Trait selection and rare mutations: the case of large diffusivities

Idriss Mazari

TRAIT SELECTION AND RARE MUTATIONS: THE CASE OF LARGE DIFFUSIVITIES

IDRISS MAZARI

Abstract. We consider a system of N competing species, each of which can access a different resources distribution and who can disperse at different speeds. We fully characterize the existence and stability of steady-states for large diffusivities. Indeed, we prove that the resources distribution yielding the largest total population size at equilibrium is, broadly speaking, always the winner when species disperse quickly. The criterion also uses the different dispersal rates. The methods used rely on an expansion of the solutions of the Lotka-Volterra sytem for large diffusivities, and is an extension of the "slowest diffuser always wins" principle.
Using this method, we also study the case of an equation modelling a trait structured population, with small mutations. We assume that each trait is characterized by its diffusivity and the resources it can access. We similarly derive a criterion mixing these diffusivities and the total population size functional for the single species model to show that for rare mutations and large diffusivities, the population concentrates in a neighbourhood of a trait maximizing this criterion.

Contents

Date: Version du July 9, 2019.
Key words and phrases. Lotka-Volterra system, Dispersal evolution, Principal eigenvalue, Total population size, Hamilton-Jacobi equations.
2010 AMS Classification: 35K57,49K20,92D15,92D25 .

1. Introduction

1.1. **Notations and comments.** The notation $\mathbb{R}_+^*$ stands for the set of positive real numbers, i.e $\mathbb{R}_+^* = (0; +\infty)$.
For any integer $k \in \mathbb{N}$, the set $\mathbb{N}_k$ is defined as $\mathbb{N}_k = \{1, \dots, k\}$.
In this article, all the equations will be understood in a weak $W^{1,2}$ sense. Furthermore, when the equation is set on a smooth domain Ω, the notation $\frac{\partial}{\partial \nu}$ denotes the derivative with respect to the unit outward normal vector.

1.2. The diffusive Lotka-Volterra system and our prototypical result.

1.2.1. *Model and assumptions.* We consider the diffusive Lotka-Volterra system modeling the interaction between N species, where $N \in \mathbb{N}^*$. Let $\mathbb{N}_N$ be the set $\{1, \dots, N\}$. Throughout this article, Ω stands for a bounded $\mathscr{C}^2$ domain in $\mathbb{R}^n$.
In order to describe the interspecific interactions, we parameterize the model with the following quantities :

(1) N positive diffusion rates $\mu_i > 0$ where $i \in \mathbb{N}_N$,
(2) N functions $m_i \in L^\infty(\Omega)$ where $i \in \mathbb{N}_N$. For a fixed $i \in \mathbb{N}_N$, m_i stands for the resources distribution available to the i-th species. **The spatial heterogeneity will be accounted for by the resources distributions m_i's.**

The diffusive Lotka-Volterra system reads as follows:

$$(1.1) \qquad \begin{cases} \dfrac{\partial u_i}{\partial t} = \mu_i \Delta u_i + u_i \left(m_i - \displaystyle\sum_{j=1}^N u_j \right) & \text{in } \Omega, \\ \frac{\partial u_i}{\partial \nu} = 0 & \text{on } \partial\Omega, \\ u_i(t=0, \cdot) = u_{i,0}, \end{cases} , i \in \mathbb{N}_N,$$

where, for every $i \in \mathbb{N}_N$, $u_{i,0}$ denotes a non-negative initial condition in $W^{1,2}(\Omega)$.

For further explanations about modeling issues we refer to [10–12, 29, 30] and to the references therein. Our main interest here is the investigation of the influence of spatial heterogeneity on the existence and stability of steady states (also called equilibria) of (1.1) in the setting of large diffusivities.

Formal presentation of our main focus. We use a criterion related to single species models for large diffusivities, to derive results about existence and stability results for the system (1.1). This criterion was already studied in the case $N = 2$ by He and Ni (see [14–16]). We will further comment on their works in upcoming sections of the introduction.
Let $i \in \mathbb{N}_N$. It will be convenient to introduce the positive solution $\theta_i = \theta_{m_i,\mu_i}$ of the so-called logistic diffusive equation:

$$(1.2) \qquad \begin{cases} \mu_i \Delta \theta_i + \theta_i(m_i - \theta_i) = 0 & \text{in } \Omega, \\ \frac{\partial \theta_i}{\partial \nu} = 0 & \text{on } \partial\Omega. \\ \theta_i > 0. \end{cases}$$

Existence and Uniqueness issues: Existence and uniqueness of a positive solution to equation (1.2) is classical and has been answered in different frameworks. In [9], the existence and uniqueness of a solution to (1.2) is investigated in bounded domains and, in [2], the same question is investigated in a periodic setting. A study of the influence of spatial heterogeneity on species persistence is carried out. We also refer to [12, 16] and to the references therein for more information regarding the influence of concentration and fragmentation of resources. We will come back to [2] later on, when giving biological interpretations of our results. Here, in the case of Neumann boundary conditions, we recall that the question of existence and uniqueness of a solution to (1.2) boils down to the study of the principal eigenvalue $\lambda_1(\mu_i, m_i)$ of the elliptic operator $\mu_i \Delta + m_i$. Recall that this eigenvalue can be defined using Rayleigh quotients, that is:

$$\lambda_1(\mu_i, m_i) := \sup_{f \in W^{1,2}(\Omega)\,, \fint_\Omega f^2 = 1} \left\{ -\mu \fint_\Omega |\nabla f|^2 + \fint_\Omega m_i f^2 \right\}.$$

This eigenvalue is simple. Furthermore, any eigenfunction φ_i associated with $\lambda_1(\mu_i, m_i)$ has a constant sign, and can hence be chosen to be positive. Any eigenfunction φ_i satisfies

$$\begin{cases} \mu_i \Delta \varphi_i + m_i \varphi_i = \lambda_1(\mu_i, m_i)\varphi_i, \\ \frac{\partial \varphi_i}{\partial \nu} = 0, \end{cases}$$

in a weak $W^{1,2}(\Omega)$ sense. Existence and uniqueness of a solution to (1.2) is equivalent to requiring that

$$\lambda_1(\mu_i, m_i) > 0.$$

Using $f = \frac{1}{|\Omega|^{\frac{1}{2}}}$ as a test function, existence and uniqueness is guaranteed if

$$\fint_\Omega m_i > 0. \tag{1.3}$$

Thus, we assume that, for every $i \in \mathbb{N}_N$, we have

$$\fint_\Omega m_i > 0.$$

Semi-trivial equilibria Coming back to system (1.1), note that, for any i, if θ_i solves (1.2), then the state

$$\overline{u}_i := (0, \dots, \theta_i, 0, \dots, 0) \tag{ST}$$

is an equilibrium of (1.1). These equilibria can be referred to as *semi-trivial.* A question that has been intensely studied over the last decades is wether or not these equilibria are the only one and if they are linearly or globally asymptotically stable. We introduce the following definition:

Definition 1.1. *Any equilibrium of the form* (ST) *will be called a semi-trivial equilibrium of* (1.1). *Any equilibrium $u := (u_1, \dots, u_N)$ such that at least two components u_i are non zero in Ω will be called a coexistence state of* (1.1).

Broadly speaking, the criterion for existence and stability of equilibria will be the total population size associated with the resources distribution m_i, reading

$$\fint_\Omega \theta_i, \tag{1.4}$$

that is, the total population size of a single species, moving at rate μ_i with a resources distribution m_i, **in the case where all the diffusivities μ_i's are large.** Our prototypical result reads:

If the m_i's are ordered with respect to criterion (1.4) and to the diffusivities, that is

$$\fint_\Omega \theta_1 > \dots > \fint_\Omega \theta_N,$$

and if the μ_i's are "large enough", then the $\overline{u}_i = (0, \dots, \theta_i, 0, \dots, 0)$'s are the only equilibria, and $\overline{u}_1=(\theta_1,0,\dots,0)$ is the only stable one.

1.2.2. *Bibliographical remarks.* A much more thorough analysis of the existence and/or stability of coexistence and semi-trivial equilibria of (1.1) was carried out by He and Ni in the three parts of their paper [14–16] in the case $N=2$, with two different resources distributions m_1 and m_2. They give, most notably in parts II and III of their paper, a global characterization of the sets

$$\Sigma_1:=\left\{(\mu_1,\mu_2)\in(\mathbb{R}_+^*)^2\,,(\theta_{\mu_1,m_1},0)\text{ is stable}\right\}$$

and

$$\Sigma_2:=\left\{(\mu_1,\mu_2)\in(\mathbb{R}_+^*)^2\,,(0,\theta_{\mu_2,m_2})\text{ is stable}\right\}$$

as epigraphs: for instance, Σ_1 can be described as

$$\{\mu_2>f(\mu_1)\},$$

for a function f whose asymptotic behaviour, as, $\mu_1\to\infty$ is then analyzed using asymptotic expansions of θ_{μ_1,m_1} as μ_1 goes to ∞. Our criterion here is the same as theirs. Their paper is written under the assumption that $m\in\mathscr{C}^{0,\alpha}(\Omega)$ (although adapting these methods enables to derive the same asymptotic expansions for $m\in L^\infty(\Omega)$). Our contribution in this article is to study the case of an arbitrary number N of competing species and to give new proofs of the asymptotic expansions in the case $m_i\in L^\infty(\Omega)$. This enables us to encompass the case of patch models (see for instance [2,10] for the relevance of such models).
We also give interpretations in terms of concentrations of resources, and expand on the paradigm He and Ni introduce at the end of [16, Corollary 1.8]: for large diffusivities, the lesser spatial oscillation in resources the better for competition.
Furthermore, in the second part of this article, we consider the case of a continuum of traits with a small mutation parameters.

1.2.3. *Assumptions and comments.* In this section, we introduce and comment on the assumptions we will be led to make later on.

Assumption on diffusivities: Another way to consider stability is to try to understand the influence of the diffusivities on equilibria. In this paper, we work under the hypothesis that **diffusivities are large.**
In [11], the diffusive Lotka-Volterra system is studied under the assumptions that $m_i=m_j$ for any i,j (all the species are considered with respect to the same resources distribution), and the diffusivities are ordered (but not necessarily large), that is, $\mu_1>\dots>\mu_N$. It is proved that the slowest diffuser always wins: the $\overline{u}_i$'s defined by (ST) are the only equilibria, $\overline{u}_1$ is stable, while the other $\overline{u}_i$'s are unstable. Our work encompasses this result in the case of large diffusivities.

Assumption and comments on interactions: In this paper, we will work under the hypothesis that **all the interaction coefficients are equal to 1.**
To understand the interactions between the different species, consider the general system:

$$\forall i\in\mathbb{N}_N\,,\mu_i\Delta u_i+u_i\left(m_i-\sum_{j=1}^N b_{i,j}u_j\right)=\frac{\partial u_i}{\partial t}\quad\text{ in }\mathbb{R}_+\times\Omega,$$

with Neumann boundary conditions in space and with a non-negative initial condition. Here, $(b_{i,j})_{i,j\in\mathbb{N}_N}$ is a matrix with non-negative coefficients and such that, for any $i\in\mathbb{N}_N$, $b_{i,i}>0$.

Many results are devoted to studying the existence of coexistence equilibria and the importance of the heterogeneity. See for instance [5–7, 17, 26]. We highlight in particular two of them. They hold in the case $N = 2$, $b_{1,1} = b_{2,2} = 1$ and $m_1 = m_2 = m$. It has been shown that

(1) the map $\mu \mapsto \fint_\Omega \theta_{m,\mu}$ has at least one maximum on $\mathbb{R}_+^*$ and that, if $b_{2,1} < \inf_{\mu>0} \frac{\fint_\Omega m}{\fint_\Omega \theta_{m,\mu}} = b_{2,1}^*$, then $\overline{u}_1$ is unstable. If $b_{2,1} > b_{2,1}^*$, then $\overline{u}_1$ can change stability. This result is due to Lou, see [22].
(2) if $b_{2,1} = \alpha b_{1,2}$ and if $b_{1,2}$ is large enough, then $\overline{u}_1$ is stable, $\overline{u}_2$ is stable, and any coexistence state is unstable. This result is due to Girardin, see [13, Theorem 1.2].

In other words, the magnitude of the interspecies interaction can influence in many ways the stability of equilibria, so that we will not consider this influence in this paper. We believe that our method enables us to recover these results in the case of large diffusivities.

Assumption on the resources distributions: In this paper, we will successively work under two hypotheses: first, that **all species can access the same amount of resources** and, later, under the hypothesis that **the species have access to different amounts of resources**. Many efforts have been done in the last decade to understand the influence of the distribution of resources on the persistence of a species. For instance, in [2] it is proved that the concentration of resources in the logistic diffusive model (1.2) favors the persistence of the species. In [16, Corollary 1.8], the authors conclude that concentration of resources is better than fragmentation for competition. We will give further details on these interpretations at the end of this Introduction, see Section 2.

1.3. **The rare mutations model for trait selection.** In the second part of this article, we are interested in the trait selection process occurring for small mutations. This encompasses the evolution phenomena occurring in population dynamics.
More precisely, we consider a set $\Xi \subset \mathbb{R}^d$, assumed to be $\mathscr{C}^2$ and compact, accounting for the different traits (e.g length of the legs, age...), and a domain $\Omega \subset \mathbb{R}^n$, also $\mathscr{C}^2$ and compact, accounting for the spatial environment. We consider a population density in both trait and space, denoted as $u = u(\xi, x)$ where $\xi \in \Xi$ and $x \in \Omega$. For any $\xi \in \Xi, x \in \Omega$, the quantity $u(\xi, x)dx$ represents the number of members of the species with trait ξ located at position x. Note that here, we are primarily interested in the steady-state situation, where an equilibrium has already been reached.
Our hypothesis regarding the spatial evolution of the density are standard: if we consider, for a trait ξ, a diffusivity $\mu(\xi) > 0$, the spatial evolution will be described by $\mu(\xi)\Delta_x u$. We also assume that each trait can access some finite amount of resources $m = m(\xi, \cdot)$. The hypothesis on the resources distributions are the same as in the previous section: we assume that there exists a constant $\delta > 0$ such that, for any $\xi \in \Xi$,

$$\fint_\Omega m(\xi, x)dx \geq \delta > 0.$$

Finally, we account for the mutation (i.e the possibility for individuals to acquire a new trait) via some small mutation rate, $\varepsilon^2 \Delta_\xi u$. Here, $\varepsilon > 0$ is a small parameter.
In other words, we consider the following trait mutation model:

$$(1.5) \qquad \begin{cases} \mu(\xi)\Delta_x u(\xi, x) + \varepsilon^2 \Delta_\xi u(\xi, x) + u(\xi, x)\Big(m(\xi, x) - \int_\Xi u(\xi, x)d\xi.\Big) = 0 \text{ in } \Omega, \\ \frac{\partial u}{\partial \nu} = 0 \text{ on } \partial\Omega \times \partial\Xi, \end{cases}$$

in a weak sense. For notational convenience, we now define

$$\Phi(x) = \int_\Xi u(\xi,x)d\xi.$$

It is expected that, as $\varepsilon \to 0$, the density $u = u_\varepsilon$ concentrates at particular traits, accounting for a natural selection process: there exists a collection of traits $(\xi_j)_{j\in J} \in \Xi^J$ and a collection of functions $(\psi_j)_{j\in J} \in W^{1,2}(\Omega)^I$ such that, for any sequence $\varepsilon_k \underset{k\to\infty}{\to} 0$, there exists a subsequence and there exists some $j \in J$ satisfying, in the sense of distributions and along this subsequence:

$$u_{\varepsilon_k}(\xi,x) \underset{k\to\infty}{\to} \delta_{\xi_j}(\xi)\psi_j(x). \tag{1.6}$$

In other words, when mutations are rare, a trait selection process happens. This problem was introduced in [1]. This selection was proved rigorously in different settings; we refer to [27] for the case where Ω and Ξ are convex and where the resources distribution does not depend on the trait $\xi \in \Xi$. We note here that, provided m is $\mathscr{C}^2$ in $x \in \Omega$ and $\xi \in \Xi$, up to minor modifications of the technical proof of [27], the same result holds.
A lot of attention has been devoted to identifying the possible limit traits $\{\xi_j\}_{j\in J}$. For instance, in [20, 27] it is shown that, provided the distribution resources m do not depend on ξ and provided $\mu = \mu(\xi)$ has a unique minimum ξ_* in Ξ, then the only possible limit trait is ξ_*, extending the aforementioned result of [11] (i.e, the slowest diffuser always wins). In [20], the same result is proved under the condition that Ξ is a one-dimensional interval, and the convergence rates are made sharp. For further references regarding the study of selection processes in unbounded domains and time-dependant problems, most noticeably the traveling-waves solutions to this equation, we refer to [4, 31] and to the references therein.
Our contribution in this article consists in a study of the case where the resources distributions depend on the trait ξ. We do so in the setting of large diffusivities.
Just as in the first part of the article, for a particular trait $\xi \in \Xi$, the function $\theta = \theta(\xi,x)$ will denote the solution of the following logistic diffusive equation:

$$\begin{cases} \mu(\xi)\Delta_x\theta(\xi,x) + \theta(\xi,x)(m(\xi,x)-\theta(\xi,x)) = 0 & \text{in } \Omega, \\ \frac{\partial\theta(\xi,x)}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{cases} \tag{1.7}$$

We will prove the same kind of results as in the first part of this article:

Assume that the map $\xi \mapsto \fint_\Omega \theta(\xi,x)dx$ has a finite number of maximizers in Ξ. If all the $\mu(\xi)$ are "large enough", then any limit traits will be close to one of these maximizers.

In other words, the total population size criterion is, in the case of large diffusivities, a selection criterion.

1.4. **Introducing the criterion for both models.** We first assume that all the species can access the same amount of resources.

<u>The class of admissible distribution resources:</u> Since we want to order the resources distributions with respect to the total population size, it is natural to assume the following on the distribution resources (that is, either m_i or $m(\xi,\cdot)$ depending on the model): in the case of the Lotka-Volterra system, for any $i \in \mathbb{N}_N$, $m_i \in \mathcal{M}(\Omega)$, and, in the case of the mutation diffusion model, for any $\xi \in \Xi$, $m(\xi,\cdot) \in \mathcal{M}(\Omega)$, where

$$\mathcal{M}(\Omega) = \left\{ m \in L^\infty(\Omega)\,, 0 \le m \le \kappa \text{ a.e}\,, \fint_\Omega m = m_0 \right\}. \tag{1.8}$$

The relevance of this admissible class is detailed in [23,25]. Broadly speaking, these are the minimal assumptions we can make on resources distributions so that the optimization problem

$$\sup_{m\in\mathcal{M}(\Omega)} \fint_\Omega \theta_{m,\mu}$$

has a solution.

Note that, if $m \in \mathcal{M}(\Omega)$ and if $\mu > 0$, then the unique positive solution of the logistic diffusive equation

$$\left\{\begin{array}{ll} \mu\Delta\theta_{m,\mu} + \theta_{m,\mu}(m-\theta_{m,\mu}) = 0, & \text{in } \Omega \\ \frac{\partial\theta_{m,\mu}}{\partial\nu} = 0 & \text{on } \partial\Omega, \end{array}\right. \tag{1.9}$$

satisfies

$$0 < \inf_{\overline{\Omega}}\theta_{m,\mu} \leq \kappa\,, \quad \theta_{m,\mu} \in W^{2,p}(\Omega)\,, \quad \forall p \in [1;+\infty).$$

Ordering the resources distributions with respect to our criterion. We have mentioned that our main criterion will be the total population size functional, and that our results hold for large diffusivities. Consider the logistic diffusive equation with a resources distribution m satisfying $\fint_\Omega m = m_0 > 0$. Introduce, for a positive diffusivity $\mu > 0$, the functional $\mathcal{F}_\mu : \mathcal{M}(\Omega) \to \mathbb{R}$ defined by

$$\mathcal{F}_\mu : m \mapsto \fint_\Omega \theta_{m,\mu}.$$

The question that arises is that of the behavour of $\mathcal{F}_\mu$ as $\mu \to +\infty$. In order to adress this question, we recall the classical result (see [22] and the references therein) that for any $p \in [1;+\infty)$,

$$\theta_{m,\mu} \underset{\mu\to\infty}{\to} m_0$$

in $W^{1,p}(\Omega)$. We now look for a second order term, that is for $\eta_{1,m}$ such that

$$\theta_{m,\mu} = m_0 + \frac{\eta_{1,m}}{\mu} + \underset{\mu\to\infty}{o}\left(\frac{1}{\mu}\right) \text{ in } W^{1,2}(\Omega), \tag{1.10}$$

and where $\underset{\mu\to\infty}{o}\left(\frac{1}{\mu}\right)$ is uniform in $m \in \mathcal{M}(\Omega)$. This gives rise to the following equation on $\eta_{1,m}$:

$$\left\{\begin{array}{ll} \Delta\eta_{1,m} + m_0(m-m_0) = 0 & \text{in } \Omega, \\ \frac{\partial\eta_{1,m}}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{array}\right. \tag{1.11}$$

This is not enough to fully characterize $\eta_{1,m}$. In order to do so, we introduce the solution $\hat{\eta}_{1,m}$ to

$$\left\{\begin{array}{ll} \Delta\hat{\eta}_{1,m} + m_0(m-m_0) = 0 & \text{in } \Omega, \\ \frac{\partial\hat{\eta}_{1,m}}{\partial\nu} = 0 & \text{on } \partial\Omega, \\ \fint_\Omega \hat{\eta}_{1,m} = 0 & . \end{array}\right. \tag{1.12}$$

We therefore know that there exists a constant $\beta_{1,m}$ such that $\eta_{1,m} = \hat{\eta}_{1,m} + \beta_{1,m}$. To determine this constant, we integrate the logistic diffusive equation (1.2):

$$\fint_\Omega \theta_{m,\mu}(m-\theta_{m,\mu}) = 0,$$

so that, identifiying at order $\frac{1}{\mu}$, we get

$$\beta_{1,m} = \frac{1}{m_0}\fint_\Omega \hat{\eta}_{1,m}(m-m_0) = \frac{1}{m_0^2}\fint_\Omega |\nabla\hat{\eta}_{1,m}|^2. \tag{1.13}$$

We can prove (see [16, 25]) that Equation (1.10) holds strongly in $W^{1,2}(\Omega)$. This means that the following first-order expansion of $\mathcal{F}_\mu$ holds:

$$\boxed{\mathcal{F}_\mu : m \mapsto m_0 + \frac{1}{\mu} \fint_\Omega \eta_{1,m} + \underset{\mu\to\infty}{o}\left(\frac{1}{\mu}\right).}$$

1.5. **Bibliographical remarks.** If we go back to [16], we recall that for instance the set

$$\Sigma_1 := \left\{(\mu_1, \mu_2) \in (\mathbb{R}_+^*)^2 \,, (\theta_{\mu_1, m_1}, 0) \text{ is stable}\right\}$$

is described by the authors as

$$\{\mu_2 > f(\mu_1)\}.$$

The content of their Theorem 1.6 is a precise asymptotic expansion of f as $\mu \to \infty$; if we truncate their results at order μ_1, it reads

$$f(\mu_1) \underset{\mu_1\to\infty}{\sim} \mu_1 \frac{\fint_\Omega \eta_{1,m_2}}{\fint_\Omega \eta_{1,m_1}}$$

and that, if $(\mu_1, \mu_2) \in \Sigma_1$ then $(\theta_{\mu_1,m_1}, 0)$ is globally asymptotically stable. Our theorem reads the same for the existence part in the setting of large diffusivities, but is less precise, for these results by He and Ni encompass our own and are completed by a study of the precise zones of stability, both local and global of these semi-trivial equilibria. As mentioned earlier, our goal here is to provide a partial study for the case of an arbitrary number of competing species and for a rare mutations equation.

1.6. **Main results of the papers for the Lotka-Volterra system.** For the sake of clarity, we will first state the results in the case of the Lotka-Volterra system.

<u>Same amount of resources and same scale of dispersal:</u> Here and throughout we parameterize the diffusivities as functions of μ_1, i.e we work with a collection of functions $\mu_2, \dots, \dots \mu_n$ of the variable μ_1. For this first result, we assume that all species move at the same scale that is, for any $i \in \mathbb{N}_N$, there exists $d_i > 0$ such that

$$\text{(A1)} \qquad \frac{\mu_i(\mu_1)}{\mu_1} \underset{\mu_1\to\infty}{\to} d_i,$$

and that the resources distributions are ordered with respect to the criterion:

$$\text{(A2)} \qquad \frac{1}{d_1}\fint_\Omega \eta_{1,m_1} > \dots > \frac{1}{d_N}\fint_\Omega \eta_{1,m_N}.$$

We recall that, for any $i \in \mathbb{N}_N$, $\fint_\Omega \eta_{1,m_i} = \frac{1}{m_0^2}\fint_\Omega |\nabla \hat{\eta}_{1,m_i}|^2$, and $\hat{\eta}_{1,m_i}$ is defined by equation (1.12).

Theorem 1.1. *Assume that, for any $i \in \mathbb{N}_N, m_i \in \mathcal{M}(\Omega)$. Assume that* (A1) *and* (A2) *are satisfied.*
There exists $\mu^* = \mu^*(\Omega, m_0, \kappa, m_1, \dots, m_N) > 0$ such that, for any $\mu_1 > \mu^*$ and such that, for any $i = 2, \dots, N$, $\mu_i(\mu_1) > \mu^*$:

(1) The $\overline{u}_i$'s are the only non-zero equilibria of the system (1.1). *There are no coexistence states.*
(2) $\overline{u}_1$ is linearly stable, while the other $\overline{u}_i$'s are linearly unstable.

Under the hypothesis of this theorem, we can rewrite the arguments of [11, Theorem 3.4] and we obtain the following result:

Theorem 1.2. *Let $M = (m_{i,j})_{i,j\in \mathbb{N}_N}$ be a matrix such that, for any $i \in \mathbb{N}_N$ we have $m_{i,i} < 0$ and, for $i \neq j$, $m_{i,j} \geq 0$.*
Consider the system with mutation:

$$(1.14)\qquad \begin{cases} \frac{\partial u_i}{\partial t} = \mu_i \Delta u_i + u_i(m_i - \sum_{j=1}^N u_j) + \varepsilon \sum_{j=1}^n m_{i,j} u_j & \text{in } \Omega, \\ \frac{\partial u_i}{\partial \nu} = 0 & \text{on } \partial\Omega, \\ u_i(t=0,\cdot) = u_{i,0}, \end{cases} \quad , i \in \mathbb{N}_N,$$

where, for every $i \in \mathbb{N}_N$, $u_{i,0}$ denotes a non-negative initial condition in $W^{1,2}(\Omega)$. Then, under the assumptions of Theorem 1.1: there exists $\varepsilon_0 > 0$ such that, for any $\varepsilon < \varepsilon_0$, there exists a non-negative equilibrium $u_1(\varepsilon)$, varying analytically in ε, such that $u_1(0) = \overline{u}_1$ (i.e $\overline{u}_1$ perturbs analytically in the cone of non-negative n-tuples of functions). Furthermore, this equilibria is linearly stable.

We will not prove this result, for it is a straightforward adaptation of the arguments of [11, Theorem 3.4] .

Same amount of resources and different scales of dispersal: A bit of notation is required to give a clear statement of the two next results. Henceforth, we will parameterize diffusivities as functions of μ_1, that is, $\mu_i = \mu_i(\mu_1)$.
As we have mentioned, we have to understand the interplay between the scale of dispersal and the total population size functional. To do so, the most convenient way is to introduce the notion of **size-scale order**.
We recall that we assume

$$\mu_i(\mu_1) \underset{\mu_1\to\infty}{\rightarrow} \infty.$$

For a subset of indexes $\{i_1, \dots, i_k\}$ of $\mathbb{N}_N$, we say it is **size-scaled ordered** if the two following conditions hold:

(1) For any $j \geq 1$, there exists $d_{i_j} \in (0;\infty)$ such that

$$\text{(H1)}\qquad \boxed{\frac{\mu_{i_j}(\mu_1)}{\mu_{i_1}(\mu_1)} \underset{\mu_1\to\infty}{\rightarrow} d_{i_j},}$$

and this hypothesis will be referred to as the **same diffusivity scale** hypothesis,

(2) Furthermore,

$$\text{(H2)}\qquad \boxed{\forall j \neq j' \in \{i_1, \dots, i_k\}\ \frac{1}{d_{i_j}} \fint_\Omega \eta_{1,m_{i_j}} \neq \frac{1}{d_{i_{j'}}} \fint_\Omega \eta_{1,m_{i_{j'}}}.}$$

Furthermore, if we are given a set of indexes $\Gamma \subset \{1, \dots, N\}$, it is always possible to split it into t same diffusivity scale sets

$$\Gamma = \Gamma_1 \sqcup \dots \sqcup \Gamma_t,$$

and we assume that the same diffusivity scale sets are maximal, that is, for any $i \in \{1, \dots, t-1\}$,

$$\frac{\mu_{\min\{k,k\in\Gamma_i\}}(\mu_1)}{\mu_{\min\{k,k\in\Gamma_{i+1}\}}(\mu_1)} \underset{\mu_1\to\infty}{\rightarrow} 0.$$

We call it a **scale partition of the set**.

Remark 1.1. *The hypothesis of Theorem 1.1 were in fact the hypothesis that the set $\mathbb{N}_N$ itself was size-scale ordered.*

Theorem 1.3. *Assume that, for any $i \in \mathbb{N}_N, m_i \in \mathcal{M}(\Omega)$. Let us write the scale partition of $\mathbb{N}_N$:*

$$\mathbb{N}_N = I_1 \sqcup \cdots \sqcup I_\ell$$

and assume each of the I_j is size-scale ordered i.e satisfies (H1) *and* (H2)*. Then there exists $\mu^* > 0$ such that for any N-tuple $(\mu_1, \ldots, \mu_N)$ satisfying , for any $i \in \mathbb{N}_n$, $\mu_i > \mu^*$:*

(1) the $\overline{u}_i$'s are the only non-zero equilibria of the system (1.1)*. There are no coexistence states.*
(2) Furthermore, if $i_1 \in I_1$ satisfies

$$F_1(m_{i_1}) = \max_{i \in I_1} F_1(m_i) \text{ (i.e it is the optimal resources distribution among the slowest diffusers)}$$

then $\overline{u}_{i_1}$ is the only stable equilibria.

Different amounts of resources and different scale of dispersal. Let us drop the assumption that $m_i \in \mathcal{M}(\Omega)$. We write $\mathbb{N}_N$ as

$$\mathbb{N}_N = J_1 \sqcup \cdots \sqcup J_\omega$$

as follows: for any $k \in \mathbb{N}_\omega$, there exists $m_{0,k}$ such that, for any $i \in J_k$,

$$\fint_\Omega m_i = m_{0,k} > 0.$$

Each of the set J_i is then split as before according to the scale of dispersal rates, that is,

$$J_k = \Gamma_{k,1} \sqcup \cdots \sqcup \Gamma_{k,\gamma_k},$$

with the same notations as in the previous paragraph. We now assume that each of the $\Gamma_{i,j}$ is size-scale ordered.

Theorem 1.4. *Assume the $\Gamma_{i,j}$ are size-scale ordered i.e satisfy both conditions* (H1) *and* (H2)*. Then there exists μ^* such that for any N-tuple $(\mu_1, \ldots, \mu_N)$ satisfying, for any $i \in \mathbb{N}_N$, $\mu_i > \mu^*$:*

(1) the $\overline{u}_i$'s are the only non-zero equilibria of the system (1.1)*. There are no coexistence states.*
(2) Furthermore, let $k_1 \in \mathbb{N}_\omega$ be such that

$$\forall i \in J_{k_1}, \forall j \notin J_{k_1}, \overline{m} := \fint_\Omega m_i > \fint_\Omega m_j$$

and let $i_1 \in \Gamma_{k_1,1}$ (that is, among the slowest diffusers for the maximal amount of resources $\overline{m}$) be such that

$$F_1(m_{i_1}) = \max_{i \in \Gamma_{k_1,1}} F_1(m_i).$$

Then, $\overline{u}_{i_1}$ is the only stable equilibria.

1.7. **Main result of the paper for the mutation diffusion system.** We will make the following assumptions on the dispersal rate μ and on the resources distributions, strongly resembling the hypothesis of the first part. We introduce a reference scale $\underline{\mu} > 0$ and parameterize $\mu = \mu(\xi)$ as a function $\mu = \mu(\xi, \underline{\mu})$ and assume that

$$\text{(H1)} \qquad \mu(\xi, \underline{\mu}) \underset{\underline{\mu} \to \infty}{\to} \infty$$

uniformly in $\xi \in \Xi$. We also assume that all the species move at the same-scale: this means that there exists a trait $\xi_0 \in \Xi$ and a function $d : \Xi \to \mathbb{R}_+^*$ bounded above such that, for any $\xi \in \Xi$,

$$\text{(H2)} \qquad \frac{\mu(\xi, \underline{\mu})}{\mu(\xi_0, \underline{\mu})} \underset{\underline{\mu} \to \infty}{\longrightarrow} d(\xi).$$

Furthermore, we also assume that, for each $\xi \in \Xi$

$$\text{(H3)} \qquad 0 \leq m \leq \kappa \text{ a.e in } \Omega \times \xi \,, \fint_\Omega m(\xi,x)dx = m_0 \,, \text{i.e } m(\xi,\cdot) \in \mathcal{M}(\Omega).$$

Finally, for technical reasons, we will also assume the following regularity property on Ω and Ξ:

$$\text{(H4)} \qquad \Omega \text{ and } \Xi \text{ are convex.}$$

We could expect, as was the case in the first part of this article, to be able to handle different amounts of resources. It is the case: as will be noted through the proof, if you assume that there is an above bound on the amount of resources, then the limit traits will be in a neigbourhood of the maximizers of the functional

$$\xi \mapsto \fint_\Omega m(\xi,x)dx.$$

Thus, for the sake of simplicity, we will assume (H3) as of now.
As was the case in the first part, we can consider, for a trait ξ, the solution θ_ξ to the logistic diffusive equation with resources distribution $m(\xi,\cdot)$.

Finally, for each resources distribution $m(\cdot,\xi)$, denote by η_ξ the solution of the equation

$$\text{(1.15)} \qquad \begin{cases} \Delta\eta_\xi + \fint_\Omega m(\xi,x)dx \left(m(\xi,x) - \fint_\Omega m(\xi,x)dx\right) = 0 & \text{in } \Omega, \\ \frac{\partial \eta_\xi}{\partial \nu} = 0 & \text{on } \partial\Omega, \\ \fint_\Omega \eta_\xi = \frac{1}{(\fint_\Omega m(\xi,\cdot))^2} \fint_\Omega |\nabla \eta_\xi|^2. \end{cases}$$

As was recalled in the first part of the introduction, this accounts for the first-order term of the total population size for the single - species logistic-diffusive model. We recall that for any $\xi \in \Xi$, $\theta(\xi,\cdot)$ is the solution of (1.7). Our criterion is then, for a fixed trait ξ_0,

$$F(\xi) = \frac{1}{d(\xi)} \fint_\Omega \eta_\xi$$

Our hypothesis is then
(H4)
F has a unique maximizer ξ^* and there exists $t > 0 \,, C \geq 0$ such that $F(\xi^*) - F(\xi) \geq C|\xi - \xi^*|^t$.

Our theorem reads as follows, and bears a strong resemblance to the theorems of the first part.

Theorem 1.5. *We work under assumption* (H4). *Asume m is $\mathscr{C}^2$ in $x \in \Omega$ and $\xi \in \Xi$. Let $r > 0$ and $\mathbb{B}(\xi^*, r)$ be the euclidean ball centered at ξ^* with radius r. Let $\{\xi_i\}_{i\in I}$ be the set of all limit traits for $u = u_\varepsilon(\xi,x)$ as $\varepsilon \to 0$ in the sense of distributions: up to a subsequence,*

$$u_\varepsilon \underset{\varepsilon\to 0}{\overset{\mathcal{D}'(\Xi\times\Omega)}{\longrightarrow}} \delta_{\xi_i}\theta(\xi,\cdot) \,, \theta(\xi,\cdot) \textit{ solution of } (1.7).$$

Then there exists $\mu^* = \mu^*(\Omega,\Xi)$ such that, for any $\underline{\mu}$ such that $\inf_{\xi\in\Xi} \mu(\xi,\underline{\mu}) \geq \mu^*$,

$$\text{(1.16)} \qquad \forall i \in I \,, \xi_i \in \mathbb{B}(\xi^*, r).$$

Remark 1.2. *In other words, for large diffusivities, the traits that are selected are close to the trait accessing the resources distribution maximizing the criterion involving the total population size and the diffusivity for the logistic diffusive model.*

2. Regarding the criterion: What is known concerning the shape optimization problem

The results of this paper thus indicates that a relevant criterion for studying local linear stability of semi-trivial equilibria of the system (1.1) (or for the trait structured population) is the functional

$$F_1(m) := \fint_\Omega |\nabla \hat{\eta}_{1,m}|^2$$

where $\hat{\eta}_{1,m}$ solves (1.12). Here, for notational simplicity, we have considered that, in the case of (1.1), all diffusivities are equal (i.e $\mu_i = \mu_1$ for all i) and, in the case of the trait structured model, all diffusivities are equal ($\mu(\xi) = \underline{\mu}$ for all ξ). In this setting, the relevant optimization problem then is

$$\text{(PV1)} \qquad \max_{m \in \mathcal{M}(\Omega)} \fint_\Omega |\nabla \hat{\eta}_{1,m}|^2.$$

Here, the fact that the sup is in fact a max (i.e that the variational problem has a solution) is a straightforward consequence of the direct method in the calculus of variations.

As was recalled earlier, F_1 is the first order expansion of the total population size functional in the sense that, uniformly in $m \in \mathcal{M}(\Omega)$,

$$\fint_\Omega \theta_{m,\mu_1} = m_0 + \frac{1}{\mu_1} F_1(m) + \underset{\mu_1 \to \infty}{o} \left(\frac{1}{\mu_1} \right).$$

2.0.1. *Pointwise properties of the resources distributions.* The first thing that comes to mind when dealing with optimization problem such as (PV1) is the question of pointwise properties of maximizers: are they bang-bang type functions, i.e, if m^* is a solution of (PV1), do we have $m^* = 0$ or κ almost everywhere? In [25], calculations are carried out to prove that the functional F_1 is strictly convex, in the sense that its second Gâteaux-derivative is always positive. Since we are maximizing on a convex set $\mathcal{M}(\Omega)$, the following result follows:

Theorem 2.1 ([25], Step 1 of the Proof of Theorem 1)**.** *The maximizers of F_1 over the set $\mathcal{M}(\Omega)$ are of bang-bang type.*

In other words: for competitions, it is better to split the domain into two zones $\Omega = \{m = 0\} \sqcup \{m = \kappa\}$ and oscillations between 0 and κ for large diffusivities are counterproductive. Thus, the optimization problem (PV1) can be recast as a shape optimization problem, since it is equivalent to

$$\sup_{E \text{ measurable subset of } \Omega\,, |E| = \frac{m_0}{\kappa}} F_1(\kappa \chi_E).$$

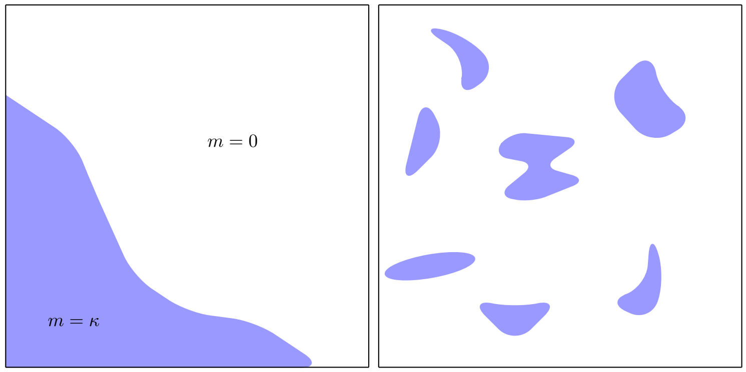
It thus seems that patch models are relevant for such studies.

2.0.2. *Geometric properties: concentration and fragmentation.* We have also recalled some results from [16], most notably [16, Corollary 1.8] that, among other things, state that, for large diffusivities, in the one dimensional case (on $\Omega = (0;1)$), if $N = 2$ and if

$$m_1(x) = 1 + \cos(2\pi k_1 x)\,, m_2(x) = 1 + \cos(2\pi k_2 x)\,, k_i \in \mathbb{N}\,, k_1 < k_2$$

then the semi-trivial equilibrium $(\theta_{m_1,\mu_1}, 0)$ is globally asymptotically stable, indicating that the lesser spatial oscillations, the better for competition.
Here, we expand on results proved in [25] in the n-dimensional case: namely, should we expect concentration or fragmentation of resources for the total population size and/or stability?

To give a feeling of what concentration-fragmentation means, consider the two following resources distributions (here, Ω is a box):



This first distribution is more ”concentrated” than the second one.

The results we give are in the following setting: Ω is a n dimensional orthotope, namely

$$\Omega = \prod_{i=1}^{n} [0; a_i], \forall i \in \mathbb{N}_n \, , a_i > 0.$$

We also introduce the following notion of **decreasing rearrangement** due to Berestycki and Lachand-Robert (see [3]):

Definition 2.1. *(1) <u>The one dimensional case:</u> For a given function $b \in L^1(0, a_i)$, one defines its monotone decreasing rearrangement b_{dr} on $(0, a_i)$ by $b_{dr}(x) = \sup\{c \in I\!R \mid x \in \Omega_c^*\}$, where $\Omega_c^* = (a_i - |\Omega_c|, a_i)$ with $\Omega_c = \{b > c\}$.*

(2) <u>The n-dimensional case:</u> For a given function $b \in L^1(\Omega)$, one defines its symmetric decreasing rearrangement b_{ds} on Ω as follows: first fix the $n-1$ variables $x_2, \dots, x_n$. Define $b_{1,sd}$ as the monotone decreasing rearrangement of $x \mapsto b(x, x_2, \dots, x_n)$. Then fix $x_1, x_3, \dots, x_n$ and define $b_{2,sd}$ as the monotone decreasing rearrangement of $x \mapsto b_{1,sd}(x_1, x, \dots, x_n)$. Perform such monotone decreasing rearrangements successively. The resulting function is the symmetric decreasing rearrangement of b.

In both cases, the decreasing rearrangement will be denoted by $b^\#$.

This rearrangement was first put to use in the context of the study of spatial heterogeneity by Berestycki, Hamel and Roques in [2], where they prove that concentration of resources favors the survival of the species in the sense that, for any $m \in \mathcal{L}^\infty(\Omega)$ and any diffusivity μ we have

$$\lambda_1(m^\#, \mu) \geq \lambda_1(m, \mu).$$

This is an application of the Polya-Szego inequality for the decreasing rearrangement. For applications of numerous rearrangements for spectral quantities in elliptic equations, we refer for instance to [2, 18]. For the specific case of optimal location of resources (with respect to the eigenvalues) and the study of different phenomena arising in it, we refer to [21]. In [25] we prove the following theorem:

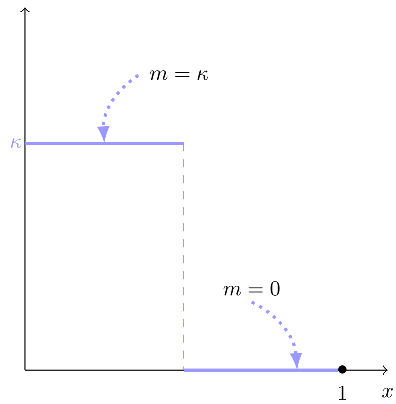
Theorem 2.2 ([25],Theorem 2, Theorem 3)**.** *Any maximizer m^* of F_1 satisfies*

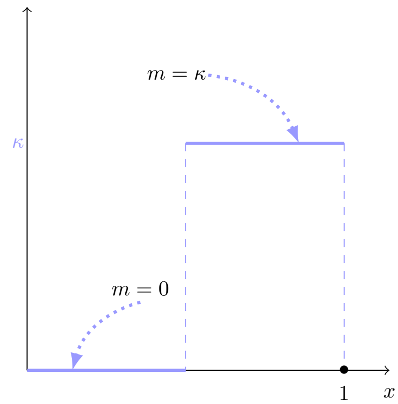
$$m^* = (m^*)^\#.$$

In other words, any maximizer of F_1 is decreasing in every direction.
Furthermore, in the one dimensional case (in $\Omega = (0;1)$), there are only two maximizers of F_1, namely,

$$m_1^* := \kappa \mathbb{1}_{[0;\ell]} \text{ and } m_2^* := \kappa \mathbb{1}_{[1-\ell;1]}, \text{ with } \kappa\ell = m_0.$$

Thus, in the one dimensional case and for large diffusivities, the following resources distributions are always better for competition with another species:



and


Thus, this means that the single step is, in the case of large diffusivities, always a winner for competition.

3. Proof of Theorem 1.1

A few facts about principal eigenvalues. Let us recall a few facts about principal eigenvalues, which are of paramount importance in studying the stability and existence of equilibria of systems (it is the main tool to prove the results we have recalled). In a general setting, for any $h \in L^\infty(\Omega)$, the principal eigenvalue of $\mu\Delta + h$ will be denoted by $\lambda_1(h,\mu)$. We recall that $\lambda_1(h,\mu)$ can be seen as the solution of the following variational problem:

$$\lambda_1(h,\mu) = \sup_{f \in W^{1,2}(\Omega), \fint_\Omega f^2 = 1} \left\{ -\mu \fint_\Omega |\nabla f|^2 + \fint_\Omega f^2 h \right\}.$$

The quantity

$$\frac{-\mu \fint_\Omega |\nabla f|^2 + \fint_\Omega f^2 h}{\fint_\Omega f^2}$$

is the associated Rayleigh quotient. It is also clear, since $\theta_i > 0$ is a principal eigenfunction of the operator $\mu_i\Delta + (m_i - \theta_i)$ that

$$\lambda_1(\mu_i, m_i - \theta_i) = 0.$$

We finally recall the following results (see [11]): for any $h \in L^\infty(\Omega)$, the map $\mu \mapsto \lambda_1(h,\mu)$ is non-increasing, and $\lambda_1(h,\mu) \underset{\mu\to+\infty}{\longrightarrow} \fint_\Omega h$.

3.1. Proof of statement 1: non-existence of coexistence equilibria.

Let us first comment on notations.

Regarding notations. Recall that we parameterized diffusivities as functions of μ_1, that is, $\mu_i = \mu_i(\mu_1)$. In the sequel, we consider a sequence $\{U_{\mu_1}\}_{\mu_1>0} \in (W^{1,2}(\Omega)^N)^{\mathbb{R}_+^*}$ of equilibria. Here, what we mean is that, for each $\mu_1 > 0$, U_{μ_1} is a N-tuple of functions $(u_{\mu_1,1}, u_{\mu_2(\mu_1),2}, \dots, u_{\mu_N(\mu_1),N})$ that is a steady-state of equation (1.1).We will write either $u_{\mu_1,k}$ or u_k (when no confusion is possible) to denote the k-th component of this equilibrium. Since in the framework of this theorem $\mathbb{N}_N$ is size-scale ordered, we know that **we can fix μ_1 as a reference diffusivity**, and note that any function behaving as $\underset{\mu_1\to\infty}{o}\left(\frac{1}{\mu_1}\right)$ behaves as $\underset{\mu_i\to\infty}{o}\left(\frac{1}{\mu_i}\right)$ and conversely. We have already defined, for any $i \in \mathbb{N}_N$,

$$d_i := \lim_{\mu_1\to\infty} \frac{\mu_i(\mu_1)}{\mu_1} \in]0;\infty[. \tag{3.1}$$

Consider, for some N-tuple $(\mu_1,\dots,\mu_N)$, a non-zero equilibrium $U_{\mu_1} = (u_1,\dots,u_N)$ and define

$$\Phi_{\mu_1} = \Phi := \sum_{i=1}^N u_i,$$

so that each u_i solves the following equation:

$$\mu_i \Delta u_i + u_i(m_i - \Phi) = 0 \text{ in } \Omega, \tag{3.2}$$

along with Neumann boundary conditions. Now, assume that there exists a sequence $\{U_{\mu_1} = (u_1,\dots,u_N)\}_{\mu>0}$ of coexistence state as $\mu_1 \to \infty$. Up to an extraction, we can split the set $\mathbb{N}_N$ into two subsets:

$$I_1 = \{i\,,\ \text{for all } \mu \text{ large enough } u_i = U_{\mu_1,i} \neq 0\}\ , I_2 = \{i\,,\ \text{for all } \mu \text{ large enough } u_i = U_{\mu_1,i} = 0\}\,.$$

We will only focus on the set I_1.
Assume that U_{μ_1} is not one of the $\overline{u}_j$'s. This means that at least two components u_i, u_j of u do not vanish, so that u_i is an eigenvalue of the operator

$$\mu_i\Delta + (m_i - \Phi),$$

while u_j is an eigenvalue of

$$\mu_j\Delta + (m_j - \Phi).$$

In particular,

$$0 = \lambda_1(\mu_i, m_i - \Phi) = \lambda_1(\mu_j, m_j - \Phi) \text{ for a subsequence } \mu_1 \to \infty.$$

We will show that, under the assumptions (A1)-(A2), the latter eigenvalues can never be equal for large enough dispersal rates. This will be done in several steps, aimed at providing an asymptotic expansion of $\lambda_1(\mu_i, m_i - \Phi)$ and $\lambda_1(\mu_j, m_j - \Phi)$. Note that this kind of asymptotic expansions was studied in the case $N = 2$ in [16].

Asymptotic behaviour of Φ. We first note that Φ satisfies the following partial differential equation:

$$\Delta\Phi - \left(\sum_{i=1}^N \frac{u_i}{\mu_i}\right)\Phi + \sum_{i=1}^N \frac{u_i m_i}{\mu_i} = 0,$$

with Neumann boundary conditions in a weak $W^{1,2}(\Omega)$ sense.
Under assumption (A1), and since Φ satisfies Neumann boundary conditions, it is classical to see that Φ converges, in $W^{1,2}(\Omega)$, to m_0 as $\mu_1 \to \infty$. We refine this result:

Lemma 3.1. *There exists $\Phi_1 = \Phi_{1,m_1,\dots,m_N} \in W^{1,2}(\Omega)$ such that there holds, strongly in $W^{1,2}(\Omega)$,:*

$$\Phi = m_0 + \frac{\Phi_1}{\mu_1} + \underset{\mu_1\to\infty}{o}\left(\frac{1}{\mu_1}\right). \tag{3.3}$$

Proof of Lemma 3.1. We proceed in several distinct steps:

First order expansion: We first prove the first order expansion, i.e that there holds, strongly in $W^{1,2}(\Omega)$, the following expansion:

$$\Phi = m_0 + \underset{\mu_1\to\infty}{O}\left(\frac{1}{\mu_1}\right). \tag{3.4}$$

Proof of Claim (3.4). In order to do so, we are going to proceed as follows:

(1) We first prove that Φ converges to m_0 in $L^2(\Omega)$ as μ_1 goes to ∞.
(2) We give an estimate on $\nabla\Phi$ in $L^2(\Omega)$ to prove that this convergence in fact holds in $W^{1,2}(\Omega)$, and that this convergence has a rate $\frac{1}{\mu_1}$.

Let's proceed to the proofs:

(1) First of all, it is standard that u_i converges, strongly in $L^2(\Omega)$,to some constant $u_i^{(0)} \geq 0$ in $W^{1,2}(\Omega)$. Thus, we know that

$$\Phi \underset{\mu\to\infty}{\to} \sum_{j=1}^N u_i^{(0)} =: \Phi^{(0)} \text{ in } W^{1,2}(\Omega).$$

Furthermore, we assumed that we were working along a sequence μ_1 going to ∞ such that there always exists an index $i \in \mathbb{N}_N$ satisfying $u_i = u_{\mu_i,i} \neq 0$. Fix such an index i. Dividing Equation (3.2) by u_i and integrating it by parts yields

$$\mu_i \fint_\Omega \frac{|\nabla u_i|^2}{u_i^2} + m_0 = \fint_\Omega \Phi. \tag{3.5}$$

Thus, there always holds

$$\fint_\Omega \Phi \geq m_0 > 0.$$

Since $\Phi \underset{\mu_1\to\infty}{\to} \Phi^{(0)}$ in $W^{1,2}$ and since this convergence ensures the strong L^1 convergence of Φ to $\Phi^{(0)}$, this entails that

$$\Phi^{(0)} = \lim_{\mu_1\to\infty} \fint_\Omega \Phi \geq m_0 > 0. \tag{3.6}$$

Finally, if we integrate Equation (3.2), we get

$$\fint_\Omega u_i\left(m_i - \Phi\right) = 0.$$

We now pass to the limit as $\mu_1 \to \infty$ in these equations, leading to

$$\forall i \in \mathbb{N}_N\,, u_i^{(0)} m_0 - u_i^{(0)}\Phi^{(0)} = 0.$$

Summing these identities for $i = 1, \dots, N$ leads to

$$\Phi^{(0)} m_0 - \left(\Phi^{(0)}\right)^2 = 0.$$

Since $\Phi^{(0)} \neq 0$ by (3.6), this readily gives

$$\Phi^{(0)} = m_0.$$

(2) We now have to give an estimate on the decay rate; namely, we need to prove the following Claim: there exists a constant A_1 depending on m_0, κ and Ω such that

$$||\Phi - m_0||_{W^{1,2}(\Omega)} \leq \frac{A_1}{\mu_1}. \tag{3.7}$$

Proof of Claim (3.7). To prove this claim, we need to prove that there exist constants A_0 and A_0' such that

$$||\Phi - m_0||_{L^2(\Omega)} \leq \frac{A_0}{\mu_1} \tag{3.8}$$

and

$$||\nabla(\Phi - m_0)||_{L^2(\Omega)} \leq \frac{A_0'}{\mu_1}.$$

Since m_0 is a constant, it suffices to prove the existence of a constant A_0 such that

$$||\nabla\Phi||_{L^2(\Omega)} \leq \frac{A_0'}{\mu_1}.$$

To prove the existence of a constant A_0 such that (3.8) holds, we proceed in two steps: first, we prove that there exists a constant a_0 such that

$$\left|\left|\Phi - \fint_\Omega \Phi\right|\right|_{L^2(\Omega)} \leq \frac{a_0}{\mu_1}$$

and then that there exists a constant a_0' such that

$$\left|\fint_\Omega \Phi - m_0\right| \leq \frac{a_0'}{\mu_1}.$$

Setting $A_0 = a_0 + a_0'$ yields the desired estimate. For the first step (i.e to prove the existence of a_0), define

$$z_0 := \Phi - \fint_\Omega \Phi.$$

It is clear that z_0 satisfies the elliptic equation

$$\begin{cases} \Delta z_0 + \sum_{i=1}^N \frac{u_i m_i}{\mu_i} - \Phi \sum_{i=1}^N \frac{u_i}{\mu_i} = 0, \\ \frac{\partial z_0}{\partial \nu} = 0, \end{cases}$$

in a weak $W^{1,2}(\Omega)$ sense.
Multiplying this equation by z_0, integrating by parts and using the Cauchy-Schwarz inequality gives

$$\fint_\Omega |\nabla z_0|^2 \leq \sum_{i=1}^N \frac{1}{\mu_i} ||u_i m_i||_{L^2(\Omega)} ||z_0||_{L^2(\Omega)} + ||z_0||_{L^2(\Omega)} \sum_{i=1}^N \frac{1}{\mu_i} ||u_i \Phi||_{L^2(\Omega)}.$$

We now recall that each u_i converges, as μ_1 goes to ∞, to a constant $u_i^{(0)}$ and that Φ converges, as μ_1 goes to ∞, to m_0. Thus, each of these functions can be bounded from above by a constant that does not depend on the index i. Furthermore, each m_i can be bounded from above by κ, because $m \in \mathcal{M}(\Omega) = \{0 \leq m \leq \kappa\,, \fint_\Omega m = m_0\}$. There thus exists a universal constant α such that

$$\fint_\Omega |\nabla z_0|^2 \leq ||z_0||_{L^2(\Omega)}\alpha \sum_{i=1}^N \frac{1}{\mu_1}.$$

Using Hypothesis (A1), i.e the fact that, for each $i \in \mathbb{N}_N$, $\frac{\mu_i(\mu_1)}{\mu_1} \underset{\mu_1\to\infty}{\to} d_i > 0$, there exists a constant α' that does not depend on $i \in \mathbb{N}_N$ such that

$$\frac{\mu_i(\mu_1)}{\mu_1} \leq \alpha'.$$

This gives

$$\fint_\Omega |\nabla z_0|^2 \leq N\alpha\alpha' \frac{||z_0||_{L^2(\Omega)}}{\mu_1}.$$

We now use the Poincaré-Wirtinger inequality: there exists a constant $C_{PW}(\Omega)$ such that, for any $f \in W^{1,2}(\Omega)$, there holds

$$\left|\left|f - \fint_\Omega f\right|\right|_{L^2(\Omega)} \leq C_{PW}(\Omega)||\nabla f||_{L^2(\Omega)}.$$

Since $\fint_\Omega z_0 = 0$, this inequality entails

$$||\nabla z_0||^2_{L^2(\Omega)} \leq \frac{N\alpha\alpha' C_{PW}(\Omega)}{\mu_1}||\nabla z_0||_{L^2(\Omega)}.$$

Setting

$$a_0 := N\alpha\alpha' C_{PW}(\Omega),$$

the conclusion immediately follows.
We now need to prove that there exists a_0' such that

$$\left|\fint_\Omega \Phi - m_0\right| \leq \frac{a_0'}{\mu_1}.$$

We use the integral identity giving an expression of $\fint_\Omega \Phi$: if we choose an index i such that $u_i \underset{\mu_1\to\infty}{\to} u_i^{(0)} \neq 0$ (we know this is possible, since, from the proof of the Claim (3.4), Φ converges to $m_0 \neq 0$, and Φ converges also to $\sum_{i=1}^N u_i^{(0)}$. Furthermore, $u_i^{(0)} \geq 0$, so that at least one of the $u_i^{(0)}$ is positive), then there holds, by Equation (3.5),

$$0 < \fint_\Omega \Phi - m_0 = \mu_i \fint_\Omega \frac{|\nabla u_i|^2}{u_i^2}.$$

From this we first note that $\left|\fint_\Omega \Phi - m_0\right| = \fint_\Omega \Phi - m_0$. Now, set

$$\zeta_i := \mu_i\left(u_i - \fint_\Omega u_i\right).$$

The previous integral identity yields

$$\fint_\Omega \Phi - m_0 = \frac{1}{\mu_i}\fint_\Omega \frac{|\nabla \zeta_i|^2}{u_i^2}.$$

Since u_i converges to $u_i^{(0)} > 0$ in $L^2(\Omega)$, we know that, almost everywhere and as μ_1 goes to ∞, u_i is bounded below by a constant β. Furthermore, Hypothesis (A1) gives the existence of a universal constant α' such that

$$\frac{\mu_1}{\mu_i} \leq \alpha'.$$

Thus, there holds, for μ_1 large enough,

$$\fint_\Omega \Phi - m_0 \leq \frac{\alpha'}{\beta}\frac{1}{\mu_1}\fint_\Omega |\nabla\zeta_i|^2.$$

If we can bound $||\nabla\zeta_i||^2_{L^2(\Omega)}$ from above by a constant β' that only depends on m_0, κ and Ω, then setting $A_0' := \frac{\beta'\alpha'}{\beta}$ gives the desired inequality.
Let us then prove the existence of β' depending only on m_0, κ and Ω such that

$$||\nabla\zeta_i||^2_{L^2(\Omega)} \leq \beta'.$$

The function ζ_i satisfies

$$\Delta\zeta_i + u_i(m_i - \Phi) = 0.$$

Since $\fint_\Omega \zeta_i = 0$, the Poincaré-Wirtinger inequality yields

$$||\nabla\zeta_i||_{L^2(\Omega)} \leq C_{PW}(\Omega)||\zeta_i||_{L^2(\Omega)}.$$

We also know that, as μ_1 goes to ∞, u_i converges to $u_i^{(0)} \leq m_0$ and that Φ converges to m_0. Thus u_i and Φ are bounded above, as $\mu_1 \to \infty$, by a constant β''. Multiplying the equation on ζ_i by ζ_i, integrating by parts and using the Cauchy-Schwarz and Poincaré-Wrtinger inequalities, along with the definition of β'', we get

$$\begin{aligned}
\fint_\Omega |\nabla\zeta_i|^2 &= \fint_\Omega \zeta_i u_i(m_i - \Phi) && \text{by the Cauchy-Schwarz Inequality} \\
&\leq ||\zeta_i||_{L^2}||u_i(m_i - \Phi)||_{L^2(\Omega)} && \text{by the Poincaré-Wirtinger Inequality} \\
&\leq C_{PW}||\nabla\zeta_i||_{L^2(\Omega)}||\beta''(\kappa + \beta'').
\end{aligned}$$

This gives the conclusion. ☐

This concludes the proof of Claim (3.4). ☐

We now prove there exists $\Phi_1 \in W^{1,2}(\Omega)$ such that (3.4) holds.
The Rellich-Kondrachov theorem gives the existence of a function $\Phi_1 \in W^{1,2}(\Omega)$ such that

$$\mu_1(\Phi - m_0) \underset{\mu_1\to\infty}{\rightharpoonup} \Phi_1 \text{ in } W^{1,2}(\Omega),$$

and

$$\mu_1(\Phi - m_0) \underset{\mu_1\to\infty}{\to} \Phi_1 \text{ in } L^2(\Omega).$$

Thus we have, in a weak sense, established the expansion (4.2). We want to show that this expansion holds in a strong sense in $W^{1,2}(\Omega)$. To do so, we split our proof in several steps:

(1) First of, we need to identify the equation satisfied by Φ_1.
(2) Using this equation, we give an $L^2(\Omega)$ estimate on the gradient $\nabla(\mu_1(\Phi - m_0) - \Phi_1)$ as $\mu_1 \to \infty$ to prove that it converges strongly in $L^2(\Omega)$ to 0. Since we already know that the sequence $\{\mu_1(\Phi - m_0)\}_{\mu_1>0}$ converges strongly in $L^2(\Omega)$ to Φ_1, this is enough to ensure that (4.2) holds in $W^{1,2}(\Omega)$ strong.

We need to know what equation Φ_1 satisfies. Recall the weak formulation on the equation on Φ, that, is, for any $v \in W^{1,2}(\Omega)$,

$$-\int_\Omega \langle \nabla \Phi, \nabla v\rangle + \int_\Omega v \left(\sum_{j=1}^N \frac{u_i m_i}{\mu_i} - \Phi \frac{u_i}{\mu_i}\right) = 0.$$

Using hypothesis (A1) and passing to the limit, it follows that Φ_1 solves

$$\Delta \Phi_1 + \sum_{i=1}^N \frac{u_i^{(0)}}{d_i}(m_i - m_0) = 0$$

along with Neumann boundary conditions, in a weak sense. To ensure that the expansion (4.2) holds in $W^{1,2}(\Omega)$ strong, we only need to guarantee that

$$||\mu_1 \nabla \left(\Phi - m_0\right) - \nabla \Phi_1||_{L^2(\Omega)} = \underset{\mu_1 \to \infty}{o}(1). \tag{3.9}$$

Consider

$$z := \mu_1 \left(\Phi - m_0\right) - \Phi_1$$

and

$$\zeta := z - \fint_\Omega z.$$

Given that $\nabla z = \nabla \zeta$, it suffices to establish that

$$||\nabla \zeta||_{L^2(\Omega)} \underset{\mu_1 \to \infty}{\to} 0.$$

It is clear from the equation on Φ and on Φ_1 that ζ satisfies, in a weak sense, the equation

$$\begin{cases} \Delta \zeta + \sum_{i=1}^N m_i \left(u_i \frac{\mu_1}{\mu_i} - u_i^{(0)} \frac{1}{d_i}\right) - \sum_{i=1}^N \left(u_i^{(0)} m_0 \frac{1}{d_i} - \Phi u_i \frac{\mu_1}{\mu_i}\right) = 0 \\ \frac{\partial \zeta}{\partial \nu} = 0, \end{cases}$$

in a weak $W^{1,2}(\Omega)$ sense. For notational convenience, define ω as

$$\omega = \omega_{\mu_1} := \sum_{i=1}^N m_i \left(u_i \frac{\mu_1}{\mu_i} - u_i^{(0)} \frac{1}{d_i}\right) - \sum_{i=1}^N \left(u_i^{(0)} m_0 \frac{1}{d_i} - \Phi u_i \frac{\mu_1}{\mu_i}\right),$$

so that

$$\Delta \zeta + \omega = 0.$$

Furthermore, the convergences $\Phi \underset{\mu_1 \to \infty}{\to} m_0$ strongly in $L^2(\Omega)$ and $u_i \underset{\mu_1 \to \infty}{\to} u_i^{(0)}$ strongly in $L^2(\Omega)$ entail

$$||\omega||_{L^2(\Omega)} \underset{\mu_1 \to \infty}{\to} 0.$$

Since $\fint_\Omega \zeta = 0$ we also know, thanks to the Poincaré-Wirtinger inequality, that

$$||\zeta||_{L^2(\Omega)} \leq C_{PW}(\Omega) ||\nabla \zeta||_{L^2(\Omega)}.$$

Multiplying the equation on ζ by ζ, integrating by part and using the Cauchy-Schwarz inequality gives us

$$\begin{aligned}\fint_\Omega |\nabla\zeta|^2 &= \fint_\Omega \zeta\omega \\ &\leq ||\zeta||_{L^2(\Omega)}||\omega||_{L^2(\Omega)} \\ &\leq C_{PW}(\Omega)||\nabla\zeta||_{L^2(\Omega)}||\omega||_{L^2(\Omega)},\end{aligned}$$

so that

$$||\nabla\zeta||_{L^2(\Omega)} \leq C_{PW}(\Omega)||\omega||_{L^2(\Omega)}.$$

As was noted before,

$$||\omega||_{L^2(\Omega)} \underset{\mu_1\to\infty}{\to} 0,$$

concluding the proof of Estimate (3.9), and thus ending the proof of Lemma (3.1). □

<u>Asymptotic behaviour of $\lambda_1(\mu_i, m_i - \Phi)$.</u> Now assume that there are two different indices $i \neq j$ in I_1, i.e such that $u_i\,, u_j \neq 0$. As was mentioned before, this implies that

$$\lambda_1(\mu_i, m_i - \Phi) = \lambda_1(\mu_j, m_j - \Phi) = 0.$$

For $\ell = i, j$, we consider the associated eigenfunction ψ_ℓ normalized with respect to the $L^1(\Omega)$-norm, that is, the unique solution to

$$\begin{cases} \mu_\ell\Delta\psi_\ell + \psi_\ell(m_\ell - \Phi) = 0 & \text{in } \Omega, \\ \frac{\partial\psi_\ell}{\partial\nu} = 0 & \text{on } \partial\Omega, \\ \fint_\Omega \psi_\ell = 1. \end{cases} \tag{3.10}$$

We are going to use ψ_ℓ as a test function in the Rayleigh quotient of $\lambda_1(\mu_\ell, m_\ell - \Phi)$, so we need to have information about its behaviour, as $\mu_1 \to \infty$.

Lemma 3.2. *Define*

$$\psi_\ell^{(1)} := \frac{1}{d_\ell m_0}\hat{\eta}_{1,m_\ell}.$$

There holds:

$$\psi_\ell = 1 + \frac{\psi_\ell^{(1)}}{\mu_1} + \underset{\mu_1\to\infty}{o}\left(\frac{1}{\mu_1}\right) \textit{ strongly in } W^{1,2}(\Omega). \tag{3.11}$$

Proof of Lemma 3.2. As for the asymptotic expansion of Φ, we proceed in two steps: we first prove that there exists a constant A such that

$$||\psi_\ell - 1||_{W^{1,2}(\Omega)} \leq \frac{A}{\mu_1}. \tag{3.12}$$

We then prove that

$$\mu_1(\psi_\ell - 1) \underset{\mu_1\to\infty}{\rightharpoonup} \psi_\ell^{(1)} \text{ in } W^{1,2}(\Omega)$$

and

$$\mu_\ell(\psi_\ell - 1) \underset{\mu_1\to\infty}{\to} \psi_\ell^{(1)} \text{ in } L^2(\Omega).$$

We conclude by proving that

$$\left|\left|\mu_\ell\nabla\psi_\ell - \nabla\psi_\ell^{(1)}\right|\right|_{L^2(\Omega)} \underset{\mu_1\to\infty}{\to} 0. \tag{3.13}$$

Proof of Estimate (3.12). Define $\zeta_\ell := \psi_\ell - 1$. Given the normalization of the eigenfunction, it is clear that

$$\fint_\Omega \zeta_\ell = 0$$

so that, using the Poincaré-Wirtinger inequality, we get

$$||\zeta_\ell||_{L^2(\Omega)} \leq C_{PW}(\Omega)||\nabla\zeta_\ell||_{L^2(\Omega)}.$$

Furthermore, ζ_ℓ satisfies, in a weak sense,

$$\begin{cases} \mu_\ell\Delta\zeta_\ell + \zeta_\ell(m_\ell - \Phi) + (m_\ell - \Phi) = 0, \\ \frac{\partial\zeta_\ell}{\partial\nu} = 0. \end{cases}$$

Recall that $\Phi \underset{\mu_1\to\infty}{\to} m_0$ in $W^{1,2}(\Omega)$, so that Φ is uniformly bounded, as $\mu_1 \to \infty$, by $2m_0$. Multiplying the equation on ζ_ℓ by ζ_ℓ, integrating it by parts and successively using the Cauchy-Schwarz and the Poincaré-Wirtinger inequalities, we are led to

$$\begin{aligned} \mu_\ell \fint_\Omega |\nabla\zeta_\ell|^2 &= \fint_\Omega \zeta_\ell^2(m_\ell - \Phi) + \fint_\Omega \zeta_\ell(m_\ell - \Phi) \\ &\leq (\kappa + 2m_0)\fint_\Omega \zeta_\ell^2 + ||m_\ell - \Phi||_{L^2(\Omega)}||\zeta_\ell||_{L^2(\Omega)} \\ &\leq (\kappa + 2m_0)C_{PW}(\Omega)^2 \fint_\Omega |\nabla\zeta_\ell|^2 + (2m_0 + \kappa)C_{PW}(\Omega)||\nabla\zeta_\ell||_{L^2(\Omega)}. \end{aligned}$$

This leads to

$$\Big(\mu_\ell - (\kappa + 2m_0)C_{PW}(\Omega)^2\Big)\fint_\Omega |\nabla\zeta_\ell|^2 \leq (2m_0 + \kappa)||\nabla\zeta_\ell||_{L^2(\Omega)}.$$

Since $\mu_\ell(\mu_1) \to \infty$ as $\mu_1 \to \infty$, it follows that

$$\mu_\ell - (\kappa + 2m_0)C_{PW}(\Omega)^2 \underset{\mu_1\to\infty}{\sim} \mu_\ell,$$

1 so there exists a constant A_0 such that

$$||\nabla\zeta_\ell||_{L^2(\Omega)} \leq \frac{A_0}{\mu_\ell}. \tag{3.14}$$

Thanks to Hypothesis (A1), this is equivalent to requiring that there exist a constant A such that

$$||\nabla\zeta||_{L^2(\Omega)} \leq \frac{A}{\mu_1}.$$

Using the Poincaré-Wirtinger inequality, it follows that

$$||\zeta_\ell||_{L^2(\Omega)} \leq \frac{C_{PW}(\Omega)A}{\mu_1} \underset{\mu_1\to\infty}{\to} 0.$$

2 This concludes the proof of (3.12). $\square$

In this first step, we have proved that

$$||\mu_1(\psi_\ell - 1)||_{L^2(\Omega)}$$

is bounded and that

$$||\nabla\mu_\ell\psi_\ell||_{L^2(\Omega)} = ||\nabla\mu_\ell(\psi_\ell - 1)||_{L^2(\Omega)}$$

is bounded too (by Estimate (3.14)), as $\mu_1 \to \infty$. The Rellich-Kondrachov theorem ensures that there exists ψ_1 such that

$$\mu_\ell(\mu_1)(\psi_\ell - 1) \underset{\mu_1 \to \infty}{\to} \psi_1$$

weakly in $W^{1,2}(\Omega)$ and strongly in $L^2(\Omega)$. Using the weak formulation of the eigenequation (3.10), we are led to the conclusion that ψ_1 satisfies, in the weak $W^{1,2}(\Omega)$ sense, the equation

$$\Delta\psi_1 + \frac{1}{d_\ell}(m_\ell - m_0) = 0,$$

along with Neumann boundary conditions.
The function $\psi_\ell^{(1)} := \frac{1}{d_\ell m_0}\hat{\eta}_{1,m_\ell}$ satisfies the same equation with Neumann boundary conditions (because $\hat{\eta}_{1,m_\ell}$ solves (1.12)), thus there exists a constant α_1 such that

$$\psi_1 = \psi_\ell^{(1)} + \alpha.$$

Note that

$$\fint_\Omega \psi_\ell^{(1)} = 0.$$

But the condition $\fint_\Omega \psi_\ell = 1$ forces

$$\fint_\Omega \psi_1 = 0 = \fint_\Omega \psi_\ell^{(1)},$$

so that $\alpha = 0$ and, finally,

$$\psi_1 = \psi_\ell^{(1)}.$$

So far, we have proved that

$$\mu_1(\psi_\ell - 1) \underset{\mu_1 \to \infty}{\to} \psi_\ell^{(1)}$$

weakly in $W^{1,2}(\Omega)$ and strongly in $L^2(\Omega)$. It remains to prove that this convergence is strong in $W^{1,2}(\Omega)$; to do so, we only need to prove (3.13) i.e that $||\mu_\ell \nabla\psi_\ell - \nabla\psi_\ell^{(1)}||_{L^2(\Omega)} \underset{\mu_1 \to \infty}{\to} 0$.

Proof of Estimate (3.13). Define

$$z_\ell := \mu_1(\psi_\ell - 1) - \psi_\ell^{(1)}.$$

We need to prove that

$$||\nabla z_\ell||_{L^2(\Omega)} \underset{\mu_1 \to \infty}{\to} 0.$$

It is easy to see that z_ℓ satisfies

$$\Delta z_\ell + \frac{\mu_1}{\mu_\ell}\psi_\ell(m_\ell - \Phi) - \frac{1}{d_\ell}(m_\ell - m_0) = 0,$$

along with Neumann boundary conditions in a weak $W^{1,2}(\Omega)$ sense, and that

$$\fint_\Omega z_\ell = 0$$

so that the Poincaré-Wirtinger inequality ensures that

$$||z_\ell||_{L^2(\Omega)} \leq C_{PW}(\Omega)||\nabla\zeta_\ell||_{L^2(\Omega)}.$$

Multiplying the equation on z_ℓ by z_ℓ, integrating by parts and using the Poincaré-Wirtinger and the Cauchy-Schwarz Inequalities once again lead to the estimate

$$||\nabla z_\ell||_{L^2(\Omega)} \leq C_{PW}(\Omega) \left|\left| \frac{\mu_1}{\mu_\ell}\psi_\ell(m_\ell - \Phi) - \frac{1}{d_\ell}(m_\ell - m_0) \right|\right|_{L^2(\Omega)}.$$

We now just have to use the fact that

$$\frac{\mu_1}{\mu_\ell} \underset{\mu_1\to\infty}{\to} \frac{1}{d_\ell}$$

and that

$$\Phi \underset{\mu_1\to\infty}{\to} m_0$$

strongly in $L^2(\Omega)$ to conclude that the right hand term goes to zero as μ_1 goes to ∞. This concludes the proof. □

These two estimates combined end the proof of Lemma 3.1.

□

Let us now prove the first part of our theorem.

Proof of statement 1. We want to show that, under assumption (A1)-(A2), it is impossible to have

$$\lambda_1(\mu_j, m_j - \Phi) = \lambda_1(\mu_i, m_i - \Phi) \tag{3.15}$$

for μ_1 large enough. Consider then the quantity $\mu_1\lambda_1(\mu_\ell, m_\ell - \Phi)$ for $\ell = 1, j$. Using the Rayleigh quotients formulation of pricipal eigenvalues, Lemmas 3.1,3.2 and the weak formulation of the equation on $\varphi_\ell^{(1)}$, we know that

$$\begin{aligned}
\mu_1\lambda_1(\mu_\ell, m_\ell - \Phi) &= \frac{-\mu_1\mu_\ell \fint_\Omega |\nabla\psi_\ell|^2 + \mu_1 \fint_\Omega \psi_\ell^2(m_\ell - \Phi)}{\fint_\Omega \psi_\ell^2} \\
&= \frac{1}{1 + \underset{\mu_1\to\infty}{o}(1)} \left\{ -\frac{\mu_\ell}{\mu_1} \fint_\Omega |\nabla\psi_\ell|^2 + \underset{\mu_1\to\infty}{o}(1) - \fint_\Omega \Phi_1 \right. \\
&\left. +2\fint_\Omega \psi_\ell(m_\ell - m_0) + \underset{\mu_1\to\infty}{o}(1) \right\} \\
&= \left\{ d_\ell \fint_\Omega |\nabla\psi_\ell|^2 - \fint_\Omega \Phi_1 \right\} + \underset{\mu_1\to\infty}{o}(1).
\end{aligned}$$

Recall now that

$$\fint_\Omega \eta_{1,m_i} = \frac{1}{m_0^2}\fint_\Omega |\nabla\hat{\eta}_{1,m_i}|^2 = \frac{1}{d_\ell^2}\fint_\Omega |\nabla\psi_\ell|^2.$$

Thus, if equality (3.15) were true for two indexes $i \neq j$ and for a sequence of diffusivities going to $+\infty$, we would have

$$\frac{1}{d_i}\fint_\Omega \eta_{1,m_i} = \frac{1}{d_j}\fint_\Omega \eta_{1,m_j} + \underset{\mu_1\to\infty}{o}(1),$$

leading to a contradiction.

3.2. **Proof of statement 2: the stability of semi-trivial equilibria.** We have established that all the non zero equilibria are exactly the semi-trivial equilibria. It is then relevant to study the stablity of these equilibria. Consider $i \in \mathbb{N}_N$, and the associated equilibrium $\overline{u}_i$.
As is well-known (see e.g. [11]), the stability of $\overline{u}_i$ is determined by the sign of the eigenvalues associated with the operators

$$\mu_i\Delta + (m_i - 2\theta_i)\,, \mu_j\Delta + (m_j - \theta_i)\,, j \neq i.$$

Thus, the linear stability of $\overline{u}_i$ is determined by the signs of

$$\lambda_1(\mu_i, m_i - 2\theta_i)\,, \sup_{j\in\mathbb{N}_n\,, j\neq i} \lambda_1(\mu_j, m_j - \theta_i).$$

The first of these tho quantities is negative; this can be seen as a consequence of the monotony of the map $h \mapsto \lambda_1(\mu, h)$ (see [11]) and of the fact that $\lambda_1(\mu_i, m_i - \theta_i) = 0$.
Now, consider any index $j \neq i$. We are going to show that

$$\boxed{\mu_1\lambda_1(\mu_j, m_j - \theta_i) = \left(\frac{1}{d_j}\fint_\Omega \eta_{1,m_j} - \frac{1}{d_i}\fint_\Omega \eta_{1,m_i}\right) + \underset{\mu_1\to\infty}{o}(1).} \tag{3.16}$$

This, along with hypothesis (A2), leads to the desired result: $\overline{u}_1$ is linearly stable, while $\overline{u}_i$ is linearly unstable for any $i \neq 1$.
We will proceed as before, by studying the asymptotic behaviour of eigenfunctions: consider a L^1 normalized eigenfunction $\varphi_{i,j}$ associated with $\lambda_1(\mu_j, m_j - \theta_i)$, that is, the positive function such that

$$\begin{cases} \mu_j\Delta\varphi_{i,j} + \varphi_{i,j}(m_j - \theta_i) = 0, \\ \frac{\partial\varphi_{i,j}}{\partial\nu} = 0, \\ \fint_\Omega \varphi_{i,j} = 1. \end{cases} \tag{3.17}$$

in a weak $W^{1,2}(\Omega)$ sense.
According to [16, Proposition 2.4], we know that the following first order expansion holds:

$$\theta_i = m_0 + \frac{\eta_{1,m_i}}{\mu_i} + \underset{\mu_i\to\infty}{o}\left(\frac{1}{\mu_i}\right) \text{ in } W^{1,2}(\Omega).$$

By adapting slightly the proof of (3.11) we get the following result:

Lemma 3.3. *Define*

$$\varphi_{i,j}^{(1)} = \frac{1}{d_j m_0}\hat{\eta}_{1,m_j}. \tag{3.18}$$

There holds:

$$\varphi_{i,j} = 1 + \frac{\varphi_{i,j}^{(1)}}{\mu_1} + \underset{\mu_1\to\infty}{o}\left(\frac{1}{\mu_1}\right) \text{ in } W^{1,2}(\Omega), \tag{3.19}$$

This leads to the first order expansion of the eigenvalues, by using Lemma 3.3:

$$\begin{aligned}\mu_1\lambda_1(\mu_j, m_j-\theta_i) &= \frac{1}{|\Omega| + \underset{\mu_1\to\infty}{o}(1)}\left\{-d_j \fint_\Omega |\nabla\varphi_{i,j}^{(1)}|^2 + 2\fint_\Omega \varphi_{i,j}^{(1)}(m_j-m_0)\right.\\ &\left.-\frac{1}{d_i}\fint_\Omega \eta_{1,m_i} + \underset{\mu_1\to\infty}{o}(1)\right\}\\ &= \left(\frac{1}{d_j}\fint_\Omega \eta_{1,m_j} - \frac{1}{d_i}\fint_\Omega \eta_{1,m_i}\right) + \underset{\mu_i\to\infty}{o}(1).\end{aligned}$$

We have thus derived the desired identity, and the conclusion readily follows. This concludes the proof.

4. Proof of Theorem 1.3

4.1. **Proof of Statement 1: non-existence of coexistence equilibria.** Using Theorem 1.1, we only have to prove that there cannot exists two indexes i and j in $\mathbb{N}_N$ such that there exist $k \neq k'$ satisfying:

$$i \in \Gamma_k\,, j \in \Gamma_{k'}, u_i \neq 0 \text{ and } u_j \neq 0. \tag{4.1}$$

In other words, species with different scales of dispersal cannot coexist. If we can indeed prove this, it will mean that, up to a subsequence, all the indexes i such that $u_i \neq 0$ belong to the same set Γ_ℓ for some index ℓ. It will only remain to prove that there is no coexistence state in Γ_ℓ for large enough diffusivities, but this is exactly the point of the first theorem.
To prove Claim (4.1), we argue by contradiction: let $i_1, \dots, i_k$ be indexes such that, as $\mu_1 \to \infty$, along a subsequence, $u_{i_1} \neq 0, \dots, u_{i_k} \neq 0$ and for any index $j \notin \{i_1, \dots, i_k\}$, $u_j = 0$. Up to relabelling, we can assume that i_1 is the slowest diffuser, that is:

$$\exists D\,, \forall t \in \{2, \dots, k\}\,, \frac{\mu_{i_1}}{\mu_{i_t}}(\mu_1) \leq D.$$

Once again, our method relies on asymptotic expansions.

<u>Asymptotic behaviour of Φ.</u> Up to relabelling, we can assume that $i_1 \in \Gamma_1$, that is, we are working with the slowest disperser.
A straightforward adaptation of Lemmas 3.1 and 3.2 yields the two following results:

Lemma 4.1. *There exists $\Phi_1 \in W^{1,2}(\Omega)$ such that there holds:*

$$\Phi = m_0 + \frac{\Phi_1}{\mu_{i_1}} + \underset{\mu_1\to\infty}{o}\left(\frac{1}{\mu_{i_1}}\right) \text{ in } W^{1,2}(\Omega). \tag{4.2}$$

Using this lemma, assume there exists an index $j \in \{i_1, \dots, i_k\}$ such that

$$\mu_{i_1}(\mu_1) \underset{\mu_1\to\infty}{\to} \infty\,, \quad \mu_j(\mu_1) \underset{\mu_1\to\infty}{\to} \infty\,, \frac{\mu_{i_1}}{\mu_j}(\mu_1) \underset{\mu_1\to\infty}{\to} 0.$$

The existence of a coexistence state entails

$$\lambda_1(\mu_{i_1}, m_{i_1} - \Phi) = \lambda_1(\mu_j, m_j - \Phi) = 0. \tag{4.3}$$

We introduce the two normalized eigenfunctions associated with $\lambda_1(\mu_{i_1}, m_{i_1} - \Phi)$ and $\lambda_1(\mu_j, m_j - \Phi)$: for $\ell = i_1, j$,

$$\left\{\begin{array}{ll} \mu_\ell \Delta\psi_\ell + \psi_\ell(m_\ell - \Phi) = 0 & \text{in } \Omega, \\ \frac{\partial \psi_\ell}{\partial \nu} = 0 & \text{on } \partial\Omega, \\ \fint_\Omega \psi_\ell = 1. & \end{array}\right. \tag{4.4}$$

We then give the asymptotic expansion of ψ_ℓ:

Lemma 4.2. *Define*

$$\psi_{i_1}^{(1)} := \frac{1}{m_0}\hat{\eta}_{1,m_{i_1}} \, , \psi_j^{(1)} = \frac{1}{m_0}\hat{\eta}_{1,m_j}.$$

Then there holds:

$$\psi_{i_1} = 1 + \frac{\psi_{i_1}^{(1)}}{\mu_i} + \underset{\mu_i \to \infty}{o}\left(\frac{1}{\mu_{i_1}}\right) \, , \quad \psi_j = 1 + \frac{\psi_j^{(1)}}{\mu_j} + \underset{\mu_j \to \infty}{o}\left(\frac{1}{\mu_j}\right) \text{ in } W^{1,2}(\Omega). \tag{4.5}$$

Coming back to the proof of the theorem, identity (4.3) is

$$\mu_{i_1}\lambda_1(\mu_{i_1}, m_{i_1} - \Phi) = \mu_{i_1}\lambda_1(\mu_j, m_j - \Phi) = 0.$$

Expand each of these two quantities separately by adapting the proof of (3.16):

$$\mu_{i_1}\lambda_1(\mu_{i_1}, m_{i_1} - \Phi) = \frac{1}{1 + \underset{\mu_{i_1} \to \infty}{o}(1)} \left\{ \fint_\Omega |\nabla \psi_{i_1}^{(1)}|^2 - \fint_\Omega \Phi_1 + \underset{\mu_{i_1} \to \infty}{o}(1) \right\},$$

$$\mu_{i_1}\lambda_1(\mu_j, m_j - \Phi) = \frac{1}{1 + \underset{\mu_j \to \infty}{o}(1)} \left\{ \frac{\mu_{i_1}}{\mu_j} \fint_\Omega |\nabla \psi_j^{(1)}|^2 - \fint_\Omega \Phi_1 + \underset{\mu_j \to \infty}{o}(1) + \underset{\mu_i \to \infty}{o}\left(\frac{\mu_{i_1}}{\mu_j}\right) \right\},$$

Lemma 4.3. *Assume*

$$\fint_\Omega |\nabla \psi_{i_1}^{(1)}|^2 = 0.$$

Then m_i is constant.

This is a simple consequence of the fact that, if $\psi_{i_1}^{(1)}$ is a constant, then so is $\hat{\eta}_{1,m_{i_1}}$. Thus, since

$$\Delta \hat{\eta}_{1,m_{i_1}} + m_0(m_{i_1} - m_0) = 0$$

it follows that $m_{i_1} = m_0$. Note first that the asymptotic expansions of these eigenvalues, along with the fact that

$$\frac{\mu_{i_1}}{\mu_j}(\mu_1) \underset{\mu_1 \to \infty}{\to} 0$$

lead to

$$\fint_\Omega \Phi_1 = 0.$$

Using the asymptotic expansion of $\mu_{i_1}\lambda_1(\mu_{i_1}, m_{i_1} - \Phi)$, this in turn guarantees that

$$\fint_\Omega |\nabla \psi_{i_1}^{(1)}|^2 = 0.$$

Since

$$\mu_j \lambda_1(\mu_j, m_j - \Phi) = 0$$

we use the asymptotic expansion of this quantity to ensure that

$$\fint_\Omega |\nabla \psi_j^{(1)}|^2 = 0.$$

We now use Lemma 4.3: we have

$$m_{i_1} = m_j = m_0.$$

But our assumption on diffusivity implies that, whenever μ_1 is large enough, we have

$$\mu_i = \mu_{i_1}(\mu_1) < \mu_j = \mu_j(\mu_1).$$

By monotonicity of the principal eigenvalue with respect to diffusivity, we should get, for μ_1 large enough

$$\lambda_1(\mu_{i_1}, m_0 - \Phi) < \lambda_1(\mu_j, m_0 - \Phi).$$

1 This is a contradiction, and thus concludes the proof of Statement 1 of Theorem 1.3.

4.2. **Proof of Statement 2: The stability of semi-trivial equilibria.** We now fix an index $i \in \{1, \dots, N\}$ and linearize the system (1.1) at the equilibrium $\overline{u}_i$. As was recalled, the stability of this equilibrium is determined by the sign of the eigenvalues

$$\lambda_1(\mu_j, m_j - \theta_i)\,, j \in \{1, \dots, N\}\,, j \neq i.$$

2 If we can prove that:

$$\text{If } \frac{\mu_i}{\mu_j}(\mu_1) \underset{\mu_1 \to \infty}{\to} +\infty\,, \text{ then } \mu_j \lambda_1(\mu_j, m_j - \theta_i) \underset{\mu_1 \to \infty}{\to} d > 0 \tag{4.6}$$

3 then we are almost reduced to the setting of the first theorem, Theorem 1.1 provided we also prove

$$\text{If } \frac{\mu_i}{\mu_j}(\mu_1) \underset{\mu_1 \to \infty}{\to} 0\,, \text{ then } \mu_j \lambda_1(\mu_j, m_j - \theta_i) \underset{\mu_1 \to \infty}{\to} d < 0 \tag{4.7}$$

Proof of Claim (4.6). To prove this claim, we use once again asymptotic expansions of eigenvalues. Fix two indexes i and j satisfying the hypotheses of Claim (4.6). Introduce the associated eigenfunction $\varphi_{i,j}$, that is, the solution in a weak $W^{1,2}(\Omega)$ sense of

$$\begin{cases} \mu_j \Delta \varphi_{i,j} + \varphi_{i,j}(m_j - \theta_i) = \lambda_1(\mu_j, m_j - \theta_i)\varphi_{i,j}, \\ \frac{\partial \varphi_{i,j}}{\partial \nu} = 0, \\ \fint_\Omega \varphi_{i,j} = 1. \end{cases}$$

4 $\square$

5 We then have the following Lemma, that directly ensures the validity of Claim (4.6).

Lemma 4.4. *Assume* $\frac{\mu_i}{\mu_j}(\mu_1) \underset{\mu_1 \to \infty}{\to} 0$. *Let* $\varphi_{i,j}^{(1)} := \frac{1}{m_0}\hat{\eta}_{1,m_j}$. *There holds, in* $W^{1,2}(\Omega)$*:*

$$\varphi_{i,j} = 1 + \frac{\varphi_{i,j}^{(1)}}{\mu_j} + \underset{\mu_1 \to \infty}{o}\left(\frac{1}{\mu_j}\right).$$

There also holds

$$\lambda_1(\mu_j, m_j - \theta_{m_i,\mu_i}) = \frac{1}{\mu_j}\fint_\Omega |\nabla \varphi_{i,j}^{(1)}|^2 + \underset{\mu_1 \to \infty}{o}\left(\frac{1}{\mu_j}\right).$$

The proof of this lemma is a straightforward adaptation of all the previous asymptotic expansions. This concludes the proof of Claim (4.6).
In the very same way, we prove the Claim (4.7), by showing that, if $\frac{\mu_j}{\mu_i}(\mu_1) \underset{\mu_1\to\infty}{\to} 0$, then

$$\lambda_1(\mu_j, m_j-\theta_i) \underset{\mu_1\to\infty}{\sim} -\frac{1}{\mu_i}\fint_\Omega |\nabla\varphi_{i,j}^{(1)}|^2.$$

Thus, we are reduced to the stting of Theorem 1.1. We have thus completed the proof of Theorem 1.3.

5. Proof of Theorem 1.4

To prove this Theorem, we simply prove that we can reduce ourselves to the setting of Theorem 1.3.
If we can prove that, if all the diffusivities are large enough, then all the indexes $i_1,\dots,i_p$ of all the positive components $u_{i_1},\dots,u_{i_p}$ of an equilibrium lie in one of the J_i (i.e, if we can prove that all species can acces the same amount of resources), then the problem is reduced to the setting of Theorem 1.3. We can thus conclude.
Let us argue by contradiction and assume that there exists two positive components u_i, u_j such that

$$\fint_\Omega m_i \neq \fint_\Omega m_j.$$

In fact, if the non-zero components are $u_{i_1},\dots,u_{i_K}$, up to relabelling, you can assume that i_1 is the slowest diffuser: for any $j\in\{2,\dots,K\}$,

$$\frac{\mu_{i_1}}{\mu_{i_j}}(\mu_1)\underset{\mu_1\to\infty}{}d\in[0;+\infty).$$

Pick another $j\in\{2,\dots,K\}$. Our hypothesis entails

$$\lambda_1(\mu_i, m_i-\Phi)=\lambda_1(\mu_j,m_j-\Phi)=0.$$

We know, using the same techniques, that there exist an index k and a function $\Phi_1\in W^{1,2}(\Omega)$ such that there holds:

$$\Phi=\fint_\Omega m_k+\frac{\Phi_1}{\mu_i}+\underset{\mu_i\to\infty}{o}\left(\frac{1}{\mu_i}\right)\text{ in } W^{1,2}(\Omega).$$

Fix such an index k. We first prove the claim

Claim 5.1. *If $u_{i_1}, u_{i,j}\neq 0$ along a subsquence $\mu_1\to\infty$, then*

$$\fint_\Omega m_{i_1}=\fint_\Omega m_{i_j}=\fint_\Omega m_k.$$

Proof of Claim (5.1). This follows by identifying the first order of the expansion with respect to μ_1 in the identity

$$\lambda_1(\mu_i, m_i-\Phi)=\lambda_1(\mu_j,m_j-\Phi)=0.$$

Recall that one has

$$\lambda_1(\mu_i,m_i-\Phi)=\frac{1}{|\Omega|+\underset{\mu_i\to\infty}{o}(1)}\left\{\fint_\Omega m_i-\fint_\Omega m_k+\underset{\mu_i\to\infty}{o}(1)\right\}.$$

for every i such that $u_i\neq 0$. This immediately concludes the proof of Claim (5.1). □

This means that, if u_i and u_j are non-zero, then $\fint_\Omega m_i = \fint_\Omega m_j$, bringing us back to Theorem 1.3. The conclusions (on existence and stability of equilibria) of Theorem 1.4 then follow in the very same way.

6. Proof of Theorem 1.5

6.1. **Formal Hopf-Cole transform.** In this section, we recall the heuristics underlying the selection of traits for the sake of convenience for the reader and in order to fix some notations. We assume that ε is going to zero.
We use the Hopf-Cole transform: we write u_ε as

$$u_\varepsilon(\xi,x) := e^{\frac{\psi_\varepsilon(\xi,x)}{\varepsilon}},$$

which gives rise to the following equation:

$$\left\{\begin{array}{l}\mu(\xi)\frac{|\nabla_x\psi_\varepsilon|^2}{\varepsilon^2}+\mu(\xi)\frac{\Delta_x\psi_\varepsilon}{\varepsilon}+|\nabla_\xi\psi_\varepsilon|^2+\varepsilon\Delta_\xi\psi_\varepsilon+(m-\Phi)=0 \text{ in } \Omega,\\ \frac{\partial\psi_\varepsilon}{\partial\nu}=0 \text{ on } \partial\Omega.\end{array}\right. \tag{6.1}$$

Standard elliptic regularity arguments yield that Φ_ε converges, as $\varepsilon\to 0$, to some function $\Phi_{0,\mu}$.
In other words, we look for an asymoptotic development of ψ_ε of the form

$$\psi_\varepsilon(\xi,x)\approx\psi_0(\xi)+\varepsilon\ln\left(\psi_1(\xi,x)\right),\psi_1>0. \tag{6.2}$$

Plugging the previous expansion in the previous equation and identifying at the order 0 leads to

$$\mu(\xi)\Delta_x\psi_1(\xi,x)+\psi_1(\xi,x)\left(m(\xi,x)-\Phi_{0,\mu}(x)\right)=-|\nabla_\xi\psi_0|^2\psi.$$

We will use the fact that $|\nabla_\xi\psi_0|^2$ does not depend on x.
Since $\psi_1>0$, we can conclude that ψ_1 is a principal eigenfunction to a principal eigenvalue of the operator

$$\mathcal{L}: u\mapsto\mu(\xi)\Delta_x u+u(\xi,x)(m(\xi,x)-\Phi_{0,\mu}).$$

For the sake of notational convenience, we will write, for a trait ξ, $\lambda_1(\mu(\xi),m(\xi,\cdot)-\Phi_{\varepsilon,\mu})$ the principal eigenvalue associated with this operator. If we sum it all up, we get

$$\boxed{|\nabla_\xi\psi_0|^2=-\lambda_1(\mu(\xi),m(\xi,\cdot)-\Phi_{0,\mu}),\max_\xi\psi_0(\xi)=0,} \tag{6.3}$$

and

$$\boxed{\left\{\begin{array}{l}\mu(\xi)\Delta_x\psi_1+\psi_1(m(\xi,\cdot)-\Phi_{0,\mu})=\lambda_1(\mu(\xi),m(\xi,\cdot)-\Phi_{0,\mu})\psi_1 \text{ in } \Omega,\\ \dfrac{\partial\psi_1}{\partial\nu}=0 \text{ on } \partial\Omega.\end{array}\right.} \tag{6.4}$$

6.2. **Analysis of the limit equations.** For a fixed $\underline{\mu}$, it is known (see e.g [27]) that, as $\varepsilon\to 0$, we indeed have the uniform convergence of $\varepsilon\ln(u_{\varepsilon,\mu})$, up to a subsequece, to a solution of (6.3), and that, in fact, (6.4) also holds. Now, the main difference with [27] is that we assume a trait dependence on the resources distribution. Our regularity hypotheses on m enables us to mimick their arguments in order to derive continuity estimates of Bernstein type. Thus, we get convergence along subsequences, and it now remains to identify the possible limiting traits.
Let $\xi\in\Xi$ be a maximum point for φ_0. Then the equation (6.3) yields

$$-\lambda_1(\mu(\xi),m(\xi,\cdot)-\Phi_{0,\mu})=0.$$

We will show that, for large enough diffusivities, this can only happen in a neighbourhood of one of the maximizer ξ^*.
We claim the following:

Proposition 6.1. *For any $\xi \in \Xi$,*

$$\lambda_1\Big(\mu(\xi), m(\xi,\cdot) - \Phi_{0,\mu}\Big) \leq 0. \tag{6.5}$$

Proof. Let $\underline{\mu}$ be fixed. Then we know that, as $\varepsilon \to 0$, the function $z_\varepsilon := \varepsilon \ln(\psi_\varepsilon)$ converges uniformly in $\Omega \times \Xi$ to a solution of (6.3), so that

$$\lambda_1\Big(\mu(\xi), m(\xi,\cdot) - \Phi_{0,\mu}\Big) < 0.$$

□

To conclude, we only need the following proposition:

Proposition 6.2. *Assume the set is size-scale ordered. Let ξ^* be such that*

$$\forall \xi \in \Xi\,, \xi \neq \xi^*\,, F(\xi^*) > F(\xi).$$

There holds

$$\forall \xi \in \Xi$$

$$\mu(\xi)\Big(\lambda_1(\mu(\xi), m(\xi,\cdot) - \Phi_{0,\mu}) - \lambda_1(\mu(\xi^*), m(\xi^*,\cdot) - \Phi_{0,\mu})\Big) = F(\xi^*) - F(\xi) + \underset{\underline{\mu}\to\infty}{O}\left(\frac{1}{\underline{\mu}}\right).$$

These two propositions combined immediately lead to the conclusion.

Proof. The first thing to do is to control the behaviour of $\Phi_{0,\mu}$. But we know that there exists a trait $\xi \in \Xi$ such that

$$\Phi_{0,\mu} = \theta_\xi.$$

The asymptotic results recalled in the first part yield

$$\Phi_{0,\mu} = m_0 + \underset{\underline{\mu}\to\infty}{O}\left(\frac{1}{\underline{\mu}}\right).$$

Furthermore, a straightforward adaptation of the proofs of [4,27] yields the existence of a constant M uniform in $\varepsilon \in (0;1)$ and $\mu > 1$ such that

$$||\Phi_{\varepsilon,\mu}||_{L^\infty(\Omega)}\,, ||\Phi_{\varepsilon,\mu}||_{W^{2,p}(\Omega)} \leq M.$$

The proposition is then an easy consequence of the asymptotic expansion recalled in the introduction and of the use of the Rayleigh quotient. Indeed, consider, for $\xi \in \Xi$, an eigenfunction ζ_ξ associated with $\mu(\xi), m(\xi,\cdot) = m_\xi$:

$$\begin{cases} \mu(\xi)\Delta\zeta_\xi + \zeta_\xi(m_\xi - \Phi_{0,\mu}) = \lambda_1(\mu(\xi), m(\xi,\cdot) - \Phi_{\varepsilon,\mu})\zeta_\xi & \text{in } \Omega, \\ \frac{\partial \zeta_\xi}{\partial \nu} = 0 & \text{on } \partial\Omega, \\ \fint_\Omega \zeta_\xi = 1. \end{cases}$$

Standard elliptic estimates, along with the Poincaré-Wirtinger inequality, yield the following asymptotic expansion for ζ_ξ:

$$\zeta_\xi = 1 + \frac{\hat{\eta}_\xi}{\mu(\xi)} + \underset{\mu(\xi)\to\infty}{o}\left(\frac{1}{\mu(\xi)}\right),$$

where $\hat{\eta}_\xi$, as recalled in the introduction, solves

$$\begin{cases} \Delta\hat{\eta}_\xi + m_0\left(m(\xi,x) - \fint_\Omega m(\xi,x)dx\right) = 0 & \text{in } \Omega, \\ \frac{\partial\hat{\eta}_\xi}{\partial\nu} = 0 & \text{on } \partial\Omega, \\ \fint_\Omega \hat{\eta}_\xi = 0. & \end{cases}$$

We now conclude in the same fashion as was used in the proof of Proposition 1. This leads to

$$\lambda_1\left(\mu(\xi), m(\xi,\cdot) - \Phi_{\varepsilon,\mu}\right) = \frac{1}{\mu(\xi,\underline{\mu})}\fint_\Omega |\nabla\eta_\xi|^2 + \underset{\underline{\mu}\to\infty}{O}\left(\frac{1}{\underline{\mu}}\right).$$

The conclusion follows easily. □

References

[1] O. Bénichou, V. Calvez, N. Meunier, and R. Voituriez. Front acceleration by dynamic selection in fisher population waves. *Phys. Rev. E*, 86:041908, Oct 2012.

[2] H. Berestycki, F. Hamel, and L. Roques. Analysis of the periodically fragmented environment model : I – species persistence. *Journal of Mathematical Biology*, 51(1):75–113, 2005.

[3] H. Berestycki and T. Lachand-Robert. Some properties of monotone rearrangement with applications to elliptic equations in cylinders. *Mathematische Nachrichten*, 266(1):3–19, mar 2004.

[4] E. Bouin and S. Mirrahimi. A hamilton-jacobi approach for a model of population structured by space and trait. *Communications in Mathematical Sciences*, 13, 07 2013.

[5] R. Cantrell and C. Cosner. Diffusive logistic equations with indefinite weights: population models in disrupted environments. II. *SIAM J. Math. Anal.*, 22(4):1043–1064, 1991.

[6] R. Cantrell, C. Cosner, and V. Hutson. Permanence in ecological systems with spatial heterogeneity. *Proceedings of the Royal Society of Edinburgh Section A: Mathematics*, 123(3):533–559, 1993.

[7] R. Cantrell, C. Cosner, and V. Hutson. Ecological models, permanence and spatial heterogeneity. *Rocky Mountain J. Math.*, 26(1):1–35, 03 1996.

[8] R. S. Cantrell and C. Cosner. The effects of spatial heterogeneity in population dynamics. *J. Math. Biol.*, 29(4):315–338, 1991.

[9] R. S. Cantrell and C. Cosner. On the effects of spatial heterogeneity on the persistence of interacting species. *Journal of Mathematical Biology*, 37(2):103–145, Aug 1998.

[10] R. S. Cantrell and C. Cosner. *Spatial Ecology via Reaction-Diffusion Equations*. John Wiley & Sons Ltd., Chichester, UK, 2003.

[11] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski. The evolution of slow dispersal rates: a reaction diffusion model. *Journal of Mathematical Biology*, 37(1):61–83, 1998.

[12] R. A. Fisher. The wave of advance of advantageous genes. *Annals of Eugenics*, 7(4):355–369, 1937.

[13] L. Girardin. Competition in periodic media: I – Existence of pulsating fronts. *Discrete and Continuous Dynamical Systems - Series B*, 22(4), June 2017.

[14] X. He and W.-M. Ni. Global dynamics of the lotka-volterra competition-diffusion system: Diffusion and spatial heterogeneity is. *Communications on Pure and Applied Mathematics*, 69(5):981–1014, 2015.

[15] X. He and W.-M. Ni. Global dynamics of the lotka–volterra competition–diffusion system with equal amount of total resources, ii. *Calculus of Variations and Partial Differential Equations*, 55, 04 2016.

[16] X. He and W.-M. Ni. Global dynamics of the Lotka–Volterra competition–diffusion system with equal amount of total resources, III. *Calculus of Variations and Partial Differential Equations*, 56(5):56:132, 2017.

[17] V. Hutson, Y. Lou, and K. Mischaikow. Spatial heterogeneity of resources versus lotka-volterra dynamics. *Journal of Differential Equations*, 185(1):97 – 136, 2002.

[18] B. Kawohl. *Rearrangements and Convexity of Level Sets in PDE*. Springer Berlin Heidelberg, 1985.

[19] A. Kolmogorov, I. Pretrovski, and N. Piskounov. étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. *Moscow University Bulletin of Mathematics*, 1:1–25, 1937.

[20] K.-Y. Lam and Y. Lou. An integro-PDE model for evolution of random dispersal. *Journal of Functional Analysis*, 272(5):1755–1790, 2017.

[21] J. Lamboley, A. Laurain, G. Nadin, and Y. Privat. Properties of optimizers of the principal eigenvalue with indefinite weight and Robin conditions. *Calc. Var. Partial Differential Equations*, 55(6):55:144, 2016.
[22] Y. Lou. On the effects of migration and spatial heterogeneity on single and multiple species. *Journal of Differential Equations*, 223(2):400 – 426, 2006.
[23] Y. Lou. *Tutorials in Mathematical Biosciences IV: Evolution and Ecology*, chapter Some Challenging Mathematical Problems in Evolution of Dispersal and Population Dynamics, pages 171–205. Springer Berlin Heidelberg, Berlin, Heidelberg, 2008.
[24] D. Ludwig, D. G. Aronson, and H. F. Weinberger. Spatial patterning of the spruce budworm. *Journal of Mathematical Biology*, 8(3):217–258, 1979.
[25] I. Mazari, G. Nadin, and Y. Privat. Optimal location of resources maximizing the total population size in logistic models. working paper or preprint, Oct. 2017.
[26] S. Pacala and J. Roughgarden. Spatial heterogeneity and interspecific competition. *Theoretical Population Biology*, 21(1):92 – 113, 1982.
[27] B. Perthame and P. E. Souganidis. Rare mutations limit of a steady state dispersion trait model. 2015.
[28] L. Roques and F. Hamel. Mathematical analysis of the optimal habitat configurations for species persistence. *Math. Biosci.*, 210(1):34–59, 2007.
[29] N. Shigesada and K. Kawasaki. *Biological Invasions: Theory and Practice*. Oxford University Press, 1997.
[30] J. G. Skellam. Random dispersal in theoretical populations. *Biometrika*, 38:196–218, 1951.
[31] O. Turanova. On a model of a population with variable motility. *Mathematical Models and Methods in Applied Sciences*, 25(10):1961–2014, 2015.

Acknowledgment. The author was partially supported by the "Project Analysis and simulation of optimal shapes - application to lifesciences" of the Paris City Hall.
The author also wishes to thank Grégoire Nadin and Yannick Privat for their help and support in writing this article.

E-mail address: `idriss.mazari@upmc.fr`