{ij}(x_j(t) - x_i(t)) \\ &\geq x_i(t)(1 - x_i(t)) - \frac{a_i y_i(t)(x_i(t) - m_i)_+}{k_{1i} + (x_i(t) - m_i)_+}. \end{aligned} \quad (4.3)$$

For any  $t$  such that  $\underline{x}(t) < \underline{m}$ , the last term disappears. So we have

$$\dot{\underline{x}}^d(t) \geq \underline{x}(t)(1 - \underline{x}(t)) \text{ for every } t \text{ such that } \underline{x}(t) < \underline{m} \quad (4.4)$$

From the comparison theorem [42, Th.1.4.1], we deduce that, if  $\underline{x}(t_0) < \underline{m}$  for a  $t_0 \geq 0$ , we have

$$\underline{x}(t_0) \geq u(t) \text{ as long as } \underline{x}(t) \leq \underline{m},$$

where, for  $t \geq t_0$ ,  $u(t)$  is the solution to

$$\dot{u} = u(1 - u), \quad u(t_0) = \underline{x}(t_0).$$

Since  $\lim_{t \rightarrow +\infty} u(t) = 1$  (logistic equation), we deduce that  $\underline{x}(t)$  hits  $\underline{m}$  in finite time. We note also that, for  $\underline{x}(t) \geq \underline{m}$ , we have again

$$\dot{\underline{x}}^d(t) \geq \underline{x}(t)(1 - \underline{x}(t)) - \frac{a\bar{y}(t)(\underline{x}(t) - \underline{m})_+}{k_{1i} + (\underline{x}(t) - \underline{m})_+}.$$

By continuity of  $x \mapsto \frac{a\bar{y}(t)(x(t) - \underline{m})_+}{k_{1i} + (x(t) - \underline{m})_+}$  and by continuity of  $\bar{y}$ , we see that there exists  $\delta > 0$  (depending on  $\bar{y}$  and  $t$ ), such that, for  $\underline{m} \leq \underline{x} \leq \underline{m} + \delta$ , we have  $\dot{\underline{x}}^d(t) > 0$ . Therefore, the value  $\underline{m}$  can be crossed by  $\underline{x}$  only upwards.

Thus, there exists  $t_m > 0$  such that  $t \geq t_m \Rightarrow \underline{x}(t) \geq \underline{m}$ .

Similarly, we have for all  $t \geq 0$ ,

$$\dot{\bar{x}}^d(t) \leq \bar{x}(1 - \bar{x}). \quad (4.5)$$

Hence, from the comparison theorem

- $\lim_{t \rightarrow +\infty} \dot{\bar{x}}^d(t) \leq 1$
- $\overline{x(t_0)} \leq 1 \Rightarrow \forall t \geq t_0, \bar{x}(t) \leq 1$ .

Similarly, we have

$$\dot{\underline{y}}^d(t) \geq \underline{y}(1 - \frac{\underline{y}}{k_2})$$

and

$$\dot{\bar{y}}(t) \leq b\bar{y}(t)(1 - \frac{\bar{y}}{1 + k_2 + \epsilon - \underline{m}})$$

for  $t$  large enough such that  $\bar{x}(t) \leq 1 + \epsilon$ . We deduce as in [74], that

$$k_2 \leq \underline{\lim} \underline{y} \leq \overline{\lim} \bar{y}(t) \leq 1 + k_2 - \underline{m}.$$

This shows that  $\mathcal{A}$  is an attractor, and the point  $(x_1, y_1, \dots, x_n, y_n)$  enters in any neighborhood of  $\mathcal{A}$  in finite time.

### 4.3 Stochastic coupled system

We now investigate the stochastically perturbed system

$$\left\{ \begin{array}{l} dx_i(t) = \left( x_i(t)(1 - x_i(t)) - \frac{a_i y_i(t)(x_i(t) - m_i)_+}{k_{1i} + (x_i(t) - m_i)_+} + \sum_{j=1}^n c_{ij}(x_j(t) - x_i(t)) \right) dt \\ \quad + \sigma_{1i} x_i(t) dw_{1i}(t) \\ dy_i(t) = \left( b_i y_i(t) \left( 1 - \frac{y_i(t)}{k_{2i} + (x_i(t) - m_i)_+} \right) + \sum_{j=1}^n d_{ij}(y_j(t) - y_i(t)) \right) dt \\ \quad + \sigma_{2i} y_i(t) dw_{2i}(t), \end{array} \right. \quad (4.6)$$

with the initial conditions

$$x_i(0) = x_{0i}, \quad y_i(0) = y_{0i},$$

where,  $(w_{1i}, w_{2i})$  are independent standard Brownian motions in  $\mathbf{R}^2$ .

In the sequel, we denote

$$x_0 = (x_{01}, \dots, x_{0n}), \quad y_0 = (y_{01}, \dots, y_{0n}), \quad z_0 = ((x_{01}, y_{01}), \dots, (x_{0n}, y_{0n})). \quad (4.7)$$

For this system we begin to show the existence and uniqueness of the global positive solution with any initial positive value in section 4.4. In the second section, we obtain sufficient conditions for the existence of an ergodic stationary distribution of the system (4.6). Finally, in Section 4.6, we make numerical simulations to confirm the effect of white noise and the diffusion coefficient on the species.

## 4.4 Existence and uniqueness of the bounded solution

**Theorem 4.4.** *For any initial condition  $(x_0, y_0) = ((x_{01}, y_{01}), \dots, (x_{0n}, y_{0n})) \in \mathbb{R}_+^{2n}$ , the system (4.6) admits a unique solution  $(x_i(t), y_i(t)) = ((x_1(t), y_1(t)), \dots, (x_n(t), y_n(t)))$ , defined for all  $t \geq 0$  a.s, and this solution remains in  $(]0, +\infty[ \times ]0, +\infty])^n$ .*

**Proof.** Let  $\tau_e$  be the explosion time of the solution of (4.6). We have to prove that  $(x_i(t), y_i(t)) \in \mathbb{R}_+^{2n}$  for every  $t \in [0, \tau_e[$  and that  $\tau_e = \infty$  a.s. The proof of the first assertion is adapted from [49]. Indeed, the coefficients in System (4.6) are locally Lipschitz, so there is exists a unique local solution for all  $t \in [0, \tau_e[$  and for all  $(x_i(0), y_i(0)) \in (]0, +\infty[ \times ]0, +\infty])^n$ . To show that this solution is global, it suffices to show that  $\tau_e = \infty$ . For that, let  $k_0 > 0$  be large enough, such that  $(x_{0i}, y_{0i}) \in [\frac{1}{k_0}, k_0] \times [\frac{1}{k_0}, k_0]$ . For each integer  $k \geq k_0$  we define the stopping time

$$\tau_k = \inf \left\{ t \in [0, \tau_e) : x \notin \left(\frac{1}{k}, k\right) \text{ ou } y \notin \left(\frac{1}{k}, k\right) \text{ for some } i = 1, \dots, n \right\}.$$

The sequence  $(\tau_k)$  is increasing as  $k \rightarrow \infty$ . Set  $\tau_\infty = \lim_{k \rightarrow \infty} \tau_k$ , whence  $\tau_\infty \leq \tau_e$ , (in fact, as  $(x(t), y(t)) > 0$  a.s., we have  $\tau_\infty = \tau_e$ ). It suffices to prove that  $\tau_\infty = \infty$  a.s.. Assume that this statement is false, then there exist  $T > 0$  and  $\varepsilon \in ]0, 1[$  such that  $\mathbb{P}(\{\tau_\infty \leq T\}) > \varepsilon$ . Since  $(\tau_k)$  is increasing we have

$$\mathbb{P}(\{\tau_k \leq T\}) > \varepsilon.$$

Now, consider the positive definite function  $V : (]0, +\infty[ \times ]0, +\infty])^n \rightarrow (]0, +\infty[ \times ]0, +\infty])^n$  given by

$$V(x, y) = \sum_{i=1}^n (x_i + 1 - \log x_i + y_i + 1 - \log y_i).$$

Applying Itô's formula, we get

$$dV(x, y) = \sum_{i=1}^n \left( (x_i - 1)(1 - x_i) - \frac{a_i y_i (x_i - m)}{k_{1i} + x_i} + \frac{\sigma_{1i}^2}{2} + \sum_{j=1}^n c_{ij} (x_j - x_i) \right)$$

$$\begin{aligned}
& + b_i(y_i - 1)\left(1 - \frac{y_i}{k_{2i} + x_i}\right) + \sum_{j=1}^n d_{ij}(y_j - y_i) + \frac{\sigma_{2i}^2}{2} \Big) dt \\
& + \sum_{i=1}^n \sigma_{1i}(x_i - 1)dW_{1i} + \sum_{i=1}^n \sigma_{2i}(y_i - 1)dW_{2i}.
\end{aligned}$$

The positivity of  $x_i(t)$  and  $y_i(t)$  implies

$$\begin{aligned}
dV(x, y) & \leq \sum_{i=1}^n \left( 2x_i + \left(a_i + b_i + \frac{1}{k_{2i}}\right)y_i + \frac{\sigma_{1i}^2 + \sigma_{2i}^2}{2} + \sum_{j=1}^n c_{ij}x_j \right) dt \\
& + \sum_{i=1}^n \sigma_{1i}(x_i - 1)dW_{1i} + \sum_{i=1}^n \sigma_{2i}(y_i - 1)dW_{2i}.
\end{aligned}$$

Let  $C_{1i} = a_i + b_i + \frac{1}{k_{2i}}$ ,  $C_{2i} = \frac{\sigma_{1i}^2 + \sigma_{2i}^2}{2}$ ,  $i = 1, \dots, n$ . Using [20, lemma 4.1], we can write

$$\begin{aligned}
2x_i + C_{1i}y_i & \leq 4(x_i + 1 - \log x_i) + 2C_{1i}(y_i + 1 - \log y_i) \\
& \leq C_{3i}V_i(x_i, y_i),
\end{aligned}$$

where  $C_{3i} = \max(4, 2C_{1i})$ , hence

$$dV(x, y) \leq C_4(1 + V(x, y))dt + \sum_{i=1}^n \sigma_{1i}(x_i - 1)dW_{1i} + \sum_{i=1}^n \sigma_{2i}(y_i - 1)dW_{2i},$$

where  $C_4 = \max(C_{2i}, C_{3i})$ ,  $i = 1, \dots, n$ .

Integrating both sides from 0 to  $\tau_k \wedge T$ , and taking expectations, we get

$$\mathbb{E}V(x(\tau_k \wedge T), y(\tau_k \wedge T)) \leq V(x_0, y_0) + C_4T + C_4 \int_0^T \mathbb{E}V(x(\tau_k \wedge t), y(\tau_k \wedge t))dt.$$

By Gronwall's inequality, this yields

$$\mathbb{E}V(x(\tau_k \wedge T), y(\tau_k \wedge T)) \leq C_5, \quad (4.8)$$

where  $C_5$  is the finite constant given by

$$C_5 = (V(x_0, y_0) + C_4T)e^{C_4T}. \quad (4.9)$$

Let  $\Omega_k = \{\tau_k \leq T\}$ . We have  $\mathbb{P}(\Omega_k) \geq \varepsilon$ , thus for all  $\omega \in \Omega_k$ , there exists at least one element of  $x(\tau_k, \omega), y(\tau_k, \omega)$  which is equal either to  $k$  or to  $\frac{1}{k}$ , hence

$$V(x(\tau_k), y(\tau_k)) \geq (k + 1 - \log k) \wedge \left(\frac{1}{k} + 1 + \log k\right).$$

Therefore, by (4.8),

$$C_5 \geq \mathbb{E}[1_{\Omega_k}(\omega)V(x(\tau_k, \omega), y(\tau_k, \omega))] \geq \varepsilon \left[ (k + 1 - \log k) \wedge \left(\frac{1}{k} + 1 + \log k\right) \right],$$

where  $1_{\Omega_k}$  is the indicator function of  $\Omega_k$ . Letting  $k \rightarrow \infty$ , we get  $C_5 = \infty$ , which contradicts (4.9). So we must have  $\tau_\infty = \infty$  a.s.  $\square$

## 4.5 Stationary distribution

In this section, we show that there is a stationary distribution for System (4.6) instead of asymptotically stable equilibria.

**Theorem 4.5.** *Assume that  $0 < \sigma_{1i}^2 < 2$  and  $0 < \sigma_{2i}^2 < 2b_i$  and  $m_i > 0$ ,  $i = 1, \dots, n$ . Then the system (4.6) has a unique stationary distribution  $\mu$  on  $(]0, +\infty[ \times ]0, +\infty[)^n$ . Moreover, the system (4.6) is ergodic and its transition probability  $P(z_0, t, \cdot)$  satisfies*

$$P((z_0), t, \varphi) \rightarrow \mu(\varphi) \text{ when } t \rightarrow \infty$$

for each  $z_0 \in (]0, +\infty[ \times ]0, +\infty[)^n$  and each bounded continuous function  $\varphi : (]0, +\infty[ \times ]0, +\infty[)^n \rightarrow \mathbf{R}$ .

The proof of Theorem 4.5 follows the same lines as in [74]. First, as in [74], applying locally the comparison theorem for SDEs (see [22, Theorem 1]), we have a.s., for each  $i \in \{1, \dots, n\}$ , and for each  $t \geq 0$ ,

$$\begin{aligned} 0 &\leq \check{u}_i(t) \leq x_i(t) \leq u_i(t) \\ 0 &\leq \check{v}_i(t) \leq y_i(t) \leq v_i(t), \end{aligned} \tag{4.10}$$

where

$$\begin{aligned} du_i(t) &= \left( u_i(t)(1 - u_i(t)) + \sum_{j=1}^n c_{ij}(u_j(t) - u_i(t)) \right) dt \\ &\quad + \sigma_{1i}u_i(t)dw_{1i}(t), \end{aligned} \tag{4.11}$$

$$\begin{aligned} dv_i(t) &= \left( b_i v_i(t) \left( 1 - \frac{v_i(t)}{k_{2i} + u_i(t)} \right) + \sum_{j=1}^n d_{ij}(v_j(t) - v_i(t)) \right) dt \\ &\quad + \sigma_{2i}v_i(t)dw_{2i}(t), \end{aligned} \tag{4.12}$$

$$\begin{aligned} d\check{u}_i(t) &= \left( \check{u}_i(t)(1 - \check{u}_i(t)) - a_i v_i(t) + \sum_{j=1}^n c_{ij}(\check{u}_j(t) - \check{u}_i(t)) \right) dt \\ &\quad + \sigma_{1i}\check{u}_i(t)dw_{1i}(t), \end{aligned} \tag{4.13}$$

$$\begin{aligned} d\check{v}_i(t) &= \left( b_i \check{v}_i(t) \left( 1 - \frac{\check{v}_i(t)}{k_{2i}} \right) + \sum_{j=1}^n d_{ij}(\check{v}_j(t) - \check{v}_i(t)) \right) dt \\ &\quad + \sigma_{2i}\check{v}_i(t)dw_{2i}(t), \end{aligned} \tag{4.14}$$

with

$$u_i(0) = \check{u}(0) = x_{0i} = x_i(0), \quad v_i(0) = \check{v}(0) = y_{0i} = y_i(0).$$

Note that the equations (4.11) and (4.14) stand alone, while (4.12) and (4.13) depend on the processes  $u_i$  and  $v_i$  respectively.

For a Lyapunov function  $V = V(x_1, y_1, \dots, x_n, y_n)$ , the contribution of the coupling of prey densities  $x_i$  is

$$\sum_{i=1}^n \frac{\partial V}{\partial x_i} \sum_{j=1}^n c_{ij}(x_j - x_i).$$

whereas that of the coupling of predator densities is

$$\sum_{i=1}^n \frac{\partial V}{\partial y_i} \sum_{j=1}^n d_{ij}(y_j - y_i).$$

We consider Lyapunov functions of the form

$$V(x_1, y_1, \dots, x_n, y_n) = \sum_{i=1}^n V_i(x_i) + \sum_{i=1}^n \mathfrak{V}_i(y_i),$$

for some Lyapunov functions  $V_i$  and  $\mathfrak{V}_i$ . For  $V_i(x_i) = x_i + x_i^{-\eta}$ , with  $\eta > 0$ , since  $c_{ij} = c_{ji}$ , we get

$$\begin{aligned} \sum_{i=1}^n \frac{\partial V}{\partial x_i} \sum_{j=1}^n c_{ij}(x_j - x_i) &= \sum_{i,j} \left(1 - \frac{\eta}{x_i^{1+\eta}}\right) c_{ij}(x_j - x_i) \\ &= \sum_{1 \leq i < j \leq n} c_{ij}(x_j - x_i) \left(-\frac{\eta}{x_i^{1+\eta}} + \frac{\eta}{x_j^{1+\eta}}\right) \\ &= -\eta \sum_{1 \leq i < j \leq n} c_{ij}(x_i - x_j) \frac{x_i^{1+\eta} - x_j^{1+\eta}}{x_i^{1+\eta} x_j^{1+\eta}} < 0. \end{aligned} \quad (4.15)$$

Similarly, for  $\mathfrak{V}_i(y_i) = y_i^{-1} + \log(y_i)$ , we have

$$\begin{aligned} \sum_{i=1}^n \frac{\partial \mathfrak{V}}{\partial y_i} \sum_{j=1}^n d_{ij}(y_j - y_i) &= \sum_{i,j} \left(-\frac{1}{y_i^2} - \frac{1}{y_i}\right) d_{ij}(y_j - y_i) \\ &= \sum_{1 \leq i < j \leq n} d_{ij}(y_j - y_i) \left(-\frac{1}{y_i^2} - \frac{1}{y_i} + \frac{1}{y_j^2} + \frac{1}{y_j}\right) \\ &= -\sum_{1 \leq i < j \leq n} d_{ij} \left(\frac{(y_i - y_j)(y_i^2 - y_j^2)}{y_i^2 y_j^2} + \frac{(y_i - y_j)^2}{y_i y_j}\right) < 0. \end{aligned} \quad (4.16)$$

The proofs of [74, Lemmas 3.11 and 3.12] rely on [50, Theorem 3.2], where a one-dimensional Lyapunov function of the form  $V(x) = x + x^{-\eta}$ , is used, for some  $\eta > 0$ . Using (4.15), and (4.16) these proofs can be adapted to show :

**Lemma 4.6.** *For  $R, r > 0$ , let*

$$\tau_1^{(R)}(x_0) = \inf\{t \geq 0; \max_{1 \leq i \leq n} u_i(t) < R\},$$

$$\check{\tau}_1^{(r)}(x_0) = \inf\{t \geq 0; \min_{1 \leq i \leq n} x_i(t) > r\},$$



$$\tilde{\tau}_2^{(r)}(y_0) = \inf\{t \geq 0; \min_{1 \leq i \leq n} \check{v}(t) > r\}.$$

Assume that  $0 < \sigma_{1i}^2 < 2$  and  $0 < \sigma_{2i}^2 < 2b_i$ ,  $i = 1 \dots, n$ . There exists  $R_1 > 0$  sufficiently large, depending on  $x_0$ , and  $r_1 > 0$  and  $r_2 > 0$  sufficiently small, depending respectively on  $x_0$  and  $y_0$ , such that  $E\left(\tau_1^{(R_1)}(x_0)\right)$ ,  $E(\tilde{\tau}_1^{(r_1)}(x_0))$  and  $E\left(\tilde{\tau}_2^{(r_2)}(y_0)\right)$  are finite and uniformly bounded on compact subsets of  $[R_1, +\infty[^n$ ,  $]0, r_1]^n$  and  $]0, r_2]^n$  respectively.

Similarly, the proof of [74, Lemma 3.13] uses the two-dimensional Lyapunov function  $V(x, y) = x + x^{-1} + \log(y) + y^{-1}$ . By (4.15) and (4.16), we can adapt its proof to show :

**Lemma 4.7.** *Let*

$$\tau_2^{(R)}(z_0) = \inf\{t \geq 0; \max_{1 \leq i \leq n} v_i(t) < R\},$$

(Recall that  $z_0$  has been defined in (4.7)), assume that  $0 < \sigma_{1i}^2 < 2$ ,  $i = 1 \dots, n$ . There exists  $R_2$  sufficiently large, depending on  $z_0$ , such that  $E(\tau_2^{(R_2)}(z_0))$  is finite and uniformly bounded on compact subsets of  $]0, +\infty[ \times [R_2, +\infty[^n$ .

**Proof of Theorem 4.5.** By Lemmas 4.6 and 4.7, taking  $r = r(z_0) < R = R(z_0)$  such that  $r \leq \min\{r_1, r_2\}$  and  $R \geq \max\{R_1, R_2\}$ , and  $U = ]r, R[ \times ]r, R[^n$ , the stopping time

$$\tau^U = \inf\{t > 0; ((x_1(t), y_1(t)), \dots, (x_n(t), y_n(t))) \in U$$

is finite, and  $\sup_{x \in K} E^x \tau^U < \infty$  for every compact subset  $K$  of  $]0, +\infty[ \times ]0, +\infty[^n$ .

As in [74, Theorem 3.7], the rest of the proof of Theorem 4.5 follows from classical results in [38, Chapter 4]. □

## 4.6 Numerical Simulation

To illustrate our results, we consider the two-species nonlinear dispersal system with  $n = 2$ .

$$\begin{aligned} dx_1 &= \left[ x_1(1 - x_1) - \frac{a_1 y_1 (x_1 - m)_+}{k_{11} + (x_1 - m)_+} + c_{12}(x_2 - x_1) \right] dt + \sigma_{11} x_1 dW_{11}(t), \\ dy_1 &= b_1 y_1 \left[ 1 - \frac{y_1}{k_{21} + (x_1 - m)_+} + d_{12}(y_2 - y_1) \right] dt + \sigma_{21} y_1 dW_{21}(t), \\ dx_2 &= \left[ x_2(1 - x_2) - \frac{a_2 y_2 (x_2 - m)_+}{k_{12} + (x_2 - m)_+} + c_{21}(x_1 - x_2) \right] dt + \sigma_{12} x_2 dW_{12}(t), \\ dy_2 &= b_2 y_2 \left[ 1 - \frac{y_2}{k_{22} + (x_2 - m)_+} + d_{21}(y_1 - y_2) \right] dt + \sigma_{22} y_2 dW_{22}(t), \end{aligned} \tag{4.17}$$

We numerically simulate the solution of System (4.17). By the Milstein scheme mentioned in [39], we consider the following discretized system :

$$\begin{aligned}
x_{1,k+1} &= x_{1,k} + \left[ x_{1,k}(1 - x_{1,k}) - \frac{a_1 y_{1,k}(x_{1,k} - m)}{k_{11} + x_{1,k} - m} + c_{12}(x_{2,k} - x_{1,k}) \right] h \\
&\quad + \sigma_{11} x_{1,k} \sqrt{h} \xi_{1,k}^2 + \frac{1}{2} \sigma_{11}^2 x_{1,k} (h \xi_{1,k}^2 - h), \\
y_{1,k+1} &= y_{1,k} + b_1 y_1 \left[ 1 - \frac{y_1}{k_{21} + x_1 - m} + d_{12}(y_{2,k} - y_{1,k}) \right] h + \sigma_{21} y_{1,k} \sqrt{h} \xi_{2,k}^2 + \frac{1}{2} \sigma_{21}^2 y_{1,k} (h \xi_{2,k}^2 - h) \\
x_{2,k+1} &= x_{2,k} + \left[ x_{2,k}(1 - x_{2,k}) - \frac{a_2 y_{2,k}}{k_{12} + x_{2,k} - m} + c_{21}(x_{1,k} - x_{2,k}) \right] h \\
&\quad + \sigma_{12} x_{2,k} \sqrt{h} \xi_{3,k}^2 + \frac{1}{2} \sigma_{12}^2 x_{2,k} (h \xi_{3,k}^2 - h), \\
y_{2,k+1} &= y_{2,k} + b_2 y_2 \left[ 1 - \frac{y_2}{k_{22} + x_2 - m} + d_{21}(y_{1,k} - y_{2,k}) \right] h + \sigma_{22} y_{2,k} \sqrt{h} \xi_{4,k}^2 + \frac{1}{2} \sigma_{22}^2 y_{2,k} (h \xi_{4,k}^2 - h).
\end{aligned} \tag{4.18}$$

For the numerical simulation, we choose  $a_1 = 0.4$ ,  $k_{11} = 0.08$ ,  $k_{21} = 0.2$ ,  $b_1 = 0.1$ ,  $a_2 = 0.5$ ;  $k_{12} = 0.4$ ,  $k_{22} = 0.25$ ,  $b_2 = 1$ , and the time step  $h = 0.01$ . In Figure 1, we assume that  $c_{12} = d_{12} = 1.5$ ,  $c_{21} = d_{21} = 1.6$ , with  $\sigma_{11} = 0.3$ ,  $\sigma_{21} = 0.01$ , and  $\sigma_{12} = 0.01$ ,  $\sigma_{22} = 0.01$ . The initial value  $(x_1(0), y_1(0)) = ((0.55, 0, 6), (0.5, 0, 61))$ . In this case, the deterministic model has a globally stable equilibrium point  $(x^*, y^*) = ((x_1^*, y_1^*), (x_2^*, y_2^*)) = ((0.55, 0.75), (0.576, 0.825))$ .

Obviously, the conditions of Theorem (3.8) are satisfied, so there is a stationary distribution. In Figure 2, we choose  $\sigma_{11} = 0.3$ ,  $\sigma_{21} = 0.2$ , and  $\sigma_{12} = 0.1$ ,  $\sigma_{22} = 0.3$ . The populations of  $(x_1, y_1)$  and  $(x_2, y_2)$  suffer relatively large white noise.

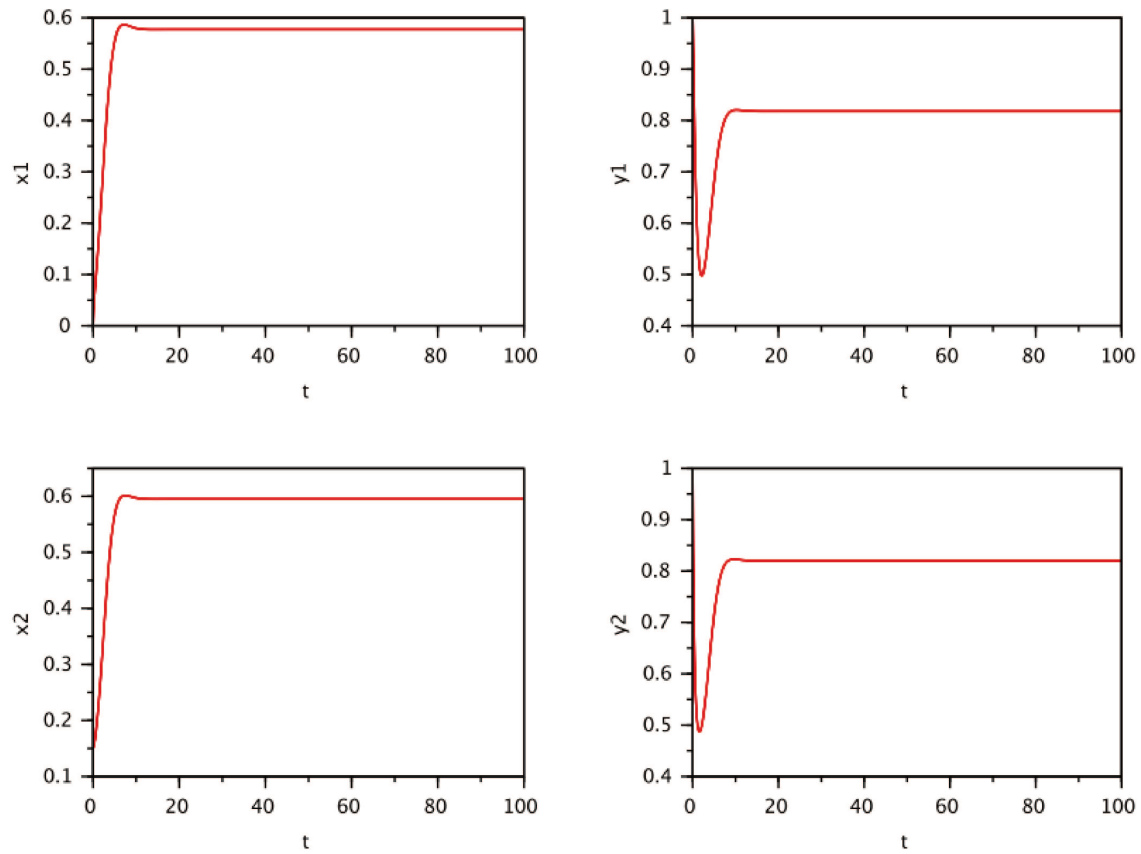


FIGURE 4.1 – Trajectories of the solutions of the system (4.17) with the absence of stochastic perturbation. The system is uniformly persistent.

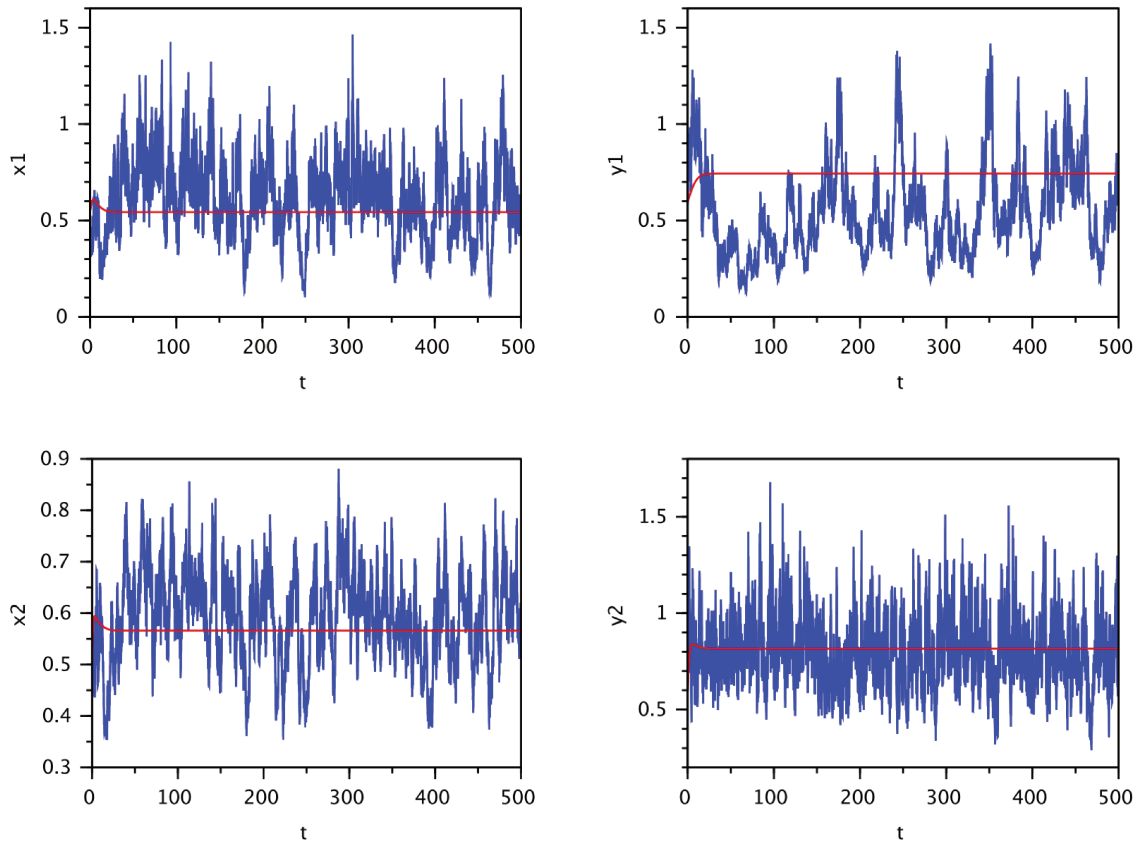


FIGURE 4.2 – Trajectories of the solutions of stochastic system (4.17) and the corresponding deterministic system, the blue lines and the red lines represent them, respectively.  $\sigma_{11} = 0.3$ ,  $\sigma_{21} = 0.2$ ,  $\sigma_{12} = 0.1$ ,  $\sigma_{22} = 0.3$ .

By comparing Figure 1, we can see that in Figure 2 the curves fluctuations are more large. In Figure 3, we choose  $c_{12} = 0$ ,  $c_{21} = 0.01$  and  $\sigma_{11} = 0.3$ ,  $\sigma_{21} = 0.2$ , and  $\sigma_{12} = 0.1$ ,  $\sigma_{22} = 0.3$ . Figure 2 and 3 have the same white noise intensity but have different diffusion coefficients. because there is no diffusion effects, we can see that  $(x_1, y_1)$  will die.

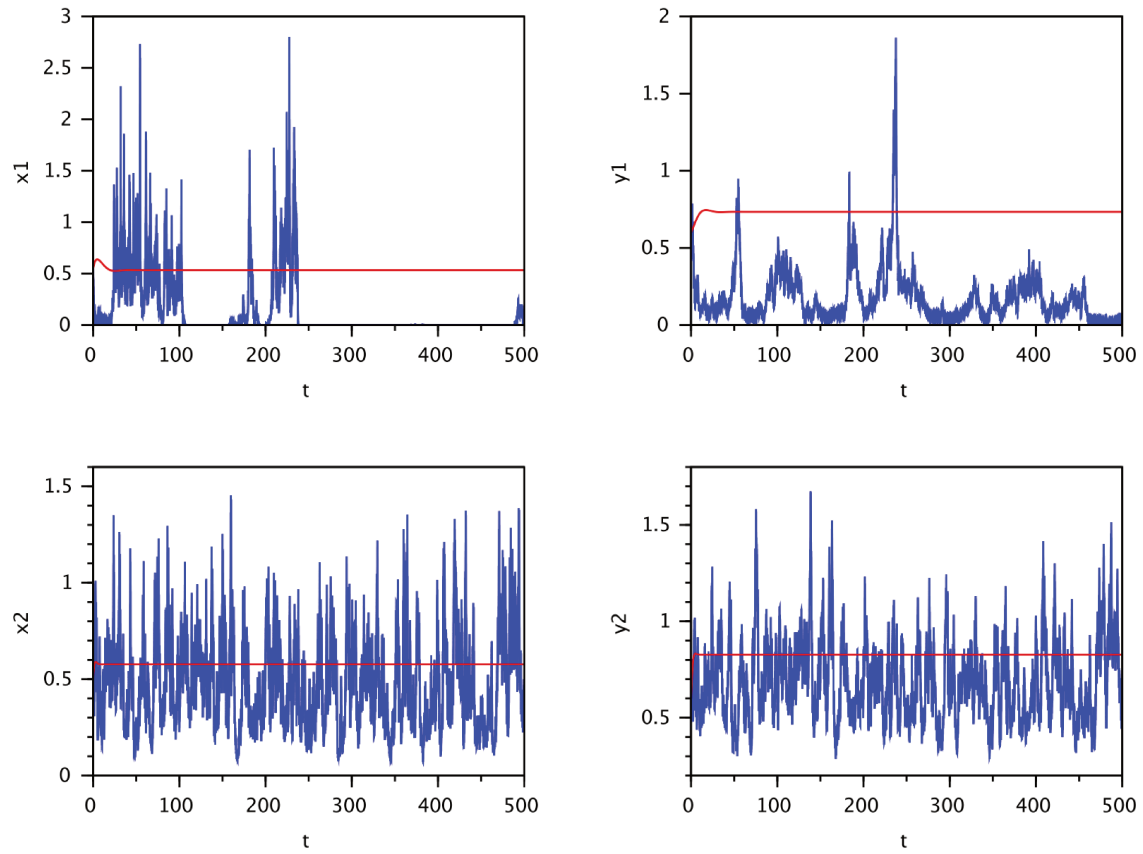


FIGURE 4.3 – Trajectories of the solutions of stochastic coupled system (4.17) with absence of diffusion effects, we can see that  $(x_1, y_1)$  will die;  $c_{12} = d_{12} = 0$ ,  $c_{21} = d_{21} = 0.01$  and  $\sigma_{11} = 0.3$ ,  $\sigma_{21} = 0.2$ , and  $\sigma_{12} = 0.1$ ,  $\sigma_{22} = 0.3$ .

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