

THE PRINCIPAL FLOQUET BUNDLE AND THE DYNAMICS OF FAST DIFFUSING COMMUNITIES

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ABSTRACT. For $N \geq 2$, consider the system of N competing species which are ecologically identical and having distinct diffusion rates $\{D_i\}_{i=1}^N$, in an environment with the carrying capacity $m(x, t)$. For a generic class of $m(x, t)$ that varies with space and time, we show that there is a positive number D_* independent of N so that if $D_i \geq D_*$ for all $1 \leq i \leq N$, then the slowest diffusing species is able to competitively exclude the rest of the species. In the case when the environment is temporally constant or temporally periodic, our result provides some further evidence in the affirmative direction regarding the conjecture by Dockery et al. in 1998. The main tool is the theory of the principal Floquet bundle for linear parabolic equations.

1. INTRODUCTION

We consider the following Lotka-Volterra model for N competing species, all of which are subject to unbiased dispersal:

$$\begin{cases} \partial_t u_i(x, t) = D_i \Delta u_i(x, t) + u_i(x, t) \left[m(x, t) - \sum_{j=1}^N u_j(x, t) \right] & \text{for } x \in \Omega, t > 0, 1 \leq i \leq N, \\ \partial_\nu u_i(x, t) = 0 & \text{for } x \in \partial\Omega, t > 0, 1 \leq i \leq N, \\ u_i(x, 0) = u_{i,0}(x) & \text{for } x \in \Omega. \end{cases} \quad (1.1)$$

These N species are assumed to be identical except for their dispersal rates, denoted by D_i , $1 \leq i \leq N$. Without loss of generality, we may assume $0 < D_1 < \dots < D_N$. Here Ω is a bounded domain in \mathbb{R}^n with smooth boundary $\partial\Omega$ and outer unit normal vector ν , $\Delta = \sum_{j=1}^n \partial_{x_j x_j}$ is the Laplacian operator in \mathbb{R}^n , $\partial_\nu := \nu \cdot \nabla$ is the outer-normal derivative on $\partial\Omega$. The initial data $\{u_{i,0}\}_{i=1}^N$ are assumed to

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be continuous and componentwise non-negative. The assumptions on $m(x, t)$ will be specified later.

How are the dispersal strategies of organisms shaped by their ambient environment? In the seminal paper [17], Hastings formulated this question in terms of a system of two reaction-diffusion equations modeling the competition of two phenotypes of the same species which are identical except for their dispersal rates. Assuming the environment to be spatially heterogeneous but temporally constant, and that the two phenotypes disperse unconditionally, Hastings showed that the slower diffuser can invade the faster diffuser when rare but not vice versa. Subsequently, Dockery et al. [12] introduced the system (1.1) of N competing species. When $N = 2$, they proved that the slower diffuser always competitively exclude the faster diffuser, regardless of the initial data; see also [27] for similar results in patch models.

Theorem 1.1 ([12]). *Suppose $N = 2$ and $m = m(x)$ is nonnegative, nonconstant and independent of t . If $D_1 < D_2$, then every positive solution of (1.1) satisfies*

$$\lim_{t \rightarrow \infty} (u_1(\cdot, t), u_2(\cdot, t)) = (\Theta_{D_1}(\cdot), 0) \quad \text{uniformly in } x \in \Omega,$$

where for $D > 0$, Θ_D is the unique positive solution of

$$D\Delta\Theta + \Theta(m(x) - \Theta) = 0 \quad \text{in } \Omega, \quad \text{and} \quad \partial_\nu\Theta|_{\partial\Omega} = 0. \quad (1.2)$$

Moreover, it is conjectured that for nonconstant $m = m(x)$ and $N \geq 3$, the slower diffuser equilibrium $E_1 = (\Theta_{D_1}, 0, \dots, 0)$ likewise attracts all positive solutions of (1.1). See Subsection 1.2 for further discussion on the recent progress on this conjecture.

While the above results suggest that spatial heterogeneity selects against dispersal, the interaction between phenotypes becomes more subtle when there is a mixture of spatial and temporal heterogeneity [24, 47]. For instance, the conjecture that slower diffuser wins does not hold for time-periodic environment $m = m(x, t)$. In fact, it is proved by Hutson et al. [24] that when $m(x, t)$ is time-periodic, either the slower or faster diffuser may be selected, or there may be coexistence of phenotypes. See [3] for further progress in this regard.

The work of Hastings and Dockery et al. has stimulated substantial mathematical analysis of competition models involving two species. While early models on the evolution of dispersal focused on the evolution of fixed, unconditional dispersal [20, 24, 32, 34], more recent studies have investigated conditional dispersal [2, 6, 9, 10, 26, 28, 29]. An interesting application concerns the evolution of dispersal in stream populations, which are subject to an uni-directional drift [40]. It has been shown that in some circumstances, faster dispersal is sometimes selected for [35, 38]. See also [16, 30, 37].

Most of the existing results are restricted to the case when the number of species is equal to two. In this case, the theory of monotone dynamical systems [25, 31, 48] can be applied to determine the global dynamics of the competition system. Results for three or more competing species are mostly restricted to the

discussion of permanence or the existence of time-independent solutions [5, 8, 13, 14, 36, 41]. As such, the determination of long time dynamics remains an open and challenging problem.

1.1. Main Result. In this paper, we consider the dynamics of (1.1) for general environments $m(x, t) \in C^{\beta, \beta/2}(\bar{\Omega} \times [0, \infty))$ satisfying a generic condition

$$\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} |m(x, t) - \bar{m}(t)|^2 dx dt > 0, \quad (1.3)$$

where $\bar{m}(t) = \int_{\Omega} m(x, t) dx$. We fix the exponent $0 < \beta < 1$ throughout this paper. Condition (1.3) says that the environment is spatially heterogeneous, on an average sense in time.

On the one hand, condition (1.3) is obviously satisfied for any non-constant function $m(x)$ in $C^{\beta}(\bar{\Omega})$. On the other hand, such a condition is necessary, as it is demonstrated by McPeck and Holt [42] (and is rigorously proven in [24]) that diffusion rates are a selectively neutral trait in spatially homogeneous environments. Here $C^{\beta}(\bar{\Omega})$ and $C^{\beta, \beta/2}(\bar{\Omega} \times [0, \infty))$ are respectively the usual Hölder and parabolic Hölder spaces with exponent β (see, e.g. [33, Chap. IV.1]).

Our main result states that, among phenotypes performing unbiased dispersal, excessive dispersal is always selected against.

Theorem 1.2. *Given $m(x, t) \in C^{\beta, \beta/2}(\bar{\Omega} \times [0, \infty))$ satisfying (1.3), there exists $B_0 > 0$ such that for any $N \geq 1$ and diffusion rates*

$$D_N > D_{N-1} > \dots > D_1 \geq B_0, \quad (1.4)$$

every positive solution $(u_i)_{i=1}$ of (1.1) satisfies

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |u_i(\cdot, t)| = 0 \quad \text{for } 2 \leq i \leq N. \quad (1.5)$$

If, in addition, $\liminf_{t \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} m(x, t) dx dt > 0$ holds, then

$$\liminf_{t \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} u_1(x, t) dx dt > 0. \quad (1.6)$$

Remark 1.3. It is well known that excessive dispersal is selected against when dispersal is costly [15]. Here we demonstrate that spatial heterogeneity alone leads to selection against excessive dispersal for a wide range of environments.

If m is asymptotically periodic in time, or asymptotically autonomous, we obtain stronger convergence results.

Corollary 1.4. *Given $m(x, t) \in C^{\beta, \beta/2}(\bar{\Omega} \times [0, \infty))$. Suppose there is a T^* -periodic function $m^* \in C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})$ such that*

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |m(x, t) - m^*(x, t)| = 0$$

where m^* satisfies

$$\int_0^{T^*} \int_{\Omega} m^*(x, t) dx dt > 0, \quad \text{and} \quad \int_0^{T^*} \int_{\Omega} |m^*(x, t) - \overline{m^*}(t)|^2 dx dt > 0.$$

Then there exists $B_0 > 0$ such that for any $N \geq 1$ and diffusion rates $(D_i)_{i=1}^N$ satisfying (1.4), every positive solution $u = (u_1, \dots, u_N)$ of (1.1) satisfies

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |u_1(x, t) - \theta_{D_1}(x, t)| = 0 \quad (1.7)$$

and

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |u_i(x, t)| = 0 \quad \text{for } 2 \leq i \leq N, \quad (1.8)$$

where $\theta_{D_1}(x, t)$ is the unique T^* -periodic, positive solution of

$$\partial_t \theta = D_1 \Delta \theta + \theta(m^*(x, t) - \theta) \quad \text{in } \Omega \times \mathbb{R}, \quad \text{and} \quad \partial_\nu \theta|_{\partial\Omega \times \mathbb{R}} = 0. \quad (1.9)$$

Remark 1.5. Note that B_0 can be chosen independent of $N \geq 2$. When $N = 2$ and m is periodic in time, the above result is contained in [3] by the method of monotone dynamical systems.

Corollary 1.6. *Given $m(x, t) \in C^{\beta, \beta/2}(\bar{\Omega} \times [0, \infty))$. Suppose there is a nonconstant function $\tilde{m} \in C^\beta(\bar{\Omega})$ such that*

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |m(x, t) - \tilde{m}(x)| = 0 \quad \text{and} \quad \int_{\Omega} \tilde{m} dx > 0, \quad (1.10)$$

then there exists $B_0 > 0$ such that for any $N \geq 1$ and diffusion rates $(D_i)_{i=1}^N$ satisfying (1.4), every positive solution $u = (u_1, \dots, u_N)$ of (1.1) satisfies

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |u_1(x, t) - \Theta_{D_1}(x)| = 0 \quad (1.11)$$

and

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |u_i(x, t)| = 0 \quad \text{for } 2 \leq i \leq N, \quad (1.12)$$

where $\Theta_{D_1}(x)$ is the unique positive solution of (1.2) with $D = D_1$.

1.2. Temporally constant environments. In this subsection, we discuss our result in connection with a conjecture of Dockery et al. [12]. Suppose

$$m \in C^\beta(\bar{\Omega}) \text{ is non-constant, and } \int_{\Omega} m(x) \geq 0. \quad (1.13)$$

If $0 < D_1 < D_2 < \dots < D_N$, then it follows from [12, Theorem 3.2] that the system (1.1) has exactly $N + 1$ equilibria, which are given by

$$E_i = (0, \dots, 0, \Theta_{D_i}, 0, \dots, 0) \quad \text{for } 1 \leq i \leq N, \quad \text{and} \quad E_0 = (0, \dots, 0),$$

where for $D > 0$ the function $\Theta_D(x)$ denotes the unique positive solution of (1.2). In case $N = 2$, Dockery et al. obtained a complete description of the dynamics of (1.1) by applying the abstract tools of monotone dynamical systems.

Theorem 1.7 ([12, Lemmas 3.9 and 4.1]). *Suppose $N = 2$, and let $0 < D_1 < D_2$ be given. Let (u_1, u_2) be a nonnegative and nontrivial solution of (1.1), then*

$$\lim_{t \rightarrow \infty} (u_1, u_2) = E_{i_0} \quad \text{uniformly in } \Omega,$$

where $i_0 = 1$ or 2 is the least number i such that $u_i(x, 0) \not\equiv 0$.

When $N \geq 3$, it is conjectured in [12] that the slowest diffuser continues to win the competition.

Conjecture 1. *Let $N \geq 2$, $D_1 < \dots < D_N$ be given. Let $u = (u_1, \dots, u_N)$ be a nonnegative and nontrivial solution of (1.1), then $u \rightarrow E_{i_0}$ uniformly in Ω as $t \rightarrow \infty$, where $i_0 \in \{1, \dots, N\}$ is the minimal number i such that $u_i(x, 0) \not\equiv 0$.*

Define \mathcal{D} to be the collection of all finite subsets of \mathbb{R}_+ sets of positive real numbers such that Conjecture 1 holds; i.e.

$$\mathcal{D} = \cup_{N=1}^{\infty} \{(D_i)_{i=1}^N : 0 < D_1 < \dots < D_N \text{ and Conjecture 1 holds}\}.$$

By the result of Dockery et al., the family \mathcal{D} contains all singleton and doubleton sets of positive numbers. Can we say more about \mathcal{D} ?

The following stability result is contained in [7], which provides a step towards an affirmative answer to Conjecture 1.

Theorem 1.8 ([7, Theorem 1.4]). *The collection \mathcal{D} is open in the space of finite sets relative to the Hausdorff metric.*

We recall that the Hausdorff metric is given by

$$\text{dist}_H(A, B) = \max \left\{ \sup_{x \in A} \inf_{y \in B} |x - y|, \sup_{y \in B} \inf_{x \in A} |x - y| \right\}$$

for any two non-empty subsets A, B of \mathbb{R} . In particular, the collection of finite subsets of \mathbb{R}_+ forms a metric space under the Hausdorff metric.

Corollary 1.6 implies that Conjecture 1 holds for all finite sets of diffusion rates that is bounded from below by a sufficiently large constant.

Theorem 1.9. *Given $m \in C^\beta(\overline{\Omega})$ which is non-constant and $\int_{\Omega} m \, dx > 0$, there exists B_0 such that for any $N \in \mathbb{N}$ and diffusion rate $(D_i)_{i=1}^N$ such that (1.4) holds, the equilibrium E_1 attracts all positive solutions of (1.1). Furthermore, the collection \mathcal{D} contains all finite subsets of \mathbb{R}_+ which is bounded from below by B_0 , i.e.*

$$\mathcal{D} \supseteq \bigcup_{N=2}^{\infty} \{(D_i)_{i=1}^N : B_0 \leq D_1 < \dots < D_N\}.$$

Proof. In this case, $m = m(x)$ satisfies the hypotheses of Corollary 1.6. Given $N \geq 3$, $0 < D_1 < \cdots < D_N$ and a nonnegative, nontrivial solution u of (1.1), we can assume without loss that $u_i(x, 0) \not\equiv 0$ for all i . Furthermore, by strong maximum principle, we may perform a translation in time and further assume that $u_i(x, 0) > 0$ in $\bar{\Omega}$ for all i . We can then conclude that $u \rightarrow E_1$ as $t \rightarrow \infty$, by Corollary 1.6. \square

Remark 1.10. A closely related theorem was obtained in [41], where it is proved that if all species are fast diffusing, and if the carrying capacity of the i -th species is equal to $m_i(x)$ such that $\int_{\Omega} m_i dx$ is strictly decreasing in i , then the first species (the one with the highest total carrying capacity) excludes the other species. To study the evolution of dispersal, we are interested in the case when carrying capacity $m(x)$ is the same for all species, and our analysis requires a higher order expansion of the principal Floquet bundle, which we introduce in Section 2.

1.3. Organization of the paper. In Section 2, we will recall the existence and uniqueness of principal Floquet bundle, and its adjoint bundle. Using the principal Floquet bundle and its smooth dependence on coefficients, which is established recently in [7], we will derive some quantitative estimates of the asymptotic behavior of the principal Floquet bundle for large diffusion rate. A key conclusion says that the growth of the principal bundle is strictly increasing in diffusion rate, on an average sense. In Section 3, we establish some *a priori* estimates of solution $(u_i)_{i=1}^N$ of (1.1), which is independent of the largeness of N . In Section 4, we prove the main result, namely, Theorem 1.2. In Section 5, we prove Corollaries 1.4 and 1.6.

2. THE PRINCIPAL FLOQUET BUNDLE

Let Ω be a bounded domain in \mathbb{R}^n with smooth boundary $\partial\Omega$ and outward unit normal vector $\nu(x)$. Consider the linear elliptic operator of divergence form (repeated indices are summed from 1 to n):

$$\mathcal{L}\varphi := -\partial_{x_i}(a_{ij}(x)\partial_{x_j}\varphi) \quad \text{for } x \in \Omega, \quad (2.1)$$

endowed with the no-flux boundary operator:

$$\mathcal{B}\varphi := \nu_i(x)a_{ij}(x)\partial_{x_j}\varphi \quad \text{for } x \in \partial\Omega, \quad (2.2)$$

where $a(x) = (a_{ij}(x))_{i,j=1}^n \in C^{1+\beta}(\overline{\Omega}; \mathbb{R}^{n^2})$ for some $0 < \beta < 1$ is symmetric and satisfies, for some $\Lambda > 1$

$$\frac{1}{\Lambda}|\xi|^2 \leq a_{ij}(x)\xi_i\xi_j \leq \Lambda|\xi|^2 \quad \text{for } x \in \Omega, \xi \in \mathbb{R}^n. \quad (2.3)$$

Definition 2.1. For $D > 0$, $a_{ij} \in C^{1+\beta}(\overline{\Omega})$ satisfying (2.3), and $c(x, t) \in C^{\beta, \beta/2}(\overline{\Omega} \times \mathbb{R})$, we say that $(\varphi, H(t))$ is the *principal Floquet bundle* corresponding to (D, a_{ij}, c) if they satisfy

$$\begin{cases} \partial_t\varphi + D\mathcal{L}\varphi = c(x, t)\varphi + H(t)\varphi & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B}\varphi = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \varphi > 0 & \text{in } \overline{\Omega} \times \mathbb{R}, \\ \int_{\Omega} \varphi(x, t) dx = 1 & \text{for all } t \in \mathbb{R}. \end{cases} \quad (2.4)$$

We say that $\psi(x, t)$ is the *adjoint bundle* if it satisfies

$$\begin{cases} -\partial_t\psi + D\mathcal{L}\psi = c(x, t)\psi + H(t)\varphi & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B}\psi = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \psi > 0 & \text{in } \overline{\Omega} \times \mathbb{R}, \\ \int_{\Omega} \varphi(x, 0)\psi(x, 0) dx = 1. \end{cases} \quad (2.5)$$

For linear parabolic equations in one space dimension, the existence and uniqueness of Floquet bundles, as characterized by the nodal properties of solutions as in the classical Sturm–Liouville theory, was obtained by Chow et al. [11]. Subsequently, Mierczyński [43] generalized the existence and uniqueness of the principal Floquet bundle when the spatial dimension is greater than one, by invoking the general exponential separation results due to Poláčik and Tereščák [46]. Later on, Huska and collaborators [21, 22, 23] significantly weakened the smoothness assumptions on coefficients, and proved continuous dependence of the principal Floquet bundle on coefficients of the linear problem. More recently, the smooth dependence on coefficients was obtained in [7]. The notion of principal Floquet bundle generalizes the principal eigenvalue and eigenfunctions of uniformly elliptic, or periodic-parabolic operators.

By a rescaling, we will assume without loss of generality that $|\Omega| = 1$ throughout this paper. Since the choices of Ω, a_{ij} are fixed throughout this paper, we

sometimes suppress the dependence of various constants on Ω and a_{ij} . For any function $c(x, t)$, set $\bar{c}(t) := \int_{\Omega} c(x, t) dx$, i.e. the spatial average of c at time t .

Theorem 2.2. *Given $(D, a_{ij}, c) \in \mathbb{R}_+ \times C^{1+\beta}(\bar{\Omega}) \times C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})$, there is a unique triplet $(\varphi(x, t), \psi(x, t), H(t))$ satisfying (2.4)-(2.5). Moreover, the mapping*

$$\begin{aligned} \mathbb{R}_+ \times [C^{1+\beta}(\bar{\Omega})]^{n \times n} \times C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R}) &\rightarrow [C^{2+\beta, 1+\beta/2}(\bar{\Omega} \times \mathbb{R})]^2 \times C^{\beta/2}(\mathbb{R}) \\ (D, a_{ij}, c) &\mapsto (\varphi, \psi, H) \end{aligned}$$

is smooth. Furthermore,

- (a) $\sup_{\Omega \times \mathbb{R}} |H(t)| \leq \sup_{\Omega \times \mathbb{R}} |c(x, t)|$.
- (b) Let (a_{ij}) be fixed. For each $M > 0$, there exists $C_h = C_h(M)$ such that for any $D \geq 1$ and $c(x, t)$ satisfying $\sup_{\Omega \times \mathbb{R}} |c(x, t) - \bar{c}(t)| \leq M$, we have

$$\frac{1}{C_h} \leq \varphi(x, t) \leq C_h \quad \text{and} \quad \frac{1}{C_h} \leq \psi(x, t) \leq C_h \quad \text{in } \bar{\Omega} \times \mathbb{R}. \quad (2.6)$$

Proof. By replacing $c(x, t)$ by $c(x, t) - \bar{c}(t)$ and $H(t)$ by $H(t) + \bar{c}(t)$, we may assume, without loss of generality, that $\bar{c}(t) \equiv 0$. We first prove the statements concerning the principal bundle (φ, H) , and then move on to prove properties of the adjoint bundle ψ . Let $\tilde{\varphi}$ be the unique positive solution to

$$\begin{cases} \partial_t \tilde{\varphi} - D\mathcal{L}\tilde{\varphi} = c(x, t)\tilde{\varphi} & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B}\tilde{\varphi} = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \int_{\Omega} \tilde{\varphi}(x, 0) dx = 1. \end{cases} \quad (2.7)$$

The existence and uniqueness of $\tilde{\varphi}(x, t)$ are proved in [43, Theorem 2.1(iii) and Corollary 2.4] using a general framework in [46]. By the standard parabolic regularity theory, we observe that $\tilde{\varphi} \in C_{loc}^{2+\beta, 1+\beta/2}(\bar{\Omega} \times \mathbb{R})$. Now, letting

$$H(t) = -\frac{d}{dt} [\log \|\tilde{\varphi}\|_{L^1(\Omega)}] = -\frac{\int_{\Omega} \partial_t \tilde{\varphi} dx}{\int_{\Omega} \tilde{\varphi} dx}$$

and $\varphi(x, t) = \tilde{\varphi}(x, t) \exp\left(\int_0^t H(s) ds\right)$, it follows that $(\varphi(x, t), H(t))$ satisfies (2.4), including the normalization $\int_{\Omega} \varphi(x, t) dx \equiv 1$ for all $t \in \mathbb{R}$. By verifying that $H(t)$ is (globally) bounded in $C^{\beta/2}(\mathbb{R})$, we can use standard Schauder's estimates to show that φ is also globally bounded in $C^{2+\beta, 1+\beta/2}(\bar{\Omega} \times \mathbb{R})$. We omit the details and refer the readers to [7, Proof of Theorem A.1]. The smooth dependence of $(\varphi(x, t), H(t))$ on coefficients is established in [7, Proposition A.3] in a slightly more general setting.

Next, integrate the first equation of (2.4) over $x \in \Omega$ and use the no-flux boundary condition we get

$$\frac{d}{dt} \int_{\Omega} \varphi dx = \int_{\Omega} c\varphi dx + H(t) \int_{\Omega} \varphi dx.$$

Using the fact that $\int_{\Omega} \varphi \, dx \equiv 1$ for all $t \in \mathbb{R}$, we deduce $H(t) = -\int_{\Omega} c\varphi \, dx$, from which (a) follows:

$$|H(t)| \leq \int_{\Omega} |c(x, t)| \varphi(x, t) \, dx \leq \left[\sup_{\Omega} |c(\cdot, t)| \right] \int_{\Omega} \varphi(x, t) \, dx = \sup_{\Omega} |c(\cdot, t)|.$$

To prove (b), we define $\hat{\varphi}(x, \tau) = \varphi(x, \tau/D)$, then $\hat{\varphi}$ satisfies the no-flux boundary condition $\mathcal{B}\hat{\varphi} = 0$ on $\partial\Omega$ and

$$\partial_{\tau}\hat{\varphi} - \mathcal{L}\varphi = \hat{c}(x, \tau)\varphi \quad \text{in } \Omega \times \mathbb{R},$$

where $\hat{c}(x, \tau) = [c(x, \tau/D) + H(\tau/D)]/D$ satisfies

$$\|\hat{c}\|_{L^{\infty}(\Omega \times \mathbb{R})} \leq 2\|c\|_{L^{\infty}(\Omega \times \mathbb{R})}/D \leq 2M,$$

where we used (a) and $D \geq 1$. Then $\hat{\varphi}$ satisfies the uniform Harnack inequality [22, Theorem 2.5], i.e. there exists $C_M > 1$ (hereafter C_M represents a generic constant that depends only on M) such that $\sup_{\Omega} \hat{\varphi}(\cdot, \tau) \leq C_M \inf_{\Omega} \hat{\varphi}(\cdot, \tau)$ for all $\tau \in \mathbb{R}$, which is the same as

$$\varphi(x, t) \leq C_M \varphi(y, t) \quad \text{for all } x, y \in \Omega, \, t \in \mathbb{R}. \quad (2.8)$$

Using $|\Omega| = 1$ and $\int_{\Omega} \varphi \, dx \equiv 1$ for $t \in \mathbb{R}$, we can integrate the above inequality in x or in y to deduce

$$\frac{1}{C_M} \leq \varphi(x, t) \leq C_M \quad \text{for all } (x, t) \in \Omega \times \mathbb{R}. \quad (2.9)$$

Having defined $\varphi(x, t)$ and $H(t)$, we observe that $\tilde{\psi}(x, t) = \psi(x, -t)e^{\int_{-t}^0 H(\tau) \, d\tau}$ is the positive solution corresponding to (2.7) with $c(x, t)$ replaced by $\tilde{c}(x, t) := c(x, -t)$. So that by previous arguments $\tilde{\psi}$ (and hence ψ) exists in $C_{loc}^{2+\beta, 1+\beta/2}(\overline{\Omega} \times \mathbb{R})$ and is uniquely determined by $\int_{\Omega} \varphi(x, 0)\tilde{\psi}(x, 0) \, dx = 1$.

To show that ψ is (globally) bounded in $C^{2+\beta, 1+\beta/2}(\overline{\Omega} \times \mathbb{R})$, we observe that $\int_{\Omega} \varphi\psi \, dx \equiv 1$ for all t . Indeed, by direct calculation,

$$\begin{aligned} \frac{d}{dt} \int_{\Omega} \varphi\psi \, dx &= \int_{\Omega} (\varphi\partial_t\psi + \psi\partial_t\varphi) \, dx \\ &= - \int_{\Omega} \varphi(D\mathcal{L}\psi + (h+H)\psi) \, dx + \int_{\Omega} \psi(D\mathcal{L}\varphi + (h+H)\varphi) \, dx. \end{aligned}$$

Using the no-flux boundary conditions $\mathcal{B}\varphi = 0 = \mathcal{B}\psi$, we can integrate by parts and deduce that the last expression is zero. By (2.9) and $\int_{\Omega} \varphi\psi \, dx \equiv 1$, we have

$$\frac{1}{C_M} \leq \int_{\Omega} \psi(x, t) \, dx \leq C_M \quad \text{for all } (x, t) \in \Omega \times \mathbb{R}.$$

Now, note that ψ also satisfies the Harnack inequality (2.8) with the same constant C_M , we deduce the uniform upper and lower bounds for $\psi(x, t)$. This and (2.9) completes the proof of (b).

Having proved that ψ is (globally) bounded in $C^0(\overline{\Omega} \times \mathbb{R})$, we can apply the standard parabolic estimate to deduce that ψ is (globally in time) bounded in

$C^{2+\beta,1+\beta/2}(\overline{\Omega} \times \mathbb{R})$. Finally, the smooth dependence of ψ on coefficients can be established similar as φ and we omit the details. \square

Next, we fix our choice of a_{ij} , c and consider the dependence on diffusion rate D of the corresponding principal bundle and its adjoint (φ_D, ψ_D, H_D) . We will analyze asymptotic behavior of (φ_D, ψ_D, H_D) as $D \rightarrow \infty$. Recall also that (φ_D, H_D) is differentiable in D . Denote by $(\varphi'_D, H'_D) \in C^{2+\beta,1+\beta/2}(\overline{\Omega} \times \mathbb{R}) \times C^{\beta/2}(\mathbb{R})$ their Fréchet derivatives with respect to D .

Definition 2.3. Given $\mathcal{L} = -\partial_{x_i}(a_{ij}\partial_{x_j})$ as in (2.1).

- (1) We define the inner-product in $H^1(\Omega)$ induced by (a_{ij}) as follows:

$$\langle p, q \rangle_a := \int_{\Omega} a_{ij} \partial_{x_i} p \partial_{x_j} q \, dx.$$

- (2) We regard \mathcal{L} as a sectorial operator in $X = L^2(\Omega)$ with domain

$$\text{Dom}(\mathcal{L}) = \{u_0 \in W^{2,2}(\Omega) : \mathcal{B}u_0|_{\partial\Omega} = 0\}.$$

- (3) Let $e^{-t\mathcal{L}} : X \rightarrow X$ be the analytic semigroup generated by \mathcal{L} , i.e. $e^{-t\mathcal{L}}[\phi_0] = \phi(\cdot, t)$, where $\phi(x, t)$ is the unique solution to

$$\begin{cases} \phi_t + \mathcal{L}\phi = 0 & \text{in } \Omega \times (0, \infty), \\ \mathcal{B}\phi = 0 & \text{on } \partial\Omega \times (0, \infty), \\ \phi(x, 0) = \phi_0(x) & \text{in } \Omega. \end{cases}$$

- (4) For given $h \in L^\infty(\mathbb{R}; L^2(\Omega))$, we define the quantities $\Gamma_h(x, t)$, $\Psi_D[h](x, t)$ and $\hat{\Psi}_D[h](x, t)$ as follows:

$$\Gamma_h(\cdot, t) = \int_0^\infty e^{-\tau\mathcal{L}}[h(\cdot, t) - \bar{h}(t)] \, d\tau \quad \text{for } t \in \mathbb{R}, \quad (2.10)$$

$$\Psi_D[h](\cdot, t) = D \int_{-\infty}^t e^{-D(t-s)\mathcal{L}}[h(\cdot, s) - \bar{h}(s)] \, ds \quad \text{for } t \in \mathbb{R}, \quad (2.11)$$

$$\hat{\Psi}_D[h](\cdot, t) = D \int_t^\infty e^{-D(s-t)\mathcal{L}}[h(\cdot, s) - \bar{h}(s)] \, ds \quad \text{for } t \in \mathbb{R}. \quad (2.12)$$

Remark 2.4. Let

$$X_2 = \left\{ u_0 \in L^2(\Omega) : \int_{\Omega} u_0 = 0 \right\},$$

then the quantities Γ_h , $\Psi_D[h]$ and $\hat{\Psi}_D[h]$ are well-defined functions in $L^\infty(\mathbb{R}; X_2 \cap H^1(\Omega))$ thanks to the fact that $e^{-t\mathcal{L}} : X_2 \rightarrow X_2$ is well-defined, and that there exists positive constants C_1, ν such that the following semigroup estimates

$$\|e^{-t\mathcal{L}}u_0\|_{L^2(\Omega)} \leq C_1 e^{-\nu t} \|u_0\|_{L^2(\Omega)} \quad \text{and} \quad \|e^{-t\mathcal{L}}u_0\|_{H^1(\Omega)} \leq \frac{C_1}{\sqrt{t}} e^{-\nu t} \|u_0\|_{L^2(\Omega)}$$

hold for all $t > 0$ and $u_0 \in X_2$. See (A.2) and (A.3). Further properties of Ψ_D and $\hat{\Psi}_D$ are proved in Appendix A.

Proposition 2.5. *There exist positive constants $C_1^* = C_1^*(M)$ and $\underline{D}_1 = \underline{D}_1(M)$ such that for arbitrary $c(x, t) \in C^{\beta, \beta/2}(\bar{\Omega})$ such that $\|c - \bar{c}\|_{C^0(\bar{\Omega} \times \mathbb{R})} \leq M$, the corresponding principal Floquet bundle (φ_D, ψ_D, H_D) has the following asymptotic behavior for all $D \geq \underline{D}_1$:*

$$\sup_{t \in \mathbb{R}} |H_D(t) + \bar{c}(t)| \leq \frac{C_1^*}{D}, \quad (2.13)$$

and

$$\limsup_{T \rightarrow \infty} \left| \frac{1}{T} \int_0^T H'_D(t) dt - \frac{1}{D^2} \cdot \frac{1}{T} \int_0^T \langle \Psi_D[c], \hat{\Psi}_D[c] \rangle_a dt \right| \leq \frac{C_1^*}{D^3}, \quad (2.14)$$

where the integral operators $\Psi_D, \hat{\Psi}_D$ are given in (2.11)-(2.12).

The operators $\Psi_D, \hat{\Psi}_D$ are difficult to compute as they are nonlocal in time. For the purpose of applications, one needs to impose further regularity on the potential function $c(x, t)$ to determine the first order asymptotic behavior of the principal bundle, as the following result illustrates.

Theorem 2.6. *Given any $M > 0$, there exist $C_2^* = C_2^*(M)$ and $\underline{D}_2 = \underline{D}_2(M)$ such that if $c(x, t) \in C^{\beta, \beta/2}(\bar{\Omega})$ can be written as $c(x, t) = m(x, t) + U(x, t)$ for some m, U satisfying*

$$\|m - \bar{m}\|_{C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})} + \|U - \bar{U}\|_{L^\infty(\Omega \times \mathbb{R})} \leq M, \quad (2.15)$$

(recall that $\bar{m}(t) = \int_\Omega m(x, t) dx$ and $\bar{U}(t) = \int_\Omega U(x, t) dx$), then the corresponding principal Floquet bundle (φ_D, ψ_D, H_D) has the following asymptotic behavior in $D \gg 1$:

$$\begin{aligned} \limsup_{T \rightarrow \infty} & \left| \frac{1}{T} \int_0^T (H_D(t) - H_{D^*}(t)) dt + \left(\frac{1}{D} - \frac{1}{D^*} \right) \frac{1}{T} \int_0^T \langle \Gamma_m(\cdot, t), \Gamma_m(\cdot, t) \rangle_a dt \right| \\ & \leq C_2^* \left| \frac{1}{D} - \frac{1}{D^*} \right| \left[\frac{\|m - \bar{m}\|_{C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})}}{D^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U(\cdot, t) - \bar{U}(t)\|_{L^2(\Omega)} + \frac{1}{D} \right] \end{aligned} \quad (2.16)$$

holds for $D^* > D \geq \underline{D}_2$, where $\Gamma_m(x, t)$ is given by (A.1). Furthermore,

$$\begin{aligned} \limsup_{T \rightarrow \infty} & \left| \frac{1}{T} \int_0^T H_D(t) dt + \frac{1}{T} \int_0^T \bar{c}(t) dt + \frac{1}{D} \frac{1}{T} \int_0^T \langle \Gamma_m(\cdot, t), \Gamma_m(\cdot, t) \rangle_a dt \right| \\ & \leq \frac{C_2^*}{D} \left[\frac{\|m - \bar{m}\|_{C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})}}{D^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U(\cdot, t) - \bar{U}(t)\|_{L^2(\Omega)} + \frac{1}{D} \right] \end{aligned} \quad (2.17)$$

holds for $D \geq \underline{D}_2$.

By (2.16), we observe that $H_D(t)$ is monotone increasing in large diffusion rates $D \gg 1$, on an average sense in time; see (2.18) below. This generalizes the

well known monotonicity property of self-adjoint elliptic operators with respect to diffusion rate; see [1]. On the other hand, the monotonicity cannot be improved to all positive diffusion rate. In fact, when $c(x, t)$ is \tilde{T} -periodic in time, then $\frac{1}{\tilde{T}} \int_t^{t+\tilde{T}} H_D(s) ds$ is independent of t and is given by the principal eigenvalue μ_D of certain periodic-parabolic eigenvalue problem. It is proved in [3, 24] that μ_D is not increasing in D for certain time-periodic $m(x, t)$.

Corollary 2.7. *Suppose $c(x, t) = m(x, t) + U(x, t)$ for some m, U such that (2.15) holds for some constant $M > 0$, and that there is $B \geq \underline{D}_2$ and $\delta_0 > 0$ such that*

$$\begin{aligned} & \liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \langle \Gamma_m(\cdot, t), \Gamma_m(\cdot, t) \rangle_a dt \\ & \geq C_2^*(M) \left[\frac{\|m - \bar{m}\|_{C^{\beta, \beta/2}}}{B^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U(\cdot, t) - \bar{U}(t)\|_{L^2(\Omega)} + \frac{1}{B} \right] + \delta_0 \end{aligned}$$

where $C_2^*(M)$ and \underline{D}_2 are given in Theorem 2.6. Then

$$\liminf_{T \rightarrow \infty} \left[\frac{1}{T} \int_0^T H_{D^*}(t) dt - \frac{1}{T} \int_0^T H_D(t) dt \right] \geq \delta_0 \left(\frac{1}{D} - \frac{1}{D^*} \right) \quad (2.18)$$

for any D, D^* satisfying $D^* > D \geq B$.

Proof of Corollary 2.7. It is a direct consequence of (2.16). \square

The proof of Proposition 2.5 is split into several lemmas. Inspired by [3], we first obtain an asymptotic expansion of φ_D (and respectively of ψ_D) for $D \gg 1$. For this purpose, define $\varphi_2(x, t)$ and $\psi_2(x, t)$ by writing

$$\begin{aligned} \varphi_D(x, t) &= 1 + \frac{\Psi_D[c](x, t)}{D} + \frac{\varphi_2(x, t)}{D^2}, \\ \psi_D(x, t) &= 1 + \frac{\hat{\Psi}_D[c](x, t)}{D} + \frac{\psi_2(x, t)}{D^2}, \end{aligned} \quad (2.19)$$

where the operators Ψ_D and $\hat{\Psi}_D$ are defined in (2.11) and (2.12). By Theorem 2.2 and Lemma A.3, $\varphi_D, \psi_D, \Psi[c], \hat{\Psi}[c] \in C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})$, and therefore $\varphi_2, \psi_2 \in C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})$ for each fixed D . By noting also that $\varphi_D - 1, \psi_D - 1, \Psi_D[c], \hat{\Psi}_D[c]$ all have zero spatial averages (see Remark 2.4), it is clear that

$$\int_{\Omega} \varphi_2(x, t) dx = 0 \quad \text{and} \quad \int_{\Omega} \psi_2(x, t) dx = 0 \quad \text{for } t \in \mathbb{R}. \quad (2.20)$$

Lemma 2.8. *There exist constants $C_3^* = C_3^*(M)$ and $\underline{D}_3 = \underline{D}_3(M)$ such that*

$$\frac{1}{T} \int_0^T \int_{\Omega} |\nabla \varphi_2|^2 dx dt + \frac{1}{T} \int_0^T \int_{\Omega} |\nabla \psi_2|^2 dx dt \leq C_3^* \left(\frac{1}{DT} + 1 \right) \quad (2.21)$$

for $D \geq \underline{D}_3$ and $T \geq 1$.

Proof. We only estimate φ_2 , as the adjoint bundle ψ_2 can be estimated in a similar manner. By replacing $c(x, t)$ and $H_D(t)$ by $c(x, t) - \bar{c}(t)$ and $H_D(t) + \bar{c}(t)$ respectively, we may assume without loss of generality that c satisfies

$$c \in C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R}), \quad \bar{c}(t) \equiv 0 \quad \text{and} \quad \|c\|_{L^\infty(\Omega \times \mathbb{R})} \leq M. \quad (2.22)$$

It follows from Lemma A.3 that $\Psi_D[c]$ belongs to $C^{2+\beta, 1+\beta/2}(\bar{\Omega} \times \mathbb{R})$, hence φ_2 belongs to $C^{2+\beta, 1+\beta/2}(\bar{\Omega} \times \mathbb{R})$ by construction.

Using (2.19) and direct computation,

$$\begin{cases} \partial_t \varphi_2 + D\mathcal{L}\varphi_2 = (c + H_D)\varphi_2 + D(c + H_D)\Psi_D[c] + \zeta_1(t) & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B}\varphi_2 = 0 & \text{on } \partial\Omega \times \mathbb{R}, \end{cases} \quad (2.23)$$

where $\zeta_1(t)$ is a function depending on t only. By Lemma B.2, we have

$$\begin{aligned} \frac{1}{T} \int_0^T \int_\Omega |\nabla \varphi_2|^2 dx dt &\leq C_M \left(\frac{1}{DT} + 1 \right) \sup_{t \in \mathbb{R}} \int_\Omega |(c + H_D)\Psi_D[c]|^2 dx \\ &\leq C'_M \left(\frac{1}{DT} + 1 \right), \end{aligned}$$

provided $D \geq 4\Lambda M/c_p$. Here we used (B.5) for the first inequality; and used Theorem 2.2(a), $\|c\|_\infty \leq M$ and Lemma A.2 for the second one. \square

Lemma 2.9. *There exist C_4^*, \underline{D}_4 depending only on M , and $C_{M,D}$ depending on M and D , such that for any $D \geq \underline{D}_4$, $T \geq 1$ and $\|c - \bar{c}\|_\infty \leq M$, we have*

$$\left| \frac{1}{T} \int_0^T H'_D(t) dt - \frac{1}{D^2 T} \int_0^T \langle \Psi_D[c], \hat{\Psi}_D[c] \rangle_a dt \right| \leq \frac{C_4^*}{D^3} + \frac{C_{M,D}}{T}. \quad (2.24)$$

Proof. Again, we may assume without loss of generality that (2.22) holds. Differentiating (2.4) with respect to D , we have

$$\begin{cases} \partial_t \varphi'_D + D\mathcal{L}\varphi'_D = c(x, t)\varphi'_D + H'_D(t)\varphi'_D - \mathcal{L}\varphi_D + H'_D(t)\varphi_D & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B}\varphi'_D = 0 & \text{on } \partial\Omega \times \mathbb{R}. \end{cases} \quad (2.25)$$

Multiplying the first equation in (2.25) by ψ_D and integrating in Ω , we have

$$\begin{aligned} \int_\Omega \psi_D \partial_t \varphi'_D dx &= \int_\Omega \psi_D (-D\mathcal{L}\varphi'_D + (c + H_D)\varphi'_D) dx - \langle \varphi_D, \psi_D \rangle_a \\ &\quad + H'_D(t) \int_\Omega \varphi_D \psi_D dx. \end{aligned}$$

Integrating by parts and using (2.5) and $\int_\Omega \varphi_D \psi_D dx \equiv 1$, we have

$$H'_D(t) = \langle \varphi_D, \psi_D \rangle_a + \frac{d}{dt} \int_\Omega \psi_D \varphi'_D dx.$$

Integrating over $[0, T]$ and dividing by T , we have

$$\frac{1}{T} \int_0^T H'_D(t) dt = \frac{1}{T} \int_0^T \langle \varphi_D, \psi_D \rangle_a dt + \frac{1}{T} \left[\int_\Omega \psi_D \varphi'_D dx \right]_{t=0}^T. \quad (2.26)$$

Now, using the expansion (2.19), we have

$$\begin{aligned} & \frac{1}{T} \int_0^T H_D'(t) dt - \frac{1}{D^2 T} \int_0^T \langle \Psi_D[c], \hat{\Psi}_D[c] \rangle_a dt \\ &= \frac{\zeta_2(T)}{D^3} + \frac{1}{T} \left[\int_{\Omega} \psi_D \varphi_D' dx \right]_{t=0}^T \\ &= \frac{C_M}{D^3} + \frac{C_{M,D}}{T}. \end{aligned}$$

Here we apply the observation that $\sup_{t \in \mathbb{R}} |\int \psi_D \varphi_D' dx| < \infty$, which uses crucially the smoothness of $D \mapsto \varphi_D$ as a mapping from \mathbb{R} to $C^{2+\beta, 1+\beta/2}(\bar{\Omega} \times \mathbb{R})$, so that

$$\sup_{t \in \mathbb{R}} \|\varphi_D'(\cdot, t)\|_{L^2(\Omega)} < \infty;$$

and that

$$\zeta_2(T) = \frac{1}{T} \int_0^T \left[\langle \Psi_D[c], \psi_2 \rangle_a + \langle \hat{\Psi}_D[c], \varphi_2 \rangle_a \right] dt + \frac{1}{DT} \int_0^T \langle \varphi_2, \psi_2 \rangle_a dt$$

is bounded by a constant C_M depending only on M but is independent of $T \geq 1$, by Lemmas 2.8 and A.2. \square

Proof of Proposition 2.5. Given any $M > 0$ and fix any (a_{ij}) and $c \in C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})$ such that (2.22) holds. For each $D \geq 1$, let $(\varphi_D(x, t), \psi_D(x, t), H_D(t))$ be the principal Floquet bundle and its adjoint as given by Theorem 2.2. We will study the asymptotic behavior of (φ_D, ψ_D, H_D) for $D \gg 1$.

By Theorem 2.2(b), there exists $C_h = C_h(M)$ such that for $D \geq 1$,

$$\frac{1}{C_h} \leq \varphi_D(x, t) \leq C_h \quad \text{in } \Omega \times \mathbb{R}. \quad (2.27)$$

By Theorem 2.2(a), $\|c + H_D\|_{L^\infty(\Omega \times \mathbb{R})} \leq 2\|c\|_{L^\infty(\Omega \times \mathbb{R})} \leq 2M$, so that we can apply Lemma B.2 with $g(x, t) = c(x, t) + H_D(t)$, $F \equiv 0$ and $\zeta_0 \equiv 0$, such that (B.3) says

$$\begin{aligned} \sup_{t \in \mathbb{R}} \|\varphi_D(\cdot, t) - 1\|_{L^2(\Omega)} &\leq \sqrt{2} \frac{\Lambda(2M)}{c_p D} \sup_{t \in \mathbb{R}} \|\varphi_D(\cdot, t)\|_{L^2(\Omega)} \\ &\leq 2\sqrt{2} \frac{\Lambda M}{c_p D} \cdot C_h := \frac{C'_M}{D}, \end{aligned} \quad (2.28)$$

where we used $\overline{\varphi_D}(t) = \int_{\Omega} \varphi_D dx \equiv 1$, and $\int_{\Omega} (\varphi_D)^2 dx \leq |C_h|^2 |\Omega| = |C_h|^2$. Hence, integrating the first equation of (2.4) over Ω , and using $\int_{\Omega} \varphi_D dx \equiv 1$ for all t and the no-flux boundary conditions, we have $H_D(t) = - \int_{\Omega} c(x, t) \varphi_D(x, t) dx$, so that

$$\begin{aligned} H_D(t) + \bar{c}(t) &= - \int_{\Omega} (c(x, t) - \bar{c}(t)) \varphi_D(x, t) dx \\ &= - \int_{\Omega} (c(x, t) - \bar{c}(t)) (\varphi_D(x, t) - 1) dx \end{aligned}$$

and hence

$$\sup_{t \in \mathbb{R}} |H_D(t) + \bar{c}(t)| \leq \sup_{t \in \mathbb{R}} \|c - \bar{c}(t)\|_{L^2(\Omega)} \cdot \|\varphi_D(x, t) - 1\|_{L^2(\Omega)} \leq \frac{MC'_M}{D}.$$

This proves (2.13). Finally, (2.14) is proved by letting $T \rightarrow \infty$ in (2.24) and noting that the constant C_4^* is independent of $T \gg 1$. \square

Lemma 2.10. *Suppose $c \in C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})$ can be written as $c(x, t) = m(x, t) + U(x, t)$, where m, U satisfy (2.15) for some $M > 0$, then there exist $C_5^* = C_5^*(M)$ and $\underline{D}_5 = \underline{D}_5(M)$ such that for $D \geq \underline{D}_5$,*

$$\begin{aligned} & \sup_{t \in \mathbb{R}} \left| \langle \Psi_D[c], \hat{\Psi}_D[c] \rangle_a - \langle \Gamma_m, \Gamma_m \rangle_a \right| \\ & \leq C_5^* \left[\frac{\|m - \bar{m}\|_{C^{\beta, \beta/2}(\Omega \times \mathbb{R})}}{D^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U - \bar{U}\|_{L^2(\Omega)} \right]. \end{aligned} \quad (2.29)$$

Proof. Observe that

$$\begin{cases} \Psi_D[c] = \Gamma_m + I_1 + I_2 := \Gamma_m + (\Psi_D[m] - \Gamma_m) + \Psi_D[U], \\ \hat{\Psi}_D[c] = \Gamma_m + I_3 + I_4 := \Gamma_m + (\hat{\Psi}_D[m] - \Gamma_m) + \hat{\Psi}_D[U], \end{cases}$$

where, by Lemmas A.2 – A.4, the terms on the right can be estimated as follows:

$$\begin{cases} \sup_{t \in \mathbb{R}} \|\Gamma_m\|_{H^1(\Omega)} \leq M, \\ \sup_{t \in \mathbb{R}} [\|I_2\|_{H^1(\Omega)} + \|I_4\|_{H^1(\Omega)}] \leq C \sup_{t \in \mathbb{R}} \|U - \bar{U}\|_{L^2(\Omega)}, \\ \sup_{t \in \mathbb{R}} (\|I_1\|_{H^1(\Omega)} + \|I_3\|_{H^1(\Omega)}) \leq CD^{-\beta/4} \|m - \bar{m}\|_{C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})}. \end{cases} \quad (2.30)$$

We estimate the inner product $\langle \Psi_D[c], \hat{\Psi}_D[c] \rangle_a$ by Cauchy-Schwartz inequality:

$$\begin{aligned} & \sup_{t \in \mathbb{R}} \left| \langle \Psi_D[c], \hat{\Psi}_D[c] \rangle_a - \langle \Gamma_m, \Gamma_m \rangle_a \right| \\ & \leq \Lambda \sup_{t \in \mathbb{R}} \|\Gamma_m\|_{H^1} \sum_{k=1}^4 \|I_k\|_{H^1} + \Lambda \sum_{k=1}^4 \|I_k\|_{H^1}^2 \\ & \leq C \left[\frac{\|m - \bar{m}\|_{C^{\beta, \beta/2}(\Omega \times \mathbb{R})}}{D^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U - \bar{U}\|_{L^2(\Omega)} \right], \end{aligned}$$

where we used $|\langle p, q \rangle_a| \leq \Lambda \int_{\Omega} |\nabla p| \cdot |\nabla q| dx \leq \Lambda \|\nabla p\|_{L^2(\Omega)} \|\nabla q\|_{L^2(\Omega)}$, which follows from (2.3). \square

Proof of Theorem 2.6. Using Lemma 2.10, we can rewrite (2.24) into

$$\begin{aligned} & \left| \frac{1}{T} \int_0^T H'_D(t) dt - \frac{1}{D^2 T} \int_0^T \langle \Gamma_m, \Gamma_m \rangle_a dt \right| \\ & \leq \frac{C_M}{D^2} \left[\frac{\|m - \bar{m}\|_{C^{\beta, \beta/2}}}{D^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U - \bar{U}\|_{L^2(\Omega)} + \frac{1}{D} \right] + \frac{C_{M,D}}{T} \end{aligned}$$

which holds for each $D \geq \underline{D}_6 := \max\{\underline{D}_4, \underline{D}_5\}$ and all $T \geq 1$. Integrating from D to D^* , we obtain

$$\begin{aligned} & \left| \frac{1}{T} \int_0^T H_D(t) dt - \frac{1}{T} \int_0^T H_{D^*}(t) dt + \left[\frac{1}{D} - \frac{1}{D^*} \right] \frac{1}{T} \int_0^T \langle \Gamma_m, \Gamma_m \rangle_a dt \right| \\ & \leq C_M \left| \frac{1}{D} - \frac{1}{D^*} \right| \left[\frac{\|m - \bar{m}\|_{C^{\beta, \beta/2}}}{D^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U - \bar{U}\|_{L^2(\Omega)} + \frac{1}{D} \right] + \frac{C_{M,D}|D^* - D|}{T} \end{aligned}$$

for each $D^* > D \geq \underline{D}_6$ and all $T \geq 1$. Letting $T \rightarrow \infty$, we obtain (2.16). Finally, (2.17) can be obtained by letting $D^* \rightarrow +\infty$ in (2.16) and using (2.13). \square

3. UNIFORM IN N ESTIMATES FOR THE SEMIFLOW

Define

$$M_0 := 2|\Omega| \|m\|_{L^\infty(\Omega \times \mathbb{R}_+)}.$$

Lemma 3.1. *Let $(u_i)_{i=1}^N$ be a non-negative solution of (1.1) then*

$$\sup_{t \geq 0} \sum_{i=1}^N \|u_i(\cdot, t)\|_{L^1(\Omega)} \leq \max \left\{ \sum_{i=1}^N \|u_i(\cdot, 0)\|_{L^1(\Omega)}, |\Omega| \sup_{\Omega \times \mathbb{R}_+} m \right\},$$

and

$$\limsup_{t \rightarrow \infty} \sum_{i=1}^N \|u_i(\cdot, t)\|_{L^1(\Omega)} < M_0.$$

In particular, the set \mathcal{N} , given by

$$\mathcal{N} := \left\{ \tilde{u} \in C^0(\bar{\Omega}; \mathbb{R}_+^N) : \sum_{i=1}^N \|\tilde{u}_i\|_{L^1(\Omega)} < M_0 \right\},$$

is forward-invariant with respect to (1.1).

Proof. Integrate (1.1) over Ω and sum over $1 \leq i \leq N$, we have

$$\begin{aligned} \frac{d}{dt} \left\| \sum_{i=1}^N u_i(\cdot, t) \right\|_{L^1(\Omega)} &= \left\| \sum_{i=1}^N u_i(\cdot, t) m \right\|_{L^1(\Omega)} - \left\| \sum_{i=1}^N u_i(\cdot, t) \right\|_{L^2(\Omega)}^2 \\ &\leq \left(\sup_{\Omega \times \mathbb{R}_+} m \right) \left\| \sum_{i=1}^N u_i(\cdot, t) \right\|_{L^1(\Omega)} - \frac{1}{|\Omega|} \left\| \sum_{i=1}^N u_i(\cdot, t) \right\|_{L^1(\Omega)}^2, \end{aligned}$$

where we used Cauchy-Schwartz inequality for the last inequality. The assertions follow from the properties of the solution to the logistic type ODE. \square

Let $(u_i)_{i=1}^N$ be a positive solution to (1.1). To emphasize that the constants obtained in the following lemmas are independent of the number N of the species in (1.1), we define the following notation:

Definition 3.2. Let $B > 0$ be given. We say that the triple (N, \vec{D}, \vec{u}) such that

$$N \in \mathbb{N}, \quad \text{and} \quad (\vec{D}, \vec{u}) = ((D_i)_{i=1}^N, (u_i)_{i=1}^N) \in [\mathbb{R}_+]^N \times [C^{2,1}(\bar{\Omega} \times \mathbb{R}_+)]^N$$

satisfies condition (\mathbf{H}_B) if \vec{u} is a solution of (1.1) with diffusion rates \vec{D} , and

$$\begin{cases} B \leq D_1 < D_2 < \dots < D_N, \\ \inf_{\Omega} u_i(\cdot, 0) > 0 \text{ for all } 1 \leq i \leq N, \text{ and } \sum_{i=1}^N \|u_i(\cdot, 0)\|_{L^1(\Omega)} < M_0. \end{cases} \quad (3.1)$$

Lemma 3.3. Suppose (N, \vec{D}, \vec{u}) satisfy condition (\mathbf{H}_B) for some $B > 0$, then

$$D_i \|u_i\|_{L^1(\Omega \times [t-1/D_i, t])} \leq e^{\frac{1}{B} \|m\|_{L^\infty(\Omega \times \mathbb{R})}} \|u_i(\cdot, t-1/B)\|_{L^1(\Omega)} \quad (3.2)$$

for $1 \leq i \leq N$ and $t \geq 1/B$.

Proof. The spatial average $\bar{u}_i(t)$ of $u_i(x, t)$ satisfies the differential inequality $\frac{d}{dt} \bar{u}_i(t) \leq \|m\| \bar{u}_i(t)$, so that

$$D_i \|u_i\|_{L^1(\Omega \times [t-1/D_i, t])} \leq \sup_{[t-1/B, t]} \bar{u}_i(t) \leq e^{\frac{1}{B} \|m\|_\infty} \bar{u}_i(t-1/B),$$

where we used $D_i \geq B$ in the first inequality. \square

Lemma 3.4. There exists $C_6^* = C_6^*(\|m\|_\infty)$ such that if (N, \vec{D}, \vec{u}) satisfy condition (\mathbf{H}_B) for some $B \geq 1$, then

$$\sup_{t \geq 2} \left[\sum_{i=1}^N \|u_i(\cdot, t)\|_{C^{1+\beta}(\bar{\Omega})} \right] \leq C_6^*. \quad (3.3)$$

Proof. Suppose $B \geq 1$, so that $D_i \geq 1$ for all i . Fix $t \geq 1$ and define $v_i(x, \tau; t) = u_i(x, t + \tau/D_i)$ for each $1 \leq i \leq N$, then

$$\begin{cases} \partial_\tau v_i - \Delta v_i = \frac{m(x, \tau/D_i) - \sum_{j=1}^N u_j(x, \tau/D_j)}{D_i} v_i & \text{in } \Omega \times [-1, \infty), \\ \partial_\nu v_i = 0 & \text{on } \partial\Omega \times [-1, \infty), \\ v_i(x, 0; t) = u_i(x, t) & \text{in } \Omega. \end{cases} \quad (3.4)$$

Next, we drop the nonlinear terms so that v_i satisfies the differential inequality $\partial_\tau v_i - \Delta v_i \leq \frac{m(x, \tau/D_i)}{D_i} v_i$. By the local maximum principle [33, Theorem 7.36], there exists C independent of $B \geq 1$, $t \geq 1$ and i (and any information of \vec{u}) such that $\|v_i(\cdot, 0)\|_{C^0(\bar{\Omega})} \leq C \|v_i\|_{L^1(\Omega \times [-1, 0])}$, i.e.

$$\|u_i(\cdot, t)\|_{C^0(\bar{\Omega})} \leq C D_i \|u_i\|_{L^1(\Omega \times [t-1/D_i, t])}. \quad (3.5)$$

Using Lemma 3.3 and (3.5), we get

$$\|u_i(\cdot, t)\|_{C^0(\bar{\Omega})} \leq C D_i \|u_i\|_{L^1(\bar{\Omega} \times [t-1/D_i, t])} \leq C' \|u_i(\cdot, t-1/B)\|_{L^1(\Omega)}.$$

Since C' is independent of $B \geq 1$, $t \geq 1$ and $1 \leq i \leq N$, we can take summation in i to get

$$\sum_{i=1}^N \|u_i(\cdot, t)\|_{C^0(\bar{\Omega})} \leq C' \sum_{i=1}^N \|u_i(\cdot, t-1/B)\|_{L^1(\Omega)} \leq C' M_0$$

for $t \geq 1$. Hence,

$$\sum_{i=1}^N \|u_i\|_{C^0(\Omega \times [1, \infty))} \leq C'' \quad (3.6)$$

for some $C'' = C''(\|m\|_\infty)$ that is uniform across all (N, \vec{D}, \vec{u}) satisfying condition (\mathbf{H}_B) .

Having shown the L^∞ boundedness of $m - \sum u_i$, we now apply parabolic L^p estimate to (3.4) (which can be regarded as a linear parabolic equation of v_i with L^∞ bounded coefficients) and the Sobolev embedding theorem, to get

$$\|v_i(\cdot, \cdot; t)\|_{C^{1+\alpha, (1+\alpha)/2}(\bar{\Omega} \times [0, 1])} \leq C' \sup_{t \geq 1} \|v_i(\cdot, \cdot; t)\|_{L^\infty(\Omega \times [-1, 1])}, \quad (3.7)$$

from which we yield the following concerning u_i for $t \geq 2$:

$$\|u_i(\cdot, t)\|_{C^{1+\alpha}(\bar{\Omega})} \leq C' \|u_i\|_{L^\infty(\Omega \times [t-1, t+1])} \leq \|u_i\|_{C^0(\bar{\Omega} \times [1, \infty))} \quad (3.8)$$

where C' is independent of i and $t \geq 2$. The estimate (3.3) follows upon taking summation in i and using (3.6). \square

Lemma 3.5. *There exists $C_7^* = C_7^*(\|m\|_\infty) > 0$ such that if (N, \vec{D}, \vec{u}) satisfy condition (\mathbf{H}_B) for some $B \geq 1$, then*

$$\sup_{t \geq 3} \sum_{i=1}^N \|u_i(\cdot, t) - \bar{u}_i(t)\|_{L^2(\Omega)} \leq \frac{C_7^*}{B}, \quad (3.9)$$

where the constant $C_7^* = C_7^*(\Omega, \|m\|_{L^\infty})$ is independent of $B \geq 1$.

Proof. First, since $B \geq 1$, we can use Lemma (3.4) to find $C' = 2C_6^* + \|m\|_\infty$ such that

$$\sup_{t \geq 2} \sum_{i=1}^N \bar{u}_i(t) + \sup_{t \geq 2} \|h(\cdot, t)\|_{C^0(\bar{\Omega})} \leq C',$$

where $h(x, t) = m(x, t) - \sum_{i=1}^N u_i(x, t)$, and that C' is chosen uniformly over all $N \in \mathbb{N}$, diffusion rates satisfying $\min(D_i)_{i=1}^N \geq B$, and initial data in \mathcal{N} .

Let $\tilde{u}_i(x, t) = u_i(x, t) - \bar{u}_i(t)$, then $\int_\Omega \tilde{u}_i dx = 0$ for all t and

$$\frac{1}{D_i} \partial_t \tilde{u}_i - \Delta \tilde{u}_i = \frac{1}{D_i} h(x, t) u_i - \frac{1}{D_i} \int_\Omega h(x, t) u_i(x, t) dx.$$

Multiply the above by \tilde{u}_i and integrate over x , then

$$\begin{aligned} \frac{1}{2D_i} \frac{d}{dt} \int_\Omega |\tilde{u}_i|^2 dx + \int_\Omega |\nabla \tilde{u}_i|^2 dx &= \int_\Omega \frac{h(x, t)}{D_i} u_i \tilde{u}_i dx \\ &\leq \delta \int_\Omega |\tilde{u}_i|^2 dx + \frac{C_\delta}{(D_i)^2} \int_\Omega |u_i|^2 dx. \end{aligned} \quad (3.10)$$

By Poincaré's inequality, there exists a constant $c_p = c_p(\Omega) > 0$ depending only on Ω such that $2c_p \int_{\Omega} |\tilde{u}_i|^2 dx \leq \int_{\Omega} |\nabla \tilde{u}_i|^2 dx$, and so

$$\frac{1}{2D_i} \frac{d}{dt} \int_{\Omega} |\tilde{u}_i|^2 dx + c_p \int_{\Omega} |\tilde{u}_i|^2 dx \leq \frac{C'}{D_i^2} \|u_i\|_{C^0(\bar{\Omega})}^2 \quad \text{for } t \geq 2,$$

where we have taken $\delta = c_p$. Solving the above differential inequality in $t \mapsto \frac{d}{dt} \int_{\Omega} |\tilde{u}_i|^2 dx$, we obtain

$$\begin{aligned} \int_{\Omega} |\tilde{u}_i(\cdot, t)|^2 dx &\leq e^{-2D_i c_p(t-2)} \int_{\Omega} |\tilde{u}_i(\cdot, 2)|^2 dx + \frac{C}{D_i^2 c_p} \|u_i\|_{C^0(\bar{\Omega} \times [2, \infty))}^2 \\ &\leq C' \left(e^{-2D_i c_p} + \frac{1}{D_i^2} \right) \|u_i\|_{C^0(\bar{\Omega} \times [2, \infty))}^2 \end{aligned}$$

for $t \geq 3$ and $1 \leq i \leq N$, i.e.

$$\sup_{t \geq 3} \|\tilde{u}_i(\cdot, t)\|_{L^2(\Omega)} \leq \frac{C''}{D_i} \|u_i\|_{C^0(\bar{\Omega} \times [2, \infty))} \leq \frac{C''}{B} \|u_i\|_{C^0(\bar{\Omega} \times [2, \infty))},$$

where we used $D_i \geq B$. We may now sum over i to obtain (3.9). □

Remark 3.6. By interpolating (3.3) and (3.9), we can show

$$\sup_{t \geq 3} \sum_{i=1}^N \|u_i(\cdot, t) - \bar{u}_i(t)\|_{C^0(\bar{\Omega})} \leq \frac{C}{|\min_{1 \leq i \leq N} D_i|^\theta} \quad \text{for some } 0 < \theta < 1.$$

The constant C only depends on β , and $\|m\|_\infty$ (via $C_6^*(\|m\|_\infty)$ and $C_7^*(\|m\|_\infty)$).

4. PROOF OF MAIN THEOREM

In this section, we set $a_{ij} = \delta_{ij}$, so that

$$\mathcal{L} = -\Delta, \quad \text{and} \quad \mathcal{B} = \nu \cdot \nabla.$$

For given $m(x, t) \in C^{\beta, \beta/2}(\bar{\Omega} \times [0, \infty))$ satisfying (1.3), the function $\Gamma_m(x, t)$, as defined in (2.10), can be written as

$$\Gamma_m(\cdot, t) = (-\Delta)^{-1}[m(\cdot, t) - \bar{m}(t)] \in C^{2+\beta}(\bar{\Omega}) \quad \text{for each } t \geq 0,$$

where $(-\Delta)^{-1}$ is the inverse of the sectorial operator $-\Delta$ on Ω with homogeneous Neumann boundary condition in the space $X^\perp = \{\varphi \in C^\beta(\bar{\Omega}) : \int_{\Omega} \varphi dx = 0\}$.

Proof of Theorem 1.2. Step 1. Define $M > 0$ and δ_0 by

$$M := 1 + 2\|m\|_{C^0(\bar{\Omega} \times [0, \infty))},$$

and

$$\delta_0 := \min \left\{ 1, \frac{1}{3} \liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} |\nabla \Gamma_m(x, t)|^2 dx dt \right\}.$$

Since m satisfies (1.3), Lemma A.5 implies $0 < \delta_0 \leq 1$. Having chosen $M > 0$ and $0 < \delta_0 \leq 1$, we can fix $B_0 \geq 1$ so that

$$B_0 \geq C_7^*, \quad \text{and} \quad \delta_0 \geq C_2^* \left[\frac{M}{B_0^{\beta/4}} + \frac{C_7^*}{B_0} + \frac{1}{B_0} \right] \quad (4.1)$$

where $C_2^* = C_2^*(M)$ and $C_7^* = C_7^*(\|m\|_\infty)$ are given in Theorem 2.6 and Lemma 3.5 respectively.

Step 2. For $N \geq 2$, $D_N > D_{N-1} > \dots > D_1 \geq B_0$ and $(u_i)_{i=1}^N$ be an arbitrary positive solution of (1.1). We will show that

$$\max_{2 \leq i \leq N} \sup_{\Omega} u_i \rightarrow 0 \quad \text{uniformly as } t \rightarrow \infty.$$

By Lemma 3.1, we can perform a translation in time and assume without loss of generality that $\sup_{t \geq 0} \sum_{i=1}^N \|u(\cdot, t)\|_{L^1(\Omega)} < 2|\Omega|\|m\|_\infty$. By Lemmas 3.4 and 3.5, we can further assume that

$$\sup_{t \geq 0} \left\| \sum_{i=1}^N u_i(\cdot, t) \right\|_{C^{1+\beta}(\bar{\Omega})} \leq C_6^* \quad \text{and} \quad \sup_{t \geq 0} \left\| \sum_{i=1}^N (u_i(\cdot, t) - \bar{u}_i(t)) \right\|_{L^2(\Omega)} \leq \frac{C_7^*}{B}, \quad (4.2)$$

where $C_6^* = C_6^*(\|m\|_\infty)$ and $C_7^* = C_7^*(\|m\|_\infty)$.

Step 3. Extend the domain of definition of m to $\Omega \times \mathbb{R}$ by

$$m(x, t) = \begin{cases} m(x, t) & \text{in } \Omega \times [0, \infty), \\ m(x, 0) & \text{in } \Omega \times (-\infty, 0) \end{cases}$$

and extend $(u_i)_{i=1}^N$ to $\Omega \times \mathbb{R}$ in the same way. By standard Schauder estimate, the extended m and $(u_i)_{i=1}^N$ are in $C^{\beta, \beta/2}(\bar{\Omega})$. By setting $a_{ij} = \delta_{ij}$ (so that $\mathcal{L} = \Delta$ and $\mathcal{B} = \nu \cdot \nabla$) and setting

$$c(x, t) = m(x, t) + U(x, t) = m(x, t) - \sum_{i=1}^N (u_i(x, t) - \bar{u}_i),$$

we can define the corresponding principal Floquet bundle (φ_D, ψ_D, H_D) for any $D > 0$. Now, we use (4.1) and (4.2) to verify that for $D \geq B_0$,

$$\begin{aligned} & \liminf_{T \rightarrow \infty} \int_0^T \int_{\Omega} |\nabla \Gamma_m(x, t)|^2 dx dt \\ & \geq C_2^* \left[\frac{\|m - \bar{m}\|_\infty}{D^{\beta/4}} + \sup_{t \in \mathbb{R}} \|U(\cdot, t) - \bar{U}(t)\|_{L^2(\Omega)} + \frac{1}{D} \right] + \delta_0. \end{aligned}$$

Hence, we can apply Corollary 2.7 to deduce that

$$\liminf_{T \rightarrow \infty} \left[\int_0^T H_{D_i}(t) dt - \int_0^T H_{D_1}(t) dt \right] \geq \delta_0 \left(\frac{1}{D_1} - \frac{1}{D_i} \right) > 0 \quad (4.3)$$

holds for $2 \leq i \leq N$.

Step 4. Since (u_i) is componentwise positive, we may assume, without loss of generality, that

$$0 < \inf_{x \in \Omega} u_i(x, 0) \leq \sup_{x \in \Omega} u_i(x, 0) < \infty. \quad (4.4)$$

Noting that $u_i(x, t)$ and $C\varphi_{D_i}(x, t)e^{-\int_0^t H_{D_i}(\tau) d\tau}$ satisfy the same linear heat equation in $\Omega \times [0, \infty)$ with diffusion rate D_i and weight $h(x, t) = m - \sum u_i$, and the Neumann boundary condition on $\partial\Omega \times [0, \infty)$, we can apply the comparison principle, so that

$$\underline{c}_i \varphi_{D_i}(x, t) e^{-\int_0^t H_{D_i}(\tau) d\tau} \leq u_i(x, t) \leq \bar{c}_i \varphi_{D_i}(x, t) e^{-\int_0^t H_{D_i}(\tau) d\tau} \quad (4.5)$$

in $\Omega \times [0, \infty)$ for $1 \leq i \leq N$ and for some positive constants $\underline{c}_i, \bar{c}_i$. Using (4.5), we deduce that for each $i \geq 2$,

$$\begin{aligned} \frac{u_i(x, t)}{u_1(x, t)} &\leq C \left[e^{-\int_0^t H_{D_i}(\tau) d\tau + \int_0^t H_{D_1}(\tau) d\tau} \right] \frac{\varphi_{D_i}(x, t)}{\varphi_{D_1}(x, t)} \\ &\leq C \left[e^{-t[\frac{1}{i} \int_0^t H_{D_i}(\tau) d\tau + \frac{1}{i} \int_0^t H_{D_1}(\tau) d\tau]} \right] (C_h)^2 \end{aligned} \quad (4.6)$$

where we used the fact that the constant C_h in Theorem 2.2 is independent of $D \geq B$ for the last inequality. Using (4.3), we deduce that for each $2 \leq i \leq N$,

$$\sup_{x \in \mathbb{R}} \frac{u_i(x, t)}{u_1(x, t)} \leq C' e^{-t[\delta_0(\frac{1}{D_1} - \frac{1}{D_i}) + o(1)]} \quad \text{for } t \gg 1.$$

Using the fact that $\|u_1\|_{C^0(\bar{\Omega} \times [0, \infty))} \leq C$ (by (4.2)), we can take $t \rightarrow \infty$ and get

$$\lim_{t \rightarrow \infty} \sup_{x \in \Omega} u_i(x, t) = 0 \quad \text{for } 2 \leq i \leq N.$$

Step 5. It remains to assume $\liminf_{T \rightarrow \infty} \int_0^T \bar{m}(t) dt > 0$ and show the weak persistence of u_1 . For this purpose, fix $\delta_1 > 0$ such that

$$\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T (\bar{m}(t) - \delta_1) dx > 0.$$

Using Remark 3.6 and by taking B larger, we may assume that

$$m(x, t) - \sum_{i=1}^N u_i(x, t) \geq m(x, t) - \bar{u}_1(t) - \delta_1 \quad \text{in } \Omega \times [T_0, \infty)$$

for some $T_0 \gg 1$. Hence, the function $\bar{u}_1(t)$ satisfies the differential inequality

$$\frac{d}{dt} \bar{u}_1(t) \geq (\bar{m}(t) - \delta_1 - \bar{u}_1(t)) \bar{u}_1(t) \quad \text{for } t \geq T_0.$$

First, observe that $\sup_{[T_0, \infty)} \bar{u}_1 \leq \max\{\bar{u}_1(T_0), \sup \bar{m}\}$. For $T > t > T_0$, divide both sides by $\frac{\bar{u}_1(t)}{T}$ and integrate t over the interval $[T_0, T]$, we have

$$\frac{1}{T} \log \frac{\bar{u}_1(T_0) \vee \sup \bar{m}}{\bar{u}_1(T_0)} \geq \frac{1}{T} \log \frac{\bar{u}_1(T)}{\bar{u}_1(T_0)} = \frac{1}{T} \int_{T_0}^T \bar{m}(t) dt - \delta_1 - \frac{1}{T} \int_{T_0}^T \bar{u}_1(t) dt$$

where $a \vee b = \max\{a, b\}$ for $a, b \in \mathbb{R}$. Moving $\frac{1}{T} \int_{T_0}^T \bar{u}_1(t) dt$ to the left hand side, and taking $T \rightarrow \infty$, we obtain

$$\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \bar{u}_1(t) dt = \liminf_{T \rightarrow \infty} \frac{1}{T} \int_{T_0}^T \bar{u}_1(t) dt \geq \liminf_{T \rightarrow \infty} \frac{1}{T} \int_{T_0}^T \bar{m}(t) dt - \delta_1 > 0.$$

This proves the weak persistence of the slowest diffuser u_1 [49]. \square

Remark 4.1. If $m = m(x)$, or if $m(x, t)$ is periodic in t , then we will see that u_1 converges to $E_1 = (\Theta_{D_1}, 0, \dots, 0)$ (Θ_{D_1} being the positive equilibrium or periodic solution of the single species problem). In such cases, strong persistence holds:

$$\liminf_{t \rightarrow \infty} \inf_{\Omega} u_1(x, t) > 0. \quad (4.7)$$

However, we do not expect strong persistence to hold in general. Consider the case when $m(x, t) = p(t) - q(x)$ where $0 < q(x) \leq 1/2$ is nonconstant, $|p(t)| \leq 1$ and satisfies

$$p(t) = \begin{cases} -1 & \text{for } t \in \cup_{k=2}^{\infty} [k^2, k^2 + k] \\ 1 & \text{for } t \notin \cup_{k=2}^{\infty} [k^2 - 1, k^2 + k + 1]. \end{cases}$$

Then the hypotheses of Theorem 1.2 is satisfied, namely, (1.3) holds, and

$$\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} m(x, t) dx dt \geq \liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} \left[p(t) - \frac{1}{2} \right] dx dt = \frac{1}{2}.$$

Now, let u_1 be a positive solution to

$$\begin{cases} \partial_t u_1 = \Delta u_1 + u_1(m(x, t) - u_1) & \text{in } \Omega \times (0, \infty), \\ \partial_{\nu} u_1 = 0 & \text{on } \partial\Omega \times (0, \infty), \\ 0 < u(x, 0) \leq 1 & \text{in } \Omega. \end{cases}$$

Then the spatial average $\bar{u}_1(t) = \int_{\Omega} u_1(x, t) dx$ satisfies

$$\frac{d}{dt} \bar{u}_1 \leq \bar{u}_1(p(t) - \bar{u}_1) \quad \text{with } \bar{u}_1(0) \leq 1,$$

and it is easy to see that $\sup \bar{u}_1 \leq 1$. But since

$$\frac{d}{dt} \bar{u}_1(t) \leq -\bar{u}_1(t) \quad \text{in } [k^2, k^2 + k], \quad \bar{u}_1(k^2) \leq 1,$$

we deduce that there exists $t_k := k^2 + k \rightarrow \infty$ such that

$$\bar{u}_1(t_k) \leq e^{-k} \rightarrow 0 \quad \text{as } k \rightarrow \infty,$$

i.e. (4.7) does not hold in this case.

For general sectorial operator \mathcal{L} given in (2.1) with boundary operator \mathcal{B} be given by (2.2), consider

$$\begin{cases} \partial_t u_i(x, t) = D_i \mathcal{L} u_i(x, t) + u_i(x, t) \left[m(x, t) - \sum_{j=1}^N u_j(x, t) \right] & \text{for } x \in \Omega, t > 0, 1 \leq i \leq N, \\ \mathcal{B} u_i(x, t) = 0 & \text{for } x \in \partial\Omega, t > 0, 1 \leq i \leq N. \end{cases} \quad (4.8)$$

By repeating our proofs, one can show the counterpart of Theorem 1.2 for (4.8):

Theorem 4.2. *Given $a_{ij} \in C^{1+\beta}(\overline{\Omega})$, and $m(x, t) \in C^{\beta, \beta/2}(\overline{\Omega} \times [0, \infty))$ satisfying (1.3), there exists $B_0 > 0$ such that for any $N \geq 1$ and diffusion rates*

$$D_N > D_{N-1} > \dots > D_1 \geq B_0, \quad (4.9)$$

any positive solution $(u_i)_{i=1}$ of (4.8) satisfies

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |u_i(\cdot, t)| = 0 \quad \text{for } 2 \leq i \leq N.$$

If we assume, in addition, $\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} m(x, t) dx dt > 0$, then we have

$$\liminf_{t \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} u_1(x, t) dx dt > 0.$$

5. PROOF OF COROLLARIES 1.4 AND 1.6

We only prove Corollary 1.6, as the proof of Corollary 1.4 is analogous.

Proof of Corollary 1.6. First, let $\tilde{m}(x)$ be nonconstant, independent of time, and satisfies $\int_{\Omega} \tilde{m} dx > 0$, it is well-known (see [4]) that the single species problem

$$\begin{cases} \tilde{u}_t = D_1 \Delta \tilde{u} + \tilde{u}(\tilde{m} - \tilde{u}) & \text{in } \Omega \times (0, \infty), \\ \partial_{\nu} \tilde{u} = 0 & \text{on } \partial\Omega \times (0, \infty), \\ \tilde{u}(x, 0) = \tilde{u}_0(x) & \text{in } \Omega \end{cases} \quad (5.1)$$

has a unique positive equilibrium $\Theta_{D_1}(x)$ that is globally asymptotically stable among all nonnegative, nontrivial solutions.

Let $m \in C^{\beta, \beta/2}(\overline{\Omega})$ be given such that (1.10) holds, i.e. $m(x, t)$ is asymptotic to $\tilde{m}(x)$. Then it obviously satisfies (1.3) and

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} m(x, t) dx dt = \int_{\Omega} \tilde{m}(x) dx > 0.$$

By Theorem 1.2, there exists $B_0 > 0$ such that for any $N \geq 2$ and any $D_N > D_{N-1} > \dots > D_1 \geq B_0$, each positive solution $u = (u_i)_{i=1}^N$ of (1.1) satisfies

$$\limsup_{t \rightarrow \infty} \sup_{x \in \Omega} |u_i(x, t)| = 0 \quad \text{for } 2 \leq i \leq N$$

and

$$\liminf_{t \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} u_1(x, t) dx dt > 0. \quad (5.2)$$

Consider the ω -limit set ω_1 given by

$$\omega_1 := \{\hat{u} \in C(\overline{\Omega}) : u_1(\cdot, t_n) \rightarrow \hat{u} \text{ for some } t_n \rightarrow \infty\}.$$

Then it follows [19] that ω_1 is an internally chain transitive set of the semiflow generated by the limiting equation (5.1). Since (5.1) has one trivial equilibrium, and a unique positive equilibria Θ_{D_1} which attracts all nonnegative, nontrivial solutions, it follows that $\omega_1 = \{0\}$ or $\omega_1 = \{\Theta_{D_1}\}$. In view of (5.2), we must have $\omega_1 = \{\Theta_{D_1}\}$. Hence, $u_1 \rightarrow \Theta_{D_1}$ as $t \rightarrow \infty$. This completes the proof. \square

APPENDIX A. ESTIMATES

Let $\mathcal{L} = -\partial_{x_j}(a_{ij}\partial_{x_i})$ be the sectorial operator in $X = L^2(\Omega)$, with domain $\text{Dom}(\mathcal{L}) = \{u_0 \in W^{2,2}(\Omega) : \mathcal{B}u_0 = 0\}$, where \mathcal{L} and its associated conormal derivative operator \mathcal{B} are defined in Section 2. Since \mathcal{L} is self-adjoint, all of its eigenvalues are real and can be enumerated as $0 = \nu_0 < \nu_1 < \nu_2 < \dots$. Moreover, the principal eigenvalue $\nu_0 = 0$ is simple and the principal eigenfunction ϕ_0 is a constant. It follows from [18, Theorem 1.5.2] that $X = X_1 \oplus X_2$, where

$$X_1 := \text{span}\{1\} \quad \text{and} \quad X_2 := \{u_0 \in L^2(\Omega) : \int_{\Omega} u_0 dx = 0\}$$

are invariant under the action of the semigroup operator $e^{-t\mathcal{L}}$, and that the spectrum $\sigma(\mathcal{L}|_{X_2})$ satisfies

$$\sigma(\mathcal{L}|_{X_2}) = \{\nu_k\}_{k=1}^{\infty} \subset \{z \in \mathbb{C} : \text{Re } z > \nu\} \quad \text{for some } \nu > 0. \quad (\text{A.1})$$

Hence, it follows from [18, Theorem 1.5.4] that there exists $C_1 > 0$ such that

$$\|e^{-t\mathcal{L}}u_0\|_{L^2(\Omega)} \leq C_1 e^{-\nu t} \|u_0\|_{L^2(\Omega)} \quad \text{for all } u_0 \in X_2 \text{ and } t > 0 \quad (\text{A.2})$$

and

$$\|e^{-t\mathcal{L}}u_0\|_{H^1(\Omega)} \leq \frac{C_1}{\sqrt{t}} e^{-\nu t} \|u_0\|_{L^2(\Omega)} \quad \text{for all } u_0 \in X_2 \text{ and } t > 0. \quad (\text{A.3})$$

Let $h(x, t) \in L^\infty(\Omega \times \mathbb{R})$ be given. We define $\Gamma_h(x, t)$, $\Psi_D[h](x, t)$ and $\hat{\Psi}_D[h](x, t)$ as follows:

$$\Gamma_h(\cdot, t) = \int_0^\infty e^{-\tau\mathcal{L}}[h(\cdot, t) - \bar{h}(t)] d\tau \quad (\text{A.4})$$

$$\Psi_D[h](x, t) = D \int_{-\infty}^t e^{-D(t-s)\mathcal{L}}[h(\cdot, s) - \bar{h}(s)] ds \quad (\text{A.5})$$

and

$$\hat{\Psi}_D[h](x, t) = D \int_t^\infty e^{-D(s-t)\mathcal{L}}[h(\cdot, s) - \bar{h}(s)] ds. \quad (\text{A.6})$$

Note that they are well defined in $L^\infty(\mathbb{R}; X_2 \cap H^1(\Omega))$, by (A.2).

Lemma A.1. *Let $h(x, t) \in L^\infty(\Omega \times \mathbb{R})$ be given.*

(a) *For each t , $x \mapsto \Gamma_h(x, t)$ is the unique solution to*

$$\mathcal{L}\Gamma_h = h(x, t) - \bar{h}(t) \quad \text{in } \Omega, \quad \mathcal{B}\Gamma_h = 0 \quad \text{on } \partial\Omega, \quad \text{and} \quad \int_{\Omega} \Gamma_h dx = 0. \quad (\text{A.7})$$

(b) *The function $w_{D,h}(x, t) = \Psi_D[h](x, t)$ satisfies*

$$w_{D,h}(x, t) = \int_0^\infty e^{-\tau\mathcal{L}}[h(\cdot, t - \frac{\tau}{D}) - \bar{h}(t - \frac{\tau}{D})] d\tau \quad (\text{A.8})$$

and is the unique solution to

$$\begin{cases} \frac{1}{D}\partial_t w_{D,h} + \mathcal{L}w_{D,h} = h(x, t) - \bar{h}(t) & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B}w_{D,h} = 0 & \text{on } \partial\Omega \times \mathbb{R} \quad \text{and} \quad \limsup_{t \rightarrow -\infty} \|w_{D,h}(\cdot, t)\|_{L^2(\Omega)} < +\infty. \end{cases} \quad (\text{A.9})$$

(c) The function $v_{D,h}(x, t) = \hat{\Psi}_D[h](x, t)$ satisfies

$$v_{D,h}(x, t) = \int_0^\infty e^{-\mathcal{L}\tau} [h(\cdot, t + \frac{\tau}{D}) - \bar{h}(t + \frac{\tau}{D})] d\tau \quad (\text{A.10})$$

and is the unique solution to

$$\begin{cases} -\frac{1}{D} \partial_t v_{D,h} + \mathcal{L} v_{D,h} = h(x, t) - \bar{h}(t) & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B} v_{D,h} = 0 & \text{on } \partial\Omega \times \mathbb{R} \quad \text{and} \quad \limsup_{t \rightarrow +\infty} \|v_{D,h}(\cdot, t)\|_{L^2(\Omega)} < +\infty. \end{cases} \quad (\text{A.11})$$

Proof. See [18]. □

Lemma A.2. *There exists C_ν depending only on ν and C_1 such that*

$$\sup_{t \in \mathbb{R}} \|\Psi_D[h](\cdot, t)\|_{H^1(\Omega)} + \sup_{t \in \mathbb{R}} \|\hat{\Psi}_D[h](\cdot, t)\|_{H^1(\Omega)} \leq C_\nu \sup_{t \in \mathbb{R}} \|h(\cdot, t) - \bar{h}(t)\|_{L^2(\Omega)}.$$

Proof. For $t \in \mathbb{R}$, we apply (A.3) to (A.8) to get

$$\begin{aligned} \|\Psi_D[h](\cdot, t)\|_{H^1(\Omega)} &\leq \int_0^\infty \frac{C_1}{\sqrt{\tau}} e^{-\nu\tau} ds \sup_{s \in \mathbb{R}} \|h(\cdot, s) - \bar{h}(s)\|_{L^2(\Omega)} \\ &\leq C_\nu \sup_{s \in \mathbb{R}} \|h(\cdot, s) - \bar{h}(s)\|_{L^2(\Omega)}. \end{aligned}$$

The proof for $\hat{\Psi}_D[h]$ is analogous. □

Lemma A.3. *If $h \in C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})$, then $\Psi_D[h], \hat{\Psi}_D[h] \in C^{2+\beta, 1+\beta/2}(\bar{\Omega} \times \mathbb{R})$.*

Proof. By Lemma A.3, $\sup_{t \in \mathbb{R}} \|\Psi_D[h]\|_{L^2(\Omega \times [t-2, t])} < \infty$. Hence, by applying standard parabolic estimates on the equation (A.9), we have

$$\sup_{t \in \mathbb{R}} \|\Psi_D[h]\|_{C^{2+\beta, 1+\beta/2}(\bar{\Omega} \times [t-1, t])} < \infty,$$

although the bound may generally depend on D . The proof for $\hat{\Psi}_D[h]$ is analogous and is omitted. □

Lemma A.4. *There exists C_ν depending only on ν and C_1 such that*

$$\begin{cases} \sup_{t \in \mathbb{R}} \|\Psi_D[h](\cdot, t) - \Gamma_h(\cdot, t)\|_{H^1(\Omega)} \leq C_\nu D^{-\beta/4} \|h - \bar{h}\|_{C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})}, \\ \sup_{t \in \mathbb{R}} \|\hat{\Psi}_D[h](\cdot, t) - \Gamma_h(\cdot, t)\|_{H^1(\Omega)} \leq C_\nu D^{-\beta/4} \|h - \bar{h}\|_{C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})}. \end{cases}$$

Proof. Combining (A.4) and (A.8), we write $\Psi_D[h](x, t) - \Gamma_h(x, t) = J_1 + J_2$, where

$$\begin{cases} J_1 = \int_0^{\sqrt{D}} e^{-\tau\mathcal{L}} [h(\cdot, t - \frac{\tau}{D}) - h(\cdot, t) - \bar{h}(t - \frac{\tau}{D}) + \bar{h}(t)] d\tau, \\ J_2 = \int_{\sqrt{D}}^\infty e^{-\tau\mathcal{L}} [h(\cdot, t - \frac{\tau}{D}) - h(\cdot, t) - \bar{h}(t - \frac{\tau}{D}) + \bar{h}(t)] d\tau. \end{cases}$$

We use (A.3) to estimate J_1 and J_2 . Indeed, we have

$$\|J_1\|_{H^1(\Omega)} \leq \int_0^{\sqrt{D}} \frac{C_1}{\sqrt{\tau}} e^{-\nu\tau} \|h(\cdot, t - \frac{\tau}{D}) - h(\cdot, t) - \bar{h}(t - \frac{\tau}{D}) + \bar{h}(t)\|_{L^2(\Omega)} d\tau$$

$$\begin{aligned}
&\leq C(1/\sqrt{D})^{\beta/2} \|h - \bar{h}\|_{C^{\beta/2}(\mathbb{R}; C^0(\Omega))} \int_0^{\sqrt{D}} \frac{C_1}{\sqrt{\tau}} e^{-\nu\tau} d\tau \\
&\leq CD^{-\beta/4} \|h - \bar{h}\|_{C^{\beta, \beta/2}(\bar{\Omega} \times \mathbb{R})}
\end{aligned}$$

and

$$\begin{aligned}
\|J_2\|_{H^1(\Omega)} &\leq \int_{\sqrt{D}}^{\infty} \frac{C_1}{\sqrt{\tau}} e^{-\nu\tau} \|h(\cdot, t - \frac{\tau}{D}) - h(\cdot, t) - \bar{h}(t - \frac{\tau}{D}) + \bar{h}(t)\|_{L^2(\Omega)} d\tau \\
&\leq 2\|h - \bar{h}\|_{C^0(\bar{\Omega} \times \mathbb{R})} e^{-\nu\sqrt{D}} \int_{\sqrt{D}}^{\infty} \frac{C_1}{\sqrt{\tau - \sqrt{D}}} e^{-\nu(\tau - \sqrt{D})} d\tau \\
&\leq Ce^{-\nu\sqrt{D}} \|h - \bar{h}\|_{C^0(\bar{\Omega} \times \mathbb{R})}.
\end{aligned}$$

The proof for $\hat{\Psi}_D[h]$ is analogous and is omitted. \square

Lemma A.5. *Given $h \in L^\infty((0, \infty); C^\beta(\bar{\Omega}))$. If*

$$\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} |h(x, t) - \bar{h}(t)|^2 dx dt > 2\eta > 0 \quad \text{for some } \eta > 0, \quad (\text{A.12})$$

then

$$\liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} |\nabla \Gamma_h(x, t)|^2 dx dt > 0.$$

Proof. Define

$$A_\eta := \{t : \int_{\Omega} |h(x, t) - \bar{h}(t)|^2 dx \geq \eta\}.$$

Step 1. We claim that $\liminf_{T \rightarrow \infty} \frac{1}{T} \int_{[0, T] \cap A_\eta} \int_{\Omega} |h(x, t) - \bar{h}(t)|^2 dx dt > \eta$.

This is a consequence of (A.12) and $\frac{1}{T} \int_{[0, T] \setminus A_\eta} \int_{\Omega} |h(x, t) - \bar{h}(t)|^2 dx dt \leq \eta$.

Step 2. We claim that $\liminf_{T \rightarrow \infty} \frac{1}{T} |[0, T] \cap A_\eta| > 0$.

Indeed, we have

$$\liminf_{T \rightarrow \infty} \frac{1}{T} |[0, T] \cap A_\eta| \geq \frac{\liminf_{T \rightarrow \infty} \frac{1}{T} \int_{[0, T] \cap A_\eta} \int_{\Omega} |h(x, t) - \bar{h}(t)|^2 dx dt}{4|\Omega| \|h\|_{L^\infty(\bar{\Omega} \times \mathbb{R})}^2} > 0.$$

Step 3. We claim that there is a constant $c_\eta > 0$ such that

$$\inf_{t \in A_\eta} \int_{\Omega} |\nabla \Gamma_h(x, t)|^2 dx \geq c_\eta. \quad (\text{A.13})$$

Suppose not, then there exists a sequence $t_k \in A_\eta$ such that as $t_k \rightarrow \infty$,

$$\int_{\Omega} |\nabla \Gamma_h(x, t_k)|^2 dx \searrow 0.$$

Since $h \in L^\infty(\mathbb{R}; C^\beta(\bar{\Omega}))$, we may assume without loss of generality that $h(\cdot, t_k) \rightarrow h_\infty(\cdot)$ strongly in $L^2(\Omega)$. Hence, $\int_{\Omega} |h_\infty(x) - \bar{h}_\infty|^2 dx \geq \eta > 0$ and hence $\mathcal{L}^{-1}h_\infty \in H^1(\Omega)$ is non-constant. Recall that the sectorial operator \mathcal{L} is invertible in X_2 (the

space of L^2 functions with zero spatial average). Moreover that $\mathcal{L}^{-1} : X_2 \rightarrow H^1(\Omega)$ is compact, so that

$$\Gamma_h(\cdot, t_k) = \mathcal{L}^{-1}h(\cdot, t_k) \rightarrow \mathcal{L}^{-1}h_\infty \quad \text{in } H^1(\Omega),$$

and hence we reach a contradiction:

$$0 = \lim_{k \rightarrow \infty} \int_{\Omega} |\nabla \Gamma_h(x, t_k)|^2 dx = \int_{\Omega} |\nabla \mathcal{L}^{-1}[h_\infty]|^2 dx > 0.$$

This proves the claim.

Finally, we use Steps 3 and 4 to deduce

$$\begin{aligned} & \liminf_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} |\nabla \Gamma_h(x, t)|^2 dx dt \\ & \geq \left[\inf_{t \in A_\eta} \int_{\Omega} |\nabla \Gamma_h(x, t)|^2 dx \right] \liminf_{T \rightarrow \infty} \frac{1}{T} |[0, T] \cap A_\eta| > 0. \end{aligned}$$

This completes the proof. \square

APPENDIX B. CALCULUS LEMMAS

Lemma B.1. *Suppose $p(t)$ satisfies $\sup_{t \in \mathbb{R}} p(t) < +\infty$ and the differential inequality*

$$p'(t) + A_1 p(t) \leq B_1 \quad \text{for } t \in \mathbb{R},$$

where $A_1 > 0$ and $B_1 \in \mathbb{R}$ are constants, then $\sup_{t \in \mathbb{R}} p(t) \leq B_1/A_1$.

Proof. Multiply the differential inequality by $e^{A_1 t}$ and integrate from s to t , then

$$p(t) \leq e^{-A_1(t-s)} p(s) + \frac{B_1}{A_1} (1 - e^{-A_1(t-s)}) \quad \text{for any } -\infty < s < t < \infty.$$

Fix t and send $s \rightarrow -\infty$, by $\sup_{s \in \mathbb{R}} p(s) < +\infty$ we obtain the desired estimate. \square

Given a smooth bounded domain Ω in \mathbb{R}^n . The Poincaré's inequality asserts the existence of a positive constant c_p which depends only on Ω and n such that

$$2c_p \int_{\Omega} |\phi(x) - \bar{\phi}|^2 dx \leq \int_{\Omega} |\nabla \phi|^2 dx \quad \text{for all } \phi \in H^1(\Omega), \quad (\text{B.1})$$

where we recall that $\bar{\phi} = \frac{1}{|\Omega|} \int_{\Omega} \phi(y) dy$.

Lemma B.2. *Let $v(x, t)$ be a classical solution of*

$$\begin{cases} \partial_t v - D\mathcal{L}v = F(x, t) + g(x, t)v(x, t) + \zeta_0(t) & \text{in } \Omega \times \mathbb{R}, \\ \mathcal{B}v = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \sup_{t \in \mathbb{R}} \left[\int_{\Omega} |v(x, t)|^2 dx \right] < \infty, \end{cases} \quad (\text{B.2})$$

where $\mathcal{L} = \partial_{x_i}(a_{ij}\partial_j)$ and $\mathcal{B} = \nu_i a_{ij}\partial_j$ are given in (2.1)-(2.2) such that a_{ij} satisfies (2.3) for some constant $\Lambda > 1$, and

$$\|g\|_{L^\infty(\Omega \times \mathbb{R})} + \sup_{t \in \mathbb{R}} \|F(\cdot, t)\|_{L^2(\Omega)} < +\infty.$$

Then

$$\sup_{t \in \mathbb{R}} \int_{\Omega} |v(x, t) - \bar{v}(t)|^2 dx \leq 2 \left(\frac{\Lambda}{c_p D} \right)^2 \left[\sup_{t \in \mathbb{R}} \|F\|_{L^2(\Omega)}^2 + \|g\|_{L^\infty(\Omega \times \mathbb{R})}^2 \sup_{t \in \mathbb{R}} \|v\|_{L^2(\Omega)}^2 \right]. \quad (\text{B.3})$$

Assume, in addition, $\bar{v}(t) \equiv 0$ for all $t \in \mathbb{R}$ and $D \geq 2\Lambda \|g\|_{L^\infty(\Omega \times \mathbb{R})}/c_p$, then

$$\sup_{t \in \mathbb{R}} \int_{\Omega} |v(x, t)|^2 dx \leq 4 \left(\frac{\Lambda}{c_p D} \right)^2 \sup_{t \in \mathbb{R}} \int_{\Omega} |F(x, t)|^2 dx, \quad (\text{B.4})$$

and

$$\frac{1}{T} \int_0^T \int_{\Omega} |\nabla v|^2 dx dt \leq 4\Lambda^2 \left[\frac{2\Lambda}{Dc_p^2 T} + \frac{1}{c_p} \right] \sup_{t \in \mathbb{R}} \int_{\Omega} \frac{|F(x, t)|^2}{D^2} dx. \quad (\text{B.5})$$

Proof. Let $\tilde{v}(x, t) = v(x, t) - \bar{v}(t)$, then $\mathcal{B}\tilde{v} = 0$ on $\partial\Omega \times \mathbb{R}$ and

$$\partial_t \tilde{v} - D\mathcal{L}\tilde{v} = F + gv + \zeta_1(t), \quad (\text{B.6})$$

where $\zeta_1(t) = \zeta_0(t) - \overline{(F + gv)}(t)$. Multiply (B.6) by \tilde{v} and integrate by parts, we have

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} \tilde{v}^2 + D \int_{\Omega} a_{ij} \tilde{v}_{x_i} \tilde{v}_{x_j} = \int_{\Omega} F \tilde{v} + \int_{\Omega} gv \tilde{v}$$

where we used $\int_{\Omega} \tilde{v}(x, t) \zeta_1(t) dx \equiv 0$.

Using (2.3), we have, for any $\delta > 0$,

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} \tilde{v}^2 + \frac{D}{\Lambda} \int_{\Omega} |\nabla \tilde{v}|^2 \leq 2\delta \int_{\Omega} \tilde{v}^2 + \frac{1}{4\delta} \int_{\Omega} F^2 + \frac{1}{4\delta} \int_{\Omega} g^2 v^2.$$

Taking $\delta = \frac{Dc_p}{4\Lambda}$, and using (B.1) we have

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} \tilde{v}^2 + \frac{D}{2\Lambda} \int_{\Omega} |\nabla \tilde{v}|^2 \leq \frac{\Lambda}{c_p D} \left[\int_{\Omega} F^2 + \|g\|_{L^\infty(\Omega \times \mathbb{R})}^2 \int_{\Omega} v^2 \right] \quad \text{for } t \in \mathbb{R}. \quad (\text{B.7})$$

Applying (B.1) on the second term on the left side, we have

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} \tilde{v}^2 + \frac{c_p D}{2\Lambda} \int_{\Omega} |\tilde{v}|^2 \leq \frac{\Lambda}{c_p D} \left[\int_{\Omega} F^2 + \|g\|_{L^\infty(\Omega \times \mathbb{R})}^2 \int_{\Omega} v^2 \right] \quad \text{for } t \in \mathbb{R}. \quad (\text{B.8})$$

By our assumption, the right hand side of (B.8) is bounded uniformly in $t \in \mathbb{R}$, so we can apply Lemma B.1 to deduce (B.3).

Next, assume

$$\bar{v}(t) \equiv 0 \quad \text{and} \quad D \geq 2\Lambda \|g\|_{L^\infty(\Omega \times \mathbb{R})}/c_p,$$

then $\tilde{v} = v$ and (B.4) follows from (B.3).

Substituting (B.4) into (B.7), we get

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} v^2 + \frac{D}{2\Lambda} \int_{\Omega} |\nabla v|^2 \leq \frac{2\Lambda}{c_p D} \int_{\Omega} F^2 \quad \text{for } t \in \mathbb{R}.$$

Integrate the above over $[0, T]$, and divide by DT , we get

$$\frac{1}{2DT} \left[\int_{\Omega} v^2 dx \right]_{t=0}^T + \frac{1}{2\Lambda T} \int_0^T \int_{\Omega} |\nabla v|^2 \leq \frac{2\Lambda}{c_p D^2 T} \int_0^T \int_{\Omega} F^2.$$

Hence,

$$\frac{1}{2\Lambda T} \int_0^T \int_{\Omega} |\nabla v|^2 dx dt \leq \frac{1}{DT} \sup_{t \in \mathbb{R}} \int_{\Omega} v^2 dx + \frac{2\Lambda}{c_p D^2} \sup_{t \in \mathbb{R}} \int_{\Omega} F^2 dx.$$

Upon combining with (B.4), we obtain (B.5). □

Remark B.3. By letting $T \rightarrow \infty$ in (B.5),

$$\limsup_{T \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} |\nabla v(x, t)|^2 dx dt \leq \frac{4\Lambda^2}{c_p D^2} \limsup_{t \rightarrow \infty} \frac{1}{T} \int_0^T \int_{\Omega} |F(x, t)|^2 dx \quad (\text{B.9})$$

holds uniformly for $D \geq 2\Lambda \|g\|_{L^\infty(\Omega \times \mathbb{R})}/c_p$.

REFERENCES

- [1] L. Altenberg, Resolvent positive linear operators exhibit the reduction phenomenon. *Proc. Natl. Acad. Sci. USA* **109** (2012) 3705-3710.
- [2] I. Averill, K.-Y. Lam and Y. Lou, The role of advection in a two-species competition model: a bifurcation approach, *Mem. Amer. Math. Soc.* **245** (2017), no. 1161, v+117pp.
- [3] X. Bai, X. He and W.-M. Ni, Dynamics of a periodic-Parabolic Lotka-Volterra competition-diffusion system in heterogeneous environments, *J. Eur. Math. Soc.*, 2021, accepted.
- [4] R.S. Cantrell, C. Cosner, Spatial ecology via reaction-diffusion equations. *Wiley Series in Mathematical and Computational Biology*. John Wiley & Sons, Ltd., Chichester, 2003.
- [5] R.S. Cantrell, C. Cosner, V. Hutson, Permanence in some diffusive Lotka-Volterra models for three interacting species, *Dynam. Systems Appl.* **2** (1993) 505-530.
- [6] R.S. Cantrell, C. Cosner, Y. Lou, Advection-mediated coexistence of competing species, *Proc. Roy. Soc. Edinburgh Sect. A* **137** (2007) 497-518.
- [7] R.S. Cantrell and K.-Y. Lam, On the evolution of slow dispersal in multi-species communities, *SIAM J. Math. Anal.*, **53** (2021), 4933-4964.
- [8] R.S. Cantrell and J.R. Ward, On competition-mediated coexistence, *SIAM J. Appl. Math.* **57** (1997) 1311-1327.
- [9] X. Chen and Y. Lou, Principal eigenvalue and eigenfunctions of an elliptic operator with large advection and its application to a competition model, *Indiana Univ. Math. J.* **57** (2008) 627-658.
- [10] E. Cho and Y.-J. Kim, Starvation driven diffusion as a survival strategy of biological organisms, *Bull. Math. Biol.* **75** (2013) 845-870.
- [11] S.-N. Chow, K. Lu, and J. Mallet-Paret, Floquet bundles for scalar parabolic equations. *Arch. Rational Mech. Anal.* **129** (1995), no. 3, 245-304.
- [12] J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, The evolution of slow dispersal rates: a reaction diffusion model, *J. Math. Biol.* **37** (1998) 61-83.
- [13] E.N. Dancer and Y. Du, Positive solutions for a three-species competition system with diffusion – I. General existence results, *Nonlinear Anal.* **24** (1995) 337-357.
- [14] E.N. Dancer, K. Wang, Z. Zhang, Dynamics of strongly competing systems with many species, *Trans. Amer. Math. Soc.* **364** (2012) 961-1005.
- [15] D.L. DeAngelis, G.S. Wolkowicz, Y. Lou, Y. Jiang, M. Novak, R. Svanbäck, M.S. Araujo, Y. Jo, and E.A. Cleary, . The effect of travel loss on evolutionarily stable distributions of populations in space. *The American Naturalist*, **178** (2011), 15-29.
- [16] W. Hao, K.-Y. Lam and Y. Lou, Ecological and evolutionary dynamics in advective environments: critical domain size and boundary conditions, *Discrete Cont. Dyn. Syst. Ser. B* **26** (2021) 367-400.
- [17] A. Hastings, Can spatial variation alone lead to selection for dispersal?, *Theor. Pop. Biol.* **24** (1983) 224-251.
- [18] D. Henry, Geometric theory of semilinear parabolic equations. *Lecture Notes in Mathematics*, 840. Springer-Verlag, Berlin-New York, 1981.
- [19] M.W. Hirsch, H.L. Smith, X.-Q. Zhao, Chain transitivity, attractivity, and strong repellers for semidynamical systems, *J. Dynam. Differential Equations* **13** (2001) 107-131.
- [20] X. He and W.-M. Ni, Global dynamics of the Lotka-Volterra competition-diffusion system: diffusion and spatial heterogeneity I, *Comm. Pure Appl. Math.* **69** (2016) 981-1014.
- [21] J. Hůska and P. Poláčik, The principal Floquet bundle and exponential separation for linear parabolic equations, *J. Dynam. Differential Equations* **24** (2004) 1312-1330.
- [22] J. Hůska, Harnack inequality and exponential separation for oblique derivative problems on Lipschitz domains, *J. Differential Equations* **226** (2006) 541-557.
- [23] J. Hůska, P. Poláčik, and M. V. Safonov, Harnack inequalities, exponential separation, and perturbations of principal Floquet bundles for linear parabolic equations, *Ann. Inst. H. Poincaré Anal. Non Linéaire* **24** (2007) 711-739.

- [24] V. Hutson, K. Mischaikow, P. Poláčik, The evolution of dispersal rates in a heterogeneous time-periodic environment, *J. Math. Biol.* **43** (2001) 501-533.
- [25] S.B. Hsu, H.L. Smith and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered banach spaces, *Trans. Amer. Math. Soc.* **348** (1996) 4083-4094.
- [26] Y.-J. Kim, O. Kwon and F. Li, Evolution of dispersal toward fitness. *Bull. Math. Biol.* **75** (2013), no. 12, 2474-2498.
- [27] S. Kirkland, C.-K. Li and S.J. Schreiber, On the evolution of dispersal in patchy landscapes. *SIAM J. Appl. Math.* **66** (2006), no. 4, 1366-1382.
- [28] L. Korobenko, E. Braverman, On evolutionary stability of carrying capacity driven dispersal in competition with regularly diffusing populations, *J. Math. Biol.* **69** (2014) 1181-1206.
- [29] K.-Y. Lam and Y. Lou, Evolution of conditional dispersal: evolutionarily stable strategies in spatial models, *J. Math. Biol.* **68** (2014) 851-877.
- [30] K.-Y. Lam, Y. Lou and F. Lutscher, Evolution of dispersal in closed advective environments, *J. Biol. Dyn.* **9** (2015) 188-212.
- [31] K.-Y. Lam and D. Munther, A remark on the global dynamics of competitive systems on ordered Banach spaces, *Proc. Amer. Math. Soc.* **144** (2016) 1153-1159.
- [32] K.-Y. Lam and W.-M. Ni, Uniqueness and complete dynamics in heterogeneous competition-diffusion systems, *SIAM J. Appl. Math.* **72** (2012) 1695-1712.
- [33] G. M. Lieberman. Second order parabolic differential equations. World Scientific Publishing Co., Inc., River Edge, NJ, 1996.
- [34] Y. Lou, On the effects of migration and spatial heterogeneity on single and multiple species, *J. Differential Equations* **223** (2006) 400-426.
- [35] Y. Lou and F. Lutscher, Evolution of dispersal in open advective environments, *J. Math. Biol.* **69** (2014) 1319-1342.
- [36] Y. Lou and D. Munther, Dynamics of a three species competition model, *Discrete Contin. Dyn. Syst.* **32** (2012) 3099-3131.
- [37] Y. Lou, X.-Q. Zhao and P. Zhou, Global dynamics of a Lotka-Volterra competition-diffusion-advection system in heterogeneous environments, *J. Math. Pures Appl.* **121** (2019) 47-82.
- [38] Y. Lou and P. Zhou, Evolution of dispersal in advective homogeneous environment: the effect of boundary conditions, *J. Differential Equations* **259** (2015) 141-171.
- [39] A. Lunardi, Analytic semigroups and optimal regularity in parabolic problems. Modern Birkhäuser Classics. Birkhäuser/Springer Basel AG, Basel, 1995. xviii+424 pp.
- [40] F. Lutscher, E. Pachepsky, and M.A. Lewis, The effect of dispersal patterns on stream populations, *SIAM Rev.* **47** (2005) 749-772.
- [41] I. Mazari, Trait selection and rare mutations: the case of large diffusivities, *Discrete Contin. Dyn. Syst. Ser. B* **24** (2019) 6693-6724.
- [42] M.A. McPeck and R.D. Holt, The evolution of dispersal in spatially and temporally varying environments, *Am. Nat.* **6** (1992), 1010-1027.
- [43] J. Mierczyński, Globally positive solutions of linear parabolic PDEs of second order with Robin boundary conditions, *J. Math. Anal. Appl.* **209** (1997) 47-59.
- [44] W.-M. Ni, The mathematics of diffusion, CBMS-NSF Regional Conference Series in Applied Mathematics, 82. Society for Industrial and Applied Mathematics (SIAM), Philadelphia, PA, 2011. xii+110 pp.
- [45] M. Patrão, Morse decomposition of semiflows on topological spaces. *J. Dynam. Differential Equations* **19** (2007) 181-198.
- [46] P. Poláčik and I. Tereščák, Exponential separation and invariant bundles for maps in ordered Banach spaces with applications to parabolic equations, *J. Dynam. Differential Equations* **5** (1993) 279-303.
- [47] S.J. Schreiber and C.-K. Li, Evolution of unconditional dispersal in periodic environments. *J. Biol. Dyn.* **5** (2011), no. 2, 120-134.

- [48] H. L. Smith, Monotone Dynamical Systems, An Introduction to the Theory of Competitive and Cooperative Systems, Mathematical Surveys and Monographs, 41 American Mathematical Society, Providence, RI, 1995.
- [49] H. L. Smith and H. R. Thieme, Dynamical systems and population persistence. Graduate Studies in Mathematics, 118. American Mathematical Society, Providence, RI, 2011.