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Equilibria and stability issues for diffusive Lotka-Volterra system in a heterogeneous setting for large diffusivities

Idriss Mazari*

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Abstract

We consider a system of $N$ competing species, each of which can access a different resources distribution. We fully characterize the existence and stability of steady-states for large diffusivities. Indeed, we prove that the resources distribution yielding the largest population size at equilibrium is, broadly speaking, always the winner when species disperse quickly. The methods used rely on an expansion of the solutions of the Lotka-Volterra system for large diffusivities.

Keywords: Diffusive Lotka-Volterra system, principal eigenvalue, coexistence steady-states, stability.

AMS classification: 34E10,35J47,35Q92,49K20,49R05,92D25.

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1 Introduction

1.1 The diffusive Lotka-Volterra system and our prototypical result

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 $\{1, \ldots, N\}$. Throughout this article, $\Omega$ will stand for a bounded $C^2$ 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, $\mu_i$ ($i = 1, \ldots, N$),

2. $N$ functions $m_i \in L^\infty(\Omega)$ ($i = 1, \ldots, N$) standing for resources distribution. The spatial heterogeneity will be accounted for by the resources distributions $m_i$’s.

The diffusive Lotka-Volterra system reads as follows:

\[
\begin{aligned}
\frac{\partial u_i}{\partial t} &= \mu_i \Delta u_i + u_i(m_i - \sum_{j=1}^{N} u_j) \quad \text{in } \Omega, \\
\frac{\partial u_i}{\partial \nu} &= 0 \quad \text{on } \partial \Omega, \\
u_i(t = 0, \cdot) &= u_{i,0},
\end{aligned}
\]  

(1)

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 [6, 20, 8, 7, 19] and the references therein. Our main interest here is the investigation of the influence of spatial heterogeneity on the existence and stability of steady states of (1), which we will also call equilibria, in the setting of large diffusivities.

**Formal presentation of our main focus.** We will use a criterion related to single species models for large diffusivities, to derive results about existence and stability results for the system (1).

It will be convenient to introduce the positive solution $\theta_i = \theta_{m_i, \mu_i}$ of the so-called logistic diffusive equation:

\[
\begin{aligned}
\mu_i \Delta \theta_i + \theta_i(m_i - \theta_i) = 0 \quad \text{in } \Omega, \\
\frac{\partial \theta_i}{\partial \nu} &= 0 \quad \text{on } \partial \Omega.
\end{aligned}
\]  

(2)

Existence and uniqueness of a positive solution to this equation is classical, see [1]. We recall that this question boils down to the study of the principal eigenvalue $\lambda_1(m_i, \mu_i)$ of the elliptic operator $\mu_i \Delta + m_i$, and that existence and uniqueness is guaranteed if

\[
\int_{\Omega} m_i > 0. 
\]  

(3)

It is then natural to assume that, for every $i \in \mathbb{N}_N$, we have

\[
\int_{\Omega} m_i > 0.
\]

Note that, for any $i$, the state

$$(\bar{u}_i, 0, \ldots, \bar{u}_i, 0, \ldots, 0)$$

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

\[
\int_{\Omega} \theta_i. 
\]  

(4)
that is, the total population size of a single species, moving at rate $\mu_i$ with a resources distribution $m_i$, in the case where all the diffusivities $\mu_i$’s are large. In other words, a criterion on the equations regarding a single species yields results for the whole system. Our prototypical result reads:

If the $m_i$’s are ordered with respect to criterion (4), that is

$$\frac{1}{\mu_1} \int_{\Omega} \theta_1 > \cdots > \frac{1}{\mu_N} \int_{\Omega} \theta_N,$$

and if the $\mu_i$’s are "large enough", then the $\pi_i$’s are the only equilibria, and $\pi_1$ is the only stable one.

1.2 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 and understand the influence of the diffusivities on equilibria. In this paper, we will work under the hypothesis that diffusivities are large.

In [7], 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, $\mu_1 > \cdots > \mu_N$. It is proved that the slowest diffuser always wins: the $u_i$’s are the only equilibria, $u_1$ is stable, while the other $u_i$’s are unstable.

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, let us 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 an with a non-negative initial condition. Many results are devoted to studying the existence of coexistence equilibria and the importance of the heterogeneity. See for instance [2, 4, 3, 11, 17]. We highlight in particular two of them. They hold in the case $N = 2$, $b_{1,1} = b_{2,2} = 1$ and $m_1 = m_2 = m$, and it has been shown that

1. In [13], the map $\mu \mapsto \int_{\Omega} \theta_{m,\mu}$ has at least one maximum on $\mathbb{R}_+$ and that, if $b_{2,1} < \inf_{\mu > 0, \mu_1 \theta_{m,\mu} = b_{1,1}^*}$, then $\pi_1$ is unstable. If $b_{2,1} > b_{1,1}^*$, then $\pi_1$ can change stability.

2. In [9], if $b_{2,1} = \alpha b_{1,2}$ and if $b_{1,2}$ is large enough, then $\pi_1$ and $\pi_2$, no linearly stable coexistence state can exist.

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 hypothesis: 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 this distributions on the persistence of a species. For instance, in [1] it is proved that the concentration of resources in the logistic diffusive model (6) favors the persistence of a species.

We conclude this introduction by mentioning a recent result by He and Ni, in [10]. In this paper, the two authors study the case $N = 2$, with two different resources distributions $m_1$ and $m_2$. Using a technique of asymptotic expansion, the precisely study the set

$$Q := \{(\mu_1, \mu_2), (\theta m_1, \mu_1, 0) \text{ is linearly stable}\}$$

and prove that

$$Q = \{\mu_2 > f(\mu_1)\}$$

where

$$f(\mu_1) \to \infty, f(\mu_1) \to 0.$$ 

We insist upon the fact that, to the best of our knowledge, our criterion, which we believe is relevant, as not yet been used in studying the existence of equilibria.

It is notable that the technique we use here was also used and generalized in [16] to tackle a shape optimization problem involving the total population size functional, as we will recall in the main part of this article, and that it is this technique is extended here to the case of $N$ species.

## 2 Main results

### 2.1 With the same amount of resources

We first assume that all the species can access the same amount of resources.

**The class of admissible distribution resources.** 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 $m_i$'s: for any $i \in \mathbb{N}_N$, $m_i \in \mathcal{M}_{m_0}(\Omega)$, where

$$\mathcal{M}_{m_0}(\Omega) = \left\{ m \in L^\infty(\Omega), 0 \leq m \leq \kappa \text{ a.e.}, \int_\Omega m = m_0 \right\}. \quad (5)$$

The relevance of this admissible class is detailed in [14].

Note that, if $m \in \mathcal{M}_{m_0}(\Omega)$ and if $\mu > 0$, then the unique positive solution of the logistic diffusive equation

$$\begin{cases} 
\mu \Delta \theta_{m,\mu} + \theta_{m,\mu}(m - \theta_{m,\mu}) = 0, & \text{in } \Omega \\
\frac{\partial \theta_{m,\mu}}{\partial \nu} = 0 & \text{on } \partial \Omega,
\end{cases} \quad (6)$$

satisfies

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

**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 \( \int_{\Omega} m = m_0 > 0 \). Introduce, for a diffusivity \( \mu \), the functional \( \mathcal{F}_\mu : \mathcal{M}_{m_0}(\Omega) \to \mathbb{R} \) defined by

\[
\mathcal{F}_\mu : m \mapsto \int_{\Omega} \theta_{m,\mu}.
\]

The question that arises is that of the behaviour of \( \mathcal{F}_\mu \) as \( \mu \to +\infty \). In order to address this question, we recall the classical result (see [13] and the references therein) that for any \( p \in [1; +\infty) \),

\[
\theta_{m,\mu} \to \mu \to \infty m_0 \text{ in } W^{1,p}(\Omega).
\]

We now look for a second order term, that is for \( \eta_{1,m} \) such that

\[
\theta_{m,\mu} = m_0 + \frac{\eta_{1,m}}{\mu} + o\left(\frac{1}{\mu}\right) \text{ in } W^{1,2}(\Omega),
\]

and where \( o\left(\frac{1}{\mu}\right) \) is uniform in \( m \in \mathcal{M}_{m_0}(\Omega) \). This gives rise to the following equation on \( \eta_{1,m} \):

\[
\begin{cases}
\Delta \eta_{1,m} + m_0 (m - m_0) = 0 & \text{in } \Omega, \\
\frac{\partial \eta_{1,m}}{\partial \nu} = 0 & \text{on } \partial \Omega.
\end{cases}
\]

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

\[
\begin{cases}
\Delta \hat{\eta}_{1,m} + m_0 (m - m_0) = 0 & \text{in } \Omega, \\
\frac{\partial \hat{\eta}_{1,m}}{\partial \nu} = 0 & \text{on } \partial \Omega, \\
\int_{\Omega} \hat{\eta}_{1,m} = 0.
\end{cases}
\]

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 (6):

\[
\int_{\Omega} \theta_{m,\mu} (m - \theta_{m,\mu}) = 0,
\]

so that, identifying at order \( \frac{1}{\mu} \), we get

\[
\beta_{1,m} = \frac{1}{m_0} \int_{\Omega} \hat{\eta}_{1,m} (m - m_0) = \frac{1}{m_0^2} \int_{\Omega} |\nabla \hat{\eta}_{1,m}|^2.
\]

This will be our criterion. This means that the following first-order expansion of \( \mathcal{F}_\mu \) holds:

\[
\mathcal{F}_\mu : m \mapsto m_0 + \frac{1}{\mu} \int_{\Omega} \eta_{1,m} + o\left(\frac{1}{\mu}\right).
\]

### 2.2 Main results of the papers

**Same amount of resources and same scale of dispersal.** 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 \( d_i \in \mathbb{R}^* \) such that

\[
\frac{\mu_i(\mu_1)}{\mu_1} \to d_i, \quad (A1)
\]

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

\[
\frac{1}{d_1} \int_{\Omega} \eta_{1,m_1} > \cdots > \frac{1}{d_N} \int_{\Omega} \eta_{1,m_N}. \quad (A2)
\]
Theorem 1. Assume that, for any $i \in \mathbb{N}_N, m_i \in \mathcal{M}_{m_0}(\Omega)$. Assume that (A1) and (A2) are satisfied.

There exists $\mu^* = \mu^*$ such that, for any $N$-tuple $(\mu_1, \ldots, \mu_N)$ satisfying, for any $i \in \mathbb{N}_n, \mu_i > \mu^*$:

1. The $\pi_i$'s are the only non-zero equilibria of the system (1). There are no coexistence states.
2. $\pi_1$ is linearly stable, while the other $\pi_i$'s are linearly unstable.

Under the hypothesis of this theorem, we can rewrite the arguments of [7, Theorem 3.4] and we obtain the following result:

Theorem 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:

\[
\begin{aligned}
\frac{\partial u_i}{\partial t} &= \mu_i \Delta u_i + u_i (m_i - \sum_{j=1}^N u_j) + \epsilon \sum_{j=1}^n m_{i,j} u_j \quad \text{in } \Omega, \\
\frac{\partial u_i}{\partial \nu} &= 0 \quad \text{on } \partial \Omega, \\
u_i(t = 0, \cdot) &= u_{i,0},
\end{aligned}
\]

(10)

where, for every $i \in \mathbb{N}_N$, $u_{i,0}$ denotes a non-negative initial condition in $W^{1,2}(\Omega)$. Under the assumptions of theorem 1: there exists $\epsilon_0 > 0$ such that, for any $\epsilon < \epsilon_0$, there exists a non-negative equilibrium $u_1(\epsilon)$, varying analytically in $\epsilon$, such that $u_1(0) = \pi_1$ (i.e $\pi_1$ perturbs analytically in the cone of non-negative $N$-tuples of functions). There also exists $\delta > 0$ such that, for $\epsilon < \epsilon_0$, any positive (componentwise) steady-state $u_\epsilon$ of the system with mutations satisfy: for any $i > 1$,

\[\|u_\epsilon - \pi_i\|_{C^1(\Omega)} \geq \delta,\]

i.e the unstable equilibria do not perturb into equilibria of the system with mutations.

We will not prove this result, for it is a straightforward adaptation of the arguments of [7, Theorem 3.4].

**Same amount of resources and different scales of dispersal.** A bit of notation is required to be able to give a clear statement of the two next results. As we have mentioned, we will 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. Henceforth, we will parameterize diffusivities as functions of $\mu_1$, that is, $\mu_i = \mu_i(\mu_1)$, and we recall that we assume

\[\mu_i(\mu_1) \to \infty \quad \text{as } \mu_1 \to \infty.\]

For a subset of indexes $\{i_1, \ldots, i_k\}$ 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

\[\frac{\mu_i(\mu_1)}{\mu_1} \to d_{i_j}, \quad \text{as } \mu_1 \to \infty, \quad (H1)\]

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

2. Furthermore,

\[\forall j, j' \in \{i_1, \ldots, i_k\}, \frac{1}{d_{i_j}} \int_\Omega \eta_1.m_{i,j} \neq \frac{1}{d_{i_j'}} \int_\Omega \eta_1.m_{i,j'}, \quad (H2)\]
Furthermore, if we are given a set of indexes $\Gamma \subset \mathbb{N}_N$, it is always possible to split it into same diffusivity scale sets

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

and we assume that the same diffusivity scale sets are maximal, that is, for any $i \in [1; t - 1]$,

$$\frac{\mu_i(\mu_1)}{\mu_{i+1}(\mu_1)} \to 0 \text{ as } \mu_i \to \infty.$$

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

The hypothesis of Theorem 1 were in fact the hypothesis that the set $\mathbb{N}_N$ itself was size-scale ordered.

**Theorem 3.** Assume that, for any $i \in \mathbb{N}_N, m_i \in \mathcal{M}_{m_0}(\Omega)$. Let us write the scale partition of $\mathbb{N}_N$:

$$\mathbb{N}_N = I_1 \sqcup \cdots \sqcup I_L$$

and assume each of the $I_j$ is size-scale ordered i.e satisfy (H1) and (H2). Then there exists $\mu^*$ such that for any $N$-tuple $(\mu_1, \ldots, \mu_N)$ satisfying, for any $i \in \mathbb{N}_n, \mu_i > \mu^*$, The $\pi_i$’s are the only non-zero equilibria of the system (1). There are no coexistence states.

**Different amounts of resources and different scale of dispersal.** Let us drop the assumption that $m_i \in \mathcal{M}_{m_0}(\Omega)$. 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 $i \in J_k$,

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

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. The

**Theorem 4.** Assume the $\Gamma_{i,j}$ are size-scale ordered i.e satisfy both conditions (H1) and (H2). Then there exists $\mu^*$ such that for any $N$-tuple $(\mu_1, \ldots, \mu_N)$ satisfying, for any $i \in \mathbb{N}_n, \mu_i > \mu^*$, the $\pi_i$’s are the only non-zero equilibria of the system (1). There are no coexistence states.

### 3 Proof of theorem 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 that we have recalled). In a more 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:

$$\lambda_1(h, \mu) = \sup_{f \in W^{1,2}(\Omega), \int_\Omega f^2 = 1} \left\{ -\mu \int_\Omega |\nabla f|^2 + \int_\Omega f^2 h \right\}.$$
The quantity
\[
\left\{-\mu \int_{\Omega} |\nabla f|^2 + \int_{\Omega} f^2 h\right\}
\]
is the associated Rayleigh quotient. It is also clear, since \(\theta_i\) is an eigenfunction of the operator \(\mu_i \Delta + (m_i - \theta_i)\) that
\[
\lambda_1(m_i - \theta_i) = 0.
\]
We finally recall the following results (\cite{7}): for any \(h \in L^\infty(\Omega)\), the map \(\mu \mapsto \lambda_1(h, \mu)\) is non-increasing, and \(\lambda_1(h, \mu) \xrightarrow{h \to +\infty} \int_{\Omega} h\).

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

Regarding notations. In the sequel, we will consider a sequence \(\{U_\mu\}_{\mu>0}\) of equilibria, and we will write either \(U_{\mu,k}\) or \(u_k\) to denote the \(k\)-th component of this equilibrium. Since in the framework of this theorem \(N\) is size-scale ordered, we know that we can fix \(\mu_1\) as a reference diffusivity, and note that any function behaving as \(o_{\mu \to \infty} \left(\frac{1}{\mu_1}\right)\) behaves as \(o_{\mu \to \infty} \left(\frac{1}{\mu_i}\right)\) and conversely. We have already defined, for any \(i \in \mathbb{N}\),
\[
d_i := \lim_{\mu \to \infty} \frac{\mu_i(\mu_1)}{\mu_1} \in ]0; \infty[.
\]
Consider, for some \(N\)-tuple \((\mu_1, \ldots, \mu_N)\), a non-zero equilibrium \(u = (u_1, \ldots, u_N)\) and define
\[
\Phi := \sum_{i=1}^{N} u_i,
\]
so that each \(u_i\) solves the following equation:
\[
\mu_i \Delta u_i + u_i(m_i - \Phi) = 0 \text{ in } \Omega,
\]
along with Neumann boundary conditions. Now, assume that there exists a sequence \(\{U_\mu\}_{\mu>0}\) of coexistence equilibria as \(\mu \to \infty\). Up to an extraction, we can split the set \(\mathbb{N}\) into two subsets:
\[
I_1 = \{i, \text{ for all } \mu \text{ large enough } U_{\mu,i} \neq 0\}, \quad I_2 = \{i, \text{ for all } \mu \text{ large enough } U_{\mu,i} = 0\}.
\]
We will only focus on the set \(I_1\).
Assume that \(U_\mu\) is not one of the \(\pi_i\)'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,
\[
0 = \lambda_1(m_i - \Phi, \mu_i) = \lambda_1(m_j - \Phi, \mu_j).
\]
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. We will need some background results about principal eigenvalues.
Asymptotic behaviour of $\Phi$. We first note that $\Phi$ satisfies the following partial differential equation:

$$\Delta \Phi - \left( \sum_{i=1}^{N} \frac{1}{\mu_i} \right) \Phi^2 + \sum_{i=1}^{N} \frac{u_i m_i}{\mu_i} = 0,$$

with Neumann boundary conditions.

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

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

$$\Phi = m_0 + \frac{\Phi_1}{\mu_1} + o_{\mu_1 \to \infty} \left( \frac{1}{\mu_1} \right). \quad (13)$$

**Proof of Lemma 1.** The weak formulation of the equation on $\Phi$, readily gives, thanks to assumption (A1):

$$||\nabla \Phi||_{L^2(\Omega)} \leq A \mu_1,$$

where $A$ is a positive constant depending on $m_0, \kappa$ and $\Omega$.

It is standard that $u_i$ converges to some constant $u_i^{(0)} \geq 0$ in $W^{1,2}(\Omega)$. Since $\Phi$ converges to $m_0$, at least one of the $u_i^{(0)}$ is positive. Fix such an index $i$. We now use the Poincaré-Wirtinger inequality

$$\forall f \in W^{1,2}(\Omega), ||f - f||_{L^2(\Omega)} \leq C_{PW}(\Omega)||\nabla f||_{L^2(\Omega)}.$$

It just remains to prove that

$$\left| \int_{\Omega} \Phi - m_0 \right| \leq \frac{B}{\mu_i}. \quad (14)$$

Integrating equation (12) yields

$$\mu_i \int_{\Omega} \frac{\nabla u_i}{u_i^2} + m_0 = \int_{\Omega} \Phi. \quad (15)$$

Now introduce

$$z_i := \mu_i (u_i - \int_{\Omega} u_i).$$

It is clear that $|\nabla z|$ is uniformly bounded in $L^2(\Omega)$ by the same arguments, and identity (15) becomes

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

This, combined with the Poincaré-Wirtinger inequality and the fact that $u_i \to u_i^{(0)}$ as $\mu_1 \to 0$, yields the fact that the sequence $\{\mu_i (\Phi - m_0)\}^{\mu_i > 0}$ is bounded in $W^{1,2}(\Omega)$, so that there exists a closure point $\Phi_1$, strong in $L^2$ and weak in $W^{1,2}(\Omega)$. □

Asymptotic behaviour of $\lambda_1(\mu_i, m_i - \Phi)$. Now assume that there are two different indices $i \neq j$ in $I_1$. 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 eigenfunction $\varphi_{\ell}$ normalized with respect to the $L^1(\Omega)$-norm, that is, the unique solution to
\[
\begin{cases}
\Delta \varphi_{\ell} + \varphi_{\ell}(m_{\ell} - \Phi) = 0 & \text{in } \Omega, \\
\frac{\partial \varphi_{\ell}}{\partial \nu} = 0 & \text{on } \partial \Omega, \\
\int_{\Omega} \varphi_{\ell} = 1.
\end{cases}
\]  
(16)

We are going to use $\varphi_{\ell}$ as a test function in the Rayleigh quotient, so we need to have information about its $L^2$-norm and about its behaviour, as $\mu_1 \to \infty$.

**Lemma 2.**
1. There holds: for $\ell = i,j$,
\[
\int_{\Omega} \varphi_{\ell}^2 \to 1. 
\]  
(17)

2. Define
\[
\varphi_{\ell}^{(1)} := \frac{1}{d_{\ell} m_0} \hat{\eta}_{1,m_{\ell}}.
\]

There holds:
\[
\varphi_{\ell} = 1 + \frac{\varphi_{\ell}^{(1)}}{\mu_1} + o(\frac{1}{\mu_1}) \text{ in } W^{1,2}(\Omega). 
\]  
(18)

**Proof of Lemma 2.** The proof that $\varphi_{\ell}$ converges to a constant as $\mu_1 \to \infty$ follows the same lines as the proof that $\Phi$ converges to a constant. By using the constraint
\[
\int_{\Omega} \varphi_{\ell} = 1
\]
we prove that this constant equals 1. We then apply the Poincaré-Wirtinger inequality to prove that, by the Rellich-Kondrachov theorem, the sequence $\{\mu_1(\varphi_{\ell} - 1)\}_{\mu_1 > 0}$ has a $W^{1,2}$-weak, $L^2$-strong limit $\varphi_{\ell}^{(1)}$ satisfying
\[
d_{\ell} \Delta \varphi_{\ell}^{(1)} + (m_{\ell} - m_0) = 0,
\]
along with Neumann boundary conditions. The condition
\[
\int_{\Omega} \varphi_{\ell} = 1
\]
indicates that we have
\[
\int_{\Omega} \varphi_{\ell}^{(1)} = 0.
\]
Coming back to equation (8), this gives
\[
\varphi_{\ell}^{(1)} = \frac{1}{d_{\ell} m_0} \hat{\eta}_{1,m_{\ell}}.
\]

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
\[ \lambda_1(\mu_j, m_j, \Phi) = \lambda_1(\mu_i, m_i - \Phi) \] (19)
for \(\mu_1\) 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 principal eigenvalues, to lemmas 1,2 and to the weak formulation of the equation on \(\varphi^{(1)}_\ell\), we know that
\[ \mu_1 \lambda_1(\mu_\ell, m_\ell - \Phi) = -\mu_1 \delta_\ell \Omega |\nabla \varphi^{(1)}_\ell|^2 + \mu_1 \int_\Omega \varphi^{(1)}_\ell^2(m_\ell - \Phi) = -\mu_1 \delta_\ell \Omega |\nabla \varphi^{(1)}_\ell|^2 + o_{\mu_1 \to \infty}(1) - \int_\Omega \Phi_1 \]
\[ + 2 \int_\Omega \varphi^{(1)}_\ell (m_\ell - m_0) + o_{\mu_1 \to \infty}(1) \]
\[ = \{d_\ell \int_\Omega |\nabla \varphi^{(1)}_\ell|^2 - \int_\Omega \Phi_1 \} + o_{\mu_1 \to \infty}(1). \]
Recall now that
\[ \int_\Omega \eta_{1,m_i} = \frac{1}{m_{i0}} \int_\Omega |\nabla \eta_{1,m_i}|^2 = \frac{1}{d_i} \int_\Omega |\nabla \varphi^{(1)}_i|^2. \]
Thus, if the equality (19) were true, we would have
\[ \frac{1}{d_i} \int_\Omega \eta_{1,m_i} = \frac{1}{d_j} \int_\Omega \eta_{1,m_j} + o_{\mu_1 \to \infty}(1), \]
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 stability of these equilibria. Consider \(i \in \mathbb{N}_N\), and the associated equilibrium \(u_i\).

As is well-known (see e.g. [7]), the stability of \(\pi_i\) is determined by the sign of the eigenvalues associated with the operators
\[ \mu_i \Delta + (m_i - 2u_i), \mu_j \Delta + (m_j - u_i), j \neq i. \]
Thus, the linear stability of \(\pi_i\) 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 two quantities is negative; this can be seen as a consequence of the monotony of the map \(h \mapsto \lambda_1(\mu, h)\) 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
\[ \mu_1 \lambda_1(\mu_j, m_j - \theta_i) = \left( \frac{1}{d_j} \int_\Omega \eta_{1,m_j} - \frac{1}{d_i} \int_\Omega \eta_{1,m_i} \right) + o_{\mu_1 \to \infty}(1). \] (20)
to conclude that \(\pi_1\) is linearly stable, while \(\pi_i\) is linearly unstable for any \(i \neq 1\).

We will proceed as before, by studying the asymptotic behaviour of eigenfunctions: consider an eigenfunction \(\varphi_{i,j}\) associated with \(\lambda_1(\mu_j, m_j - \theta_i)\), that is a non-negative function such that
\[ \mu_j \Delta \varphi_{i,j} + \varphi_{i,j}(m_j - \theta_i) = 0, \]
along with Neumann boundary conditions. We assume furthermore that
\[ \int_\Omega \varphi_{i,j} = 1. \]

According to [16, section 2.2], we know that the following first order expansion holds:
\[ \theta_i = m_0 + \frac{\eta_{1,m_i}}{\mu_i} + \frac{1}{\mu_i \rightarrow \infty} \left( \frac{1}{\mu_i} \right) \text{ in } W^{1,2}(\Omega). \]

By adapting slightly the proof of (18) we get the following result:

**Lemma 3.** There holds:
\[ \varphi_{i,j} = 1 + \frac{\varphi_{i,j}^{(1)}}{\mu_1} + \frac{o}{\mu_1 \rightarrow \infty} \left( \frac{1}{\mu_1} \right) \text{ in } W^{1,2}(\Omega), \tag{21} \]
where
\[ \varphi_{i,j}^{(1)} = \frac{1}{d_j m_0} \eta_{1,m_j}. \tag{22} \]

This leads to the first order expansion of the eigenvalues, by using lemma 2:
\[
\mu_1 \lambda_1 (\mu_j, m_j - \theta_i) = \frac{1}{|\Omega|} + \frac{o}{\mu_1 \rightarrow \infty} (1) \left\{ -d_j \int_\Omega |\nabla \varphi_{i,j}^{(1)}|^2 + 2 \int_\Omega \varphi_{i,j}^{(1)} (m_j - m_0) \right. \\
- \frac{1}{d_i} \int_\Omega \eta_{1,m_i} + \frac{o}{\mu_1 \rightarrow \infty} (1) \right\} \\
= \left( \frac{1}{d_j} \int_\Omega \eta_{1,m_j} - \frac{1}{d_i} \int_\Omega \eta_{1,m_i} \right) + \frac{o}{\mu_1 \rightarrow \infty} (1). \]

We have thus derived the desired identity.

## 4 Proof of theorem 3

Using theorem 1, we only have to prove that there cannot exist two indexes \( i \) and \( j \) in \( \mathbb{N}_N \) such that there exist \( k \neq k' \) satisfying:
\[ i \in \Gamma_k, j \in \Gamma_{k'}, u_i u_j > 0. \]

In other words, species with different scales of dispersal cannot coexist. If we can indeed prove this, it will only remain to prove that there is no coexistence state in \( \Gamma \) for large enough diffusivities, but this is exactly the point of the first theorem. We argue by contradiction, and assume two such indices exist.

**Asymptotic behaviour of \( \Phi \).** We note that, by definition, \( \mu_i \) represents the slowest diffusional rate. Up to relabelling, we can assume that \( i \in \Gamma_1 \), that is, we are working with the slowest disperser.

A straightforward adaptation of lemmas 1 and 2 yields the two following results:

**Lemma 4.** There exists \( \Phi_1 \in W^{1,2}(\Omega) \) such that there holds:
\[ \Phi = m_0 + \frac{\Phi_1}{\mu_i} + \frac{o}{\mu_1 \rightarrow \infty} \left( \frac{1}{\mu_i} \right) \text{ in } W^{1,2}(\Omega). \tag{23} \]
For notational simplicity, we will assume that we are working with two indices $i \neq j$ such that $$\mu_i(\mu_1) \to \infty, \quad \mu_j(\mu_1) \to \infty, \quad \frac{\mu_i}{\mu_j}(\mu_1) \to 0.$$ The existence of a coexistence state entails

$$\lambda_1(d, m_i - \Phi) = \lambda_1(d, m_j - \Phi) = 0.$$ (24)

We introduce the two $L^1$ normalized eigenfunctions associated with $\lambda_1(d, m_i - \Phi)$ and $\lambda_1(d, m_j - \Phi)$:

for $\ell = i, j$,

$$\begin{cases}
\Delta \varphi_\ell + \varphi_\ell(m_\ell - \Phi) = 0 & \text{in } \Omega, \\
\frac{\partial \varphi_\ell}{\partial \nu} = 0 & \text{on } \partial \Omega, \\
\int_\Omega \varphi_\ell = 1.
\end{cases}$$ (25)

We recall that $i \in \Gamma_k, j \in \Gamma_{k'}$.

Lemma 5. 1. There holds:

$$\int_\Omega \varphi_\ell^2 = 0, \quad \ell = i, j.$$ (26)

2. Define

$$\varphi_i^{(1)} := \frac{1}{\mu_i m_0} \hat{\eta}_{1, m_i}, \quad \varphi_j^{(1)} := \frac{1}{\mu_j m_0} \hat{\eta}_{1, m_j}.$$ Then there holds:

$$\varphi_i = 1 + \varphi_i^{(1)} + o(1), \quad \varphi_j = 1 + \varphi_j^{(1)} + o(1).$$ (27)

Coming back to the proof of the theorem, identity (24) is

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

Expand each of these two quantities separately:

$$\mu_i \lambda_1(d, m_i - \Phi) = \frac{1}{1 + o(1)} \left\{ \int_\Omega |\nabla \varphi_i^{(1)}|^2 - \int_\Omega \Phi_1 + o(1) \right\},$$

$$\mu_i \lambda_1(d, m_j - \Phi) = \frac{1}{1 + o(1)} \left\{ \int_\Omega |\nabla \varphi_j^{(1)}|^2 - \int_\Omega \Phi_1 + o(1) + o(\frac{\mu_i}{\mu_j}) \right\},$$

by adapting the proof of (20)

Lemma 6. Assume

$$\int_\Omega |\nabla \varphi_i^{(1)}|^2 = 0.$$ Then $m_i$ is constant.

We postpone the proof of this lemma to the end of the section. If $\int_\Omega |\nabla \varphi_i^{(1)}|^2 \neq 0$, in other words if $m_i$ is non constant, then the conclusion follows immediately.

If $\int_\Omega |\nabla \varphi_i^{(1)}|^2 = 0$, then one has that $\int_\Omega |\nabla \varphi_j^{(1)}|^2 = 0$ as well. Indeed, note first that the condition $\lambda_1(d, m_i - \Phi) = 0$ leads to

$$\int_\Omega \Phi_1 = 0.$$
Since 
\[ \mu_j \lambda_1(\mu_j, m_j - \Phi) = 0 \]
the desired inequality follows. So far, we have 
\[ m_i = m_j = m_0. \]
But our assumption on diffusivity implies that, whenever \( \mu_1 \) is large enough, we have 
\[ \mu_i = \mu_i(\mu_1) < \mu_j = \mu_j(\mu_1). \]
By monotonicity of the principal eigenvalue with respect to diffusivity, we should get, for \( \mu_1 \) large enough
\[ \lambda_1(\mu_i, m_0 - \Phi) < \lambda_1(\mu_j, m_0 - \Phi). \]

**Proof of lemma 6.** Note that the condition \( \int_{\Omega} |\nabla \varphi_i^{(1)}|^2 = 0 \) is equivalent to requiring 
\[ \eta_{1,m_i} = 0. \]
Now using the asymptotic expansion that was proved in [16, section 2.3], there exists a sequence \( \{\eta_{k,m_i}\}_{k \in \mathbb{N}} \in W^{1,2}(\Omega)^{\mathbb{N}} \) such that 
\[ \theta_i = \sum_{k=0}^{\infty} \frac{\eta_{k,m_i}}{\mu_i^k}, \]
where this sequence can be described as 
\[ \eta_{k,m_i} = \hat{\eta}_{k,m_i} + \beta_{k,m_i}, \]
where \( \{\hat{\eta}_{k,m_i}\}_{k \in \mathbb{N}} \) solves the following cascade system 
\[
\begin{cases}
\Delta \hat{\eta}_{k+1,m_i} + (m_i - 2m_0)\eta_{k,m_i} - \sum_{\ell=1}^{k-1} \eta_{\ell,m_i} \eta_{k-\ell,m_i} = 0 & \text{in } \Omega \\
\frac{\partial \hat{\eta}_{k+1,m_i}}{\partial n} = 0 & \text{on } \partial \Omega \\
\int_{\Omega} \hat{\eta}_{k+1,m_i} = 0, \quad (28)
\end{cases}
\] 
with \( \beta_{k,m_i} \) is defined by 
\[ \beta_{k+1,m_i} = \frac{1}{m_0} \int_{\Omega} m_i \hat{\eta}_{k+1,m_i} - \frac{1}{m_0} \sum_{\ell=1}^{k} \int_{\Omega} \eta_{\ell,m_i} \eta_{k+1-\ell,m_i}. \]
Proceeding by induction we prove that, for any \( k \geq 1 \), we have \( \eta_{k,m_i} = 0 \), so that \( \theta_i = m_0 \), which in turn leads to 
\[ m_i = m_0, \]
thus proving the desired result.

## 5 Proof of theorem 4

If we can prove that, if all the diffusivities are large enough, then all the indexes \( i_1, \ldots, i_p \) of all the positive components \( u_{i_1}, \ldots, u_{i_p} \) of an equilibrium lie in one of the \( J_i \), then the problem is reduced to the setting of theorem 3. We can thus conclude.
Let us argue by contradiction and assume that there exists two positive components $u_i, u_j$ such that
\[
\int_\Omega m_i \neq \int_\Omega m_j.
\]
We assume that $\mu_i$ is the slowest scale for which this is possible. 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:
\[
\Phi = \int_\Omega m_k + \frac{\Phi_1}{\mu_i} + \frac{o}{\mu_i \to \infty} \left( \frac{1}{\mu_i} \right) \text{ in } W^{1,2}(\Omega).
\]
We first note that
\[
\int_\Omega m_i = \int_\Omega m_j = \int_\Omega m_k.
\]
This follows by identifying the first order of the expansion with respect to $\mu_1$ in the identity
\[
\lambda_1(\mu_i, m_i - \Phi) = \lambda_1(\mu_j, m_j - \Phi).
\]
Recall that one has
\[
\lambda_1(\mu_i, m_i - \Phi) = \frac{1}{|\Omega| + \frac{o}{\mu_i \to \infty}(1)} \left\{ \int_\Omega m_i - \int_\Omega m_k + \frac{o}{\mu_i \to \infty}(1) \right\}.
\]
for every $j$ such that $u_j > 0$.

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