ON THE EVOLUTION OF SLOW DISPERSAL IN MULTI-SPECIES COMMUNITIES

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Abstract. For any $N \geq 2$, we show that there are choices of diffusion rates $\{d_i\}_{i=1}^N$ such that for N competing species which are ecologically identical and having distinct diffusion rates, the slowest diffuser is able to competitive exclude the remainder of the species. In fact, the choices of such diffusion rates is open in the Hausdorff topology. Our result provdes some evidence in the affirmative direction regarding the conjecture by Dockery et al. in [15]. The main tools include Morse decomposition of the semiflow, as well as the theory of normalized principal bundle for linear parabolic equations.

1. Introduction

Many organisms adapt to the surrounding environment through their dispersal behavior. It is important to determine the circumstances in which organisms modify their dispersal strategies under the driving forces of evolution. In a pioneering paper, Hastings introduced the point of view of studying the effect of individual factors on the evolution of dispersal independently, using mathematical modeling [20]. By analyzing the outcome of invasion between two competing species, assuming they are identical except for their dispersal rates, Hastings showed that passive diffusion is selected against in an environment that is constant in time, but varies in space. Subsequently, Dockery et al. [15] refined Hastings findings via a more explicit Lotka-Volterra model. They showed that it is impossible for two or more ecologically identical species, moving randomly at different rates, to coexist at an equilibrium. When the number of species is equal to two, they determined the global dynamics of the competition system completely

2010 *Mathematics Subject Classification.* 35Q92,37B35,37L45,35B40 .

Key words and phrases. evolution of dispersal, reaction-diffusion, Perturbation of Morse decomposition, principal bundle, competition exclusion .

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RSC is partially supported by NSF grant DMS-1853478; KYL is partially supported by NSF grant DMS-1853561.

by demonstrating the faster disperser is always driven to extinction by the slower disperser, regardless of initial conditions.

The work of Hastings and Dockery et al. have been highly influential in prompting advances in both mathematical and biological aspects of the evolution of dispersal. In [1] Altenberg showed a reduction principle, which says that the growth bounds for certain class of linear operators exhibit monotone dependence on the mixing coefficient. This principle gives a mathematical explanation of the relative proliferative advantage of slower dispersers in a static, but spatially varying environment.

The theory of habitat selection can also explain the evolution of slow dispersal among passive dispersers. As observed by Hastings, passive diffusion transports individuals from more favorable locations to less favorable ones in an average sense, rendering passive diffusion to be selected against. The picture is different, however, if the dispersal is conditional on the local environment. An important class of dispersal strategies consists of ones enabling a population to become perfectly aligned with the heterogeneous resource distribution, thus achieving the so called ideal free distribution [17]. In this circumstance, it is shown that such a dispersal strategy is selected for, in the sense that it is both an evolutionarily stable strategy and a neighborhood invader strategy. See [3, 5, 12, 29] for results on reaction-diffusion models; and [6, 7, 8, 14] for results in other modeling settings.

The work of Hastings and Dockery et al. has also stimulated substantial mathematical analysis of competition models involving two species. We mention the work of [21, 36, 38] for passive dispersal, and [2, 4, 11, 10, 26, 32, 33] for conditional dispersal. An interesting application concerns the evolution of dispersal in stream populations, which are subject to a unidirectional drift [44, 47]. It has been shown that in some circumstances, faster dispersal is sometimes selected for [39, 42]. See also [19, 34, 41]. We also mention the work [28] on the evolution of dispersal in phytoplankton populations, where individuals compete non-locally for sunlight.

Most of the above results are restricted to the case when the number of species is equal to two. In this case, the abstract tools of monotone dynamical systems [27, 35, 49] can be applied to determine the global dynamics of the competition system. Results for three or more competing species are relatively rare [16, 30, 31, 40], and the question of global dynamics remains an open and challenging problem. In the following, we will address two conjectures of Dockery et al. concerning a model involving N competing species, which are identical except for the passive dispersal rates.

1.1. **Two conjectures of Dockery et al.** The following Lotka-Volterra model of N competing species, which are subject to passive dispersal, was introduced by Dockery et al. [15].

$$\begin{cases} \partial_t u_i(x,t) = d_i \Delta u_i(x,t) + u_i(x,t)\left[m(x) - \sum_{j=1}^N u_j(x,t)\right] \\ \partial_\nu u_i(x,t) = 0 \end{cases} \tag{1.1}$$

These N species are assumed to be identical except for their dispersal rates $0 < d_1 < ... < d_N$. Here Ω is a bounded domain in $\mathbb{R}^n$ with smooth boundary $\partial\Omega$, $\Delta = \sum_{j=1}^n \partial_{x_j x_j}$ is the Laplacian operator, ∂_ν is the outer-normal derivative on $\partial\Omega$. We also assume

$$m(x) \in C^\alpha(\overline{\Omega}) \text{ is non-constant, and } \int_\Omega m\,dx \geq 0.$$

In the following we denote

$$E_i = (0, ..., 0, \theta_{d_i}, 0, ..., 0) \quad \text{for} \quad 1 \leq i \leq N, \quad \text{and} \quad E_0 = (0, ..., 0) \tag{1.2}$$

to be the corresponding equilibria of (1.1), where for $d > 0$ the function $\theta_d(x)$ denotes the unique positive solution of

$$d\Delta\theta_d + \theta_d(m(x) - \theta_d) = 0 \text{ in } \Omega, \text{ and } \partial_\nu \theta_d = 0 \text{ on } \partial\Omega. \tag{1.3}$$

In case $N = 2$, Dockery et al. obtained a complete description of the dynamics of (1.1) by applying the abtract tools of monotone dynamical systems.

Theorem 1.1 ([15, Lemmas 3.9 and 4.1])**.** *Suppose $N = 2$ and $d_1 < d_2$. Then every positive solution of (1.1) converges to the equilibrium $(\theta_{d_1}, 0)$. Furthermore, a Morse decomposition for* $\operatorname{Inv} K^+$ *is given by*

$$M(1) = \{E_1\} \quad M(2) = \{E_2\}, \quad M(3) = \{E_0\},$$

where $\operatorname{Inv} K^+$ *denotes the maximal bounded invariant set of the dynamical system generated in $K^+ = \{(u_i)_{i=1}^N \in [C(\overline{\Omega})]^N : u_i \geq 0\}$ under (1.1).*

Roughly speaking, we say that $\{M(1), M(2), M(3)\}$ is a Morse decomposition of $\operatorname{Inv} K^+$ if any bounded trajectory $\gamma(t)$ converges to some equilibrium, and that, if $\gamma(t)$ is defined for $t \in \mathbb{R}$, then $\gamma(\infty) \subset M(i)$ and $\gamma(-\infty) \subset M(j)$ for some $i < j$. The precise definition of a Morse decomposition will be given in Subsection 1.2, after some related dynamical system concepts are introduced.

When $N \geq 3$, it is conjectured in [15] that the slowest disperser continues to win the competition.

Conjecture 1. *Let $N \geq 3$ and $0 < d_1 < ... < d_N$. Then the equilibrium $E_1 = (\theta_{d_1}, 0, ..., 0)$ is globally asymptotically stable among all positive solutions of (1.1).*

Another version of the conjecture, also due to Dockery et al., can be formulated in terms of the concept of Morse Decomposition.

Conjecture 2. *Let $N \geq 3$ and $0 < d_1 < ... < d_N$. Then a Morse decomposition for* Inv K^+ *is given by*

$$M(i) = \{E_i\} \quad \text{for } 1 \leq i \leq N, \quad \text{and} \quad M(N+1) = \{E_0\}.$$

Define $\mathcal{D}$ to be the collection of all finite sets of positive real numbers such that Conjecture 2 holds; i.e.

$$\mathcal{D} = \cup_{N=2}^{\infty}\{(d_i)_{i=1}^N \,:\, \text{Conjecture 2 holds.}\}.$$

We first observe that Conjecture 2 implies Conjecture 1, for any N.

Proposition 1.2. *Let $0 < d_1 < d_2 < ... < d_N$ be given. If $(d_i)_{i=1}^N \in \mathcal{D}$, then every interior trajectory of* (1.1) *converges to E_1.*

Moreover, if $N = 3$, the two conjectures are equivalent.

Proposition 1.3. *Let $0 < d_1 < d_2 < d_3$ be given. Then $(d_i)_{i=1}^3 \in \mathcal{D}$ if and only if every interior trajectory of* (1.1) *converges to E_1.*

The goal of this paper is to prove the following stability result.

Theorem 1.4. *The collection $\mathcal{D}$ is open in the space of finite sets relative to the Hausdorff metric.*

By the theorem of Dockery et al., the family $\mathcal{D}$ contains any doubleton sets of positive numbers. Our result thus gives a step towards an affirmative answer to Conjectures 1 and 2.

As a corollary, we obtain some global stability results for (1.1) with no restriction on the number of species N.

Corollary 1.5. *Given $0 < \hat{d}_1 < \hat{d}_2$, there exists $\varepsilon > 0$ such that for any integer $N \geq 3$ and any $(d_i)_{i=1}^N$ such that*

$$0 < d_1 < d_2 < ... < d_N \quad \text{and} \quad \text{dist}_H((d_i)_{i=1}^N, \{\hat{d}_1, \hat{d}_2\}) < \varepsilon,$$

then for the problem (1.1) *of N species, every positive solution converges to the equilibrium $E_1 = (\theta_{d_1}, 0, ..., 0)$. Here $dist_H$ is the Hausdorff metric.*

Finally, we also mention that the dynamics of arbitrary number of competing species was considered in the paper [6] in the context of patch models, which are discrete in space version of (1.1). When at least one of the patches is a sink (which is equivalent to $m(x)$ changes sign in the reaction-diffusion context), they showed that the zero disperser can competitively exclude all other species, by the construction a Lyapunov function.

1.2. **Definitions.** Let $X = [C(\overline{\Omega})]^N$ be the Banach space with norm $\|u\| = \max\limits_{1\leq i\leq N} \sup_\Omega |u_i|$, and let K^+ be the cone of non-negative functions in X. Then the Neumann Laplacian operator Δ is a sectorial operator with domain

$$D(\Delta) = \cap_{r>1}\{u \in W^{2,r}(\Omega) : \Delta u \in C(\overline{\Omega}),\ \text{ and } \partial_\nu u = 0 \text{ on } \partial\Omega\};$$

and we denote the fractional power of Δ by Δ^ξ for some $0 < \xi < 1$ (see [43, Ch. 2]). It is a standard fact that the reaction-diffusion system (1.1) generates a semiflow in X, which we will denote here by $\Psi : [0,\infty) \times X$, i.e., for the solution $u(x,t)$ of (1.1) it holds that

$$u(\cdot, t + t_0) = \Psi(t, u(\cdot, t_0)) \quad \text{ for } t, t_0 \geq 0.$$

We say that a function $\gamma : \mathbb{R} \to X$ is a full trajectory if

$$\gamma(t + t_0) = \Psi(t, \gamma(t_0)) \quad \text{ for all } t \geq 0,\ t_0 \in \mathbb{R}.$$

A subset A of X is an invariant set if every $a \in A$ lies on a full trajectory $\gamma(t)$ such that $\{\gamma(t) : t \in \mathbb{R}\} \subset A$. Let $\operatorname{Inv} K^+$ denote the maximal bounded invariant set in K^+ under (1.1). It is not difficult to see that $\operatorname{Inv} K^+$ is compact, and attracts every trajectory in K^+.

Recall also that the ω- and α-limit sets of a point $u_0 \in K^+$ are given by

$$\begin{cases} \omega(u_0) = \{\tilde{u} \in X : \tilde{\Phi}(t_j, u_0) \to \tilde{u} \quad \text{for some } t_j \to \infty.\}, \\ \alpha(u_0) = \{\tilde{u} \in X : \tilde{\Phi}(t_j, u_0) \to \tilde{u} \quad \text{for some } t_j \to -\infty.\}, \end{cases}$$

where the latter is well-defined if and only if u lies on a full trajectory.

Next, we define the concept of Morse decomposition, which is relevant in considering the global dynamics of (1.1). We say that a finite collection of disjoint compact invariant subsets of $\operatorname{Inv} K^+$,

$$\{M(i) \subset \operatorname{Inv} K^+ \,:\, 1 \leq i \leq m\},$$

is a Morse decomposition if, for every $u_0 \in K^+ \setminus \cup_{i=1}^m M(p)$ with bounded trajectory, there exists i with $1 \leq i \leq m$ such that $\omega(u_0) \subset M(i)$, and if u lies on a full trajectory, then there exists j such that $i < j \leq m$ and $\alpha(u_0) \subset M(j)$.

1.3. **Proofs of Propositions 1.2 and 1.3.** First, we recall the statement of [15, Lemma 3.9]. (See also Lemma 4.2.)

Lemma 1.6. *Fix $0 < d_1 < ... < d_N$. For any $u_0 \in \operatorname{Int} K^+$, if the trajectory $\Psi(t, u_0)$ converges to an equilibrium, i.e.*

$$\lim_{t\to\infty} \Psi(t, u_0) = E_i \quad \textit{for some } i \in \{0, 1, 2, 3, ..., N\},$$

then necessarily $i = 1$; i.e. $\Psi(t, u_0) \to E_1$. Here E_i is defined in (1.2).

Proof of Proposition 1.2. Suppose $(\hat{d}_k)_{k=1}^K \in \mathcal{D}$, then the system (1.1) admits a Morse decomposition where the Morse sets consist of the $(N+1)$ equilbria. Hence, every internal trajectory converges to an equilibrium E_i (see (1.2)). By Lemma 1.6, it can only converge to E_1. □

Proof of Proposition 1.3. It suffices to show the converse. Suppose $0 < d_1 < d_2 < d_3$ are given such that all interior trajectories of (1.1) converge to E_1. We need to show that

$$M(1) = E_1, \quad M(2) = E_2, \quad M(3) = E_3, \quad M(4) = (0,0,0)$$

is a Morse decomposition of the semiflow.

For the trajectories starting at $u_0 \in K^+ \setminus (\operatorname{Int} K^+)$, by strong maximum principle, it either enters the $\operatorname{Int} K^+$ for all $t > 0$, or there is at least one component that is identically zero for all $t > 0$. In the first case, the trajectory also converges to E_1. In the second case, the system reduces to the two-species case, so that the solution converges to E_i, where $i = 1, 2$ is the smallest integer such that the i-th component of u_0 is non-zero. Moreover, there is no cycle of fixed points, since if E_i is chained to E_j (i.e. there is a full trajectory connecting from E_i to E_j), then the trajectory a positive solution of either the full three-species system, or a two-species subsystem. In either case, we have $i > j$. It therefore follows from [50, Theorem 3.2] that any compact internally chain transitive set is an equilibrium point. Since any omega (resp. alpha) limit set is internally chain transitive, it can only be one of the E_i. The proof of the proposition is completed. □

1.4. **Setting up the proof of Theorem 1.4.** Suppose $K \geq 2$ and a finite increasing sequence $(\hat{d}_k)_{k=1}^K \subset \mathcal{D}$ are given. Consider, for a small $\epsilon > 0$, any $N \geq 2$ and any finite increasing sequence $(d_i)_{i=1}^N$ such that

$$N \geq K \quad \text{and} \quad (d_i)_{i \in I_k} \subset (\hat{d}_k - \varepsilon, \hat{d}_k + \varepsilon) \tag{1.4}$$

for some partition $\{I_k\}_{k=1}^K$ of $\{1, ..., N\}$. We introduce three closely related dynamical systems.

Let $\Phi : [0, \infty) \times X \to X$ be the semigroup operator generated by the unperturbed problem of K species:

$$\begin{cases} \partial_t \hat{U}_k(x,t) = \hat{d}_k \Delta \hat{U}_k(x,t) + \hat{U}_k(x,t) \left[m(x) - \sum_{j=1}^K \hat{U}_j(x,t) \right] & \text{for } 1 \leq k \leq K \\ \partial_\nu \hat{U}_k(x,t) = 0 & \text{for } 1 \leq k \leq K \end{cases} \tag{$\hat{P}_0$}$$

Let $\varphi : [0,\infty) \times X \to X$ be the semigroup operator generated by the unperturbed problem of N species (with non-distinct diffusion rates):

$$\begin{cases} \partial_t u_i(x,t) = \hat{d}_k \Delta u_i(x,t) + u_i(x,t)\left[m(x) - \sum_{j=1}^N u_j(x,t)\right] & \text{for } i \in I_k,\ 1 \le k \le K, \\ \partial_\nu u_i(x,t) = 0 & \text{for } i \in I_k,\ 1 \le k \le K, \end{cases} \tag{P_0}$$

Let $\varphi_\varepsilon : [0,\infty) \times X \to X$ be the semigroup operator generated by the perturbed problem of N species (with distinct diffusion rates):

$$\begin{cases} \partial_t u_i(x,t) = d_i \Delta u_i(x,t) + u_i(x,t)\left[m(x) - \sum_{j=1}^N u_j(x,t)\right] & \text{for } 1 \le i \le N, \\ \partial_\nu u_i(x,t) = 0 & \text{for } 1 \le i \le N. \end{cases} \tag{P_ε}$$

Then, define the projection $\mathcal{P} : \mathbb{R}^N \to \mathbb{R}^K$ by

$$[\mathcal{P}(y_1,\dots,y_N)]_k = \sum_{i\in I_k} y_i \quad \text{for } 1 \le k \le K. \tag{1.5}$$

and denote $U = \mathcal{P}u$, i.e.

$$U_k := \sum_{i\in I_k} u_i \quad \text{for } 1 \le k \le K. \tag{1.6}$$

Remark 1.7. Note that $\Phi(t, \mathcal{P}u_0) = \mathcal{P}\varphi(t,u_0)$ for all $t \ge 0$ and $u_0 \in K^+$.

1.5. **Outline of the proof.** Let $(\hat{d}_k)_{k=1}^K$ and $(d_i)_{i=1}^N$ be two finite subsets of $\mathbb{R}_+$, which are close in Hausdorff topology such that $(\hat{d}_k)_{k=1}^K \in \mathcal{D}$. We need to show that $(d_i)_{i=1}^N \in \mathcal{D}$ by examining the semiflow generated by (P_ε). The strategy of our proof is to first obtain a rough Morse decomposition of the flow of (P_ε) by relating it to ($\hat{P}_0$). This is based on the existence of a complete Lyapunov function for the unperturbed semiflow Φ corresponding to the Morse decomposition (Section 2), and some *a priori* parabolic estimates that imply uniform continuity of the intermediate and perturbed semiflows (Section 3). Then the rough Morse decomposition implies that every interior trajectory of the perturbed semiflow is ultimately dominated by the group of slowest dispersers whose diffusion rates are in a neighborhood of $\hat{d}_1$ (Section 4). In Section 5 we define the notion of normalized principal bundle, which is a generalization of the notion of principal eigenvalue for elliptic or periodic-parabolic problems and observe its smooth dependence with respect to the coefficients of the linear parabolic problem. This is the main technical tool to refine the Morse decomposition and complete the proof of the main theorem (Section 6). (A proof of the smooth dependence is provided in the Appendix. We believe this tool will also be useful in the study of dynamics of general reaction-diffusion systems which are not necessarily of Lotka-Volterra type; see, e.g. [9].) Some concluding remarks are presented in Section 7.

2. The complete Lyapunov function for the unperturbed semiflow Φ

Since $(\hat{d}_k)_{k=1}^K \in \mathcal{D}$, i.e. the semiflow Φ genereated by ($\hat{P}_0$) admits a Morse decomposition $\{M(k)\}_{k=1}^{K+1}$, the classical theorem due to Conley [13, P. 39] (see also [22, 46] and [15, Remark 1]) guarantees the existence of a continuous function $V : \mathcal{U}' \to \mathbb{R}$, in some neighborhood $\mathcal{U}'$ of $\operatorname{Inv} K^+$ relative to K^+, with the following properties:

- $M(k) \in V^{-1}(k)$ for each $k = 1, ..., K+1$,
- If $\Phi([0,T], U_0) \subset [\mathcal{U}' \setminus \cup_{k=1}^{K+1} M(k)]$, then

$$V(U_0) > V(\Phi(t, U_0)) \quad \text{for all } t \in (0, T]. \tag{2.1}$$

By Remark 1.7, the function V is the Lyapunov function of the semiflows Φ and φ, which are generated by ($\hat{P}_0$) and (P_0). It will be the main tool allowing us to control and compare the dynamics generated by the three semiflows given in Subsection 1.4. In the following, we recall [15, Lemma 4.4].

Lemma 2.1. *For given $0 < \hat{d}_1 < ... < \hat{d}_K$, consider the semigroup operator Φ generated by problem ($\hat{P}_0$). For any $r > 0$ and $\mu > 0$, there exist $T > 0$ and a neighborhood $\mathcal{U}$ of $\operatorname{Inv} K^+$ contained in $\mathcal{U}'$, such that if $\Phi(t, U_0)$ is a solution of ($\hat{P}_0$) such that*

$$\Phi([0,t], U_0) \subset \mathcal{U} \setminus \left[\cup_{k=1}^{K+1} B_r(M(k))\right] \qquad \text{for some } t \geq T,$$

then

$$V(U_0) - V(\Phi(t, U_0)) > \mu.$$

Proof. Let $r > 0$ and $\mu > 0$ be given. We first prove that there exists a neigborhood $\mathcal{U}$ of $\operatorname{Inv} K^+$ such that

$$\tilde{\mu} := \inf\,[V(U_0) - V(\Phi(1, U_0)] > 0, \tag{2.2}$$

where the infimum is taken over all initial data U_0 satisfying

$$\Phi([0,1], U_0) \subset \mathcal{U} \setminus [\cup_{k=1}^{K+1} B_r(M(k))].$$

Suppose to the contrary that (2.2) fails for every neighborhood $\mathcal{U}$ of $\operatorname{Inv} K^+$, then there exist sequences $\{U^n\} \subset \mathcal{U}'$ and $\{\mu_n\} \subset (0, \infty)$ such that

$$\Phi([0,1], U^n) \subset \mathcal{U}' \setminus [\cup_{k=1}^{K+1} B_r(M(k))], \quad \operatorname{dist}(U^n, \operatorname{Inv} K^+) \to 0, \quad \mu_n \to 0.$$

and

$$V(U^n) - V(\Phi(1, U^n)) \leq \mu_n. \tag{2.3}$$

By the compactness of $\operatorname{Inv} K^+$, we may pass to a subsequence so that

$$U^n \to \overline{U} \in \operatorname{Inv} K^+ \setminus [\cup_{k=1}^{K+1} B_r(M(k))].$$

By continuous dependence on initial data, $\Phi([0,1], \overline{U}) \subset \operatorname{Inv} K^+ \setminus [\cup_{k=1}^{K+1} B_r(M(k))]$, hence

$$\begin{aligned} 0 &< V(\overline{U}) - V(\Phi(1, \overline{U})) \\ &= \lim_{n\to\infty} (V(U^n) - V(\Phi(1, U^n)) \\ &\le \lim_{n\to\infty} \mu_n = 0, \end{aligned}$$

a contradiction. This shows the existence of a neighborhood $\mathcal{U}$ of $\operatorname{Inv} K^+$ and a positive number $\tilde{\mu} > 0$ such that (2.2) holds.

Finally, observe that for given $\mu > 0$, if $\mu \in (0, \tilde{\mu}]$, then we can take $T = 1$ and (2.2) implies the desired conclusion. In case $\mu > \tilde{\mu}$, it suffices to choose T to be an integer such that $\tilde{\mu} T \ge \mu$. □

3. Uniform continuity of the intermediate semiflow φ and perturbed semiflow φ_ε

Recall that φ is the semiflow generated by (P_0) with diffusion rates $(\hat{d}_k)_{k=1}^K$, and φ_ε is the semiflow generated by (P_ε) with diffusion rates $(d_i)_{i=1}^N$ satisfying (1.4). The purpose of this section is to establish some parabolic estimates and show that the trajectories of φ and φ_ε stays close in any finite time interval. (In the following, $\|\cdot\| = \|\cdot\|_{C(\overline{\Omega})}$ or $\|\cdot\|_{[C(\overline{\Omega})]^n}$ for some n, unless otherwise specified.)

Lemma 3.1. *Let $(u_i)_{i=1}^N$ be a non-negative solution of (P_ε) (or (P_0)), such that*

$$\sum_{i=1}^N \|u_i(\cdot, 0)\|_{L^1(\Omega)} \le M,$$

then

$$\begin{cases} \sup_{t\ge 0} \sum_{i=1}^N \|u_i(\cdot, t)\|_{L^1(\overline{\Omega})} \le \max\{M, |\Omega| \sup_\Omega m\}, \\ \limsup_{t\to\infty} \sum_{i=1}^N \|u_i(\cdot, t)\|_{L^1(\overline{\Omega})} < 2|\Omega| \sup_\Omega m. \end{cases} \tag{3.1}$$

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

$$\mathcal{N} = \{u \in K^+ : \sum_{i=1}^N \|u_i\|_{L^1(\Omega)} < 2|\Omega| \sup_\Omega m\}, \tag{3.2}$$

is open in X and forward-invariant with respect to both (P_0) and (P_ε), and hence contains the respective maximal bounded invariant sets $\operatorname{Inv} K^+$ *and* $\operatorname{Inv} K_\varepsilon^+$.

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

$$\frac{d}{dt}\left\|\sum_{i=1}^N u_i\right\|_{L^1(\Omega)} = \left\|\sum_{i=1}^N u_i m(x)\right\|_{L^1(\Omega)} - \left\|\sum_{i=1}^N u_i\right\|^2_{L^2(\Omega)}.$$
$$\leq (\sup_\Omega m)\left\|\sum_{i=1}^N u_i\right\|_{L^1(\Omega)} - \frac{1}{|\Omega|}\left\|\sum_{i=1}^N u_i\right\|^2_{L^1(\Omega)},$$

where we used Cauchy-Schwartz inequality for the last inequality. □

Lemma 3.2. *Let $(\hat{u}_i)_{i=1}^N$ (resp. $(u_i)_{i=1}^N$) be a non-negative solution of (P_0) (resp. (P_ε)) with initial data in $\mathcal{N}$. If $\epsilon \in (0, \hat{d}_1/2)$, then there exists $C_1 = C_1((\hat{d}_k)_{k=1}^K, \Omega, m)$ (but otherwise independent of N and $(d_i)_{i=1}^N$ satisfying (1.4)) such that*

$$\sum_{i=1}^N \|\hat{u}_i(x,t)\|_{C^{1+\alpha,(1+\alpha)/2}(\overline{\Omega}\times[1,\infty))} + \sum_{i=1}^N \|u_i(x,t)\|_{C^{1+\alpha,(1+\alpha)/2}(\overline{\Omega}\times[1,\infty))} \leq C_1. \tag{3.3}$$

Proof. By Lemma 3.1, we have

$$\sup_{t\geq 1}\sum_{j=1}^N \|u_i\|_{L^1(\Omega\times[t-1,t+1])} \leq 4|\Omega|\sup_\Omega m.$$

Since $\partial_t u_i - d_i\Delta u_i \leq m(x)u_i$, we can apply the local maximum principle to deduce that

$$\sup_{t\geq 1}\|u_i\|_{L^\infty(\overline{\Omega}\times[t-1/2,t+1])} \leq C\sup_{t\geq 1}\|u_i\|_{L^1(\Omega\times[t-1,t+1])}. \tag{3.4}$$

(It is essential that we have dropped the nonlinear terms involving $u_i u_j$ and work with the differential inequality when applying the local maximum principal for strong sub-solutions, otherwise the constant in (3.4) may depend on initial data.)

Applying parabolic L^p estimate to the parabolic equation $\partial_t u_i - d_i\Delta u_i = (m(x) - \sum u_j)u_i$ (which can be regarded as a linear parabolic equation of u_i with L^∞ bounded coefficients) and by the Sobolev embedding theorem, the above can be improved to

$$\sup_{t\geq 1}\|u_i\|_{C^{1+\alpha,(1+\alpha)/2}(\overline{\Omega}\times[t,t+1])} \leq C'\sup_{t\geq 1}\|u_i\|_{L^1(\Omega\times[t-1,t+1])}. \tag{3.5}$$

And the desired conclusion follows by summing i from 1 to N,

$$\sum_{j=1}^N \|u_i\|_{C^{1+\alpha,(1+\alpha)/2}(\overline{\Omega}\times[1,\infty))} \leq C'\sup_{t\geq 1}\sum_{j=1}^N \|u_i\|_{L^1(\Omega\times[t-1,t+1])} \leq C'''.$$

Since d_i are uniformly bounded from above and below from zero, the constants C, C', C'' in the above estimates can be chosen to be independent of N and $(d_i)_{i=1}^N$. This completes the proof. $\square$

In summary, we have the following.

Corollary 3.3. *Fix* $0 < \hat{d}_1 < \ldots < \hat{d}_K$, $\epsilon \in (0, \hat{d}_1/2)$ *and consider arbitrary* $N \geq K$ *and* $(d_i)_{i=1}^N$ *satisfying* (1.4)*. Then we have*

$$\left(\operatorname{Inv} K^+ \cup \operatorname{Inv} K_\varepsilon^+\right) \subset \mathcal{N},$$

where $\operatorname{Inv} K^+$ *and* $\operatorname{Inv} K_\varepsilon^+$ *are the invariant sets generated by* (P_0) *and* (P_ε) *respectively. Furthermore, there exists* C_0 *(dependent on* $\hat{d}_k$*, but independent of* $\varepsilon \in (0, \hat{d}_1/2)$*,* N *and* d_i*) such that for any solution* u *of* (P_ε) *(resp.* $\hat{u}$ *of* (P_0)*) with initial data* $u_0 \in \varphi(1, \mathcal{N}) \cup \varphi_\varepsilon(1, \mathcal{N})$*, we have*

$$\sum_{i=1}^N \|u_i(\cdot, t)\|_{C(\overline{\Omega})} + \sum_{i=1}^N \|\hat{u}_i(\cdot, t)\|_{C(\overline{\Omega})} \leq C_0 \quad \text{for } t \geq 0, \tag{3.6}$$

and for some $0 < \xi < 1/2$*,*

$$\sum_{i=1}^N \|\Delta^\xi u_i(\cdot, t)\|_{C(\overline{\Omega})} \leq C_0(1 + t^{-\xi}) \quad \text{for } t \geq 0. \tag{3.7}$$

Proof. Fix initial data $u_0 \in \varphi(1, \mathcal{N}) \cup \varphi_\varepsilon(1, \mathcal{N})$. Then by Lemma 3.2, there exists C_1 depending on $(\hat{d}_k)_{k=1}^K, \Omega$, and $m(x)$ but independent of N and $(d_i)_{i=1}^N$ such that (here $(u_0)_j$ denotes the j-th components of u_0)

$$\sum_{j=1}^N \|(u_0)_j\|_{C(\overline{\Omega})} \leq C_1 \quad \text{and} \quad \partial_\nu u_0 = 0 \quad \text{on } \partial\Omega.$$

We claim that

$$\sup_{0 \leq t \leq 1} \sum_{j=1}^N \|u_j(\cdot, t)\|_{C(\overline{\Omega})} \leq C_1 e^{\sup_\Omega m}.$$

Indeed, by using the differential inequality

$$\begin{cases} \partial_t u_i - d_i \Delta u_i \leq (\sup_\Omega m) u_i & \text{in } \Omega \times [0, \infty). \\ \partial_\nu u_i = 0 & \text{on } \partial\Omega \times [0, \infty), \\ u_i(x, 0) = (u_0)_i(x) & \text{in } \Omega, \end{cases} \tag{3.8}$$

we can compare each u_i with the super-solution $\overline{u}_i$ of (3.8), given by

$$\overline{u}_i(x, t) := e^{(\sup_\Omega m)t} \|(u_0)_i\|_{C(\overline{\Omega})} \quad \text{in } \Omega \times [0, \infty),$$

to deduce that

$$\|u_i(\cdot,t)\|_{C(\overline{\Omega})} \leq e^{\sup_\Omega m}\|(u_0)_i\|_{C(\overline{\Omega})} \quad \text{ for } t\in[0,1].$$

Hence we have

$$\sup_{0\leq t\leq 1}\sum_{i=1}^N \|u_i(\cdot,t)\|_{C(\overline{\Omega})} \leq e^{\sup_\Omega m}\sum_{j=1}^N \|(u_0)_j\|_{C(\overline{\Omega})} \leq C_1 e^{\sup_\Omega m}.$$

Combining with (3.3), we deduce the boundedness of $\sup_{t\geq 0}\sum_{i=1}^N \|u_i(\cdot,t)\|_{C(\overline{\Omega})}$. Since the proof for the boundeness of $\sup_{t\geq 0}\sum_{i=1}^N \|\hat{u}_i(\cdot,t)\|_{C(\overline{\Omega})}$ is similar, we omit the proof. This establishes (3.6).

Finally, we observe that each u_i satisfies a non-autonomous linear parabolic equation with regular coefficients, so that (3.7) follows from [43, Theorem 5.1.17]. □

Recalling that φ (resp. φ_ε) is the semiflow generated by (P_0) (resp. (P_ε)), we now prove the main theorem of this section.

Proposition 3.4. *Fix $(\hat{d}_k)_{k=1}^K \in \mathcal{D}$. For each $T>0$ and $\eta>0$, there exists ε_1 such that for $\varepsilon\in(0,\varepsilon_1)$, and arbitrary $N\in\mathbb{N}$, $(d_i)_{i=1}^N$ satisfying (1.4), we have*

$$\|\mathcal{P}\varphi(t,u_0) - \mathcal{P}\varphi_\varepsilon(t,u_0)\| < \eta \quad \text{for } \ 0\leq t\leq T, \quad u_0\in\varphi(1,\mathcal{N})\cup\varphi_\varepsilon(1,\mathcal{N}). \tag{3.9}$$

where $\mathcal{P}$ is the projection operator given in (1.5) and the open set $\mathcal{N}$ is defined in (3.2).

Proof. Let $\operatorname{Inv} K^+$ (resp. $\operatorname{Inv} K^+_\varepsilon$) denote the maximal invariant set in K^+ of the semiflow φ generated by (P_0) (resp. the semiflow φ_ε generated by (P_ε)). Let $\mathcal{N}$ be the neighborhood of $\operatorname{Inv} K^+$ specified by (3.2).

Let $(\hat{u}_i)_{i=1}^N = \varphi(t,u_0)$ and $(u_i)_{i=1}^N = \varphi_\varepsilon(t,u_0)$. Since $u_0\in\varphi(1,\mathcal{N})\cup\varphi_\varepsilon(1,\mathcal{N})$, we can apply Corollary 3.3 to obtain the estimates

$$\sum_{i=1}^N [\|u_i(t)\| + \|\hat{u}_i(t)\|] \leq C \quad \text{ and } \quad \sum_{i=1}^N \|\Delta^{1/2}u_i(t)\| \leq C(1+t^{-1/2}) \tag{3.10}$$

for $t\geq 0$, where C is independent of N.

We will estimate u_i by the variation of constants formula. Recall the partition $\{I_k\}_{k=1}^K$ of $\{1,2,...,N\}$ given in (1.4). For $i\in I_k$, we have

$$\begin{cases} \hat{u}_i(t) &= e^{t\hat{d}_k\Delta}(u_0)_i + \int_0^t e^{(t-s)\hat{d}_k\Delta}[\hat{u}_i(s)(m-\sum_{j=1}^N \hat{u}_j(s))]\,ds,\\ u_i(t) &= e^{t\hat{d}_k\Delta}(u_0)_i + \int_0^t e^{(t-s)\hat{d}_k\Delta}[u_i(s)(m-\sum_{j=1}^N u_j(s))]\,ds \\ & \qquad +(d_i-\hat{d}_k)\int_0^t e^{(t-s)\hat{d}_k\Delta}\Delta u_i(s)\,ds \end{cases} \tag{3.11}$$

Denoting $\hat{U} = \mathcal{P}\hat{u}$, $U = \mathcal{P}u$, and W as follows

$$\hat{U}_k = \sum_{i\in I_k} \hat{u}_i, \quad U_k = \sum_{i\in I_k} u_i, \quad W_k = \sum_{i\in I_k} \frac{d_i - \hat{d}_k}{\varepsilon} u_i, \qquad \text{for } 1 \le k \le K,$$

and then adding (3.11) over $i \in I_k$, we deduce

$$\begin{cases} \hat{U}_k(t) & = e^{t\hat{d}_k\Delta}(U_0)_k + \int_0^t e^{(t-s)\Delta}[\hat{U}_k(s)(m - \sum_{j=1}^N \hat{u}_j(s))]\, ds, \\ U_k(t) & = e^{t\hat{d}_k\Delta}(U_0)_k + \int_0^t e^{(t-s)\Delta}[U_k(s)(m - \sum_{j=1}^N u_j(s))]\, ds \\ & \qquad +\varepsilon \int_0^t e^{(t-s)\hat{d}_k\Delta}\Delta W_k(s)\, ds \end{cases} \tag{3.12}$$

Denoting $Q_k(t) = U_k(t) - \hat{U}_k(t)$, then by subtracting the first equation of (3.12) from the second equation, we have

$$\begin{aligned} Q_k(t) = &\int_0^t e^{(t-s)\hat{d}_k\Delta}[U_k(s)(m - \sum_{\ell=1}^K U_\ell(s)) - \hat{U}_k(s)(m - \sum_{\ell=1}^K \hat{U}_\ell(s))]\, ds \\ &+ \varepsilon \int_0^t e^{(t-s)\hat{d}_k\Delta}\Delta W_k(s)\, ds \\ := &\, I_1(k) + \varepsilon I_2(k). \end{aligned}$$

Now, by the first estimate of (3.10), we have

$$\sum_{k=1}^K \|I_1(k)\| \le C_1 \int_0^t \sum_{k=1}^K \|Q_k(s)\|\, ds,$$

where we have used the uniform boundedness of trajectories in X. Moreover, let $\xi \in (0, 1/2)$ be as given in Corollary 3.3, then

$$\begin{aligned} \sum_{k=1}^K \|I_2(k)\| &\le \sum_{k=1}^K \sum_{i\in I_k} |d_i - \hat{d}_k| \int_0^t \left\| e^{(t-s)\hat{d}_k\Delta}\Delta^{1-\xi}\right\| \left\|\Delta^\xi u_i(s)\right\|\, ds \\ &\le \sum_{i=1}^N \varepsilon \int_0^t C_T(t-s)^{-(1-\xi)} \left\|\Delta^\xi u_i(s)\right\|\, ds \\ &\le \varepsilon C_T \int_0^t (t-s)^{-(1-\xi)} \sum_{i=1}^N \left\|\Delta^\xi u_i(s)\right\|\, ds \end{aligned}$$

where the constant C_T can be chosen to be uniform for $t \in [0, T]$. Note that we used $\sum_{k=1}^K \sum_{i\in I_k} = \sum_{i=1}^N$ and that $\left\| e^{(t-s)\hat{d}_k\Delta}\Delta^{1-\xi}\right\| \le C_T(t-s)^{-(1-\xi)}$

(see [43, Chapter 2]) to derive the first inequality. Then,

$$\begin{aligned}\sum_{k=1}^K \|Q_k(t)\| &\leq C_T\left[\int_0^t \sum_{k=1}^K \|Q_k(s)\|\,ds + \varepsilon\int_0^t (t-s)^{-(1-\xi)}\sum_{i=1}^N \left\|\Delta^\xi u_i(s)\right\|\,ds\right]\\ &\leq C_T'\left[\int_0^t \sum_{k=1}^K \|Q_k(s)\|\,ds + \varepsilon\int_0^t (t-s)^{-(1-\xi)}(1+s^{-\xi})\,ds\right]\\ &\leq C_T''\left[\int_0^t \sum_{k=1}^K \|Q_k(s)\|\,ds + \varepsilon\right],\end{aligned}$$

where we used (3.10). Hence, by the Gronwall's inequality, we have

$$\sup_{0\leq t\leq T}\sum_{k=1}^K \|Q_k(t)\| \leq \varepsilon C_T'' e^{C_T'' T} = \varepsilon C_T'''. \tag{3.13}$$

This proves Proposition 3.4. □

4. Ultimate bounds for the perturbed semiflow

Definition 4.1. Let $d' > 0$ and $h' \in L^\infty(\Omega)$, define $\mu_1(d', h')$ to be the principal eigenvalue of

$$d'\Delta\psi + h'(x)\psi + \lambda\psi = 0 \text{ in } \Omega, \quad \text{and} \quad \partial_\nu\psi = 0 \text{ on } \partial\Omega.$$

The following is adapted from [15, Lemma 3.9].

Lemma 4.2. *Fix $(\hat{d}_k)_{k=1}^K$. There exists $\delta > 0$ such that for any $\varepsilon \in (0, \hat{d}_1/2, (\hat{d}_2 - \hat{d}_1)/2)$, and any $u_0 \in \operatorname{Int} K^+$, the omega limit set $\omega(u_0, \varphi_\varepsilon)$ under the semiflow of (P_ε) satisfies*

$$\mathcal{P}\omega(u_0,\varphi_\varepsilon) \not\subset B_\delta(M(k_0)) \quad \text{for any } k_0 \in \{2, ..., K+1\}.$$

Proof. Suppose to the contrary that there is $2 \leq k_0 \leq K+1$ and T_0 such that the solution $(u_i)_{i=1}^N = \varphi_\varepsilon([T_0,\infty), u_0)$ satisfies

$$\mathcal{P}\varphi_\varepsilon([T_0,\infty), u_0) \subset B_\delta(M(k_0)). \tag{4.1}$$

Define, $h(x,t) := m(x) - \sum_{j=1}^N u_j(x,t)$ and

$$h_\delta(x) := \inf_{(\hat{v}_k)\in B_\delta(M(k_0))}\left(m(x) - \sum_{k=1}^K \hat{v}_k\right),$$

then $h(x,t) \geq h_\delta(x)$ for all $t \geq T_0$. We claim that $\mu_1(d_1, h_\delta) < 0$ for all sufficiently small δ.

We first discuss the case $2 \leq k_0 < K+1$. By continuity, it suffices to show that $\mu_1(d_1, m - \theta_{\hat{d}_{k_0}}) < 0$. Since $d_1 < \hat{d}_{k_0}$ (as $d_1 < \hat{d}_1 + \varepsilon < \hat{d}_2 \leq \hat{d}_{k_0}$), we can apply the classical fact that μ_1 is strictly increasing in d [45, Proposition 4.4], to deduce that

$$\mu_1(d_1, m - \theta_{\hat{d}_{k_0}}) < \mu_1(d_{\hat{d}_{k_0}}, m - \theta_{\hat{d}_{k_0}}) = 0.$$

(The last equality holds since 0 is the eigenvalue with a positive eigenfunction $\theta_{\hat{d}_{k_0}}$.)

In case $k_0 = K + 1$, then it suffices to show that $\mu_1(d_1, m) < 0$. Indeed, if $\psi > 0$ is the principal eigenfunction of $\mu_1(d_1, m)$, then

$$d_1 \Delta\psi + m\psi + \mu_1(d_1, m)\psi = 0 \ \text{ in } \Omega, \ \text{ and } \ \partial_\nu \psi = 0 \ \text{ on } \partial\Omega.$$

Divide the above by ψ and integrate by parts, we have

$$d_1 \int_\Omega \frac{|\nabla\psi|^2}{\psi^2}\, dx + \int_\Omega m\, dx + \mu_1(d_1, m)|\Omega| = 0 \tag{4.2}$$

Since (i) $\int_\Omega m\, dx \geq 0$ and that (ii) $m(x)$, and thus $\psi(x)$, is non-constant, we deduce from (4.2) that $\mu_1(d_1, m) < 0$.

In conclusion, there exists $\delta > 0$ such that the principal eigenvalue λ of

$$d_1 \Delta\psi + h_\delta(x)\psi + \lambda\psi = 0 \ \text{ in } \Omega, \ \text{ and } \ \partial_\nu\psi = 0 \ \text{ on } \partial\Omega.$$

is negative. We also normalize the corresponding positive eigenfunction ψ to ensure $\inf_\Omega \psi = 1$. Now, since $h(x,t) \geq h_\delta(x)$, we can show that $u_1(x,t)$ and

$$\underline{u}_1(x,t) := 2\delta e^{-\lambda(t-t_0)}\psi(x),$$

where $t_0 \in [T_0, \infty)$ is to be specified, together form a pair of super- and sub-solutions of the linear parabolic equation

$$\partial_t w - d_1 \Delta w = h(x,t) w \quad \text{ in } \Omega \times [T_0, \infty),$$

under the Neumann boundary condition. By taking $t_0 \geq T_0$ sufficiently large, we have also $u_1(x, T_0) \geq \underline{u}_1(x, T_0)$. By the method of sub- and super-solutions, $u_1(x,t) \geq \underline{u}_1(x,t)$ for all $t \geq T_0$. However, when $t = t_0$, we have

$$u_1(x, t_0) \geq 2\delta\psi(x) \geq 2\delta \quad \text{ for all } x \in \Omega,$$

but this contradicts (4.1) when $t = t_0$. □

Proposition 4.3. *Given $(\hat{d}_k)_{k=1}^K \in \mathcal{D}$ and a sufficiently small $r > 0$, then there exists $\varepsilon > 0$ such that for any $N \in \mathbb{N}$ and $(d_i)_{i=1}^N$ such that (1.4) holds, and any solution u of (P_ε) with initial data $u_0 \in \operatorname{Int} K^+$, we have*

$$\limsup_{t\to\infty} \Big\| \sum_{i=1}^N u_i - \theta_{\hat{d}_1}(x) \Big\| < 2r, \tag{4.3}$$

Proof. Let φ (resp. φ_ε) be the semiflow operator corresponding to (P_0) (resp. (P_ε)), and denote its maximal bounded invariant set to be $\mathrm{Inv}\, K^+$ (resp. $\mathrm{Inv}\, K^+_\varepsilon$). Fix $\mu = 3/4$ and $r \in (0, \min\{1/4, \delta/2\})$ small enough (with δ given by Lemma 4.2) so that

$$|V(U) - V(\tilde{U})| < \frac{1}{4} \quad \text{if } U, \tilde{U} \in B_{2r}(M(k)), \text{ for some } 1 \leq k \leq K+1. \tag{4.4}$$

Since $V(M(k)) = k$, it follows that

$$V(B_{2r}(M(k))) \subset \left(k - \frac{1}{4}, k + \frac{1}{4}\right) \quad \text{for each } k. \tag{4.5}$$

Having chosen μ and r, we then choose $T > 1$ and $\mathcal{U}$ so that the conclusion of Lemma 2.1 holds. (Since $\mathrm{Inv}\, K^+ \cup \mathrm{Inv}\, K^+_\varepsilon \subset \mathcal{N}$, we can also assume that $\mathcal{U} \subset \mathcal{N}$.)

By Lemma 3.2, $\Phi(1, \mathcal{N}_0) = \mathcal{P}\varphi(1, \mathcal{N})$ is compact, where

$$\mathcal{N}_0 := \mathcal{P}\mathcal{N} = \{(U_k)_{k=1}^K \in K^+ : \sum_{k=1}^K \|U_k\|_{L^1(\Omega)} < 2|\Omega| \sup_\Omega m\}.$$

Since $\mathcal{U}$ is a neighborhood of the maximal bounded invariant set of the K-species problem ($\hat{P}_0$), there exists a finite time $T_0 > 1$ such that $\Phi(T_0, \mathcal{N}_0) \subset \mathcal{U}$. By Remark 1.7, this means $\mathcal{P}\varphi(T_0, \mathcal{N}) \subset \mathcal{U}$ and thus $\mathcal{P}\mathrm{Inv}\, K^+ \subset \mathcal{U}$.

Claim 1. *There exists $\epsilon_1 \in (0, \hat{d}_1/2)$ such that for all $\varepsilon \in (0, \varepsilon_1)$ and any N and $(d_i)_{i=1}^N$ satisfying (1.4), we have*

$$(\mathcal{P}\mathrm{Inv}\, K^+) \cup (\mathcal{P}\mathrm{Inv}\, K^+_\varepsilon) \subset \mathcal{U}.$$

By Lemma 3.2, there exists a compact set $\mathcal{K}$ independent of $\varepsilon \in (0, \hat{d}_1/2)$, N and $(d_i)_{i=1}^N$ such that

$$\mathcal{P}\varphi_\varepsilon(1, \mathcal{N}) \subset \mathcal{K} \subset \mathcal{N} \quad \text{and} \quad \mathcal{P}\varphi(T_0, \mathcal{K}) \subset \mathcal{U}.$$

Hence, we can apply Proposition 3.4 to show that there exists $\epsilon_1 \in (0, \hat{d}_1/2)$ so that for any $N \in \mathbb{N}$ and $(d_i)_{i=1}^N$ satisfying (1.4),

$$\mathcal{P}\varphi_\varepsilon(T_0 + 1, \mathcal{N}) \subset \mathcal{P}\varphi_\varepsilon(T_0, \mathcal{K}) \subset \mathcal{U}.$$

In particular, the maximal bounded invariant set $\mathrm{Inv}\, K^+_\varepsilon$ of the semiflow φ_ε generated by (P_ε) is also contained in $\mathcal{U}$. We emphasize that such a choice of ε_1 is uniform across all possible N and $(d_i)_{i=1}^N$ satisfying (1.4).

Next, by Proposition 3.4, there exists $\varepsilon_2 \in (0, \varepsilon_1)$ such that for all $\varepsilon \in (0, \varepsilon_2)$ and $u_0' \in \varphi(1, \mathcal{N}) \cup \varphi_\varepsilon(1, \mathcal{N})$, we have

$$\sup_{0 \leq t \leq 2T} \|\mathcal{P}\varphi(t, u_0') - \mathcal{P}\varphi_\varepsilon(t, u_0')\| < r, \tag{4.6}$$

and, provided $\mathcal{P}\varphi([0,2T],u_0') \subset \mathcal{U}$ and $\mathcal{P}\varphi_\varepsilon([0,2T],u_0') \subset \mathcal{U}$, that

$$\sup_{0\le t\le 2T} \|V(\mathcal{P}\varphi(t,u_0')) - V(\mathcal{P}\varphi_\varepsilon(t,u_0'))\| < \frac{\mu}{3}. \tag{4.7}$$

Now, fix an arbitrary trajectory $\varphi_\varepsilon(t,u_0)$ of (P_ε) with initial data $u_0 \in \operatorname{Int} K^+$. We will show (4.3). By Claim 1, we may perform a translation in time and assume without loss of generality that

$$\mathcal{P}\varphi(t,u_0) \in \mathcal{U}, \quad \text{and} \quad \mathcal{P}\varphi_\varepsilon(t,u_0) \in \mathcal{U} \quad \text{for all } t \ge 0.$$

Claim 2. *Let $\varepsilon \in (0,\varepsilon_2)$. Suppose there is $t_1 \ge 1$ such that*

$$V(\mathcal{P}\varphi_\varepsilon(t_1,u_0)) = k_1 + \frac{1}{2}, \quad \textit{for some } k_1 \in \{1,...,K+1\}, \tag{4.8}$$

then

$$\sup_{t_1<t<t_1+T} V(\mathcal{P}\varphi_\varepsilon(t,u_0)) < k_1 + \frac{3}{4}, \tag{4.9}$$

and

$$V(\mathcal{P}\varphi_\varepsilon(t_2,u_0)) \le k_1 + \frac{1}{2} \quad \textit{for some } t_2 \in (t_1, t_1+T]. \tag{4.10}$$

Denote $u_0' = \varphi_\varepsilon(t_1,u_0)$. Then (4.4) and (4.8) imply $u_0' \notin \cup_{k=1}^{K+1} B_r(M(k))$. Then, we have

$$V(\mathcal{P}\varphi_\varepsilon(t,u_0')) < V(\mathcal{P}\varphi(t,u_0')) + \frac{\mu}{3} \le V(\mathcal{P}u_0') + \frac{\mu}{3} = k_1 + \frac{3}{4} \quad \text{for } t \in [0,T],$$

where the first inequality is due to (4.7) and the second one is due to $\mathcal{P}\varphi(t,u_0') = \Phi(t,\mathcal{P}u_0')$ and the property of Lyapunov function. This proves (4.9).

Next, we show (4.10) by dividing into two cases:

(i) $\mathcal{P}\varphi([0,T],u_0') \cap \left[\cup_{k=1}^{K+1} B_r(M(k))\right] = \emptyset$

(ii) $\mathcal{P}\varphi([0,T],u_0') \cap \left[\cup_{k=1}^{K+1} B_r(M(k))\right] \ne \emptyset$

In case (i), we use (4.7) and then Lemma 2.1 to obtain

$$V(\mathcal{P}\varphi_\varepsilon(T,u_0')) < V(\mathcal{P}\varphi(T,u_0')) + \frac{\mu}{3} < V(\mathcal{P}u_0') - \frac{2\mu}{3} = k_1.$$

In case (ii), (2.1) implies there is an interger k_1' and $t_1' \in (0,T]$ such that $\mathcal{P}\varphi(t_1',u_0') \in B_r(M(k_1'))$. Furthermore, since V is decreasing along trajectories of $\Phi = \mathcal{P}\varphi$, we have $k_1' \le k_1$. Then,

$$V(\mathcal{P}\varphi_\varepsilon(t_1',u_0')) < V(\mathcal{P}\varphi(t_1',u_0')) + \frac{\mu}{3} < k_1' + \frac{1}{4} + \frac{\mu}{3} \le k_1 + \frac{1}{2},$$

where the first and second inequalities are due to (4.7) and (4.4), respectively. This proves (4.10) and completes the proof of Claim 2.

Claim 3. *There exists k_0 and T_ε such that*

$$k_0 - \frac{1}{2} < V(\mathcal{P}\varphi_\varepsilon(t,u_0)) < k_0 + \frac{3}{4} \quad \textit{for all } t \geq T_\varepsilon. \tag{4.11}$$

Remark 4.4. It follows from (4.5) and (4.11) that for $t \geq T_\varepsilon$, we have $\mathcal{P}\varphi_\varepsilon(t,u_0) \notin B_{2r}(M(k))$ for any $k \neq k_0$.

Define

$$k_0 = \min\left\{k \in \mathbb{N} \,:\, V(\mathcal{P}\varphi_\varepsilon(t_0,u_0)) \leq k + \frac{1}{2} \text{ for some } t_0 \geq 1\right\}.$$

By construction, $V(\mathcal{P}\varphi_\varepsilon(t,u_0)) > (k_0 - 1) + 1/2$ for all $t \geq 1$ and the lower bound of (4.11) holds. Moreover, there is $T_\varepsilon \geq 1$ such that $V(\mathcal{P}\varphi_\varepsilon(T_\varepsilon,u_0)) \leq k_0 + \frac{1}{2}$. Denote, for simplicity, $u_0' = \varphi_\varepsilon(T_\varepsilon,u_0)$. Suppose to the contrary that

$$V(\mathcal{P}\varphi_\varepsilon(t_3,u_0') \geq k_0 + \frac{3}{4} \quad \text{for some } t_3 > 0.$$

Define the set

$$S = \left\{t \in [0,t_3) \,:\, V(\mathcal{P}\varphi_\varepsilon(t_3,u_0')) \leq k_0 + \frac{1}{2}\right\},$$

then S is non-empty since $0 \in S$. Let $t_4 = \sup S$. By (4.9) we have $t_3 - t_4 > T$. By (4.10), we have $t_5 \in (t_4,t_3)$ such that $t_5 \in S$. This contradicts the definition of t_4. This proves (4.11).

Claim 4. *There exists $\epsilon_3 \in (0,\epsilon_2)$ such that if $\epsilon \in (0,\varepsilon_3)$, for any $u_0 \in$* Int K^+ *with a certain k_0 guaranteed by Claim 3, it follows that*

$$\mathcal{P}\omega(u_0,\varphi_\varepsilon) \subset B_{2r}(M(k_0)). \tag{4.12}$$

Suppose to the contrary that there is a certain $1 \leq k_0 \leq K+1$, a sequence $\varepsilon \to 0$ and $N = N^\varepsilon$ and $(d_i^\varepsilon)_{i=1}^{N^\varepsilon}$ and $u_0 = u_0^\varepsilon$ such that the conclusions of Claim 3 hold for that k_0 but (4.12) is false. Let $v_\varepsilon = \varphi_\varepsilon(T_\varepsilon,u_0^\varepsilon)$. Then $\mathcal{P}\omega(v_\varepsilon,\varphi_\varepsilon) \not\subset B_{2r}(M(k_0))$. Let $w_\varepsilon \in \omega(v_\varepsilon,\varphi_\varepsilon)$ such that $\mathcal{P}w_\varepsilon \notin B_{2r}(M(k_0))$.

Thanks to the *a priori* estimates developed in Lemma 3.2, $\{\mathcal{P}w_\varepsilon\}$ belongs to a compact set. Therefore, we can pass to a sequence $\varepsilon \to 0$ such that $\mathcal{P}w_\varepsilon \to \hat{W}$. Taking (4.11) into account,

$$k_0 - \frac{1}{2} \leq V(\mathcal{P}\varphi_\varepsilon(t,w_\varepsilon)) \leq k_0 + \frac{3}{4} \quad \text{for all } t \in \mathbb{R}.$$

As a result, we have $\hat{W} \in \operatorname{Inv} K^+$ and $k_0 - \frac{1}{2} \leq V(\Phi(\mathbb{R},\hat{W})) \leq k_0 + \frac{3}{4}$, where we implicitly used the observation in by Remark 1.7. However, since $M(k_0)$ is the maximal invariant set in

$$\big\{W \in \operatorname{Inv} K^+ \,:\, k_0 - \frac{1}{2} \leq V(W) \leq k_0 + \frac{3}{4}\big\},$$

we are led to the conclusion that $\{\hat{W}\} = M(k_0)$. This is a contradiction since $\hat{W} \notin B_{2r}(M(k_0))$. The proves Claim 4.

Now, in view of Lemma 4.2, $\mathcal{P}\omega(u_0, \varphi_\varepsilon) \not\subset B_{2r}(M(k))$ for all $k > 1$. Hence, for any $u_0 \in \operatorname{Int} K^+$, (4.12) holds with $k_0 = 1$. Since $M(1) = \{(\theta_{\hat{d}_1}, 0, ..., 0)\}$, this means

$$\limsup_{t\to\infty} \left\| \mathcal{P}\varphi_\varepsilon(t, u_0) - (\theta_{\hat{d}_1}, 0, ..., 0) \right\| < 2r.$$

This proves (4.3) and completes the proof of the proposition. □

5. The normalized principal bundle

In this section, we define the notion of a normalized principal bundle, which is a generalization of the notion of principal eigenfunction of an elliptic, or periodic-parabolic operator. We give a theorem concerning its smooth dependence on parameters, which is crucial in the completion of the proof of Theorem 1.4.

5.1. **The normalized principal bundle.** Given $d > 0$ and $h(x,t) \in C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R})$, we say that the pair $(\psi_1(x,t), H_1(t))$ is the corresponding normalized principal bundle if it satisfies

$$\begin{cases} \partial_t \psi_1(x,t) - d\Delta\psi_1(x,t) - h(x,t)\psi_1(x,t) = H_1(t)\psi_1(x,t) & \text{for } x \in \Omega,\ t \in \mathbb{R}, \\ \partial_\nu \psi_1(x,t) = 0 & \text{for } x \in \partial\Omega,\ t \in \mathbb{R}, \\ \int_D |\psi_1(x,t)|^2\, dx = 1 & \text{for } t \in \mathbb{R}, \\ \psi_1(x,t) > 0 & \text{for } x \in \Omega,\ t \in \mathbb{R}. \end{cases} \tag{5.1}$$

The existence and uniqueness of $(\psi_1(x,t), H_1(t))$ is proved in Theorem A.1.

Remark 5.1. If $h(x,t) = \hat{h}(x)$ for some time-independent function $\hat{h}$, then ψ_1 and H_1 are time-independent, and coincide with the principal eigenfunction and principal eigenvalue $(\psi_e(x), \lambda)$ of

$$-d\Delta\psi_e - \hat{h}(x)\psi_e = \lambda\psi_e \quad \text{in } \Omega, \quad \partial_\nu\psi_e = 0 \quad \text{on } \partial\Omega. \tag{5.2}$$

The main result of this section is the smooth dependence of the principal bundle on the coefficients.

Proposition 5.2. *The normalized principal bundle, as a mapping*

$$\begin{aligned} (d,h) &\mapsto (\psi_1, H_1) \\ \mathbb{R}_+ \times C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R}) &\to C^{2+\beta,1+\beta/2}(\overline{\Omega} \times \mathbb{R}) \times C^{1+\beta/2}(\mathbb{R}), \end{aligned}$$

is smooth.

Since the proof of Proposition 5.2 is self-contained, we will postpone it to the Appendix. See Proposition A.3 for details.

Corollary 5.3. *Let $\delta > 0$ and $\hat{h}(x) \in C^{\beta}(\overline{\Omega})$ be a non-constant function. There exists $r' > 0$ such that for any $d > 0$ and any function $h(x,t) \in C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R})$, if*

$$\delta < d < 1/\delta, \quad \|h(x,t) - \hat{h}(x)\|_{C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})} < r', \tag{5.3}$$

then the partial derivative $\partial_d H_1(t)$ of $H_1(t)$, with respect to the diffusion coefficient d, satisfies

$$\inf_{t\in\mathbb{R}} \partial_d H_1(t) \geq r'.$$

Proof. Denote by $(\psi_1(x,t;d,h), H_1(t;d,h))$ the normalized principal bundle satisfying (5.1) for some constant $d > 0$ and function h. By Remark 5.1, we see that

$$(\psi_1(x,t;d,\hat{h}), H_1(t;d,\hat{h}) = (\psi_e(x), \lambda)$$

where $(\psi_e(x), \lambda)$ is the principal eigenpair (5.2).

Next, we claim that $\partial_d\lambda > 0$ for all $d > 0$. Indeed, if we differentiate (5.2) with respect to d, (and denote the derivative as $'$)

$$\begin{cases} -d\Delta\psi_e' - \hat{h}\psi_e' - \Delta\psi_e = \lambda\psi_e' + \lambda'\psi_e & \text{in } \Omega, \\ \partial_\nu\psi_e' = 0 & \text{on } \partial\Omega. \end{cases}$$

Multiplying the above by ψ_e and integrating by parts, we obtain

$$0 < \int_\Omega |\nabla\psi_e|^2\,dx = \lambda' \int_\Omega |\psi_e|^2\,dx.$$

Note that the strict inequality follows from the fact that $\hat{h}$ is non-constant, so that ψ_e is also non-constant. In particular,

$$r_0 := \inf_{\delta\leq d\leq 1/\delta} \partial_d\lambda > 0$$

Now it follows from Proposition 5.2 that there exists $r' \in (0, r_0/2)$ such that if (5.3) holds, then

$$\|\partial_d H_1(\cdot;d,h) - \partial_d H_1(\cdot;d,\hat{h})\|_{C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})} = \|\partial_d H_1(\cdot;d,h) - \partial_d\lambda\|_{C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})} < \frac{r_0}{2}.$$

Hence

$$\inf_{t\in\mathbb{R}} \partial_d H_1(t;d,h) > \partial_d\lambda - \frac{r_0}{2} \geq \frac{r_0}{2}.$$

This proves the corollary. □

6. Completion of the proof of main theorem

Proposition 6.1. *Given $\delta > 0$ and a non-constant function $\hat{h}(x) \in C^\beta(\overline{\Omega})$ that depends on x only, there exists $r > 0$ such that for any $N \in \mathbb{N}$ and $(d_i)_{i=1}^N$ satisfying*

$$\delta < d_1 < ... < d_N < \frac{1}{\delta},$$

if a positive solution u of (1.1) satisfies

$$\limsup_{t\to\infty} \left\| \left(m(x) - \sum_{i=1}^N u_i\right) - \hat{h}(x) \right\|_{C(\overline{\Omega})} < r,$$

then $u \to (\theta_{d_1}, 0, ..., 0)$ as $t \to \infty$.

Before we give the proof of Proposition 6.1, we give an immediate consequence as follows.

Corollary 6.2. *Given constants $0 < \hat{d}_1 < ... < \hat{d}_K$ such that $(\hat{d}_k)_{k=1}^K \in \mathcal{D}$, there exists $r > 0$ such that for any $N \in \mathbb{N}$ and $(d_i)_{i=1}^N$ satisfying*

$$\mathrm{dist}_H((d_i)_{i=1}^N, (\hat{d}_k)_{k=1}^K) < \frac{1}{2}\hat{d}_1,$$

if a positive solution u of (P_ε) satisfies (4.3), then $u \to (\theta_{d_1}, 0, ..., 0)$ as $t \to \infty$.

Proof of Corollary 6.2. To apply Proposition 6.1, it suffices to check that, for each $\hat{d} > 0$, the function $\hat{h}(x) = m(x) - \theta_{\hat{d}}(x)$ is non-constant in x. Suppose to the contrary that, $m(x) - \theta_{\hat{d}}(x) = \lambda$ for some constant λ. Then

$$\hat{d}\Delta\theta_{\hat{d}} + \lambda\theta_{\hat{d}} = 0 \quad \text{in } \Omega, \quad \text{and} \quad \partial_\nu\theta_{\hat{d}} = 0 \quad \text{on } \partial\Omega.$$

i.e. $\lambda/\hat{d}$ is an eigenvalue of the Laplacian operator in the domain Ω subject to the Neumann boundary condition. Since the eigenfunction $\theta_{\hat{d}}$ is positive, it must be the case that $\lambda = 0$ and $\theta_{\hat{d}} = C$ for some constant C. However, this implies that $m(x) = \theta_{\hat{d}} = C$ as well. This is a contradiction to the standing assumption that $m(x)$ is a non-constant function. □

Proof of Proposition 6.1. Given $\delta > 0$ and $\hat{h}(x)$, let $r' > 0$ be as given in Corollary 5.3. We claim that there is r such that

$$\limsup_{t\to\infty} \left\| \left(m(x) - \sum_{i=1}^N u_i\right) - \hat{h}(x) \right\|_{C^{\beta,\beta/2}(\overline{\Omega}\times[t,t+1])} < r'. \tag{6.1}$$

Indeed, in view of (4.3) and the *a priori* estimate (3.3), we can use interpolation to estimate

$$\begin{aligned}&\Big\|\Big(m(x)-\sum_{i=1}^N u_i\Big)-\hat{h}(x)\Big\|_{C^{\beta,\beta/2}(\overline{\Omega}\times[t,t+1])}\\&\leq C\Big\|\Big(m(x)-\sum_{i=1}^N u_i\Big)-\hat{h}(x)\Big\|^{\gamma}_{C(\overline{\Omega}\times[t,t+1])}\leq Cr^{\gamma}\quad \text{for } t\gg 1,\end{aligned}$$

where C and γ are some positive constants in the interpolation inequality. Hence, we deduce (6.1) upon taking $r\in(0,(r'/C)^{1/\gamma}]$.

Next, define $h(x,t)=m(x)-\sum_{j=1}^N u_j(x,t)$. After an appropriate translation in time, we may assume without loss of generality that

$$\|h(\cdot,t)-\hat{h}(\cdot)\|_{C^{\alpha,\alpha/2}(\overline{\Omega}\times[0,\infty))}<r'. \tag{6.2}$$

Extend $h(x,t)$ evenly in t, so that it is defined for $(x,t)\in\Omega\times\mathbb{R}$. Let $\psi_1(x,t;d,h)$ and $H_1(t;d,h)$ be the normalized principal bundle guaranteed by Section 5. By an application of Corollary 5.3, we have for any $d\in[\delta,1/\delta]$,

$$\inf_{t\in\mathbb{R}}\partial_d H_1(t;d,h)\geq r'>0. \tag{6.3}$$

For each i, we claim that there is $\overline{c}_i>\underline{c}_i>0$ such that

$$\underline{c}_i e^{-\int_0^t H_1(s;d_i,h)\,ds}\psi_1(x,t;d_i,h)\leq u_i(x,t)\leq \overline{c}_i e^{-\int_0^t H_1(s;d_i,h)\,ds}\psi_1(x,t;d_i,h) \tag{6.4}$$

for $(x,t)\in\Omega\times\mathbb{R}$.

Indeed, the left and right hand sides of (6.4) satisfy the same equation as u_i. Hence we can choose $\overline{c}_i$ large enough and $\underline{c}_i$ small enough to deduce (6.4) from classical comparison theorem of linear parabolic equations. This proves (6.4).

By (6.3), we have

$$H_1(t;d_{i+1},h)-H_1(t;d_i,h)\geq(d_{i+1}-d_i)r'>0\quad \text{for all } 1\leq i<N, \text{ and all } t\in\mathbb{R}.$$

Hence, we derive from (6.4) that, for $i>1$,

$$\begin{aligned}\frac{u_i(x,t)}{u_1(x,t)}&\leq C\exp\left(-\int_0^t(H_1(s;d_i)-H_1(s;d_1))\,ds\right)\frac{\psi_1(x,t;d_i,h)}{\psi_1(x,t;d_1,h)}\\&\leq C\exp\left(-(d_i-d_1)r't\right)\to 0\quad \text{as } t\to\infty.\end{aligned}$$

Note that we have used the Harnack inequailty (see also [24, Theorem 2.5]) which says that there is $C=C_\delta>0$ such that

$$\frac{1}{C_\delta}\leq\psi_1(x,t;d,h)\leq C_\delta\quad \text{in } \Omega\times\mathbb{R},\ d\in[\delta,1/\delta].$$

This follows from the facts that $\psi_i(x,t) > 0$ satisfies a linear parabolic equation with L^∞ bounded coefficients in $\Omega \times (-\infty, \infty)$, and that $\int_\Omega |\psi_i(x,t)|^2\, dx = 1$ for all $t \in \mathbb{R}$.

Since we also have $\limsup_{t\to\infty} \sum_{i=1}^N \|u_i\| \leq C_1$ (by Lemma 3.2), we deduce that $u_i \to 0$ uniformly for $i = 2, .., N$. Hence the semiflow φ_ε generated by (P_ε) is asymptotic to the single species model consisting of only the first species u_1. Since the trivial solution is repelling by our assumption $\int_\Omega m\, dx \geq 0$ and m being non-constant (see Lemma 4.2), we deduce that $u_1 \to \theta_{d_1}$ uniformly as $t \to \infty$. □

Recall that a subset A of K^+ is said to be *internally chain transitive* with respect to the semiflow φ if, for two points $u_0, v_0 \in A$, and any $\delta > 0$, $T > 0$, there is a finite sequence

$$\mathcal{C}_{\delta,T} = \{u^{(1)} = u_0, u^{(2)}, ..., u^{(m)} = v_0; t_1, ..., t_{m-1}\}$$

with $u^{(j)} \in A$ and $t_j \geq T$, such that $\|\varphi(t_j, u^{(j)}) - u^{(j+1)}\| < \delta$ for all $1 \leq i \leq m-1$. The sequence $\mathcal{C}_{\delta,T}$ is called a (δ, T)-chain connecting u_0 and v_0. Let E, E' be two equilibrium points. E is said to be chained to E', written as $E \to E'$, if there exists a full trajectory $\varphi(t, u_0)$ (though some u_0 distinct from E, E') such that $\alpha(u_0, \varphi) = E$ and $\omega(u_0, \varphi) = E'$. We will henceforth use E_i to denote the equilibrium $(0, ..., 0, \theta_{d_i}, 0, ..., 0)$ of the semiflow φ_ε.

Proof of Theorem 1.4. Let $\{\hat{d}_k\}_{k=1}^K \in \mathcal{D}$. Then let $r > 0$ be given by Corollary 6.2. By Proposition 4.3, there exists $\overline{\epsilon} \in (0, \hat{d}_1/2)$ such that for any $N \in \mathbb{N}$ and any choice of diffusion rates $(d_i)_{i=1}^N$ such that $\mathrm{dist}_H((d_i), (\hat{d}_k)) < \overline{\varepsilon}$, the estimate (4.3) holds for all positive solutions. Hence by Corollary 6.2, the equilibrium E_1 attracts all solutions of (1.1) with initial data in $\mathrm{Int}\, K^+$.

It remains to verify that $(d_i)_{i=1}^N \in \mathcal{D}$, i.e. that the semiflow φ_ε under (P_ε) admits the desired Morse decomposition. This follows from similar lines in the proof of Proposition 1.3. For the trajectory starting at $u_0 \in K^+ \setminus (\mathrm{Int}\, K^+)$, by strong maximum principle, it either enters the $\mathrm{Int}\, K^+$ for all $t > 0$, or there is at least one component that is identically zero for all $t > 0$. In the first case, the trajectory also converges to E_1. In the second case, it suffices to repeat the proofs for a suitable subset $(\tilde{d}_j)$ of (d_i), to deduce again the convergence to the equilibria E_i, where i is the smallest integer such that the i-th component of u_0 is non-zero. Moreover, there is no cycle of fixed points, since if E_i is chained to E_j, then necessarily $i > j$. It therefore follows from [50, Theorem 3.2] that any compact internally chain transitive set is an equilibrium point. Since any omega (resp. alpha) limit set is internally chain transitive, it can only be one of the E_i.

In conclusion, for any choice of diffusion rates $(d_i)_{i=1}^N$ that is sufficiently close to $(\hat{d}_k)$ in the Hausdorff sense, the set of equilibria with the obvious ordering gives a Morse decomposition of the dynamics of (P_ε). i.e. $(d_i)_{i=1}^N \in \mathcal{D}$. □

7. Conclusion

In his seminal paper [20], Hastings showed that for two competing species that are ecologically identical but having distinct diffusion rates, the slower diffuser can invade the faster diffuser when rare, but not vice versa. Later, Dockery et al. [15] proved that the slower diffuser always competitively excludes the faster diffuser, regardless of initial conditions, and conjectured that the same is true for any number of species.

In this paper, we show that for any number of competing species which are ecologically identical and having distinct diffusion rates $\{d_i\}_{i=1}^N$, there are choices of $\{d_i\}_{i=1}^N$ for which the slowest diffuser is able to competitive exclude the remainder of the species. In fact, the choices of such diffusion rates is open in the space of finite sets of $\mathbb{R}_+$ endowed with the Hausdorff topology. Our result provdes some evidence in the affirmative direction regarding the conjecture by Dockery et al. in [15].

Appendix A. The normalized principal bundle

A.1. **Existence and uniqueness results.** Let $\Omega \subset \mathbb{R}^n$ be a smooth bounded domain, and consider the linear parabolic operator of non-divergence form:

$$\partial\psi_t - \mathcal{L}\psi = \partial_t\psi - a_{ij}(x,t)\partial^2_{x_ix_j}\psi - b_j(x,t)\partial_{x_j}\psi - c(x,t)\psi$$

where the coefficients a_{ij}, b_j, c are continuous in x, t and satisfy, for some fixed $\Lambda > 1$ and $\beta \in (0,1)$,

$$\|a\|_{C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})} + \|b\|_{C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})} + \|c\|_{C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})} \leq \Lambda, \tag{A.1}$$

where Ω is a smooth bounded domain in $\mathbb{R}^n$, and

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

In the following C denotes generic constants that depend on Λ but are independent of the coefficients $\mathcal{A} := (a_{ij}, b_j, c)$.

Theorem A.1. *There exists a unique pair* $(\psi_1(x,t), H_1(t)) \in C_N^{2+\beta,1+\beta/2}(\overline{\Omega}\times \mathbb{R}) \times C^{\beta/2}(\mathbb{R})$ *satisfying, in classical sense,*

$$\begin{cases} \partial_t \psi - \mathcal{L}\psi = H(t)\psi & \textit{for } x\in\Omega,\ t\in\mathbb{R},\\ \partial_\nu \psi(x,t) = 0 & \textit{for } x\in\partial\Omega,\ t\in\mathbb{R},\\ \int_\Omega |\psi(x,t)|^2\,dx = 1 & \textit{for } t\in\mathbb{R},\\ \psi(x,t) > 0 & \textit{for } x\in\Omega,\ t\in\mathbb{R}. \end{cases} \tag{A.3}$$

Remark A.2. The uniform Harnack inequality [24, Theorem 2.5] says that there exists some positive constant C' independent of the coefficients $\mathcal{A}$ and t such that

$$\sup_{x\in\Omega} \psi(x,t) \le C' \inf_{x\in\Omega} \psi(x,t) \quad \text{ for } t\in\mathbb{R}.$$

By the normalization $\int_\Omega \psi(x,t)^2\,dx = 1$, it is not difficult to show that there exists C such that

$$\frac{1}{C} \le \psi(x,t) \le C \quad \text{ for all } x\in\Omega,\ t\in\mathbb{R}. \tag{A.4}$$

Proof. Let $\tilde\psi(x,t)$ be the unique positive entire solution to

$$\begin{cases} \partial_t \tilde\psi - \mathcal{L}\tilde\psi = 0 & \text{for } x\in\Omega,\ t\in\mathbb{R},\\ \partial_\nu \tilde\psi(x,t) = 0 & \text{for } x\in\partial\Omega,\ t\in\mathbb{R},\\ \int_D |\tilde\psi(x,0)|^2\,dx = 1, & \\ \tilde\psi(x,t) > 0 & \text{for } x\in\Omega,\ t\in\mathbb{R}. \end{cases} \tag{A.5}$$

The uniqueness of $\tilde\psi(x,t)$ follows from [24, Proposition 2.7] (see also [48]), while the existence follows by a limiting argument based on the existence of solutions of suitable related periodic parabolic problems. For the details we refer readers to [23, Section 4]. By the standard parabolic regularity theory, $\tilde\psi \in C_{loc}^{2+\beta,1+\beta/2}(\overline{\Omega}\times\mathbb{R})$. Furthermore, the uniform Harnack inequality [24, Theorem 2.5] holds, i.e. there exists C such that

$$\sup_{x\in\Omega} \tilde\psi(x,t) \le C \inf_{x\in\Omega} \tilde\psi(x,t) \quad \text{ for all } t\in\mathbb{R}. \tag{A.6}$$

We proceed to normalize the principal bundle $\tilde\psi$; i.e. if we define

$$H_1(t) = -\frac{d}{dt}\left[\log \|\tilde\psi(\cdot\,,t)\|_{L^2(\Omega)}\right] = -\frac{\int_\Omega \tilde\psi \partial_t \tilde\psi\,dx}{\int_\Omega \tilde\psi^2\,dx}$$

and

$$\psi_1(x,t) = \exp\left(\int_0^t H_1(s)\,ds\right)\tilde\psi(x,t)$$

then it is obvious that $H_1 \in C^{\beta/2}_{loc}(\mathbb{R})$ and $\psi_1 \in C^{2+\beta,1+\beta/2}_{loc}(\overline{\Omega}\times\mathbb{R})$ and that (ψ_1, H_1) satisfies (A.3). To conclude the proof, it remains to show that

$$\|H_1\|_{C^{\beta/2}(\mathbb{R})} \leq C \quad \text{for some constant } C. \tag{A.7}$$

To this end, we claim that

$$\inf_{x\in\Omega} \tilde{\psi}(x,t) \geq e^{-\|c\|(t-t_0)} \inf_{x\in\Omega} \tilde{\psi}(x,t_0) \quad \text{for } t > t_0, \tag{A.8}$$

where $\|c\|$ is the supremum norm of the zero-th order coefficient of $\mathcal{L}$ in $\Omega\times\mathbb{R}$. Indeed, if we fix s, then $\tilde{\psi}(x,t)$ and $e^{-\|c\|(t-t_0)}\inf_\Omega \psi(\cdot,t)$ form a pair of super- and sub-solutions of (A.5). The inequality (A.8) thus follows by comparison.

By parabolic estimates, there exists C independent of t such that

$$\|\tilde{\psi}\|_{C^{\beta,\beta/2}(\overline{\Omega}\times[t-1/2,t])} + \|\partial_t\tilde{\psi}\|_{C^{\beta,\beta/2}(\overline{\Omega}\times[t-1/2,t])} \leq C\|\tilde{\psi}\|_{L^\infty(\Omega\times(t-1,t))} \tag{A.9}$$

for all $t\in\mathbb{R}$. Combining with (A.6) and (A.8), we have

$$\|\tilde{\psi}\|_{C^{\beta,\beta/2}(\overline{\Omega}\times[t-1/2,t])} + \|\partial_t\tilde{\psi}\|_{C^{\beta,\beta/2}(\overline{\Omega}\times[t-1/2,t])} \leq C \inf_{x\in\Omega}\tilde{\psi}(x,t).$$

for all $t\in\mathbb{R}$. In particular, if we define

$$a(t) = -\int_\Omega \tilde{\psi}(x,t)\partial_t\tilde{\psi}(x,t)\,dx \quad \text{and} \quad b(t) = \int_\Omega \psi^2(x,t)\,dx,$$

then there is C independent of t such that

$$|a(t)| + \frac{|a(t)-a(s)|}{|t-s|^{\beta/2}} + \frac{|b(t)-b(s)|}{|t-s|^{\beta/2}} \leq Cb(t) \quad \text{for } s\in[t-1/2,t).$$

Since $H_1(t) = a(t)/b(t)$, we obtain $\|H_1\|_{C^0(\mathbb{R})} \leq C$ and

$$\frac{|H_1(t)-H_1(s)|}{|t-s|^{\beta/2}} \leq \frac{1}{b(t)}\frac{|a(t)-a(s)|}{|t-s|^{\beta/2}} + \frac{|a(s)|}{b(s)b(t)}\frac{|b(t)-b(s)|}{|t-s|^{\beta/2}} \leq C$$

for $s\in[t-1/2,t)$. This proves (A.7). □

A.2. **The decomposition and exponential separation.** For fixed functions $a_{ij}, b_j, c \in C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})$, let $(\psi_1(x,t), H_1(t))$ be given as in Theorem A.1. Consider the non-autonomous problem

$$\begin{cases} \partial_t u - \mathcal{L}u = H_1(t)u & \text{for } x\in\Omega,\ t\geq s,\\ \partial_\nu u = 0 & \text{for } x\in\partial\Omega,\ t\geq s,\\ u(x,s) = u_0(x) & \text{for } x\in\Omega. \end{cases} \tag{A.10}$$

We follow the notation of [43] and, for $t\geq s$, let $U(t,s)$ be the evolution operator to (A.10) i.e. $u(x,t) = U(t,s)[u_0](x)$ is the unique solution to (A.10). Then

$$U(t,s)\psi_1(\cdot,s) = \psi_1(\cdot,t) \quad \text{whenever } t\geq s.$$

Define, for each $t \in \mathbb{R}$, $X^1(t) := \text{span}\,\{\psi_1(\cdot, t)\}$, and

$$X^2(t) := \left\{u_0 \in L^2(\Omega) : U(\tilde{t}, t)[u_0](x) \text{ has a zero in } D \text{ for all } \tilde{t} \in (t, \infty)\right\}$$

Then $X^1(t)$ and $X^2(t)$ are forward-invariant under $U(t, s)$, i.e.

$$U(t, s)(X^1(s)) = X^1(t) \quad \text{and} \quad U(t, s)(X^2(s)) \subseteq X^2(t) \quad \text{for } t \geq s.$$

Also, it follows by [24, 25] that

$$L^2(\Omega) = X^1(t) \oplus X^2(t) \quad \text{for each } t \in \mathbb{R}, \tag{A.11}$$

and there are constants $C, \gamma > 0$ that depend on the bound M in (A.1) and (A.2) only, such that

$$\|U(t, s)u_0\|_{L^2(\Omega)} \leq Ce^{-\gamma(t-s)}\|u_0\|_{L^2(\Omega)} \quad \text{for any } t \geq s \text{ and } u_0 \in X^2(s). \tag{A.12}$$

(Here we made use of [24, Theorem 2.1] and the fact that $\|U(t, s)u_0\|_{L^2(\Omega)} = \|u_0\|_{L^2(\Omega)}$ for $u_0 \in X^1(s)$, which follows by the definition of the normalized principal bundle ψ_1.)

A.3. **Smooth dependence on coefficients.** Proposition 5.2 is a particular case of the following result.

Proposition A.3. *The quantities* (ψ_1, H_1) *depend smoothly on the coefficients* $\mathcal{A} = (a_{ij}, b_j, c) \in C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R}; \mathbb{R}^{N^2+N+1})$.

Proof. We consider general parabolic operator $\partial_t - \mathcal{L}$ with coefficients $\mathcal{A}$. We denote $\psi_1 = \psi_1(x, t; \mathcal{A})$ and $H_1 = H_1(t; \mathcal{A})$ to stress the dependence of the normalized principal bundle on the coefficients $\mathcal{A} = (a_{ij}, b_j, c)$ of $\mathcal{L}$. First, the continuous dependence of (ψ_1, H_1) on $\mathcal{A}$ follows readily from the uniqueness of the pair and standard parabolic regularity. (See [24] for details.) In the following, we will prove the smooth dependence.

Consider the mapping

$$\mathcal{F} : C_N^{2+\beta,1+\beta/2}(\overline{\Omega} \times \mathbb{R}) \times C^{\beta/2}(\mathbb{R}) \times C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R}; \mathbb{R}^{N^2+N+1}) \longrightarrow C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R}) \times C^{1+\beta/2}(\mathbb{R})$$

defined by

$$\mathcal{F}(\psi(x, t), H(t), \mathcal{A}) := \begin{pmatrix} \partial_t\psi(x, t) - \mathcal{L}\psi(x, t) - H(t)\psi(x, t) \\ \frac{1}{2}\int_\Omega |\psi(x, t)|^2\, dx - \frac{1}{2} \end{pmatrix},$$

where

$$C_N^{2+\beta,1+\beta/2}(\overline{\Omega} \times \mathbb{R}) = \{u \in C^{2+\beta,1+\beta/2}(\overline{\Omega} \times \mathbb{R}) : \partial_\nu u = 0 \text{ in } \partial D \times \mathbb{R}\}.$$

Then for each fixed $\mathcal{A} = (a_{ij}, b_j, c) \in C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R}; \mathbb{R}^{N^2+N+1})$ satisfying (A.1) and (A.2),

$$\mathcal{F}(\psi_1(\cdot, \cdot; \mathcal{A}), H_1(\cdot; \mathcal{A}), \mathcal{A}) = 0.$$

To prove the smooth dependence on $\mathcal{A}$, it suffices to show that

$$D_{(\psi,H)}\mathcal{F} = D_{(\psi,H)}\mathcal{F}(\psi_1(\cdot,\cdot;\mathcal{A}), H_1(\cdot;\mathcal{A}), \mathcal{A}), \tag{A.13}$$

as a mapping from $C_N^{2+\beta,1+\beta/2}(\overline{\Omega}\times\mathbb{R}) \times C^{\beta/2}(\mathbb{R})$ to $C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R}) \times C^{1+\beta/2}(\mathbb{R})$, is invertible. To this end, given $(f(x,t), G(t)) \in C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R}) \times C^{1+\beta/2}(\mathbb{R})$, we need to prove the existence and uniqueness of $(w(x,t), Y(t))$ in $C_N^{2+\beta,1+\beta/2}(\overline{\Omega}\times\mathbb{R}) \times C^{\beta/2}(\mathbb{R})$ such that

$$\begin{cases} \partial_t w - \mathcal{L}w - H_1 w - Y(t)\psi_1 = f(x,t) & \text{for } t\in\mathbb{R},\ x\in\Omega, \\ \int_D w(x,t)\psi_1\,dx = G(t) & \text{for } t\in\mathbb{R}, \end{cases} \tag{A.14}$$

where $H_1 = H_1(t;\mathcal{A})$ and $\psi_1 = \psi_1(x,t;\mathcal{A})$. First, we show the existence. We start by choosing $w^\perp$ as

$$w^\perp(x,t) = \int_{-\infty}^t U(t,\sigma)[P^2(s)f(\cdot,\sigma)]\,d\sigma,$$

where, for $i = 1,2$, $P^i : L^2(\Omega) \to L^2(\Omega)$ is the projection operator corresponding to the decomposition given in (A.11). We claim that $w^\perp$ is well defined. Indeed, by (A.12), we have

$$\begin{aligned} \sup_{t\in\mathbb{R}} \|w^\perp(\cdot,t)\|_{L^2(\Omega)} &\le \sup_{t\in\mathbb{R}} \left\| \int_{-\infty}^t U(t,\sigma)[P^2(\sigma)[f(\cdot,\sigma)]]\,d\sigma \right\|_{L^2(\Omega)} \\ &\le C \sup_{t\in\mathbb{R}} \int_{-\infty}^t e^{-\gamma(t-s)} \|f(\cdot,\sigma)\|_{L^2(\Omega)}\,d\sigma \\ &\le C \sup_{t\in\mathbb{R}} \|f(\cdot,t)\|_{L^2(\Omega)} < \infty \end{aligned} \tag{A.15}$$

Moreover, since it defines an entire solution of $\partial_t w^\perp - \mathcal{L}w^\perp - H_1(t)w^\perp = P^2(t)[f(\cdot,t)]$ with Neumann boundary condition, it follows by parabolic regularity estimates that $w^\perp \in C_N^{2+\beta,1+\beta/2}(\overline{\Omega}\times\mathbb{R})$. Next, define $w \in C_N^{2+\beta,1+\beta/2}(\overline{\Omega}\times\mathbb{R})$ to be

$$w(x,t) = w^\perp(x,t) + \left[-\int_\Omega w^\perp(y,t)\psi_1(y,t)\,dy + G(t)\right]\psi_1(x,t).$$

Then w satisfies the second part of (A.14). Moreover, we have

$$\begin{aligned} &\partial_t w - \mathcal{L}w - H_1(t)w \\ &= P^2(t)[f(\cdot,t)] + \left\{-\frac{d}{dt}\Big[\int_\Omega w^\perp(y,t)\psi_1(y,t)\,dy\Big] + G'(t)\right\}\psi_1(x,t). \end{aligned}$$

It therefore suffices to choose $Y \in C^{\beta,\beta/2}(\overline{\Omega}\times\mathbb{R})$ such that

$$Y(t)\psi_1(x,t) + P^1(t)[f(\cdot,t)] = \left\{-\frac{d}{dt}\Big[\int_\Omega w^\perp(y,t)\psi_1(y,t)\,dy\Big] + G'(t)\right\}\psi_1(x,t).$$

Then $(w, Y) \in C_N^{2+\beta,1+\beta/2}(\overline{\Omega} \times \mathbb{R}) \times C^{\beta,\beta/2}(\overline{\Omega} \times \mathbb{R})$ satisfies (A.14). This proves existence.

For the uniqueness, set $f = 0$ and $G = 0$, then using the the variation of constants formula for $\partial_t w - \mathcal{L}w - H_1(t)w = Y(t)\psi_1(x,t)$, we get

$$\begin{aligned} w(\cdot,t) &= U(t,s)w(\cdot,s) + \int_s^t U(t,\sigma)[Y(\sigma)\psi_1(\cdot,\sigma)]\,d\sigma \\ &= U(t,s)w(\cdot,s) + \int_s^t Y(\sigma)\{U(t,\sigma)[\psi_1(\cdot,\sigma)]\}\,d\sigma \\ &= U(t,s)w(\cdot,s) + \int_s^t Y(\sigma)\psi_1(\cdot,t)\,d\sigma \\ &= U(t,s)w(\cdot,s) + \left[\int_s^t Y(\sigma)\,d\sigma\right]\psi_1(\cdot,t). \end{aligned}$$

Hence, we deduce

$$w(\cdot,t) = U(t,s)w(\cdot,s) + \left[\int_s^t Y(\sigma)\,d\sigma\right]\psi_1(\cdot,t) \qquad \text{for any } t,s \in \mathbb{R},\ t > s. \tag{A.16}$$

Next, apply the projection $P^2(t)$ on both sides of (A.16),

$$P^2(t)[w(\cdot,t)] = P^2(t)[U(t,s)w(\cdot,s)] = U(t,s)P^2(s)[w(\cdot,s)].$$

provided $t, s \in \mathbb{R}$ and $t > s$. This implies

$$\|P^2(t)[w(\cdot,t)]\|_{L^2(\Omega)} \leq Ce^{-\gamma(t-s)}\|P^2(s)[w(\cdot,s)]\|_{L^2(\Omega)} \leq Ce^{-\gamma(t-s)}, \tag{A.17}$$

where we used (A.12) for the first inequality and the fact that $w \in C^{2+\beta,1+\beta/2}(\overline{\Omega}\times \mathbb{R})$ for the second one. Letting $s \to -\infty$ in (A.17), we deduce that $P^2(t)[w(\cdot,t)] = 0$ for each $t \in \mathbb{R}$. Hence, $w(\cdot,t) \in X^1(t)$ and thus $w(\cdot,t) = p(t)\psi_1(\cdot,t)$ for some function $p(t)$. Now, using $G(t) \equiv 0$, the second equation in (A.14) gives

$$0 = \int_\Omega w(x,t)\psi_1(x,t)\,dx = p(t)\int_\Omega |\psi_1(x,t)|^2\,dx = p(t)$$

for each $t \in \mathbb{R}$. This implies $w(x,t) \equiv 0$. Substituting into (A.16), we have

$$\int_s^t Y(\sigma)\,d\sigma = 0 \qquad \text{for any } t,s \in \mathbb{R},\ t > s,$$

which means $Y(t) \equiv 0$ as well. This proves uniqueness.

Having shown that $D_{(\psi,H)}\mathcal{F}$ given in (A.13) is an isomorphism, we may apply the implicit function theorem to conclude the smooth dependence of the normalized principal bundle $(\psi_1(x,t), H_1(t))$ on the coefficients $\mathcal{A}$. This concludes the proof. □

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