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CONVERGENCE TO THE EQUILIBRIUM IN A LOTKA-VOLTERRA ODE COMPETITION SYSTEM WITH MUTATIONS

JÉRÔME COVILLE AND FRÉDÉRIC FABRE

ABSTRACT. In this paper we are investigating the long time behaviour of the solution of a mutation competition model of Lotka-Volterra's type. Our main motivation comes from the analysis of the Lotka-Volterra's competition system with mutation which simulates the demo-genetic dynamics of diverse virus in their host:

$$\frac{dv_i(t)}{dt} = v_i \left[r_i - \frac{1}{K} \Psi_i(v) \right] + \sum_{i=1}^N \mu_{ij} (v_j - v_i).$$

In a first part we analyse the case where the competition terms Ψ_i are independent of the virus type i. In this situation and under some rather general assumptions on the functions Ψ_i , the coefficients r_i and the mutation matrix μ_{ij} we prove the existence of a unique positive globally stable stationary solution i.e. the solution attracts the trajectory initiated from any nonnegative initial datum. Moreover the unique steady state \bar{v} is strictly positive in the sense that $\bar{v}_i>0$ for all i. These results are in sharp contrast with the behaviour of Lotka-Volterra without mutation term where it is known that multiple non negative stationary solutions exist and an exclusion principle occurs (i.e For all $i\neq i_0, \bar{v}_i=0$ and $\bar{v}_{i_0}>0$). Then we explore a typical example that has been proposed to explain some experimental data. For such particular models we characterise the speed of convergence to the equilibrium. In a second part, under some additional assumption, we prove the existence of a positive steady state for the full system and we analyse the long term dynamics. The proofs mainly rely on the construction of a relative entropy which plays the role of a Lyapunov functional.

Keywords: Demo-genetic dynamics, Lokta-Volterra competition system with mutation, equilibria, Relative entropy, Global stability.

2010 Mathematics Subject Classification: 34A34, 34A40, 34D05, 34D23, 92D15, 92D25.

1. Introduction

In this paper we are investigating the long time behaviour of the solution of some models that have been recently used in epidemiology. Our analysis focuses on a Lotka-Volterra competition system with mutation which basically simulates the demo-genetic dynamic of a genetically diverse virus population in its hosts, highliting the numerous links existing between ecological and within-host infection dynamics. Such type of model has been proposed to explain some experimental data e.g.[16, 22, 37]. To be more specific the demo-genetic dynamic is modelled by N ordinary differential equations which simulates at host scale the dynamics of $v_i(t)$ the number of virus particles of genotype i at time t:

(1.1)
$$\frac{dv_i(t)}{dt} = v_i \left[r_i - \frac{1}{K} \Psi_i(v) \right] + \sum_{j=1}^N \mu_{ij} (v_j - v_i)$$

where r_i, K and μ_{ij} represent respectively the growth rate for each genotype, the total carrying capacity of the host and a nonnegative matrix characterising the rate of mutation from a virus of genotype i to a virus of genotype j. For each $i, \Psi_i(v) : \mathbb{R}^N \to \mathbb{R}$ is a locally Lipschitz application describing the intensity of the interaction between a virus of genotype i with all its competitors.

The mutation term of the system can also be interpreted as a dispersal term. Indeed, mutation naturally corresponds to dispersal into the discrete space of genotype. But the mutation term can

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also handle dispersal between physical patches. With this in mind, the above system of equation can also be used to model the demo-genetic dynamic of a diverse virus population in structured hosts, each host tissue types being virus "habitats" connected to each others by dispersal via fluid flow (e.g. [38]). Ways of derive results for this interpretation are discussed in the biological comments subsection.

In what follows we will always make the following assumptions on r_i , Ψ_i and μ_{ij}

$$\begin{cases} \text{ For all } i, r_i > 0, \\ \text{ The matrix } (\mu_{ij}) \text{ is nonnegative symmetric and irreducible} \\ \Psi_i(v) \in C^{0,1}_{loc}(\mathbb{R}^N, \mathbb{R}), \Psi_i(0) = 0 \\ \Psi_i \text{ is monotone increasing with respect to the natural order of } \mathbb{R}^N \end{cases}$$

Furthermore we will assume that for all i there exists positive constants R_i, k_i, c_i with $k_i > 0$ so that the function Ψ_i satisfies for all $v \in \mathbb{R}^{N,+} \setminus Q_{R_i}(0)$,

$$(1.3) c_i \left(\sum_{j=1}^N v_j\right)^{k_i} \le \Psi_i(v),$$

where $Q_{R_i}(0)$ denotes the ball of radius R_i and centred at 0 associated to the l^1 norm. A typical example of model satisfying our assumption is given by

$$\frac{dv_i(t)}{dt} = v_i \left[r_i - \frac{1}{K} \sum_{j=1}^4 \beta_{ij} v_j \right] + Mv$$

with

$$M := \begin{pmatrix} (1-\mu)^2 - 1 & \mu(1-\mu) & \mu(1-\mu) & \mu^2 \\ \mu(1-\mu) & (1-\mu)^2 - 1 & \mu^2 & \mu(1-\mu) \\ \mu(1-\mu) & \mu^2 & (1-\mu)^2 - 1 & \mu(1-\mu) \\ \mu^2 & \mu(1-\mu) & \mu(1-\mu) & (1-\mu)^2 - 1 \end{pmatrix},$$

where μ is a parameter giving the point mutation rate per replication cycle and per nucleotide. This mutation matrix corresponds to a viral population composed of 4 variants differing only by one or two substitutions involved in adaptative proprieties (e.g. pathogenicity). The interactions terms $\Psi_i := \sum_{j=1}^4 \beta_{ij} v_j$ can handle a wide range of possible inter-specific (inter-variants) competition rates between any pairs of virus variants.

This particular structure has been used recently to model the adaptation of plant virus to resistance genes [21, 22]. This particular form of competition is commonly used to model virus evolution,[16, 32, 37]. Without the mutation's matrix (μ_{ij}) , the system (1.1) reduces to a classical competition system in the sense of Hirsch [26, 27, 28]

(1.4)
$$\frac{dv_i(t)}{dt} = v_i \left[r_i - \frac{1}{K} \Psi_i(v) \right].$$

Such systems has been intensively studied and many aspects are now well understood see for example [1, 5, 6, 13, 15, 19, 24, 26, 27, 28, 29, 30, 31, 33, 39] and references therein. In particular, the existence of stationary solution and the asymptotic behaviour of the solution has been obtained in [12, 13, 31, 39]. Those systems are characterised by the existence of at least as many equilibrium states that the number of competiting species (or genotypes) involved. In addition, the dynamics exhibit a competitive exclusion principle which state that the fittest species initially present will overcome all the other ones.

When the mutations's matrix (μ_{ij}) is non trivial, the system (1.1) does not fall into Hirsch's definition of competitive system and less results are known. If for reasonably smooth interaction functions, the existence of solution of (1.1) defined for all times is not an issue, the existence of a non trivial stationary solution and the analysis of the asymptotic behaviour are challenging questions.

Most of the known results concerns either particular interaction functions Ψ_i for which the existence of steady states and their local stability are investigated [4, 15, 24, 29] or for some ODE's systems (1.1) where the mutation matrix μ_{ij} is considered as a small parameter. In the latter the system (1.1) is seen as a perturbation of (1.4) and analysed using perturbative techniques [6, 7, 8]. Recently, there has been an intense activity on continuous trait version of (1.1) where some of the techniques can be used to obtain the existence of locally stable steady states for (1.1) see for example [3, 7, 8, 9, 10, 11, 12, 13, 18, 19, 31, 39, 40, 41]. However, to our knowledge there is no results on global stability of the steady states for systems like(1.1) neither for its continuous trait version.

In this direction, our first results concern the systems (1.1) where the competition terms Ψ_i are independent of i. A typical case is $\Psi_i(v) = \sum_{j=1}^N v_j$ which corresponds to a situation where inter- and intra-species (genotypes) competitions are equals (i.e. blind and uniform competition between variants, see Lafforgue et al. [32]). In this situation one can show that there exists a unique positive stationary solution of (1.1) $\bar{v} \in \mathbb{R}^N$, which attracts all the trajectories initiated from any nonnegative and non zero initial data. Namely we show that

Theorem 1.1. Assume that the interaction Ψ_i is independent of i and is satisfying the assumptions (1.2)–(1.3), then there exists a unique positive stationary solution \bar{v} to (1.1). Moreover for any nonnegative initial datum v(0) not identically zero, the corresponding solution v(t) of (1.1) converges to \bar{v} .

A case of particular interest is when the interactions Ψ_i take the following form $\Psi_i(v) = \sum_{j=1}^N r_j v_j$. This particular structure of interaction was initially introduced on a theoretical ground by Sole et al. [44] to model the competition between viruses. Recently, this form of interactions has been used to explain experimental results of virus evolution [16, 22, 37]. Sole et al. showed that Eigen's model of molecular quasi-species [20] was to a large extent equivalent to the Lotka-Volterra competition equations under this assumption.

For this type of interaction, we can rewrite the system (1.1) as follows

(1.5)
$$\frac{dv_i(t)}{dt} = v_i \left[r_i - \frac{1}{K} \sum_{j=1}^N r_j v_j \right] + \sum_{j=1}^N \mu_{ij} (v_j - v_i).$$

For (1.5) besides the asymptotic behaviour of the solution obtained as an application of Theorem 1.1 we can precise the speed of convergence to the equilibrium. Furthermore we can give an estimate of the time to reach near the equilibrium. In epidemiology, this type of informations is of practical use for building tractable nested models. Nested models are a class of model which explicitly links the relationships between processes at different levels of biological organization. They are often used to study the pathogen evolution by linking the disease dynamic of within- and between-host, see Mideo et al. [36]. Their formalisation becomes more simple when the within-host pathogen dynamic is faster than the between-hosts dynamic. Indeed, in such cases, using for example slow-fast reduction techniques commonly used in ecology [2], the within-host dynamic can be approximated by its equilibrium, see for example [23].

More precisely, we show that

Theorem 1.2. Assume that the interactions Ψ_i take the form $\Psi_i(v) = \sum_{j=1}^N r_j v_j$ then for any nonnegative initial datum v(0) not identically zero, the solution v(t) of (1.5) converges exponentially fast to its unique equilibrium. That is to say there exists two positive constants C_1 and C_2 so that

$$||v - \bar{v}||_{\infty} \le C_1 e^{-C_2 t}$$
.

Next, we analyse the situation where the functions Ψ_i are not reduced to a single function. From a biological point of view, this situation could appears as, often, genotypes (species) exhibit particular association patterns (see for example [45] in the case of plant viruses). A way to model such phenomena is to take Ψ_i of the form $\Psi_i(v) = \sum_{j=1}^N \alpha_{i,j} r_j v_j$ where $\alpha_{i,j}$ are crowing index [34, 25]. This index is equal to 1 when the 2 species are distributed independently and ranges from 0 (complete avoidance) to a large constant (near overlap) according to patterns of species association.

In this general context, our first result concerns the existence of a positive stationary solution for the system (1.1) assuming we have the following extra condition

$$(1.6) \forall i \quad \sum_{j=1}^{N} \mu_{ij} \le \frac{r_i}{2}.$$

This condition makes senses in our application framework since mutation rates (expressed as substitutions per nucleotide per cell infection) range from 10^{-8} to 10^{-6} for DNA viruses and from 10^{-6} to 10^{-3} for RNA viruses [43] whereas growth rates r_i are of the order of the unit or higher. For example, the overall growth rate of the RNA virus VSV was estimated to 0.6 virus/hour [17]. Each cell infected by a single VSV particle produces from 50 to 8000 progeny virus particle/ cell infection [47].

Under the extra assumption (1.6) we prove

Theorem 1.3. Assume that r_i , Ψ_i and μ_{ij} satisfy the assumptions (1.2)–(1.3). Assume further that (1.6) holds. Then there exists a positive stationary solution \bar{v} to the system (1.1).

Lastly, we obtain the convergence to the equilibria for some general interactions Ψ_i . Namely, we show that

Theorem 1.4. Assume that r_i, Ψ_i and μ_{ij} satisfy (1.2)–(1.3). Assume further that (1.6) holds and $\Psi_i(v) = \alpha(v) + \epsilon \psi_i(v)$ with $\psi_i \in C^1_{loc}$ uniformly bounded and $\alpha \in C^1_{loc}$ satisfying (1.2)–(1.3) is so that $\forall x \in \mathbb{R}^N$, $\nabla \alpha(x) > 0$. Then there exists ϵ_0 so that, for all $\epsilon \leq \epsilon_0$, the positive stationary solution \bar{v}_{ϵ} of (1.1) attracts all the possible trajectories initiated from any non zero and nonnegative initial data.

Note that C^1_{loc} perturbation of the particular interaction function $\alpha(v) = \sum_{j=1}^N r_j v_j$ satisfied the assumptions of the above Theorem.

1.1. General remarks.

Before going to the proofs, we want to make some general remarks and comments.

Mathematical comments: First as remarked in [13], we can interpret the system of equations (1.5) as a discrete version of the continuous model

$$(1.7) \qquad \frac{\partial v(t,x)}{\partial t} = v(t,x) \left[r(x) - \frac{1}{K} \int_{\mathbb{R}^n} r(y) v(t,dy) \right] + \int_{\mathbb{R}^n} \mu(x,y) v(t,dy) - \mu(x) v(t,x)$$

by posing for each sub-population corresponding to a typical trait $x_i \in \mathbb{R}^d$,

$$v(t,x) = \sum_{i=1}^{N} v_i(t)\delta_{x_i}, \ r(x_i) = r_i, \ \mu(x_i,x_j) = \mu_{ij} \ \text{and} \ \mu(x) = \int_{\mathbb{R}^n} \mu(x,y)dy.$$

Recently there have been a lot of works dealing with (1.7) and generalisation of it, see for example [3, 5, 7, 8, 9, 10, 11, 13, 12, 18, 19, 31, 39, 40, 41] and references therein. A large part of the analysis are concerning (1.7) in absence of mutation (ie $\mu \equiv 0$) or in the limit $\mu \rightarrow 0$. In the latter case, much have been done in developing a constrained Hamilton-Jacobi approach to analyse the long time behaviour of positive solution of this type of models see for instance [3, 19]. Other approaches based on semigroup theory have also been developed to analyse the asymptotic behaviour and local stability of the stationary solution of (1.7) see [7, 8]. Although some of the techniques developed in this two frameworks may be adapted to analyse the system (1.1) most of them fail when we try to prove the global stability of the stationary states. To tackle this difficulty we construct a set of Lyapunov functionals for the solution of (1.1) when the interactions Ψ_i are independent of i. Properly used these Lyapunov functionals enable us to analyse the asymptotic behaviour of the solution of (1.1) in this particular situation. From this analysis, we derive some consideration on the asymptotic behaviour of the solution of (1.1) in a general situation. The Lyapunov functionals are constructed in the spirit of the relative entropy introduced for linear parabolic operators in [35]. Even if our problem is nonlinear such type of relative entropy can still be constructed. These is an interesting new feature of nonlinear dissipative system.

It is worth noticing that a similar construction can be made for (1.7) giving us access to a simple way of analysing the asymptotic behaviour and the global stability of steady solution of (1.7), see [14].

Along some of the proofs we notice that the existence of a steady state in Theorem 1.1 and Theorem 1.3 can be generalised to situation where the mutation matrix (μ_{ij}) is not symmetric. Indeed, when the interactions Ψ_i are independent of i (Theorem 1.1), the construction of a unique stationary solution relies only on the Perron-Frobenius Theorem which holds true for non symmetric matrices. However, for the general case (Theorem 1.3) to obtain the existence of a steady state, we do require that the condition (1.6) is replaced by

(1.8)
$$\forall i \quad \sum_{j=1}^{N} \left(\frac{\mu_{ij} + \mu_{ji}}{2} \right) \le \frac{r_i}{3}.$$

Biological comments: First, we emphasize the biological interpretation of our result and particularly the role of the mutation term. Indeed, under biological compatible assumptions concerning the competition ψ_i , the mutation matrix (μ_{ij}) and the growth rate r_i we have shown that, in sharp contrast with the classical results known for the Lotka-Volterra system without mutation, the mutation term deeply changes the dynamics of the system. On one hand, the mutation term stabilizes the dynamic of system by reducing the number of equilibrium up to a single equilibrium and on the other hand, the mutation term precludes the competitive exclusion principle to occur.

Second, we emphasize the biological relevance of relaxing some hypothesis regarding (i) the monotony of Ψ_i and (ii) the symmetry of the mutation matrix μ_{ij} to study viral demo-genetics dynamics in structured hosts. To illustrate this point, let consider 2 patches p_1 and p_2 , and 2 virus genotypes v_1 and v_2 . The demo-genetics dynamics of the viral population in this system can be modelled by

$$\frac{dw}{dt} = Mw + Rw - \Psi(w)w$$

where w is the vector $(v_{1,p_1}, v_{2,p_1}, v_{1,p_2}, v_{2,p_2})$ and R, M and $\Psi(w)$ are the following matrices $R := (r_i \delta_{ij})$,

$$\Psi(w) := \begin{pmatrix} r_1 v_{1,p_1} + r_2 v_{2,p_1} & 0 & 0 & 0 \\ 0 & r_1 v_{1,p_1} + r_2 v_{2,p_1} & 0 & 0 \\ 0 & 0 & r_1 v_{1,p_2} + r_2 v_{2,p_2} & 0 \\ 0 & 0 & 0 & r_1 v_{1,p_2} + r_2 v_{2,p_2} \end{pmatrix}.$$

In structured hosts some tissue types often act as virus "sources" and others are "sinks", creating an asymmetry in the exchange between patches. In the above example this implies that $d_1 > d_2$ if the patch p_1 is a "source" and the patch p_2 is a "sink", making the mutation matrix M nonsymmetric. Moreover, in this example since the competition takes place only inside a given patch, we can check that the two monotone interaction functionals involved $\Psi_1(v) := r_1 v_{1,p_1} + r_2 v_{2,p_1}$ and $\Psi_2(v) := r_1 v_{1,p_2} + r_2 v_{2,p_2}$ do not satisfy the monotone properties (1.2).

Such type of structure, inducing asymmetries in the exchanges and some weak interaction functionals, are expected to play a role in constraining or facilitating adaptive evolution of viruses in heterogeneous host environment [38]. It is then relevant to study extension of our results in a context of more general assumptions on μ_{ij} and Ψ_i .

Organization of the Paper: In Section 2 we start by establishing some preliminaries results about the system (1.1). We derive the relative entropy identities in 3 Then in Section 4 we analyse in details the system (1.1) for a particular type of interactions and we prove the Theorem 1.1. We show Theorem 1.2 in Section 5. Finally, we are proving the Theorems 1.3 and 1.4 in Sections 6 and 7.

2. Global facts on the system (1.1)

In this section we establish some useful properties of solution of (1.1) and prove the existence of a positive global in time solution of the system (1.1), that for convenience we rewrite

(2.1)
$$\frac{dv}{dt} = A(\Psi(t))v$$

where $A(\Psi(t))$ is the following matrix:

$$A := \begin{pmatrix} (r_1 - \frac{1}{K}\Psi_1(t)) - \mu_1 + \mu_{11} & \mu_{ij} \\ & \ddots & \\ \mu_{ij} & & (r_N - \frac{1}{K}\Psi_N(t)) - \mu_N + \mu_{NN} \end{pmatrix},$$

with $\Psi_i(t) := \Psi_i(v(t))$ and $\mu_i = \sum_{j=1}^N \mu_{ij}$. Since the function Ψ_i are locally Lipschitz the local existence of a solution of (2.1) is a straightforward application of the Cauchy-Lipschitz Theorem. To obtain a global solution starting with non-negative initial data, we need more *a priori* estimates on the solutions $(v_i)_{i \in \{1,\dots,N\}}$. Let us first show that the system (2.1) preserve the positivity.

2.1. Positivity.

Lemma 2.1 (Positivity). The system (2.1) preserves the positivity. That is to says that if v(0) is a non-negative initial value, then the solution v of (2.1) stays nonnegative. Moreover, for all i $v_i(t) > 0$ for all times $t \in (0,T]$.

Proof:

We argue by contradiction and assume that v changes its sign. Let $t_1 \in (0,T]$ be the first time where $v_i(t_1)=0$ for some i,v(t)>0 for all $t\in (0,t_1)$ and there exists $t>t_1$ so that v(t)<0. $t_1>0$ is well defined since v changes its sign and $v_i(0)\geq 0$ for all $i,v_i(0)>0$ for some i and $\lim_{t\to 0^+}\frac{dv_i(t)}{dt}>0$. Now at the time t_1 , we have

$$0 \ge \frac{dv_i(t_1)}{dt} = \sum_j \mu_{ij} v_j(t_1) \ge 0.$$

Therefore for all i $v_i(t_1)=0=\frac{dv_i(t_1)}{dt}$ and by the Cauchy-Lipschitz Theorem we deduce that for all i and all $t\in[t_1,T]$ $v_i(t)=0$. Thus $v\geq 0$ in (0,T] which contradicts that v changes its sign.

Next we show that $v_i(t)>0$ for all times $t\in(0,T]$. From the above argumentation, v is nonnegative for all times. To show that v stays positive for all time, we can see that it is enough to show that $\mathcal{N}(t)=\sum_{i=1}^N v_j(t)>0$ for all times $t\in[0,T]$. Indeed, if there is $t_1\in(0,T]$ so that t_1 is the first time where for some $i,v_i(t_1)=0$ then arguing as above we see that for all i and $T\geq t_1$ $v_i(t)=0$ so $\mathcal{N}(t)=0$ for all $t\geq t_1$.

Now, let us denote Q(0,1) the following set

$$Q(0,1) := \left\{ x \in \mathbb{R}^N \mid \sum_{i=1}^N |x_i| \le 1 \right\}.$$

Since Ψ_i is locally Lipschitz, we have on Q(0,1),

(2.2)
$$\forall i, \exists \kappa_i \text{ so that } \Psi_i(x) \leq \kappa_i \sum_{i=1}^N |x_i|.$$

Let $\kappa_0 := \sum_{i=1}^N \kappa_i$ and δ a positive constant so that $\delta < \min\left\{1, \frac{\mathcal{N}(0)}{2}, \frac{r_{min}}{2\kappa_0}\right\}$. We will prove that $\mathcal{N} \geq \delta$ for all times in (0,T]. We argue by contradiction and assume there exists $t_1 < t_2$ so that $\mathcal{N}(t_1) = \delta$ and $\mathcal{N}(t) \leq \delta$ in $(t_1, t_2]$. Using that the v_i are non negative functions and (2.2), from our assumption we deduce that on $[t_1, t_2]$ and for all i,

$$\frac{dv_i}{dt} \ge v_i (r_{min} - \kappa_i \mathcal{N}) + \sum_{j=1}^{N} \mu_{ij} (v_j - v_i).$$

By summing over all the possible i we end up with the following equation

(2.3)
$$\frac{d\mathcal{N}}{dt} \ge \mathcal{N}(r_{min} - \mathcal{N}\kappa_0),$$

$$\mathcal{N}(t_1) = \delta.$$

Using the comparison principle on the latter equation, we achieve on $[t_1, t_2]$, $\mathcal{N} \geq \widetilde{\mathcal{N}}$ where $\widetilde{\mathcal{N}}$ is the solution of the logistic type equation (2.3). By construction we have $\widetilde{\mathcal{N}} > \delta$ for all times $t > t_1$. Thus we get the contradiction $\delta < \mathcal{N} \leq \delta$. Hence $\mathcal{N} > \delta$ for all $t \in (0, T]$.

Remark 2.2. Of the above proof, we also have a bound from below for \mathcal{N} . Namely, we have for all t

$$\mathcal{N}(t) \geq \min \left\{ 1, \frac{\mathcal{N}(0)}{2}, \frac{r_{min}}{2\kappa_0} \right\}.$$

2.2. Existence of a global solution.

Next we show the following estimate an

Lemma 2.3. Let v(t) be a solution of the Cauchy problem (2.1), then there exists two constants C_0 and C_1 and a positive vector v_p so that $v(t) \leq C_0 e^{C_1 t} v_p$

Proof:

From Lemma 2.1 we know that the v_i are non negative functions. Therefore by (2.1) we can see that the v_i satisfy

(2.5)
$$\frac{dv_i}{dt} \le r_i v_i + \sum_{j=1}^N \mu_{ij} (v_j - v_i).$$

Let us denote M and R the two following matrices

$$M := \begin{pmatrix} -\mu_1 + \mu_{11} & \mu_{ij} \\ & \ddots & \\ \mu_{ij} & -\mu_N + \mu_{NN} \end{pmatrix}, \qquad R := \begin{pmatrix} r_1 & 0 \\ & \ddots & \\ 0 & r_N \end{pmatrix}.$$

We can then rewrite the inequalities (2.5) as follows

$$\frac{dv}{dt} \le (R+M)v.$$

By choosing $\bar{\mu}=\sup_{i\in\{1,\ldots,N\}}\mu_i$, we can see that $R+M+\bar{\mu}$ is nonnegative matrix. Since $R+M+\bar{\mu}$ $\bar{\mu}Id$ is also irreducible, by the Perron-Frobenius Theorem $R+M+\bar{\mu}Id$ posses a unique principal eigenpair (ν_p, v_p) so that v_p is a positive vector, i.e. there exists (ν_p, v_p) so that $v_p > 0$ and

$$(R + M + \bar{\mu}Id)v_p = \nu_p v_p.$$

Note that $e^{(\nu_p - \bar{\mu})t} ||v(0)||_{\infty} v_p$ satisfies

$$\frac{du}{dt} = (R+M)u.$$

So, by the Cauchy-Lipschitz Theorem, from (2.6) we deduce that $v \leq e^{(\nu_p - \bar{\mu})t} ||v(0)||_{\infty} v_p$ for all times t.

The existence of a global in time solution for the system (2.1) is then a consequence of the Cauchy-Lipschitz Theorem and the above a priori estimates.

Remark 2.4. By adapting some ideas in [39] and for a particular type of Ψ_i , we can derive an explicit formula for the solution of (2.1). Indeed when the interaction terms take the form $\Psi_i(v) = \alpha(v) = \sum_{i=1}^N \alpha_i v_i$ for all i then the solution $v_i(t)$ can be expressed by the formula

(2.7)
$$v_i(t) = \frac{\left(e^{(R+M)t}v(0)\right)_i}{1 + \sum_{j=1}^N \alpha_j \int_0^t \left(e^{(R+M)s}v(0)\right)_j ds}.$$

To obtain this formula we argue as in [39] (Chapter 2 Section 2.1) and we start by introducing the functions

$$\alpha(t) := \sum_{i=1}^{N} \alpha_j v_j$$
 and $V_i(t) := e^{\int_0^t \alpha(s) \, ds} v_i(t).$

We remark that the V_i satisfy the linear equation

(2.8)
$$\frac{dV_i(t)}{dt} = r_i V_i + \sum_{j=1}^{N} \mu_{ij} (V_j - V_i).$$

Thus $V_i(t) := (e^{(R+M)t}v(0))_i$ and $v_i(t)$ is implicitly given by the formula

$$v_i(t) = e^{-\int_0^t \alpha(s) ds} \left(e^{(R+M)t} v(0) \right)_i.$$

Now let us evaluate the term $e^{-\int_0^t \alpha(s) ds}$. By differentiating $e^{-\int_0^t \alpha(s) ds}$ one has

$$\frac{d}{dt}(e^{\int_0^t \alpha(s) ds}) = \alpha(t)e^{\int_0^t \alpha(s) ds} = \sum_{j=1}^N \alpha_j V_j(t).$$

Therefore we have

$$e^{\int_0^t \alpha(s) \, ds} = 1 + \int_0^t \sum_{j=1}^N \alpha_j V_j(s) \, ds = 1 + \sum_{j=1}^N \alpha_j \int_0^t \left(e^{(R+M)s} v(0) \right)_j \, ds.$$

Hence

$$v_i(t) = \frac{\left(e^{(R+M)t}v(0)\right)_i}{1 + \sum_{j=1}^N \alpha_j \int_0^t \left(e^{(R+M)s}v(0)\right)_j ds}.$$

3. RELATIVE ENTROPY IDENTITIES.

Here, we prove the following general principle which give us access to some useful identifies that we constantly use along this paper.

Theorem 3.1. Assume that r_i , (μ_{ij}) , Ψ_i satisfies (1.2)– (1.3). Let v and \bar{v} be respectively a positive solution and a positive stationary solution of (1.1), and let H be a smooth (at least C^1) function. Then the function $\mathcal{H}(v) := \sum_{i=1}^N \bar{v}_i^2 H\left(\frac{v_i}{\bar{v}_i}\right)$ satisfies

(3.1)
$$\frac{d\mathcal{H}(t)}{dt} = -\mathcal{D}(v) + \frac{1}{K} \sum_{i=1}^{N} \bar{v}_{i} H'\left(\frac{v_{i}}{\bar{v}_{i}}\right) \Gamma_{i} v_{i}$$

where

$$\begin{split} \mathcal{D}(v) := \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left[H\left(\frac{v_j}{\bar{v}_j}\right) - H\left(\frac{v_i}{\bar{v}_i}\right) \right] + \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j H'\left(\frac{v_i}{\bar{v}_i}\right) \left[\frac{v_i}{\bar{v}_i} - \frac{v_j}{\bar{v}_j}\right] \\ \Gamma_i := \Psi_i(\bar{v}) - \Psi_i(v) \end{split}$$

Proof:

By (1.1), for all i we have

(3.2)
$$\frac{dv_i}{dt} = \left(r_i v_i - \frac{1}{K} \Psi_i(\bar{v}) v_i + \sum_{j=1}^N \mu_{ij} (v_j - v_i)\right) + \frac{1}{K} \Gamma_i v_i$$

Using that \bar{v} is a stationary solution, we have for all i

$$(r_i - \frac{1}{K}\Psi_i(\bar{v}))\bar{v}_i = -\sum_{i=1}^N \mu_{ij}(\bar{v}_j - \bar{v}_i),$$

and we can rewrite the above equation as follows

$$\frac{dv_i}{dt} = \sum_{i=1}^{N} \mu_{ij} \left(v_j - \frac{\bar{v}_j v_i}{\bar{v}_i} \right) + \frac{1}{K} \Gamma_i v_i.$$

By multiplying the above equality by $\bar{v}_i H'\left(\frac{v_i}{\bar{v}_i}\right)$ and by summing over all i we achieve

$$\sum_{i=1}^{N} \bar{v}_i H'\left(\frac{v_i}{\bar{v}_i}\right) \frac{dv_i}{dt} = \frac{1}{K} \sum_{i=1}^{N} \bar{v}_i H'\left(\frac{v_i}{\bar{v}_i}\right) \Gamma_i v_i + \sum_{i=1}^{N} \bar{v}_i H'\left(\frac{v_i}{\bar{v}_i}\right) \sum_{j=1}^{N} \mu_{ij} \left(v_j - \frac{\bar{v}_j v_i}{\bar{v}_i}\right).$$

Thus we have

$$\frac{d\mathcal{H}(t)}{dt} = \frac{1}{K} \sum_{i=1}^{N} \bar{v}_i H'\left(\frac{v_i}{\bar{v}_i}\right) \Gamma_i v_i - \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j H'\left(\frac{v_i}{\bar{v}_i}\right) \left(\frac{v_i}{\bar{v}_i} - \frac{v_j}{\bar{v}_j}\right).$$

Hence we have

$$\frac{d\mathcal{H}(t)}{dt} = \frac{1}{K} \sum_{i=1}^{N} \bar{v}_i H'\left(\frac{v_i}{\bar{v}_i}\right) \Gamma_i v_i - \mathcal{D}(v).$$

since by symmetry of μ_{ij} ,

$$\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left[H\left(\frac{v_j}{\bar{v}_j}\right) - H\left(\frac{v_i}{\bar{v}_i}\right) \right] = 0.$$

As immediate corollary of the Theorem 3.1, we have the following identities that we constantly used along this paper,

Lemma 3.2. Assume that r_i , (μ_{ij}) , Ψ_i satisfies (1.2)– (1.3). Let v and \bar{v} be respectively a positive solution and a positive stationary solution of (1.1), then we have

$$\frac{d}{dt} \left(\sum_{i=1}^{N} v_i \bar{v}_i \right) = \frac{1}{K} \sum_{i=1}^{N} (\Psi_i(\bar{v}) - \Psi_i(v)) v_i \bar{v}_i$$

(ii)
$$\frac{d}{dt} \left(\sum_{i=1}^{N} v_i^2 \right) = -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{v_j}{\bar{v}_j} - \frac{v_j}{\bar{v}_j} \right)^2 + \frac{2}{K} \sum_{i=1}^{N} v_i^2 \left(\Psi_i(\bar{v}) - \Psi_i(v) \right).$$

Proof:

(i) and (ii) can be obtained straightforwardly from the Theorem 3.1. Indeed, by using H(s) = s in Theorem 3.1, and by observing that from the symmetry of μ_{ij} ,

$$\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left[\frac{v_i}{\bar{v}_i} - \frac{v_j}{\bar{v}_j} \right] = 0,$$

we easily get

$$\frac{d\mathcal{H}(t)}{dt} = \frac{1}{K} \sum_{i=1}^{N} \Gamma_i \bar{v}_i v_i,$$

which proves (i) since for the function H(s)=s, we have $\mathcal{H}(t)=\sum_{i=1}^N \bar{v}_i v_i$. We can obtain (ii) in a similar way by using the function $H(s)=s^2$ in the Theorem 3.1 and by observing that

$$\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(2 \frac{v_i}{\bar{v}_i} \right) \left[\frac{v_i}{\bar{v}_i} - \frac{v_j}{\bar{v}_j} \right] = \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left[\frac{v_i}{\bar{v}_i} - \frac{v_j}{\bar{v}_j} \right]^2.$$

4. The special case
$$\Psi_i(.) = \alpha(.)$$
:

In this section we analyse in details the asymptotic behaviour of a positive solution of (1.1) when the competition functional Ψ_i is independent of i, i.e for all $i, \Psi_i(v) = \alpha(v)$ where α is a function from $\mathbb{R}^N \to \mathbb{R}$ which satisfies (1.2) –(1.3). As we expressed in Theorem 1.1 that we recall below, in this situation the system (1.1) has a unique positive stationary solution which attracts all the trajectories initiated from any nonnegative and non zero initial data. More precisely, we prove

Theorem 4.1. Assume that for all i the function $\Psi_i(.) = \alpha(.)$, then there exists a unique stationary solution \bar{v} of (2.1). Moreover, for all nonnegative and non zero initial datum v(0), the corresponding solution v(t) converges to \bar{v} .

To prove the Theorem, we first analyse the existence of stationary solution

4.1. Study of the existence of equilibria.

Recall that we look for a stationary solution of

$$\frac{dv}{dt} = A(\alpha(t))v.$$

Therefore if there exists a stationary equilibria for the system (4.1) the v_i must satisfies the following equations:

$$A(\bar{\alpha})v = 0$$

$$\bar{\alpha} = \alpha(v)$$

where $A(\bar{\alpha})$ is the matrix

$$A(\bar{\alpha}) := \begin{pmatrix} (r_1 - \frac{\bar{\alpha}}{K}) - \mu_1 + \mu_{11} & \mu_{ij} \\ & \ddots & \\ \mu_{ij} & (r_N - \frac{\bar{\alpha}}{K}) - \mu_N + \mu_{NN} \end{pmatrix}.$$

Note that we can rewrite the matrix $A(\bar{\alpha}) := \left(R - \left(\frac{\bar{\alpha}}{K}\right)Id + M\right)$ where R and M are matrices defined in Section 2.

Therefore, a solution v to (4.2) is a solution to

$$(M+R)v = \left(\frac{\bar{\alpha}}{K}\right)v.$$

Let us now establish some important property of the equilibrium.

Lemma 4.2. If v is a nonnegative stationary solution of (4.1), then either $v \equiv 0$ or v > 0 (i.e $\forall i, v_i > 0$).

Proof:

First, we observe that 0 is a solution of the problem (4.2). Now let v be nonnegative stationary solution of (4.1) so that $v_i = 0$ for some i. From (4.4) we see that

$$(M+Rv)_i = \left(\frac{\bar{\alpha}}{K}\right)v_i = 0.$$

Therefore

$$0 = r_i v_i + \sum_{j=1}^{N} \mu_{ij} (v_j - v_i) = \sum_{j=1}^{N} \mu_{ij} v_j.$$

Thus $v_j = 0$ for all j since by assumption $v_j \ge 0$ and (μ_{ij}) is irreducible. Hence any nonnegative stationary solution is either positive or the zero solution.

Observe that from the above Lemma and (4.4), one can see that v is a positive eigenvector of the matrix M+R associated to the eigenvalue $\frac{\bar{\alpha}}{K}$. Now we are in position to prove that there exists a unique positive stationary solution to (4.4).

Lemma 4.3. There exists a unique $(\bar{\alpha}, \bar{v})$ solution of the equations (4.2) and (4.3). Moreover v satisfies $\alpha(v) = \nu_p$.

Proof:

By choosing $\bar{\mu}=\sup_{i\in\{1,\dots,N\}}\mu_i$, we can see that $R+M+\bar{\mu}$ is nonnegative matrix. Since $R+M+\bar{\mu}Id$ is also irreducible, by the Perron-Frobenius Theorem $R+M+\bar{\mu}Id$ posses a unique principal eigenpair (ν_p,v_p) so that v_p is a positive vector, i.e. there exists (ν_p,v_p) so that $v_p>0$ and

(4.5)
$$(R + M + \bar{\mu}Id)v_p = \nu_p v_p.$$

Moreover, the linear subspace associated to the eigenvalue ν_p is one dimensional [46]. So without any loss of generality we can assume that $\sum_{i=1}^N (v_p)_i^2 = 1$. From the equation (4.5) we deduce that the vector v_p is a positive eigenvector of the matrix M+R associated with the eigenvalue $\lambda_p := (\nu_p - \bar{\mu})$. By construction one can see that λ_p is the unique eigenvalue of the matrix M+R associated with a positive eigenvector. A quick computation shows that $\lambda_p = (\nu_p - \bar{\mu}) > 0$. Indeed, if not we have

$$(R+M)v_p \leq 0.$$

Thus for all $i \in \{1, ..., N\}$ we have

$$r_i(v_p)_i + \sum_{j=1}^N \mu_{ij} ((v_p)_j - (v_p)_i) \le 0.$$

Let $(v_p)_{i_0} := \min_{i \in \{1,...,N\}} (v_p)_i$ then for $(v_p)_{i_0}$ we have

$$\sum_{j=1}^{N} \mu_{ij} ((v_p)_j - (v_p)_{i_0}) \ge 0.$$

Since R is a positive matrix we achieve the contradiction

$$0 < r_{i_0}(v_p)_{i_0} + \sum_{j=1}^{N} \mu_{ij} ((v_p)_j - (v_p)_{i_0}) \le 0.$$

Now from (4.4) we deduce that there exists an unique positive $\bar{\alpha}$ so that $\frac{\bar{\alpha}}{K} = \lambda_p$. Let us now construct our solution. Note that for any $\mu \in \mathbb{R}$, the vector μv_p is also a solution to (4.4) with the eigenvalue λ_p . So to obtain a solution \bar{v} to (4.2) and (4.3) we only have to adjust μ in such a way that $\alpha(\mu v_p) = \bar{\alpha}$. This is always possible for a unique μ since $\alpha(0) = 0$, $\lim_{\mu \to \infty} \alpha(\mu v_p) = +\infty$ and α is an increasing function.

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4.2. Convergence to the unique equilibrium.

Let us look at the convergence of v(t) toward its equilibrium. Let us first establish some useful identities.

Lemma 4.4. Let us denote $(\bar{\alpha}, \bar{v})$ the stationary solution constructed above. Let v be a solution of (4.1) then v satisfies the following identities

$$\frac{d}{dt} \left(\sum_{i=1}^{N} v_i \bar{v}_i \right) = \frac{1}{K} (\bar{\alpha} - \alpha(t)) \left(\sum_{i=1}^{N} v_i \bar{v}_i \right).$$
(ii)
$$\frac{d}{dt} \sum_{i=1}^{N} (v_i)^2 = -\sum_{i=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{v_j}{\bar{v}_i} - \frac{v_j}{\bar{v}_i} \right)^2 + \frac{2}{K} (\bar{\alpha} - \alpha(t)) \sum_{i=1}^{N} (v_i)^2.$$

Proof:

Since here for all $i, \Psi_i = \alpha$, from Lemma 3.2 we deduce that

$$\frac{d}{dt} \left(\sum_{i=1}^{N} v_i \bar{v}_i \right) = \frac{1}{K} \left(\sum_{i=1}^{N} (\alpha(\bar{v}) - \alpha(v(t))) v_i \bar{v}_i \right),$$

$$\frac{d}{dt} \sum_{i=1}^{N} (v_i)^2 = -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{v_j}{\bar{v}_j} - \frac{v_j}{\bar{v}_j} \right)^2 + \frac{2}{K} (\bar{\alpha} - \alpha(t)) \sum_{i=1}^{N} (\alpha(\bar{v}) - \alpha(v)) (v_i)^2.$$

Thus (i) and (ii) hold true.

From the above Lemma we can derive a useful Lyapunov functional.

Lemma 4.5. Let \bar{v} be the positive stationary solution of (4.1). For any positive solution v of (4.1), let us denote \mathcal{E} , β and F the following quantities

$$\mathcal{E}(v) := \sum_{i=1}^{N} (v_i)^2, \quad \beta(v) := \sum_{i=1}^{N} v_i \bar{v}_i \quad F(v) := \log \left[\frac{\mathcal{E}(v)}{(\beta(v))^2} \right].$$

Then $F \ge \log(\frac{1}{\sup_i \bar{v}_i})$ and for any positive solution v of (4.1) we have

$$\frac{d}{dt}F(v) = -\frac{1}{\mathcal{E}(v)} \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_{j} \bar{v}_{i} \left(\frac{v_{j}}{\bar{v}_{j}} - \frac{v_{i}}{\bar{v}_{i}}\right)^{2} < 0.$$

Proof:

First let us show that F is bounded from below. By construction and using a standard convexity argument, we see that $\beta^2(v) \leq (\sup_i \bar{v}_i)\mathcal{E}(v)$. So from the monotonicity of the log, we conclude that $F(v) \geq \log(\frac{1}{\sup_i \bar{v}_i})$.

Now let us show that F is non increasing. To do so let us compute $\frac{d}{dt}F(v)$. From the definition of F we see that

$$\frac{d}{dt}F(v) = \frac{d_t \mathcal{E}(v)}{\mathcal{E}(v)} - 2\frac{d_t \beta(v)}{\beta(v)},$$

where d_t denotes $\frac{d}{dt}$. By Lemmas 4.4 we have

$$\frac{d_t \mathcal{E}(v)}{\mathcal{E}(v)} = -\frac{1}{\mathcal{E}(v)} \sum_{i,j=1}^N \mu_{ij} \bar{v}_j \bar{v}_i \left(\frac{v_j}{\bar{v}_j} - \frac{v_i}{\bar{v}_i}\right)^2 + \frac{2}{K} (\bar{\alpha} - \alpha(t))$$
$$\frac{d_t \beta(v)}{\beta(v)} = \frac{1}{K} (\bar{\alpha} - \alpha(t)).$$

Thus,

$$\frac{d}{dt}F(v) = -\frac{1}{\mathcal{E}(v)} \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_j \bar{v}_i \left(\frac{v_j}{\bar{v}_j} - \frac{v_i}{\bar{v}_i}\right)^2 \le 0.$$

Next we derive some $a \ priori$ estimates on the solution v of (4.1) from the previous Lemmas. Namely, we show that

Lemma 4.6. Let v be a positive solution of (4.1), then there exists C_1 so that

$$\mathcal{E}(v) + \beta(v) \le C_1.$$

Proof:

Observe that from Lemma 4.5, to obtain the bound it is sufficient to have a uniform bound on β . Indeed, since F is decreasing in time, we have for all times

$$\mathcal{E}(v) \le \beta^2(t) \frac{\mathcal{E}(v(0))}{\beta^2(v(0))}.$$

Now recall that by Lemma 4.4, $\beta(v)$ satisfies the following equation

$$\frac{d\beta(t)}{dt} = \frac{1}{K}(\bar{\alpha} - \alpha(t))\beta(t).$$

Since α satisfies the assumptions (1.2)–(1.3), there exists $R_{\alpha}, c_{\alpha}, k_{\alpha}$ so that for all $x \in \mathbb{R}^{N,+} \setminus Q_{R_{\alpha}}(0)$,

$$(4.6) c_{\alpha} \left(\sum_{i=1}^{N} x_{i}\right)^{k_{\alpha}} \leq \alpha(x).$$

Assume that for some $t > 0, v(t) \in \mathbb{R}^{N,+} \setminus \bar{Q}_{R_\alpha}(0)$ otherwise we are done since

$$\beta(v) \le \left(\max_{i \in \{1,\dots,N\}} \bar{v}_i\right) \sum_{j=1}^N |v_j|.$$

Let Σ be

$$\Sigma := \{ t \in \mathbb{R}^+ \, | \, \mathcal{N}(t) > R_{\alpha} \}.$$

From (4.6) and using that the v_i are non negative, we see that for all $t \in \Sigma$

$$\alpha(t) \ge c_{\alpha} \mathcal{N}(t)^{k_{\alpha}} \ge c_{\alpha} \left(\frac{1}{\bar{v}_{max}}\right)^{k_{\alpha}} \beta(t)^{k_{\alpha}},$$

where $\bar{v}_{max} := \max_{i \in \{1,...,N\}} \bar{v}_i$. Therefore, on Σ we have

$$\frac{d\beta(t)}{dt} \le \frac{1}{K} \left(\bar{\alpha} - \tilde{c}_0 \beta^{k_\alpha}(t) \right) \beta(t).$$

Using the logistic character of the above equation, we can check that

$$\beta(v(t)) \le \sup \left\{ \beta(v(0)), \max_{x \in \bar{Q}_{R_{\alpha}}(0)} \beta(x), \left(\frac{\bar{\alpha}}{\tilde{c}_0}\right)^{\frac{1}{k_{\alpha}}} \right\}.$$

We are now in position to prove the convergence of v toward its equilibrium.

Lemma 4.7. Let $(\bar{v}_i)_{i=1...N}$ be the unique stationary solution of (4.1). Then for any non negative initial datum $(v_i(0))_{i=1...N}$ not identically zero, the corresponding solution $(v_i(t))_{i=1...N}$ of (4.1) converges to $(\bar{v}_i)_{i=1...N}$ as t goes to infinity.

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Proof:

For simplicity we denote <, > the standard scalar product in \mathbb{R}^N .

Now, since $\bar{v} \neq 0$ and for all times t, $v(t) = (v_1, \dots, v_N)$ is a vector of \mathbb{R}^N , we can write $v(t) := \lambda(t)\bar{v} + h(t)$ with for all t, $< h(t), \bar{v} >= 0$. Substituting v by this decomposition in (4.1), it follows that

(4.7)
$$\lambda'(t)\bar{v} + \frac{dh(t)}{dt} = \lambda(t)A(\alpha(t))\bar{v} + A(\alpha(t))h,$$

(4.8)
$$= \frac{1}{K} (\bar{\alpha} - \alpha(t)) \lambda(t) \bar{v} + A(\alpha(t)) h.$$

Therefore, we have

$$<\lambda'(t)\bar{v}+\frac{dh(t)}{dt}, h>=<\frac{1}{K}(\bar{\alpha}-\alpha(t))\bar{v}+A(\alpha(t))h, h>.$$

Thus

$$<\frac{dh(t)}{dt}, h> = \frac{1}{2}\frac{d\mathcal{E}(h)}{dt} = < A(\alpha(t))h, h>.$$

By following the computation developed for the proof of (ii) in Lemma 4.4, we see that

$$\frac{d\mathcal{E}(h)}{dt} = -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2 + \frac{2}{K} (\bar{\alpha} - \alpha(t)) \mathcal{E}(h).$$

Since $\mathcal{E}(h) \geq 0$ for all times, we will analyse separately two situations: Either $\mathcal{E}(h(t)) > 0$ for all times t or there exists $t_0 \in \mathbb{R}$ so that $\mathcal{E}(h(t_0)) = 0$. In the latter case, from the above equation we see that we must have $\mathcal{E}(h(t)) = 0$ for all $t \geq t_0$ and so for all $t \geq t_0$, we must have $v(t) = \lambda(t)\bar{v}$. Hence from (4.8) we are reduced to analyse the following ODE equation

$$\lambda'(t) = \frac{\lambda(t)}{K} (\bar{\alpha} - \tilde{\alpha}(\lambda(t)))$$

where $\widetilde{\alpha}$ is the increasing locally Lipschitz function defined by $\widetilde{\alpha}(s) := \alpha(s\overline{v})$. Note that since $\lambda(t) < \overline{v}, \overline{v} >= \beta(v) > 0$, we have $\lambda(t) \geq 0$ for all times t. The above ODE is of logistic type with non negative initial datum therefore by a standard argumentation we see that $\lambda(t)$ converges to $\overline{\lambda} > 0$ where $\overline{\lambda}$ is the unique solution of $\widetilde{\alpha}(\overline{\lambda}) = \overline{\alpha}$. By construction we have $\widetilde{\alpha}(1) = \overline{\alpha}$, so we deduce that $\overline{\lambda} = 1$. Hence, in this situation, v converges to \overline{v} as time goes to infinity.

In the other situation, $\mathcal{E}(h(t)) > 0$ for all t and we claim that

Claim 4.8.
$$\mathcal{E}(h(t)) \to 0$$
 as $t \to +\infty$.

Assume the Claim holds true then we can conclude the proof by arguing as follows. From the decomposition $v(t) = \lambda(t)\bar{v} + h(t)$, we can express the function $\beta(v(t))$ by $\beta(v(t)) = \langle v, \bar{v} \rangle = \lambda(t) \langle \bar{v}, \bar{v} \rangle$. Therefore from Lemma 4.4 we deduce that

(4.9)
$$\lambda'(t) = \frac{1}{K} (\bar{\alpha} - \alpha(\lambda(t)\bar{v} + h(t)))\lambda(t).$$

Now by using $\mathcal{E}(h) \to 0$, we deduce that $h \to 0$ as $t \to \infty$ and from (4.9) we are reduced to analyse the ODE

$$\lambda'(t) = \frac{1}{K} (\bar{\alpha} - \tilde{\alpha}(\lambda(t)))\lambda(t) + \lambda(t)(\tilde{\alpha}(\lambda(t)\bar{v}) - \alpha(\lambda(t)\bar{v} + h(t)))$$
$$= \frac{1}{K} (\bar{\alpha} - \tilde{\alpha}(\lambda(t)))\lambda(t) + \lambda(t)o(1)$$

where $|o(1)| = |\widetilde{\alpha}(\lambda(t)\overline{v}) - \alpha(\lambda(t)\overline{v} + h(t))| \le C\sqrt{\mathcal{E}(h)} \to 0$ as $t \to \infty$. As before we can conclude that $\lambda(t) \to 1$ and v converges to \overline{v} .

Proof of Claim 4.8:

Since $\mathcal{E}(h(t)) > 0$ for all t, as in Lemma 4.5 we have

(4.10)
$$\frac{d}{dt} \log \left[\frac{\mathcal{E}(h)}{(\beta(v))^2} \right] = -\frac{1}{\mathcal{E}(h)} \sum_{i,j=1}^N \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j} \right)^2.$$

Thus the function $\widetilde{F} := \log \left[\frac{\mathcal{E}(h)}{(\beta(v))^2} \right]$ is a decreasing smooth function.

First we observe that the claim is proved if there exists a sequence $(t_n)_{n\in\mathbb{N}}$ converging to infinity so that $\mathcal{E}(h(t_n))\to 0$. Indeed, assume such sequence exists and let $(s_k)_{k\in\mathbb{N}}$ be a sequence converging to $+\infty$. Then there exists k_0 and a subsequence $(t_{n_k})_{k\in\mathbb{N}}$ of $(t_n)_{n\in\mathbb{N}}$ so that for all $k\geq k_0$, we have $s_k\geq t_{n_k}$. Therefore from the monotonicity of \widetilde{F} we have for all $k\geq k_0$

$$\log \left[\frac{\mathcal{E}(h(s_k))}{(\beta(v(s_k)))^2} \right] \le \log \left[\frac{\mathcal{E}(h(t_{n_k}))}{(\beta(v(t_{n_k})))^2} \right].$$

By letting k to infinity in the above inequality, we deduce that

$$\lim_{k \to \infty} \log \left[\frac{\mathcal{E}(h(s_k))}{(\beta(v(s_k)))^2} \right] = -\infty,$$

which implies that $\mathcal{E}(h(s_k)) \to 0$, since by Lemma 4.6 $(\beta(v(t_k)))_{k \in \mathbb{N}}$ is uniformly bounded. The sequence $(s_k)_{k \in \mathbb{N}}$ being chosen arbitrarily this implies that $\mathcal{E}(h(t)) \to 0$ as $t \to +\infty$.

Let us now prove that such sequence $(t_n)_{n\in\mathbb{N}}$ exists. We argue by contradiction and assume that $\inf_{t\in\mathbb{R}^+} \mathcal{E}(h(t))>0$. Therefore from the monotonicity and the smoothness of \widetilde{F} we deduce that there is $c_0\in\mathbb{R}$ so that

$$\widetilde{F}(h(t)) \to c_0$$
 and $\frac{d}{dt}\widetilde{F}(h(t)) \to 0$ as $t \to +\infty$.

Thus by Lemma 4.6 and (4.10) it follows that

(4.11)
$$\lim_{t \to \infty} \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_j \bar{v}_i \left(\frac{h_j}{\bar{v}_j} - \frac{h_i}{\bar{v}_i} \right)^2 = 0.$$

From the *a priori* estimates of Lemma 4.6, there exists a sequence $t_n \to \infty$ so that for all i $h_i(t_n) \to \widetilde{h}_i$. Passing to the limit along this sequence in the equation (4.11) it yields

$$0 = \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_j \bar{v}_i \left(\frac{\tilde{h}_j}{\bar{v}_j} - \frac{\tilde{h}_i}{\bar{v}_i} \right)^2.$$

By using the irreducibility assumption on the nonnegative matrix μ_{ij} and the positivity of the quantities \bar{v}_i , one can deduce from the above equality that we must have for all i and j

$$\frac{\widetilde{h}_j}{\overline{v}_i} = \frac{\widetilde{h}_i}{\overline{v}_i}.$$

Thus if we set $\lambda := \frac{\widehat{h}_1}{\overline{v}_1}$ we have $\widetilde{h} = \lambda \overline{v}$. So by using that $\langle h, \overline{v} \rangle = 0$ for all time it follows that $\lambda = 0$. Hence, we get the contradiction

$$0 < \inf_{t \in \mathbb{R}} \mathcal{E}(h(t)) \le \mathcal{E}(h(t_n)) \to 0.$$

5. A CASE OF INTEREST

In this section we analyse more precisely the dynamics of the solution v of (1.1) when the interactions Ψ_i take the form $\Psi_i(v) := \sum_{j=1}^N r_j v_j$. We prove the Theorem 1.2 that we recall below.

Theorem 5.1. Assume that the interactions Ψ_i take the form $\Psi_i(v) = \sum_{j=1}^N r_j v_j$ then for any nonnegative initial datum v(0) not identically zero, the solution v(t) of (1.5) converges exponentially fast to its unique equilibrium. That is to say there exists two positive constants C_1 and C_2 so that

$$||v - \bar{v}||_{\infty} \le C_1 e^{-C_2 t}$$
.

Before proving this Theorem we establish two auxiliary results that for convenience we present in two separate subsections. We prove Theorem 1.2 at the end of this section.

5.1. Study of the evolution of the total population.

Let us denote $\mathcal{N}(t) = \sum_{i=1}^{N} v_i$ the total population. A straightforward computation shows that for the interactions Ψ_i of the form $\Psi_i(v) := \sum_{j=1}^{N} r_j v_j$ we see that $\mathcal{N}(t)$ satisfies the equation :

(5.1)
$$\frac{d\mathcal{N}}{dt} = \alpha(t) \left(1 - \frac{\mathcal{N}}{K} \right),$$

which written with the new variable $P(t) = K - \mathcal{N}(t)$ takes the form

$$\frac{dP}{dt} = -\frac{\alpha(t)}{K}P.$$

The dynamic of the above equation is strongly related to the behaviour of $\alpha(t)$ and we have

(5.3)
$$|P(t)| = |P_0|e^{-\frac{1}{K}\int_0^t \alpha(s) \, ds}.$$

Lemma 5.2. For any nonnegative initial datum v(0) not identically zero, $\mathcal{N}(t)$ converges exponentially fast toward its unique equilibrium K. Moreover \mathcal{N} satisfies identically

(5.4)
$$\min\{\mathcal{N}_{min}(t), \mathcal{N}_{max}(t)\} \le \mathcal{N}(t) \le \max\{\mathcal{N}_{min}(t), \mathcal{N}_{max}(t)\},$$

where \mathcal{N}_{min} and \mathcal{N}_{max} are the solutions of the logistic equations:

$$\frac{du}{dt} = \xi^{\pm} u \left(1 - \frac{u}{K} \right)$$
$$u(0) = \mathcal{N}(0)$$

with respectively $\xi^- = \min\{r_1, \dots, r_N\}$ and $\xi^+ = \max\{r_1, \dots, r_N\}$

Proof:

Assume for the moment that (5.4) holds then the convergence exponentially fast to K is a straightforward consequence of (5.3). Indeed by (5.4) we deduce that $R_{min}\min(\mathcal{N}_{min},\mathcal{N}_{max}) \leq \alpha(s) \leq R_{max}\min(\mathcal{N}_{min},\mathcal{N}_{max})$ where $R_{\max} := \max\{r_1,\ldots,r_N\}$ and $R_{\min} := \min\{r_1,\ldots,r_N\}$. Therefore $\alpha(s) > C_0$, since \mathcal{N}_{min} and \mathcal{N}_{max} converge to K.

To obtain (5.4) we investigate the following three cases, $\mathcal{N}(0) = K$, $\mathcal{N}(0) < K$ and $\mathcal{N}(0) > K$. In the first case $\mathcal{N}(0) = K$, we see that (5.4) holds true trivially, since $\mathcal{N}_{max} = \mathcal{N}_{min} = \mathcal{N}(t) \equiv K$ for all t. Let us now investigate the two other situations. The argumentation in both situation being similar we expose only the case $\mathcal{N}(0) < K$.

In this situation, \mathcal{N}_{min} and \mathcal{N}_{max} being the solutions of logistic equations they are increasing functions. Moreover wa have $\mathcal{N}_{min}(t) \leq \mathcal{N}_{max}(t) < K$ for all t. On another hand, by continuity of $\mathcal{N}(t)$, there exists also $t_1 > 0$ so that $\mathcal{N}(t) < K$ on $[0, t_1)$. Furthermore on $(0, t_1)$ we can see that $\mathcal{N}(t)$ satisfies the following differential inequalities

(5.5)
$$\frac{d\mathcal{N}}{dt} \ge R_{min} \mathcal{N} \left(1 - \frac{\mathcal{N}}{K} \right)$$

(5.6)
$$\frac{d\mathcal{N}}{dt} \le R_{max} \mathcal{N} \left(1 - \frac{\mathcal{N}}{K} \right).$$

From the above differentials inequalities, by comparing $\mathcal{N}, \mathcal{N}_{min}$ and \mathcal{N}_{max} via the Cauchy Lipschitz Theorem, we obtain $\mathcal{N}_{\min} \leq \mathcal{N} \leq \mathcal{N}_{max}$ for all $t \in [0,t_1)$. Since $\mathcal{N}_{max}(t_1) < K$, we can bootstrap the above argument and show that (5.4) holds true for all t.

5.2. A useful functional inequality.

Next we establish a useful functional inequality satisfied by vectors $h \in \bar{v}^{\perp}$ where \bar{v}^{\perp} denotes the linear subspace of \mathbb{R}^N orthogonal to \bar{v} .

Lemma 5.3. There exists $C_1 > 0$ so that for all $h \in \bar{v}^{\perp}$

$$C_1 \mathcal{E}(h) \leq \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2.$$

Moreover $C_1 = \lambda_2$ where λ_2 is the minimal eigenvalue strictly positive of the linear eigenvalue problem

$$h_i \sum_{j=1}^{N} \mu_{ij} \frac{\bar{v}_j}{\bar{v}_i} - \sum_{j=1}^{N} \mu_{ij} h_j = \lambda h_i.$$

Proof:

Let \mathcal{I} be the following Rayleigh quotient

$$\mathcal{I}(h) := \frac{1}{\mathcal{E}(h)} \sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j} \right)^2.$$

Observe that the first part of the Lemma is proved if we show that

$$\inf_{h \in \bar{\eta}^{\perp}} \mathcal{I}(h) > 0,$$

or equivalently

(5.8)
$$\inf_{h \in \bar{v}^{\perp}, \mathcal{E}(h) = 1} \mathcal{I}(h) = \inf_{h \in \bar{v}^{\perp}} \mathcal{I}(h) > 0,$$

since for all real μ , $\mathcal{I}(h) = \mathcal{I}(\mu h)$.

To obtain (5.7), we argue by contradiction and assume that $\inf_{h\in \bar{v}^\perp}\mathcal{I}(h)=0$. By (5.8) we can take $(h_n)_{n\in\mathbb{N}}$ a minimising sequence so that $h_n\in \bar{v}^\perp,\mathcal{E}(h_n)=1$ for all n. Since $\{x\in\mathbb{R}^N\,|\,x\in\bar{v}^\perp,\mathcal{E}(x)=1\}$ is a closed bounded set, $(h_n)_{n\in\mathbb{N}}$ is uniformly bounded and we can extract a subsequence $(h_{n_k})_{k\in\mathbb{N}}$ which converges to $\bar{h}\in\bar{v}^\perp$ with $\mathcal{E}(\bar{h})=1$. Passing to the limit along this subsequence, we see that $\mathcal{I}(\bar{h})=0$ which combined with $\bar{h}\in\bar{v}^\perp$ implies that $\bar{h}=0$. Thus we get the contradiction $0=\mathcal{E}(\bar{h})=1$. Hence (5.7) holds true.

Let C_1 be defined by $C_1 = \inf_{h \in \bar{v}^{\perp}, \mathcal{E}(h) = 1} \mathcal{I}(h)$, let us try to compute C_1 . By construction C_1 is the result of a constrained minimisation problem. Therefore, by the standard optimization Theory [42], the minimizers must satisfy the following Euler-Lagrange equations

$$(5.9) (D - \widetilde{M})h = \lambda h,$$

$$\mathcal{E}(h) = 1,$$

$$(5.11) < h, \bar{v} > = 0,$$

where $\lambda \in \mathbb{R}$ is a Lagrange Multiplier to be determined and M and D are the following matrices

$$\widetilde{M} := \begin{pmatrix} \mu_{11} & \mu_{ij} \\ & \ddots & \\ \mu_{ij} & & \mu_{NN} \end{pmatrix}, \quad D := \begin{pmatrix} \frac{1}{\bar{v}_1} \sum_{j=1}^N \mu_{1j} \bar{v}_j & 0 \\ & & \ddots & \\ 0 & & \frac{1}{\bar{v}_N} \sum_{j=1}^N \mu_{Nj} \bar{v}_j \end{pmatrix}.$$

By taking k>0 large enough, the irreducible matrix $\widetilde{M}-D+kId$ becomes non-negative and so $\widetilde{M}-D+kId$ is a symmetric positive definite matrix. As a consequence, the eigenvectors associated to the eigenvalue ν_i of $\widetilde{M}-D+kId$ form an a orthogonal basis of \mathbb{R}^N , i.e. $\mathbb{R}^N=\bigoplus^{\perp} E_{\nu_i}$, where E_{ν_i} denotes the eigenspace associated to the eigenvalue ν_i .

Since $\widetilde{M}-D+kId$ is non negative and irreducible by the Perron-Frobenius Theorem there exists a unique eigenvalue, says ν_1 associated with a positive eigenvector ϕ_1 . Furthermore ν_1 is the largest eigenvalue and is algebraically simple. By a direct computation one can see that $(\widetilde{M}-D+kId)\overline{v}=k\overline{v}$, thus $\nu_1=k$ and $\phi_1=\gamma\overline{v}$. From the properties of ν_1 we have $E_{\nu_1}=lin(\overline{v})$, for all $i\neq 1, \nu_i<\nu_1=k$ and $\overline{v}^\perp=\bigoplus_{i\neq 1}^\perp E_{\nu_i}$.

By construction, the $\lambda_i := \nu_i - k \le 0$ are the eigenvalues of $\widetilde{M} - D$ and we can see that for all $h \in \overline{v}^{\perp}, \mathcal{E}(h) = 1$ we have

$$\mathcal{I}(h) = {}^{t}h(\widetilde{M} - D)h \ge \min_{i \ne 1} \{-\lambda_i\}.$$

Let $\lambda_2<0$ be second largest eigenvalue of $\widetilde{M}-D$ and ϕ_2 an associated eigenvector. By normalising ϕ_2 properly and since $\phi_2\in \bar{v}^\perp$ a straightforward computation shows that

$$\mathcal{I}(\phi_2) = {}^t\phi_2(D - \widetilde{M})\phi_2 = -\lambda_2 = \min_{i \neq 1} \{-\lambda_i\}.$$

Hence, $\min_{h \in \bar{v}^{\perp}} \mathcal{I}(h) = -\lambda_2$.

5.3. Asymptotic behaviour of the solution.

We are now in position to obtain the exponential rate of convergence for any solution v of (1.5). **Proof of Theorem 1.2:**

First we claim that

(5.12)
$$\sum_{i=1}^{N} \bar{v}_i = K.$$

Indeed from Lemma 4.3 we deduce that $\bar{v} = \frac{K\lambda_p}{\sum_{i=1}^N r_i(v_p)_i} v_p$ where v_p is the positive normalised eigenvector associated to the principal eigenvalue λ_p of the matrix R+M. A straightforward computation shows that

$$\sum_{i=1}^{N} r_i(v_p)_i = \sum_{i=1}^{N} ((R+M)v_p)_i = \lambda_p \sum_{i=1}^{N} (v_p)_i.$$

Since $\lambda_p > 0$ it follows that

$$\frac{\sum_{i=1}^{N} (v_p)_i}{\sum_{i=1}^{N} r_i(v_p)_i} = \frac{1}{\lambda_p}.$$

Thus

$$\frac{K\lambda_p}{\sum_{i=1}^{N} r_i(v_p)_i} \sum_{i=1}^{N} (v_p)_i = K.$$

Now recall that in the proof of Lemma 4.7 from the orthogonal decomposition $v(t) = \lambda(t)\bar{v} + h(t)$ we have

$$\frac{d\mathcal{E}(h)}{dt} = -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2 + \frac{2}{K} (\bar{\alpha} - \alpha(t)) \mathcal{E}(h).$$

By Lemma 5.3 we obtain

$$\frac{d\mathcal{E}(h)}{dt} \le -C_1 \mathcal{E}(h) + \frac{2}{K} (\bar{\alpha} - \alpha(t)) \mathcal{E}(h).$$

Now arguing as in the proof of Lemma 4.5, we end up with

$$\frac{d}{dt}\log\left(\frac{\mathcal{E}(h)}{\beta(v)^2}\right) \le -C_1.$$

Therefore, thanks to Lemma 4.6 we deduce that

(5.13)
$$\mathcal{E}(h) \le \left(\frac{\mathcal{E}(h(0))}{\beta(v(0))^2}\right) e^{-C_1 t} \beta^2(v) \le C_2 e^{-C_1 t}.$$

Finally we get the exponential rate of convergence, by observing that

$$\mathcal{N}(t) = \langle v, 1 \rangle = \lambda(t) \langle \bar{v}, 1 \rangle + \langle h, 1 \rangle$$

which thanks to (5.3) implies that

$$\lambda(t) = \frac{K}{\langle \bar{v}, 1 \rangle} + \frac{\langle h, 1 \rangle}{\langle \bar{v}, 1 \rangle} + \frac{|\mathcal{N}(0) - K|e^{-\frac{1}{K} \int_0^t \alpha(s) \, ds}}{\langle \bar{v}, 1 \rangle}.$$

By Lemma 5.2 and the estimates (5.13), (5.12), using standard norm estimates, we have

$$||v - \bar{v}||_{\infty} \le \left| \frac{\langle h, 1 \rangle}{K} + \frac{|\mathcal{N}(0) - K|e^{-\frac{1}{K}\int_{0}^{t}\alpha(s)\,ds}}{K} \right| ||\bar{v}||_{\infty} + N\mathcal{E}(h)$$

$$\le \frac{|\mathcal{N}(0) - K|||\bar{v}||_{\infty}}{K} e^{-\frac{1}{K}\int_{0}^{t}\alpha(s)\,ds} + \left(1 + \frac{||\bar{v}||_{\infty}}{K}\right) \widetilde{C}_{2}e^{-C_{1}t}.$$

6. THE GENERAL CASE: THE STATIONARY SOLUTION

In this section we investigate the existence of a positive stationary solution of (2.1) under the additional condition (1.6) on the matrices R and M that we recall below,

$$\forall i \quad \sum_{i=1}^{N} \mu_{ij} \le \frac{r_i}{2}.$$

This assumption has for consequence that the matrix R + M is positive definite. Indeed, we have

$${}^{t}h(R+M)h = \sum_{i=1}^{N} r_{i}h_{i}^{2} - \frac{1}{2}\sum_{i,j=1}^{N} \mu_{ij}(h_{i} - h_{j})^{2} \ge 2\sum_{i,j=1}^{N} \mu_{ij}h_{i}^{2} - \frac{1}{2}\sum_{i,j=1}^{N} \mu_{ij}(h_{i} - h_{j})^{2}$$

$$\ge \sum_{i,j=1}^{N} (\mu_{ij} \left(h_{i}^{2} + h_{j}^{2} - \frac{1}{2}(h_{i} - h_{j})^{2}\right)$$

$$\ge \frac{1}{2} \left(\sum_{i,j=1}^{N} \mu_{ij}(h_{i} + h_{j})^{2}\right).$$

Thus $kern(R+M)=\{0\}$ and the matrix R+M is invertible. Moreover from the last inequality we see that there exists positive constants c_0 and C_0 so that

(6.1)
$$c_0 < u, u >_{R+M} \le \mathcal{E}(u) \le C_0 < u, u >_{R+M},$$

where $< u, u>_{R+M} := {}^{t}u(R+M)u$.

Let $\Xi(v)$ be the diagonal matrix defined by

$$(\Xi(v))_{ij} = \delta_{ij}\Psi_i(v).$$

With this notation, a positive stationary solution of (2.1) is then a non negative solution of the following problem:

$$(6.2) (R+M)v = \Xi(v)v$$

Note that when $\Xi(v)$ can be written as $\Xi(v) = \alpha(v)Id$, the construction of a positive solution has already been made in Section 4. So in the later, we will assume that $\Xi(v)$ cannot be written as $\Xi(v) = \alpha(v)Id$. It is worth mentioning that in this situation the method used in Section 4 does not work and we have to use another strategy.

Let *T* be the following map

$$T: \mathbb{R}^N \to \mathbb{R}^N$$

$$v \mapsto Tv := (R+M)^{-1} [\Xi(v)v] .$$

Since R + M is invertible, T is well defined and one can easily check that a positive solution of (6.2) is a positive fixed point of the map T. To check that T has a positive fixed point we use a degree argument.

Let $\Psi_i(v)^s$ and $\Xi(v)^s$ defined by

$$\Psi_i^s := s\Psi_i + (1-s)\Psi_1, \qquad (\Xi^s(v))_{ij} := \delta_{ij}\Psi_i^s(v),$$

we consider the homotopy $H \in C([0,1] \times \mathbb{R}^N, \mathbb{R}^N)$ defined by

$$\begin{array}{cccc} H:[0,1]\times\mathbb{R}^N & \to & \mathbb{R}^N \\ (s,v) & \mapsto & H(s,v):=(R+M)^{-1}[\Psi^s(v)v]. \end{array}$$

One can see that H(1,.) = T and $H(0,.) = T_0$ where T_0 corresponds to the map

$$T_0: \mathbb{R}^N \to \mathbb{R}^N$$

$$v \mapsto T_0 v := \Psi_1(v)(R+M)^{-1}v.$$

Note that there exists a unique positive fixed point to T_0 which can be constructed by arguing as in Section 4.

The next step in this degree argument is to obtain for all s, a good a priori estimates on the fixed point of the map H(s,v), i.e. a good estimate on the positive solutions of the following problem:

(6.3)
$$(R+M)V = \Psi^s(V)V.$$

In this direction we show the following:

Lemma 6.1. Let V be a non negative solution of (6.3). Then either $V \equiv 0$ or V > 0 and there exists \bar{c}_1 and \bar{C}_1 independent of s so that

$$\bar{c}_1 \le \sum_i V_i \le \bar{C}_1.$$

Proof:

To obtain that V is either positive or V=0 we can argue as in the proof of Lemma 2.1. So assume that there exists a i_0 so that $V_{i_0}=0$. By construction V_{i_0} is a minimum of the V_i and from the equation satisfied by V_{i_0} we get

$$0 \le \sum_{j=1}^{N} \mu_{i_0 j} (V_j - V_{i_0}) = 0.$$

Therefore $V_j=V_{i_0}$ for all j where $\mu_{i_0j}\neq 0$. Since M is irreducible there exists $j\neq i_0$ so that $\mu_{i_0j}\neq 0$. Let $\rho:=\{k\,|\,V_k=0\}$ then i_0 and all j so that $\mu_{i_0j}\neq 0$ belongs to ρ . In the previous argument, by replacing i_0 by any $k\in \rho$, we see that all j so that $\mu_{kj}\neq 0$ belongs to the set ρ . By iterating enough times the above argument and using the irreducibility of the matrix M we can see that $\rho=\{1,\ldots,N\}$ so $V_i=V_{i_0}=0$ for all i. Therefore a nonnegative solution of (6.3) is either $V\equiv 0$ or V>0.

Now let us assume that V > 0. Recall that by (6.1) there exists positive constants c_0 and C_0 so that for all $u \in \mathbb{R}^N$

$$c_0 < u, u >_{R+M} \le \mathcal{E}(u) \le C_0 < u, u >_{R+M}$$
.

So for a solution V of (6.3) one has

$$< V, V>_{R+M} = \sum_{i} \Psi_{i}^{s}(V) V_{i}^{2} \ge \left(s \min_{i \in \{2, ..., N\}} \Psi_{i}(V) + \Psi_{1}(V) \right) < V, V>$$

 $\ge c_{0} \Psi_{1}(V) < V, V>_{R+M},$

and we also get

$$< V, V>_{R+M} \le C_0 \left(s \max_{i \in \{2, \dots, N\}} \Psi_i(V) + \Psi_1(V) \right) < V, V>_{R+M}.$$

Therefore we have

$$(6.4) \Psi_1(V) \le \frac{1}{c_0},$$

(6.5)
$$\frac{1}{C_0} \le s \max_{i \in \{2, \dots, N\}} \Psi_i(V) + \Psi_1(V).$$

Now thanks to the assumptions (1.2)–(1.3) made on the functions Ψ_i , there exists R_1, c_1, k_1 and N positive constants κ_i so that :

(6.6) For all
$$x \in \mathbb{R}^{N,+} \setminus Q_{R_1}(0)$$
, $c_1 \left(\sum_{i=1}^{N} x_i \right)^{k_1} \le \Psi_1(x)$,

(6.7) For all
$$i$$
, and for all $x \in Q_{R_1}(0)$, $\Psi_i(x) \le \kappa_i \sum_{j=1}^N |x_j|$.

By combining (6.4),(6.6), (6.5) and (6.7) we deduce that

$$\mathcal{N} = \sum_{j=1}^{N} V_j \le \sup \left\{ \left(\frac{1}{c_0 c_1} \right)^{\frac{1}{k_1}}, R_1 \right\},$$

$$\mathcal{N} = \sum_{j=1}^{N} V_j \ge \min \left\{ R_1, \frac{1}{C_0 (\kappa_1 + \sup_i \kappa_i)} \right\}.$$

6.1. Computation of the degree.

We are now in position to prove the existence of a positive solution to the equation (6.2) by means of the computation of the topological degree of T-id on a well chosen set $\Omega\subset\mathbb{R}^{N,+}$. Now we take two positive constants c_2 and C_2 so that $c_2<\bar{c}_1$ and $C_2>\bar{C}_1$ where \bar{c}_1 and \bar{C}_1 are the constants obtained in Lemma 6.1. Let Ω be the following open set

$$\Omega := \left\{ v \in \mathbb{R}^{N,+} \, | \, c_2 \le \sum_{i=1}^{N} v_i \le C_2 \right\}$$

and let us compute $deg(T - Id, \Omega, 0)$.

By Lemma 6.1 for all $s\in [0,1]$ in $H(s,v)-v\neq 0$ on $\partial\Omega$. Therefore using that H(.,.) is an homotopy, we conclude that $deg(T-Id,\Omega,0)=deg(H(1,.)-Id,\Omega,0)=deg(H(0,.)-Id,\Omega,0)$. By construction, from Section 4.1, one can check that $deg(H(0,.)-Id,\Omega,0)\neq 0$ since the map T_0 has an unique stable and positive fixed point. Thus $deg(T-Id,\Omega,0)\neq 0$ which shows that T has a fixed point in Ω .

7. The General Case: Asymptotic Behaviour

In this section we prove Theorem 1.4. That is to say, under the extra assumption (1.6) we analyse the asymptotic behaviour of the solution v(t) when for all i the interaction Ψ_i can be expressed like: $\Psi_i(v) = \alpha(v) + \epsilon \psi_i(v)$ with ψ_i uniformly bounded. To obtain the asymptotic behaviour in this case, we follow the strategy developed in Subsection 4.2. Namely, we start by showing some *a priori* estimates on the solution, then we analyse the convergence by means of a Lyapunov functional. For convenience we dedicate a subsection to each essential part of the proof.

7.1. A priori estimate.

We start by establishing some useful differential inequalities. Namely we show that

Lemma 7.1. Assume that r_i , (μ_{ij}) , Ψ_i satisfies (1.2), (1.3) and (1.6). Assume further that $\Psi_i(v) = \alpha(v) + \epsilon \psi_i(v)$ with ψ_i uniformly bounded. Then there exists $\epsilon_0 > 0$ so that for all $0 \le \epsilon \le \epsilon_0$ there exists $\omega^+ \in \mathbb{R}^N$, ω^+ positive and a positive real γ so that

(i)

$$\frac{d\sum_{i=1}^{N} \bar{\omega}_{i}^{+} v_{i}}{dt} \leq \frac{1}{K} (\alpha(\bar{\omega}^{+}) - \alpha(v)) \sum_{j=1}^{N} \bar{\omega}_{i}^{+} v_{i}$$
$$\frac{d\sum_{i=1}^{N} \bar{\omega}_{i}^{+} v_{i}}{dt} \geq \frac{1}{K} (\alpha(\gamma \bar{\omega}^{+}) - \alpha(v)) \sum_{i=1}^{N} \bar{\omega}_{i}^{+} v_{i}$$

$$\frac{d\mathcal{E}(v)}{dt} \le -\sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{+} \bar{\omega}_{j}^{+} \left(\frac{v_{i}}{\bar{\omega}_{i}^{+}} - \frac{v_{j}}{\bar{\omega}_{j}^{+}}\right)^{2} + \frac{2}{K} (\alpha(\omega^{+}) - \alpha(v)) \mathcal{E}(v)$$

$$\frac{d\mathcal{E}(v)}{dt} \ge -\sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{+} \bar{\omega}_{j}^{+} \left(\frac{v_{i}}{\bar{\omega}_{i}^{+}} - \frac{v_{j}}{\bar{\omega}_{j}^{+}}\right)^{2} + \frac{2}{K} (\alpha(\gamma\bar{\omega}^{+}) - \alpha(v)) \mathcal{E}(v)$$

(iii)

$$\frac{d}{dt} \log \left[\frac{\mathcal{E}(v)}{(\sum_{i=1}^{N} \bar{\omega}_{i}^{+} v_{i})^{2}} \right] \leq -\frac{1}{\mathcal{E}(v)} \sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{+} \bar{\omega}_{j}^{+} \left(\frac{v_{i}}{\bar{\omega}_{i}^{+}} - \frac{v_{j}}{\bar{\omega}_{j}^{+}} \right)^{2} + \frac{2}{K} (\alpha(\bar{\omega}^{+}) - \alpha(\gamma\bar{\omega}^{+}))$$

$$\frac{d}{dt} \log \left[\frac{\mathcal{E}(v)}{(\sum_{i=1}^{N} \bar{\omega}_{i}^{+} v_{i})^{2}} \right] \geq -\frac{1}{\mathcal{E}(v)} \sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{+} \bar{\omega}_{j}^{+} \left(\frac{v_{i}}{\bar{\omega}_{i}^{+}} - \frac{v_{j}}{\bar{\omega}_{j}^{+}} \right)^{2} + \frac{2}{K} (\alpha(\gamma\bar{\omega}^{+}) - \alpha(\bar{\omega}^{+}))$$

Proof:

First, we observe that (iii) can be straightforwardly obtained by combining (i) and (ii). So we deal only with (i) and (ii).

Let us denote $\sigma := \epsilon \|\psi\|_{\infty}$. Then since v is positive, from (1.1) it follows that

$$\frac{dv_i}{dt} \le (r_i + \sigma - \alpha(v))v_i + \sum_{j=1}^N \mu_{ij}(v_j - v_i),$$

$$\frac{dv_i}{dt} \ge (r_i - \sigma - \alpha(v))v_i + \sum_{j=1}^N \mu_{ij}(v_j - v_i).$$

Let $\bar{\omega}^+$ and $\bar{\omega}^-$ be the stationary solutions of the corresponding equations

$$\frac{d\omega_{i}^{+}}{dt} = (r_{i} + \sigma - \alpha(\omega^{+}))\omega_{i}^{+} + \sum_{j=1}^{N} \mu_{ij}(\omega_{j}^{+} - \omega_{i}^{+}),$$
$$\frac{d\omega_{i}^{-}}{dt} = (r_{i} - \sigma - \alpha(\omega^{-}))\omega_{i}^{-} + \sum_{j=1}^{N} \mu_{ij}(\omega_{j}^{-} - \omega_{i}^{-}).$$

Now, let us fix ϵ small enough so that $\bar{\omega}^{\pm}$ exists. Then by arguing as in the proof of Lemma 3.2, we obtain

$$\frac{d}{dt} \sum_{i=1}^{N} \bar{\omega}_{i}^{+} v_{i} \leq \frac{1}{K} (\alpha(\bar{\omega}^{+}) - \alpha(v)) \sum_{j=1}^{N} \bar{\omega}_{i}^{+} v_{i},$$

$$\frac{d}{dt} \sum_{i=1}^{N} \bar{\omega}_{i}^{-} v_{i} \geq \frac{1}{K} (\alpha(\bar{\omega}^{-}) - \alpha(v)) \sum_{j=1}^{N} \bar{\omega}_{i}^{-} v_{i},$$

$$\frac{d\mathcal{E}(v)}{dt} \leq -\sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{+} \bar{\omega}_{j}^{+} \left(\frac{v_{i}}{\bar{\omega}_{i}^{+}} - \frac{v_{j}}{\bar{\omega}_{j}^{+}} \right)^{2} + \frac{2}{K} (\alpha(\bar{\omega}^{+}) - \alpha(v)) \mathcal{E}(v),$$

$$\frac{d\mathcal{E}(v)}{dt} \geq -\sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{-} \bar{\omega}_{j}^{-} \left(\frac{v_{i}}{\bar{\omega}_{i}^{-}} - \frac{v_{j}}{\bar{\omega}_{j}^{-}} \right)^{2} + \frac{2}{K} (\alpha(\bar{\omega}^{-}) - \alpha(v)) \mathcal{E}(v).$$

Note that by Lemma 4.3, $\bar{\omega}^{\pm}$ are positive eigenvectors of the matrices $R+M\pm\sigma Id$. Thus $\bar{\omega}$ are eigenvectors of the matrix R+M associated to the principal eigenvalue of R+M. Since R+M is irreducible, the eigenspace associated to the principal eigenvalue is unidimensional. So, we have $\omega^+=\gamma\omega^-$ for some positive γ . Hence (i) and (ii) hold true since

$$\sum_{i,j=1}^N \mu_{ij} \bar{\omega}_i^- \bar{\omega}_j^- \left(\frac{v_i}{\bar{\omega}_i^-} - \frac{v_j}{\bar{\omega}_j^-} \right)^2 = \sum_{i,j=1}^N \mu_{ij} \bar{\omega}_i^+ \bar{\omega}_j^+ \left(\frac{v_i}{\bar{\omega}_i^+} - \frac{v_j}{\bar{\omega}_j^+} \right)^2.$$

Next, we derive some *a priori* estimates for the solution v for an interaction Ψ as in Theorem 1.4. We first prove some sharp *a priori* estimates for stationary solution \bar{v}_{ϵ} of (1.1).

Lemma 7.2. Assume that r_i , (μ_{ij}) , Ψ_i satisfies (1.2), (1.3) and (1.6). Assume further that $\Psi_i(v) = \alpha(v) + \epsilon \psi_i(v)$ with ψ_i uniformly bounded. Then there exists $\bar{c}_1 < \bar{C}_1$ and ϵ_1 so that for all $0 \le \epsilon \le \epsilon_1$ and for any positive stationary solution \bar{v}_{ϵ} of (1.1), we have

$$\bar{c}_1 \le \sum_{i=1}^N \bar{v}_{\epsilon,i} < \bar{C}_1.$$

Moreover, there exists r_0 so that for all $\epsilon \leq \epsilon_1, \bar{v}_{\epsilon} \in Q_{\sqrt{\epsilon}r_0}(\bar{\omega}^+)$. Furthermore, for any nonnegative initial datum $v_i(0)$ not identically zero there exists two constants $\bar{c}_2(v(0)), \bar{C}_2(v(0))$ so that for all $0 \leq \epsilon \leq \epsilon_1$ the solution v_{ϵ} satisfies for all t,

$$\bar{c}_2 \le \beta(v_{\epsilon}(t)) := \sum_{i=1}^{N} \bar{v}_{\epsilon,i} v_{\epsilon,i}(t) \le \bar{C}_2.$$

Proof:

Let us first observe that for $\epsilon \leq \epsilon_0$ by replacing v_{ϵ} by \bar{v}_{ϵ} in (i) of Lemma 7.1, we get

(7.1)
$$0 \le \frac{1}{K} (\alpha(\bar{\omega}^+) - \alpha(\bar{v}_{\epsilon})) \sum_{i=1}^N \bar{\omega}_i^+ \bar{v}_{\epsilon,i},$$

(7.2)
$$0 \ge \frac{1}{K} (\alpha(\gamma \bar{\omega}^+) - \alpha(\bar{v}_{\epsilon})) \sum_{i=1}^{N} \bar{\omega}_i^+ \bar{v}_{\epsilon,i}.$$

From the proof of Lemma 4.3, we also see that

(7.3)
$$\alpha(\bar{\omega}^+) = K(\lambda_p + \sigma), \qquad \alpha(\bar{\omega}^-) = K(\lambda_p - \sigma),$$

where λ_p is the positive principal eigenvalue of the matrix R+M. By using the monotonicity of α , we deduce that the maps $\sigma \mapsto \omega^{\pm}$ are monotone. Moreover, we have $0 \le \alpha(\bar{\omega}^+) - \alpha(\bar{\omega}^-) \le 2\sigma K$.

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To obtain \bar{c}_1 and \bar{C}_1 we argue as follows. Let us fix $\epsilon_1 := \min\{\epsilon_0, \frac{\lambda_p}{4\|\psi\|_{\infty}}\}$. Then by (7.3), for all $\epsilon \in [0, \epsilon_1]$ we have

(7.4)
$$\alpha(\bar{\omega}^+) \le \alpha(\omega_{\epsilon_1}^+) = \frac{5K\lambda_p}{4}, \qquad \alpha(\bar{\omega}^-) \ge \alpha(\omega_{\epsilon_1}^-) = \frac{3K\lambda_p}{4}.$$

Now thanks to the assumptions (1.2)–(1.3) satisfied by α , there exists R_{α} , c_{α} , k_{α} and κ_{α} so that :

(7.5) For all
$$x \in \mathbb{R}^{N,+} \setminus Q_{R_{\alpha}}(0)$$
, $c_{\alpha} \left(\sum_{i=1}^{N} x_{i}\right)^{k_{\alpha}} \leq \alpha(x)$,

(7.6) For all
$$i$$
, and for all $x \in Q_{R_{\alpha}}(0)$, $\alpha(x) \le \kappa_{\alpha} \sum_{j=1}^{N} |x_{j}|$.

So for $\epsilon \in [0, \epsilon_1]$, by combining (7.1), (7.2),(7.3),(7.4), (7.5) and (7.6) we achieve

(7.7)
$$\sum_{j=1}^{N} \bar{v}_{\epsilon,j} \le \sup \left\{ \left(\frac{5K\lambda_p}{4c_{\alpha}} \right)^{\frac{1}{k_{\alpha}}}, R_{\alpha} \right\} =: \bar{C}_1,$$

(7.8)
$$\sum_{j=1}^{N} \bar{v}_{\epsilon,j} \ge \min \left\{ R_{\alpha}, \frac{3K\lambda_{p}}{4\kappa_{\alpha}} \right\} =: \bar{c}_{1}.$$

To obtain a more precise estimate on \bar{v}_{ϵ} , we argue as follows. Let us decompose $\bar{v}_{\epsilon} := \lambda_{\epsilon}\bar{\omega}^+ + h_{\epsilon}$ where h_{ϵ} is orthogonal to $\bar{\omega}^+$. Then by replacing v_{ϵ} by \bar{v}_{ϵ} in (iii) of Lemma 7.1, and using that $|\alpha(\bar{\omega}^+) - \alpha(\bar{\omega}^-)| \leq 2\sigma K$ we get

$$(7.9) 0 \le -\frac{1}{\mathcal{E}(\bar{v}_{\epsilon})} \sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{+} \bar{\omega}_{j}^{+} \left(\frac{h_{\epsilon,i}}{\bar{\omega}_{i}^{+}} - \frac{h_{\epsilon,j}}{\bar{\omega}_{j}^{+}} \right)^{2} + 4\sigma,$$

(7.10)
$$0 \ge -\frac{1}{\mathcal{E}(\bar{v}_{\epsilon})} \sum_{i,j=1}^{N} \mu_{ij} \bar{\omega}_{i}^{+} \bar{\omega}_{j}^{+} \left(\frac{h_{\epsilon,i}}{\bar{\omega}_{i}^{+}} - \frac{h_{\epsilon,j}}{\bar{\omega}_{j}^{+}} \right)^{2} - 4\sigma.$$

From (7.7) and using the functional inequality, Lemma 5.3, we deduce that

(7.11)
$$\mathcal{E}(h_{\epsilon}) \leq \frac{4\sigma \bar{C}_{1}^{2}}{C(\bar{\omega}^{+})}.$$

Combining the latter estimate with (7.7) and the positivity of $\bar{\omega}^+$ and \bar{v}_{ϵ} , we have the estimate

$$\lambda_{\epsilon} \leq \frac{\bar{C}_1}{\sum_{i=1}^{N} \bar{\omega}_i} \left(1 + 2\sqrt{\frac{N\sigma}{C(\bar{\omega})}} \right),$$

where $\bar{\omega}$ is the stationary solution with $\epsilon=0$. Let $R_0:=\bar{C}_1\left(1+2\sqrt{\frac{N\sigma}{C(\bar{\omega})}}\right)$, and choose ϵ_1 smaller if necessary to have $R_0\leq 2\bar{C}_1$. Next consider the set $\bar{Q}_{R_0}(0)\subset Q_{2\bar{C}_1}(0)$. From the above estimates on λ_ϵ and h_ϵ , since α is Lipschitz continuous in $Q_{2\bar{C}_1}(0)$ there exists κ_0 so that for all ϵ ,

$$|\alpha(\lambda_{\epsilon}\bar{\omega}^{+}) - \alpha(\lambda_{\epsilon}\bar{\omega}^{+} + h_{\epsilon})| \leq \kappa_{0}\sqrt{N\mathcal{E}(h_{\epsilon})},$$

which combine with (7.11) enforces

(7.12)
$$|\alpha(\lambda_{\epsilon}\bar{\omega}^{+}) - \alpha(\lambda_{\epsilon}\bar{\omega}^{+} + h_{\epsilon})| \leq 2\bar{C}_{1}\kappa_{0}\sqrt{\frac{N\sigma}{C(\bar{\omega})}}.$$

Thus from (7.1), (7.2) and (7.12) we deduce that

(7.13)
$$|\alpha(\bar{\omega}^+) - \alpha(\lambda_{\epsilon}\bar{\omega}^+)| \le 2K\sigma + 2\bar{C}_1\kappa_0\sqrt{\frac{N\sigma}{C(\bar{\omega})}} \le C\sqrt{\sigma},$$

with C independent of ϵ . Observe that by construction there exists two positives constants $0 < \iota_0 < 1 < \iota_1$ so that for all $\epsilon \leq \epsilon_1$, there exists $\iota_\epsilon \in (\iota_0, \iota_1)$ so that $\bar{\omega}^+ = \iota_\epsilon \bar{\omega}$. Recall now that by assumption $\nabla \alpha > 0$, then the real map $s \mapsto \alpha(s\bar{\omega})$ is smooth $(C^1(\mathbb{R}))$ and increasing. It is therefore an homeomorphism in \mathbb{R}^+ and a local diffeomorphism in \mathbb{R}^+ . So by the Inverse Function Theorem, we deduce that for all $s,t \in (0,C)$,

$$|s-t| \le \frac{k}{\iota_0} |\alpha(s\bar{\omega}^+) - \alpha(t\bar{\omega}^+)|,$$

where

$$C := \sup \left\{ \frac{\iota_1}{\iota_0}, \frac{\bar{C}_1}{\sum_{i=1}^N \bar{\omega}_i} \left(1 + 2\sqrt{\frac{N\sigma}{C(\bar{\omega})}} \right) \right\}$$
$$k := \frac{1}{\min_{s \in (0,C)} (\langle \nabla(\alpha(s\bar{\omega})), \bar{\omega} \rangle)}.$$

In particular, we have

$$|s-1| \le \frac{k}{\iota_0} |\alpha(s\bar{\omega}^+) - \alpha(\bar{\omega}^+)|,$$

which combined with (7.13) enforces

$$|\lambda_{\epsilon} - 1| \le \frac{k}{\iota_0} C \sqrt{\sigma}.$$

Hence from the latter estimate and (7.11) we have for all $\epsilon \leq \epsilon_1$, $\bar{v}_{\epsilon} \in Q_{C\sqrt{\epsilon}}(\bar{\omega}^+)$.

Next, we derive an uniform upper bound for $\beta(v_{\epsilon})$ when $\epsilon \in [0, \epsilon_1]$. In the sequel of this proof, for convenience we drop the subscript ϵ on v.

First, we observe that by Lemma 3.2 we have

$$\frac{d}{dt} \left(\sum_{i=1}^{N} v_i \bar{v}_i \right) = \frac{1}{K} \sum_{i=1}^{N} (\Psi_i(\bar{v}) - \Psi_i(v)) v_i \bar{v}_i,$$

$$= \left(\frac{1}{K} (\alpha(\bar{v}) - \alpha(t)) \right) \sum_{i=1}^{N} v_i \bar{v}_i + \frac{\epsilon}{K} \sum_{i=1}^{N} (\psi_i(\bar{v}) - \psi_i(v)) v_i \bar{v}_i.$$

Since the functions ψ_i are uniformly bounded, we achieve

$$\frac{d}{dt} \left(\sum_{i=1}^{N} v_i \bar{v}_i \right) \le \left(\frac{1}{K} (\alpha(\bar{v}) + 2\epsilon \|\psi\|_{\infty} - \alpha(t)) \right) \sum_{i=1}^{N} v_i \bar{v}_i.$$

By using (7.1) and (7.4), it follows

$$\frac{d}{dt} \left(\sum_{i=1}^{N} v_i \bar{v}_i \right) \le \frac{1}{K} \left[\frac{7K\lambda_p}{4} - \alpha(t) \right] \sum_{i=1}^{N} v_i \bar{v}_i.$$

Again using that α satisfies the assumptions (1.2)–(1.3), there exists $R_{\alpha}, c_{\alpha}, k_{\alpha}$ so that for all $x \in \mathbb{R}^{N,+} \setminus Q_{R_{\alpha}}(0)$,

(7.14)
$$c_{\alpha} \left(\sum_{i=1}^{N} x_{i} \right)^{k_{\alpha}} \leq \alpha(x).$$

Now, let us assume that for some $t>0, v(t)\in\mathbb{R}^{N,+}\setminus \bar{Q}_{R_\alpha}(0)$ otherwise the proof is done since we have

$$\beta(v) \le \left(\max_{i \in \{1,\dots,N\}} \bar{v}_i\right) \sum_{j=1}^N |v_j| \le \bar{C}_1 R_\alpha,$$

where \bar{C}_1 is the bound obtained above. Let Σ be the following set

$$\Sigma := \{ t \in \mathbb{R}^+ \, | \, \mathcal{N}(t) > R_{\alpha} \}.$$

From (7.14), (7.7) and using that the v_i are non negative, we see that for all $t \in \Sigma$

$$\alpha(t) \ge c_{\alpha} \mathcal{N}(t)^{k_{\alpha}} \ge c_{\alpha} \left(\frac{1}{\overline{C}_{1}}\right)^{k_{\alpha}} \beta(t)^{k_{\alpha}}.$$

Therefore, with $\widetilde{c}_0 := c_{\alpha} \left(\frac{1}{C_1} \right)^{k_{\alpha}}$ we have for $t \in \Sigma$

$$\frac{d\beta(t)}{dt} \le \frac{1}{K} \left(\frac{7K\lambda_p}{4} - \widetilde{c}_0 \beta^{k_\alpha}(t) \right) \beta(t).$$

Using the logistic character of the above equation, we can check that

$$\beta(v(t)) \le \sup \left\{ \beta(v(0)), \sup_{x \in Q_{R_{\alpha}}(0)} \beta(x), \left(\frac{7K\lambda_p}{4\widetilde{c}_0}\right)^{\frac{1}{k_{\alpha}}} \right\}.$$

Thus, by using (7.7), we achieve for all $\epsilon \in [0, \epsilon_1]$

$$\beta(v_{\epsilon}(t)) \leq \bar{C}_2 := \sup \left\{ \beta(v(0)), \bar{C}_1 R_{\alpha}, \bar{C}_1 \left(\frac{7K\lambda_p}{4c_{\alpha}} \right)^{\frac{1}{k_{\alpha}}} \right\}.$$

To obtain the lower bound for $\beta(v_{\epsilon})$ we argue as follows. First let us observe that by taking ϵ_1 smaller if necessary, since $\bar{\omega}^+ \to \bar{\omega}$ as $\epsilon \to 0$ and $\bar{v}_{\epsilon} \in Q_{C\sqrt{\epsilon}}(\bar{\omega}^+)$, there exists a positive constant c_0 independent of $\epsilon \in [0, \epsilon_1]$ so that for all stationary solution \bar{v}_{ϵ} we have

$$\min_{i \in \{1, \dots, N\}} \bar{v}_{\epsilon, i} \ge c_0$$

Now by (7.8), for all $\epsilon \in [0, \epsilon_1]$ we have

(7.15)
$$\beta(v_{\epsilon}) \ge \min_{i \in \{1, \dots, N\}} \bar{v}_{\epsilon, i} \sum_{i=1}^{N} v_{\epsilon, i} \ge c_0 \sum_{i=1}^{N} v_{\epsilon, i}.$$

Therefore to obtain an uniform lower bound for $\beta(v_{\epsilon})$ it is enough to obtain an uniform lower bound for $\mathcal{N}_{\epsilon} := \sum_{i=1}^{N} v_{\epsilon,i}$. From (1.1) by summing over all i and by using the definition of Ψ and the boundedness of the ψ_{i} we deduce that \mathcal{N}_{ϵ} satisfies the following inequality

$$\frac{d\mathcal{N}_{\epsilon}}{dt} \ge \frac{1}{K} \left(\alpha(\bar{v}_{\epsilon}) - 2\epsilon \|\psi\|_{\infty} - \alpha(t) \right) \mathcal{N}_{\epsilon}.$$

Thanks to (7.1) and (7.4), we have

$$\frac{d\mathcal{N}_{\epsilon}}{dt} \ge \frac{1}{K} \left(\frac{K\lambda_p}{4} - \alpha(t) \right) \mathcal{N}_{\epsilon}.$$

By reproducing the argumentation of the proof of Lemma 2.1 and by using Remark 2.2 we can check that

(7.16)
$$\mathcal{N}_{\epsilon}(t) \ge \min \left\{ 1, \frac{K\lambda_p}{4\kappa_1}, \frac{\mathcal{N}(0)}{2} \right\},\,$$

where κ_1 denotes the Lipschitz constant of the function α in the unit cube. Hence, by collecting (7.15) -(7.16) we achieve for all $\epsilon \leq \epsilon_1$ and all t > 0,

$$\beta(v_{\epsilon}(t)) \geq \frac{\bar{c}_1}{N} \min \left\{ 1, \frac{K\lambda_p}{4\kappa_1}, \frac{\sum_{j=1}^N v_i(0)}{2} \right\} =: \bar{c}_2.$$

Remark 7.3. Note that from the above argumentation, using the Logistic character of the equations, we can get that for all $\epsilon \le \epsilon_1$ and all initial data $v(0) \ge 0$, there exists t_0 so that for all $t \ge t_0$ we have

$$\frac{1}{2}\frac{\bar{c}_1}{N}\min\left\{1,\frac{K\lambda_p}{4\kappa_1}\right\} \leq \beta(v) \leq 2\sup\left\{\bar{C}_1R_\alpha,\bar{C}_1\left(\frac{7K\lambda_p}{4c_\alpha}\right)^{\frac{1}{k_\alpha}}\right\}.$$

Lastly, we obtain some uniform control on a continuous set of homeomorphisms

$$\widetilde{\Psi}_v(s) := \sum_{i=1}^N \Psi_i(sv) v_i^2$$

where $v \in U \subset \mathbb{R}^{N,+}$.

Namely, we show that

Lemma 7.4. Assume that r_i , (μ_{ij}) , Ψ_i satisfies (1.2), (1.3) and (1.6). Assume further that $\Psi_i(v) = \alpha(v) + \epsilon \psi_i(v)$ with $\alpha \in C^1_{loc}$ satisfying (1.2), (1.3) and $\psi_i \in C^1_{loc}$ uniformly bounded. Then there exists ϵ_2 and $\tau_0 > 0$ so that for for all $\epsilon \leq \epsilon_2$ and for all \bar{v}_{ϵ} stationary solution of (1.1) we have

$$\bar{c}_3 \le \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) \le \bar{C}_3 \le 2\bar{C}_3 \le \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1+\tau_0).$$

Moreover there exists ϵ_3 and k > 0 so that for all $\epsilon \le \epsilon_3$ we have for all \bar{v}_{ϵ} stationary solution of (1.1) and $t, s \in (0, 1 + \tau_0)$

$$|t-s| \le k|\widetilde{\Psi}_{\bar{v}_{\epsilon}}(t) - \widetilde{\Psi}_{\bar{v}_{\epsilon}}(s)|.$$

Proof:

Recall that from the proof of Lemma 7.2 for all $\epsilon \leq \epsilon_1$, for any stationary solution of (1.1) \bar{v}_{ϵ} , we have $\alpha(\bar{\omega}^-) \leq \alpha(\bar{v}_{\epsilon}) \leq \alpha(\bar{\omega}^+)$. So, for all $\epsilon \leq \epsilon_1$ and for all stationary solution of (1.1) we have

$$<\bar{v}_{\epsilon}, \bar{v}_{\epsilon}>(\alpha(\bar{\omega}^{-})-\sigma)\leq \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1)\leq (\alpha(\bar{\omega}^{+})+\sigma)<\bar{v}_{\epsilon}, \bar{v}_{\epsilon}>,$$

where $\sigma = \epsilon \|\psi\|_{\infty}$. Let us fix $\epsilon_2 := \min\{\epsilon_1, \frac{\lambda_p}{4K\|\psi\|_{\infty}}\}$. From (7.4) and Lemma 7.2 we get

$$\bar{c}_3 := \frac{\bar{c}_1^2 K \lambda_p}{2N} \le \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) \le \frac{3\bar{C}_1^2 K \lambda_p}{2} =: \bar{C}_3,$$

for all $\epsilon \le \epsilon_2$ and for any stationary solution of (1.1).

By using to the monotonicity of the map $\sigma \to \bar{\omega}^{\pm}$ and Lemma 7.2, we can choose ϵ_2 smaller if necessary to achieve for any $\epsilon \le \epsilon_2$ and any stationary solution \bar{v}_{ϵ} ,

$$s_0 \bar{\omega}_{\epsilon_1}^- \le s_0 \bar{v}_{\epsilon} \le s_0 \bar{\omega}_{\epsilon_1}^+$$
 for all $s_0 > 0$.

The latter inequalities imply that we have for all $\epsilon \leq \epsilon_2$ and for any stationary solution \bar{v}_{ϵ} ,

$$\widetilde{\Psi}_{\bar{v}_{\epsilon}}(s_0\bar{v}_{\epsilon}) \ge \alpha(s_0\bar{\omega}_{\epsilon_1}^-) - \frac{\lambda_p}{4K}.$$

Let us fix s_0 such that

$$\alpha(s_0\bar{\omega}_{\epsilon_1}^-) - \frac{\lambda_p}{4K} = 2\bar{C}_3.$$

This is always possible since α is monotone increasing and $\lim_{\mu\to\infty}\alpha(\mu\omega_{\epsilon_1}^-)=+\infty$. By construction, $s_0>1$, since $\widetilde{\Psi}_{\bar{v}_{\epsilon}}$ is monotone increasing and we have

$$\widetilde{\Psi}_{\bar{v}_{\epsilon}}(s_0) \geq 2\widetilde{\Psi}_{\bar{v}_{\epsilon}}(1).$$

Let us denote $\tau_0 := s_0 - 1$.

Now since for each i the function Ψ_i satisfies (1.2), (1.3) and that α and the ψ_i are $C^1_{loc}(\mathbb{R}^N)$, the function $\widetilde{\Psi}_{\bar{v}_{\epsilon}}(s) := \sum_{i=1}^N \Psi_i(s\bar{v}_{\epsilon})\bar{v}^2_{\epsilon,i}$ is $C^1_{loc}(\mathbb{R})$ and monotone increasing. Therefore, for any stationary solution of (1.1) \bar{v}_{ϵ} , the function $\widetilde{\Psi}_{\bar{v}_{\epsilon}}$ is a \mathbb{R}^+ homeomorphism.

Next, we check that for a fixed ϵ and a fixed stationary solution \bar{v}_{ϵ} , the homeomorphism $\tilde{\Psi}_{\bar{v}_{\epsilon}}$ is a C^1 diffeomorphism on $(0,1+\tau_0)\to \widetilde{\Psi}_{\bar{v}_{\epsilon}}((0,1+\tau_0))$. Thanks to the Inverse Function Theorem, to show that $\widetilde{\Psi}_{\bar{v}_{\epsilon}}$ is a local C^1 diffeomorphism it is sufficient to prove that for all $s\in(0,1+\tau_0)$, $\widetilde{\Psi}'_{\bar{v}_{\epsilon}}(s)\neq 0$. By a straightforward computation we have:

$$(\Psi_{\bar{v}_{\epsilon}})'(s) = <\nabla\alpha(s\bar{v}_{\epsilon}), \bar{v}_{\epsilon} > \mathcal{E}(\bar{v}) + \epsilon \sum_{i=1}^{N} <\nabla\psi_{i}(s\bar{v}_{\epsilon}), \bar{v} > \bar{v}_{\epsilon,i}^{2}.$$

For all $s \in (0, 1 + \tau_0)$, and for any stationary solution $\bar{v}_{\epsilon} \in Q_{(1+\tau_0)\bar{C}_1}(0)$ we have:

$$\begin{split} |\nabla \psi_i(s\bar{v}_\epsilon)| &\leq \sup_{v \in Q_{(1+\tau_0)\bar{C}_1}(0)} |\nabla \psi_i(v)| := \zeta_1, \\ \nabla \alpha(s\bar{v}_\epsilon) &\leq \sup_{v \in Q_{(1+\tau_0)\bar{C}_1}(0)} \nabla \alpha(v) := \zeta_2 > 0, \\ \nabla \alpha(s\bar{v}_\epsilon) &\geq \inf_{v \in Q_{(1+\tau_0)\bar{C}_1}(0)} \nabla \alpha(v) := \zeta_3 > 0. \end{split}$$

Therefore, by Lemma 7.2 we deduce that

$$(\Psi_{\bar{v}_{\epsilon}})'(s) \ge \frac{\bar{c}_1^3}{N} \zeta_3 - \epsilon \zeta_1 \bar{C}_1^3.$$

By choosing $\epsilon \leq \epsilon_3 := \min\left\{\epsilon_2, \frac{\bar{c}_1^3 \zeta_3}{2N\zeta_1 C_1^3}\right\}$, we get for all ϵ , $s \in (0, 1 + \tau_0)$ and for any stationary solution of (1.1) \bar{v}_{ϵ} ,

$$0 < \frac{\bar{c}_1^3 \zeta_3}{2N} \le \left(\Psi_{\bar{v}_{\epsilon}}\right)'(s) \le \bar{C}_1^3 \left(\zeta_2 + \frac{\zeta_3}{2N}\right).$$

From the latter *a priori* bounds, we see that for all $\epsilon \le \epsilon_3$, $s \in (0, 1 + \tau_0)$ and for any stationary solution of (1.1) \bar{v}_{ϵ} , we get the following *a priori* estimate

$$\frac{1}{\bar{C}_{1}^{3}\left(\zeta_{2}+\frac{\zeta_{3}}{2N}\right)}\leq\left(\widetilde{\Psi}_{\bar{v}_{\epsilon}}^{-1}\right)'\left[\widetilde{\Psi}_{\bar{v}_{\epsilon}}(s)\right]=\frac{1}{\left(\Psi_{\bar{v}_{\epsilon}}\right)'\left(s\right)}\leq\frac{2N}{\bar{c}_{1}^{2}\zeta_{3}}.$$

Hence, we deduce that for all $\epsilon \le \epsilon_3$, $s,t \in (0,1+\tau_0)$ and for any stationary solution of (1.1) \bar{v}_{ϵ} , we have

$$|s-t| \le k |\widetilde{\Psi}_{\bar{v}_{\epsilon}}(s) - \widetilde{\Psi}_{\bar{v}_{\epsilon}}(t)|,$$

with

$$k := \frac{2N}{\bar{c}_1^2 \zeta_3}.$$

7.2. Asymptotic Behaviour.

We are now in position to obtain the asymptotic behaviour of the solution $v_{\epsilon}(t)$ as t goes to $+\infty$ for $\epsilon \in [0, \epsilon^*]$, where ϵ^* is to be determined later on.

Let us fix $\epsilon \in [0, \epsilon_1]$ where ϵ_1 is obtained in Lemma 7.2 and let \bar{v}_{ϵ} be a stationary solution of (1.1). For simplicity we denote <,> the standard scalar product in \mathbb{R}^N .

As in the proof of Lemma 4.7, we start by observing that since $\bar{v}_{\epsilon} \neq 0$ we can write $v_{\epsilon}(t) := \lambda(t)\bar{v}_{\epsilon} + h(t)$ with for all $t, < h, \bar{v}_{\epsilon} >= 0$. In the sequel of this subsection, for more clarity in the presentation we drop the subscript ϵ on v and \bar{v} .

First, we note that from this decomposition we can derive the following equalities:

(7.17)
$$\lambda < \bar{v}, \bar{v} > = \sum_{i=1}^{N} v_i \bar{v}_i,$$

(7.18)
$$\frac{d\mathcal{E}(h)}{dt} = \frac{d\mathcal{E}(v)}{dt} - 2\lambda\lambda' < \bar{v}, \bar{v} > .$$

By Lemma 7.2 and (7.17), we can check that for all $\epsilon \le \epsilon_1$ and for all t > 0, we have

$$\frac{\bar{c}_2}{\bar{C}_1^2} \le \lambda(t) \le \frac{N\bar{C}_2}{\bar{c}_1^2}.$$

Similarly, by using (7.19), Lemma 7.2 and $\sum_{i=1}^N |h_i| \le \lambda(t) \sum_{i=1}^N \bar{v}_i + \sum_{i=1}^N v_i$, we deduce from $\mathcal{E}(v) = \mathcal{E}(h) + \lambda^2 \mathcal{E}(\bar{v})$ that

(7.20)
$$\mathcal{E}(h) \le \frac{N\bar{C}_2^2}{\bar{c}_1^2}(N+1),$$

(7.21)
$$\sum_{i=1}^{N} |h_i| \le \frac{N\bar{C}_2}{\bar{c}_1} \left(1 + \frac{\bar{C}_1}{\bar{c}_1} \right).$$

By (7.19),(7.20),(7.21), Lemma 7.2,and by using the Lipschitz regularity of Ψ_i and the Cauchy-Schwartz inequality we can check that for some constant C > 0 independent of ϵ and v

(7.22)
$$\sum_{i=1}^{N} |\Psi_i(\lambda(t)\bar{v}) - \Psi_i(v(t))| \bar{v}_i^2 \le C\sqrt{\mathcal{E}(h)},$$

(7.23)
$$\sum_{i=1}^{N} |(\psi_i(\bar{v}) - \psi_i(v))\bar{v}_i h_i| \le C\sqrt{\mathcal{E}(h)}.$$

Indeed by (7.19)–(7.21) and Lemma 7.2, $\lambda \bar{v}$ and h are uniformly bounded and we have

$$\sum_{i=1}^{N} |\psi_i(\bar{v}) - \psi_i(v)| |h_i| \bar{v}_i \le \sum_{i=1}^{N} \kappa_i \left(\sum_{j=1}^{N} |\bar{v}_j - v_j| \right) |h_i| \bar{v}_i,$$

where κ_i are the Lipschitz constant of ψ_i on the set $Q_{R_0}(0)$ with $R_0 := \frac{N\bar{C}_2\bar{C}_1}{\bar{c}_1^2}\left(1+2\frac{\bar{C}_1}{\bar{c}_1}\right)$. From the decomposition of v and by using the Cauchy-Schwartz inequality, we get

$$(7.24) \qquad \sum_{i=1}^{N} |(\psi_{i}(\bar{v}) - \psi_{i}(\lambda(t)\bar{v} + h))\bar{v}_{i}h_{i}| \leq \bar{\kappa} \left(|1 - \lambda(t)| \sum_{j=1}^{N} \bar{v}_{j} + \sum_{j=1}^{N} |h_{j}| \right) \sum_{i=1}^{N} |h_{i}|\bar{v}_{i}$$

$$\leq N\bar{\kappa} \sqrt{\mathcal{E}(h)\mathcal{E}(\bar{v})} \left[|1 - \lambda(t)| \sqrt{\mathcal{E}(\bar{v})} + \sqrt{\mathcal{E}(h)} \right],$$

where $\bar{\kappa} := \sup_{i \in \{1, \dots, N\}} \kappa_i$. Therefore, by (7.20) and Lemma 7.2, the inequality (7.23) holds true for some positive constant C independent of $\epsilon \le \epsilon_1$. A similar argumentation holds to get (7.22). Next, we show that

Lemma 7.5. There exists $\epsilon^* \leq \min\{\epsilon_0, \epsilon_1, \epsilon_3\}$, so that for all $\epsilon \leq \epsilon^*$, $\mathcal{E}(h_{\epsilon}(t)) \to 0$ as $t \to +\infty$.

Assume the lemma holds true, then we can conclude the proof of Theorem 1.4 by arguing as follows

By combining (7.17) and Lemma 3.2, we achieve

(7.26)
$$\lambda'(t) < \bar{v}, \bar{v} > = \frac{d}{dt} \sum_{i=1}^{N} v_i \bar{v}_i = \frac{1}{K} \sum_{i=1}^{N} \Gamma_i v_i \bar{v}_i.$$

Now by using $\mathcal{E}(h) \to 0$, we deduce that $h \to 0$ as $t \to \infty$ and from the latter equality we are reduced to analyse the ODE

$$\lambda'(t)\mathcal{E}(\bar{v}) = \frac{\lambda(t)}{K} \sum_{i=1}^{N} (\Psi_i(\bar{v}) - \Psi_i(\lambda(t)\bar{v}))\bar{v}_i^2 + o(1),$$

where

$$o(1) := \sum_{i=1}^{N} (\Psi_i(\lambda(t)\bar{v}) - \Psi_i(v))\bar{v}_i v_i,$$

which by (7.22) and (7.23) satisfies

(7.27)
$$|o(1)| \le \frac{C(1+\epsilon)}{K} \sqrt{\mathcal{E}(h)} \to 0 \quad \text{as} \quad t \to +\infty.$$

By Lemma 7.2, for all $\epsilon \leq \epsilon^* \leq \epsilon_1$ we have $\bar{c}_2 \leq \sum_{i=1}^N \bar{v}_i v_i \leq \bar{C}_2$ with \bar{c}_2 and \bar{C}_2 independent of ϵ . Therefore by (7.17) $\frac{\bar{c}_1}{\mathcal{E}(\bar{v})} \leq \lambda(t) \leq \frac{\bar{C}_2}{\mathcal{E}(\bar{v})}$ for all t > 0. Thus λ satisfies an ODE of the form

$$\lambda'(t) = \frac{\lambda(t)}{K\mathcal{E}(\bar{v})} (\theta - \widetilde{\Psi}(\lambda(t))) + \frac{\lambda(t)}{K\mathcal{E}(\bar{v})} o(1),$$

which can be rewritten

(7.28)
$$\lambda'(t) = \frac{\lambda(t)}{K\mathcal{E}(\bar{v})} (\theta + o(1) - \widetilde{\Psi}(\lambda(t))),$$

where $\theta:=\sum_{i=1}^N \Psi_i(\bar{v})\bar{v}_i^2$ and $\widetilde{\Psi}(s):=\sum_{i=1}^N \Psi_i(s\bar{v})\bar{v}_i^2$. By construction, $\widetilde{\Psi}\in C^1_{loc}(\mathbb{R})$ and is monotone increasing.

The above ODE is of logistic type with a perturbation $o(1) \to 0$ with a non negative initial datum. Therefore, by a standard argumentation, we see that $\lambda(t)$ converges to $\bar{\lambda} > 0$ where $\bar{\lambda}$ is the unique solution of $\widetilde{\Psi}(\bar{\lambda}) = \theta$. By construction, we have $\widetilde{\Psi}(1) = \theta$, so we deduce that $\bar{\lambda} = 1$. Hence, $\lambda(t) \to 1$ and we can conclude that v converges to \bar{v} .

Let us now turn our attention to the proof of the Lemma 7.5.

Proof of Lemma 7.5:

First, let us denote $\Gamma_i := \Psi_i(\bar{v}) - \Psi_i(v)$. Then, by combining (7.17), (7.18)and Lemma 3.2, we achieve

(7.29)
$$\lambda'(t) < \bar{v}, \bar{v} > = \frac{d}{dt} \sum_{i=1}^{N} v_i \bar{v}_i = \frac{1}{K} \sum_{i=1}^{N} \Gamma_i v_i \bar{v}_i$$

and

$$\begin{split} \frac{d\mathcal{E}(h)}{dt} &= -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2 + \frac{2}{K} \sum_{i=1}^{N} \Gamma_i h_i^2 + \frac{2\lambda}{K} \sum_{i=1}^{N} \Gamma_i h_i \bar{v}_i, \\ &= -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2 + \frac{2}{K} \sum_{i=1}^{N} \Gamma_i v_i h_i. \end{split}$$

Therefore using the definition of Ψ_i and with the notation $\gamma_i := \psi_i(\bar{v}) - \psi_i(v)$, we have

$$\frac{d\mathcal{E}(h)}{dt} = -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2 + \frac{2}{K} (\alpha(\bar{v}) - \alpha(v)) \mathcal{E}(h) + \frac{2\epsilon}{K} \sum_{i=1}^{N} \gamma_i h_i^2 + \frac{2\epsilon\lambda(t)}{K} \sum_{i=1}^{N} \gamma_i \bar{v}_i h_i,$$

which implies that

$$(7.30) \quad \frac{d\mathcal{E}(h)}{dt} \leq -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2 + \frac{2}{K} (\alpha(\bar{v}) + 2\epsilon \|\psi\|_{\infty} - \alpha(v)) \mathcal{E}(h)$$

$$+ \frac{2\epsilon \lambda(t)}{K} \sum_{i=1}^{N} \gamma_i \bar{v}_i h_i.$$

By (7.29), using the definition of Ψ_i we also have

$$\frac{d}{dt} \sum_{i=1}^{N} \bar{v}_i v_i = \frac{1}{K} (\alpha(\bar{v}) - \alpha(v)) \sum_{i=1}^{N} \bar{v}_i v_i + \frac{\epsilon}{K} \sum_{i=1}^{N} \gamma_i \bar{v}_i v_i,$$

$$\geq \frac{1}{K} (\alpha(\bar{v}) - 2\epsilon \|\psi\|_{\infty} - \alpha(v)) \sum_{i=1}^{N} \bar{v}_i v_i.$$

By Lemma 7.2, for all $\epsilon \leq \epsilon_1, \bar{c}_2 \leq \beta(v) = \sum_{i=1}^N \bar{v}_i v_i \leq \bar{C}_2$ with \bar{c}_2 and \bar{C}_2 independent of ϵ . So we

$$\frac{d}{dt}\log(\beta(v(t))) \ge \frac{1}{K}(\alpha(\bar{v}) - 2\epsilon \|\psi\|_{\infty} - \alpha(v)),$$

which combined with (7.30) leads to

$$\frac{d\mathcal{E}(h)}{dt} \le -\sum_{i,j=1}^{N} \mu_{ij} \bar{v}_i \bar{v}_j \left(\frac{h_j}{\bar{v}_j} - \frac{h_j}{\bar{v}_j}\right)^2 + \frac{d}{dt} \log(\beta^2(v(t))) \mathcal{E}(h) + \frac{8\epsilon \|\psi\|_{\infty}}{K} \mathcal{E}(h) + \frac{2\epsilon \lambda(t)}{K} \sum_{i=1}^{N} \gamma_i \bar{v}_i h_i.$$

By using the functional inequality, Lemma 5.3, and rearranging the terms in the above inequality

$$(7.31) \qquad \frac{d\mathcal{E}(h)}{dt} - \mathcal{E}(h)\frac{d}{dt}\log(\beta^2(v(t))) \le \left(-C_1(\bar{v}_{\epsilon}) + \frac{8\epsilon\|\psi\|_{\infty}}{K}\right)\mathcal{E}(h) + \frac{2\epsilon\lambda(t)}{K}\sum_{i=1}^N \gamma_i \bar{v}_i h_i,$$

where $C_1(\epsilon)$ is the second largest eigenvalue of some associated linear problem.

Now, we estimate the last term of the above inequality. Recall that by (7.25) we have

$$\sum_{i=1}^{N} |\gamma_i \bar{v}_i h_i| \le N \bar{\kappa} \sqrt{\mathcal{E}(h) \mathcal{E}(\bar{v})} \left[|1 - \lambda(t)| \sqrt{\mathcal{E}(\bar{v})} + \sqrt{\mathcal{E}(h)} \right].$$

By combining the above estimate and (7.31), we achieve

$$(7.32) \frac{d\mathcal{E}(h)}{dt} - \mathcal{E}(h)\frac{d}{dt}\log(\beta^2(v(t))) \le (-C_1(\bar{v}_{\epsilon}) + \epsilon C_5)\mathcal{E}(h) + \epsilon C_4|1 - \lambda(t)|\sqrt{\mathcal{E}(h)},$$

where
$$C_5:=\frac{2}{K}\left(4\|\psi\|_{\infty}+\frac{N^2\bar{\kappa}\bar{C}_2}{\bar{c}_1}\right)$$
 and $C_4:=\frac{2\bar{C}_2N\bar{\kappa}}{K}$.

Recall that $C_1(\bar{v})$ is an eigenvalue, therefore for ϵ small enough, say $\epsilon \leq \epsilon_4$, since $\bar{v} \in Q_{C\sqrt{\epsilon}}(\bar{\omega}^+)$ and $\bar{\omega}^+ \to \bar{\omega}$ as $\epsilon \to 0$ one has $C_1(\bar{v}) \geq \frac{C(\omega^+)}{2}$. With the latter estimate and by choosing $\epsilon \leq \min(\epsilon_1, \epsilon_4)$ smaller if necessary, we get

(7.33)
$$\frac{d\mathcal{E}(h)}{dt} - \mathcal{E}(h)\frac{d}{dt}\log(\beta^2(v(t))) \le -\frac{C_1(\bar{\omega}^+)}{4}\mathcal{E}(h) + \epsilon C_4|1 - \lambda(t)|\sqrt{\mathcal{E}(h)}.$$

The proof now will follow several steps:

Step One: Since by (7.19) we have $|1 - \lambda(t)| \leq \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right]$ for all t, we claim that

Claim 7.6. For all $\epsilon \leq \min(\epsilon_1, \epsilon_4)$, there exists t_0 so that for all $t \geq t_0$ we have

$$\sqrt{\mathcal{E}(h)} \le 2\epsilon \left(\frac{\bar{C}_2}{\bar{c}_2}\right) \frac{4C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right]}{C_1(\bar{\omega}^+)}$$

Indeed, by (7.17), and Lemma 7.2 we have

$$(7.34) \qquad \frac{d\mathcal{E}(h)}{dt} - \mathcal{E}(h)\frac{d}{dt}\log(\beta^2(v(t))) \le -\frac{C_1(\bar{\omega}^+)}{4}\mathcal{E}(h) + \epsilon C_4\left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right]\sqrt{\mathcal{E}(h)}$$

and we can check that there exists $t_0 > 0$ so that $\sqrt{\mathcal{E}(h(t_0))} \le 2 \frac{\epsilon^4 C_4 \left[1 + \frac{NC_2}{c_1^2}\right]}{C_1(\bar{\omega}^+)}$. If not, then for all t>0 $\sqrt{\mathcal{E}(h(t))}>2\frac{\epsilon^4C_4\left\lfloor1+\frac{NC_2}{\tilde{c}_1^2}\right\rfloor}{C_1(\bar{\omega}^+)}$ and by dividing (7.34) by $\sqrt{\mathcal{E}(h)}$ and rearranging the terms, we

$$(7.35) \qquad \sqrt{\mathcal{E}(h)} \frac{d}{dt} \log \left(\frac{\mathcal{E}(h)}{\beta^2(v(t))} \right) \leq -\frac{C_1(\bar{\omega}^+)}{4} \sqrt{\mathcal{E}(h)} + \epsilon C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2} \right] < -\epsilon C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2} \right].$$

Thus $F(t) := \log \left(\frac{\mathcal{E}(h)}{\beta^2(v(t))} \right)$ is a decreasing function which by Lemma 7.2, is bounded from below.

Moreover, we have for all t>0 $\sqrt{\mathcal{E}(h(t))}>2\frac{\epsilon^4C_4\left[1+\frac{NC_2}{\tilde{c}_1^2}\right]}{C_1(\bar{\omega}^+)}$. Therefore F converges as t tends to $+\infty$ and $\frac{dF}{dt}\to 0$. Thus for t large enough, we get the contradiction

$$-\frac{1}{2}\epsilon C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2} \right] \le \sqrt{\mathcal{E}(h)} \frac{d}{dt} \log \left(\frac{\mathcal{E}(h)}{\beta^2(v(t))} \right) \le \epsilon C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2} \right].$$

Let Σ be the set $\Sigma:=\left\{t>t_0|\sqrt{\mathcal{E}(h(t))}>2\frac{\epsilon^4C_4\left[1+\frac{N\bar{C}_2}{\bar{c}_1^2}\right]}{C_1(\bar{\omega}^+)}\right\}$. Assume that Σ is non empty

otherwise the claim is proved since $\frac{\bar{C}_2}{\bar{c}_2} > 1$. Let us denote $t^* := \inf \Sigma$. So at t^* we have $\sqrt{\mathcal{E}(h(t^*))} = 2\frac{\epsilon^4 C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right]}{C_1(\bar{\omega}^+)}$. Again, by dividing(7.34) by $\sqrt{\mathcal{E}(h)}$ and rearranging the terms, on the set Σ we have

$$(7.36) \sqrt{\mathcal{E}(h)} \frac{d}{dt} \log \left(\frac{\mathcal{E}(h)}{\beta^2(v(t))} \right) \le -\frac{C_1(\bar{\omega}^+)}{4} \sqrt{\mathcal{E}(h)} + \epsilon C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2} \right] \le 0.$$

Thus $\log\left(\frac{\mathcal{E}(h)}{\beta^2(v(t))}\right)$ is a decreasing function of t for all $t \in \Sigma$. By arguing on each connected component of Σ , we can check that for all $t \in \Sigma$

$$\sqrt{\mathcal{E}(h(t))} \le \frac{\beta(v(t))}{\bar{c}_2} \frac{\epsilon 4C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right]}{C_1(\bar{\omega}^+)}.$$

Therefore by using Lemma 7.2 for $t \ge t^*$ we have

$$\sqrt{\mathcal{E}(h)} \le 2\frac{\bar{C}_2}{\bar{c}_2} \frac{\epsilon 4C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right]}{C_1(\bar{\omega}^+)}.$$

Hence, since $\frac{\bar{C}_2}{\bar{c}_2} > 1$ we get for all $t \geq t_0$,

$$\sqrt{\mathcal{E}(h)} \leq 2 \frac{\bar{C}_2}{\bar{c}_2} \frac{\epsilon 4 C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right]}{C_1(\bar{\omega}^+)}.$$

Step Two: First, we define some constant quantities:

(7.37)
$$\delta_0 := 2 \frac{\bar{C}_2}{\bar{c}_2} \frac{4C_4 \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2} \right]}{C_1(\bar{\omega}^+)},$$

$$(7.38) d := \left[1 + \frac{N\bar{C}_2}{\bar{c}_1^2}\right],$$

(7.39)
$$\epsilon^* := \min \left\{ \epsilon_1, \epsilon_2, \epsilon_3, \epsilon_4, \frac{d}{4kC\delta_0}, \frac{\bar{c}_3}{4C\delta_0} \right\},$$

where the constants C, k are respectively defined in (7.22),(7.23) and in the Lemma 7.4. By the previous step, we have that for all $\epsilon \leq \epsilon^*$, all $t \geq t_0$

$$\sqrt{\mathcal{E}(h)} \le \epsilon \delta_0.$$

We claim that

Claim 7.7. For all $\epsilon \leq \epsilon^*$ there exists $t_{\epsilon\delta_0}$ such that for all $t \geq t_{\epsilon\delta_0}$

$$\sqrt{\mathcal{E}(h(t))} \leq \frac{\epsilon \delta_0}{2}.$$

Proof:

First, we can check that for $\epsilon \leq \epsilon^*$ there exists t^* so that for all $t \geq t^*$

$$|1 - \lambda(t)| \le 2kC\epsilon\delta_0.$$

Indeed, by (7.28) and (7.27), we have

(7.40)
$$\lambda'(t) = \frac{\lambda(t)}{K\mathcal{E}(\bar{v})} (\theta + o(1) - \widetilde{\Psi}(\lambda(t))),$$

with $o(1) \le C\epsilon \delta_0$ for $t \ge t_0$. Let $\lambda_{\pm C\epsilon \delta_0}$ be the solution of the ODE

(7.41)
$$\lambda'_{\pm C\epsilon\delta_0}(t) = \frac{\lambda_{\pm C\epsilon\delta_0}(t)}{K\mathcal{E}(\bar{v})} (\widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) \pm C\epsilon\delta_0 - \widetilde{\Psi}_{\bar{v}_{\epsilon}}(\lambda_{\pm C\epsilon\delta_0}(t))).$$

Since $\epsilon \leq \frac{\bar{c}_3}{4C\delta_0}$, for $t \geq t_0$ we have

$$\frac{3\bar{c}_3}{4} \le \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) \pm C\epsilon \delta_0 \le \frac{5\bar{C}_3}{4}.$$

Therefore $\lambda_{\pm C\epsilon\delta_0} \to \bar{\lambda}_{\pm C\epsilon\delta_0}$ where $\bar{\lambda}_{\pm C\epsilon\delta_0}$ are the unique positive solutions of $\widetilde{\Psi}_{\bar{v}_{\epsilon}}(\bar{\lambda}_{\pm C\epsilon\delta_0}) = \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) \pm C\epsilon\delta_0$.

Thanks to the strict monotonicity of $\widetilde{\Psi}_{\bar{v}_{\epsilon}}$, we also have

$$\bar{\lambda}_{-2C\epsilon\delta_0} < \bar{\lambda}_{-C\epsilon\delta_0} < \bar{\lambda}_{C\epsilon\delta_0} < \bar{\lambda}_{2C\epsilon\delta_0},$$

where $\bar{\lambda}_{\pm 2C\epsilon\delta_0}$ are the unique positive solutions of $\widetilde{\Psi}_{\bar{v}_{\epsilon}}(\bar{\lambda}_{\pm 2C\epsilon\delta_0}) = \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) \pm 2C\epsilon\delta_0$. Since $\epsilon \leq \epsilon^* \leq \frac{\bar{c}_3}{4C\delta_0}$, it follows that

$$\frac{\bar{c}_3}{2} \le \widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) \pm 2C\epsilon \delta_0 \le \frac{3\bar{C}_3}{2}$$

and therefore, by Lemma (7.4), we have

$$(7.42) 0 < \bar{\lambda}_{\pm 2C\epsilon\delta_0} < 1 + \tau_0.$$

Now, recall that for $t \ge t_0$, $\lambda(t)$ satisfies

$$\lambda'(t) \leq \frac{\lambda(t)}{K\mathcal{E}(\bar{v})} (\widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) + C\epsilon\delta_0 - \widetilde{\Psi}_{\bar{v}_{\epsilon}}(\lambda(t))),$$

$$\lambda'(t) \ge \frac{\lambda(t)}{K\mathcal{E}(\bar{v})} (\widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) - C\epsilon\delta_0 - \widetilde{\Psi}_{\bar{v}_{\epsilon}}(\lambda(t))).$$

Thus, by a standard argumentation, we can show that for $t \geq t^*$ we have

$$\bar{\lambda}_{-2C\epsilon\delta_0} \le \lambda(t) \le \bar{\lambda}_{+2C\epsilon\delta_0}.$$

Therefore, for $t > t^*$ we have

$$|1 - \lambda(t)| \le \sup\{|1 - \bar{\lambda}_{-2C\epsilon\delta_0}|, |1 - \lambda_{+2C\epsilon\delta_0}|\}.$$

By (7.42) and Lemma 7.4, since $\epsilon \leq \epsilon^* \leq \epsilon_3$, we deduce that for $t \geq t^*$,

$$|1-\lambda(t)| \leq k \sup\{|\widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) - \widetilde{\Psi}_{\bar{v}_{\epsilon}}(\bar{\lambda}_{-2C\epsilon\delta_0})|, |\widetilde{\Psi}_{\bar{v}_{\epsilon}}(1) - \widetilde{\Psi}_{\bar{v}_{\epsilon}}(\lambda_{+2C\epsilon\delta_0})|\} \leq 2kC\epsilon\delta_0.$$

From the latter estimate, by using (7.33), we see that for $t \ge t^*$

(7.43)
$$\frac{d\mathcal{E}(h)}{dt} - \mathcal{E}(h)\frac{d}{dt}\log(\beta^2(v(t))) \le -\frac{C_1(\bar{\omega}^+)}{4}\mathcal{E}(h) + 2\epsilon^2 C_4 kC\delta_0 \sqrt{\mathcal{E}(h)}.$$

By following the argumentation of Step one, we can show that there exists $t_{\epsilon\delta_0}$ such that for $t \ge t_{\epsilon\delta_0}$ we have

$$\sqrt{\mathcal{E}(h)} \le \frac{2kC\epsilon^2\delta_0^2}{d}.$$

Hence, we have for all $t \geq t_{\epsilon\delta_0}$

$$\sqrt{\mathcal{E}(h)} \le \frac{\epsilon \delta_0}{2},$$

since $\epsilon \delta_0 < \frac{d}{4kC}$.

Step Three: Since for all $t \geq t_{\epsilon \delta_0}$,

$$\sqrt{\mathcal{E}(h(t))} \leq \frac{\epsilon \delta_0}{2},$$

by arguing as in the proof of Claim 7.7, we show that for all $\epsilon \leq \epsilon^*$ there exists $t_{\epsilon \frac{\delta_0}{2}}$ so that for all $t \geq t_{\epsilon \frac{\delta_0}{2}}$

$$\sqrt{\mathcal{E}(h)} \le \frac{\epsilon \delta_0}{4}.$$

By reproducing inductively the above argumentation, for all $\epsilon \leq \epsilon^*$ we can construct a sequence $(t_n)_{n\in\mathbb{N}}$ so that for all $t\geq t_n$ we have

$$\sqrt{\mathcal{E}(h(t))} \le \frac{\epsilon \delta_0}{2^n}.$$

Hence, for all $\epsilon \leq \epsilon^*$ we deduce that

$$\lim_{t\to\infty} \mathcal{E}(h(t))\to 0.$$

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REFERENCES

- [1] E. Akin. The geometry of population genetics. In *The geometry of population genetics*, volume 31 of *Lectures Notes in Biomathematics*. Springer, 1979.
- [2] P. Auger, R. Bravo de la Parra, J.C. Poggiale, E. Sanchez, and L. Sanz. Aggregation methods in dynamical systems and applications in population and community dynamics. *Physics of Life Reviews*, 5(2):79 105, 2008.
- [3] G. Barles and B. Perthame. Dirac concentrations in lotka-volterra parabolic pdes. *Indiana Univ. Math. J.*, 57:3275–3302, 2008.
- [4] Peter W. Bates and Fengxin Chen. Structure of principal eigenvectors and genetic diversity. *Nonlinear Analysis: Theory, Methods & Applications*, 74(18):7285 7295, 2011.
- [5] R. Bürger. *The mathematical theory of selection, recombination, and mutation*. Wiley series in mathematical and computational biology. John Wiley, 2000.
- [6] R Bürger and J Hofbauer. Mutation load and mutation -selection -balance in quantitative genetic traits. *Journal of Mathematical Biology*, 32(3):193–218, 1994.
- [7] A Calsina and S Cuadrado. Stationary solutions of a selection mutation model: The pure mutation case. *Mathematical Models, Methods, in Applied Sciences*, 15(7):1091–1117, 2005.
- [8] A. Calsina and S. Cuadrado. Asymptotic stability of equilibria of selection-mutation equations. *Journal of Mathematical Biology*, 54(4):489–511, 2007.
- [9] A. Calsina, S. Cuadrado, L. Desvillettes, and G. Raoul. Asymptotics of steady states of a selection mutation equation for small mutation rate. *Mathematical Bioscience and Engineering*, preprint.
- [10] J.A. Canizo, J.A. Carrillo, and S. Cuadrado. Measure solutions for some models in population dynamics. preprint.
- [11] J. A. Carrillo, S. Cuadrado, and B. Perthame. Adaptive dynamics via hamilton-jacobi approach and entropy methods for a juvenile-adult model. *Mathematical Biosciences*, 205(1):137–161, JAN 2007.
- [12] N. Champagnat and PE. Jabin. The evolutionary limit for models of populations interacting competitively via several resources. *Journal of Differential Equations*, 251(1):176–195, 2011.
- [13] N. Champagnat, PE. Jabin, and G. Raoul. Convergence to equilibrium in competitive lotka-volterra and chemostat systems. *Comptes Rendus Mathematique*, 348(23-24):1267–1272, 2010.
- [14] J. Coville. Convergence to the equilibria on some mutation selection model. preprint, 2012.
- [15] J.F. Crow and M. Kimura. An introduction to population genetics theory. New-York, Harper and Row, 1970.
- [16] J. M. Cuevas, A. Moya, and S. F. Elena. Evolution of rna virus in spatially structured heterogeneous environments. *Journal of Evolutionary Biology*, 16(3):456–466, 2003.
- [17] Jose. Cuevas, Andres Moya, and Rafael Sanjuan. Following the very initial growth of biological rna viral clones. *Journal of General Virology*, 86(2):435–443, 2005.
- [18] L. Desvillettes, P.E. Jabin, S. Mischler, and G. Raoul. On selection dynamics for continuous structured populations. *Communication in Mathematical Sciences*, 6(3):729–747, 2008.
- [19] O; Diekmann, PE. Jabin, S. Mischler, and B. Perthame. The dynamics of adaptation: An illuminating example and a hamilton-jacobi approach. *Theoretical Population Biology*, 67(4):257 271, 2005.

- [20] Manfred Eigen, John McCaskill, and Peter Schuster. Molecular quasi-species. *The Journal of Physical Chemistry*, 92(24):6881–6891, 1988.
- [21] F. Fabre, C. Bruchou, A. Palloix, and B. Moury. Key determinants of resistance durability to plant viruses: Insights from a model linking within- and between-host dynamics. *Virus Research*, 141(2):140 149, 2009.
- [22] F. Fabre, J. Montarry, J. Coville, R. Senoussi, V. Simon, and B. Moury. Modelling the evolutionary dynamics of viruses within their hosts: A case study using high-throughput sequencing. *PLoS Pathog*, 8(4):e1002654, 2012.
- [23] Frederic Fabre, Elsa Rousseau, Ludovic Mailleret, and Benoit Moury. Durable strategies to deploy plant resistance in agricultural landscapes. *New Phytologist*, 193(4):1064–1075, 2012.
- [24] K. P. Hadeler. Stable polymorphisms in a selection model with mutation. SIAM Journal on Applied Mathematics, 41(1):pp. 1–7, 1981.
- [25] Stephen Hartley and Bryan Shorrocks. A general framework for the aggregation model of coexistence. *Journal of Animal Ecology*, 71(4):651–662, 2002.
- [26] M. W. Hirsch. Systems of differential equations which are competitive or cooperative: I. limit sets. SIAM Journal on Mathematical Analysis, 13(2):167–179, 1982.
- [27] M. W. Hirsch. Systems of differential equations that are competitive or cooperative ii: Convergence almost everywhere. SIAM Journal on Mathematical Analysis, 16(3):423–439, 1985.
- [28] M. W. Hirsch. Systems of differential equations which are competitive or cooperative: Iii. competitive species. Non-linearity, 1:51–71, 1988.
- [29] J. Hofbauer. The selection mutation equation. Journal of Mathematical Biology, 23:41-53, 1985.
- [30] J. Hofbauer, V. Hutson, and W. Jansen. Coexistence for systems governed by difference equations of lotka-volterra type. *Journal of Mathematical Biology*, 25:553–570, 1987.
- [31] PE. Jabin and G. Raoul. On selection dynamics for competitive interactions. *Journal of Mathematical Biology*, 63:493–517, 2011.
- [32] Guillaume Lafforgue, Josep Sardanyes, and Santiago F. Elena. Differences in accumulation and virulence determine the outcome of competition during tobacco etch virus coinfection. *PLoS ONE*, 6(3):e17917, 03 2011.
- [33] X.Z. Li, C.L. Tang, and Ji X.H. The criteria for globally stable equilibrium in n-dimensional lotka-volterra systems. *Journal of Mathematical Analysis and Applications*, 240(2):600 – 606, 1999.
- [34] M. Lloyd. Mean crowding. Journal of Animal Ecology, 36:1–30, 1967.
- [35] P. Michel, S. Mischler, and B. Perthame. General relative entropy inequality: an illustration on growth models. *J. Math. Pures Appl.* (9), 84(9):1235–1260, 2005.
- [36] Nicole Mideo, Samuel Alizon, and Troy Day. Linking within- and between-host dynamics in the evolutionary epidemiology of infectious diseases. Trends in Ecology and Evolution, 23(9):511 517, 2008.
- [37] R. Miralles, R. Ferrer, R. V. Sole, A. Moya, and S. F. Elena. Multiple infection dynamics has pronounced effects on the fitness of rna viruses. *Journal of Evolutionary Biology*, 14(4):654–662, 2001.
- [38] Maria E. Orive, Miles N. Stearns, John K. Kelly, Michael Barfield, Marilyn S. Smith, and Robert D. Holt. Viral infection in internally structured hosts. i. conditions for persistent infection. *Journal of Theoretical Biology*, 232(4):453 466, 2005.
- [39] B. Perthame. Transport equations in biology. In *Transport Equations in Biology*, volume 12 of *Frontiers in Mathematics*, pages 1–26. Birkhauser Basel, 2007.
- [40] G. Raoul. Long time evolution of populations under selection and vanishing mutations. *Acta Applicandae Mathematica*, 114, 2011.
- [41] G. Raoul. Local stability of evolutionary attractors for continuous structured populations. *Monatshefte fur Mathematik*, 165:117–144, 2012. 10.1007/s00605-011-0354-9.
- [42] R.T. Rockafellar. Convex Analysis. Princeton Mathematical Series. Princeton University Press, 1997.
- [43] Rafael Sanjuan, Miguel R. Nebot, Nicola Chirico, Louis M. Mansky, and Robert Belshaw. Viral mutation rates. *Journal of Virology*, 84(19):9733–9748, 2010.
- [44] R.V. Sole, R. Ferrer, I. Gonzalez-Garcia, J. Quer, and E. Domingo. Red queen dynamics, competition and critical points in a model of rna virus quasispecies. *Journal of Theoretical Biology*, 198(1):47 59, 1999.
- [45] Tsubasa Takahashi, Tomohiko Sugawara, Tsubasa Yamatsuta, Masamichi Isogai, Tomohide Natsuaki, and Nobuyuki Yoshikawa. Analysis of the spatial distribution of identical and two distinct virus populations differently labeled with cyan and yellow fluorescent proteins in coinfected plants. *Phytopathology*, 97(10):1200–1206, September 2007.
- [46] E. Zeidler. *Nonlinear functional analysis and its applications. I.* Springer-Verlag, New York, 1986. Fixed-point theorems, Translated from the German by Peter R. Wadsack.
- [47] Ying Zhu, Andrew Yongky, and John Yin. Growth of an rna virus in single cells reveals a broad fitness distribution. *Virology*, 385(1):39 46, 2009.
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