HAL open science

Dynamique de concentration dans des équations aux dérivées partielles non locales issues de la biologie

Cécile Taing

▶ **To cite this version:**

Cécile Taing. Dynamique de concentration dans des équations aux dérivées partielles non locales issues de la biologie. Mathématiques [math]. Sorbonne Université, UPMC University of Paris 6, Laboratoire Jacques-Louis Lions, 2018. Français. NNT : . tel-02485006v1

HAL Id: tel-02485006

https://theses.hal.science/tel-02485006v1

Submitted on 14 Nov 2018 (v1), last revised 19 Feb 2020 (v2)

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

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

Sorbonne Université - Faculté des Sciences et Ingénierie

Laboratoire Jacques-Louis Lions

Thèse de doctorat

Discipline : Mathématiques Appliquées

présentée par

Cécile Taing

Dynamique de concentration dans des équations aux dérivées partielles non locales issues de la biologie

---

sous la direction d'Alexander Lorz et de Benoît Perthame

Soutenue publiquement le 1er juin 2018 devant le jury composé de :

M.	Arnaud Ducrot (Univ. Bordeaux)	Rapporteur
Mme	Céline Grandmont (Inria Paris)	Examinatrice
Mme	Sylvie Méléard (École Polytechnique)	Examinatrice
M.	Benoît Perthame (Sorbonne Université)	Directeur de Thèse
Mme	Magali Ribot (Univ. Orléans)	Examinatrice
M.	Panagiotis E. Souganidis (Univ. Chicago)	Examinateur
M.	Nicolas Vauchelet (Univ. Paris-XIII)	Examinateur

après avis favorable des rapporteurs :

M.	Arnaud Ducrot (Univ. Bordeaux)	MCF HDR
M.	José Antonio Carrillo de la Plata (Imperial College, Londres)	Professeur

Remerciements

Ma gratitude va bien sûr, pour commencer, à mes directeurs de thèse, Alexander Lorz et Benoît Perthame. Le soutien, la gentillesse, la disponibilité et les conseils avisés de Benoît ont certainement été pour moi autant de raisons de mener à bien ce travail. Alexander a su guider mes premiers pas dans le monde de la recherche, et cela compte forcément beaucoup.

Je remercie Arnaud Ducrot et José Antonio Carrillo de m'avoir fait l'honneur de rapporter ma thèse. Céline Grandmont, Sylvie Méléard, Magali Ribot, Takis Souganidis et Nicolas Vauchelet ont accepté de faire partie du jury, et je leur en suis vraiment très reconnaissante.

Mes remerciements vont ensuite à Hélène Hivert, Samuel Nordmann et Martin Strugarek, avec qui j'ai eu grand plaisir à discuter de modèles, d'estimations *a priori*, de schéma numérique ou de comportement asymptotique, mais aussi d'autres sujets, moins mathématiques.

Dans ces lignes, je ne saurais oublier Sepideh Mirrahimi pour sa gentillesse, sa patience et pour avoir toujours pris le temps de répondre à mes questions, toujours avec clarté et précision. Gaël Raoul et Vincent Calvez m'ont fait le plaisir de considérer ma candidature en postdoc, ce qui a donné lieu à de prometteuses discussions prospectives. Dans des moments où l'avenir est incertain, avoir de telles discussions permet de reprendre courage.

Je remercie sincèrement Sébastien Benzekry et Olivier Saut, qui ont accepté de m'accueillir en postdoc dans l'équipe-projet Monc à Bordeaux, que je rejoindrai bientôt.

Aussi, c'est avec un certain serrement au cœur que je quitterai le laboratoire Jacques-Louis Lions et le campus de Jussieu. Merci à Salima, Catherine, Malika, Nathalie, Francelise et Corentin d'avoir toujours œuvré pour faciliter le travail et la vie des doctorants au laboratoire et dans l'UFR. Merci à Khashayar, Christian, Hugues, Stephan, Clément, Julie et Kevin pour m'avoir apporté leur aide lorsque j'avais des soucis informatiques. Enfin, merci à vous toutes et tous, membres du laboratoire. Il serait trop long de décrire aujourd'hui tout ce que vous m'avez apporté[1].

Pour finir, je ne peux que remercier du fond du cœur ma famille, mes amis, mes proches, aujourd'hui présents physiquement ou par le pensée, qui m'ont accompagné tout au long de ces années de thèse. À vous aussi, je dois bien plus que quelques lignes.

[1] Je le ferai dans la version définitive de ce manuscrit, promis...

Table des matières

Remerciements **i**

Introduction **1**

1 Dirac concentration in a chemostat model **23**
1.1 Introduction . . . 24
1.2 The weak theory: assumptions and main results . . . 25
1.3 BV estimates on $\rho_\varepsilon^2(t)$ and $S_\varepsilon(t)$ . . . 27
1.3.1 Bounds for ρ_ε . . . 27
1.3.2 Local BV estimates . . . 28
1.4 Concentration and constrained Hamilton-Jacobi equation . . . 31
1.4.1 Local bounds and equi-continuity in space . . . 31
1.4.2 The equi-continuity in time . . . 32
1.4.3 Passing to the limit . . . 34
1.4.4 Properties of the concentration points . . . 35
1.5 The monomorphic case in dimension $d = 1$ . . . 37
1.6 The concavity framework in $\mathbb{R}^d$ . . . 38
1.6.1 Uniform concavity of u_ε . . . 39
1.6.2 BV estimates on $\rho_\varepsilon^2, S_\varepsilon$ and their limits . . . 41
1.6.3 The limit of the Hamilton-Jacobi equation . . . 42
1.6.4 The canonical equation . . . 42
1.7 Numerical results . . . 44
1.8 Discussion . . . 46

2 Population structured by and a phenotypical trait **49**
2.1 Introduction . . . 50
2.2 Assumptions . . . 52
2.3 Case without mutations . . . 53
2.3.1 The eigenproblem . . . 54
2.3.2 Concentration . . . 55
2.3.3 Properties of concentration points . . . 58
2.4 Case with mutations . . . 60
2.4.1 Saturation and stationary problem . . . 61
2.4.2 The Hamilton-Jacobi equation . . . 62
2.4.3 Global existence and a priori estimate . . . 63
2.4.4 The semi-relaxed limits . . . 64

2.4.5 Uniqueness result . . . 67
2.5 Numerical simulations . . . 70
2.6 Conclusion . . . 72
2.7 Appendices . . . 73
2.7.1 Saturation of the population denstity . . . 73
2.7.2 Proof of Theorem 2.12 and Theorem 2.2 . . . 73
2.7.3 Proof of Proposition 2.13 . . . 74
2.7.4 Proof of Proposition 2.17 . . . 75

3 Selection-mutation models with sexual reproduction 79
3.1 Introduction . . . 80
3.2 Main results . . . 82
3.2.1 Assumptions and statements . . . 82
3.2.2 Boundedness of ρ_ε and non-extinction . . . 84
3.3 The model without mutations (3.5) . . . 85
3.3.1 Proof of Theorem 3.1 . . . 86
3.3.2 Concentration of Dirac masses . . . 87
3.4 BV estimates on the total population . . . 88
3.4.1 Linear dependency on the competition variable in the AF model . . . 88
3.4.2 Linear dependency on the competition variable in the ATH model . . . 90
3.4.3 Questions and difficulties for the general case . . . 92
3.5 The Hamilton-Jacobi equation . . . 94
3.5.1 A priori bounds . . . 96
3.5.2 Regularity in space . . . 97
3.5.3 Regularity in time . . . 99
3.5.4 A more precise upper bound . . . 100
3.5.5 Discussion on the formal limiting equation . . . 101
3.6 Conclusion and perspectives . . . 103

Bibliographie 107

Introduction

Motivations

La concentration en masse de Dirac des solutions d'équations aux dérivées partielles et intégro-différentielles issues de la dynamique des populations représente la sélection naturelle telle qu'elle intervient en écologie. L'objectif de cette thèse est d'expliquer mathématiquement les phénomènes de sélection au sein d'une population présentant une variabilité phénotypique et sujette aux mutations.

Nous nous intéressons à des équations de la forme suivante

$$\begin{cases} \partial_t n(t,x) = n(t,x)R(x,\rho(t)) + \displaystyle\int_{\mathbb{R}} M(x,y)b(y,\rho(t))n(t,y)\,dy, \quad t \geq 0,\, x \in \mathbb{R}, \\ \rho(t) = \displaystyle\int_{\mathbb{R}} n(t,x)\,dx. \end{cases}$$

Ici, $n(t,\cdot)$ est la distribution de la population sur un espace de traits phénotypiques au temps t. Un *trait phénotypique* est une variation d'un caractère visible chez un individu, par exemple la couleur des yeux, et x est la variable de trait. La fonction R est un taux de croissance dépendant de la variable de trait et de la taille de la population ρ. Dans le deuxième terme, M est un noyau de mutations : il mesure la probabilité qu'un individu de trait y donne naissance à un individu de trait x, et b est un taux de naissance.

Une caractéristique importante de cette équation est la présence du terme non local ρ. Ce terme décrit les interactions entre les différents individus et leurs conséquences sur la reproduction.

Cette équation a pour propriété, sous des hypothèses appropriées, que sa solution se concentre en une masse de Dirac en temps long, ce qui signifie qu'un trait dominant est sélectionné et que les individus portant ce trait sont les plus adaptés et vont se reproduire plus que les autres.

Nous expliquerons dans la suite les méthodes qui permettent de démontrer ce type de résultat. Nous commençons d'abord par quelques bases de biologie.

Concepts de base

Nous considérons dans cette thèse des populations structurées en traits phénotypiques. Commençons par préciser les termes "génotype" et "phénotype", inventés par Wilhelm Johannsen au début du XXème siècle [3] :

- Le **génome** est l'ensemble du matériel génétique d'un organisme, soit les **gènes**, contenu dans chacune de ses cellules sous forme d'ADN. Un **allèle** est une variation d'un gène.

- Le **génotype** est l'ensemble des informations génétiques d'un individu, soit la composition allélique de tous ses gènes. Il détermine les caractères d'un individu, constituant le **phénotype**, et se transmet des parents à leurs descendants.

- Le **phénotype** est l'ensemble des caractères observables d'un individu, provenant à la fois de l'expression du génotype de l'individu et de son interaction avec l'environnement dans lequel il vit. On appelle trait phénotypique un sous-ensemble du phénotype d'un individu. Voici quelques exemples de traits phénotypiques : la taille, la couleur des yeux, la morphologie.

La théorie de la sélection naturelle telle qu'elle a été décrite par Charles Darwin [63] repose sur les trois principes suivants :

- **Hérédité :** transmission de caractéristiques individuelles d'une génération à une autre. Dans le cas d'une population asexuée, l'ensemble des informations génétiques du parent est copié à l'identique et transmis aux descendants. Dans le cas d'une population sexuée, le patrimoine génétique des parents n'est pas reproduit à l'identique. Un enfant n'a pas les mêmes combinaisons d'allèles que son père ou sa mère mais un mélange des deux.

- **Variation :** Les individus d'une population donnée doivent présenter des variations phénotypiques. La variabilité phénotypique d'une population résulte généralement de sa diversité génétique et des influences environnementales. Les mutations peuvent également créer des variations phénotypiques. Une mutation est une modification de la séquence d'ADN d'un gène. Les mutations sont rares en général.

- **Adaptation :** Lorsque certains individus portent des variations phénotypiques qui leur permettent de se reproduire davantage que les autres dans un milieu précis, ils bénéficient d'un avantage sélectif. Ces individus avantagés sont mieux adaptés à l'environnement et ont ainsi de plus grandes chances de survivre et de se reproduire.

Ces trois principes conduisent au processus de sélection naturelle, c'est-à-dire l'augmentation de la fréquence des individus portant les traits qui favorisent la survie et la reproduction dans un environnement donné, et la diminution de la fréquence des individus portant des traits désavantageux jusqu'à une éventuelle disparition.

À partir des principes de base de la théorie de la sélection naturelle, nous essayons d'illustrer les phénomènes de sélection. Ces principes ont été décrits en divers termes mathématiques :

- la théorie des jeux qui s'intéresse aux invasions successives et qui a laissé la terminologie de "stratégie" [85, 103],

- une théorie de stabilité dans des systèmes différentiels qui est considérée comme la dynamique adaptative classique [67, 82, 107, 109, 110],

- une théorie probabiliste qui s'intéresse à des modèles individus centrés et analyse des limites en grandes populations avec des changements d'échelle [47, 48, 50] et des limites en temps long [54],

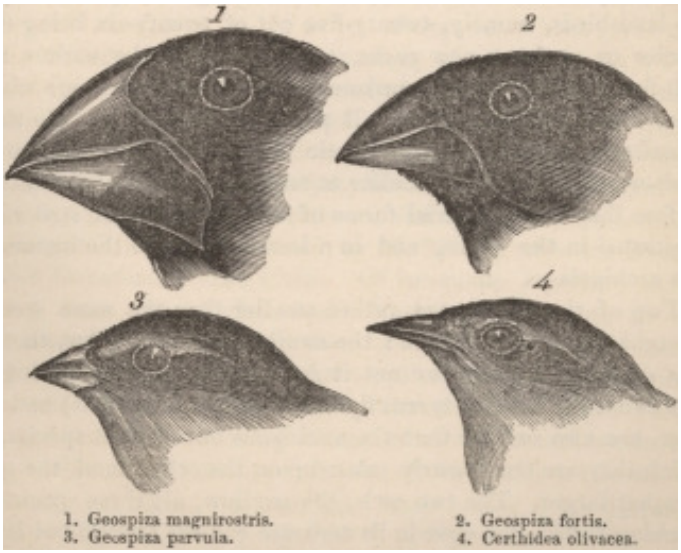

FIGURE 0.1 : Les *pinsons de Darwin*, vus par le naturaliste dans les îles Galapagos, ont participé à sa réflexion sur la théorie de la sélection naturelle. Un lien est notamment établi entre le régime alimentaire de chaque espèce et leurs caractéristiques morphologiques, notamment la forme du bec.

- une théorie de dynamique des populations qui utilise des modèles d'équations intégro-différentielles et aux dérivées partielles [64, 131].

Nous considérons ce dernier formalisme pour étudier des modèles de populations structurées en traits phénotypiques. En particulier nous cherchons à montrer qu'asymptotiquement, en temps long et à la limite des mutations rares, seul un nombre fini de traits phénotypiques peut subsister, ce que l'on traduit par la convergence de la distribution de la population vers une somme de masses de Dirac. Comme les traits dominants évoluent en temps, nous nous intéressons au devenir de ces traits. Une population monomorphique, c'est-à-dire concentrée autour d'un seul trait dominant, peut persister ou s'éteindre. Une population initialement monomorphique peut se diviser en deux ou plusieurs sous-populations de types dominants différents, ce phénomène a reçu le nom de **branchement évolutif** [109]. À la suite d'un branchement évolutif à deux branches, il peut y avoir coévolution, c'est-à-dire que les deux traits dominants résultat du branchement coexistent, ou bien extinction de l'une des branches et la population devient à nouveau monomorphique. Le branchement évolutif a été proposé comme un mécanisme pouvant être à l'origine de la spéciation sympatrique (sans séparation géographique) mais le lien entre branchement et spéciation reste encore discuté.

Nous ne cherchons pas à décrire la théorie de l'évolution dans son ensemble mais à en expliquer quelques idées simples. Dans cette thèse, nous nous concentrons sur la théorie de la sélection naturelle et nous intéressons au monomorphisme ; le branchement évolutif ne sera pas abordé. Nous commençons par présenter la théorie de la dynamique adaptative, à partir de laquelle ont été développées les théories probabilistes et déterministes évoquées.

Théorie de la dynamique adaptative

La *théorie de la dynamique adaptative* est l'étude de la dynamique en temps long de traits phénotypiques en présence de mutations rares. Cette théorie s'intéresse uniquement aux populations asexuées et aux interactions entre évolution et écologie, par conséquent la génétique n'est pas prise en compte. Nous ne décrivons ici que certains concepts de cette théorie qui sont importants pour la suite de ce mémoire.

L'idée principale de la théorie de la dynamique adaptative est de mesurer dans un environnement donné la capacité d'invasion d'un mutant dans une population résidente. Pour cela, on utilise la **fitness** ou **valeur sélective** [110]. On appelle fitness d'un trait y au sein d'une population de trait résident x la différence du taux de natalité et du taux de mortalité du trait y, lorsque la population est majoritairement du trait x. Historiquement, cette idée a été initialement développée dans un contexte de théorie des jeux où les traits sont des stratégies. Cette définition de fitness permet de construire dans l'espace des traits un paysage de valeurs sélectives en fonction des traits des mutants, ceux des résidents et des interactions écologiques de la population.

Une hypothèse fondamentale de cette théorie est la **séparation des échelles de temps** entre mutations et interactions écologiques : les mutations sont observées sur une échelle de temps plus longue que l'échelle de temps de la convergence de la population vers son état stationnaire attracteur. Nous parlerons dans la suite d'échelles de temps *évolutives* et *écologiques*. Sur le plan biologique, l'étude des dynamiques adaptatives se fait sous les hypothèses de grandes populations et de mutations rares. Ces hypothèses permettent d'étudier de manière dynamique les invasions successives de mutants et les états stationnaires successifs de la population.

L'identification des états stationnaires possibles, ou **stratégies singulières**, nécessite l'étude du gradient de la fitness et une classification des différentes stratégies a été établie. On retiendra notamment la terminologie d'ESS pour "Evolutionary Stable Strategy" qui décrit les stratégies singulières non envahissables. En particulier, un critère de branchement évolutif est spécifié à travers les dérivées de la fonction de fitness en les points de l'espace des traits où le branchement évolutif est susceptible de se produire.

Un autre outil de la théorie de la dynamique adaptative est **l'équation canonique** [66]. Il s'agit d'une équation différentielle décrivant la dynamique du trait dominant d'une population monomorphique. Cette équation différentielle comporte un terme décrivant l'effet des mutations et un terme de gradient de fitness décrivant la sélection.

La théorie de la dynamique adaptative propose des méthodes simples pour décrire la dynamique d'un trait dominant dans une population et qui peuvent être utilisées dans beaucoup de situations écologiques, par exemple pour traiter les interactions compétitives, proie-prédateurs, hôtes-parasites, *etc.* Mais cette théorie comporte aussi des limites. Elle donne notamment les conditions pour observer le branchement évolutif mais elle ne le décrit pas de manière dynamique.

Approche WKB

Le formalisme des équations de sélection et mutations sous forme d'équations aux dérivées partielles et d'équations intégro-différentielles a permis une approche plus générale que la théorie de la dynamique adaptative qui considérait des systèmes différentiels. Ces équations définies sur des espaces de traits continus ont été introduites pour la première fois par

Kimura [90] pour expliquer le maintien de la variabilité génétique au sein d'une population. La notion d'ESD pour "Evolutionary Stable Distribution" a été définie dans [88], donnant ainsi une extension de la notion d'ESS aux modèles structurés en traits continus. Les auteurs montrent la convergence de distributions de populations sous la forme $\sum \rho_i \delta_{x_i}$ vers des ESD par des études de stabilité, en utilisant des méthodes d'entropie. Notons qu'il est possible de trouver des ESD qui ne sont pas des distributions de masses de Dirac [4,5,36].

Les modèles macroscopiques étudiés ont été obtenus rigoureusement à partir de modèles stochastiques individus-centrés dans la limite de grandes populations [46,48–50,105]. L'idée est de partir d'un modèle microscopique qui détaille la dynamique de chaque individu et, après changement d'échelles, à la limite de grandes populations, on obtient une limite macroscopique sous forme d'équations intégro-différentielles.

Un point de vue asymptotique a été introduit pour la première fois par Diekmann, Jabin, Mischler et Perthame dans [68]. Il est basé sur les équations de Hamilton-Jacobi sous contraintes. L'idée principale est de partir d'un modèle continu et d'introduire un petit paramètre ε afin de faire un changement d'échelle de temps et de considérer des mutations rares ou petites. Ce changement d'échelle en temps nous permet de nous placer sur une échelle de temps évolutive, où l'équilibre écologique est atteint et où l'on observe l'effet des mutations. En procédant à l'étude du comportement asymptotique lorsque ε tend vers 0, on s'attend à la convergence de la densité de population vers une somme de masses de Dirac, c'est-à-dire une combinaison de traits dominants qui évoluent dans le temps. Une étape importante dans la dérivation de ces limites consiste à contrôler la population totale afin d'en déduire une contrainte sur la solution de l'équation de Hamilton-Jacobi.

Un premier modèle général étudié est le suivant

$$\begin{aligned} &\varepsilon \partial_t n_\varepsilon(t,x) = n_\varepsilon R(x, I_\varepsilon(t)) + \varepsilon^2 \Delta n_\varepsilon(t,x), \qquad x \in \mathbb{R}^d,\ t \geq 0, \\ &I_\varepsilon(t) := \int_{\mathbb{R}^d} \psi(x) n_\varepsilon(t,x)\, dx, \end{aligned} \tag{0.1}$$

où x est la variable de trait, t le temps et n_ε la densité de population. La fonction R est le taux de croissance de la population, soit la fonction de fitness dans le langage de la dynamique adaptative. Elle dépend du trait et du terme non local I_ε qui peut être interprété comme un terme de compétition ou une quantité de ressources. L'approche Hamilton-Jacobi repose sur le changement de fonction inconnue suivant, que l'on appelle aussi ansatz WKB,

$$n_\varepsilon(t,x) = e^{\frac{u_\varepsilon(t,x)}{\varepsilon}},$$

comme dans la méthode KPP ou l'étude des fronts de propagation [12,76,78,81,104].

Deux cadres ont été développés pour prouver la convergence de la suite u_ε et la concentration de la distribution n_ε.

- Un cadre de régularité et concavité fortes : on suppose que la fonction de fitness et la donnée initiale u_ε^0 sont concaves. Ce cadre permet de décrire la dynamique de masses de Dirac et d'obtenir rigoureusement un équivalent de l'équation canonique pour la dynamique adaptative. L'équation canonique est une équation différentielle sur la position de la masse de Dirac. C'est un cadre qui permet de décrire un comportement monomorphique dans un espace de trait multidimensionnel.
- Un cadre de régularité faible : les hypothèses autorisent une régularité faible de la fonction de fitness et des données initiales. On montre dans ce cadre la convergence

de u_ε vers une fonction u solution de viscosité de l'équation limite. La convergence de la distribution de la population vers une masse de Dirac est prouvée sous des hypothèses particulières sur la fonction de fitness et lorsque l'espace des traits est de dimension 1.

Lorsque ε tend vers 0, on montre dans [16,96] que dans ces deux cadres d'hypothèses u_ε converge vers u solution au sens de la viscosité de l'équation de Hamilton-Jacobi sous contrainte

$$\begin{cases} \partial_t u(t,x) = R(x,\bar{I}(t)) + |\nabla u|^2, \\ \max_{x\in\mathbb{R}^d} u(t,x) = 0, \quad \forall t > 0, \end{cases}$$

où $\bar{I}$ est la limite de I_ε quand ε tend vers 0. La théorie des solutions de viscosité est un cadre naturel pour déterminer le comportement asymptotique de solutions de ce type d'équation, voir [7,9,77].

Le contrôle de la population totale permet d'obtenir la contrainte, et $\bar{I}$ en est le multiplicateur de Lagrange associé. On en déduit ainsi que le support de n_ε lorsque ε tend vers 0 est inclus dans l'ensemble des points de maximum de u, soit

$$\text{supp } n \subset \{(t,x) | R(x,\bar{I}(t)) = 0\}.$$

On en déduit la concentration en masse de Dirac lorsque le support de n est discret dans l'espace de traits. Lorsque ce trait est unique, alors la population est monomorphique et on définit le trait le plus adapté $\bar{x}(t)$ pour tout temps t. Avec des hypothèses de régularité forte, on peut obtenir rigoureusement l'équivalent de l'équation canonique de la théorie de la dynamique adaptative

$$\dot{\bar{x}}(t) = \left(-D^2 u(t,\bar{x}(t))\right)^{-1} . \nabla_x R(\bar{x}(t),\bar{I}(t)), \quad \bar{x}(0) = \bar{x}^0.$$

Cette équation contient deux éléments caractéristiques de la théorie de la dynamique adaptative : la hessienne de u qui mesure la diversité locale autour du trait dominant, et le gradient de la fitness R évalué en $\bar{x}(t)$, qui indique localement le sens dans lequel le trait dominant $\bar{x}$ évolue. Cette équation donne l'évolution en temps du trait dominant.

L'unicité de la solution $(u,\bar{I})$ est une question ouverte en général. Elle a été prouvée dans certains cas particuliers, à savoir le cadre de la concavité, dans le cadre de régularité faible lorsque R a une forme particulière et pour un modèle structuré en espace.

Le but de notre travail est d'étendre la méthode décrite à des problèmes prenant en compte d'autres paramètres biologiques et environnementaux. La double structure en trait et en espace a été étudiée dans divers travaux pour comprendre l'incidence de l'hétérogénéité spatiale sur la dynamique adaptative d'une population. En particulier, dans [23–26, 143] les auteurs décrivent des fronts d'invasion pour des populations présentant des mobilités variables qui sont considérées comme des traits. Divers modèles structurés en trait et espace ont été abordés dans d'autres contextes, par exemple [6,18,79,89,92]. L'étude de fronts d'invasion a aussi été réalisée pour des populations sexuées [121,132]. Dans [115,116], les auteurs s'intéressent à la dynamique adaptative de populations pouvant migrer entre différents habitats, mettant plutôt l'accent sur l'étude de la sélection de traits dominants. Des modèles de populations structurées en trait pouvant consommer différents types de nutriments ont aussi été abordés, par exemple dans [51–53,119].

Cette thèse est composée de trois chapitres : dans le chapitre 1 nous nous intéressons à un modèle de population asexuée évoluant dans un chémostat. Le chémostat est un système expérimental fermé dans lequel des individus interagissent à travers la consommation de ressources limitées. Dans le chapitre 2, nous étudions la dynamique de concentration d'une population dont le taux de croissance dépend à la fois d'une variable de trait et d'une variable non héréditaire mais évoluant au cours de la vie d'un individu, comme l'âge. Dans le dernier chapitre, nous étudions une série de modèles de population sexuée ayant comme propriété une asymétrie d'hérédité des traits entre mâles et femelles.

Dynamique de concentration dans un modèle de chémostat

Dans le chapitre 1, nous étudions un modèle de chémostat initialement abordé dans [97] dans le cas sans mutation. Le chémostat est un bioréacteur dans lequel on observe l'évolution d'une population de micro-organismes alors qu'un substrat y est versé continûment. Afin que le volume du milieu de culture reste constant, l'excès contenant à la fois des individus et du substrat est évacué par un trop-plein. Ainsi, le chémostat permet d'observer les phénomènes de sélection avec un contrôle sur la quantité de ressources disponibles. Ce dispositif est considéré par les biologistes comme une bonne représentation de la réalité et de nombreux modèles mathématiques ont été étudiés pour en décrire le mécanisme.

Dans le cas du chémostat, la compétition entre organismes portant des traits différents est indirecte, elle se fait à travers la consommation d'une même ressource limitée. En termes mathématiques, la compétition indirecte peut être représentée par un noyau de consommation de ressources. Des modèles de compétition directe entre individus ont aussi été étudiés, par exemple dans [59, 120].

Nous considérons le modèle suivant, qui est en fait une extension du modèle classique (0.1) au chémostat

$$\begin{aligned}
&\varepsilon\partial_t n_\varepsilon(t,x) = n_\varepsilon R(x, S_\varepsilon(t)) + \varepsilon^2 \Delta n_\varepsilon(t,x), \qquad x \in \mathbb{R}^d, t \geq 0,\\
&\varepsilon\beta \frac{d}{dt} S_\varepsilon(t) = Q(S_\varepsilon(t), \rho_\varepsilon(t)),\\
&\rho_\varepsilon(t) := \int_{\mathbb{R}^d} n_\varepsilon(t,x)dx,
\end{aligned} \tag{0.2}$$

où n_ε est la distribution de la population par rapport à la variable de trait x, S_ε est la quantité de nutriments et ρ_ε la densité de population totale. Le terme laplacien représente les mutations. Ici la compétition indirecte pour les ressources est illustrée par la deuxième équation de (0.2). La quantité de nutriments évolue avec la pression exercée par la population, représentée par ρ_ε, et influe sur la fonction de croissance R.

Le paramètre β est utilisé ici pour mesurer la rapidité de réaction à la compétition. À la limite $\beta \to 0$, nous obtenons, à partir de la deuxième équation de (0.2), l'égalité $Q(S, \rho) = 0$ et, sous des hypothèses appropriées, nous déduisons, par le théorème des fonctions implicites, l'existence d'une fonction f vérifiant $S = f(\rho)$, ce qui permet de se ramener à l'équation dont nous connaissons les résultats de concentration.

Le paramètre ε permet de faire un changement d'échelle de temps et de considérer les mutations rares. Le but de cette étude est de retrouver les résultats de concentrations énoncés pour le modèle classique. Nous étudions la limite asymptotique lorsque ε tend

vers 0 pour montrer la concentration de la densité de population dans les deux cadres que nous avons décrit et en suivant les idées des méthodes développées dans [14, 96, 128].

Afin d'atteindre ces objectifs, nous utilisons les hypothèses suivantes sur R et Q, que l'on suppose lipschitziennes, soit

$$Q(0,\rho) > 0, \quad \max_{\rho\geq 0} Q(S_0,\rho) = 0, \tag{0.3}$$

$$Q_S(S,\rho) \leq -K_Q, \quad Q_\rho(S,\rho) \leq -K_Q, \tag{0.4}$$

$$0 < \underline{K}_1 \leq R_S(x,S) \leq \overline{K}_1. \tag{0.5}$$

L'hypothèse (0.3) illustre les limites physiques du chémostat : la quantité de nutriments est limitée et S_0 est la valeur de saturation. L'interprétation de l'hypothèse (0.4) est qu'une population plus grande ou une hausse des ressources impliquent un ralentissement du renouvellement des ressources disponibles.

Une première conséquence est le contrôle des quantités ρ_ε et S_ε et en particulier un résultat de non extinction.

Proposition 0.1. *Sous les hypothèses* (0.3)–(0.5)*, il existe des bornes* ρ_m*,* ρ_M *et* $S_m > 0$ *telles que*

$$0 < \rho_m \leq \rho_\varepsilon(t) \leq \rho_M, \quad S_m \leq S_\varepsilon(t) \leq S_0,$$

où S_m *est définie à travers l'égalité* $Q(\rho_M, S_m) = 0$.

Cadre faible

On complète les hypothèses précédentes avec les conditions sur la donnée initiale u_ε^0

$$u_\varepsilon^0(x) \leq A - K_2\sqrt{1+|x|^2}, \qquad ||\nabla u_\varepsilon^0|| \leq B, \qquad \forall x \in \mathbb{R}^d,$$

et une condition de régularité "faible"

$$\sup_{0\leq S\leq S_0} \|R(\cdot,S)\|_{W^{2,\infty}(\mathbb{R}^d)} \leq K_2,$$

où A, B, et K_2 ne dépendent pas de ε. Pour déduire estimations BV sur ρ_ε et S_ε, on a besoin de l'hypothèse suivante sur le paramètre β, soit

$$\min_{\substack{0\leq\rho\leq\rho_M,\\ S_m\leq S\leq S_0}} \frac{|Q_S|}{|Q_\rho|} \geq 4\beta \max_{\substack{0\leq\rho\leq\rho_M,\\ S_m\leq S\leq S_0}} \frac{\overline{K}_1\rho_M}{|Q_S|}. \tag{0.6}$$

Sous ces hypothèses et en utilisant la proposition 0.1, on prouve le théorème suivant.

Theorème 0.2. *Sous les hypothèses* (0.3)–(0.6)*,* ρ_ε *et* S_ε *sont uniformément bornés en* ε *dans* $BV_{loc}(0,\infty)$*. Par conséquent, il existe des fonctions limites* $\bar\rho$ *et* $\bar S$ *telles que, à extraction de sous-suites près, on a les convergences*

$$\rho_\varepsilon(t) \xrightarrow[\varepsilon\to 0]{} \bar\rho(t), \quad S_\varepsilon(t) \xrightarrow[\varepsilon\to 0]{} \bar S(t), \quad p.p.\ t > 0,$$

et en particulier l'égalité $Q(\bar\rho(t), \bar S(t)) = 0$ *est valable pour presque tout* t.

Avec ce résultat, on obtient ensuite la convergence de u_ε.

Theorème 0.3. *Sous les hypothèses* (0.3)–(0.6), *il existe une sous-suite de* $(u_\varepsilon)_\varepsilon$ *qui converge localement uniformément vers une fonction limite* u *lipschitzienne. Cette fonction* u *est solution au sens de la viscosité de l'équation de Hamilton-Jacobi sous contrainte*

$$\begin{cases} \partial_t u(t,x) = R(x,\bar{S}(t)) + |\nabla u|^2, \\ \max_{x\in\mathbb{R}^d} u(t,x) = 0, \quad \forall t > 0. \end{cases} \tag{0.7}$$

Ce résultat est obtenu grâce à des estimations Lipschitz sur u_ε, on utilise ensuite la stabilité des solutions de viscosité.

Cadre de concavité stricte

On utilise les hypothèses de concavité suivantes sur la fonction de fitness

$$-\underline{K}_2|x|^2 \leq R(x,S) \leq \overline{K}_0 - \overline{K}_2|x|^2, \quad -2\underline{K}_2 \leq D^2R(x,S) \leq -2\overline{K}_2. \tag{0.8}$$

De même, on suppose également de la concavité sur la données initiale

$$-\underline{L}_0 - \underline{L}_1|x|^2 \leq u_\varepsilon^0 \leq \overline{L}_0 - \overline{L}_1|x|^2, \quad -2\underline{L}_1 \leq D^2u_\varepsilon^0 \leq -2\overline{L}_1. \tag{0.9}$$

Sous ces hypothèses de concavité, on retrouve les résultats établis dans le théorème 0.2 sur les estimations BV de ρ_ε et S_ε. Ces hypothèses de concavité permettent d'obtenir le résultat suivant.

Theorème 0.4. *Sous les hypothèses* (0.8)–(0.9), *à extraction de sous-suite près, la suite* (n_ε) *converge faiblement en mesure vers une masse de Dirac*

$$n_\varepsilon(t,x) \xrightarrow[\varepsilon\to 0]{} \bar{\rho}(t)\delta(x-\bar{x}(t)).$$

En outre, on obtient l'égalité $R(\bar{x}(t),\bar{S}(t)) = 0$ *presque partout.*

L'idée essentielle de ce théorème est que la concavité de $R(\cdot,S)$ et de la donnée initiale entraîne la concavité de u, solution de (0.7). De plus, la concavité de u implique qu'il existe un unique point $\bar{x}(t)$ vérifiant la contrainte sur u. Ainsi, le support de n, limite de n_ε lorsque ε tend vers 0, est constitué d'un point isolé, on en déduit la concentration de n au point $(t,\bar{x}(t))$ pour preque tout temps $t \in (0,\infty)$.

Si on suppose plus de régularité sur la donnée initiale u_ε^0, on peut établir rigoureusement une forme d'équation canonique sur la dynamique du trait dominant. On utilise l'hypothèse suivante :

$$D^3R(\cdot,S) \in L^\infty(\mathbb{R}^d), \quad \|D^3u_\varepsilon^0\|_{L^\infty(\mathbb{R}^d)} \leq C, \tag{0.10}$$

où C ne dépend pas de ε : la majoration précédente est uniforme en ε.

Theorème 0.5. *Sous les hypothèses* (0.8)–(0.10), $\bar{x}$ *appartient à* $W^{1,\infty}(\mathbb{R}_+,\mathbb{R}^d)$ *et satisfait l'équation*

$$\dot{\bar{x}}(t) = \left(-D^2u(t,\bar{x}(t))\right)^{-1}.\nabla_x R(\bar{x}(t),\bar{S}(t)), \quad \bar{x}(0) = \bar{x}^0.$$

De plus, $\bar{S}(t) \in W^{1,\infty}(\mathbb{R}_+,\mathbb{R}^d)$ *et on en déduit que* $\bar{S}(t)$ *est une fonction décroissante et*

$$S(t) \xrightarrow[t\to\infty]{} S_m, \quad \bar{x}(t) \xrightarrow[t\to\infty]{} 0.$$

L'unicité est souvent une question ouverte, sauf dans certains cas particuliers. Dans le cas concave, l'unicité a été prouvée pour l'équation (0.1). On trouve également un résultat d'unicité dans un modèle structuré en espace et en trait dans [117] qui permet de se passer des estimations BV.

Pour terminer, la figure 0.2 montre le comportement de la densité n_ε pour deux valeurs de ε, avec une donnée initiale dépendant aussi de ε, soit $n_\varepsilon^0 = C_{mass}\exp(-(x-0.8)^2/\varepsilon)$.

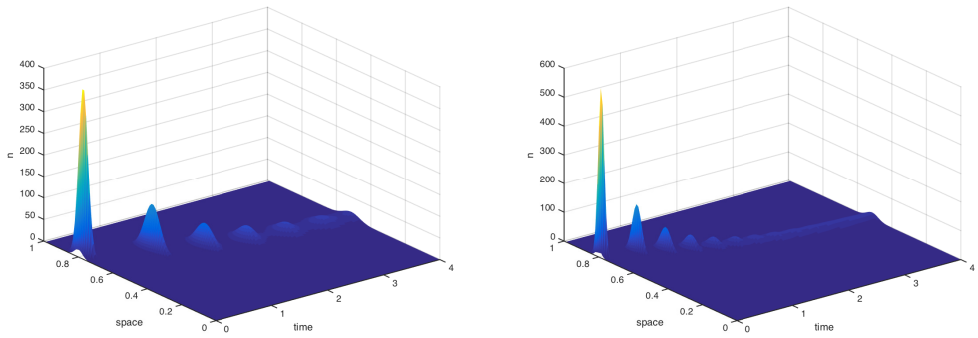

FIGURE 0.2 : Dynamique de la densité n_ε pour $\beta = 2\cdot 10^3$ et (a) $\varepsilon = 10^{-3}$, (b) $\varepsilon = 5\cdot 10^{-4}$.

Dynamique de concentration dans un modèle structuré en âge et en trait

Dans le chapitre 2, nous étudions un modèle de population structurée en trait et en âge. Nous nous référons à l'âge, mais les hypothèses sont assez générales pour pouvoir considérer d'autres variables biologiques : la taille par exemple. Néanmoins cette variable biologique n'est pas une caractéristique héréditaire et doit avoir comme propriété d'évoluer au cours de la vie d'un individu. Divers modèles structurés en âge ont été traités [37, 38, 60, 74].

Le but de cette étude est de déterminer l'évolution d'une population lorsque ses paramètres démographiques dépendent à la fois d'une variable d'âge et d'une variable de trait. En particulier, nous cherchons à identifier les traits dominants d'une telle population. La question du couplage des structures d'âge et de trait est naturelle, car certains gènes conférant un avantage sélectif à un jeune âge peuvent s'avérer moins avantageux, voire délétères à des âges plus avancés. Il s'agit donc de déterminer les traits qui offrent le meilleur compromis sélectif lorsque leurs effets évoluent en fonction de l'âge. Divers modèles structurés en traits et en âge ont été abordés dans différents contextes [34, 69, 70, 100, 133], ainsi que des extensions à la division cellulaire [111] et aux stades proliférants et quiescents de cellules tumorales [83]. On retrouve le même type d'équations par passage à la limite en grandes populations de processus stochastiques [39, 40, 106, 141].

Dans cet article, nous proposons une alternative à la méthode WKB qui a été expliquée dans le chapitre précédent. On part d'une équation de renouvellement à laquelle on ajoute

la structure de trait et le terme de compétition

$$\begin{cases} \varepsilon\partial_t m_\varepsilon(t,x,y) + \partial_x\left[A(x,y)m_\varepsilon(t,x,y)\right] + \left(\rho_\varepsilon(t) + d(x,y)\right) m_\varepsilon(t,x,y) = 0, \\ A(x=0,y)m_\varepsilon\left(t,x=0,y\right) = \dfrac{1}{\varepsilon^n}\displaystyle\int_{\mathbb{R}_+}\int_{\mathbb{R}^n} M(\frac{y'-y}{\varepsilon})b(x',y')m_\varepsilon(t,x',y')dx'dy', \\ \rho_\varepsilon(t) = \displaystyle\int_{\mathbb{R}_+}\int_{\mathbb{R}^n} m_\varepsilon(t,x,y)dxdy, \\ m_\varepsilon(t=0,x,y) = m_\varepsilon^0(x,y) > 0. \end{cases}$$

Précisons les notations : x est la variable d'âge et y la variable de trait, on note m_ε la distribution de la population. La fonction A désigne la vitesse de vieillissement, la fonction b le taux de naissance et la fonction d le taux de mortalité. Ici ρ_ε est le terme de compétition. On suppose que l'effet des mutations est observé à la naissance, l'apparition des mutations est mesurée par le noyau M sur la distance entre le trait du parent et celui du descendant.

Le paramètre ε est introduit d'une part pour considérer des petites mutations, d'autre part pour effectuer un changement d'échelle de temps $t \mapsto \frac{t}{\varepsilon}$ afin de se placer sur une échelle de temps évolutive et observer les mutations.

L'étude de ce modèle est divisée en deux cas : le premier cas sans mutation, le deuxième avec mutations.

Cas sans mutation

Nous commençons par le cas sans mutation, c'est-à-dire lorsque $M(z) = \delta_0(z)$, on obtient ainsi le modèle simplifié

$$\begin{cases} \varepsilon\partial_t m_\varepsilon(t,x,y) + \partial_x\left[A(x,y)m_\varepsilon(t,x,y)\right] + \left(\rho_\varepsilon(t) + d(x,y)\right) m_\varepsilon(t,x,y) = 0, \\ A(x=0,y)m_\varepsilon\left(t,x=0,y\right) = \displaystyle\int_{\mathbb{R}_+} b(x',y)m_\varepsilon(t,x',y)dx', \\ \rho_\varepsilon(t) = \displaystyle\int_{\mathbb{R}^n}\int_{\mathbb{R}_+} m_\varepsilon(t,x,y)dxdy, \\ m_\varepsilon(t=0,x,y) = m_\varepsilon^0(x,y) > 0. \end{cases} \tag{0.11}$$

Il s'agit en fait d'une équation de renouvellement avec un paramètre y. Il est déjà bien connu que l'étude en temps long des solutions d'équations de renouvellement repose sur l'analyse du problème spectral associé à l'équation stationnaire [72, 73, 127]. Plus précisément, on prouve en pratique l'existence d'éléments propres principaux, λ la valeur propre principale et $P(x)$ le vecteur propre associé (unique par normalisation) et on cherche à prouver que les solutions sont de la forme $P(x)\exp(\lambda t)$, soit d'un profil stationnaire en âge multiplié par une croissance exponentielle, par une méthode d'entropie [112, 113]. En suivant cette approche, notre idée est d'effectuer une factorisation de la densité de population en deux profils, l'un en âge et l'autre en trait. Nous écrivons la densité de population sous la forme

$$m_\varepsilon(t,x,y) = p_\varepsilon(t,x,y)e^{\frac{u_\varepsilon(t,y)}{\varepsilon}}. \tag{0.12}$$

Les principaux résultats de l'analyse du modèle sans mutations sont la convergence du profil en âge p_ε et de u_ε. La limite est donnée par la solution du problème spectral suivant

$$\begin{cases} \partial_x \left[A(x,y)Q(x,y)\right] + d(x,y)Q(x,y) = \Lambda(y)Q(x,y), \\ A(x=0,y)Q(x=0,y) = \displaystyle\int_{\mathbb{R}_+} b(x',y)Q(x',y)dx', \\ Q(x,y) > 0, \quad \displaystyle\int_{\mathbb{R}^+} b(x',y)Q(x',y)dx' = 1, \end{cases} \tag{0.13}$$

où $\Lambda(y)$ est la valeur propre principale et $Q(x,y)$ le vecteur propre associé. L'existence et l'unicité de ces éléments propres sont obtenus par un calcul direct. En effet, dans le cas sans mutation, la variable y est un paramètre, ainsi le problème aux valeurs propres devient une équation différentielle en la variable x. On obtient une formule explicite pour Q en fonction de Λ, et la condition de normalisation donne une définition implicite de Λ. Nous utilisons les hypothèses suivantes sur les coefficients

$$\lim_{x\to+\infty} d(x,y) = +\infty, \tag{0.14}$$

$$0 < \underline{r} \leq b(x,y) - d(x,y) \leq \overline{r}, \tag{0.15}$$

$$0 < A_0 \leq A(x,y) \leq A_\infty. \tag{0.16}$$

Afin de réaliser une décomposition unique de m_ε, on définit d'abord u_ε et on utilise l'unicité de Λ. On définit u_ε comme la solution de l'équation suivante

$$\begin{cases} \partial_t u_\varepsilon(t,y) = -\Lambda(y) - \rho_\varepsilon(t), \quad t > 0,\, y \in \mathbb{R}^n, \\ u_\varepsilon(0,y) = u_\varepsilon^0, \quad y \in \mathbb{R}^n. \end{cases} \tag{0.17}$$

Ainsi, on obtient l'équation sur p_ε

$$\begin{cases} \varepsilon\partial_t p_\varepsilon(t,x,y) + \partial_x \left[A(x,y)p_\varepsilon(t,x,y)\right] + d(x,y)p_\varepsilon(t,x,y) = \Lambda(y)p_\varepsilon(t,x,y), \\ A(x=0,y)p_\varepsilon\left(t,x=0,y\right) = \displaystyle\int_{\mathbb{R}_+} b(x',y)p_\varepsilon(t,x',y)dx'. \end{cases}$$

On a alors le résultat suivant.

Theorème 0.6. *Soit m_ε la solution de* (0.11)*, u_ε la solution de* (0.17)*, p_ε défini par la factorisation* (0.12) *et* (Λ, Q) *solution de* (0.13)*. Sous les hypothèses* (0.14)-(0.16) *et en utilisant des conditions adéquates sur les données initiales, les assertions suivantes sont vérifiées :*

1. *$\rho_\varepsilon = \int_{\mathbb{R}^n}\int_{\mathbb{R}_+} m_\varepsilon(\cdot,x,y)dxdy$ converge vers une fonction limite ρ lorsque ε tend vers 0 dans $L^\infty(0,\infty)$ faible-$\star$.*

2. *p_ε converge vers un multiple du vecteur propre normalisé Q pour une norme L^1 pondérée.*

3. *u_ε converge localement uniformément quand ε tend vers 0 vers une fonction continue u solution de l'équation*

$$\begin{cases} \partial_t u(t,y) = -\Lambda(y) - \rho(t), \quad t > 0,\, y \in \mathbb{R}^n, \\ \sup\limits_{y\in\mathbb{R}^n} u(t,y) = 0, \quad \forall t > 0, \\ u(0,y) = u^0(y), \quad y \in \mathbb{R}^n. \end{cases}$$

4. *Ainsi, m_ε converge faiblement lorsque ε tend vers 0 vers une mesure μ dont le support est inclus dans l'ensemble $\{(t,y) \in (0,\infty) \times \mathbb{R}^n \,|\, u(t,y) = 0\}$.*

5. *De plus, en supposant que u^0 et $-\Lambda$ sont strictement concaves, on a*

$$m_\varepsilon(t,x,y) \underset{\varepsilon\to 0}{\rightharpoonup} \rho(t)\frac{Q(x,y)}{\|Q(\cdot,y)\|_{L^1}}\delta_{y=\bar{y}(t)},$$

où $\bar{y}(t) \in \mathbb{R}^n$ satisfait une équation canonique.

On déduit que la population totale ρ_ε est bornée grâce à un principe de comparaison et en utilisant la convergence de m_ε lorsque x tend vers $+\infty$. La convergence du profil p_ε vers le vecteur propre Q est établie par le théorème suivant.

Theorème 0.7. *Soit (Q,Φ) solution de (0.13), sous les hypothèses (0.14)-(0.16) et en utilisant des conditions adéquates sur les données initiales, les assertions suivantes sont vérifiées :*

1. *$\underline{\gamma}(y)Q(x,y) \le p_\varepsilon(t,x,y) \le \overline{\gamma}(y)Q(x,y)$ pour tous $t \ge 0, x \ge 0, y \in \mathbb{R}^n$,*

2. *de plus, le profil p_ε converge vers le vecteur propre Q pour une norme L^1 pondérée quand ε tend vers 0. Plus précisément, pour γ^0 défini dans les conditions initiales, on a uniformément en (t,y)*

$$\int_{\mathbb{R}^+} \left|\frac{p_\varepsilon}{Q}(t,x,y) - \gamma^0(y)\right| Q(x,y)\Phi(x,y)dx \to 0 \quad \textit{lquand } \varepsilon \to 0.$$

Contrairement au chapitre 1 et aux cas classiques évoqués, le problème sur u_ε est simple et nous permet d'écrire une formule explicite pour u_ε. En fait, toute la difficulté a été reportée sur p_ε. La preuve de la convergence de p_ε repose sur des estimations d'entropie. Il s'agit d'une méthode classique pour montrer que le profil en âge se rapproche du profil stationnaire en temps long. Ici, on a besoin d'une convergence quand ε tend vers 0. On définit alors ce qu'on appelle l'entropie relative généralisée

$$E_\varepsilon(t,y) := \int_{\mathbb{R}^+} \left|\frac{p_\varepsilon}{Q}(t,x,y) - \gamma^0(y)\right| Q(x,y)\Phi(x,y)dx.$$

On montre que l'entropie E_ε décroît en temps pour tout y, elle est donc bornée par sa donnée initiale. En supposant que cette donnée initiale converge vers 0 uniformément en y, on obtient le résultat du théorème 0.7.

Par ailleurs, p_ε est borné uniformément en ε, ce qui permet d'en déduire la contrainte sur $u \leq 0$. Une condition de non extinction impose $\max u = 0$. La convergence de u_ε est triviale à extraction de sous-suite près. Par ailleurs, on a un résultat d'unicité

$$\int_0^t \rho(s)ds = \sup_{y\in\mathbb{R}^n} [u^0(y) - t\Lambda(y)], \quad \forall t \geq 0. \tag{0.18}$$

Cette unicité permet d'affirmer que les résultats de convergence s'appliquent aux suites entières, et non plus seulement à extraction de sous-suite près. On en déduit ainsi la convergence au sens des mesures de m_ε vers une mesure dont le support est donné par l'ensemble des points d'annulation de u. Le même type de résultat d'unicité est obtenu dans [117].

En comparaison avec la méthode WKB appliquée au modèle de chémostat, la méthode d'entropie relative et le résultat d'unicité (0.18) permettent de contourner la difficulté des estimations BV et de démontrer *a posteriori* la convergence de u_ε.

On a formellement la concentration de la densité de population. L'étude de la dynamique évolutive est différente des cas classiques car la fitness est donnée ici par la valeur propre principale Λ. Cette fitness est donc déterminée de manière implicite, ce qui rend l'étude de la dynamique de concentration plus difficile.

La concentration est étudiée à travers la valeur propre principale de l'opérateur (0.13). Une équation canonique peut être obtenue ; dans ce cas, elle a la forme suivante :

$$\dot{\bar{y}}(t) = \left(-D^2u(t,\bar{y}(t))\right)^{-1}.\nabla\Lambda(\bar{y}(t)), \quad \bar{y}(0) = \bar{y}^0.$$

Cas avec mutations

Le cas avec mutations est plus complexe. Nous étudions un problème approché et démontrons un résultat d'unicité de la solution du problème au sens de la viscosité. L'intérêt de ce problème consiste à trouver un résultat de stabilité alors que le hamiltonien n'est pas donné explicitement. En appliquant la transformation $m_\varepsilon = p_\varepsilon e^{u_\varepsilon/\varepsilon}$ et en passant à la limite $\varepsilon \to 0$, on obtient formellement le terme de renouvellement limite

$$A(x=0,y)p(t,x=0,y) = \int_{\mathbb{R}^n} M(z)e^{\nabla_y u(t,y)\cdot z}dz \int_{\mathbb{R}_+} b(x',y)p(t,x',y)\,dx'.$$

Avec la définition

$$\eta(t,y) := \int_{\mathbb{R}^n} M(z)e^{\nabla_y u(t,y)\cdot z}\,dz,$$

l'équation limite sur le profil p s'écrit

$$\begin{cases} \partial_x\left[A(x,y)p(t,x,y)\right] + d(x,y)p(t,x,y) = -(\rho(t)+\partial_t u(t,y))p(t,x,y), \\ A(x=0,y)p(t,x=0,y) = \eta(t,y)\displaystyle\int_{\mathbb{R}_+} b(x',y)p(t,x',y)\,dx', \\ p(t=0,x,y) = p^0(x,y) > 0. \end{cases}$$

Ainsi, on en déduit le problème spectral

$$\begin{cases} \partial_x \left[A(x,y)Q(x,y,\eta)\right] + d(x,y)Q(x,y,\eta) = \Lambda(y,\eta)Q(x,y,\eta), \\ A(x=0,y)Q(x=0,y,\eta) = \eta \displaystyle\int_{\mathbb{R}_+} b(x',y)Q(x',y,\eta)\,dx', \\ Q(x,y,\eta) > 0, \quad \displaystyle\int_{\mathbb{R}_+} b(x,y)Q(x,y,\eta)\,dx = 1, \end{cases}$$

où η est un paramètre. L'existence et l'unicité d'éléments propres principaux sont établis par les mêmes arguments que dans le cas sans mutation. En utilisant la même factorisation que dans le cas sans mutation et en définissant $H(y,p) = -\Lambda\left(y, \int M(z)e^{\nabla_y p\cdot z}dz\right)$, on cherche à montrer que la limite formelle u est solution de l'équation

$$\partial_t u(t,y) = H(y,\nabla_y u(t,y)) - \rho(t) = -\Lambda\left(y, \int_{\mathbb{R}^n} M(z)e^{\nabla_y u(t,x)\cdot z}dz\right) - \rho(t).$$

Pour contourner la difficulté de la régularité de ρ_ε, on définit $U_\varepsilon = u_\varepsilon + \int_0^t \rho_\varepsilon$ qui vérifie

$$\partial_t U_\varepsilon(t,y) = -\Lambda\left(y, \int_{\mathbb{R}^n} M(z)e^{\frac{U_\varepsilon(t,y+\varepsilon z)-U_\varepsilon(t,y)}{\varepsilon}}dz\right). \tag{0.19}$$

On cherche à construire une solution U_ε qui approche la solution de l'équation limite. On a besoin des hypothèses suivantes : pour tout intervalle fermé I, on suppose qu'il existe deux constantes L_0 et $L_1 > 0$, dépendant de I, telles que

$$\forall y \in \mathbb{R}^n,\ \forall \eta \in I, \quad \begin{cases} |\Lambda(y,\eta)| \le L_0, \\ |\partial_\eta \Lambda(y,\eta)| \le L_1. \end{cases} \tag{0.20}$$

On suppose aussi

$$|\Lambda(y,\eta)| \to +\infty \text{ quand } \eta \to +\infty \text{ ou } \eta \to 0, \text{ uniformément par rapport à } y \in \mathbb{R}^n. \tag{0.21}$$

Pour tout compact $K_p \subset \mathbb{R}^n$, on suppose qu'il existe $C > 0, \gamma_1 \in [0,4), \gamma_2 \in [0,1)$ tels que

$$\forall y \in \mathbb{R}^n, \forall p \in K_p, \quad \begin{cases} |\nabla_y H(y,p)| \le C\left(1+|y|^{\gamma_1}\right), \\ |\nabla_p H(y,p)| \le C\left(1+|y|^{\gamma_2}\right). \end{cases} \tag{0.22}$$

Theorème 0.8. *Sous les hypothèses* (0.20)–(0.22)*, il existe une unique solution U_ε à l'équation* (0.19)*. De plus, quand ε tend vers 0, U_ε converge localement uniformément vers une fonction limite U qui est solution, au sens de la viscosité, de l'équation de Hamilton-Jacobi*

$$\partial_t U(t,y) = H(y,\nabla_y U(t,y)) = -\Lambda\left(y, \int_{\mathbb{R}^n} M(z)e^{\nabla_y U(t,x)\cdot z}dz\right).$$

Les équations de Hamilton-Jacobi comportant une croissance sur-linéaire en le gradient de la solution ont motivé de nombreux travaux sur la régularité des solutions [10, 41–43].

Nous prouvons la convergence de U_ε vers l'unique solution de l'équation limite au sens de la viscosité. Pour cela, nous utilisons la méthode des semi-limites relaxées [8]. On définit

$$\overline{U}(t,y) = \limsup_{\substack{x\to y\\ s\to t\\ \varepsilon\to 0}} U_\varepsilon(s,x), \quad \underline{U}(t,y) = \liminf_{\substack{x\to y\\ s\to t\\ \varepsilon\to 0}} U_\varepsilon(s,x).$$

Par stabilité des solutions de viscosité discontinues, $\overline{U}$ et $\underline{U}$ sont respectivement sous-solution et sur-solution. Le principal résultat est l'unicité forte de la solution de l'équation limite.

Theorème 0.9. *Sous les hypothèses* (0.20)–(0.22), *on a* $\underline{U} = \overline{U}$.

Ce résultat d'unicité permet de déduire *a posteriori* la convergence uniforme de U_ε vers $U = \underline{U} = \overline{U}$. Le point-clé de la preuve du résultat d'unicité est le caractère lipschitzien au sens de la viscosité de la sur-solution $\underline{U}$. La preuve de ce résultat repose sur la borne uniforme de $\partial_t U_\varepsilon$.

La convergence du profil p_ε dans ce cas reste une question ouverte.

Populations sexuées

Dans le chapitre 3, nous étudions une série de modèles de populations sexuées. On suppose que mâles et femelles sont identifiés par la même distribution. Cette hypothèse est valable lorsque la proportion des sexes dans la population reste constante en tout temps, ou lorsque la population est hermaphrodite par exemple. Cette simplification permet de réduire le problème une seule équation au lieu d'un système. Nous supposons également que l'accouplement se fait de manière aléatoire et uniforme. Les modèles que nous étudions s'écrivent sous la forme générale

$$\varepsilon \partial_t n_\varepsilon(t,x) = \int_{\mathbb{R}\times\mathbb{R}} K_\varepsilon(x,y,z) \frac{n_\varepsilon(t,y)}{\rho_\varepsilon(t)} n_\varepsilon(t,z)\, dy\, dz - R(x,\rho_\varepsilon(t)) n_\varepsilon(t,x). \tag{0.23}$$

La fonction K_ε est le noyau de reproduction et contient aussi les mutations. R est le terme de saturation, comprenant un taux de mortalité dépendant de la variable de trait et le terme de compétition ρ_ε, la taille de population. On considérera toujours la variable y comme le trait de la femelle, et z comme le trait du mâle.

Les principales difficultés techniques de ce modèle sont liées au facteur $\frac{1}{\rho_\varepsilon}$ dans le terme de naissance. Ce terme de naissance est ainsi non linéaire et non local, bien que 1-homogène. Cela vient du fait que le nombre de naissances doit être proportionnel à la densité de population. Cela peut aussi s'interpréter par le fait que le choix d'un partenaire se fait de manière uniforme dans toute la population.

L'étude de modèles de populations sexuées est plus complexe que dans le cas asexué. En effet, la reproduction sexuée assure un brassage génétique et donc une variabilité phénotypique plus grande dans la population. L'objectif de cette étude est de comprendre les effets de la reproduction sexuée sur la dynamique adaptative d'une population structurée en trait. Nous cherchons notamment à obtenir des propriétés et méthodes générales pour traiter des modèles de populations comprenant un terme de naissance non linéaire et non local avec un aspect quadratique. Notons que cette structure d'équation apparaît également dans des modèles d'échange d'information génétique [20, 21, 99, 102] ou de protéines [84, 101].

Des modèles de reproduction sexuée ont déjà été étudiés dans différents contextes. Des études numériques de modèles individu-centrés sexués ont été faites afin de déterminer les conditions nécessaires au branchement évolutif dans des populations sexuées, par exemple [71, 134].

Du côté stochastique, on trouve divers travaux sur des modèles de populations mendeliennes, c'est-à-dire structurées en traits génétiques [56–58, 136, 137].

D'un point de vue populationnel, un certain intérêt s'est porté vers le modèle infinitésimal [17]. Il s'agit d'un modèle structuré en phénotype de la forme (0.23) avec une distribution des traits de la progéniture de type gaussien centré en la moyenne des traits des parents et une variance constante. Dans le cas où R est constant, on a existence et unicité d'un état stable qui est gaussien [32, 144]. Dans le cas où R dépend de x, les auteurs de [28] étudient deux modèles, l'un structuré en trait et l'autre en âge et en trait, et obtiennent l'existence d'éléments propres principaux associés aux problèmes stationnaires.

Des modèles structurés en trait et en espace ont également été abordés. Dans [121], la population vit dans un environnement non homogène et le résultat principal est une estimation de la vitesse d'invasion ou d'extinction, d'après une étude asymptotique et une simplification du modèle. Dans [132], une limite macroscopique est obtenue par une approche faisant appel à la distance de Wasserstein, utilisée aussi dans [135].

On s'intéresse également à deux modèles généraux de populations sexuées, mais dont les noyaux de naissance présentent une asymétrie. D'abord, un modèle d'hérédité asymétrique ou ATH pour "asymmetric trait heredity" :

$$\varepsilon\partial_t n_\varepsilon(t,x) = \int_{\mathbb{R}} K_0(x-z)\frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)}dz \cdot \int_{\mathbb{R}} G_\varepsilon(y-x)n_\varepsilon(t,y)dy - R(x,\rho_\varepsilon(t))n_\varepsilon(t,x),$$

où K_0 est un noyau symétrique et positif, G_ε la densité gaussienne centrée et d'écart type ε. On peut considérer pour G_ε des noyaux non gaussiens s'ils vérifient une convergence en mesure vers une masse de Dirac.

On s'intéresse également à un modèle comportant une fécondité asymétrique : la fécondité dépend uniquement du trait de la femelle. Dans la suite on utilise la terminologie de modèle AF pour "asymmetric fecundity", et on a

$$K_\varepsilon(x,y,z) = B(y)\alpha_\varepsilon(x,y,z) \text{ avec } \int_{\mathbb{R}} \alpha(x,y,z)dx = 1 \text{ pour tout } y,z. \tag{0.24}$$

Ces modèles sont motivés par la problématique des maladies transmises par des vecteurs, en particulier l'espèce de moustiques *Aedes aegypti*, principal vecteur de la dengue, du virus Zika, du chikungunya et de la fièvre jaune, qui semble développer rapidement des résistances aux insecticides. L'hypothèse d'asymétrie de la fécondité se justifie par le fait que les moustiques mâles fécondent tôt dans leur vie et sur un temps court, la résistance aux insecticides aurait donc plus d'incidence sur la fécondité de la femelle. Ce travail fait partie d'un programme sur l'analyse de modèles et leur contrôle dans le contexte de l'épidémiologie évolutive [22, 139].

Dans un premier temps, nous étudions le modèle simplifié suivant,

$$\varepsilon\partial_t n_\varepsilon(t,x) = \left(\int_{\mathbb{R}} K_0(x-z)\frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)}dz - \nu\rho_\varepsilon(t)\right) n_\varepsilon(t,x), \tag{0.25}$$

qui est en fait un cas particulier des modèles ATH et AF. Dans ce cas, on suppose que tout individu hérite de son trait directement de la mère et que l'hérédité du père présente une variabilité mesurée par le noyau K_0. Nous essayons d'étendre les méthodes développées initialement pour les modèles asexués au cas sexué.

Estimations BV

On obtient des estimations BV sur ρ_ε lorsque $R = \nu\rho$ avec $\nu > 0$ une constante. Dans ce cas, R ne dépend pas de la variable de trait et ne contient que les effets de la compétition.

Pour les modèles sans mutations et ATH, on suppose le noyau K_0 symétrique, continu et borné. On obtient alors le résultat suivant.

Theorème 0.10 (Estimation BV pour le modèle sans mutations)**.** *Soit $T > 0$ et n_ε solution de* (0.25) *avec la donnée initiale n_ε^0.*

Sous des hypothèses de non extinction de la population, ρ_ε est uniformément borné dans $BV(0,T)$. Ainsi, il existe une fonction $\bar\rho$ et une mesure $\bar n$ telles que, à extraction de sous-suites près, on a les convergences $\rho_\varepsilon \to \bar\rho$ in $L^1(0,T)$, et $n_\varepsilon \rightharpoonup \bar n \in L^\infty(0,T;M^1)$ au sens des mesures lorsque ε tend vers 0.

De plus, on a l'estimation

$$\left|\int_0^T \int_{\mathbb{R}} n_\varepsilon \left(\frac{K_0 * n_\varepsilon}{\rho_\varepsilon} - \nu\rho_\varepsilon\right)^2 dxdt\right| \leq C\varepsilon.$$

Cette dernière estimation est reliée à la notion d'ESD [88], il s'agit d'une distribution satisfaisant les conditions suivantes

$$\begin{aligned} &K_0 * \overline{n} = \nu\overline{\rho}^2 \text{ sur } \mathrm{supp}(\overline{\mathrm{n}}),\\ &K_0 * \overline{n} \leq \nu\overline{\rho}^2 \text{ sur } \mathbb{R}, \end{aligned}$$

où $\overline{\rho} = \int \overline{n}$. Les masses de Dirac peuvent justement satisfaire ce type de conditions.

On a le même type de résultat pour les autres modèles avec d'autres hypothèses. Dans le cas AF, on a besoin de la condition suivante

$$\begin{aligned} &\exists C > 0, \forall \varepsilon > 0, \forall \phi \in M^1 \text{ avec } \|\phi\|_{M^1} = 1,\\ &\iiint \alpha_\varepsilon(x,y,z)B(x)B(y)\phi(y)\phi(z)\,dx\,dy\,dz - \left(\int B(y)\phi(y)\,dy\right)^2 \geq -C\varepsilon. \end{aligned}$$

Cette condition signifie que les variations de la fécondité doivent être bornées. Pour le cas ATH, on a besoin de la condition suivante : pour tout $\phi \in L^1 \cap W^{1,\infty}$ on a $G_\varepsilon * \phi = \phi + O(\varepsilon)$, dans le sens

$$\frac{1}{\varepsilon\|\phi\|_{Lip}}\|G_\varepsilon * \phi - \phi\|_{L^1} \text{ est uniformément borné en } \varepsilon.$$

Dans le cas où R est une fonction dépendant à la fois de la variable de trait et de la taille de la population, la dérivation d'estimations BV uniformes pour ρ_ε est difficile. Des conditions restrictives ont été détaillées dans le chapitre 3, pour lesquelles le théorème précédent est toujours valable.

Approche Hamilton-Jacobi dans le cas sexué

Une structure d'équation de Hamilton-Jacobi apparaît pour ces modèles de populations sexuées. Après changement de variable par la transformation de Hopf-Cole et en posant

$$a_\varepsilon(t,x) = \frac{1}{\rho_\varepsilon(t)}\int_{\mathbb{R}} K(x,z)n_\varepsilon(t,z)dz, \quad b_\varepsilon(t,x) = R(x,\rho_\varepsilon(t)),$$

on obtient, dans le cas du modèle ATH avec un noyau gaussien pour l'hérédité venant de la mère

$$\partial_t u_\varepsilon(t,x) = a_\varepsilon(t,x)\int_{\mathbb{R}} \frac{1}{\sqrt{\pi}} e^{-|y|^2} e^{\frac{u_\varepsilon(t,x-\varepsilon y)-u_\varepsilon(t,x)}{\varepsilon}} dy - b_\varepsilon(t,x), \tag{0.26}$$

où K est un noyau plus général que K_0 mais qui reste symétrique. On cherche à montrer la convergence de u_ε vers u solution de l'équation limite

$$\partial_t u(t,x) = a(t,x)e^{(\partial_x u(t,x))^2/2} - b(t,x). \tag{0.27}$$

Pour le modèle AF, on obtient à ε fixé

$$\partial_t u_\varepsilon(t,x) = \int_{\mathbb{R}} B(y) q_\varepsilon(t,y) \int_{\mathbb{R}} \alpha(z,y) e^{\frac{u_\varepsilon(t,x-\varepsilon y)-u_\varepsilon(t,x)}{\varepsilon}} dz dy - b_\varepsilon(t,x), \tag{0.28}$$

où $q_\varepsilon(t,x) = \frac{n_\varepsilon(t,x)}{\rho_\varepsilon(t)}$ et à la limite ε tendant vers 0,

$$\partial_t u(t,x) = \int_{\mathbb{R}} B(y) q(t,y) \int_{\mathbb{R}} \alpha(z,y) e^{-\partial_x u(t,x)\cdot z} dz dy - b(t,x). \tag{0.29}$$

Pour les deux modèles, on réussit à obtenir des estimations Lipschitz sur u_ε uniformes en ε (voir [11, 55] pour des résultats de régularité pour les hamiltoniens sous forme intégrale). Cependant, le résultat de stabilité des solutions de viscosité est assuré si les coefficients convergent également. La dérivation d'estimations pour les coefficients des équations en u_ε pour les cas ATH et AF est une question ouverte, la difficulté venant de la dépendance en temps.

Pour obtenir les estimations Lipschitz sur u_ε, on a besoin des hypothèses suivantes sur la donnée initiale.

$$u_\varepsilon^0(x) \le -A|x| + C, \quad \|\partial_x u_\varepsilon^0\| \le L_0. \tag{0.30}$$

On parvient alors au résultat suivant.

Theorème 0.11. *Sous l'hypothèse* (0.30)*, pour les deux équations* (0.26) *et* (0.28)*, les solutions correspondantes u_ε sont localement uniformément lipschitziennes en ε.*

De plus, on obtient une majoration globale de u_ε. Plus précisément,

$$u_\varepsilon(t,x) \le \varepsilon \ln\left(C + \frac{C(1+t)}{\varepsilon}\right),$$

où C est une constante strictement positive.

L'idée de la preuve est la suivante : on démontre d'abord que u_ε est localement uniformément lipschitzienne en espace. On réussit à contrôler la borne Lipschitz en espace par $-u_\varepsilon$ qui croît au plus linéairement vers $+\infty$ lorque x tend vers l'infini. Ensuite, l'estimation de la dérivée en temps de u_ε découle du caractère lipschitzien en espace et de la décroissance de K vers 0 en l'infini. La borne globale résulte également de l'estimation Lipschitz en espace et des estimations sur ρ_ε.

Comme la population totale est bornée, on obtient la contrainte $\max_x u = 0$ en tout temps, ce qui permet d'identifier l'ensemble des possibles points de concentration, c'est-à-dire

$$\operatorname{supp} \bar{n} \subset \{(t,x) \in (0,\infty)\times\mathbb{R} \,|\, B(x) - b(t,x) = 0\} \quad \text{dans le cas AF,}$$
$$\operatorname{supp} \bar{n} \subset \{(t,x) \in (0,\infty)\times\mathbb{R} \,|\, a(t,x) - b(t,x) = 0\} \quad \text{dans le cas ATH.}$$

L'étape suivante est donc de trouver les hypothèses appropriées pour caractériser la concentration de la population.

Avant de commencer

Pour résumer, le chapitre 1 évoque les dynamiques des masses de Dirac dans le modèle du chémostat. Il fait l'objet de l'article [98] en collaboration avec Alexander Lorz et Benoît Perthame, publié dans *Chinese Annals of Mathematics, Series B*.

Le chapitre 2 est consacré aux dynamiques de concentration dans le modèle structuré en âge et en traits phénotypiques. Il s'agit de l'article [125] réalisé en collaboration avec Samuel Nordmann et Benoît Perthame, publié dans *Acta Applicandae Mathematicae*.

Le chapitre 3 est dédié aux modèles de sélection-mutation avec noyaux de reproduction sexuée et compétition. Ce travail a été effectué en collaboration avec Benoît Perthame et Martin Strugarek et sera présenté prochainement sous forme d'article.

Chapter 1

Dirac concentrations in a chemostat model of adaptive evolution

We consider a non-local parabolic equation of Lotka-Volterra type that describe the evolution of phenotypically structured populations. Nonlinearities appear in these systems to model interactions and competition phenomena leading to selection. In this paper, the equation on the structured population is coupled with a differential equation on the nutrient concentration that changes as the total population varies.

We review different methods aimed at showing the convergence of the solutions to a moving Dirac mass. Using either weak or strong regularity assumptions we study the concentration of the solution. To this end, we state BV estimates in time on appropriate quantities and derive a constrained Hamilton-Jacobi equation to identify where the solutions concentrates as Dirac masses.

1.1 Introduction

We survey several methods developed to study concentration effects in parabolic equations of Lotka-Volterra type. Furthermore, we extend the theory to a coupled system motivated by models of chemostat where we observe very rare mutations for a long time. These equations have been established with the aim of describing how speciation occurs in biological populations, taking into account competition for resources and mutations in the populations. There is a large literature on the subject where the mutation-competition principles are illustrated in various mathematical terms: for instance in [67,82,107] for an approach based on the study of the stability of differential systems, in [85,86,103] for the evolutionary games theory, in [45] for the study of stochastic individual based models, or in [16,114,130] for the study of integro-differential models. We choose here the formalism using parabolic partial differential equations, widely developed in [14,64,127,128] to describe the competition dynamics in a chemostat.

The chemostat is a bioreactor to which fresh medium containing nutrients is continuously added, while culture liquid is continuously removed to keep the culture volume constant. This device is used as an experimental ecosystem in evolutionary biology to observe mutation and selection processes driven by competition for resources. From the mathematical point of view, the theoretical description of the population dynamics in a chemostat leads to highly nonlinear models and questions of long term behaviour and convergence to an evolutionary steady state naturally arise (see [1,53,68,118,138]).

Our aim is to study a generalization of the chemostat model introduced in [97] with a representation of mutations by a diffusion term. In this model, each individual in the population is characterized by a quantitative phenotypic trait $x \in \mathbb{R}^d$ and $n_\varepsilon(t,x)$ denotes the population density at time t with the trait x. We study the following equations

$$\varepsilon \partial_t n_\varepsilon(x,t) = n_\varepsilon R(x, S_\varepsilon(t)) + \varepsilon^2 \Delta n_\varepsilon(x,t), \qquad x \in \mathbb{R}^d, t \geq 0, \tag{1.1}$$

$$\varepsilon\beta \frac{d}{dt} S_\varepsilon(t) = Q(S_\varepsilon(t), \rho_\varepsilon(t)), \tag{1.2}$$

$$\rho_\varepsilon(t) := \int_{\mathbb{R}^d} n_\varepsilon(t,x)dx, \tag{1.3}$$

where the function $R(x, S_\varepsilon)$ represents a trait-dependent birth-death rate and S_ε denotes the nutrient concentration which changes over time with rate Q. Here ε is a small parameter which allows to consider very rare mutations and large times of order ε^{-1}. The idea of an ε^{-1} rescaling in the space and time variables goes back to [80,81] to study propagation for systems of reaction-diffusion PDE. The parameter β, introduced first in [97], gives a time scale which, as $\beta \to 0$, leads to the equation $Q(\rho, S) = 0$. In this case, under suitable assumptions, we deduce the existence of a function f by Implicit Function Theorem, such that $S = f(\rho)$ and the concentration results are known to hold [96,128].

Such models can be derived from stochastic individual based models in the limit of large populations (refer to [48,50]).

A possible way to express mathematically the emergence of the fittest traits among the population is to prove that n_ε concentrates as a Dirac mass centered on a point $\bar{x}$ (or a sum of Dirac masses) when ε vanishes. This means the phenotypic selection of a quantitative trait denoted by $\bar{x}$ in long times. The main results of the paper can be summarized as

Theorem 1.1. *For well-prepared initial data and two classes of assumptions (monotonic*

in one dimension or concavity in multi-dimensions), then the solution $n_\varepsilon(t,x)$ concentrates i.e.

$$n_\varepsilon(t,x) \underset{\varepsilon\to 0}{\longrightarrow} \bar{\rho}(t)\delta(x-\bar{x}(t)) \qquad \textit{in the sense of measure,}$$

where the pair $(\bar{x}(t),\bar{\rho}(t))$ can be determined thanks to a constrained Hamilton-Jacobi equation given later on.

In order to describe these concentration effects and following earlier works on similar issues [14, 44, 128], we will use the Hopf-Cole transformation defining $u_\varepsilon(t,x) = \varepsilon \ln n_\varepsilon(t,x)$ and derive a Hamilton-Jacobi equation. Then we obtain by passing to the limit $\varepsilon \to 0$ a constrained Hamilton-Jacobi equation, whose solutions have a maximum value of 0. The point is that the concentration locations in the limit $\varepsilon \to 0$ can be identified among the maximum points of these solutions. This method, introduced in [68] and used for instance in [130, 131] is very general and has been extended to various systems (see [51, 96, 127]).

Singular perturbation problems in PDEs is a classical subject that has been studied from different viewpoints. For instance a seminal paper on parabolic equations involving measures is [30]. Also the above rescaling in parabolic equations or systems has been deeply studied in reaction-diffusion equations (see [12, 76]) leading to front propagation where a state invades another as in the Fishher-KPP equation where the stable state $n_\varepsilon = 1$ invades the unstable state $n_\varepsilon = 0$. This is also the case of Ginzburg-Landau equations (see [19]) where the quadratic observable $n_\varepsilon = |u_\varepsilon|^2$ takes asymptotically the value 1. This is different from our case, as one can see in the above theorem and since we essentially derive L^1 bounds from the presented model.

To prove the main convergence results of this paper, we will adapt the method introduced in [14, 97, 128] to find BV estimates for the appropriate quantities as a first step. Then we will use the theory of viscosity solutions to Hamilton-Jacobi equations (see [7, 9, 62, 77] for general introduction to this theory) to obtain the Dirac locations. In the first part, we proceed with assumptions of weak regularity of the growth rate in a first instance, and then we resume the study under concavity assumptions.

This paper is organized as follows. We first state (see Section 1.2) the framework of the general weak theory and its main results. We start the study by establishing BV estimates on ρ_ε^2 and S_ε in Section 1.3. Section 1.4 is devoted to the analysis of the solutions to the constrained Hamilton-Jacobi equations. We first prove some regularity results for u_ε. Then we study the asymptotic behaviour of u_ε and deduce properties of the concentration points. In Section 1.5 we set the simple case of our results when the dimension d equals 1 and prove concentration effects. In Section 1.6 we review the d-dimensional framework where we assume uniform concavity of the growth rate and initial conditions. We establish again the BV estimates in this specific case and prove the uniform concavity of u_ε. The regularity obtained for u_ε allows us to derive the dynamics of the concentration points in the form of a *canonical equation*. We complete these results by numerics in Section 1.7.

1.2 The weak theory: assumptions and main results

First of all, we give assumptions to set a framework for the general weak theory. We use the same assumptions as in [97].

For the Lipschitz continuous functions R and Q, we assume that there are constants $S_0 > 0$, $K_Q > 0$, $\underline{K}_1 > 0$ and $\overline{K}_1 > 0$ such that

$$Q(0,\rho) > 0, \quad \max_{\rho \geq 0} Q(S_0,\rho) = 0, \qquad Q_S(S,\rho) \leq -K_Q, \quad Q_\rho(S,\rho) \leq -K_Q, \tag{1.4}$$

$$0 < \underline{K}_1 \leq R_S(x,S) \leq \overline{K}_1, \tag{1.5}$$

$$\sup_{0 \leq S \leq S_0} \|R(\cdot,S)\|_{W^{2,\infty}(\mathbb{R}^d)} \leq K_2. \tag{1.6}$$

We complete the system with the initial conditions S_ε^0, n_ε^0 such that

$$S_m < S_\varepsilon^0 < S_0, \qquad n_\varepsilon^0(x) > 0, \ \forall x \in \mathbb{R}^d, \quad 0 < \rho_m \leq \rho_\varepsilon^0 := \int_{\mathbb{R}^d} n_\varepsilon^0(x)dx \leq \rho_M, \tag{1.7}$$

where ρ_m, ρ_M and S_m are defined below.

We add to these assumptions a smallness condition on β which can be written as

$$\min_{\substack{0 \leq \rho \leq \rho_M, \\ S_m \leq S \leq S_0}} \frac{|Q_S|}{|Q_\rho|} \geq 4\beta \max_{\substack{0 \leq \rho \leq \rho_M, \\ S_m \leq S \leq S_0}} \frac{\overline{K}_1 \rho_M}{|Q_S|}, \tag{1.8}$$

with the definition of ρ_M stated below.
Note that from assumption (1.4), we directly obtain the bounds

$$n_\varepsilon(t,x) > 0, \qquad 0 < S_\varepsilon(t) \leq S_0. \tag{1.9}$$

First we recall the following lemma, whose proof is given in [97]:

Lemma 1.2. *Under the assumptions* (1.4)-(1.7)*, there are constants* ρ_m*,* ρ_M *and* $S_m > 0$ *such that*

$$0 < \rho_m \leq \rho_\varepsilon(t) \leq \rho_M \qquad \text{and} \qquad S_m \leq S_\varepsilon(t) \leq S_0,$$

where the value $S_m < S_0$ *is defined by* $Q(S_m, \rho_M) = 0$.

This result is required to prove the following theorem.

Theorem 1.3. *Assuming also* (1.8)*,* $\rho_\varepsilon(t)$ *and* $S_\varepsilon(t)$ *have locally bounded total variation uniformly in* ε*. Consequently, there are limit functions* $\rho_m \leq \overline{\rho} \leq \rho_M$*,* $S_m \leq \overline{S} \leq S_0$ *such that, after extraction of a subsequence, we have*

$$S_{\varepsilon_k}(t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{S}(t) \qquad \text{and} \qquad \rho_{\varepsilon_k}(t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\rho}(t), \qquad a.e.,$$

and

$$Q(\bar{\rho}, \bar{S}) = 0 \qquad a.e.$$

The next section is devoted to the proof of Theorem 1.3. Contrary to what we could expect, the establishment of the BV estimates will be more complicated than in the previous works (see [96, 128]) where the nutrients are represented by an integral term as $\int \psi(x) n_\varepsilon(t,x)dx$. Here the main challenge comes from the equation (1.2) that we also have to consider to obtain BV estimates on S_ε. Another difficulty comes from the parameter β. For β large, it seems that we cannot derive BV estimates with our approach, but anyway we do observe the convergence of the solutions in the numerics we performed. This is not the case for inhibitory integrate-and-fire models for instance (see [31]) where delays generate periodic solutions.

In the following proofs, C denotes a constant which may change from line to line.

1.3 BV estimates on $\rho_\varepsilon^2(t)$ and $S_\varepsilon(t)$

1.3.1 Bounds for ρ_ε

We follow the lines of [97] to give the bounds ρ_m and ρ_M. By integrating the equation (1.1) and using the assumptions (1.5) and (1.6), we arrive to the inequalities

$$\varepsilon \frac{d}{dt}\rho_\varepsilon \leq \rho_\varepsilon(K_2 + \overline{K_1}S_\varepsilon),$$

and

$$\varepsilon \frac{d}{dt}\ln\rho_\varepsilon \leq K_2 + \overline{K_1}S_0.$$

Notice that $Q(S_\varepsilon, \rho_\varepsilon) \leq -K_Q\rho_\varepsilon + Q(0,0)$ from the assumptions in (1.4). By adding the equation (1.2) to the inequation above, we arrive to

$$\varepsilon \frac{d}{dt}(\ln\rho_\varepsilon + \beta S_\varepsilon) \leq K_2 + \overline{K_1}S_0 + Q(0,0) - K_Q\rho_\varepsilon \tag{1.10}$$

$$\leq K_2 + \overline{K_1}S_0 + Q(0,0) - \frac{K_Q}{e^{\beta S_0}}e^{\ln\rho_\varepsilon + \beta S_\varepsilon}. \tag{1.11}$$

It follows that, for C_2 the root in $\ln\rho_\varepsilon + \beta S_\varepsilon$ of the right hand side,

$$\ln\rho_\varepsilon \leq \ln\rho_\varepsilon + \beta S_\varepsilon \leq \max(\ln\rho_\varepsilon^0 + \beta S_0, C_2).$$

Hence the upper bound ρ_M for $\rho_\varepsilon(t)$.

Thanks to this upper bound, we obtain the lower bound S_m on $S_\varepsilon(t)$, since, by using the assumption (1.4) on Q, we remark that

$$\varepsilon\beta \frac{d}{dt}S_\varepsilon(t) = Q(S_\varepsilon(t), \rho_\varepsilon(t)) \geq Q(S_\varepsilon(t), \rho_M).$$

Then there is a unique value S_m such that $Q(S_m, \rho_M) = 0$, and from the initial conditions (1.7), we deduce that $S_m \leq S_\varepsilon(t)$ for $t \geq 0$.

Next, let us look for the lower bound. It follows, from the integration of (1.1) as above, that we have

$$\varepsilon \frac{d}{dt}\ln\rho_\varepsilon \geq -K_2 + \underline{K_1}S_m.$$

By subtracting (1.2) and still using (1.4), we obtain

$$\varepsilon \frac{d}{dt}(\ln\rho_\varepsilon - \beta S_\varepsilon) \geq -K_2 + \underline{K_1}S_m - Q(S_\varepsilon, \rho_\varepsilon) \tag{1.12}$$

$$\geq -K_2 - Q(0,0) + K_Q\rho_\varepsilon \tag{1.13}$$

$$\geq -K_2 - Q(0,0) + K_Q e^{\ln\rho_\varepsilon - \beta S_\varepsilon}e^{\beta S_m}. \tag{1.14}$$

Taking C_3 the root in $\ln\rho_\varepsilon - \beta S_\varepsilon$ of the right hand side in (1.12), we have the lower bound

$$\ln\rho_\varepsilon(t) \geq \min(\ln\rho_\varepsilon^0 - \beta S_0, C_3),$$

which ends the proof of the Lemma 1.2.

1.3.2 Local BV estimates

To find local BV bounds for ρ_ε and S_ε which are uniform in $\varepsilon > 0$, we apply the method described in [97] that we explain in detail in this section.

Let us first define $J_\varepsilon := \dot{S}_\varepsilon$ and $P_\varepsilon := \dot{\rho_\varepsilon}$. With these definitions, we have the equations

$$\varepsilon P_\varepsilon = \int n_\varepsilon R(x, S_\varepsilon(t))\, dx, \qquad \varepsilon\beta J_\varepsilon = Q(\rho_\varepsilon(t), S_\varepsilon(t)). \tag{1.15}$$

Defining α_ε and γ_ε as

$$\alpha_\varepsilon(t) := \int n_\varepsilon R_S(x, S_\varepsilon(t))\, dx \qquad \text{and} \qquad \gamma_\varepsilon(t) := \int n_\varepsilon R^2\, dx,$$

we differentiate both equations above, then we obtain the following equations on J_ε and P_ε

$$\varepsilon \dot{P}_\varepsilon = J_\varepsilon \int n_\varepsilon R_S(x, S_\varepsilon(t))\, dx + \int \partial_t n_\varepsilon R(x, S_\varepsilon(t))\, dx \tag{1.16}$$

$$= \alpha_\varepsilon(t) J_\varepsilon + \varepsilon \int n_\varepsilon \Delta R dx + \frac{1}{\varepsilon}\gamma_\varepsilon(t), \tag{1.17}$$

$$\varepsilon\beta \dot{J}_\varepsilon = Q_S J_\varepsilon + Q_\rho P_\varepsilon. \tag{1.18}$$

However at this stage we cannot obtain directly the BV bounds on ρ_ε and S_ε we expect. Thus we consider a linear combination of P_ε and J_ε. Let $\mu_\varepsilon(t)$ be a function we will determine later. By combining the equalities above, we obtain the following equation on $P_\varepsilon + \mu_\varepsilon J_\varepsilon$:

$$\varepsilon \frac{d}{dt}(P_\varepsilon + \beta\mu_\varepsilon J_\varepsilon) = \alpha_\varepsilon J_\varepsilon + \varepsilon \int n_\varepsilon \Delta R dx + \beta \dot{\mu_\varepsilon} J_\varepsilon + \mu_\varepsilon (Q_S J_\varepsilon + Q_\rho P_\varepsilon) + \frac{1}{\varepsilon}\gamma_\varepsilon \tag{1.19}$$

$$= \mu_\varepsilon Q_\rho (P_\varepsilon + \beta\mu_\varepsilon J_\varepsilon) + (\varepsilon\beta\dot{\mu_\varepsilon} - \beta Q_\rho \mu_\varepsilon^2 + \mu_\varepsilon Q_S + \alpha_\varepsilon) J_\varepsilon \tag{1.20}$$

$$+ \varepsilon \int n_\varepsilon \Delta R dx + \frac{1}{\varepsilon}\gamma_\varepsilon. \tag{1.21}$$

First we prove the following result.

Lemma 1.4. *Considering the solution μ_ε of the differential equation*

$$\varepsilon\beta\dot{\mu}_\varepsilon = -\beta|Q_\rho|\mu_\varepsilon^2 + \mu_\varepsilon|Q_S| - \alpha_\varepsilon,$$

there exist constants $0 < \mu_m < \mu_M$ such that, choosing initially $\mu_m < \mu_\varepsilon(0) < \mu_M$, we have

$$\mu_m \le \mu_\varepsilon(t) \le \mu_M, \qquad \forall t \ge 0.$$

Furthermore, we have the following estimate concerning the negative part of the linear combination

$$\big(P_\varepsilon(t) + \beta\mu(t)J_\varepsilon(t)\big)_- \le \big(P_\varepsilon(0) + \beta\mu(0)J_\varepsilon(0)\big)_- e^{\frac{-K_Q\mu_m}{\varepsilon}t} + \varepsilon C(1 - e^{\frac{-K_Q\mu_m}{\varepsilon}t}). \tag{1.22}$$

Proof. Our goal is to choose a function $\mu_\varepsilon(t)$ which solves the differential equation

$$\varepsilon\beta\dot{\mu_\varepsilon} = -\beta|Q_\rho|\mu_\varepsilon^2 + \mu_\varepsilon|Q_S| - \alpha_\varepsilon. \tag{1.23}$$

We use the same argument as in [97]. Therefore we concentrate on the main ideas.
Note that, because the solution might blow up to $-\infty$ in finite time, we need to prove that solutions of (1.23) remain strictly positive for all times. To do so, we first notice that the zeroes of $-\beta|Q_\rho|\mu_\varepsilon^2 + \mu_\varepsilon|Q_S| - \alpha_\varepsilon$ are

$$\mu_{\varepsilon,\pm}(t) := \frac{1}{2\beta|Q_\rho|}\big(|Q_S| \pm \sqrt{Q_S^2 - 4\alpha_\varepsilon\beta|Q_\rho|}\big)$$

and from the smallness condition (1.8), both zeros are positive.
We need to find two constants $0 < \mu_m < \mu_M$ such that, choosing initially $\mu_m < \mu_\varepsilon(0) < \mu_M$, then we have for all times

$$0 < \mu_m \leq \mu_\varepsilon(t) \leq \mu_M. \tag{1.24}$$

This condition is satisfied with the following constants

$$\mu_M := \frac{1}{\beta} \max_{\substack{\rho_m \leq \rho \leq \rho_M, \\ S_m \leq S \leq S_0}} \frac{|Q_S|}{|Q_\rho|}, \tag{1.25}$$

and μ_m defined as

$$\max_t \mu_{\varepsilon,-}(t) \leq \mu_m := \min_t \mu_{\varepsilon,+}(t), \tag{1.26}$$

which defines a positive constant because of the smallness condition for β (1.8).

Coming back to equation (1.19), we arrive to

$$\varepsilon\frac{d}{dt}(P_\varepsilon + \beta\mu J_\varepsilon) \geq -\mu\,|Q_\rho|\,(P_\varepsilon + \beta\mu J_\varepsilon) + \varepsilon\int n_\varepsilon\Delta R dx \geq -\mu|Q_\rho|(P_\varepsilon + \beta\mu J_\varepsilon) - \varepsilon C,$$

and we conclude that, for all $t \geq 0$,

$$\big(P_\varepsilon(t) + \beta\mu(t)J_\varepsilon(t)\big)_- \leq \big(P_\varepsilon(0) + \beta\mu(0)J_\varepsilon(0)\big)_- e^{\frac{-K_Q\mu_m}{\varepsilon}t} + \varepsilon C(1 - e^{\frac{-K_Q\mu_m}{\varepsilon}t}),$$

which concludes the proof of the Lemma 1.4. □

From the estimate of the Lemma 1.4, we can deduce the local BV bounds uniform in ε. We start with P_ε. Adding $\alpha_\varepsilon\frac{P_\varepsilon}{\beta\mu_\varepsilon}$ to (1.17) and using (1.6) and Lemma 1.2, we find

$$\varepsilon\frac{d}{dt}P_\varepsilon + \alpha_\varepsilon\frac{P_\varepsilon}{\beta\mu_\varepsilon} = \alpha_\varepsilon\left(J_\varepsilon + \frac{P_\varepsilon}{\beta\mu_\varepsilon}\right) + \varepsilon\int n_\varepsilon\Delta R dx + \frac{1}{\varepsilon}\gamma_\varepsilon \geq -\alpha_\varepsilon\left(J_\varepsilon + \frac{P_\varepsilon}{\beta\mu_\varepsilon}\right)_- - C\varepsilon.$$

Notice that $0 < \underline{K}_1\rho_\varepsilon(t) \leq \alpha_\varepsilon(t) \leq \bar{K}_1\rho_M$. By considering the negative parts of P_ε and using (1.5) and (1.22), we arrive to the inequality

$$\begin{aligned}\varepsilon\frac{d}{dt}\left(P_\varepsilon\right)_- + \alpha_\varepsilon\frac{(P_\varepsilon)_-}{\beta\mu_\varepsilon} &\leq \alpha_\varepsilon\left(J_\varepsilon + \frac{P_\varepsilon}{\beta\mu_\varepsilon}\right)_- + C\varepsilon \\ &\leq \alpha_\varepsilon\left(P_\varepsilon(0) + \beta\mu_\varepsilon(0)J_\varepsilon(0)\right)_- \frac{e^{\frac{-\mu_m K_Q}{\varepsilon}t}}{\beta\mu_m} + \varepsilon\alpha_\varepsilon C(1 - e^{\frac{-\mu_m K_Q}{\varepsilon}t}) + C\varepsilon \\ &\leq \bar{K}_1\rho_M\left(P_\varepsilon(0) + \beta\mu_\varepsilon(0)J_\varepsilon(0)\right)_- \frac{e^{\frac{-\mu_m K_Q}{\varepsilon}t}}{\beta\mu_m} + C\varepsilon. \quad (1.27)\end{aligned}$$

With this inequality, the BV bounds follow. Since $\varepsilon P_\varepsilon$ is bounded, by integrating the inequality above, we have

$$\int_0^T \alpha_\varepsilon(t)\left(P_\varepsilon(t)\right)_- dt \leq C_1(T) + \varepsilon C_2(T), \qquad \forall T \geq 0.$$

Consequently, we obtain

$$\underline{K}_1\int_0^T \rho_\varepsilon\left(\frac{d}{dt}\rho_\varepsilon\right)_- dx = \frac{\underline{K}_1}{2}\int_0^T\left(\frac{d}{dt}\rho_\varepsilon^2\right)_- dt \leq C_1(T) + \varepsilon C_2(T), \qquad \forall T \geq 0.$$

Since $\rho_\varepsilon(t)$ is bounded, we have finally that ρ_ε^2 has local bounded variations. Therefore up to an extraction, there exists a function $\bar{\rho}$ on $(0,\infty)$ satisfying

$$\rho_\varepsilon \longrightarrow \bar{\rho} \qquad \text{in } L^1_{loc}(0,\infty).$$

Since we have the lower bound $\rho_\varepsilon \geq \rho_m$ by Lemma 1.2, we obtain the bound for the negative part of the derivative of ρ_ε:

$$\int_0^T (\frac{d}{dt}\rho_\varepsilon)_- dx \leq \frac{C_1 + C_2\varepsilon}{\underline{K}_1\rho_m}.$$

Finally, it remains to study S_ε. To do so, we rewrite (1.18) as

$$\varepsilon\beta\frac{d}{dt}J_\varepsilon = Q_S J_\varepsilon + Q_\rho P_\varepsilon = Q_S J_\varepsilon + Q_\rho\frac{(\dot{\rho_\varepsilon^2})}{2\rho_\varepsilon}. \quad (1.28)$$

With our assumptions (1.4) on the Lipschitz function Q, we have

$$\varepsilon\beta\frac{d}{dt}(-J_\varepsilon) = Q_S(-J_\varepsilon) - Q_\rho\frac{(\dot{\rho_\varepsilon^2})}{2\rho} \leq Q_S(-J_\varepsilon) + L_Q\frac{|(\dot{\rho_\varepsilon^2})|}{2\rho_m}, \quad (1.29)$$

and

$$\varepsilon\beta\frac{d}{dt}(J_\varepsilon)_- \leq -K_Q(J_\varepsilon)_- + L_Q\frac{|(\dot{\rho_\varepsilon^2})|}{2\rho_m}. \quad (1.30)$$

The term $\varepsilon J_\varepsilon$ is bounded because of our assumptions on Q. Then, integrating this equation, we have, for $T > 0$,

$$\int_0^T (J_\varepsilon)_- \leq C + \frac{L_Q}{2\rho_m K_Q}\int_0^T |(\dot{\rho_\varepsilon^2})|, \quad (1.31)$$

and we deduce that $\int_0^T (J_\varepsilon)_-$ is uniformly bounded from our previous result on ρ_ε^2.

Then, since S_ε is uniformly bounded, we conclude that there exists a function $\bar{S}$ such that, after extraction of a subsequence,

$$S_\varepsilon \longrightarrow \bar{S} \qquad \text{in } L^1_{loc}(0,\infty) \qquad \text{and} \qquad Q(S_\varepsilon,\rho_\varepsilon) \underset{\varepsilon\to 0}{\longrightarrow} Q(\bar{S},\bar{\rho}) \quad \text{a.e.}$$

To conclude, it follows that $\varepsilon\frac{d}{dt}S_\varepsilon$ converges in measure to 0 as ε vanishes and thus, $Q(\bar{S},\bar{\rho}) = 0$.

1.4 Concentration and constrained Hamilton-Jacobi equation

In order to prove the concentration of n_ε in a sum of Dirac masses as ε vanishes, we perform the change of unknown $n_\varepsilon(t,x) = e^{u_\varepsilon(t,x)/\varepsilon}$ and we study the regularity properties of $u_\varepsilon(t,x)$. With the definition of u_ε, we obtain the following equation which is equivalent to (1.1):

$$\begin{cases} \partial_t u_\varepsilon(t,x) = |\nabla u_\varepsilon|^2 + R(x,S_\varepsilon(t)) + \varepsilon\Delta u_\varepsilon, \\ \\ u_\varepsilon(t=0,x) = u^0_\varepsilon(x) := \varepsilon \ln n^0_\varepsilon. \end{cases} \tag{1.32}$$

We complete assumption (1.7) on the initial data with

$$u^0_\varepsilon(x) \le A - K_2\sqrt{1+|x|^2}, \qquad ||\nabla u^0_\varepsilon|| \le B, \qquad \forall x \in \mathbb{R}^d, \tag{1.33}$$

with $A, B > 0$.

We prove in this section the following result

Theorem 1.5. *Under the assumptions* (1.4)-(1.8) *and* (1.33)*, then after extraction of a subsequence,* $(u_\varepsilon)_\varepsilon$ *converges locally uniformly to a Lipschitz continuous viscosity solution* u *to the constrained Hamilton-Jacobi equation*

$$\begin{cases} \partial_t u(t,x) = |\nabla u|^2 + R(x,\bar{S}(t)), \\ \\ \max\limits_{x\in\mathbb{R}^d} u(t,x) = 0, \qquad \forall t \ge 0. \end{cases} \tag{1.34}$$

In the simple case when dimension d is equal to 1 and when $R(x,S)$ is monotonic in x for all S, n concentrates in one single point.

We first prove that u_ε is equi-bounded, then the equi-continuity, and finally we explain how to pass to the limit in (1.32).

1.4.1 Local bounds and equi-continuity in space

We first set the upper bound for u_ε. Let $T > 0$ be given. Defining $\bar{u}(t,x) = A + Ct - K_2\sqrt{1+|x|^2}$ with $C = K_2(1+K_2)$, we have

$$\partial_t\bar{u} - \varepsilon\Delta\bar{u} - |\nabla\bar{u}|^2 - R(x,S_\varepsilon(t)) \ge C + \varepsilon K_2\frac{d-1}{\sqrt{1+|x|^2}} - K_2^2 - K_2 \ge 0.$$

Since $\bar{u}(0,x) \geq u_\varepsilon^0(x)$ from initial data (1.33), we conclude that $\bar{u}$ is a super-solution and $u_\varepsilon(t,x) \leq A + CT - K_2\sqrt{1+|x|^2}$, for all $t \in [0,T]$.

Next we prove that u_ε is uniformly Lipschitz continuous in space on $[0,T] \times \mathbb{R}^d$. We define for h small $w_\varepsilon(t,x) = u_\varepsilon(t,x+h) - u_\varepsilon(t,x)$. Since the initial condition u_ε^0 are uniformly continuous, given $\delta > 0$, for h small enough, we have $|w_\varepsilon(0,x)| < \frac{\delta}{2}$. From (1.32), we arrive to

$$\partial_t w_\varepsilon(t,x) - \varepsilon\Delta w_\varepsilon(t,x) - (\nabla u_\varepsilon(t,x+h) + \nabla u_\varepsilon(t,x)) \cdot \nabla w_\varepsilon(t,x) \tag{1.35}$$

$$= R(x+h, S_\varepsilon(t)) - R(x, S_\varepsilon(t)) \leq K_2 h. \tag{1.36}$$

Thus by the maximum principle we deduce that

$$|w_\varepsilon(t,x)| \leq |\max_{\mathbb{R}^d} w_\varepsilon(0,x)| + K_2|h|t \leq (||\nabla u_\varepsilon^0||_{L^\infty(\mathbb{R}^d)} + K_2 t)|h|.$$

We conclude that u_ε is uniformly Lipschitz in space on $[0,T] \times \mathbb{R}^d$ and set

$$L(t) = \sup_{\varepsilon \leq \varepsilon_0, 0 \leq s \leq t, x \in \mathbb{R}^d} ||\nabla u_\varepsilon(s,x)||_{L^\infty}. \tag{1.37}$$

To conclude we show that u_ε is also uniformly bounded from below on compact subsets of $[0,\infty) \times \mathbb{R}^d$. Let $0 < T$ and $r > 0$. For all $t \in [0,T]$ and $x \in B(0,r)$, we recall that $u_\varepsilon(t,x) \leq A + CT - K_2\sqrt{1+|x|^2}$ and thus

$$\int_{|x|>r} e^{\frac{u_\varepsilon}{\varepsilon}} dx < \int_{|x|>r} e^{\frac{A+CT-K_2|x|}{\varepsilon}} < \frac{\rho_m}{2},$$

for $0 < \varepsilon < \varepsilon_0$, ε_0 small enough and r large enough. We also have from Lemma 1.2 that $\rho_\varepsilon \geq \rho_m$, then for $0 < \varepsilon < \varepsilon_0$ and r large enough, we obtain

$$\frac{\rho_m}{2} < \int_{|x|\leq r} e^{\frac{u_\varepsilon}{\varepsilon}} \leq B_r e^{\max_{B_r} \frac{u_\varepsilon}{\varepsilon}}.$$

This implies

$$\max_{B_r} u_\varepsilon \geq \varepsilon \ln \frac{\rho_m}{2|B_r|}.$$

Using the Lipschitz bound (1.37) we obtain

$$u_\varepsilon(t,x) > \varepsilon \ln \frac{\rho_m}{2|B_r|} - 2L(t)r, \qquad \forall x \in B(0,r).$$

Hence we have the local lower bound on u_ε.

1.4.2 The equi-continuity in time

For given T, η and $r > 0$, we fix $(s,x) \in [0,T[\times B(0,\frac{r}{2})$ and define

$$\xi_\varepsilon(t,y) = u_\varepsilon(s,x) + \eta + E|y-x|^2 + D(t-s), \qquad \text{for } (t,y) \in [s,T] \times B(0,r),$$

where E and D are constants to be determined. We prove in this section the uniform continuity in time. The idea of the proof is to find constants E and D large enough such that, for any $x \in R(0, \frac{r}{2})$, and for all $\varepsilon < \varepsilon_0$

$$u_\varepsilon(t,y) \leq \xi_\varepsilon(t,y) = u_\varepsilon(s,x) + \eta + E|y-x|^2 + D(t-s), \qquad \forall (t,y) \in [0,T] \times B(0,r), \quad (1.38)$$

and

$$u_\varepsilon(t,y) \geq \phi_\varepsilon(t,y) := u_\varepsilon(s,x) - \eta - E|y-x|^2 - D(t-s), \qquad \forall (t,y) \in [0,T] \times B(0,r). \quad (1.39)$$

Then by taking $y = x$, we have the uniform continuity in time on compact subsets of $[0,\infty) \times \mathbb{R}^d$. We prove here inequality (1.38), the proof of (1.39) is analogous.

First we prove that $\xi_\varepsilon(t,y) > u_\varepsilon(t,y)$ on $[s,T] \times \partial B(0,r)$, for all η, D and $x \in B(0, \frac{r}{2})$. Since u_ε are locally uniformly bounded according to Sections 1.4.1 and 1.4.2, by taking E large enough such that

$$E \geq \frac{8||u_\varepsilon||_{L^\infty([0,T]\times B(0,r))}}{r^2},$$

we obtain

$$\begin{aligned} \xi_\varepsilon(t,y) &\geq u_\varepsilon(t,x) + \eta + 2||u_\varepsilon||_{L^\infty([0,T]\times B(0,r))} + D(t-s) && (1.40)\\ &\geq ||u_\varepsilon||_{L^\infty([0,T]\times B(0,r))} && (1.41)\\ &\geq u_\varepsilon(t,y). && (1.42) \end{aligned}$$

Next we prove that, for E large enough, $\xi_\varepsilon(s,y) \geq u_\varepsilon(s,y)$ for all $y \in B(0,r)$. We argue by contradiction. Assume that there exists $\eta > 0$ such that for all constants $E > 0$ there exists $y_E \in B(0,r)$ such that

$$u_\varepsilon(s,y_E) - u_\varepsilon(s,x) > \eta + E|y_E - x|^2.$$

This implies

$$|y_E - x| \leq \sqrt{\frac{2M}{E}},$$

where M is a uniform upper bound for $||u_\varepsilon||_{L^\infty([0,T]\times B(0,r))}$. For $E \to \infty$, we have that $|y_E - x| \to 0$. Since u_ε are uniformly continuous in space, this is a contradiction.

Finally, from assumption (1.6), if D is large enough, ξ_ε is a super-solution to (1.34) in $[s,T] \times B(0,r)$,

$$u_\varepsilon(t,y) \leq u_\varepsilon(s,x) + \eta + E|y-x|^2 + D(t-s), \qquad \forall (t,y) \in [0,T] \times B(0,r).$$

With the proof of (1.39) which is similar, we deduce that the sequence u_ε is uniformly continuous in time on compact subsets of $[0,\infty) \times \mathbb{R}^d$.

1.4.3 Passing to the limit

We proceed as in [14] to prove the convergence of (1.32) to (1.34) as ε goes to 0. Considering the regularity results above, the point at this step is to pass to the limit in the term $R(x, S_\varepsilon)$. To avoid the complications of the discontinuity, we define

$$\phi_\varepsilon(t,x) := u_\varepsilon(t,x) - \int_0^t R(x, S_\varepsilon(s))ds,$$

and it follows that ϕ_ε satisfies the equation:

$$\partial_t \phi_\varepsilon(t,x) - \varepsilon\Delta\phi_\varepsilon(t,x) - |\nabla\phi_\varepsilon(t,x)|^2 - 2\nabla\phi_\varepsilon(t,x).\int_0^t \nabla R(x, S_\varepsilon(s))ds \tag{1.43}$$

$$= \varepsilon\int_0^t \Delta R(x, S_\varepsilon(s))ds + |\int_0^t \nabla R(x, S_\varepsilon(s))ds|^2. \tag{1.44}$$

As $S_\varepsilon(t)$ converges to $\bar{S}(t)$ for all $t \geq 0$ and $R(x, I)$ is a Lipschitz continuous function, we have

$$\lim_{\varepsilon\to 0}\int_0^t R(x, S_\varepsilon(s))ds = \int_0^t R(x, \bar{S}(s))ds,$$

$$\lim_{\varepsilon\to 0}\int_0^t \nabla R(x, S_\varepsilon(s))ds = \int_0^t \nabla R(x, \bar{S}(s))ds,$$

$$\lim_{\varepsilon\to 0}\int_0^t \Delta R(x, S_\varepsilon(s))ds = \int_0^t \Delta R(x, \bar{S}(s))ds,$$

for all $t \geq 0$. Furthermore the limit functions $\int_0^t R(x, \bar{S}(s))ds, \int_0^t \nabla R(x, \bar{S}(s))ds$ and $\int_0^t \Delta R(x, \bar{S}(s))ds$ are locally uniformly continuous.

After extraction of a subsequence by the Arzela-Ascoli Theorem, $u_\varepsilon(t,x)$ converges locally uniformly to the continuous function $u(t,x)$ as ε vanishes. Consequently $\phi_\varepsilon(t,x)$ converges locally uniformly to the continuous function $\phi(t,x) = u(t,x) - \int_0^t R(x, \bar{S}(s))ds$ and ϕ is a viscosity solution to the equation

$$\partial_t\phi(t,x) - |\nabla\phi(t,x)|^2 - 2\nabla\phi(t,x).\int_0^t \nabla R(x, \bar{S}(s))ds = |\int_0^t \nabla R(x, \bar{S}(s))ds|^2. \tag{1.45}$$

Then u is a solution to the following equation in the viscosity sense

$$\partial_t u(t,x) = |\nabla u|^2 + R(x, \bar{S}(t)).$$

It remains to prove that $\max_{x\in\mathbb{R}^d} u(t,x) = 0$ for all $t \geq 0$. We argue by contradiction. Assume that there exists $a > 0$ such that for some $t > 0$ and $x \in \mathbb{R}^d$ we have $0 < a \leq u(t,x)$. It follows that, from the continuity of u, $u(t,y) \geq \frac{a}{2}$ on $B(x,r)$ for some $r > 0$, and then $n_\varepsilon(t,y) \to \infty$ as ε goes to 0, which is a contradiction to the statements of Lemma 1.2. Thus we have $\max_{x\in\mathbb{R}^d} u(t,x) \leq 0$ for all $t \geq 0$.

From Subsection 1.4.1, we have for $0 < \varepsilon < \varepsilon_0$ and for some $r > 0$ large enough

$$\lim_{\varepsilon\to 0}\int_{|x|\leq r} n_\varepsilon(t,x)dx > \frac{\rho_m}{2}, \qquad t \geq 0. \tag{1.46}$$

Furthermore, recall that we have

$$u_\varepsilon(t,x) \leq A + Ct - K_2\sqrt{1+|x|^2} \leq A + Ct - K_2|x|, \qquad \forall t \geq 0, x \in \mathbb{R}^d.$$

Then it follows that, for r large enough

$$\lim_{\varepsilon\to 0} \int_{|x|\geq r} n_\varepsilon(t,x)dx \leq \lim_{\varepsilon\to 0} \int_{|x|\geq r} e^{\frac{A+Ct-K_2|x|}{\varepsilon}} dx = 0.$$

We argue by contradiction again. Assume that $u(t,x) < 0$ for all $t \geq 0$ and $|x| < r$. It implies that $\lim_{\varepsilon\to 0} n_\varepsilon(t,x) = 0$ and thus $\lim_{\varepsilon\to 0} \int_{|x|<r} n_\varepsilon(t,x)dx = 0$. This is a contradiction with (1.46) and it follows that $\max_{x\in\mathbb{R}^d} u(t,x) = 0$ for all $t \geq 0$.

It is an open problem to know if the full sequence u_ε converges and it is equivalent to the question of uniqueness of the solution to the Hamilton-Jacobi equation. We will consider in Section 1.5 a special case where uniqueness holds.

In the next section we derive some properties of the concentration points that also hold in the concavity framework (Section 1.6) and will be useful in what follows.

1.4.4 Properties of the concentration points

We prove in the rest of this section the following theorem

Theorem 1.6. *Let assumption* (1.6) *hold. For any* $u^0 \in W^{1,\infty}(\mathbb{R}^d)$*, the solution to* (1.34) *is semi-convex in* x *for any* $t > 0$*, i.e. there exists a* $C(t)$ *such that, for any unit vector* $\xi \in \mathbb{R}^d$*, we have the following inequality*

$$\frac{\partial^2}{\partial \xi^2} u \geq -C(t).$$

Consequently, $u(t,\cdot)$ *is differentiable in* x *at maximum points and we have*

$$\nabla u(t, \bar{x}(t)) = 0$$

where $\bar{x}(t)$ *is a maximum point of* $u(t,\cdot)$*.*
Furthermore, for all Lebesgue points of $\bar{S}$ *we have*

$$R(\bar{x}(t), \bar{S}(t)) = 0.$$

First step: the semi-convexity. To increase readability we use the notation $u_\xi := \frac{\partial u_\varepsilon}{\partial \xi}, u_{\xi\xi} := \frac{\partial^2 u_\varepsilon}{\partial \xi^2}$ for a unit vector ξ. We obtain from equation (1.32)

$$\frac{\partial}{\partial t} u_\xi = 2\nabla u_\varepsilon \cdot \nabla u_\xi + R_\xi(x, S_\varepsilon(t)) + \varepsilon \Delta u_\xi, \tag{1.47}$$

and

$$\frac{\partial}{\partial t} u_{\xi\xi} = 2\nabla u_\varepsilon \cdot \nabla u_{\xi\xi} + 2|\nabla u_\xi|^2 + R_{\xi\xi}(x, S_\varepsilon(t)) + \varepsilon \Delta u_{\xi\xi}. \tag{1.48}$$

Notice that $|\nabla u_\xi| \geq |u_{\xi\xi}|$ because $u_{\xi\xi} = \nabla u_\xi \cdot \xi$. Therefore the function $w := u_{\xi\xi}$ satisfies

$$\frac{\partial}{\partial t} w \geq 2\nabla u_\varepsilon \cdot \nabla w + 2w^2 - K_2 + \varepsilon \Delta w,$$

from the assumption (1.6). The semi-convexity follows from the comparison principle with the subsolution given by the solution to the ODE $\dot{y} = 2y^2 - K_2, y(0) = -\infty$.

Second step: $\nabla u(t, \bar{x}(t)) = 0$. The semi-convexity implies that u is differentiable at its maximum points. Therefore we have for $t > 0$

$$\nabla u(t, \bar{x}(t)) = 0.$$

Moreover, we also have the property that, for any sequence (t_k, x_k) of x- differentiability point of u which converges to $(t, \bar{x}(t))$, we have

$$\nabla u(t_k, x_k) \to 0 \qquad as \qquad k \to \infty.$$

In fact, we deduce that, for $h, r > 0, h, r \to 0$

$$\frac{1}{rh} \int_t^{t+h} \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} |\nabla u(s, y)|^2 dsdy \to 0,$$

and

$$\frac{1}{rh} \int_{t-h}^{t} \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} |\nabla u(s, y)|^2 dsdy \to 0.$$

We obtain these convergence results by applying Lebesgue's dominated convergence Theorem to the integral

$$\int_0^1 \int_{-1}^1 |\nabla u(t + h\tau, x(t) + r\sigma)|^2 d\tau d\sigma$$

given by a change of variable, combined with the local Lipschitz continuity of u.

Third Step: Proof of $R(\bar{x}(t), \bar{S}(t)) = 0$. We first integrate the equation on rectangles $(t, t + h) \times (\bar{x}(t) - r, \bar{x}(t) + r)$. We obtain

$$\int_{\bar{x}(t)-r}^{\bar{x}(t)+r} [u(t + h, y) - u(t, y)]dy$$
$$= \int_t^{t+h} \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} R(y, \bar{S}(s))dsdy + \int_t^{t+h} \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} |\nabla u(s, y)|^2 dsdy.$$

By the semi-convexity, we have

$$0 \geq u(t, y) \geq u(t, \bar{x}(t)) - C(t)|y - \bar{x}(t)|^2 = O(r^2),$$

and also $u(t + h, y) \leq 0$. We deduce

$$\frac{1}{rh} \int_t^{t+h} \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} R(y, \bar{S}(s))dsdy + \frac{1}{rh} \int_t^{t+h} \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} |\nabla u(s, y)|^2 dsdy \leq \frac{1}{rh} O(r^2).$$

Therefore we obtain

$$\frac{1}{rh} \int_t^{t+h} \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} R(y, \bar{S}(s))dsdy \leq \frac{1}{rh} O(r^2).$$

We conclude that at any Lebesgue point of $\bar{S}$ we have

$$R(\bar{x}(t), \bar{S}(t)) \leq 0.$$

Next, we prove the opposite inequality. By integrating on the rectangle $(t-h, t) \times (\bar{x}(t) - r, \bar{x}(t) + r)$.

$$\int_{\bar{x}(t)-r}^{\bar{x}(t)+r} (u(t,y) - u(t-h,y))dy \geq \int_{\bar{x}(t)-r}^{\bar{x}(t)+r} u(t,y)dy,$$

and

$$\frac{1}{rh}\int_{t-h}^{t}\int_{\bar{x}(t)-r}^{\bar{x}(t)+r} R(y, \bar{S}(s))dsdy + \frac{1}{rh}\int_{t-h}^{t}\int_{\bar{x}(t)-r}^{\bar{x}(t)+r} |\nabla u(s,y)|^2 dsdy \geq \frac{O(r)}{h}.$$

Hence, we have that, at any Lebesgue point of $\bar{S}$,

$$R(\bar{x}(t), \bar{S}(t)) \geq 0.$$

Hence the statement of Theorem 1.6.

1.5 The monomorphic case in dimension $d = 1$

In the case when dimension d equals 1 and $R(x, S)$ is monotonic in x for each S, we have the expected convergence toward a single Dirac mass under the additional assumption (which holds for instance when R is monotonic in x)

$$\forall S_m < S < S_0, \text{ there is a unique } X(S) \in \mathbb{R} \text{ such that } R(X(S), S) = 0. \tag{1.49}$$

Theorem 1.7. *Assume* (1.4)-(1.8)*, that* u_ε^0 *are uniformly continuous in* $\mathbb{R}^d$ *and* (1.49)*. Then, the solution* n_ε *to* (1.1)*, still after extraction of a subsequence, converges in the weak sense of measures*

$$n_{\varepsilon_k}(t,x) \longrightarrow n(t,x) := \bar{\rho}(t)\delta(x - \bar{x}(t)), \tag{1.50}$$

and we also obtain the relations

$$\bar{x}(t) = X\big(\overline{S}(t)\big), \qquad R\big(\bar{x}(t), \overline{S}(t)\big) = 0 \qquad a.e.$$

Moreover, the full sequence n_ε *converges when* R *has one of the following form, for some functions* $b > 0, d > 0, F > 0$*,*

$$R(x,S) = b(x) - d(x)F(S) \qquad \textit{with } F'(S) < 0, \tag{1.51}$$

or

$$R(x,S) = b(x)F(S) - d(x) \qquad \textit{with } F'(S) > 0. \tag{1.52}$$

We do not prove this result in detail. It is a consequence of the following observation. As the measure n defined in (1.50) satisfies the condition *supp* $n(t,\cdot) \subset \{u(t,\cdot)\}$ from the properties obtained in the previous section (see details in [14, 128]), n is monomorphic. Indeed, from the condition (1.49) the set $\{u(t,\cdot)\}$ is reduced to an isolated point for all

$t \geq 0$. The uniqueness of the solution when R is written as (1.51) or (1.52) is entirely explained in [128]. The idea of the proof is to consider for instance the function

$$\phi(t,x) = u(t,x) - b(x)\int_0^t F(S(\sigma))d\sigma,$$

and, by noticing that ϕ satisfies the equation

$$\partial_t\phi(t,x) = -d(x) + |\nabla(\phi(t,x) + b(x))\int_0^t F(S(\sigma))d\sigma|,$$

to derive an estimate on the derivative of the difference between two different solutions ϕ_1 and ϕ_2 with the same initial data. By considering the different quantities at the maximum points of $u(t,\cdot)$, we see that there exists a constant $C > 0$ such that

$$\frac{d}{dt}||\phi_1 - \phi_2||_\infty \leq C||\phi_1 - \phi_2||_\infty,$$

and the uniqueness follows.

1.6 The concavity framework in $\mathbb{R}^d$

In this section we are going to assume more regularity in order to prove the convergence of n_ε to a Dirac mass in the sense of measure. The specific feature of this framework is that uniform concavity of the growth rate and initial data induce uniform concavity of the solutions u_ε to the Hamilton-Jacobi equations, which implies that u_ε has only one maximum point. The main technical difficulty is that uniform bounds are not possible because of the quadratic growth at infinity. Therefore, following the work [96], we start with assumptions on $R \in C^2$:

$$\max_{x\in\mathbb{R}^d} R(x,S_m) = 0 = R(0,S_m), \tag{1.53}$$

$$-\underline{K}_2|x|^2 \leq R(x,S) \leq \overline{K}_0 - \overline{K}_2|x|^2, \tag{1.54}$$

$$0 < \underline{K}_1 \leq R_S(x,S) \leq \overline{K}_1, \tag{1.55}$$

$$-2\underline{K}_2 \leq D^2R(x,S) \leq -2\overline{K}_2. \tag{1.56}$$

We also need the uniform concavity of the initial data

$$n_\varepsilon^0 = e^{\frac{u_\varepsilon^0}{\varepsilon}}, \tag{1.57}$$

$$-\underline{L}_0 - \underline{L}_1|x|^2 \leq u_\varepsilon^0 \leq \overline{L}_0 - \overline{L}_1|x|^2, \tag{1.58}$$

$$-2\underline{L}_1 \leq D^2u_\varepsilon^0 \leq -2\overline{L}_1, \tag{1.59}$$

and we add some compatibility conditions

$$4\overline{L}_1^2 \leq \overline{K}_2 \leq \underline{K}_2 \leq 4\underline{L}_1^2. \tag{1.60}$$

For this section, we will need

$$D^3R(\cdot,S) \in L^\infty(\mathbb{R}^d), \tag{1.61}$$

$$D^3 u_\varepsilon^0 \in L^\infty(\mathbb{R}^d) \qquad \text{uniformly in } \varepsilon, \tag{1.62}$$

$$n_\varepsilon^0(x) \longrightarrow \bar{\rho}^0 \delta(x - \bar{x}^0) \qquad \text{weakly in the sense of measures.} \tag{1.63}$$

We keep the same assumptions on Q and S_ε as in the previous section. Next we are going to prove the following result:

Theorem 1.8. *Under assumptions* (1.54)-(1.60) *and the assumptions on Q, ρ_ε and S_ε have locally bounded total variations uniformly in ε. Therefore there exist functions $\overline{\rho}$ and $\overline{S}$ such that, after extraction of a subsequence, we have*

$$S_{\varepsilon_k}(t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{S}(t) \qquad \textit{and} \qquad \rho_{\varepsilon_k}(t) \underset{\varepsilon_k \to 0}{\longrightarrow} \bar{\rho}(t), \qquad \textit{a.e.}$$

Furthermore we have weakly in the sense of measures for a subsequence n_ε

$$n_\varepsilon(t,x) \underset{\varepsilon \to 0}{\longrightarrow} \overline{\rho}(t)\delta(x - \overline{x}(t)), \tag{1.64}$$

and the pair $(\bar{x}(t), \overline{S}(t))$ also satisfies

$$R(\bar{x}(t), \overline{S}(t)) = 0, \qquad \textit{a.e.} \tag{1.65}$$

As a first step, we will give estimates on u_ε. Next, we will adapt the proof of Section 1.3 to give BV estimates on ρ_ε and S_ε and then pass to the limit as ε goes to 0. Finally we prove the following theorems:

Theorem 1.9. *Assuming* (1.53)-(1.63), *$\bar{x}(t)$ is a $W^{1,\infty}(\mathbb{R}_+, \mathbb{R}^d)$-function and its dynamics is described by the equation*

$$\dot{\bar{x}}(t) = (-D^2 u(t, \bar{x}(t)))^{-1} \cdot \nabla_x R(\bar{x}(t), \bar{S}(t)), \qquad \bar{x}(0) = \overline{x}^0 \tag{1.66}$$

with $u(t,x)$ given below in (1.83) *and $\overline{x}^0$ in* (1.63). *Furthermore, $\bar{S}(t)$ is a $W^{1,\infty}(\mathbb{R}_+)$-function. From this equation, it follows that $\bar{S}(t)$ is a decreasing function and*

$$\bar{S}(t) \underset{t \to \infty}{\longrightarrow} S_m, \qquad \bar{x}(t) \underset{t \to \infty}{\longrightarrow} 0. \tag{1.67}$$

1.6.1 Uniform concavity of u_ε

Again we use the Hopf-Cole transformation defining $u_\varepsilon = \varepsilon \ln n_\varepsilon$ and we obtain the same equation as in Section 4

$$\begin{cases} \partial_t u_\varepsilon(t,x) = |\nabla u_\varepsilon|^2 + R(x, S_\varepsilon(t)) + \varepsilon \Delta u_\varepsilon, \\ \\ u_\varepsilon(t=0,x) = u_\varepsilon^0(x) := \varepsilon \ln n_\varepsilon^0. \end{cases} \tag{1.68}$$

We focus now on the study of the properties of the sequence u_ε.

We first prove the following lemma

Lemma 1.10. *Under assumptions* (1.54) *and* (1.60), *we have for $t \geq 0$ and for $x \in \mathbb{R}^d$*

$$-\underline{L}_0 - \underline{L}_1 |x|^2 - \varepsilon(2d\underline{L}_1)t \leq u_\varepsilon(t,x) \leq \overline{L}_0 - \overline{L}_1 |x|^2 + (\overline{K}_0 + 2d\varepsilon \overline{L}_1)t. \tag{1.69}$$

Proof. First we achieve an upper bound for u_ε. By defining $\overline{u}_\varepsilon(t,x) := \overline{L}_0 - \overline{L}_1|x|^2 + C_0(\varepsilon)t$ with $C_0(\varepsilon) := \overline{K}_0 + 2d\varepsilon\overline{L}_1$, we obtain from assumptions (1.54), (1.58) and (1.60) that $\overline{u}_\varepsilon(t=0) \geq u_\varepsilon^0$ and

$$\partial_t \overline{u}_\varepsilon - |\nabla \overline{u}_\varepsilon|^2 - R(x, I_\varepsilon) - \varepsilon\Delta\overline{u}_\varepsilon \geq C_0(\varepsilon) - 4\overline{L}_1^2|x|^2 - \overline{K}_0 + \overline{K}_2|x|^2 - 2d\varepsilon\overline{L}_1 \geq 0.$$

Then by a comparison principle, we conclude that $u_\varepsilon(t,x) \leq \overline{L}_0 - \overline{L}_1|x|^2 + (\overline{K}_0 + 2d\varepsilon\overline{L}_1)t$ for all $t \geq 0$ and $x \in \mathbb{R}^d$.

Next for the lower bound, we define $\underline{u}_\varepsilon(t,x) := -\underline{L}_0 - \underline{L}_1|x|^2 - \varepsilon C_1 t$ with $C_1 := 2d\underline{L}_1$. Thus we have $\underline{u}_\varepsilon(t=0) \leq u_\varepsilon^0$ and

$$\partial_t \underline{u}_\varepsilon - |\nabla \underline{u}_\varepsilon|^2 - R(x, I_\varepsilon) - \varepsilon\Delta\underline{u}_\varepsilon \leq -\varepsilon C_1 - 4\underline{L}_1^2|x|^2 + \underline{K}_2|x|^2 + \varepsilon 2d\underline{L}_1 \leq 0.$$

Consequently, we obtain that $u_\varepsilon(t,x) \geq -\underline{L}_0 - \underline{L}_1|x|^2 - \varepsilon(2d\underline{L}_1)t$ for all $t \geq 0$ and $x \in \mathbb{R}^d$. Hence the estimates on u_ε. □

The next point is to show that the semi-convexity and the concavity of the initial data are preserved by equation (1.1). In other words, we are going to show the following lemma

Lemma 1.11. *Under assumptions* (1.54)-(1.60)*, we have for* $t \geq 0$ *and* $x \in \mathbb{R}^d$

$$-2\underline{L}_1 \leq D^2 u_\varepsilon(t,x) \leq -2\overline{L}_1. \tag{1.70}$$

Proof. For a unit vector ξ, we use the notation $u_\xi := \nabla_\xi u_\varepsilon$ and $u_{\xi\xi} := \nabla^2_{\xi\xi} u_\varepsilon$ to obtain

$$\begin{aligned} u_{\xi t} &= R_\xi(x, I) + 2\nabla u \cdot \nabla u_\xi + \varepsilon\Delta u_\xi, \\ u_{\xi\xi t} &= R_{\xi\xi}(x, I) + 2\nabla u_\xi \cdot \nabla u_\xi + 2\nabla u \cdot \nabla u_{\xi\xi} + \varepsilon\Delta u_{\xi\xi}. \end{aligned}$$

By using $|\nabla u_\xi| \geq |u_{\xi\xi}|$ and the definition $\underline{w}(t,x) := \min_\xi u_{\xi\xi}(t,x)$ we arrive at the inequality

$$\partial_t \underline{w} \geq -2\underline{K}_2 + 2\underline{w}^2 + 2\nabla u \cdot \nabla \underline{w} + \varepsilon\Delta\underline{w}.$$

And finally by a comparison principle and assumptions (1.59) and (1.60), we obtain

$$\underline{w} \geq -2\underline{L}_1. \tag{1.71}$$

Hence the uniform semi-convexity of u_ε.

To prove the uniform concavity, we first recall that, at every point $(t,x) \in \mathbb{R}^+ \times \mathbb{R}^d$, we can choose an orthonormal basis such that $D^2 u_\varepsilon(t,x)$ is diagonal. Thus we can estimate the mixed second derivatives in terms of $u_{\xi\xi}$ and consequently we have

$$|\nabla u_\xi| = |u_{\xi\xi}|. \tag{1.72}$$

By defining $\overline{w}(t,x) := \max_\xi u_{\xi\xi}(t,x)$ and using assumptions (1.56) and (1.72), we obtain the following inequality

$$\partial_t \overline{w} \leq -2\overline{K}_2 + 2\overline{w}^2 + 2\nabla u \cdot \nabla \overline{w} + \varepsilon\Delta\overline{w}.$$

By a comparison principle and assumption we obtain the estimate

$$\overline{w} \leq -2\overline{L}_1, \tag{1.73}$$

which ends the proof of Lemma 1.11. □

1.6.2 BV estimates on $\rho_\varepsilon^2, S_\varepsilon$ and their limits

We use exactly the same proof as in Section 1.3 to obtain BV estimates on ρ_ε^2 and S_ε. To obtain these estimates, an important point was the bounds on $\varepsilon P_\varepsilon$. We need to confirm that $\varepsilon P_\varepsilon$ is bounded, which was clear in Section 1.3 thanks to the bounds on the growth rate. Here the growth rate has a quadratic decrease at infinity, which does not give an immediate lower bound on $\varepsilon P_\varepsilon$. Furthermore we do not have a lower bound on ρ_ε either because of the same argument and we cannot obtain directly a BV estimate on S_ε as in Section 1.3.2. However we derive a lower bound for $\varepsilon P_\varepsilon$ and we use the uniform concavity of u_ε for that purpose.

By definition of P_ε, it follows from (1.54) and (1.69) that

$$\varepsilon P_\varepsilon = \int_{\mathbb{R}^d} n_\varepsilon R(x, S_\varepsilon(t))dx \geq \int_{\mathbb{R}^d} e^{\frac{1}{\varepsilon}(-\underline{L}_0 - \underline{L}_1|x|^2 - \varepsilon C_1 t)}(-\underline{K}_2|x|^2)dx, \tag{1.74}$$

$$\geq -\underline{K}_2 e^{\frac{1}{\varepsilon}(-\underline{L}_0 - \varepsilon C_1 t)} \int_{\mathbb{R}^d} e^{-\frac{1}{\varepsilon}\underline{L}_1|x|^2}|x|^2 dx, \tag{1.75}$$

$$= -\underline{K}_2 e^{\frac{1}{\varepsilon}(-\underline{L}_0 - \varepsilon C_1 t)} \frac{d\varepsilon}{2\underline{L}_1}\left(\sqrt{\frac{\pi\varepsilon}{\underline{L}_1}}\right)^{d-1}. \tag{1.76}$$

And we have a bound for $(\varepsilon P_\varepsilon)_-$.

We recall inequality (1.27) that also holds true in this framework

$$\varepsilon\frac{d}{dt}(P_\varepsilon)_- + \alpha_\varepsilon\frac{(P_\varepsilon)_-}{\beta\mu_\varepsilon} \leq \bar{K}_1\rho_M\left(P_\varepsilon(0) + \beta\mu_\varepsilon(0)J_\varepsilon(0)\right)_- \frac{e^{\frac{-\mu_m K_Q}{\varepsilon}t}}{\beta\mu_m} + C\varepsilon.$$

Then, we integrate this inequality over $[0,T]$ for $T>0$ and by the same arguments used in Section 1.3.2 it follows that ρ_ε^2 has local BV bounds and therefore there exists a function $\overline{\rho}$ such that after extraction of a subsequence

$$\rho_\varepsilon \longrightarrow \overline{\rho} \qquad \text{in } L^1_{loc}(0,\infty).$$

The next aim is to show that S_ε has local BV bounds. We go back to equation (1.18) and we recall

$$\varepsilon\beta\frac{d}{dt}J_\varepsilon = Q_S J_e + Q_\rho P_\varepsilon.$$

Then we have the following inequality

$$\varepsilon\beta\frac{d}{dt}(-J_\varepsilon) \leq Q_S(-J_\varepsilon) + L_Q|P_\varepsilon| \tag{1.77}$$

and

$$\varepsilon\beta\frac{d}{dt}(J_\varepsilon)_- \leq Q_S(J_\varepsilon)_- + L_Q((P_\varepsilon)_+ + (P_\varepsilon)_-). \tag{1.78}$$

By integrating this inequality over $[0,T]$ for $T>0$, using

$$\int_0^T L_Q|P_\varepsilon| \leq L_Q\left(\int_0^T(\dot{\rho}_\varepsilon)_+ + \int_0^T(P_\varepsilon)_-\right), \tag{1.79}$$

and since ρ_ε is bounded above, we deduce from (1.27) that

$$\int_0^T (J_\varepsilon)_- \leq C_1 T + \underset{\varepsilon\to 0}{o}(1). \tag{1.80}$$

To conclude, we can extract a subsequence from S_ε which locally converges in $L^1_{loc}(0,\infty)$ to a limit function $\overline{S}$.

1.6.3 The limit of the Hamilton-Jacobi equation

From the estimates obtained above on u_ε and $D^2 u_\varepsilon$, we can deduce that ∇u_ε is locally uniformly bounded and thus from (1.32) for $\varepsilon < \varepsilon_0$ that $\partial_t u_\varepsilon$ is also locally uniformly bounded. Therefore there exists a function u such that, after extraction of a subsequence (see [29, 75] for compactness properties), we have for $T > 0$

$$u_\varepsilon(t,x) \underset{\varepsilon\to 0}{\longrightarrow} u(t,x) \text{ strongly in } L^\infty\left(0,T; W^{1,\infty}_{loc}(\mathbb{R}^d)\right),$$

$$u_\varepsilon(t,x) \underset{\varepsilon\to 0}{\longrightarrow} u(t,x) \text{ weakly-* in } L^\infty\left(0,T; W^{2,\infty}_{loc}(\mathbb{R}^d)\right) \cap W^{1,\infty}\left(0,T; L^\infty_{loc}(\mathbb{R}^d)\right),$$

and

$$-\underline{L}_0 - \underline{L}_1|x|^2 \leq u(t,x) \leq \overline{L}_0 - \overline{L}_1|x|^2 + \overline{K}_0 t, \quad -2\underline{L}_1 \leq D^2 u(t,x) \leq -2\overline{L}_1 \quad \text{a.e.} \tag{1.81}$$

$$u \in W^{1,\infty}_{\text{loc}}(\mathbb{R}^+ \times \mathbb{R}^d). \tag{1.82}$$

Then, passing to the limit as $\varepsilon \to 0$ in equation (1.32), we deduce that u satisfies in the viscosity sense the equation

$$\begin{cases} \dfrac{\partial}{\partial t} u = R\big(x, \overline{S}(t)\big) + |\nabla u|^2, \\ \max\limits_{\mathbb{R}^d} u(t,x) = 0. \end{cases} \tag{1.83}$$

In particular u is strictly concave, therefore it has exactly one maximum. This proves n stays monomorphic and characterizes the Dirac location by

$$\max_{\mathbb{R}^d} u(t,x) = 0 = u\big(t, \bar{x}(t)\big). \tag{1.84}$$

This completes the proof of Theorem 1.8.

1.6.4 The canonical equation

In this section, we establish from the regularity properties proved in the previous sections a form of the so-called *canonical equation* in the language of adaptive dynamics (see [47,66]):

$$\dot{\bar{x}}(t) = (-D^2 u(t, \bar{x}(t)))^{-1} \cdot \nabla_x R(\bar{x}(t), \bar{S}(t)).$$

This equation was formally introduced in [68] and holds true in our framework. The point of this differential equation is to describe the long time behaviour of the concentration

point $\bar{x}(t)$.

First step: Bounds on third derivatives of u_ε. For the unit vectors ξ and η, we use the notation $u_\xi := \nabla_\xi u_\varepsilon, u_{\xi\eta} := \nabla^2_{\xi\eta} u_\varepsilon$ and $u_{\xi\xi\eta} := \nabla^3_{\xi\xi\eta} u_\varepsilon$ to derive

$$\partial_t u_{\xi\xi\eta} = 4\nabla u_{\xi\eta} \cdot \nabla u_\xi + 2\nabla u_\eta \cdot \nabla u_{\xi\xi} + 2\nabla u \cdot \nabla u_{\xi\xi\eta} + R_{\xi\xi\eta} + \varepsilon \Delta u_{\xi\xi\eta}.$$

Let us define

$$M_1(t) := \max_{x,\xi,\eta} u_{\xi\xi\eta}(t,x).$$

Again, at every $(t,x) \in \mathbb{R}_+ \times \mathbb{R}^d$, we choose an orthogonal basis such that $D^2(\nabla_\eta u_\varepsilon(t,x))$ is diagonal. And since $-u_{\xi\xi\eta}(t,x) = \nabla_{-\eta} u_{\xi\xi}(t,x)$, we have $M_1(t) = \max_{x,\xi,\eta} |u_{\xi\xi\eta}(t,x)|$. Then we obtain the following inequality

$$\frac{d}{dt} M_1 \leq 4dM_1 ||D^2 u_\varepsilon||_\infty + 2dM_1 ||D^2 u_\varepsilon||_\infty + R_{\xi\xi\eta}.$$

As assumption (1.62) gives a bound on $M_1(t=0)$, by using the Grönwall lemma we obtain a L^∞-bound on the third derivative uniform in ε.

Second step : Maximum point of u_ε We denote the maximum point of $u_\varepsilon(t,\cdot)$ by $\bar{x}_\varepsilon(t)$. Since we have $\nabla u_\varepsilon(t, \bar{x}_\varepsilon(t)) = 0$, we obtain

$$\frac{d}{dt} \nabla u_\varepsilon(t, \bar{x}_\varepsilon(t)) = 0.$$

Then the chain rule gives

$$\frac{\partial}{\partial t} \nabla u_\varepsilon(t, \bar{x}_\varepsilon(t)) + D^2_x u_\varepsilon(t, \bar{x}_\varepsilon(t)) \dot{\bar{x}}_\varepsilon(t) = 0$$

and using equation (1.68), it follows that, for all $t \geq 0$, we have

$$D^2_x u_\varepsilon(t, \bar{x}_\varepsilon(t)) \dot{\bar{x}}_\varepsilon(t) = -\frac{\partial}{\partial t} \nabla u_\varepsilon(t, \bar{x}_\varepsilon(t)) = -\nabla_x R(\bar{x}_\varepsilon(t), S_\varepsilon(t)) - \varepsilon \Delta \nabla_x u_\varepsilon.$$

Thanks to the uniform bound on $D^3 u_\varepsilon$ and the regularity on R, we pass to the limit

$$\dot{\bar{x}}(t) = (-D^2 u(t, \bar{x}(t)))^{-1} \cdot \nabla_x R(\bar{x}(t), \bar{S}(t)) \qquad \text{a.e.}$$

As we have $R(\bar{x}(t), \overline{S}(t)) = 0$ and assumption (1.54), $\bar{x}(t)$ is bounded in $L^\infty(\mathbb{R}_+)$. Then it implies from the canonical equation that $\bar{x}(t)$ is bounded in $W^{1,\infty}(\mathbb{R}_+)$ and $\overline{S}(t)$ is also bounded in $W^{1,\infty}(\mathbb{R}^d)$ since $S \mapsto R(\cdot, S)$ is invertible by the Implicit Function Theorem. We differentiate (1.65) and obtain the following differential equation

$$\dot{\bar{x}}(t) \cdot \nabla_x R + \dot{\overline{S}}(t) \nabla_S R = 0.$$

Third step: Long time behaviour. Using the canonical equation we obtain

$$\frac{d}{dt} R(\bar{x}(t), \overline{S}(t)) = \nabla R(\bar{x}(t), \overline{S}(t)) \frac{d}{dt} \bar{x}(t) + \partial_S R(\bar{x}(t), \overline{S}(t)) \frac{d}{dt} \overline{S}(t)$$

$$= \nabla R(\bar{x}(t), \overline{S}(t))(-D^2u)^{-1}\nabla R(\bar{x}(t), \overline{S}(t)) + \partial_S R(\bar{x}(t), \overline{S}(t))\frac{d}{dt}\overline{S}(t).$$

Since the left hand side equals 0 from (1.65), it follows that

$$\frac{d}{dt}\overline{S}(t) = \frac{-1}{\partial_S R(\bar{x}(t), \overline{S}(t))}\nabla R(\bar{x}(t), \overline{S}(t))(-D^2u)^{-1}\nabla R(\bar{x}(t), \overline{S}(t)) \leq 0.$$

We deduce that $\bar{S}(t)$ decreases. Consequently $\bar{S}(t)$ converges and subsequences of $\bar{x}(t)$ also converge since $\bar{x}(t)$ is bounded. However the possible limits $\bar{x}_\infty$ and $\bar{S}_\infty$ have to satisfy $\nabla R(\bar{x}_\infty, \bar{S}_\infty) = 0$. Then from (1.53), (1.55) and (1.65), we conclude that

$$\bar{S}(t) \underset{t\to\infty}{\longrightarrow} S_m, \qquad \bar{x}(t) \underset{t\to\infty}{\longrightarrow} \bar{x}_\infty = 0,$$

which ends the proof of Theorem 1.9.

1.7 Numerical results

We illustrate in this section the evolution of $n_\varepsilon, \rho_\varepsilon$ and S_ε in time with different values of β. We choose the following initial data

$$n_\varepsilon^0 = C_{mass}\exp(-(x-0.8)^2/\varepsilon), \tag{1.85}$$

and growth rate R and Q as follows

$$R(x,S) = 0.2(-0.6 + 0.3S - (x-0.5)^2), \tag{1.86}$$

$$Q(\rho, S) = 10 - (1.5+\rho)S. \tag{1.87}$$

The numerics have been performed in Matlab with parameters as follows. We consider the solution on interval $[0,1]$. We use a uniform grid with 1000 points on the segment and denote by n_i^k and S^k the numerical solutions at grid point $x_i = i\Delta x$ and at time $t_k = k\Delta t$. We choose as initial value of the nutrient concentration $S_\varepsilon(t=0) = 5$. We also choose β to be $2\cdot 10^3$, the time step $\Delta t = 10^{-4}$ and C_{mass} such as the initial mass of the population in the computational domain is equal to 1. The equation is solved by an implicit-explicit finite-difference method with the following scheme:

$$n_i^{k+1} = n_i^k + \frac{\Delta t}{\varepsilon}((R_i^k)_+ n_i^k + (R_i^k)_- n_i^{k+1}) + \varepsilon\frac{\Delta t}{\Delta x^2}(n_{i+1}^{k+1} - 2n_i^{k+1} + n_{i-1}^{k+1}), \tag{1.88}$$

$$S^{k+1} = S^k + \frac{\Delta t}{\varepsilon\beta}(10 - (1.5+\rho^k)S^{k+1}). \tag{1.89}$$

We use Neumann boundary conditions $n_0^{k+1} = n_1^{k+1}$ and $n_{N-1}^{k+1} = n_N^{k+1}$. We use an implicit-explicit scheme for the growth term in order to maintain the positivity of the numerical solution.

Figure 1.1 shows the dynamics for $\varepsilon = 1\cdot 10^{-3}$ and Figure 1.2 for $\varepsilon = 5\cdot 10^{-4}$. We observe that, since ε is smaller in Figure 1.2, the concentration location of the population moves to the maximum point of fitness more quickly than in Figure 1.1, which illustrates

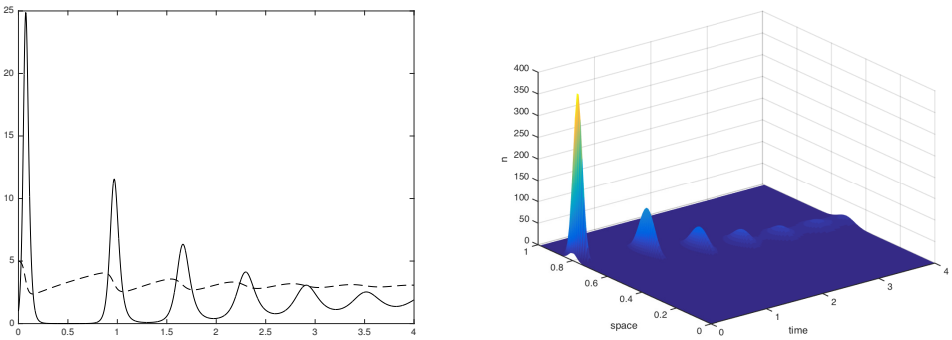

Figure 1.1: Dynamics of ρ_ε (_____) and S_ε $(- - - -)$ (left) and dynamics of the density n_ε for $\beta = 2 \cdot 10^3$ and $\varepsilon = 10^{-3}$.

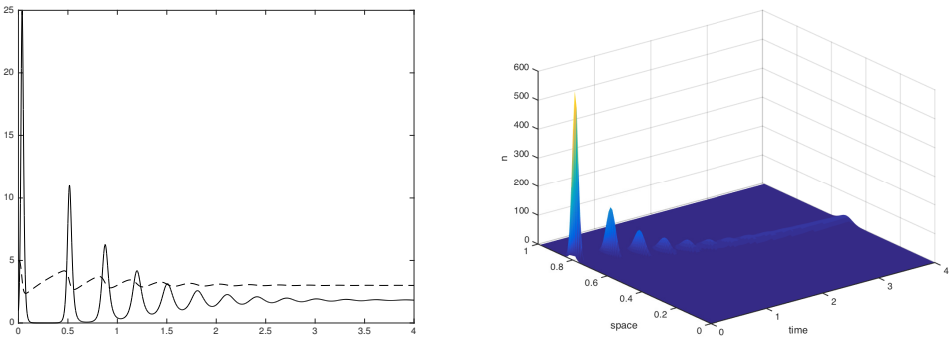

Figure 1.2: Dynamics of ρ_ε (_____) and S_ε $(- - - -)$ (left) and dynamics of the density n_ε for $\beta = 2 \cdot 10^3$ and $\varepsilon = 5 \cdot 10^{-4}$.

the dynamics given by the canonical equation, and then the concentration point and the population density become stable.

In Figure 1.3, we show the numerical results corresponding to the same data as in Figure 1.1, except that we choose $\beta = 2 \cdot 10^2$. We can observe oscillations of ρ_ε and S_ε in the first case ($\beta = 2 \cdot 10^3$), whereas there are very few variations of these quantities when β is smaller. Indeed the parameter β can be considered as a measure of the ecological dynamics: as β goes to 0, we approach the case of the quasi-stationary state of the resource level and we then observe mostly the dynamics of the concentration location. However as explained in the next section, the convergence to the quasi-stationary solutions as β goes to 0 cannot be proved with our approach and remains an open problem.

In Figure 1.4, we show the numerical results for the 2-dimensional model with $\beta = 2 \cdot 10^2$, $\varepsilon = 1 \cdot 10^{-2}$ and $S_\varepsilon(t = 0) = 5$. We choose the time step Δt to be $5 \cdot 10^{-3}$ and Δx to be equal to $1 \cdot 10^{-2}$. We also choose the initial condition

$$n_\varepsilon^0(x, y) = \exp(-\frac{(x - 0.8)^2}{\varepsilon} - \frac{(y - 0.2)^2}{\varepsilon}), \tag{1.90}$$

and the functions

$$R(x, y, S) = 0.2(-0.6 + 0.3S - (1 + (x - 0.3)^2)(1 + (y - 0.6)^2)), \tag{1.91}$$

$$Q(\rho, S) = 10 - (1.5 + \rho)S. \tag{1.92}$$

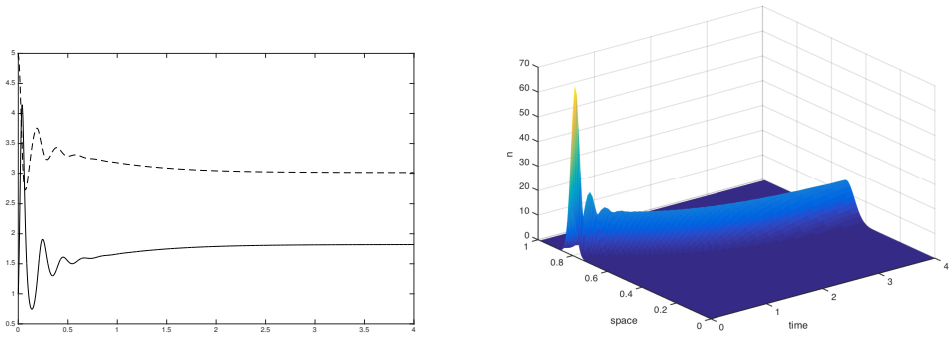

Figure 1.3: Dynamics of ρ_ε (_____) and S_ε $(- - - -)$ (left) and dynamics of the density n_ε for $\beta = 2 \cdot 10^2$ and $\varepsilon = 10^{-3}$

As confirmed by the analysis we conducted, the population density concentrates at the maximum point of the growth rate.

1.8 Discussion

The weak assumptions provide a generic framework to study the asymptotic behaviour of u_ε but do not enable us to derive a canonical equation describing the dynamics of the concentration points and we can observe jump phenomena of the concentration location. Indeed the lack of regularity can produce a discontinuity of $\rho(t)$ and local maxima of $u(t,x)$ can become global maxima and jumps from a given concentration location to an other can occur, which means the extinction of a population quickly invaded by an other growing one (see [128] for further details). The concavity assumptions are suitable to avoid the jump cases because these assumptions preserve regularity and they ensure that the global maximum of u is the only maximum. The canonical equation derived in this framework describes the evolution of the selected trait in an evolutionary time scale.

Many models have been studied to illustrate the diversity of evolutionary problems. For instance the problem of coevolution has been tackled in [128], [51] and [96]. The branching phenomenon where a monomorphic population at some point becomes dimorphic is described in [68,127]. In the chemostat model, the spatial component has been neglected here with the hypothesis that the content of the chemostat is well-mixed, it has been taken into account in [27,115,117].

The inclusion of mutations in structured population models is necessary to generate phenotypic variability in a given population, which is a fundamental ingredient of the selection process. It implies the separation of the ecological time scale and the evolutionary one. In the presented model the mutation term has little phenotypic effects due to the parameter ε. Especially in the canonical equation form we observe that the pressure of mutants on the dynamics of $\bar{x}$ is small and, as ε goes to 0, it does not change the convergence of $\bar{x}_\varepsilon$ to the maximum point of fitness $\bar{x}$. It means that only the mutations with positive effects on the phenotypic trait can influence the dynamics: mutants emerging with a better fitness than the residents can invade, while the other mutants go to extinction.

However some open questions arise from the present study. First it seems that the

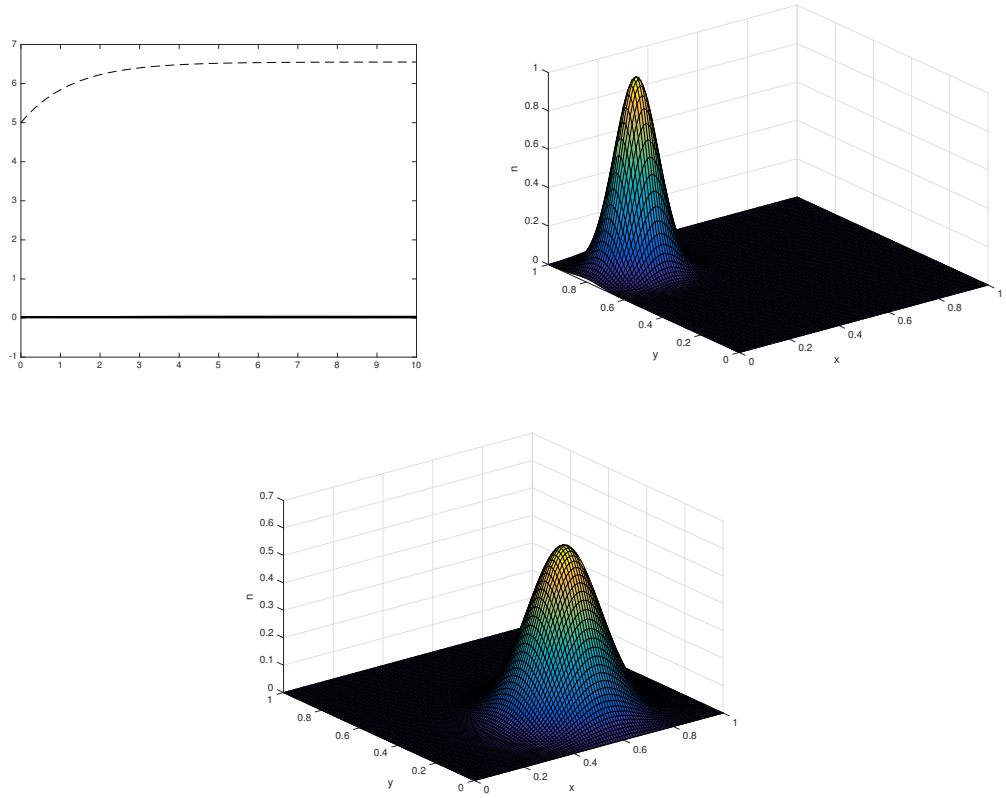

Figure 1.4: Dynamics in dimension 2 of ρ_ε (_____) and S_ε (− − −−) (at top left), the initial condition for n_ε (at top right) and the stationary state n_ε converges to (at bottom), with $\beta = 2 \cdot 10^2$ and $\varepsilon = 10^{-2}$.

method developed in this work does not give TV bounds for the full range $[0, \beta_0]$ for some small β_0 since the estimates providing the uniform BV estimates on ρ^2 in Section 3.2 are local in time and then it is not possible to prove uniform convergence of $S(t)$ as $\beta \to 0$ on $[0, \infty)$ at this stage. Thus we cannot obtain the asymptotic behaviour of the limit functions as β goes to 0, while the convergence of ε to 0 describes the dynamics of the presented system on a larger time scale, therefore local estimates are enough.

As mentioned in Section 1.4, the uniqueness of the solution to the Hamilton-Jacobi equation (1.83) has up to now been an open problem, apart from very particular cases (see for instance [16]), and the issue of the convergence of the full sequence u_ε has remained unsolved. However a recent work of S. Mirrahimi and J.-M. Roquejoffre [122] has shown uniqueness of the constrained Hamilton-Jacobi equation related to the following selection-mutation model in the concavity framework

$$\varepsilon \partial_t n_\varepsilon(t,x) = n_\varepsilon(t,x) R(x, I_\varepsilon(t)) + \varepsilon^2 \Delta n_\varepsilon(t,x), \quad \text{with} \quad I_\varepsilon(t) = \int_{\mathbb{R}^d} \psi(x) n_\varepsilon(t,x) dx,$$

and generalizes a result on a selection model with spatial structure [117], where the proof relies on the uniqueness of the solution to the corresponding constrained Hamilton-Jacobi equation.

Chapter 2

Dynamics of concentration in a population model structured by age and a phenotypical trait

We study a mathematical model describing the growth process of a population structured by age and a phenotypical trait, subject to aging, competition between individuals and rare mutations. Our goals are to describe the asymptotic behavior of the solution to a renewal type equation, and then to derive properties that illustrate the adaptive dynamics of such a population. We begin with a simplified model by discarding the effect of mutations, which allows us to introduce the main ideas and state the full result. Then we discuss the general model and its limitations.

Our approach uses the eigenelements of a formal limiting operator, that depend on the structuring variables of the model and define an effective fitness. Then we introduce a new method which reduces the convergence proof to entropy estimates rather than estimates on the constrained Hamilton-Jacobi equation. Numerical tests illustrate the theory and show the selection of a fittest trait according to the effective fitness. For the problem with mutations, an unusual Hamiltonian arises with an exponential growth, for which we prove existence of a global viscosity solution, using an uncommon a priori estimate and a new uniqueness result.

2.1 Introduction

The mathematical description of competition between populations and selection phenomena leads to the use of nonlocal equations that are structured by a quantitative trait. A mathematical way to express the selection of the fittest trait is to prove that the population density concentrates as a Dirac mass (or a sum of Dirac masses) located on this trait. This result has been obtained for various models with parabolic ([14,96,128]) and integro-differential equations ([16, 64, 94]). More generally, convergence to positive measures in selection-mutation models has been studied by many authors, see [1, 34, 36] for example. The question that we pose in the present paper is the long time behavior of the population density when the growth rate depends both on phenotypical fitness and age. This question brings up to consider the aging parameter and to use renewal type equations. Accordingly, the aim of this paper is to study the asymptotic behavior of the solutions, as $\epsilon \to 0$, to the following model, with $x \geq 0$ and $y \in \mathbb{R}^n$:

$$\begin{cases} \epsilon \partial_t m_\epsilon(t,x,y) + \partial_x \left[A(x,y) m_\epsilon(t,x,y)\right] + \left(\rho_\epsilon(t) + d(x,y)\right) m_\epsilon(t,x,y) = 0, \\ A(x=0,y) m_\epsilon\left(t, x=0, y\right) = \dfrac{1}{\epsilon^n} \displaystyle\int_{\mathbb{R}^n} \int_{\mathbb{R}_+} M(\frac{y'-y}{\epsilon}) b(x',y') m_\epsilon(t,x',y') dx' dy', \\ \rho_\epsilon(t) = \displaystyle\int_{\mathbb{R}_+} \int_{\mathbb{R}^n} m_\epsilon(t,x,y) dx dy, \\ m_\epsilon(t=0,x,y) = m_\epsilon^0(x,y) > 0. \end{cases} \tag{2.1}$$

We choose $m_\epsilon(t,x,y)$ to represent the population density of individuals which, at time t, have age x and trait y. The function $A(x,y)$ is the speed of aging for individuals with age x and trait y. We denote with $\rho_\epsilon(t)$ the total size of the population at time t. Here the mortality effect features the nonlocal term $\rho_\epsilon(t)$, which represents competition, and an intrinsic death rate $d(x,y) > 0$. The condition at the boundary $x = 0$ describes the birth of newborns that happens with rate $b(x,y) > 0$ and with the probability kernel of mutation M. The terminology of "renewal equation" comes from this boundary condition. It is related to the McKendrick-von Foerster equation which is only structured in age (see [127] for a study of the linear equation). This model has been extended with other structuring variables as size for example (see [108, 123]) and then with more variables (representing DNA content, maturation, etc.) to illustrate biological phenomena, among many others, like cell division (see [73,111]), proliferative and quiescent states of tumour cells (see [2,83]). Space structured problems have also been extensively studied (see [89, 115, 117, 129]). The variable x can represent different biological quantities that evolve throughout the individual lifespan and that are not inherited at birth. These can be as diverse as, for example, the size of individuals, a physiological age, a parasite load and many others. Therefore we assume that the propgression speed A depends both on x and the trait y to keep the model (2.1) quite general. In the present paper, we refer to x as the age for simplicity. Studies in these contexts can be found in [37] about the existence of steady states for a selection-mutation model structured by physiological age and maturation age, which is considered as a phenotypical trait.

The parameter $\epsilon > 0$ is used for a time rescaling, since we consider selection-mutation phenomena that occur in a longer time scale than in an individual life cycle. It is also introduced to consider rare mutations. This rescaling is a classical way to give a continuous formulation of the adaptive evolution of a phenotypically structured population, in

particular to analyze the dynamics of "$\bar{y}_\epsilon(t)$", the fittest trait at time t, which is solution to a form of a canonical equation from the framework of adaptive dynamics (see [47,67,68,96]).

Here we observe two different time scales for our model. The first one is the individual life cycle time scale, i.e. the time for the population to reach the dynamical equilibrium for a fixed y. The second one is the evolutionary time scale, corresponding to the evolution of the population distribution with respect to the variable y. The mathematical expression of these two time scales is the property of variable separation

$$m_\epsilon(t,x,y) \simeq \bar{\rho}(t)Q(x,y)\delta_{y=\bar{y}(t)}, \tag{2.2}$$

when ϵ is close to 0, where $Q(x,y)$ is a normalized equilibrium distribution over age for a fixed y, $\bar{\rho}(t)$ the total population density and $\bar{y}(t)$ the fittest trait at the limit $\epsilon \to 0$. In order to observe the asymptotic behavior of the solution to (2.1), the key point is to prove convergence results when ϵ vanishes, that is when the two time scales become totally separated. In other words, as ϵ vanishes, we observe the ecological equilibrium and we focus on the evolutionary dynamics of the population density to identify $\bar{y}(t)$.

As a first step, we ignore mutations, i.e. we take $M(z) = \delta_0(z)$. Equation (2.1) becomes, for $t, x \geq 0$ and $y \in \mathbb{R}^n$,

$$\begin{cases} \epsilon\partial_t m_\epsilon(t,x,y) + \partial_x\left[A(x,y)m_\epsilon(t,x,y)\right] + \left(\rho_\epsilon(t) + d(x,y)\right)m_\epsilon(t,x,y) = 0, \\ A(x=0,y)m_\epsilon\left(t,x=0,y\right) = \displaystyle\int_{\mathbb{R}_+} b(x',y)m_\epsilon(t,x',y)dx', \\ \rho_\epsilon(t) = \displaystyle\int_{\mathbb{R}^n}\int_{\mathbb{R}_+} m_\epsilon(t,x,y)dxdy, \\ m_\epsilon(t=0,x,y) = m_\epsilon^0(x,y) > 0. \end{cases} \tag{2.3}$$

The analysis of this simplified model allows us to introduce the main ideas of our work. In order to study the asymptotic behavior of the solution to (2.3), we consider the associated eigenproblem, that is to find, for each $y \in \mathbb{R}^n$, the solution $(\Lambda(y), Q(x,y))$ to

$$\begin{cases} \partial_x\left[A(x,y)Q(x,y)\right] + d(x,y)Q(x,y) = \Lambda(y)Q(x,y), \\ A(x=0,y)Q(x=0,y) = \displaystyle\int_{\mathbb{R}_+} b(x',y)Q(x',y)dx', \\ Q(x,y) > 0, \quad \displaystyle\int_{\mathbb{R}^+} b(x',y)Q(x',y)dx' = 1. \end{cases} \tag{2.4}$$

We also define Φ, solution of the dual problem

$$\begin{cases} A(x,y)\partial_x\Phi(x,y) + \left[\Lambda(y) - d(x,y)\right]\Phi(x,y) = -b(x,y)\Phi(0,y), \\ \displaystyle\int_{\mathbb{R}_+} Q(x,y)\Phi(x,y)dx = 1. \end{cases} \tag{2.5}$$

The purpose of this paper is to introduce an alternative to the usual WKB method (see [68, 128]) to prove the concentration phenomenon in the y variable for the model (2.3).

Indeed we propose a new approach that consists in firstly introducing the exponential concentration singularity and secondly in estimating the corresponding age profile. The main idea is to define a function $u_\epsilon(t,y)$ independent of x, and an "age profile" $p_\epsilon(t,x,y)$, such that we can write $m_\epsilon(t,x,y) = p_\epsilon(t,x,y)\mathrm{e}^{\frac{u_\epsilon(t,y)}{\epsilon}}$. Then we prove that u_ϵ converges uniformly to a function u, which zeros correspond to the potential concentration points of the population density when ϵ vanishes. Moreover, following earlier works, we prove that $p_\epsilon(t,x,y)$ converges to the first eigenvector of the stationary problem introduced in (2.4) using the general relative entropy (GRE) principle (see [113] for an introduction).

This convergence result does not apply for the model (2.1) with mutations. Because of several technical obstructions we cannot prove the full result. However, we are able to derive some estimates resulting from the study of the formal limiting problem. Then we derive an approximation problem with a Hamilton-Jacobi equation satisfied by a sequence u_ϵ that we build and we prove its convergence to the solution to the constrained Hamilton-Jacobi equation coming from the formal limiting problem. This constrained Hamilton-Jacobi formally determines the locations of the concentration points.

Recently, the asymptotic behavior of an age-structured equation with spatial jumps has been determined in [38] when the death rate vanishes and with a slowly decaying birth rate b; then the eigenproblem (2.4) does not have a solution. Also in [70], a concentration result has been proved for a model representing the evolutionary epidemiology of spore producing plant pathogens in a host population, with infection age and pathogen strain structures.

More generally, the Hamilton-Jacobi approach to prove the concentration of the population density goes back to [68] and has been extensively used in works on the similar issue (see [51] for example). It also has been used in the context of front propagation theory for reaction-diffusion equations (see [12, 13, 76]). For example in the case of the simple Fisher-KPP equation, the dynamics of the front are described by the level set of a solution of a Hamilton-Jacobi equation. In this framework, it is naturally appropriate to use the theory of viscosity solutions to derive the convergence of the sequence u_ϵ (see [7, 9, 77] for an introduction to this notion). In this paper we also prove a uniqueness result in the viscosity sense that is not standard because the Hamiltonian under investigation has exponential growth.

The paper is organized as follows. We first state the general assumptions in section 2.2. Section 2.3 is devoted to the formulation and the proof of the convergence results in the case without mutation. In section 2.4, we discuss the case with mutations and tackle the formal limit of the stationary problem. Finally we present some numerics in section 2.5.

2.2 Assumptions

Since the analysis requires several technical assumptions on the coefficients and the initial data, we present them first.

Regularity of the coefficients. We assume that $x \mapsto b(x,y) > 0$ and $x \mapsto d(x,y) > 0$ are uniformly continuous, that $x \mapsto A(x,y)$ is $\mathcal{C}^1$ and such that, for all $y \in \mathbb{R}^n$,

$$\lim_{x\to+\infty} d(x,y) = +\infty, \tag{2.6}$$

$$0 < \underline{r} \leq b(x,y) - d(x,y) \leq \overline{r}, \tag{2.7}$$

$$0 < A_0 \leq A(x,y) \leq A_\infty, \quad \text{for two positive constants } A_0 \text{ and } A_\infty. \tag{2.8}$$

This set of assumptions is an example. It serves mostly to guarantee some properties of the spectral problem which are stated in Theorem 2.2. Only the conclusions of Theorem 2.2 are used in the present approach to the concentration phenomena.

Conditions on the initial data. We suppose that the total density is initially bounded

$$0 < \underline{\rho}^0 \leq \rho_\epsilon^0 \leq \overline{\rho}^0, \tag{2.9}$$

with $\underline{\rho}_0$ and $\overline{\rho}_0$ two constants. Besides we assume the population to be well prepared for concentration, that is, we can write

$$m_\epsilon^0(x,y) = p_\epsilon^0(x,y) e^{\frac{u_\epsilon^0(y)}{\epsilon}}, \tag{2.10}$$

where u_ϵ^0 is uniformly Lipschitz continuous and

$$\begin{cases} \exists k_0 > 0, \forall \epsilon > 0, \forall (y,y') \in \mathbb{R}^{2n}, |u_\epsilon^0(y) - u_\epsilon^0(y')| \leq k_0 |y - y'|, \\ u_\epsilon^0(y) \to u^0(y) \leq 0 \text{ uniformly in } y, \\ \exists!\ \bar{y}^0 \in \mathbb{R}^n, \max\limits_{y \in \mathbb{R}^n} u^0(y) = u^0(\bar{y}^0) = 0, \\ e^{\frac{u_\epsilon^0}{\epsilon}} \underset{\epsilon \to 0}{\longrightarrow} \delta_{\bar{y}^0}. \end{cases} \tag{2.11}$$

Finally, we assume that, for all $y \in \mathbb{R}^d$, there exist $\underline{\gamma}(y)$, $\overline{\gamma}(y)$ and $\gamma^0(y)$ positive such that, for all $\epsilon > 0, x \in \mathbb{R}_+$,

$$\underline{\gamma}(y) Q(x,y) \leq p_\epsilon^0(x,y) \leq \overline{\gamma}(y) Q(x,y), \tag{2.12}$$

$$\int_{\mathbb{R}_+} \left| p_\epsilon^0(x,y) - \gamma^0(y) Q(x,y) \right| \Phi(x,y) dx \underset{\epsilon \to 0}{\longrightarrow} 0, \quad \text{uniformly in } y, \tag{2.13}$$

where Q, Φ are eigenelements associated with the eigenproblem (2.4)-(2.5) which properties are analyzed in section 2.3.1.

Some notations: We define, for $x \in \mathbb{R}_+$, $y \in \mathbb{R}^n$ and $\lambda \in \mathbb{R}$, the functions

$$f(x,y,\lambda) = \frac{b(x,y)}{A(x,y)} \exp\left(- \int_0^x \frac{d(x',y) - \lambda}{A(x',y)} dx' \right), \quad F(y,\lambda) = \int_{\mathbb{R}_+} f(x,y,\lambda) dx. \tag{2.14}$$

2.3 Case without mutations

We present our new approach to understand how solutions of (2.3) behave when ϵ vanishes. To prove that a concentration in the y variable may occur, we first consider the principal eigenvalue $\Lambda(y)$ of (2.4), and define u_ϵ as the solution of the equation

$$\begin{cases} \partial_t u_\epsilon(t,y) = -\Lambda(y) - \rho_\epsilon(t), \quad t > 0, y \in \mathbb{R}^n, \\ u_\epsilon(0,y) = u_\epsilon^0, \quad y \in \mathbb{R}^n. \end{cases} \tag{2.15}$$

Then, we define p_ϵ such that

$$m_\epsilon(t,x,y) = p_\epsilon(t,x,y)e^{\frac{u_\epsilon(t,y)}{\epsilon}}, \tag{2.16}$$

and we prove that p_ϵ converges when $\epsilon \to 0$ respectively to the eigenvector Q associated to Λ in some way that we will specify, using an entropy method. Thereafter we prove that u_ϵ converges locally uniformly as ϵ goes to 0. This section is devoted to the proof of the following theorem, which states the concentration of the population density on the fittest traits.

Theorem 2.1. Assume (2.6)–(2.13). Let m_ϵ be the solution of (2.3), u_ϵ the solution of (2.15), p_ϵ defined by the factorization (2.16) and (Λ, Q) defined in (2.4). Then, the following assertions hold true:

(i) $\rho_\epsilon(t) = \int_{\mathbb{R}^n}\int_{\mathbb{R}_+} m_\epsilon(t,x,y)dxdy$ converges to a function ρ when ϵ vanishes in $L^\infty(0,\infty)$ weak-$\star$.

(ii) p_ϵ converges to a multiple of the normalized eigenvector Q for a weighted L^1 norm.

(iii) u_ϵ converges locally uniformly when ϵ vanishes to a continuous function u solution of

$$\begin{cases} \partial_t u(t,y) = -\Lambda(y) - \rho(t), \quad t > 0, y \in \mathbb{R}^n, \\ \sup\limits_{y\in\mathbb{R}^n} u(t,y) = 0, \quad \forall t > 0, \\ u(0,y) = u^0(y), \quad y \in \mathbb{R}^n. \end{cases} \tag{2.17}$$

(iv) Hence, m_ϵ converges weakly as ϵ vanishes to a measure μ which support is included in $\{(t,y) \in (0,\infty) \times \mathbb{R}^n | u(t,y) = 0\}$.

(v) Furthermore, assuming u^0 and $-\Lambda$ to be strictly concave

$$m_\epsilon(t,x,y) \underset{\epsilon\to 0}{\rightharpoonup} \rho(t)\frac{Q(x,y)}{\|Q(\cdot,y)\|_{L^1}}\delta_{y=\bar{y}(t)},$$

where $\bar{y}(t) \in \mathbb{R}^n$ satisfies a canonical differential equation.

2.3.1 The eigenproblem

We first study the eigenproblem (2.4) and the associated dual problem (2.5). The operator in (2.4), which is time independent, is obtained by formally taking $\epsilon = 0$ in system (2.3) and by removing the formal limiting term $\rho(t)$. We point out that this approach relies on the observation that $\rho_\epsilon(t)$ operates linearly on m_ϵ, therefore its effect on the eigenvalue Λ is no more than a shift. The following theorem states existence and uniqueness for these eigenelements as well as some properties.

Theorem 2.2. We assume (2.6)–(2.8). For a given $y \in \mathbb{R}^n$, there exists a unique triplet $(\Lambda(y), Q(x,y), \Phi(x,y))$ solution of (2.4)-(2.5). Moreover, the function $x \mapsto Q(x,y)$ is bounded and belongs to $L^1(0,\infty)$, the function $y \mapsto \Lambda(y)$ is $\mathcal{C}^1$ and we have

$$\partial_\lambda F > 0, \quad F(y,\Lambda(y)) = 1, \tag{2.18}$$

$$\nabla_y \Lambda(y) = -\frac{\nabla_y F(y, \Lambda(y))}{\partial_\lambda F(y, \Lambda(y))}, \quad \underline{r} \leq -\Lambda(y) \leq \overline{r}, \tag{2.19}$$

where F is defined in (2.14).

The complete proof, which only uses classical arguments, is postponed to Appendix 2.7.2. We give here a formal idea of the method. The eigenfunction Q satisfies a linear differential equation that allows us to derive

$$Q(x, y) = \frac{1}{A(x, y)} \exp\left(- \int_0^x \frac{d(x', y) - \Lambda(y)}{A(x', y)} dx' \right). \tag{2.20}$$

From this formulation, we deduce that the eigenvalue $\Lambda(y)$ must satisfy $F(y, \Lambda(y)) = 1$, for all $y \in \mathbb{R}^d$, where F is defined in (2.14). Since $\partial_\lambda F > 0$, the above equality determines a unique Λ, and therefore a unique Q. Similarly, we derive an explicit formula for Φ.

Note that Q represents the age distribution at equilibrium for a fixed y, thus it seems natural that it exponentially decreases. The eigenvalue Λ defines what we call the "effective fitness". It drives the adaptive dynamics of the population, as discussed in what follows.

2.3.2 Concentration

Saturation of the population density

The nonlocal term ρ_ϵ in (2.3), which is also called competition term, can be interpreted as the pressure exerted by the total population on the survival of individuals with trait y. It leads the total population to be bounded. This saturation property also holds for the general model with mutations and is stated in its general form in Proposition 2.11.

Proposition 2.3. *We assume* (2.6)-(2.9) *and* (2.12)*, then,*

$$\forall t \geq 0, \quad \rho_m \leq \rho_\epsilon(t) \leq \rho_M, \tag{2.21}$$

where $\rho_m := \min(\underline{r}, \underline{\rho}^0)$ *and* $\rho_M := \max(\overline{r}, \overline{\rho}^0)$*. Hence, after extraction of a subsequence,* ρ_ϵ *converges weakly-*$\star$ *to a function* ρ *in* $L^\infty(0, +\infty)$*.*

The proof of this result, using classical arguments, is postponed to Appendix A and is given as a particular case of Proposition 2.11.

Thereafter, in order to remove the restriction to a subsequence, we need a uniqueness statement to prove the assertion (i) of Theorem 2.1. This is done in Section 2.3.2.

We now introduce u_ϵ solution to (2.15), and we define $p_\epsilon(t, x, y)$ by the factorization (2.16) that we recall

$$m_\epsilon(t, x, y) = p_\epsilon(t, x, y) e^{\frac{u_\epsilon(t, y)}{\epsilon}}.$$

We first prove the convergence of p_ϵ. This convergence result is needed to prove the convergence of u_ϵ and then the uniqueness of ρ and u.

Convergence of p_ϵ

We state the following theorem on the convergence of p_ϵ, which details the statement (ii) of Theorem 2.1.

Theorem 2.4. We assume (2.6)–(2.13). With the constants defined in (2.12)–(2.13) and (Q, Φ) defined in Theorem 2.2,

(i) we have $\underline{\gamma}(y)Q(x,y) \leq p_\epsilon(t,x,y) \leq \overline{\gamma}(y)Q(x,y)$ for all $t \geq 0$,

(ii) moreover, the profile p_ϵ converges to the eigenfunction Q for a weighted L^1 norm. Namely, for γ^0 defined in assumption (2.13) we have, uniformly in (t,y),

$$\int_{\mathbb{R}^+} \left| \frac{p_\epsilon}{Q}(t,x,y) - \gamma^0(y) \right| Q(x,y)\Phi(x,y)dx \to 0 \quad \text{when } \epsilon \to 0,$$

The main ingredients of the proof are as follows: in a first step we prove that $\frac{p_\epsilon}{Q}$ is bounded. Then we use an entropy method to prove that the convergence occurs in a weighted L^1 space. Our approach follows closely [113, 127].

Proof of Theorem 2.4. First step: bounds on $\frac{p_\epsilon}{Q}$. From (2.3) and (2.15)-(2.16), we infer that p_ϵ satisfies

$$\begin{cases} \epsilon\partial_t p_\epsilon(t,x,y) + \partial_x \left[A(x,y)p_\epsilon(t,x,y)\right] + \left[d(x,y) - \Lambda(y)\right] p_\epsilon(t,x,y) = 0, \\ A(x=0,y)p_\epsilon(t,x=0,y) = \displaystyle\int_{\mathbb{R}^+} b(x',y)p_\epsilon(t,x',y)dx'. \end{cases} \tag{2.22}$$

Moreover Q satisfies the same linear equation. Assumption (2.12) and the comparison principle for transport equations prove the first statement of Theorem 2.4.

Second step: Entropy inequality. In the sequel, we consider

$$v_\epsilon(t,x,y) := \frac{p_\epsilon(t,x,y)}{Q(x,y)} - \gamma^0(y). \tag{2.23}$$

We also define, for any function $f(t,x,y)$, the average

$$\langle f \rangle(t,y) := \int_{\mathbb{R}_+} f(t,x,y)b(x,y)Q(x,y)dx,$$

and we notice that a direct computation gives

$$\begin{cases} \epsilon\partial_t v_\epsilon(t,x,y) + A(x,y)\partial_x v_\epsilon(t,x,y) = 0, \\ v_\epsilon(t,x=0,y) = \langle v_\epsilon \rangle(t,y). \end{cases} \tag{2.24}$$

Thus we have, in distribution sense

$$\epsilon\partial_t |v_\epsilon(t,x,y)| + A(x,y)\partial_x |v_\epsilon(t,x,y)| = 0. \tag{2.25}$$

We now introduce the generalized relative entropy

$$E_\epsilon(t,y) = \int_{\mathbb{R}_+} |v_\epsilon(t,x,y)| Q(x,y)\Phi(x,y)dx$$

and compute

$$\begin{aligned}\epsilon\partial_t E_\epsilon(t,y) &= \int_{\mathbb{R}_+} \epsilon|\partial_t v_\epsilon(t,x,y)|Q(x,y)\Phi(x,y)dx \\ &= -\int_{\mathbb{R}_+} A(x,y)|\partial_x v_\epsilon(t,x,y)|Q(x,y)\Phi(x,y)dx \\ &= -\left[|v_\epsilon|AQ\Phi\right]_{x=0}^{\infty} + \int_{\mathbb{R}_+} |v_\epsilon|\partial_x\left(AQ\Phi\right)dx.\end{aligned}$$

The function $|v_\epsilon|AQ\Phi$ converges to 0 when x goes to infinity,. Indeed, v_ϵ is bounded from the assertion (i) of Theorem 2.4, A is bounded and, since an explicit computation of $Q\Phi$ gives

$$Q(x,y)\Phi(x,y) = \frac{\Phi(0,y)}{A(x,y)}\left(1 - \int_0^x \frac{b(x',y)}{A(x',y)}\exp\left(\int_0^{x'} \frac{\Lambda(y)-d(x'',y)}{A(x'',y)}dx''\right)dx'\right), \quad (2.26)$$

from the equality $F(y,\Lambda(y)) = 1$ in (2.18), we deduce that $Q\Phi$ goes to 0 as $x \to \infty$. Then,

$$\epsilon\partial_t E_\epsilon(t,y) = \Phi(0,y)\left|\langle v_\epsilon\rangle\right|(t,y) - \Phi(0,y)\int_{\mathbb{R}_+} bQ|v_\epsilon|dx.$$

Hence, using the Cauchy-Schwarz inequality,

$$\epsilon\partial_t E_\epsilon(t,y) = -\Phi(0,y)\left(\langle|v_\epsilon|\rangle - |\langle v_\epsilon\rangle|\right) \leq 0. \quad (2.27)$$

Therefore $0 \leq E_\epsilon(t,y) \leq E_\epsilon(0,y)$, and we conclude for (ii) using (2.13). □

Remark 2.5. As v_ϵ is bounded, the convergence stated in (iii) occurs in all weighted L^p norms. Namely, for all $p \geq 1$

$$\int_{\mathbb{R}_+}\left|\frac{p_\epsilon}{Q}(t,x,y) - \gamma^0(y)\right|^p Q\Phi dx \longrightarrow 0, \quad \text{when } \epsilon \to 0.$$

Convergence of u_ϵ

Integrating (2.15), we obtain the explicit formula

$$u_\epsilon(t,y) = u_\epsilon^0(y) - t\Lambda(y) - \int_0^t \rho_\epsilon(s)ds. \quad (2.28)$$

Hence, by (2.11) and Proposition 2.3, after extraction of a subsequence, u_ϵ converges locally uniformly to a function u which is given by

$$u(t,y) = u^0(y) - t\Lambda(y) - \int_0^t \rho(s)ds. \quad (2.29)$$

Next, we claim that

$$\sup_{y\in\mathbb{R}^n} u(t,y) = 0, \quad \forall t \geq 0. \quad (2.30)$$

Indeed, we recall $m_\epsilon(t,x,y) = p_\epsilon(t,x,y)e^{\frac{u_\epsilon(t,y)}{\epsilon}}$ and $p_\epsilon(t,x,y)$ converges in virtue of Theorem 2.4. If there existed a point y_0 for some t such that $u(t,y_0) > 0$, $\rho_\epsilon(t)$ would diverge, which is a contradiction with Proposition 2.3. In a similar way, $\sup_y u(t,\cdot) < 0$ would imply $\rho_\epsilon(t) \to 0$, which also contradicts Proposition 2.3. Hence (2.30) must hold.

Thus, up to extraction of a subsequence, m_ϵ weakly converges to a measure which support is included in the set $\{(t,y) \in [0,+\infty) \times \mathbb{R}^n | u(t,y) = 0\}$. Outside of this set, we know that the population density vanishes locally uniformly as $\epsilon \to 0$.

Finally we prove the convergence of the whole sequence u_ϵ. From (2.29) and (2.30) we obtain

$$\int_0^t \rho(s)ds = \sup_{y\in\mathbb{R}^n} [u^0(y) - t\Lambda(y)], \quad \forall t \geq 0. \tag{2.31}$$

The uniqueness of the limit function ρ is therefore ensured, which implies that the full sequence ρ_ϵ converges to ρ. Then, the convergence of the full family u_ϵ follows from (2.28). Hence the statements (i),(iii) and (iv) of Theorem 2.1.

2.3.3 Properties of concentration points

Since we can explicitly integrate (2.15) to obtain (2.29), we are able to identify the points where the population concentrates, which are the points where u vanishes.

Proposition 2.6. *Let $t \in (0,\infty)$ and $\bar{y}(t) \in \mathbb{R}^n$ such that $u(t,\bar{y}(t)) = 0$, where u is given in (2.29). As $\bar{y}(t)$ is a maximum point of $u(t,\cdot)$, it satisfies*

$$\nabla_y u^0(\bar{y}(t)) = t\nabla_y \Lambda\left(\bar{y}(t)\right), \tag{2.32}$$

and we have

$$u^0(\bar{y}(t)) = \int_0^t \rho(t')dt' - t\rho(t). \tag{2.33}$$

Proof. From equation (2.29) we derive

$$u^0(\bar{y}(t)) = t\Lambda(\bar{y}(t)) + \int_0^t \rho(t')dt'. \tag{2.34}$$

Besides, $\bar{y}(t)$ is a maximum point of $u(t,\cdot)$, therefore $\nabla_y u(t,\bar{y}(t)) = 0$ which proves (2.32). Moreover $\partial_t u(t,\bar{y}(t)) = 0$, and using (2.15) we obtain

$$\Lambda(\bar{y}(t)) = -\rho(t). \tag{2.35}$$

Thus, combining (2.34) and (2.35), we obtain equation (2.33) □

At this stage, the concentration of the population density on a single trait $\bar{y}(t)$ cannot be concluded yet because the above relation defines a hypersurface. There are two frameworks in which one can prove that the population is monomorphic, that is, the population converges in measure toward a Dirac mass located on a unique point $\bar{y}(t)$ at each time $t \geq 0$. The first framework assumes that y is one dimensional, and $y \mapsto \Lambda(y)$ is strictly monotonic. The second assumes, for $y \in \mathbb{R}^d$, that $u_\epsilon^0(\cdot)$ and $-\Lambda(\cdot)$ are strictly concave uniformly in ϵ. The interested reader can refer to [128] and [96] for a complete analysis of these two cases.

In the framework of uniform strict concavity, we obtain the additional result of uniform regularity on u_ϵ and u, which enables to rigorously derive a form of canonical equation in the language of adaptive dynamics. This canonical equation gives the dynamics of the selected trait, that is, the evolution of the concentration point in an evolutionary time scale.

Theorem 2.7. Assume that u^0 and $-\Lambda$ are strictly concave in a neighborhood of $\bar{y}^0$ defined in (2.11). Then $u(t,\cdot)$, given in (2.29), is locally strictly concave and there exists $T>0$ such that for all $t\in(0,T)$, $u(t,\cdot)$ reaches its maximum 0 on a unique point $\bar{y}(t)$. Moreover $t\mapsto\bar{y}(t)\in\mathcal{C}^1(0,T)$ and its dynamics is described by the equation

$$\dot{\bar{y}}(t)=\left(\nabla_y^2 u(t,\bar{y}(t))\right)^{-1}\cdot\nabla_y\Lambda\left(\bar{y}(t)\right),\quad \bar{y}(0)=\bar{y}^0. \tag{2.36}$$

Proof. We are interested in the solutions $\bar{y}(t)\in\mathbb{R}^n$ of

$$\nabla_y u(t,\bar{y}(t))=0. \tag{2.37}$$

Note that u is strictly concave, because u^0 and $-\Lambda$ are. Therefore, such a $\bar{y}(t)$ must satisfy $u(t,\bar{y}(t))=\max_y u(t,y)=0$.

From (2.11) we know that at initial time there exists a unique solution $\bar{y}^0$ of (2.37). Besides, as u is strictly concave, $\nabla_y^2 u$ is invertible. Hence, thanks to the implicit functions theorem, there exists $T>0$ such that for all $t\in(0,T)$, there exists a unique $\bar{y}(t)\in\mathbb{R}^n$ satisfying (2.37). Moreover, $t\mapsto\bar{y}(t)$ is a $\mathcal{C}^1$ function, and then differentiating (2.37) with respect to t, we obtain, using (2.29),

$$0=\frac{\mathrm{d}}{\mathrm{d}t}\left[\nabla_y u(t,\bar{y}(t))\right]=-\nabla_y\Lambda(\bar{y}(t))+\left(\nabla_y^2 u(t,\bar{y}(t)\right)\cdot\dot{\bar{y}}(t),$$

and (2.36) follows. □

Remark 2.8. Note that we have

$$\frac{\mathrm{d}}{\mathrm{d}t}\left[\Lambda\left(\bar{y}(t)\right)\right]=\left(\nabla_y\Lambda(\bar{y}(t))\right)\cdot\left(\nabla_y^2 u(t,\bar{y}(t))\right)^{-1}\cdot\left(\nabla_y\Lambda(\bar{y}(t))\right). \tag{2.38}$$

Then, we deduce that $\frac{\mathrm{d}}{\mathrm{d}t}\left[\Lambda\left(\bar{y}(t)\right)\right]\le 0$. Therefore, if at initial time $\bar{y}^0$ belongs to a potential well of Λ, then $\bar{y}(t)$ remains bounded. Thus Theorem 2.7 holds globally in time and $\bar{y}(t)$ converges to a local minimum of Λ when t goes to infinity.

From Theorem 2.7 we infer the statement (v) of Theorem 2.1. We also give the following additional results. The first one is derived directly from (2.19), the second one from (2.35) and (2.38).

Corollary 2.9. *Under the same hypothesis as in Theorem 2.7, the critical points for evolutionary dynamics satisfy* $\nabla_y F(y^*,\Lambda(y^*))=0$.

Corollary 2.10. *Under the same hypothesis as in Theorem 2.7, we have* $t\mapsto\rho(t)\in\mathcal{C}^1(0,T)$ *and* $\dot{\rho}(t)\ge 0$ *for all* $t\in(0,T)$.

2.4 Case with mutations

We turn to the model (2.1) including mutations. We use the same approach as in the previous section, that is, we write $m_\epsilon(t,x,y) = p_\epsilon(t,x,y)e^{\frac{u_\epsilon(t,y)}{\epsilon}}$ and insert this form in (2.1). We obtain

$$\begin{cases} \epsilon\partial_t p_\epsilon(t,x,y) + \partial_x\left[A(x,y)p_\epsilon(t,x,y)\right] + d(x,y)p_\epsilon(t,x,y) \\ \qquad\qquad\qquad\qquad = -(\rho_\epsilon(t) + \partial_t u_\epsilon(t,y))p_\epsilon(t,x,y), \\ A(x=0,y)\,p_\epsilon\,(t,x=0,y) \\ \qquad\qquad = \dfrac{1}{\epsilon^n}\displaystyle\int_{\mathbb{R}^n}\int_{\mathbb{R}_+} M(\frac{y'-y}{\epsilon})b(x',y')p_\epsilon(t,x',y')e^{\frac{u_\epsilon(t,y')-u_\epsilon(t,y)}{\epsilon}}dx'dy', \\ \rho_\epsilon(t) = \displaystyle\int_{\mathbb{R}^n}\int_{\mathbb{R}_+} m_\epsilon(t,x,y)dxdy, \\ p_\epsilon(t=0,x,y) = p^0_\epsilon(x,y) > 0. \end{cases} \tag{2.39}$$

With the change of variable $z = \frac{y'-y}{\epsilon}$, the renewal term is written as

$$\begin{aligned} &A(x=0)\,p_\epsilon(t,x=0,y) \\ &\qquad = \int_{\mathbb{R}^n}\int_{\mathbb{R}_+} M(z)e^{\frac{u_\epsilon(t,y+\epsilon z)-u_\epsilon(t,y)}{\epsilon}}b(x',y+\epsilon z)p_\epsilon(t,x',y+\epsilon z)dx'dz. \end{aligned} \tag{2.40}$$

By taking formally the limit $\epsilon \to 0$, we obtain

$$A(x=0)p(t,x=0,y) = \int_{\mathbb{R}^n} M(z)e^{\nabla_y u(t,y)\cdot z}dz \int_{\mathbb{R}_+} b(x',y)p(t,x',y)dx'.$$

Denoting

$$\eta(t,y) := \int_{\mathbb{R}^n} M(z)e^{\nabla_y u(t,y)\cdot z}dz, \tag{2.41}$$

the formal limit of (2.39) is written as

$$\begin{cases} \partial_x\left[A(x,y)p(t,x,y)\right] + d(x,y)p(t,x,y) = -(\rho(t) + \partial_t u(t,y))p(t,x,y), \\ A(x=0)p(t,x=0,y) = \eta(t,y)\displaystyle\int_{\mathbb{R}_+} b(x',y)p(t,x',y)dx', \\ \rho(t) = \displaystyle\int_{\mathbb{R}^n}\int_{\mathbb{R}_+} m(t,x,y)dxdy, \\ p(t=0,x,y) = p^0(x,y) > 0, \quad u(t=0,y) = u^0(y). \end{cases}$$

With this form, one can consider the following eigenproblem: for fixed $(y,\eta) \in \mathbb{R}^n \times (0,+\infty)$, find $(\Lambda(y,\eta), Q(x,y,\eta))$, solution of

$$\begin{cases} \partial_x\left[A(x,y)Q(x,y,\eta)\right] + d(x,y)Q(x,y,\eta) = \Lambda(y,\eta)Q(x,y,\eta), \\ A(x=0,y)Q(x=0,y,\eta) = \eta\displaystyle\int_{\mathbb{R}_+} b(x',y)Q(x',y,\eta)dx', \\ Q(x,y,\eta) > 0, \quad \displaystyle\int_{\mathbb{R}_+} b(x,y)Q(x,y,\eta)dx = 1. \end{cases} \tag{2.42}$$

Using this eigenproblem, we will firstly compute the formal limit u of the sequence u_ϵ, and prove that it satisfies the following Hamilton-Jacobi equation

$$\begin{cases} \partial_t u(t,y) = -\Lambda\left(y, \int_{\mathbb{R}^n} M(z) e^{\nabla_y u(t,y)\cdot z} dz\right) - \rho(t), \quad t \geq 0, y \in \mathbb{R}^n, \\ u(0,y) = u^0(y), \quad y \in \mathbb{R}^n. \end{cases} \tag{2.43}$$

In this way, we formally recover the limit profile p using (2.42) with $\eta = \eta(t,y)$. Back to the question of adaptive dynamics, $\Lambda(y, \eta(t,y))$ defines the effective fitness of the population with trait y.

In what follows, we study this limit problem and construct a solution u. Actually the convergence of p_ϵ towards the solution Q of the eigenproblem (2.42) is an unsolved question. Indeed because of the particular form of the boundary condition (2.40), we do not know how to study the asymptotic of p_ϵ as $\epsilon \to 0$. However, we construct a sequence u_ϵ from an approximation problem of (2.43) that is well defined and we prove it converges to the solution of (2.43) in the viscosity sense.

To begin with, we state the saturation of the population density, and the existence and uniqueness of the eigenelements of (2.42).

2.4.1 Saturation and stationary problem

As in the case without mutations in the previous section, it still holds that the total population is bounded.

Proposition 2.11. *We assume* (2.6)–(2.9) *and* (2.12). *Then there exist two constants* $\rho_m, \rho_M > 0$ *such that*

$$\forall t \geq 0, \ 0 < \rho_m \leq \rho_\epsilon(t) \leq \rho_M.$$

where $\rho_m := \min(\underline{r}, \underline{\rho}^0)$ *and* $\rho_M := \max(\bar{r}, \bar{\rho}^0)$. *Hence, after extracting a subsequence,* ρ_ϵ *converges to a function* ρ *in weak*-*$L^\infty(0, +\infty)$.

We now establish the existence and uniqueness of the eigenelements in (2.42). Thus we introduce the associated dual problem: find $\Phi(x,y,\eta)$ solution of

$$\begin{cases} A(x,y)\partial_x \Phi(x,y,\eta) + [\Lambda(y,\eta) - d(x,y)]\,\Phi(x,y,\eta) = -\eta b(x,y)\Phi(0,y,\eta), \\ \int_{\mathbb{R}^+} Q(x,y,\eta)\Phi(x,y,\eta)dx = 1. \end{cases} \tag{2.44}$$

We also recall the definition (2.14) for the function F. The proof of the following theorem is given in Appendix 2.7.2.

Theorem 2.12. We assume (2.6)–(2.8). Given $y \in \mathbb{R}^n$ and $\eta \in \mathbb{R}_+$, there exists a unique triplet $(\Lambda(y,\eta), Q(x,y,\eta), \Phi(x,y,\eta))$ solution of (2.42) and (2.44). The map $x \mapsto Q(x,y,\eta)$ is bounded and integrable, $y \mapsto \Lambda(y,\eta)$ is $\mathcal{C}^1$ and we have

$$\partial_\lambda F > 0, \quad F(y, \Lambda(y,\eta)) = \frac{1}{\eta}, \tag{2.45}$$

$$\nabla_y \Lambda(y,\eta) = -\frac{\nabla_y F(y,\Lambda(y,\eta))}{\partial_\lambda F(y,\Lambda(y,\eta))}, \quad \partial_\eta \Lambda(y,\eta) = -\frac{1}{\eta^2 \partial_\lambda F(y,\Lambda(y,\eta))} < 0. \tag{2.46}$$

In the sequel we consider the effective Hamiltonian (fitness)

$$H(y,p) := -\Lambda\big(y,\eta(p)\big), \quad \eta(p) := \int_{\mathbb{R}^n} M(z)e^{p\cdot z}dz > 0. \tag{2.47}$$

Before constructing a solution to the associated Hamilton-Jacobi equation in the next section, we state the following result, which is proved in Appendix 2.7.3.

Proposition 2.13. *The mapping $p \mapsto H(y,p)$ is convex, for all $y \in \mathbb{R}^n$.*

2.4.2 The Hamilton-Jacobi equation

Here we consider the Hamilton-Jacobi equation (2.43) that we may write from (2.47) as

$$\begin{cases} \partial_t u(t,y) = H(y,\nabla_y u) - \rho(t), \\ u(0,y) = u^0(y), \quad y \in \mathbb{R}^n. \end{cases}$$

Our goal is to build a solution to this equation. Therefore, we introduce u_ϵ solution of an approximate problem motivated by the form in (2.39), which reads

$$\begin{cases} \partial_t u_\epsilon(t,y) = -\Lambda\left(y, \displaystyle\int_{\mathbb{R}^n} M(z)e^{\frac{u_\epsilon(t,y+\epsilon z)-u_\epsilon(t,y)}{\epsilon}}dz\right) - \rho_\epsilon(t), \\ u_\epsilon(0,y) = u_\epsilon^0(y), \quad y \in \mathbb{R}^n. \end{cases} \tag{2.48}$$

To simplify the Hamiltonian in equation (2.48), we set $U_\epsilon(t,y) := u_\epsilon(t,y) + \int_0^t \rho_\epsilon(t')dt$, which satisfies

$$\partial_t U_\epsilon(t,y) = -\Lambda\left(y, \int_{\mathbb{R}^n} M(z)e^{\frac{U_\epsilon(t,y+\epsilon z)-U_\epsilon(t,y)}{\epsilon}}dz\right). \tag{2.49}$$

For clarity, we set

$$\eta_\epsilon(t,y) = \int_{\mathbb{R}^n} M(z)e^{\frac{U_\epsilon(t,y+\epsilon z)-U_\epsilon(t,y)}{\epsilon}}dz.$$

We state the following theorem, which is the main result of this section. The set of assumptions $(\mathcal{H})$ is presented below.

Theorem 2.14. Assuming $(\mathcal{H})$ there exists a unique solution U_ϵ to (2.49). Furthermore, U_ϵ converges locally uniformly to a function U which is a viscosity solution of the equation

$$\partial_t U(t,y) = H(y,\nabla_y U) = -\Lambda\left(y, \int_{\mathbb{R}^n} M(z)e^{\nabla_y U\cdot z}dz\right). \tag{2.50}$$

In other words, we prove a stability result in the language of the viscosity solutions theory (see [9]) in a situation where the Hamiltonian depends on $\nabla_y U$ with an exponential growth, which is the main difficulty here. The plan of the proof is as follows. Firstly we consider the truncated equation associated to (2.49), for which classical results give existence and uniqueness of a global solution. Then we provide a uniform a priori estimate on the time derivative of the solution. It allows us to remove the truncation and to infer a global solution U_ϵ of (2.49). This proves the first step.

Secondly, we consider the semi-relaxed limits $\overline{U} := \limsup U_\epsilon$ and $\underline{U} := \liminf U_\epsilon$, and prove that they are respectively subsolution and supersolution of (2.50) in the viscosity sense. Then, an assumption of coercivity of $\eta \mapsto \Lambda(y,\eta)$ in (2.52), allows us to state that $\underline{U}$ is a Lipschitz function. Finally, using an uncommon uniqueness result on the Hamiltonian H, we prove that $\overline{U} = \underline{U}$, and conclude that U_ϵ converges locally uniformly to a viscosity solution of (2.50).

Assumptions ($\mathcal{H}$). We assume (2.11). In addition, for any compact interval I, we assume there exist two constants L_0, $L_1 > 0$, (depending on I) such that

$$\forall y \in \mathbb{R}^n, \forall \eta \in I, \quad \begin{cases} |\Lambda(y,\eta)| \leq L_0, \\ |\partial_\eta \Lambda(y,\eta)| \leq L_1. \end{cases} \tag{2.51}$$

We also assume

$$|\Lambda(y,\eta)| \to +\infty \text{ when } \eta \to +\infty \text{ or } \eta \to 0, \text{ uniformly in } y \in \mathbb{R}^n. \tag{2.52}$$

Finally, the following assumption is required for our uniqueness result, stated in Theorem 2.18. For all compact set $K_p \subset \mathbb{R}^n$, we assume there exist $C > 0, \gamma_1 \in [0,4), \gamma_2 \in [0,1)$ such that

$$\forall y \in \mathbb{R}^n, \forall p \in K_p, \quad \begin{cases} |\nabla_y H(y,p)| \leq C\left(1 + |y|^{\gamma_1}\right), \\ |\nabla_p H(y,p)| \leq C\left(1 + |y|^{\gamma_2}\right). \end{cases} \tag{2.53}$$

2.4.3 Global existence and a priori estimate

This section is devoted to the proof of the following Theorem, which is the first step towards Theorem 2.14.

Theorem 2.15. Assume (2.51). Then, for all $\epsilon > 0$, there exists a unique global solution U_ϵ to the equation (2.49), such that $|\partial_t U_\epsilon(t,y)| \leq L$ for a constant $L > 0$, uniformly in $\epsilon > 0,\ t > 0,\ y \in \mathbb{R}^n$.

The truncated problem

We first consider a truncated problem associated to (2.49). For a fixed $R > 0$, we define the function $\phi_R : \mathbb{R} \to \mathbb{R}$ which is smooth, increasing and satisfies the following conditions:

- $\phi_R(r) = r$ for $r \in [-\frac{R}{2}, \frac{R}{2}]$,
- $\phi_R(r) = R$ for $r \geq 2R$,
- $\phi_R(r) = -R$ for $r \leq -2R$,
- $\phi_R' \geq 0$ is uniformly bounded.

Let $\epsilon > 0$ be fixed. We consider the Cauchy problem

$$\begin{cases} \partial_t U_\epsilon^R(t,y) = \phi_R\left(-\Lambda\left(y, \int_{\mathbb{R}^n} M(z) e^{\frac{U_\epsilon^R(t,y+\epsilon z) - U_\epsilon^R(t,y)}{\epsilon}} dz\right)\right), \\ U_\epsilon^R(0,\cdot) = u_\epsilon^0. \end{cases} \tag{2.54}$$

We state the following result

Lemma 2.16. *Assuming* (2.51)*, there exists a unique solution of* (2.54)*, defined globally in time.*

The proof is based on the Cauchy-Lipschitz Theorem and uses only classical arguments. It is left to the reader.

Estimate on the time derivative

The particular form of (2.54) allows us to infer uniform a priori estimates on $\partial_t U_\epsilon^R$. It is stated in the following result.

Proposition 2.17. *For all $R > 0, \epsilon > 0$, we have*

$$\|\partial_t U_\epsilon^R\|_\infty \leq \|\partial_t u_\epsilon^0\|_\infty := \|\Lambda(y, \eta_\epsilon(0,y))\|_\infty .$$

As a consequence, there exists a positive constant L, independent of R and ϵ such that

$$\forall \epsilon > 0, \forall R > 0, \forall t \geq 0, \forall y \in \mathbb{R}^n, \quad |\partial_t U_\epsilon^R(t,y)| \leq L. \tag{2.55}$$

The complete proof is postponed to Appendix 2.7.4. However we give the formal idea here. As R is fixed, we simply write U_ϵ instead of U_ϵ^R. We set $V_\epsilon(t,y) := \partial_t U_\epsilon(t,y)$. Differentiating (2.50) with respect to t, we obtain

$$\partial_t V_\epsilon(t,y) = \int_{\mathbb{R}^n} K_\epsilon(t,y,z) \left(\frac{V_\epsilon(t, y+\epsilon z) - V_\epsilon(t,y)}{\epsilon} \right) dz, \tag{2.56}$$

where $K_\epsilon(t,y,z) := -\partial_\eta \Lambda\left(y, \eta_\epsilon(t,y)\right) M(z) e^{\frac{U_\epsilon(t,y+\epsilon z) - U_\epsilon(t,y)}{\epsilon}}$. Note that, thanks to (2.46), K_ϵ is positive. Then, if for some $t > 0$, $V_\epsilon(t,\cdot)$ reaches its maximum at $\bar{y} \in \mathbb{R}^n$, we obtain the inequality

$$\partial_t V_\epsilon(t,\bar{y}) = \int_{\mathbb{R}^n} K_\epsilon(t,\bar{y},z) \left(\frac{V_\epsilon(t, \bar{y}+\epsilon z) - V_\epsilon(t,\bar{y})}{\epsilon} \right) dz \leq 0.$$

Formally, it shows that the maximum value of V_ϵ is decreasing with time, that is,

$$\sup_y V_\epsilon(t,y) \leq \sup_y V_\epsilon(0,y) = \sup_y \partial_t u_\epsilon^0.$$

With the same method we show $\inf_y \partial_t U_\epsilon \geq \inf_y \partial_t u_\epsilon^0$, which completes the first step of the proof. Then, using (2.51) and that u_ϵ^0 is a Lipschitz function from (2.11), we deduce an estimate on $\partial_t U_\epsilon$, uniform in $R > 0$ and $\epsilon > 0$.

Removing the truncation

From Proposition 2.17, $\partial_t U_\epsilon^R(t,y) = \phi_R\left(-\Lambda\left(y, \eta_\epsilon(t,y)\right)\right)$ is bounded uniformly in R. As $\phi_R \equiv \mathrm{Id}$ on $[-\frac{R}{2}, \frac{R}{2}]$, then, for R large enough, U_ϵ^R is also solution to the non-truncated problem (2.49). Conversely, a solution to (2.49) with a bounded time derivative is a solution to the truncated problem (2.54) for R large enough. Thus $U_\epsilon := U_\epsilon^R$ is the unique solution of (2.49) with $\|\partial_t U_\epsilon\|_\infty \leq L$, for R large enough. The proof of Theorem 2.15 is thereby complete.

2.4.4 The semi-relaxed limits

We assume (2.51). Thanks to Theorem 2.15, there exists a constant $C > 0$ such that

$$|U_\epsilon(t,y)| \leq |u_\epsilon^0(y)| + Lt \leq C + Lt + k_0|y|, \quad \forall t > 0, \ \forall y \in \mathbb{R}^n, \tag{2.57}$$

uniformly in $\epsilon > 0$. This allows us to consider the following semi-relaxed limits (see [15,87])

$$\overline{U}(t,y) = \limsup_{\substack{x\to y\\ s\to t\\ \epsilon\to 0}} U_\epsilon(s,x), \quad \underline{U}(t,y) = \liminf_{\substack{x\to y\\ s\to t\\ \epsilon\to 0}} U_\epsilon(s,x). \tag{2.58}$$

Note that accordingly $\underline{U}$ and $\overline{U}$ satisfy the inequality (2.57). More precisely, from the uniform estimate on the time derivative stated in Theorem 2.15 we have

$$|\overline{U}(t,y) - u^0(y)| \le Lt, \quad |\underline{U}(t,y) - u^0(y)| \le Lt. \tag{2.59}$$

In this section, we prove

Theorem 2.18. Assuming (2.51)–(2.53), we have $\overline{U} = \underline{U}$.

This result implies that U_ϵ converges locally uniformly to a solution U of equation (2.50), which completes the proof of Theorem 2.14.

Subsolution and supersolution

The following proposition is adapted from classical stability results for viscosity solutions of Hamilton-Jacobi equations (see [9]). Note that it slightly differs from the usual framework because of the nonlocal term $\eta_\epsilon(t,y)$.

Proposition 2.19. *The semi-continuous functions $\overline{U}$ and $\underline{U}$ defined in* (2.58) *are respectively subsolution and supersolution of* (2.50) *in the viscosity sense in* $(0,\infty)\times\mathbb{R}^n$. *Also, for all $T > 0$, the viscosity inequalities stand for $t \in (0,T]$.*

Proof of Proposition 2.19. In order to prove that $\overline{U}$ is a viscosity subsolution of (2.50), since $\overline{U}$ is upper semi-continuous, let us consider a test function φ and a point (t_0,y_0) such that $\overline{U}-\varphi$ reaches a global maximum at (t_0,y_0). From classical results, there exists (t_ϵ,y_ϵ) such that

$$\begin{cases} (t_\epsilon,y_\epsilon) \underset{\epsilon\to 0}{\longrightarrow} (t_0,y_0), \\ \max\limits_{t,y} U_\epsilon - \varphi = (U_\epsilon - \varphi)(t_\epsilon,y_\epsilon). \end{cases}$$

Besides, note that for all $z \in \mathbb{R}^n$, $\varphi(t_\epsilon,y_\epsilon+\epsilon z) - U_\epsilon(t_\epsilon,y_\epsilon+\epsilon z) \ge \varphi(t_\epsilon,y_\epsilon) - U_\epsilon(t_\epsilon,y_\epsilon)$, thus we have

$$\frac{\varphi(t_\epsilon,y_\epsilon+\epsilon z)-\varphi(t_\epsilon,y_\epsilon)}{\epsilon} \ge \frac{U_\epsilon(t_\epsilon,y_\epsilon+\epsilon z)-U_\epsilon(t_\epsilon,y_\epsilon)}{\epsilon}.$$

Since $\partial_\eta\Lambda < 0$ from (2.46), equation (2.49) gives

$$\begin{aligned}\partial_t\varphi(t_\epsilon,y_\epsilon) &= -\Lambda\left(y_\epsilon, \int_{\mathbb{R}^n} M(z) e^{\frac{U_\epsilon(t_\epsilon,y_\epsilon+\epsilon z)-U_\epsilon(t_\epsilon,y_\epsilon)}{\epsilon}} dz\right) \\ &\le -\Lambda\left(y_\epsilon, \int_{\mathbb{R}^n} M(z) e^{\frac{\varphi(t_\epsilon,y_\epsilon+\epsilon z)-\varphi(t_\epsilon,y_\epsilon)}{\epsilon}} dz\right).\end{aligned}$$

As ϵ goes to 0,

$$\partial_t\varphi(t_0,y_0) \le -\Lambda\left(y_0, \int_{\mathbb{R}^n} M(z) e^{\nabla_y\varphi(t_0,y_0)\cdot z}\right) = H(y_0,\nabla_y\varphi(t_0,y_0)),$$

then $\overline{U}$ is a viscosity subsolution of (2.50). With the same method, we prove that $\underline{U}$ is a viscosity supersolution. It completes the first part of the proof. The second part of the statement is a well-known result, and a proof can be found in [9]. □

A posteriori Lipschitz estimate on $\underline{U}$

The announced Lipschitz continuity of $\underline{U}$ is stated in the following result.

Proposition 2.20. *Assume* (2.51)–(2.52). *Then the lower semi-continuous function* $\underline{U}$ *defined in* (2.58) *is a* L*-Lipschitz function with* $L > 0$ *defined below.*

We first prove these two preliminary lemmas. We point out that (2.52) plays a crucial role in the proof.

Lemma 2.21. *Assume* (2.51)–(2.52). *Then there exist some positive constants* $\underline{\eta}, \bar{\eta}, L_1$ *such that, uniformly in* ϵ, $\forall (t,y) \in (0,+\infty) \times \mathbb{R}^n$,

$$\underline{\eta} \leq \eta_\epsilon(t,y) \leq \bar{\eta}, \tag{2.60}$$

$$|\partial_\eta \Lambda\left(y, \eta_\epsilon(t,y)\right)| \leq L_1. \tag{2.61}$$

Proof. From Theorem 2.15, we know $\partial_t U_\epsilon(t,y) = -\Lambda(y, \eta_\epsilon(t,y))$ is bounded for $(t,y) \in (0,+\infty) \times \mathbb{R}^n$, uniformly in $\epsilon > 0$. From (2.52), we deduce that $\eta_\epsilon(t,y)$ is bounded, which proves (2.60). Then we derive (2.61) directly from assumption (2.51). □

In what follows, we use the notation $\nabla U = (\partial_t U, \nabla_y U)$.

Lemma 2.22. *In the viscosity sense,* $\nabla \underline{U}$ *is bounded, that is, there exists a constant* $L \geq k_0$ *such that if* ψ *is a smooth function and* $\underline{U} - \psi$ *reaches its minimum at* $(t_0, y_0) \in (0,+\infty) \times \mathbb{R}^n$, *then*

$$|\partial_t \psi(t_0, y_0)| \leq L,$$

$$\|\nabla_y \psi(t_0, y_0)\|_\infty \leq L.$$

Proof. Let ψ be a smooth function such that $\underline{U} - \psi$ reaches its minimum at (t_0, y_0). Similarly to the proof of Proposition 2.19, up to extraction of a subsequence, there exists a sequence of minimum points (t_ϵ, y_ϵ) of $U_\epsilon - \psi$ which converges to (t_0, y_0). As $\underline{U}$ is a supersolution, we obtain

$$\begin{aligned} &-\Lambda\left(y_\epsilon, \int_{\mathbb{R}^n} M(z) e^{\frac{\psi(t_\epsilon, y_\epsilon + \epsilon z) - \psi(t_\epsilon, y_\epsilon)}{\epsilon}} dz\right) \\ &\qquad \leq \partial_t \psi(t_\epsilon, y_\epsilon) = \partial_t U_\epsilon(t_\epsilon, y_\epsilon) = -\Lambda\left(y_\epsilon, \eta_\epsilon(t_\epsilon, y_\epsilon)\right). \end{aligned} \tag{2.62}$$

From the estimate on $\partial_t U_\epsilon$ given by Theorem 2.15, we have, when ϵ goes to 0,

$$|\partial_t \psi(t_0, y_0)| \leq L. \tag{2.63}$$

Thus, from $\partial_\eta \Lambda < 0$, (2.60) and (2.62), we derive, as ϵ goes to 0,

$$\int_{\mathbb{R}^n} M(z) e^{\nabla_y \psi(t_0, y_0) \cdot z} dz \leq \overline{\eta}.$$

Since $M(z) > 0$, we deduce

$$\|\nabla_y \psi(t_0, y_0)\|_\infty \leq L', \tag{2.64}$$

for some constant L'. Setting $L := \max(L, L', k_0)$ achieves the proof. □

Proof of Proposition 2.20. We want to prove that

$$\forall (t,t') \in (0,\infty)^2, (y,y') \in (\mathbb{R}^n)^2, \quad \underline{U}(t',y') - \underline{U}(t,y) \leq L(|t-t'| + |y-y'|).$$

By contradiction, we assume that there exists $K > L$ such that, for some $(t_0, t_0') \in (0,\infty)^2$ and $(y_0, y_0') \in (\mathbb{R}^n)^2$,

$$\underline{U}(t_0', y_0') - \underline{U}(t_0, y_0) - K(|t_0 - t_0'| + |y_0 - y_0'|) > 0. \tag{2.65}$$

Let us define the test function $\psi(t,y) := \underline{U}(t_0', y_0') - K(|t - t_0'| + |y - y_0'|)$. As $k_0 < K$, from (2.57) we derive that $\psi(t,y) - \underline{U}(t,y) \to -\infty$ when $|y| \to \infty$. Because this function is upper semicontinuous, it reaches its maximum at a point $(\bar{t}, \bar{y}) \in [0,\infty) \times \mathbb{R}^n$. In order to apply Lemma 2.22 at $(\bar{t}, \bar{x})$, we have to prove that $\bar{t} > 0$ and that ψ is smooth in a neighborhood of $\bar{x}$. We prove the first assertion by contradiction. We assume $\bar{t} = 0$. From (2.59) and the Lipschitz continuity of u^0, we have

$$\underline{U}(t_0', y_0') - \underline{U}(\bar{t}, \bar{y}) \leq \underline{U}(t_0', y_0') - u^0(y_0') + u^0(y_0') - u^0(\bar{y}) \leq L(|t_0' - \bar{t}| + |\bar{y} - y_0'|), \tag{2.66}$$

which contradicts (2.65). Thus $\bar{t} > 0$. Besides, using (2.65) we deduce $\bar{x} \neq x_0$, therefore ψ is smooth in a neighborhood of $\bar{x}$. Thus we can apply Lemma 2.22 and obtain $\|\nabla\psi(\bar{t}, \bar{y})\|_\infty = K \leq L$, which is a contradiction. □

2.4.5 Uniqueness result

We prove Theorem 2.18. This implies that U_ϵ converges locally uniformly to a function U solution of (2.50) in the viscosity sense. Therefore, it completes the proof of Theorem 2.14.

In fact, we prove that a Lipschitz continuous supersolution remains above a subsolution provided it is the case at initial time. Namely, we prove $\underline{U} \equiv \overline{U}$, with the notations introduced in (2.58). We point out that this uniqueness result is not standard since our assumption (2.53) allows the Hamiltonian to have superlinear growth. The fact that $\underline{U}$ is Lipschitz continuous, as stated in Proposition 2.20, is used as a key ingredient.

Proof of Theorem 2.18. From the definition of $\overline{U}$ and $\underline{U}$ given in (2.58), we know that $\underline{U} \leq \overline{U}$. We prove the reverse inequality. We fix $T > 0$. By contradiction, we assume

$$\sigma := \sup_{\substack{y \in \mathbb{R}^n \\ t \in [0,T]}} (\overline{U}(t,y) - \underline{U}(t,y)) > 0. \tag{2.67}$$

From (2.57) and (2.58), there exists a constant $C > 0$ such that

$$\forall t > 0, \forall y \in \mathbb{R}^n, \quad |\underline{U}(t,y)| + |\overline{U}(t,y)| \leq C + 2k_0|y|, \tag{2.68}$$

The same estimate also holds for $\underline{U}$. We use the classical method of doubling the variables in the framework of viscosity solutions (see [61,62]). Let us fix $\alpha > 0$, $\delta \in [0,1]$ and set for all $t \in [0,T], t' \in [0,T], y \in \mathbb{R}^n, y' \in \mathbb{R}^n$, we define

$$V_\delta(t,y,t',y') := \left[\overline{U}(t,y) - \alpha t - \delta|y|^2\right] - \left[\underline{U}(t',y') + \alpha t' + \delta|y'|^2\right] - \frac{|y-y'|^2}{\delta^2} - \frac{|t-t'|^2}{\delta^2}. \tag{2.69}$$

Thanks to (2.68), V_δ reaches its maximum M_δ at a point $(t_\delta, y_\delta, t_\delta', y_\delta')$. In what follows we use the following lemma.

Lemma 2.23. *When δ vanishes, the estimates hold*

1. $|t_\delta - t'_\delta|, |y_\delta - y'_\delta| = O(\delta^2)$,
2. $|y_\delta|, |y'_\delta| = O(\frac{1}{\sqrt{\delta}})$,
3. $\liminf_{\delta\to 0} t_\delta, \liminf_{\delta\to 0} t'_\delta > 0$.

The proof of Lemma 2.23 is essentially technical. Note that the Lipschitz continuity of $\underline{U}$ is a key ingredient, since usual estimates cannot give any better result than $|y_\delta - y'_\delta| = O(\delta)$.

Proof of Lemma 2.23. First, we prove that $|y_\delta|, |y'_\delta| = O(\frac{1}{\delta})$. For simplicity, all constants that do not depend on δ are denoted by K. We have

$$\begin{aligned}\forall (t,y,t',y') \in ([0,T]\times\mathbb{R}^n)^2, V_\delta(t,y,t',y') &\le K + k_0(|y|+|y'|) - \delta(|y|^2+|y'|^2)\\ &\le K + Kz - \delta z^2,\end{aligned}$$

where $z = \max(|y|,|y'|)$. This means that V_δ can be bounded from above by a second order polynomial function of z. Consequently, the points (y_δ, y'_δ) where V_δ reaches its maximum are bounded by z_0, maximum solution to the equation

$$V_\delta(0,0,0,0) - 1 = K + Kz - \delta z^2,$$

which writes under the form

$$z_0 = \frac{K + \sqrt{K+\delta K}}{\delta} = O(\frac{1}{\delta}).$$

Thus we infer

$$|y_\delta|,\ |y'_\delta| = O(\frac{1}{\delta}). \tag{2.70}$$

Now we prove the assertion 1 of Lemma 2.23. As $M_\delta \ge V_\delta(t_\delta, y_\delta, t_\delta, y_\delta)$, we have

$$\begin{aligned}\alpha(t'_\delta - t_\delta) + \delta(|y'_\delta|^2 - |y_\delta|^2) + \frac{|y_\delta - y'_\delta|^2}{\delta^2} + \frac{|t_\delta - t'_\delta|^2}{\delta^2}&\\ \le \overline{U}(t_\delta, y_\delta) - \underline{U}(t'_\delta, y'_\delta) - \overline{U}(t_\delta, y_\delta) + \underline{U}(t_\delta, y_\delta)&\\ \le \underline{U}(t_\delta, y_\delta) - \underline{U}(t'_\delta, y'_\delta) \le L\left(|t_\delta - t'_\delta| + |y_\delta - y'_\delta|\right),&\end{aligned} \tag{2.71}$$

from the Lipschitz continuity of $\underline{U}$ stated in Proposition 2.20. Besides, from (2.70) we obtain

$$\delta\left(|y_\delta|^2 - |y'_\delta|^2\right) \le \delta(|y_\delta| + |y'_\delta|)(|y_\delta| - |y'_\delta|) \le K|y_\delta - y'_\delta|. \tag{2.72}$$

Consequently, using (2.72) in (2.71), we have

$$\frac{|y_\delta - y'_\delta|^2}{\delta^2} + \frac{|t_\delta - t'_\delta|^2}{\delta^2} \le K\left(|t_\delta - t'_\delta| + |y_\delta - y'_\delta|\right). \tag{2.73}$$

Then, using the inequality

$$(|y_\delta - y'_\delta| + |t_\delta - t'_\delta|)^2 \le 2(|y_\delta - y'_\delta|^2 + |t_\delta - t'_\delta|^2),$$

we deduce

$$\frac{(|y_\delta - y'_\delta| + |t_\delta - t'_\delta|)^2}{\delta^2} \leq K\left(|t_\delta - t'_\delta| + |y_\delta - y'_\delta|\right).$$

Then, we obtain the estimates

$$|y_\delta - y'_\delta|, |t_\delta - t'_\delta| = O\left(\delta^2\right). \tag{2.74}$$

Hence the assertion 1 of Lemma 2.23.

Next, we prove the assertion 2. From $M_\delta \geq V_\delta(0,0,0,0)$, (2.59) and Proposition 2.20 we infer

$$\begin{aligned} \alpha(t_\delta + t'_\delta) + \delta\left(|y_\delta|^2 + |y'_\delta|^2\right) \leq & \ \overline{U}(t_\delta, y_\delta) - \underline{U}(t'_\delta, y'_\delta) \\ = & \ \left[\overline{U}(t_\delta, y_\delta) - u^0(y_\delta)\right] + \left[u^0(y_\delta) - \underline{U}(t_\delta, y_\delta)\right] \\ & + \left[\underline{U}(t_\delta, y_\delta) - \underline{U}(t'_\delta, y'_\delta)\right] \\ \leq & \ 2Lt_\delta + L(|t_\delta - t'_\delta| + |y_\delta - y'_\delta|). \end{aligned} \tag{2.75}$$

We deduce $\delta(|y_\delta|^2 + |y'_\delta|^2) = O(1)$, hence the assertion 2.

Finally, we prove the last assertion. By contradiction, we assume, up to extraction of a subsequence, that $t'_\delta \to 0$ as δ goes to 0. From (2.74), we deduce that t_δ converges to 0 as δ vanishes and then, from (2.75), we obtain $\delta(|y_\delta|^2 + |y'_\delta|^2) = o(1)$. We set $M := \max_{(t,y)\in[0,T]\times\mathbb{R}^n} V_\delta(t,y,t,y)$ and choose δ and α small enough to ensure $M \geq \frac{\sigma}{2}$. We write

$$\begin{aligned} \frac{\sigma}{2} \leq M \leq M_\delta \leq & \ \overline{U}(t_\delta, y_\delta) - \underline{U}(t'_\delta, y'_\delta) \\ = & \ [\overline{U}(t_\delta, y_\delta) - u^0(y_\delta)] + [u^0(y_\delta) - u^0(y'_\delta)] + [u^0(y'_\delta) - \underline{U}(t'_\delta, y'_\delta)] \\ \leq & \ L(t_\delta + t'_\delta) + k_0|y_\delta - y'_\delta|, \end{aligned}$$

where we used (2.59) for the last inequality. As δ goes to 0, we deduce from the previous inequality that $\sigma \leq 0$, contradiction. Thus $t'_\delta > 0$ uniformly in δ when δ goes to 0. Moreover we have $t_\delta - t'_\delta = o(1)$, hence the result. □

Now we go back to the proof of Theorem 2.18. We use that $\overline{U}$ and $\underline{U}$ are subsolution and supersolution in the viscosity sense. We define the test function

$$\varphi_{\alpha,\delta}(t,y) := \alpha t + \delta|y|^2 + \left[\underline{U}(t'_\delta, y'_\delta) + \alpha t'_\delta + \delta|y'_\delta|^2\right] + \frac{|y - y'_\delta|^2}{\delta^2} + \frac{|t - t'_\delta|^2}{\delta^2},$$

which is smooth and is such that $\overline{U} - \varphi_{\alpha,\delta}$ reaches its global maximum at the point (t_δ, y_δ). Since $\overline{U}$ is a subsolution of (2.50) ands $t_\delta \in (0,T]$, the viscosity inequality holds

$$\partial_t \varphi_{\alpha,\delta}(t_\delta, y_\delta) = \alpha + \frac{2}{\delta^2}(t_\delta - t'_\delta) \leq H\left(y_\delta, 2\delta y_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right).$$

In the same way, since $\underline{U}$ is a supersolution, we derive

$$-\alpha + \frac{2}{\delta^2}(t_\delta - t'_\delta) \geq H\left(y'_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right).$$

Subtracting this last inequality from the previous one and using Lemma 2.23, we obtain

$$\begin{aligned}
2\alpha &\leq H\left(y_\delta, 2\delta y_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) - H\left(y'_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) \\
&\leq \left[H\left(y_\delta, 2\delta y_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) - H\left(y_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right)\right] \\
&\quad + \left[H\left(y_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right) - H\left(y'_\delta, -2\delta y'_\delta + \frac{2}{\delta^2}(y_\delta - y'_\delta)\right)\right] \\
&\leq 2\delta C(1 + |y_\delta|^{\gamma_2})|y_\delta + y'_\delta| + C(1 + |y_\delta|^{\gamma_1} + |y'_\delta|^{\gamma_1})|y_\delta - y'_\delta| \\
&= O(\delta^{\frac{1}{2} - \frac{\gamma_2}{2}}) + O(\delta^{2 - \frac{\gamma_1}{2}}),
\end{aligned}$$

From assumption (2.53) we have $2\alpha = o(1)$ as δ goes to 0, thus we find $\alpha \leq 0$, which is a contradiction. Therefore $\sigma = 0$ and we have $\overline{U} = \underline{U}$. The proof of Theorem 2.18 is thereby complete. □

2.5 Numerical simulations

In order to complete the theory, we present numerical results in the case without mutations studied in Section 2.3. We perform a simulation of equation (2.3) with $\epsilon = 5 \cdot 10^{-3}$. The numerical results allow to visualize u_ϵ and then the concentration dynamics of the population density. We choose the variable pair (x, y) to be in the set $[0, 1] \times [0, 4]$ which we discretize with the steps $\Delta x = \frac{1}{M}$ and $\Delta y = \frac{1}{N}$ with $M = 90, N = 40$. The time step Δt is chosen to be $5 \cdot 10^{-5}$ according to the CFL condition. We denote by $m^k_{i,j}$ the numerical solution at grid point $x_i = i\Delta x$, $y_j = j\Delta y$ and time $t_k = k\Delta t$. Equation (2.3) is solved by an implicit-explicit finite-difference method with the following scheme: for $i = 1, \ldots, N$ and $j = 1, \ldots, M$,

$$m^{k+1}_{i,j} = m^k_{i,j} - \frac{\Delta t}{\epsilon} \frac{A(x_i, y_j)m^k_{i,j} - A(x_{i-1}, y_j)m^k_{i-1,j}}{\Delta x} - \frac{\Delta t}{\epsilon}\left(\rho^k m^k_{i,j} - d(x_i, y_j)m^{k+1}_{i,j}\right), \tag{2.76}$$

and the boundary term is discretized as

$$A(0, y_j)m^{k+1}_{0,j} = \sum_{i=1}^{M} b(x_i, y_j)m^k_{i,j},$$

which is necessary for computing when $i = 0$ in (2.76).

The numerics is performed using Matlab with parameters as follows. We choose the initial number of individuals to be 1000 and the final time $T = 1.5$. We choose the following functions A, b and d as follows

$$A(x, y) = 1, \qquad b(x, y) = 10 \cdot \frac{y}{1 + x^2}, \qquad d(x, y) = y^3 \cdot (2 + x/3),$$

and the initial data

$$m^0(x, y) = p^0(x, y)e^{\frac{u^0(y)}{\epsilon}},$$

with

$$p^0(x, y) = \exp(-0.8x), \qquad u^0(y) = -\frac{(y - 0.5)^2}{2}.$$

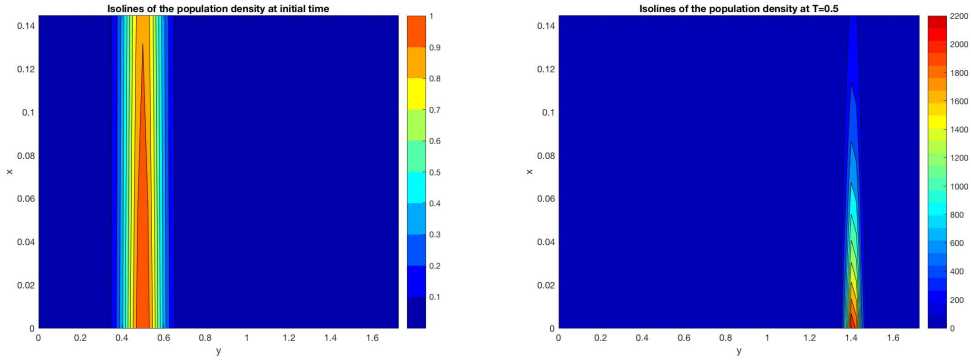

Figure 2.1: Isolines in (x, y) of the population distribution

We choose to create a trade-off between the birth and death rates with regards to the y variable, by assuming that $y \mapsto b(x, y)$ and $y \mapsto d(x, y)$ are increasing, which means that a greater natality also induces a greater mortality. This assumption allows to determine an Evolutionary Stable Distribution or ESD from the language of adaptive dynamics, which gives the repartition of the fittest traits (see [35, 67, 88]). We do not know this ESD from the beginning, however it is important to select, according to assumptions (2.6)-(2.7), a death rate with a stronger increase for large x than the growth rate with regards to the trait variable in order to avoid that the dominant traits go to infinity.

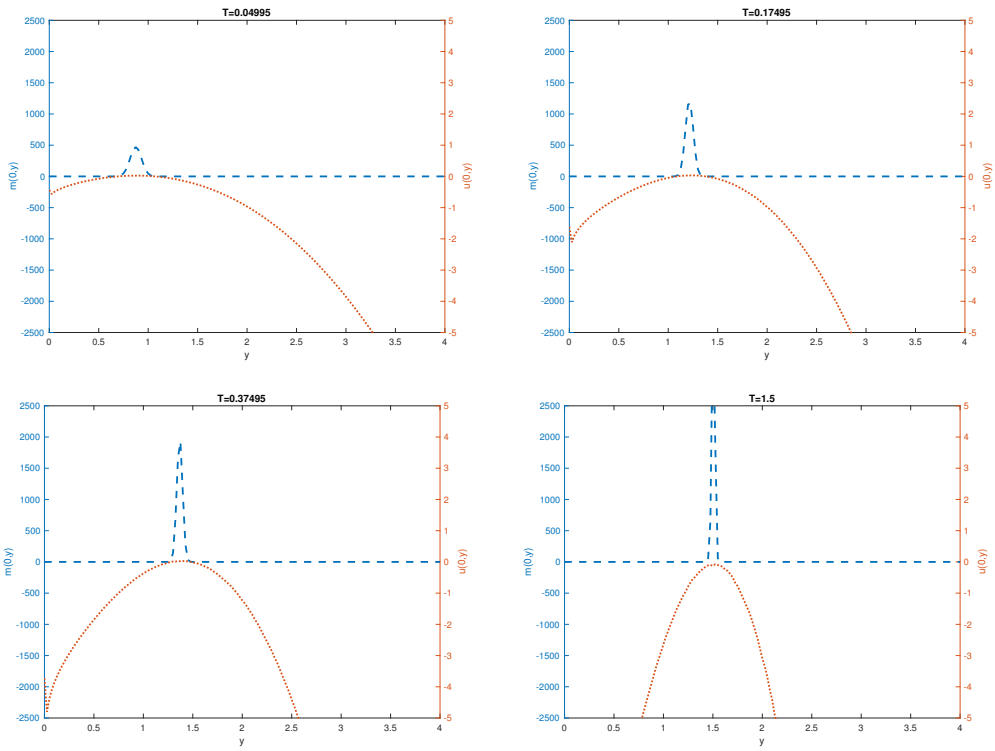

Figure 2.2: Concentration dynamics: snapshots of the population distribution in y at four different times with respect to the trait variable. Blue dashed line= m_ϵ, red dotted line = u_ϵ.

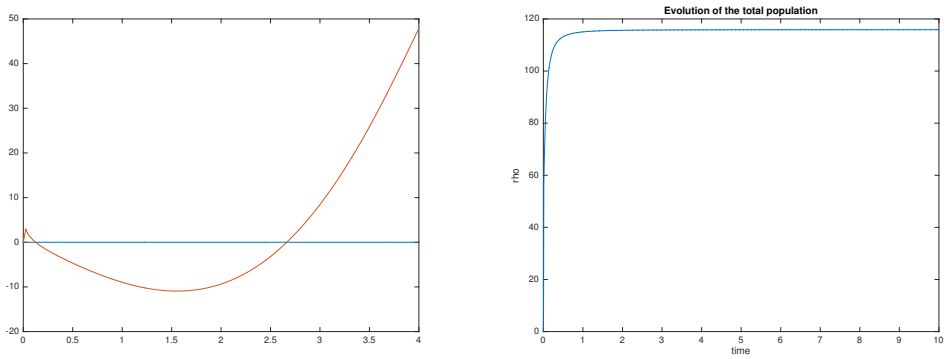

Figure 2.3: Left: Principal eigenvalue $\Lambda(y)$. Right: Evolution of ρ over time

Figure 2.1 shows the population distribution with regards to y (abscissa) and x (ordinates) at two different times. The population has moved and concentrated to a location which is different from its initial one. One can observe this continuous evolution of the population distribution in Figure 2.2 where we show the distribution of individuals with age $x = 0$ at different times and identify an ESD.

The ESD can also be identified thanks to the principal eigenvalue. We show in Figure 2.3 the eigenvalue $\Lambda(y)$ solved by the Newton method using (2.18). From equation (2.36) one can notice that the equilibrium points have to satisfy $\nabla_y \Lambda(y) = 0$ and moreover that the dynamics of the concentration is directed towards the minimum points of $\Lambda(y)$, as predicted by our analysis.

2.6 Conclusion

The approach we develop here, based on the transformation $m_\epsilon = p_\epsilon e^{\frac{u_\epsilon}{\epsilon}}$, seems convenient for the study concentration phenomena. In the case without mutations, we get precise results on the concentration points as well as on the asymptotic age profile of the population. In particular we have developed a method where the asymptotic analysis is not performed on u_ϵ but on p_ϵ, using relative entropy methods. Because of technical difficulties, we are not able yet to infer the same conclusion for the case with mutations. However the result seems to hold, at least for short time, more precisely before the Hamilton-Jacobi singularities occur in (2.50). Indeed, denoting $Q_\epsilon(t,x,y) = Q(x,y,\eta_\epsilon(t,y))$ we have that $v_\epsilon = \frac{p_\epsilon}{Q_\epsilon}$ satisfies a transport equation with a source term which reads

$$\epsilon \partial_t v_\epsilon(t,x,y) + A(x,y)\partial_x v_\epsilon(t,x,y) = \epsilon \frac{\partial_\eta Q(x,y,\eta_\epsilon(t,y))}{Q(x,y,\eta_\epsilon(t,y))} \partial_t \eta_\epsilon(t,y) v_\epsilon(t,x,y).$$

If $\partial_t \eta_\epsilon$ is bounded uniformly, we can deduce that v_ϵ is also bounded uniformly, which implies a weak concentration of the population on the set $\{(t,y) \ / \ u(t,y) = 0\}$. A rigorous proof of this result along with an entropy method to prove strong convergence of p_ϵ will be proposed in a forthcoming paper.

2.7 Appendices

2.7.1 Saturation of the population denstity

We prove Proposition 2.3 and Proposition 2.11. Integrating (2.1) and using (2.7), we obtain

$$\epsilon \frac{\mathrm{d}}{\mathrm{d}t}\rho_\epsilon(t) = -\int_{\mathbb{R}^n}\int_{\mathbb{R}_+} \big(\partial_x[A(x,y)m_\epsilon(t,x,y)]dxdy + (d(x,y)+\rho_\epsilon(t))m_\epsilon(t,x,y)\big)dxdy. \tag{2.77}$$

First we prove that $A(x,y)m_\epsilon(t,x,y)$ converges to 0 when x goes to infinity. Note that from (2.6) and the explicit formula for Q given in (2.20), we have

$$\forall y \in \mathbb{R}^n, \quad \lim_{x\to\infty} Q(x,y) = \lim_{x\to\infty} \frac{1}{A(x,y)}\exp\left(-\int_0^x \frac{d(x',y)-\Lambda(y)}{A(x',y)}dx'\right) = 0.$$

Since p_ϵ^0 is bounded from (2.12), we deduce that m_ϵ^0 converges to 0 when x goes to infinity. Besides, as A is bounded and m_ϵ satisfies (2.1) which is a transport equation, then a classical result implies that m_ϵ converges to 0 when x goes to infinity.

Then, integrating by parts in (2.77), we obtain

$$\begin{aligned}\epsilon \frac{\mathrm{d}}{\mathrm{d}t}\rho_\epsilon(t) &= \int_{\mathbb{R}^n}\int_{\mathbb{R}_+}\left[\left(\frac{1}{\epsilon^n}\int_{\mathbb{R}^n} M(\frac{y'-y}{\epsilon})dy\right)b(x,y') - d(x,y')\right]m_\epsilon(t,x,y')dxdy' - \rho_\epsilon^2(t)\\ &\le \overline{r}\rho_\epsilon(t) - \rho_\epsilon^2(t).\end{aligned}$$

Therefore, using (2.9), we conclude

$$0 \le \rho_\epsilon(t) \le \max\left(\overline{r}, \rho_\epsilon^0\right).$$

The other inequality can be proved in the same way.

2.7.2 Proof of Theorem 2.12 and Theorem 2.2

We only prove Theorem 2.12, as Theorem 2.2 is a particular case with $\eta = 1$. Equation (2.42) is equivalent to write

$$Q(x,y,\eta) = Q(0,y,\eta)\exp\left(-\int_0^x \frac{\partial_x A(x',y) + d(x',y) - \Lambda(y,\eta)}{A(x',y)}dx'\right),$$

and thanks to the condition at $x = 0$,

$$Q(x,y,\eta) = \eta\frac{1}{A(x,y)}\exp\left(-\int_0^x \frac{d(x',y)-\Lambda(y,\eta)}{A(x',y)}dx'\right). \tag{2.78}$$

Multiplying by $b(x,y)$ and integrating with regard to the x variable, we obtain

$$\frac{1}{\eta} = F(y,\Lambda(y,\eta)). \tag{2.79}$$

A direct calculation gives $\partial_\lambda F > 0$, thus (2.79) ensures uniqueness for Λ and then for Q.

Moreover, as $F(y,+\infty) = +\infty$ and $F(y,-\infty) = 0$, there exists such a $\Lambda(y,\eta)$. Besides, defining Q as in (2.78) implies that Q is in $L^1 \cap L^\infty$, thanks to (2.6), thus it proves

existence. Finally, using the implicit function theorem in (2.79) we deduce that $\Lambda(y,\eta)$ is $\mathcal{C}^1$ and (2.46) holds true.

For the dual equation (2.44), a simple calculation shows that the solution Φ must be given by

$$\Phi(x,y,\eta) = \Phi(0,y,\eta)e^{-\int_0^x \frac{\Lambda(y,\eta)-d(x',y)}{A(x',y)}dx'}\left(1-\eta\int_0^x \frac{b(x',y)}{A(x',y)}e^{\int_0^{x'}\frac{\Lambda(y,\eta)-d(x'',y)}{A(x'',y)}dx''}\right), \quad (2.80)$$

where $\Phi(0,y,\eta)>0$ is determined by the normalization $\int_{\mathbb{R}_+} Q(x,y,\eta)\Phi(x,y,\eta)dx = 1$.

Finally, we prove in the case without mutations

$$\forall y \in \mathbb{R}^n, \quad \underline{r} \leq -\Lambda(y) \leq \overline{r}. \quad (2.81)$$

Integrating (2.4) with respect to x, we have

$$-\Lambda(y) = \frac{\int_{\mathbb{R}_+}(b(x,y)-d(x,y))Q(x,y)dx}{\int_{\mathbb{R}_+} Q(x,y)dx}. \quad (2.82)$$

Thus, using (2.7), we obtain the announced result.

2.7.3 Proof of Proposition 2.13

We first state the following lemma. We recall that the definitions of $F(y,\lambda), \Lambda(y,\eta)$ and $\eta(p)$ are given in (2.14), (2.45) and (2.47).

Lemma 2.24. *We have*

$$\eta(p)\big[\partial_\lambda F\big(y,\Lambda(y,\eta(p))\big)\big]^2 \leq \partial_\lambda^2 F\big(y,\Lambda(y,\eta(p))\big), \quad (2.83)$$

and

$$\big[\partial_{p_i}\eta(p)\big]^2 \leq \eta(p)\partial_\partial^2\eta(p). \quad (2.84)$$

Proof of Lemma 2.24. We define and compute using (2.14)

$$g(x,y) := \int_0^x \frac{1}{A(x',y)}\mathrm{d}x', \quad \partial_\lambda F(y,\lambda) = \int_0^\infty g(x,y)f(x,y,\lambda)dx,$$

With these notations we may write

$$\partial_\lambda^2 F(y,\lambda) = \int_0^\infty g(x,y)^2 f(x,y,\lambda)dx.$$

Using the Cauchy-Schwarz inequality we obtain

$$\big[\partial_\lambda F\big(y,\Lambda(y,\eta(p))\big)\big]^2 \leq \partial_\lambda^2 F\big(y,\Lambda(y,\eta(p))\big)\cdot F\big(y,\Lambda(y,\eta(p))\big),$$

and then thanks to (2.45) the first inequality follows. The second inequality is a simple consequence of the Cauchy-Schwarz inequality on $\eta(p) = \int_{\mathbb{R}^n} M(z)e^{p\cdot z}dz$. □

We go back to the proof of Proposition 2.13. By differentiating twice (2.45) with respect to p_i, we obtain

$$\partial_\lambda F\big(y, \Lambda(y, \eta(p))\big) D_{p_i}\Lambda(y, \eta(p)) = -\frac{\partial_{p_i}\eta(p)}{\eta(p)^2}, \tag{2.85}$$

$$\partial_\lambda F \cdot D^2_{p_i}\Lambda(y, \eta(p)) + \partial^2_\lambda F \cdot \big[D_{p_i}\Lambda(y, \eta(p))\big]^2 = -\frac{\partial_{p_i^2}\eta(p)}{\eta(p)^2} + 2\frac{\partial_{p_i}\eta(p)}{\eta(p)^3}.$$

Then using (2.83), (2.84) and (2.85), we derive

$$\begin{aligned}
\partial_\lambda F \cdot D^2_{p_i}\Lambda(y, p) &= -\partial^2_\lambda F \left[\frac{\partial_{p_i}\eta(p)}{\eta(p)^2 \partial_\lambda F}\right]^2 - \frac{\partial_{p_i^2}\eta(p)}{\eta(p)^2} + 2\frac{\big[\partial_{p_i}\eta(p)\big]^2}{\eta(p)^3} \\
&\leq -\frac{\big[\partial_{p_i}\eta(p)\big]^2}{\eta(p)^3} - \frac{\partial_{p_i^2}\eta(p)}{\eta(p)^2} + 2\frac{\big[\partial_{p_i}\eta(p)\big]^2}{\eta(p)^3} \\
&= -\frac{1}{\eta(p)^3}\Big(\eta(p)\partial^2_{p_i}\eta(p) - \big[\partial_{p_i}\eta(p)\big]^2\Big) \leq 0,
\end{aligned}$$

hence the announced convexity result on $p \mapsto H(y, p)$.

2.7.4 Proof of Proposition 2.17

Our goal is to prove

$$\partial_t U^R_\epsilon(t, y) \leq \sup_{y \in \mathbb{R}^d} \partial_t U^{R,0}_\epsilon := \sup_{y \in \mathbb{R}^n} \partial_t u^0_\epsilon(0, y), \quad \forall R > 0, \forall y \in \mathbb{R}^n, \forall t > 0. \tag{2.86}$$

The reverse inequality can be obtained similarly. Note that from (2.51) we have that

$$\partial_t U^{0,R}_\epsilon = -\Lambda\left(y, \int_{\mathbb{R}^n} M(z) e^{\frac{u^0_\epsilon(y+\epsilon z) - u^0_\epsilon(y)}{\epsilon}} dz\right) \text{ is bounded uniformly in } \epsilon,$$

thus (2.86) allows us to conclude that $\partial_t U^R_\epsilon$ is bounded uniformly in R and ϵ.

We prove (2.86) by contradiction. We assume that there exists $(T, y_0) \in (0, +\infty) \times \mathbb{R}^n$ such that

$$\partial_t U^R_\epsilon(T, y_0) - \sup \partial_t U^{R,0}_\epsilon > 0. \tag{2.87}$$

For conciseness, we define $V^R_\epsilon(t, y) := \partial_t U^R_\epsilon(t, y)$. For $\beta > 0$, $\alpha > 0$ small and for $t \in [0, T], y \in \mathbb{R}^n$, we also introduce

$$\varphi_{\alpha,\beta}(t, y) := V^R_\epsilon(t, y) - \alpha t - \beta|y - y_0|.$$

We choose α small enough to ensure $\varphi_{\alpha,\beta}(T, y_0) > \varphi_{\alpha,\beta}(0, y_0) = \partial_t U^{R,0}_\epsilon(y_0)$, which is possible thanks to assumption (2.87). From the definition of ϕ_R, we have $|V^R_\epsilon(t, y)| \leq R$, therefore $\varphi_{\alpha,\beta}$ decreases to $-\infty$ as $|y| \to \infty$ and reaches its maximum on $[0, T] \times \mathbb{R}^n$ at a point $(\bar{t}, \bar{y})$. We have

$$\varphi_{\alpha,\beta}(\bar{t}, \bar{y} + \epsilon z) \leq \varphi_{\alpha,\beta}(\bar{t}, \bar{y}), \quad \forall z \in \mathbb{R}^n,$$

and thus

$$\frac{V^R_\epsilon(\bar{t}, \bar{y} + \epsilon z) - V^R_\epsilon(\bar{t}, \bar{y})}{\epsilon} \leq \beta \frac{|\bar{y} + \epsilon z| - |\bar{y}|}{\epsilon} \leq \beta|z|, \quad \forall z \in \mathbb{R}^n. \tag{2.88}$$

Moreover, as u_ϵ^0 is k_0-Lipschitz continuous from (2.11), then we obtain for all $t > 0$, $(y, y') \in \mathbb{R}^{2n}$,

$$\begin{aligned}
&|U_\epsilon^R(t,y) - U_\epsilon^R(t,y')| \\
&\qquad \leq |U_\epsilon^R(t,y) - U_\epsilon^{0,R}(y)| + |U_\epsilon^{0,R}(y) - U_\epsilon^{0,R}(y')| + |U_\epsilon^{0,R}(y') - U_\epsilon^R(t,y')| \\
&\qquad\qquad \leq 2RT + k_0|y - y'|. \qquad (2.89)
\end{aligned}$$

Next, we set

$$\eta_\epsilon^R(t,y) := \int_{\mathbb{R}^n} M(z) e^{\frac{U_\epsilon^R(t,y+\epsilon z) - U_\epsilon^R(t,y)}{\epsilon}} dz, \qquad (2.90)$$

$$\eta_\epsilon^\pm := \int_{\mathbb{R}^n} M(z) e^{\pm\left(\frac{2RT}{\epsilon} + k_0|z|\right)} dz, \qquad (2.91)$$

and notice that $0 < \eta_\epsilon^- \leq \eta_\epsilon^R(t,y) \leq \eta_\epsilon^+$.

We have chosen α such that $\varphi_{\alpha,\beta}(0,y_0) < \varphi_{\alpha,\beta}(T,y_0)$, then we know that $\bar{t} > 0$. Hence $\partial_t \varphi_{\alpha,\beta}(\bar{t},\bar{y}) \geq 0$, that is $\partial_t V_\epsilon^R(\bar{t},\bar{y}) \geq \alpha$ (if $\bar{t} = T$ then $\partial_t V_\epsilon^R(\bar{t},\bar{y})$ stands for the left-derivative). Differentiating (2.54), we have

$$\partial_t V_\epsilon^R(t,y) = \phi_R'\left(-\Lambda\left(y,\eta_\epsilon^R\right)\right)\left(-\partial_\eta \Lambda\left(y,\eta_\epsilon^R\right)\right)\Gamma_\epsilon^R(t,y), \qquad (2.92)$$

where $\Gamma_\epsilon^R(t,y) := \int_{\mathbb{R}^n} M(z) e^{\frac{U_\epsilon^R(t,y+\epsilon z) - U_\epsilon^R(t,y)}{\epsilon}} \left(\frac{V_\epsilon^R(t,y+\epsilon z) - V_\epsilon^R(t,y)}{\epsilon}\right) dz$.

Writing (2.92) at $(\bar{t},\bar{y})$, using (2.46) and (2.88)-(2.89), we have

$$\begin{aligned}
\alpha &\leq \partial_t V_\epsilon^R(\bar{t},\bar{y}) = \phi_R'\left(-\Lambda\left(y,\eta_\epsilon^R(\bar{t},\bar{y})\right)\right)\left(-\partial_\eta \Lambda\left(y,\eta_\epsilon^R(\bar{t},\bar{y})\right)\right)\Gamma_\epsilon^R(\bar{t},\bar{y}) \\
&\leq \beta \sup_{r\in\mathbb{R}} \phi_R'(r) \sup_{\substack{\eta\in(\eta_\epsilon^-,\eta_\epsilon^+)\\ y\in\mathbb{R}^n}} \left[-\partial_\eta \Lambda\left(y,\eta\right)\right]\left(\int_{\mathbb{R}^n} M(z) e^{\frac{U_\epsilon^R(\bar{t},\bar{y}+\epsilon z) - U_\epsilon^R(\bar{t},\bar{y})}{\epsilon}} |z| dz\right) \\
&\leq \beta \sup_{r\in\mathbb{R}} \phi_R'(r) \sup_{\substack{\eta\in(\eta_\epsilon^-,\eta_\epsilon^+)\\ y\in\mathbb{R}^n}} \left[-\partial_\eta \Lambda\left(y,\eta\right)\right]\left(\int_{\mathbb{R}^n} M(z) e^{\frac{2RT}{\epsilon} + k_0|z|} |z| dz\right).
\end{aligned} \qquad (2.93)$$

Hence $\alpha \leq \bar{C}\beta$, where $\bar{C}$ is a constant that does not depend on β. Then as β goes to 0, we obtain $\alpha \leq 0$, which is absurd. The proof is thereby achieved.

Chapter 3

Selection-mutation models with sexual reproduction kernels and competition

We study a family of selection-mutation models of a sexual population structured by a phenotypical trait. The main feature of these models is the asymmetric trait heredity or fecundity between the parents: we assume that each individual inherits mostly its traits from the female. Following previous works inspired from principles of adaptive dynamics, we rescale time and assume that mutations have limited effects on the phenotype. Our goal is to study the asymptotic behavior of the population distribution. We derive non-extinction conditions and BV estimates on the total population. We also obtain Lipschitz estimates on the solutions of Hamilton-Jacobi equations that arise from the study of the population distribution concentration at fittest traits.

3.1 Introduction

We introduce and study mathematically a family of models of selection-mutation for a continuous phenotype, which we call "trait", denoted by $x \in \mathbb{R}$. We always assume that all individuals compete for survival because they share the same resources.

Although our approach is formal and mathematical, the models under study are motivated by the issue of insecticide resistance. This phenomenon has appeared in many insects of interest in human health, in particular in species of mosquitoes that are vectors for dengue (of the genus *Aedes*) or malaria (of the genus *Anopheles*). For this specific problem of selection-mutation, the trait variable should contain, for instance, the expression level for the gene *kdr* (*knock-down resistance*, see [126]). The present study is part of a more general program on the analysis of models, and their control, in the context of evolutionary epidemiology (see [22, 124, 139, 140]).

Because of this motivation, and as a new feature, our models have a sexual reproduction kernel. This is not the case in similar selection-mutation models developed for bacteria or resistance to treatment in cancer (see [95]), where the reproduction is clonal. The major feature of equations for sexual reproduction is to yield nonlinear and nonlocal birth terms with a quadratic aspect though 1-homogeneous. All models studied in the present paper are derived from the general form

$$\begin{aligned} &\varepsilon \partial_t n_\varepsilon(t,x) = \frac{1}{\rho_\varepsilon(t)} \iint K_\varepsilon(x,y,z) n_\varepsilon(t,y) n_\varepsilon(t,z) dy\, dz - R(x, \rho_\varepsilon(t)) n_\varepsilon(t,x), \quad x \in \mathbb{R}, t \geq 0, \\ &\rho_\varepsilon(t) = \int n_\varepsilon(t,x) dx. \end{aligned} \tag{3.1}$$

The variable t stands for time, $n_\varepsilon(t,x) \in [0, +\infty)$ is the population distribution at time t and trait x. The positive function R is here the saturation term, which contains the death rate and the insecticide effect. Competition is taken into account through the dependency of R in its second variable.

In equation (3.1), we interpret y, the second variable for K_ε, as the female trait, and z, the third variable, as the male trait. The kernel $K_\varepsilon(x,y,z)$ is thus equal to the number of individuals with trait x that are born from any encounter between a female of trait y and a male of trait z per unit of time. This model is valid only if we assume that the sex ratio is constant in time and the same for each value of the trait. We make this simplification in order to obtain a single equation rather than a system.

To justify this assumption, it is worth highlighting that we aim here at general properties and methods for dealing with the nonlinear and nonlocal birth term, rather than at a realistic model for the evolution of a specific trait (see [142, 144] for more realistic models). We hope that the techniques developed here will be successfully applied to specific contexts. We also point out that the same kind of equation sturctures appears in models of cell population exchanging genetic information (see [20, 99]) or proteins (see [101]).

The relations between sexual selection and speciation are not well understood. Models of sexual reproduction have already been discussed in different contexts. Studies of individual-based models of sexual population were performed to determine the necessary conditions to evolutionary branching in [65, 91, 145]. Mendelian populations, i.e. structured by genetic types, were also considered (see [32, 33]). In [56] for instance, the authors investigate a stochastic birth and death process model for sexually reproducing diploids

with Lotka-Volterra type dynamics and single locus genetics. At the small mutation steps limit, they derive a differential equation in allele space, referred to as a form of the canonical equation of the adaptive dynamics. In [58], another stochastic birth and death process model is studied with sexual reproduction according to mating preferences and a space structure with patches. In this case, reproductive isolation between patches occurs, and the authors prove that the time needed for this isolation to occur is a function of the population size.

From a full population point of view, in [121] the authors considered sexual populations structured by a trait and a space variable in a non-homogeneous environment, and after performing an asymptotic limit and a simplification of the model, derived an estimate of the invasion speed or extinction speed of the population. In [28], the authors study the same kind of models as in the present paper, where the traits of the newborns are distributed through a gaussian kernel centered on the mean of the parents' traits and with a constant variance, as in [71]. They prove the existence of principal eigenelements for the corresponding eigenproblem, using the Schauder fixed point theorem.

The main results of this paper regard the behavior of ρ_ε and n_ε in the asymptotic of large time scale and mutations with limited effect on the phenotype, for several models of the form (3.1). We also identify some difficulties raised by the application of our methods to the general case of (3.1).

In the present paper, we study two classes of models with the common idea that new individuals inherit mostly their trait from the female. We consider a first model with **asymmetric fecundity** (AF in short)

$$\varepsilon\partial_t n_\varepsilon(t,x) = \frac{1}{\rho_\varepsilon(t)}\iint B(y)\alpha_\varepsilon(x,y,z)n_\varepsilon(t,y)n_\varepsilon(t,z)dy\,dz - R(x,\rho_\varepsilon(t))n_\varepsilon(t,x), \tag{3.2}$$

where, with B, α_ε positive functions,

$$K_\varepsilon(x,y,z) = B(y)\alpha_\varepsilon(x,y,z), \qquad \int \alpha_\varepsilon(x,y,z)\,dx = 1 \text{ for all } y,z.$$

The second model features an **asymmetric trait heredity** (ATH in short), which reads

$$\varepsilon\partial_t n_\varepsilon(t,x) = \frac{1}{\rho_\varepsilon(t)}\iint K_0(x-z)G_\varepsilon(x-y)n_\varepsilon(t,y)n_\varepsilon(t,z)dy\,dz - R(x,\rho_\varepsilon(t))n_\varepsilon(t,x), \tag{3.3}$$

where

$$K_\varepsilon(x,y,z) = K_0(x-z)G_\varepsilon(x-y), \tag{3.4}$$

with K_0, G_ε positive functions, and

$$G_\varepsilon(x-z) = \frac{1}{\varepsilon}G\left(\frac{x-z}{\varepsilon}\right) \text{ and } \int G(z)\,dz = 1.$$

As in the other chapters, we study two ingredients of proof for convergence: first, identifying a consistent limit object as $\varepsilon \to 0$, which is here a constrained Hamilton-Jacobi equation; secondly, obtaining time compactness estimates on the solutions at the ε-level in order to be able to extract converging subsequences and to use the stability property

of viscosity solutions. The first and most intricate step to obtain this second ingredient is the study of the variations of ρ_ε.

For simplification, we first study a model without mutations, which is a particular case of the two models presented above, in order to introduce the ingredients that we use and to highlight the new arguments of the proofs. This model without mutations reads

$$\varepsilon\partial_t n_\varepsilon(t,x) = \left(\frac{1}{\rho_\varepsilon(t)} K_0 * n_\varepsilon(t,\cdot)(x) - \nu\rho_\varepsilon(t)\right) n_\varepsilon(t,x), \tag{3.5}$$

with $\nu > 0$. This equation can be written under the form of equation (3.2) with

$$B \equiv 1 \text{ and } \alpha_\varepsilon(x,y,z) = K_0(x-z)\delta_0(x-y),$$

and also under the form of (3.3) with

$$G_\varepsilon = \delta_0.$$

The paper is organized as follows. In Section 3.2, we state the results of this work and the assumptions associated. We also establish some non-extinction conditions and a control on the total population. In Section 3.3, we focus on the model without mutations in order to indroduce the main arguments that will be used for the general cases. In particular we derive BV estimates for the total population and discuss the formal limit of the population distribution. In Section 3.4, we address the derivation of BV estimates for the ATH and AF models when R only depends on the total population variable and we explain the difficulties encountered when R is generic. In Section 3.5, we deal with the Hamilton-Jacobi approach.

3.2 Main results

3.2.1 Assumptions and statements

The function R stands for the death rate and the competition effects. Therefore we use the standard hypotheses

$$\forall x, \rho, \quad \partial_\rho R(x,\rho) > 0. \tag{3.6}$$

We use the notation L^1_+ for the set of almost-everywhere non-negative functions in L^1.

The main results of this paper are obtained under the following assumption on R

$$R(x,\rho) = \nu\rho, \quad \forall x \in \mathbb{R}, \text{ with } \nu > 0. \tag{3.7}$$

We also assume on the initial data

$$\varepsilon(\dot\rho_\varepsilon)_-(0) = \left(\int n^0_\varepsilon(x)\frac{K_0 * n^0_\varepsilon}{\rho^0_\varepsilon}(x)\,dx - (\rho^0_\varepsilon)^2\right)_- \text{ is uniformly bounded.} \tag{3.8}$$

For the model without mutations and the one with asymmetric trait heredity, we assume

$$K_0 \in \mathcal{C}_b(\mathbb{R},\mathbb{R}_+) \text{ is a symmetric kernel,} \tag{3.9}$$

where $\mathcal{C}_b(\mathbb{R},\mathbb{R}_+)$ is the space of continuous and bounded functions defined $\mathbb{R}$ and taking values in $\mathbb{R}_+$.

We state the following result for the model without mutations whose proof is given in Section 3.3.

Theorem 3.1 (BV bound for model (3.5))**.** *Let $T > 0$ and let n_ε be the solution to* (3.5) *associated with initial data n_ε^0. We assume* (3.8) *and* (3.9).

Then, ρ_ε is uniformly bounded in $BV(0,T)$. Namely, we obtain

$$\int_0^T |\dot{\rho}_\varepsilon(t)|\,dt \leq \rho_M + 2(\dot{\rho}_\varepsilon)_-(0)\frac{\varepsilon}{\kappa_m''}\big(1 - e^{-\frac{\kappa_m'' T}{\varepsilon}}\big),$$

with ρ_M and κ_m'' defined later on. This implies that, up to extraction of subsequences, there exist limits $\rho_\varepsilon \to \rho$ in $L^1(0,T)$, and $n_\varepsilon \rightharpoonup n \in L_t^\infty(0,T;M_x^1)$ in the sense of measures.

Moreover, we have

$$\int_0^T \int_{\mathbb{R}} n_\varepsilon\big(\frac{K_0 * n_\varepsilon}{\rho_\varepsilon} - \nu\rho_\varepsilon\big)^2 dx\,dt = O(\varepsilon). \tag{3.10}$$

For the model with asymmetric fecundity, we need the following assumption on B and α.

$$\begin{aligned} &\exists C > 0, \forall \varepsilon > 0, \forall \phi \in M^1 \text{ with } \|\phi\|_{M^1} = 1, \\ &\iiint \alpha_\varepsilon(x,y,z)B(x)B(y)\phi(y)\phi(z)dx\,dy\,dz - \left(\int B(y)\phi(y)dy\right)^2 \geq -C\varepsilon. \end{aligned} \tag{3.11}$$

This means that the fecundity variation is controlled. We obtain the following result whose proof is given in Section 3.4.

Theorem 3.2 (BV bound for model (3.2))**.** *Let $T > 0$ and let n_ε be the solution to* (3.2) *associated with initial data n_ε^0. Assume* (3.7) *and* (3.11).

Then, ρ_ε is uniformly bounded in $BV(0,T)$. Namely, we have

$$\int_0^T |\dot{\rho}_\varepsilon(t)|\,dt \leq \rho_M + 2(\dot{\rho}_\varepsilon)_-(0)\frac{\varepsilon}{\nu\rho_m}\big(1 - e^{-\frac{\nu\rho_m T}{\varepsilon}}\big) + 2\frac{C}{\nu\rho_m}\left(T + \frac{\varepsilon}{\nu\rho_m}(e^{-\frac{\nu\rho_m T}{\varepsilon}} - 1)\right).$$

with C, ρ_M and ρ_m defined later on. This implies that, up to extraction of subsequences, there exist limits $\rho_\varepsilon \to \rho$ in $L^1(0,T)$, and $n_\varepsilon \rightharpoonup n \in L_t^\infty(0,T;M_x^1)$ in the sense of measures.

For the model with asymmetric trait heredity, we also need to assume that, for all $\phi \in L^1 \cap W^{1,\infty}, G_\varepsilon * \phi = \phi + O(\varepsilon)$, in the sense that

$$\frac{1}{\varepsilon\|\phi\|_{Lip}}\|G_\varepsilon * \phi - \phi\|_{L^1} \text{ is uniformly bounded in } \varepsilon. \tag{3.12}$$

Additionally, we assume that K_0 is Lipschitz in this case. We obtain the following result which proof is given in Section 3.4.

Theorem 3.3 (BV bound for model (3.3))**.** *Let n_ε be the solution to* (3.3) *associated with initial data n_ε^0. Assume* (3.8), (3.9) *and* (3.12). *Assume also the following ("non-extinction" in this case) condition*

$$\exists \eta_0 > 0, \quad \forall \varepsilon > 0, \quad \eta_\varepsilon := \inf_{\substack{\phi \in L_+^1 \\ \|\phi\|_{L^1} = 1}} \int K_0 * \phi \cdot G_\varepsilon * \phi\,dx \geq \eta_0. \tag{3.13}$$

Then ρ_ε is uniformly bounded in $BV(0,T)$. Namely, we have

$$\int_0^T |\dot\rho_\varepsilon(t)|\,dt \le \rho_M + 2(\dot\rho_\varepsilon(0))_- \frac{\varepsilon}{C_1}(1-e^{-C_1T/\varepsilon}) + 2\frac{\varepsilon C_2}{C_1^2}(e^{-C_1T/\varepsilon}-1) + 2\frac{C_2}{C_1}T.$$

Then, up to extraction there exist $\rho \in L^1_{loc}(0,\infty)$ and $n \in L^\infty_t(0,T;M^1_x)$ such that (ρ_ε) converges towards ρ in $L^1_{loc}(0,\infty)$, and (n_ε) towards n in the sense of measures, when ε goes to 0.

Moreover, for all $T>0$, we have

$$\int_0^T \int_x (G_\varepsilon * n_\varepsilon)\left[\frac{K_0 * n_\varepsilon}{\rho_\varepsilon} - \nu\rho_\varepsilon\right]^2 dx\,dt = O(\varepsilon),$$

In the general case of a death rate depending on both traits and the total population, we can perform the Hopf-Cole transform

$$u_\varepsilon(t,x) = \varepsilon \ln n_\varepsilon(t,x),$$

and apply the Hamilton-Jacobi approach that we exposed previously. For the models under investigation, we obtain the following result that is the topic of Section 3.5.

Theorem 3.4 (Lipschitz estimates for u_ε)**.** *Under some assumptions on the initial data u^0_ε, for both models* (3.2) *and* (3.3)*, the corresponding u_ε are locally Lipschitz uniformly in ε.*

Moreover, we have a global upper bound on u_ε. Namely, there exists a constant C, such that

$$u_\varepsilon(t,x) \le \varepsilon \ln\left(C + \frac{C(1+t)}{\varepsilon}\right).$$

The assumptions required for the proof of this theorem in each case are specified in the corresponding section.

3.2.2 Boundedness of ρ_ε and non-extinction

The total population ρ_ε satisfies

$$\varepsilon\dot\rho_\varepsilon(t) = \int \Big(\iint K_\varepsilon(x,y,z)\frac{n_\varepsilon(t,z)}{\rho_\varepsilon(t)} n_\varepsilon(t,y)dy\,dz - R(x,\rho_\varepsilon(t))n_\varepsilon(t,x)\Big)\,dx.$$

To ensure that ρ_ε remains bounded along all trajectories, we complement (3.6) with

$$\begin{aligned} &\exists R_m : \mathbb{R}_+ \to \mathbb{R}_+, \text{ increasing, with } R_m(0)=0, \\ &R_m(+\infty) = +\infty \text{ and } \forall x, \quad R(x,\rho) \ge R_m(\rho). \end{aligned} \tag{3.14}$$

We also assume that

$$K_M := \sup_{0<\varepsilon\le 1} \sup_{\substack{\phi\in L^1_+ \\ \|\phi\|_{L^1}=1}} \sup_y \iint K_\varepsilon(x,y,z)dx\,\phi(z)dz < +\infty. \tag{3.15}$$

Then, let $\rho_M := R_m^{-1}(K_M)$. The following boundedness result is straightforward:

Proposition 3.5 (Upper bound for ρ_ε). *Under assumptions* (3.6), (3.14) *and* (3.15), *all trajectories of* (3.1) *are forward-ρ_M-bounded from above in ρ_ε, by which we mean that $\dot\rho_\varepsilon(t) < 0$ as long as $\rho_\varepsilon(t) > \rho_M$.*

Conversely, we can study conditions that ensure non-extinction of the population: $\rho_\varepsilon(t) \geq \rho_m > 0$. For instance, let

$$\kappa_m(\rho) := \inf_{0<\varepsilon\leq 1} \inf_{\substack{\phi\in L^1_+ \\ \|\phi\|_{L^1_+}=1}} \inf_y \iint K_\varepsilon(x,y,z)dx\,\phi(z)dz - R(y,\rho). \tag{3.16}$$

Proposition 3.6 (Lower bound for ρ_ε under assumption (3.16)). *Under assumption* (3.6) *and if there exists $\rho_m > 0$ such that $\kappa_m(\rho_m) = 0$, with κ_m defined in* (3.16), *then all trajectories of* (3.1) *are forward-ρ_m-bounded from below in ρ_ε, by which we mean that $\dot\rho_\varepsilon(t) > 0$ as long as $\rho_\varepsilon(t) < \rho_m$.*

However, $\kappa_m(0) > 0$ is not expected to be a necessary condition. It is an open and challenging question to determine more general conditions for non-extinction, and study the set of extinction trajectories in cases when these conditions are not met.

For instance, let

$$\kappa'_m(\rho) := \inf_{0<\varepsilon\leq 1} \inf_{\substack{\phi\in L^1_+ \\ \|\phi\|_{L^1}=1}} \int \Big(\iint K_\varepsilon(x,y,z)dx\,\phi(z)dz - R(y,\rho)\Big)\phi(y)dy. \tag{3.17}$$

Proposition 3.7 (Lower bound for ρ_ε with a condition on (3.17)). *Under assumption* (3.6) *and if there exists $\rho_m > 0$ such that $\kappa'_m(\rho_m) = 0$ then all trajectories of* (3.1) *are forward-ρ_m-bounded from below in ρ_ε.*

And likewise, let

$$\kappa''_m := \inf_{0<\varepsilon\leq 1} \inf_{\substack{\phi\in L^1_+ \\ \|\phi\|_{L^1}=1}} \iiint K_\varepsilon(x,y,z)\phi(y)\phi(z)\,dx\,dy\,dz. \tag{3.18}$$

Then, assuming also

$$\begin{aligned} &\exists R_M : \mathbb{R}_+ \to \mathbb{R}_+, \text{ increasing, with } R_M(0) \geq 0, \\ &R_M(+\infty) = +\infty \text{ and } \forall x, \quad R(x,\rho) \leq R_M(\rho), \end{aligned} \tag{3.19}$$

we have $\dot\rho \geq \big(\kappa''_m - R_M(\rho)\big)\rho$.

Proposition 3.8 (Lower bound for ρ_ε with a condition on (3.18)). *Assume* (3.19) *holds and $\kappa''_m > R_M(0)$ defined in* (3.18). *Then all trajectories of* (3.1) *are forward-ρ_m-bounded from below in ρ_ε, with $\rho_m = R_M^{-1}(\kappa''_m) > 0$.*

3.3 The model without mutations (3.5)

In order to see clearly the kind of results to be expected, we first study in detail a very simple example, which is equation (3.5). The form of the birth rate assumes that the trait

is perfectly transmitted from the females to their progeny, and the cross-fecundity between a male of trait z and a female of trait x depends only on the distance between x and z through K_0.

Assumptions (3.6) and (3.14) (for $R_m = \nu\rho$) obviously hold in case (3.5). Assumption (3.15) holds with $K_M = \max_x K_0(x)$. However, $\kappa_m(\rho) = \inf K_0 - \rho$ so the non-extinction condition from Proposition 3.6 holds if and only if $\inf_x K_0(x) > 0$.

Even though $\inf_x K_0(x) = 0$, it seems standard to assume that K_0 is such that Proposition 3.8 holds, that is

$$\kappa_m'' = \inf_{\substack{\phi \in L^1_+ \\ \|\phi\|_{L^1}=1}} \int \big(K_0 * \phi\big)(x)\phi(x)\, dx > 0.$$

Notice that, for all $\phi \in L^1/\{0\}$ satisfying $\|\phi\|_{L^1} = 1$, we have the equality

$$\int (K_0 * \phi)(x)\phi(x)dx = \int \widehat{K_0}(\xi) \left(\widehat{\phi}(\xi)\right)^2 d\xi,$$

which suggests that, if K_0 is chosen such that its Fourier transform is positive, we can define another non-extinction condition without sign condition on ϕ, that is

$$\kappa_m''' = \inf_{\substack{\phi \in L^1/\{0\} \\ \|\phi\|_{L^1}=1}} \int \widehat{K_0}(\xi) \left(\widehat{\phi}(\xi)\right)^2 d\xi > 0.$$

The same kind of assumption is used in [88] to prove an entropy-based stability result.

3.3.1 Proof of Theorem 3.1

In this section we prove Theorem 3.1. From equation (3.5) we can compute

$$\varepsilon\dot{\rho}_\varepsilon(t) = \int n_\varepsilon(t,x)\frac{K_0 * n_\varepsilon(t,\cdot)}{\rho_\varepsilon(t)}(x)\, dx - \nu\rho_\varepsilon^2.$$

Assuming (3.9) yields $\frac{d}{dt}\int nK_0 * n = 2\int nK_0 * (\partial_t n)$. Hence

$$\varepsilon\ddot{\rho}_\varepsilon = -\nu\rho_\varepsilon\dot{\rho}_\varepsilon - \nu\rho_\varepsilon\dot{\rho}_\varepsilon - \frac{\dot{\rho}_\varepsilon}{\rho_\varepsilon^2}\int n_\varepsilon K_0 * n_\varepsilon + \frac{1}{2\rho_\varepsilon}\frac{d}{dt}\int n_\varepsilon K_0 * n_\varepsilon + \frac{1}{\rho_\varepsilon}\int \partial_t n_\varepsilon K_0 * n_\varepsilon.$$

We rewrite this as

$$\varepsilon\ddot{\rho}_\varepsilon = -\nu\rho_\varepsilon\dot{\rho}_\varepsilon - \frac{\dot{\rho}_\varepsilon}{2\rho_\varepsilon^2}\int n_\varepsilon K_0 * n_\varepsilon + \frac{1}{2}\frac{d}{dt}\Big(\frac{1}{\rho_\varepsilon}\int n_\varepsilon K_0 * n_\varepsilon - \nu\rho_\varepsilon^2\Big) + \frac{1}{\varepsilon}\int \Big(\frac{n_\varepsilon(K_0 * n_\varepsilon)^2}{\rho_\varepsilon^2} - \nu n_\varepsilon K_0 * n_\varepsilon\Big),$$

and since $\varepsilon\dot{\rho}_\varepsilon = \frac{1}{\rho_\varepsilon}\int n_\varepsilon K_0 * n_\varepsilon - \nu\rho_\varepsilon^2$, we get

$$\frac{\varepsilon}{2}\ddot{\rho}_\varepsilon = -\frac{\dot{\rho}_\varepsilon}{2\rho_\varepsilon^2}\int n_\varepsilon K_0 * n_\varepsilon + \frac{1}{\varepsilon}\int n_\varepsilon\Big(\frac{K_0 * n_\varepsilon}{\rho_\varepsilon} - \nu\rho_\varepsilon\Big)^2. \tag{3.20}$$

From (3.20) a lot can be said. First, $\ddot{\rho}_\varepsilon \geq -\frac{\dot{\rho}_\varepsilon}{\varepsilon\rho_\varepsilon^2}\int n_\varepsilon K_0 * n_\varepsilon$, hence if $\dot{\rho}_\varepsilon = 0$ then $\ddot{\rho}_\varepsilon \geq 0$. In particular, ρ_ε has no strict local maximum. We can conclude that ρ_ε is either decreasing, increasing or decreasing-increasing, and since it is bounded, $\rho_\varepsilon(t)$ must converge to some finite value ρ_ε^∞ as t goes to $+\infty$.

For $a \in \mathbb{R}$, let $a_- = \max(-a, 0)$. Let $b_\varepsilon(t) := \frac{1}{\rho_\varepsilon^2(t)}\int n_\varepsilon(t,x)(K_0 * n_\varepsilon(t,\cdot))(x)dx \geq \kappa_m'' > 0$. Then from (3.20),

$$\frac{d}{dt}(\dot{\rho}_\varepsilon)_- \leq -\frac{\kappa_m''}{\varepsilon}(\dot{\rho}_\varepsilon)_-.$$

Hence $(\dot{\rho}_\varepsilon)_-(t) \leq e^{-\frac{\kappa_m'' t}{\varepsilon}}(\dot{\rho}_\varepsilon)_-(0)$. We write

$$\begin{aligned}\int_0^T |\dot{\rho}_\varepsilon(t)|\,dt &\leq \int_0^T \dot{\rho}_\varepsilon(t)\,dt + 2\int_0^T (\dot{\rho}_\varepsilon)_-(t)dt \\ &\leq \rho_M + 2(\dot{\rho}_\varepsilon)_-(0)\int_0^T e^{-\frac{\kappa_m'' t}{\varepsilon}}dt \\ &\leq \rho_M + 2(\dot{\rho}_\varepsilon)_-(0)\frac{\varepsilon}{\kappa_m''}\big(1 - e^{-\frac{\kappa_m'' T}{\varepsilon}}\big).\end{aligned}$$

Therefore, under the mild assumption (3.8), the family $(\rho_\varepsilon)_\varepsilon$ is uniformly bounded in $BV(\mathbb{R}_+)$.

We now establish equation (3.10). Going back to equation (3.20), and integrating this one over $[0,T]$ for $T > 0$, we obtain

$$\int_0^T\int_{\mathbb{R}} n_\varepsilon\big(\frac{K_0 * n_\varepsilon}{\rho_\varepsilon} - \nu\rho_\varepsilon\big)^2 dx\,dt = \varepsilon\int_0^T \frac{\dot{\rho}_\varepsilon}{2\rho^2}\int n_\varepsilon K_0 * n_\varepsilon\,dx\,dt + \frac{\varepsilon^2}{2}(\dot{\rho}_\varepsilon(T) - \dot{\rho}_\varepsilon(0)). \quad (3.21)$$

Since ρ_ε is locally BV uniformly in ε and using (3.8) and (3.9), we deduce that

$$\int_0^T\int_{\mathbb{R}} n_\varepsilon\big(\frac{K_0 * n_\varepsilon}{\rho_\varepsilon} - \nu\rho_\varepsilon\big)^2 dx\,dt = O(\varepsilon),$$

which is equation (3.10).

3.3.2 Concentration of Dirac masses

In the limit $\varepsilon \to 0$, equation (3.10) gives formally

$$\int n(t,x)\Big(\frac{K_0 * n(t,\cdot)}{\rho(t)}(x) - \nu\rho(t)\Big)^2 dx = 0. \quad (3.22)$$

It turns out that combinations of Dirac masses are admissible solutions to (3.22), $n(x) = \sum_{i=1}^N \rho_i\delta_{x=x_i}$, $\rho_i > 0$ with $\sum_{i=1}^N \rho_i = \rho$, and

$$\sum_{i=1}^N \rho_i\Big(\sum_{j=1}^N \frac{\rho_j}{\rho}K_0(x_i - x_j) - \nu\rho\Big)^2 = 0,$$

so for all $i \in \{1,\dots,N\}$,

$$\sum_{j=1}^N \frac{\rho_j}{\rho}K_0(x_i - x_j) = \nu\rho. \quad (3.23)$$

We define the matrix $\underline{\mathbf{K}}$, whose coefficient with indices (i,j) is equal to $K_0(x_i - x_j)$. $\underline{\mathbf{K}}$ is symmetric with positive coefficients and constant main diagonal (equal to $K_0(0)$). If the family $(x_i)_{1\le i\le N}$ is given, the problem amounts to finding a positive vector P such that $\underline{\mathbf{K}}P = \mathbb{1}$. (Then $\rho = 1/\mathbb{1}^T P$ and $\rho_i = P_i\rho^2$).

It is easily checked that if

$$\max_{i\neq j} K_0(x_i - x_j) < \frac{K_0(0)}{N-1}$$

then $\underline{\mathbf{K}}$ is invertible (in this case indeed, $\underline{\mathbf{K}}$ is strictly diagonally dominant). It is worth noting that if $N = 2$ and $\max K_0 = K_0(0)$, with the maximum of K_0 being reached only at 0, then this is always satisfied. However, in the generic case when $(x_i)_i$ is such that $\underline{\mathbf{K}}$ is invertible, it remains unclear whether $P := \underline{\mathbf{K}}^{-1}\mathbb{1} > 0$ or not.

In order to study in more details the structure of solutions, we might use the Hopf-Cole transformation $n_\varepsilon = e^{u_\varepsilon/\varepsilon}$. We obtain

$$\partial_t u_\varepsilon(t,x) = \frac{K * n_\varepsilon(t,\cdot)}{\rho_\varepsilon(t)}(x) - \nu\rho_\varepsilon(t).$$

An analysis of a general form of this equation is performed in Section 4.

3.4 BV estimates on the total population

In this section, we derive BV estimates assuming that R is independent from the trait variable and features a linear dependency on ρ, which is specified by assumption (3.7). Thereafter we address the difficulties encountered when R has a general form.

3.4.1 Linear dependency on the competition variable in the AF model

Although the asymptotic behavior of n_ε solution to (3.1) may be difficult to obtain in general, under some assumptions on K and R, the total population ρ_ε can be proved to have bounded variations.

Recall that, integrating equation (3.1), we have

$$\varepsilon\dot{\rho}_\varepsilon = \frac{1}{\rho_\varepsilon}\iiint K_\varepsilon(x,y,z)n_\varepsilon(t,y)n_\varepsilon(t,z)dx\,dy\,dz - \int R(x,\rho_\varepsilon)n_\varepsilon(t,x)\,dx.$$

The proofs of Theorems 3.2 and 3.3 rely on estimates obtained through the equation satisfied by $\ddot{\rho}_\varepsilon$. In general, we start from

$$\begin{aligned}\varepsilon\ddot{\rho}_\varepsilon = &-\frac{\dot{\rho}_\varepsilon}{\rho_\varepsilon^2}\iiint K_\varepsilon(x,y,z)n_\varepsilon(t,y)n_\varepsilon(t,z)dx\,dy\,dz\\ &+\frac{1}{\rho_\varepsilon}\iiint K_\varepsilon(x,y,z)\big(\partial_t n_\varepsilon(t,y)n_\varepsilon(t,z) + n_\varepsilon(t,y)\partial_t n_\varepsilon(t,z)\big)dx\,dy\,dz\\ &-\dot{\rho}_\varepsilon\int \partial_\rho R(x,\rho)n_\varepsilon(t,x)dx\\ &-\int R(x,\rho_\varepsilon)\Big(\frac{1}{\varepsilon\rho_\varepsilon}\iint K_\varepsilon(x,y,z)n_\varepsilon(t,y)n_\varepsilon(t,z)dy\,dz - R(x,\rho_\varepsilon)n_\varepsilon(t,x)\Big)dx. \quad (3.24)\end{aligned}$$

Proof of Theorem 3.2. We treat the case of the model with asymmetric fecundity. Then, ρ_ε satisfies

$$\varepsilon\dot{\rho}_\varepsilon = \int B(x)n_\varepsilon(t,x)dx - \nu\rho_\varepsilon^2,$$

and (3.24) reads

$$\begin{aligned}\varepsilon\ddot{\rho} &= \int B(x)\partial_t n_\varepsilon(t,x)dx - 2\nu\rho_\varepsilon\dot{\rho}_\varepsilon \\ &= -\nu\rho_\varepsilon\dot{\rho}_\varepsilon + \frac{\nu^2}{\varepsilon}\rho_\varepsilon^3 - \frac{\nu\rho_\varepsilon}{\varepsilon}\int B(x)n_\varepsilon(t,x)dx \\ &+ \frac{1}{\varepsilon\rho_\varepsilon}\iiint \alpha_\varepsilon(x,y,z)B(x)B(y)n_\varepsilon(t,y)n_\varepsilon(t,z)dx\,dy\,dz - \frac{\nu\rho_\varepsilon}{\varepsilon}\int B(x)n_\varepsilon(t,x)dx.\end{aligned}$$

Which we rewrite as

$$\begin{aligned}\varepsilon\frac{d}{dt}\dot{\rho}_\varepsilon = -\nu\rho_\varepsilon\dot{\rho}_\varepsilon + \overbrace{\frac{\rho_\varepsilon}{\varepsilon}\left(\frac{\int B(x)n_\varepsilon(t,x)dx}{\rho_\varepsilon} - \nu\rho_\varepsilon\right)^2}^{\text{demographic stabilization}} \\ + \underbrace{\frac{1}{\varepsilon\rho_\varepsilon}\Big(\iiint \alpha_\varepsilon(x,y,z)B(x)B(y)n_\varepsilon(t,y)n_\varepsilon(t,z)dx\,dy\,dz - \big(\int B(x)n_\varepsilon(t,x)dx\big)^2\Big)}_{\text{mixing-induced fecundity variation}}.\end{aligned} \tag{3.25}$$

In order to apply the same technique as for the simple case (3.5), we need to assume that the mixing-induced fecundity variation term is bounded from below.

Under (3.11), we obtain from (3.25) and Proposition 3.5

$$\varepsilon\frac{d}{dt}\dot{\rho}_\varepsilon \geq -\nu\rho_\varepsilon\dot{\rho}_\varepsilon - C. \tag{3.26}$$

And from Proposition 3.8, we deduce

$$\frac{d}{dt}(\dot{\rho}_\varepsilon)_- \leq -\frac{\nu\rho_m}{\varepsilon}(\dot{\rho}_\varepsilon)_- + \frac{C}{\varepsilon},$$

and thus $(\dot{\rho}_\varepsilon)_-(t) \leq e^{-\frac{\nu\rho_m t}{\varepsilon}}(\dot{\rho}_\varepsilon)_-(0) + \frac{C}{\nu\rho_m}\big(1 - e^{-\frac{\nu\rho_m t}{\varepsilon}}\big)$. Then we use the same argument we used to treat case without mutations in the previous section, which proves uniform boundedness of $(\rho_\varepsilon)_\varepsilon$ in $BV(0,T)$, for all $T > 0$. □

We discuss assumption (3.11). Firstly, if B is constant then it is obviously satisfied.

Secondly, by taking ϕ concentrated at a point x_M where B reaches its maximum, we obtain

$$\int \alpha_\varepsilon(x,x_M,x_M)B(x)dx \geq B(x_M) - C\epsilon.$$

Recalling that $\int \alpha_\varepsilon(x,y,z)dx = 1$ for all y,z, this implies that as ε goes to 0, $\alpha_\varepsilon(\cdot,x_M,x_M)$ is concentrated at points where B is equal to its maximum $B(x_M)$, which is a restrictive necessary condition for (3.11) to hold.

Thirdly, we state a sufficient condition: if $\alpha_\varepsilon(\cdot, y, z) \to \alpha_0(y, z) \in \mathcal{M}^1$ with either

$$\forall y, z, \quad \int \alpha_0(y, z)(x)B(x)dx \geq B(y)$$

or

$$\forall y, z, \quad \int \alpha_0(y, z)(x)B(x)dx \geq B(z),$$

and if convergence is sufficiently fast, then (3.11) holds. In the first case this is a consequence of the Cauchy-Schwarz inequality, and in the second case we simply obtain that the left-hand side in (3.11) converges to 0 as $\varepsilon \to 0$. In particular, we may assume $\alpha_\varepsilon(x, y, z) = \frac{1}{\varepsilon}G\big(\frac{x-y}{\varepsilon}\big)$ or $\frac{1}{\varepsilon}G\big(\frac{x-z}{\varepsilon}\big)$ for some appropriate kernel G. These situations are those we have in mind, although (3.11) in all generality may allow for some other cases.

All in all, (3.11) means that the trait inheritance pattern α_ε does not allow next-generation's fecundity to get smaller than the current one's as $\varepsilon \to 0$. Unsurprisingly, this dissipative feature implies that the variations of ρ can be controlled as $\varepsilon \to 0$, as stated in Theorem 3.2.

3.4.2 Linear dependency on the competition variable in the ATH model

We now address the case of the model with asymmetric trait heredity, which we refer to as the ATH model.

Remark 3.9. *In order to apply the same technique as for the model without mutations addressed in Section 3.3, we need a convergence assumption on G_ε as ε goes to 0. Specifically, we use the following assumption: for all Lipschitz function ϕ, we have*

$$G_\varepsilon * \phi = \phi + O(\varepsilon). \tag{3.27}$$

This assumption on the convergence of G_ε as ε goes to 0 holds in the typical example where G_ε is Gaussian with variance ε^2. It means that there exists $C \in \mathbb{R}_+^*$ such that for all $\varepsilon > 0$, $\phi \in W^{1,\infty}$ with $\|\phi\|_{Lip} \leq 1$ and $\psi \in L^\infty$ with $\|\psi\|_{L^\infty} \leq 1$,

$$\Big| \int \psi(x)(G_\varepsilon * \phi)(x)dx - \int \psi(x)\phi(x)dx \Big| \leq C\varepsilon.$$

Specifically, we write $G_\varepsilon(x) = \frac{1}{(2\pi\varepsilon^2)^{d/2}} e^{-x^2/2\varepsilon^2}$. Then we compute

$$\begin{aligned}\delta &:= \Big| \int \psi(x)(G_\varepsilon * \phi)(x)dx - \int \psi(x)\phi(x)dx \Big| \\ &\leq \int |\psi(x)||G_\varepsilon * \phi(x) - \phi(x)|dx \leq \int \int \frac{1}{(2\pi\varepsilon^2)^{d/2}} e^{-\frac{(x-y)^2}{2\varepsilon^2}} |\phi(y) - \phi(x)|dydx.\end{aligned}$$

We apply the change of variables $\hat{y} = (2\varepsilon)^{-1}(y - x)$, so $d\hat{y} = (2\varepsilon)^{-d}dy$, to get

$$\delta \leq \pi^{-d/2} \int \int e^{-\hat{y}^2} |\phi(x + 2\varepsilon\hat{y}) - \phi(x)|d\hat{y}dx \leq \frac{2\|\phi\|_{Lip}}{(2\pi)^{d/2}}\varepsilon.$$

Proof of Theorem 3.3. Departing from (3.3), the equation satisfied by ρ_ε reads

$$\varepsilon \frac{d}{dt}\rho_\varepsilon(t) = \int_{\mathbb{R}} \left(\frac{1}{\rho_\varepsilon(t)} K * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) - \nu \rho_\varepsilon(t) n_\varepsilon(t,x) \right) dx.$$

Differentiating this equation, we obtain

$$\begin{aligned}
\varepsilon \ddot{\rho}_\varepsilon(t) = \; & \frac{1}{\rho_\varepsilon(t)} \int_{\mathbb{R}} \left[K_0 * \partial_t n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) + K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * \partial_t n_\varepsilon(t,\cdot)(x) \right] dx \\
& - \nu \rho_\varepsilon(t) \frac{d}{dt}\rho_\varepsilon(t) - \nu \int \partial_t n_\varepsilon(t,x) \rho_\varepsilon(t) dx \\
& - \frac{\dot{\rho}_\varepsilon(t)}{\rho_\varepsilon^2(t)} \int \left[K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) \right] dx
\end{aligned}$$

By the same trick as in Section 3.3, assuming (3.9) induces

$$\begin{aligned}
\varepsilon \ddot{\rho}_\varepsilon(t) = \; & \frac{1}{2\rho_\varepsilon(t)} \frac{d}{dt} \left[\int K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) dx \right] \\
& + \frac{1}{\rho_\varepsilon(t)} \int \left[G_\varepsilon * (K_0 * n_\varepsilon(t,\cdot))(x) \partial_t n_\varepsilon(t,x) \right] dx \\
& - \nu \rho_\varepsilon(t) \frac{d}{dt}\rho_\varepsilon(t) - \nu \int \partial_t n_\varepsilon(t,x) \rho_\varepsilon(t) dx \\
& - \frac{\dot{\rho}_\varepsilon(t)}{\rho_\varepsilon^2(t)} \int \left[K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) \right] dx.
\end{aligned}$$

Then we compute

$$\begin{aligned}
\varepsilon \ddot{\rho}_\varepsilon(t) = & \frac{1}{2\rho_\varepsilon(t)} \frac{d}{dt} \left[\int K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) dx \right] \\
& + \frac{1}{\varepsilon} \frac{1}{\rho_\varepsilon(t)} \int G_\varepsilon * (K_0 * n_\varepsilon(t,\cdot))(x) \left[\frac{1}{\rho_\varepsilon(t)} K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) - \nu n_\varepsilon(t,x) \rho_\varepsilon(t) \right] dx \\
& - \nu \rho_\varepsilon(t) \frac{d}{dt}\rho_\varepsilon(t) - \frac{\nu}{\varepsilon} \rho_\varepsilon(t) \int \left[\frac{1}{\rho_\varepsilon(t)} K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) - \nu n_\varepsilon(t,x) \rho_\varepsilon(t) \right] dx \\
& - \frac{\dot{\rho}_\varepsilon(t)}{\rho_\varepsilon^2(t)} \int \left[K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) \right] dx,
\end{aligned}$$

and get

$$\begin{aligned}
\varepsilon \ddot{\rho}_\varepsilon(t) = & -\nu \rho_\varepsilon(t) \frac{d}{dt}\rho_\varepsilon(t) + \frac{1}{2} \frac{d}{dt} \left[\int \frac{1}{\rho_\varepsilon(t)} K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) dx \right] \\
& - \frac{1}{2} \frac{\dot{\rho}_\varepsilon(t)}{\rho_\varepsilon^2(t)} \int \left[K_0 * n_\varepsilon(t,\cdot)(x) G_\varepsilon * n_\varepsilon(t,\cdot)(x) \right] dx \\
& + \frac{1}{\varepsilon} \int (G_\varepsilon * n_\varepsilon) \left[G_\varepsilon * (K_0 * n_\varepsilon) \frac{(K_0 * n_\varepsilon)}{\rho_\varepsilon^2} - 2\nu K_0 * n \right] dx + \frac{1}{\varepsilon} \nu^2 \rho_\varepsilon^2 \int G_\varepsilon * n_\varepsilon \, dx.
\end{aligned}$$

We rewrite this as

$$\varepsilon\ddot{\rho}_\varepsilon(t) = -\nu\rho_\varepsilon(t)\dot{\rho}_\varepsilon(t) - \frac{1}{2}\frac{\dot{\rho}_\varepsilon(t)}{\rho_\varepsilon^2(t)}\int K_0 * n_\varepsilon(t,\cdot)G_\varepsilon * n_\varepsilon(t,\cdot)$$
$$+\frac{1}{\varepsilon}\int (G_\varepsilon * n_\varepsilon)\left[\frac{(K_0 * n_\varepsilon)}{\rho_\varepsilon} - \nu\rho_\varepsilon\right]^2 dx$$
$$+\frac{1}{\varepsilon\rho_\varepsilon^2(t)}\int (K_0 * n_\varepsilon)(G_\varepsilon * n_\varepsilon)\Big(G_\varepsilon * (K_0 * n_\varepsilon) - K_0 * n_\varepsilon\Big)dx.$$

Now we use the convergence assumption (3.27) on G_ε. We simply need to check that $\phi(x) := \int K_0(x-y)n_\varepsilon(t,y)dy$ is Lipschitz. But obviously, $|\phi'| \le \|K_0'\|_{L^\infty}\rho_\varepsilon(t)$. Hence

$$\begin{aligned}\frac{\varepsilon}{2}\ddot{\rho}_\varepsilon(t) &= -\nu\rho_\varepsilon(t)\dot{\rho}_\varepsilon(t) - \frac{1}{2}\frac{\dot{\rho}_\varepsilon(t)}{\rho_\varepsilon^2(t)}\int K_0 * n_\varepsilon(t,\cdot)G_\varepsilon * n_\varepsilon(t,\cdot)\\ &+\frac{1}{\varepsilon}\int (G_\varepsilon * n_\varepsilon)\left[\frac{(K_0 * n_\varepsilon)}{\rho_\varepsilon} - \nu\rho_\varepsilon\right]^2 dx + O(1).\end{aligned} \tag{3.28}$$

Thanks to (3.13), we obtain

$$\frac{\varepsilon}{2}\frac{d}{dt}(\dot{\rho}_\varepsilon(t))_- \le -\big(\frac{1}{2}\eta_0 + \nu\rho_\varepsilon(t)\big)(\dot{\rho}_\varepsilon(t))_- + O(1).$$

Then, ρ_ε is bounded in $BV_{\text{loc}}(\mathbb{R}_+)$ uniformly in ε. Indeed, we obtain that for some constants $C_1, C_2 > 0$,

$$(\dot{\rho}_\varepsilon(t))_- \le e^{-C_1 t/\varepsilon}\Big((\dot{\rho}_\varepsilon(0))_- + \frac{C_2}{\varepsilon}\int_0^t e^{C_1 t'/\varepsilon}dt'\Big),$$

hence

$$(\dot{\rho}_\varepsilon(t))_- \le (\dot{\rho}_\varepsilon(0))_- e^{-C_1 t/\varepsilon} + \frac{C_2}{C_1}\big(1 - e^{-C_1 t/\varepsilon}\big).$$

As in the proof of Theorem 3.1, we deduce that for all $T > 0$, $(\rho_\varepsilon)_\varepsilon$ is uniformly (in ε) bounded in $BV([0,T])$.

Going back to (3.28), we deduce the estimate, for $T > 0$

$$\int_0^T\int_x (G_\varepsilon * n_\varepsilon)\left[\frac{K_0 * n_\varepsilon}{\rho_\varepsilon} - \nu\rho_\varepsilon\right]^2 dxdt = O(\varepsilon),$$

as in the proof of Theorem 3.1.

□

3.4.3 Questions and difficulties for the general case

Firstly, we address the case of a general saturation term for the AF model, featuring the competition effect and the trait-dependency:

$$R \in \mathcal{C}^1(\mathbb{R}^d \times \mathbb{R}_+; \mathbb{R}_+), \quad K(x,y,z) = B(y)\alpha_\varepsilon(x,y,z), \quad \forall y, z, \int \alpha_\varepsilon(x,y,z)dx = 1.$$

Then, we find

$$\varepsilon\frac{d}{dt}\dot{\rho}_\varepsilon = \int \big(B(x) - R(x,\rho_\varepsilon)\big)\partial_t n_\varepsilon(t,x)dx - \dot{\rho}_\varepsilon\int \partial_\rho R(x,\rho_\varepsilon)n_\varepsilon(t,x)dx$$

$$= -\dot{\rho}_\varepsilon \int \partial_\rho R(x,\rho_\varepsilon) n_\varepsilon(t,x)dx + \frac{1}{\varepsilon}\int n_\varepsilon(t,x)\big(R(x,\rho_\varepsilon)-B(x)\big)^2$$
$$+\frac{1}{\varepsilon}\int \big(B(x)-R(x,\rho_\varepsilon)\big)\Big(\frac{1}{\rho_\varepsilon}\iint \alpha_\varepsilon(x,y,z)B(y)n_\varepsilon(t,y)n_\varepsilon(t,z)dy\,dz - B(x)n_\varepsilon(t,x)\Big)dx$$

The last term can be seen as the integral of the net fitness $B - R(\cdot,\rho_\varepsilon)$ weighted by a fecundity variation $\Delta_{n_\varepsilon(t,\cdot)}B$ (with $\int \Delta_{n_\varepsilon(t,\cdot)}B(x)dx = 0$).

To apply the same argument as before, we need to assume

$$\begin{aligned}&\exists C>0,\ \forall\varepsilon>0,\ \forall y,z,\ \forall\phi\in L^1_+ \text{ with } \|\phi\|_{L^1}=1,\\ &\Big\|\iint \alpha_\varepsilon(\cdot,y,z)B(y)\phi(y)\phi(z)dydz - B(\cdot)\phi(\cdot)\Big\|_{L^1}\le C\varepsilon,\end{aligned} \tag{3.29}$$

and we also assume that

$$\forall\rho\le\rho_M, C_f(\rho) := \|B(\cdot)-R(\cdot,\rho)\|_\infty<\infty,\quad \overline{C_f} = \sup_{0\le\rho\le\rho_M} C_f(\rho). \tag{3.30}$$

Under assumptions (3.29) and (3.30), this additional term is treated as in the case (3.7), replacing the negative constant on the right-hand side of (3.26) by $-\rho_M C\overline{C_f}$, which gives

$$\varepsilon\frac{d}{dt}\dot{\rho}_\varepsilon(t) \ge -\dot{\rho}_\varepsilon\int \partial_\rho R(x,\rho_\varepsilon)n_\varepsilon(t,x)dx - \rho_M C\overline{C_f}.$$

Therefore, similarly to the proof of Theorem 3.2, we obtain

Lemma 3.10. *Assume* (3.29) *and* (3.30). *Then, for all* $T>0$, $(\rho_\varepsilon)_\varepsilon$ *is uniformly in* ε *bounded in* $BV([0,T])$.

Secondly, we address the case of a general death term for the ATH model:

$$R\in\mathcal{C}^1(\mathbb{R}^d\times\mathbb{R}_+;\mathbb{R}_+),\quad K_\varepsilon(x,y,z) = G_\varepsilon(x-z)K_0(x-y).$$

To see clearly where the difficulty lies, we replace $G_\varepsilon(x-z)$ by $\delta_{x=z}$ (letting $\varepsilon\to0$ in this term only). For simplicity, we define

$$\zeta(t,x) := \frac{K_0 * n_\varepsilon(t,\cdot)}{\rho_\varepsilon(t)},\quad Q(t) := \int \partial_\rho R(x,\rho_\varepsilon(t))n_\varepsilon(t,x)dx.$$

After computations similar to the previous ones, we find

$$\frac{1}{2}\varepsilon\frac{d}{dt}\dot{\rho}_\varepsilon = -\frac{\dot{\rho}_\varepsilon}{2\rho_\varepsilon}\int n_\varepsilon\zeta + \frac{1}{\varepsilon}\int n_\varepsilon\Big[\zeta^2 - R\zeta + \frac{R+Q}{2}(R-\zeta)\Big], \tag{3.31}$$

and the term in $\frac{1}{\varepsilon}$ rewrites

$$\int n(\zeta - \frac{R+Q}{2})(\zeta-R).$$

Meanwhile, one can check that

$$\varepsilon\dot{\rho}_\varepsilon = \int n_\varepsilon(\zeta-R).$$

When $\dot{\rho}_\varepsilon \leq 0$ we would like to prove that the term in $\frac{1}{\varepsilon}$ in (3.31) is non-negative. We could be less restrictive and simply require $\ddot{\rho}_\varepsilon \geq 0$. This reads (with $q_\varepsilon(t,x) = n_\varepsilon(t,x)/\rho_\varepsilon(t)$):

$$\int q_\varepsilon(t,x)\big(\zeta(t,x) - R(x,\rho_\varepsilon(t))\big)\Big(\zeta(t,x) - \frac{R(x,\rho_\varepsilon(t)) + Q(t)}{2} - \int q_\varepsilon(t,y)\zeta(t,y)dy\Big)dx \geq 0$$

if

$$\int q_\varepsilon(t,x)\big(\zeta(t,x) - R(x,\rho_\varepsilon(t))\big)dx \leq 0.$$

By a straightforward computation, we deduce

Lemma 3.11. *If $R(x,\rho) = R_0(\rho)$ and $\rho R_0'(\rho) \geq R_0(\rho)$, then $\dot{\rho}_\varepsilon \leq 0$ implies $\ddot{\rho}_\varepsilon \geq -\frac{\dot{\rho}_\varepsilon}{2\rho_\varepsilon}\int n\zeta$. Then in particular for all $T > 0$, $(\rho_\varepsilon)_\varepsilon$ is uniformly in ε bounded in $BV([0,T])$.*

For instance, this is the case if $R_0(\rho) = \nu\rho^\gamma$ for some $\gamma \geq 1$. In general however, this is an inequality which is still to be understood.

3.5 The Hamilton-Jacobi equation

In our context, the Hamilton-Jacobi approach has been introduced in [68] and then developped in [96, 128] to study the concentration effect for phenotypically structured PDEs. This consists in determining the possible Dirac distributions through the zeroes of u_ε defined from the Hopf-Cole transform

$$u_\varepsilon(t,x) = \varepsilon \ln n_\varepsilon(t,x).$$

In the mentioned works, the convergence of u_ε as ε goes to 0 is rigorously established and the limit u satisfies a constrained Hamilton-Jacobi equation, using the theory of viscosity solutions (see [9] for an introduction). The constraint on the solution u reads

$$\max_{x\in\mathbb{R}} u(t,x) = 0, \quad \forall t > 0$$

and comes from the control in L^1 of the total population. Then, some properties on the concentration points can be derived from the study of the constrained Hamilton-Jacobi equation and the solution u. In some particular cases, it is proved that the population density remains monomorphic, that is composed of a single Dirac mass, and then a form of canonical equation is derived, giving the dynamics of the dominant trait.

In the present work, a Hamilton-Jacobi structure arises in the different situations presented above. We show in this section different results obtained by applying the Hamilton-Jacobi approach, especially on the regularity of u_ε. The main difficulties that we encounter are the time-dependency of the coefficients and their lack of regularity.

Asymmetric fecundity: we use the particular form

$$K_\varepsilon(x,y,z) = B(y)\frac{1}{\varepsilon}\alpha\left(\frac{x-z}{\varepsilon}, y\right) \text{ with } \int \alpha(z',y)dz' = 1 \text{ for all } y,$$

and define

$$b_\varepsilon(t,x) := R(x,\rho_\varepsilon(t)), \quad q_\varepsilon(t,y) = \frac{n_\varepsilon(t,y)}{\rho_\varepsilon(t)}. \tag{3.32}$$

In this case, the equation on u_ε reads

$$\partial_t u_\varepsilon(t,x) = \int B(y) q_\varepsilon(t,y) \int \alpha(z,y) e^{\frac{u_\varepsilon(t,x-\varepsilon z)-u_\varepsilon(t,x)}{\varepsilon}} dz dy - b_\varepsilon(t,x), \tag{3.33}$$

and we compute the formal limiting equation

$$\begin{aligned} \partial_t u(t,x) &= \int B(y) q(t,y) \int \alpha(z,y) e^{-\partial_x u(t,x)\cdot z} dz dy - b(t,x) \\ &= \int B(y) q(t,y) \mathcal{L}[\alpha(\cdot,y)](\partial_x u(t,x)) dy - b(t,x), \end{aligned} \tag{3.34}$$

with $\mathcal{L}[\alpha(\cdot,y)]$ the Laplace transform of $\alpha(\cdot,y)$ for all y:

$$\mathcal{L}[\alpha](p) := \int \alpha(z) e^{-p\cdot z} dz,$$

for α a probability density function.

Assymetric trait heredity: The interest of this problem comes from the time- and trait-dependent coefficients of the Hamiltonian. We use the generic form

$$K_\varepsilon(x,y,z) = G_\varepsilon(x-z) K_1(x,y).$$

After the change of variable $z' = \frac{x-z}{\varepsilon}$, the equation on u_ε reads

$$\partial_t u_\varepsilon(t,x) = \frac{1}{\rho_\varepsilon(t)} \int K_1(x,y) n_\varepsilon(t,y) dy \cdot \int G(z') e^{\frac{u_\varepsilon(t,x-\varepsilon z')-u_\varepsilon(t,x)}{\varepsilon}} dz' - b_\varepsilon(t,x). \tag{3.35}$$

For clarity, we define

$$a_\varepsilon(t,x) := \int K_1(x,y) q_\varepsilon(t,y) dy \geq 0. \tag{3.36}$$

At the limit $\varepsilon \to 0$, we obtain the formal limiting equation

$$\begin{aligned} \partial_t u(t,x) &= a(t,x) \int G(z) e^{-\partial_x u(t,x)\cdot z} dz - b(t,x) \\ &= a(t,x) \mathcal{L}[G](\partial_x u(t,x)) - b(t,x), \end{aligned} \tag{3.37}$$

with a and b the formal limits of a_ε and b_ε defined in (3.36) and (3.32), and $\mathcal{L}[G]$ the Laplace transform of G. From now on, we choose G such that its Laplace transform is well defined on $\mathbb{R}$.

In the case G is the gaussian density, the equation on u_ε reads

$$\partial_t u_\varepsilon(t,x) = a_\varepsilon(t,x) \int \frac{1}{\sqrt{2\pi}} e^{-\frac{|z|^2}{2}} e^{\frac{u_\varepsilon(t,x-\varepsilon z)-u_\varepsilon(t,x)}{\varepsilon}} dz - b_\varepsilon(t,x). \tag{3.38}$$

Then, passing formally to the limit $\varepsilon \to 0$, we arrive at

$$\begin{aligned} \partial_t u(t,x) &= a(t,x) \int \frac{1}{\sqrt{2\pi}} e^{-\frac{|z|^2}{2}} e^{-\partial_x u(t,x)\cdot z} dz - b(t,x) \\ &= a(t,x) e^{(\partial_x u(t,x))^2/2} - b(t,x). \end{aligned}$$

The purpose of this section is to prove for these models the convergence of u_ε as ε vanishes. To this end, we derive a priori estimates on the sequence u_ε in order to use compactness arguments. The uniqueness of the solution to the limit equation has not been determined, thus we only derive convergence up to extraction of subsequences. Moreover, the stability result is not complete, since we do not have convergence results on the coefficients.

We mostly focus on the equation on u_ε (3.38) for the proof of Theorem 3.4, but the arguments are identical for the generic ATH case. The proof of the theorem in the AF case is similar and we also give the formal ideas where it is necessary.

Assumptions: We assume on the function R

$$\exists C_0 > 0,\, \forall \rho_m \leq \rho \leq \rho_M,\, \forall x \in \mathbb{R}, \quad R(x,\rho) \leq C_0(1+|x|), \tag{3.39}$$

$$\exists L_b > 0, \forall \rho_m \leq \rho \leq \rho_M,\, \forall x \in \mathbb{R}, \quad |\partial_x R(x,\rho)| \leq L_b. \tag{3.40}$$

We choose the positive function K_1 bounded

$$\exists \bar{K} > 0, \forall x, y \in \mathbb{R}, \quad K_1(x,y) \leq \bar{K}, \tag{3.41}$$

and such that,

$$\exists \lambda > 0, \exists C_\lambda > 0, \forall \varepsilon > 0, t \geq 0, x \in \mathbb{R}, \quad e^{\frac{|\partial_x a_\varepsilon(t,x)|}{\lambda a_\varepsilon(t,x)}} \lambda a_\varepsilon(t,x) \leq C_\lambda. \tag{3.42}$$

This assumption is satisfied for example when K_1 is bounded and there exists a constant L_K such that

$$|\partial_x K_1(x,y)| \leq L_K |K_1(x,y)|, \quad \forall x, y \in \mathbb{R},$$

or, when K_1 induces a gaussian type distribution for a_ε, that is,

$$a_\varepsilon(t,x) \sim C e^{\frac{-(x-m)^2}{\sigma^2}}.$$

We also assume on the initial condition

$$u_\varepsilon^0(x) \leq -A|x| + C, \quad \|\partial_x u_\varepsilon^0\| \leq L_0. \tag{3.43}$$

For the model with asymmetric fecundity, we assume that B and α are positive and bounded. For both models under investigation, we prove Theorem 3.4.

3.5.1 A priori bounds

We begin with the estimates for the ATH case, and especially with a gaussian trait female heredity distribution.

Lemma 3.12. *Let u_ε be solution to equation* (3.38)*. Then, there exist constants $C_1 > 0$ and $C_2 > 0$, such that for all $t > 0, x \in \mathbb{R}$ and $\varepsilon > 0$ we have*

$$-C_1(1+t)(1+|x|) \leq u_\varepsilon(t,x) \leq -A|x| + C_2(1+t).$$

We prove this lemma in the case of a gaussian trait female heredity distribution, but the argument exactly applies to equation (3.35) in the generic ATH case.

Proof. We first prove the lower bound

$$u_\varepsilon(t,x) \geq -C_1(1+t)(1+|x|).$$

Indeed, because $a_\varepsilon \geq 0$ and $\mathcal{L}(G) \geq 0$, we deduce from (3.39) that

$$\partial_t u_\varepsilon \geq -b_\varepsilon(t,x) \geq -C_0(1+|x|).$$

From (3.43) we obtain

$$u_\varepsilon(t,x) \geq \inf_\varepsilon u_\varepsilon^0(0) - \inf_\varepsilon \|\partial_x u_\varepsilon^0\| - C_0 t(1+|x|).$$

Hence the lower bound.

We also derive the inequality

$$u_\varepsilon(t,x) \leq -A|x| + C_2(1+t),$$

where $C_2 = \bar{K}\frac{1}{\sqrt{2\pi}}\int e^{-|z|^2/2}e^{A|z|}dz$. Indeed, defining $v(t,x) := -A|x| + C_2(1+t)$, we compute

$$\partial_t v(t,x) - a_\varepsilon(t,x)\int \frac{1}{\sqrt{2\pi}}e^{-|z|^2/2}e^{\frac{v(t,x-\varepsilon z)-v(t,x)}{\varepsilon}}dz \geq C_2 - \bar{K}\frac{1}{\sqrt{2\pi}}\int e^{-|z|^2/2}e^{A|z|}dz \geq 0.$$

Thus, v is a supersolution of (3.38), and since $u^0(x) \leq v(0,x)$ we deduce that $u_\varepsilon(t,x) \leq v(t,x)$ by a comparison principle argument. □

We obtain the same kind of bounds for the asymmetric fecundity case.

Lemma 3.13. *Let u_ε be solution to equation* (3.33)*. Then, there exist constants $C_1 > 0$ and $C_2 > 0$, such that for all $t > 0, x \in \mathbb{R}$ and $\varepsilon > 0$ we have*

$$-C_1(1+t)(1+|x|) \leq u_\varepsilon(t,x) \leq -A|x| + C_2(1+t),$$

where $C_2 = \sup_y B(y)\int \alpha(z,y)e^{|A|z}dz$.

3.5.2 Regularity in space

We prove the following

Lemma 3.14. *Let u_ε be the solution to the equation* (3.38)*. For $\lambda > 0$ given by* (3.42) *and for all $t > 0, x \in \mathbb{R}$, we have*

$$|\partial_x u_\varepsilon(t,x)| \leq \|\partial_x u_\varepsilon^0\|_{L^\infty} + (C_\lambda + L_b)t + \lambda\left(\sup_\varepsilon \|u_\varepsilon^0\|_{L^\infty} + C_1(1+t)(1+|x|)\right).$$

This implies that u_ε is Lipschitz in space, uniformly in ε and locally in time.

Proof. We use the notations

$$p_\varepsilon(t,x) = \partial_x u_\varepsilon(t,x), \quad p(t,x) = \partial_x u(t,x).$$

Differentiating (3.38), p_ε satisfies

$$\begin{aligned}\partial_t p_\varepsilon(t,x) &= \partial_x a_\varepsilon(t,x) \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{\frac{u_\varepsilon(t,x-\varepsilon z)-u_\varepsilon(t,x)}{\varepsilon}} dz \\ &\quad + a_\varepsilon(t,x) \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{\frac{u_\varepsilon(t,x-\varepsilon z)-u_\varepsilon(t,x)}{\varepsilon}} \left(\frac{p_\varepsilon(t,x-\varepsilon z) - p_\varepsilon(t,x)}{\varepsilon} \right) dz - \partial_x b_\varepsilon(t,x).\end{aligned}$$

Let $\lambda > 0$. We define

$$w_\varepsilon^\lambda(t,x) = p_\varepsilon(t,x) + \lambda u_\varepsilon(t,x), \quad D_\varepsilon(t,x,z) = \frac{u_\varepsilon(t,x-\varepsilon z) - u_\varepsilon(t,x)}{\varepsilon}.$$

Then, w_ε^λ satisfies

$$\begin{aligned}\partial_t w_\varepsilon^\lambda &= a_\varepsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\varepsilon(t,x,z)} \left(\frac{w_\varepsilon^\lambda(t,x-\varepsilon z) - w_\varepsilon^\lambda(t,x)}{\varepsilon} \right) dz \\ &\quad - \lambda \left[a_\varepsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\varepsilon(t,x,z)} (D_\varepsilon(t,x,z) - 1) \right] dy \\ &\quad + \partial_x a_\varepsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\varepsilon(t,x,z)} dz - (\partial_x b_\varepsilon + \lambda b_\varepsilon).\end{aligned}$$

Then, using (3.40), we have

$$\begin{aligned}&\partial_t w_\varepsilon^\lambda - L_b - a_\varepsilon \cdot \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\varepsilon} \left(\frac{w_\varepsilon^\lambda(t,x-\varepsilon z) - w_\varepsilon^\lambda(t,x)}{\varepsilon} \right) dz \\ &\quad \le \int \frac{1}{\sqrt{\pi}} e^{-|z|^2} e^{D_\varepsilon} \left[\partial_x a_\varepsilon + \lambda a_\varepsilon - \lambda a_\varepsilon D_\varepsilon \right] dz.\end{aligned}$$

Defining $f(D) := e^D(\partial_x a_\varepsilon + \lambda a_\varepsilon - \lambda a_\varepsilon D)$, the maximum of f is reached on $D^* := \frac{\partial_x a_\varepsilon}{\lambda a_\varepsilon}$ and equals

$$e^{\frac{\partial_x a_\varepsilon}{\lambda a_\varepsilon}} \lambda a_\varepsilon \le C_\lambda,$$

from (3.42). Then we have the upper bound

$$w_\varepsilon^\lambda(t,x) \le \max_{\mathbb{R}} w_\varepsilon^\lambda(0,x) + Ct, \quad C = C_\lambda + L_b,$$

which implies the upper bound on p_ε

$$p_\varepsilon(t,x) \le \|\partial_x u_\varepsilon^0\|_{L^\infty} + Ct + \lambda \left(\sup_\varepsilon \|u_\varepsilon^0\|_{L^\infty} + C_1(1+t)(1+|x|) \right).$$

We have the same estimate for $-p_\varepsilon$. □

For the AF model, we have the following estimate on the derivative in space of u_ε:

Lemma 3.15. *Let u_ε be the solution of equation* (3.33)*. Then, for all $t > 0, x \in \mathbb{R}$ and $\varepsilon > 0$, we have*

$$|\partial_x u_\varepsilon(t,x)| \leq \|\partial_x u_\varepsilon^0\|_{L^\infty} + L_b t.$$

This implies that u_ε is Lipschitz in space, uniformly in ε and locally in time.

We address the limit equation

$$\partial_t p(t,x) = (-\partial_x p(t,x)) \int B(y)q(t,y) \int z\alpha(z,y)e^{-p(t,x)\cdot z} dz dy - \partial_x b(t,x), \tag{3.44}$$

and give formal arguments, since the proof for the ε-level problem is similar to the one of the ATH case. We compute that $w(t) := \|\partial_x u_\varepsilon^0\|_{L^\infty} + L_b t$ is a supersolution of (3.44). Since $p(0,x) \leq w(0)$ for all $x \in \mathbb{R}$, we deduce that, from the comparison principle, u_ε is Lipschitz in space, uniformly in ε and locally in time.

3.5.3 Regularity in time

In the ATH case, since we proved that u_ε is uniformly Lipschitz in space locally in time, we can deduce that $\partial_t u_\varepsilon$ is locally uniformly bounded.

Lemma 3.16. *Let u_ε be the solution to equation* (3.35) *and let $T > 0$ and $r > 0$ be fixed. Assume* (3.40) *and* (3.41)*. Then, there exists $C(T,r) > 0$ such that, for all $t \in [0,T], x \in B(0,r)$, we have*

$$|\partial_t u_\varepsilon| \leq C(T,r) + \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot,\rho)\|_{L^\infty(B(0,r))}.$$

This implies that u_ε is Lipschitz in time, uniformly in ε.

Proof. Let $T > 0$ and $R > r > 0$ be fixed with R large enough. We choose some constants L_1 and L_2 such that

$$u_\varepsilon(t,x) < -L_1, \quad \forall (t,x) \in [0,T] \times \mathbb{R} \backslash B(0,R),$$

$$|p_\varepsilon| < L_2, \quad \forall (t,x) \in [0,T] \times B(0,R).$$

Then, we obtain for $t \in [0,T], x \in B(0,r)$,

$$|\partial_t u_\varepsilon| \leq \sup_{0 \leq \rho \leq \rho_M} \|R(\cdot,\rho)\|_{L^\infty(B(0,r))}$$
$$+ \frac{1}{\rho_\varepsilon(t)} \int K(x,z) n_\varepsilon(t,z) dz \cdot \left(\int_{|x-\varepsilon y|<R} e^{-|y|^2} e^{L_2 y} dy + \int_{|x-\varepsilon y|>R} e^{-|y|^2} e^{\frac{u_\varepsilon(t,x-\varepsilon y) - u_\varepsilon(t,x)}{\varepsilon}} dy \right).$$

Thus, for ε small enough, and assuming that

$$u_\varepsilon(t,x) > -L_1, \quad \forall t \in [0,T], \forall x \in B(0,r),$$

$$u_\varepsilon(t,x) < -L_1, \quad \forall t \in [0,T], \forall x \in \mathbb{R} \backslash B(0,R),$$

we have

$$
\begin{aligned}
|\partial_t u_\varepsilon| &\leq \overline{K}\left(\int_{|x-\varepsilon y|<R} e^{-|y|^2} e^{L_2 y} dy + \int_{|x-\varepsilon y|>R} e^{-|y|^2} e^{\frac{-L_1-u_\varepsilon(t,x)}{\varepsilon}} dy\right) + \sup_{0\leq\rho\leq\rho_M} \|R(\cdot,\rho)\|_{L^\infty(B(0,r))} \\
&\leq \overline{K}\left(\int e^{-|y|^2} e^{L_2 y} dy + \int_{|x-\varepsilon y|>R} e^{-|y|^2} dy\right) + \sup_{0\leq\rho\leq\rho_M} \|R(\cdot,\rho)\|_{L^\infty(B(0,r))} \\
&\leq \overline{K}\left(\int e^{-|y|^2} e^{L_2 y} dy + \sqrt{\pi}\right) + \sup_{0\leq\rho\leq\rho_M} \|R(\cdot,\rho)\|_{L^\infty(B(0,r))}.
\end{aligned}
$$

Hence the local uniform bound on $\partial_t u_\varepsilon$. □

The proof is similar for the AF case.

Lemma 3.17. *Let u_ε be the solution to equation (3.33) and let $T > 0$ and $r > 0$ be fixed. Then, there exists $C(T,r) > 0$ such that, for all $t \in [0,T], x \in B(0,r)$, we have*

$$
|\partial_t u_\varepsilon| \leq C(T,r) + \sup_{0\leq\rho\leq\rho_M} \|R(\cdot,\rho)\|_{L^\infty(B(0,r))}.
$$

This implies that u_ε is Lipschitz in time, uniformly in ε.

3.5.4 A more precise upper bound

The following argument concerns both cases and gives a sharper upper bound on u_ε.

Lemma 3.18. *Let u_ε be the solution to equation (3.33) or (3.35). Then, for all $x, y \in \mathbb{R}$, we have*

$$
u_\varepsilon(t,x) \leq \varepsilon \ln\left(\rho_M m_{x,\frac{C(1+t)}{\varepsilon}}\right),
$$

where $m_{x,A} > 0$ is the minimum on $\mathbb{R}$ of $g_{x,A} : y \mapsto A\frac{1+\max(|x|,|y|)}{1-e^{-|y-x|A(1+\max(|x|,|y|))}}$.

In addition, if $A > 0$ we have $A < m_{x,A} \leq A + 3/2$. Thus, we obtain the global upper bound

$$
u_\varepsilon(t,x) \leq \varepsilon \ln\left(\rho_M(3/2 + C(1+t)/\varepsilon)\right) \xrightarrow{\varepsilon\to 0} 0.
$$

Proof. For all $z \in (x,y)$, by the mean value theorem there exists $\theta_\varepsilon(t,x,z)$ between x and y such that

$$
u_\varepsilon(t,z) = u_\varepsilon(t,x) + (z-x)\partial_x u_\varepsilon(t,\theta_\varepsilon(t,x,z)).
$$

In addition, by the previous point there exists C (independent of t, x and ε) such that for all t, x, $|\partial_x u_\varepsilon(t,x)| \leq C(1+t)(1+|x|)$. Hence

$$
u_\varepsilon(t,z) \geq u_\varepsilon(t,x) - (z-x)C(1+t)\big(1+\max(|x|,|y|)\big).
$$

Since we have, for $x < y$,

$$
\int_x^y e^{\frac{u_\varepsilon(t,z)}{\varepsilon}} dz \leq \rho_M,
$$

we deduce that

$$
\varepsilon e^{\frac{u_\varepsilon(t,x)}{\varepsilon}} \frac{1-e^{-(y-x)\frac{C(1+t)(1+\max(|x|,|y|))}{\varepsilon}}}{C(1+t)\big(1+\max(|x|,|y|)\big)} \leq \rho_M, \quad \forall y.
$$

Then, we compute

$$u_\varepsilon(t,x) \le \varepsilon \ln\Big(\frac{\rho_M C(1+t)\big(1+\max(|x|,|y|)\big)}{\varepsilon\big(1-e^{-(y-x)\frac{C(1+t)(1+\max(|x|,|y|))}{\varepsilon}}\big)}\Big),$$

and this holds for all $y > x$. We can also choose $y < x$ and get in more generality

$$u_\varepsilon(t,x) \le \varepsilon \ln\Big(\frac{\rho_M C(1+t)\big(1+\max(|x|,|y|)\big)}{\varepsilon\big(1-e^{-|y-x|\frac{C(1+t)(1+\max(|x|,|y|))}{\varepsilon}}\big)}\Big) = \varepsilon \ln\big(\rho_M g_{x,\frac{C(1+t)}{\varepsilon}}(y)\big).$$

Observe that $g_{x,A}$ is positive and goes to $+\infty$ at $y = \pm\infty$ and at $y = x$. Minimizing in y, we find that

$$u_\varepsilon(t,x) \le \varepsilon \ln\big(\rho_M m_{x,\frac{C(1+t)}{\varepsilon}}\big).$$

To conclude we first remark that if $A > 0$ and $x, y \in \mathbb{R}$, then we have

$$\frac{1+\max(|x|,|y|)}{1-e^{-|y-x|A(1+\max(|x|,|y|)}} > 1,$$

so $g_{x,A}(y) > A$ for all $y \in \mathbb{R}$ and thus $m_{x,A} > A$. Then, with $A > 0$ we also have

$$g_{1/A,A}(-1/A) = \frac{A+1}{1-e^{-2(1+A)}} \le A + 3/2,$$

which implies $m_{x,A} \le A + 3/2$. Thus, we obtain the global upper bound

$$u_\varepsilon(t,x) \le \varepsilon \ln\big(\rho_M(3/2 + C(1+t)/\varepsilon)\big) \xrightarrow{\varepsilon\to 0} 0.$$

□

The proof of Theorem 3.4 is achieved.

3.5.5 Discussion on the formal limiting equation

As in the previous chapters, using the Lipschitz regularity, the limit function u satisfies the constraint

$$\max_{x\in\mathbb{R}} u(t,x) = 0, \quad \forall t > 0.$$

Then, when u is differentiable at maximum points, we deduce that $\partial_t u$ equals 0 and, going back to (3.34) and (3.37), we obtain

$$\text{supp } \bar{n} \subset \{(t,x) \in (0,\infty)\times\mathbb{R} | B(x) - b(t,x) = 0\}, \quad \text{in the AF case,}$$

$$\text{supp } \bar{n} \subset \{(t,x) \in (0,\infty)\times\mathbb{R} | a(t,x) - b(t,x) = 0\}, \quad \text{in the ATH case.}$$

It would be then interesting to determine the conditions required to have these null sets reduced to an isolated point. If, for all $t > 0$, we identify a unique point $\bar{x}(t)$ satisfying

$$B(\bar{x}(t)) - b(t,\bar{x}(t)) = B(\bar{x}(t)) - R(\bar{x}(t),\bar{\rho}(t)) = 0, \quad \text{in the AF case,}$$

$$a(t,\bar{x}(t)) - R(\bar{x}(t),\bar{\rho}(t)) = 0, \quad \text{in the ATH case,}$$

then the population is monomorphic, that composed of a single Dirac mass located on $\bar{x}(t)$. Provided some regularity properties on u_ε, we can derive a form of a canonical equation for both AF and ATH, as it is detailed in the previous chapters.

Another viewpoint to investigate the stationary equilibria of these models is the entropy approach for stability. We focus on the model without mutations and consider the stationary problem associated. Let $\overline{n}$ be an Evolutionary Stable Distribution (ESD) in the sense of Jabin-Raoul defined in [88]

$$K_0 * \overline{n} = \nu \overline{\rho}^2 \text{ on } \mathrm{supp}(\overline{n}), \tag{3.45}$$

$$K_0 * \overline{n} \leq \nu \overline{\rho}^2 \text{ on } \mathbb{R}, \tag{3.46}$$

where $\overline{\rho} = \int \overline{n}$.

Let $J(\phi) := \int \big(K_0 * \phi\big)(x)\phi(x)dx$, for $\phi \in \mathcal{M}^1 = \{\psi \geq 0, \int \psi = 1\}$. The functional J is defined over the set of probability measures. We claim that $\overline{n}$ **is an ESD if and only if** $\overline{q} := \overline{n}/\overline{\rho}$ **is a local maximizer of** J. Indeed, let ϕ^* be a local maximizer of J. It is so if and only if for all admissible perturbation h of ϕ^* we have

$$0 \geq \langle dJ(\phi^*), h\rangle = 2\int (K_0 * \phi^*)h.$$

Thus, if $x_1, x_2 \in \mathrm{supp}(\phi^*)$, since $h = \delta_{x_1} - \delta_{x_2}$ is admissible (that is, by definition, $\phi^* + th \in \mathcal{M}^1$ for $t > 0$ small enough), necessarily $(K_0 * \phi^*)(x_1) \leq (K_0 * \phi^*)(x_2)$. The argument is symmetric in x_1, x_2 and thus $K_0 * \phi^*$ must be equal to some constant C on $\mathrm{supp}(\phi^*)$, whence (3.45). Now, if $x_2 \in \mathrm{supp}(\phi^*)$ and $x_1 \in X \backslash \mathrm{supp}(\phi^*)$ then by using the first part of the previous argument we find that $(K_0 * \phi^*)(x_1) \leq C$, whence (3.46). The converse is proved easily.

We now look at the behavior of $J(q)$. Recalling that $q(t,x) = \frac{n(t,x)}{\rho(t)}$, a straightforward computation shows that

$$\begin{aligned}
\partial_t q &= \frac{\partial_t n}{\rho} - \frac{\dot{\rho}}{\rho} q \\
&= q\big(K_0 * q - \nu\rho\big) - q\big(J(q) - \nu\rho\big) \\
&= q\big(K_0 * q - J(q)\big).
\end{aligned}$$

Then, computing $\frac{d}{dt}J(q)$, we arrive at

$$\begin{aligned}
\frac{d}{dt}J(q) &= 2\int \partial_t q \, K_0 * q \\
&= 2\left[\int q(K_0 * q)^2 - \left(\int qK_0 * q\right)^2\right] \\
&\geq 0.
\end{aligned}$$

This is Cauchy-Schwarz inequality, which also implies that equality holds if and only if $K_0 * q$ is constant on the support of q. Since K_0 is bounded, we deduce that $J(q)$ is bounded from above and then converges to a finite value $\overline{J}$ as t goes to $+\infty$.

We also deduce the following equation on ρ

$$\dot{\rho} = \rho(J(q) - \nu\rho).$$

Since $J(q)$ is an increasing function and converges to $\overline{J}$, we obtain by a comparison principle that

$$\rho(t) \xrightarrow[t\to\infty]{} \frac{\bar{J}}{\nu}.$$

Since $\overline{n} = \overline{\rho q}$ (with $\overline{q}$ a probability measure on $\mathbb{R}$) is an ESD if and only if $\overline{q}$ is a local maximizer of J and $\overline{\rho} = J(\overline{q})/\nu$, we hope that these elements will lead to the convergence of $n = \rho q$ to an ESD, combining the convergence of q to a local maximizer of J and the convergence of ρ.

If we assume that K_0 is radial-decreasing, then it can be proved that extremal points in $\text{supp}(\overline{n})$ (if it is bounded) cannot support a positive Dirac mass, by using (3.46). In particular, among all combinations of Dirac masses, only the single-point measure $\overline{n}_{\overline{x}}(x) := K_0(0)/\nu\delta_{x=\overline{x}}$ is an ESD. Indeed, assume that $\bar{n}$ is composed of $k \geq 2$ Dirac masses located on $(x_i)_{1\leq i\leq k}$, then defining

$$\overline{K}(x) := K_0 * \bar{n}(x) = \sum_{i=1}^{k} \rho_i K_0(x - x_i),$$

we deduce from (3.45) and (3.46) that $\overline{K}$ is maximal on the support of $\bar{n}$, that is the points x_i. With no loss of generality, we assume that the sequence (x_i) is ordered and $x_1 = \min_i x_i$. Then, differentiating $\overline{K}$, we obtain

$$\overline{K}'(x_1) = \sum_{i\geq 1} \rho_i K_0'(x_1 - x_i) > 0,$$

which contradicts the optimality of $\overline{K}$ on the support of $\bar{n}$.

3.6 Conclusion and perspectives

Our models under investigation extend to sexual reproduction the studies of the two first chapters when the trait is mainly inherited from the mother. We determined non-extinction conditions and a control on the total population. In the particular case of a saturation term R depending only on the competition, we derived BV estimates on the total population. In general, estimating the variations of ρ_ε when R depends on both trait variable and competition seems difficult. More appropriate assumptions need to be considered.

Concerning the sequences $u_\varepsilon = \varepsilon \ln n_\varepsilon$ associated to each model, we obtained local Lipschitz estimates uniform in ε. To deduce the convergence of u_ε to the solution of the limiting Hamilton-Jacobi equation with constraint, we still need time compactness on the coefficients of (3.33) and (3.35). In the case without mutations (3.5), if we provide some convergence result on $K * q_\varepsilon$, then, up to extraction of a subsequence, the limit function u has an explicit formulation and its maximum points can be described. In general, Hamilton-Jacobi equations with time- and space-dependent coefficients are difficult to deal with when there is a lack of regularity. The authors in [93] developed a theory of stochastic viscosity solutions to tackle nonlinear stochastic PDEs. In particular, they prove existence, regularity and uniqueness results for the viscosity solution when the time-dependent coefficient of the Hamiltonian can be written as the derivative of a trajectory. This theory does not apply to our models since the coefficients in front of the gradient-dependent term are not under the form of a time derivative.

Another question is the determination of a convenient framework to observe Dirac concentrations. The convergence of the population distribution to a sum of Dirac masses illustrates the selection of well-adapted or dominant phenotypical traits. In [96], the Hamilton-Jacobi approach enables to characterize the dynamics of the dominant traits under specific

assumptions of regularity. The required hypotheses to observe Dirac concentrations are to be clarified.

Another viewpoint has been recently developed in [132] using the Wasserstein distance to study a spatial infinitesimal model. It is proved that the sexual reproduction operator in the infinitesimal model induces a contraction for the Wasserstein distance on the phenotypic trait space, which enables to derive a macroscopic limit for the model, using also some parabolic estimates for the space regularity of the solution. It would be interesting then to explore the Wasserstein approach to investigate general sexual population models.

Bibliographie

[1] A. S. Ackleh, B. G. Fitzpatrick, and H. R. Thieme. Rate distributions and survival of the fittest : a formulation on the space of measures. *Discrete Contin. Dyn. Syst. Ser. B*, 5(4) :917–928, 2005.

[2] M. Adimy, F. Crauste, and S. Ruan. A mathematical study of the hematopoiesis process with applications to chronic myelogenous leukemia. *SIAM J. Appl. Math.*, 65(4) :1328–1352, 2005.

[3] B. Alberts, A. Johnson, J. Lewis, M. Raff, K. Robert, and P. Walter. *Molecular Biology of the Cell.* Garland Science, Taylor & Francis, 2008.

[4] M. Alfaro and R. Carles. Explicit solutions in evolutionary genetics and applications. *C. R. Math. Acad. Sci. Paris*, 353(3) :225–228, 2015.

[5] M. Alfaro and R. Carles. Replicator-mutator equations with quadratic fitness. *Proc. Amer. Math. Soc.*, 145(12) :5315–5327, 2017.

[6] M. Alfaro, J. Coville, and G. Raoul. Travelling waves in a nonlocal reaction-diffusion equation as a model for a population structured by a space variable and a phenotypic trait. *Comm. Partial Differential Equations*, 38(12) :2126–2154, 2013.

[7] M. Bardi and I. Capuzzo-Dolcetta. *Optimal control and viscosity solutions of Hamilton-Jacobi-Bellman equations.* Systems & Control : Foundations & Applications. Birkhäuser Boston, Inc., Boston, MA, 1997. With appendices by Maurizio Falcone and Pierpaolo Soravia.

[8] G. Barles. Regularity results for first order Hamilton-Jacobi equations. *Differential Integral Equations*, 3(1) :103–125, 1990.

[9] G. Barles. *Solutions de viscosité des équations de Hamilton-Jacobi*, volume 17 of *Mathématiques & Applications (Berlin) [Mathematics & Applications].* Springer-Verlag, Paris, 1994.

[10] G. Barles and E. Chasseigne. On the regularizing effect for unbounded solutions of first-order Hamilton-Jacobi equations. *J. Differential Equations*, 260(9) :7020–7031, 2016.

[11] G. Barles, E. Chasseigne, and C. Imbert. Hölder continuity of solutions of second-order non-linear elliptic integro-differential equations. *J. Eur. Math. Soc. (JEMS)*, 13(1) :1–26, 2011.

[12] G. Barles, L. C. Evans, and P. E. Souganidis. Wavefront propagation for reaction-diffusion systems of PDE. *Duke Math. J.*, 61(3) :835–858, 1990.

[13] G. Barles, C. Georgelin, and P. E. Souganidis. Front propagation for reaction-diffusion equations arising in combustion theory. *Asymptot. Anal.*, 14(3) :277–292, 1997.

[14] G. Barles, S. Mirrahimi, and B. Perthame. Concentration in Lotka-Volterra parabolic or integral equations : a general convergence result. *Methods Appl. Anal.*, 16(3) :321–340, 2009.

[15] G. Barles and B. Perthame. Exit time problems in optimal control and vanishing viscosity method. *SIAM J. Control Optim.*, 26(5) :1133–1148, 1988.

[16] G. Barles and B. Perthame. Concentrations and constrained Hamilton-Jacobi equations arising in adaptive dynamics. In *Recent developments in nonlinear partial differential equations*, volume 439 of *Contemp. Math.*, pages 57–68. Amer. Math. Soc., Providence, RI, 2007.

[17] N. Barton, A. Etheridge, and A. Véber. The infinitesimal model : Definition, derivation, and implications. *Theor. Popul. Biol.*, 118 :50–73, 2017.

[18] H. Berestycki, T. Jin, and L. Silvestre. Propagation in a non local reaction diffusion equation with spatial and genetic trait structure. *Nonlinearity*, 29(4) :1434–1466, 2016.

[19] F. Bethuel, H. Brézis, and F. Hélein. *Ginzburg-Landau vortices*, volume 13 of *Progress in Nonlinear Differential Equations and their Applications*. Birkhäuser Boston, Inc., Boston, MA, 1994.

[20] S. Billiard, P. Collet, R. Ferrière, S. Méléard, and V. C. Tran. Stochastic dynamics for adaptation and evolution of microorganisms. *ArXiv e-prints*, Oct. 2016.

[21] S. Billiard, P. Collet, R. Ferrière, S. Méléard, and V. C. Tran. The effect of competition and horizontal trait inheritance on invasion, fixation, and polymorphism. *J. Theoret. Biol.*, 411 :48–58, 2016.

[22] P.-A. Bliman and N. Vauchelet. Establishing Traveling Wave in Bistable Reaction-Diffusion System by Feedback. *ArXiv e-prints*, Mar. 2017.

[23] E. Bouin and V. Calvez. Travelling waves for the cane toads equation with bounded traits. *Nonlinearity*, 27(9) :2233–2253, 2014.

[24] E. Bouin, V. Calvez, N. Meunier, S. Mirrahimi, B. Perthame, G. Raoul, and R. Voituriez. Invasion fronts with variable motility : phenotype selection, spatial sorting and wave acceleration. *C. R. Math. Acad. Sci. Paris*, 350(15-16) :761–766, 2012.

[25] E. Bouin, M. H. Chan, C. Henderson, and P. S. Kim. Influence of a mortality trade-off on the spreading rate of cane toads fronts. *ArXiv e-prints*, Feb. 2017.

[26] E. Bouin, C. Henderson, and L. Ryzhik. Super-linear spreading in local and non-local cane toads equations. *J. Math. Pures Appl. (9)*, 108(5) :724–750, 2017.

[27] E. Bouin and S. Mirrahimi. A Hamilton-Jacobi approach for a model of population structured by space and trait. *Commun. Math. Sci.*, 13(6) :1431–1452, 2015.

[28] T. Bourgeron, V. Calvez, J. Garnier, and T. Lepoutre. Existence of recombination-selection equilibria for sexual populations. *ArXiv e-prints*, Mar. 2017.

[29] H. Brézis. *Functional analysis, Sobolev spaces and partial differential equations.* Universitext. Springer, New York, 2011.

[30] H. Brézis and A. Friedman. Nonlinear parabolic equations involving measures as initial conditions. *J. Math. Pures Appl. (9)*, 62(1) :73–97, 1983.

[31] N. Brunel and V. Hakim. Fast global oscillations in networks of integrate-and-fire neurons with low firing rates. *Neural comput.*, 11(7) :1621–1671, 1999.

[32] M. G. Bulmer. *The mathematical theory of quantitative genetics.* The Clarendon Press, Oxford University Press, New York, 1980. Oxford Science Publications.

[33] R. Bürger. *The mathematical theory of selection, recombination, and mutation.* Wiley Series in Mathematical and Computational Biology. John Wiley & Sons, Ltd., Chichester, 2000.

[34] J.-E. Busse, P. Gwiazda, and A. Marciniak-Czochra. Mass concentration in a nonlocal model of clonal selection. *J. Math. Biol.*, 73(4) :1001–1033, 2016.

[35] W. Cai, P.-E. Jabin, and H. Liu. Time-asymptotic convergence rates towards the discrete evolutionary stable distribution. *Math. Models Methods Appl. Sci.*, 25(8) :1589–1616, 2015.

[36] À. Calsina, S. Cuadrado, L. Desvillettes, and G. Raoul. Asymptotics of steady states of a selection-mutation equation for small mutation rate. *Proc. Roy. Soc. Edinburgh Sect. A*, 143(6) :1123–1146, 2013.

[37] À. Calsina and J. M. Palmada. Steady states of a selection-mutation model for an age structured population. *J. Math. Anal. Appl.*, 400(2) :386–395, 2013.

[38] V. Calvez, P. Gabriel, and Á. Mateos González. Limiting Hamilton-Jacobi equation for the large scale asymptotics of a subdiffusion jump-renewal equation. *ArXiv e-prints*, Sept. 2016.

[39] F. Campillo, N. Champagnat, and C. Fritsch. Links between deterministic and stochastic approaches for invasion in growth-fragmentation-death models. *J. Math. Biol.*, 73(6-7) :1781–1821, 2016.

[40] F. Campillo, N. Champagnat, and C. Fritsch. On the variations of the principal eigenvalue with respect to a parameter in growth-fragmentation models. *Commun. Math. Sci.*, 15(7) :1801–1819, 2017.

[41] P. Cardaliaguet, A. Porretta, and D. Tonon. Sobolev regularity for the first order Hamilton-Jacobi equation. *Calc. Var. Partial Differential Equations*, 54(3) :3037–3065, 2015.

[42] P. Cardaliaguet and C. Rainer. Hölder regularity for viscosity solutions of fully nonlinear, local or nonlocal, Hamilton-Jacobi equations with superquadratic growth in the gradient. *SIAM J. Control Optim.*, 49(2) :555–573, 2011.

[43] P. Cardaliaguet and L. Silvestre. Hölder continuity to Hamilton-Jacobi equations with superquadratic growth in the gradient and unbounded right-hand side. *Comm. Partial Differential Equations*, 37(9) :1668–1688, 2012.

[44] J. A. Carrillo, S. Cuadrado, and B. Perthame. Adaptive dynamics via Hamilton-Jacobi approach and entropy methods for a juvenile-adult model. *Math. Biosci.*, 205(1) :137–161, 2007.

[45] N. Champagnat. *Mathematical study of stochastic models of evolution belonging to the ecological theory of adaptive dynamics.* PhD thesis, Université de Nanterre - Paris X, Dec. 2004.

[46] N. Champagnat. A microscopic interpretation for adaptive dynamics trait substitution sequence models. *Stochastic Process. Appl.*, 116(8) :1127–1160, 2006.

[47] N. Champagnat, R. Ferrière, and G. Ben Arous. The canonical equation of adaptive dynamics : A mathematical view. *Selection*, 2(1-2) :73–83, 2002.

[48] N. Champagnat, R. Ferrière, and S. Méléard. Unifying evolutionary dynamics : From individual stochastic processes to macroscopic models. *Theor. Popul. Biol.*, 69(3) :297–321, 2006.

[49] N. Champagnat, R. Ferrière, and S. Méléard. From individual stochastic processes to macroscopic models in adaptive evolution. *Stoch. Models*, 24(suppl. 1) :2–44, 2008.

[50] N. Champagnat, R. Ferrière, and S. Méléard. *Individual-based probabilistic models of adaptive evolution and various scaling approximations*, volume 59 of *Progr. Probab.*, pages 75–113. Birkhäuser, Basel, 2008.

[51] N. Champagnat and P.-E. Jabin. The evolutionary limit for models of populations interacting competitively via several resources. *J. Differential Equations*, 251(1) :176–195, 2011.

[52] N. Champagnat, P.-E. Jabin, and S. Méléard. Adaptation in a stochastic multi-resources chemostat model. *J. Math. Pures Appl. (9)*, 101(6) :755–788, 2014.

[53] N. Champagnat, P.-E. Jabin, and G. Raoul. Convergence to equilibrium in competitive Lotka-Volterra and chemostat systems. *C. R. Math. Acad. Sci. Paris*, 348(23-24) :1267–1272, 2010.

[54] N. Champagnat and A. Lambert. Evolution of discrete populations and the canonical diffusion of adaptive dynamics. *Ann. Appl. Probab.*, 17(1) :102–155, 2007.

[55] E. Chasseigne. The Dirichlet problem for some nonlocal diffusion equations. *Differential Integral Equations*, 20(12) :1389–1404, 2007.

[56] P. Collet, S. Méléard, and J. A. J. Metz. A rigorous model study of the adaptive dynamics of Mendelian diploids. *J. Math. Biol.*, 67(3) :569–607, 2013.

[57] C. Coron. Stochastic modeling of density-dependent diploid populations and the extinction vortex. *Adv. in Appl. Probab.*, 46(2) :446–477, 2014.

[58] C. Coron, M. Costa, H. Leman, and C. Smadi. A stochastic model for speciation by mating preferences. *J. Math. Biol., to be published*, 2018.

[59] M. Costa, C. Hauzy, N. Loeuille, and S. Méléard. Stochastic eco-evolutionary model of a prey-predator community. *J. Math. Biol.*, 72(3) :573–622, 2016.

[60] J. Coville. On a simple criterion for the existence of a principal eigenfunction of some nonlocal operators. *J. Differential Equations*, 249(11) :2921–2953, 2010.

[61] M. G. Crandall, L. C. Evans, and P.-L. Lions. Some properties of viscosity solutions of Hamilton-Jacobi equations. *Trans. Amer. Math. Soc.*, 282(2) :487–502, 1984.

[62] M. G. Crandall, H. Ishii, and P.-L. Lions. User's guide to viscosity solutions of second order partial differential equations. *Bull. Amer. Math. Soc. (N.S.)*, 27(1) :1–67, 1992.

[63] C. R. Darwin. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, 1859.

[64] L. Desvillettes, P.-E. Jabin, S. Mischler, and G. Raoul. On selection dynamics for continuous structured populations. *Commun. Math. Sci.*, 6(3) :729–747, 2008.

[65] U. Dieckmann and M. Doebeli. On the origin of species by sympatric speciation. *Nature*, 400 :354–357, 1999.

[66] U. Dieckmann and R. Law. The dynamical theory of coevolution : a derivation from stochastic ecological processes. *J. Math. Biol.*, 34(5-6) :579–612, 1996.

[67] O. Diekmann. A beginner's guide to adaptive dynamics. In *Mathematical modelling of population dynamics*, volume 63 of *Banach Center Publ.*, pages 47–86. Polish Acad. Sci. Inst. Math., Warsaw, 2004.

[68] O. Diekmann, P.-E. Jabin, S. Mischler, and B. Perthame. The dynamics of adaptation : an illuminating example and a Hamilton-Jacobi approach. *Theor. Popul. Biol.*, 67(4) :257–271, 2005.

[69] R. Djidjou-Demasse and A. Ducrot. An age-structured within-host model for multistrain malaria infections. *SIAM J. Appl. Math.*, 73(1) :572–593, 2013.

[70] R. Djidjou-Demasse, A. Ducrot, and F. Fabre. Steady state concentration for a phenotypic structured problem modeling the evolutionary epidemiology of spore producing pathogens. *Math. Models Methods Appl. Sci.*, 27(2) :385–426, 2017.

[71] M. Doebeli, H. J. Blok, O. Leimar, and U. Dieckmann. Multimodal pattern formation in phenotype distributions of sexual populations. *Proc. R. Soc. B*, 274(1608) :347–357, 2007.

[72] M. Doumic. Analysis of a Population Model Structured by the Cells Molecular Content. *Math. Model. Nat. Phenom.*, 2(3) :121–152, 2007.

[73] M. Doumic Jauffret and P. Gabriel. Eigenelements of a general aggregation-fragmentation model. *Math. Models Methods Appl. Sci.*, 20(5) :757–783, 2010.

[74] A. Ducrot and P. Magal. Travelling wave solutions for an infection-age structured epidemic model with external supplies. *Nonlinearity*, 24(10) :2891–2911, 2011.

[75] L. C. Evans. *Partial differential equations*, volume 19 of *Graduate Studies in Mathematics*. American Mathematical Society, Providence, RI, 1998.

[76] L. C. Evans and P. E. Souganidis. A PDE approach to geometric optics for certain semilinear parabolic equations. *Indiana Univ. Math. J.*, 38(1) :141–172, 1989.

[77] W. H. Fleming and H. M. Soner. *Controlled Markov processes and viscosity solutions*, volume 25 of *Applications of Mathematics (New York)*. Springer-Verlag, New York, 1993.

[78] W. H. Fleming and P. E. Souganidis. PDE-viscosity solution approach to some problems of large deviations. *Ann. Scuola Norm. Sup. Pisa Cl. Sci. (4)*, 13(2) :171–192, 1986.

[79] J. Fontbona and S. Méléard. Non local Lotka-Volterra system with cross-diffusion in an heterogeneous medium. *J. Math. Biol.*, 70(4) :829–854, 2015.

[80] M. Freidlin. *Functional integration and partial differential equations*, volume 109 of *Annals of Mathematics Studies*. Princeton University Press, Princeton, NJ, 1985.

[81] M. Freidlin. Limit theorems for large deviations and reaction-diffusion equations. *Ann. Probab.*, 13(3) :639–675, 1985.

[82] S. A. H. Geritz, E. Kisdi, G. Meszena, and J. A. J. Metz. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, 12(1) :35–57, 1998.

[83] M. Gyllenberg and G. F. Webb. A nonlinear structured population model of tumor growth with quiescence. *J. Math. Biol.*, 28(6) :671–694, 1990.

[84] P. Hinow, F. Le Foll, P. Magal, and G. F. Webb. Analysis of a model for transfer phenomena in biological populations. *SIAM J. Appl. Math.*, 70(1) :40–62, 2009.

[85] J. Hofbauer and K. Sigmund. *Evolutionary games and population dynamics*. Cambridge University Press, Cambridge, 1998.

[86] J. Hofbauer and K. Sigmund. Evolutionary game dynamics. *Bull. Amer. Math. Soc. (N.S.)*, 40(4) :479–519, 2003.

[87] H. Ishii. Hamilton-Jacobi equations with discontinuous Hamiltonians on arbitrary open sets. *Bull. Fac. Sci. Engrg. Chuo Univ.*, 28 :33–77, 1985.

[88] P.-E. Jabin and G. Raoul. On selection dynamics for competitive interactions. *J. Math. Biol.*, 63(3) :493–517, 2011.

[89] P.-E. Jabin and R. Strother Schram. Selection-Mutation dynamics with spatial dependence. *ArXiv e-prints*, Jan. 2016.

[90] M. Kimura. A stochastic model converning the maintenance of genetic variability in quantitative characters. *Proc. Natl. Acad. Sci. USA*, 54 :731–736, 1965.

[91] E. Kisdi and S. A. H. Geritz. Adaptive Dynamics in Allele Space : Evolution of Genetic Polymorphism by Small Mutations in a Heterogeneous Environment. *Evolution*, 53(4) :993–1008, 1999.

[92] H. Leman, S. Méléard, and S. Mirrahimi. Influence of a spatial structure on the long time behavior of a competitive Lotka-Volterra type system. *Discrete Contin. Dyn. Syst. Ser. B*, 20(2) :469–493, 2015.

[93] P.-L. Lions and P. E. Souganidis. Fully nonlinear stochastic partial differential equations : non-smooth equations and applications. *C. R. Acad. Sci. Paris Sér. I Math.*, 327(8) :735–741, 1998.

[94] T. Lorenzi, A. Lorz, and G. Restori. Asymptotic dynamics in populations structured by sensitivity to global warming and habitat shrinking. *Acta Appl. Math.*, 131 :49–67, 2014.

[95] A. Lorz, T. Lorenzi, J. Clairambault, A. Escargueil, and B. Perthame. Modeling the effects of space structure and combination therapies on phenotypic heterogeneity and drug resistance in solid tumors. *Bull. Math. Biol.*, 77(1) :1–22, 2015.

[96] A. Lorz, S. Mirrahimi, and B. Perthame. Dirac mass dynamics in multidimensional nonlocal parabolic equations. *Comm. Partial Differential Equations*, 36(6) :1071–1098, 2011.

[97] A. Lorz and B. Perthame. Long-term behaviour of phenotypically structured models. *Proc. R. Soc. Lond. Ser. A Math. Phys. Eng. Sci.*, 470(2167) :20140089, 10, 2014.

[98] A. Lorz, B. Perthame, and C. Taing. Dirac concentrations in a chemostat model of adaptive evolution. *Chin. Ann. Math. Ser. B*, 38(2) :513–538, 2017.

[99] P. Magal. Mutation and recombination in a model of phenotype evolution. *J. Evol. Equ.*, 2(1) :21–39, 2002.

[100] P. Magal, C. C. McCluskey, and G. F. Webb. Lyapunov functional and global asymptotic stability for an infection-age model. *Appl. Anal.*, 89(7) :1109–1140, 2010.

[101] P. Magal and G. Raoul. Dynamics of a kinetic model describing protein exchanges in a cell population. *ArXiv e-prints*, Nov. 2015.

[102] P. Magal and G. F. Webb. Mutation, selection, and recombination in a model of phenotype evolution. *Discrete Contin. Dynam. Systems*, 6(1) :221–236, 2000.

[103] J. Maynard Smith. *Evolution and the Theory of Games.* Cambridge University Press, Cambridge, 1982.

[104] S. Méléard and S. Mirrahimi. Singular limits for reaction-diffusion equations with fractional Laplacian and local or nonlocal nonlinearity. *Comm. Partial Differential Equations*, 40(5) :957–993, 2015.

[105] S. Méléard and V. C. Tran. Trait substitution sequence process and canonical equation for age-structured populations. *J. Math. Biol.*, 58(6) :881–921, 2009.

[106] S. Méléard and V. C. Tran. Slow and fast scales for superprocess limits of age-structured populations. *Stochastic Process. Appl.*, 122(1) :250–276, 2012.

[107] G. Meszéna, M. Gyllenberg, F. J. Jacobs, and J. A. J. Metz. Link between Population Dynamics and Dynamics of Darwinian Evolution. *Phys. Rev. Lett.*, 95 :078105, Aug 2005.

[108] J. A. J. Metz and O. Diekmann, editors. *The dynamics of physiologically structured populations*, volume 68 of *Lecture Notes in Biomathematics*. Springer-Verlag, Berlin, 1986. Papers from the colloquium held in Amsterdam, 1983.

[109] J. A. J. Metz, S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. van Heerwaarden. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and spatial structures of dynamical systems (Amsterdam, 1995)*, volume 45 of *Konink. Nederl. Akad. Wetensch. Verh. Afd. Natuurk. Eerste Reeks*, pages 183–231. North-Holland, Amsterdam, 1996.

[110] J. A. J. Metz, R. M. Nisbet, and S. A. H. Geritz. How should we define 'fitness' for general ecological scenarios ? *Trends Ecol. Evol.*, 7(6) :198–202, 1992.

[111] P. Michel. Existence of a solution to the cell division eigenproblem. *Math. Models Methods Appl. Sci.*, 16(7, suppl.) :1125–1153, 2006.

[112] P. Michel, S. Mischler, and B. Perthame. General entropy equations for structured population models and scattering. *C. R. Math. Acad. Sci. Paris*, 338(9) :697–702, 2004.

[113] P. Michel, S. Mischler, and B. Perthame. General relative entropy inequality : an illustration on growth models. *J. Math. Pures Appl. (9)*, 84(9) :1235–1260, 2005.

[114] S. Mirrahimi. *Phénomènes de concentration dans certaines EDPs issues de la biologie*. PhD thesis, Université Pierre et Marie Curie-Paris VI, 2011.

[115] S. Mirrahimi. Adaptation and migration of a population between patches. *Discrete Contin. Dyn. Syst. Ser. B*, 18(3) :753–768, 2013.

[116] S. Mirrahimi. A Hamilton-Jacobi approach to characterize the evolutionary equilibria in heterogeneous environments. *Math. Models Methods Appl. Sci.*, 27(13) :2425–2460, 2017.

[117] S. Mirrahimi and B. Perthame. Asymptotic analysis of a selection model with space. *J. Math. Pures Appl. (9)*, 104(6) :1108–1118, 2015.

[118] S. Mirrahimi, B. Perthame, E. Bouin, and P. Millien. Population formulation of adaptative meso-evolution : theory and numerics. In *The mathematics of Darwin's legacy*, Math. Biosci. Interact., pages 159–174. Birkhäuser/Springer Basel AG, Basel, 2011.

[119] S. Mirrahimi, B. Perthame, and J. Y. Wakano. Evolution of species trait through resource competition. *J. Math. Biol.*, 64(7) :1189–1223, 2012.

[120] S. Mirrahimi, B. Perthame, and J. Y. Wakano. Direct competition results from strong competition for limited resource. *J. Math. Biol.*, 68(4) :931–949, 2014.

[121] S. Mirrahimi and G. Raoul. Population structured by a space variable and a phenotypical trait. *Theor. Popul. Biol.*, 84 :87–133, 2013.

[122] S. Mirrahimi and J.-M. Roquejoffre. Uniqueness in a class of Hamilton-Jacobi equations with constraints. *C. R. Math. Acad. Sci. Paris*, 353(6) :489–494, 2015.

[123] S. Mischler, B. Perthame, and L. Ryzhik. Stability in a nonlinear population maturation model. *Math. Models Methods Appl. Sci.*, 12(12) :1751–1772, 2002.

[124] G. Nadin, M. Strugarek, and N. Vauchelet. Hindrances to bistable front propagation : application to Wolbachia invasion. *J. Math. Biol.*, Sep 2017.

[125] S. Nordmann, B. Perthame, and C. Taing. Dynamics of concentration in a population model structured by age and a phenotypical trait. *Acta Appl. Math.*, 155 :197–225, 2018.

[126] N. Pasteur and M. Raymond. Insecticide resistance genes in mosquitoes : their mutations, migration, and selection in field populations. *J. Hered.*, 87(6) :444–449, 1996.

[127] B. Perthame. *Transport equations in biology.* Frontiers in Mathematics. Birkhäuser Verlag, Basel, 2007.

[128] B. Perthame and G. Barles. Dirac concentrations in Lotka-Volterra parabolic PDEs. *Indiana Univ. Math. J.*, 57(7) :3275–3301, 2008.

[129] B. Perthame and P. E. Souganidis. Rare mutations limit of a steady state dispersal evolution model. *Math. Model. Nat. Phenom.*, 11(4) :154–166, 2016.

[130] G. Raoul. *Étude qualitative et numérique d'équations aux dérivées partielles issues des sciences de la nature.* PhD thesis, ENS Cachan, 2009.

[131] G. Raoul. Local stability of evolutionary attractors for continuous structured populations. *Monatsh. Math.*, 165(1) :117–144, 2012.

[132] G. Raoul. Macroscopic limit from a structured population model to the Kirkpatrick-Barton model. *ArXiv e-prints*, June 2017.

[133] T. Roget. On the long-time behaviour of an age and trait structured population dynamics. *ArXiv e-prints*, Nov. 2017.

[134] R. Rudnicki and R. Wieczorek. Does assortative mating lead to a polymorphic population ? A toy model justification. *Discrete Contin. Dyn. Syst. Ser. B*, 23(1) :459–472, 2018.

[135] R. Rudnicki and P. Zwoleński. Model of phenotypic evolution in hermaphroditic populations. *J. Math. Biol.*, 70(6) :1295–1321, 2015.

[136] C. Smadi. An eco-evolutionary approach of adaptation and recombination in a large population of varying size. *Stochastic Process. Appl.*, 125(5) :2054–2095, 2015.

[137] C. Smadi. The effect of recurrent mutations on genetic diversity in a large population of varying size. *Acta Appl. Math.*, 149 :11–51, 2017.

[138] H. L. Smith and P. Waltman. *The theory of the chemostat : dynamics of microbial competition.* Cambridge University Press, Cambridge, 1994.

[139] M. Strugarek and N. Vauchelet. Reduction to a single closed equation for 2-by-2 reaction-diffusion systems of Lotka-Volterra type. *SIAM J. Appl. Math.*, 76(5) :2060–2080, 2016.

[140] M. Strugarek, N. Vauchelet, and J. Zubelli. Quantifying the Survival Uncertainty of Wolbachia-infected Mosquitoes in a Spatial Model. *ArXiv e-prints*, Aug. 2016.

[141] V. C. Tran. Large population limit and time behaviour of a stochastic particle model describing an age-structured population. *ESAIM Probab. Stat.*, 12 :345–386, 2008.

[142] J. Tufto. Quantitative genetic models for the balance between migration and stabilizing selection. *Genet. Res.*, 76(3) :285–293, 2000.

[143] O. Turanova. On a model of a population with variable motility. *Math. Models Methods Appl. Sci.*, 25(10) :1961–2014, 2015.

[144] M. Turelli and N. H. Barton. Genetic and Statistical Analyses of Strong Selection on Polygenic Traits : What, Me Normal ? *Genetics*, 138(3) :913–941, 1994.

[145] G. G. van Doorn and U. Dieckmann. The Long-Term Evolution of Multilocus Traits under Frequency-Dependent Disruptive Selection. *Evolution*, 60(11) :2226–2238, 2006.

Résumé

Cette thèse porte sur l'étude des dynamiques de masses de Dirac dans des équations aux dérivées partielles et intégro-différentielles issues de la biologie évolutive. Nous nous intéressons à des modèles de populations structurées en trait phénotypique en tenant compte des phénomènes d'adaptation et de mutations, afin de montrer la sélection d'individus les plus adaptés dans un environnement donné. La description de ces problèmes biologiques conduit à l'étude d'équations non linéaires et non locales, avec la présence d'un petit paramètre qui induit deux échelles de temps. Les solutions asymptotiques de ces équations sont des distributions de populations dans l'espace des traits et se concentrent en masses de Dirac en les traits dominants. Dans une première partie, nous nous intéressons à la dynamique des masses de Dirac dans un modèle de chémostat en utilisant une formulation Hamilton-Jacobi. Le modèle de chémostat est constitué d'un système d'équations décrivant la dynamique consommateurs-nutriment dans un système fermé. Dans une deuxième partie, nous étudions un modèle de compétition structuré en âge et en trait. Grâce à une factorisation adaptée, nous obtenons la limite asymptotique de la solution comme le produit d'un profil en âge et d'un profil en trait. Lorsque les mutations sont introduites, une équation d'Hamilton-Jacobi apparaît et nous démontrons un résultat d'unicité associé dans le cadre des solutions de viscosité. La dernière partie s'intéresse aux populations sexuées. Nous étudions une famille de modèles de populations sexuées présentant une asymétrie dans l'hérédité ou la fécondité : chaque individu hérite principalement des traits de la mère.

Abstract

This thesis focuses on the dynamics of Dirac mass concentrations in non-local partial differential and integro-differential equations motivated by evolutionary biology. We consider population models structured in phenotypical traits and, taking into account adaptation and mutation phenomena, we aim to describe the selection of the fittest traits in a given environment. The mathematical modeling of these biological problems leads to nonlinear and nonlocal equations, with a small parameter that induces two time-scales. The asymptotic solutions to these equations are population distributions on the traits space and concentrate in Dirac masses located on the dominant traits. In the first part, we study the Dirac mass dynamics in a chemostat model, using a Hamilton-Jacobi formulation. The chemostat model is a system of equations describing the dynamics of consumers and nutrients in a bioreactor. In a second part, we investigate a competition model structured in age and phenotypical traits. By means of an appropriate factorization, we obtain the asymptotic limit of the solution as a decomposition into two profiles, one in age, the other in traits. When mutations are introduced, a Hamilton-Jacobi equation arises and we prove a uniqueness result of the solution to this equation in the framework of viscosity solutions. The last part is devoted to sexual population models. These models under investigation include asymmetric trait heredity or asymmetric trait-dependent fecundity between the parents : each individual inherits mostly its traits from the female.