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Sujet de la thèse :

# Phénomènes de concentration dans certaines EDPs issues de la biologie

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# Table des matières

**Chapitre 2**

**Généralisation des résultats de convergence à des cas moins réguliers**

Methods and Applications of Analysis (MAA). Vol. 16.3., pp. 321 – 340 (2009).

**Chapitre 3**

**Modèle singulier pour éviter la queue de distribution**

Soumis

# Introduction

## 1 Motivations et dynamique adaptative

Cette thèse porte sur l'étude de phénomènes de concentrations dans certaines équations intégro-différentielles issues de la dynamique des populations. Nous nous intéressons principalement à l'évolution Darwinienne (voir [41]) de populations asexuées. Dans le dernier chapitre nous étudions en outre un modèle de populations sexuées.

Ce sujet a connu, récemment un développement rapide dans la littérature mathématique car plusieurs théories ont permis de l'aborder :

- La théorie des jeux qui a laissé la terminologie "stratégie" utilisée ultérieurement par d'autres théories [87, 70].
- Une théorie de stabilité de systèmes différentiels (la dynamique adaptative classique) que nous rappelons ci-dessous. Elle date des années 80's [66, 46, 65, 49, 91].
- Une théorie probabiliste qui considère des populations finies et analyse soit des limites en grandes populations en mettant à l'échelle les naissances/mortalités/mutations [93, 29, 31, 32], soit des limites en temps long [35].
- Une théorie populationnelle qui utilse des modèles intégro-différentiels [50, 45, 111, 110, 74].

**Quelques concepts de base.**

Nous considérons des populations structurées (voir [92, 43, 42, 48, 44]) par des traits phénotypiques. Tout d'abord, précisons ce que signifient des termes, "génotype" et "phénotype" introduits en 1911 par Wilhelm Johannsen [76].

**Définition 1**
- *Génome : Ensemble des gènes d'un organisme, présent dans chacune de ses cellules.*
- *Génotype : Ensemble des informations génétiques d'un organisme portées par ses gènes, qu'elles soient exprimées ou non. Des individus avec le même génotype peuvent paraitre différents. De même, des individus qui nous paraissent similaires peuvent avoir des génotypes différents.*
- *Phénotype : Ensemble des caractères observables d'un individu. Le phénotype provient de l'expression du génotype de l'individu et de son interaction avec le milieu dans lequel il se développe. Nous négligeons ici l'effet de l'environnement sur le phénotype. On appelle trait phénotypique, un sous-ensemble du phénotype d'un individu.*

Quelques exemples de traits phénotypiques sont la taille, la couleur, l'âge à maturité, la composition de l'alimentation et le comportement.

Les points de départ de l'étude de l'évolution d'une population structurée sont trois mécanismes de bases qui s'appuient sur l'explication de Darwin concernant l'évolution [41] :

- **Hérédité :** Reproduction et transmission des caractéristiques individuelles d'une génération à une autre. Dans une reproduction asexuée l'ensemble des informations génétiques du parent est copié et se transmet au descendant (sauf en cas de mutation) par le moyen de l'ADN. Dans le cas de la reproduction sexuée, le matériel génétique n'est pas reproduit. Un enfant n'a pas les mêmes chromosomes que son père ou sa mère mais un mélange des deux. Ceci rend l'étude des populations sexuées plus complexe.
- **Mutations :** Modification irréversible d'une information génétique lors de la réplication de l'ADN. La présence de mutations crée de la variabilité dans les traits phénotypiques. Les mutations sont en général rares (voir [71, 52, 99, 121]). Par exemple le taux d'erreurs lors de réplication pour les bactéries est estimé à environ $10^{-8}$ ou $10^{-7}$ par nucléotide et par réplication ou bien environ 0.004 erreurs par génome et par réplication [52]. Les erreurs qui modifient le trait phénotypique sont encore plus rares.
- **Sélection naturelle :** Une conséquence de l'interaction des individus entre eux et avec leur environnement. Parmi les individus, ceux qui sont mieux adaptés à l'environnement et plus avantagés pour accéder à des ressources, ont plus de chance pour survivre et se reproduire. Ceci entraine la sélection naturelle.

Avec une étude mathématique de la dynamique Darwinienne de traits phénotypiques, ayant comme base les principes ci-dessus, nous essayons d'expliquer ce qui s'observe dans la nature. En particulier, nous cherchons à expliquer des phénomènes liés à l'arbre de Darwin (voir figure 1). Nous montrons qu'asymptotiquement, dans la limite de mutations rares et en temps long, seul un nombre fini de traits phénotypiques peuvent survivre, ce que nous interprétons comme une somme de masses de Dirac à la limite. Autrement dit, une distribution continue de traits phénotypiques présents n'est pas possible dans la plupart des cas. Ces traits dominants évoluent dans le temps. Un trait phénotypique peut disparaître au bout d'un certain temps (extinction). L'évolution d'un trait peut aussi mener à un branchement : l'apparition de deux ou plusieurs traits à partir d'un seul trait. Notre approche est très liée, bien que plus générale, à la théorie de la Dynamique Adaptative introduite ci-dessous.

### Dynamique Adaptative.

La théorie de la dynamique adaptative [66, 46, 65, 49, 91] est développée depuis les années 1980 pour étudier la dynamique en temps long de traits phénotypiques en présence de mutations rares. Elle suppose que le trait est un paramètre $x \in I$, avec $I$ un intervalle de $\mathbb{R}$. Elle met l'accent sur l'étude de stabilité de populations avec un (ou plusieurs) trait particulier. Cette théorie est apparue à la suite d'études sur l'évolution des populations en utilisant des techniques de la théorie de jeux [87, 70].

Nous ne décrivons ici que certains concepts et idées de bases de cette théorie en se concentrant sur les phénomènes dont nous aurons besoin dans la suite de ce rapport. En général, dans cette approche, on suppose qu'un nombre fini de traits phénotypiques est présent. Ici nous présentons le cas où un seul trait unidimensionnel est présent, i. e. $n(t,\cdot) = \rho(t)\delta_{\bar{x}(t)}(\cdot)$. Nous appelons ce trait $\bar{x}(\cdot)$ le "**résident**".

Une hypothèse fondamentale dans cette théorie est que les mutants apparaissent dans une échelle de temps qui est longue par rapport à l'échelle de temps de la convergence de la population vers son état stationnaire attracteur. On peut alors supposer que la densité de population à l'échelle écologique, s'écrit sous la forme $\bar{n}(t,\cdot) = \bar{\rho}(t)\delta_{\bar{x}(t)}(\cdot)$, où $\bar{x}(t)$ est le trait résident en temps $t$ et $\bar{\rho}(t)$ est tel que $\bar{n}(t,\cdot)$ est un état stationnaire, en absence de mutations. On appelle un tel état $\bar{n}$ une "**stratégie**".

On définit ensuite la fonction fitness comme ci-dessous [94]

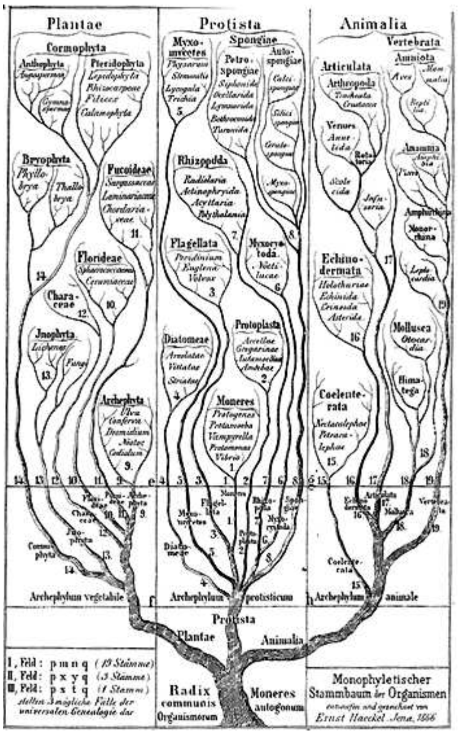


FIGURE 1 – Arbre phylogénétique de Haeckel. Issu de "http ://bioinfo.uqam.ca/bif7002/archives/Hiver2005/Phylogenie"

**Définition 2** *On appelle* **fitness** *du trait $y$ au sein d'une population du trait résident $x$, et on le note $F_x(y)$, la différence de taux de natalité et de taux de mortalité du trait $y$, lorsque la population est majoritairement du trait $x$. Autrement dit, la fitness $F_x(y)$ désigne le taux de croissance initial d'un mutant $y$, lorsque les résidents sont du trait $x$.*

D'après les explications ci-dessus, on a

$$F_x(x) = 0.$$

Le trait dominant $x$ évolue dans le sens du gradient de la fitness, lorsque celui-ci est non nul

$$(\nabla_y F_x(y))_{y=x} \neq 0.$$

Ici on suppose qu'un envahissement réussi implique une fixation du trait (voir par exemple [64] pour justification de ce dernier).

Lorsque

$$(\nabla_y F_{\bar{x}}(y))_{y=\bar{x}} = 0,$$

on dit que $\bar{x}$ est une **stratégie singulière**. Voici quelques questions qu'on aimerait pouvoir aborder pour $\bar{x}$ une stratégie singulière :

- Si le trait résident est $\bar{x}$, est-ce qu'un mutant avec un trait $x$ proche de $\bar{x}$ peut envahir la population ? Si non il s'agit d'une "Evolutionary stable strategy" (ESS). Voir ci-dessous pour une définition plus détaillée.
- Si le résident a un trait $x$ proche de $\bar{x}$, les mutants gagnants sont-ils plus proches de $\bar{x}$ ? Si oui on dit que $\bar{x}$ est une "Convergence stable strategy".

- Y a-t-il des stratégies $y$ et $z$ proches de $\bar{x}$ qui peuvent envahir la population et coexister ? Si oui il s'agit d'une "invasion mutuelle" qui peut entrainer un "branchement".

On renvoie à [65, 49] pour une classification des stratégies singulières. Les dérivées secondes de la fonction de fitness d'une stratégie singulière $F_{\bar{x}}(y)$, si celle-ci est régulière, nous aident à décrire la nature de ce point. Une classification de stratégies singulières a été effectué dans [49] à l'aide des constantes

$$c_{11} = \frac{\partial^2}{\partial x^2} F_{\bar{x}}(\bar{x}), \qquad c_{22} = \frac{\partial^2}{\partial y^2} F_{\bar{x}}(\bar{x}), \qquad c_{12} = \frac{\partial^2}{\partial x \partial y} F_{\bar{x}}(\bar{x}), \qquad c_{21} = \frac{\partial^2}{\partial y \partial x} F_{\bar{x}}(\bar{x}).$$

On observe que, puisque $F_x(x) = 0$, le long de la diagonale $x = y$ on a

$$\frac{\partial F}{\partial x} + \frac{\partial F}{\partial y} = 0, \qquad \frac{\partial^2 F}{\partial x^2} + 2\frac{\partial^2 F}{\partial x \partial y} + \frac{\partial^2 F}{\partial y^2} = 0.$$

On en déduit que

$$c_{12} = c_{21} = -\frac{c_{11} + c_{22}}{2}.$$

Désormais on peut introduire deux notions de stabilité qui sont fondamentales dans la théorie classique de la dynamique adaptative (voir [88, 53]) :

**Définition 3** *On dit que la stratégie singulière $\bar{x}$ est une* **"Evolutionary stable strategy" (ESS)**, *si tous les mutants $y \neq \bar{x}$, avec $y$ proche de $\bar{x}$, ont une fonction de fitness $F_{\bar{x}}(y)$ négative. Cela est vérifié lorsque*

$$c_{22} < 0.$$

*On dit que la stratégie singulière $\bar{x}$ est une* **"Convergence stable strategy" (CSS)**, *si le gradient de fitness est positif pour $x < \bar{x}$ et négatif pour $x > \bar{x}$ :*

$$c_{12} + c_{22} = \left( \frac{d}{dx} \left( \frac{\partial}{\partial y} F_x(y) \right)_{y=x} \right)_{x=\bar{x}} < 0,$$

*ou en d'autres termes*

$$c_{22} < c_{11}.$$

On tient à préciser qu'une ESS n'est pas toujours un attracteur. Pour qu'une stratégie singulière soit un attracteur évolutif, elle doit être à la fois ESS et CSS.

Bien que la théorie classique de la dynamique adaptative nous fournisse des méthodes simples pour décrire la dynamique d'un trait existant dans la population, elle présente certaines limites. En particulier, cette théorie ne peut pas expliquer la présence de traits spécifiques dans la population qui ne se présentent pas comme un continuum de traits. Elle donne des conditions pour le branchement mais elle ne peut pas le décrire. L'hypothèse d'avoir une population monomorphique en tout temps et la séparation d'échelle entre l'échelle écologique et l'échelle évolutionnaire est très simplifiée et doit être justifiée par des modèles continus. C'est pourquoi l'utilisation de méthodes plus générales est cruciale.

Divers travaux, en utilisant des modèles intégro-différentiels, retrouvent toutefois des résultats de la théorie classique de la dynamique adaptative. En partant de distributions de populations sous forme $n = \sum \rho_i \delta_{x_i}(x)$ et en utilisant un modèle intégro-différentiel, L. Desvillettes, P. E. Jabin, S. Mischler et G. Raoul montrent la convergence de la solution, vers une ESS lorsque le temps tend vers l'infini [45]. Voir aussi [111, 110, 74] pour une étude de stabilité des attracteurs évolutifs ainsi que des résultats de convergence vers des ESS.

# 2 Dynamique des populations : Approche Hamilton-Jacobi

Les équations de sélection et mutations, sous forme continue, ont été introduites pour la première fois par M. Kimura [78] pour expliquer le maintien de la variabilité génétique au sein d'une population. Voir aussi [23] pour une suite de ce travail. Dans cette thèse nous nous intéressons à une formulation continue sous formes d'EDP comme cela est standard sous la terminologie "équations structurées". Divers travaux [24, 25, 26] ont utilisé ce formalisme. Dans le cadre de l'évolution Darwinienne, un point de vue asymptotique a été introduit pour la première fois par O. Diekmann, P. Jabin, S. Mischler et B. Perthame dans [50]. Le but est de décrire la dynamique d'une population caractérisée par des traits phénotypiques. L'outil principal dans cette approche est l'équation de Hamilton-Jacobi. Cette formulation a été étendue au cas des systèmes par J. Carrillo, S. Cuadrado et B. Perthame dans [28].

L'idée principale dans cette méthode est de partir d'un modèle continu qui décrit la compétition entre les traits et qui contient un terme de mutations modélisé soit par un Laplacien soit par un noyau intégral. On introduit ensuite un petit terme $\varepsilon$ devant le Laplacien ou dans le terme intégral des mutations pour considérer les mutations rares ou petites. On effectue aussi un changement de variable en temps $t \mapsto \frac{t}{\varepsilon}$ pour accélérer le temps. On étudie ensuite le comportement asymptotique de la dynamique lorsque $\varepsilon \to 0$. Cette dynamique asymptotique est décrite à l'aide d'une équation de Hamilton-Jacobi avec contrainte. Le changement d'échelle en temps nous permet de nous placer à l'échelle écologique et d'observer l'effet de mutation dans la dynamique. Sans ce changement d'échelle cet effet ne serait pas visible. En général, on s'attend à obtenir à la limite une somme de masses de Dirac, i.e. qu'à chaque instant un ou plusieurs traits soit présents et les autres traits disparaissent. Ces traits dominants évoluent dans le temps. L'évolution d'un trait peut mener à son extinction ou bien à un branchement.

Les modèles macroscopiques que nous étudions, sans le paramètre $\varepsilon$, ont été obtenu rigoureusement à partir des modèles stochastiques individus centrés dans les travaux de S. Méléard, R. Ferrière, N. Champagnat [31, 32] dans la limite de populations grandes. Ils partent d'un modèle microscopique qui détaille la dynamique de chaque individu en considérant l'interaction des individus entre eux et avec leur environnement et en supposant que le nouveau-né a le même trait que celui de son géniteur sauf dans le cas des mutations. En faisant des changements d'échelles, notamment pour considérer de grandes populations, ils obtiennent une limite macroscopique soit déterministe sous forme d'équations intégro-différentielles ou d'équations différentielles partielles soit stochastique et sous forme d'équation différentielle stochastique ou de superprocessus. Les modèles déterministes ainsi obtenus ressemblent à certains modèles qu'on étudie.

## 2.1 Deux modèles principaux

Un premier modèle général (modèle à une seule ressource) que nous étudions est le suivant

$$\frac{\partial}{\partial_t} n_\epsilon - \epsilon \Delta n_\epsilon = \frac{n_\epsilon}{\epsilon} R\big(x, I_\epsilon(t)\big), \qquad t > 0,\ x \in \mathbb{R}^d, \tag{1}$$

avec

$$I_\epsilon(t) = \int_{\mathbb{R}^d} \psi(x) n_\epsilon(t,x) dx. \tag{2}$$

La donnée initiale $n_\varepsilon^0$, et sa forme asymptotique pour $\varepsilon$ petit, sera précisée ultérieurement. Dans ce modèle on suppose qu'un seul nutriment est présent. Le terme $\psi(x)$ correspond au taux de consommation associé au trait $x$ et $I(t)$ est la consommation totale de la population. Le terme $R(x, I)$ représente le taux de naissance et de mortalité d'un individu de trait $x$, dépendant du paramètre de l'environnement $I(t)$. Le terme de Laplace représente des mutations. On introduit un paramètre $\varepsilon$ petit pour considérer des mutations rares. On fait aussi un changement d'échelle en temps $t \mapsto \frac{t}{\varepsilon}$ pour étudier l'évolution en temps grand, afin d'observer l'effet de mutations. Un deuxième modèle est le modèle de compétition directe

$$\frac{\partial}{\partial_t} n_\epsilon(t,x) = \frac{1}{\epsilon} n_\epsilon(t,x)\left(r(x) - \int_{\mathbb{R}^d} C(x,y) n_\epsilon(t,y)\,dy\right) + \epsilon \Delta n_\epsilon(t,x). \tag{3}$$

Dans ce modèle on ne suppose plus la présence d'une seule ressource. Au contraire on modélise la compétition avec un noyau de compétition directe sans faire références directement à des ressources dans le modèle. Le terme $r(x)$ correspond au taux de naissance et de mortalité intrinsèque et $C(x,y)$ est le noyau de compétition entre les traits. Les autres termes sont comme dans le modèle (1).

Une formulation Hamilton-Jacobi de (1)–(2) et (3) a été introduite dans [103] et [104]. Cette approche repose sur le changement de variable

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

comme dans la méthode KPP réelle ou l'étude des fronts propagatifs (voir [58, 56, 9]). En faisant tendre $\varepsilon$ vers 0, les auteurs de [103, 104] montrent que $u_\varepsilon$ converge vers $u$ une solution au sens de viscosité d'une équation de Hamilton-Jacobi avec contrainte pour les deux modèles (1)–(2) et (3). Voici l'équation limite associée au modèle (1)–(2)

$$\begin{cases} \frac{\partial}{\partial t} u = R\big(x, I(t)\big) + |\nabla u|^2, \\ \\ \max_{\mathbb{R}^d} u(t,x) = 0, \end{cases} \tag{4}$$

avec $I$ la limite de $I_\varepsilon$, lorsque $\varepsilon$ tend vers 0. Quant à celle associée au modèle (3), elle s'écrit

$$\begin{cases} \frac{\partial}{\partial t} u = F(x,t) + |\nabla u|^2, \\ \max_{\mathbb{R}^d} u(t,x) = 0, \end{cases} \tag{5}$$

avec

$$F(x,t) = \lim_{\varepsilon \to 0} r(x) - \int C(x,y) n(y,t) dy.$$

Une étape dans la dérivation des limites ci-dessus, consiste à contrôler la population totale et à en déduire la contrainte. Le paramètre $I$ est le multiplicateur de Lagrange associé à cette dernière.

Pour comprendre comment ces résultats nous aident à déterminer la limite de $n_\varepsilon$ et à décrire concentrations de masse, nous citons un théorème introduit dans [103], pour le cas où le trait phéotypique $x$ est unidimensionnel, $x \in \mathbb{R}$. D'après ce résultat la population devient immédiatement monomorphique à la limite de $\varepsilon$ petit et le point de concentration $\bar{x}(t)$ peut être décrit, à tout instant $t$, à l'aide du couple $(u, I)$.

**Théorème 4 (Barles, Perthame)** *On suppose que $x \in \mathbb{R}$ et $R(x, I)$ est monotone en $x$. Alors $n_\varepsilon$ la solution de (1)–(2) converge en mesure vers une masse de Dirac*

$$n_\varepsilon(t,x) \underset{\varepsilon \to 0}{\longrightarrow} \rho(t)\delta(x - \bar{x}(t)), \tag{6}$$

*avec*

$$u(t, \bar{x}(t)) = R(\bar{x}(t), I(t)) = 0, \tag{7}$$

*où le couple $(u, I)$ satisfait l'équation de Hamilton-Jacobi avec contrainte (4).*

Une observation importante qui aide à comprendre ce théorème est que le support de $n$, la limite de $n_\varepsilon$ lorsque $\varepsilon$ tend vers 0, est inclus dans l'ensemble des points de maximum de $u(t,x)=0$ :

$$\operatorname{supp} n(t,x) \subset \mathcal{A} = \{(t,x) \,|\, u(t,x) = 0\}. \tag{8}$$

De plus, de la forme particulière de l'équation de Hamilton-Jacobi (4), on déduit que $u$ est semi-convexe. On en déduit que $u$ est dérivable à ses points de maximum. Cette dernière propriété et (8) entrainent

$$\operatorname{supp} n(t,x) \subset \mathcal{A} = \{(t,x) \,|\, R(x,I) = 0\}.$$

Les équations (6)–(7) s'en déduisent.

Avant de décrire des résultats mathématiques, nous présentons un exemple biologique pour le modèle (1)–(2) :

### Chemostat

Un exemple simple de modèle mathématique autonome pour l'évolution adaptative est le chemostat (cet exemple est extrait de [96], voir aussi [49, 50]). Il s'agit de micro-organismes (bactéries, phytoplanctons, algues,...) caractérisés par un paramètre $x \in \mathbb{R}$ (on peut considérer par exemple le logarithme de la taille ou la proportion de divers composants chimiques dans leur métabolisme) qui vivent dans un bain de nutriments où les nutriments sont renouvelés avec un taux constant $d > 0$. La concentration de nutriments est représentée par $S(t) \geq 0$ et les nutriments frais par $S_{\text{in}} > 0$. La densité de micro-organismes est représentée par $n(x,t)$ et le taux de consommation d'un individu du trait $x$ par $\eta(x) > 0$.

L'équation décrivant la dynamique du chemostat s'écrit

$$\begin{cases} \frac{d}{dt}S(t) = d\big(S_{\text{in}} - S(t)\big) - S(t)\int_{-\infty}^{\infty}\eta(x)n(x,t)dx, \\ \frac{\partial}{\partial t}n(x,t) = -dn(x,t) + (1-\mu)S(t)\eta(x)n(x,t) + \mu S(t)\int_{-\infty}^{\infty} M(y,x)\eta(y)n(y,t)dy. \end{cases}$$

Ici la croissance de la population est régie par l'équation sur $n(x,t)$ et la compétition s'explique par le fait que la ressource est limitée (on a $S(t) \leq max(S(0), S_{\text{in}})$). Le terme $(1-\mu)\eta(x)n(x,t)$ correspond au taux de naissance sans mutations et le paramètre $0 < \mu < 1$ représente le taux de naissance avec mutations. Le terme $M(y,x)$ est la probabilité qu'un nouveau-né ait le trait $x$ alors que son parent a le trait $y$. On suppose donc que $M(y,x) \geq 0$, $\int_0^\infty M(y,x)dx = 1$.

On suppose maintenant que les nutriments atteignent un équilibre rapidement par rapport à l'échelle de l'évolution de la population. On peut alors remplacer l'équation sur $S(t)$ par

$$S(t) = \frac{dS_{\text{in}}}{d + \int_{-\infty}^{\infty}\eta(x)n(x,t)dx}.$$

On remplace aussi le terme de mutations par une diffusion

$$\frac{\partial}{\partial t}n(x,t) = -dn(x,t) + S(t)\eta(x)n(x,t) + \lambda\Delta n(x,t).$$

On peut enfin écrire la dynamique sous forme du problème (1)–(2),

$$\begin{cases} \frac{\partial}{\partial t}n(x,t) = n(x,t)\ R\big(x, I(t)\big) + \lambda\Delta n(x,t), \quad x \in \mathbb{R},\ t > 0, \\ I(t) = \int_{-\infty}^{\infty}\eta(x)n(x,t)dx, \end{cases}$$

avec le terme de croissance

$$R(x,I) = -d + \frac{dS_{\text{in}}}{d+I}\eta(x).$$

## 2.2 Dynamique de masses de Dirac

Une dérivation rigoureuse de la limite de $n_\varepsilon$ en forme de masses de Dirac à partir de la formulation Hamilton-Jacobi présentée ci-dessus était établie dans [103] seulement pour le cas $x \in \mathbb{R}$ et pour le modèle (1)–(2). Dans le chapitre 1 nous utilisons ces formulations pour les deux modèles présentés ci-dessus, en faisant des hypothèses de régularité, pour montrer la convergence vers une masse de Dirac dans le cas $x \in \mathbb{R}^d$ et donner une description générale de la dynamique de masses de Dirac dans la limite asymptotique. Cette étude met donc en évidence l'intérêt de cette méthode pour étudier ce genre de modèles (voir aussi [11, 10]).

Pour atteindre cet objectif, il faut faire des hypothèses de concavité sur $R$ ou sur $r(x) - C(x,y)\rho(t)$. Voici les hypothèses que nous utilisons

$$-2\underline{K}_1 \leq D^2 R(x,I) \leq -2\overline{K}_1 < 0 \text{ pour } 0 \leq I \leq I_M, \tag{9}$$

$$-2\underline{K}_1' \leq D^2 r(x) - \sup_y \big(D^2 C(x,y)\big)_+ \rho_M \leq D^2 r(x) + \sup_y \big(D^2 C(x,y)\big)_- \rho_M \leq -2\overline{K}_1'. \tag{10}$$

De même, il faut faire une hypothèse de concavité sur la donnée initiale

$$-2\underline{L}_1 \leq D^2 u_\epsilon^0 \leq -2\overline{L}_1. \tag{11}$$

Sous les hypothèses précédentes nous montrons la convergence de la densité $n_\varepsilon$ vers une masse de Dirac (population monomorphique) :

**Théorème 5 (Lorz, M., Perthame. Convergence 1)** *Sous hypothèses (9) et (11), quitte à extraire une sous-suite, la suite* $(n_\varepsilon)_\varepsilon$*, avec* $n_\varepsilon$ *la solution de (1)–(2), converge faiblement en mesure vers une masse de Dirac*

$$n_\epsilon(t,x) \underset{\epsilon \to 0}{\longrightarrow} \bar{\rho}(t)\, \delta\big(x - \bar{x}(t)\big).$$

*En outre, les propriétés suivantes sont vraies, quitte à encore extraire une sous-suite,*

$$I_\epsilon(t) \underset{\epsilon \to 0}{\longrightarrow} \bar{I}(t) \quad \text{dans } L^1_{loc}(\mathbb{R}^+), \qquad R\big(\bar{x}(t), \bar{I}(t)\big) = 0 \quad p.p.$$

*avec* $\bar{I}(t)$ *une fonction croissante.*

Un résultat similaire est obtenu pour le modèle (3) :

**Théorème 6 (Lorz, M., Perthame. Convergence 2)** *Sous hypothèses (10) et (11), quitte à extraire une sous-suite, la suite* $(n_\varepsilon)_\varepsilon$*, avec* $n_\varepsilon$ *la solution de (3), converge faiblement en mesure vers une masse de Dirac*

$$n_\epsilon(t,x) \underset{\epsilon \to 0}{\longrightarrow} \bar{\rho}(t)\, \delta\big(x - \bar{x}(t)\big).$$

*De plus, les propriétés suivantes sont vraies, quitte à encore extraire une sous-suite,*

$$\rho_\epsilon(t) \underset{\epsilon \to 0}{\longrightarrow} \bar{\rho}(t) \quad \text{faible-}\star\ L^\infty(\mathbb{R}^+), \qquad \bar{\rho}(t)\big[r\big(\bar{x}(t)\big) - \bar{\rho}(t) C\big(\bar{x}(t), \bar{x}(t)\big)\big] \geq 0.$$

Nous précisons que le modèle (3) ne conduit pas toujours à des limites en forme de mesure de Dirac et des limites continues sont possible (voir [104, 17, 74]). Nous détaillerons plus cela dans le chapitre 4. Ici, une mesure de Dirac est obtenue comme limite grâce à l'hypothèse de concavité. En outre, grâce à cette hypothèse nous pouvons dériver une équation de Hamilton-Jacobi plus précise que (5)

$$\begin{cases} \frac{\partial}{\partial t} u = r(x) - \bar{\rho}(t) C\big(x, \bar{x}(t)\big) + |\nabla u|^2, \\ \max_{\mathbb{R}^d} u(t,x) = 0. \end{cases}$$

Ici il faut comprendre que $\bar\rho(t)$ et $\bar x(t)$ sont reliés par $r(\bar x(t)) = \bar\rho(t)C(\bar x(t), \bar x(t))$, et $\bar\rho(t)$ joue le rôle de multiplicateur de Lagrange pour la contrainte.

L'idée essentielle dans les théorèmes 5 et 6, est que la concavité de $R(x, I)$ (ou de $r(x) - \rho(t)C(x, y)$) et de la donnée initiale imposent la concavité de $u(t, x)$, la solution de (1)–(2) (ou de (3)). De plus, le support de $n$, la limite de $n_\varepsilon$ lorsque $\varepsilon$ tend vers 0, est inclus dans l'ensemble $\mathcal{A}$ des points de maximum de $u(t, x) = 0$ comme expliqué dans la section 2.1. La fonction $u(t, \cdot)$ étant concave, pour tout $t$ fixé, il existe un unique point $\bar x(t)$ tel que $(t, \bar x(t)) \in \mathcal{A}$. D'où la concentration de masse $n$ au point $(t, \bar x(t))$, pour tout $t \in \mathbb{R}^+$.

Enfin la semi-convexité (voir section 2.1), et la concavité de $u$ imposent sa régularité. Avec ces propriétés, on peut montrer que $\bar x(t)$ est une fonction régulière de $t$ et en déduire une sorte d'équation canonique.

**L'équation canonique**, introduite dans la théorie de la dynamique adaptative [49, 47], est une équation différentielle sur la position de la masse de Dirac $\bar x(t)$.

Pour établir l'équation canonique, il est nécessaire de supposer plus de régularité sur $R$ et sur la donnée initiale :

$$D^3 R(\cdot, I) \in L^\infty(\mathbb{R}^d), \qquad D^3 u^0_\varepsilon(\cdot) \in L^\infty(\mathbb{R}^d). \tag{12}$$

**Théorème 7 (Lorz, M., Perthame. Forme d'équation canonique 1)** *Sous les hypothèses (9), (11) et (12),* $\bar x(\cdot)$ *le point de concentration associé au modèle (1)–(2), est dans* $W^{1,\infty}(\mathbb{R}^+; \mathbb{R}^d)$ *et il satisfait*

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

*En particulier* $u(t, x)$*, la solution de (4), est une fonction* $C^2$*.*

Nous précisons que cette équation canonique était déjà établie dans [103] formellement. Nous avons un résultat similaire pour (3)

**Théorème 8 (Lorz, M., Perthame. Forme d'équation canonique 2)** *Sous les hypothèses (10), (11) et (12),* $\bar x(\cdot)$ *le point de concentration associé au modèle (3), est dans* $W^{1,\infty}(\mathbb{R}^+; \mathbb{R}^d)$ *et elle satisfait*

$$\dot{\bar x}(t) = \big(-D^2 u\big(t, \bar x(t)\big)\big)^{-1} \cdot \big[\nabla_x r\big(\bar x(t)\big) - \bar\rho(t)\nabla_x C\big(\bar x(t), \bar x(t)\big)\big].$$

*En particulier* $u(t, x)$*, la solution de (5), est une fonction* $C^2$*. En outre,* $\rho_\epsilon$ *converge fortement et on a persistence*

$$r\big(\bar x(t)\big) - \bar\rho(t)C\big(\bar x(t), \bar x(t)\big) = 0, \qquad \bar\rho(t) \geq \rho^0 e^{-Kt}.$$

Enfin, en utilisant une sorte de fonctionnelle de Lyapunov, obtenue à partir de l'équation canonique nous pouvons dériver le comportement en temps long du point de concentration.

**Théorème 9 (Lorz, M., Perthame. Comportement en temps long 1)** *Sous les hypothèses (9), (11) et (12), dans le cas du modèle (1)–(2),* $\bar I(t)$ *est croissante et*

$$\bar I(t) \underset{t\to\infty}{\longrightarrow} I_M, \quad \bar x(t) \underset{t\to\infty}{\longrightarrow} \bar x_\infty.$$

*Enfin, la limite peut être déterminée par* $\nabla R(\bar x_\infty, I_M) = 0$*.*

**Théorème 10 (Lorz, M., Perthame. Comportement en temps long 2)** *Dans le cas du modèle (3), on suppose (9), (11), (12),* $C(x, y) = C(y, x)$ *et*

$$x \mapsto \Phi(x) := \ln r(x) - \ln C(x, x) \quad \textit{est strictement concave dans } \{r > 0\}.$$

*Alors on a* $\bar\rho(t) \to \bar\rho_\infty > 0$ *et* $\bar x(t) \to \bar x_\infty$*, lorsque* $t \to \infty$*, avec* $\bar x_\infty$ *un point de maximum de* $\Phi$*.*

Nous avons ainsi terminé la description de la dynamique de la masse de Dirac dans ce cas de populations monomorphiques. Ces résultats peuvent être étendus au modèle suivant où la diffusion n'est plus constante

$$\frac{\partial}{\partial_t} n_\epsilon - \epsilon \nabla \cdot \left(b(x) \nabla n_\epsilon\right) = \frac{n_\epsilon}{\epsilon} R\big(x, I_\epsilon(t)\big), \qquad t > 0,\ x \in \mathbb{R}^d.$$

Voir le chapitre 1 pour plus de détail.

## 2.3 Modèles moins réguliers ; données initiales mal préparées

La dérivation de l'équation de Hamilton-Jacobi (4) à partir du modèle (1)–(2) a été effectuée dans [103] sous l'hypothèse de régularité de la donnée initiale $u_\varepsilon^0 = \varepsilon \ln n_\varepsilon^0$. Dans cet article les auteurs supposent que la donnée initiale est uniformément Lipschitz. Un résultat plus général est souhaité pour pouvoir admettre les données initiales plus générales et en particulier inclure les cas où $u_\varepsilon^0$ n'est pas initialement uniformément Lipschitz. Dans le chapitre 2 nous montrons la convergence de $u_\varepsilon$ vers l'équation de Hamilton-Jacobi (4) sans hypothèse de régularité sur $u_\varepsilon^0$.

Pour montrer le résultat on a besoin des hypothèses suivantes sur le terme de croissance $R(x, I)$, avec $I_m < I_M$ et $K_1$ des constantes positives,

$$\min_{x \in \mathbb{R}^d} R(x, I_m) = 0, \qquad \max_{x \in \mathbb{R}^d} R(x, I_M) = 0, \tag{13}$$

$$-K_1 \leq \frac{\partial R}{\partial I}(x, I) \leq -K_1^{-1} < 0. \tag{14}$$

L'interprétation de l'hypothèse (13) est que si la consommation totale $I$ est trop élevée ($I = I_M$), alors il n'y a pas assez de ressource pour la population et le taux de croissance est négatif pour tout trait $x$. De même, si la consommation totale $I$ est peu élevée ($I = I_m$), il y a assez de ressource pour toute la population et le taux de croissance $R(x, I)$ est positif pour tout trait $x$. L'hypothèse (14) implique que le taux de croissance est une fonction décroissante de la consommation totale $I$.

On a également besoin des hypothèses suivantes sur la donnée initiale

$$I_m \leq \int_{\mathbb{R}^d} \psi(x) n_\epsilon^0(x) \leq I_M, \quad \text{et} \quad \exists\, A,\, B > 0\,,\ n_\epsilon^0 \leq e^{\frac{-A|x|+B}{\epsilon}}. \tag{15}$$

**Théorème 11 (Barles, M., Perthame)** *On suppose (13), (14) et (15). Soit* $n_\epsilon$ *la solution de (1)–(2), et* $u_\epsilon = \epsilon \ln(n_\epsilon)$*. Alors, quitte à extraire une sous-suite,* $u_\epsilon$ *converge localement uniformément vers une fonction continue* $u \in \mathrm{C}((0,\infty) \times \mathbb{R}^d)$*, une solution de viscosité de l'équation suivante*

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

*avec*

$$I_\epsilon(t) \underset{\epsilon \to 0}{\longrightarrow} I(t) \quad p.p., \qquad \int \psi(x) n(t,x) dx = I(t) \quad p.p..$$

*En particulier, supp* $n(t,\cdot) \subset \{u(t,\cdot) = 0\}$ *p.p en* $t$*, où* $n$ *est la limite faible de* $n_\epsilon$ *lorsque* $\epsilon$ *tend vers* $0$*. Si de plus,* $(u_\epsilon^0)_\epsilon = \epsilon \ln(n_\epsilon^0)$ *est une suite de fonctions continues qui convergent localement uniformément vers* $u^0$*, on a alors* $u \in \mathrm{C}([0,\infty) \times \mathbb{R}^d)$ *et* $u(0,x) = u^0(x)$ *dans* $\mathbb{R}^d$*.*

Ce résultat est obtenu à l'aide d'une estimation BV sur $I_\varepsilon$ et d'une estimation Lipschitz sur $u_\varepsilon$. Les estimations Lipschitz, en absence de régularité de la donnée initiale, provient des propriétés régularisantes de l'équation eikonale (voir [82, 3, 4]). Le résultat peut être ensuite dérivé par la stabilité de solutions de viscosité (voir [38, 5]).

Dans les modèles qu'on a présentés précédemment, les mutations ont été modélisées à l'aide d'un terme de Laplace. Une façon plus naturelle de modéliser les mutations est en ajoutant un terme intégral au modèle :

$$\begin{cases}\partial_t n_\epsilon = \frac{n_\epsilon}{\epsilon} R(x, I_\epsilon(t)) + \frac{1}{\epsilon} \int \frac{1}{\epsilon^d} K(\frac{y-x}{\epsilon})\, b(y, I_\epsilon)\, n_\epsilon(t,y)\, dy, \qquad x \in \mathbb{R}^d,\ t \geq 0,\\ n_\epsilon(t=0) = n_\epsilon^0 \in L^1(\mathbb{R}^d), \qquad n_\epsilon^0 \geq 0,\end{cases} \tag{16}$$

$$I_\epsilon(t) = \int_{\mathbb{R}^d} n_\epsilon(t,x) dx. \tag{17}$$

Ici $K(x-y)$ est la probabilité d'avoir une mutation de trait $y$ vers trait $x$, et $b(y,I)$ est le taux de naissances avec mutation. On suppose

$$\int e^{|z|^2} K(z) dz < \infty, \tag{18}$$

et que $K$ est assez régulier. Le paramètre $\varepsilon$ dans le terme intégral permet de considérer les mutations petites et $\frac{1}{\varepsilon}$ devant le terme à droite est le résultat du changement d'échelle $t \mapsto \frac{t}{\varepsilon}$ comme dans le cas du modèle (1)–(2). Ce modèle, ainsi que les modèle (1)–(2) et (3) ont été dérivés des modèles stochastiques à la limite des grandes populations [31, 32]. Ici les mutations, au contraire des modèles avec un terme de Laplace, ne sont pas considérées homogènes et elles peuvent dépendre de trait à travers le terme $b(y,I)$.

Une difficulté dans l'étude de ce modèle, est que la borne Lipschitz de la donnée initiale n'est plus propagée et peut exploser en temps fini (voir [19, 8, 36] pour des résultats de régularité pour les Hamiltoniens sous forme intégral). On surmonte toutefois cette difficulté, en contrôlant la norme Lipschitz par $-u_\varepsilon$ qui tend en effet vers $+\infty$, lorsque $x$ tend vers l'infini. Pour obtenir le résultat principal on a besoin de remplacer les hypothèses (13)-(14) par

$$\min_{x\in\mathbb{R}^d} \big[R(x, I_m) + b(x, I_m)\big] = 0, \qquad \max_{x\in\mathbb{R}^d} \big[R(x, I_M) + b(x, I_M)\big] = 0, \tag{19}$$

$$-K_2 \leq \frac{\partial (R+b)}{\partial I}(x, I) \leq -K_2^{-1} < 0. \tag{20}$$

Dans le chapitre 2 nous montrons le résultat suivant qui était déjà obtenu formellement dans [11] :

**Théorème 12 (Barles, M., Perthame)** *On suppose (15), (18), (19), (20), et que* $(u_\epsilon^0)_\epsilon = (\epsilon \ln(n_\epsilon^0))_\varepsilon$ *est une suite de fonctions continues qui convergent localement uniformément vers* $u^0$*. Soit* $n_\epsilon$ *la solution de (16)–(17), et* $u_\epsilon = \epsilon \ln(n_\epsilon)$*. Alors, quitte à extraire une sous-suite,* $u_\epsilon$ *converge localement uniformément vers une fonction continue* $u \in \mathrm{C}((0,\infty)\times\mathbb{R}^d)$*, une solution de viscosité de l'équation suivante*

$$\begin{cases}\partial_t u = R(x, I(t)) + b(x, I(t)) \int K(z) e^{\nabla u \cdot z} dz,\\ \max\limits_{x\in\mathbb{R}^d} u(t,x) = 0, \quad \forall t > 0,\\ u(0,x) = u^0(x),\end{cases} \tag{21}$$

$$I_\epsilon(t) \xrightarrow[\epsilon\to 0]{} I(t) \quad p.p., \qquad \int n(t,x) dx = I(t) \quad p.p..$$

*En particulier, supp* $n(t,\cdot) \subset \{u(t,\cdot) = 0\}$ *p.p en* $t$*, où* $n$ *est la limite faible de* $n_\epsilon$ *lorsque* $\epsilon$ *tend vers* $0$*.*

Une question naturelle est alors de savoir si le couple $(u, I)$ solution de (4) ou de (21) est unique. Cette question a été répondue positivement pour les deux modèles dans [11, 103], dans le cas particulier de

$$R(x, I) = b(x) - d(x) Q_1(I), \qquad \text{avec } Q_1(I) > 0 \text{ croissante,}$$

ou

$$R(x,I) = b(x)Q_2(I) - d(x), \qquad \text{avec } Q_2(I) > 0 \text{ décroissante},$$

et avec

$$0 < b_m \leq b(x), \qquad 0 < d_m \leq d(x).$$

L'unicité dans le cas général est une question ouverte.

Pour les deux modèles (1)–(2) et (16)–(17), on suppose qu'il y a une seule ressource dans l'environnement. Le principe d'exclusion compétitive de Volterra-Gause (voir [80, 114] implique qu'en présence d'une seule ressource, un seul trait puisse survivre, c'est-à-dire que la population devienne monomorphique. Des phénomènes comme le branchement ne peuvent donc pas être expliqués par ces modèles. Un modèle avec plusieurs ressources, où $R(x,I)$ est remplacé par $R(x, I_1, \cdots, I_k)$, a été récemment étudié dans [33].

## 2.4 Eviter la queue de distribution

En comparant les simulations numériques stochastiques et déterministes, des différences apparaissent dans la vitesse de l'évolution, le nombre de branchements, et la régularité de ces derniers. L'évolution dans le cas des modèles déterministes est plus rapide et les branchements sont plus nombreux et moins réguliers que le cas des modèles stochastiques. Une possibilité pour l'origine de ces différences est le phénomène de stochasticité démographique, (voir [107, 37]). Il s'agit d'un manque de fiabilité des modèles déterministes dans le cas des petites populations. Comme indiqué ci-dessus, les modèles présentés précédemment sont dérivées de modèles stochastiques dans la limite des grandes populations. Ils sont alors moins appropriés que les modèles stochastiques pour décrire la dynamique des petites populations, ce qui peut entrainer des artéfacts dans la dynamique. Notamment, dans ces modèles la solution a une queue de distribution exponentielle. En réalité, dans les endroits où la densité est très petite, aucun individu n'est présent et la densité devrait s'annuler, car on ne peut pas avoir moins d'un individu. Mais dans nos modèles continus, il peut exister des masses très petites qui peuvent croître, si elles sont dans les zones favorables. En particulier, cela peut entrainer un saut dans la localisation de la masse de Dirac, qui ne devrait pas arriver naturellement (voir figure 2). Dans le chapitre 3 nous étudions un modèle où les traits qui sont représentés par une faible densité vont disparaître immédiatement. On évite ainsi les queues de distributions.

L'idée du modèle consiste à ajouter un terme de mortalité au modèle (1)–(2)

$$\begin{cases} \frac{\partial}{\partial_t} n_\varepsilon - \varepsilon \Delta n_\varepsilon = \frac{1}{\varepsilon} n_\varepsilon R(\cdot, I) - \frac{1}{\varepsilon}\sqrt{\beta_\varepsilon n_\varepsilon} \quad \text{dans } \mathbb{R}^d \times (0, +\infty), \\ n_\varepsilon = e^{u_\varepsilon^0/\varepsilon} \quad \text{dans} \quad \mathbb{R}^d \times \{0\}, \end{cases} \tag{22}$$

avec le seuil

$$\beta_\varepsilon = e^{u_m/\varepsilon} \quad \text{avec} \quad u_m < 0.$$

Ainsi, si la densité $n_\varepsilon(x,t)$ devient inférieure au seuil $\beta_\varepsilon$, le terme de croissance devient fortement négatif, et donc la densité du trait $x$ diminue et tend vers 0. L'idée d'ajouter un terme de décroissance en racine carrée de $n_\varepsilon$ a été proposée pour la première fois dans [60] pour le modèle (3). Dans ce dernier article, les simulations numériques confirment qu'en ajoutant ce terme de mortalité, la dynamique obtenue se rapproche des modèles stochastiques. Nous présentons aussi, dans figure 2, un exemple où l'ajout de terme de mortalité entraine la disparition de la discontinuité de masse de Dirac pour le modèle (1)–(2).

L'étude mathématique de (22) est difficile. Nous étudions alors une équation plus simple où le terme de croissance $R$ ne dépend plus de la consommation totale $I(t)$ :

$$\begin{cases} \frac{\partial}{\partial_t} n_\varepsilon(x,t) - \varepsilon \Delta n_\varepsilon(x,t) = \frac{1}{\varepsilon} n_\varepsilon(x,t) R(x) - \frac{1}{\varepsilon}\sqrt{\beta_\varepsilon n_\varepsilon(x,t)} \quad \text{dans } \mathbb{R}^d \times (0, +\infty), \\ n_\varepsilon = e^{u_\varepsilon^0/\varepsilon} \quad \text{dans} \quad \mathbb{R}^d \times \{0\}. \end{cases} \tag{23}$$

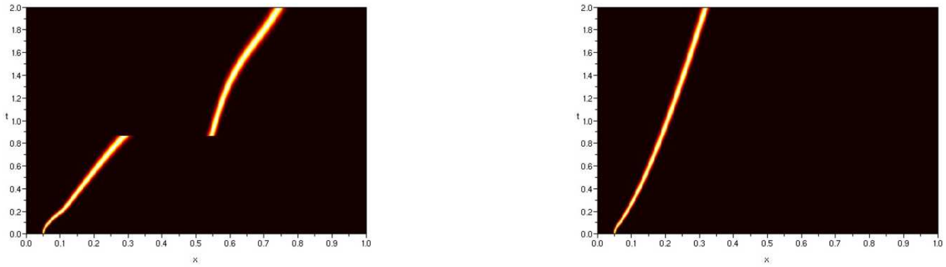


FIGURE 2 – La dynamique avec $R = (x, I) = (x - x^2 + 3x^4)(9 - (1+x)^3) - I$ pour le modèle (22). A Gauche : sans le terme de mortalité ($\beta_\varepsilon = 0$). A droite : avec le terme de mortalité et avec le seuil $\beta_\varepsilon = \exp(-\frac{0.001}{\varepsilon}) = \exp(-10)$.

On ne peut plus considérer ce dernier comme un modèle de dynamique des populations. Cependant, l'étude analytique de ce modèle simplifié, nous permet de comprendre comment le terme de mortalité modifie la solution. Nous montrons en particulier, que la forme spécifique du terme de mortalité ne change pas la dynamique asymptotique, i.e. si on remplace la racine carré par une puissance $\gamma \in (0,1)$ la solution limite ne changera pas.

La présence du terme en racine carrée de $n_\varepsilon$ complique l'étude de ce problème. L'étude de ce genre de non-linéarités, à notre connaissance remonte à [55] où il est montré que la solution pourrait s'annuler localement. Le fait que la solution d'un problème parabolique s'annule localement est un effet surprenant et aussi singulier que l'explosion de la solution pour des équations avec termes de réactions supercritiques ([108]).

Comme dans les cas précédents, nous utilisons la transformation $u_\varepsilon = \varepsilon \ln n_\varepsilon$, avec $u_\varepsilon$ solution de l'équation suivante

$$\begin{cases} \frac{\partial}{\partial_t} u_\varepsilon - \varepsilon \Delta u_\varepsilon - |Du_\varepsilon|^2 = R - \exp\big((2\varepsilon)^{-1}(u_m - u_\varepsilon)\big) \quad \text{in} \quad \mathbb{R}^d \times (0, +\infty), \\ \\ u_\varepsilon = u_\varepsilon^0 \quad \text{dans } \mathbb{R}^d \times \{0\}. \end{cases}$$

Dans le cas où le terme de croissance $R$ ne prend pas des valeurs positives, le problème est plus facile à étudier et on peut montrer que le terme de mortalité ne modifie pas significativement la dynamique. On peut en effet identifier la limite de $u_\varepsilon$ dans ce cas, lorsque $\varepsilon \to 0$, à l'aide de la solution limite $u^1$ du problème sans le terme racine carrée,

$$\begin{cases} \frac{\partial}{\partial_t} u^1 = |Du^1|^2 + R \quad \text{dans} \;\; \mathbb{R}^d \times (0, +\infty), \\ \\ u^1 = u^0 \quad \text{dans} \;\; \mathbb{R}^d \times \{0\}. \end{cases} \tag{24}$$

On montre en fait que la suite $(u_\varepsilon)_\varepsilon$ converge vers la fonction $u^1$ tronquée à $u_m$. Pour présenter notre résultat nous avons besoins de définir l'ensemble $\Omega^1$ :

$$\Omega^1 = \{(x,t) \,|\, u^1(x,t) > u_m\}. \tag{25}$$

Nous pouvons maintenant présenter notre résultat dans le cas $R \leq 0$ :

**Théorème 13 (M., Barles, Perthame, Souganidis)** *On suppose que $R \leq 0$ dans $\mathbb{R}^d$. Alors, lorsque $\varepsilon \to 0$ et quitte à extraire une sous-suite, la suite $(u_\varepsilon)_\varepsilon$ converge localement uniformément dans $\Omega^1 \cup \mathbb{R}^d \backslash \overline{\Omega^1}$, vers*

$$u(x,t) = \begin{cases} u^1(x,t) & \textit{for} \quad (x,t) \in \Omega^1, \\ -\infty & \textit{for} \quad (x,t) \in \mathbb{R}^d \backslash \overline{\Omega^1}, \end{cases}$$

*avec $u^1$ et $\Omega^1$ définis par (24) et (25). En particulier, $u(x,t) \to u_m$ lorsque $(x,t) \to \partial\Omega^1$.*

Ce cas présenté ci-dessus est plus facile à étudier que le cas général, car on peut utiliser la propriété que pour un Hamiltonien concave, le maximum de deux sur-solutions est une sur-solution. La difficulté dans le cas où $R$ peut prendre des valeurs positive est qu'on ne dispose pas de sur-solution triviale. On doit alors effectuer une analyse plus poussée.

Dans le cas général, on peut observer facilement, au moins formellement, que la solution $u_\varepsilon$ devrait converger vers $u$ la solution de viscosité de l'équation suivante

$$\begin{cases} \frac{\partial}{\partial_t} u = |Du|^2 + R \quad \text{in} \quad \Omega \subset \mathbb{R}^d \times (0,\infty), \\ u = -\infty \quad \text{in} \quad \overline{\Omega}^c \cap (\mathbb{R}^d \times (0,\infty)), \\ u \geq u_m \quad \text{in} \quad \overline{\Omega}, \\ u = u^0 \quad \text{in} \quad \overline{\Omega} \cap \{0\}, \end{cases} \tag{26}$$

avec l'ensemble ouvert $\Omega$ défini par

$$\Omega = \mathcal{I}nt \left\{(x,t) \in \mathbb{R}^d \times (0,\infty) : \lim_{\varepsilon\to 0} u_\varepsilon(x,t) > -\infty\right\}.$$

On constate que (26) ressemble à un problème avec obstacle où l'obstacle dépend de la solution-même. L'ensemble $\Omega$ a un rôle important ici et le problème est de trouver un couple $(u,\Omega)$ qui vérifie (26). La difficulté ici est qu'un tel problème admet plusieurs solutions. Il faudrait alors choisir de bonnes conditions aux bords pour obtenir la bonne solution. Les conditions aux bords naturelles pour ce problème sont la condition de Dirichlet

$$\lim_{(x,t)\to(x_0,t_0)\in\partial\Omega} u(x,t) = u_m, \tag{27}$$

et la condition de contrainte d'état (voir [116])

$$u \quad \text{est une sur-solution dans } \Omega \quad \text{et une sous-solution dans } \overline{\Omega}\ .$$

Cependant, à notre connaissance, les problèmes de contrainte d'état n'ont pas été étudiés pour les domaines qui varient avec le temps et les domaines non-réguliers. Ici le domaine $\Omega$ varie avec le temps et peut être très irrégulier. On ne peut donc pas utiliser directement les résultats existants dans cette théorie. L'idée sous-jacente à nos calculs vient toutefois de cette théorie.

Pour présenter notre résultat, nous avons besoin de définir

$$\overline{u}(x) = \limsup_{\varepsilon\to 0, y\to x} u_\varepsilon(y) \quad \text{et} \quad \underline{u}(x) = \liminf_{\varepsilon\to 0, y\to x} u_\varepsilon(y).$$

Voici notre résultat pour le cas général

**Théorème 14 (M., Barles, Perthame, Souganidis)** *Soit $n_\varepsilon$ la solution de (23) et $u_\varepsilon = \varepsilon \ln(n_\varepsilon)$. On a alors, pour tout $\mu > 0$,*

$$\overline{u} \leq U[u_0] \quad \textit{in} \quad \mathbb{R}^d \times [0,\infty) \quad \textit{et} \quad U[u_0-\mu] + \mu \leq \underline{u} \quad \textit{in} \quad \Omega[u_0-\mu].$$

La fonction $U[u_0]$ et le domaine $\Omega[u_0]$ sont définis dans le chapitre 3 par un algorithme itératif. Notre conjecture est que la sous-solution $\overline{u}$ et la sur-solution $\underline{u}$ sont en fait égales, mais nous ne pouvons le montrer que pour le cas où $R$ est strictement positive :

$$R \geq a > 0 \quad \text{in} \quad \mathbb{R}^d, \tag{28}$$

et, sous l'hypothèse que pour $\mu > \delta > 0$ suffisamment petits, il existe $\rho_{\delta,\mu} > 0$ tel que

$$\lim_{\mu\to 0}\lim_{\delta\to 0} \rho_{\delta,\mu} = 0 \quad \text{et, si } u_0(y) > u_m - \delta, \quad \text{alors} \quad \sup_{|y-z|\leq\rho_{\delta,\mu}} u_0(z) > u_m - \delta + \mu. \tag{29}$$

**Théorème 15 (M., Barles, Perthame, Souganidis)** *Sous les hypothèses (28) et (29), on a*

$$\lim_{\varepsilon\to 0} u_\varepsilon = U[u_0] \quad \textit{dans} \quad \cup_{\mu>0}\ \Omega[u_0-\mu]. \tag{30}$$

# 3 Méthodes numériques et exemples biologiques

## 3.1 Modèle de compétition directe

Dans le modèle (1)–(2), on considère la situation où une seule ressource est présente et que la compétition entre traits se fait à travers le paramètre $I(t)$ qui représente la consommation totale de cette ressource. La compétition entre les individus ne dépend donc pas de leurs traits. Dans un grand nombre de situations, cela n'est pas le cas. Il est en particulier plus naturel de supposer que les individus avec des traits proches ont une compétition plus importante entre eux. C'est pourquoi d'autres modèles ont été proposés où la compétition dépend du trait. En particulier, un modèle qui a été proposé est le modèle de compétition directe (voir [91, 45, 62, 61, 17])

$$\frac{\partial n(x,t)}{\partial t} - \lambda \frac{\partial^2 n(x,t)}{\partial x^2} = n(x,t)\big(r(x) - K * n(x,t)\big), \qquad t \geq 0,\ x \in \mathbb{R}. \tag{31}$$

On constate que ce modèle de type Lotka-Volterra est le même que (3) avant le changement d'échelle $t \mapsto \frac{t}{\varepsilon}$. La signification des termes est alors inchangée. Comme indiqué auparavant, ce modèle est dérivée des modèles d'individu-centré [113, 31, 32].

Dépendant de la structure du terme de croissance et du noyau de la compétition, la solution de cette équation peut soit converger vers un état continue, en temps long, soit se concentrer sous forme de masses de Dirac. Il existe plusieurs résultats théoriques pour déterminer dans laquelle de ces deux situations le modèle se situe. Par exemple, dans le cas où il n'y a pas de mutations et le terme de croissance et le noyau de compétition sont des Gaussiennes,

$$\lambda = 0, \qquad r(x) = \frac{1}{\sqrt{2\pi\sigma_1}} e^{-\frac{|x|^2}{2\sigma_1}}, \qquad K(z) = \frac{1}{\sqrt{2\pi\sigma_2}} e^{-\frac{|x|^2}{2\sigma_2}},$$

on peut dériver facilement le résultat suivant.

**Proposition 16** *Pour $\sigma_1 > \sigma_2$ il existe un état stationnaire régulier pour* (31) *donné par*

$$N(x) = \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{|x|^2}{2\sigma}}, \qquad \sigma = \sigma_1 - \sigma_2,$$

*et les masses de Dirac ne sont pas des états stationnaires stables.*

*Pour $\sigma_1 < \sigma_2$ la masse de Dirac $\bar{\rho}\delta(x)$ est un état stationnaire stable (et la seule masse de Dirac stable est celle à l'origine).*

Les auteurs de [74] montrent de plus que les états stables correspondants sont, de même, les limites en temps long de la dynamique décrite par (31).

Un autre cas qu'on peut décrire est le cas de l'équation Fisher-Non-locale, où

$$r \equiv 1. \tag{32}$$

Alors on a la

**Proposition 17 ([62])** *On suppose $r \equiv 1$ et qu'il exite $\xi_0$ tel que*

$$\widehat{K}(\xi_0) < 0,$$

*alors pour $\lambda$ suffisamment petit, l'état stationnaire $N \equiv 1$ est linéairement instable (au sense de Turing; les modes instables sont bornés).*

On dispose aussi d'un résultat avec les conditions opposées :

**Théorème 18 ([17])** *On suppose* $r \equiv 1$ *et*

$$\widehat{K}(\xi) > 0 \qquad \forall \xi \in \mathbb{R}. \tag{33}$$

*Alors* $n \equiv 0$ *et* $n \equiv 1$ *sont les seuls états stationnaires non-négatifs et bornés pour l'équation* (31)*. En outre, il existe des fronts propagatifs qui connectent les états* $n = 0$ *et* $n = 1$*.*

Le résultat de ce Théorème correspond à la situation $\sigma_1 > \sigma_2$ dans la Proposition 16.

Dans le chapitre 4 nous présentons des simulations numériques dans le cas où (32) et (33) sont vérifiés. Nous supposons notamment que le noyau de compétition est Gaussien. Pour les simulations numériques nous utilisons les deux méthodes des différences finies et de Monte-Carlo. Les deux méthodes confirment la convergence de la solution vers l'état stationnaire $n \equiv 1$, conformément au Théorème 18. Voir figures 3 et 4.

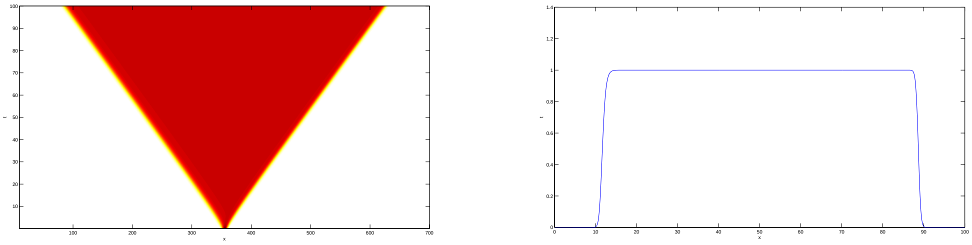


FIGURE 3 – A gauche : Simulation numérique de la dynamique d'une densité de population pour le modèle (31) où les paramètres vérifient (32) et (33) et la population initiale est concentrée au centre du domaine de calcul. Horizontalement on a représenté $x$ et verticalement $t$. Dans la zone en gris $n \equiv 1$ et la zone en blanc correspond à $n \equiv 0$. A droite : la densité de population $n(x, T)$ au temps final. Un schéma déterministe des différences finies a été utilisé (voir le chapitre 4). On observe la convergence vers la solution constante conformément au Théorème 18.

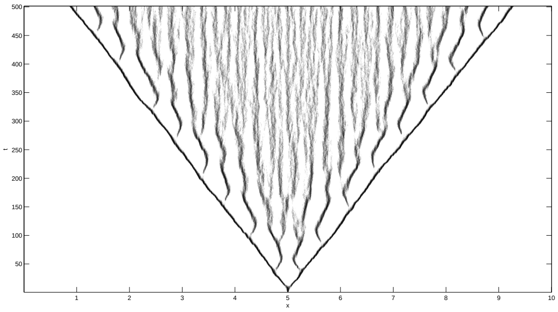


FIGURE 4 – Simulation numérique avec l'algorithme de Monte-Carlo présenté dans la section 4.2.2. Horizontalement on a représenté le trait $x$ et verticalement le temps $t$. Initialement la population est concentrée au centre du domaine. On observe que la distribution de la population converge faiblement vers l'état constant. Cela est en accord avec les simulations déterministes.

Dans les simulations Monte-Carlo, on observe notamment une somme de masses de Dirac, qui se soumettent à des branchements et deviennent de plus en plus nombreuses. Cela peut être expliqué par le fait que pour de petites perturbations du noyau, seulement des états stationnaires stables discrets pourraient exister, où ces états discrets convergent faiblement vers l'état constant $n \equiv 1$ (voir [68, 74]).

Pour les simulations stochastiques, dans le calcul de la convolution, il est important de considérer des bonnes conditions aux bords. Dans [20, 115] les auteurs utilisent une formule pour la convolution qui consiste à imposer des conditions périodiques. Cela revient à choisir comme le noyau de convolution, une gaussienne périodique. On se place alors dans le cadre de la Proposition 17 plutôt que celui du Théorème 18. Les simulations montrent aussi la convergence vers les masses de Dirac, en accord avec la Proposition 17. Voir figures 5 et 6 et le chapitre 4 pour plus de détail.

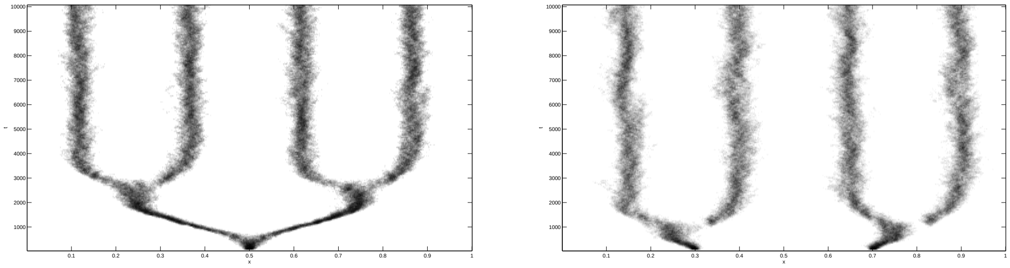


FIGURE 5 – Dynamique des points de concentration avec l'algorithme de Monte-Carlo présenté dans la section 4.2.3 avec les conditions aux bords périodiques. Horizontalement on a représenté le trait $x$ et verticalement le temps $t$. Initialement la solution est concentrée en une masse de Dirac à gauche et en deux masses de Dirac à droite.

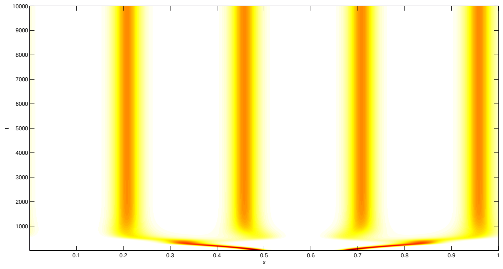


FIGURE 6 – Dynamique des points de concentration avec un algorithme déterministe des différences finies présenté dans la section 4.2.3 avec les conditions aux bords périodiques. Horizontalement on a représenté le trait $x$ et verticalement le temps $t$.

## 3.2 Modèle de compétition pour des ressources limitées

La plupart des résultats existant dans la littérature concerne les modèles de compétition directe comme (31). La compétition entre traits se fait cependant en général pour des ressources limitées, comme des nutriments ou des proies. Par exemple, les oiseaux avec des becs similaires sont en compétition parce qu'ils utilisent des nutriments similaires. Il est alors plus réaliste d'étudier un modèle où la compétition a lieu non pas directement entre individus, mais pour obtenir des ressources. En termes mathématiques, cela correspond à utiliser un noyau de ressource-consommation, à la place d'un noyau de compétition directe.

Dans le chapitre 5 nous étudions un tel modèle pour modéliser un chemostat. Nous avons donné un exemple de modèle simple de type chemostat dans la section 2.1. Ce modèle diffère des précédents par le fait que les nutriments possèdent aussi des traits continus et les consommateurs utilisent des ressources qui ont des traits similaires aux leurs.

Voici le modèle que nous étudions

$$\begin{cases} \partial_t n(x,t) = n(x,t)\big(-m_1(x) + r(x)\int K(x,y)R(y,t)dy\big) + \varepsilon\Delta n(x,t), \\ \\ \partial_t R(y,t) = -m_2(y)R(y,t) + R_{in}(y) - R(y,t)\int r(x)K(x,y)n(x,t)dx, \end{cases} \tag{34}$$

avec la donnée initiale

$$n(0,x) = n^0(x) \geq 0, \qquad R(0,y) = R^0(y) \geq 0.$$

Dans ce modèle nous avons deux espèces ; le consommateur et la ressource. La variable $x$ représente le trait du consommateur et $y$ représente celui de la ressource. En outre, $n(x,t) \geq 0$ correspond à la densité du consommateur du trait $x$ et $R(y,t) \geq 0$ correspond à la densité de la ressource du trait $y$. La ressource est fournie perpétuellement (comme il est souvent le cas pour un modèle du chemostat) avec le taux $R_{in}(y) > 0$. Les taux de mortalité (où le taux de l'écoulement du chemostat) des consommateurs et des ressources sont représentés respectivement par $m_1(x)$ et $m_2(y)$. La consommation de la ressource est modélisée à l'aide d'un paramètre d'efficacité $r(x)$ et d'un noyau de ressource-consommation $K(x,y)$ qui détermine comment les consommateurs du trait $x$ dépendant de la ressource du trait $y$. Enfin comme auparavant, le terme de Laplace correspond aux mutations et $\varepsilon$ est un petit terme qui correspond au taux de mutations. Voir le tableau 5.1.

Ce système est une généralisation du modèle de MacArthur dans [85]. Il peut aussi être considéré comme le modèle de la dynamique des populations dans un environnement hétérogène, où le taux de consommation de la ressource, la décroissance de la ressource, et la mortalité des consommateurs sont des fonctions de la position spatiale, $x$ (voir [112]).

Certains de nos résultats ne sont vrais que pour le modèle réduit suivant

$$\begin{cases} \partial_t n(x,t) = n(x,t)\big(-m_1(x) + r(x)\int K(x,y)R(y,t)dy\big) + \varepsilon\Delta n(x,t), \\ \\ R(y,t) = \frac{R_{in}(y)}{m_2(y)+\int r(x)K(x,y)n(x,t)dx}. \end{cases} \tag{35}$$

L'idée sous-jacente à ce modèle vient du fait que la dynamique des consommateurs a lieu dans une échelle de temps qui est lente par rapport à celle de la dynamique des ressources.

Nous donnons une condition pour la survie de la population

**Théorème 19 (M., Perthame, Wakano. Condition pour la survie)** *Soit le couple* $(n,R)$ *une solution du système* (34) *ou de* (35). *Etant donné que* $\int \frac{R_{in}(y)}{m_2(y)} |\ln R^0(y)| dy < \infty$ *et*

$$m_1(x) \geq r(x) \int K(x,y) \frac{R_{in}(y)}{m_2(y)} dy, \qquad \textit{pour tout } x \in \mathbb{R}, \tag{36}$$

*la population disparaît, i.e.* $\int n(x,t)dx$ *tend vers* 0 *et* $R(y,t)$ *converge p.p. vers* $\frac{R_{in}(y)}{m_2(y)}$, *lorsque* $t$ *tend vers* $+\infty$.

*Si (36) n'est pas vérifiée alors la population va survivre, i.e.* $\int n(x,t)dx$ *ne tend pas vers* 0 *, au moins lorsque il n'y a pas de mutations et la donnée initiale* $n^0$ *est positive partout.*

La démonstration de ce résultat utilise une fonctionnelle de Lyapunov classique. Notons toutefois qu'une autre fonctionnelle est introduite dans [34].

## 3.3 Etats stationnaires et étude de leur stabilité

Dans le chapitre 5 nous étudions les formes possibles d'états stationnaires pour le modèle (34), sans le terme de mutations ($\varepsilon = 0$). Nous montrons que le modèle n'admet pas d'état stationnaire continu, contrairement au cas de compétition directe (31) (voir [63, 45, 74, 113] et aussi le chapitre 4).

**Théorème 20 (M., Perthame, Wakano. Non-existence d'état stationnaire non-nul)** *Le système* (34)*, avec* $\varepsilon = 0$*, n'admet pas d'état stationnaire strictement positive.*

En outre, nous montrons que le modèle (34) admet toutefois des états stationnaires sous forme de masse de Dirac. Ces propriétés nous confirment que ce modèle est commode pour observer des concentrations de populations sous forme de deltas de Dirac comme on pourrait s'y attendre pour un modèle de dynamique de populations.

Nous montrons en particulier que des états stationnaires monomorphiques existent :

**Théorème 21 (M., Perthame, Wakano. Etats stationnaires monomorphiques)** *On considère le système* (34) *avec* $\varepsilon = 0$*. Pour tout* $\bar{x}$ *tel que*

$$m_1(\bar{x}) < r(\bar{x}) \int \frac{K(\bar{x}, y) R_{in}(y)}{m_2(y)} dy, \tag{37}$$

*il existe un unique état stationnaire monomorphique* $\bar{n} = \overline{\rho} \delta_{\bar{x}}$ *avec* $\overline{\rho} > 0$*.*

Pour présenter notre résultat pour le cas dimorphique il nous faut une hypothèse de symétrie

$$\begin{gathered} R_{in}(y) = R_{in}(-y), \qquad m_1(x) = m_1(-x), \qquad m_2(y) = m_2(-y), \\ r(x) = r(-x), \qquad K(x,y) = K(-x,-y). \end{gathered} \tag{38}$$

Nous pouvons maintenant énoncer le

**Théorème 22 (M., Perthame, Wakano. Etats stationnaires dimorphiques)** *Sous l'hypothèse de symétrie* (38)*, pour tout* $\bar{x}$ *qui vérifie* (37) *il existe un unique état stationnaire dimorphique pour le système* (34) *avec* $\varepsilon = 0$*, sous la forme*

$$\bar{n} = \overline{\rho} \left( \delta_{\bar{x}} + \delta_{-\bar{x}} \right).$$

Dans le chapitre 5 nous montrons de même certaines propriétés de stabilité pour les états stationnaires. Pour pouvoir présenter ces propriétés, nous donnons d'abord une définition de la fonction fitness plus générale que dans la définition 2 (voir [45]).

**Définition 23 (Fitness)** *On appelle fitness du trait* $y$ *au sein d'une population de densité* $n(x)$*, et on le note* $F[n](y)$*, la différence de taux de natalité et de taux de mortalité du trait* $y$*, lorsque la population est de la densité* $n(x)$*.*

Ensuite nous énonçons la définition de "Evolutionary stable distribution" (ESD) qui est une phénomène proche de "Evolutionary stable state" (ESS) (voir la définition 3).

**Définition 24 (Evolutionary Stable Distribution (ESD), [74])** *Une mesure non-négative bornée* $\overline{n}$ *(i.e.* $\int \overline{n} < \infty$*), est appelée "Evolutionary Stable Distribution" si*

$$\begin{cases} F[\overline{n}](x) = 0, & \forall\, x \in \operatorname{supp} \overline{n}, \\ F[\overline{n}](x) \le 0, & \forall\, x \in \mathbb{R}, \end{cases}$$

*où* $F[\overline{n}]$ *est la fonction fitness d'une population de densité* $\overline{n}$*.*

Nous avons alors tous les éléments permettant de présenter les résultats de stabilité suivants :

**Théorème 25 (M., Perthame, Wakano. Convergence globale vers une ESD)** *On considère les systèmes* (34) *ou* (35) *avec* $\varepsilon = 0$. *On suppose que* $(\overline{n}, \overline{R})$ *est une ESD bornée et que* $\int \overline{n}(x) |\ln n^0(x)| dx$ *et* $\int \overline{R}(y) |\ln R^0(y)| dy$ *sont bien définis. Alors* $R(y,t) \to \overline{R}(y)$ *p. p. lorsque* $t \to +\infty$. *En particulier ceci est vrai lorsque supp* $n^0 =$ *Supp* $\overline{n}$.

La démonstration de ce théorème a également été effectuée à l'aide d'une fonctionnelle de Lyapunov. Nos méthodes sont en effet très liées à la méthode utilisée dans [74] pour montrer la convergence vers une ESD pour le modèle de compétition directe (voir aussi [34] pour une version discrète). Nous précisons que le théorème 25 n'implique pas la convergence de $n$ vers $\overline{n}$ dans le cas général. Pour obtenir cette convergence nous avons besoin des hypothèses sur $r$ et $K$ qui entrainent l'unicité de l'ESD comme dans [74]. Cependant en général les ESD ne sont pas uniques et elles ne sont pas toujours des "convergence stable distributions" (voir [49, 111]).

Nous pensons que le théorème 25 est aussi vrai lorsque $\overline{n}$ est une mesure. Il s'agirait d'adapter l'estimation logarithmique de [74]. Mais celui-ci n'est pas démontré dans cette thèse. Nous présentons toutefois un résultat similaire pour les solutions sous formes $n(t) = \rho(t)\delta(x - \bar{x})$.

**Théorème 26 (M., Perthame, Wakano)** *Pour les solutions sous forme* $n(t) = \rho(t)\delta(x - \bar{x})$ *avec* $\bar{x}$ *satisfaisant* (37), *la population converge vers l'unique état stationnaire monomorphique dans le Théorème 21, i.e.* $\rho(t) \to \overline{\rho}$ *et* $R(y,t) \to \overline{R}(y)$ *lorsque* $t \to \infty$, *avec* $\overline{R}(y) = \frac{R_{in}(y)}{m_2(y) + r(\bar{x})\overline{\rho}K(\bar{x},y)}$.

Dans le cas particulier où le noyau de ressource-consommation et le débit entrant de la ressource $R_{in}$ sont des gaussiennes et les taux de mortalité et le paramètre d'efficacité sont des constantes :

$$\begin{array}{ll} K(x,y) = \frac{1}{\sigma_K\sqrt{2\pi}} \exp(-\frac{|x-y|^2}{2\sigma_K^2}), \qquad R_{in}(y) = \frac{M_{in}}{\sigma_{in}\sqrt{2\pi}} \exp(-\frac{y^2}{2\sigma_{in}^2}), \\ m_1(x) \equiv \overline{m}_1, \qquad m_2(y) \equiv \overline{m}_2, \qquad \overline{m}_0 = \min(\overline{m}_1, \overline{m}_2) \qquad r(x) \equiv r, \end{array} \tag{39}$$

nous disposons d'une condition suffisante pour que l'état monomorphique soit une ESD.

**Théorème 27 (M., Perthame, Wakano. Condition suffisante pour une ESD)** *On considère le cas gaussien* (39) *avec la condition*

$$\frac{\sigma_{in}^2}{(\sigma_{in}^2 + \sigma_K^2)^{\frac{3}{2}}} < \frac{\overline{m}_1\overline{m}_2}{rM_{in}}\sqrt{2\pi} < \frac{1}{\sqrt{\sigma_{in}^2 + \sigma_K^2}}.$$

*Alors il existe une unique* $\overline{\rho}$ *tel que* $n = \overline{\rho}\delta_0$ *est une ESD locale pour le système* (34) *avec* $\varepsilon = 0$.

## 3.4 Concentration de masse

Nous effectuons, en outre, une analyse asymptotique analogue à celle présentée dans les chapitres 1 et 2, pour le modèle (35). Après un changement d'échelle $\tau = \varepsilon t$, le modèle s'écrit

$$\begin{cases} \frac{\partial}{\partial\tau} n_\varepsilon = \frac{n_\varepsilon}{\varepsilon}\big( - m_1(x) + r(x) \int K(x,y) R_\varepsilon(y,\tau) dy \big), \\ R_\varepsilon(y,\tau) = \frac{R_{in}(y)}{m_2(y) + \int r(x)K(x,y)n_\varepsilon(x,\tau)dx}. \end{cases}$$

Nous utilisons comme précédemment la transformation $\varphi_\varepsilon = \varepsilon \ln(n_\varepsilon)$ et avec des arguments similaires à ceux présentés dans les chapitres 1 et 2 nous montrons que, quitte à extraire une sous-suite, $\varphi_\varepsilon$ converge

$$\varphi_\varepsilon \underset{\varepsilon\to 0}{\to} \varphi, \qquad n_\varepsilon \rightharpoonup n,$$

avec

$$\varphi \leq 0, \qquad \text{et} \qquad \operatorname{supp} n \subset \{\varphi = 0\}.$$

Ensuite en supposant des hypothèses de concavité sur les données, des techniques proches du chapitre 1 nous permettent de montrer que la fonction $\varphi$ est strictement concave proche des points où $\varphi = 0$. En conséquence, $n$ est une somme de masses de Dirac. Ces résultats sont rassemblés dans le

**Théorème 28 (M., Perthame, Wakano. Effet de concentration)** *On suppose que, des constantes $a_0$ et $\mu_1 \in \mathbb{R}$ sont telles que la donnée initiale vérifie*

$$\varphi^0_{\varepsilon,xx}(x) - \mu_1\, \varphi^0_\varepsilon(x) \leq a_0, \tag{40}$$

*(i) et qu'il existe $a_1 > 0$ et $\mu_2 \geq 0$ tel que*

$$m_1''(x) - m_1(x)\mu_1 - \int \frac{\mu_2(y)}{m_2(y)} R_{in}(y)dy \geq a_1, \qquad \big(r(x)K(x,y)\big)_{xx} \leq \mu_1 r(x)K(x,y) + \mu_2(y). \tag{41}$$

*Alors on a*

$$\varphi_{xx} - \mu_1\, \varphi \leq a_0 - a_1\tau,$$

*dans le sens des distributions et p.p.. En particulier si $a_0 \leq 0$, on déduit que $\varphi_{xx} - \mu_1\varphi \leq 0$. Cette propriété entraine que, quitte à extraire une sous-suite, la suite $(n_\varepsilon)_\varepsilon$ converge au sens des mesures vers une somme de masses de Dirac :*

$$n_\varepsilon(x,\tau) \rightharpoonup n(x,\tau) = \sum_i \overline{\rho}_i(\tau)\delta_i(x - \bar{x}_i(\tau)). \tag{42}$$

*(ii) Si (41) est vrai avec $\mu_1 \geq 0$ alors, la population, si elle survit, est asymptotiquement monomorphique.*

$$n_\varepsilon(x,\tau) \rightharpoonup n(x,\tau) = \overline{\rho}(\tau)\delta(x - \bar{x}(\tau)). \tag{43}$$

Nous avons également obtenu une forme d'équation canonique.

**Théorème 29 (M., Perthame, Wakano. Forme d'équation canonique)** *On suppose (41) avec $\mu_1 \geq 0$, (40) avec $a_0 \leq 0$ et donc (43). Alors, le point de concentration $\bar{x}$ défini par (43) est dans $W^{1,\infty}$ et il satisfait*

$$\dot{\bar{x}}(\tau) = \big( - D^2\varphi(\bar{x}(\tau),\tau)\big)^{-1} \quad \Big(-\nabla m_1(\bar{x}(\tau)) + r\,(\bar{x}(\tau)) \int \nabla_x K(\bar{x}(\tau),y)R(y,\tau)dy$$
$$+\nabla r\,(\bar{x}(\tau)) \int K(\bar{x}(\tau),y)R(y,\tau)dy\Big).$$

*De plus, la famille $\rho_\varepsilon$ converge p.p. vers $\overline{\rho} \in W^{1,\infty}$,*

$$-m_1(\bar{x}(\tau)) + \int K(\bar{x}(\tau),y)R(y,\tau)dy = 0, \qquad R(y,\tau) = \frac{R_{in}(y)}{m_2(y) + \overline{\rho}(\tau)r(\bar{x}(\tau))K(\bar{x}(\tau),y)},$$

$$\overline{\rho}(t) \geq \rho^0 e^{-K\tau}.$$

*Par conséquent, la population survit.*

Voir section 5.6.3 pour des interprétations biologiques plus détaillées des théorèmes 28 et 29.

On constate que les résultats de concentration de masses (42) et (43) sont vrais sous l'hypothèse (40) sur la donnée initiale avec $a > 0$. Cette hypothèse revient à dire que la population est initialement concentrée sur des traits séparés. Une question naturelle est alors de savoir si, partant des données initiales continues, la population se concentre sous forme de masse de Dirac. Dans la section 5.7 nous répondons positivement à cette question (sous certaines hypothèses).

**Théorème 30 (M., Perthame, Wakano. Distribution continue vers des masses de Dirac)** *Soit $n(x,t)$ la solution de (35) et $\varphi(x,t) = \ln n(x,t)$.*
*(i) Si la condition (41) est satisfaite avec $\mu_1 \geq 0$, la fonction $\varphi$ est concave pour $t$ assez long et la population, à condition qu'elle survive, est asymptotiquement monomorphique,*

$$\limsup_{t\to\infty} \frac{\varphi_{xx}(x,t)}{t} \leq -a_1.$$

*(ii) Si la condition (41) est satisfaite avec $\mu_1 < 0$, alors*

$$\limsup_{t\to\infty} \frac{\varphi_{xx}(x,t) - \mu_1 \varphi(x,t)}{t} \leq -a_1.$$

*Par conséquent, la population se concentre sur des traits bien-séparés et la distribution ne peut pas être continue.*

# 4 Populations sexuées

La modélisation de la dynamique des populations sexuées est plus compliquée que celle de populations asexuées, puisqu'il faudrait considérer deux densités de populations, mâles et femelles. En outre, la reproduction exige deux parents, de traits $v_*$ et $v'_*$, qui donnent naissance à un individu de trait $v$, souvent différent de $v_*$ ou $v'_*$. L'analyse et la modélisation de l'accouplement et de la distribution de traits des nouveau-nées en fonction de distributions de traits des parents, ne sont pas des tâches faciles et les phénomènes biologiques sous-jacents ne sont pas entièrement compris. Voir les détails ci-dessous.

Dans le chapitre 6, nous étudions un modèle simple de la dynamique des populations sexuées où l'on identifie des mâles et des femelles. Nous étudions la dynamique d'une population structurée par un trait phénotypique $v \in \mathbb{R}$ et par une variable d'espace $x \in \mathbb{R}$, qui vit dans un environnement hétérogène. On suppose que le trait optimal à tout point $x$ de l'espace, est indiqué par $\theta(x) = bx$. Voir [100, 79, 101] pour des études de modèles similaires utilisant des méthodes numériques.

Ce type de modèle peut être utilisé pour étudier la distribution et l'aire de répartition des espèces le long d'un gradient d'environnement, comme le gradient nord-sud de la température dans l'hémisphère du nord [72, 79, 105, 15]. Il est utile en particulier pour étudier l'impact d'un changement dans l'environnement, par exemple le réchauffement climatique, sur une population (voir [100, 79, 105]).

Le processus de la reproduction sexuée est le phénomène qui distingue la dynamique des populations sexuées de celle des populations asexuées. En particulier, le fait que le nouveau-né ait un trait $v$ différent de celui de ses deux parents, $v_*$ et $v'_*$, induit une plus grande variété dans la population et apparaît comme un obstacle pour la spéciation (voir [51]). En outre, la répartition géographique pour ces deux dernières populations peut être très différente. En particulier, dans le chapitre 6 on observe que la population soit se propage dans tout l'espace, soit elle survit mais reste restreinte à une partie de l'espace (notre modèle présuppose qu'il n'y a pas d'extinction). Dans un modèle équivalent pour les populations asexuées, cela n'est pas le cas. Dans ce dernier cas, la population, à condition qu'elle survive, se propage à tout l'espace (voir [98]). Une origine de cette différence, est le phénomène de "gene flow"; les traits des individus qui sont sur le bord du domaine de répartition de l'espèce sont très influencés par les traits des individus qui sont au centre du domaine. Les traits des individus sur le bord sont donc loin d'être optimaux par rapport à leurs positions dans l'espace (voir [79]).

Dans la section 6.2.1 nous présentons un modèle de populations structurées pour modéliser la dynamique d'une population sexuée. A partir de cette dernière, nous obtenons formellement une équation différentielle sur les deux premiers moments de la densité de la population $n$ :

$$N(t,x) := \int n(t,x,v)\,dv, \quad Z(t,x) := \int v\frac{n(t,x,v)}{N(t,x)}\,dv.$$

Voici l'équation sur $Z$ et $N$ :

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \big(1 - \frac{A}{2}(Z(t,x)-Bx)^2 - N(t,x)\big)\,N(t,x), \\ \partial_t Z(t,x) - \Delta_x Z(t,x) = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x)). \end{cases} \tag{44}$$

Cette équation a été introduite dans [79] où les auteurs ont étudié la répartition géographique de la population dû au "gene flow". Ainsi, nous justifions le choix de ce modèle en mettant en évidence les hypothèses nécessaires sur les paramètres pour que ce dernier soit valable.

Dans l'équation (44), le paramètre $A$ peut être interprété comme le potentiel d'adaptation vers le trait optimal. Le paramètre $B$ indique la vitesse de changement de l'environnement. En particulier, on s'attend à ce que la population disparaisse si $B$ est grand, qu'elle se propage à l'espace entier si $B$ est petit, et qu'elle survive et reste restreinte à une partie de l'espace pour les valeurs intermédiaires de $B$. Ici, en supposant qu'il n'y a pas d'extinction, nous étudions l'existence de fronts propagatifs et de solutions stationnaires qui correspondent respectivement au deuxième et le troisième cas.

En effectuant un changement d'échelle et en supposant que $A$ est petit, on obtient le modèle simplifié suivant

$$N(t,x) \sim 1 - (Z(t,x) - (B/\sqrt{2})x)^2.$$

$$\begin{aligned} \partial_t Z(t,x) - \Delta_x Z(t,x) &= -4\frac{(\partial_x Z(t,x) - B/\sqrt{2})(Z(t,x) - (B/\sqrt{2})x)}{1 - (Z(t,x) - (B/\sqrt{2})x)^2}\partial_x Z(t,x) \\ &\quad + ((B/\sqrt{2})x - Z(t,x)), \end{aligned}$$

En remplaçant $Z(t,x) - (B/\sqrt{2})x$ par $W(t,x)$ cette dernière équation s'écrit

$$\partial_t W - \triangle_x W = -4\frac{\partial_x W W}{1-W^2}(\partial_x W + B/\sqrt{2}) - W, \tag{45}$$

avec

$$-1 \le W^0 \le 1.$$

Cette équation a des singularités aux points $\pm 1$. La présence des singularités est un obstacle pour avoir un modèle bien défini. Cependant, la présence de ces dernières est cruciale pour observer des fronts propagatifs. Dans les modèles habituels, les fronts propagatifs connectent deux états stationnaires. La situation pour le modèle (45) est différente. Ici les fronts connectent un état stationnaire instable, correspondant à $W = 0$ à un point de singularité, qui correspond à $W = -1$.

Puisque le modèle est singulier, on introduit le modèle approché suivant

$$\partial_t W_\delta - \triangle_x W_\delta = -4\frac{\partial_x W_\delta W_\delta}{1 - W_\delta^2 + \delta}(\partial_x W_\delta + B/\sqrt{2}) - \frac{(1 - W_\delta^2)W_\delta}{1 - W_\delta^2 + \delta}, \tag{46}$$

$$-1 \leq W_\delta(t=0) \leq 1. \tag{47}$$

Avec ce choix de modèle on évite les points de singularités, et on remplace le point singulier $-1$ par un état stationnaire stable (la stabilité est pour une formulation EDO présentée dans la section 6.3.2).

A l'aide de ce modèle approché nous obtenons le résultat d'existence suivant :

**Théorème 31 (M., Raoul)** *Sous hypothèse (47), les solutions de (46) sont localement uniformément bornées et Lipschitz :*

$$-1 \leq W_\delta(t,x) \leq 1, \qquad |\partial_x W_\delta(t,x)| \leq C_2, \qquad \text{pour tout } (t,x) \in \mathbb{R}^+ \times \mathbb{R}.$$

*De plus, quitte à extraire une sous-suite,* $(W_\delta)_\delta$ *converge vers une fonction continue* $W$*, une solution de viscosité de*

$$(1-W^2)\partial_t W - (1-W^2)\triangle_x W = -4\partial_x W W(\partial_x W + B/\sqrt{2}) - (1-W^2)W. \tag{48}$$

L'équation (48) est en effet l'équation (45) multipliée par $1 - W^2$. Le critère de viscosité n'est malheureusement pas suffisant pour sélectionner une unique solution. Voir la section 6.3 pour un contre-exemple.

Nous montrons que ce problème admet des fronts propagatifs :

**Théorème 32 (M., Raoul)** *Pour tout* $B > 0$*, il existe* $\nu_B \in \mathbb{R}$ *tel que* (45) *admet un front propagatif de vitesse* $\nu$*,* $W(t,x) = U(x-\nu t)$*, avec*

$$U(x) \to 0 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ as } x \to +\infty,$$

*si et seulement si* $\nu > \nu_B$*.*

*Le front propagatif de vitesse* $\nu$ *est unique, à une translation près. De plus* $\nu_B$ *est une fonction décroissante de* $B$*.*

Pour tout $B > 0$, il existe une famille de fronts propagatifs. Par analogie avec le cas de l'équation de Fisher-KPP, on peut s'attendre à ce que le seul front stable soit celui avec la vitesse minimale $\nu_B$. Le front associé à $\nu_B$ serait un front d'invasion si $\nu_B > 0$, et un front d'extinction si $\nu_B < 0$. Nous montrons que des états stationnaires existent seulement dans le cas de $\nu_B < 0$. Ces observations sont en accord avec notre première intuition, où on s'attendait à ce que pour $B$ grand il y ait propagation de la population à l'espace entier et que pour $B$ petit, la population reste restreinte à une partie de l'espace.

On précise que, puisque ce modèle n'admet pas de principe de comparaison, on ne peut pas utiliser les méthodes habituelles pour étudier la stabilité des fronts propagatifs. Cependant, on arrive à montrer un principe de comparaison pour le modèle approché (46). Alors, si on définit la solution comme limite de solutions du modèle approché (46), il est naturel de s'attendre à ce que le principe de comparaison soit vrai pour ces solutions limites. Le principe de comparaison nous permettrait notamment de comparer les solutions avec les fronts propagatifs et de montrer la propagation de la population avec la vitesse minimale.

Voici enfin le résultat d'existence d'états stationnaires :

**Théorème 33** *L'équation* (45) *a un état stationnaire non-trivial si et seulement si* $\nu_B < 0$*. Les états stationnaires* $W(t,x) = U(x)$ *satisfont*

$$U(x) \to 1 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ lorsque } x \to +\infty.$$

## 5 Perspectives

**Unicité pour le problème de Hamilton-Jacobi avec contrainte :**

Comme nous avons constaté auparavant, l'étude asymptotique de l'équation (1)–(2) est liée à l'étude de l'équation Hamilton-Jacobi suivante

$$\begin{cases} \frac{\partial}{\partial_t} u = |\nabla u|^2 + R(x, I), \\ \max_{\mathbb{R}^d} u(x, t) = 0. \end{cases}$$

Une question ouverte est de savoir si cette équation avec contrainte, admet une unique solution $(u, I)$. L'unicité a été démontrée par Benoît Perthame et Guy Barles, seulement dans le cas particulier où

$$R(x, I) = b(x) - d(x)Q_1(I),$$

ou

$$R(x, I) = b(x)Q_2(I) - d(x).$$

Ici $Q_1(I) > 0$ et $Q_2(I) > 0$ sont respectivement des fonctions croissantes et décroissantes de $I$ et $b(x) \geq b_m$, $d(x) \geq d_m$ (voir [11, 103]).

**Evolution et propagation de traits phénotypiques dans l'espace pour les populations asexuées :**

Avec Gaël Raoul nous nous intéressons aussi à l'étude de la dynamique des populations asexuées structurées par une variable d'espace et un trait phénotypique. Donc, comme dans le cas des populations sexuées dans le chapitre 6, il y a deux paramètres dans le modèle :

$v$ : le trait phénotypique, et $x$ : la position en espace.

La dynamique s'écrit

$$\frac{\partial}{\partial_t} n - \varepsilon \triangle_x n - \varepsilon^2 \triangle_v n = \frac{n}{\varepsilon} R(x, v, I(t, x)),$$

avec $I$ le paramètre de ressource :

$$I(t, x) = \int \psi(v) n(t, x, v) dv.$$

Dans ce problème, on s'attend à observer la propagation en direction de l'espace, et des masses de Dirac dans la direction du trait phénotypique.

La différence de celui-ci avec les modèles étudiés auparavant est la dépendance de $I$ en $x$ ainsi que la présence de deux échelles différentes pour les mutations et la diffusion. Cette différence de l'échelle s'explique par le fait que la diffusion en espace a lieu plus rapidement que les mutations.

**Modèle de compétition pour des ressources vers modèle de compétition directe :**

Avec Benoît Perthame et Joe Yuichiro Wakano, nous nous intéressons à comprendre mieux le lien entre le modèle de compétition pour des ressources limitées présenté dans le chapitre 5 et le modèle de compétition directe (3) déjà étudié dans la littérature. Nous partons de notre travail précédent dans le chapitre 5 où on étudie un modèle de type chemostat où des micro-organismes consomment des ressources fournies perpétuellement, en supposant que des consommateurs et des ressources sont tous deux caractérisés par des traits continus. Nous souhaitons en particulier de dériver le modèle de compétition directe à partir du modèle de compétition pour des ressources comme une limite asymptotique.

**Approche homogénéisation :**

J'ai commencé récemment, lors d'une visite à l'université de Chicago avec Panagiotis E. Souganidis, une étude d'un problème de l'évolution Darwinienne avec une approche d'homogénéisation. Il s'agit de l'étude de la dynamique d'une population structurée par des traits phénotypiques dans un environnement avec de grandes oscillations à l'échelle microscopique. La motivation principale de la théorie de l'homogénéisation est de comprendre des propriétés macroscopiques des modèles avec de grandes oscillations à l'échelle microscopique. Il s'agit d'une équation aux dérivées partielles dépendant d'une variable lente et d'une variable rapide. Le but est de d'obtenir une solution homogénéisée qui ne dépend que de la variable lente.

Lions, Papanicolaou et Varadhan étaient les premiers à étudier l'homogénéisation des équations de Hamilton Jacobi [83] dans un milieu périodique. Ceci a été aussi étudié par Evans, Caffarelli, Majda, Souganidis, Arisawa et Ishii,.... Dans le cas de la dynamique des populations on peut étendre nos modèles à des problèmes d'homogénéisation en ajoutant une variable rapide au modèle :

$$\frac{\partial}{\partial_t} n_\varepsilon - \varepsilon \triangle n_\varepsilon = \frac{n_\varepsilon}{\varepsilon} R(x, \frac{x}{\varepsilon}, I_\varepsilon),$$

$$I_\varepsilon(t) = \int \psi(t,x) n_\varepsilon(t,x) dx,$$

avec $R$ périodique par rapport à la deuxième variable. Dans le cas du modèle avec oscillations, nous espérons pouvoir décrire la solution limite sous forme de concentration en masses de Dirac, à l'aide d'un hamiltonien effectif qui ne dépend que de la variable lente $x$ et non de la variable rapide $\frac{x}{\varepsilon}$.

**Mutations avec de grandes amplitudes et le Laplacien fractionnaire :**

Dans les modèles présentés dans cette thèse, on a supposé que les noyaux de mutations ressemblent à des noyaux Gaussien. Dans un article récent, B. Jourdain, S. Méléard et W. A. Woyczynski [77] étudient avec une approche stochastique une situation où les mutations peuvent avoir, au contraire, une grande amplitude, i.e. le mutant peut être considérablement différent de son ancêtre. L'hypothèse de grande queue de distribution pour les mutations, peut être justifiée notamment lorsqu'un mutant qui a un trait trop proche de son parent est nocif. Cela est vrai en particulier pour un trait qui mesure le niveau d'agressivité de l'individu. Dans cet article, les auteurs obtiennent à la limite des grandes populations une équation déterministe qui ressemble à l'équation (3) où le Laplacien est remplacé par un Laplacien fractionnaire. Une version simplifiée du modèle déterministe obtenu est le suivant

$$\frac{\partial}{\partial_t} n(x,t) - \triangle^\alpha n(x,t) = n(x,t) \left( r(x) - \int C(x,y) n(y,t) dy \right),$$

avec le Laplacien fractionnaire

$$\triangle^\alpha f(x) = \int_{\mathbb{R}} \left( f(x+h) - f(x) - f'(x) h \mathbb{1}_{|h|\le 1} \right) \frac{dx}{|h|^{1+\alpha}}.$$

L'opérateur de Laplacien fractionnaire généralise le Laplacien classique et il a la propriété que sa fonction de distribution décroît comme une puissance plutôt que exponentiellement.

L'étude de ce dernier rentre dans le cadre de solutions de viscosité (voir par exemple [1, 7, 75]). Une direction de recherche éventuelle consisterait à comprendre les propriétés analytiques de l'équation ci-dessus et à effectuer une étude asymptotique de la dynamique pour cette nouvelle équation.

# Première partie

# Dynamique de masses de Dirac décrite par des équations de Hamilton-Jacobi

# Chapitre 1

# Dynamique de masses de Dirac dans un domaine multidimensionnel

Le travail dans ce chapitre a été effectué en collaboration avec Alexander Lorz et Benoît Perthame. Nous étudions des modèles de type Lotka-Volterra non-local pour étudier l'évolution Darwinienne d'une population asexuée à la limite des petites mutations. Nous décrivons la dynamique à l'aide d'une équation de Hamilton-Jacobi avec contrainte. En faisant des hypothèses de régularité, nous nous plaçons dans un cadre où les solutions régulières existent. Cela nous permet de décrire la dynamique des masses de Dirac et établir rigoureusement une forme d'équation canonique. Nous montrons de plus que l'équation canonique nous fournit avec une sorte de fonctionnelle Lyapunov. Simulations numériques montrent qu'une dynamique inattendue des trajectoires peut avoir lieu. Ce travail reprend l'article [84].

## 1.1 Motivation

The nonlocal Lotka-Volterra parabolic equations arise in several areas such as ecology, adaptative dynamics and can be derived from stochastic individual based models in the limit of infinite population. The simplest example assumes competition between individuals with a trait $x$, through a single resource and reads

$$\partial_t n_\epsilon - \epsilon \Delta n_\epsilon = \frac{n_\epsilon}{\epsilon} R\big(x, I_\epsilon(t)\big), \qquad t>0,\ x \in \mathbb{R}^d, \tag{1.1}$$

with a nonlinearity driven by the integral term

$$I_\epsilon(t) = \int_{\mathbb{R}^d} \psi(x) n_\epsilon(t,x) dx. \tag{1.2}$$

Another and more interesting example is with direct competition

$$\partial_t n_\epsilon(t,x) = \frac{1}{\epsilon} n_\epsilon(t,x) \left( r(x) - \int_{\mathbb{R}^d} C(x,y) n_\epsilon(t,y)\, dy \right) + \epsilon \Delta n_\epsilon(t,x). \tag{1.3}$$

We denote by $n^0_\epsilon \geq 0$ the initial data.

These are called 'mutation-competition' models because the Laplace term is used for modeling mutations in the population. Competition is taken into account in the second model by the competition kernel $C(x,y) \geq 0$ and in the first model by saying that $R$ can be negative for $I_\epsilon$ large enough (it is a measure of how the total population influences birth and death rates). Such models can be derived from stochastic individual based models in the limit of large populations, [40, 31, 32]. There is a large literature on the subject, in terms of modeling and analysis, we just refer the interested reader to [49, 50, 96, 109].

We have already normalized the model with a small positive parameter $\varepsilon$ since it is our goal to study the behaviour of the solution as $\varepsilon \to 0$. The interesting qualitative outcome is that solutions concentrate as Dirac masses

$$n_\epsilon(t,x) \approx \bar{\rho}(t) \delta\big(x - \bar{x}(t)\big).$$

For equation (1.1), we can give an intuitive explanation; in this limit, we expect that the relation $n(t,x) R\big(x, I(t)\big) = 0$ holds. In dimension 1 and for $x \mapsto R(x,I)$ monotonic, there is a single point $x = X(I)$ where $R$ will vanish and, consequently, where $n$ will not vanish. A priori control of the total mass on $n$ from below implies the result with $\bar{x}(t) = X(I(t))$.

In several studies, we have established these singular limits with weak assumptions [10, 103]. A main new concept arises in this limit, the *constrained Hamilton-Jacobi* equation introduced in [50] which occurs by some kind of real phase WKB ansatz (as for fronts propagations in [58, 56, 9])

$$n_\epsilon(t,x) = e^{u_\epsilon(t,x)/\epsilon}. \tag{1.4}$$

Here we have in mind the simple example of Dirac masses approximated by gaussians

$$\delta(x-\bar{x}) \approx \frac{1}{\sqrt{2\pi\epsilon}} e^{-|x-\bar{x}|^2/2\epsilon} = e^{(-|x-\bar{x}|^2 - \epsilon ln(2\pi\epsilon))/2\epsilon}.$$

It is much easier to describe the limit of $-|x-\bar{x}|^2 - \epsilon ln(2\pi\epsilon)$! Dirac concentration points are understood as maximum points of $u_\epsilon(t,x)$ in (1.4). As it is well understood, these Hamilton-Jacobi equations develop singularities in finite time [5, 54, 81] which is a major technical difficulty both for proving the limit and for analyzing properties of the concentration points $\bar{x}(t)$.

This method in [50] of using $\epsilon \ln(n_\epsilon)$ to prove concentration has been followed in several subsequent studies. For long time asymptotics (and not $\epsilon \to 0$ but the two issues are connected as we explain in section 1.2) it was introduced in [45] and used in [111, 109]. More recently in [33] the authors come back on the Hamilton-Jacobi equation and prove that it makes sense still with weak assumptions for several nonlocal quantities $I_k = \int \psi_k n_\epsilon(t,x)dx$ which can be characterized in the limit.

Here we take the counterpart and develop a framework where we can prove smoothness of the various quantities arising in the theory. This opens up the possibility to address many questions that seem impossible to attain directly

- Do the Dirac concentrations points appear spontaneously at their optimal location or do they move regularly?
- In the later case, is there a differential equation on the concentration point $\bar{x}(t)$? It follows from regularity that we can establish a form of the so-called *canonical equation* in the language of adaptive dynamics [49, 47]. This equation has been established *assuming* smoothness in [50], in our framework it holds true.
- In higher dimensions, why is a single Dirac mass naturally sustained (and not the hypersurface $R(\cdot, I) = 0$ for instance)? The canonical equation enforces constraints on the dynamics which give the explanation.
- What is the long time behaviour of the concentration points $\bar{x}(t)$? A simple route is that the canonical equation comes with a kind of Lyapunov functional.

We develop the theory separately for the simpler case of the model with competition through a single resource (1.1) and for the direct competition model (1.3). For the model with a single resource we rely on assumptions stated in section 1.3 and we give all the details of the proofs in the three subsequent sections. We illustrate the results with numerical simulations that are presented in section 1.7. We give several extensions afterwards; in section 1.8 we treat the case with non-constant diffusion, and finally the case of direct competition in section 1.9.

## 1.2 A simple example: no mutations

The Laplace term in the asymptotic analysis of (1.1) and (1.3) is at the origin of several assumptions and technicalities. In order to explain our analysis in a simpler framework, we begin with the case of the two equations without mutations set for $t > 0$, $x \in \mathbb{R}^d$,

$$\partial_t n = nR\big(x, I(t)\big), \qquad I(t) = \int_{\mathbb{R}^d} \psi(x) n(t,x) dx. \tag{1.5}$$

$$\partial_t n(t,x) = n(t,x)\left(r(x) - \int_{\mathbb{R}^d} C(x,y) n(t,y)\, dy\right) := n(t,x) R\big(x, I(t,x)\big). \tag{1.6}$$

Also, we give a formal analysis, that shows the main ideas and avoids writing a list of assumptions; those of the section 1.3 and 1.9 are enough for our purpose.

In both cases one can easily see the situation of interest for us. The models admit a continuous family of singular, Dirac masses, steady states parametrized by $y \in \mathbb{R}^d$ and the question is to study their stability and, when unstable, how the dynamics can generate a moving Dirac mass.

The Dirac steady states are given by

$$\bar{n}(x; y) = \underline{\rho}(y) \delta(x - y).$$

The total population size $\underline{\rho}(y)$ is defined in both models by the constraint

$$R\big(y, \underline{I}(y)\big) = 0,$$

with respectively for (1.5) and (1.6)

$$\underline{I}(y)) = \psi(y)\underline{\rho}(y), \qquad \text{resp. } \underline{I}(y) = \underline{\rho}(y)C(y,y).$$

A monotonicity assumption in $I$ for model (1.5), namely $R_I(x,I) < 0$ shows uniqueness of $\underline{I}(y)$ for a given $y$. In case of (1.6) it is necessary that $r(y) > 0$ for the positivity of $\underline{\rho}(y)$.

In both models a 'strong' perturbation in measures is stable, i.e. only on the weight; for $n^0 = \rho^0\delta(x-y)$, the solution is obviously $n(t,x) = \rho(t)\delta(x-y)$ with

$$\frac{d}{dt}\rho(t) = \rho(t)R\big(y, \psi(y)\rho(t)\big), \qquad \text{resp. } \frac{d}{dt}\rho(t) = \rho(t)[r(y) - \rho(t)C(y,y)],$$

and

$$\rho(t) \underset{t\to\infty}{\longrightarrow} \underline{\rho}(y).$$

This simple remark explains why, giving $I$ now, the hypersurface $\{x,\ R(x,I) = 0\}$ is a natural candidate for the location of a possible Dirac curve (see the introduction).

Apart from this stable one dimensional manifold, the Dirac steady states are usually unstable by perturbation in the weak topology. A way to quantify this instability is to follow the lines of [50] and consider at $t = 0$ an exponentially concentrated initial data

$$n^0(x) = e^{u^0_\epsilon(x)/\epsilon} \underset{\epsilon\to 0}{\longrightarrow} \underline{\rho}(\bar{x}^0)\delta(x - \bar{x}^0).$$

It is convenient to restrict our attention to $u^0_\epsilon$ uniformly concave, having in mind the gaussian case mentioned in the introduction. Then, $\epsilon$ measures the deviation from the initial Dirac state and to see motion it is necessary to consider long times as $t/\epsilon$ or, equivalently, rescale the equation as

$$\epsilon\, \partial_t n_\epsilon = n_\epsilon R\big(x, I_\epsilon(t,x)\big),$$

and our goal is to prove that

$$n_\epsilon(t,x) \underset{\epsilon\to 0}{\longrightarrow} \bar{n}(t,x) = \bar{\rho}(t)\delta\big(x - \bar{x}(t)\big).$$

Also the deviation to a Dirac state turns out to stay at the same size for all times and we can better analyze this phenomena using the WKB ansatz (1.4). Indeed, $u_\epsilon$ satisfies the equation

$$\partial_t u_\epsilon = R\big(x, I_\epsilon(t,x)\big).$$

As used by [45], because $u^0$ is concave, assuming $x \mapsto R(x, I_\epsilon(t,x))$ is also concave (this only relies on assumptions on the data), we conclude that $u_\epsilon(t,\cdot)$ is also concave and thus has a *unique* maximum point $\bar{x}_\epsilon(t)$. The Laplace formula shows that, with $\bar{x}(t)$ the strong limit of $\bar{x}_\epsilon(t)$,

$$\frac{n_\epsilon(t,x)}{\int_{\mathbb{R}^d} n_\epsilon(t,x)dx} \underset{\epsilon\to 0}{\longrightarrow} \delta\big(x - \bar{x}(t)\big).$$

With some functional analysis, we are able to pass to the strong limit in $I_\varepsilon$ and $u_\epsilon$. Despite its nonlinearity, we find the same limiting equation,

$$\partial_t u = R\big(x, I(t,x)\big), \qquad u(t=0) = u^0. \tag{1.7}$$

Still following the idea introduced in [50], we may see $I(t,x)$ or $\rho(t)$ as a Lagrange multiplier for the constraint

$$\max_{\mathbb{R}^d} u(t,x) = 0 = u\big(t,\bar{x}(t)\big), \tag{1.8}$$

which follows from the a priori bound $0 < \rho(t) \leq \rho_M < \infty$. The mathematical justification of these developments is rather easy here. For model (1.5) it uses a $BV$ estimate proved in [11]. For model (1.6) one has to justify persistence (that is $\rho_\epsilon$ stays uniformly positive) and strong convergence of $\rho_\epsilon(t)$. All this work is detailed below with the additional Laplace terms.

The constraint (1.8) allows us to recover the 'fast' dynamics of $I(t)$ and $\rho(t)$. Indeed, combined with (1.7), it yields

$$R\big(\bar{x}(t), I(t)\big) = 0, \qquad \text{resp.} \quad R\big(\bar{x}(t), I(t,\bar{x}(t))\big) = 0. \tag{1.9}$$

Assuming regularity on the data, $u(t,x)$ is three times differentiable and the constraint (1.8) also gives

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

Differentiating in $t$, we establish the analogue of the canonical equations in [47] (see also [30, 50, 111, 90])

$$\dot{\bar{x}}(t) = \big(-D^2 u\big(t,\bar{x}(t)\big)\big)^{-1} . D_x R\big(\bar{x}(t), \bar{I}(t,\bar{x}(t))\big), \quad \bar{x}(0) = \bar{x}^0, \tag{1.10}$$

(in the case of model (1.6), this means the derivative with respect to $x$ in both places). Inverting $I$ from the identities (1.9) gives an autonomous equation.

This differential equation has a kind of Lyapunov functional and this makes it easy to analyze its long time behaviour. It is closely related to know what are the stable Dirac states for the weak topology; the so-called Evolutionary attractor or Convergence Stable Strategy in the language of adaptive dynamics [49, 111]. Eventhough this is less visible, it also carries regularity on the Lagrange multiplier $\rho(t)$ which helps for the functional analytic work in the case with mutations. Another use of (1.10) is to explain why, generically, only one pointwise Dirac mass can be sustained; as we explained earlier, the equation on $\dot{\bar{x}}(t)$ also gives the global unknown $I(t)$ by coupling with (1.9) and this constraint is very strong. See section 1.7 for an example.

To conclude this quick presentation, we notice that the time scale (in $\epsilon$ here) has to be precisely adapted to the specific initial state under consideration. The initial state itself also has to be 'exponentially' concentrated along with our construction; this is the only way to observe the regular motion of the Dirac concentration point. This is certainly implicitly used in several works where such a behaviour is displayed, at least numerically. Of course, there are many other ways to concentrate the initial state with a 'tail' covering the full space so as to allow that any trait $x$ can emerge; these are not covered by the present analysis.

## 1.3 Competition through a single resource: assumptions and main results

As used by [45], concavity assumptions on the function $u_\epsilon$ in (1.4) are enough to ensure concentration of $n_\epsilon(t,\cdot)$ as a *single* Dirac mass. We follow this line and make the necessary assumptions.

We start with assumptions on $\psi$:

$$0 < \psi_m \leq \psi \leq \psi_M < \infty, \qquad \psi \in W^{2,\infty}(\mathbb{R}^d). \tag{1.11}$$

The assumptions on $R \in C^2$ are that there is a constant $I_M > 0$ such that (fixing the origin in $x$ appropriately)

$$\max_{x\in\mathbb{R}^d} R(x, I_M) = 0 = R(0, I_M), \tag{1.12}$$

$$-\underline{K}_1|x|^2 \leq R(x, I) \leq \overline{K}_0 - \overline{K}_1|x|^2, \qquad \text{for } \; 0 \leq I \leq I_M, \tag{1.13}$$

$$-2\underline{K}_1 \leq D^2R(x, I) \leq -2\overline{K}_1 < 0 \text{ as symmetric matrices for } \; 0 \leq I \leq I_M, \tag{1.14}$$

$$-\underline{K}_2 \leq \frac{\partial R}{\partial I} \leq -\overline{K}_2, \qquad \Delta(\psi R) \geq -K_3. \tag{1.15}$$

At some point we will also need that (uniformly in $0 \leq I \leq I_M$)

$$D^3R(\cdot, I) \in L^\infty(\mathbb{R}^d). \tag{1.16}$$

Next the initial data $n^0_\epsilon$ has to be chosen compatible with the assumptions on $R$ and $\psi$. We require that there is a constant $I^0$ such that

$$0 < I^0 \leq I_\epsilon(0) := \int_{\mathbb{R}^d} \psi(x)n^0_\epsilon(x)dx < I_M, \tag{1.17}$$

that we can write

$$n^0_\epsilon = e^{u^0_\epsilon/\epsilon}, \qquad \text{with } \; u^0_\epsilon \in C^2(\mathbb{R}^d) \quad \text{(uniformly in } \epsilon\text{)},$$

and we assume uniform concavity on $u^\epsilon$ too. Namely, there are positive constants $\underline{L}_0, \overline{L}_0, \underline{L}_1, \overline{L}_1$ such that

$$-\underline{L}_0 - \underline{L}_1|x|^2 \leq u^0_\epsilon(x) \leq \overline{L}_0 - \overline{L}_1|x|^2, \tag{1.18}$$

$$-2\underline{L}_1 \leq D^2u^0_\epsilon \leq -2\overline{L}_1. \tag{1.19}$$

For Theorems 1.3.2 and 1.3.3 we also need that

$$D^3u^0_\epsilon \in L^\infty(\mathbb{R}^d) \quad \text{componentwise uniformly in } \epsilon, \tag{1.20}$$

$$n^0_\epsilon(x) \underset{\epsilon\to 0}{\longrightarrow} \bar{\rho}^0 \; \delta\big(x - \bar{x}^0\big) \text{ weakly in the sense of measures.} \tag{1.21}$$

Next we need to restrict the class of initial data to fit with $R$ through some compatibility conditions

$$4\overline{L}_1^2 \leq \overline{K}_1 \leq \underline{K}_1 \leq 4\underline{L}_1^2. \tag{1.22}$$

In the concavity framework of these assumptions, we are going to prove the following

**Theorem 1.3.1 (Convergence)** *Assume* (1.11)-(1.15), (1.17)-(1.19) *and* (1.22). *Then for all* $T > 0$, *there is a* $\epsilon_0 > 0$ *such that for* $\epsilon < \epsilon_0$ *and* $t \in [0, T]$, *the solution* $n_\epsilon$ *to* (1.1) *satisfies,*

$$0 < \rho_m \leq \rho_\epsilon(t) := \int_{\mathbb{R}^d} n_\epsilon \, dx \leq \rho_M + C\epsilon^2, \qquad 0 < I_m \leq I_\epsilon(t) \leq I_M + C\epsilon^2 \quad a.e. \tag{1.23}$$

*for some constant* $\rho_m$, $I_m$. *Moreover,* $I_\varepsilon$ *is uniformly bounded in* $BV(\mathbb{R}^+)$ *and after extraction of a subsequence* $I_\epsilon$

$$I_\epsilon(t) \underset{\epsilon\to 0}{\longrightarrow} \bar{I}(t) \quad \text{ in } L^1_{loc}(\mathbb{R}^+), \quad I_m \leq \bar{I}(t) \leq I_M \quad a.e., \tag{1.24}$$

*and* $\bar{I}(t)$ *is non-decreasing. We also have weakly in the sense of measures for a subsequence* $n_\epsilon$

$$n_\epsilon(t,x) \underset{\epsilon\to 0}{\longrightarrow} \bar{\rho}(t)\ \delta\big(x-\bar{x}(t)\big). \tag{1.25}$$

*Finally, the pair* $\big(\bar{x}(t),\bar{I}(t)\big)$ *also satisfies*

$$R\big(\bar{x}(t),\bar{I}(t)\big)=0 \quad a.e. \tag{1.26}$$

In particular, there can be an initial layer on $I_\epsilon$ that makes a possible rapid variation of $I_\epsilon$ at $t\approx 0$ so that the limit satisfies $R(\bar{x}^0, I(0^+))=0$, a relation that might not hold true, even with $O(\epsilon)$, at the level of $n_\epsilon$.

**Theorem 1.3.2 (Form of canonical equation)** *Assume* (1.11)-(1.22). *Then,* $\bar{x}(\cdot)$ *belongs to*
$W^{1,\infty}(\mathbb{R}^+;\mathbb{R}^d)$ *and satisfies*

$$\dot{\bar{x}}(t)=\big(-D^2u\big(t,\bar{x}(t)\big)\big)^{-1}.\nabla_x R\big(\bar{x}(t),\bar{I}(t)\big), \quad \bar{x}(0)=\bar{x}^0, \tag{1.27}$$

*with* $u(t,x)$ *a* $C^2$*-function given below in* (1.42)*,* $D^3u\in L^\infty(\mathbb{R}^d)$*, and initial data* $\bar{x}^0$ *given in* (1.21)*. Furthermore, we have* $\bar{I}(t)\in W^{1,\infty}(\mathbb{R}^+)$*.*

We insist that the Lipschitz continuity at $t=0$ is with the value $I(0)=\lim_{t\to 0^+} I(t)\neq \lim_{\epsilon\to 0} I_\epsilon^0$; the equality might hold if the initial data is well-prepared.

**Theorem 1.3.3 (Long-time behaviour)** *With the assumptions* (1.11)-(1.22)*, equation* (1.27) *has a kind of Lyapunov functional, the limit* $\bar{I}(t)$ *is increasing and*

$$\bar{I}(t) \underset{t\to\infty}{\longrightarrow} I_M, \quad \bar{x}(t) \underset{t\to\infty}{\longrightarrow} \bar{x}_\infty = 0. \tag{1.28}$$

*Finally, the limit is identified by* $\nabla R(\bar{x}_\infty=0, I_M)=0$ *(according to* (1.12)*).*

It is an open question to know if the full sequence converges. This is to say if the solution to the Hamilton-Jacobi equation is unique. The only uniqueness case in [11] assumes a very particular form of $R(\cdot,\cdot)$.

## 1.4 A-priori bounds on $\rho_\epsilon$, $I_\epsilon$ and their limits

Here, we establish the first statements of Theorem 1.3.1. As in [10] we can show with (1.12) and (1.15) that $I_\epsilon\le I_M + C\epsilon^2$. With (1.11) (the bounds on $\psi$), we also have that

$$\rho_\epsilon(t)\le I_M/\psi_m + C\epsilon^2. \tag{1.29}$$

To achieve the lower bound away from 0 is more difficult. We multiply the equation (1.1) by $\psi$ and integrate over $\mathbb{R}^d$, to arrive at

$$\frac{d}{dt}I_\epsilon(t)=\frac{1}{\epsilon}\int \psi R n_\epsilon\, dx + \epsilon\int n_\epsilon \Delta\psi\, dx. \tag{1.30}$$

We define $J_\epsilon(t) := \frac{1}{\epsilon}\int \psi R n_\epsilon\, dx$ and calculate its time derivative

$$\frac{d}{dt}J_\epsilon(t)=\frac{1}{\epsilon}\int \psi R\left(\frac{1}{\epsilon}Rn_\epsilon+\epsilon\Delta n_\epsilon\right)\,dx+\frac{1}{\epsilon}\int \psi n_\epsilon \frac{\partial R}{\partial I}\left(J_\epsilon+\epsilon\int n_\epsilon\Delta\psi\, dy\right)\,dx.$$

So we estimate it from below using (1.11), (1.15) and (1.29) by

$$\frac{d}{dt}J_\epsilon(t) \geq -C + \frac{1}{\epsilon}J_\epsilon(t)\int \psi n_\epsilon \frac{\partial R}{\partial I}\,dx,$$

and we may bound the negative part of $J_\epsilon$ by

$$\frac{d}{dt}(J_\epsilon(t))_- \leq C - \frac{\overline{K}_2}{\epsilon}I_\epsilon(t)(J_\epsilon(t))_-. \tag{1.31}$$

Now for $\epsilon$ small enough, we can estimate $I_\epsilon(t)$ as

$$I_\epsilon(t) = I_\epsilon(0) + \int_0^t \dot{I}_\epsilon(s)\,ds = I_\epsilon(0) + \int_0^t J_\epsilon(s)\,ds + O(\epsilon) \geq I^0/2 - \int_0^t (J_\epsilon(s))_-\,ds, \tag{1.32}$$

and plugging this in the estimate (1.31) leads to

$$\frac{d}{dt}(J_\epsilon(t))_- \leq C - \frac{\overline{K}_2}{\epsilon}\left(I^0/2 - \int_0^t (J_\epsilon(s))_-\,ds\right)(J_\epsilon(t))_-.$$

Now for $T > 0$ fixed. If there exists $T' \leq T$ such that $\int_0^{T'}(J_\epsilon(s))_-\,ds = I^0/4$, then we have

$$\frac{d}{dt}(J_\epsilon(t))_- \leq C - \frac{\overline{K}_2}{\epsilon}\frac{I^0}{4}(J_\epsilon(t))_-, \qquad 0 \leq t \leq T'.$$

Thus we obtain

$$(J_\epsilon(t))_- \leq (J_\epsilon(t=0))_- e^{-\overline{K}_2 I^0 t/(4\epsilon)} + \frac{4C\epsilon}{\overline{K}_2 I^0}\left(1 - e^{-\overline{K}_2 I^0 t/(4\epsilon)}\right).$$

Then for $\epsilon < \epsilon_0(T)$ small enough, we conclude that such a $T'$ does not exist *i.e.*

$$\int_0^T (J_\epsilon(s))_-\,ds \leq I^0/4. \tag{1.33}$$

So from (1.32), we obtain

$$I_\epsilon(t) \geq I^0/4, \qquad (J_\epsilon(t))_- \underset{\epsilon\to 0}{\longrightarrow} 0 \qquad \text{a. e. in } [0,T]. \tag{1.34}$$

This also gives the lower bound $\rho_m \leq \rho_\epsilon(t)$ with $\rho_m := I^0/(4\psi_M)$.

Finally, the estimate (1.33) and the $L^\infty$ bounds on $I_\epsilon(t)$ give us a local BV bound, which will eventually allow us to extract a convergent subsequence for which (1.24) holds. The obtained limit function $\bar{I}(t)$ is non-decreasing because in the limit the right-hand side of (1.30) is almost everywhere non-negative.

## 1.5 Estimates on $u_\epsilon$ and its limit $u$

In this section we introduce the major ingredient in our study, the function $u_\epsilon := \epsilon\ln(n_\epsilon)$. We calculate

$$\partial_t n_\epsilon = n_\epsilon \partial_t u_\epsilon/\epsilon, \quad \nabla n_\epsilon = n_\epsilon \nabla u_\epsilon/\epsilon, \quad \Delta n_\epsilon = n_\epsilon \Delta u_\epsilon/\epsilon + n_\epsilon|\nabla u_\epsilon|^2/\epsilon^2.$$

Plugging this in (1.1), we obtain that $u_\epsilon$ satisfies the Hamilton-Jacobi equation

$$\begin{cases} \partial_t u_\epsilon = |\nabla u_\epsilon|^2 + R(x, I_\epsilon(t)) + \epsilon\Delta u_\epsilon, & x \in \mathbb{R}^d,\ t \geq 0, \\ u_\epsilon(t=0) = \epsilon\ln(n_\epsilon^0) := u_\epsilon^0. \end{cases} \tag{1.35}$$

Our study of the concentration effect relies mainly on the asymptotic analysis of the family $u_\epsilon$ and in particular on its uniform regularity. We will pass to the (classical) limit in (1.35), and this relies on the

**Lemma 1.5.1** *With the assumptions of Theorem 1.3.1, we have for* $t \geq 0$,

$$-\underline{L}_0 - \underline{L}_1|x|^2 - \epsilon 2d\underline{L}_1 t \leq u_\epsilon(t,x) \leq \overline{L}_0 - \overline{L}_1|x|^2 + \left(\overline{K}_0 + 2d\epsilon\overline{L}_1\right)t, \tag{1.36}$$

$$-2\underline{L}_1 \leq D^2 u_\epsilon(t,x) \leq -2\overline{L}_1. \tag{1.37}$$

This Lemma relies on a welknown (and widely used) fact that the Hamilton-Jacobi equations have a regime of regular solutions with concavity assumptions, [5, 81].

### 1.5.1 Quadratic estimates on $u_\epsilon$

First we achieve an upper bound, defining $\overline{u}_\epsilon(t,x) := \overline{L}_0 - \overline{L}_1|x|^2 + C_0(\epsilon)t$ with $C_0(\epsilon) := \overline{K}_0 + 2d\epsilon\overline{L}_1$, we obtain thanks to (1.13), (1.18) and (1.22) that $\overline{u}_\epsilon(t=0) \geq u_\epsilon^0$ and

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

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

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

This concludes the proof of the first part of Lemma 1.5.1 *i.e.* inequality 1.36.

### 1.5.2 Bounds on $D^2u_\epsilon$

We show that the semi-convexity and the concavity of the initial data is preserved by equation (1.35). For a unit vector $\xi$, we use the notation $u_\xi := \nabla_\xi u_\epsilon$ and $u_{\xi\xi} := \nabla^2_{\xi\xi}u_\epsilon$ to obtain

$$u_{\xi t} = R_\xi(x,I) + 2\nabla u \cdot \nabla u_\xi + \epsilon\Delta u_\xi,$$
$$u_{\xi\xi t} = R_{\xi\xi}(x,I) + 2\nabla u_\xi \cdot \nabla u_\xi + 2\nabla u \cdot \nabla u_{\xi\xi} + \epsilon\Delta u_{\xi\xi}.$$

The first step is to obtain a lower bound on the second derivative *i.e.* semi-convexity. It can be obtained in the same way as in [103]: Using $|\nabla u_\xi| \geq |u_{\xi\xi}|$ and the definition $\underline{w}(t,x) := \min_\xi u_{\xi\xi}(t,x)$ leads to the inequality

$$\partial_t\underline{w} \geq -2\underline{K}_1 + 2\underline{w}^2 + 2\nabla u \cdot \nabla\underline{w} + \epsilon\Delta\underline{w}.$$

By a comparison principle and assumptions (1.19), (1.22), we obtain

$$\underline{w} \geq -2\underline{L}_1. \tag{1.38}$$

At every point $(t,x) \in \mathbb{R}^+ \times \mathbb{R}^d$, we can choose an orthonormal basis such that $D^2u_\epsilon(t,x)$ is diagonal because it is a symmetric matrix. So we can estimate the mixed second derivatives in terms of $u_{\xi\xi}$. In particular, for each element $\xi$ of the latter basis, we have $\nabla u_\xi = u_{\xi\xi}\xi$ and $|\nabla u_\xi| = |u_{\xi\xi}|$.

This enables us to show concavity in the next step. We start from the definition $\overline{w}(t,x) := \max_\xi u_{\xi\xi}(t,x)$ and the inequality

$$\partial_t\overline{w} \leq -2\overline{K}_1 + 2\overline{w}^2 + 2\nabla u \cdot \nabla\overline{w} + \epsilon\Delta\overline{w}.$$

By a comparison principle and assumptions (1.19), (1.22), we obtain

$$\overline{w} \leq -2\overline{L}_1. \tag{1.39}$$

From the space regularity gained and (1.19), we obtain $\nabla u_\epsilon$ locally uniformly bounded and thus from (1.35) for $\epsilon < \epsilon_0$ that $\partial_t u_\epsilon$ is locally uniformly bounded.

### 1.5.3 Passing to the limit

From the regularity obtained in section 1.5.2, it follows that we can extract a subsequence such that, for all $T > 0$,

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

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

and

$$-\underline{L}_0 - \underline{L}_1|x|^2 \le u(t,x) \le \overline{L}_0 - \overline{L}_1|x|^2 + \overline{K}_0 t, \quad -2\underline{L}_1 \le D^2u(t,x) \le -2\overline{L}_1 \quad \text{a.e.} \tag{1.40}$$

$$u \in W^{1,\infty}_{\text{loc}}(\mathbb{R}^+ \times \mathbb{R}^d). \tag{1.41}$$

Notice that the uniform $W^{2,\infty}_{loc}(\mathbb{R}^d)$ regularity also allows to differentiate the equation in time, and find

$$\frac{\partial^2}{\partial t^2}u = \frac{\partial}{\partial I}R\big(x,I(t)\big)\frac{dI(t)}{dt} + 2\nabla u.[\nabla R(x,I(t)) + D^2u.\nabla u].$$

This is not enough to have $C^1$ regularity on $u$.

We also obtain that $u$ satisfies in the viscosity sense (modified as in [11, 103]) the equation

$$\begin{cases} \frac{\partial}{\partial t}u = R\big(x,I(t)\big) + |\nabla u|^2, \\ \\ \max_{\mathbb{R}^d} u(t,x) = 0. \end{cases} \tag{1.42}$$

The constraint that the maximum vanishes is achieved, as in [10], from the a priori bounds on $I_\epsilon$ and (1.40).

In particular $u$ is strictly concave, therefore it has exactly one maximum. This proves (1.25) *i.e.* $n$ stays monomorphic and characterizes the Dirac location by

$$\max_{\mathbb{R}^d} u(t,x) = 0 = u\big(t,\bar{x}(t)\big). \tag{1.43}$$

Moreover, as in [103] we can achieve (1.26) at each Lebesgue point of $I(t)$.

This completes the proof of Theorem 1.3.1.

## 1.6 Canonical equation, time asymptotic

With the additional assumptions (1.16) and (1.20), we can write our form of the canonical equation and show long-time behavior. To do so, we first show that the third derivative is bounded. This allows us to establish rigorously the canonical equation while it was only formally given in [50, 103]. From this equation, we obtain regularity on $\bar{x}$ and $\bar{I}$. For long-time behavior we show that $\bar{I}$ is strictly increasing as long as $\nabla R\big(\bar{x},\bar{I}\big) \neq 0$ and this is based on a kind of Lyapunov functional.

### 1.6.1 Bounds on third derivatives of $u_\epsilon$

For the unit vectors $\xi$ and $\eta$, we use the notation $u_\xi := \nabla_\xi u_\epsilon$, $u_{\xi\eta} := \nabla^2_{\xi\eta}u_\epsilon$ and $u_{\xi\xi\eta} := \nabla^3_{\xi\xi\eta}u_\epsilon$ to derive

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

Again we can fix a point $(t,x)$ and choose an orthonormal basis such that $D^2\left(\nabla_\eta u_\epsilon(t,x)\right)$ is diagonal. Let us define

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

Since $-u_{\xi\xi\eta}(t,x) = \nabla_{-\eta} u_{\xi\xi}(t,x)$, we have $M_1(t) = \max\limits_{x,\xi,\eta} |u_{\xi\xi\eta}(t,x)|$. So with the maximum principle we obtain

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

Assumption (1.20) gives us a bound on $M_1(t=0)$. So we obtain a $L^\infty$-bound on the third derivative uniform in $\epsilon$.

### 1.6.2 Maximum points of $u_\epsilon$

Now we wish to establish the canonical equation. We denote the maximum point of $u_\epsilon(t,\cdot)$ by $\bar{x}_\epsilon(t)$.

Since $u_\epsilon \in C^2$, at maximum points we have $\nabla u_\epsilon(t, \bar{x}_\epsilon(t)) = 0$ and thus

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

The chain rule gives

$$\frac{\partial}{\partial t} \nabla u_\epsilon\big(t, \bar{x}_\epsilon(t)\big) + D_x^2 u_\epsilon\big(t, \bar{x}_\epsilon(t)\big) \dot{\bar{x}}_\epsilon(t) = 0,$$

and using the equation (1.35), it follows further that, for almost every $t$,

$$D_x^2 u_\epsilon\big(t, \bar{x}_\epsilon(t)\big) \dot{\bar{x}}_\epsilon(t) = -\frac{\partial}{\partial t} \nabla u_\epsilon\big(t, \bar{x}_\epsilon(t)\big) = -\nabla_x R\big(\bar{x}_\epsilon(t), I_\epsilon(t)\big) - \epsilon \Delta \nabla_x u_\epsilon.$$

Due to the uniform in $\epsilon$ bound on $D^3 u_\epsilon$ and $R \in C^2$, we can pass to the limit in this equation and arrive at

$$\dot{\bar{x}}(t) = \big(-D^2 u\big(\bar{x}(t), t\big)\big)^{-1} . \nabla_x R\big(\bar{x}(t), \bar{I}(t)\big) \quad a.e.$$

But we have further regularity in the limit and obtain the equations in the classical sense. We first notice that, from $R\big(\bar{x}(t), \bar{I}(t)\big) = 0$ and the assumptions (1.13), $\bar{x}(t)$ is bounded in $L^\infty(\mathbb{R}^+)$. So we obtain that $\bar{x}(t)$ is bounded in $W^{1,\infty}(\mathbb{R}^+)$. Because $I \mapsto R(\cdot, I)$ is invertible, it follows that $\bar{I}(t)$ is bounded in $W^{1,\infty}(\mathbb{R}^+)$; more precisely we may differentiate the relation (1.26) (because $R \in C^2$) and find a differential equation on $I(t)$ that will be used later:

$$\dot{\bar{x}}(t) \cdot \nabla_x R + \dot{\bar{I}}(t) \nabla_I R = 0 \quad a.e.$$

This completes the proof of Theorem 1.3.2.

### 1.6.3 Long-time behaviour

It remains to prove the long time behaviour stated in Theorem 1.3.3.

We start from the canonical equation

$$\frac{d}{dt} \bar{x}(t) = (-D^2 u)^{-1} \nabla R\big(\bar{x}(t), \bar{I}(t)\big),$$

and use some kind of Lyapunov functional. We calculate

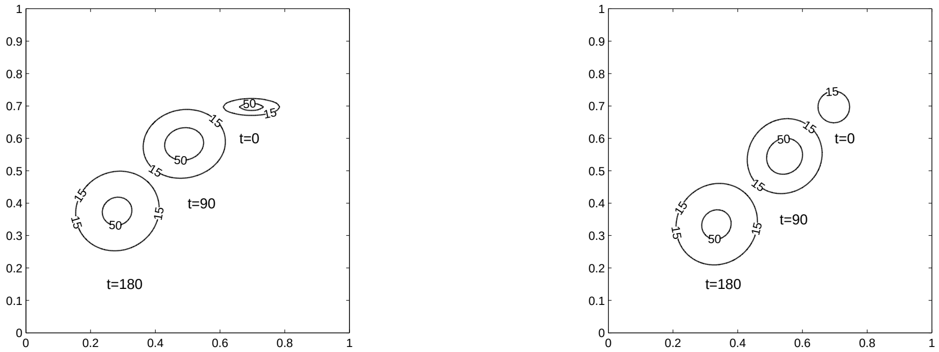
$$\begin{aligned}\frac{d}{dt}R\big(\bar{x}(t),\bar{I}(t)\big) &= \nabla R\big(\bar{x}(t),\bar{I}(t)\big)\frac{d}{dt}\bar{x}(t) + R_I\big(\bar{x}(t),\bar{I}(t)\big)\frac{d\bar{I}}{dt}\\ &= \nabla R\big(\bar{x}(t),\bar{I}(t)\big)(-D^2u)^{-1}\nabla R\big(\bar{x}(t),\bar{I}(t)\big) + R_I\big(\bar{x}(t),\bar{I}(t)\big)\frac{d\bar{I}}{dt}.\end{aligned}$$

Now we also know from (1.26) that the left hand side vanishes. Then, we obtain

$$\frac{d}{dt}\bar{I}(t) = \frac{-1}{R_I\big(\bar{x}(t),\bar{I}(t)\big)}\nabla R\big(\bar{x}(t),\bar{I}(t)\big)(-D^2u)^{-1}\nabla R\big(\bar{x}(t),\bar{I}(t)\big) \geq 0.$$

The inequality is strict as long as $\bar{I}(t) < I_M$. Consequently, we recover that $\bar{I}(t)$ is non-decreasing, as $t \to \infty$, $\bar{I}(t)$ converges, and subsequences of $\bar{x}(t)$ converge also (recall that $\bar{x}(t)$ is bounded). But we discover that the only possible limits are such that $\nabla R(\bar{x}_\infty, I_\infty) = 0$. With relation (1.26), assumptions (1.12) and (1.15) this identifies the limit as announced in Theorem 1.3.3.

## 1.7 Numerics



(a) asymmetric I.D.

(b) symmetric I.D.

Figure 1.1: Dynamics of the density $n$ with asymmetric initial data (1.44) (left) and symmetric initial data (1.45) (right). These computations illustrate the effect of the matrix $(-D^2u)^{-1}$ in the dynamics of the concentration point according to the form of canonical equation (1.27). The plots show the level sets $\{(x,y)|n(x,y)=15\}$ and $\{(x,y)|n(x,y)=50\}$.

The canonical equation is not self-contained because the effect of mutations appears through the matrix $(-D^2u)^{-1}$. Nevertheless it can be used to explain several effects. The purpose of this section is firstly to illustrate how it acts on the dynamics, secondly to see the effect of $\epsilon$ being not exactly zero, and thirdly to explain why it is generic, in high dimensions as well as in one dimension [103] that pointwise Dirac masses (and not on curves) can exist.

We first illustrate the fact that a isotropic approximation of a Dirac mass will give rise to different dynamics than an anisotropic. This anisotropy is measured with $u$ and we choose two initial data. In the first case $-D^2u^0$ is "far" from the identity matrix and in the second case it is isotropic:

$$n_0^\epsilon(x,y) = C_{\text{mass}}\exp(-(x-.7)^2/\epsilon - 12(y-.7)^2/\epsilon), \tag{1.44}$$

$$n_0^\epsilon(x,y) = C_{\text{mass}} \exp(-2.4(x-.7)^2/\epsilon - 2.4(y-.7)^2/\epsilon). \tag{1.45}$$

We also choose a growth rate $R$ with gradient along the diagonal:

$$R(x,y,I) = 2 - I - 0.6(x^2+y^2). \tag{1.46}$$

Here although, we start with initial data centered on the diagonal and $\nabla R$ pointing along the diagonal to the origin, the concentration point with the anisotropic initial data (1.44) leaves the diagonal (cf. Figure 1.1 (a)). The isotropic initial data moves along the diagonal as expected by symmetry reasons (cf. Figure 1.1 (b)).

The numerics has been performed in Matlab with parameters as follows. The plots show the level sets $\{(x,y)|n(x,y)=15\}$ and $\{(x,y)|n(x,y)=50\}$ corresponding to $t=0$, 90 and 180 (time in units of $dt$): $\epsilon$ is chosen to be 0.005 and $C_{\text{mass}}$ such that the initial mass in the computational domain is equal to 0.3. The equation is solved by an implicit-explicit finite-difference method on square grid consisting of $100 \times 100$ points (time step $dt = 0.005$).

The second example is to illustrate the role of the parameter $\epsilon$ for symmetric initial data:

$$n_0^\epsilon(x,y) = C_{\text{mass}} \exp(-(x-.3)^2/\epsilon - (y-.3)^2/\epsilon), \tag{1.47}$$

$$R(x,y,I(t)) = 0.9 - I + 5(y-.3)_+^2 + 2.3(x-.3) \quad \text{with } I(t) := \int n(t,x)\,dx. \tag{1.48}$$

In this example, we start with symmetric initial data centered on the line $y = 0.3$ and the gradient of $R$ along this line ($y = 0.3$) is $(1,0)$. Hence, the canonical equation in the limit $\epsilon = 0$ predicts a motion in the $x$ direction on this line. One however observes in Figure 1.2 that the maximum point leaves this line because $\epsilon$ does not vanish. Notice that $\partial_y R \equiv 0$ below the line $y = 0.3$.

In this computation, performed with Matlab, $\epsilon$ is chosen to be 0.004, $C_{\text{mass}}$ such that the initial mass in the computational domain is equal to 0.3 and square grid consisting of $150 \times 150$ points (time step $dt = 8.8889 \cdot 10^{-4}$).

With our third example we wish to illustrate that, except in particular symmetric geometries, only a single Dirac mass can be sustained by the Lotka-Volterra equations with a single resource in the framework of section 1.3. We place initially two symmetric deltas on the $x$ and the $y$-axis:

$$n_0^\epsilon(x,y) = C_{\text{mass}} \left[\exp\left(-\frac{2.4}{\epsilon}\left((x-.25\sqrt{2})^2+y^2\right)\right) + \exp\left(-\frac{2.4}{\epsilon}\left((y-.25\sqrt{2})^2+x^2\right)\right)\right], \tag{1.49}$$

We seek for asymmetry in the growth rate $R$ under the form

$$R(x,y,I) = 3 - 1.5I - 5.6(y^2 + R_e x^2). \tag{1.50}$$

In the special case $R_e = 1$, all isolines of $R$ are circles then the two concentration points just move symmetrically to the origin cf. Figure 1.3 (b). However, if we choose $R_e = 1.1$ *i.e.* all isolines of $R$ are ellipses then one of the two concentration points disappears cf. Figure 1.3 (a). The intuition behind is that the canonical equation (1.27) should hold for the two points. However the constraint (1.26) given by $\rho(t)$ is the same for the two points and this is a contradiction. One of the two points has to disappear right away.

The numerics is performed with $\epsilon = 0.003$ and $C_{\text{mass}}$ such that the initial mass in the computational domain is equal to 0.3. The equation is solved by an implicit-explicit finite-difference method on square grid consisting of $100 \times 100$ points (time step $dt = 0.001$).

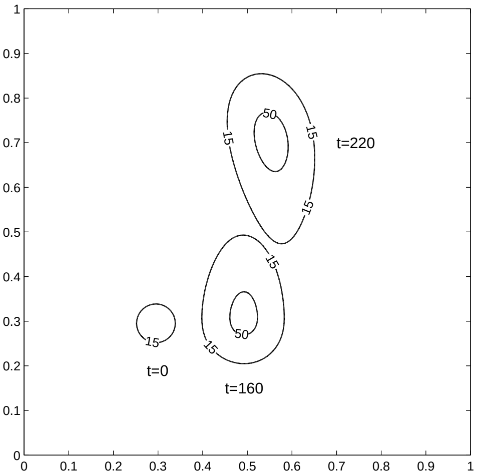


Figure 1.2: This figure illustrates the effect of $\epsilon$ being not exactly zero. The dynamics of the density $n$ with symmetric initial data is plotted for $t = 0$, 160 and 220 in units of $dt$ and the limiting behavior is a motion along the axis $y = 0.3$. The plot shows the level sets $\{(x, y)|n(x, y) = 15\}$ and $\{(x, y)|n(x, y) = 50\}$.

## 1.8 Extension: non-constant diffusion

Our results can be extended to include a diffusion coefficient depending on $x$. This leads to the equation

$$\partial_t n_\epsilon - \epsilon\nabla \cdot (b(x)\nabla n_\epsilon) = \frac{n_\epsilon}{\epsilon} R\big(x, I_\epsilon(t)\big), \qquad t > 0,\ x \in \mathbb{R}^d. \tag{1.51}$$

Our assumptions on $b$ are that there are positive constants $b_m$, $b_M$, $B_1$, $B_2$ and $B_3$ such that

$$b_m \le b \le b_M, \qquad |\nabla b(x)| \le B_1 \frac{1}{1+|x|}, \qquad \big|Tr(D^2 b(x))\big| \le B_2 \frac{1}{(1+|x|)^2}, \qquad \big|D^3 b\big| \le B_3. \tag{1.52}$$

Our assumptions on the initial data and on $R$ are the same, as before (1.11)–(1.21). However, we have to supplement the assumption (1.15) to take $b$ into account:

$$\nabla b \cdot \nabla(\psi R) \ge -K_3. \tag{1.53}$$

These assumptions will in the following allow us to obtain a gradient bound

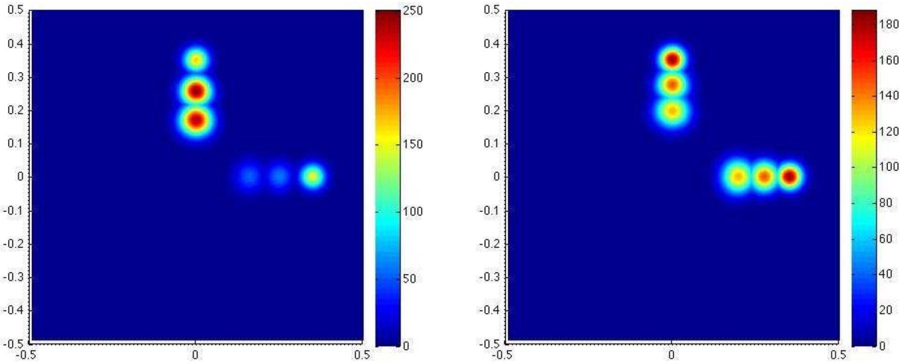
$$|\nabla u_\epsilon(t, x)| \le C_{\nabla u}(1 + |x|). \tag{1.54}$$

This bound enables us to formulate the compatibility conditions which replace (1.18): we need

$$B_2 C_{\nabla u}^2 - 2\overline{K}_1 < 0 \tag{1.55}$$

and define

$$\overline{K}_b := \frac{2B_1 - \sqrt{4B_1^2 - 2b_M\left(B_2 C_{\nabla u}^2 - 2\overline{K}_1\right)}}{b_M},$$



(a) asymmetric R (b) symmetric R

Figure 1.3: This figure illustrates that, except for particular symmetry conditions, a single Dirac mass is exhibited by Lotka-Volterra equations. We depict the density $n$ with asymmetric (left) and symmetric (right) growth rate $R$ plotted for $t = 5$, 90 and 180 in units of $dt$.

$$\underline{K}_b := \frac{-2B_1 - \sqrt{4B_1^2 + 2b_m\left(B_2 C_{\nabla u}^2 + 2\underline{K}_1\right)}}{b_m},$$

to require

$$-\underline{K}_b \leq D^2 u_\epsilon^0 \leq -\overline{K}_b, \tag{1.56}$$

$$4b_M \overline{L}_1^2 \leq \overline{K}_1 \leq \underline{K}_1 \leq 4b_m \underline{L}_1^2. \tag{1.57}$$

Our goal is to prove the following

**Theorem 1.8.1 (Convergence)** *Assume* (1.11)-(1.15), (1.18), (1.52), (1.53), (1.55), (1.56) *and* (1.57). *Then the solution $n_\epsilon$ to* (1.51) *satisfies for all $T > 0$, for $\epsilon$ small enough and $t \in [0, T]$*

$$0 < \rho_m \leq \rho_\epsilon(t) \leq \rho_M + C\epsilon^2, \qquad I_m \leq I_\epsilon(t) \leq I_M + C\epsilon^2 \quad a.e. \tag{1.58}$$

*Moreover, there is a subsequence $I_\epsilon$ such that*

$$I_\epsilon(t) \underset{\epsilon\to 0}{\longrightarrow} \bar{I}(t) \quad \text{ in } L^1_{loc}(\mathbb{R}^+), \quad I_m \leq \bar{I}(t) \leq I_M \quad a.e., \tag{1.59}$$

*and $\bar{I}(t)$ is non-decreasing. Furthermore, we have weakly in the sense of measures for a subsequence $n_\epsilon$*

$$n_\epsilon(t,x) \underset{\epsilon\to 0}{\longrightarrow} \bar{\rho}(t)\, \delta\big(x - \bar{x}(t)\big), \tag{1.60}$$

*and the pair $\big(\bar{x}(t), \bar{I}(t)\big)$ also satisfies*

$$R\big(\bar{x}(t), \bar{I}(t)\big) = 0 \quad a.e. \tag{1.61}$$

**Theorem 1.8.2 (Form of canonical equation)** *With the assumptions* (1.11)-(1.18), (1.20), (1.21), (1.52), (1.53), (1.55), (1.56) *and* (1.57), *$\bar{x}$ is a $W^{1,\infty}(\mathbb{R}^+)$-function satisfying*

$$\dot{\bar{x}}(t) = \big(-D^2 u\big(t, \bar{x}(t)\big)\big)^{-1} . \nabla_x R\big(\bar{x}(t), \bar{I}(t)\big), \quad \bar{x}(0) = \bar{x}^0, \tag{1.62}$$

*with $u(t,x)$ a $C^2$-function given below in* (1.71), *$D^3 u \in L^\infty(\mathbb{R}^d)$, and initial data $\bar{x}^0$ given in* (1.21). *Furthermore, we have $\bar{I}(t) \in W^{1,\infty}(\mathbb{R}^+)$.*

The end of this section is devoted to the proof of these Theorems. The a priori bounds (1.58), (1.59) on $\rho_\epsilon$ and $I_\epsilon$ can be established as before.

As before we study the function $u_\epsilon := \epsilon \ln(n_\epsilon)$. We obtain that $u_\epsilon$ satisfies the Hamilton-Jacobi equation

$$\begin{cases} \partial_t u_\epsilon = R\big(x, I_\epsilon(t)\big) + b|\nabla u_\epsilon|^2 + \epsilon \nabla b \cdot \nabla u_\epsilon + \epsilon b \Delta u_\epsilon, & t > 0,\ x \in \mathbb{R}^d, \\ u_\epsilon(t=0) = \epsilon \ln(n_\epsilon^0). \end{cases} \tag{1.63}$$

In order to adapt our method to this equation we need a bound on the gradient of $u_\epsilon$. We achieve this following arguments in [82, 10]:

**gradient bound** Let us define $v(t,x)$ by $u_\epsilon = K_v - v^2$ where we choose $K_v$ large enough to have $v > \delta > 0$ on $[0,T]$ uniform in $\epsilon$. We calculate

$$\nabla u_\epsilon = -2v\nabla v \quad \text{and} \quad \Delta u_\epsilon = -2v\Delta v - 2|\nabla v|^2$$

and obtain from (1.63)

$$-2v\partial_t v = R + 4bv^2|\nabla v|^2 - 2\epsilon \nabla b \cdot v\nabla v - 2\epsilon v b \Delta v - 2\epsilon b |\nabla v|^2. \tag{1.64}$$

Dividing by $-2v$, taking the derivative with respect to $x_i$ and defining $p := \nabla v$, we have

$$\partial_t p_i = -\left(\frac{R}{2v}\right)_{x_i} - 2p_i b|p|^2 - 2vb_{x_i}|p|^2 - 4vbp \cdot \nabla p_i + \epsilon \nabla b_{x_i} \cdot p + \epsilon \nabla b \cdot \nabla p_i$$
$$+ \epsilon b_{x_i} \Delta v + \epsilon b \Delta p_i + \epsilon \frac{b_{x_i}}{v}|p|^2 - \epsilon \frac{b}{v^2}|p|^2 p_i + 2\epsilon \frac{b}{v} p \cdot \nabla p_i.$$

Multiplying (1.64) by $\dfrac{b_{x_i}}{2bv}$ and adding to the equation above, we obtain

$$\partial_t \left(p_i - \frac{b_{x_i} v}{b}\right) = -\left(\frac{R}{2v}\right)_{x_i} - 2p_i b|p|^2 - 2vb_{x_i}|p|^2 - 4vbp \cdot \nabla p_i + \epsilon \nabla b_{x_i} \cdot p + \epsilon \nabla b \cdot \nabla p_i$$
$$+ \epsilon b \Delta p_i + \epsilon \frac{b_{x_i}}{v}|p|^2 - \epsilon \frac{b}{v^2}|p|^2 p_i + 2\epsilon \frac{b}{v} p \cdot \nabla p_i + \frac{b_{x_i} R}{2bv} + 2b_{x_i} v |p|^2 - \epsilon \frac{b_{x_i}}{b} \nabla b \cdot p - \epsilon \frac{b_{x_i}}{v}|p|^2.$$

Now we define

$$M_b(t) := \max_{i,x} \left[(p_i)_-, (p_i)_+\right] \geq 0. \tag{1.65}$$

If $\max_{i,x}(p_i)_- \leq \max_{i,x}(p_i)_+$, we have

$$\partial_t \left(M_b - \frac{b_{x_i} v}{b}\right) \leq C - 2b_m M_b^3 + 2|v||b_{x_i}|d^2 M_b^2 + \epsilon d\, |\nabla b_{x_i}|\, M_b$$
$$+ \epsilon \frac{|b_{x_i}|}{\delta} d^2 M_b^2 + C + 2|b_{x_i}||v| d^2 M_b^2 + \epsilon \frac{|b_{x_i}|}{b_m} d |\nabla b| M_b + \epsilon \frac{|b_{x_i}|}{\delta} d^2 M_b^2.$$

Since $\dfrac{b_{x_i} v}{b}$ is bounded, we have $M_b$ bounded from above.

If $\max_{i,x}(p_i)_- > \max_{i,x}(p_i)_+$, we show similarly a bound on $M_b$ and therefore achieve (1.54).

To prove the concavity and semi-convexity results, we only give formal arguments for the limit case. To adapt the argument for the $\epsilon$-case is purely technical:

For a unit vector $\xi$, we define $u_\xi := \nabla_\xi u_\epsilon$ and $u_{\xi\xi} := \nabla_{\xi\xi} u_\epsilon$ to obtain

$$\partial_t u_\xi = R_\xi + b_\xi |\nabla u|^2 + 2b \nabla u \cdot \nabla u_\xi, \tag{1.66}$$

and

$$\partial_t u_{\xi\xi} = R_{\xi\xi} + b_{\xi\xi}|\nabla u|^2 + 4b_\xi \nabla u \cdot \nabla u_\xi + 2b\nabla u \cdot \nabla u_{\xi\xi} + 2b|\nabla u_\xi|^2. \tag{1.67}$$

With the definition $\overline{w}(t,x) := \max_\xi u_{\xi\xi}(t,x)$ and assumptions (1.52) we have

$$\partial_t \overline{w} \leq -2\overline{K}_1 + B_2 C^2_{\nabla u} + 4B_1 C_{\nabla u}|\overline{w}| + 2b\nabla u \cdot \nabla \overline{w} + 2b_M \overline{w}^2.$$

With assumption (1.55), 0 is a supersolution to

$$\partial_t \overline{w}^* = -2\overline{K}_1 + B_2 C^2_{\nabla u} - 4B_1 C_{\nabla u} \overline{w}^* + 2b\nabla u \cdot \nabla \overline{w}^* + 2b_M (\overline{w}^*)^2,$$

so we know from assumption (1.56) that $\overline{w} \leq 0$. Therefore it follows further that

$$\overline{w} \leq \overline{K}_b.$$

For the lower bound, we use the definition $\underline{w}(t,x) := \min_\xi u_{\xi\xi}(t,x)$ and the inequality

$$\partial_t \underline{w} \geq -2\underline{K}_1 - B_2 C^2_{\nabla u} - 4B_1 C_{\nabla u}|\underline{w}| + 2b\nabla u \cdot \nabla \underline{w} + 2b_m \underline{w}^2.$$

Since we already know that $\underline{w} \leq 0$, we obtain

$$\underline{w} \geq \underline{K}_b.$$

We can achieve this at the $\epsilon$-level using the equation

$$\partial_t u_\xi = R_\xi + b_\xi|\nabla u|^2 + 2b\nabla u \cdot \nabla u_\xi + \epsilon \nabla b_\xi \cdot \nabla u + \epsilon \nabla b \cdot \nabla u_\xi + \epsilon b_\xi \Delta u + \epsilon b \Delta u_\xi, \tag{1.68}$$

and

$$\begin{aligned} \partial_t u_{\xi\xi} = {} & R_{\xi\xi} + b_{\xi\xi}|\nabla u|^2 + 4b_\xi \nabla u \cdot \nabla u_\xi + 2b\nabla u \cdot \nabla u_{\xi\xi} + 2b|\nabla u_\xi|^2 \\ & + \epsilon \nabla b_{\xi\xi} \cdot \nabla u + 2\epsilon \nabla b_\xi \cdot \nabla u_\xi + \epsilon \nabla b \cdot \nabla u_{\xi\xi} + \epsilon b_{\xi\xi} \Delta u + 2\epsilon b_\xi \Delta u_\xi + \epsilon b \Delta u_{\xi\xi}. \end{aligned} \tag{1.69}$$

Now we define

$$f := \frac{2b_\xi}{b} \text{ and } g := \frac{bb_{\xi\xi} - 2b_\xi^2}{b^2},$$

multiply (1.68) by $f$, substract it from (1.69), multiply (1.63) by $g$, substract it to obtain

$$\begin{aligned} \partial_t(u_{\xi\xi} - fu_\xi - gu) = {} & R_{\xi\xi} + 2b\nabla u \cdot \nabla u_{\xi\xi} + 2b|\nabla u_\xi|^2 + \epsilon \nabla b_{\xi\xi} \cdot \nabla u \\ & + 2\epsilon \nabla b_\xi \nabla u_\xi + \epsilon \nabla b \cdot \nabla u_{\xi\xi} + \epsilon b \Delta u_{\xi\xi} - fR_\xi - \epsilon f \nabla b_\xi \cdot \nabla u - \epsilon f \nabla b \cdot \nabla u_\xi - gR - \epsilon g \nabla b \cdot \nabla u. \end{aligned} \tag{1.70}$$

The remaining steps can be done similar as before. For the Hamilton-Jacobi-equation on $u$, we obtain the variant

$$\begin{cases} \partial_t u = R\big(x, \bar{I}(t)\big) + b(x)\, |\nabla u|^2, \\ \max\limits_{x \in \mathbb{R}^d} u(t,x) = 0, \qquad \forall t \geq 0. \end{cases} \tag{1.71}$$

## 1.9 Direct competition

The other class of models we handle are populations with direct competition kernel $C(x,y) \geq 0$, that is

$$\partial_t n_\epsilon(t,x) = \frac{1}{\epsilon} n_\epsilon(t,x) \left( r(x) - \int_{\mathbb{R}^d} C(x,y) n_\epsilon(t,y)\, dy \right) + \epsilon \Delta n_\epsilon(t,x). \tag{1.72}$$

The term $r(x)$ is the intra-specific growth rate (and has a priori no sign) and the integral term models an additional contribution to the death rate due to competition between different traits. Notice that the choice $C(x,y)=\psi(y)\Phi(x)$ will reduce this model to a particular case of those in (1.1). This class of model is also very standard, see [40, 91, 31, 32, 109] and the references therein. We call it direct competition in opposition to more realistic models where competition is through resources [97].

For the initial data, we assume as before (1.18)–(1.21). Concerning $r(x)$ and $C(x,y)$ we assume $C^1$ regularity and that there are constants $\rho_M>0$, $\underline{K}'_1>0$... such that

$$C(x,x)>0 \qquad \forall x\in\mathbb{R}^d, \tag{1.73}$$

$$\int_{\mathbb{R}^d}\int_{\mathbb{R}^d} n(x)C(x,y)n(y)\,dydx \geq \frac{1}{\rho_M}\int_{\mathbb{R}^d} n(x)\,dx\int_{\mathbb{R}^d} r(x)n(x)\,dx \qquad \forall n\in L^1_+(\mathbb{R}^d). \tag{1.74}$$

This assumption is weaker than easier conditions of the type

$$C(x,y)\geq\frac{1}{\rho_M}r(x) \quad \text{or} \quad C(x,y)\geq\frac{1}{2\rho_M}[r(x)+r(y)].$$

Because it is restricted to positive functions, it is a pointwise positivity condition on $C(x,y)$ in opposition to the positivity as operator that occurs for the entropy method in [74].

Then, we make again concavity assumptions. Namely that concavity on $r$ is strong enough to compensate for concavity in $C$

$$-\underline{K}'_1|x|^2\leq r(x)-\sup_y C(x,y)\rho_M\leq r(x)\leq\overline{K}'_0-\overline{K}'_1|x|^2, \tag{1.75}$$

$$-2\underline{K}'_1\leq D^2r(x)-\sup_y\big(D^2C(x,y)\big)_+\rho_M\leq D^2r(x)+\sup_y\big(D^2C(x,y)\big)_-\rho_M\leq-2\overline{K}'_1, \tag{1.76}$$

as symmetric matrices, where the positive and negative parts are taken componentwise. As for regularity, we will use

$$D^3r-\sup_y\big(D^3C(\cdot,y)\big)_+\rho_M, \qquad D^3r+\sup_y\big(D^3C(\cdot,y)\big)_-\rho_M\in L^\infty(\mathbb{R}^d). \tag{1.77}$$

The initial data is still supposed to concentrate at a point $\bar{x}^0$ following (1.18)–(1.21). But because persistence, i.e. that $n_\varepsilon$ does not vanish, is more complicated to control, we need two new conditions

$$r(\bar{x}^0)>0, \tag{1.78}$$

$$\int_{\mathbb{R}^d} n_\epsilon(t,x)dx\leq\rho^0_M. \tag{1.79}$$

We also need a compatibility condition with $R$

$$4\overline{L}_1^2\leq\overline{K}'_1\leq\underline{K}'_1\leq4\underline{L}_1^2. \tag{1.80}$$

The interpretation of our assumptions is that the intra-specific growth rate $r$ dominates strongly the competition kernel. This avoids the branching patterns that are usual in this kind of models [91, 63, 61, 109]. Our concavity assumptions also implies that there is no continuous solution $N$ to the steady state equation without mutations $N(x)\big(r(x)-\int_{\mathbb{R}^d}C(x,y)N(y)\,dy\big)=0$. This makes a difference with the entropy method used in [74] as well as the positivity condition on the kernel that, compared to (1.74), also involves $r(x)$.

Our goal is to prove the following results

**Theorem 1.9.1 (Convergence)** *With the assumptions* (1.73)–(1.76) *and* (1.18), (1.79)–(1.80), *the solution* $n_\epsilon$ *to* (1.72) *satisfies,*

$$0 \leq \rho_\epsilon(t) := \int_{\mathbb{R}^d} n_\epsilon(t,x)dx \leq \rho_M \quad a.e. \tag{1.81}$$

*and there is a subsequence such that*

$$\rho_\epsilon(t) \underset{\epsilon\to 0}{\longrightarrow} \bar\rho(t) \quad \text{in weak-}\star\ L^\infty(\mathbb{R}^+), \qquad 0 \leq \bar\rho(t) \leq \rho_M \quad a.e. \tag{1.82}$$

*Furthermore, we have weakly in the sense of measures for a subsequence* $n_\epsilon$

$$n_\epsilon(t,x) \underset{\epsilon\to 0}{\longrightarrow} \bar\rho(t)\ \delta\big(x-\bar x(t)\big), \qquad \frac{n_\epsilon(t,x)}{\int_{\mathbb{R}^d} n_\epsilon(t,x)dx} \underset{\epsilon\to 0}{\longrightarrow} \delta\big(x-\bar x(t)\big), \tag{1.83}$$

*and the pair* $\big(\bar x(t), \bar\rho(t)\big)$ *also satisfies*

$$\bar\rho(t)\big[r\big(\bar x(t)\big) - \bar\rho(t) C\big(\bar x(t), \bar x(t)\big)\big] \geq 0. \tag{1.84}$$

With the assumptions of Theorem 1.9.1, we do not know if $\rho_\epsilon$ converges strongly because we do not have the equivalent of the $BV$ quantity in Theorem 1.3.1. We can only prove it with stronger assumptions. This is stated in the

**Theorem 1.9.2 (Form of canonical equation)** *We assume* (1.18)–(1.21) *and* (1.74)–(1.80). *Then, for the* $C^2$*-function* $u(t,x)$ *given below in* (1.95) *with* $D_x^3 u \in L^\infty_{\text{loc}}\big(\mathbb{R}^+; L^\infty(\mathbb{R}^d)\big)$, $\bar x \in W^{1,\infty}(\mathbb{R}^+)$ *satisfies*

$$\dot{\bar x}(t) = \big(-D^2 u\big(t, \bar x(t)\big)\big)^{-1} \cdot \big[\nabla_x r\big(\bar x(t)\big) - \bar\rho(t) \nabla_x C\big(\bar x(t), \bar x(t)\big)\big]\,, \tag{1.85}$$

*with initial data* $\bar x^0$ *given in* (1.21). *Furthermore,* $\rho_\epsilon$ *converges strongly and we have* $\bar\rho(t) \in W^{1,\infty}(\mathbb{R}^+)$,

$$r\big(\bar x(t)\big) - \bar\rho(t) C\big(\bar x(t), \bar x(t)\big) = 0, \tag{1.86}$$

$$r\big(\bar x(t)\big) \geq r(\bar x^0) e^{-Kt}, \qquad \bar\rho(t) \geq \rho^0 e^{-Kt}. \tag{1.87}$$

We may find some kind of gradient flow structure for the canonical equation when $C(x,y)$ is symmetric and obtain

**Theorem 1.9.3 (Long time behavior)** *We make the assumptions of Theorem 1.9.2,* $C(x,y) = C(y,x)$ *and*

$$x \mapsto \Phi(x) := \ln r(x) - \ln C(x,x) \quad \text{is strictly concave in the set } \{r>0\}. \tag{1.88}$$

*Then, as* $t\to\infty$, $\bar\rho(t) \to \bar\rho_\infty > 0$, $\bar x(t) \to \bar x_\infty$ *and* $\bar x_\infty$ *is the maximum point of* $\Phi$.

### 1.9.1 A-priori bounds on $\rho_\epsilon$

The main new difficulty with the competition model comes from a priori bounds on the total population. In particular it is not known if there are $BV$ quantities proving that $\rho_\epsilon(t)$ converges strongly. Even non extinction is not longer automatic.

One side of the inequality (1.81) is given by $n_\epsilon \geq 0$, for the other side we integrate (1.72) over $\mathbb{R}^d$ and use (1.74) to write

$$\begin{aligned}\frac{d}{dt}\int_{\mathbb{R}^d} n_\epsilon(t,x)\,dx &= \frac{1}{\epsilon}\int_{\mathbb{R}^d} n_\epsilon(t,x) r(x)\,dx - \frac{1}{\epsilon}\int_{\mathbb{R}^d}\int_{\mathbb{R}^d} n_\epsilon(t,x) C(x,y) n_\epsilon(t,y)\,dydx \\ &\leq \frac{1}{\epsilon}\int_{\mathbb{R}^d} n_\epsilon(t,x) r(x)\,dx \left[1 - \frac{\int_{\mathbb{R}^d} n_\epsilon(t,x)\,dx}{\rho_M}\right],\end{aligned}$$

therefore (and even though $r$ can change sign) we conclude thanks to (1.79)

$$\int_{\mathbb{R}^d} n_\epsilon(t,x)\,dx \leq \rho_M.$$

### 1.9.2 Passing to the limit

The proofs of the remaining parts of Theorems are close to those already written before. We only give the main differences here. They rely again on the WKB ansatz $u_\epsilon := \epsilon \ln(n_\epsilon)$. We obtain as before that $u_\epsilon$ satisfies the Hamilton-Jacobi equation

$$\begin{cases} \frac{\partial}{\partial t} u_\epsilon(t,x) = r(x) - \displaystyle\int_{\mathbb{R}^d} C(x,y) n_\epsilon(t,y)\, dy + |\nabla u_\epsilon|^2 + \epsilon \Delta u_\epsilon, \qquad t>0,\ x\in\mathbb{R}^d, \\ u_\epsilon(t=0) = u_\epsilon^0. \end{cases} \tag{1.89}$$

Similarly to Lemma 1.5.1 we can prove the

**Lemma 1.9.4** *With the assumptions of Theorem 1.9.1, we have for all* $t \geq 0$

$$-\underline{L}_0 - \underline{L}_1 |x|^2 - \epsilon 2d \underline{L}_1 t \leq u_\epsilon(t,x) \leq \overline{L}_0 - \overline{L}_1 |x|^2 + \left( \overline{K}'_0 + 2d\epsilon \overline{L}_1 \right) t,$$

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

**Proof**. The first line holds because the right (resp. left) hand side of the inequality is a super (resp. sub) solution thanks to assumption (1.75) and using the control of $n_\varepsilon$ by $\rho_M$. For the second line, the upper and lower bound use the maximum principle on the equation for $D^2 u_\varepsilon$ and the compatibility conditions (1.80) as in section 1.5.2. □

From the regularity obtained, it follows that we can extract a subsequence such that $u_\epsilon(t,x) \underset{\epsilon\to 0}{\longrightarrow} u(t,x)$, locally uniformly as in section 1.5.3. We also obtain from Lemma 1.9.4

$$-\underline{L}_0 - \underline{L}_1 |x|^2 \leq u(t,x) \leq \overline{L}_0 - \overline{L}_1 |x|^2 + \overline{K}'_0 t, \qquad -2\underline{L}_1 \leq D^2 u(t,x) \leq -2\overline{L}_1 \quad \text{a.e.} \tag{1.90}$$

and that $u$ satisfies, in the viscosity sense (modified as in [11, 103, 10]), the equation

$$\begin{cases} \frac{\partial}{\partial t} u = r(x) - \bar\rho(t) C\big(x, \bar x(t)\big) + |\nabla u|^2, \\ \max_{\mathbb{R}^d} u(t,x) \leq 0. \end{cases} \tag{1.91}$$

The constraint is now relaxed to an inequality because we know that the total mass is bounded but we do not control the mass from below at this stage. In the framework of Theorem 1.9.2, we prove later on that the constraint is always an equality (see (1.95)).

It might be that $\bar\rho(t)$ vanishes and then $\bar x(t)$ does not matter here, nevertheless we still have

$$\max_{\mathbb{R}^d} u(t,x) = u\big(t, \bar x(t)\big). \tag{1.92}$$

Using the control (1.90) and this Hamilton-Jacobi equation we obtain (1.83) with the same arguments as in Section 1.5.3. The new difficulty is that $\rho(t)$ might vanish in particular when the constraint is strict $\max_{\mathbb{R}^d} u(t,x) < 0$, an option that we will discard later. Because of that, we also obtain the restriction on times in (1.84) which can be completed as (in the viscosity sense)

$$\frac{d}{dt} u\big(t, \bar x(t)\big) = r\big(\bar x(t)\big) - \bar\rho(t) C\big(\bar x(t), \bar x(t)\big). \tag{1.93}$$

We also have, as in section 1.9.1,

$$\epsilon \frac{d}{dt} \rho_\epsilon(t) = \int_{\mathbb{R}^d} n_\epsilon(t,x) r(x)\, dx - \int_{\mathbb{R}^d}\int_{\mathbb{R}^d} n_\epsilon(t,x) C(x,y) n_\epsilon(t,y)\, dy dx.$$

Passing to the weak limit (integration by parts and using boundedness of $\rho_\epsilon$), we find that

$$\bar\rho(t) r\big(\bar x(t)\big) = \text{ w-lim} \int_{\mathbb{R}^d}\int_{\mathbb{R}^d} n_\epsilon(t,x) C(x,y) n_\epsilon(t,y)\, dy dx \geq \bar\rho(t)^2 C\big(\bar x(t), \bar x(t)\big). \tag{1.94}$$

This proves (1.84) and concludes the proof of Theorem 1.9.1.

### 1.9.3 Form of the canonical equation

We continue with the proof of Theorem 1.9.2 and we begin with the derivation of (1.85).

The third derivative of $u_\varepsilon$ is bounded using assumption (1.77) and following the same arguments in Section 1.6.1. Then similarly to Section 1.6.2, we have the regularity $D_x^3 u \in L^\infty\big((0,T)\times\mathbb{R}^d\big)$ for all $T>0$, $\frac{\partial}{\partial t}u$ and $D^3_{txx}u \in L^\infty_{\text{loc}}\big(\mathbb{R}^+\times\mathbb{R}^d\big)$.

The canonical equation (1.85) is established a.e. as in section 1.6.2 using the maximum points of $u_\epsilon$ and passing to the limit. From (1.81), (1.85) and (1.90), we next obtain that $|\frac{d}{dt}\bar{x}(t)|$ is uniformly bounded.

### 1.9.4 Persistence

Now we prove that $u\big(t,\bar{x}(t)\big)=0$ for all $t\geq 0$ and that $\bar{\rho}(t)>0$ a.e. $t$. We cannot obtain this directly and thus we begin with proving $r(\bar{x}(t))>0$. We prove indeed the first part of the inequality (1.87).

We prove this by contradiction. We suppose that $t_0$ is the first point such that $r(\bar{x}(t_0))=0$. We notice that $\bar{x}(t)$ being lipschitzian and using assumption (1.78), for all $t<t_0$, we have $r(\bar{x}(t))>0$. Therefore with assumption (1.75) we deduce that $\bar{x}(t)$ remains bounded for $t\in[0,t_0]$. Using (1.85) and (1.90) we have

$$\begin{aligned}\frac{d}{dt}r(\bar{x}(t)) &= \nabla_x r(\bar{x}(t))\cdot\dot{\bar{x}}(t)\\ &= \nabla_x r(\bar{x}(t))\cdot\big(-D^2u\big(t,\bar{x}(t)\big)\big)^{-1}\cdot\big[\nabla_x r\big(\bar{x}(t)\big)-\bar{\rho}(t)\nabla_x C\big(\bar{x}(t),\bar{x}(t)\big)\big]\\ &\geq -\bar{\rho}(t)|\nabla_x r(\bar{x}(t))||\nabla_x C\big(\bar{x}(t),\bar{x}(t)\big)|.\end{aligned}$$

Consequently, using (1.84), we obtain

$$\frac{d}{dt}r(\bar{x}(t)) \geq -r(\bar{x}(t))|\nabla_x r(\bar{x}(t))|\frac{|\nabla_x C\big(\bar{x}(t),\bar{x}(t)\big)|}{C\big(\bar{x}(t),\bar{x}(t)\big)}.$$

Moreover we know that $\bar{x}(t)$ remains bounded for $t\in[0,t_0]$ and thus we have $\inf\limits_{t\in[0,t_0]} C(\bar{x}(t),\bar{x}(t))\geq\eta_2>0$. We conclude that, for $K$ a positive constant,

$$\frac{d}{dt}r(\bar{x}(t))\geq -Kr(\bar{x}(t)),\qquad \text{for } 0\leq t\leq t_0.$$

Starting with $r(\bar{x}^0)>0$ according to (1.78), this inequality is in contradiction with $r(\bar{x}(t_0))=0$. Therefore for all $t>0$ we have $r(\bar{x}(t))>0$ and thus this inequality is true for all $t>0$. Thereby we obtain the first part of (1.87). From the latter and using again (1.75), we also deduce that $\bar{x}(t)$ remains bounded for all $t>0$.

Next we use (1.84), (1.93) and the positivity of $r(\bar{x}(t))$ to obtain

$$u(t,\bar{x}(t))-u^0(\bar{x}^0)=\int r(\bar{x}(t))-\bar{\rho}(t)C(\bar{x}(t),\bar{x}(t))dt\geq \mathbf{1}_{\bar{\rho}(t)=0}r(\bar{x}(t))\geq 0.$$

We deduce, using (1.21), that $u(t,\bar{x}(t))=0$ for all $t\geq 0$. Thus the equation on $u$ is in fact

$$\begin{cases}\frac{\partial}{\partial t}u = r(x)-\bar{\rho}(t)C\big(x,\bar{x}(t)\big)+|\nabla u|^2,\\ \max_{\mathbb{R}^d}u(t,x)=0.\end{cases}\tag{1.95}$$

This identity also proves the identity (1.86) and thus that (1.94) holds as an equality, which is equivalent to say that the weak limit of $\rho_\epsilon(t)$ is in fact a strong limit.

We may now use (1.86) to conclude that $\bar\rho(t)$ is also bounded in $W^{1,\infty}(\mathbb{R}^+)$. To do so, we first differentiate (1.86) and find again some kind of gradient flow structure

$$\nabla r\big(\bar x(t)\big)\cdot\dot{\bar x}(t)-\dot{\bar\rho}(t)C\big(\bar x(t),\bar x(t)\big)-\bar\rho(t)\left[\nabla_x C\big(\bar x(t),\bar x(t)\big)+\nabla_y C\big(\bar x(t),\bar x(t)\big)\right]\dot{\bar x}(t)=0.$$

With (1.85), it follows that

$$\dot{\bar x}(t)\cdot\big(-D^2u\big)\cdot\dot{\bar x}(t)=\dot{\bar\rho}(t)C\big(\bar x(t),\bar x(t)\big)+\bar\rho(t)\nabla_y C\big(\bar x(t),\bar x(t)\big)\dot{\bar x}(t). \tag{1.96}$$

From the uniform bounds proved before, there is a constant $\eta_3$ such that

$$\frac{\nabla_y C\big(\bar x(t),\bar x(t)\big)\cdot\dot{\bar x}(t)}{C\big(\bar x(t),\bar x(t)\big)}\le\eta_3. \tag{1.97}$$

Using the latter and (1.90) we conclude that, for $K$ a positive constant,

$$\dot{\bar\rho}(t)\ge-K\bar\rho(t).$$

Thus we obtain (1.87). This completes the proof of Theorem 1.9.2.

### 1.9.5 Long time behavior

It remains to prove Theorem 1.9.3. Assuming that $C(x,y)$ is symmetric, we can find a quantity which is non-decreasing in time, which replaces the quantity $\bar I$ in section 1.6.3. We compute, from the relation (1.96),

$$\begin{aligned}\frac{d}{dt}\left[\bar\rho^2(t)C\big(\bar x(t),\bar x(t)\big)\right](2\bar\rho(t))^{-1}&=\dot{\bar\rho}(t)C\big(\bar x(t),\bar x(t)\big)+\bar\rho(t)(\nabla_y C)\dot{\bar x}(t)\\&=\dot{\bar x}(t)\cdot\big(-D^2u\big)\cdot\dot{\bar x}(t)\ge0.\end{aligned}\tag{1.98}$$

As $t$ tends to infinity, we may consider a subsequence $t_n$ such that $\bar\rho(t_n)\to\bar\rho_\infty$, $\bar x(t_n)\to\bar x_\infty$. From (1.98), we may also assume $\dot{\bar x}(t_n)\to0$. Therefore

$$\nabla r(\bar x_\infty)=\bar\rho_\infty\nabla_x C(\bar x_\infty,\bar x_\infty),\qquad r(\bar x_\infty)=\bar\rho_\infty C(\bar x_\infty,\bar x_\infty).$$

From these relations, we first conclude that $\bar\rho_\infty$ is positive because $r$ is concave and its gradient only vanishes at a point where $r$ is positive.

Then we combine the relations and conclude that

$$\frac{\nabla r(\bar x_\infty)}{r(\bar x_\infty)}=\frac{\nabla_x C(\bar x_\infty,\bar x_\infty)}{C(\bar x_\infty,\bar x_\infty)}.$$

The assumption (1.88) then concludes on the uniqueness of such a point $\bar x_\infty$ and thus on the convergence of $\bar x(t)$. $\square$

# Chapitre 2

# Généralisation des résultats de convergence à des cas moins réguliers

---

Le travail dans ce chapitre a été effectué en collaboration avec Guy Barles et Benoît Perthame. On étudie deux équations de type Lotka-Volterra décrivant l'évolution Darwinienne d'une densité de population. Ce travail s'inscrit dans la continuité de l'article [103] où les auteurs étudient un modèle avec un terme de croissance et de mortalité non-linéaire et un terme de Laplace représentant des mutations. Ils ont montré qu'à la limite des mutations rares ou petites la solution converge vers une somme de masses de Dirac qui évoluent dans le temps. La limite est décrite par une équation de Hamilton-Jacobi avec contrainte.
Dans ce chapitre on montre le même résultat, mais en relaxant les hypothèses de régularité sur la donnée initiale. En outre, on montre des propriétés équivalentes pour un autre modèle où l'on remplace le laplacien par un noyau intégral pour des mutations. L'avantage de ce dernier modèle est que les mutations peuvent dépendre du trait phénotypique et elles ne sont plus considérées homogènes. Ce travail reprend l'article [10].

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## 2.1 Introduction

We continue the study, initiated in [103], of the asymptotic behavior of Lotka-Volterra parabolic equations. The model we use describes the dynamics of a population density. Individuals respond differently to the environment, i.e. they have different abilities to use the available resources. To take this fact into account, population models can be structured by a parameter, representing a physiological (phenotypical) trait inherited from the parent, and that we denote by $x \in \mathbb{R}^d$. We denote by $n(t,x)$ the density of trait $x$. The mathematical modeling in accordance with Darwin's theory consists of two effects: natural selection and mutations between the traits (see [49, 66, 91, 65] for literature in adaptive evolution). We represent the birth and death rates of the phenotypical traits by a net growth rate $R(x,I)$. The term $I(t)$ is an ecological parameter that corresponds to a measure of the total population, whatever the trait, and that represents in the simpler possible way the resources (more precisely the inverse of it). We use two different models for mutations. A first possibility is to represent them by a Laplacian and, in an extreme and irrealistic simplification, we take them independent of birth, so as to write

$$\begin{cases} \partial_t n_\epsilon - \epsilon \triangle n_\epsilon = \frac{n_\epsilon}{\epsilon} R(x, I_\epsilon(t)), \qquad x \in \mathbb{R}^d,\ t \geq 0, \\ n_\epsilon(t=0) = n_\epsilon^0 \in L^1(\mathbb{R}^d), \qquad n_\epsilon^0 \geq 0, \end{cases} \tag{2.1}$$

$$I_\epsilon(t) = \int_{\mathbb{R}^d} \psi(x)\, n_\epsilon(t,x) dx. \tag{2.2}$$

Here $\epsilon$ is a small term that we introduce to consider only rare mutations. It is also used to re-scale time to consider a much larger time than a generation scale.

A more natural way to model mutations is to use, instead of a Laplacian, an integral term that describes directly the mutation probability to generate a new-born of trait $x$ from a mother with trait $y$. This yields

$$\begin{cases} \partial_t n_\epsilon = \frac{n_\epsilon}{\epsilon} R(x, I_\epsilon(t)) + \frac{1}{\epsilon} \int \frac{1}{\epsilon^d} K(\frac{y-x}{\epsilon})\, b(y, I_\epsilon)\, n_\epsilon(t,y)\, dy, \qquad x \in \mathbb{R}^d,\ t \geq 0, \\ n_\epsilon(t=0) = n_\epsilon^0 \in L^1(\mathbb{R}^d), \qquad n_\epsilon^0 \geq 0, \end{cases} \tag{2.3}$$

$$I_\epsilon(t) = \int_{\mathbb{R}^d} n_\epsilon(t,x) dx. \tag{2.4}$$

Both types of models can be derived from individual based stochastic processes in the limit of large populations depending on the scales in mutations birth and death (see [31, 32]).

In this paper, we study the asymptotic behavior of equations (2.1)–(2.2) and (2.3)–(2.4) when $\epsilon$ vanishes. Our purpose is to show that under some assumptions on $R(x,I)$, $n_\epsilon(t,x)$ concentrates as a sum of Dirac masses that are traveling. In biological terms, at every moment one or several dominant traits coexist while other traits disappear. The dominant traits change in time due to the presence of mutations.

We use the same assumptions as [103]. We assume that there exist two constants $\psi_m$, $\psi_M$ such that

$$0 < \psi_m < \psi < \psi_M < \infty, \qquad \psi \in W^{2,\infty}(\mathbb{R}^d). \tag{2.5}$$

We also assume that there are two constants $0 < I_m < I_M < \infty$ such that

$$\min_{x \in \mathbb{R}^d} R(x, I_m) = 0, \qquad \max_{x \in \mathbb{R}^d} R(x, I_M) = 0, \tag{2.6}$$

and there exists constants $K_i > 0$ such that, for any $x \in \mathbb{R}^d$, $I \in \mathbb{R}$,

$$-K_1 \leq \frac{\partial R}{\partial I}(x,I) \leq -K_1^{-1} < 0, \tag{2.7}$$

$$\sup_{\frac{I_m}{2} \leq I \leq 2I_M} \parallel R(\cdot, I) \parallel_{W^{2,\infty}(\mathbb{R}^d)} < K_2. \tag{2.8}$$

We also make the following assumptions on the initial data

$$I_m \leq \int_{\mathbb{R}^d} \psi(x) n_\epsilon^0(x) \leq I_M, \quad \text{and} \quad \exists\, A,\, B > 0\,,\; n_\epsilon^0 \leq e^{\frac{-A|x|+B}{\epsilon}}. \tag{2.9}$$

Here we take $\psi(x) \equiv 1$ for equations (2.3)–(2.4) because replacing $n$ by $\psi n$ leaves the model unchanged. For equation (2.3) we assume additionally that the probability kernel $K(z)$ and the mutation birth rate $b(z)$ verify

$$0 \leq K(z), \qquad \int K(z)\, dz = 1, \qquad \int K(z) e^{|z|^2}\, dz < \infty, \tag{2.10}$$

$$b_m \leq b(z,I) \leq b_M, \quad |\nabla_x b(z,I)| < L_1\, b(z,I), \quad |b(x,I_1) - b(x,I_2)| < L_2 |I_1 - I_2|, \tag{2.11}$$

where $b_m$, $b_M$, $L_1$ and $L_2$ are positive constants. Finally for equation (2.3) we replace (2.6) and (2.7) by

$$\min_{x\in\mathbb{R}^d} \big[R(x,I_m) + b(x,I_m)\big] = 0, \qquad \max_{x\in\mathbb{R}^d} \big[R(x,I_M) + b(x,I_M)\big] = 0, \tag{2.12}$$

$$|R(x,I_1) - R(x,I_2)| < K_3 |I_1 - I_2| \quad \text{and} \quad -K_4 \leq \frac{\partial(R+b)}{\partial I}(x,I) \leq -K_4^{-1} < 0, \tag{2.13}$$

where $K_3$ and $K_4$ are positive constants.

In both cases, in the limit we expect $n(t,x) = 0$ or $R(x,I) = 0$, where $n(t,x)$ is the weak limit of $n_\epsilon(t,x)$ as $\epsilon$ vanishes. If we suppose that the latter is possible at only isolated points, we expect $n$ to concentrate as Dirac masses. Following earlier works on the similar issue [50, 11, 103, 93], in order to study $n$, we make a change of variable $n_\epsilon(t,x) = e^{\frac{u_\epsilon(t,x)}{\epsilon}}$. It is easier to study the asymptotic behavior of $u_\epsilon$ instead of $n_\epsilon$. In section 2.5 we study the asymptotic behavior of $u_\epsilon$ while $\epsilon$ vanishes. We show that $u_\epsilon$, after extraction of a subsequence, converge to a function $u$ that satisfies a constrained Hamilton-Jacobi equation in the viscosity sense (see [5, 54, 38, 57] for general introduction to the theory of viscosity solutions). Our main results are as follows.

**Theorem 2.1.1** *Assume (2.5)–(2.9). Let $n_\epsilon$ be the solution of (2.1)–(2.2), and $u_\epsilon = \epsilon \ln(n_\epsilon)$. Then, after extraction of a subsequence, $u_\epsilon$ converges locally uniformly to a function $u \in \mathrm{C}((0,\infty) \times \mathbb{R}^d)$, a viscosity solution to the following equation:*

$$\begin{cases} \partial_t u = |\nabla u|^2 + R(x, I(t)), \\ \max_{x\in\mathbb{R}^d} u(t,x) = 0, \quad \forall t > 0, \end{cases} \tag{2.14}$$

$$I_\epsilon(t) \underset{\epsilon\to 0}{\longrightarrow} I(t) \quad a.e., \qquad \int \psi(x) n(t,x) dx = I(t) \quad a.e.. \tag{2.15}$$

*In particular, a.e. in $t$, supp $n(t,\cdot) \subset \{u(t,\cdot) = 0\}$. Here the measure $n$ is the weak limit of $n_\epsilon$ as $\epsilon$ vanishes. If additionally $(u_\epsilon^0)_\epsilon := \epsilon \ln(n_\epsilon^0)$ is a sequence of uniformly continuous functions which converges locally uniformly to $u^0$ then $u \in \mathrm{C}([0,\infty)\times\mathbb{R}^d)$ and $u(0,x) = u^0(x)$ in $\mathbb{R}^d$.*

**Theorem 2.1.2** *Assume (2.8)–(2.13), and* $(u_\epsilon^0)_\epsilon$ *is a sequence of uniformly Lipschitz-continuous functions which converges locally uniformly to* $u^0$. *Let* $n_\epsilon$ *be the solution of (2.3)–(2.4) with* $n_\epsilon^0 = e^{\frac{u\epsilon^0}{\epsilon}}$, *and* $u_\epsilon = \epsilon \ln(n_\epsilon)$. *Then, after extraction of a subsequence,* $u_\epsilon$ *converges locally uniformly to a function* $u \in \mathrm{C}([0,\infty) \times \mathbb{R}^d)$, *a viscosity solution to the following equation:*

$$\begin{cases} \partial_t u = R(x, I(t)) + b(x, I(t)) \int K(z) e^{\nabla u \cdot z} dz, \\ \max\limits_{x \in \mathbb{R}^d} u(t,x) = 0, \quad \forall t > 0, \\ u(0,x) = u^0(x), \end{cases} \tag{2.16}$$

$$I_\epsilon(t) \underset{\epsilon \to 0}{\longrightarrow} I(t) \quad a.e., \qquad \int n(t,x) dx = I(t) \quad a.e.. \tag{2.17}$$

*In particular, a.e. in* $t$, *supp* $n(t,\cdot) \subset \{u(t,\cdot) = 0\}$. *As above, the measure* $n$ *is the weak limit of* $n_\epsilon$ *as* $\epsilon$ *vanishes.*

These theorems improve previous results proved in [50, 103, 11, 102] in various directions. For the case where mutations are described by a Laplace equation, i.e. (2.1)–(2.2), Theorem 2.1.1 generalizes the assumptions on the initial data. This generalization derives from regularizing effects of Eikonal Hamiltonian (see [82, 3, 4]). But our motivation is more in the case of equations (2.3)–(2.4) where mutations are described by an integral operator. Then we can treat cases where the mutation rate $b(x, I)$ really depends on $x$, which was not available until now. The difficulty here is that Lipschitz bounds on the initial data are not propagated on $u_\epsilon$ and may blow up in finite time (see [19, 8, 36] for regularity results for integral Hamiltonian). However, we achieve to control the Lipschitz norm by $-u_\epsilon$, that goes to infinity as $|x|$ goes to $+\infty$.

We do not discuss the uniqueness for equations (2.14) and (2.16) in this paper. The latter is studied, for some particular cases, in [103, 11].

A related, but different, situation arises in reaction-diffusion equations as in combustion (see [9, 13, 12, 56, 58, 117]). A typical example is the Fisher-KPP equation, where the solution is a progressive front. The dynamics of the front is described by a level set of a solution of a Hamilton-Jacobi equation.

The paper is organized as follows. In section 2.2 we state some existence results and bounds on $n_\epsilon$ and $I_\epsilon$. In section 2.3 we prove some regularity results for $u_\epsilon$ corresponding to equations (2.1)–(2.2). We show that $u_\epsilon$ are locally uniformly bounded and continuous. In section 2.4 we prove some analogous regularity results for $u_\epsilon$ corresponding to equations (2.3)–(2.4). Finally, in section 2.5 we describe the asymptotic behavior of $u_\epsilon$ and deduce the constrained Hamilton-Jacobi equation (2.14)–(2.15).

## 2.2 Preliminary results

We recall the following existence results for $n_\epsilon$ and a priori bounds for $I_\epsilon$ (see also [103, 45]).

**Theorem 2.2.1** *With the assumptions (2.5)–(2.8), and* $I_m - C\epsilon^2 \le I_\epsilon(0) \le I_M + C\epsilon^2$, *there is a unique solution* $n_\epsilon \in \mathrm{C}(\mathbb{R}^+; L^1(\mathbb{R}^d))$ *to equations (2.1)–(2.2) and it satisfies*

$$I'_m = I_m - C\epsilon^2 \le I_\epsilon(t) \le I_M + C\epsilon^2 = I'_M, \tag{2.18}$$

*where* $C$ *is a constant. This solution,* $n_\epsilon(t,x)$, *is nonnegative for all* $t \ge 0$.

We recall a proof of this theorem in Appendix 2.6.1. We have an analogous result for equations (2.3)–(2.4):

**Theorem 2.2.2** *With the assumptions (2.8), (2.10))–(2.13), and* $I_m \le I_\epsilon(0) \le I_M$*, there is a unique solution* $n_\epsilon \in \mathrm{C}(\mathbb{R}^+; L^1 \cap L^\infty(\mathbb{R}^d))$ *to equations (2.3)–(2.4) and it satisfies*

$$I_m \le I_\epsilon(t) \le I_M. \tag{2.19}$$

*This solution,* $n_\epsilon(t,x)$*, is nonnegative for all* $t \ge 0$*.*

This theorem can be proved with similar arguments as Theorem 2.2.1. A uniform BV bound on $I_\epsilon(t)$ for equations (2.1)–(2.2) is also proved in [103]:

**Theorem 2.2.3** *With the assumptions (2.5)–(2.9), we have additionally to the uniform bounds (2.18), the locally uniform BV and sub-Lipschitz bounds*

$$\frac{d}{dt} I_\epsilon(t) \ge -\epsilon C + e^{\frac{-Lt}{\epsilon}} \int \psi(x) n_\epsilon^0(x) \frac{R(x, I_\epsilon^0)}{\epsilon} dx, \tag{2.20}$$

$$\frac{d}{dt} \varrho_\epsilon(t) \ge -Ct + \int (1+\psi(x)) n_\epsilon^0(x) \frac{R(x, I_\epsilon^0)}{\epsilon} dx, \tag{2.21}$$

*where* $C$ *and* $L$ *are positive constants and* $\varrho_\epsilon(t) = \int_{\mathbb{R}^d} n_\epsilon(t,x)dx$*. Consequently, after extraction of a subsequence,* $I_\epsilon(t)$ *converges a.e. to a function* $I(t)$*, as* $\epsilon$ *goes to* 0*. The limit* $I(t)$ *is nondecreasing as soon as there exists a constant* $C$ *independent of* $\epsilon$ *such that*

$$\int \psi(x) n_\epsilon^0(x) \frac{R(x, I_\epsilon^0)}{\epsilon} \ge -Ce^{\frac{o(1)}{\epsilon}}.$$

We also have a local BV bound on $I_\epsilon(t)$ for equations (2.3)–(2.4):

**Theorem 2.2.4** *With the assumptions (2.8)–(2.13), we have additionally to the uniform bounds (2.19), the locally uniform BV bound*

$$\frac{d}{dt} I_\epsilon(t) \ge -C' + e^{\frac{-L't}{\epsilon}} \int n_\epsilon^0(x) \frac{R(x, I_\epsilon^0) + b(x, I_\epsilon^0)}{\epsilon} dx, \tag{2.22}$$

$$\int_0^T |\frac{d}{dt} I_\epsilon(t)| dt \le 2C'T + C'', \tag{2.23}$$

*where* $C'$*,* $C''$ *and* $L'$ *are positive constants. Consequently, after extraction of a subsequence,* $I_\epsilon(t)$ *converges a.e. to a function* $I(t)$*, as* $\epsilon$ *goes to* 0*.*

This theorem is proved in Appendix 2.6.2.

## 2.3 Regularity results for equations (2.1)–(2.2)

In this section we study the regularity properties of $u_\epsilon = \epsilon \ln n_\epsilon$, where $n_\epsilon$ is the unique solution of equations (2.1)–(2.2). We have

$$\partial_t n_\epsilon = \frac{1}{\epsilon} \partial_t u_\epsilon \, e^{\frac{u_\epsilon}{\epsilon}}, \quad \nabla n_\epsilon = \frac{1}{\epsilon} \nabla u_\epsilon \, e^{\frac{u_\epsilon}{\epsilon}}, \quad \triangle n_\epsilon = (\frac{1}{\epsilon} \triangle u_\epsilon + \frac{1}{\epsilon^2} |\nabla u_\epsilon|^2) e^{\frac{u_\epsilon}{\epsilon}}.$$

Consequently $u_\epsilon$ is a smooth solution to the following equation

$$\begin{cases} \partial_t u_\epsilon - \epsilon \triangle u_\epsilon = |\nabla u_\epsilon|^2 + R(x, I_\epsilon(t)), & x \in \mathbb{R}, \, t \ge 0, \\ u_\epsilon(t=0) = \epsilon \ln n_\epsilon^0. \end{cases} \tag{2.24}$$

We have the following regularity results for $u_\epsilon$.

**Theorem 2.3.1** *Assume (2.5)–(2.9) and let $T > 0$ be given. Set $D = B + (A^2 + K_2)T$. Then we have $u_\epsilon \leq D^2$. For all $t_0 > 0$, $v_\epsilon = \sqrt{2D^2 - u_\epsilon}$ are locally uniformly bounded and Lipschitz in $[t_0, T] \times \mathbb{R}^d$,*

$$|\nabla v_\epsilon| \leq C(T) + \frac{1}{2\sqrt{t_0}}, \tag{2.25}$$

*where $C(T)$ is a constant depending on $T$, $K_1$, $K_2$, $A$ and $B$. Moreover, if we assume that $(u_\epsilon^0)_\epsilon := \epsilon \ln(n_\epsilon^0)$ is a sequence of uniformly continuous functions, then $u_\epsilon$ are locally uniformly bounded and continuous in $[0, \infty[\times \mathbb{R}^d$.*

We prove Theorem 2.3.1 in several steps. We first prove an upper bound, then a regularizing effect in $x$, then local $L^\infty$ bounds, and finally a regularizing effect in $t$.

### 2.3.1 An upper bound for $u_\epsilon$

From assumption (2.9) we have $u_\epsilon^0(x) \leq -A|x| + B$. We claim that, with $C = A^2 + K_2$,

$$u_\epsilon(t, x) \leq -A|x| + B + Ct, \quad \forall t \geq 0. \tag{2.26}$$

Define $\phi(t, x) = -A|x| + B + Ct$. We have

$$\partial_t \phi - \epsilon \triangle \phi - |\nabla \phi|^2 - R(x, I_\epsilon(t)) \geq C + \epsilon \frac{A(d-1)}{|x|} - A^2 - K_2 \geq 0.$$

Here $K_2$ is an upper bound for $R(x, I)$ according to (2.8). We have also $\phi(0, x) = -A|x| + B \geq u_\epsilon^0(x)$. So $\phi_\epsilon$ is a super-solution to (2.24) and (2.26) is proved.

### 2.3.2 Regularizing effect in space

Let $u = f(v)$, where $f$ is chosen later. We have

$$\partial_t u = f'(v)\partial_t v, \quad \partial_x u = f'(v)\partial_x v, \quad \triangle u = f'(v)\triangle v + f''(v)|\nabla v|^2.$$

So equation (2.24) becomes

$$\partial_t v - \epsilon \triangle v - \left[\epsilon \frac{f''(v)}{f'(v)} + f'(v)\right] |\nabla v|^2 = \frac{R(x, I)}{f'(v)}. \tag{2.27}$$

Define $p = \nabla v$. By differentiating (2.27) we have

$$\partial_t p_i - \epsilon \triangle p_i - 2\left[\epsilon \frac{f''(v)}{f'(v)} + f'(v)\right] \nabla v \cdot \nabla p_i - \left[\epsilon \frac{f'''(v)}{f'(v)} - \epsilon \frac{f''(v)^2}{f'(v)^2} + f''(v)\right] |\nabla v|^2 p_i$$
$$= -\frac{f''(v)}{f'(v)^2} R(x, I) p_i + \frac{1}{f'(v)} \frac{\partial R}{\partial x_i}.$$

We multiply the equation by $p_i$ and sum over $i$:

$$\partial_t \frac{|p|^2}{2} - \epsilon \sum (\triangle p_i) p_i - 2\left[\epsilon \frac{f''(v)}{f'(v)} + f'(v)\right] \nabla v \cdot \nabla \frac{|p|^2}{2} - \left[\epsilon \frac{f'''(v)}{f'(v)} - \epsilon \frac{f''(v)^2}{f'(v)^2} + f''(v)\right] |p|^4$$
$$= -\frac{f''(v)}{f'(v)^2} R(x, I)|p|^2 + \frac{1}{f'(v)} \nabla_x R \cdot p.$$

First, we compute $\sum_i (\triangle p_i) p_i$.

$$\begin{aligned}\sum_i (\triangle p_i)p_i &= \sum_i \triangle \frac{p_i^2}{2} - \sum |\nabla p_i|^2 \\ &= \triangle \frac{|p|^2}{2} - \sum |\nabla p_i|^2 \\ &= |p|\triangle|p| + |\nabla|p||^2 - \sum_i |\nabla p_i|^2.\end{aligned}$$

We also have

$$|\nabla|p||^2 = \sum_i \frac{|p\cdot \partial_{x_i} p|^2}{|p|^2} \leq \sum_i |\partial_{x_i} p|^2 = \sum_{i,j} |\partial_{x_i} p_j|^2 = \sum_j |\nabla p_j|^2.$$

It follows that

$$\sum_i (\triangle p_i)p_i \leq |p|\triangle|p|.$$

We deduce

$$\begin{aligned}\partial_t|p| - \epsilon\triangle|p| - 2\left[\epsilon\frac{f''(v)}{f'(v)} + f'(v)\right] p\cdot\nabla|p| - \left[\epsilon\frac{f'''(v)}{f'(v)} - \epsilon\frac{f''(v)^2}{f'(v)^2} + f''(v)\right]|p|^3 \\ \leq -\frac{f''(v)}{f'(v)^2}R(x,I)|p| + \frac{1}{f'(v)}\nabla_x R\cdot\frac{p}{|p|}.\end{aligned} \tag{2.28}$$

From (2.26) we know that, for $0 \leq t \leq T$, $u_\epsilon \leq D(T)^2$, where $D(T) = \sqrt{B+CT}$. Then we define $f(v) = -v^2 + 2D^2$, for $v$ positive, and thus

$$D(T) \leq v,$$

$$f'(v) = -2v, \quad \text{and} \quad |\frac{1}{f'(v)}| = \frac{1}{2v} \leq \frac{1}{2D},$$

$$f''(v) = -2, \quad \text{and} \quad |\frac{f''(v)}{f'(v)^2}| = \frac{1}{2v^2} \leq \frac{1}{2D^2},$$

$$f'''(v) = 0, \quad -\left[\epsilon\frac{f'''(v)}{f'(v)} - \epsilon\frac{f''(v)^2}{f'(v)^2} + f''(v)\right] = 2 + \epsilon\frac{1}{v^2} > 2.$$

From (2.28), Theorem 2.2.1, assumption (2.8) and these calculations we deduce

$$\frac{\partial|p|}{\partial t} - \epsilon\triangle|p| - 2\left[\epsilon\frac{f''(v)}{f'(v)} + f'(v)\right] p\cdot\nabla|p| + 2|p|^3 - \frac{K_2}{2D^2}|p| - \frac{K_2}{2D} \leq 0.$$

Thus for $\theta(T)$ large enough we can write

$$\frac{\partial |p|}{\partial t} - \epsilon \triangle |p| - 2\left[\epsilon \frac{f''(v)}{f'(v)} + f'(v)\right] p \cdot \nabla |p| + 2(|p| - \theta)^3 \leq 0. \tag{2.29}$$

Define the function

$$y(t,x) = y(t) = \frac{1}{2\sqrt{t}} + \theta.$$

Since $y$ is a solution to (2.29), and $y(0) = \infty$ and $|p|$ being a sub-solution we have

$$|p|(t,x) \leq y(t,x) = \frac{1}{2\sqrt{t}} + \theta.$$

Thus for $v_\epsilon = \sqrt{2D^2 - u_\epsilon}$, we have

$$|\nabla v_\epsilon|(t,x) \leq \frac{1}{2\sqrt{t}} + \theta(T), \quad 0 < t \leq T. \tag{2.30}$$

### 2.3.3 Regularity in space of $u_\epsilon$ near $t = 0$

Assume that $u_\epsilon^0$ are uniformly continuous. We show that $u_\epsilon$ are uniformly continuous in space on $[0,T] \times \mathbb{R}^d$.

For $\delta > 0$ we prove that for $h$ small $|u_\epsilon(t,x+h) - u_\epsilon(t,x)| < \delta$. To do so define $w_\epsilon(t,x) = u_\epsilon(t,x+h) - u_\epsilon(t,x)$. Since $u_\epsilon^0$ are uniformly continuous, for $h$ small enough $|w_\epsilon(0,x)| < \frac{\delta}{2}$. Besides $w_\epsilon$ satisfies the following equation:

$$\partial_t w_\epsilon(t,x) - \epsilon \triangle w_\epsilon(t,x) - (\nabla u_\epsilon(t,x+h) + \nabla u_\epsilon(t,x)) \cdot \nabla w_\epsilon(t,x) = R(x+h, I_\epsilon(t)) - R(x, I_\epsilon(t)).$$

From Theorem 2.2.1 and using assumption (2.8) we have

$$\partial_t w_\epsilon(t,x) - \epsilon \triangle w_\epsilon(t,x) - (\nabla u_\epsilon(t,x+h) + \nabla u_\epsilon(t,x)) \cdot \nabla w_\epsilon(t,x) \leq K_2 |h|.$$

Therefore by the maximum principle we arrive at

$$\max_{\mathbb{R}^d} |w_\epsilon(t,x)| < \max_{\mathbb{R}^d} |w_\epsilon(0,x)| + K_2 |h| t.$$

So for $h$ small enough $|u_\epsilon(t,x+h) - u_\epsilon(t,x)| < \delta$ on $[0,T] \times \mathbb{R}^d$.

### 2.3.4 Local bounds for $u_\epsilon$

We show that $u_\epsilon$ are bounded on compact subsets of $]0,\infty[\times \mathbb{R}^d$. We already know from section 2.3.1 that $u_\epsilon$ is locally bounded from above. We show that it is also bounded from below on $\mathcal{C} = [t_0, T] \times \mathrm{B}(0,R)$, for all $R > 0$ and $0 < t_0 < T$.

From section 2.3.1 we have $u_\epsilon(t,x) \leq -A|x| + B + CT$. So for $R$ large enough there exists $\epsilon_0$ such that for $\epsilon < \epsilon_0$

$$\int_{|x|>R} e^{\frac{u_\epsilon}{\epsilon}} dx < \int_{|x|>R} e^{\frac{-A|x|+B+CT}{\epsilon}} dx < \frac{I'_m}{2\psi_M}.$$

We have also from (2.18) that

$$\int_{\mathbb{R}^d} e^{\frac{u_\epsilon}{\epsilon}}dx > \frac{I'_m}{\psi_M}.$$

We deduce that for $R$ large enough and for all $0<\epsilon<\epsilon_0$

$$\int_{|x|<R} e^{\frac{u_\epsilon}{\epsilon}}dx > \frac{I'_m}{2\psi_M}.$$

Therefore there exists $\epsilon_1>0$ such that, for all $\epsilon<\epsilon_1$

$$\exists x_0 \in \mathbb{R}^d; \quad |x_0|<R,\ u_\epsilon(t,x_0)>-1, \ \text{ thus } \ v_\epsilon(t,x_0)<\sqrt{2D^2+1}.$$

From Section 2.3.2 we know that $v_\epsilon$ are locally uniformly Lipschitz

$$|v_\epsilon(t,x+h)-v_\epsilon(t,x)| < \big(C(T)+\frac{1}{2\sqrt{t_0}}\big)|h|,$$

Thus for all $(t,x)\in\mathcal{C}$ and $\epsilon<\epsilon_1$

$$v_\epsilon(t,x) < E(t_0,T,R) := \sqrt{2D^2(T)+1}+2\big(C(T)+\frac{1}{2\sqrt{t_0}}\big)R.$$

It follows that

$$u_\epsilon(t,x) > 2D^2(T)-E^2(t_0,T,R).$$

We conclude that $u_\epsilon$ are uniformly bounded from below on $\mathcal{C}$.

If we assume additionally that $u_\epsilon^0$ are uniformly continuous, with similar arguments we can show that $u_\epsilon$ are bounded on compact subsets of $[0,\infty[\times\mathbb{R}^d$. To prove the latter we use uniform continuity of $u_\epsilon$ instead of the Lipschitz bounds of $v_\epsilon$.

### 2.3.5 Regularizing effect in time

From the above uniform bounds and continuity results we can also deduce uniform continuity in time i.e. for all $\eta>0$, there exists $\theta>0$ such that for all $(t,s,x)\in[0,T]\times[0,T]\times \mathrm{B}(0,\frac{R}{2})$, such that $0<t-s<\theta$, and for all $\epsilon<\epsilon_0$ we have:

$$|u_\epsilon(t,x)-u_\epsilon(s,x)|\le 2\eta.$$

We prove this with the same method as that of Lemma 9.1 in [6] (see also [16] for another proof of this claim). We prove that for any $\eta>0$, we can find positive constants $A$, $B$ large enough such that, for any $x\in \mathrm{B}(0,\frac{R}{2})$, $s\in[0,T]$ and for every $\epsilon<\epsilon_0$,

$$u_\epsilon(t,y)-u_\epsilon(s,x)\le \eta + A|x-y|^2+B(t-s), \quad \text{for every } (t,y)\in[s,T]\times \mathrm{B}(0,R), \tag{2.31}$$

and

$$u_\epsilon(t,y)-u_\epsilon(s,x)\ge -\eta - A|x-y|^2-B(t-s), \quad \text{for every } (t,y)\in[s,T]\times \mathrm{B}(0,R). \tag{2.32}$$

We prove inequality (2.31), the proof of (2.32) is analogous. We fix $(s,x)$ in $[0,T[\times \mathrm{B}(0,\frac{R}{2})$. Define

$$\xi(t,y)=u_\epsilon(s,x)+\eta+A|y-x|^2+B(t-s), \qquad (t,y)\in[s,T[\times \mathrm{B}(0,R),$$

where $A$ and $B$ are constants to be determined. We prove that, for $A$ and $B$ large enough, $\xi$ is a super-solution to (2.24) on $[s,T]\times \mathrm{B}(0,R)$ and $\xi(t,y)>u_\epsilon(t,y)$ for $(t,y)\in\{s\}\times$

$\mathrm{B}(0,R) \cup [s,T] \times \partial \mathrm{B}(0,R)$.

According to section 2.3.4, $u_\epsilon$ are locally uniformly bounded, so we can take $A$ a constant such that for all $\epsilon < \epsilon_0$,

$$A \geq \frac{8 \parallel u_\epsilon \parallel_{L^\infty([0,T]\times \mathrm{B}(0,R))}}{R^2}.$$

With this choice, $\xi(t,y) > u_\epsilon(t,y)$ on $[0,T] \times \partial\mathrm{B}(0,R)$, for all $\eta$, $B$ and $x \in \mathrm{B}(0,\frac{R}{2})$. Next we prove that, for $A$ large enough, $\xi(s,y) > u_\epsilon(s,y)$ for all $y \in \mathrm{B}(0,R)$. We argue by contradiction. Assume that there exists $\eta > 0$ such that for all constants $A$ there exists $y_{A,\epsilon} \in \mathrm{B}(0,R)$ such that

$$u_\epsilon(s,y_{A,\epsilon}) - u_\epsilon(s,x) > \eta + A|y_{A,\epsilon} - x|^2. \tag{2.33}$$

It follows that

$$|y_{A,\epsilon} - x| \leq \sqrt{\frac{2M}{A}},$$

where $M$ is a uniform upper bound for $\parallel u_\epsilon \parallel_{L^\infty([0,T]\times\mathrm{B}(0,R))}$. Now let $A \to \infty$. Then for all $\epsilon$, $|y_{A,\epsilon} - x| \to 0$. According to Section 2.3.3, $u_\epsilon$ are uniformly continuous on space. Thus there exists $h > 0$ such that if $|y_{A,\epsilon} - x| \leq h$ then $|u_\epsilon(s,y_{A,\epsilon}) - u_\epsilon(s,x)| < \frac{\eta}{2}$, for all $\epsilon$. This is in contradiction with (2.33). Therefore $\xi(s,y) > u_\epsilon(s,y)$ for all $y \in \mathrm{B}(0,R)$. Finally, noting that $R$ is bounded we deduce that for $B$ large enough, $\xi$ is a super-solution to (2.24) in $[s,T] \times \mathrm{B}(0,R)$. Since $u_\epsilon$ is a solution of (2.24) we have

$$u_\epsilon(t,y) \leq \xi(t,y) = u_\epsilon(s,x) + \eta + A|y-x|^2 + B(t-s) \quad \text{for all } (t,y) \in [s,T]\times\mathrm{B}(0,R).$$

Thus (2.31) is satisfied for $t \geq s$. We can prove (2.32) for $t \geq s$ analogously. Then we put $x = y$ and we conclude taking $\theta < \frac{\eta}{B}$.

## 2.4 Regularity results for equations (2.3)–(2.4)

In this section we study the regularity properties of $u_\epsilon = \epsilon \ln n_\epsilon$, where $n_\epsilon$ is the unique solution of equations (2.3)–(2.4) as given in Theorem 2.2.2. From equation (2.3) we deduce that $u_\epsilon$ is a solution to the following equation

$$\begin{cases} \partial_t u_\epsilon = R(x, I_\epsilon(t)) + \int K(z) b(x+\epsilon z, I_\epsilon) e^{\frac{u_\epsilon(t,x+\epsilon z) - u_\epsilon(t,x)}{\epsilon}} dz, & x \in \mathbb{R},\ t \geq 0, \\ u_\epsilon(t=0) = \epsilon \ln n_\epsilon^0. \end{cases} \tag{2.34}$$

We have the following regularity results for $u_\epsilon$.

**Theorem 2.4.1** *Let $n_\epsilon$ be the solution of (2.3)–(2.4) with $n_\epsilon^0 = e^{\frac{u_\epsilon^0}{\epsilon}}$, and $u_\epsilon = \epsilon \ln(n_\epsilon)$. With the assumptions (2.8)–(2.13), and if we assume that $(u_\epsilon^0)_\epsilon$ is a sequence of uniformly bounded functions in $W^{1,\infty}$, then $u_\epsilon$ are locally uniformly bounded and Lipschitz in $[0,\infty[\times\mathbb{R}^d$.*

As in section 2.3 we prove Theorem 2.4.1 in several steps. We first prove an upper and a lower bound on $u_\epsilon$, then local Lipschitz bounds in space and finally a regularity result in time.

### 2.4.1 Upper and lower bounds on $u_\epsilon$

From assumption (2.9) we have $u_\epsilon^0(x) \le -A|x| + B$. As in section 2.3.1 we claim that

$$u_\epsilon(t,x) \le -A|x| + B + Ct, \ \ \forall t \ge 0. \tag{2.35}$$

Define $v(t,x) = -A|x| + B + Ct$, where $C = b_M \int K(z) e^{A|z|} dz + K_2$. Using (2.8) and (2.11) we have

$$\partial_t v - R(x, I_\epsilon(t)) - \int K(z) b(x+\epsilon z, I_\epsilon) e^{\frac{v(t,x+\epsilon z)-v(t,x)}{\epsilon}} dz \ge C - K_2 - b_M \int K(z) e^{A|z|} dz \ge 0.$$

We also have $v(0,x) = -A|x| + B \ge u_\epsilon^0(x)$. So $v$ is a supersolution to (2.34). Since (2.3) verifies the comparison property, equation (2.34) verifies also the comparison property, i.e. if $v$ and $u$ are respectively super and subsolutions of (2.34) then $u \le v$. Thus (2.35) is proved.

To prove a lower bound on $u_\epsilon$ we assume that $u_\epsilon^0$ are locally uniformly bounded. Then from equation (2.34) and assumption (2.8) we deduce

$$\partial_t u_\epsilon(t,x) \ge -K_2,$$

and thus

$$u_\epsilon(t,x) \ge -\|u_\epsilon^0\|_{L^\infty(\mathrm{B}(0,R))} - K_2 t, \quad \forall x \in \mathrm{B}(0,R).$$

Moreover, $|\nabla u_\epsilon^0|$ being bounded, we can give a lower bound in $\mathbb{R}^d$

$$u_\epsilon(t,x) \ge \inf_\epsilon u_\epsilon^0(0) - \|\nabla u_\epsilon^0\|_{L^\infty} |x| - K_2 t, \quad \forall x \in \mathbb{R}^d. \tag{2.36}$$

### 2.4.2 Lipschitz bounds

Here we assume that $u_\epsilon$ is differentiable in $x$ (See [36]). See also Appendix 2.6.3 for a proof without any regularity assumptions on $u_\epsilon$.

Let $p_\epsilon = \nabla u_\epsilon \cdot \chi$, where $\chi$ is a fixed unit vector. By differentiating (2.34) with respect to $\chi$ we obtain

$$\begin{aligned} \partial_t p_\epsilon(t,x) = \nabla R(x, I_\epsilon(t)) \cdot \chi + \int K(z) \nabla b(x+\epsilon z, I_\epsilon) \cdot \chi \, e^{\frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}} dz \\ + \int K(z) b(x+\epsilon z, I_\epsilon) \frac{p_\epsilon(t,x+\epsilon z) - p_\epsilon(t,x)}{\epsilon} e^{\frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}} dz. \end{aligned}$$

Thus, using assumptions (2.8) and (2.11), we have

$$\begin{aligned} \partial_t p_\epsilon(t,x) \le K_2 + L_1 \int K(z) b(x+\epsilon z, I_\epsilon) e^{\frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}} dz \\ + \int K(z) b(x+\epsilon z, I_\epsilon) \frac{p_\epsilon(t,x+\epsilon z) - p_\epsilon(t,x)}{\epsilon} e^{\frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}} dz. \end{aligned} \tag{2.37}$$

Define $w_\epsilon(t,x) = p_\epsilon(t,x) + L_1 u_\epsilon(t,x)$ and $\Delta_\epsilon(t,x,z) = \frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}$. From (2.37) and (2.34) we deduce

$$\begin{aligned}
&\partial_t w_\epsilon - K_2(1+L_1) - \int K(z)b(x+\epsilon z, I_\epsilon)\frac{w_\epsilon(t,x+\epsilon z)-w_\epsilon(t,x)}{\epsilon}e^{\Delta_\epsilon(t,x,z)}dz\\
&\leq 2L_1\int K(z)b(x+\epsilon z, I_\epsilon)e^{\Delta_\epsilon(t,x,z)}dz\\
&- L_1\int K(z)b(x+\epsilon z, I_\epsilon)\Delta_\epsilon(t,x,z)e^{\Delta_\epsilon(t,x,z)}dz\\
&= L_1\int K(z)b(x+\epsilon z, I_\epsilon)e^{\Delta_\epsilon(t,x,z)}\big(2-\Delta_\epsilon(t,x,z)\big)dz\\
&\leq L_1 b_M e,
\end{aligned}$$

noticing that $e$ is the maximum of the function $g(t) = e^t(2-t)$ in $\mathbb{R}$. Therefore by the maximum principle, with $C_1 = K_2(1+L_1) + L_1 b_M e$, we have

$$w_\epsilon(t,x) \leq C_1 t + \max_{\mathbb{R}^d} w_\epsilon(0,x).$$

It follows that

$$\begin{aligned}
p_\epsilon(t,x) &\leq C_1 t + \parallel \nabla u_\epsilon^0 \parallel_{L^\infty} + L_1(B+Ct) + L_1\big(\|\nabla u_\epsilon^0\|_{L^\infty}|x| + K_2 t - u_\epsilon^0(x=0)\big) \qquad (2.38)\\
&= C_2 t + C_3|x| + C_4,
\end{aligned}$$

where $C_2$, $C_3$ and $C_4$ are constants. Since this bound is true for any $|\chi| = 1$, we obtain a local bound on $|\nabla u_\epsilon|$.

### 2.4.3 Regularity in time

In section 2.4.2 we proved that $u_\epsilon$ is locally uniformly Lipschitz in space. From this we can deduce that $\partial_t u_\epsilon$ is also locally uniformly bounded.

Let $\mathcal{C} = [0,T] \times \mathrm{B}(x_0,R)$ and $S_1$ be a constant such that $\parallel u_\epsilon \parallel_{L^\infty(\mathcal{C})} < S_1$ for all $\epsilon > 0$. Assume that $R'$ is a constant large enough such that we have $u_\epsilon(t,x) < -S_1$ in $[0,T] \times \mathbb{R}^d \backslash \mathrm{B}(x_0,R')$. According to (2.35) there exists such constant $R'$. We choose a constant $S_2$ such that $\parallel \nabla u_\epsilon \parallel_{L^\infty([0,T]\times \mathrm{B}(x_0,R'))} < S_2$ for all $\epsilon > 0$. We deduce

$$\begin{aligned}
|\partial_t u_\epsilon| &\leq |R(x, I_\epsilon(t))| + \int K(z)b(x+\epsilon z, I_\epsilon)e^{\frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}}\big(\mathbb{1}_{|x+\epsilon z|<R'} + \mathbb{1}_{|x+\epsilon z|\geq R'}\big)dz\\
&\leq K_2 + b_M\int K(z)e^{S_2|z|}\mathbb{1}_{|x+\epsilon z|<R'}dz + b_M\int K(z)\mathbb{1}_{|x+\epsilon z|\geq R'}dz\\
&\leq K_2 + b_M\big(1 + \int K(z)e^{S_2|z|}dz\big).
\end{aligned}$$

This completes the proof of Theorem 2.4.1.

## 2.5 Asymptotic behavior of $u_\epsilon$

Using the regularity results in sections 2.3 and 2.4, we can now describe the asymptotic behavior of $u_\epsilon$ and prove Theorems 2.1.1 and 2.1.2. Here we prove Theorem 2.1.1. The proof of Theorem 2.1.2 is analogous, except the limit of the integral term in equation (2.16). The latter has been studied in [50, 19, 11, 102].

**Proof**. [Proof of theorem 2.1.1]

**step 1 (Limit)** According to section 2.3, $u_\epsilon$ are locally uniformly bounded and continuous. So by Arzela-Ascoli Theorem after extraction of a subsequence, $u_\epsilon$ converges locally uniformly to a continuous function $u$.

**step 2 (Initial condition)** We proved that if $u_\epsilon^0$ are uniformly continuous then $u_\epsilon$ will be locally uniformly bounded and continuous in $[0,T]\times\mathbb{R}^d$. Thus we can apply Arzela-Ascoli near $t=0$ as well. Therefore we have $u(0,x)=\lim\limits_{\epsilon\to 0}u_\epsilon(0,x)=u^0(x)$.

**step 3** $\big(\max\limits_{x\in\mathbb{R}^d}u=0\big)$ Assume that for some $t,x$ we have $0<a\leq u(t,x)$. Since $u$ is continuous $u(t,y)\geq\frac{a}{2}$ on $\mathrm{B}(x,r)$, for some $r>0$. Thus we have $n_\epsilon(t,y)\to\infty$, while $\epsilon\to 0$. Therefore $I_\epsilon(t)\to\infty$ while $\epsilon\to 0$. This is a contradiction with (2.18).

To prove that $\max\limits_{x\in\mathbb{R}^d}u(t,x)=0$, it suffices to show that $\lim\limits_{\epsilon\to 0}n_\epsilon(t,x)\neq 0$, for some $x\in\mathbb{R}^d$. From (2.26) we have

$$u_\epsilon(t,x)\leq -A|x|+B+Ct.$$

It follows that for $M$ large enough

$$\lim_{\epsilon\to 0}\int_{|x|>M}n_\epsilon(t,x)dx\leq\lim_{\epsilon\to 0}\int_{|x|>M}e^{\frac{-A|x|+B+Ct}{\epsilon}}=0. \tag{2.39}$$

From this and (2.18) we deduce

$$\lim_{\epsilon\to 0}\int_{|x|\leq M}n_\epsilon(t,x)dx\geq\frac{I'_m}{\psi_M}.$$

If $u(t,x)<0$ for all $|x|<M$ then $\lim\limits_{\epsilon\to 0}e^{\frac{u_\epsilon(t,x)}{\epsilon}}=0$ and thus $\lim\limits_{\epsilon\to 0}\int_{|x|\leq M}n_\epsilon(t,x)dx=0$. This is a contradiction with (2.39). It follows that $\max\limits_{x\in\mathbb{R}^d}u(t,x)=0,\quad\forall t>0$.

**step 4** ($supp\ n(t,\cdot)\subset\{u(t,\cdot)=0\}$) Assume that $u(t_0,x_0)=-a<0$. Since $u_\epsilon$ are uniformly continuous in a small neighborhood of $(t_0,x_0)$, $(t,x)\in[t_0-\delta,t_0+\delta]\times\mathrm{B}(x_0,\delta)$, we have $u_\epsilon(t,x)\leq-\frac{a}{2}<0$ for $\epsilon$ small. We deduce that $\int_{[t_0-\delta,t_0+\delta]\times\mathrm{B}(x_0,\delta)}n\,dtdx=\int_{[t_0-\delta,t_0+\delta]\times\mathrm{B}(x_0,\delta)}\lim\limits_{\epsilon\to 0}e^{\frac{u_\epsilon(t,x)}{\epsilon}}dtdx=0$. Therefore we have $supp\ n(t,\cdot)\subset\{u(t,\cdot)=0\}$ for almost every $t$.

**step 5 (Limit equation)** Finally we recall, following [103], how to pass to the limit in the equation. Since $u_\epsilon$ is a solution to (2.24), it follows that $\phi_\epsilon(t,x)=u_\epsilon(t,x)-\int_0^t R(x,I_\epsilon(s))ds$ is a solution to the following equation

$$\begin{aligned}\partial_t\phi_\epsilon(t,x)-\epsilon\triangle\phi_\epsilon(t,x)-|\nabla\phi_\epsilon(t,x)|^2-2\nabla\phi_\epsilon(t,x)\cdot\int_0^t\nabla R(x,I_\epsilon(s))ds\\=\epsilon\int_0^t\triangle R(x,I_\epsilon(s))ds+|\int_0^t\nabla R(x,I_\epsilon(s))ds|^2.\end{aligned}$$

Note that we have $I_\epsilon(s)\to I(s)$ for all $s\geq 0$ as $\epsilon$ goes to 0, and on the other hand, the function $R(x,I)$ is smooth. It follows that we have the locally uniform limits

$$\lim_{\epsilon\to 0}\int_0^t R(x,I_\epsilon(s))ds=\int_0^t R(x,I(s))ds,$$

$$\lim_{\epsilon\to 0}\int_0^t \nabla R(x,I_\epsilon(s))ds = \int_0^t \nabla R(x,I(s))ds,$$
$$\lim_{\epsilon\to 0}\int_0^t \triangle R(x,I_\epsilon(s))ds = \int_0^t \triangle R(x,I(s))ds,$$

for all $t\geq 0$. Moreover the functions $\int_0^t R(x,I(s))ds$, $\int_0^t \nabla R(x,I(s))ds$ and $\int_0^t \triangle R(x,I(s))ds$ are continuous. According to step 1, $u_\epsilon(t,x)$ converge locally uniformly to the continuous function $u(t,x)$ as $\epsilon$ vanishes. Therefore $\phi_\epsilon(t,x)$ converge locally uniformly to the continuous function $\phi(t,x)=u(t,x)-\int_0^t R(x,I(s))ds$ as $\epsilon$ vanishes. It follows that $\phi(t,x)$ is a viscosity solution to the equation

$$\partial_t\phi(t,x)-|\nabla\phi(t,x)|^2-2\nabla\phi(t,x)\cdot\int_0^t \nabla R(x,I(s))ds$$
$$=|\int_0^t \nabla R(x,I)ds|^2.$$

In other words $u(t,x)$ is a viscosity solution to the following equation

$$\partial_t u(t,x)=|\nabla u(t,x)|^2+R(x,I(t)).$$

## 2.6 Appendix

### 2.6.1 Proof of theorem 2.2.1

**Existence**

Let $T>0$ be given and A be the following closed subset:

$$\mathrm{A}=\{u\in \mathrm{C}\big([0,T],L^1(\mathbb{R}^d)\big),\ u\geq 0,\ \|\ u(t,\cdot)\ \|_{L^1}\leq a\},$$

where $a=\left(\int n_\epsilon^0 dx\right)e^{\frac{K_2T}{\epsilon}}$. Let $\Phi$ be the following application:

$$\Phi:\mathrm{A}\to\mathrm{A}$$
$$u\mapsto v,$$

where $v$ is the solution to the following equation

$$\begin{cases}\partial_t v-\epsilon\triangle v=\frac{v}{\epsilon}\bar{R}(x,I_u(t)), & x\in\mathbb{R},\ t\geq 0,\\ v(t=0)=n_\epsilon^0.\end{cases}\tag{2.40}$$

$$I_u(t)=\int_{\mathbb{R}^d}\psi(x)u(t,x)dx,\tag{2.41}$$

and $\bar{R}$ is defined as below

$$\bar{R}(x,I)=\begin{cases}R(x,I) & \text{if } \frac{I_m}{2}<I<2I_M,\\ R(x,2I_M) & \text{if } 2I_M\leq I,\\ R(x,\frac{I_m}{2}) & \text{if } I\leq\frac{I_m}{2}.\end{cases}$$

We prove that

1. $\Phi$ defines a mapping of $A$ into itself,

2. $\Phi$ is a contraction for $T$ small.

With these properties, we can apply the Banach-Picard fixed point theorem and iterate the construction with $T$ fixed.

Assume that $u \in \mathrm{A}$. In order to prove (a) we show that $v$, the solution to (2.40), belongs to A. By the maximum principle we know that $v \geq 0$. To prove the $L^1$ bound we integrate (2.40)

$$\frac{d}{dt}\int v dx = \int \frac{v}{\epsilon}\bar{R}(x, I_u(t))dx \leq \frac{1}{\epsilon}\max_{x\in\mathbb{R}^d}\bar{R}(x, I_u(t))\int v dx \leq \frac{K_2}{\epsilon}\int v dx,$$

and we conclude from the Gronwall Lemma that

$$\| v \|_{L^1} \leq \left(\int n_\epsilon^0 dx\right) e^{\frac{K_2 T}{\epsilon}} = a.$$

Thus (a) is proved. It remains to prove (b). Let $u_1,\ u_2 \in \mathrm{A}$, $v_1 = \Phi(u_1)$ and $v_2 = \Phi(u_2)$. We have

$$\partial_t(v_1 - v_2) - \epsilon\triangle(v_1 - v_2) = \frac{1}{\epsilon}\left[(v_1 - v_2)\bar{R}(x, I_{u_1}) + v_2\left(\bar{R}(x, I_{u_1}) - \bar{R}(x, I_{u_2})\right)\right].$$

Noting that $\| v_2 \|_{L^1} \leq a$, and $|\bar{R}(x, I_{u_1}) - \bar{R}(x, I_{u_2})| \leq K_1|I_{u_1} - I_{u_2}| \leq K_1\psi_M \| u_1 - u_2 \|_{L^1}$ we obtain

$$\frac{d}{dt}\| v_1 - v_2 \|_{L^1} \leq \frac{K_2}{\epsilon}\| v_1 - v_2 \|_{L^1} + \frac{aK_1\psi_M}{\epsilon}\| u_1 - u_2 \|_{L^1}.$$

Using $v_1(0,\cdot) = v_2(0,\cdot)$ we deduce

$$\| v_1 - v_2 \|_{L_t^\infty L_x^1} \leq \frac{aK_1\psi_M}{K_2}(e^{\frac{K_2 T}{\epsilon}} - 1)\| u_1 - u_2 \|_{L_t^\infty L_x^1}.$$

Thus, for $T$ small enough such that $e^{\frac{K_2 T}{\epsilon}}(e^{\frac{K_2 T}{\epsilon}} - 1) < \frac{K_2}{2K_1\psi_M\int n_\epsilon^0}$, $\Phi$ is a contraction. Therefore $\Phi$ has a fixed point and there exists $n_\epsilon \in \mathrm{A}$ a solution to the following equation

$$\begin{cases}\partial_t n_\epsilon - \epsilon\triangle n_\epsilon = \frac{n_\epsilon}{\epsilon}\bar{R}(x, I(t)), & x \in \mathbb{R},\ 0 \leq t \leq T,\\ n_\epsilon(t=0) = n_\epsilon^0.\end{cases}$$

$$I(t) = \int_{\mathbb{R}^d}\psi(x)n_\epsilon(t,x)dx,$$

With the same arguments as 2.6.1 we prove that $\frac{I_m}{2} < I(t) < 2I_M$ and thus $n_\epsilon$ is a solution to equations (2.1)–(2.2) for $t \in [0,T]$. We fix $T$ small enough such that $e^{\frac{K_2 T}{\epsilon}}(e^{\frac{K_2 T}{\epsilon}} - 1) < \frac{K_2\psi_m}{4K_1\psi_M I_M}$. Then we can iterate in time and find a global solution to equations (2.1)–(2.2).

### Uniform bounds on $I_\epsilon(t)$

We have

$$\frac{dI_\epsilon}{dt} = \frac{d}{dt}\int_{\mathbb{R}^d}\psi(x)n_\epsilon(t,x)dx = \epsilon\int_{\mathbb{R}^d}\psi(x)\triangle n_\epsilon(t,x)dx + \frac{1}{\epsilon}\int_{\mathbb{R}^d}\psi(x)n_\epsilon(t,x)R(x, I_\epsilon(t))dx.$$

We define $\psi_L = \chi_L \cdot \psi \in \mathbf{W}^{\infty}_{2,c}(\mathbb{R}^d)$, where $\chi_L$ is a smooth function with a compact support such that $\chi_L|_{\mathrm{B}(0,L)} \equiv 1$, $\chi_L|_{\mathbb{R}\setminus \mathrm{B}(0,2L)} \equiv 0$. Then by integration by parts we find

$$\int_{\mathbb{R}^d} \psi_L(x) \triangle n_\epsilon(t,x)dx = \int_{\mathbb{R}^d} \triangle \psi_L(x) n_\epsilon(t,x)dx.$$

As $L \to \infty$, $\psi_L$ converges to $\psi$ in $W^{2,\infty}_{\mathrm{loc}}(\mathbb{R}^d)$. Therefore we obtain

$$\lim_{L\to\infty} \int_{\mathbb{R}^d} \triangle \psi_L(x) n_\epsilon dx = \int_{\mathbb{R}^d} \triangle \psi(x) n_\epsilon dx,$$
$$\lim_{L\to\infty} \int_{\mathbb{R}^d} \psi_L(x) \triangle n_\epsilon(t,x)dx = \int_{\mathbb{R}^d} \psi(x) \triangle n_\epsilon(t,x)dx.$$

From these calculations we conclude

$$\frac{dI_\epsilon}{dt} = \epsilon \int_{\mathbb{R}^d} \triangle \psi(x) n_\epsilon(t,x)dx + \frac{1}{\epsilon}\int_{\mathbb{R}^d} \psi(x) n_\epsilon(t,x) R(x, I_\epsilon(t))dx.$$

It follows that

$$-\epsilon \frac{C_1}{\psi_m} I_\epsilon + \frac{1}{\epsilon} I_\epsilon \min_{x\in\mathbb{R}^d} R(x,I_\epsilon) \leq \frac{dI_\epsilon}{dt} \leq \epsilon \frac{C_1}{\psi_m} I_\epsilon + \frac{1}{\epsilon} I_\epsilon \max_{x\in\mathbb{R}^d} R(x,I_\epsilon).$$

Let $C = \frac{C_1 K_1}{\psi_m}$. As soon as $I_\epsilon$ overpasses $I_M + C\epsilon^2$, we have $R(x, I_\epsilon) < -\frac{C\epsilon^2}{K_1} = -\epsilon^2 \frac{C_1}{\psi_m}$ and thus $\frac{dI_\epsilon}{dt}$ becomes negative. Similarly, as soon as $I_\epsilon$ becomes less than $I_m - C\epsilon^2$, $\frac{dI_\epsilon}{dt}$ becomes positive. Thus (2.18) is proved.

### 2.6.2 A locally uniform BV bound on $I_\epsilon$ for equations (2.3)–(2.4)

In this appendix we prove Theorem 2.2.4. We first integrate (2.3) over $\mathbb{R}^d$ to obtain

$$\frac{d}{dt} I_\epsilon(t) = \frac{1}{\epsilon} \int n_\epsilon(t,x) \big( R\left(x, I_\epsilon(t)\right) + b\left(x, I_\epsilon(t)\right) \big) dx.$$

Define $J_\epsilon(t) = \frac{d}{dt} I_\epsilon(t)$. We differentiate $J_\epsilon$ and we obtain

$$\begin{aligned}\frac{d}{dt} J_\epsilon(t) = {} & \frac{1}{\epsilon} J_\epsilon(t) \int n_\epsilon(t,x) \frac{\partial (R+b)}{\partial I}(x, I_\epsilon(t))dx \\ & + \frac{1}{\epsilon^2} \int \big(R(x,I_\epsilon) + b(x,I_\epsilon)\big)\big[ n_\epsilon(t,x)R(x,I_\epsilon) + \int K_\epsilon(y-x) b(y,I_\epsilon) n_\epsilon(t,y)dy \big] dx.\end{aligned}$$

We rewrite this equality in the following form

$$\begin{aligned}\frac{d}{dt} J_\epsilon(t) = {} & \frac{1}{\epsilon} J_\epsilon(t) \int n_\epsilon(t,x) \frac{\partial (R+b)}{\partial I}\big(x, I_\epsilon(t)\big)dx + \frac{1}{\epsilon^2} \int n_\epsilon(t,x) \Big( R\big(x, I_\epsilon(t)\big) + b\big(x, I_\epsilon(t)\big)\Big)^2 dx \\ & + \frac{1}{\epsilon^2} \int\int K_\epsilon(y-x) \Big( R\big(x, I_\epsilon(t)\big) - R\big(y, I_\epsilon(t)\big)\Big) b\big(y, I_\epsilon(t)\big) n_\epsilon(t,y) dy dx \\ & + \frac{1}{\epsilon^2} \int\int K_\epsilon(y-x) \Big( b\big(x, I_\epsilon(t)\big) - b\big(y, I_\epsilon(t)\big)\Big) b\big(y, I_\epsilon(t)\big) n_\epsilon(t,y) dy dx.\end{aligned}$$

It follows that

$$\begin{aligned}\frac{d}{dt}J_\epsilon(t) \geq & \frac{1}{\epsilon}J_\epsilon(t)\int n_\epsilon(t,x)\frac{\partial(R+b)}{\partial I}\big(x,I_\epsilon(t)\big)dx + \frac{1}{\epsilon^2}\int n_\epsilon(t,x)\Big(R\big(x,I_\epsilon(t)\big)+b\big(x,I_\epsilon(t)\big)\Big)^2 dx \\ & - \frac{K_2+b_M\,L_1}{\epsilon}\int\int K(z)|z|b\big(x+\epsilon z,I_\epsilon(t)\big)n_\epsilon(t,x+\epsilon z)dzdx \\ \geq & \frac{1}{\epsilon}J_\epsilon(t)\int n_\epsilon(t,x)\frac{\partial(R+b)}{\partial I}\big(x,I_\epsilon(t)\big)dx + \frac{1}{\epsilon^2}\int n_\epsilon(t,x)\Big(R\big(x,I_\epsilon(t)\big)+b\big(x,I_\epsilon(t)\big)\Big)^2 dx - \frac{C_1}{\epsilon},\end{aligned}$$

where $C_1$ is a positive constant. Consequently, using (2.13) we obtain

$$\frac{d}{dt}(J_\epsilon(t))_- \leq \frac{C_1}{\epsilon} - \frac{C_2}{\epsilon}(J_\epsilon(t))_-,$$

with $(J_\epsilon(t))_- = \max(0,-J_\epsilon(t))$. From this inequality we deduce

$$(J_\epsilon(t))_- \leq \frac{C_1}{C_2} + (J_\epsilon(0))_- e^{-\frac{C_2 t}{\epsilon}}.$$

With similar arguments we obtain

$$(J_\epsilon(t))_+ \geq -\frac{C_1'}{C_2'} + (J_\epsilon(0))_+ e^{-\frac{C_2' t}{\epsilon}},$$

with $(J_\epsilon(t))_+ = \max(0,J_\epsilon(t))$. Thus (2.22) is proved. Finally, we deduce the locally uniform BV bound (2.23)

$$\begin{aligned}\int_0^T |\frac{d}{dt}I_\epsilon(t)|dt &= \int_0^T \frac{d}{dt}I_\epsilon(t)dt + 2\int_0^T (\frac{d}{dt}I_\epsilon(t))_- dt \\ &\leq I_M - I_m + 2C'T + O(1).\end{aligned}$$

### 2.6.3 Lipschitz bounds for equations (2.3)–(2.4)

Here we prove that $u_\epsilon$ are locally uniformly Lipschitz without assuming that the latter are differentiable. The proof follows the same ideas as in section 2.4.2.

Let $\overline{c} = \frac{2L_1 b_M}{b_m}$. From (2.34) we have

$$\begin{aligned}&\partial_t\big(u_\epsilon(t,x+h)-u_\epsilon(t,x)+\overline{c}h\big(2u_\epsilon(t,x+h)-u_\epsilon(t,x)\big)\big) - (1+2\overline{c}h)R(x+h,I_\epsilon) + (1+\overline{c}h)R(x,I_\epsilon) \\ &= \int K(z)b(x+h+\epsilon z,I_\epsilon)e^{\frac{u_\epsilon(t,x+h+\epsilon z)-u_\epsilon(t,x+h)}{\epsilon}}dz - \int K(z)b(x+\epsilon z,I_\epsilon)e^{\frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}}dz \\ &+ \overline{c}h\Big(\int K(z)2b(x+h+\epsilon z,I_\epsilon)e^{\frac{u_\epsilon(t,x+h+\epsilon z)-u_\epsilon(t,x+h)}{\epsilon}}dz - \int K(z)b(x+\epsilon z,I_\epsilon)e^{\frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}}dz\Big)\end{aligned}$$

Define $\alpha = \frac{u_\epsilon(t,x+\epsilon z)-u_\epsilon(t,x)}{\epsilon}$, $\beta = \frac{u_\epsilon(t,x+h+\epsilon z)-u_\epsilon(t,x+h)}{\epsilon}$, $\varDelta(t,x) = 2u_\epsilon(t,x+h)-u_\epsilon(t,x)$ and $w_\epsilon(t,x) = \frac{u_\epsilon(t,x+h)-u_\epsilon(t,x)}{h} + \overline{c}\varDelta(t,x)$. Using the convexity inequality

$$e^\beta \leq e^\alpha + e^\beta(\beta-\alpha),$$

we deduce

$$\begin{aligned}
&h\partial_t w_\epsilon(t,x) - (1+2\overline{c}h)R(x+h,I_\epsilon) + (1+\overline{c}h)R(x,I_\epsilon)\\
&\quad\leq \int K(z)b(x+h+\epsilon z,I_\epsilon)\big(e^\alpha + e^\beta(\beta-\alpha)\big)dz - \int K(z)b(x+\epsilon z,I_\epsilon)e^\alpha dz\\
&\quad+ \overline{c}h\Big(\int 2K(z)b(x+h+\epsilon z,I_\epsilon)e^\beta dz - \int K(z)b(x+\epsilon z,I_\epsilon)e^\alpha dz\Big)\\
&\quad\leq \int K(z)\big(b(x+h+\epsilon z,I_\epsilon) - b(x+\epsilon z,I_\epsilon)\big)e^\alpha dz\\
&\quad+ \int K(z)b(x+h+\epsilon z,I_\epsilon)e^\beta\big(\beta-\alpha+\overline{c}h\frac{\Delta(t,x+\epsilon z)-\Delta(t,x)}{\epsilon}\big)dz\\
&\quad+ \overline{c}h\int K(z)b(x+h+\epsilon z,I_\epsilon)e^\beta(2-2\beta+\alpha)dz - \overline{c}h\int K(z)b(x+\epsilon z,I_\epsilon)e^\alpha dz.
\end{aligned}$$

From assumptions (2.8) and (2.11) it follows that

$$\begin{aligned}
\partial_t w_\epsilon(t,x) \leq& \int K(z)b(x+h+\epsilon z,I_\epsilon)e^\beta\frac{w_\epsilon(t,x+\epsilon z)-w_\epsilon(t,x)}{\epsilon}dz\\
&+ K_2 + 3\overline{c}K_2 + \int K(z)\big(\overline{c}b_M e^\beta(2-2\beta+\alpha) + (L_1 b_M - \overline{c}b_m)e^\alpha\big)dz.
\end{aligned}$$

Notice that

$$\overline{c}b_M e^\beta(2-2\beta+\alpha) + (L_1 b_M - \overline{c}b_m)e^\alpha = \overline{c}b_M e^\beta(2-2\beta+\alpha) - L_1 b_M e^\alpha,$$

is bounded from above. Indeed if we first maximize the latter with respect to $\beta$ and then with respect to $\alpha$ we obtain

$$\overline{c}b_M e^\beta(2-2\beta+\alpha) - L_1 b_M e^\alpha \leq 2\overline{c}b_M e^{\frac{\alpha}{2}} - L_1 b_M e^\alpha \leq \frac{b_M\overline{c}^2}{L_1}.$$

We deduce

$$\partial_t w_\epsilon(t,x) \leq \int K(z)b(x+h+\epsilon z,I_\epsilon)e^\beta\frac{w_\epsilon(t,x+\epsilon z)-w_\epsilon(t,x)}{\epsilon}dz + G,$$

where $G$ is a constant. Therefore by the maximum principle, (2.35) and (2.36), we have

$$w_\epsilon(t,x) \leq Gt + \parallel \nabla u_\epsilon^0 \parallel_{L^\infty} - 2\overline{c}A|x+h| + 2\overline{c}B - \overline{c}u_\epsilon^0(x=0) + \overline{c} \parallel \nabla u_\epsilon^0 \parallel_{L^\infty} |x|.$$

Using again (2.35) and (2.36) we conclude that

$$\begin{aligned}
\frac{u_\epsilon(t,x+h)-u_\epsilon(t,x)}{h} \leq& (G+2\overline{c}K_2)t + \overline{c}\big(-A + \parallel \nabla u_\epsilon^0 \parallel_{L^\infty}\big)\big(|x| + 2|x+h|\big)\\
&+ 3\overline{c}B + \parallel \nabla u_\epsilon^0 \parallel_{L^\infty} - 3\overline{c}\inf u_\epsilon^0(x=0).
\end{aligned} \tag{2.42}$$

# Chapitre 3

# Modèle singulier pour éviter la queue de distribution

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Le travail présenté ici est issu d'une collaboration avec Guy Barles, Benoît Perthame et Panagiotis E. Souganidis. Nous ajoutons un terme de mortalité aux modèles précédents pour éviter les queues exponentielles de distribution. Il s'agit d'ajouter un seuil de survie, en dessous duquel, la densité s'annule immédiatement. Ceci mène à des inégalités variationnelles de type Hamilton-Jacobi avec obstacle, où l'obstacle dépend de la solution même. Cela définit de plus un ensemble ouvert où la solution limite ne s'annule pas. Des contre-exemples montrent un manque non-trivial d'unicité pour l'inégalité variationnelle, dépendant des conditions imposées aux bords de cet ensemble ouvert. Les deux conditions aux bords de Dirichlet et de contrainte d'état jouent un rôle. Lorsque le terme de compétition ne change pas de signe, nous pouvons identifier la limite, alors que dans le cas général, nous trouvons des bornes inférieures et supérieures pour la limite. Nous montrons notamment que le seuil de mortalité a un impact sur le profil de la population, sauf dans le cas particulier où la compétition est non-positive. En outre, la forme précise de terme de mortalité ne modifie pas la dynamique asymptotique. Ce travail reprend l'article [95].

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## 3.1 Introduction

We consider the following reaction-diffusion equations with a singular reaction term

$$\begin{cases} n_{\varepsilon,t} - \varepsilon \Delta n_\varepsilon = \frac{1}{\varepsilon} n_\varepsilon R - \frac{1}{\varepsilon}\sqrt{\beta_\varepsilon n_\varepsilon} & \text{in } \mathbb{R}^d \times (0,+\infty), \\ n_\varepsilon = e^{u_\varepsilon^0/\varepsilon} \quad \text{on} \quad \mathbb{R}^d \times \{0\}, \end{cases} \tag{3.1}$$

with threshold

$$\beta_\varepsilon = e^{u_m/\varepsilon} \qquad \text{for some} \qquad u_m < 0. \tag{3.2}$$

The parameter $\varepsilon > 0$ is introduced by a hyperbolic scaling with the aim to describe the long time and long range behavior of the unscaled problem (corresponding to $\varepsilon = 1$).

The limiting behavior of scaled reaction-diffusion equations with KPP-type reaction has been studied extensively in, among other places, the theory of front propagation ([9, 117, 56]) using the so called WKB-(exponential) change of the unknown.

The novelty of the problem we are considering here is the negative square root term in the right-hand side. To the best of our knowledge the first study of such nonlinearity goes back to [55] where it is proved that local extinction occurs, i.e., the solution can vanish in a domain and stay positive in another region. That a solution of a parabolic problem can vanish locally is a surprising effect and as singular as the blow-up phenomena for supercritical reactions terms ([108]).

In population biology such behavior prevents the so-called "tail problem" where very small (and thus meaningless) populations can generate artifacts ([60]). Although the mathematical analysis of the limit in (3.1) turns out to be a full subject in itself, our primary motivation comes from qualitative questions in population dynamics.

Along the same lines, in the context of front propagation, one may consider the modified Fisher–KPP equation

$$n_{\varepsilon,t} - \varepsilon \Delta n_\varepsilon = \frac{1}{\varepsilon} n_\varepsilon (1 - n_\varepsilon) - \frac{1}{\varepsilon}\sqrt{\beta_\varepsilon n_\varepsilon} \quad \text{in } \mathbb{R}^d \times (0,+\infty),$$

and ask the question whether the square root term changes fundamentally the study in [56] and [60] of the propagation of the invading/combustion fronts.

An elementary model in adaptive evolution is the non-local reaction-diffusion equation

$$n_{\varepsilon,t} - \varepsilon \Delta n_\varepsilon = \frac{1}{\varepsilon} n_\varepsilon R(x, I_\varepsilon) - \frac{1}{\varepsilon}\sqrt{\beta_\varepsilon n_\varepsilon} \quad \text{in } \mathbb{R}^d \times (0,+\infty),$$

where $n_\varepsilon$ is the population density of individuals with phenotypical trait $x$ and, for $t > 0$,

$$I_\varepsilon(t) = \int \psi(x) n_\varepsilon(x,t) dx.$$

Here $x$ denotes the trait, $R$ represents the net growth rate while $\psi$ is the consumption rate of individuals and $I(t)$ is the total consumption of the resource at time $t$. The survival threshold is as in [60]. Finally $\varepsilon$ may represent large time and rare mutations as introduced in [10, 11, 103].

It is known that under some assumptions the density concentrates as an evolving Dirac mass for the fittest trait. In biological terms this means that one or several dominant traits survive while others become extinct. Some phenomena as the discontinuous jumps of the fittest trait, non smooth branching and fast dynamics compared to stochastic simulations, motivated [60] to improve the model by including a survival threshold. Numerical results confirm that this modification gives dynamics comparable to stochastic models. It is interesting to investigate rigorously whether the dynamics of the Dirac concentration points are really changed by the survival threshold and to explain why its specific form (square root versus $n_\varepsilon^\alpha$ with $0 < \alpha < 1$) seems irrelevant.

A way to approach these questions is through the asymptotic analysis of $n_\varepsilon$. Since, as in the classical case (i.e., the Fisher-KPP equation without the square root term (see [56]), $n_\varepsilon$ decays exponentially, the limit is better described using the Hopf-Cole transformation

$$u_\varepsilon = \varepsilon \ln n_\varepsilon, \tag{3.3}$$

which, for $u^0_\varepsilon = \varepsilon \ln n^0_\varepsilon$, leads to

$$\begin{cases} u_{\varepsilon,t} - \varepsilon\Delta u_\varepsilon - |Du_\varepsilon|^2 = R - \exp\big((2\varepsilon)^{-1}(u_m - u_\varepsilon)\big) \quad \text{in} \quad \mathbb{R}^d \times (0,+\infty), \\ u_\varepsilon = u^0_\varepsilon \quad \text{in } \mathbb{R}^d \times \{0\}. \end{cases} \tag{3.4}$$

Throughout the paper we assume that there exist $C > 0$ and $u^0 \in C^{0,1}(\mathbb{R}^d)$ such that

$$\|R\|_{C^{0,1}} \leq C \quad \text{and} \quad \|u^0\|_{C^{0,1}} \leq C, \tag{3.5}$$

and

$$u^0_\varepsilon \in C(\mathbb{R}^d), \quad u^0_\varepsilon \leq C \qquad u^0_\varepsilon \underset{\varepsilon\to 0}{\longrightarrow} u^0 \quad \text{in} \quad C(\mathbb{R}^d). \tag{3.6}$$

It is easy to see, at least formally, that the $u_\varepsilon$'s converge, as $\varepsilon \to 0$, to some $u$ satisfying, in the viscosity sense ([39]), the Hamilton-Jacobi problem

$$\begin{cases} u_t = |Du|^2 + R \quad \text{in} \quad \Omega \subset \mathbb{R}^d \times (0,\infty), \\ u = -\infty \quad \text{in} \quad \overline{\Omega}^c \cap (\mathbb{R}^d \times (0,\infty)), \\ u \geq u_m \quad \text{in} \quad \overline{\Omega}, \\ u = u^0 \quad \text{in} \quad \overline{\Omega} \cap (\mathbb{R}^d \times \{0\}), \end{cases} \tag{3.7}$$

with the space-time open set $\Omega$ is defined by

$$\Omega = \mathcal{I}nt\,\big\{(x,t) \in \mathbb{R}^d \times (0,\infty) : \lim_{\varepsilon\to 0} u_\varepsilon(x,t) > -\infty\big\}.$$

Note that (3.7) resembles an obstacle problem where the obstacle depends on the solution itself. As a matter of fact the open set $\Omega$ plays an important role and, hence, the problem may be better stated in terms of the pair $(u,\Omega)$. The difficulty is that there are many viscosity solutions (see Appendix 3.7.1 for examples) to this problem and the boundary conditions on $\partial\Omega$ are of real importance.

The "natural" boundary conditions for (3.7) are the Dirichlet and state constraint ones. The former is

$$\lim_{(x,t)\to(x_0,t_0)\in\partial\Omega} u(x,t) = u_m, \tag{3.8}$$

while the latter says (see [116]) that

$$u \quad \text{is a super-solution in} \quad \Omega \text{ and a sub-solution in} \quad \overline{\Omega}\,. \tag{3.9}$$

The basic questions are:

- What boundary condition should be satisfied by the limit of the $u_\varepsilon$'s on $\partial\Omega$? Dirichlet or state constraint ? The latter at least plays a fundamental role. To the best of our knowledge, however, there are no available results for state constraint problems with time varying and non smooth domains. Most of the work in this paper is geared towards going around this difficulty.
- What stability is induced by the selection of the correct solution to (3.7)? Is it the maximal subsolution?
- Does the limit of the $u_\varepsilon$'s depend on the specific form of the survival threshold, i.e., can

we replace $(\beta_\varepsilon n_\varepsilon)^{1/2}$ by $(\beta_\varepsilon n_\varepsilon)^\alpha$ with $\alpha \in (0,1)$ without affecting the limit?

To study (3.1) it is useful to consider the problem

$$\begin{cases} n^1_{\varepsilon,t} - \varepsilon \Delta n^1_\varepsilon = \frac{n^1_\varepsilon}{\varepsilon} R \quad \text{in} \quad \mathbb{R}^d \times (0,+\infty), \\ n^1_\varepsilon = \exp(\varepsilon^{-1} u^0_\varepsilon) \quad \text{in } \mathbb{R}^d \times \{0\}. \end{cases} \tag{3.10}$$

In view of the above assumptions the theory of viscosity solutions yields that the $u^1_\varepsilon$'s defined by

$$u^1_\varepsilon = \varepsilon \ln n^1_\varepsilon, \tag{3.11}$$

converge, as $\varepsilon \to 0$, locally uniformly to $u^1 \in C(\mathbb{R}^d \times (0,\infty))$, the unique solution of the eikonal -type equation

$$\begin{cases} u^1_t = |Du^1|^2 + R \quad \text{in } \ \mathbb{R}^d \times (0,+\infty), \\ u^1 = u^0 \quad \text{in } \ \mathbb{R}^d \times \{0\}. \end{cases} \tag{3.12}$$

The maximum principle yields the comparison $n_\varepsilon \le n^1_\varepsilon$, which in turn implies that $u_\varepsilon \le u^1_\varepsilon$ and, in the limit (this has to be stated more carefully), $u \le u^1$. It also follows from (3.4), at least formally, that, as $\varepsilon \to 0$,

$$u_\varepsilon \to -\infty \qquad \text{in } \ (\mathbb{R}^d \times (0,\infty)) \backslash \overline{\Omega^1},$$

where

$$\Omega^1 = \{(x,t) \mid u^1(x,t) > u_m\}. \tag{3.13}$$

It turns out that the case of nonpositive rate is particularly illuminating and the above questions can be answered completely and positively using $u^1$ (see Section 3.2).

The problem is considerably more complicated when $R$ takes positive values. In this case we introduce an iterative procedure to build successive sub- and super-solutions (Section 3.3). This construction gives the complete limit of $u_\varepsilon$ in the case where $R$ is constant (Section 3.4). It follows that the limit is not the maximal subsolution of (3.7) and the Dirichlet condition is not enough to select it. In Section 3.5, we analyze the case of strictly positive spatially dependent $R$ and provide a complete answer in terms of the iterative procedure. The relative roles of the Dirichlet and state constraint boundary conditions appear clearly in this case. In Appendix we present some examples as well as the proofs of few technical facts used earlier.

We conclude Introduction with the definition and the notation of the half-relaxed limits that we will be using throughout the paper. To this end, if $(w_\varepsilon)_{\varepsilon>0}$ is a family of bounded functions, the upper and lower limits, which are denoted by $\bar{w}$ and $\underline{w}$ respectively, are given by

$$\overline{w}(x) = \limsup_{\varepsilon \to 0, y \to x} w_\varepsilon(y) \qquad \text{and} \qquad \underline{w}(x) = \liminf_{\varepsilon \to 0, y \to x} w_\varepsilon(y). \tag{3.14}$$

## 3.2 Nonpositive growth rate

In this section we assume that

$$R \le 0 \quad \text{in} \quad \mathbb{R}^d. \tag{3.15}$$

When (3.15) holds, the behavior of the $u_\varepsilon$'s, in the limit $\varepsilon \to 0$, can be described completely and the solution $u^1$ of (3.12) carries all the information.

We have:

**Theorem 3.2.1** *Assume (3.5), (3.6) and (3.15). Then, as* $\varepsilon \to 0$*, the* $u_\varepsilon$*'s converge, locally uniformly in* $\Omega^1 \cup (\mathbb{R}^d \backslash \overline{\Omega^1})$*, to*

$$u(x,t) = \begin{cases} u^1(x,t) & \textit{for} \quad (x,t) \in \Omega^1, \\ -\infty & \textit{for} \quad (x,t) \in \mathbb{R}^d \backslash \overline{\Omega^1}, \end{cases} \tag{3.16}$$

*with* $u^1$ *and* $\Omega^1$ *defined by (3.12) and (3.13) respectively. In particular,* $u(x,t) \to u_m$ *as* $(x,t) \to \partial\Omega^1$*.*

Before we begin with the proof we discuss below several observations which are important to explain the meaning of the results.

Firstly, by 'uniform convergence' to $-\infty$, we mean $\limsup_{\varepsilon\to 0, y \to x, s\to t} u_\varepsilon(y,s) = -\infty$.

Secondly, the $u$ associated with the open set $\Omega^1$ is the maximal solution to (3.7). Indeed any other solution $\widetilde{u}$, with the corresponding open set $\widetilde{\Omega}$, satisfies $\widetilde{u} \le u^1$ and thus $\widetilde{\Omega} \subset \Omega^1$ and $\widetilde{u} \le u$. It also satisfies the Dirichlet and state constraint boundary conditions. To verify the latter we notice, using the standard optimal control formula ([81, 57, 2]), that

$$u^1(x,t) = \sup_{\substack{(x(s),s)\in\mathbb{R}^d\times[0,\infty) \\ x(t)=x}} \left\{ \int_0^t \left( -\frac{|\dot{x}(s)|^2}{4} + R(x(s)) \right) ds + u_0(x(0)) \right\}.$$

If $\widetilde{x}(\cdot)$ is an optimal trajectory, the Dynamic Programming Principle implies that, for any $0 < \tau < t$,

$$u^1(x,t) = \int_\tau^t \left( -\frac{|\dot{\widetilde{x}}(s)|^2}{4} + R(\widetilde{x}(s)) \right) ds + u^1(\widetilde{x}(\tau),\tau).$$

Since $R$ is nonpositive, $u^1$ is decreasing along the optimal trajectory. It follows that, if $u^1(x,t) > u_m$, then, for all $0 \le \tau < t$, $u^1(\widetilde{x}(\tau),\tau) > u_m$.

Hence, for all $(x,t) \in \Omega^1$,

$$u(x,t) = \sup_{\substack{(x(s),s)\in\Omega^1 \\ x(t)=x}} \left\{ \int_0^t \left( -\frac{|\dot{x}(s)|^2}{4} + R(x(s)) \right) ds + u_0(x(0)) \right\},$$

and, therefore, $u$ verifies the state constraint condition.

Finally, the limit $u$ does not depend on the details on the extra death term. In particular it is the same for a term like $-n_\varepsilon^\gamma \exp(\varepsilon^{-1}\gamma u_m)$ with $0 < \gamma < 1$.

We continue with the **Proof**. [Proof of Theorem 3.2.1] As already discussed, we know that $u_\varepsilon \le u_\varepsilon^1$ but we cannot obtain directly the other inequality. It is therefore necessary to introduce a pair of auxiliary functions $v_\varepsilon^A$ and $v_\varepsilon^{A,1}$ which converge, as $\varepsilon \to 0$, in $C(\mathbb{R}^d \times (0,\infty))$ to $\max(u^1, -A)$. Using this information for appropriate values of the parameter $A$, we then prove that, as $\varepsilon \to 0$, $u_\varepsilon \to u^1$ locally uniformly in the open set

$$\mathcal{A} = \{(x,t) : \ u^1(x,t) > u_m\}, \tag{3.17}$$

and $u_\varepsilon \to -\infty$ locally uniformly in the open set

$$\mathcal{B} = \{(x,t) : \ u^1(x,t) < u_m\}. \tag{3.18}$$

To this end, for $A$ such that

$$0 < A < -u_m, \tag{3.19}$$

we consider the functions $v_\varepsilon^A$ and $v_\varepsilon^{A,1}$ given by

$$n_\varepsilon + \exp(\frac{-A}{\varepsilon}) = \exp(\frac{v_\varepsilon^A}{\varepsilon}) \quad \text{and} \quad n_\varepsilon^1 + \exp(\frac{-A}{\varepsilon}) = \exp(\frac{v_\varepsilon^{A,1}}{\varepsilon}). \tag{3.20}$$

We have:

**Proposition 3.2.2** *Assume (3.5), (3.6), (3.19) and (3.15). The* $v_\varepsilon^{A,1}$*'s and* $v_\varepsilon^A$*'s converge, as* $\varepsilon \to 0$*, in* $C(\mathbb{R}^d \times [0,\infty))$ *to the unique solution* $v^{A,1}$ *of*

$$\begin{cases} \min\left(v^{A,1} + A, v_t^{A,1} - |Dv^{A,1}|^2 - R\right) = 0 \quad in \quad \mathbb{R}^d \times (0,\infty), \\ \\ v^{A,1} = \max(u^0, -A) \quad on \quad \mathbb{R}^d \times \{0\}. \end{cases} \tag{3.21}$$

*Consequently, as* $\varepsilon \to 0$*, the* $v_\varepsilon^A \to v^{A,1} = \max(u^1, -A)$ *in* $C(\mathbb{R}^d \times [0,\infty))$*.*

We present the proof at the end of this section and next we prove the convergence of the $u_\varepsilon$'s in the sets $\mathcal{A}$ and $\mathcal{B}$. We begin with the former.

To this end fix $(x_0, t_0) \in \mathcal{A}$. By the definition of $\mathcal{A}$ we have $u^1(x_0, t_0) > u_m$ and, hence, we can choose $A$ such that $u^1(x_0, t_0) > -A > u_m$. It follows from Proposition 3.2.2 that, as $\varepsilon \to 0$ and uniformly in any neighborhood of $(x_0, t_0)$,

$$v_\varepsilon^A \to v^{A,1} = \max(-A, u^1) = u^1.$$

Using the latter, the choice of $A$ and the fact that

$$u_\varepsilon = v_\varepsilon^A + \varepsilon \ln(1 - \exp(\varepsilon^{-1}(-A - v_\varepsilon^A))),$$

we deduce that, as $\varepsilon \to 0$, $u_\varepsilon \to u^1$ uniformly in any neighborhood of $(x_0, t_0)$.

Next we consider the limiting behavior in the set $\mathcal{B}$. To this end, observe that, using (3.3), (3.11) and a sub-solution argument, we find $u_\varepsilon \le u_\varepsilon^1$ and, thus, $\overline{u} \le u^1$, and

$$\overline{u} < u_m \quad \text{in} \quad \mathcal{B}.$$

Next assume that, for some $(x_0, t_0) \in \mathcal{B}$, $\overline{u}(x_0, t_0) > -\infty$. Since $\overline{u}$ is upper semi-continuous, there exists a family $(\phi_\alpha)_{\alpha>0}$ of smooth functions such that $\overline{u} - \phi_\alpha$ attains a strict local maximum at some $(x_\alpha, t_\alpha)$ and, as $\alpha \to 0$,

$$(x_\alpha, t_\alpha) \to (x_0, t_0), \quad \overline{u}(x_\alpha, t_\alpha) \ge \overline{u}(x_0, t_0) \quad \text{and} \quad \overline{u}(x_\alpha, t_\alpha) \to \overline{u}(x_0, t_0).$$

It follows that there exists points $(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon})$ such that $u_\varepsilon - \phi_\alpha$ attains a local maximum at $(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon})$, $(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon}) \to (x_\alpha, t_\alpha)$, as $\varepsilon \to 0$, and, in view of (3.4), at $(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon})$,

$$\phi_{\alpha,t} - \varepsilon \Delta \phi_\alpha - |D\phi_\alpha|^2 - R \le -\exp((2\varepsilon)^{-1}(u_m - u_\varepsilon)).$$

Letting $\varepsilon \to 0$ we obtain, at $(x_\alpha, t_\alpha)$,

$$\phi_{\alpha,t} - |D\phi_\alpha|^2 - R \le \limsup_{\varepsilon \to 0} [-\exp((2\varepsilon)^{-1}(u_m - u_\varepsilon(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon})))].$$

The definition of $\overline{u}$ yields

$$\limsup_{\varepsilon \to 0} u_\varepsilon(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon}) \le \overline{u}(x_\alpha, t_\alpha)$$

and, since, for $\alpha$ sufficiently small, $\overline{u}(x, t) < u_m$, we have $\overline{u}(x_\alpha, t_\alpha) < u_m$,

$$\limsup_{\varepsilon \to 0} [-\exp((2\varepsilon)^{-1}(u_m - u_\varepsilon(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon})))] = -\infty$$

and, finally, at $(x_\alpha, t_\alpha)$,

$$\phi_{\alpha,t} - |D\phi_\alpha|^2 - R \le -\infty,$$

which is not possible because $\phi_\alpha$ is a smooth function.

The claim about the uniform convergence on compact is an immediate consequence of the upper semicontinuity of $\overline{u}$ and the previous argument.

We conclude the section with the proof of Proposition 3.2.2. Since it is long, before entering in the details, we briefly describe the main steps. Then we establish that the half relaxed upper and lower limits $\overline{v}^\alpha$ and $\underline{v}^\alpha$ are respectively sub- and super-solutions of (3.21). We conclude by identifying the limit.

We have:

**Proof**. [Proof of Proposition 3.2.2] By the definition of $v_\varepsilon^A$, we have $v_\varepsilon^A > -A$ and, thus, the family $(v_\varepsilon^A)_\varepsilon > 0$ is bounded from below.

To prove an upper bound we first notice that on $\mathbb{R}^d \times \{0\}$

$$v_\varepsilon^A = u_\varepsilon^0 + \varepsilon \ln(1 + e^{\frac{-A-u_\varepsilon^0}{\varepsilon}}) \quad \text{and} \quad v_\varepsilon^A = -A + \varepsilon \ln(1 + e^{\frac{A+u_\varepsilon^0}{\varepsilon}}), \tag{3.22}$$

and, hence,

$$v_\varepsilon^A \le \max(u_\varepsilon^0 + \varepsilon \ln(2), -A + \varepsilon \ln(2)) \quad \text{on} \quad \mathbb{R}^d \times \{0\},$$

and, in view of (3.6),

$$v_\varepsilon^A \le C_A \quad \text{on} \quad \mathbb{R}^d \times \{0\},$$

for $C_A > 0$ such that $\max(-A, u_\varepsilon^0) \le C_A$.

Moreover, since $R \le 0$, we have

$$v_{\varepsilon,t}^A - \varepsilon \Delta v_\varepsilon^A - |Dv_\varepsilon^A|^2 = \frac{n_\varepsilon}{n_\varepsilon + \exp(\frac{-A}{\varepsilon})} R - \frac{\sqrt{\beta_\varepsilon n_\varepsilon}}{n_\varepsilon + \exp(\frac{-A}{\varepsilon})} \le 0 \quad \text{in} \quad \mathbb{R}^d \times (0, \infty). \tag{3.23}$$

It follows from the maximum principle that

$$v_\varepsilon^A \le C_A + \varepsilon \ln(2) \quad \text{in} \quad \mathbb{R}^d \times (0, \infty).$$

Next we show that $\underline{v}^A$ is a super-solution of (3.21). Since $u_m < -A$,

$$0 \le \frac{n_\varepsilon}{n_\varepsilon + \exp(\frac{-A}{\varepsilon})} \le 1,$$

and

$$\frac{\sqrt{\beta_\varepsilon n_\varepsilon}}{n_\varepsilon + \exp(\frac{-A}{\varepsilon})} \le \frac{\sqrt{\beta_\varepsilon n_\varepsilon}}{2\sqrt{n_\varepsilon \exp(\frac{-A}{\varepsilon})}} = \frac{1}{2} \exp(\frac{u_m + A}{2\varepsilon}),$$

as $\varepsilon \to 0$ and uniformly on $\mathbb{R}^d \times (0, \infty)$, we have

$$\frac{\sqrt{\beta_\varepsilon n_\varepsilon}}{n_\varepsilon + \exp(\frac{-A}{\varepsilon})} \to 0. \tag{3.24}$$

From (3.15) and (3.23) we then deduce that, in $\mathbb{R}^d \times (0, \infty)$,

$$v_{\varepsilon,t}^A - \varepsilon \Delta v_\varepsilon^A - |Dv_\varepsilon^A|^2 \ge R - O(\varepsilon), \tag{3.25}$$

while by the definition of $v_\varepsilon^A$ we also have

$$v_\varepsilon^A + A \ge 0. \tag{3.26}$$

Combining (3.25) and (3.26) and using the basic stability properties of the viscosity solutions (see [5]) we find that the lower semi-continuous function $\underline{v}^A$ is a viscosity super-solution of (3.21).

To prove that $\overline{v}^A$ is a sub-solution to (3.21) we assume that, for some smooth $\phi$, $\overline{v}^A - \phi$ has a strict local maximum at $(x_0, t_0)$. It follows that there exists a family, which for notational simplicity we denote again by $\varepsilon$, of points $(x_\varepsilon, t_\varepsilon)_{\varepsilon>0} \in \mathbb{R}^d \times (0,\infty)$ such that $v_\varepsilon^A - \phi$ has a local maximum at $(x_\varepsilon, t_\varepsilon)$, and, as $\varepsilon \to 0$, $(x_\varepsilon, t_\varepsilon) \to (x_0, t_0)$ and $v_\varepsilon^A(x_\varepsilon, t_\varepsilon) \to \overline{v}^A(x_0, t_0)$ (See [5]).

We also know, still using (3.23) and (3.24), that $v_\varepsilon^A$ solves

$$v_{\varepsilon,t}^A - \varepsilon \Delta v_\varepsilon^A - |Dv_\varepsilon^A|^2 = \big(1 - \exp(\frac{-A - v_\varepsilon^A}{\varepsilon})\big)R - O(\varepsilon).$$

It then follows that, at $(x_\varepsilon, t_\varepsilon)$,

$$\phi_t - \varepsilon\Delta\phi - |D\phi|^2 - \big(1 - \exp(\varepsilon^{-1}(-A - v_\varepsilon^A)\big)R \le O(\varepsilon). \tag{3.27}$$

Recall that $\lim_{\varepsilon\to 0} v_\varepsilon^A(x_\varepsilon, t_\varepsilon) = \overline{v}^A(x_0, t_0) \ge -A$. Hence, if $\overline{v}^A(x_0, t_0) > -A$, then

$$\lim_{\varepsilon\to 0} \exp(\varepsilon^{-1}(-A - v_\varepsilon^A(x_\varepsilon, t_\varepsilon))) = 0.$$

From this and (3.27) we deduce that, if $\overline{v}^A(x_0, t_0) > -A$, then, at $(x_0, t_0)$,

$$\phi_t - |D\phi|^2 - R \le 0,$$

and, hence, the claim.

Next we show that $\overline{v}$ and $\underline{v}$ satisfy the appropriate initial conditions. Indeed, in view of (3.6) and (3.22) we know that, as $\varepsilon \to 0$,

$$v_\varepsilon^A \to \max(-A, u^0) \quad \text{on} \quad \mathbb{R}^d \times \{0\}.$$

It also follows from a classical argument in theory of viscosity solutions ([5, 9]) that, on $\mathbb{R}^d \times \{0\}$,

$$\overline{v}^A - \max(-A, u^0) \le 0 \quad \text{and} \quad \underline{v}^A - \max(-A, u^0) \ge 0.$$

Hence $\overline{v}^A$ ($\underline{v}^A$ resp.) satisfies the discontinuous viscosity sub-solution (super-solution resp.) initial condition corresponding to (3.21). (See [5], [9]).

We already know from the definition of $\overline{v}^A$ and $\underline{v}^A$ that

$$\underline{v}^A \le \overline{v}^A,$$

while from the comparison property for (3.21) in the class of semi-continuous viscosity solutions (see [2, 5, 38]) we conclude from the steps above that

$$\overline{v}^A \le \underline{v}^A \quad \text{in} \quad \mathbb{R}^d \times (0,\infty).$$

Hence $\underline{v}^A = \overline{v}^A = v^{A,1}$ is the unique continuous viscosity solution of (3.21) and consequently $v_\varepsilon^A$ and $v_\varepsilon^{A,1}$ converge, as $\varepsilon \to 0$ and locally uniformly, to $v^{A,1}$.

Combining (3.3) and (3.20) we find

$$v_\varepsilon^{A,1} = u_\varepsilon^1 + \varepsilon \ln(1 + e^{\frac{-A-u_\varepsilon^1}{\varepsilon}}) \quad \text{and} \quad v_\varepsilon^{A,1} = -A + \varepsilon \ln(1 + e^{\frac{A+u_\varepsilon^1}{\varepsilon}}).$$

Moreover, from the general Hamilton-Jacobi theory [103, 10] we know that, as $\varepsilon \to 0$, $u_\varepsilon^1 \to u^1$ locally uniformly. Hence, still for $A < -u_m$, we obtain that, as $\varepsilon \to 0$,

$$v_\varepsilon^{A,1} \to \max(u^1, -A) \quad \text{in} \quad \mathbb{R}^d \times [0,\infty).$$

It also follows that the $v_\varepsilon^A$'s converge, as $\varepsilon \to 0$, locally uniformly to $v^{A,1} = \max(u^1, -A)$.

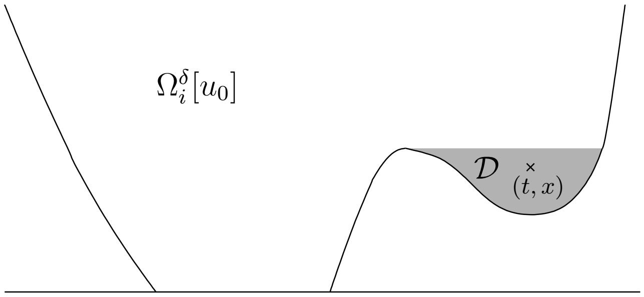

Figure 3.1: An example of the space-time set $\Omega_i^\delta[u_0]$. The point $(x,t) \in \Omega_i^\delta[u^0]$ cannot be connected to 0 by a trajectory $(x(s),s)$ staying within $\Omega_i^\delta[u^0]$. More generally, for the points in the hatched area, called $\mathcal{D}$, there is no admissible trajectory. We have indeed $\mathcal{C}_{i+1}^\delta[u_0] = \Omega_i^\delta[u_0] \setminus \mathcal{D}$.

## 3.3 The limit for general rate

When $R$ changes sign, the situation is much more complicated and (3.16) does not hold in general. In this case we are able to provide only inequalities for the limsup and liminf of the $u_\varepsilon$'s, which we use later to characterize the limit when $R$ is positive.

Given $u_0$, $\delta > 0$ and $u^1$ defined by (3.12) with $u^1 = u_0$ on $\mathbb{R}^d \times \{0\}$, we introduce the family $(u_i^\delta[u_0], \mathcal{C}_i^\delta[u_0], \Omega_i^\delta[u_0])_{i\in\mathbb{Z}^+}$ in $C(\mathbb{R}^d \times [0,\infty)) \times (\mathbb{R}^d \times [0,\infty)) \times (\mathbb{R}^d \times [0,\infty))$ which is defined iteratively as follows:

$$u_1^\delta[u_0] = u^1,\ \mathcal{C}_1^\delta[u_0] = \mathbb{R}^d \times [0,\infty) \ \text{ and } \ \Omega_1^\delta[u_0] = \{(x,t) \in \mathbb{R}^d \times [0,\infty) : u_1^\delta[u_0](x,t) > u_m - \delta\}, \tag{3.28}$$

and, given $u_i^\delta[u_0], \mathcal{C}_i^\delta[u_0]$, and $\Omega_i^\delta[u_0]$, we define

$$u_{i+1}^\delta[u_0](x,t) = \sup_{\substack{(x(s),s)\in\Omega_i^\delta[u_0] \\ x(t)=x}} \int_0^t \left[ -\frac{|\dot{x}(s)|^2}{4} + R(x(s)) \right] ds + u_0(x(0)), \tag{3.29}$$

with the sup taken over only $C^1$-trajectories $s \longmapsto x(s)$,

$$\mathcal{C}_{i+1}^\delta[u_0] = \{(x,t) \in \Omega_i^\delta[u_0] :\ u_{i+1}^\delta[u_0](x,t) > -\infty\}, \tag{3.30}$$

and

$$\Omega_{i+1}^\delta[u_0] = \{(x,t) \in \Omega_i^\delta[u_0] :\ u_{i+1}^\delta[u_0](x,t) > u_m - \delta\} \subset \mathcal{C}_{i+1}^\delta[u_0]. \tag{3.31}$$

It follows from (3.5), (3.28) and the theory of Optimal Control [81, 57, 2, 27] that, for all $i \in \mathbb{Z}^+$, the sets $\mathcal{C}_i^\delta[u_0]$ and $\Omega_i^\delta$ are open and $u_i^\delta[u_0] \in C(\mathcal{C}_i^\delta[u_0])$.

Note that the state constraint boundary condition is hidden in the control formula. On the other hand we do not write it explicitly, because, to the best of our knowledge, there is no general theory, as in [116], for state constraint problem with time varying domains, and, in particular, in this context where we have no regularity properties for these domains.

We notice that in general

$$\mathcal{C}_{i+1}^\delta[u_0] \subsetneq \Omega_i^\delta[u_0].$$

The reason that $\mathcal{C}_{i+1}^\delta[u_0]$ is different from $\Omega_i^\delta[u_0]$ is that there can be points $(\bar{x},\bar{t}) \in \Omega_i^\delta[u_0]$ which cannot be connected to 0 by a trajectory $(x(t),t)$ in $\Omega_i^\delta[u^0]$. (See Figure 3.1.)

It follows from the optimal control theory formula that, given $\mathcal{C}_{i+1}^\delta[u_0]$ from (3.30), $u_{i+1}^\delta[u_0]$ is the minimal viscosity solution to

$$\begin{cases} u_{i+1,t}^\delta[u_0] = |Du_{i+1}^\delta[u_0]|^2 + R \quad \text{in} \quad \mathcal{C}_{i+1}^\delta[u_0], \\ u_{i+1}^\delta[u_0] = u_0 \quad \text{in } \mathcal{C}_{i+1}^\delta[u_0] \cap (\mathbb{R}^d \times \{0\}). \end{cases} \tag{3.32}$$

We refer to [2, 5] for the property that $u^\delta_{i+1}[u_0]$ is a viscosity solution to (3.32). The minimality of $u^\delta_{i+1}[u_0]$ is proved in Appendix 3.7.2.

The sequence $(u^\delta_i[u_0])_{i\in\mathbb{Z}^+}$ is non-increasing. Therefore there exists $U^\delta[u_0] \geq -\infty$, such that, as $i \to +\infty$,

$$u^\delta_i[u_0] \searrow U^\delta[u_0] \quad \text{in} \quad \mathbb{R}^d \times [0,\infty).$$

Let $U[u_0]$ to be the non-increasing limit, as $\delta \to 0$, in $\mathbb{R}^d \times [0,\infty)$

$$U^\delta[u_0] \searrow U[u_0],$$

and, for $\mu > 0$, consider the nonincreasing family of sets

$$\Omega^\delta[u_0] = \bigcap_{i\in\mathbb{Z}^+} \Omega^\delta_i[u_0] \quad \text{and} \quad \Omega[u_0-\mu] = \bigcap_{\delta>0} \Omega^\delta[u_0-\mu]. \tag{3.33}$$

**Theorem 3.3.1** *Let $n_\varepsilon$ the solution to (3.1), $u_\varepsilon = \varepsilon \ln(n_\varepsilon)$, and assume (3.5). Then, for any $\mu > 0$,*

$$\overline{u} \leq U[u_0] \quad \text{in} \quad \mathbb{R}^d \times [0,\infty) \quad \text{and} \quad U[u_0-\mu]+\mu \leq \underline{u} \quad \text{in} \quad \Omega[u_0-\mu]. \tag{3.34}$$

We remark that, by definition, we have $u^\delta_i[u_0] = -\infty$ in $\left(\mathcal{C}^\delta_i[u_0]\right)^c$. Therefore $U^\delta[u_0] = -\infty$ in $(\Omega^\delta[u_0])^c$ and, finally, $U[u_0] = -\infty$ in $(\Omega[u_0])^c = \left(\bigcap_{i,\delta} \mathcal{C}^\delta_i[u_0]\right)^c = \left(\bigcap_\delta \Omega^\delta[u_0]\right)^c$. It follows that

$$\overline{u} = -\infty \quad \text{in} \quad (\Omega[u_0])^c.$$

Moreover, since $u^\delta_i[\cdot] \geq u_m - \delta$ in $\Omega^\delta[\cdot]$, by passing to the limit as $\delta \to 0$ we also obtain

$$U[\cdot] \geq u_m \quad \text{in} \quad \Omega[\cdot].$$

An important question is whether, as $\mu \to 0$, $U[u_0-\mu] \to U[u_0]$. This is wrong in general. A counterexample can be found for $u^0 = u_m$ and $R > 0$. Then $\Omega^\delta_1[u_0-\mu]$ cannot touch $\mathbb{R}^d \times \{0\}$ and $u^\delta_i[u_0-\mu] \equiv -\infty$. Therefore $U[u_0-\mu] \equiv -\infty$, for any positive constant $\mu$. On the other hand $u^\delta_i[u_0] > u_m$ and $U[u_0] = u^1$.

We continue with the

**Proof**. [Proof of Theorem 3.3.1] First we show by induction that, for all $\delta > 0$ and all $i \in \mathbb{Z}^+$, $\overline{u} \leq u^\delta_i[u_0]$.

Since $n^1_\varepsilon$ is a super-solution to (3.1), by the comparison principle, we obtain $n_\varepsilon \leq n^1_\varepsilon$, and, hence, $\overline{u} \leq u^\delta_1[u_0] = u^1$.

Next assume that $\overline{u} \leq u^\delta_i[u_0]$, and, arguing by contradiction, we show, following an argument similar to that in Section 3.2, that $\overline{u} \leq u^\delta_{i+1}[u_0] = -\infty$ in $(\Omega^\delta_i[u_0])^c$.

To this end, suppose that, for some $(x_0,t_0) \in (\Omega^\delta_i[u_0])^c$, $\overline{u}(x_0,t_0) > -\infty$. Since $\overline{u}$ is an upper semi-continuous function, there exists a family $(\phi_\alpha)_{\alpha>o}$ of smooth functions $(\phi_\alpha)_\alpha$ such that $\overline{u}-\phi_\alpha$ attains a strict local maximum at $(x_\alpha,t_\alpha)$ and, as $\alpha \to 0$,t $(x_\alpha,t_\alpha) \to (x_0,t_0)$, $\overline{u}(x_\alpha,t_\alpha) \geq \overline{u}(x_0,t_0)$, and, consequently, $\overline{u}(x_\alpha,t_\alpha) \to u(x_0,t_0)$.
It follows that there exists a family of points $(x_{\alpha,\varepsilon},t_{\alpha,\varepsilon})$ such that $u_\varepsilon - \phi_\alpha$ attains a local maximum at $(x_{\alpha,\varepsilon},t_{\alpha,\varepsilon})$, and, as $\varepsilon \to 0$, $(x_{\alpha,\varepsilon},t_{\alpha,\varepsilon}) \to (x_\alpha,t_\alpha)$.

Moreover, in view of (3.4), at $(x_{\alpha,\varepsilon},t_{\alpha,\varepsilon})$,

$$\phi_{\alpha,t} - \varepsilon\Delta\phi_\alpha - |D\phi_\alpha|^2 - R \leq -\exp((2\varepsilon)^{-1}(u_m - u_\varepsilon)).$$

Letting $\varepsilon \to 0$ yields, at $(x_\alpha,t_\alpha)$,

$$\phi_{\alpha,t} - |D\phi_\alpha|^2 - R \leq \limsup_{\varepsilon\to 0}(-\exp[(2\varepsilon)^{-1}(u_m - u_\varepsilon(x_{\alpha,\varepsilon},t_{\alpha,\varepsilon}))]).$$

Since, by the definition of $\overline{u}$, we have $\limsup_{\varepsilon\to 0} u_\varepsilon(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon}) \leq \overline{u}(x_\alpha, t_\alpha)$, using the assumption of the induction we find that, for $\alpha$ small enough, $\overline{u}(x_\alpha, t_\alpha) \leq u_i^\delta[u_0](x_\alpha, t_\alpha) \leq u_m - \delta/2$.

It follows that

$$\limsup_{\varepsilon\to 0}(-\exp[(2\varepsilon)^{-1}(u_m - u_\varepsilon(x_{\alpha,\varepsilon}, t_{\alpha,\varepsilon}))]) = -\infty,$$

and, hence, at $(x_\alpha, t_\alpha)$,

$$\phi_{\alpha,t} - |D\phi_\alpha|^2 - R \leq -\infty,$$

which, of course, is not possible because $\phi_\alpha$ is a smooth function.

It follows that $\overline{u} = -\infty$ in $(\Omega_i^\delta)^c$ and, in particular, $\overline{u} = -\infty$ on $\partial\Omega_i^\delta[u_0]$.

Next we show that

$$\overline{u} \leq u_{i+1}^\delta[u_0] = -\infty \quad \text{in} \quad (\mathcal{C}_{i+1}^\delta[u_0])^c.$$

To this end, let $(\bar{x}, \bar{t}) \in (\mathcal{C}_{i+1}^\delta[u_0])^c \setminus (\Omega_i^\delta[u_0])^c$. Note that the existence of such a point means that $(\bar{x}, \bar{t})$ cannot be connected to $\mathbb{R}^d \times \{0\}$ by a $C^1$-trajectory staying in $\Omega_i^\delta[u_0]$. Hence $(\bar{x}, \bar{t})$ belongs to a connected component $\mathcal{D}$ of $\omega_i^\delta[u_0] = \{(y, s) \in \Omega_i^\delta[u_0] : s \leq \bar{t}\}$, such that the set $\mathcal{D}$ does not touch $\mathbb{R}^d \times \{0\}$. (See Figure 3.1.)

Therefore $\partial_p\mathcal{D} \subset \partial\Omega_i^\delta[u_0]$, where $\partial_p\mathcal{D} = \{(y, s) \in \partial\mathcal{D} : s < \bar{t}\}$ is the parabolic boundary of $\mathcal{D}$. From the previous argument we obtain

$$\overline{u} = -\infty \qquad \text{on } \partial_p\mathcal{D}. \tag{3.35}$$

As in (3.20), for $A > 0$, we define $w_\varepsilon^A$ by

$$n_\varepsilon + \exp\big(\frac{-A}{\varepsilon}\big) = \exp\big(\frac{w_\varepsilon^A}{\varepsilon}\big).$$

Arguing as in the previous section, we deduce that, for all $A > 0$,

$$\overline{w}^A = \max(-A, \overline{u}) \quad \text{and} \quad \min(\overline{w}^A + A, \overline{w}_t^A - |D\overline{w}^A|^2 - R) \leq 0,$$

and, in view of (3.35), that $\overline{w}^A$ solves the initial value problem

$$\begin{cases} \min(\overline{w}^A + A, \overline{w}_t^A - |D\overline{w}^A|^2 - R) \leq 0 & \text{in} \quad \mathcal{D}, \\ \overline{w}^A = -A \quad \text{in} \quad \partial_p\mathcal{D}, \end{cases}$$

which admits, for some $C_1 > 0$,

$$\phi(x, t) = -A + C_1 t,$$

as a super-solution.

It follows from the comparison principle that, for all $A > 0$,

$$\overline{u} \leq \overline{w}^A \leq -A + C_1 t \quad \text{in} \quad \mathcal{D}.$$

Letting $A \to \infty$ yields $\overline{u} = -\infty$ in $\mathcal{D}$ and, consequently, $\overline{u}(\bar{x}, \bar{t}) = -\infty$. Observe that $\overline{u} = -\infty$ in $(\mathcal{C}_{i+1}^\delta[u_0])^c$ implies that $\overline{u} = -\infty$ on $\partial\mathcal{C}_{i+1}^\delta[u_0] \cap (\mathbb{R}^d \times [0, \infty))$.

Finally we show that

$$\overline{u} \leq u_{i+1}^\delta[u_0] \quad \text{in} \quad \mathcal{C}_{i+1}^\delta[u_0].$$

To this end, define $z_\varepsilon$ by

$$n_\varepsilon + \exp\big(\frac{u^\delta_{i+1}[u_0]}{\varepsilon}\big) = \exp\big(\frac{z_\varepsilon}{\varepsilon}\big),$$

and notice that

$$\overline{z} = \max(\overline{u},\, u^\delta_{i+1}[u_0]).$$

We claim that $\overline{z}$ is a sub-solution of

$$\overline{z}_t - |D\overline{z}|^2 - R \le 0 \quad \text{in} \quad \mathcal{C}^\delta_{i+1}[u_0]. \tag{3.36}$$

We postpone the proof of (3.36) and proceed by noticing that, in view of the above,

$$\overline{u} = -\infty \quad \text{on} \quad \partial\mathcal{C}^\delta_{i+1} \cap (\mathbb{R}^d \times (0,+\infty)).$$

It follows that

$$\overline{z} = u^\delta_{i+1}[u_0] \quad \text{on} \quad \partial\mathcal{C}^\delta_{i+1}[u_0],$$

and, hence,

$$\overline{z} \le u^\delta_{i+1}[u_0] \quad \text{on} \quad \partial\mathcal{C}^\delta_{i+1}[u_0].$$

Therefore, by the comparison principle for (3.32), we obtain

$$\overline{z} \le u^\delta_{i+1}[u_0] \quad \text{in} \quad \mathcal{C}^\delta_{i+1}[u_0],$$

and we conclude that $\overline{u} \le u^\delta_{i+1}[u_0]$.

It remains to prove (3.36). Let $\phi$ be a smooth test function and assume that $\overline{z} - \phi$ achieves a local maximum at $(\bar{x}, \bar{t})$ and, without loss of generality, $\overline{z}(\bar{x},\bar{t}) = \phi(\bar{x},\bar{t})$. In a neighborhood of $(\bar{x},\bar{t})$ we have

$$\overline{u}(x,t) \le \overline{z}(x,t) \le \phi(x,t) \quad \text{and} \quad u^\delta_{i+1}[u_0](x,t) \le \overline{z}(x,t) \le \phi(x,t).$$

If $\overline{z}(\bar{x},\bar{t}) = u^\delta_{i+1}[u_0](\bar{x},\bar{t})$, then $u^\delta_{i+1}[u_0] - \phi$ achieves a local maximum at $(\bar{x},\bar{t})$, and, since $u^\delta_{i+1}[u_0]$ is a sub-solution of (3.36) in $\mathcal{C}^\delta_{i+1}[u_0]$, at $(\bar{x},\bar{t})$ we get

$$\phi_t - |D\phi|^2 - R \le 0.$$

If $\overline{z}(\bar{x},\bar{t}) = \overline{u}(\bar{x},\bar{t})$, then $\overline{u}(\bar{t},\bar{x}) > -\infty$ and $\overline{u} - \phi$ achieves a local maximum at $(\bar{x},\bar{t})$. Using (3.4) and the stability of viscosity sub-solutions we find, at $(\bar{x},\bar{t})$,

$$\phi_t - |D\phi|^2 - R \le 0,$$

and we conclude that $\overline{z}$ is a sub-solution of (3.36).

The fact that, at $(\bar{x},\bar{t})$, $\overline{u} \le u^\delta_i[u_0]$ yields that, for all $\delta > 0$, $\overline{u} \le \lim_{i\to\infty} u^\delta_i[u_0] = U^\delta[u_0]$. Letting $\delta \to 0$ we obtain

$$\overline{u} \le \lim_{\delta\to 0} U^\delta[u_0] = U[u_0] \quad \text{in} \quad \mathbb{R}^d,$$

which concludes the proof of the first part of the claim.

For the second part we need the following Lemma. Its proof is postponed to the end of this section.

**Lemma 3.3.2** *For all $i \in \mathbb{Z}^+$ the lower semi-continuous function*

$$v_i^\delta = \max(u_i^\delta[u_0 - \mu] + 2\delta, \underline{u}), \tag{3.37}$$

*is a super-solution of*

$$\begin{cases} v_{i,t}^\delta - |Dv_i^\delta|^2 - R \geq 0 \quad \textit{in} \quad \Omega_i^\delta[u_0 - \mu], \\ v_i^\delta = u_0 \quad \textit{in } \{u_0 - \mu > u_m - \delta\} \cap (\mathbb{R}^d \times \{0\}). \end{cases} \tag{3.38}$$

Since $u_{i+1}^\delta[u_0 - \mu]$ is a minimal solution of (3.32) in $\mathcal{C}_{i+1}^\delta[u_0 - \mu] \subset \Omega_i^\delta[u_0 - \mu]$ with $u_{i+1}^\delta[u_0 - \mu] = u_0 - \mu$ on $\mathbb{R}^d \times \{0\}$ (see Appendix 3.7.2), it follows that

$$u_{i+1}^\delta[u_0 - \mu] \leq v_i^\delta - \mu \quad \text{in} \quad \mathcal{C}_{i+1}^\delta[u_0 - \mu],$$

and, hence,

$$u_{i+1}^\delta[u_0 - \mu] + \mu \leq \max(u_i^\delta[u_0 - \mu] + 2\delta, \underline{u}) \quad \text{in} \quad \mathcal{C}_{i+1}^\delta[u_0 - \mu].$$

Letting $i \to \infty$ yields

$$U^\delta[u_0 - \mu] + \mu \leq \max(U^\delta[u_0 - \mu] + 2\delta, \underline{u}) \quad \text{in} \quad \Omega^\delta[u_0 - \mu].$$

Choosing $\mu > 2\delta$ we also get

$$U^\delta[u_0 - \mu] + 2\delta < U^\delta[u_0 - \mu] + \mu \quad \text{in} \quad \Omega^\delta[u_0 - \mu],$$

and, therefore,

$$U^\delta[u_0 - \mu] + \mu \leq \underline{u} \quad \text{in} \quad \Omega^\delta[u_0 - \mu].$$

Finally letting $\delta \to 0$ we obtain

$$U[u_0 - \mu] + \mu = \lim_{\delta \to 0} U^\delta[u_0 - \mu] + \mu \leq \underline{u} \quad \text{in} \quad \Omega[u_0 - \mu].$$

We conclude with the

**Proof**. [Proof of Lemma 3.3.2] The argument relies on the property that, for concave Hamiltonians, the maximum of two super-solutions is a super-solution, which we prove in the present context of semi-continuous super-solutions in a space-time domains. The key ideas are from [14].

To this end, fix $i \in \mathbb{Z}^+$ and $(x,t) \in \mathcal{C}_i^\delta[u_0 - \mu]$. Since $\mathcal{C}_i^\delta[u_0 - \mu]$ is an open set, there exists $\rho > 0$ such that $B_\rho(x,t) \in \mathcal{C}_i^\delta[u_0 - \mu]$, where $B_\rho(x,t)$ denotes the open ball of radius $\rho$ centered at $(x,t)$.

For $\alpha > 0$, let

$$u_i^{\delta,\alpha}(x,t) = \inf_{(y,s) \in B_\rho(x,t)} \{u_i^\delta[u_0 - \mu](y,s) + (2\alpha)^{-1}(|x-y|^2 + |t-s|^2)\},$$

and

$$u_i^{\delta,\alpha,\beta} = u_i^{\delta,\alpha} * \chi_\beta,$$

where $(\chi_\beta)_\beta$ is a standard smoothing mollifier. Since $u_i^{\delta,\alpha}$ is an inf-convolution of the continuous function $u_i^\delta$, it is locally Lipschitz continuous and semi-concave with semi-concavity constant $1/\alpha$.

It follows that $u_i^{\delta,\alpha,\beta}$ is a smooth semi-concave function with semi-concavity constant $1/\alpha$, and, moreover,

$$\liminf_{\substack{(y,s) \to (\bar{y},\bar{s}) \\ \alpha,\, \beta \to 0}} u_i^{\delta,\alpha,\beta}(y,s) = u_i^\delta[u_0 - \mu](\bar{y},\bar{s}).$$

Using Jensen's inequality and the concavity of the Hamiltonian, we obtain, for some $K>0$,

$$u_{i,t}^{\delta,\alpha,\beta}-\varepsilon\Delta u_i^{\delta,\alpha,\beta}-|Du_i^{\delta,\alpha,\beta}|^2-R*\chi_\beta\geq -K\alpha-\varepsilon/\alpha \quad \text{in} \quad B_\rho(x,t); \tag{3.39}$$

notice that, since $u_i^{\delta,\alpha,\beta}$ is smooth, the above inequality holds in the classical sense.

To prove (3.38) we use the smooth approximations $v_i^{\delta,\alpha,\beta,\varepsilon}$ of $v_i^\delta$ in $B_\rho(x,t)$ given by

$$n_\varepsilon+\exp\big(\frac{u_i^{\delta,\alpha,\beta}+2\delta}{\varepsilon}\big)=\exp\big(\frac{v_i^{\delta,\alpha,\beta,\varepsilon}}{\varepsilon}\big), \tag{3.40}$$

and, we show that they are almost super-solutions to (3.38) for $\alpha$, $\beta$ and $\varepsilon$ small. Notice that in (3.40) we use $2\delta$ instead of $\delta$.

Replacing $n_\varepsilon$ by $\exp\big(\frac{v_i^{\delta,\alpha,\beta,\varepsilon}}{\varepsilon}\big)-\exp\big(\frac{u_i^{\delta,\alpha,\beta}+2\delta}{\varepsilon}\big)$ in (3.1) we get

$$\begin{aligned}Rn_\varepsilon-\beta_\varepsilon\sqrt{n_\varepsilon}=&\big(v_{i,t}^{\delta,\alpha,\beta,\varepsilon}-\varepsilon\Delta v_i^{\delta,\alpha,\beta,\varepsilon}-|Dv_i^{\delta,\alpha,\beta,\varepsilon}|^2\big)\exp(\varepsilon^{-1}v_i^{\delta,\alpha,\beta})\\&-\big(u_{i,t}^{\delta,\alpha,\beta}-\varepsilon\Delta u_i^{\delta,\alpha,\beta}-|Du_i^{\delta,\alpha,\beta}|^2\big)\exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta)),\end{aligned}$$

and, in view of (3.40),

$$\begin{aligned}v_{i,t}^{\delta,\alpha,\beta,\varepsilon}-\varepsilon\Delta v_i^{\delta,\alpha,\beta,\varepsilon}-|Dv_i^{\delta,\alpha,\beta,\varepsilon}|^2=&\,(u_{i,t}^{\delta,\alpha,\beta}-\varepsilon\Delta u_i^{\delta,\alpha,\beta}-|Du_i^{\delta,\alpha,\beta}|^2\\&-R*\chi_\beta)\exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta-v_i^{\delta,\alpha,\beta,\varepsilon}))\\&+(R*\chi_\beta-R)\exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta-v_i^{\delta,\alpha,\beta}))\\&+R-\beta_\varepsilon\sqrt{n_\varepsilon}\exp(-\varepsilon^{-1}v_i^{\delta,\alpha,\beta,\varepsilon}).\end{aligned}$$

Using that, in view of (3.40), $\exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta-v_i^{\delta,\alpha,\beta,\varepsilon}))\leq 1$, and (3.39) we find

$$\begin{aligned}v_{i,t}^{\delta,\alpha,\beta,\varepsilon}-\varepsilon\Delta v_i^{\delta,\alpha,\beta,\varepsilon}-|Dv_i^{\delta,\alpha,\beta,\varepsilon}|^2-R\geq&-K\alpha-\varepsilon/\alpha\\&+(R*\chi_\beta-R)\exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta-v_i^{\delta,\alpha,\beta}))\\&-\beta_\varepsilon\sqrt{n_\varepsilon}\exp(\varepsilon^{-1}v_i^{\delta,\alpha,\beta}).\end{aligned}$$

Define

$$v_i^{\delta,\alpha,\beta}(\bar y,\bar s)=\liminf_{\substack{\varepsilon\to0\\(y,s)\to(\bar y,\bar s)}} v_i^{\delta,\alpha,\beta,\varepsilon}(y,s).$$

Letting $\varepsilon\to0$ and using the stability of viscosity super-solutions we obtain

$$\begin{aligned}v_{i,t}^{\delta,\alpha,\beta}-|Dv_i^{\delta,\alpha,\beta}|^2-R\geq&-K\alpha\\&+\liminf_{\substack{\varepsilon\to0\\(y,s)\to(\bar y,\bar s)}}(R*\chi_\beta-R)\exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta-v_i^{\delta,\alpha,\beta}))-\beta_\varepsilon\sqrt{n_\varepsilon}\exp(\varepsilon^{-1}v_i^{\delta,\alpha,\beta}).\end{aligned} \tag{3.41}$$

Recalling that $u_i^\delta+2\delta>u_m+\delta$ in $\Omega_i^\delta[u_0-\mu]$, we deduce that, as $\varepsilon,\alpha,\beta\to0$, in $B_\rho(x,t)$,

$$\beta_\varepsilon\sqrt{n_\varepsilon}\exp(-\varepsilon^{-1}v_i^{\delta,\alpha,\beta})=\beta_\varepsilon\sqrt{n_\varepsilon}(n_\varepsilon+\exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta)))^{-1}\leq(1/2)\beta_\varepsilon\exp(-(2\varepsilon)^{-1}(u_i^{\delta,\alpha,\beta}+2\delta))\to0. \tag{3.42}$$

Moreover, as $\varepsilon,\beta\to0$, we also have

$$R*\chi_\beta-R\to0 \quad \text{and} \ \exp(\varepsilon^{-1}(u_i^{\delta,\alpha,\beta}+2\delta-v_i^{\delta,\alpha,\beta}))<1. \tag{3.43}$$

Finally notice that

$$v_i^\delta=\liminf_{\substack{\alpha,\beta\to0\\(y,s)\to(\bar y,\bar s)}} v_i^{\delta,\alpha,\beta}(y,s). \tag{3.44}$$

Using (3.41), (3.42), (3.43), (3.44) and the stability of viscosity super-solutions we get

$$v^\delta_{i,t} - |Dv^\delta_i|^2 - R \geq 0 \quad \text{in} \quad B_\rho(x,t).$$

Since all the above hold for all $(x,t) \in \Omega^\delta_i[u_0 - \mu]$, it follows that the lower semi-continuous function $v^\delta_i$ is a super-solution of

$$v^\delta_{i,t} - |Dv^\delta_i|^2 - R \geq 0 \quad \text{in} \quad \Omega^\delta_i[u_0-\mu], v^\delta_i = u_0 \quad \text{for} \quad \{u_0 - \mu > u_m - \delta\} \cap (\mathbb{R}^d \times \{0\}).$$

## 3.4 The constant rate

In this section we assume that the rate is a constant, i.e.,

$$R(x) = R \quad \text{in} \quad R^d. \tag{3.45}$$

We prove the following

**Theorem 3.4.1** *Assume (3.45) and that, if* $O = \{x \in \mathbb{R}^d : u_0(x) > u_m\}$*, then* $\overline{O} = \{x \in \mathbb{R}^d : u_0(x) \geq u_m\}$*. Then*

$$\lim_{\varepsilon \to 0} u_\varepsilon(x,t) = U[u_0](x,t) \quad \text{if} \quad U[u_0](x,t) \neq u_m, \tag{3.46}$$

*with*

$$\Omega[u_0] = \{(x,t) | \sup_{y \in \overline{O}} \{-\frac{|x-y|^2}{4t} + Rt + u_0(y)\} \geq u_m\}, \tag{3.47}$$

*and*

$$U[u_0] = \begin{cases} \sup_{y \in \overline{O}} \left\{ -\frac{|x-y|^2}{4t} + Rt + u_0(y) \right\} & \text{if} \quad (x,t) \in \Omega[u_0], \\ -\infty \quad \text{otherwise.} \end{cases} \tag{3.48}$$

We remark that, in particular, Theorem 3.4.1 shows that the limit of the $u_\varepsilon$'s is not in general defined by (3.16) (otherwise $\overline{O}$ would have been replaced by $\mathbb{R}^d$). We refer to Appendix 3.7.1 for an explicit example.

**Proof**. [Proof of Theorem 3.4.1] When the rate $R$ is constant after one iteration of (3.29), (3.30) and (3.31) we find that the set $\Omega^\delta[u_0]$ and the function $U^\delta[u_0]$, since for all $i > 1$, $j > 2$ and $\delta > 0$, we have $\Omega^\delta_i[u_0] = \mathcal{C}^\delta_j[u_0] = \Omega^\delta[u_0]$ and $u^\delta_i[u_0] = U^\delta[u_0]$.

In fact, since every optimal trajectory in $\mathcal{C}^\delta_2$ is a straight line connecting a point in $\Omega^\delta_2$ to a point in $I^\delta = \{x \in \mathbb{R}^d : u_0(x) > u_m - \delta\}$, it is included in $\Omega^\delta_2$. This is because

$$\phi(x,t) = -\frac{|x-c|^2}{4t} + Rt + u_0(c)$$

is concave in $(x,t)$ and, therefore, all the optimal trajectories of the points in $\Omega^\delta_2$ are included in $\Omega^\delta_2$. It follows that $\Omega^\delta_2 = \mathcal{C}^\delta_3$, $u^\delta_2 = u^\delta_3$ and consequently $\Omega^\delta_2 = \Omega^\delta_3$. By iteration we obtain, for all $i > 2$, $\Omega^\delta_2 = \Omega^\delta_i = \Omega^\delta$ and $u^\delta_2 = u^\delta_i = U^\delta$.

Using (3.31) and (3.29) we see that, for all $i \geq 2$,

$$\Omega^\delta[u_0] = \Omega^\delta_i[u_0] = \{(x,t) : \sup_{y \in I^\delta} \{-\frac{|x-y|^2}{4t} + Rt + u_0(y)\} > u_m - \delta\}, \tag{3.49}$$

and

$$U^\delta[u_0] = u^\delta_i[u_0](x,t) = \begin{cases} \sup_{y \in I^\delta} \left\{ -\frac{|x-y|^2}{4t} + Rt + u_0(y) \right\} & \text{if} \quad (x,t) \in \Omega^\delta[u_0], \\ -\infty \quad \text{otherwise.} \end{cases} \tag{3.50}$$

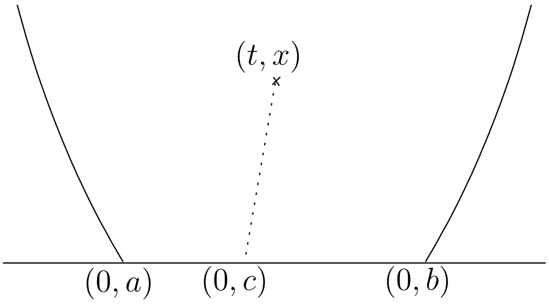

Figure 3.2: The case with $R(x)=R$ a positive constant, $\{x\in\mathbb{R}|\, u_0(x)>u_m\}=(a,b)$ and $u_0(\cdot)\geq u_m$ on an interval $[a,b]$. The set $\Omega$ is a union of hyperbolas. The optimal trajectories are straight lines and we have $U(x,t)=-\frac{|x-c|^2}{4t}+Rt+u_0(c)$, where $c$ is a point where the maximum in (3.48) is attained.

It is easy to verify that (3.32) holds, since, for all $i>2$ and $\delta>0$,

$$u^\delta_{i,t}[u_0]-|Du^\delta_i[u_0]|^2-R=0 \quad \text{in} \quad \Omega^\delta_i[u_0]=\mathcal{C}^\delta_{i+1}[u_0].$$

Letting $\delta\to 0$ in (3.49) and (3.50) we obtain (3.47)–(3.48). (See Figure 3.2.)
We also have

$$\Omega[u_0-\mu]=\bigcap_{\delta>0}\Omega^\delta[u_0-\mu]=\{(x,t):\ \sup_{y\in J^\mu}\{-\frac{|x-y|^2}{4t}+Rt+u_0(y)\}\geq u_m+\mu\},$$

with

$$J^\mu=\{(x,t):\ u_0\geq u_m+\mu\}.$$

It follows that

$$\cup_{\mu>0}\Omega[u_0-\mu]=\{(x,t):\ \sup_{y\in O}\{-\frac{|x-y|^2}{4t}+Rt+u_0(y)\}>u_m\}, \tag{3.51}$$

and

$$\lim_{\mu\to 0^+}U[u_0-\mu]=\begin{cases}\sup_{y\in O}\{-\frac{|x-y|^2}{4t}+Rt+u_0(y)\} & \text{for} \quad (x,t)\in\cup_{\mu>0}\Omega[u_0-\mu],\\ -\infty \quad \text{otherwise.}\end{cases} \tag{3.52}$$

We also notice that

$$\sup_{y\in O}\{-\frac{|x-y|^2}{4t}+Rt+u_0(y)\}=\sup_{y\in\bar{O}}\{-\frac{|x-y|^2}{4t}+Rt+u_0(y)\}. \tag{3.53}$$

Comparing (3.47), (3.48) with (3.51), (3.52) and using (3.53) we deduce that

$$\lim_{\mu\to 0}U[u_0-\mu](x,t)=U[u_0](x,t) \quad \text{for} \quad U[u_0](x,t)\neq u_m,$$

and, consequently, that

$$\lim_{\varepsilon\to 0}u_\varepsilon(x,t)=U[u_0](x,t) \quad \text{if} \quad U[u_0](x,t)\neq u_m.$$

## 3.5 Strictly positive rate

In this section we study the limiting behavior of the $u_\varepsilon$'s when

$$R \geq a > 0 \quad \text{in} \quad \mathbb{R}^d, \tag{3.54}$$

and we show that the limit is not, in general, defined by (3.16).

For this we need to assume that, for sufficiently small $\mu > \delta > 0$, there exists $\rho_{\delta,\mu} > 0$ such that

$$\lim_{\mu\to 0}\lim_{\delta\to 0}\rho_{\delta,\mu} = 0 \quad \text{and, if } u_0(y) > u_m - \delta, \quad \text{then} \quad \sup_{|y-z|\leq\rho_{\delta,\mu}} u_0(z) > u_m - \delta + \mu. \tag{3.55}$$

Notice that it is important $\rho_{\delta,\mu}$ is chosen independently of $y$. If $u_0 \in C^1$, (3.55) implies $u_m$ is never a local maximum of $u$.

We have:

**Theorem 3.5.1** *Assume (3.54) and (3.55). Then*

$$\lim_{\varepsilon\to 0} u_\varepsilon = U[u_0] \quad \textit{in} \quad \cup_{\mu>0}\,\Omega[u_0-\mu]. \tag{3.56}$$

Recall that we already know that $\lim_{\varepsilon\to 0} u_\varepsilon = -\infty$ in $\Omega[u_0]^c$. When $R$ is negative the claim of Theorem (3.5.1) together with (3.56) are equivalent to (3.16).

**Proof**. [Proof of Theorem (3.5.1)] For $h > \bar{h} = \frac{\mu}{2a} + \frac{1}{2}\sqrt{\frac{\mu^2}{a^2} + \frac{\rho_{\delta,\mu}^2}{a}}$, $(x,t) \in \mathbb{R}^d \times [0,\infty)$, $i \geq 1$ and $\mu$, $\delta > 0$, we have

$$u_i^\delta[u_0](x,t) \leq u_i^\delta[u_0-\mu](x,t+h). \tag{3.57}$$

We postpone the proof of this inequality to Appendix 3.7.3 and we continue with the ongoing one.

Letting $i \to +\infty$ and $\delta, \mu \to 0$ we obtain, for all $h > 0$ and $t > 0$,

$$U[u_0](\cdot,\cdot) \leq \lim_{\mu\to 0^+} U[u_0-\mu](\cdot,\cdot+h), \tag{3.58}$$

and, hence,

$$U[u_0](x,t) \leq \lim_{\mu\to 0^+} U[u_0-\mu](x,t+h) \leq \underline{u}(x,t+h) \leq \overline{u}(x,t+h) \quad \text{for all} \quad (x,t) \in \cup_{\mu>0}\Omega[u_0-\mu],$$

and, finally,

$$U[u_0](x,t) \leq \liminf_{h\to 0^+} \underline{u}(x,t+h) \leq \limsup_{h\to 0^+} \overline{u}(x,t+h) \quad \text{for all} \quad (x,t) \in \cup_{\mu>0}\Omega[u_0-\mu].$$

The definitions of $\underline{u}$ and $\overline{u}$ also imply that

$$\liminf_{h\to 0^+} \underline{u}(x,t+h) = \underline{u}(x,t) \quad \text{and} \quad \limsup_{h\to 0^+} \overline{u}(x,t+h) = \overline{u}(x,t).$$

Combining all the above we obtain

$$U[u_0] \leq \underline{u} \leq \overline{u} \quad \text{in} \quad \cup_{\mu>0}\,\Omega[u_0-\mu].$$

Using this last inequality and (3.34) yields

$$\underline{u} = \overline{u} = U[u_0] \quad \text{in} \quad \cup_{\mu>0}\,\Omega[u_0-\mu],$$

and, hence,

$$\lim_{\varepsilon\to 0} u_\varepsilon = U[u_0] \quad \text{in} \quad \cup_{\mu>0}\,\Omega[u_0-\mu].$$

## 3.6 Conclusions

We showed that the local uniform limit, as $\varepsilon \to 0$, for the parabolic problem (3.1) with finite time extinction is naturally set in the exponential regime (3.3) and that the formal limit is apparently the variant (3.7) of the standard eikonal equation. The new ingredient is an obstacle that depends on the solution itself.

The variational inequality admits many solutions (see Appendix 3.7.1) and the difficulty is to select the correct additional information. This is easy when the rate $R$ is negative, as shown in Section 3.2. Since, in this case it is enough to enforce the Dirichlet boundary condition on the boundary of the unknown open set $\Omega$ where the liminf of $u_\varepsilon$'s is finite. This is due to the fact that, for concave Hamiltonians, the supremum of two supersolutions is still a supersolution.

When the rate $R$ is positive we do not have easy super-solutions at hand, and the answer is more elaborate. It requires an iterative procedure which allows us to identify again the limit of the $u_\varepsilon$'s. The key ingredients are boundary conditions for (3.7) that involve state constraints and which are seen through a control problem.

If the $R$ changes sign we can only bound from above and below the limsup and liminf of the $u_\varepsilon$'s by upper and lower solutions, $\bar{u}$ and $\underline{u}$ (Section 3.3).

In terms of the biological motivation, our results qualitatively mean that the specific form of the survival threshold (a square root here) is irrelevant for the asymptotic problem. It also shows that the exponential shape is deeply influenced by the survival threshold except when $R$ is nonpositive.

We conjecture that these upper and lower solutions are in fact equal and the correct setting (implying uniqueness) is to find a pair $(u, \Omega)$ for which we can impose both Dirichlet and state constraints boundary conditions. Both establishing directly these boundary conditions for the semi-limits of the $u_\varepsilon$'s as well as developing a theory of state constraints boundary conditions for time varying, non-smooth domains are very challenging mathematical issues.

## 3.7 Apprendix

### 3.7.1 Non-uniqueness

To explain the difficulty for (3.7), we present here counter-examples for uniqueness and elaborate further conditions. Recall that the problem is to find pairs $(u, \Omega)$ such that $u$ is a viscosity solutions to (3.7).

A first source for non-uniqueness is the value of $u$ on $\partial\Omega$. Indeed assume that $R$ and $u_0$ are such that there exists a unique viscosity solution $u^1$ of (3.12) or, more generally, with $u^1$ defined in (3.10) and (3.11). For all $\eta \geq u_m$, we introduce the pair

$$\Omega_\eta = \{(x,t) :\ u^1(x,t) \geq \eta\} \quad \text{and} \quad w_\eta(x,t) = \begin{cases} u^1(x,t) & \text{if} \quad (x,t) \in \Omega_\eta, \\ -\infty & \text{otherwise.} \end{cases}$$

It can be easily verified that $(w_\eta, \Omega_\eta)$ is a viscosity solution of (3.7). In order to avoid this artefact, one can add the Dirchlet boundary condition (3.8) which appeared throughout our constructions. However in the next example we see that this Dirichlet condition is not enough to obtain uniqueness. In fact a state constraint boundary condition is hidden behind the property $u^1 = -\infty$ in the complement of $\overline{\Omega}_\eta$ and we do not take it into account here.

**Example** Let

$$R(x) = 1 \quad \text{and} \quad u_0(x) = -x^2.$$

A simple computation shows that in this case the solution $u^1$ of (3.12) is given by

$$u^1(x,t) = t - \frac{x^2}{1+4t}.$$

Therefore the first truncation of $u^1$, namely the pair $(\widetilde{u}, \widetilde{\Omega})$

$$\widetilde{u}(x,t) = \begin{cases} t - \frac{x^2}{1+4t} & \text{for} \quad t - \frac{x^2}{1+4t} \geq u_m, \\ \\ -\infty & \text{otherwise,} \end{cases}$$

and

$$\widetilde{\Omega} = \{(x,t) : \widetilde{u}(x,t) > -\infty\},$$

is a viscosity solution of (3.7). As a matter of fact this is the maximal sub-solution to (3.7), (3.8) but it does not satisfy the state constraint boundary condition. To see this choose $u_m = -0.04$. The point $(1,2)$ is included in $\widetilde{\Omega}$ since $\widetilde{u}(1,2) = 0.2 > -0.04$. The optimal trajectory associated to this point, giving the value $\widetilde{u}(1,2) = 0.2$, is the straight line that connects $(0, 0.4)$ to $(1,2)$. But we have $u_0(0.4) = -0.16 < -0.04$. So the point $(0, 0.4)$ is not included in $\widetilde{\Omega}$. Therefore a part of the optimal trajectory of the point $(1,2)$ is not included in $\widetilde{\Omega}$. Hence $\widetilde{u}$ does not satisfy the state constraint condition.

Following the arguments in Section 3.4 we can find a viscosity solution to (3.7) and (3.8). Indeed using (3.48) it is possible to compute explicitly the function $U[u_0] = \lim_{\delta\to 0} U^\delta[u_0] = \lim_{\delta\to 0} u_2^\delta[u_0]$ to find

$$\breve{u}(x,t) = \begin{cases} t - \frac{x^2}{1+4t} & \text{if} \quad -\frac{x^2}{(1+4t)^2} \geq u_m,\ t - \frac{x^2}{1+4t} \geq u_m, \\ t - \frac{(x-\sqrt{-u_m})^2}{4t} + u_m & \text{if} \quad x > 0,\ -\frac{x^2}{(1+4t)^2} \leq u_m,\ t \geq \frac{(x-\sqrt{-u_m})^2}{4t}, \\ t - \frac{(x+\sqrt{-u_m})^2}{4t} + u_m & \text{if} \quad x < 0,\ -\frac{x^2}{(1+4t)^2} \leq u_m,\ t \geq \frac{(x+\sqrt{-u_m})^2}{4t}, \\ -\infty & \text{otherwise,} \end{cases}$$

with

$$\breve{\Omega} = \{(x,t) : \breve{u}(x,t) > -\infty\}.$$

From Theorem 3.4.1 we know that $\breve{u}$ is indeed the pointwise limit of the $u_\varepsilon$'s outside the exceptional set $\{(x,t) : \breve{u}(x,t) = u_m\}$.

However, in general $\widetilde{u} \neq \breve{u}$. Consider, for instance, the value $u_m = -0.04$. Then

$$\widetilde{u}(2,1) = 0.2, \quad \breve{u}(2,1) = 0.15, \quad \widetilde{u}(2.21,1) = 0.02, \quad \breve{u}(2.21,1) = -\infty.$$

and, consequently,

$$\breve{\Omega} \subsetneq \widetilde{\Omega}.$$

According to Section 3.4, the state constraint boundary condition is satisfied for $\breve{u}$, which motivates our conjecture in Section 3.6.

### 3.7.2 $u_i^\delta[u_0]$ is a minimal solution of (3.32) in $\mathcal{C}_i^\delta[u_0]$

Here we prove that $u_i^\delta[u_0]$ is a minimal solution of (3.32) in $\mathcal{C}_i^\delta[u_0]$ by showing that, for any super-solution $w$ of (3.32) in $\mathcal{C}_i^\delta[u_0]$, we have

$$u_i^\delta[u_0] \leq w \quad \text{in} \quad \mathcal{C}_i^\delta[u_0]. \tag{3.59}$$

To this end we assume that $(\gamma(s), s) : [0,t] \to \Omega^\delta_{i-1}[u_0]$ is a $C^1$-trajectory, with $(\gamma(t), t) = (x,t) \in \mathcal{C}^\delta_i[u_0]$. Since $\mathcal{C}^\delta_i[u_0]$ is the set of points that can be connected by a $C^1$-trajectory in $\Omega^\delta_{i-1}[u_0]$ to some point in $\mathbb{R}^d$ at time $t = 0$, it follows that $\gamma$ is included in $\mathcal{C}^\delta_i[u_0]$.

Let $w$ be a super-solution of (3.32) in $\mathcal{C}^\delta_i[u_0]$ and define, for $s \in [0,t]$, $\varphi(s) = w(\gamma(s), s)$. It is clear that $\varphi$ is lower semi-continuous.

We claim that $\varphi$ is a viscosity super-solution of

$$\varphi' \geq -\frac{|\dot{\gamma}|^2}{4} + R(\gamma) \qquad \text{in} \qquad (0,t). \tag{3.60}$$

We postpone the proof of this claim to the end of the present paragraph and we proceed noticing that the function

$$\psi(t) = \int_0^t \big( -\frac{|\dot{\gamma}(s)|^2}{4} + R(\gamma(s))\big) ds + w(\gamma(0), 0),$$

is a subsolution of (3.60). Using the standard comparison principle we then obtain

$$w(x,t) = \varphi(t) \geq \int_0^t \big( -\frac{|\dot{\gamma}(s)|^2}{4} + R(\gamma(s))\big) ds + u_0(\gamma(0)),$$

and, since this is true for any $C^1$-trajectory $\gamma$, (3.59) follows.

It remains to prove (3.60). Let $\phi \in C^1((0,t))$ be a test function, assume that $\bar{t}$ is a strict minimum point of $\varphi - \phi$ and consider the function

$$F_\mu(y,t) = w(y,t) - \phi(t) + \frac{|y - \gamma(t)|^2}{\mu^2} + (t - \bar{t})^2,$$

which attains a local minimum at a point $(y_\mu, t_\mu)$ such that, as $\mu \to 0$,

$$(t_\mu - \bar{t}) \to 0 \quad \text{ and } \quad \frac{|y_\mu - \gamma(t_\mu)|^2}{\mu^2} \to 0. \tag{3.61}$$

Since $w$ is a super-solution we have

$$\phi'(t_\mu) + \frac{2\big(\gamma(t_\mu) - y_\mu\big)}{\mu^2} \cdot \dot{\gamma}(t_\mu) + 2(t_\mu - \bar{t}) \geq \big|\frac{2(y_\mu - \gamma(t_\mu))}{\mu^2}\big|^2 + R(y_\mu).$$

Using the latter and the elementary inequality

$$q \cdot \dot{\gamma}(t) - q^2 \leq \frac{|\dot{\gamma}(t_\mu)|^2}{4},$$

we obtain

$$\phi'(t_\mu) + 2(t_\mu - \bar{t}) \geq -\frac{|\dot{\gamma}(t_\mu)|^2}{4} + R(y_\mu),$$

and, after letting $\mu \to 0$, we conclude using (3.61).

### 3.7.3 Proof of (3.57)

We prove by induction on $i$ that, for all $h > \bar{h} = \frac{\mu}{2a} + \frac{1}{2}\sqrt{\frac{\mu^2}{a^2} + \frac{\rho^2_{\delta,\mu}}{a}}$, $i > 1$, $\delta > 0$, and $(x,t) \in \mathbb{R}^d \times [0,\infty)$,

$$u^\delta_i[u_0](x,t) \leq u^\delta_i[u_0 - \mu](x, t+h).$$

Recall that $u_1^\delta[u_0] = u^1[u_0]$ and $u_1^\delta[u_0-\mu] = u^1[u_0-\mu] = u^1[u_0]-\mu$, where $u^1[u_0]$ solves

$$\begin{cases} u_t^1[u_0] = |Du^1[u_0]|^2 + R \quad \text{in} \quad \mathbb{R}^d \times (0,+\infty), \\ u^1[u_0] = u_0 \quad \text{on} \quad \mathbb{R}^d \cap \{0\}. \end{cases} \tag{3.62}$$

From (3.62) and $R \geq a$ we find

$$u^1[u_0](\cdot,t) + ah - \mu \leq u^1[u_0](\cdot,t+h) - \mu = u^1[u_0-\mu](\cdot,t+h).$$

Therefore, for all $h > \bar{h} \geq \mu/a$, we have

$$u^1[u_0](\cdot,t) \leq u^1[u_0-\mu](\cdot,t+h),$$

and, consequently,

$$u_1^\delta[u_0](\cdot,t) \leq u_1^\delta[u_0-\mu](\cdot,t+h).$$

Assume next that, for all $h > \bar{h}$ and $t > 0$,

$$u_i^\delta[u_0](\cdot,t) \leq u_i^\delta[u_0-\mu](\cdot,t+h).$$

It follows that, for all $h > \bar{h}$,

$$\Omega_i^\delta[u_0] + he_t \subset \Omega_i^\delta[u_0-\mu], \tag{3.63}$$

where $e_t$ is the unit vector in the direction of time axis.

Assume that $(x,t) \in \mathcal{C}_{i+1}^\delta[u_0] \subset \Omega_i^\delta[u_0]$ and let $\gamma$ be a $C^1$-trajectory in $\Omega_i^\delta[u_0]$ connecting $(x,t)$ to a point $(y,0)$ with $u_0(y) > u_m - \delta$. It follows from (3.55) that there exists $z \in \mathbb{R}^d$ such that $|z-y| < \rho_{\delta,\mu}$ and $u_0(z) > u_m - \delta + \mu$. Without loss of generality we can take $u_0(z) \geq u_0(y)$.

The claim is that the trajectory $\widetilde{\gamma} : [0, t+h] \to \mathbb{R}^d$ defined by

$$\widetilde{\gamma}(s) = \begin{cases} h^{-1}s(y-z) + z \quad \text{if} \quad 0 \leq s \leq h, \\ \gamma(s-h) \quad \text{for} \quad h < s \leq t+h, \end{cases} \tag{3.64}$$

is included in $\Omega_i^\delta[u_0-\mu]$.

Indeed notice that, for all $h > \bar{h}$,

$$-\frac{|y-z|^2}{4h} + ah \geq \mu \geq 0.$$

Consequently, it follows from $R(x) \geq a$ and (3.49) that the straight line connecting $(y,h)$ to $(z,0)$ is included in $\Omega^\delta[u_0-\mu] = \cap_j \Omega_j^\delta[u_0-\mu]$, and, in particular, it is included in $\Omega_i^\delta[u_0-\mu]$. Therefore, for all $0 \leq s \leq h$, the point $(\widetilde{\gamma}(s), s)$ is included in $\Omega_i^\delta[u_0-\mu]$.

Moreover using (3.63) we find that $\gamma + he_t \in \Omega_i^\delta[u_0-\mu]$. Hence, for all $h < s$, $(\widetilde{\gamma}(s), s) \in \Omega_i^\delta[u_0-\mu]$. Thus we conclude that $\widetilde{\gamma}$ is included in $\Omega_i^\delta[u_0-\mu]$.

Next write

$$\begin{aligned} \int_0^{t+h} (-\frac{|\dot{\widetilde{\gamma}}(s)|^2}{4} + R(\widetilde{\gamma}(s)))ds + u_0(z) - \mu &= \int_0^t (-\frac{|\dot{\gamma}(s)|^2}{4} + R(\gamma(s)))ds \\ &+ \int_0^h (-\frac{|\dot{\widetilde{\gamma}}(s)|^2}{4} + R(\widetilde{\gamma}(s)))ds + u_0(z) - \mu. \end{aligned} \tag{3.65}$$

It follows that

$$\int_0^h \left(-\frac{|\dot{\widetilde{\gamma}}(s)|^2}{4} + R(\widetilde{\gamma}(s))\right)ds + u_0(z) - \mu \geq u_0(y). \tag{3.66}$$

If this is true, then using (3.29), (3.65) and (3.66) we obtain, for all $h > \bar{h}$ and $t > 0$,

$$u_{i+1}^{\delta}[u_0](\cdot, t) \leq u_{i+1}^{\delta}[u_0 - \mu](\cdot, t + h),$$

and we deduce (3.57).

It remains to prove (3.66). Since $R \geq a$, in view of (3.64), we have

$$\int_0^h \left(-\frac{|\dot{\widetilde{\gamma}}(s)|^2}{4} + R(\widetilde{\gamma}(s))\right)ds + u_0(z) - \mu \geq -\frac{|y - z|^2}{4h} + ah + u_0(z) - \mu,$$

$u_0(z) \geq u_0(y)$ and, for all $h > \bar{h}$,

$$-\frac{|y - z|^2}{4h} + ah \geq \mu.$$

# Deuxième partie

# Methodes Numeriques et exemples biologiques

## Chapitre 4

# Modèle de compétition directe : Illustrations

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Le travail dans ce chapitre a été effectué en collaboration avec Benoît Perthame, Emeric Bouin et Pierre Millien. Nous illustrons des simulations numériques pour un modèle de compétition directe. Nous nous intéressons notamment à observer dans quelles situations la solution se concentre sous forme de masses de Dirac et dans quelles situations, au contraire, un continuum de traits pourraient être présents. Les méthodes des différences finies et de Monte-Carlo ont été utilisées. Ces simulations numériques sont en accord avec les résultats théoriques qui existent dans la littérature. De mauvais choix de conditions aux bords pourraient cependant donner suite à des artéfacts. Ce chapitre est une partie de l'article [95].

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## 4.1 Competition models

In most of the previous models, the competition between species is global because it arises through the total resource consumption $I(t)$. All individuals are equally competing for the resource. This is not always the case and, in many situations, it is more realistic to assume that there is higher competition between individuals with closer traits. This is the reason why other models have been proposed that implement a trait dependent competition. A class of such models (see [91, 45, 62, 61, 17]) are given by the population dynamics of Lotka-Volterra type

$$\frac{\partial n(x,t)}{\partial t} - \lambda \frac{\partial^2 n(x,t)}{\partial x^2} = n(x,t)\big(r(x) - K * n(x,t)\big), \qquad t \geq 0,\ x \in \mathbb{R}. \tag{4.1}$$

The model is completed by an initial data $n(x, t = 0) = n^0(x)$ which we take highly concentrated for the numerical simulations presented below in section 4.2.

The interpretation of the quantitites arising in this model are
- $n(x,t)$ still denotes the population density at position $x$ and time $t$,
- $r(x) > 0$ is the intrinsic growth rate of individuals with trait $x$ (if isolated without competition)
- $K \in L^\infty(\mathbb{R})$ is called the competition kernel. It is a probability density: $K \geq 0$, $\int_{\mathbb{R}} K(z)dz = 1$. The convolution $K * n(x) = \int_{\mathbb{R}} K(x-y)n(y,t)dy$ represents the competition for resource,
- $\lambda$ is the mutation rate that is supposed to be a constant.

When derived from stochastic IBM, as in [113, 31, 32] such models are called *mean field* equations [20, 115]. They arise not only in evolution theory but also in ecology for non-local resources (and $x$ denotes the location then) [18, 67, 120, 59].

The large variety of regimes that can appear in such models can be seen in special cases. Below, we use simple examples to describe two of them, regularly distributed traits, or concentration as a Dirac mass. The main interest of the model (4.1) is mostly from the branching patterns that correspond to multiple concentration points which can either die out or branch again and create new structures (see [60]).

### 4.1.1 The gaussian case without mutations

Firstly we consider the case

$$\lambda = 0, \qquad r(x) = \frac{1}{\sqrt{2\pi\sigma_1}} e^{-\frac{|x|^2}{2\sigma_1}}, \qquad K(z) = \frac{1}{\sqrt{2\pi\sigma_2}} e^{-\frac{|x|^2}{2\sigma_2}}. \tag{4.2}$$

This corresponds to widely used standard forms of the input parameters because of their statistical meaning.

As usual for pure selection models, $\lambda = 0$, there are Dirac mass stationary solutions $N(x) = \bar{\rho}\delta(x - \bar{x})$ with $r(\bar{x}) = \bar{\rho}K(0)$. But this can be obtained in a long time asymptotic only when

$$r(x) < \bar{\rho}K(x - \bar{x}) \qquad \forall x \neq \bar{x},$$

or, replacing $\bar{\rho}$ from the first condition

$$\frac{r(x)}{r(\bar{x})} < \frac{K(x - \bar{x})}{K(0)} \qquad \forall x \neq \bar{x}.$$

One can deduce from this calculation the

**Proposition 4.1.1** *For $\sigma_1 > \sigma_2$ there is a smooth steady state to* (4.1) *given by*

$$N(x) = \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{|x|^2}{2\sigma}}, \qquad \sigma = \sigma_1 - \sigma_2,$$

*and Dirac masses are not stable steady states.*

*For $\sigma_1 < \sigma_2$ the Dirac mass $\bar{\rho}\delta(x)$ is a stable steady state (and only the Dirac mass at* 0 *is stable).*

The authors in [74] prove that the corresponding stable states are also the long time limits of the dynamics described by equation (4.1). They use a relative entropy method built on the corresponding steady state. The construction of this entropy is rather easy when the positive steady state exists. It is much more difficult in the case where the Dirac masses have to be handled.

### 4.1.2 The NonLocal-Fisher equation

We now consider the case

$$r \equiv 1. \tag{4.3}$$

Then, the equation (4.1) is called the *NonLocal-Fisher* (NLF) equation. It also arises in mathematical ecology, as an extension of the Fisher/KPP equation. As mentioned earlier, the non-local aspect induced by the convolution represents long range access to resources, see [67, 17, 59] and the references therein.

The positive steady state is simply given by $N \equiv 1$ but a result from [62] states that it can be Turing unstable (i.e. only a bounded set of linearly unstable modes occur). In order to explain this, we may use the Fourier transform of the competition kernel $K$ defined as

$$\widehat{K}(\xi) = \int_{\mathbb{R}} K(x) e^{-ix\xi} dx.$$

Then one has

**Proposition 4.1.2 ([62])** *Assume there is a $\xi_0$ such that*

$$\widehat{K}(\xi_0) < 0, \tag{4.4}$$

*then for $\lambda$ small enough the steady state $N \equiv 1$ is linearly unstable.*

The result of this statement corresponds qualitatively to the case $\sigma_1 < \sigma_2$ in Proposition 4.1.1 (with mutations neglected).

The Fourier transform also characterizes a nonlinear stability result; this is the case in the

**Theorem 4.1.3 ([17])** *Take $r \equiv 1$ and assume*

$$\widehat{K}(\xi) > 0 \qquad \forall \xi \in \mathbb{R}. \tag{4.5}$$

*Then $n \equiv 0$ and $n \equiv 1$ are the only two nonnegative and bounded steady states of* (31).

*Furthermore, there are traveling waves connecting the states $n = 0$ and $n = 1$.*

The result of this Theorem corresponds to the situation $\sigma_1 > \sigma_2$ in Proposition 4.1.1.
In the Turing unstable case it is possible to rescale the problem as we did it in Chapter 1 and it is observed numerically that, in general, the asymptotic limit leads to Dirac concentrations characterized again by a constrained Hamilton-Jacobi equation [61].

## 4.2 Numerical methods and branching patterns

In general it is very difficult, in the direct competition model (4.1), to distinguish between the two behaviors: convergence towards a continuous state or speciation. Numerical methods are useful to get an intuition but they can create artifacts and we explain this now.

We present two numerical approaches that allow to simulate solutions to equation (4.1). The first is a standard finite difference scheme, the second one is a Monte-Carlo simulations related to IBM that solves the same equation.

For the sake of simplicity we concentrate on the NonLocal Fisher equation as in Section 4.1.2 with a gaussian competition kernel

$$r \equiv 1, \qquad K(x) = \frac{1}{\sqrt{2\pi\sigma}}\, e^{-\frac{|x|^2}{2\sigma}}. \tag{4.6}$$

Because the Fourier transform of $K$ is positive (a gaussian), we do not expect appearance of concentrations (speciation).

At this stage we insist that the Monte-Carlo algorithms are only seen here as an approximation to (4.1). From this point of view, the closer it is from the PDE, the better it is because one looks only for possible computational cost reduction. Monte-Carlo methods also used as a modeling tool and allow to include further stochastic effects. One of them is 'demographic stochasticity' which makes that too small populations can die out by statistical effects [37, 107]. These effects are not included in the models under consideration in this chapter and give quantitatively different answers (in term of evolution speed, branching patterns). It is shown in [60] that the notion of 'survival threshold' in the equations as (4.1) is able to reproduce these effects in great details. In Chapter 3 we studied the addition of a survival threshold to the model with a single nutrient.

### 4.2.1 Finite differences

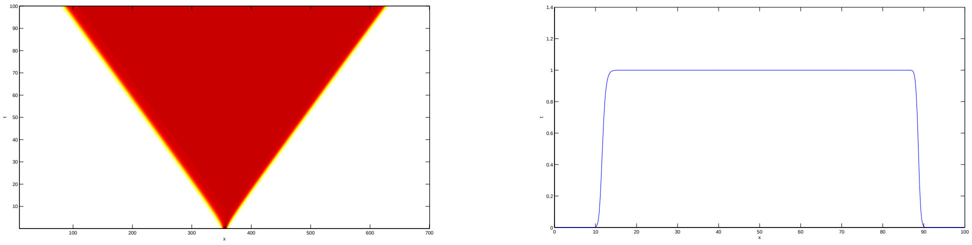

Figure 4.1: Left: Numerical population density dynamics obtained for model (4.1)–(4.6) when the initial population is concentrated in the center of the computational domain. Horizontally is $x$ and vertically is $t$, in gray zone $n \equiv 1$ and the white zone corresponds to $n \equiv 0$. Right: The population density $n(x,T)$ at final time. The deterministic finite difference scheme (4.7)–(4.9) has been used with parameters in (4.10). We observe convergence toward the constant solution in accordance with Theorem 4.1.3.

We consider the solution on interval $[-\frac{L}{2}, \frac{L}{2}]$. We use a uniform grid with $N$ points on the segment, with $\Delta x = \frac{L}{N}$ the space step. We denote by $n_i^k \geq 0$ the numerical solution at grid point $x_i = i\triangle x$, $1 \leq i \leq N$, and time $t^k = k\triangle t$ where $\triangle t$ is the time step

$$n(x_i, k\triangle t) \approx n_i^k.$$

We use a time splitting algorithm between the growth term and the diffusion that is we solve alternatively the two equations

$$\frac{d}{dt}n(x,t) = n(x,t)\ \left[1 - K * n(t)\,\right],$$

$$\frac{\partial n(x,t)}{\partial t} - \lambda\frac{\partial^2 n(x,t)}{\partial x^2} = 0.$$

**1**. First compute, with a semi-implicit method, the solution to the discrete reaction term

$$\frac{d}{dt}n_i(t) = n_i(t)\ \left[1 - K_d * n_i^k\,\right].$$

The exact solution is

$$n_i^{k+\frac{1}{2}} = n_i^k\ \exp\left(\frac{\Delta t}{\lambda}\left(1 - K_d * n_i^k\right)\right), \qquad 1 \le i \le N. \tag{4.7}$$

The discrete convolution is computed according to

$$K_d * n_i^k = \Delta x \cdot \sum_{j=-N}^{N} K_d(j\triangle x)\, n_{i-j}^k, \qquad n_{i-j}^k = 0 \ \text{ for } i-j \notin [1,N]. \tag{4.8}$$

Indeed, as a consequence of the domain truncation, only those terms satisfying $1 \le i-j \le N$ are well defined and the extension by zero amounts to extend $n$ by 0 outside $[-\frac{L}{2}, \frac{L}{2}]$. This is some kind of Dirichlet boundary condition.

**2**. As for the Laplace term, we use a three points explicit scheme

$$n_i^{k+1} = n_i^{k+\frac{1}{2}} + \frac{\lambda\Delta t}{2\Delta x^2}\left(n_{i+1}^{k+\frac{1}{2}} + n_{i-1}^{k+\frac{1}{2}} - 2\,n_i^{k+\frac{1}{2}}\right), \qquad 1 \le i \le N. \tag{4.9}$$

Because we choose $\lambda$ small, the explicit scheme is not penalizing in terms of computational time. We use Neumann boundary condition, $n_0^{k+1} = n_1^{k+1}$ and $n_N^{k+1} = n_{N-1}^{k+1}$, but as far as the wave does not reach the boundary, the Dirichlet boundary condition $n_1^{k+1} = n_N^{k+1} = 0$ gives equivalent results.

The stability of the scheme is ensured by the CFL condition $\frac{\lambda\Delta t}{2\Delta x^2} \le 1$, which is verified for

$$\lambda = 0.004, \qquad \sigma = 0.04, \qquad \Delta t = 0.025, \qquad \Delta x = 0.1, \qquad L = 100, \qquad N = 1000. \tag{4.10}$$

We have implemented this method. We choose the initial data concentrated in the center of the domain. The numerical results are depicted in Fig. 4.1. We can observe that the population propagates as a traveling wave. For $L$ large enough, for $0 \le t \le T$ the front does not reach the numerical boundary and there is almost no mass on the boundary of the interval $[-\frac{L}{2}, \frac{L}{2}]$. This is in accordance to the theory in [17] and the statement in Theorem 4.1.3.

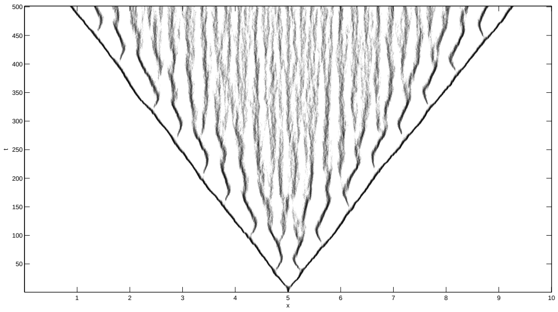

Figure 4.2: Numerical solution with the Monte-Carlo algorithm in section 4.2.2. Horizontally is the trait $x$ and vertically is time $t$. Initially the population is concentrated in one Dirac mass at the center of the domain. We observe that the population distribution converges weakly towards the constant solution as expected (see also Fig. 4.1).

### 4.2.2 The stochastic individual-based method

We also compare the finite volume simulation with a Monte-Carlo algorithm. Then, the solution is approximated by a sum of Dirac masses

$$n(t) \approx \omega \sum_{j=1}^{N(t)} \delta\big(x - y_j(t)\big).$$

Here the weight $\omega$ is taken constant. The simulation starts with a number $N(0)$ of 'individuals located' distributed on an interval of length $L$. Then $N(0)$ and $\omega$ are related by the approximation $n(0) \approx \omega \sum_{j=1}^{N(0)} \delta\big(x - y_j(0)\big)$ in the weak sense of measures.

Several Monte-Carlo algorithms are possible. See for instance [18, 59] for another algorithm motivated by models from ecology.

Here we use the method proposed in [20, 115]. The number of individuals is denoted by $N(k)$ at iteration $k$. The algorithm uses also a time splitting but not with the same operators as in Section 4.2.1. We solve alternatively the two equations

$$\frac{d}{dt} n(x,t) = -n(x,t)\ K * n(t),$$

$$\frac{\partial n(x,t)}{\partial t} - \lambda \frac{\partial^2 n(x,t)}{\partial x^2} = n(x,t).$$

Finally, in the rational of small mutations and long times, as in Chapter 1, we choose $\triangle t = 1$. Then the algorithm [20, 115] reads as follows.

**1**. The competition term is now computed as (this makes a difference with [20, 115])

$$C(x) = \frac{\omega}{\sqrt{2\pi\sigma}} \sum_{j=1}^{N(k)} \exp\left( - \frac{|x - y_j|^2}{2\sigma} \right). \tag{4.11}$$

Because the value of $C(x)$ is small, it defines the probability that an individual located at $x$ dies. For a given $j$, we compute this probability and set $N(k+1) = N(k) - 1$ if this individual dies.

**2**. If the individual survives, it reproduces. The newborn undergoes a mutation from its parent trait to a new trait given by a Gaussian distribution with variance $\lambda' = 2\lambda$. Then $N(k+1) = N(k) + 1$.

We notice that for $n$ the solution of

$$\partial_t n = \lambda' \triangle n, \qquad n(x, t^k) = n^k(x),$$

we have $n(t^{k+1}) = n^k * \frac{1}{\sqrt{4\pi\lambda'}} e^{\frac{-x^2}{4\lambda'}}$. Hence the choice $\lambda' = 2\lambda$ in the second step of the Monte-Carlo method. We act a gaussian mutation to the new-born only but with twice stronger intensity.

We have used the following parameters values which take into account the small time step in the deterministic algorithm

$$\lambda' = 10^{-6}, \qquad \sigma = 0.04, \qquad L = 10, \qquad N = 3000, \qquad \frac{\omega}{\sqrt{2\pi\sigma}} = 1/18000.$$

These values are such that the mutations are very weak compared to intraspecific competition, again in accordance with the parameters used in the finite difference method. The numerical results are depicted in Fig. 4.2. We can observe that the population propagates as a traveling wave as in Fig. 4.1 and according to the theoretical prediction in Theorem 4.1.3.

### 4.2.3 The convolution formula

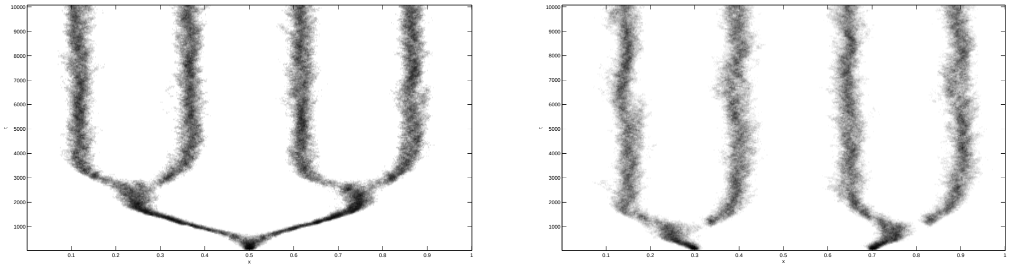

Figure 4.3: Dynamics of the concentration points with the Monte-Carlo algorithm in section 4.2.3 based on periodizing the convolution. Horizontally is the trait $x$ and vertically is time $t$. Initially the population is concentrated in one Dirac mass on the left and two Dirac masses on the right.

Surprisingly, in [20, 115] the authors observed that simulations based on this Monte-Carlo method may yield concentration patterns too (clusters). The main difference is that, rather than with 4.11, the convolution kernel is computed assuming the $y_j$ are on the circle

$$C(x) = \frac{\omega}{\sqrt{2\pi\sigma}} \sum_{j=1}^{N(k)} \exp\left(-\frac{d(x, y_j)^2}{2\sigma}\right), \tag{4.12}$$

where $d$ is the shortest distance on the circle.

This can be interpreted as periodic boundary conditions rather than extension by zero or as a periodic convolution kernel

$$K_s(x) \propto \exp\left(-\frac{(x\,[L])^2}{2\sigma}\right), \qquad x[L] = x \mod L, \;\; x \in \mathbb{R}.$$

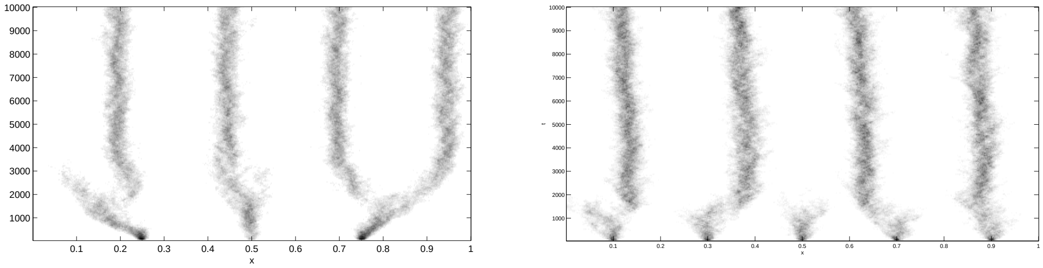

Figure 4.4: Dynamics of the concentration points. Same as above but with different initial data. A new phenomena occurs with extinction of branches.

In opposition with the Gaussian kernel because it has some Fourier coefficients with a negative real part. In this case the Fourier condition (4.4) is not fulfilled. Therefore according to the linear analysis in [62], and Proposition 4.1.2, the constant state is unstable for problem (4.1)–(4.6) and we expect to observe pattern formation.

We have run both the Monte-Carlo and finite difference approximations with this periodic kernel. The numerical results are in accordance with those obtained in different contexts in [20, 115, 62, 61]. They can be found in Fig. 4.3 and Fig. 4.4 for Monte-Carlo simulations and Fig. 4.5 for finite differences.

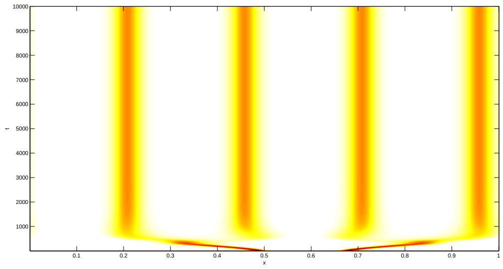

Figure 4.5: Numerical population density dynamics obtained by deterministic simulations for model (4.1)–(4.6) with periodic boundary conditions. We have used the following parameter values: $\lambda = 0.001$, $\sigma = 0.04$, $\Delta t = 0.0001$, $\Delta x = 0.001$, $L = 1$, $N = 1000$.

# Chapitre 5

# Modèle de compétition pour des ressources limitées

Le travail présenté ici a été effectué en collaboration avec Benoît Perthame et Joe Yuichiro Wakano. Nous étudions un modèle de type chemostat, où des espèces consomment des ressources qui sont perpétuellement fournies, en supposant que les consommateurs et les ressources sont tous deux caractérisés par des traits continus. Les consommateurs utilisent des ressources qui ont des traits proches des leurs. Ce modèle est plus réaliste que des modèles de compétition directe, où il n'y a pas de paramètre de ressource. Nous montrons en particulier que, contrairement au cas de la compétition directe, une distribution continue et positive de traits de consommateurs n'est pas possible. Des états stationnaires stables sous forme de masses de Dirac sont présents. Nous montrons de plus la convergence globale vers les "evolutionary steady distributions " (ESD). Ce travail reprend l'article [97].

## 5.1 Introduction

Evolutionary origin of species diversity has been one of the most important problems in evolutionary ecology. Individuals with similar traits (e.g. body size or shape) face strong competition, which might lead to the adaptive radiation. As a model of such competition-driven speciation, several theoretical studies have shown that the species distribution in continuous trait space will often evolve toward single peak or multiple peaks that are distinct from each other (see [113, 50, 45, 103, 74]). This provides a mechanism of evolution of diverse but distinct species in nature. These studies strengthen the theory of speciation by Adaptive Dynamics that usually assumes distinct species a priori [66, 65, 93].

Most of the previous results are derived from a simple model that assumes direct species competition of Lotka-Volterra type. On the other hand, competitive interaction among species generally occurs in competition for resource such as prey or nutrient. For example, birds with similar beak shapes are in competition because they utilize similar food resource. Another example is found in ecological stoichiometry where consumer species with similar C:N:P (carbon: nitrogen: phosphorus ratio) requirements experience competition for nutrient supply with their optimal C:N:P ratio (see [118]). Thus, the competitive interaction should be modeled not directly but implicitly through the resource competition. Here we study a model of evolution of traits based on this approach. Mathematically, this corresponds to assuming a resource-consumption kernel, instead of a direct competition kernel.

From Volterra-Gause's competitive exclusion principle (see [80, 114] and the references therein), it is well established that in a model with $N$ limiting factors (e.g. nutrients) at most $N$ species can generically survive. In the context of continuous traits $N$ species is represented by the sum of at most $N$ Dirac masses. For $N$ small $(1, 2, ...)$, these states are stable. Is this true asymptotically as $N$ becomes large? A way to answer this question is to study also the case of a continuous distribution of resource according to a parameter related to the predation ability of the population.

In this paper, we first describe our model of species competition through resource dynamics (section 5.2). Both consumer trait and resource trait take continuous values. First we study the condition for the survival of population (section 5.3) and the forms of steady states (section 5.4). In section 5.5, we introduce the notion of Evolutionary Stable Distribution and show nonlinear stability for large times. Our method is based on Lyapunov functionals and in particular our result covers the convergence to polymorphic ESD. To illustrate our results, we show an example case where we choose specific function form. In sections 5.6 and 5.7 we give details on the transient to polymorphic states.

## 5.2 Model

Our model is denoted as

$$\begin{cases} \partial_t n(x,t) = n(x,t)\big(-m_1(x) + r(x)\int K(x,y)R(y,t)dy\big) + \varepsilon\Delta n(x,t), \\ \\ \partial_t R(y,t) = -m_2(y)R(y,t) + R_{\text{in}}(y) - R(y,t)\int r(x)K(x,y)n(x,t)dx. \end{cases} \tag{5.1}$$

and with initial data

$$n(0,x) = n^0(x) \geq 0, \qquad R(0,y) = R^0(y) \geq 0,$$

for $x \in \mathbb{R}$ and $y \in \mathbb{R}$. Here $n(x,t) \geq 0$ is consumer species density with trait $x$ and $R(y,t) \geq 0$ is resource density with trait $y$. Resource is constantly supplied at rate $R_{\text{in}}(y) > 0$ which

| | |
|---|---|
| $x$ | Consumer species trait (evolving) |
| $y$ | Resource trait |
| $n(x,t)$ | Consumer species distribution |
| $r(x)$ | Trait dependent growth rate |
| $R(y,t)$ | Resource distribution |
| $R_{\text{in}}(y)$ | Trait dependent resource-supply rate |
| $m_1(x)$ | Mortality of consumer species |
| $m_2(y)$ | Decay rate of resource |
| $K(x,y)$ | Consumption rate of resource $y$ by individuals of trait $x$ |
| $\varepsilon$ | Mutation rate |

Table 5.1: The notations used for the chemostat models (5.1) and (5.2).

drives the system (a chemostat type model). Trait-dependent mortalities (or chemostat outflow rate or resource decay rate) are denoted by $m_1(x)$ and $m_2(y)$. Consumption of resource is denoted by a trait dependent efficiency $r(x)$ and by a resource-consumption kernel $K(x,y)$ that defines how species with trait $x$ depends on resource with trait $y$. Without loss of generality, we normalize $K(x,.)$ so that $r(x)$ represents a net growth rate

$$K(x,y) \geq 0, \qquad \int K(x,y)dy = 1.$$

We consider the evolution of a consumer trait, $x$. The change in species trait value due to mutations is modeled by a diffusion process in (5.1). To be precise the coefficient $\varepsilon$ is not the mutation rate (probability with which mutation occurs) but the product of the mutation rate and the mutation step-size. However, for brevity, we call $\varepsilon$ as mutation rate. Our system is a generalized MacArthur's model for species packing in niche space (see [85]). It can also be viewed as a model of population dynamics in spatially heterogeneous environment where resource-supply rate, resource decay rate, and consumer mortality are function of spatial position, $x$ (see [112]).

Our system consists of two species; consumer and resource. In general, two species reaction-diffusion equations are difficult to analyze. Nevertheless, our results in sections 5.3, 5.4 and 5.5 are valid for the full system (5.1) with unspecified functional forms. To obtain even stronger results in sections 5.6 and 5.7, we will later focus on a reduced system by taking the quasi-static approximation of resource dynamics as follows

$$\begin{cases} \partial_t n(x,t) = n(x,t)\big(-m_1(x) + r(x)\int K(x,y)R(y,t)dy\big) + \varepsilon\Delta n(x,t), \\ R(y,t) = \frac{R_{\text{in}}(y)}{m_2(y)+\int r(x)K(x,y)n(x,t)dx}. \end{cases} \tag{5.2}$$

The basic idea comes from the assumption that changes in species composition occur slower in consumer population than in resource population. This is because the reproduction and death of consumer species has, in many cases, slower time scale than those of prey species or resource dynamics of nutrient particles.

Finally we introduce a particular case that we will use throughout the paper to illustrate more intuitively the results; this is when $r(x)$, $m_1(x)$ and $m_2(y)$ are constant and when the resource-supply distribution and the resource-consumption kernel are gaussians:

$$\begin{aligned} &K(x,y) = \tfrac{1}{\sigma_K\sqrt{2\pi}}\exp(-\tfrac{|x-y|^2}{2\sigma_K^2}), \qquad R_{\text{in}}(y) = \tfrac{M_{\text{in}}}{\sigma_{\text{in}}\sqrt{2\pi}}\exp(-\tfrac{y^2}{2\sigma_{\text{in}}^2}), \\ &m_1(x) \equiv \overline{m}_1, \qquad m_2(y) \equiv \overline{m}_2, \qquad \overline{m}_0 = \min(\overline{m}_1, \overline{m}_2) \qquad r(x) \equiv r. \end{aligned} \tag{5.3}$$

We assume the data are smooth enough, Lipschitz continuous and we use the following notations and assumptions

$$\underline{m}_1 = \inf_x m_1(x) > 0, \qquad \underline{m}_2 = \inf_x m_2(y) > 0, \qquad \underline{m}_0 = \min(\underline{m}_1, \underline{m}_2), \qquad r_M = \sup_x r(x), \tag{5.4}$$

$$r_0 = \inf_x r(x) > 0, \qquad r_2 = \sup_x |r_x(x)|, \tag{5.5}$$

$$M_1 = \sup_x |m_{1,x}(x)|, \qquad M_2 = \sup_x |m_{2,x}(x)|, \tag{5.6}$$

$$M^0 = \int n^0(x)dx + \int R^0(y)dy, \tag{5.7}$$

$$R_1 = \sup_y R_{\text{in}}(y), \qquad R_2 = \sup_y |\nabla R_{\text{in}}(y)|, \tag{5.8}$$

$$K_M = \max_{x,y} K(x,y), \qquad M_{\text{in}} = \int R_{\text{in}}(y)dy, \qquad R_{\text{in}} \in L^2(\mathbb{R}), \tag{5.9}$$

$$K_1 = \int r(x) \int K(x,y) \frac{R_{\text{in}}(y)}{m_2(y)} dydx, \tag{5.10}$$

$$K_2 = \sup_{x,y} |K_x(x,y)|, \qquad K_3 = \sup_{x,y} |K_y(x,y)|, \tag{5.11}$$

$$K_4 = \sup_{x,y} |\Delta_x \left( r(x) K(x,y) \right)|. \tag{5.12}$$

We call the population is '(strictly) monomorphic' at $x = \bar{x}$ if $n(x) = 0$ for any $x \neq \bar{x}$ and '(strictly) polymorphic' if $n(x) = 0$ for any $x$ except for $x = \bar{x}_1, \bar{x}_2, ....$ On the other hand, we call the population is 'approximately monomorphic' if the distribution has single peak with tails. Similarly, 'approximately polymorphic' population consists of multiple peaks in its trait distribution (multimodal), see Figure 5.1.

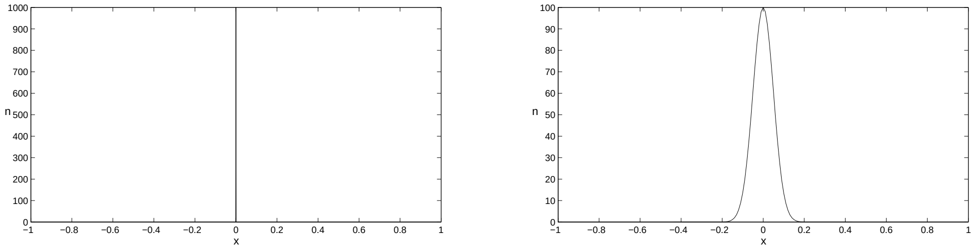

Figure 5.1: Left: a strictly monomorphic population. Right: an approximately monomorphic population.

## 5.3 Survival condition

We study whether consumer species can survive on a given rate of resource-supply in models (5.1) and (5.2). We begin with two preliminary observations: a balance law for the total flow holds which implies estimates on the total population. Next, we prove the necessary condition for survival, which implies the existence of the threshold level of resource-supply below which species go extinct, that is they reach the consumer-free steady state

$$\overline{\overline{n}}(x) := 0, \qquad \overline{\overline{R}}(y) := \frac{R_{\text{in}}(y)}{m_2(y)}. \tag{5.13}$$

We also prove that the population does not grow up to infinity; there is an upper bound.

### 5.3.1 Fundamental balance laws

Integrating and summing the two lines in the full system (5.1), we obtain the following balance law for the total flow

$$\frac{d}{dt}\left[\int n(x,t)dx + \int R(y,t)dy\right] = \int R_{\text{in}}(y)dy - \left[\int m_1(x)n(x,t)dx + \int m_2(y)R(y,t)dy\right]. \tag{5.14}$$

This indicates that the total biomass is finite and positive. Therefore competition for resource is indeed at work.

In the case of system (5.2) the biomass balance becomes

$$\frac{d}{dt}\int n(x,t)dx = \int R_{\text{in}}(y)dy - \left[\int m_1(x)n(x,t)dx + \int m_2(y)R(y,t)dy\right]. \tag{5.15}$$

### 5.3.2 Boundedness of the total population

These balance laws have the consequence that the population remains bounded.

**Theorem 5.3.1** *We define* $\rho(t) = \int n(x,t)dx$. *Then we have, for both systems* (5.1) *and* (5.2)

$$\rho(t) \le \max(M^0, \frac{M_{\text{in}}}{\underline{m}_0}) := \rho_M, \tag{5.16}$$

*with* $M^0$, $M_{\text{in}}$ *and* $\underline{m}_0$ *defined in* (5.7), (5.9) *and* (5.4). *Moreover we have, with the notation* (5.13),

$$R(y,t) \le \max\left(R(y,0), \overline{\overline{R}}(y)\right). \tag{5.17}$$

**Proof**. Proof of (5.16): For the full system (5.1), using the total biomass relation (5.14),

$$\frac{d}{dt}\left[\int n(x,t)dx + \int R(y,t)dy\right] \le M_{\text{in}} - \underline{m}_0\left[\int n(x,t)dx + \int R(y,t)dy\right].$$

Thus we obtain that

$$\frac{d}{dt}\left(\int n(t,x)dx + \int R(t,y)dy\right) \le 0, \qquad \text{if} \qquad \frac{M_{\text{in}}}{\underline{m}_0} \le \int n(t,x)dx + \int R(t,y)dy.$$

We deduce that $\int n(t,x)dx + \int R(t,y)dy \le \max(M^0, \frac{M_{\text{in}}}{\underline{m}_0})$. Hence (5.16).

In the case of system (5.2), using (5.15) we obtain that

$$\frac{d}{dt}\int n(t,x)dx \le M_{\text{in}} - \underline{m}_1\int n(t,x)dx.$$

It follows that $\rho(t) \le \max(\int n^0(x)dx, \frac{M_{\text{in}}}{\underline{m}_1}) \le \max(M^0, \frac{M_{\text{in}}}{\underline{m}_0})$.

Proof of (5.17): For the full system (5.1), we have $\frac{d}{dt}R(y,t) \le 0$ if $R(y,t) \le \frac{R_{\text{in}}(y)}{m_2(y)}$. Thus (5.17). In the case of the system (5.2) the proof is immediate. □

### 5.3.3 Necessary condition for survival

We prove that the system gets extinct if the mortality/decay rates $m_1$ and $m_2$ are too large, see Figure 5.2. This is the regime

**Theorem 5.3.2 (Condition for survival)** *We assume* (5.4), (5.7), *the first part of* (5.8), (5.9) *and* (5.12). *For the solutions to systems* (5.1) *or* (5.2), *if* $\int \overline{\overline{R}}(y)|\ln R^0(y)|dy < \infty$ *and*

$$m_1(x) \geq r(x) \int K(x,y)\overline{\overline{R}}(y)dy, \qquad \text{for all } x \in \mathbb{R}, \tag{5.18}$$

*then the solution gets extinct, that is* $\int n(x,t)dx$ *vanishes and* $R(y,t)$ *converges a.e. to* $\overline{\overline{R}}(y)$ *in* (5.13).

*Otherwise the system survives, i.e.* $\int n(x,t)dx$ *does not vanish, at least when there are no mutations and the initial data* $n^0$ *is positive everywhere.*

This condition can be made explicit for the gaussian case (5.3) and gives

$$\overline{m}_1\overline{m}_2 \geq \frac{rM_{\text{in}}}{\sqrt{2\pi(\sigma_K^2+\sigma_{\text{in}}^2)}}. \tag{5.19}$$

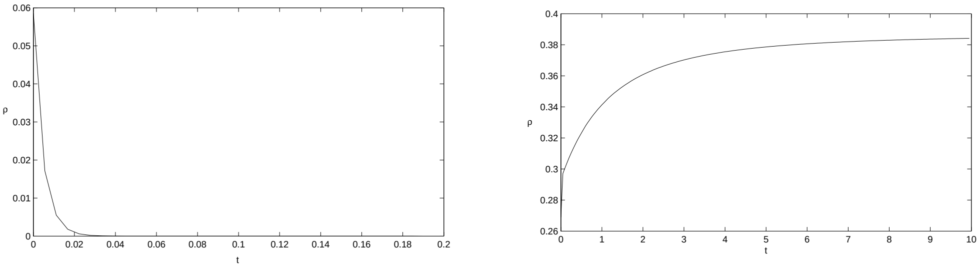

Figure 5.2: Here the horizontal axis is time and the vertical axis is $\rho$ the total mass. The model studied here is the one given in (5.2) in the particular case of (5.3) with $\varepsilon = 0.001$, $\sigma_K = 0.6$, $\sigma_{\text{in}} = 1$, $r = 1$, $M_{\text{in}} = 3$. Left: the mortality rates $\overline{m}_1 = \overline{m}_2 = 1.1$ are too large such that the non-extinction condition (5.19) is not respected and we observe extinction in finite time. Right: the mortality terms $\overline{m}_1 = \overline{m}_2 = 1$ are small enough such that the non-extinction condition (5.19) is respected and this avoids extinction. This is in accordance with the results in Theorem 5.3.2.

**Proof**. (i) We assume that the assumption (5.18) is satisfied and prove extinction.

For the system (5.1): We first prove that as $t$ goes to $+\infty$, $R(y,t)$ converges to $\overline{\overline{R}}(y)$ using the following Lyapunov functional

$$\overline{\overline{S}}(t) = -\int \overline{\overline{R}}(y)\ln R(y,t)dy + \int n(x,t)dx + \int R(y,t)dy.$$

We differentiate $\overline{\overline{S}}$ and obtain

$$\frac{d\overline{\overline{S}}}{dt}(t) = -\int \frac{m_2(y)}{R(y,t)}\left(\overline{\overline{R}}(y) - R(y,t)\right)^2 dy - \int n(x,t)\left(m_1(x) - r(x)\int K(x,y)\overline{\overline{R}}(y)dy\right)dx. \tag{5.20}$$

Thanks to assumption (5.18), we obtain that $\frac{d\overline{\overline{S}}}{dt}$ is always negative and thus $\overline{\overline{S}}$ is a decreasing function with respect to $t$. Using Theorem 5.3.1 we deduce that $\overline{\overline{S}}(t)$ is bounded from below so that

$$\int_0^\infty \int \frac{m_2(y)}{R(y,t)}\left(\overline{\overline{R}}(y) - R(y,t)\right)^2 dydt < +\infty. \tag{5.21}$$

Because $R$ is bounded from above thanks to Theorem 5.3.1, we conclude that

$$Q(t) := \int \Big(\overline{\overline{R}}(y) - R(y,t)\Big)^2 dy \quad \text{satisfies} \quad \int_0^\infty Q(t)dt < \infty.$$

But we can estimate, with the notation $K * n(y) = \int r(x)K(x,y)n(x,t)dx$

$$\begin{aligned}
\tfrac{1}{2}Q'(t) \quad &= -\textstyle\int \Big(\overline{\overline{R}}(y) - R(y,t)\Big) \frac{\partial R(y)}{\partial t} dy \\
&= -\textstyle\int \Big(\overline{\overline{R}}(y) - R(y,t)\Big) \Big(m_2 \overline{\overline{R}}(y) - m_2 R(y,t) - R(y,t) K * n(y)\Big)\, dy \\
&= -\textstyle\int \Big(\overline{\overline{R}}(y) - R(y,t)\Big)^2 (m_2 + K * n(y))\, dy - \int \Big(\overline{\overline{R}}(y) - R(y,t)\Big) \overline{\overline{R}}(y) K * n(y) dy.
\end{aligned}$$

Because $0 \leq K * n(y) \leq K_M \rho_M$, we conclude that

$$|Q'(t)| \leq C \int \Big((\overline{\overline{R}}(y) - R(y,t)\Big)^2 + \int \overline{\overline{R}}(y)^2 dy \in L^1 + L^\infty(0, +\infty).$$

With the fact that $Q \in L^1(\mathbb{R}^+)$, this is enough to conclude that $Q(t) \to 0$ as $t \to \infty$ and thus that

$$\lim_{t \to \infty} R(y,t) = \overline{\overline{R}}(y), \qquad \text{a.e.} \quad \text{and} \quad \text{in } L^1 \cap L^2(\mathbb{R}).$$

Notice that $R(t)$ is 'regularized' since initially it needs not to be square integrable.

It remains to prove that $n$ vanishes. To do so we integrate (5.14) between $t$ and $t+1$, and using (5.4) we obtain

$$\begin{aligned}
\textstyle\int n(x,t+1)dx - \int n(x,t)dx \quad &\leq -\textstyle\int R(y,t+1)dy + \int R(y,t)dy \\
&\quad + \textstyle\int_t^{t+1} \int \left[R_{in}(y)dy - m_2(y)R(y,s)\right] dyds - \underline{m}_1 \int_t^{t+1} \int n(x,s)dxds.
\end{aligned}$$

Using the dominated convergence Theorem we have

$$\alpha(t) := -\int R(y,t+1)dy + \int R(y,t)dy + \int_t^{t+1} \int \left[R_{in}(y)dy - m_2(y)R(y,s)\right] dyds \to 0,$$

while $t \to +\infty$. Now we define

$$\rho(t) := \int n(x,t)dx, \qquad H(t) := \int_t^{t+1} \rho(s)ds.$$

We have

$$\frac{d}{dt}H(t) = \rho(t+1) - \rho(t) \leq \alpha(t) - \underline{m}_1 H(t).$$

We deduce that

$$H(t) \leq e^{-\underline{m}_1 t} H(0) + e^{-\underline{m}_1 t} \int_0^t \alpha(s) e^{\underline{m}_1 s} ds.$$

It follows that

$$\int_t^{t+1} \rho(s)ds \to 0, \qquad \text{while } t \to +\infty.$$

Moreover integrating the first equation of (1) we have

$$|\frac{d}{dt}\rho(t)| \leq C,$$

for some constant $C$. We conclude that $\rho(t) \to 0$, while $t \to 0$.

For the system (5.2): We integrate the first equation, use (5.18) and arrive at

$$\frac{d}{dt}\int n(x,t)dx = \int n(x,t)\left(-m_1(x)+r(x)\int K(x,y)R(y,t)dy\right)dx \le 0.$$

Therefore $\int n(x,t)dx$ is decreasing and

$$0 \le \int_0^\infty \int n(x,t)\left(m_1(x)-r(x)\int K(x,y)R(y,t)dy\right)dx\,dt < +\infty.$$

Using (5.18) it follows that

$$0 \le \int_0^\infty \int \left(\int r(x)n(x,t)K(x,y)dx\right)\left(\frac{R_{\text{in}}(y)}{m_2(y)} - \frac{R_{\text{in}}(y)}{m_2(y)+\int r(x)n(x,t)K(x,y)dx}\right)dy\,dt < +\infty.$$

Since $\int r(x)n(x,t)K(x,y)dx$ is bounded, convexity implies that

$$\int_0^\infty \int \left(\int r(x)n(x,t)K(x,y)dx\right)^2 R_{\text{in}}(y)dydt < \infty.$$

Since $|\frac{d}{dt}\int r(x)K(x,y)n(x,t)\,dx|$ is bounded, following the arguments for the case of the system (5.1) we obtain successively that

$$\lim_{t\to\infty} R(y,t) = \overline{\overline{R}}(y) \quad \text{a.e.,} \qquad \text{and} \qquad \int n(x,t)dx \underset{t\to\infty}{\longrightarrow} 0.$$

(ii) Now we assume that the assumption (5.18) is not satisfied, i.e. for some $\bar{x} \in \mathbb{R}$ we have

$$m_1(\bar{x}) < r(\bar{x})\int K(\bar{x},y)\frac{R_{\text{in}}(y)}{m_2(y)}dy. \tag{5.22}$$

We prove that if there is no mutation, i.e. $\varepsilon = 0$, the solutions to systems (5.1) and (5.2) do not get extinct.

For system (5.1): We assume that $\int n(x,t)dx \underset{t\to\infty}{\longrightarrow} 0$. Therefore

$$\int r(x)n(x,t)K(x,y)dx \underset{t\to\infty}{\longrightarrow} 0. \tag{5.23}$$

It follows that

$$\partial_t R(y,t) = -m_2(y)R(y,t) + R_{\text{in}}(y) + \beta(t),$$

with $\beta(t) \underset{t\to\infty}{\longrightarrow} 0$. We deduce that

$$R(y,t) \underset{t\to\infty}{\longrightarrow} \overline{\overline{R}}(y).$$

Using the dominated convergence Theorem and the boundedness of $K(\cdot,\cdot)$ we obtain that $\int K(x,y)R(y,t)dy$ converges to $\int K(x,y)\overline{\overline{R}}(y)dy$, locally uniformly in $x$ as $t \to +\infty$. Therefore for $x$ in a neighborhood of $\bar{x}$ for $t > t_0$ with $t_0$ large enough, using system (5.1) with $\varepsilon = 0$ and using (5.22), we have

$$\begin{aligned}\partial_t n(x,t) &= n(x,t)\big(-m_1(x)+r(x)\textstyle\int K(x,y)R(y,t)dy\big)\\ &\approx n(x,t)\big(-m_1(x)+r(x)\textstyle\int K(x,y)\overline{\overline{R}}(y)dy\big)\\ &> an(x,t),\end{aligned}$$

with $a$ a positive constant. We deduce that $n(x,t)$ blows up when $t \to \infty$ in a neighborhood of $\bar{x}$. This is in contradiction with $\int n(x,t)dx \to 0$.

For system (5.2): In this case we deduce directly from (5.23) that $R(y,t) \underset{t\to\infty}{\longrightarrow} \overline{\overline{R}}(y)$, using the definition of $R(y,t)$. The other steps are as above. $\square$

## 5.4 Steady states

Next question we address concerns the possible shapes of stationary solutions for the model (5.1) but neglecting the mutation term. Firstly, in section 5.4.1 we show that under some general assumptions, there is no positive continuous steady solution. This distinguishes this model from that of Lotka-Volterra with direct competition where positive steady states can generally occur depending on the model coefficients (see [63, 45, 74, 113]). Secondly, in Section 5.4.2 we show that there may exist steady solutions in the form of Dirac masses. This confirms that the model is convenient to observe the high population concentrations as Dirac deltas. It means that one or several specific traits can survive while the other traits disappear.

In this section, we always consider the model without mutations that is system (5.1) with $\varepsilon = 0$. Then a steady state $(\overline{n}, \overline{R})$ satisfies

$$\int \overline{R}(y)K(x,y)dy = \frac{m_1(x)}{r(x)} \quad \forall x \in \operatorname{supp} \overline{n}, \qquad \overline{R}(y)\left(m_2(y) + \int r(x)K(x,y)\overline{n}(x)dx\right) = R_{\text{in}}(y). \tag{5.24}$$

### 5.4.1 Positive steady states

We say that the population is at positive steady state, if consumer species density $\overline{n}(x)$ is positive for all trait values.

To analyse possible solutions, we use assumptions (5.10), (5.4) and the second part of (5.9). In the one hand we have, from the second equality in (5.24) and these assumptions

$$\int r(x) \int K(x,y)\overline{R}(y)dydx \leq \int r(x) \int K(x,y)\frac{R_{\text{in}}(y)}{m_2(y)}dydx := K_1 < +\infty.$$

In the other hand we have from the first equality in (5.24) and (5.4),

$$r(x) \int K(x,y)\overline{R}(y)dy = m_1(x) \geq \underline{m}_1.$$

The latter relations are in contradiction. Thus we have proved the

**Theorem 5.4.1 (Non-existence of non-vanishing steady state with finite biomass)** *We assume* (5.10), (5.4) *and the second part of* (5.9). *Then there are no positive steady state to system* (5.1) *with* $\varepsilon = 0$.

These results suggest that steady state solutions must satisfy $\overline{n}(x) = 0$ for some values of $x$; then the first equation in (5.24) and the above argument shows that the measure of the persistence set is small; more precisely

$$\left|\{x;\, \overline{n}(x) > 0\}\right| \leq \frac{K_1}{\underline{m}_1}.$$

When outflow rate is fast enough, species are wiped out and extinction occurs as we saw it in section 5.3; this is the regime $\frac{m_0 m_2}{r_M}$ large enough. But for $\frac{m_0 m_2}{r_M}$ small compared to $R_{\text{in}}$, we may expect persistence and concentration on the fittest traits. We state later further conditions, still with finite biomass, which imply that whatever is the initial data, the solution behaves as a sum of Dirac masses.

### 5.4.2 Dirac masses (monomorphic states)

Indeed, as always in Lotka-Volterra equations, there are many possible Dirac steady states. Most of them are unstable and the issue of stability is studied later in section 5.5.3 and the present result serves as a preliminary calculation. For general coefficients $r(x)$, $m_1(x)$ and $m_2(y)$, the monomorphic steady states are characterized in the

**Theorem 5.4.2 (Monomorphic steady states)** *Consider system* (5.1) *with* $\varepsilon = 0$*. For all* $\bar{x}$ *such that*

$$m_1(\bar{x}) < r(\bar{x}) \int \frac{K(\bar{x}, y) R_{\text{in}}(y)}{m_2(y)} dy, \tag{5.25}$$

*there exists a unique monomorphic steady state* $\bar{n} = \overline{\rho}\delta_{\bar{x}}$ *with* $\overline{\rho} > 0$*.*

The biological interpretation is the following. When only one species exists (and when mutation is neglected), it can survive at a certain equilibrium density $\overline{\rho}$ if the non-extinction condition (5.25) is satisfied; this is in accordance with the condition for survival in section 5.3. Moreover, the equilibrium density is uniquely determined by the trait value of the species.

In the particular case given in (5.3), where the resource-supply distribution and the competition kernel are gaussians and $m$ and $r$ are constants, the condition (5.25) becomes

$$\frac{\overline{m}_1 \overline{m}_2}{r} < \frac{M_{\text{in}}}{\sqrt{2\pi(\sigma_{\text{in}}^2 + \sigma_K^2)}} \, e^{-\bar{x}^2/2\left(\sigma_{\text{in}}^2 + \sigma_K^2\right)}. \tag{5.26}$$

We repeat that not all these steady states are stable under regularization of the Dirac mass or under mutations. This question will be studied later on.

**Proof**. Let $\bar{n} = \overline{\rho}\delta_{\bar{x}}$, with $\overline{\rho}$ to be determined later. For $\bar{n}$ to be a steady state we must have

$$-m_1(\bar{x}) + r(\bar{x}) \int K(\bar{x}, y) R(y, t) dy = 0, \qquad R(y) = \frac{R_{\text{in}}(y)}{m_2(y) + r(\bar{x})\overline{\rho} K(\bar{x}, y)}.$$

This is equivalent to write

$$G(\overline{\rho}, \bar{x}) := \int \frac{K(\bar{x}, y) R_{\text{in}}(y)}{m_2(y) + r(\bar{x})\overline{\rho} K(\bar{x}, y)} dy = \frac{m_1(\bar{x})}{r(\bar{x})}. \tag{5.27}$$

The function $G$ is continuous and decreasing in $\overline{\rho}$. Using assumption (5.25) we have

$$\lim_{\rho \to \infty} G(\rho, \bar{x}) = 0, \qquad \lim_{\rho \to 0} G(\rho, \bar{x}) = \int \frac{K(\bar{x}, y) R_{\text{in}}(y)}{m_2(y)} dy > \frac{m_1(\bar{x})}{r(\bar{x})}.$$

We conclude that there exists $\overline{\rho} > 0$ such that $G(\overline{\rho}, \bar{x}) = \frac{m_1(\bar{x})}{r(\bar{x})}$ and consequently $\bar{n} := \overline{\rho}\delta_{\bar{x}}$ is a steady state. □

### 5.4.3 Dirac masses (dimorphic states)

The problem (5.1) with $\varepsilon = 0$ also admits polymorphic steady states. Here we consider only the case where all the functions are symmetric with respect to the origin:

$$\begin{gathered} R_{\text{in}}(y) = R_{\text{in}}(-y), \qquad m_1(x) = m_1(-x), \qquad m_2(y) = m_2(-y), \\ r(x) = r(-x), \qquad K(x, y) = K(-x, -y), \end{gathered} \tag{5.28}$$

and we show that dimorphic steady states exist:

**Theorem 5.4.3 (Dimorphic steady states)** *With the symmetry assumption* (5.28)*, for all* $\bar{x}$ *satisfying* (5.25) *there exists a unique dimorphic steady state to system* (5.1) *with* $\varepsilon = 0$ *in the form of*

$$\bar{n} = \overline{\rho}\,(\delta_{\bar{x}} + \delta_{-\bar{x}})\,.$$

We notice that the gaussian case (5.3) satisfies assumption (5.28). We deduce that, in the Gaussian case, for all $\bar{x}$ such that (5.26) is hold, there exists a unique $\overline{\rho}$ such that $\overline{\rho}\,(\delta_{\bar{x}} + \delta_{-\bar{x}})$ is a steady state. In this case indeed both monomorphic and dimorphic steady states exist (see Section 5.4.2). But we insist that we do not know yet whether these states are stable under smoothing or under mutations.

Existence and stability of steady states for such models with a finite number of resource and consumer traits have been studied in [34].

**Proof**. We determine $\overline{\rho}$ such that $\bar{n} = \overline{\rho}\,(\delta_{\bar{x}} + \delta_{-\bar{x}})$ is a steady state. We need

$$-m_1(\bar{x}) + r(\bar{x}) \int K(\bar{x},y) \frac{R_{\text{in}}(y)}{m_2(y) + r(\bar{x})\overline{\rho}K(\bar{x},y) + r(-\bar{x})\overline{\rho}K(-\bar{x},y)} dy = 0,$$

$$-m_1(-\bar{x}) + r(-\bar{x}) \int K(-\bar{x},y) \frac{R_{\text{in}}(y)}{m_2(y) + r(\bar{x})\overline{\rho}K(\bar{x},y) + r(-\bar{x})\overline{\rho}K(-\bar{x},y)} dy = 0.$$

Thanks to assumption (5.28), these two relations are equivalent. Therefore it is sufficient to find $\overline{\rho}$ such that the first relation holds. Following the arguments in section 5.4.2, this is equivalent to write

$$H(\overline{\rho},\bar{x}) := \int \frac{K(\bar{x},y)R_{\text{in}}(y)}{m_2(y) + \overline{\rho}\, r(\bar{x})[K(\bar{x},y) + K(-\bar{x},y)]} dy = \frac{m_1(\bar{x})}{r(\bar{x})}.$$

The function $H$ is continuous and decreasing in $\overline{\rho}$. Using assumption (5.25) we have

$$\lim_{\rho\to\infty} H(\rho,\bar{x}) = 0, \qquad \lim_{\rho\to 0} H(\rho,\bar{x}) = \int \frac{K(\bar{x},y)R_{\text{in}}(y)}{m_2(y)} dy > \frac{m_1(\bar{x})}{r(\bar{x})}.$$

We conclude that there exists a unique $\overline{\rho} > 0$ such that $H(\overline{\rho},\bar{x}) = \frac{m_1(\bar{x})}{r(\bar{x})}$ and consequently $\bar{n} := \overline{\rho}\,(\delta_{\bar{x}} + \delta_{-\bar{x}})$ is a steady state. □

## 5.5 Stability of steady states

We continue with the case without mutations, $\varepsilon = 0$. So far we have described possible steady states and proved that not all traits can be present; continuous distributions with small supports can exist as well as Dirac deltas. We now address the question of stability in these two classes. We recall the

**Definition 5.5.1 (Evolutionary Stable Distribution, [74])** *For a nonnegative bounded measure* $\overline{n}$ *(that is* $\int \overline{n} < \infty$*), the steady state characterized by* (5.24) *is called an Evolutionary Stable Distribution (ESD) for the equation* (5.1) *if*

$$-m_1(x) + r(x) \int K(x,y)\overline{R}(y)dy \le 0, \qquad \textit{for all } x \in \operatorname{supp} n^0 \setminus \operatorname{supp} \overline{n}. \tag{5.29}$$

### 5.5.1 Lyapunov functional and convergence to an ESD

Here we consider a non-vanishing bounded steady state $(\overline{n}, \overline{R})$. We use the same techniques as in Section 5.3.3, based on Lyapunov functionals to prove that it is nonlinearly globally attractive.

In standard analysis of adaptive dynamics, one shows the convergence and evolutionarily stability by calculating invasion fitness of rare mutants with strategy $x^m$ when resident population is monomorphic at strategy $x^r$. Our theorem extends the situation so that population consists of any (discrete or continuous) combination of strategies. The theorem strongly suggests that, if any ESD exists, any reasonable (see above) distribution of traits evolves toward the ESD. Thus, the theorem shows the convergence and evolutionarily stability of the ESD in our model against the invasion of any (discrete or continuous) combination of non-rare mutant strategies (with any densities). This is the reason we call the theorem as global convergence. In terms of the evolution of consumer trait in our chemostat model, the evolutionarily outcome is always the ESD which is determined by ecological parameters of the model (e.g., resource-supply rate, resource consumption rate) irrespective of the initial state.

**Theorem 5.5.2 (Global convergence to ESD)** *Consider systems* (5.1) *or* (5.2) *with* $\varepsilon = 0$. *We assume that* $(\overline{n}, \overline{R})$ *is a bounded ESD and that* $\int \overline{n}(x)|\ln n^0(x)|dx$ *and* $\int \overline{R}(y)|\ln R^0(y)|dy$ *are well-defined. Then* $R(y,t) \to \overline{R}(y)$ *a. e. as* $t \to +\infty$. *In particular this holds true if* $\text{supp}\, n^0 = \text{supp}\, \overline{n}$.

We would like to point out that it is fundamental to assume that $\int \overline{n}(x)|\ln n^0(x)|dx$ is well-defined; this implies that $n^0$ is a function and does not vanish where $\overline{n}$ is positive (see section 5.5.2 for $n^0$ a Dirac measure). Otherwise, not only the method collapses but it is easy to build counterexamples to the result (as monomorphic cases).

Our method is closely related to the proof in [74] for direct competition (see also [34] for a discrete version). The case of discrete ESD, that is $\overline{n}$ is a measure, can be treated as well but to the expense of technical controls which are beyond the scope of the present paper.

As we will see it in the proof, convergence of $n(t)$ to $\overline{n}$ does not always follow with our mere assumptions but is true for large class of data ($r$ and $K$). Then the uniqueness of the ESD follows and also the convergence of the population to the ESD. This shows that the systems under consideration are very particular because, in general, ESD are not always Convergence Stable Distributions (see [49, 111] and the references therein).

**Proof**. For system (5.1). With our assumptions we can define the Lyapunov functional

$$S(t) = -\int \overline{n}(x) \ln n(x,t)dx - \int \overline{R}(y) \ln R(y,t)dy + \int n(x,t)dx + \int R(y,t)dy,$$

and $S$ is bounded from below (because we assume that $\overline{n}$ is bounded). Using (5.24), we compute

$$\frac{dS}{dt}(t) = -\int \frac{R_{\text{in}}(y)}{\overline{R}(y)\, R(y,t)} \left(\overline{R}(y) - R(y,t)\right)^2 dy + \int n(x,t) \left( r(x) \int K(x,y)\overline{R}(y)dy - m_1(x) \right) dx. \tag{5.30}$$

Since $\text{supp}\, n(t,\cdot) \subseteq \text{supp}\, n^0$, assumption (5.29) shows that $S$ is a decreasing function. It follows that as $t \to \infty$, $S(t)$ converges to a finite value $\overline{S}$. We deduce that

$$\int_0^\infty \int \frac{R_{\text{in}}(y)}{\overline{R}(y)\, R(y,t)} \left(\overline{R}(y) - R(y,t)\right)^2 dy\, dt < +\infty. \tag{5.31}$$

Following the arguments in the proof of Theorem 5.3.2, we conclude that

$$\lim_{t\to\infty} R(y,t) = \overline{R}(y), \qquad \text{a.e.}$$

Furthurmore, since subsequences $n(t_k)$ converges weakly in the sense of measures to $\widetilde{n}$, following the proof of Theorem 5.3.2, we have

$$\overline{R}(y) = \frac{R_{\text{in}}(y)}{m_2(y) + \int r(x)K(x,y)\widetilde{n}(x,t)dx}.$$

This implies that for all $y$, $\int r(x)K(x,y)\widetilde{n}(x,t)dx = \int r(x)K(x,y)\overline{n}(x)dx$. However, our assumptions are not strong enough to conclude that $\widetilde{n}(x,t) \equiv \overline{n}(x)$; some operator invertibility is needed as in [74].

For system (5.2). We use the Lyapunov functional

$$S(t) = -\int \overline{n}(x)\ln n(x,t)dx + \int n(x,t)dx.$$

It still satisfies (5.30) and we can apply the same method as before. $\square$

### 5.5.2 Population dynamics of monomorphic states

With a variant of this method we can also study the solutions of the form $n(x,t) = \rho(t)\delta(x-\bar{x})$ corresponding to an initial data $n^0 = \rho^0\delta(x-\bar{x})$; indeed such a data does not satisfy the assumptions of Theorem 5.5.2 because $\ln n^0$ is not well defined.

**Theorem 5.5.3** *For the solutions of the form $n(t) = \rho(t)\delta(x-\bar{x})$ with $\bar{x}$ satisfying* (5.25)*, the population converges to the unique monomorphic steady state in Theorem 5.4.2, i.e. $\rho(t) \to \overline{\rho}$ and $R(y,t) \to \overline{R}(y)$ as $t \to \infty$, with $\overline{R}(y) = \frac{R_{\text{in}}(y)}{m_2(y)+r(\bar{x})\overline{\rho}K(\bar{x},y)}$.*

**Proof**. We treat only the case of system (5.1) and use the Lyapunov functional

$$S(t) = -\overline{\rho}\ln\rho(t) - \int \overline{R}(y)\ln\left(R(y,t)\right)dy + \rho(t) + \int R(y,t)dy,$$

$$\frac{dS}{dt}(t) = -\int \frac{R_{\text{in}}(y)}{\overline{R}(y)\;R(y,t)}\left(\overline{R}(y) - R(y,t)\right)^2 dy.$$

With similar arguments as above we obtain that $R(y,t) \underset{t\to\infty}{\longrightarrow} \overline{R}(y)$. Since there exists a unique constant $\overline{\rho}$ such that $\overline{R}(y) = \frac{R_{\text{in}}(y)}{m_2(y)+r(\bar{x})\overline{\rho}K(\bar{x},y)}$, following again the arguments in the proof of Theorem 5.5.2 we obtain that $\rho(t) \underset{t\to 0}{\longrightarrow} \overline{\rho}$. $\square$

### 5.5.3 Condition for a monomorphic state to be an ESD

With the extension in [74], we may expect that Theorem 5.5.2 applies in particular for monomorphic steady states. We consider such a monomorphic distribution $\overline{n} = \overline{\rho}\delta(x)$, restricting ourselves to a population concentrated in the origin and give a condition implying that it is evolutionary stable. Here, to simplify the analysis, we consider only the 'gaussian' case given in (5.3).

Along with section 5.4.2, we need the non-extinction condition (5.26) with $\bar{x} = 0$, that is

$$\frac{\overline{m}_1\overline{m}_2}{rM_{\text{in}}}\sqrt{2\pi} < \frac{1}{\sqrt{\sigma_{\text{in}}^2 + \sigma_K^2}}. \tag{5.32}$$

To check that the ESD condition holds locally, it is enough to check the sign of the second derivative of the fitness function (see Appendix 5.9.1). The exact condition is given by formula (5.60) which is not tractable. That is why we compute an easier sufficient condition given by the

**Theorem 5.5.4 (Sufficient condition for ESD)** *Consider the gaussian case* (5.3) *with the condition* (5.32). *Let* $n = \overline{\rho}\delta$ *with* $\overline{\rho}$ *as in* (5.27) *be a steady state. We additionally assume that*

$$\frac{\sigma_{\text{in}}^2}{(\sigma_{\text{in}}^2+\sigma_K^2)^{\frac{3}{2}}} < \frac{\overline{m}_1\overline{m}_2}{rM_{\text{in}}}\sqrt{2\pi}. \tag{5.33}$$

*Then the monomorphic state* $n = \overline{\rho}\delta_0$ *is a local ESD to system* (5.1) *with* $\varepsilon = 0$, *in other words for* supp $n^0 \supset \{0\}$ *small enough then* (5.29) *holds.*

This Theorem involves technical calculations and we prove it in Appendix 5.9.1.

In conclusion for $n = \overline{\rho}\delta_0$ to be an ESD, using (5.32), it is enough that

$$\frac{\sigma_{\text{in}}^2}{(\sigma_{\text{in}}^2+\sigma_K^2)^{\frac{3}{2}}} < \frac{\overline{m}_1\overline{m}_2}{rM_{\text{in}}}\sqrt{2\pi} < \frac{1}{\sqrt{\sigma_{\text{in}}^2+\sigma_K^2}}. \tag{5.34}$$

Roughly, it means that $\sigma_K$ is large enough compared to $\sigma_{\text{in}}$. In biological words, when the outflow rate is not too big and the resource supply distribution has a sharper peak than the competition kernel, then the species distribution is isolated.

The condition (5.34) is not a necessary condition for an ESD. We give an example where the condition is not satisfied but the origin is nevertheless an ESD. We consider the following parameter values

$$\sigma_K = 1, \qquad \sigma_{\text{in}} = 1, \qquad \overline{m}_1 = 0.5, \qquad \overline{m}_2 = 0.5, \qquad M_{\text{in}} = 3, \qquad r = 1.$$

We can easily verify that the condition (5.34) is not satisfied with these parameters. However as we see in Figure 5.3 the population goes to the origin and remains there. This is due to the estimations that we have used in our calculations. In this particular case we can compute numerically the second derivative of the fitness function using (5.60) in Appendix 5.9.1

$$D^2F_0(0) = -\frac{\overline{m}_1}{\sigma_K^2} + \frac{rM_{\text{in}}}{2\pi\sigma_K^5\sigma_{\text{in}}}\int x^2\,\frac{e^{\frac{-x^2}{2}\left(\frac{1}{\sigma_K^2}+\frac{1}{\sigma_{\text{in}}^2}\right)}}{\overline{m}_2+\overline{\rho}K(-x)}dx \approx -0.16,$$

where we estimate numerically $\overline{\rho} \approx 3.9$. This confirms that the origin is an ESD.

If we decrease $\sigma_K$ to 0.5 the origin is not ESD anymore and we observe a branching. In this case not only the condition (5.34) is satisfied but the exact amount of $D^2F_0(0) \approx 0.59$ is also positive and we estimate numerically $\overline{\rho} \approx 3.2$. This is in accordance with numerical results in Figure 5.3.

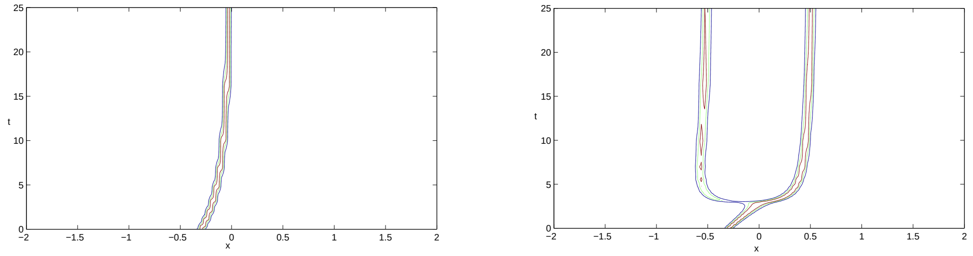

Figure 5.3: Dynamics of dominant traits begining with an initial data concentrated in −0.3. We present the dynamics of the model given in (5.2) in the particular case of (5.3) with $\varepsilon = 0.001$, $\sigma_{\text{in}} = 1$, $r = 1$, $\overline{m}_1 = \overline{m}_2 = 0.5$, $M_{\text{in}} = 3$. Left $\sigma_K = 1$. Right $\sigma_K = .5$. We observe that for $\sigma_{\text{in}}$ large comparing to $\sigma_K$ the monomorphic case is no more evolutionary attractor and we observe branching.

## 5.6 Dynamics of the fittest traits: an asymptotic point of view

We have shown that the model has monomorphic or polymorphic steady states and derived the sufficient condition for a monomorphic distribution (Dirac mass) to be evolutionarily stable. To obtain a stronger result than merely local stability, here we consider a case when a population is initially concentrated around one or several points in trait space. We establish that it stays concentrated and, using asymptotic analysis, that the fittest traits follow a form of canonical equation. We also give conditions implying that the population becomes monomorphic.

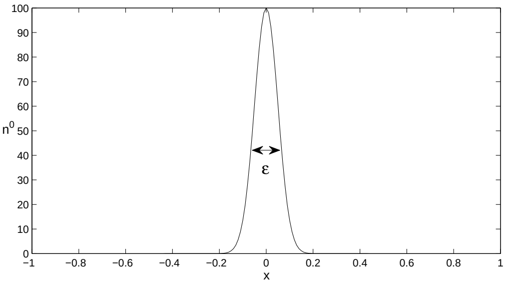

Figure 5.4: The parameter $\varepsilon$ in (5.36) measures how close is the distribution from the Dirac distribution, possibly due to mutations or, as considered here, initial variations.

We are interested in the dynamics with an initial data 'close' to a monomorphic or polymorphic state

$$n_\varepsilon(x,0) \approx \sum_{i=1,\dots,I} \overline{\rho}_i^0 \delta(x - \bar{x}_i^0).$$

To track the movements of $\bar{x}_i$ (i.e., evolutionary dynamics of traits), the initial data are chosen as a sum of concentrations with tails (non-zero variances in trait values). A parameter $\varepsilon$ denotes a small deviation of the initial data from the corresponding strictly monomorphic/polymorphic states (Dirac masses), see Figure 5.4. We also perform a change of variable $\tau = \varepsilon t$ in order to accelerate time and observe the dynamics. Note that the scaling parameter $\varepsilon$ here is no longer a mutation rate. Mathematically, however, the existence of continuously positive distribution is sufficient to track evolutionary dynamics. With this new time, the quasi-static model becomes

$$\begin{cases} \frac{\partial}{\partial \tau} n_\varepsilon = \frac{n_\varepsilon}{\varepsilon}\big( - m_1(x) + r(x) \int K(x,y) R_\varepsilon(y,\tau) dy \big), \\ R_\varepsilon(y,\tau) = \frac{R_{\text{in}}(y)}{m_2(y) + \int r(x) K(x,y) n_\varepsilon(x,\tau) dx}. \end{cases} \tag{5.35}$$

Starting from these approximately monomorphic/polymorphic populations, we show that under some assumptions the number of concentrated peaks does not change in time and no evolutionary branching can happen. However the dominant traits can evolve in time and we can describe the motion of these dominant traits with a Hamilton-Jacobi equation. We also obtain a minimum distance between the dominant traits. In section 5.6.2 we give a form of a canonical equation of the dominant traits. These results correspond to the convergence stability in Adaptive Dynamics, and the biological implications are discussed in section 5.6.3.

### 5.6.1 Polymorophic dynamics: mathematical results

According to the usual approximation of Dirac masses by gaussians, we describe it by the properties of the population potential $\varphi^0_\varepsilon(x)$ in

$$n_\varepsilon(x,0)=e^{\frac{\varphi^0_\varepsilon(x)}{\varepsilon}}. \tag{5.36}$$

The theory developed from [50] for the Lotka-Volterra equations shows that the representation $\varphi_\varepsilon(x,t):=\varepsilon\ln\big(n_\varepsilon(x,t)\big)$ makes sense for all times because it satisfies the simple equation

$$\frac{\partial}{\partial\tau}\varphi_\varepsilon(x,\tau)=-m_1(x)+r(x)\int K(x,y)R_\varepsilon(y,\tau)dy. \tag{5.37}$$

Of course there is a shortcoming in this point of view because the scaling parameter $\varepsilon>0$ is defined through the initial data which seems arbitrary. The real motivation is from modeling of mutations which we know induces this type of smoothing of the population density. See [50, 11, 103, 28]. It has been widely proved that the method may handle these mutations as well in self-contained population models as (5.1), (5.2).

Our main characterization of the population density goes through the function $\varphi_\varepsilon$ and we assume that initially

$$|\varphi^0_\varepsilon(x)|\leq C_0(R),\quad |\nabla\varphi^0_\varepsilon(x)|\leq C_1(R),\quad \forall|x|\leq R. \tag{5.38}$$

As a preliminary result, we prove in Appendix 5.9.3 the following

**Proposition 5.6.1 (Convergence)** *With the assumptions* (5.4), (5.6), (5.9), (5.8), (5.11) *and* (5.38), *after successive extractions of subsequences, the family $\varphi_\varepsilon$ converges locally uniformly to a continuous function $\varphi\leq 0$, the family $R_\varepsilon$ converges locally uniformly in space and weakly in time to a limit $R(y,\tau)$. Furthermore, we have the relation*

$$\varphi(x,\tau)=\varphi^0(x)-m_1(x)\tau+r(x)\int_0^\tau\int K(x,y)R(y,s)dyds,\qquad \varphi(x,\tau)\leq 0. \tag{5.39}$$

With these assumptions, the conclusion of Theorem 5.3.1 holds and we may extract a subsequence $(n_{\varepsilon'})_{\varepsilon'}$ that converges weakly in the sense of measures to a limit $n(x,\tau)$. The support of $n$ is included in the set $\{(\tau,x)|\varphi(x,\tau)=0\}$ (see [50, 103, 45, 84] for several uses of this property). We show below that the zeros of $\varphi(\tau)$ are isolated points, and thus the model leads to Dirac concentrations.

**Theorem 5.6.2 (Concentration effects)** *We assume that, for some constants $a_0$ and $\mu_1$,*

$$\varphi^0_{\varepsilon,xx}(x)-\mu_1\,\varphi^0_\varepsilon(x)\leq a_0. \tag{5.40}$$

*(i) If there is $a_1>0$ and $\mu_2\geq 0$ such that*

$$m_1''(x)-m_1(x)\mu_1-\int\frac{\mu_2(y)}{m_2(y)}R_{\text{in}}(y)dy\geq a_1,\qquad \big(r(x)K(x,y)\big)_{xx}\leq\mu_1 r(x)K(x,y)+\mu_2(y). \tag{5.41}$$

*Then we have*

$$\varphi_{xx}-\mu_1\,\varphi\leq a_0-a_1\tau, \tag{5.42}$$

*in the distributional sense and a.e. In particular if $a_0\leq 0$, then we have $\varphi_{xx}-\mu_1\varphi\leq 0$ and thus, after extraction of a subsequence, the $n_\varepsilon$'s converge in the weak sense of measures to a sum of Dirac masses:*

$$n_\varepsilon(x,\tau)\rightharpoonup n(x,\tau)=\sum_i\overline{\rho}_i(\tau)\delta_i(x-\bar{x}_i(\tau)). \tag{5.43}$$

*(ii) If* (5.41) *is hold with* $\mu_1 \geq 0$ *then, the population, when it persists, is asymptotically monomorphic:*

$$n_\varepsilon(x,\tau) \rightharpoonup n(x,\tau) = \overline{\rho}(\tau)\delta(x - \bar{x}(\tau)), \tag{5.44}$$

*and the pair* $(\bar{x}(\tau), \overline{\rho}(\tau))$ *also satisfies*

$$\overline{\rho}(\tau)\left(-m_1\big(\bar{x}(\tau)\big) + r(\bar{x}(\tau))\int K\big(\bar{x}(\tau), y\big)R(y,\tau)dy\right) \geq 0. \tag{5.45}$$

Also, the equation for $R(y,\tau)$ can be reduced to

$$R(y,\tau) = \frac{R_{\text{in}}(y)}{m_2(y) + \sum_i \overline{\rho}_i(\tau)r(\bar{x}_i(\tau))K(\bar{x}_i(\tau),y)} \qquad \text{(polymorphic case)}, \tag{5.46}$$

$$R(y,\tau) = \frac{R_{\text{in}}(y)}{m_2(y) + \overline{\rho}(\tau)r(\bar{x}(\tau))K(\bar{x}(\tau),y)} \qquad \text{(monomorphic case)}. \tag{5.47}$$

In order to illustrate our assumptions, we may consider the case when

$$\begin{array}{lll} r(x) = r_0, & m_1(x) = \widetilde{m}_0 + \widetilde{m}_1 \frac{|x|^2}{2}, & \widetilde{m}_2(y) \geq m_2, \\ R_{\text{in}} = \frac{M_{\text{in}}}{\sigma_{\text{in}}\sqrt{2\pi}} \exp(-\frac{y^2}{2\sigma_{\text{in}}^2}), & K(z) = \frac{1}{\sigma_K\sqrt{2\pi}} \exp(-\frac{z^2}{2\sigma_K^2}) & \end{array}$$

and $K(x,y) = K(x-y)$. We compute

$$K_{xx} = \left[-\frac{1}{\sigma_K^2} + \frac{|z|^2}{\sigma_K^4}\right]K, \qquad \mu_1 = 0, \quad \mu_2 = \frac{C}{\sigma_K^3}.$$

Therefore $\widetilde{m}_1\widetilde{m}_2$ large enough compared to $\frac{M_{\text{in}}}{\sigma_K^3}$ implies monomorphism.

We can also take $\widetilde{m}_1 = 0$, i.e., $m_1$ constant, $\mu_1 = -\frac{1}{\sigma_K^2}$. Then, $\frac{\widetilde{m}_0}{\sigma_K^2}$ large enough compared to $\frac{M_{\text{in}}}{\sigma_K^3\widetilde{m}_2}$ implies polymorphism but not continuous distribution.

**Proof**. We differentiate twice equation (5.37) and using (5.41) we obtain

$$\begin{aligned} \frac{\partial}{\partial\tau}\varphi_{\varepsilon,xx} &= -m_1''(x) + \int \big(r(x)K(x,y)\big)_{xx} R_\varepsilon(y,\tau)dy \\ &\leq -m_1''(x) + \mu_1 \int r(x)K(x,y)R_\varepsilon(y,\tau)dy + \int \mu_2(y)R_\varepsilon(y,\tau)dy \\ &\leq -m_1''(x) + \mu_1 m_1(x) + \mu_1\frac{\partial}{\partial\tau}\varphi_\varepsilon(x,\tau) + \int \frac{\mu_2(y)}{m_2(y)}R_{\text{in}}(y)dy. \end{aligned}$$

We deduce that, using again (5.41),

$$\frac{\partial}{\partial\tau}\big(\varphi_{xx} - \mu_1\varphi\big) \leq -m_1''(x) + \mu_1 m_1(x) + \int \frac{\mu_2(y)}{m_2(y)}R_{\text{in}}(y)dy \leq -a_1.$$

Therefore, using (5.40), we have

$$\varphi_{xx} - \mu_1\varphi \leq a_0 - a_1\tau.$$

In particular, if $a_0 \leq 0$, we deduce that $\varphi_{xx} < 0$ in the set $\{(t,x)|\varphi(\tau,x) = 0\}$. Therefore the zeros of $\varphi$ are isolated. Since the support of $n$ is included in this set, we conclude that $n$ is a sum of Dirac masses as stated in (5.43).

Furthermore if $\mu_1 \geq 0$ then we deduce that $\varphi \leq 0$ is a strictly concave function with respect to $x$. Thus it has a unique maximum. We conclude that the population, if it does not go extinct, is monomorphic as stated in (5.44).

Finally, we integrate (5.35) and obtain

$$\varepsilon \frac{d}{d\tau}\overline{\rho}(\tau) = -\int n_\varepsilon(\tau,x)m_1(x)dx + \int\int n_\varepsilon(\tau,x)r(x)K(x,y)\frac{R_{\text{in}}(y)}{m_2(y) + \int r(x')K(x',y)n_\varepsilon(\tau,x')dx'}dydx.$$

Passing to the weak limit we obtain that

$$\begin{aligned} 0 &= -\overline{\rho}(\tau)m_1(\bar{x}(\tau)) + \text{w-}\lim \int\int n_\varepsilon(\tau,x)r(x)K(x,y)\frac{R_{\text{in}}(y)}{m_2(y) + \int r(x')K(x',y)n_\varepsilon(\tau,x')dx'}dydx \\ &\leq \overline{\rho}(\tau)\left(-m_1(\bar{x}(\tau)) + \int r\left(\bar{x}(\tau)\right)K(\bar{x}(\tau),y)\frac{R_{\text{in}}(y)}{m_2(y) + \overline{\rho}(\tau)r\left(\bar{x}(\tau)\right)K(\bar{x}(\tau),y)}dy\right). \end{aligned}$$

Hence (5.45). □

### 5.6.2 A form of canonical equation

Within the framework of Section 5.6.1 we can go further and obtain several informations on the dynamics of the fittest trait, including a form of canonical equation as proposed initially in [47] (see also [50, 84]). For this, we need some additional regularity which relies on the assumptions

$$|D^3\varphi^0(x)| \leq D_1, \qquad |D^3 m(x)| \leq D_2, \qquad |D_x^3 K(x,y)| \leq D_3, \qquad |D^3 r(x)| \leq D_4. \tag{5.48}$$

This implies that $\varphi$ and $R$ also have bounded third derivatives in $x$. We also need the following additional assumption on the initial data

$$-m_1(\bar{x}(0)) + r(\bar{x}(0))\int K(\bar{x}(0),y)\frac{R_{\text{in}}(y)}{m_2(y)}dy > 0. \tag{5.49}$$

Within the framework of Theorem 5.6.2 and in the monomorphic case we prove the following

**Theorem 5.6.3 (Form of canonical equation)** *We assume* (5.48), (5.49) *and* (5.41) *with* $\mu_1 \geq 0$, (5.40) *with* $a_0 \leq 0$ *and thus* (5.44). *Then,* $\bar{x} \in W^{1,\infty}$ *and the following form of canonical equation for the fittest trait holds*

$$\dot{\bar{x}}(\tau) = \big(-D^2\varphi(\bar{x}(\tau),\tau)\big)^{-1}\left(-\nabla m_1(\bar{x}(\tau)) + r\left(\bar{x}(\tau)\right)\int \nabla_x K(\bar{x}(\tau),y)R(y,\tau)dy \right.$$
$$\left. + \nabla r\left(\bar{x}(\tau)\right)\int K(\bar{x}(\tau),y)R(y,\tau)dy\right). \tag{5.50}$$

*Moreover, the family* $\rho_\varepsilon$ *converges a.e. to* $\overline{\rho} \in W^{1,\infty}$*, and we have*

$$-m_1(\bar{x}(\tau)) + \int K(\bar{x}(\tau),y)R(y,\tau)dy = 0, \qquad R(y,\tau) = \frac{R_{\text{in}}(y)}{m_2(y) + \overline{\rho}(\tau)r(\bar{x}(\tau))K(\bar{x}(\tau),y)}, \tag{5.51}$$

$$\overline{\rho}(t) \geq \rho^0 e^{-K\tau}. \tag{5.52}$$

*In particular, we deduce that the population does not get extinct.*

This Theorem is proved in Appendix 5.9.4.

We notice that for any $(\tau, \bar{x}(\tau))$ there exists a unique $\overline{\rho}(\tau)$ such that (5.51) is satisfied. Therefore by eliminating $\overline{\rho}(\tau)$ from the canonical equation (5.50) we obtain an equation that depends only on the parameter $\bar{x}(\tau)$. However, we cannot write the canonical equation explicitly because the formula for $\overline{\rho}(\tau)$ is implicit.

We may also write canonical equations for dominant traits for the case with polymorphic populations within the framework of Section 5.6.1 when there are only a finite number of traits. We obtain the set of constraints and, with $R(y,t)$ given in (5.46), the canonical equation

$$\dot{\bar{x}}_i(\tau) = \big( - D^2\varphi(\bar{x}_i(\tau),\tau)\big)^{-1} \quad \Big( -\nabla m_1(\bar{x}_i(\tau)) + r\left(\bar{x}_i(\tau)\right) \int \nabla_x K(\bar{x}_i(\tau),y)R(y,\tau)dy \\ + \nabla r\left(\bar{x}_i(\tau)\right) \int K(\bar{x}_i(\tau),y)R(y,\tau)dy \Big). \tag{5.53}$$

## 5.6.3 Biological implications: Generation of species

We point out that our mathematical results in the previous sections hold for the model (5.35), where there is no mutation. Including mutations introduced a major additional difficulty with a term $|\nabla\varphi|^2$ that is against concavity. In [84], we could handle it for monomorphic populations with smallness assumptions which seem difficult to extend in the situation at hand. We now give the biological implications of our mathematical result and focus on the following two points.

(i) The interpretation of the trait concentration in terms of the function $\varphi$ is

$$n_\varepsilon(x,\tau) \approx \sum_{i=1,\dots,I} \rho_i(\tau)\delta(x-\bar{x}_i(\tau)) \Longleftrightarrow \max_x \varphi(x,\tau) = 0 = \varphi\big(\bar{x}_i(\tau),\tau\big). \tag{5.54}$$

But at the points such that $\varphi\big(\bar{x}_i(\tau),\tau\big) = 0$ for $\tau > \tau_0 := \frac{a_0}{a_1}$, using Theorem 5.6.2, we have

$$\varphi_{xx}\big(\bar{x}_i(\tau),\tau\big) \le -a_1(\tau-\tau_0) < 0.$$

We deduce that for $\tau > \tau_0$, the zeros of $\varphi$ are isolated. Therefore $n(\tau,x)$ is in the form of a sum of Dirac masses after $\tau > \tau_0$ (to be rigorous we need to complement our assumptions to ensure that $\varphi$ has three derivatives in $x$; this follows when data have three derivatives).

(ii) We can also give a minimal distance between two Dirac masses after time $\tau_0$, using the uniform Lipschitz bound on $\varphi$, see Appendix 5.9.3. Let $\varphi\big(\tau, x_i(\tau)\big) = 0$. We have

$$\begin{aligned} \varphi_{xx}(\tau,x) &\le a_0 - a_1\tau + \mu_1\, \varphi(\tau,x) \\ &\le a_0 - a_1\tau + \frac{(C_1+B_1\tau)}{\mu_1}\, |x-x_i(\tau)|. \end{aligned}$$

We deduce that $\varphi_{xx}(\tau,x) < 0$ for

$$|x-x_i(\tau)| < \frac{a_1\tau - a_0}{B_1\tau + C_1}.$$

Therefore the minimal distance between two Dirac masses at time $t$ is

$$|x_i(\tau) - x_{i+1}(\tau)| \le 2\frac{a_1\tau - a_0}{B_1\tau + C_1}. \tag{5.55}$$

Biologically, these two results mean that distinct species remain distinct after the finite time $\tau_0$. We can not observe any continuous branching or merging for $\tau > \tau_0$, because at the point where branching (or merging) happens the two new (or previous) Dirac masses will be (have been) very near each other for a while. But according to (ii) this cannot happen. Thus, the number of species does not increase (but can decrease because extinction is still possible) after this threshold time (although their trait values might keep moving). Evolutionary diversification (generation of new species) must finish until this time, so $\tau_0$ can be considered as a time scale of evolution.

Note that $\tau_0$ is measured in a slower time-scale than $t$ in the full model. This is necessary as we take $\varepsilon \to 0$, corresponding to no mutation limit, otherwise evolution requires infinitely long time. Interestingly, we still observe the dynamics in finite time in this evolutionary time scale. What is unique to the present study is that we have shown the finite threshold time after which no structural change occurs in evolutionary dynamics. This is a non-trivial result because any quantity (especially selection gradient) does not depend explicitly on time except initial data, that are chosen infinitesimally close to Dirac masses.

In some individual-based simulations of evolution of species traits (see [73]), we observe endlessly-repeated extinctions and generations of species, i.e. recurrent adaptive radiations. This has been considered as a stochastic effect, but in principle this could be possible in deterministic system as well. Our result shows that such recurrent adaptive radiation never occurs in our system.

## 5.7 Transient from continuous distribution to Dirac mass

Here we extend the analysis in section 5.6 to more general initial distribution. We give details on how an initially continuous population becomes approximately monomorphic/polymorphic in large time. Once this stage is reached, all the results and biological implications in the previous section are valid. Hence, this section is a natural extension of our results to relax our assumption of approximately monomorphic/polymorphic initial data.

We come back to the quasi-static model

$$\begin{cases} \frac{\partial n(x,t)}{\partial t} = n(x,t)\left(-m_1(x) + r(x)\int K(x,y)R(y,t)dy\right), \\ R(y,t) = \frac{R_{\text{in}}(y)}{m_2(y)+\int r(x')K(x',y)n(x',t)dx'}. \end{cases} \tag{5.56}$$

We aim to show that for large times, the population density behaves like a highly concentrated gaussian around an unknow fittest trait $\bar{x}(t)$, by example

$$n(x,t) \approx \frac{\overline{\rho}(t)}{\sqrt{2\pi t}} \exp\left(-\frac{|x-\bar{x}(t)|^2}{2t}\right).$$

The model does not impose such a quadratic type of concentration to a Dirac mass and we have to generalize the approximation as

$$n(x,t) \approx e^{\varphi(x,t)}, \qquad \text{with } \varphi \text{ a uniformly concave function in } x.$$

Then $\bar{x}(t)$ is the point where $\max_x \varphi(x,t) = \varphi\big(\bar{x}(t),t\big)$.

### 5.7.1 Pointwise estimate on the population density

We continue our analysis and prove an upper bound on pointwise growth of the population.To do so, we use the population potential

$$\varphi(x,t) = \ln\big(n(x,t)\big). \tag{5.57}$$

Here, as in (5.38), we use the following assumptions initially

$$\varphi(x,0) \le C_0, \qquad |\varphi_x(x,0)| \le C_1, \qquad |\varphi_{xx}(x,0)| \le C_2. \tag{5.58}$$

**Proposition 5.7.1 (Pointwise esimate)** *Under assumptions* (5.4), (5.9), (5.5), (5.58) *and the first parts of* (5.6) *and* (5.11), *there is a constant* $A > 0$ *(depending on* $\underline{m}_2$, $M_1$, $r_M$, $r_0$, $r_2$, $K_2$, $K_M$, $M_{\text{in}}$, $C_0$, $C_1$*) such that at all points* $x$,

$$n(x,t) \leq (2+t)^A, \qquad \varphi(x,t) \leq A \ln(2+t).$$

It turns out that the reverse inequality and polynomial growth on $n(t)$ is indeed true under some additional assumption that we mention later. This Theorem is proved in Appendix 5.9.5. This Theorem is proved in Appendix 5.9.5.

### 5.7.2 Towards monomorphism or polymorphism

We are now ready to establish the result showing strong convergence to a monomorphic or polymorphic population.

**Theorem 5.7.2 (Sufficient condition for convergence to well-separated traits)** *With the above assumptions* (5.5)–(5.11), (5.58) *and*
*(i) If* (5.41) *holds with* $\mu_1 \geq 0$, *then* $\varphi$ *is concave for* $t$ *large enough and the population, if it persists, is asymptotically monomorphic, namely*

$$\limsup_{t\to\infty} \frac{\varphi_{xx}(x,t)}{t} \leq -a_1.$$

*(ii) If* (5.41) *holds with* $\mu_1 < 0$, *then*

$$\limsup_{t\to\infty} \frac{\varphi_{xx}(x,t) - \mu_1\varphi(x,t)}{t} \leq -a_1.$$

*Consequently, the population is concentrated on well separated traits and the distribution cannot be continuous.*

The unique maximum point $\bar{x}(t)$ of $\varphi(\cdot,t)$ defines the fittest (highest represented) trait. It might be that $\bar{x}(t)$ escapes to infinity for large times, as in the cannibalism model (see [49, 102] for instance).

**Proof**. We write

$$\frac{\partial}{\partial t}\varphi(x,t) = -m_1(x) + r(x)\int K(x,y)R(y,t)dy.$$

We differentiate twice this equation and, using (5.41), we find

$$\begin{aligned}
\frac{\partial}{\partial t}\varphi_{xx}(x,t) &= -m_1''(x) + \int (r(x)K(x,y))_{xx} R(y,t)dy \\
&\leq -m_1''(x) + \mu_1 \int r(x)K(x,y)R(y,t)dy + \int \mu_2(y)R(y,t)dy \\
&\leq -m_1''(x) + \mu_1 m_1(x) + \mu_1 \frac{\partial}{\partial t}\varphi(x,t) + \int \frac{\mu_2(y)}{m_2(y)} R_{\text{in}}(y)dy \\
&\leq -a_1 + \mu_1 \frac{\partial}{\partial t}\varphi(x,t)
\end{aligned}$$

Integrating in time, we obtain

$$\varphi_{xx}(x,t) \leq \varphi^0_{xx}(x) - a_1 t + \mu_1[\varphi(t,x) - \varphi^0(x)].$$

With the help of assumptions (5.58) and Theorem 5.7.1, we conclude the first case (monomorphism).

In the case $\mu_1 < 0$, we use the same computation and arrive at

$$\frac{\partial}{\partial t}[\varphi_{xx}(x,t) - \mu_1 \varphi(x,t)] \leq -m_1''(x) + \mu_1 m_1(x) + \int \frac{\mu_2(y)}{m_2(y)} R_{\text{in}}(y) dy \leq -a_1.$$

The conclusion follows as before. □

## 5.8 Discussion

Our motivation is to explore the mechanism of the evolution of distinct species in competition-driven speciation. By analyzing a model with species and resource both of which are characterized by continuous traits, we have shown some new mathematical results. Unlike direct-competition models, our resource-competition model never allows everywhere-positive distribution even with the Gaussian kernel. We also have shown, under some conditions, global convergence to the evolutionary stable distribution, in which the population is concentrated on well separated traits.

Several studies have shown that continuous distribution cannot be a biologically relevant outcome. For a very general class of models, [68] have shown that a model allowing coexistence of infinitely many strategies is structurally unstable, i.e. with small perturbations on the coefficients of the model, the continuous steady state disappears and becomes Dirac masses. We note that the results in our paper are different, since we do not state that continuous distributions are structurally unstable but everywhere-positive steady states do not exist and that a minimal distance between traits can be calculated. In section 7, we study the transient dynamics from continuous initial distribution. Even though we know continuous distribution is impossible outcome, we can still ask how such non-steady continuous distribution develops into non-continuous distribution, steady or not. Biologically, such setting is of great interest because the distribution must be continuous (due to mutation) for evolution to occur (Note that a new trait never appears if the initial distribution is already a sum of Dirac masses). The solution to eq.(1) is always continuous when mutation exists (finite $\varepsilon$). To apply a standard method of adaptive dynamics, showing (fast) convergence to a Dirac mass is an important step. Another question is how fast the system approaches to monomorphism or to separated polymorphism, which is also studied in section 7.

In nature, the mutation rate is usually small compared with the vital rates. Thus, some of our results obtained for $\varepsilon = 0$ are considered to be good indicators of the behavior of the full system. The system with $\varepsilon = 0$ and the limiting behavior of the system in the limit $\varepsilon \to 0$ are not the same. The analysis of the latter is more difficult. By some 're-interpretation' of $\varepsilon$ (section 6), we derived canonical equation on the dynamics of the trait.

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## 5.9 Appendix

### 5.9.1 Proof of Theorem 5.5.4

With the terminology in [49, 109], we define the fitness function as

$$F_0(x) = -\overline{m}_1 + r \int K(x-z) \frac{R_{\text{in}}(z)}{\overline{m}_2 + r\overline{\rho} K(-z)} dz. \tag{5.59}$$

Ii measures the invasion ability of a mutant $x$ when the residents are all at the origin. For an ESD concentrated at the origin, the fitness function must satisfy $DF_0(0) = F_0(0) = 0$ and $D^2F_0(0) < 0$.

As we computed it in section 5.4.2, the condition $F_0(0) = 0$ follows from the choice of the weight $\overline{\rho}$ of the Dirac mass $\overline{n} = \overline{\rho}\delta$, which can also be written

$$\overline{m}_1 = rK * R(0) = r\int K(y)\frac{R_{\text{in}}(y)}{\overline{m}_2 + r\overline{\rho}K(y)}dy.$$

We also have, since $DK$ is odd and $K$ and $R_{\text{in}}$ are even,

$$DF(0) = r\int DK(-y)\frac{R_{\text{in}}(y)}{\overline{m}_2 + r\overline{\rho}K(-y)}dy = 0.$$

Finally, we analyse the sign of

$$D^2F = rD^2K * R.$$

To do so, we perform some preliminary calculation

$$\overline{m}_1 = \frac{rM_{\text{in}}}{2\pi\sigma_K\sigma_{\text{in}}}\int\frac{e^{\frac{-x^2}{2}(\frac{1}{\sigma_K^2}+\frac{1}{\sigma_{\text{in}}^2})}}{\overline{m}_2 + \overline{\rho}K(x)}dx,$$

$$D^2K(x) = \frac{1}{\sigma_R^3\sqrt{2\pi}}(-1 + \frac{x^2}{\sigma_R^2})\exp(-\frac{x^2}{2\sigma_R^2}).$$

Therefore, the condition for a local ESD is

$$D^2F_0(0) = -\frac{\overline{m}_1}{\sigma_K^2} + \frac{rM_{\text{in}}}{2\pi\sigma_K^5\sigma_{\text{in}}}\int x^2\,\frac{e^{\frac{-x^2}{2}(\frac{1}{\sigma_K^2}+\frac{1}{\sigma_{\text{in}}^2})}}{\overline{m}_2 + \overline{\rho}K(-x)}dx < 0. \tag{5.60}$$

Define $\sigma' = \frac{\sigma_K\sigma_{\text{in}}}{\sqrt{\sigma_K^2+\sigma_{\text{in}}^2}}$. We have

$$\begin{aligned}
D^2F_0(0) &\leq -\frac{\overline{m}_1}{\sigma_K^2} + \frac{rM_{\text{in}}}{2\pi\sigma_K^5\sigma_{\text{in}}\overline{m}_2}\int x^2\,e^{\frac{-x^2}{2\sigma'^2}}\,dx \\
&= -\frac{\overline{m}_1}{\sigma_K^2} + \frac{rM_{\text{in}}\sigma'^3}{\sqrt{2\pi}\sigma_K^5\sigma_{\text{in}}\overline{m}_2} \\
&= -\frac{\overline{m}_1}{\sigma_K^2} + \frac{rM_{\text{in}}}{\sqrt{2\pi}\sigma_K^2\overline{m}_2}\cdot\frac{\sigma_{\text{in}}^2}{(\sigma_{\text{in}}^2+\sigma_K^2)^{\frac{3}{2}}}.
\end{aligned}$$

We deduce from this inequality that $D^2F_0(0) < 0$ under the condition (5.33). This condition is however not sharp because we neglected the helping term $\overline{\rho}K(-x)$.

### 5.9.2 Lipschitz bounds on $\varphi$

Several steps in our estimates use Lipschitz bounds on the function $\varphi$ or $\varphi_\varepsilon$ defined through the logarithmic transform.

First we show that $|\nabla\varphi|(x,t) \leq C_1 + B_1t$, for all $x$, and for $B_1$ a constant that we determine later. We replace $n = e^\varphi$ in (5.56) and find

$$\frac{\partial}{\partial t}\varphi = -m_1(x) + r(x)\int K(x,y)R(y,t)dy. \tag{5.61}$$

Differentiating this equation we obtain

$$\frac{\partial}{\partial t}\varphi_x = -m_{1,x}(x) + r(x)\int K_x(x,y)R(y,t)dy + r_x(x)\int K(x,y)R(y,t)dy.$$

Using (5.4), (5.9), (5.6), the second part of (5.5) and the first part of (5.11) we have

$$|\frac{\partial}{\partial t}\varphi_x| \leq M_1 + \frac{r_M K_2 M_{\text{in}}}{\underline{m}_2} + \frac{r_2 K_M M_{\text{in}}}{\underline{m}_2}.$$

From this and (5.58) we deduce that

$$|\varphi_x(x,t)| \leq C_1 + B_1 t, \qquad B_1 = M_1 + \frac{r_M K_2 M_{\text{in}}}{\underline{m}_2} + \frac{r_2 K_M M_{\text{in}}}{\underline{m}_2}. \tag{5.62}$$

### 5.9.3 Proof of Theorem 5.6.1

(i) **(Lipschitz bound in space for $\varphi_\varepsilon$)** We recall the inequality (5.62) proved earlier $|\nabla\varphi_\varepsilon(x,\tau)| \leq C_1 + B_1\tau$.

(ii) **(Lipschitz bound in time for $\varphi_\varepsilon$)** Using (5.4), the first part of (5.8) and (5.37) we have

$$-m_1(x) \leq \frac{\partial}{\partial\tau}\varphi_\varepsilon = -m_1(x) + r(x)\int K(x,y)R_\varepsilon(y,\tau)dy \leq \frac{r_M R_1}{\underline{m}_2}. \tag{5.63}$$

Since $m_1(x)$ is locally bounded, we obtain that $\frac{\partial}{\partial\tau}\varphi_\varepsilon$ is locally uniformly bounded.

(iii) **(Convergence of $\varphi_\varepsilon$)** Using (5.63) and (5.58) we deduce that $\varphi_\varepsilon$ are locally uniformly bounded and its derivatives also. Thanks to the Arzela-Ascoli Theorem, we can extract a subsequence that converges locally uniformly to a continuous function $\varphi$.

Moreover $\varphi$ can not take positive values. Otherwise $\rho_\varepsilon = \int n_\varepsilon dx$ blows up in the limit as $\varepsilon$ vanishes and this is in contradiction with Theorem 5.3.1 that states $\rho_\varepsilon$ is uniformly bounded.

(iv) **(Lipschitz bound in space for $R_\varepsilon$)** We differentiate the second line of (5.56) with respect to $x$ and we obtain

$$\nabla R_\varepsilon(y,\tau) = \frac{\nabla R_{\text{in}}(y)}{m_2(y) + \int r(x)K(x,y)n_\varepsilon(x,\tau)dy} - \frac{R_{\text{in}}(y)\big(\nabla m_2(y) + \int r(x)K_y(x,y)n_\varepsilon(x,\tau)dx\big)}{\big(m_2(y) + \int r(x)K(x,y)n_\varepsilon(x,\tau)dx\big)^2}.$$

Using this equality, (5.4), (5.6), (5.8), the second part of (5.11) and (5.16) we have

$$\begin{aligned}|\nabla R_\varepsilon(y,\tau)| &\leq \frac{|\nabla R_{\text{in}}(y)|}{\underline{m}_2} + \frac{|R_{\text{in}}|\big(|\nabla m_2(y)| + r_M \sup_{x,y}|K_y|\rho_\varepsilon(\tau)\big)}{\underline{m}_2^2}\\ &\leq \frac{R_2}{\underline{m}_2} + \frac{R_1}{\underline{m}_2^2}(M_2 + r_M K_3 \rho_M).\end{aligned}$$

Therefore $R_\varepsilon$ is uniformly Lipschitz continuous in space.

It is difficult to obtain time regularity and even in the case of two nutrients, the proof is extremely technical, see [33].

(v) **(Convergence of $R_\varepsilon$ and identification of the limit)** The first parts of (5.8) and (5.4) show that $R_\varepsilon$ is uniformly bounded. Using this property together with Lipschitz bound in space we obtain that, after extraction of a subsequence, the $R_\varepsilon$'s converge weakly in time and strongly in space.

Now using the strong convergence of $\varphi_\varepsilon$ and the weak convergence of $R_\varepsilon$ together with (5.37) we obtain (5.39).

### 5.9.4 Proof of Theorem 5.6.3

We follow the arguments in [84].

Using (5.37) and (5.48) we obtain that $D^3\varphi_\varepsilon(\tau,x)$ is bounded. Therefore, after extraction of subsequence, the $D^2\varphi_\varepsilon(\tau,x)$'s converge locally uniformly to $D^2\varphi(\tau,x)$. Using (5.42) with $\mu_1 \geq 0$, we obtain that $\varphi_\varepsilon$ is concave and thus it has a unique maximum. Now we denote by $\bar{x}_\varepsilon(\tau)$ the maximum point of $\varphi_\varepsilon$. We have $\nabla\varphi_\varepsilon(\bar{x}_\varepsilon(\tau),\tau)=0$ at a maximum point and thus (using the chain rule)

$$\frac{d}{d\tau}\nabla\varphi_\varepsilon(\bar{x}_\varepsilon(\tau),\tau) = 0 = \frac{\partial}{\partial\tau}\nabla\varphi_\varepsilon(\bar{x}_\varepsilon(\tau),\tau) + D^2\varphi_\varepsilon(\bar{x}_\varepsilon(\tau),\tau)\dot{\bar{x}}_\varepsilon(\tau).$$

From (5.42) we conclude that $D^2\varphi_\varepsilon(\bar{x}(\tau),\tau)$ is invertible. Therefore, combining the above equality and (5.37) we obtain

$$\begin{aligned}\tfrac{d}{d\tau}\bar{x}_\varepsilon(\tau) &= \big(-D^2\varphi_\varepsilon(\bar{x}_\varepsilon(\tau),\tau)\big)^{-1}\big(-\nabla m_1(\bar{x}_\varepsilon(\tau)) + r(\bar{x}_\varepsilon(\tau))\textstyle\int \nabla_x K(\bar{x}_\varepsilon(\tau),y)R_\varepsilon(y,\tau)dy\\ &\quad +\nabla r(\bar{x}(\tau))\textstyle\int K(\bar{x}_\varepsilon(\tau),y)R_\varepsilon(y,\tau)dy\big).\end{aligned}$$

It remains to pass to the limit as $\varepsilon$ vanishes. Firstly, from the strong convexity of $m_1$ (from assumption (5.41) with $\mu_1>0$) and (5.37) we conclude that $\bar{x}_\varepsilon(\tau)$ is uniformly bounded. Then, from the local bounds on $R$, we deduce that $\frac{d}{d\tau}\bar{x}_\varepsilon(\tau)$ is also uniformly bounded. It follows again from Arzela-Ascoli Theorem that we may extract a subsequence of $\bar{x}_\varepsilon(\cdot)$ that converges uniformly to a Lipschitz continuous function $\bar{x}(\cdot)$. Moreover using that the $D^2\varphi_\varepsilon$'s converge locally uniformly to $D^2\varphi$, and the $R_\varepsilon$'s converge weakly to $R$ we obtain that

$$\begin{aligned}\tfrac{d}{d\tau}\bar{x}(\tau) &= \big(-D^2\varphi(\bar{x}(\tau),\tau)\big)^{-1}\big(-\nabla m_1\big(\bar{x}(\tau)\big) + r(\bar{x}(\tau))\textstyle\int \nabla_x K(\bar{x}(\tau),y)R(y,\tau)dy\\ &\quad +\nabla r(\bar{x}(\tau))\textstyle\int K(\bar{x}(\tau),y)R(y,\tau)dy\big).\end{aligned}$$

Now we prove that $\varphi(\bar{x}(\tau),\tau)=0$ for all $\tau\geq 0$ and that $\overline{\rho}(\tau) > \overline{\rho}(0)e^{-K\tau}$ for all $\tau \geq 0$ and a positive constant $K$. We cannot obtain this directly and thus we begin with proving $l(\tau)\geq 0$, with

$$l(\tau) := -m_1(\bar{x}(\tau)) + r\left(\bar{x}(\tau)\right)\int K(\bar{x}(\tau),y)\frac{R_{\text{in}}(y)}{m_2(y)}dy.$$

We define

$$\tau_0 := \inf_{s\geq 0}\,\{l(s)=0\}.$$

Since $l(\tau)$ is continuous, and $l(0)>0$ according to assumption (5.49), we have $\tau_0>0$. Assume now that $\tau_0$ is finite. We have $l(\tau)\geq 0$ in $[0,\tau_0]$. Now we write

$$\frac{d}{d\tau}\varphi(\bar{x}(\tau),\tau) = \frac{\partial}{\partial\tau}\varphi(\bar{x}(\tau),\tau) = -m_1(\bar{x}(\tau)) + r\left(\bar{x}(\tau)\right)\int K(\bar{x}(\tau),y)\frac{R_{\text{in}}(y)}{m_2(y)+\overline{\rho}(\tau)r\left(\bar{x}(\tau)\right)K(\bar{x}(\tau),y)}dy.$$

The latter is positive if $\overline{\rho}$ is positive, according to (5.45). Otherwise it is equal to $l(\tau)$ that is also positive in $[0,\tau_0]$. We obtain that

$$\frac{d}{d\tau}\varphi(\bar{x}(\tau),\tau)\geq 0, \qquad \text{for } \tau\in[0,\tau_0].$$

Starting with $\varphi(\bar{x}(0),0)=0$, we deduce that

$$\varphi(\bar{x}(\tau),\tau)=0, \qquad \text{for } \tau\in[0,\tau_0].$$

This also shows that the constraint (5.51) is satisfied and (5.45) is hold as an equality in $(0,\tau_0)$. Consequently we obtain that $\overline{\rho}$ is in fact a strong limit of $\rho_\varepsilon$ in $(0,\tau_0)$.

To gain time regularity, we use (5.51) and because $\bar{x}(\tau)$ is Lipschitz continuous, we conclude that $\overline{\rho}(\tau)$ and consequently $R(y,\tau)$ are also Lipschitz continuous in $(0,\tau_0)$. Therefore we can differentiate (5.51) a.e. with respect to $\tau$ and obtain, for all $\tau \in [0,\tau_0)$,

$$
\begin{aligned}
0 = \big( - \nabla m_1(\bar{x}(\tau) + r\,(\bar{x}(\tau)) \int \nabla_x K(\bar{x}(\tau),y) \frac{R_{\text{in}}(y)}{m_2(y) + \overline{\rho}(t) r(\bar{x}(\tau)) K(\bar{x}(\tau),y)} dy\big) \dot{\bar{x}}(\tau) \\
+ \nabla r\,(\bar{x}(\tau)) \int K(\bar{x}(\tau),y) \frac{R_{\text{in}}(y)}{m_2(y) + \overline{\rho}(t) r(\bar{x}(t)) K(\bar{x}(t),y)} dy\big) \dot{\bar{x}}(\tau) \\
- \overline{\rho}(\tau) r(\bar{x}(\tau)) \big( \int K(\bar{x}(\tau),y) \frac{R_{\text{in}}(y) \big( r(\bar{x}(\tau)) \nabla_x K(\bar{x}(\tau),y) + \nabla r(\bar{x}(\tau)) K(\bar{x}(\tau),y) \big)}{\big( m_2(y) + \overline{\rho}(\tau) r(\bar{x}(\tau)) K(\bar{x}(\tau),y) \big)^2} dy\big) \dot{\bar{x}}(\tau) \\
- \big( r(\bar{x}(\tau))^2 \int K(\bar{x}(\tau),y)^2 \frac{R_{\text{in}}(y)}{\big( m_2(y) + \overline{\rho}(\tau) r(\bar{x}(\tau)) K(\bar{x}(\tau),y) \big)^2} dy\big) \dot{\overline{\rho}}(\tau).
\end{aligned}
$$

We deduce that, for a.e. $\tau \in (0,\tau_0)$,

$$
\begin{aligned}
\dot{\bar{x}}(\tau) \big( - D^2 \varphi(\bar{x}(\tau),\tau \big) \dot{\bar{x}}(\tau) \quad &= -\dot{\overline{\rho}}(\tau)\; r(\bar{x}(\tau))^2 \textstyle\int K(\bar{x}(\tau),y)^2 \frac{R_{\text{in}}(y)}{\big( m_2(y) + \overline{\rho}(\tau) r(\bar{x}(\tau)) K(\bar{x}(\tau),y) \big)^2} dy \\
&\quad - \overline{\rho}(\tau) r(\bar{x}(\tau)) \big( \textstyle\int K(\bar{x}(\tau),y) \frac{R_{\text{in}}(y) \big( r(\bar{x}(\tau)) \nabla_x K(\bar{x}(\tau),y) + \nabla r(\bar{x}(\tau)) K(\bar{x}(\tau),y) \big)}{\big( m_2(y) + \overline{\rho}(\tau) r(\bar{x}(\tau)) K(\bar{x}(\tau),y) \big)^2} dy \big) \dot{\bar{x}}(\tau).
\end{aligned}
$$

It follows that for some constant $K$

$$
\overline{\rho}(0) e^{-K\tau} \leq \overline{\rho}(\tau).
$$

We deduce that $\overline{\rho}(s) \geq \rho_1 > 0$, for $s \in (0,\tau_0)$. Using the constraint and the latter we obtain that, for all $s \in [0,\tau_0)$,

$$
\begin{aligned}
l(s) &\geq l(s) - \big( - m_1(\bar{x}(s)) + r(\bar{x}(s)) \int K(\bar{x}(s),y) R(s,y) dy \big) \\
&= \overline{\rho}(s) r(\bar{x}(s))^2 \int K(\bar{x}(s),y)^2 \frac{R_{\text{in}}(y)}{m_2(y) \big( m_2(y) + \overline{\rho}(s) r(\bar{x}(s) K(\bar{x}(s),y) \big)} dy \\
&\geq \rho_1 \int K(\bar{x}(s),y)^2 \frac{R_{\text{in}}(y)}{C} dy.
\end{aligned}
$$

The latter is bounded from below by a positive constant because $\bar{x}(s)$ is bounded. Using the continuity of $l$ we deduce that $l(\tau_0) > 0$. This is impossible and thus contradicts that $\tau_0$ is finite.

### 5.9.5 Proof of Theorem 5.7.1

Firstly we recall the Lipschitz bound (5.62) proved in Appendix 5.9.2.

Next, our proof of Theorem 5.7.1 uses again the equation (5.61) that we write

$$
\frac{\partial}{\partial t} \varphi(x,t) = -m_1(x) + \int \frac{r(x) K(x,y) R_{\text{in}}(y)}{m_2(y) + \int r(z) K(z,y) e^{\varphi(z,t)} dz} dy.
$$

And we introduce two sets for evaluating the integral in $y$, where $B$ is a constant given later on,

$$
E_< = \{y;\ K(x,y) \leq \frac{B}{2+t}\}, \qquad E_> = \{y;\ K(x,y) \geq \frac{B}{2+t}\}.
$$

On $E_<$ we have

$$
\frac{r(x) K(x,y) R_{\text{in}}(y)}{m_2(y) + \int K(z,y) e^{\varphi(z,t)} dz} \leq \frac{r_M B}{\underline{m}_2 (2+t)} R_{\text{in}}(y).
$$

On $E_>$ we have for some constant $B_2$, $B_3$,

$$\begin{aligned}\frac{r(x)K(x,y)R_{\text{in}}(y)}{m_2(y)+\int r(z)K(z,y)e^{\varphi(z,t)}dz} &\leq e^{-\varphi(x,t)}\frac{r_M K(x,y)R_{\text{in}}(y)}{r_0\int K(z,y)e^{\varphi(z,t)-\varphi(x,t)}dz}\\ &\leq e^{-\varphi(x,t)}\frac{r_M K(x,y)R_{\text{in}}(y)}{r_0\int K(z,y)e^{-|x-z|(C_1+B_1t)}dz}\\ &\leq e^{-\varphi(x,t)}\frac{r_M K(x,y)R_{\text{in}}(y)}{r_0\int[K(x,y)-K_2|x-z|]e^{-|x-z|(C_1+B_1t)}dz}\\ &\leq e^{-\varphi(x,t)}\frac{K(x,y)R_{\text{in}}(y)}{2B_2\frac{K(x,y)}{2+t}-\frac{B_3}{(2+t)^2}}\\ &\leq e^{-\varphi(x,t)}\frac{K(x,y)R_{\text{in}}(y)}{B_2\frac{K(x,y)}{2+t}}\end{aligned}$$

and this leads our choice of $B = B_3/B_2$.

Altogether, these two controls give

$$\frac{\partial}{\partial t}\varphi(x,t) \leq M_{\text{in}}[\frac{B}{\underline{m}_2(2+t)}+\frac{2+t}{B_2}e^{-\varphi(x,t)}].$$

A supersolution to this differential equation is $\psi(t) = A\ln(2+t)$ because for $A$ large enough

$$\frac{\partial}{\partial t}\psi(t) = \frac{A}{2+t} \geq M_{\text{in}}\left[\frac{B}{\underline{m}_2(2+t)}+\frac{1}{B_2(2+t)^{(A-1)}}\right], \qquad \psi(0) \geq \varphi^0(x).$$

Therefore for for $A$ large enough, we have $\varphi(x,t) \leq A\ln(t+2)$. Written in terms on $n = e^{\varphi}$ we obtain the conclusion of Theorem 5.7.1.

# Troisième partie

# Populations sexuées

# Chapitre 6

# Evolution et propagation de traits phénotypiques en espace

---

Le travail présenté dans ce chapitre a été effectué en collaboration avec Gaël Raoul. Nous étudions des populations sexuées structurées par un trait phénotypique et une variable d'espace, dans un environnement hétérogène. En partant d'un modèle de populations structurées, nous dérivons un modèle proche des modèles existants dans le domaine de la biologie théorique. Nous étudions ensuite la dynamique à l'aide d'un modèle simplifié qui suppose la non-extinction. Nous montrons que la population soit se propage à l'espace entier, soit survit, mais reste restreinte à une partie de l'espace. Celle-ci distingue la dynamique des populations sexuées de celle des populations asexuées, où à condition que la population survive, elle se propage à l'espace entier. Pour montrer la propagation de la population à l'espace entier, nous prouvons l'existence des fronts propagatifs qui connectent un point stationnaire instable à un point singulier. Ce chapitre est une partie de l'article [98].

---

## 6.1 Introduction

In this chapter, we are interested in sexual populations that are structured by a continuous phenotypic trait $v \in \mathbb{R}$ and a continuous space variable $x \in \mathbb{R}$, living in a non-homogeneous environment: we will consider a phenotypic trait of best adaptation $\theta(x)$ that depends on the space variable. This type of population has been studied in [100, 79, 101], using mostly numerical simulations.

This type of model can in particular be used to study the distribution of a species along an environmental gradient (such as the north-south gradient of temperature in the northern hemisphere). To study the range of the species and its local adaptation, one should consider both evolution and spatial dynamics (see [72, 79, 105, 15]). These models are also useful to study the impact of an environmental change (e.g. global warming) on a population (see [100, 79, 105]).

Our work is largely based on [79], and related articles [100, 101, 105]. In [79], a partial differential equation system describing the spatial and evolutionary dynamics of a population is introduced:

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \left(1 - \frac{1}{2}(Z(t,x) - Bx)^2 - N(t,x)\right) N(t,x), \\ \partial_t Z(t,x) - \Delta_x Z(t,x) = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x)). \end{cases} \tag{6.1}$$

Here $N(t,x)$ is the population density at the location $x$ and $Z(t,x)$ is the population's mean phenotypic trait. The parameter $A$ can be interpreted as the potential for adaptation to the local optimal trait and the parameter $B$ indicates how fast the environment is changing. Numerical simulations where run for this model, and they showed that depending on $A$ and $B$, three biological scenarios were possible:

- if $B$ is large (the environment changes rapidly in space), then the population goes extinct,
- for intermediate values of $B$, the population survives, but remains in a limited area,
- if $B$ is small, the population invades the whole space.

Here, we show how (6.1) (indeed, the closely related equations (6.14)) can be derived from a sexual structured population equation. We also introduce a simplified model that allows us to investigate the existence of propagative fronts and steady states, which correspond respectively to the cases where the population invades the whole space, or it remains confined in a limited area.

In Section 6.2, we introduce a structured population model for the evolution of sexual populations structured by both a phenotypic trait and a space variable. To construct this model, we add a spatial variable to a well established local selection-mutation equation (similarly to many kinetic models in physics or chemistry, see [119]). This structured population equation can also be seen as a continuous version of the model introduced in [101]. In the description, three parameters appear: $A$, $B$, $C$. The interpretation of $A$ and $B$ is as above. Assuming that $C$ is large, which means that many generations are necessary to obtain a significant growth of the population, we show that a model very close to (6.1) can be obtained as a formal limit of our structured population model (see equation (6.14)). We explain in Remark 6.2.3 why we could not obtain exactly the system (6.1).

Moreover, we consider a formal limit of (6.14) assuming that $A$ is small. This assumption is compatible with the values of $A$ considered in [79]. With this assumption, we obtain a simpler equation on $Z(t,x)$ only:

$$\begin{aligned}\partial_t Z(t,x) - \Delta_x Z(t,x) &= -4\frac{(\partial_x Z(t,x) - B/\sqrt{2})(Z(t,x) - (B/\sqrt{2})x)}{1-(Z(t,x)-(B/\sqrt{2})x)^2}\partial_x Z(t,x) \\ &\quad +((B/\sqrt{2})x - Z(t,x)). \qquad (6.2)\end{aligned}$$

In Section 6.3, we analyze the model (6.2) derived in Section 6.2. Unfortunately, this equation has singularities that are obstacles to have a well-defined problem: we show that viscosity solutions exist, but are not unique. However, the singularities are fundamental to produce propagative fronts. We indeed prove that propagative fronts exist that connect an unstable steady state to a singular point. Thereby this simple model allows us to describe two of the three possible scenarios from [79]: invasion fronts, and populations remaining in a limited area. The extinction phenomena cannot be observed here because of our assumption that $A$ is small.

## 6.2 Sexual populations

### 6.2.1 Structured population equation

We start from a classical model describing the evolution of a population structured by a phenotypic trait only (see e.g. [22, 51, 94], and [50, 45, 84] for mathematics properties of this kind of models). Let $n(t,v)$ be the density of the population of phenotypic trait $v \in \mathbb{R}$ at time $t \geq 0$. We assume that the fitness depends on the square of distance between $v$ and an optimal adaptation trait $\theta$, and is altered by the population size. If we do not take into account the effect of sexual reproduction, under the latter assumptions, the fitness $s[n(t,\cdot)](v)$ of an individual of phenotypic trait $v$, living among a resident population $n(t,\cdot)$, is given by:

$$s[n(t,\cdot)](v) = r_{max} - \frac{1}{2V_s}(v-\theta)^2 - \frac{r_{max}}{K}\int n(t,w)\,dw, \qquad (6.3)$$

Here $r_{max} > 0$ denotes the maximal growth rate of the population, $V_s$ measures the strength of the selection toward the optimal trait $\theta$, and $K$ is the carrying capacity of the environment.

The fitness is well-defined in the case of asexual populations: it is the rate of births of offsprings of trait $x$ minus the rate of death. In the case of sexual populations, however, the situation is more complicated, since reproduction requires two parents, of traits $v_*$ and $v'_*$, that give birth to an offspring of trait $v$, usually different from $v_*$ or $v'_*$. This has two consequences (see [21]):

- We need to define $Q(\cdot, v_*, v'_*)$, the distribution function of the trait of the offspring. We will analyze the properties of $Q$ in Subsection 6.2.2.
- We have to define the birth rate and the death rate separately. Here we assume that the birth rate is a constant, denoted by $\gamma > r_{max}$.

In this model, we do not distinguish between males and females (for instance because they have the same distribution) and assume that mating is random and uniform among the population. We also assume that the number of offspring is proportional to the population density, the idea being that the number of births is proportional to the number of females. Then the evolution of the population, structured by a phenotypic trait only, is described by (see [51]):

$$\begin{aligned}\partial_t n(t,v) &= \left[-(\gamma - r_{max}) - \frac{I_s}{2} - \frac{1}{2V_s}(v-\theta)^2 - \frac{r_{max}}{K}\int n(t,w)\,dw\right] n(t,v) \\ &\quad +\gamma \int\int \frac{n(t,v_*)n(t,v'_*)}{\int n(t,w)\,dw} Q(v,v_*,v'_*)\,dv_*\,dv'_*. \qquad (6.4)\end{aligned}$$

Here $\gamma$ is the birth rate ($\gamma \geq r_{max}$), that we assume constant within the population, (the selection occurs in the death term), and $\frac{I_s}{2}$ the additional death rate due to lethal mutations (see [79]).

We next consider populations that are structured by a phenotypic trait $v$ as above, but also by a space variable $x \in \mathbb{R}$. The density is then denoted by $n(t, x, v)$. We assume that the selection-mutation process described above occurs locally in space, but that individuals move randomly in space. We model this random movement by a diffusion of rate $\sigma_x$. We additionally assume that the trait of optimal adaptation changes linearly in space:

$$\theta(x) = bx. \tag{6.5}$$

We finally obtain the following model for sexual populations:

$$\begin{aligned} &\partial_t n(t,x,v) - \sigma_x^2 \Delta_x n(t,x,v) \\ &\quad = \left[ -(\gamma - r_{max}) - \frac{I_s}{2} - \frac{1}{2V_s}(v - bx)^2 - \frac{r_{max}}{K} \int n(t,x,w)\, dw \right] n(t,x,v) \\ &\qquad + \gamma \int \int \frac{n(t,x,v_*) n(t,x,v'_*)}{\int n(t,x,w)\, dw} Q(v, v_*, v'_*)\, dv_*\, dv'_*. \end{aligned} \tag{6.6}$$

For an existence theory for (6.6), we refer to [106].

### 6.2.2 Properties of the sexual reproduction kernel $Q$

In Subsection 6.2.3, we rescale (6.6) to show that it indeed only depends on three parameters. To be able to do so, we first need to define more precisely the reproduction kernel $Q$, and analyze its properties.

The sexual reproduction has two opposite effects on the repartition of the population over the phenotypic traits:

- For each set of two chromosomes, one comes from the parent of phenotypic trait $v_*$, and one from the parent of trait $v'_*$. This process tends to give the offspring a trait between $v_*$ and $v'_*$. The effect of this phenomenon is to concentrate the population traits.
- On the contrary, a variability is maintained in the population by mutations and recombinations. Recombination is the process, occurring by the crossing-over of chromosomes during meiosis, in which DNA is exchanged between a pair of chromosomes (notice that the effect of recombinations is typically much larger than the effect of mutations, see [22]).

A reasonable assumption is that in absence of selection, a sexual population phenotypic distribution converges to a given profile that only depends on $Q$. To make this assumption precise, we consider the homogeneous sexual reproduction model (6.4) without selection, and with a constant population size, that is

$$\begin{cases} \partial_t n(t,v) = \int \int Q(v, v_*, v'_*) n(t, v_*) n(t, v'_*)\, dv_*\, dv'_* - n(t,v) \\ n(0,v) = n^0(v) \in L^1(\mathbb{R}), \text{ with } \int n^0(v)\, dv = 1. \end{cases} \tag{6.7}$$

We also assume that the long-time dynamics of this model is simple in the sense that:

**Condition 1:**

- For any $v_*$, $v'_* \in \mathbb{R}$, we have $\int Q(v, v_*, v'_*)\, dv = 1$,
- For any $v_*$, $v'_* \in \mathbb{R}$, we have $\int v\, Q(v, v_*, v'_*)\, dv = \frac{v_* + v'_*}{2}$,

- There exists $G$ (from the *genetic variance*, see [79]) such that for any initial population $n^0$, the phenotypic variance of the population converges to $G$:

$$\int\left(v-\int w\,n^0(w)\,dw\right)^2 n(t,v)\,dv\to G^2,\ \text{as } t\to\infty,$$

- For any initial population $n^0$, the third moment of the phenotypic distribution of the population converges to 0:

$$\int\left(v-\int w\,n^0(w)\,dw\right)^3 n(t,v)\,dv\to 0,\ \text{as } t\to\infty.$$

We notice that the two first parts of Condition 1 imply that

$$\int vn(t,v)dv=\int vn^0(v)dv. \tag{6.8}$$

The reproduction kernel that is typically used in structured population models for sexual populations (see [21, 51]) is:

$$Q(v,v_*,v'_*):=\frac{1}{\gamma\sqrt{2\pi}}e^{-\frac{\left(v-\frac{v_*+v'_*}{2}\right)^2}{2\gamma^2}}. \tag{6.9}$$

We show that Condition 1 is satisfied for this particular reproduction kernel:

**Proposition 6.2.1** *Condition 1 is satisfied by the reproduction kernel defined in* (6.9)*, with* $G=\sqrt{2}\gamma$.

**Remark 6.2.2** *This condition is indeed hold true for a more general reproduction kernel* $Q(v,v_*,v'_*)=\left(\widetilde\Gamma*\widetilde Q(\cdot,v_*,v'_*)\right)(v)$*, where* $\widetilde\Gamma$ *is symmetrical with a positive variance,* $\widetilde Q(\frac{v_*+v'_*}{2}+v,v_*,v'_*)=\widetilde Q(\frac{v_*+v'_*}{2}-v,v_*,v'_*)$ *for any* $v$, $v_*$, $v'_*\in\mathbb{R}$*, and*

$$\int\left(v-\frac{v_*+v'_*}{2}\right)^2\widetilde Q(v,v_*,v'_*)\,dv=C\frac{(v_*-v'_*)^2}{4},$$

*with* $C<1$*. For this and more on this type of problem, we refer to [69, 86].*

**Proof of Proposition 6.2.1:** The two first parts of Condition 1 can be easily checked. We only prove the third and fourth.

We assume, without loss of generality, that $\int v\,n^0(v)=0$. Therefore according to (6.8) we have

$$\int v\,n(t,v)=0.$$

We multiply equation (6.7) by $v^2$ and integrate to obtain

$$\begin{aligned}\frac{d}{dt}\int v^2n(t,v)\,dv &= \int\int\left(\int v^2Q(v,v_*,v'_*)\,dv\right)n(t,v'_*)n(t,v_*)\,dv_*\,dv'_*-\int v^2n(t,v)dv\\ &= \int\int\left(\gamma^2+\left(\frac{v_*+v'_*}{2}\right)^2\right)n(t,v'_*)n(t,v_*)\,dv_*\,dv'_*-\int v^2n(t,v)dv\\ &= \gamma^2-\frac{1}{2}\int v^2n(t,v)dv.\end{aligned}$$

We deduce that the variance of $n$ converges to $G = \sqrt{2}\gamma$ for any initial condition $n^0$:

$$\int v^2 n(t,v)\,dv \to G^2 = 2\gamma^2, \text{ as } t \to \infty.$$

Similarly we have

$$\begin{aligned}
\frac{d}{dt}\int v^3 n(t,v)\,dv &= \int\!\!\int \left(\int v^3 Q(v,v_*,v_*')\,dv\right) n(t,v_*)n(t,v_*')\,dv_*\,dv_*' - \int v^3 n(t,v)dv \\
&= \int\!\!\int \left(\frac{v_*+v_*'}{2}\right)^3 n(t,v_*)n(t,v_*')\,dv_*\,dv_*' - \int v^3 n(t,v)dv \\
&= -\frac{3}{4}\int v^3 n(t,v)dv.
\end{aligned}$$

It follows that $\int v^3 n(t,v) \to 0$ as $t \to \infty$.

□

### 6.2.3 Rescaling of the structured population model

To simplify (6.6), we perform the following rescaling:

$$a_1 = \left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right), \qquad a_2 = \frac{1}{\sigma_x}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{\frac{1}{2}}, \qquad a_3 = \frac{1}{G},$$

$$\widetilde{n}(\widetilde{t},\widetilde{x},\widetilde{v}) = \frac{r_{max}G}{K}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-1} n\left(\frac{\widetilde{t}}{a_1},\frac{\widetilde{x}}{a_2},\frac{\widetilde{v}}{a_3}\right),$$

$$\widetilde{Q}(v,v_*,v_*') := G\,Q\left(Gv, Gv_*, Gv_*'\right),$$

where $G$ is given by Condition 1. We notice that, the rescaled reproduction kernel $\widetilde{Q}$ satisfies Condition 1 with $\widetilde{G} = 1$. With the above rescaling, (6.6) becomes:

$$\begin{aligned}
&\partial_t n(t,x,v) - \Delta_x n(t,x,v) \\
&\quad = -\left[(C - \frac{A}{2}) + \frac{A}{2}(v - Bx)^2 + \int n(t,x,w)\,dw\right] n(t,x,v) \\
&\quad\quad +(C+1)\int\!\!\int \frac{n(t,x,v_*)n(t,x,v_*')}{\int n(t,x,w)\,dw} Q(v,v_*,v_*')\,dv_*\,dv_*',
\end{aligned} \tag{6.10}$$

with

$$\begin{aligned}
A &:= \frac{G^2}{V_s}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-1}, \\
B &:= \frac{b\sigma_x}{G}\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-\frac{1}{2}}, \\
C &:= \gamma\left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-1} - 1.
\end{aligned}$$

Here the parameter $A$ can be interpreted as the potential for adaptation to the local optimal trait. The parameter $B$ indicates how fast the environment is changing. The parameter $C$ measures the ratio between the birth rate and the maximal growth rate of the total population.

**Remark 6.2.3** *This is not the only possible rescaling for this equation. As we will see in Subsection 6.2.4, this particular scaling will allow us to obtain* (6.14) *as a formal limit of* (6.10) *when $C$ is large. In [79], the authors perform another renormalization of* (6.1) *and they obtain only two parameters $A$ and $B$. The corresponding parameters are defined as:*

$$A = \frac{G}{2V_s(r_{max} - I_s/2)}, \quad B = \frac{\sigma_x b}{\sqrt{2V_s}(r_{max} - I_s/2)}.$$

*The scaling they use does not work here, because they assume that the rescaling in the variable $v$ does not modify $G$, the typical phenotypic variance of the phenotypic distribution of the population. While with* (6.6)*, $G$ is necessarily affected by a scaling in the $v$ variable (see Condition 1). This is also why we could not obtain exactly* (6.1)*, but the slightly different model* (6.14)*.*

### 6.2.4 Formal limit of the structured population model

We denote by $N$, $Z$, $V$ the following moments of the distribution $n(t,x,\cdot)$:

$$N(t,x) := \int n(t,x,v)\,dv, \quad Z(t,x) := \int v\frac{n(t,x,v)}{N(t,x)}\,dv,$$

$$V(t,x) := \int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\,dv.$$

We show that $N$ and $Z$ satisfy the following unclosed equations:

**Proposition 6.2.4** *If $n$ is a solution of* (6.10)*, then the moments of the phenotypic distribution of $n$ satisfy:*

$$\begin{aligned}&\partial_t N(t,x) - \Delta_x N(t,x)\\ &\quad= \left[1 + \frac{A}{2}(1 - V(t,x)) - \frac{A}{2}(Z(t,x) - Bx)^2 - N(t,x)\right] N(t,x).\end{aligned} \tag{6.11}$$

$$\begin{aligned}&\partial_t Z(t,x) - \Delta_x Z(t,x)\\ &\quad= 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x))V(t,x)\\ &\qquad - \int (v - Z)^3 \frac{n(t,x,v)}{N(t,x)}\,dv.\end{aligned} \tag{6.12}$$

**Proof of Proposition 6.2.4:** To obtain (6.11), we integrate (6.10) along $v$:

$$\begin{aligned}&\partial_t N(t,x) - \Delta_x N(t,x)\\ &\quad= \int \partial_t n(t,x,v) - \Delta_x n(t,x,v)\,dv\\ &\quad= \left[1 + \frac{A}{2} - N(t,x)\right] N(t,x) - \frac{A}{2}\int (v - Bx)^2 n(t,x,v)\,dv\\ &\quad= \left[1 + \frac{A}{2}(1 - V(t,x)) - \frac{A}{2}(Z(t,x) - Bx)^2 - N(t,x)\right] N(t,x).\end{aligned}$$

The second equation, (6.12), is obtained as follows:

$$\begin{aligned}
&\partial_t Z(t,x) - \Delta_x Z(t,x)\\
&\quad = \partial_t \int v \frac{n(t,x,v)}{N(t,x)}\,dv - \Delta_x \int v \frac{n(t,x,v)}{N(t,x)}\,dv\\
&\quad = \int \frac{v}{N(t,x)} \left(\partial_t n(t,x,v) - \Delta_x n(t,x,v)\right) dv\\
&\qquad - \left(\partial_t N(t,x) - \Delta_x N(t,x)\right) \frac{Z(t,x)}{N(t,x)}\\
&\qquad + 2\partial_x(\log N(t,x))\partial_x Z(t,x),
\end{aligned}$$

and thus,

$$\begin{aligned}
&\partial_t Z(t,x) - \Delta_x Z(t,x)\\
&\quad = -\int \frac{v}{N(t,x)} \left(\left(C - \frac{A}{2}\right) + \frac{A}{2}(v - Bx)^2 + \int n(t,w)\,dw\right) n(t,x,v)\,dv\\
&\qquad + (C+1) \int \frac{v}{N(t,x)} \left(\int\int \frac{n(t,x,v_*)n(t,x,v'_*)}{\int n(t,x,w)\,dw} Q(v,v_*,v'_*)\,dv_*\,dv'_*\right) dv\\
&\qquad - \left(1 - \frac{A}{2}(Z(t,x) - Bx)^2 - N + \frac{A}{2}(1 - V(t,x))\right) N(t,x) \frac{Z(t,x)}{N(t,x)}\\
&\qquad + 2\partial_x(\log N(t,x))\partial_x Z(t,x)\\
&\quad = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x))V(t,x)\\
&\qquad - \int (v - Z)^3 \frac{n(t,x,v)}{N(t,x)}\,dv.
\end{aligned}$$

Here we use the fact that the reproduction kernel does not affect the mean phenotypic trait: $\int vQ(v,v',v'_*)\,dv = \frac{v'+v'_*}{2}$.

□

**Remark 6.2.5** *The term* $2\partial_x(\log N)\partial_x Z$ *is referred to, by biologists, as the "gene flow" term (see [89] and [100, 79, 105]). This term models the fact that the mean phenotype of low density areas are greatly influenced by the phenotypes of neighboring high density areas. It is interesting to notice that this term does not come from the sexual reproduction term, but from the diffusion term:*

$$\Delta Z(t,x) = \int v \frac{\Delta_x n(t,x,v)}{N(t,x)}\,dv - \frac{Z(t,x)}{N(t,x)} \Delta N(t,x) + 2\partial_x(\log N(t,x))\partial_x Z(t,x).$$

To close the equations on $N$ and $Z$ obtained in Proposition 6.2.4, we notice that (6.10) can be written:

$$\begin{aligned}
&\partial_t n(t,x,v) - \Delta_x n(t,x,v)\\
&\quad = C\left[\int\int \frac{n(t,x,v_*)n(t,x,v'_*)}{\int n(t,x,w)\,dw} Q(v,v_*,v'_*)\,dv_*\,dv'_* - n(t,x,v)\right]\\
&\qquad + \left[\frac{A}{2} - \frac{A}{2}(v - Bx)^2 - \int n(t,x,w)\,dw\right] n(t,x,v)\\
&\qquad + \int\int \frac{n(t,x,v_*)n(t,x,v'_*)}{\int n(t,x,w)\,dw} Q(v,v_*,v'_*)\,dv_*\,dv'_*.
\end{aligned}$$

Therefore if $C$ is very large, the first term dominates the dynamics of the population. Since this first term corresponds to the "pure" sexual reproduction equation (6.7), and since the reproduction kernel $Q$ satisfies Condition 1, it is natural to assume that at all time $t > 0$ and all locations $x \in \mathbb{R}$,

$$V(t,x) = \int (v - Z(t,x))^2 \frac{n(t,x,v)}{N(t,x)}\, dv \sim G = 1,$$
$$\int (v - Z(t,x))^3 \frac{n(t,x,v)}{N(t,x)}\, dv \sim 0. \tag{6.13}$$

We notice that here, thanks to the rescaling performed in the previous subsection, $G = 1$.

Using the latter properties to close the system of equations on $N$ and $Z$, we obtain the following model:

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \left(1 - \frac{A}{2}(Z(t,x) - Bx)^2 - N(t,x)\right) N(t,x), \\ \partial_t Z(t,x) - \Delta_x Z(t,x) = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + A(Bx - Z(t,x)). \end{cases} \tag{6.14}$$

This model is very close to the model (6.1) from [100, 79]. The model (6.1) was built directly, without the intermediate step of a structured population model, and the limits of its applications were unclear (see [101]). Our derivation shows that the model (6.14) is valid (in the sense that it is the formal limit of (6.6)) if:

- The reproduction is sexual,
- The reproduction kernel satisfies Condition 1,
- $C$ is large.

**Remark 6.2.6** $C = \gamma \left(r_{max} - \frac{G^2}{2V_s} - \frac{I_s}{2}\right)^{-1} - 1$ *is large if the birth rate is large compared to the maximal growth rate of the total population. In other words, many generations are necessary to obtain a significant growth of the population, which seems reasonable in many biological situations.*

*Notice also that in the framework of Proposition 6.2.1, the convergence criteria in Condition 1 hold true exponentially fast. Therefore the simplification* (6.13) *might be accurate even if $C$ is not very large.*

### 6.2.5 Derivation of a simplified model

To simplify (6.14), we first apply the following change of variable:

$$\widetilde{N}\left(\widetilde{t},\widetilde{x}\right) := N\left(\frac{\widetilde{t}}{A}, \frac{\widetilde{x}}{\sqrt{A}}\right), \qquad \widetilde{Z}\left(\widetilde{t},\widetilde{x}\right) := \sqrt{\frac{A}{2}}\, Z\left(\frac{\widetilde{t}}{A}, \frac{\widetilde{x}}{\sqrt{A}}\right).$$

To simplify the notations, we omit the tilde in the new unknown functions. The rescaled model becomes

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \frac{1}{A}\left(1 - (Z(t,x) - (B/\sqrt{2})x)^2 - N(t,x)\right) N(t,x), \\ \partial_t Z(t,x) - \Delta_x Z(t,x) = 2\partial_x(\log N(t,x))\partial_x Z(t,x) + ((B/\sqrt{2})x - Z(t,x)). \end{cases}$$

Now, if we assume that $A$ is very small, $N$ and $Z$ are related by the simple relation:

$$N(t,x) \sim 1 - (Z(t,x) - (B/\sqrt{2})x)^2. \tag{6.15}$$

Therefore we obtain the simpler model (6.2), on $Z$ only:

$$\begin{aligned} \partial_t Z(t,x) - \Delta_x Z(t,x) \;&=\; -4\frac{(\partial_x Z(t,x) - B/\sqrt{2})(Z(t,x) - (B/\sqrt{2})x)}{1 - (Z(t,x) - (B/\sqrt{2})x)^2}\partial_x Z(t,x) \\ &\quad + ((B/\sqrt{2})x - Z(t,x)). \end{aligned}$$

**Remark 6.2.7** *In [79], the range of $A$ that has been considered was $A \in [0.001, 1]$. Thus our approximation, assuming that $A$ is small, seems reasonable.*

*Another simplification had been proposed in [79], where the equation on $N$ was replaced by*

$$N := k \exp\left(\gamma\left(1 - A(Z - Bx)^2\right)\right). \tag{6.16}$$

*With this approximation,* (6.1) *is simplified considerably:*

$$\partial_t Z(t,x) - \Delta_x Z(t,x) = A(Bx - Z(t,x))\left[1 - 4\gamma\partial_x Z(t,x)(B - \partial_x Z(t,x))\right].$$

*However, the simplification* (6.16) *seems independent of* (6.1). *Our simplification has the advantage to rely on a clearer assumption:* (6.2) *is the formal limit of* (6.14) *when $A$ is small.*

## 6.3 Dynamics of sexual populations

### 6.3.1 Well-posedness of the model

By replacing $W = Z - (B/\sqrt{2})x$ in (6.2) we obtain the following equation

$$\partial_t W - \Delta_x W = -4\frac{\partial_x W W}{1 - W^2}(\partial_x W + B/\sqrt{2}) - W, \tag{6.17}$$

with $-1 \le W \le 1$. This equation has a singularity for $W = \pm 1$.The existence of singularities is an obstacle to have a well-defined problem. However, as we will see in section 6.3.2, the singularities are fundamental to produce propagative fronts. In most of the cases in the classical study of propagative fronts, one proves the existence of propagative fronts that connect two steady states. Here the situation is different. The propagative fronts connect the unstable steady state $W = 0$ to the singular point $W = -1$. While the presence of singularities is crucial to observe propagative fronts, it is an obstacle to prove uniqueness or a comparison principle. Nevertheless we are able to introduce an approached model where the uniqueness and the comparison principle hold.

Since (6.17) is singular, we approximate it by the following model

$$\partial_t W_\delta - \Delta_x W_\delta = -4\frac{\partial_x W_\delta W_\delta}{1 - W_\delta^2 + \delta}(\partial_x W_\delta + B/\sqrt{2}) - \frac{(1 - W_\delta^2)W_\delta}{1 - W_\delta^2 + \delta}, \tag{6.18}$$

with

$$W_\delta(t = 0, \cdot) = W_\delta^0(\cdot).$$

With this choice of approximation we avoid the singularities and transform the singularity in $-1$ into a stable steady state (the stability is for the ODE formulation presented in section 6.3.2).

Under the assumption

$$-1 \le W_\delta^0 \le 1, \tag{6.19}$$

equation (6.18) has a smooth solution that stays between $-1$ and 1 by the maximum principle. We prove a regularizing effect for equation (6.18) and we deduce that the $W_\delta$'s converge to a viscosity solution of a variant of equation (6.17) (see [38, 5] for general introduction to the theory of viscosity solutions).

**Theorem 6.3.1** *Under assumptions (6.19), $W_\delta$ the solution of (6.18) verifies, for all $(t,x) \in \mathbb{R}^+ \times \mathbb{R}$,*

$$-1 \le W_\delta(t,x) \le 1, \qquad |\partial_x W_\delta(t,x)| \le \min(L_2\,, \frac{1}{2\sqrt{t}} + L_1), \tag{6.20}$$

*with*

$$L_2 = \max\big(\sup_{x\in\mathbb{R}} |\partial_x W_\delta(x,0)|\,,\, L_1\big) \in \mathbb{R}^+ \cup +\infty,$$

*and $L_1$ a positive constant independent of $\delta$. Moreover, after extraction of a subsequence, the $W_\delta$'s converge to a continuous function $W$ that is a viscosity solution of*

$$(1-W^2)\partial_t W - (1-W^2)\Delta_x W = -4\partial_x W W(\partial_x W + B/\sqrt{2}) - (1-W^2)W. \qquad (6.21)$$

We notice that equation (6.21) is the original model (6.17) multiplied by $1-W^2$. Furthermore, the second inequality (6.20) shows that equation (6.18) has a regularizing effect and the $W_\delta$'s become uniformly Lipschitz, for all $t > t_0 > 0$, even if they are not uniformly Lipschitz initially.

**Proof of Theorem 6.3.1:** We differentiate equation (6.17) with respect to $x$ and obtain

$$\begin{aligned} \partial_t\partial_x W_\delta - \Delta_x\partial_x W_\delta \quad &= -4\tfrac{W_\delta}{1-W_\delta^2+\delta}(2\partial_x W_\delta + B/\sqrt{2})\partial_x(\partial_x W_\delta) \\ &\quad -4\partial_x W_\delta^2(\partial_x W_\delta + B/\sqrt{2})\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2} \\ &\quad -\partial_x W_\delta\left(1-\delta\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2}\right), \end{aligned} \qquad (6.22)$$

where the last term comes from

$$\partial_x\left(\frac{W_\delta(1-W_\delta^2)}{1-W_\delta^2+\delta}\right) = \partial_x\left(W_\delta - \frac{\delta W_\delta}{1-W_\delta^2+\delta}\right) = \partial_x W_\delta\left(1-\delta\frac{1-W_\delta^2+\delta+2W_\delta^2}{(1-W_\delta^2+\delta)^2}\right).$$

We multiply (6.22) by $\partial_x W_\delta$ and divide by $|\partial_x W_\delta|$ and obtain

$$\begin{aligned} \partial_t|\partial_x W_\delta| - \Delta_x|\partial_x W_\delta| \quad &\le -4\tfrac{W_\delta}{1-W_\delta^2+\delta}(2\partial_x W_\delta + B/\sqrt{2})\partial_x(|\partial_x W_\delta|) \\ &\quad -4\partial_x W_\delta^2(\partial_x W_\delta + B/\sqrt{2})\left(\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2}\right)\mathrm{sgn}(\partial_x W_\delta) \\ &\quad -\left(1-\delta\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2}\right)|\partial_x W_\delta|. \end{aligned}$$

It follows that, for $\delta < 1$,

$$\begin{aligned} \partial_t|\partial_x W_\delta| - \Delta_x|\partial_x W_\delta| \quad &\le \alpha(t,x)\partial_x|\partial_x W_\delta| + \left(\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2}\right)\cdot \\ &\quad \left(-4|\partial_x W_\delta|^3 + 2\sqrt{2}\,B|\partial_x W_\delta|^2 + |\partial_x W_\delta|\right), \end{aligned}$$

with

$$\alpha(t,x) = -4\frac{W_\delta}{1-W_\delta^2+\delta}\,(2\partial_x W_\delta + B/\sqrt{2}).$$

Therefore for $L_1$ large enough and for $\delta < 1$, we have that $|\partial_x W_\delta|$ is a subsolution of the following equation

$$\partial_t g - \Delta_x g \quad = \alpha(t,x)\partial_x g - 4\left(\tfrac{1+W_\delta^2+\delta}{(1-W_\delta^2+\delta)^2}\right)(g-L_1)^3, \qquad (6.23)$$

One can easily verify that, for $\delta < 1$, the functions $g_1(t,x) := L_2$ and $g_2(t,x) := \frac{1}{2\sqrt{t}} + L_1$ are supersolutions to equation (6.23) and they satisfy

$$|\partial_x W_\delta(0,x)| \le g_1(0,x), \qquad |\partial_x W_\delta(0,x)| \le g_2(0,x).$$

It follows that, for $\delta < 1$,

$$|\partial_x W_\delta(t,x)| \le \min(g_1(t,x), g_2(t,x)),$$

and thus (6.20).

Now we define

$$T_\delta := F(W_\delta) = (1+\delta)W_\delta - \frac{W_\delta^3}{3}.$$

We first consider the case with $L_2 < +\infty$. From (6.20), we deduce that the $T_\delta$'s are uniformly bounded and Lipschitz in $[0,+\infty)\times\mathbb{R}$. Moreover we have

$$\partial_t T_\delta - \Delta T_\delta = (1 - W_\delta^2 + \delta)\partial_t W_\delta - (1 - W_\delta^2 + \delta)\Delta W_\delta + 2W_\delta|\nabla W_\delta|^2.$$

From the latter equation, (6.18) and (6.20) we deduce that $\partial_t T_\delta - \Delta T_\delta$ is uniformly bounded in $[0,+\infty)\times\mathbb{R}$. It follows that the $T_\delta$'s are uniformly continuous in time in $[0,+\infty)\times\mathbb{R}$ (see [6]). Using the Arzela Ascoli Theorem we conclude that, after extraction of a subsequence, the $T_\delta$'s converge locally uniformly to a continuous function $T$ in $[0,+\infty)\times\mathbb{R}$.

In the case with $L_2 = +\infty$, following the arguments above we obtain that the $T_\delta$'s are uniformly bounded and locally uniformly Lipschitz in $(0,+\infty)\times\mathbb{R}$. The locally uniform convergence of the $T_\delta$'s, along subsequences, is also hold in $(0,+\infty)\times\mathbb{R}$.

Finally from the fact that

$$F'(W_\delta) = 1 + \delta - W_\delta^2 > 0, \qquad \text{for } -1 \le W_\delta \le 1,$$

we obtain that $F$ is an invertible function. We write

$$W_\delta = F^{-1}(T_\delta),$$

with $F^{-1}$ continuous. Therefore the $W_\delta$'s converge locally uniformly to the continuous function $W = F^{-1}(T)$ along subsequences. The convergence takes place in $[0,+\infty)\times\mathbb{R}$, if $L_2 < +\infty$ and in $(0,+\infty)\times\mathbb{R}$ if $L_2 = +\infty$.

By the stability of viscosity solutions (see [38, 5]), we conclude that $W$ is a viscosity solution of (6.21).

□

We proved that the equation (6.21) has a solution in the viscosity sense. Unfortunately the viscosity criterion is not enough to select a unique solution. We give a counter-example below:

**Example. Non-uniqueness for equation (6.21):** We have the two following solutions to equation (6.21):

$$W_1(t,x) = -1, \qquad \text{for all } (t,x) \in \mathbb{R}^+\times\mathbb{R},$$

$$W_2(t,x) = -e^{-t}, \qquad \text{for all } (t,x) \in \mathbb{R}^+\times\mathbb{R}.$$

Here the biological solution is the first one. Because $W = -1$ corresponds to $N = 0$. Therefore, if initially $W(0,x) = -1$ for all $x \in \mathbb{R}$, we expect that $W(t,\cdot) \equiv -1$, for all $t \in \mathbb{R}^+$. Otherwise some mass is created out of nowhere. We can easily verify that if $W_\delta(t=0,\cdot) \equiv -1$, we have $W_\delta(t,\cdot) \equiv -1$ for all $t > 0$. Therefore our approximation chooses the biological solution.

In section 6.3.2 we study the propagative fronts for this model. To be able to compare the solutions with the propagative fronts and to show the propagation of the density in space, we need a comparison principle. Unfortunately as we saw above, the equation (6.21) does not have a unique viscosity solution and therefore it does not admit a comparison principle. However we can prove a comparison principle for the approached model. We first recall its definition:

**Definition 6.3.2** *Comparison principle: Equation $L(D^2u, Du, u, x, t) = 0$ verifies a comparison principle, if for any subsolution $w^1$ and supersolution $w^2$ of $L$ such that $w^1(0, x) \leq w^2(0, x)$, we have*

$$w^1(t, x) \leq w^2(t, x), \qquad \text{for all } (t, x) \in \mathbb{R}^+ \times \mathbb{R}.$$

We prove that there is a comparison property for (6.18). In particular (6.18) has a unique solution.

**Proposition 6.3.3** *Equation (6.18) admits a comparison principle in the set of solutions $\{-1 \leq W \leq 1\}$.*

**Proof of Proposition 6.3.3:** We suppose that $W_1$ and $W_2$ are respectively subsolution and supersolution of (6.18) and

$$W_1(t = 0, \cdot) \leq W_2(t = 0, \cdot).$$

We prove that $W_1 \leq W_2$ for all $(t, x) \in \mathbb{R}^+ \times \mathbb{R}$. Let $(\bar{t}, \bar{x})$ be a maximum point of $W_1 - W_2$. Since it is a maximum point we have $\partial_x W_1(\bar{t}, \bar{x}) = \partial_x W_2(\bar{t}, \bar{x}) = p$. Therefore we have

$$\begin{aligned}
&\partial_t(W_1 - W_2)(\bar{t}, \bar{x}) - \Delta(W_1 - W_2)(\bar{t}, \bar{x}) \\
&\quad \leq -4p\,(p + B/\sqrt{2})\frac{(1 + W_1W_2 + \delta)}{(1 - W_1^2 + \delta)(1 - W_2^2 + \delta)}\,(W_1 - W_2)(\bar{t}, \bar{x}) \\
&\qquad - \frac{(1 + \delta)(1 - W_1^2 - W_1W_2 - W_2^2) + W_1W_2 + W_1^2W_2^2}{(1 - W_1^2 + \delta)(1 - W_2^2 + \delta)}\,(W_1 - W_2)(\bar{t}, \bar{x}).
\end{aligned}$$

In the previous section we proved that $|\partial_x W|$ is bounded. Thus $p(p + B/\sqrt{2})$ is bounded. Moreover $W_1$ and $W_2$ are bounded and

$$1 - W_i^2 + \delta \geq \delta, \qquad \text{for } i = 1,\ 2.$$

Therefore the coefficient of $W_1 - W_2$ is bounded. Following the classical maximum principle we deduce that equation (6.18) admits a comparison principle.

□

### 6.3.2 Existence of propagative fronts and steady populations

In this section, we study the existence of propagative fronts and steady states for equation (6.2). Since the optimal trait at the point $x$ of space is $(B/\sqrt{2})x$, we expect that a propagative front $Z$, with $Z$ a solution of (6.2), be in the following form

$$Z(t, x) = (B/\sqrt{2})x + U(x - \nu t).$$

Using the above notation, the equation (6.2) becomes

$$-\nu U' - U'' = -4\frac{U'U}{1 - U^2}(U' + B/\sqrt{2}) - U.$$

If we denote by $V := U'$, finding a propagative front is then equivalent to find a solution defined on $\mathbb{R}$ to the ODE given by the vector field

$$\begin{cases} F_U(U, V) = V, \\ F_V(U, V) = -\nu V + 4\frac{UV}{1 - U^2}(V + B/\sqrt{2}) + U. \end{cases} \tag{6.24}$$

To have a meaning with respect to (6.17), those solutions must satisfy $u(\cdot) \in [-1, 1]$.

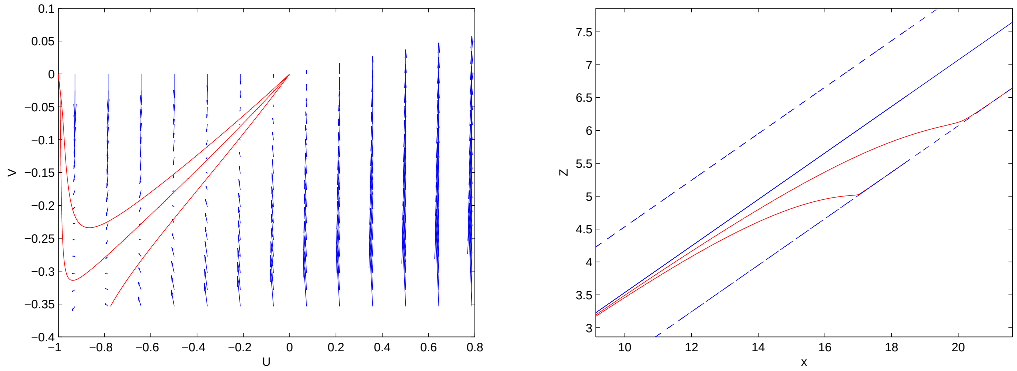

Figure 6.1: On the left, we represent solutions of the ODE defined by the vector field (6.24) for $B := 0.5$ and $\nu = 3.75,\ 4.75,\ 5.75$ (the vector field represented corresponds to $\nu = 4.75$). A propagative front exists for those two last values of $\nu$ only, which we represent on the right.

**Theorem 6.3.4** *For any positive constant $B > 0$, there exists $\nu_B \in \mathbb{R}$ such that* (6.17) *has a propagative front of speed $\nu$, $Z(t,x) = (B/\sqrt{2})x + U(x - \nu t)$, satisfying*

$$U(x) \to 0 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ as } x \to +\infty,$$

*if and only if $\nu > \nu_B$.*

*The propagative front with speed $\nu$ is unique (up to a translation), and $\nu_B$ is a decreasing function of $B$.*

The above Theorem claims that for each $B > 0$, there exists a one-parameter family of propagative fronts. By analogy to the KPP-Fisher equation, one can expect that there is only one stable propagative front, the one with the least speed. Those fronts would be invasive fronts if $\nu_B > 0$, and extinction fronts if $\nu_B < 0$. The Theorem 6.3.5 shows that steady populations exist in this second case only.

We notice that, since the model does not admit a comparison principle, we cannot use the usual methods used in the study of the KPP-Fisher equation, to study the stability of propagative fronts rigorously. Nevertheless, if we choose those solutions of (6.17) that are obtained as the limits of the approached solutions $W_\delta$'s, and since the approached model admits a comparison principle, one can expect that the comparison principle would hold for those limit solutions. The comparison principle would in particular allow us to compare the solutions with the propagative fronts and prove the propagation of the population by the minimal speed of the propagative fronts.

**Theorem 6.3.5** *The equation* (6.2) *has a non-trivial steady-state if and only if $\nu_B < 0$. Steady-states $Z(t,x) = (B/\sqrt{2})x + U(x)$ satisfy*

$$U(x) \to 1 \text{ as } x \to -\infty, \quad U(x) \to -1 \text{ as } x \to +\infty.$$

As one can see in the proof, if $\nu_B < 0$, there exists indeed a whole family of steady-states. If we assume that $U(0) = 0$ (to avoid the translation invariance of the problem), then the family of steady-states can be parameterized by $U'(0) \in (-K_B, 0)$, for some $K_B > 0$.

To prove the above Theorems, we will use the two following Lemma:

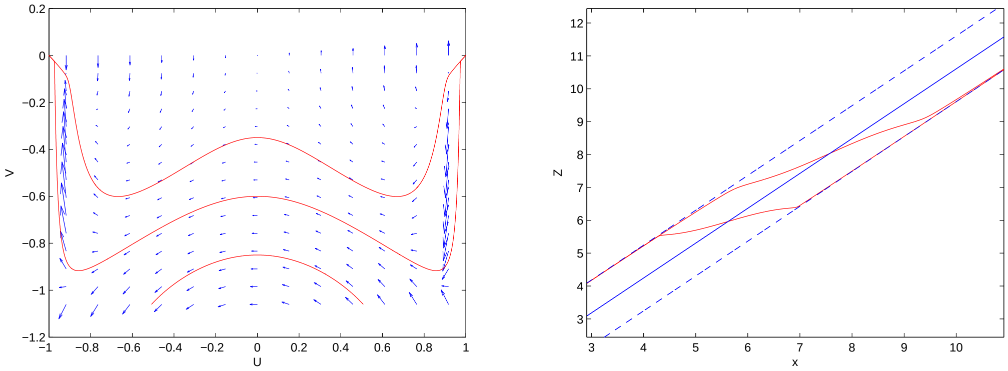

Figure 6.2: On the left, we represent solutions of the ODE defined by the vector field (6.24) for $B := 1.5$ and $\nu = 0$. Two of the three solutions represented define steady-states of (6.17), which we represent on the right.

**Lemma 6.3.6** *Let $\nu \in \mathbb{R}$. There exist only two, up to a shift in the $t$ variable, solutions $(u, v)$ to the ODE defined by the vector field (6.24) such that $(u, v)(t) \to (0, 0)$ as $t \to -\infty$. At most one of them is globally defined, which satisfies:*

$$(u, v)(t) \sim -C_- e^{\frac{\sqrt{\nu^2+4}-\nu}{2} t}(1, \frac{\sqrt{\nu^2 + 4} - \nu}{2}).$$

*Moreover, for this solution, $u$ is strictly decreasing.*

**Lemma 6.3.7** *Let $\nu_1 \leq \nu_2$, and $(u_{\nu_1}, v_{\nu_1})$, $(u_{\nu_2}, v_{\nu_2})$ be the corresponding solutions given by Lemma 6.3.6. If for $t_1$, $t_2 \in \mathbb{R}$,*

$$\begin{cases} u_{\nu_1}(t_1) = u_{\nu_2}(t_2) \\ v_{\nu_1}(t_1) \leq v_{\nu_2}(t_2), \end{cases} \tag{6.25}$$

*then, for any $t'_1 > t_1$, $t'_2 > t_2$ such that $u_{\nu_1}(t'_1) = u_{\nu_2}(t'_2)$, we have $v_{\nu_1}(t'_1) \leq v_{\nu_2}(t'_2)$, and this inequality is strict if $\nu_1 < \nu_2$.*

**Proof of Lemma 6.3.6:** The Differential of the vector field $F$ in $(0, 0)$ is

$$DF_{(0,0)} = \begin{pmatrix} 0 & 1 \\ 1 & -\nu \end{pmatrix}.$$

Therefore $(0, 0)$ is a hyperbolic equilibrium point ($\det DF_{(0,0)} < 0$). The Hartman-Grobman Theorem applies, and thus there exist only two (non-trivial) solutions $(u, v)$ satisfying $(u, v)(t) \to_{t\to-\infty} (0, 0)$. Since the eigenvector associated to the positive eigenvalue of $DF_{(0,0)}$ is $(1, \frac{\sqrt{\nu^2+4}-\nu}{2})$, the corresponding solutions are equivalent to

$$(u, v)(t) \sim_{t\to-\infty} \pm C_\pm \, e^{\frac{\sqrt{\nu^2+4}-\nu}{2} t} \left(1, \frac{\sqrt{\nu^2 + 4} - \nu}{2}\right),$$

for some $C_-$, $C_+ > 0$.

The solution such that $(u, v)(t) \sim_{t\to-\infty} C_+ e^{\frac{\sqrt{\nu^2+4}-\nu}{2} t} \left(1, \frac{\sqrt{\nu^2+4}-\nu}{2}\right)$ satisfies $u(\bar{t}) > 0$, $v(\bar{t}) > 0$ for some $\bar{t}$. Since $F_U(u(\bar{t}), V) > 0$ for $V \geq v(\bar{t})$ and $F_V(U, v(\bar{t})) \geq F_V(u(\bar{t}), v(\bar{t})) > 0$

for $U \in [u(\bar{t}), 1)$, the solution cannot escape $[u(\bar{t}), 1) \times [v(\bar{t}), \infty)$. In particular, for $t \geq \bar{t}$, $u'(t) = v(t) \geq v(\bar{t}) > 0$ and since the vector field is not defined for $U = 1$, the solution cannot be global.

The other solution satisfies $u(\bar{t}) < 0$, $v(\bar{t}) < 0$ for some $\bar{t}$ arbitrarily small. Since $F_U(0, V) \leq 0$ for $V \leq 0$ and $F_V(U, 0) \leq 0$ for $U \leq 0$, the solution cannot escape $\mathbb{R}^2_-$. In particular, we have $u'(t) = v(t) \leq 0$, which shows that $u$ is strictly decreasing with respect to $t$.

□

**Proof of Lemma 6.3.7:** Since $u_\nu$ is strictly decreasing, we can define the graph of $(u_{\nu_1}, v_{\nu_1})$.

We assume that $\bar{t}_1$, $\bar{t}_2$ are the smallest points respectively in $(t_1, \infty)$ and in $(t_2, \infty)$ such that $(u_{\nu_2}, v_{\nu_2})(\bar{t}_2) = (u_{\nu_1}, v_{\nu_1})(\bar{t}_1)$. We have,

$$\begin{aligned} v'_{\nu_1}(\bar{t}_1) &= -\nu_1 v_{\nu_1}(\bar{t}_1) + 4\frac{u_{\nu_1}(\bar{t}_1)v_{\nu_1}(\bar{t}_1)}{1 - u_{\nu_1}(\bar{t}_1)^2}\left(v_{\nu_1}(\bar{t}_1) + B/\sqrt{2}\right) + u_{\nu_1}(\bar{t}_1) \\ &= v'_{\nu_2}(\bar{t}_2) + (\nu_2 - \nu_1)v_{\nu_1}(\bar{t}_1) \\ &\leq v'_{\nu_2}(\bar{t}_2), \end{aligned}$$

this inequality being strict if $\nu_1 < \nu_2$. It follows that $\frac{v'_{\nu_1}(\bar{t}_1)}{u'_{\nu_1}(\bar{t}_1)} > \frac{v'_{\nu_2}(\bar{t}_2)}{u'_{\nu_2}(\bar{t}_2)}$. The graph of $(u_{\nu_2}, v_{\nu_2})$ can thus only cross the graph of $(u_{\nu_1}, v_{\nu_1})$ from below to above, when $t$ increases. This is enough to conclude that $v_{\nu_1}(t'_1) \leq v_{\nu_2}(t'_2)$, for all $t'_1 > t_1$ and $t'_2 > t_2$. Moreover, the latter inequality is strict if $\nu_1 < \nu_2$. This completes the proof of Lemma 6.3.7.

□

**Proof of Theorem 6.3.4:** *Step 1:* We show that the solution $(u, v)$ given by Lemma 6.3.6 satisfies either $v(\bar{t}) = -B/\sqrt{2}$ for some $\bar{t}$, or $(u, v)(t) \to (-1, 0)$ as $t \to +\infty$. Moreover, the solution is global in this last case only.

Since $u$ is strictly decreasing and $F_V(-1, V) = +\infty$ for $V \in (-B/\sqrt{2}, 0)$, only two situations are possible: either $v(\bar{t}) = -B/\sqrt{2}$ for some $\bar{t} < +\infty$, or $(u, v)(t) \to (-1, 0)$ as $t \to \bar{t} \in \mathbb{R} \cup \{+\infty\}$.

If $v(\bar{t}) = -B/\sqrt{2}$, then $v(t) < -B/\sqrt{2}$ for all $t \geq \bar{t}$. This is because

$$F_V(U, -B/\sqrt{2}) = \nu B/\sqrt{2} + U \leq F_V(u(\bar{t}), -B/\sqrt{2}) \leq 0$$

for $U \in (-1, u(\bar{t}))$ and since $u$ is decreasing. Therefore, $u'(t) = v(t) \leq -B/\sqrt{2}$ for all $t \geq \bar{t}$. From the latter, together with $F_V(-1, V) = -\infty$ for $V < -B/\sqrt{2}$, we obtain that the solution cannot be globally defined.

Now let $(u, v)(t) \to (-1, 0)$ as $t \to \bar{t} \in \mathbb{R} \cup \{\infty\}$. We prove that $\bar{t} = \infty$. For $(U, V)$ close to $(-1, 0)$, we have $F_V(U, V) \sim \frac{-2B}{\sqrt{2}}\frac{V}{1+U} - 1$. We deduce that,

$$\begin{aligned} \frac{d}{dt}\left(\frac{v}{1+u}\right)(t) &= \frac{F_V(u(t), v(t))(1 + u(t)) - v(t)F_U(u(t), v(t))}{(1 + u(t))^2} \\ &\sim \frac{1}{(1 + u(t))^2}\left[\left(\frac{-2B}{\sqrt{2}}\frac{v(t)}{1 + u(t)} - 1\right)(1 + u(t)) - v(t)^2\right] \\ &\sim \frac{1}{(1 + u(t))^2}\left[\frac{-2B}{\sqrt{2}}v(t) - v(t)^2 - (1 + u(t))\right] \\ &\geq 0, \end{aligned}$$

if $v(t) \leq \frac{-\sqrt{2}}{3B}(1+u(t))$ and $(u(t), v(t))$ is close to $(-1,0)$.

We assume that $\widetilde{t}$ is such that $(u,v)(t)$ is close to $(-1,0)$ for $t \geq \widetilde{t}$. We then have, $\frac{v(t)}{1+u(t)} \geq \min\left(\frac{v(\widetilde{t})}{1+u(\widetilde{t})}, \frac{-\sqrt{2}}{3B}\right)$ for all $t \geq \widetilde{t}$. It follows that $u'(t) = v(t) \geq -C(u(t)+1)$, which implies the estimate

$$u(t) \geq -1 + (u(\widetilde{t}\,)+1)e^{-C(t-\widetilde{t}\,)}.$$

Since $(u,v)(t) \to (-1,0)$ as $t \to \bar{t}$, we deduce that $\bar{t} = +\infty$, and $(u,v)$ is indeed globally defined.

*Step 2:* We next prove that there exists a constant $\nu_B$ such that, there exists a propagative front if and only if $\nu > \nu_B$.

If $\nu > \frac{\sqrt{2}}{B}$, we have $F_V(U, -B/\sqrt{2}) = \nu B/\sqrt{2} - U > 0$ for $U \in (-1,1)$. Therefore, the solution given by Lemma 6.3.6 cannot cross the line $V = -B/\sqrt{2}$, and thus it defines a propagative front thanks to Step 1. We deduce that, there exists a propagative front if $\nu$ is large enough.

In $[-1/\sqrt{2}, 0] \times [-B/\sqrt{2}, 0]$ and for $\nu \leq -5B$, we have

$$F_V(U,V) \leq -\nu V - 4\sqrt{2}\, V(V + B/\sqrt{2}) \leq BV \leq B\, F_U(U,V).$$

It follows that the solution given by Lemma 6.3.6 necessarily crosses the line $V = -B$, and thus it does not define a propagative front according to Step 1. We deduce that the model does not admit a propagative front if $-\nu$ is large enough.

We consider a solution $(u_{\nu_1}, v_{\nu_1})(t)$ given by Lemma 6.3.6 for some $\nu_1$, that converges to $(-1,0)$ as $t \to +\infty$, and $\nu_2 > \nu_1$. Since $\frac{\sqrt{\nu^2+4}-\nu}{2}$ is a decreasing function of $\nu$ and

$$(u_{\nu_i}, v_{\nu_i})(t) \sim -C_{\_}e^{\frac{\sqrt{\nu_{\nu_i}^2+4}-\nu_{\nu_i}}{2}}\left(1, \frac{\sqrt{\nu_{\nu_i}^2+4}-\nu_{\nu_i}}{2}\right),$$

the graph of $(u_{\nu_1}, v_{\nu_1})(t)$ is below the graph of $(u_{\nu_2}, v_{\nu_2})(t)$ for $t << 0$. Thanks to Lemma 2, this implies that the whole graph of $(u_{\nu_1}, v_{\nu_1})$ is below the graph of $(u_{\nu_2}, v_{\nu_2})$. Using the latter and Step 1 we obtain that $(u_{\nu_2}, v_{\nu_2})$ defines a propagative front.

Finally, we show that $\nu_B$ is a decreasing function of $B$. Firstly we notice that, for $B_1 \leq B_2$, we have $F_U^{B_1} = F_U^{B_2}$, and $F_V^{B_1} \leq F_V^{B_2}$ in $(-1,0] \times \mathbb{R}_-$. We deduce that, using Step 1, if the solution given by Lemma 6.3.6 for $B_1$ converges to $(-1,0)$ as $t \to \infty$, so does the one associated to $B_2$. This proves that $\nu_B$ is a decreasing function of $B$.

□

**Proof of Theorem 6.3.5:** We assume that $\nu_B < 0$. Then, for $\nu = \frac{\nu_B}{2}$, the solution $(u_{\nu_B/2}, v_{\nu_B/2})$ given by Lemma 6.3.6, is globally defined, and it satisfies $(u_{\nu_B/2}, v_{\nu_B/2})(t) \to (-1,0)$ as $t \to +\infty$. Moreover we have

$$(u_{\nu_B/2}, v_{\nu_B/2})(t) \sim_{t\to-\infty} -C_{\_}e^{\frac{\sqrt{(\nu_B/2)^2+4}-\nu_B/2}{2}t}\left(1, \frac{\sqrt{(\nu_B/2)^2+4}-\nu_B/2}{2}\right),$$

and $\frac{\sqrt{(\nu_B/2)^2+4}-\nu_B/2}{2} > 1$.

Consider now the vector field (6.24) for $\nu = 0$. Since $(u_0, v_0)(t) \sim_{t\to-\infty} -C'_{\_}e^t(1,1)$, for $\bar{t}$ small enough, $(u_0, v_0)(\bar{t}\,)$ is strictly above the graph of $(u_{\nu_B/2}, v_{\nu_B/2})$. Let $\widetilde{v}$ be such that $(u_0(\bar{t}), \widetilde{v}\,)$ is strictly between $(u_0, v_0)(\bar{t}\,)$ and the graph of $(u_{\nu_B/2}, v_{\nu_B/2})$. We define $(\bar{u}, \bar{v})$ to be the solution of the ODE given by the vector fields (6.24) such that $(\bar{u}, \bar{v})(0) = (u_0(\bar{t}\,), \widetilde{v})$ and $\nu = 0$. Then, according to Lemma 6.3.7, $(\bar{u}, \bar{v}\,)$ is defined in $\mathbb{R}_+$. Moreover, since

$(u_0, v_0)(t) \to (0,0)$ as $t \to -\infty$ and $(0,0)$ is a hyperbolic equilibrium point, there exists $\widetilde{t} > 0$ such that $\bar{u}(\widetilde{t}\,) = 0$.

By symmetry, we have $(\bar{u}, \bar{v})(\widetilde{t} + t) = (-\bar{u}, \bar{v})(\widetilde{t} - t)$. Thus, $(\bar{u}, \bar{v})$ is globally defined and satisfies $(\bar{u}, \bar{v})(t) \to (\pm 1, 0)$ as $t \to \pm\infty$. This completes the proof of Theorem 6.3.5.

$\square$

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# Résumé

Cette thèse porte sur l'étude mathématique de phénomènes de concentration en masse de Dirac apparaissant dans des problèmes issus de la biologie. Nous étudions principalement la dynamique adaptative d'un trait quantitatif en fonction de paramètres écologiques de l'environnement, comme les nutriments. La modélisation mathématique de ces problèmes mène à des équations paraboliques avec petite diffusion. La présence d'un petit terme conduit à des modèles multi-échelles. Les solutions asymptotiques de ces équations apparaissent comme une réunion de concentrations de masse en un ou plusieurs points qui se déplacent.

Dans une première partie nous présentons une formulation Hamilton-Jacobi pour une étude asymptotique des équations intégrodifférentielles qui décrivent la dynamique d'une densité de population en présence des mutations et de la compétition entre les individus. Nous donnons une description de la dynamique des masses de Dirac à l'aide de ce formalisme. Nous étudions également un modèle singulier où nous ajoutons un terme de mortalité pour les petites densités. Ce dernier nous permet d'éviter les queues exponentielles de distribution et nous fournit des résultats plus proches des modèles stochastiques. Dans la deuxième partie nous présentons quelques illustrations numériques pour le modèle de compétition directe introduite précédemment. En outre, nous appliquons nos méthodes à un modèle de type chemostat, où nous étudions un système décrivant la dynamique des consommateurs et de la ressource. La dernière partie est consacrée à l'étude de l'évolution et de la propagation en espace d'une population sexuée. Dans cette étude la population est structurée par un trait phénotypique et une variable d'espace, dans un environnement hétérogène.

**Mots-clés:** Dynamique adaptative, Équation de Lotka-Volterra, Équation de Hamilton-Jacobi, Solutions de viscosité, Concentrations en masses de Dirac, Analyses asymptotiques

# Abstract

This work is devoted to the mathematical study of concentration phenomena, that appears in problems related to biology. We study the adaptive dynamics of a quantitative trait depending on ecological parameters of the environment, such as the nutrients. The mathematical modeling of these problems gives rise to parabolic equations with small diffusion. The presence of a small term leads to multi-scale models. The asymptotic solutions of these equations concentrate on one or several points in the trait space that are evolving in time.

In the first part of this work, we introduce a Hamilton-Jacobi formulation to study some integro-differential equations that describe the asymptotic dynamics of a population density under the effect of mutations and competition between the individuals. We give a description of the dynamics of Dirac masses, using this formalism. In this part, we also study a singular model where we add a mortality rate for small densities. The latter allows us to avoid the exponential distribution tails and to obtain the results that are more in accordance with the stochastic models. In the second part we provide some numerical illustrations for the direct competition model, introduced in the previous sections. Moreover, we apply our methods to a chemostat type model, where we study a system describing the dynamics of both the consumers and the resource. The last part is devoted to the study of the evolution and the space propagation of a sexual population. In this study the population, in a heterogeneous environment, is structured by a phenotypical trait and a space variable.

**Keywords:** Adaptive evolution, Lotka-Volterra equation, Hamilton-Jacobi equation, Viscosity solutions, Dirac concentrations, Asymptotic analysis.