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Dynamics of a periodic-parabolic Lotka-Volterra competition-diffusion system in heterogeneous environments

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Abstract. The effects of spatial heterogeneity on the dynamics of reaction-diffusion models have been studied extensively. In particular, global dynamics of general spatially heterogeneous (but temporally static) Lotka-Volterra competition-diffusion systems were completely clarified by He and Ni in 2016. However, the evolutionary impacts of temporal periodicity combined with spatial heterogeneity in population ecology remain a challenging issue. In this work, we consider a population model of two competing species in a both spatially varying and temporally periodic environment, where the two species only differ in their random dispersal rates but are otherwise ecologically identical. In a pioneering 2001 work on this model by Hutson et al., by constructing various choices of resource functions and dispersal rates of the two species, the authors demonstrated that all the following three types of dynamics are possible: (i) stable coexistence of the two species; (ii) the slower diffuser invades the faster one but not vice versa; (iii) the faster diffuser invades the slower one but not vice versa. This is in drastic contrast with the spatially heterogeneous but temporally static case, where Dockery et al. showed in 1998 that the slower diffuser always wipes out the faster one. In this paper, we completely and explicitly characterize the asymptotic stability of both semitrivial periodic solutions in terms of the two dispersal rates and the resource function, when either dispersal rate is sufficiently small or large. In particular, the direction of selection on the dispersal rate during the evolution can be elucidated in these instances. Some novel analytical methods are developed to investigate asymptotic behaviors of the underlying time-periodic parabolic eigenvalue problem and its adjoint problem. We hope that these methods are of independent interest in the area of time-periodic parabolic equations.

Keywords. Evolution of dispersal, time-periodic parabolic operator, principal eigenvalue, asymptotic analysis, global dynamics, population ecology

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1. Introduction

Nonlinear periodic-parabolic equations arise naturally, e.g., in problems stemming from population ecology, where the environment depends periodically on time (seasonal or daily variations). Temporal and spatial variations of those physical conditions, such as temperature, light and nutrients, are believed to be important factors which can interrupt or even reverse competitive interactions [21].

On the other hand, dispersal is a vital life-history strategy in population ecology and evolutionary adaptability. To understand the mechanism behind the evolution of dispersal as clearly as possible, we choose the simplest dispersal strategy, namely (random) diffusion or unconditional dispersal in our model. To motivate our discussion, we consider the following two-species Lotka–Volterra competition-diffusion system:

$$\begin{cases} U_{t} = d_{1}\Delta U + U(m(x,t) - U - V) & \text{in } \Omega \times (0,\infty), \\ V_{t} = d_{2}\Delta V + V(m(x,t) - U - V) & \text{in } \Omega \times (0,\infty), \\ \partial_{\nu}U = \partial_{\nu}V = 0 & \text{on } \partial\Omega \times (0,\infty), \\ U(x,0) = U_{0}(x), \quad V(x,0) = V_{0}(x) & \text{in } \Omega, \end{cases}$$

$$(1.1)$$

where U(x,t) and V(x,t) represent the population densities of two competing species at location x and time t in a bounded domain $\Omega \subset \mathbb{R}^N$ with smooth boundary $\partial \Omega$. We are therefore only interested in nonnegative solutions $U, V \geq 0$. The parameters $d_1, d_2 > 0$ are the dispersal rates of the species with density U and V respectively; $\Delta = \sum_{i=1}^N \frac{\partial^2}{\partial x_i^2}$ is the usual Laplace operator, and $\partial_{\nu} = \nu \cdot \nabla$, where ν denotes the outward unit normal vector on $\partial \Omega$, is the normal derivative on the boundary. The zero Neumann (no-flux) boundary condition is imposed on $\partial \Omega$ to ensure that no individual crosses the boundary of the habitat. For simplicity, we assume throughout this paper that the initial data U_0 and V_0 are nonnegative and nontrivial, i.e., not identically zero. The function m(x,t) represents the local carrying capacity or intrinsic growth rate of the two species, which reflects the environmental influence on the species.

System (1.1) describes the evolution of two ecologically equivalent competitors with different dispersal rates. It seems natural to ask the following questions motivated by [9, 14, 23]:

Question. Is the fast diffuser or the slower diffuser selected for during the competition? What are the selection mechanisms behind the dispersal rates in a both spatially heterogeneous and temporally periodic environment? In particular, is there an optimal dispersal rate in the sense that the species adopting such dispersal rate can never be invaded by its competitor adopting a different dispersal rate?

When the environment is spatially heterogeneous but temporally static, the evolution of dispersal is relatively well understood. For instance, Hastings [14] considered the invasion of a small number of mutant species using a different random dispersal rate to a resident population. It is shown that the mutant species can invade when rare if and only if it has a smaller random dispersal rate. Later in 1998, Dockery et al. [9] confirmed that the slower diffuser actually always wipes out its faster counterpart regardless of their ini-

tial values – this is known as "the slower diffuser always prevails". Since then, the effects of spatial heterogeneity have been studied extensively in the past few decades, from many different perspectives. See [3–6, 9, 12, 13, 15–19, 22, 27, 31, 32] and references therein.

To state the result of Dockery et al. [9] precisely, we now introduce the following (single species) logistic equation:

$$\begin{cases} \theta_t = d\Delta\theta + \theta(m(x,t) - \theta) & \text{in } \Omega \times \mathbb{R}^+, \\ \partial_{\nu}\theta = 0 & \text{on } \partial\Omega \times \mathbb{R}^+, \end{cases}$$
(1.2)

where d>0 is the random dispersal rate of the species with density $\theta(x,t)$. Let T>0 be a fixed constant which represents the time periodicity. Throughout this paper, for any given function space E defined on $\bar{\Omega}\times\mathbb{R}$, we set

$$E_T := \{ u \in E \mid u(x,t) \text{ is } T\text{-periodic in } t \}. \tag{1.3}$$

For each $m \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ with m > 0 on $\bar{\Omega} \times \mathbb{R}$, where $C^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ is the usual "parabolic" Hölder space with $\alpha \in (0,1)$, (1.2) admits a unique positive T-periodic classical solution, denoted as θ_d . Moreover, θ_d is globally asymptotically stable with respect to positive initial conditions. For the proof of the existence and uniqueness of θ_d , see e.g. [20, Theorem 28.1].

It is easy to see that (1.1) has a trivial steady state (0,0) and two semitrivial T-periodic solutions (θ_{d_1} , 0) and (0, θ_{d_2}).

We say that m is spatially homogeneous/constant (or independent of x) if m(x,t) = m(y,t) for any $x, y \in \overline{\Omega}$ and $t \in \mathbb{R}$, and m is temporally homogeneous/constant (or independent of t) if m(x,t) = m(x,s) for any $x \in \overline{\Omega}$ and $t,s \in \mathbb{R}$.

Note that when m is temporally (resp. spatially) constant, the solution θ_d to (1.2) is also temporally (resp. spatially) constant.

We now state the result by Dockery et al. [9]:

Theorem A ([9]). Suppose that m(x,t) is spatially heterogeneous but temporally homogeneous, i.e., m(x,t) = m(x). Then the semitrivial steady state $(\theta_{d_1},0)$ of (1.1) is globally asymptotically stable when $d_1 < d_2$, i.e., every solution (U,V) of (1.1) converges to $(\theta_{d_1},0)$ as $t \to \infty$, regardless of initial data (U_0,V_0) .

Theorem A indicates that in a spatially varying but temporally constant environment, faster dispersal is always selected against if dispersal is completely random. In particular, the two species can never coexist. However, when additional temporal periodicity is incorporated into the model, the situation changes drastically. In a pioneering work by Hutson et al. [23] in 2001, by considering various choices of resource function m(x,t) and dispersal rates d_1, d_2 of the two species, the authors demonstrated that the following three outcomes of dynamics for system (1.1) are possible:

- (a) stable coexistence of the two species;
- (b) the slower diffuser invades/wipes out the faster one but not vice versa;
- (c) the faster diffuser invades/wipes out the slower one but not vice versa.

Their results indicate that the situation is substantially different from the spatially heterogeneous but temporally static case. Slower diffuser is not always selected for and interactions between spatial and temporal variations can change or even completely reverse the effects of spatial heterogeneity alone.

To study the evolution of dispersal, many researchers follow the adaptive dynamics approach [7, 8, 10, 11, 25, 26]. Roughly speaking, for a pair of given dispersal rates (d_1, d_2) , the primary focus is to determine the local stability of the two semitrivial periodic solutions $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$ of system (1.1). For instance, let the species with density U be a resident species. If $(\theta_{d_1}, 0)$ is locally stable, then biologically it means that the mutant species with density V cannot invade when rare; otherwise, the mutant species with density V may invade when rare. Mathematically, this is confirmed by studying the sign of the principal eigenvalue of the underlying time-periodic parabolic eigenvalue problem introduced in Section 3 below. In fact, the concept of principal eigenvalue of time-periodic parabolic operators plays a crucial role in the study of dynamics of system (1.1).

At this point, we would like to point out that in [23], most results concerning (a)–(c) above are obtained when one of the two dispersal rates is fixed and the other one is sufficiently small or large. In [23, Theorem 5.2], a class of resource functions m is constructed such that the faster diffuser is globally asymptotically stable when d_1 , d_2 are close to some $d_0 > 0$. However, that class of functions m and the corresponding d_0 are given in an implicit way. In other words, for a given m, it seems difficult to decide whether it belongs to that class or not.

Our goal in this paper is to understand the selection mechanisms for the evolution of different dispersal rates in a more systematic way for system (1.1) when m is both spatially heterogeneous and temporally periodic. Based in part on the foundational monograph of Hess [20] and the pioneering work of Hutson et al. [23], we develop some novel analytical methods to investigate asymptotic behaviors of a time-periodic parabolic eigenvalue problem and its adjoint problem. Note that in contrast to the study of self-adjoint elliptic eigenvalue problems, it is usually necessary to study both the time-periodic parabolic eigenvalue problem and the time-reversed adjoint problem, so that one can obtain properties of the corresponding principal eigenvalue. Therefore, temporally periodic systems are substantially more difficult to analyze than temporally static systems. We believe that our methods and results in Section 3 below are of independent interest in the area of time-periodic parabolic equations.

We briefly summarize our main results as follows:

- When one of the dispersal rates d_1 and d_2 is sufficiently large, the slower diffuser, so long as it is not too slow, wipes out its faster competitor, just as in the spatially heterogeneous but temporally static case.
- When one of the dispersal rates d_1 and d_2 is sufficiently large, while the other one is sufficiently small (relative to the larger dispersal rate), both semitrivial periodic solutions are unstable and the two species coexist regardless of their initial data.

When both dispersal rates d₁ and d₂ are sufficiently small, the situation becomes very delicate. Nevertheless, in this case, we completely characterize the dynamics of system (1.1) in terms of m, d₁ and d₂. In particular, necessary and sufficient conditions for each of the outcomes (a)–(c) listed above to take place are provided explicitly.

Based on our results, to a large extent, whether a selection on the dispersal rates or coexistence of the two species can now be determined, and our picture of understanding the underlying mechanism seems more complete.

Our paper is organized as follows. In Section 2, we state our main results. In Section 3, we recall some preliminary results concerning time-periodic parabolic eigenvalue problems. Then, we establish the asymptotic behaviors of the principal eigenvalue and the principal eigenfunction of a time-periodic parabolic operator, together with that of its adjoint operator. In Section 4, we establish properties of the solution θ_d to equation (1.2) and its asymptotic behaviors when d is small or large. Sections 5 and 6 are devoted to proving our main theorems. Some miscellaneous remarks are included in Section 7. In the Appendix, we establish an important a priori estimate for solutions of quasilinear periodic-parabolic equations by modifying the Moser-Alikakos iteration procedure [1].

2. Statement of main results

In this section, we state our main results precisely. Throughout this paper, we assume that

$$m \in C_T^{2,1}(\bar{\Omega} \times \mathbb{R})$$
 and $m > 0, \nabla m \neq 0, m_t \neq 0 \text{ on } \bar{\Omega} \times \mathbb{R}.$ (M1)

Here, for each $n, k \in \mathbb{N}$, $C^{n,k}(\bar{\Omega} \times \mathbb{R})$ is the classical space defined by

$$C^{n,k}(\bar{\Omega} \times \mathbb{R}) := \{ f \in C(\bar{\Omega} \times \mathbb{R}) \mid D^{\beta} f, f_t, \dots, f_t^{(k)} \in C(\bar{\Omega} \times \mathbb{R}) \text{ with } |\beta| \le n \},$$
 (2.1)

where $\beta = (\beta_1, \dots, \beta_N)$ is a multi-index and its order is defined as $|\beta| = \beta_1 + \dots + \beta_N$, $D^{\beta} f = \frac{\partial^{|\beta|} f}{\partial x_1^{\beta_1} \dots \partial x_N^{\beta_N}}$ and $f_t^{(i)}$ is the i-th partial derivative of f with respect to t, for $i \in \mathbb{N}$.

Note that the last two conditions in (M1) mean that m is both spatially and temporally heterogeneous.

We now introduce the following notation for the temporal and spatial averages of a function $h \in C_T(\bar{\Omega} \times \mathbb{R})$, which will be frequently used throughout this paper:

$$\hat{h}(x) := \frac{1}{T} \int_0^T h(x,t) dt, \quad \bar{h}(t) := \frac{1}{|\Omega|} \int_{\Omega} h(x,t) dx.$$

In particular, we have

$$\hat{\bar{h}} = \hat{\bar{h}} = \frac{1}{T|\Omega|} \int_0^T \int_{\Omega} h(x,t) \, dx \, dt.$$

Since system (1.1) is symmetric with respect to the line $d_1 = d_2$ in the diffusion plane

$$Q := (0, \infty) \times (0, \infty),$$

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it is sufficient to state our results only in the region $Q \cap \{(d_1, d_2) \mid d_1 < d_2\}$. In other words, we will always assume in this section that

$$0 < d_1 < d_2$$
.

Thus, the species with density U always represents the phenotype with the slower dispersal rate.

We first study linear stability of the two semitrivial periodic solutions $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$ when both d_1 and d_2 are small. For technical reasons, we need to impose the following additional condition on m(x, t):

$$\partial_{\nu} m = 0 \quad \text{on } \partial\Omega \times \mathbb{R}.$$
 (M2)

When m(x, t) has a very special form, the dynamics of system (1.1) sometimes behaves quite differently. Therefore, we exclude those situations by assuming that

$$m(x,t) \neq e^{\int_0^t b(s) \, ds} a(x) + b(t)$$
 for any functions $a(x), b(t)$. (M3)

Note that these two conditions also show up in [23, Lemma 3.4 and Theorem 4.1].

To state our results precisely, we introduce the following auxiliary function and quantity. For each $x \in \bar{\Omega}$, let p(x,t) be the unique positive solution to the following ODE:

$$\begin{cases} p_t = p(m-p), & t \in \mathbb{R}, \\ p \text{ is } T\text{-periodic in } t, \end{cases}$$
 (2.2)

and

$$I(p) := \int_{\Omega} \left[\exp\left(\frac{1}{T} \int_0^T \ln p^2 \, dt \right) \int_0^T \frac{\Delta p}{p} \, dt \right]. \tag{2.3}$$

Theorem 2.1. Assume that (M1) and (M2) hold. Then there exists some $\varepsilon_0 > 0$ small such that for all $(d_1, d_2) \in (0, \varepsilon_0)^2 \cap \{(d_1, d_2) \mid d_1 < d_2\}$, the following statements hold for system (1.1):

- (i) If I(p) > 0 and $\min_{x \in \bar{\Omega}} \int_0^T \frac{\Delta p}{p}(x,t) dt > 0$, then $(\theta_{d_1}, 0)$ is linearly unstable and $(0, \theta_{d_2})$ is linearly stable.
- (ii) If I(p) > 0 and $\min_{x \in \bar{\Omega}} \int_0^T \frac{\Delta p}{p}(x,t) dt < 0$, then $(\theta_{d_1},0)$ is linearly unstable and there exists a continuously differentiable function $\hat{d}_1: (0,\varepsilon_0) \to (0,\varepsilon_0)$ with $\hat{d}_1(d_2) \in (0,d_2)$ such that $(0,\theta_{d_2})$ is linearly unstable for all $d_1 \in (0,\hat{d}_1(d_2))$ and linearly stable for all $d_1 \in (\hat{d}_1(d_2),d_2)$. Moreover, $\lim_{d_2 \to 0} \hat{d}_1(d_2)$, $\hat{d}'_1(0)$ and $\lim_{d_2 \to 0} \hat{d}'_1(d_2)$ exist with

$$\lim_{d_2 \to 0} \hat{d}_1(d_2) = 0 \quad and \quad \lim_{d_2 \to 0} \hat{d}'_1(d_2) = \hat{d}'_1(0) \in (0, 1).$$

(iii) If I(p) < 0 and (M3) holds in addition, then $(0, \theta_{d_2})$ is linearly unstable and there exists a continuously differentiable function $\tilde{d}_1: (0, \varepsilon_0) \to (0, \varepsilon_0)$ with $\tilde{d}_1(d_2) \in (0, d_2)$ such that $(\theta_{d_1}, 0)$ is linearly unstable for all $d_1 \in (0, \tilde{d}_1(d_2))$

and linearly stable for all $d_1 \in (\tilde{d}_1(d_2), d_2)$. Moreover, $\lim_{d_2 \to 0} \tilde{d}_1(d_2)$, $\tilde{d}'_1(0)$ and $\lim_{d_2 \to 0} \tilde{d}'_1(d_2)$ exist with

$$\lim_{d_2 \to 0} \tilde{d}_1(d_2) = 0 \quad and \quad \lim_{d_2 \to 0} \tilde{d}'_1(d_2) = \tilde{d}'_1(0) \in (0, 1).$$

For an illustration of Theorem 2.1 (i)–(iii), see Figure 1 (a)–(c) respectively.

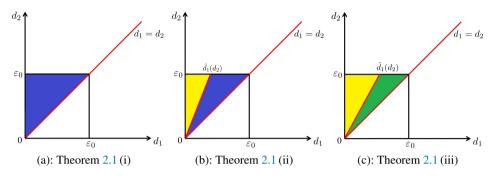


Fig. 1. An illustration of Theorem 2.1 (i)–(iii). In the blue regions, the faster diffuser can invade the slower one but not vice versa; in the green regions, the slower diffuser can invade the faster one but not vice versa; in the yellow regions, both species persist regardless of initial data.

Theorem 2.1 almost completely clarifies local dynamics around $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$ for all d_1, d_2 sufficiently small, for given m satisfying conditions (M1)–(M2), and in addition (M3) in the case of I(p) < 0. It seems interesting whether all three possibilities in (i), (ii), or (iii) of Theorem 2.1 can actually occur. The answer is affirmative – see Lemma 7.1 for explicit examples.

Our next result clarifies linear stability of the two semitrivial periodic solutions $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$ when d_2 is sufficiently large.

Theorem 2.2. Assume that (M1) holds and $0 < d_1 < d_2$. Then there exists a constant $D_2 > 0$ large such that the following statements hold:

(i) If (M2) and (M3) hold, then there exists a continuously differentiable strictly decreasing function

$$\check{d}_1:(D_2,\infty)\to(0,\infty)$$
 with $\check{d}_1(d_2)=O(1/d_2)$ as $d_2\to\infty$

such that for all $d_2 \in (D_2, \infty)$, $(\theta_{d_1}, 0)$ is linearly unstable for all $d_1 < \check{d}_1(d_2)$ and linearly stable for all $d_1 > \check{d}_1(d_2)$.

(ii) If $\hat{m} \not\equiv \text{const}$, then $(0, \theta_{d_2})$ is linearly unstable for all $d_2 > D_2$.

For an illustration of Theorem 2.2, see Figure 2(a).

We now clarify the global dynamics of system (1.1) when d_2 is large while d_1 is not too small. The conclusion is that the slower diffuser, so long as it is not too slow, still wipes out the faster diffuser, just as in spatially heterogeneous but temporally static case in Theorem A.

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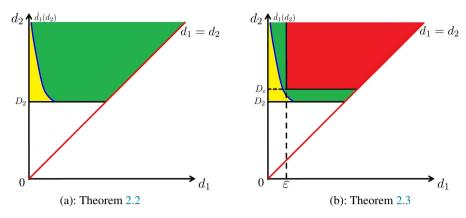


Fig. 2. An illustration of Theorems 2.2 and 2.3. The green region and the yellow region have the same meanings as in Figure 1; in the red region, the slower diffuser wipes out the faster diffuser, i.e., $(\theta_{d_1}, 0)$ is globally asymptotically stable.

Theorem 2.3. Assume that (M1) holds and $0 < d_1 < d_2$. Then for each $\varepsilon > 0$, there exists a large constant $D_{\varepsilon} > 0$ such that $(\theta_{d_1}, 0)$ is globally asymptotically stable for all $d_1 > \varepsilon$ and $d_2 > D_{\varepsilon}$.

For an illustration of Theorem 2.3, see Figure 2 (b). Note that in [23, Theorem 5.3], the authors showed that for fixed d_1 , $(\theta_{d_1}, 0)$ is globally asymptotically stable when d_2 is sufficiently large. However, their arguments cannot be applied to the case when $(d_1, d_2) \in (D_{\varepsilon}, \infty)^2$, i.e., when both d_1 and d_2 are sufficiently large.

By Lemma 5.7 below and similar arguments to those in [23, proof of Theorem 5.2], we obtain the following result where the fast diffuser is the global attractor – which is "completely opposite" to the spatially heterogeneous but temporally homogeneous case in Theorem A.

Corollary 2.4. Assume that (M1) and (M2) hold and I(p) > 0. Let $\varepsilon_0 > 0$ be as in Theorem 2.1. Then for each $d_1 \in (0, \varepsilon_0)$ and $d_2 > d_1$ sufficiently close to d_1 , the fast diffuser $(0, \theta_{d_2})$ is globally asymptotically stable.

By monotone flow theory [20], we can easily obtain conditions under which both species persist regardless of initial data. Note that in the spatially heterogeneous but temporally homogeneous case, the two species can never coexist!

Corollary 2.5. Assume that (M1) and (M2) hold and $0 < d_1 < d_2$. Then system (1.1) has a stable coexistence T-periodic solution and the two species persist regardless of initial data in each of the following cases:

- (a) I(p) > 0, $\min_{x \in \tilde{\Omega}} \int_0^T \frac{\Delta p}{p}(x, t) dt < 0$, $d_2 \in (0, \varepsilon_0)$ and $d_1 \in (0, \hat{d}_1(d_2))$;
- (b) I(p) < 0, (M3) holds, $d_2 \in (0, \varepsilon_0)$ and $d_1 \in (0, \tilde{d}_1(d_2))$;
- (c) $\hat{m} \not\equiv \text{const}$, (M3) holds, $d_2 \in (D_2, \infty)$ and $d_1 \in (0, \check{d}_1(d_2))$.

Here, ε_0 , $\hat{d}_1(\cdot)$, $\tilde{d}_1(\cdot)$ are as in Theorem 2.1, and D_2 and $\check{d}_1(\cdot)$ are as in Theorem 2.2.

3. Asymptotic behaviors of periodic-parabolic eigenvalue problems

In this section, we mainly study the asymptotic behaviors of the principal eigenvalue and the principal eigenfunction to a time-periodic parabolic eigenvalue problem, together with those of its adjoint eigenvalue problem defined below. Our results in this section will play a central role in determining the local and global stability of both semitrivial periodic solutions $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$ of system (1.1) when either of the two dispersal rates is sufficiently small or large. Furthermore, we believe that the methods and techniques developed in this section can be applied to other time-periodic parabolic equations.

We first recall some preliminary results. Given $h \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$, we introduce the following periodic-parabolic eigenvalue problem:

$$\begin{cases} \varphi_t - d\Delta\varphi = h(x, t)\varphi + \mu\varphi & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu}\varphi = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \varphi \text{ is } T\text{-periodic in } t. \end{cases}$$
(3.1)

It is well-known [20, Sect. 14] that (3.1) admits a unique principal eigenvalue μ_1 = $\mu_1(d,h)$ possessing a positive eigenfunction $\varphi \in C_T^{2+\alpha,1+\alpha/2}(\bar{\Omega} \times \mathbb{R})$ which is unique up to scaling. Furthermore, $\mu_1(d,h)$ is also the principal eigenvalue of the following adjoint eigenvalue problem:

$$\begin{cases}
-\psi_t - d\Delta\psi = h(x,t)\psi + \mu\psi & \text{in } \Omega \times \mathbb{R}, \\
\partial_\nu \psi = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\
\psi & \text{is } T\text{-periodic in } t.
\end{cases}$$
(3.2)

The sign of the principal eigenvalue $\mu_1(d, h)$ of (3.1) plays an important role in determining local stability of the two semitrivial periodic solutions of system (1.1). (See Lemma 4.5 below.) For comparison purposes, we consider a linear elliptic eigenvalue problem for $g \in L^{\infty}(\Omega)$:

$$\begin{cases} d\Delta\varphi + g(x)\varphi + \mu\varphi = 0 & \text{in } \Omega, \\ \partial_{\nu}\varphi = 0 & \text{on } \partial\Omega. \end{cases}$$
 (3.3)

Note that when h is temporally homogeneous, the periodic-parabolic eigenvalue problem (3.1) reduces to the elliptic case (3.3); see e.g. [20, Remark 16.5]. Hence, without causing any confusion, we also use $\mu_1(d, g)$ to denote the principal eigenvalue of (3.3). There are extensive studies on the principal eigenvalue of the eigenvalue problem (3.1) and its variants. For recent progress in those directions, see e.g. [24, 28-30, 39] and references therein. We now state properties of the solution $\mu_1(d,h)$ and $\mu_1(d,g)$ for (3.1) and (3.3) respectively:

Lemma 3.1. Assume that $h \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$. Then the following hold:

(i) $\frac{1}{T}\int_0^T \min_{x \in \bar{\Omega}} (-h(x,t)) dt \le \mu_1(d,h) \le -\hat{\bar{h}}$ for all d>0. Moreover, $\mu_1(d,h) = -\hat{\bar{h}}$ if and only if h is spatially homogeneous

- (ii) $\lim_{d\to 0} \mu_1(d,h) = \min_{\bar{\Omega}}(-\hat{h})$ and $\lim_{d\to \infty} \mu_1(d,h) = -\hat{\bar{h}}$.
- (iii) $\mu_1(d,h) \leq \mu_1(d,\hat{h})$ for all d > 0, where equality holds if and only if $h \hat{h}$ is spatially homogeneous.
- (iv) Assume that $g \in L^{\infty}(\Omega)$ and $g \not\equiv \text{const.}$ Then $\mu_1(d,g)$ is strictly increasing in d for all d > 0.

Lemma 3.1 (i, ii) follows from the Maximum Principle and [23, Lemma 2.4]. The proof of Lemma 3.1 (iii) can be found in [24, Theorem 2.1]. The proof of Lemma 3.1 (iv) is standard: see e.g. [6, Corollary 2.2].

It follows from Lemma 3.1 (iv) that, for a spatially heterogeneous but temporally constant function h, the corresponding principal eigenvalue is strictly increasing in d > 0. However, when h is both spatially and temporally heterogeneous, $\mu_1(\cdot,h)$ is not necessarily monotone; see [23, Theorem 2.2] for an example. Nevertheless, we will show in Lemma 3.3 below that $\mu_1(d,h)$ is still strictly increasing in d for all d sufficiently large under mild conditions on h.

3.1. Asymptotic behavior for large diffusion rates

In this subsection, we show the following result which plays a significant role in studying the dynamics of system (1.1) when either of the two dispersal rates d_1 and d_2 is sufficiently large.

To state our result precisely, we emphasize the dependence on d and h of the principal eigenfunctions φ and ψ of (3.1) and (3.2) respectively by writing them in the form of $\varphi(x,t;d,h)$ and $\psi(x,t;d,h)$. For each $t \in [0,T]$ fixed, we define $\Gamma_h(\cdot,t)$ to be the unique solution satisfying

$$\begin{cases} -\Delta\Gamma_h = h - \overline{h} \text{ in } \Omega, & \partial_{\nu}\Gamma_h = 0 \text{ on } \partial\Omega, \\ \int_{\Omega} \Gamma_h(x, t) \, dx = 0. \end{cases}$$
(3.4)

Proposition 3.2. For each constant K > 0, there exist constants d_K , $C_K > 0$ such that for any $d > d_K$ and $h \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ with $h_t \in L^2((0,T),L^2(\Omega))$ satisfying

$$||h||_{L^{\infty}(\Omega \times (0,T))} + ||h_t||_{L^2((0,T),L^2(\Omega))} \le K,$$
(3.5)

the principal eigenfunctions $\varphi(x,t;d,h)$, $\psi(x,t;d,h)$ of (3.1) and (3.2) corresponding to $\mu_1(d,h)$ respectively with normalization $\|\varphi\|_{L^2((0,T),L^2(\Omega))} = \|\psi\|_{L^2((0,T),L^2(\Omega))} = 1$ can be rewritten into the following form:

$$\varphi(x,t;d,h) = \overline{\varphi}(t;d,h) + \frac{\overline{\varphi}(t;d,h)\Gamma_h(x,t)}{d} + \frac{\varphi_2(x,t;d,h)}{d^2},$$

$$\psi(x,t;d,h) = \overline{\psi}(t;d,h) + \frac{\overline{\psi}(t;d,h)\Gamma_h(x,t)}{d} + \frac{\psi_2(x,t;d,h)}{d^2},$$
(3.6)

where the spatial averages satisfy

$$\frac{1}{C_K} \le \overline{\varphi}(t; d, h), \overline{\psi}(t; d, h) \le C_K \quad \forall t \in [0, T], \tag{3.7}$$

and $\varphi_2(x,t;d,h)$ and $\psi_2(x,t;d,h)$ satisfy

$$\|\varphi_2\|_{L^2((0,T),H^1(\Omega))} \le C_K \quad and \quad \|\psi_2\|_{L^2((0,T),H^1(\Omega))} \le C_K.$$
 (3.8)

Furthermore, for each constant $\eta > 0$, there exists a constant $d_{\eta,K} > 0$ depending only on η and K such that if h satisfies in addition

$$\|\nabla\Gamma_h\|_{L^2((0,T),L^2(\Omega))} \geq \eta,$$

then

$$\frac{\partial \mu_1(d,h)}{\partial d} > 0 \quad \text{for all } d > d_{\eta,K}. \tag{3.9}$$

Proof. For simplicity of notation, we suppress the dependence on d and h of φ , ψ , $\overline{\varphi}$, $\overline{\psi}$, φ_2 , ψ_2 and denote $\mu_1 = \mu_1(d,h)$ during this proof.

Set
$$\phi(x,t) := \overline{\varphi}(t)\Gamma_h(x,t)$$
.

Claim. There exists some constant $C_K > 0$ such that

$$\|\phi\|_{L^2((0,T),L^2(\Omega))} \le C_K,\tag{3.10}$$

$$\|\phi_t\|_{L^2((0,T),L^2(\Omega))} \le C_K. \tag{3.11}$$

We first prove (3.10). Indeed, for each $t \in [0, T]$ fixed, multiplying both sides of the equation for Γ_h in (3.4) by Γ_h and integrating over Ω , as $\overline{\Gamma_h}(t) \equiv 0$, by Hölder's inequality, Poincaré inequality and (3.5), we obtain

$$\int_{\Omega} |\nabla \Gamma_h|^2 = \int_{\Omega} \Gamma_h(h - \overline{h}) \le \left(\int_{\Omega} \Gamma_h^2\right)^{1/2} \cdot \left(\int_{\Omega} (h - \overline{h})^2\right)^{1/2} \le C_K \left(\int_{\Omega} |\nabla \Gamma_h|^2\right)^{1/2}.$$

This implies that for all $t \in [0, T]$, $\int_{\Omega} |\nabla \Gamma_h|^2 \le C_K$ and hence $\int_{\Omega} \Gamma_h^2 \le C_K$. Integrating those two inequalities from 0 to T, we see that

$$\|\Gamma_h\|_{L^2((0,T),H^1(\Omega))} \le C_K. \tag{3.12}$$

By Hölder's inequality and the normalization of φ , we see that

$$\int_0^T \int_{\Omega} \overline{\varphi}^2 \le 1. \tag{3.13}$$

Therefore, (3.10) follows from Hölder's inequality, (3.12) and (3.13).

Next we prove (3.11). Differentiating the equation for Γ_h in (3.4) with respect to t, we obtain

$$\begin{cases} -\Delta \partial_t \Gamma_h = h_t - \overline{h}_t \text{ in } \Omega, & \partial_\nu \partial_t \Gamma_h = 0 \text{ on } \partial \Omega, \\ \int_{\Omega} \partial_t \Gamma_h(x, t) \, dx = 0. \end{cases}$$

By similar arguments to the proof of (3.12), we deduce that

$$\|\partial_t \Gamma_h\|_{L^2((0,T),H^1(\Omega))} \le C_K.$$
 (3.14)

We now estimate $\overline{\varphi}(t)$. Integrating the equation for φ over Ω , we obtain

$$\overline{\varphi}_t = \overline{\varphi}(\overline{h} + \mu_1) + \frac{1}{|\Omega|} \int_{\Omega} h(\varphi - \overline{\varphi}).$$
 (3.15)

By Lemma 3.1 (i) and (3.5), $|\mu_1| \le ||h||_{L^{\infty}(\Omega \times (0,T))} \le K$. Therefore, by direct calculation,

$$\int_0^T \int_{\Omega} (\overline{\varphi}_t)^2 \le C_K. \tag{3.16}$$

Since $\phi_t = \overline{\varphi}_t \Gamma_h + \overline{\varphi} \partial_t \Gamma_h$, (3.11) follows from Hölder's inequality, (3.12)–(3.14) and (3.16).

Now, to prove the proposition, we rewrite

$$\varphi(x,t) = \overline{\varphi}(t) + \frac{\phi(x,t)}{d} + \frac{\varphi_2(x,t)}{d^2}.$$
 (3.17)

It is easy to see that φ_2 is *T*-periodic in *t* with $\overline{\varphi_2}(t) = 0$ for any *t*. Moreover, by direct computation and (3.15), it is easy to check that φ_2 satisfies the following equation:

$$\begin{cases} \frac{1}{d} \partial_t \varphi_2 - \Delta \varphi_2 - \frac{1}{d} (h + \mu_1) \varphi_2 = (h + \mu_1) \phi - \phi_t - \frac{1}{|\Omega|} \int_{\Omega} \left(\phi + \frac{1}{d} \varphi_2 \right) h & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \varphi_2 = 0 & \text{on } \partial \Omega \times \mathbb{R}. \end{cases}$$

Since $\overline{\varphi_2}(t) = 0$ for any t, $\int_0^T \int_{\Omega} \varphi_2^2 \le C \int_0^T \int_{\Omega} |\nabla \varphi_2|^2$ by Poincaré's inequality. Multiplying the equation for φ_2 by φ_2 and integrating over $\Omega \times (0, T)$, we see that

$$\begin{split} \int_0^T \int_{\Omega} |\nabla \varphi_2|^2 &= \frac{1}{d} \int_0^T \int_{\Omega} (h + \mu_1) \varphi_2^2 + \int_0^T \int_{\Omega} \varphi_2 [(h + \mu_1) \phi - \phi_t] \\ &\leq \frac{C_K}{d} \int_0^T \int_{\Omega} |\nabla \varphi_2|^2 + \int_0^T \left[\varepsilon \int_{\Omega} \varphi_2^2 + C(\varepsilon, K) \int_{\Omega} (\phi_t^2 + \phi^2) \right] \\ &\leq \left(\frac{C_K}{d} + \varepsilon C \right) \int_0^T \int_{\Omega} |\nabla \varphi_2|^2 + C(\varepsilon, K) \int_0^T \int_{\Omega} (\phi_t^2 + \phi^2). \end{split}$$

Therefore, choosing d_K even larger such that $d_K > 4C_K$ and $\varepsilon < (4C)^{-1}$, we deduce from (3.10) and (3.11) that

$$\int_0^T \int_{\Omega} |\nabla \varphi_2|^2 \le C_K \quad \text{and} \quad \int_0^T \int_{\Omega} \varphi_2^2 \le C_K \quad \forall d > d_K.$$

This finishes the proof of (3.6) for φ . By similar arguments, we can prove the inequality for ψ .

We now prove (3.7). Denote

$$\varphi_* := \varphi - \overline{\varphi} \quad \text{and} \quad \varrho(t) := \frac{1}{|\Omega|} \int_{\Omega} (\varphi - \overline{\varphi}) h = \frac{1}{|\Omega|} \int_{\Omega} \varphi_* h.$$

Using the variation of constants formula, we can solve the ODE (3.15) on [0, T] and obtain

$$\overline{\varphi}(t) = \overline{\varphi}(0) \exp\left(\int_0^t (\overline{h}(s) + \mu_1) \, ds\right) + \tau(t), \tag{3.18}$$

where

$$\tau(t) := \exp\left(\int_0^t (\overline{h}(s) + \mu_1) \, ds\right) \int_0^t \varrho(s) \exp\left(-\int_0^s (\overline{h}(\xi) + \mu_1) \, d\xi\right) ds.$$

Multiplying both sides of the equation for φ by φ and integrating over $\Omega \times (0, T)$, we obtain

 $d\int_0^T \int_{\Omega} |\nabla \varphi|^2 = \int_0^T \int_{\Omega} (h + \mu_1) \varphi^2 \le C_K.$

Since $\overline{\varphi_*}(t) = 0$ for any t and $\nabla \varphi = \nabla \varphi_*$, by Poincaré's inequality and the above estimate, we see that

$$\int_0^T \int_{\Omega} \varphi_*^2 \le \frac{C_K}{d}.\tag{3.19}$$

This implies by Hölder's inequality that for any $t \in [0, T]$,

$$|\tau(t)| \le C_K \int_0^T |\varrho(t)| \, dt \le C_K \left(\int_0^T \int_{\Omega} \varphi_*^2 \right)^{1/2} \le \frac{C_K}{\sqrt{d}}.$$

Now assume for contradiction that $\overline{\varphi}(0) \to 0$ as $d \to \infty$ (passing to a subsequence of d if necessary). Then (3.18) and the above estimate imply that $\overline{\varphi}(t) \to 0$ uniformly on [0,T]. Since $\varphi = \overline{\varphi} + (\varphi - \overline{\varphi}) = \overline{\varphi} + \varphi_*$, this combined with (3.19) ensures that $\|\varphi\|_{L^2((0,T),L^2(\Omega))} \to 0$ as $d \to \infty$, which contradicts the normalization of φ . Therefore $\overline{\varphi}(0)$ is uniformly bounded from below by a positive number depending only on K for all d sufficiently large. Similarly, we can show that $\overline{\varphi}(0)$ is uniformly bounded from above for all d sufficiently large. This finishes the proof of (3.7).

It only remains to prove (3.9). It follows from [23, proof of Lemma 2.3] that

$$\frac{\partial \mu_1(d,h)}{\partial d} = \frac{\int_0^T \int_{\Omega} \nabla \varphi \cdot \nabla \psi}{\int_0^T \int_{\Omega} \varphi \psi}.$$
 (3.20)

Therefore, by (3.6) we obtain, for all $d > d_K$,

$$\begin{split} \frac{\partial \mu_1(d,h)}{\partial d} \int_0^T \int_{\Omega} \varphi \psi &= \frac{1}{d^2} \int_0^T \overline{\varphi}(t) \overline{\psi}(t) \int_{\Omega} |\nabla \Gamma_h|^2 \\ &+ \frac{1}{d^3} \int_0^T \left(\overline{\varphi}(t) \int_{\Omega} \nabla \Gamma_h \cdot \nabla \psi_2 + \overline{\psi}(t) \int_{\Omega} \nabla \Gamma_h \cdot \nabla \varphi_2 \right) + \frac{1}{d^4} \int_0^T \int_{\Omega} \nabla \varphi_2 \cdot \nabla \psi_2. \end{split}$$

Since $\int_0^T \overline{\varphi}(t)\overline{\psi}(t) \int_{\Omega} |\nabla \Gamma_h|^2 \ge \eta^2/C_K^2 > 0$ for all $d > d_K$, choosing $d_{\eta,K} \ge d_K$ even larger if necessary, we see from (3.7), (3.8) and (3.12) that $\frac{\partial \mu_1(d,h)}{\partial d} > 0$ for all $d > d_{\eta,K}$. This finishes the proof of the proposition.

For given $h \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ fixed, actually we can obtain more precise asymptotic expansions of $\mu_1(d,h)$, φ and ψ as $d \to \infty$, based on the proof of Proposition 3.2. Although this result will not be used directly in this paper, we think it might be of independent interest.

Lemma 3.3. Let $h \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ with $h_t \in L^2((0,T),L^2(\Omega))$ be spatially heterogeneous. Then the principal eigenvalue $\mu_1(d,h)$ and the corresponding principal eigenfunctions φ, ψ of (3.1) and (3.2) respectively with normalization $\|\varphi\|_{L^2((0,T),L^2(\Omega))} = \|\psi\|_{L^2((0,T),L^2(\Omega))} = 1$ satisfy the following asymptotic expansion as $d \to \infty$:

$$\begin{split} &\mu_1(d,h) = -\hat{\bar{h}} + \frac{1}{d}\widehat{|\overline{\nabla \Gamma_h}|^2} + O\bigg(\frac{1}{d^2}\bigg), \\ &\overline{\varphi}(t) = \overline{\varphi}(0) \exp\bigg(\int_0^t \overline{h}(s) - \hat{\bar{h}}\,ds\bigg) \bigg[1 + \frac{1}{d}\bigg(\int_0^t \overline{|\nabla \Gamma_h|^2}(s) - \widehat{|\overline{\nabla \Gamma_h}|^2}\,ds\bigg)\bigg] + O\bigg(\frac{1}{d^2}\bigg), \\ &\overline{\psi}(t) = \overline{\psi}(0) \exp\bigg(-\int_0^t \overline{h}(s) - \hat{\bar{h}}\,ds\bigg) \bigg[1 - \frac{1}{d}\bigg(\int_0^t \overline{|\nabla \Gamma_h|^2}(s) - \widehat{|\overline{\nabla \Gamma_h}|^2}\,ds\bigg)\bigg] + O\bigg(\frac{1}{d^2}\bigg), \end{split}$$

where the second and third O-notations are understood in the sense of $L^2((0,T),H^1(\Omega))$ norm, and $\lim_{d\to\infty} \overline{\psi}(0)$ and $\lim_{d\to\infty} \overline{\psi}(0)$ exist.

We postpone the proof of Lemma 3.3 to the Appendix.

3.2. Asymptotic properties of linear periodic-parabolic equations with small diffusion rates

In this subsection, we establish asymptotic behavior of normalized solutions to a class of linear periodic-parabolic equations when the "diffusion rate" tends to 0.

To motivate our discussion, we first consider a simpler toy case. Let $h_d \in C_T^{\alpha,\alpha/2}(\bar{\Omega}\times\mathbb{R})$ for all d>0 small. Let $\varphi(\cdot\,;\,d)$ and $\psi(\cdot\,;\,d)$ be the principal eigenfunction and the principal adjoint eigenfunction corresponding to $\mu_1(d,h_d)$ respectively with normalization

$$\|\varphi\psi\|_{L^2((0,T),L^2(\Omega))}=1.$$

In other words, $\varphi(\cdot; d)$ and $\psi(\cdot; d)$ are strictly positive and satisfy the following equations:

$$\begin{cases} \varphi_t - d\Delta\varphi = h_d(x, t)\varphi + \mu_1(d, h_d)\varphi & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu}\varphi = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \varphi \text{ is } T\text{-periodic in } t, \end{cases}$$
(3.21)

and

$$\begin{cases} -\psi_t - d\Delta\psi = h_d(x, t)\psi + \mu_1(d, h_d)\psi & \text{in } \Omega \times \mathbb{R}, \\ \partial_\nu \psi = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \psi \text{ is } T\text{-periodic in } t. \end{cases}$$
(3.22)

Define $v(\cdot;d) := \varphi(\cdot;d)\psi(\cdot;d)$. Then $||v||_{L^2((0,T),L^2(\Omega))} = 1$ and v satisfies

$$\begin{cases} v_t = -d\nabla \cdot (\nabla v - 2v\nabla \ln \varphi) = -d(\Delta v - 2\nabla v \cdot \nabla \ln \varphi + 2v\Delta \ln \varphi) & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu}v = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ v \text{ is } T\text{-periodic in } t. \end{cases}$$
(3.23)

The above equation has a very special structure as now we can divide both sides by d and view the parameter 1/d as the time frequency. Note that the coefficients of the equation for v depend on d through $\varphi(\cdot; d)$. In general, we can ask:

Question. Assume that $\varphi(\cdot;d)$ converges in a suitable function space as $d\to 0$; can we say anything about the convergence of $v(\cdot; d)$, and in which sense?

An affirmative answer to this question means that the eigenvalue problem (3.21) and its adjoint problem (3.22) are correlated as $d \to 0$. It is this observation that gives us the key insight to the local dynamics of system (1.1) when both the dispersal rates d_1 and d_2 are small in Section 6.

Our goal in this subsection is to address the above question concerning a more general linear equation than (3.23) in the following nondivergence form (using λ as the "diffusion" parameter instead):

$$\begin{cases} \rho_t = \lambda [\Delta \rho + \nabla \rho \cdot \nabla b_{\lambda}(x, t) + c_{\lambda}(x, t) \rho] & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \rho = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \rho \text{ is } T\text{-periodic in } t, \end{cases}$$
(3.24)

where $\nabla b_{\lambda} \in (C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R}))^N$ and $c_{\lambda} \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$. For notational convenience, for any function $f \in L^{\infty}(\Omega \times (0,T))$, we use $||f||_{L^{\infty}(\Omega \times (0,T))}$ and $||f||_{\infty}$ interchangeably to denote the essential sup-norm of f. We now state the following result which plays a significant role during the study of the dynamics of system (1.1) in Section 6:

Proposition 3.4. Let ρ_{λ} be a nonnegative classical solution of (3.24) which is T-periodic in t for all λ small and

$$\|\rho_{\lambda}\|_{L^{2}((0,T),L^{2}(\Omega))} = 1. \tag{3.25}$$

Assume that

$$\lim_{\lambda \to 0} \|b_{\lambda} - b_{0}\|_{C([0,T],C^{1}(\bar{\Omega}))} = 0, \quad \lim_{\lambda \to 0} \|c_{\lambda} - c_{0}\|_{\infty} = 0.$$
 (3.26)

Then

$$\rho_{\lambda} \to \rho_0 \quad \text{in } L^2((0,T), H^1(\Omega)) \text{ as } \lambda \to 0,$$
 (3.27)

where $\rho_0 \in H^1(\Omega)$ is a weak solution to

$$\rho_{\lambda} \to \rho_{0} \quad \text{in } L^{2}((0,T), H^{1}(\Omega)) \text{ as } \lambda \to 0,$$

$$(3.27)$$

$$\text{is a weak solution to}$$

$$\begin{cases} \Delta \rho_{0} + \nabla \rho_{0} \cdot \nabla \hat{b}_{0}(x) + \hat{c}_{0}(x)\rho_{0} = 0 & \text{in } \Omega, \\ \partial_{\nu} \rho_{0} = 0 & \text{on } \partial \Omega, \end{cases}$$

$$(3.28)$$

satisfying $\|\rho_0\|_{L^2(\Omega)} = 1/\sqrt{T}$.

Before we proceed to the proof of the above proposition, we would like to mention that a similar problem has been considered in [28, 37], where the authors studied asymptotic behaviors of the principal eigenvalue to a general linear time-periodic parabolic eigenvalue problem in the following form:

$$\begin{cases} \tau \partial_t u = \nabla [\mathbf{A}(x,t) \nabla u] + \nabla b(x,t) \cdot \nabla u + c(x,t) u + \lambda u & \text{in } \Omega \times \mathbb{R}, \\ [\mathbf{A} \nabla u] \cdot v = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ u \text{ is } T\text{-periodic in } t. \end{cases}$$

Here $\tau > 0$ is a constant referred to as the frequency, and **A** is a symmetric and uniformly elliptic matrix field. Proposition 14.4 in [5] ensures the existence and uniqueness of the principal eigenvalue, denoted by $\lambda(\tau)$, of the above problem, which is real, simple, and its corresponding eigenfunction $u(\tau)$ can be chosen positive in $\bar{\Omega} \times [0, T]$. When $\tau \to \infty$, the asymptotic behavior of $(\lambda(\tau), u(\tau))$ and the limiting equation satisfied by $\lim_{\tau \to \infty} u(\tau)$ have been obtained in [28, 37].

Remark 3.5. At a first glance, Proposition 3.4 looks very similar to [37, Theorem 3.10] and [28, Theorem 1.3 (ii)]). However, we cannot apply their results directly in our paper for the following reasons:

- (i) As we pointed out at the beginning of this subsection, our study of problem (3.24) is motivated by the analysis of the local dynamics of system (1.1) in terms of the two dispersal rates d_1 and d_2 . Therefore, the coefficients in (3.24) are not fixed but naturally depend on the parameter λ involved, which would be d_1 and d_2 instead when we apply Proposition 3.4 in the study of system (1.1). This is usually the case when one studies dynamics of a system rather than a scalar equation.
- (ii) More importantly, in the proof of [37, Theorem 3.10], one only has to show that the normalized eigenfunction $u(\tau)$ converges strongly in $L^2([0,T],L^2(\Omega))$ but weakly in $L^2([0,T],H^1(\Omega))$ as $\tau\to\infty$ to get the conclusion. However, for our purposes, we need to show in Proposition 3.4 that ρ_λ converges strongly in $L^2([0,T],H^1(\Omega))$! This is the particular reason why we need to establish Lemma A.1 in the Appendix to obtain a technical uniform a priori estimate (3.29) below as a first step during our proof.

Proof of Proposition 3.4. We first claim that for each $\Lambda > 0$, if $\|b_{\lambda}\|_{C([0,T],C^{1}(\bar{\Omega}))}$, $\|c_{\lambda}\|_{\infty}$ and $\|\rho_{\lambda}\|_{L^{2}((0,T),L^{2}(\Omega))}$ are uniformly bounded in $\lambda \in (0,\Lambda]$, then there exists a constant C depending only on $\sup_{\lambda} \|b_{\lambda}\|_{C([0,T],C^{1}(\bar{\Omega}))}$, $\sup_{\lambda} \|c_{\lambda}\|_{\infty}$ and Λ such that for all $\lambda \in (0,\Lambda]$,

$$\|\rho_{\lambda}\|_{\infty} \le C. \tag{3.29}$$

Indeed, (3.29) follows directly from Lemma A.1 by choosing $\bar{k}=0$ there.

It only remains to prove (3.27). For simplicity of notation, we suppress the subscript λ in ρ_{λ} in the remainder of this proof. Multiplying both sides of the equation for ρ in (3.24)

by ρ and integrating over $\Omega \times (0, T)$, we deduce from (3.26) and (3.29) that

$$\begin{split} \int_0^T \int_{\Omega} |\nabla \rho|^2 &= \int_0^T \int_{\Omega} \rho \nabla \rho \cdot \nabla b_{\lambda} + \int_0^T \int_{\Omega} c_{\lambda} \rho^2 \\ &\leq C \bigg(\int_0^T \int_{\Omega} |\nabla \rho|^2 \bigg)^{1/2} \bigg(\int_0^T \int_{\Omega} |\nabla b_{\lambda}|^2 \bigg)^{1/2} + C. \end{split}$$

Therefore, $\int_0^T \int_{\Omega} |\nabla \rho|^2$ is uniformly bounded for all $\lambda > 0$ small, which together with (3.29) implies that for all $\lambda > 0$ small,

$$\|\rho\|_{L^2((0,T),H^1(\Omega))} \le C. \tag{3.30}$$

Next, we claim that for all $\lambda > 0$ small,

$$\|\rho_t/\lambda\|_{L^2((0,T),L^2(\Omega))} \le C.$$
 (3.31)

Indeed, multiplying both sides of the equation for ρ in (3.24) by ρ_t and integrating over $\Omega \times (0, T)$, we obtain

$$\int_0^T \int_{\Omega} \rho_t^2 = -\frac{\lambda}{2} \int_0^T \int_{\Omega} (|\nabla \rho|^2)_t + \lambda \int_0^T \int_{\Omega} \rho_t (\nabla \rho \cdot \nabla b_\lambda + c_\lambda \rho)$$

$$\leq \lambda C \left(\int_0^T \int_{\Omega} \rho_t^2 \right)^{1/2} \left[\left(\int_0^T \int_{\Omega} |\nabla \rho|^2 \right)^{1/2} + \left(\int_0^T \int_{\Omega} \rho^2 \right)^{1/2} \right],$$

which combined with (3.30) imply (3.31).

For each $t \in [0, T]$ fixed, by elliptic regularity, we see that

$$\|\rho\|_{H^2(\Omega)} \le C(\|\rho\|_{L^2(\Omega)} + \|\rho_t/\lambda\|_{L^2(\Omega)}),$$

which implies that

$$\|\rho\|_{L^2((0,T),H^2(\Omega))} \le C(\|\rho\|_{L^2((0,T),L^2(\Omega))} + \|\rho_t/\lambda\|_{L^2((0,T),L^2(\Omega))}).$$

This combined with (3.30) and (3.31) indicates that $\|\rho\|_{L^2((0,T),H^2(\Omega))}$ is uniformly bounded for all $\lambda > 0$ small. Since $H^2(\Omega) \subset H^1(\Omega) \subset L^2(\Omega)$ and the two embeddings are compact, passing to a subsequence of λ if necessary, we may apply the Aubin–Lions Lemma [41, Theorems 2.1 & 2.3] to conclude that

$$\rho \to \rho_0 \text{ in } L^2((0,T), H^1(\Omega)) \text{ as } \lambda \to 0 \text{ and } \|\rho_0\|_{L^2((0,T), L^2(\Omega))} = 1.$$
 (3.32)

Passing to a subsequence of λ again if necessary, we may assume that there exists a set $\mathcal{N} \subset [0,T]$ of measure zero such that $\rho(\cdot,t) \to \rho_0(\cdot,t)$ in $H^1(\Omega)$ for all $t \in [0,T] \setminus \mathcal{N}$ as $\lambda \to 0$. Let $\phi \in H^1(\Omega)$ be a test function. Multiplying both sides of the equation for ρ in (3.24) by ϕ and integrating from s to t, where $s,t \in [0,T] \setminus \mathcal{N}$, we see that

$$\int_{\Omega} [\rho(x,t) - \rho(x,s)] \phi(x) \, dx = -\lambda \int_{s}^{t} \int_{\Omega} \nabla \rho \cdot \nabla \phi + \lambda \int_{s}^{t} \int_{\Omega} \phi \nabla \rho \cdot \nabla b + \lambda \int_{s}^{t} \int_{\Omega} c \rho \phi$$

$$\leq \lambda \left(\int_{0}^{T} \int_{\Omega} |\nabla \rho|^{2} \right)^{1/2} \left(\int_{0}^{T} \int_{\Omega} |\nabla \phi|^{2} \right)^{1/2} + \lambda C \|\phi\|_{L^{2}(\Omega)} \|\rho\|_{L^{2}((0,T),H^{1}(\Omega))}.$$

Letting $\lambda \to 0$ in the above estimate, we find from (3.30) that

$$\int_{\Omega} [\rho_0(x,t) - \rho_0(x,s)] \phi(x) \, dx \le 0.$$

Since $\phi \in H^1(\Omega)$ is arbitrary, we may replace ϕ by $-\phi$ and still get the above inequality. This implies that

$$\int_{\Omega} [\rho_0(x,t) - \rho_0(x,s)] \phi(x) \, dx = 0 \quad \forall s,t \in [0,T] \setminus \mathcal{N}, \, \forall \phi \in H^1(\Omega).$$

By a density argument, it is easy to see that the above identity holds for all $\phi \in L^2(\Omega)$. This combined with (3.32) indicate that $\rho_0(\cdot,t)$ is independent of t for all $t \in [0,T] \setminus \mathcal{N}$. Therefore, without causing any confusion with the notations being used, we denote

$$\rho_0(x,t) = \rho_0(x) \quad \forall t \in [0,T] \setminus \mathcal{N}. \tag{3.33}$$

Multiplying both sides of the equation for ρ in (3.24) by $\phi \in H^1(\Omega)$ and integrating over $\Omega \times (0, T)$, we obtain

$$0 = -\int_0^T \int_{\Omega} \nabla \rho \cdot \nabla \phi + \int_0^T \int_{\Omega} \phi \nabla \rho \cdot \nabla b + \int_0^T \int_{\Omega} c \rho \phi.$$

Letting $\lambda \to 0$, we conclude from (3.26), (3.32) and (3.33) that

$$-T \int_{\Omega} \nabla \rho_0 \cdot \nabla \phi + T \int_{\Omega} \phi \nabla \rho_0 \cdot \widehat{\nabla b_0} + T \int_{\Omega} \hat{c}_0 \rho_0 \phi = 0$$

Therefore, $\rho_0 \in H^1(\Omega)$ is a weak solution to (3.24) with $\|\rho_0\|_{L^2(\Omega)} = 1/\sqrt{T}$. This finishes the proof of the proposition.

To end this subsection, we answer the question raised at its beginning concerning the limiting behavior of $v = \varphi \psi$ satisfying (3.23). This result will not be used in the rest of this paper, but it may be of independent interest.

Corollary 3.6. Let $h_d \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ for all d > 0 small, and let $\varphi(\cdot; d)$ and $\psi(\cdot; d)$ be the principal eigenfunction and the principal adjoint eigenfunction of (3.21) and (3.22) corresponding to $\mu_1(d,h_d)$ respectively with normalization $\|\varphi\psi\|_{L^2((0,T),L^2(\Omega))} = 1$. Assume that there exists some function φ_0 such that

$$\lim_{d\to 0} \|\ln \varphi - \ln \varphi_0\|_{C([0,T],C^1(\bar{\Omega}))} = 0 \quad and \quad \lim_{d\to 0} \|\Delta \ln \varphi - \Delta \ln \varphi_0\|_{\infty} = 0.$$

Then

$$v = \varphi \psi \to v_0 = c_0 \exp\left(\frac{1}{T} \int_0^T \ln \varphi_0^2 dt\right)$$
 in $L^2((0, T), H^1(\Omega))$ as $d \to 0$,

where $c_0 > 0$ is a constant uniquely determined such that $||v_0||_{L^2(\Omega)} = 1/\sqrt{T}$.

This follows directly from Proposition 3.4 and a direct computation to verify that v_0 is a positive solution to (3.23). Hence, we omit the proof.

4. Asymptotic behaviors of θ_d

In this section, we study the asymptotic behaviors of θ_d and its derivatives as d goes to 0 or ∞ .

Lemma 4.1. Assume $f \in C_T(\bar{\Omega} \times \mathbb{R})$. Then for each $\delta > 0$, there exists $f_{\delta} \in C_T^{\infty}(\bar{\Omega} \times \mathbb{R})$ with $\partial_{\nu} f_{\delta} = 0$ on $\partial \Omega \times \mathbb{R}$ such that

$$||f_{\delta} - f||_{C(\bar{\Omega} \times [0,T])} < \delta.$$

Furthermore, if $f \in C_T^{0,1}(\bar{\Omega} \times \mathbb{R})$, then f_{δ} can be chosen with $f_{\delta} \in C_T^{2,1}(\bar{\Omega} \times \mathbb{R})$ such that

$$||f_{\delta} - f||_{C^{0,1}(\bar{\Omega} \times [0,T])} < \delta.$$

Lemma 4.2. Assume that $f_d, h_d \in C_T(\bar{\Omega} \times \mathbb{R})$ for all d > 0 small and there exist $f_0, h_0 \in C_T(\bar{\Omega} \times \mathbb{R})$ such that

$$\lim_{d \to 0} \|f_d - f_0\|_{C(\bar{\Omega} \times [0,T])} = \lim_{d \to 0} \|h_d - h_0\|_{C(\bar{\Omega} \times [0,T])} = 0 \quad and \quad \hat{h}_0 < 0 \text{ on } \bar{\Omega}.$$

Let $u_d \in C_T(\bar{\Omega} \times \mathbb{R})$ be the unique strong solution to the linear periodic-parabolic problem

$$\begin{cases} u_t = d\Delta u + h_d u + f_d & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} u = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ u \text{ is } T\text{-periodic in } t. \end{cases}$$

$$(4.1)$$

Then

$$\lim_{d \to 0} \|u_d - u_0\|_{C(\bar{\Omega} \times [0, T])} = 0,$$

where u_0 is the unique solution to the following ODE:

$$\begin{cases} (u_0)_t = h_0 u_0 + f_0 & \text{in } \Omega \times \mathbb{R}, \\ u_0 & \text{is } T\text{-periodic in } t. \end{cases}$$

$$\tag{4.2}$$

Remark 4.3. Lemma 4.2 also holds true when the Laplacian operator Δ is replaced by a more general uniformly elliptic operator A(t) defined as in [20, Section II.12].

For the proofs of Lemmas 4.1 and 4.2, see the Appendix.

Lemma 4.4. Assume that m satisfies (M1). Then the following hold:

- (i) $\|\theta_d\|_{\infty} < \|m\|_{\infty}$ and $\|\theta_{d,t}\|_{L^2((0,T),L^2(\Omega))} \le C \|m\|_{\infty}^2$. Moreover, $\sup_{\bar{\Omega}\times[0,T]} \theta_d < \sup_{\bar{\Omega}\times[0,T]} m$ and $\inf_{\bar{\Omega}\times[0,T]} \theta_d > \inf_{\bar{\Omega}\times[0,T]} m$.
- (ii) Let (U(x,t),V(x,t)) be a coexistence T-periodic solution of system (1.1), if it exists. Then

$$\begin{split} \|U\|_{\infty} &< \|\theta_{d_1}\|_{\infty} < \|m\|_{\infty}, \quad \|V\|_{\infty} < \|\theta_{d_2}\|_{\infty} < \|m\|_{\infty}, \\ \|U_t\|_{L^2((0,T),L^2(\Omega))} &\leq C \|m\|_{\infty}^2, \quad \|V_t\|_{L^2((0,T),L^2(\Omega))} \leq C \|m\|_{\infty}^2, \end{split}$$

where C > 0 is a constant depending only on Ω and T.

Proof. The proof for part (i) is standard except for the second inequality. To prove it, multiplying the equation for θ_d by $\theta_{d,t}$ and integrating over $\Omega \times (0,T)$, we obtain

$$\begin{split} & \int_0^T \int_{\Omega} \theta_{d,t}^2 = d \int_0^T \int_{\Omega} \theta_{d,t} \Delta \theta_d + \int_0^T \int_{\Omega} \theta_{d,t} \theta_d (m - \theta_d) \\ & \leq -\frac{d}{2} \int_0^T \int_{\Omega} (|\nabla \theta_d|^2)_t - \frac{1}{3} \int_0^T \int_{\Omega} (\theta_d^3)_t + \|m\|_{\infty} \bigg(\int_0^T \int_{\Omega} \theta_d^2 \bigg)^{1/2} \bigg(\int_0^T \int_{\Omega} \theta_{d,t}^2 \bigg)^{1/2} \\ & \leq C \|m\|_{\infty}^2 \bigg(\int_0^T \int_{\Omega} \theta_{d,t}^2 \bigg)^{1/2} \,. \end{split}$$

This implies that $\|\theta_{d,t}\|_{L^2((0,T),L^2(\Omega))} \le C \|m\|_{\infty}^2$. The proof of (ii) uses the Maximum Principle and similar arguments to those above.

The linear stability of the two semitrivial periodic solutions $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$ relative to system (1.1) can be characterized as follows. For a proof, see e.g. [20, Sect. IV.31] and [23, Lemma 3.2].

Lemma 4.5. Assume that condition (M1) holds. Then the trivial solution (0,0) is linearly unstable for all $d_1, d_2 > 0$. The semitrivial periodic solution $(\theta_{d_1}, 0)$ is linearly stable (resp. linearly unstable) if $\mu_1(d_2, m - \theta_{d_1}) > 0$ (resp. $\mu_1(d_2, m - \theta_{d_1}) < 0$). Analogously, $(0, \theta_{d_2})$ is linearly stable (resp. linearly unstable) if $\mu_1(d_1, m - \theta_{d_2}) > 0$ (resp. $\mu_1(d_1, m - \theta_{d_2}) < 0$).

Now we study the asymptotic properties of θ_d as $d \to 0$.

Lemma 4.6. Assume that m satisfies (M1) and (M2). Let p(x,t) be defined in (2.2) and w(x,t) be the unique solution to the following ODE:

$$\begin{cases} w_t = w(m-2p) + \Delta p, & t \in \mathbb{R}, \\ w \text{ is } T\text{-periodic in } t. \end{cases}$$
(4.3)

Then

$$\lim_{d \to 0} \frac{1}{d} \|\theta_d - p - dw\|_{C^{0,1}(\bar{\Omega} \times [0,T])} = 0, \quad \lim_{d \to 0} \|\Delta \theta_d - \Delta p\|_{C(\bar{\Omega} \times [0,T])} = 0, \quad (4.4)$$

and for each $q \in (1, \infty)$,

$$\lim_{d \to 0} \|\theta_d(\cdot, t) - p(\cdot, t)\|_{W^{2,q}(\Omega)} = 0 \quad \text{uniformly in } t \in [0, T]. \tag{4.5}$$

In particular,

$$\lim_{d \to 0} \|\theta_d - p\|_{C([0,T],C^1(\bar{\Omega}))} = 0. \tag{4.6}$$

Proof. Since m > 0 on $\bar{\Omega} \times [0, T]$, for each $x \in \bar{\Omega}$ there is a unique positive and linearly stable T-periodic solution $p(x, \cdot)$ of (2.2). As m belongs to the classical space $C_T^{2,1}(\bar{\Omega} \times \mathbb{R})$, so does p(x, t). It follows from [23, proof of Lemma 3.4] that

$$\lim_{d \to 0} \|\theta_d - p\|_{C(\bar{\Omega} \times [0,T])} = 0 \tag{4.7}$$

and

$$\partial_{\nu} p = 0 \text{ on } \partial\Omega \times \mathbb{R}.$$
 (4.8)

Differentiating the equation for θ_d with respect to t, we can easily see that $\theta_{d,t}$ is a strong solution to

$$\begin{cases} \vartheta_t - d\Delta\vartheta = \vartheta(m - 2\theta_d) + m_t\theta_d & \text{in } \Omega \times \mathbb{R}, \\ \vartheta_{\nu}\vartheta = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \vartheta \text{ is } T\text{-periodic in } t. \end{cases}$$

Since $\mu_1(d, m - 2\theta_d) > \mu_1(d, m - \theta_d) = 0$ for all d small, the above periodic-parabolic problem has a unique strong solution, which must be $\theta_{d,t}$. By (4.7) and Lemma 4.2,

$$\lim_{d \to 0} \|\theta_{d,t} - p_t\|_{C(\bar{\Omega} \times [0,T])} = 0. \tag{4.9}$$

Denote

$$w_d := (\theta_d - p)/d$$
.

It follows from (4.8) and the equations satisfied by θ_d and p that w_d satisfies

$$\begin{cases} \partial_t w_d - d\Delta w_d = w_d (m - \theta_d - p) + \Delta p & \text{in } \Omega \times \mathbb{R}, \\ \partial_\nu w_d = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ w_d \text{ is } T\text{-periodic in } t. \end{cases}$$
(4.10)

It then follows from (4.3), (4.7) and Lemma 4.2 that

$$\lim_{d \to 0} \|(\theta_d - p)/d - w\|_{C(\bar{\Omega} \times [0, T])} = 0. \tag{4.11}$$

Differentiating the equation for w with respect to t, we see that w_t satisfies

$$\begin{cases} w_{tt} = w_t(m - 2p) + w(m_t - 2p_t) + \Delta p_t & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} w_t = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \vartheta \text{ is } T\text{-periodic in } t. \end{cases}$$

Since $m, p \in C^{2,1}(\bar{\Omega} \times [0, T])$, we see from the equation satisfied by p that $\Delta p_t \in C(\bar{\Omega} \times [0, T])$. Differentiating (4.10) with respect to t, we see that $\partial_t w_d$ is a strong solution to

$$\begin{cases} \partial_t (\partial_t w_d) - d \Delta \partial_t w_d = \partial_t w_d (m - \theta_d - p) + w_d (m_t - \theta_{d,t} - p_t) + \Delta p_t & \text{in } \Omega \times \mathbb{R}, \\ \partial_v \partial_t w_d = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \partial_t w_d & \text{is } T\text{-periodic in } t. \end{cases}$$

Hence it follows from (4.7), (4.9)–(4.11) and Lemma 4.2 that

$$\lim_{d \to 0} \|(\theta_{d,t} - p_t)/d - w_t\|_{C(\bar{\Omega} \times [0,T])} = 0.$$
(4.12)

This combined with (4.11) finishes the proof of the first equality in (4.4).

For each $t \in [0, T]$ fixed, we can rewrite (4.10) as follows:

$$\begin{cases} \Delta(\theta_d - p) = \frac{1}{d}(\theta_{d,t} - p_t) - \frac{1}{d}(\theta_d - p)(m - \theta_d - p) - \Delta p & \text{in } \Omega, \\ \partial \nu(\theta_d - p) = 0 & \text{on } \partial \Omega \end{cases}$$

By (4.3), we see that

$$\Delta(\theta_{d} - p) = \frac{1}{d}(\theta_{d,t} - p_{t}) - \frac{1}{d}(\theta_{d} - p)(m - \theta_{d} - p) - \Delta p$$

$$= \left[\frac{1}{d}(\theta_{d,t} - p_{t}) - w_{t}\right] + w(m - 2p) + \Delta p - \frac{1}{d}(\theta_{d} - p)(m - \theta_{d} - p) - \Delta p$$

$$= \left[\frac{1}{d}(\theta_{d,t} - p_{t}) - w_{t}\right] - \left[\frac{1}{d}(\theta_{d} - p) - w\right](m - 2p) + \frac{1}{d}(\theta_{d} - p)^{2}. \quad (4.13)$$

Hence, it follows from (4.7), (4.11) and (4.12) that

$$\lim_{d \to 0} \|\Delta \theta_d - \Delta p\|_{C(\bar{\Omega} \times [0,T])} = 0,$$

which finishes the proof for the second equality in (4.4). Consequently, for each $t \in [0, T]$ fixed, (4.5) follows directly from elliptic regularity theory for equation (4.13) satisfied by $\theta_d(\cdot, t) - p(\cdot, t)$. Finally, (4.6) follows from (4.5) and the Sobolev embedding theorem.

If m does not satisfy conditions (M1) or (M2), we may use Lemma 4.1 to approximate it by functions that satisfy those conditions. Then we can obtain the following result:

Lemma 4.7. Assume that
$$m \in C_T^{0,1}(\Omega \times \mathbb{R})$$
 and $m > 0$ on $\bar{\Omega} \times [0, T]$. Then

$$\|\theta_d - p\|_{C^{0,1}(\Omega \times [0,T])} \to 0 \quad as \ d \to 0.$$
 (4.14)

Since Lemma 4.7 is independent of the other parts of this paper, its proof is postponed to the Appendix.

To end this section, we characterize the behavior of θ_d when $d \to \infty$.

Lemma 4.8. Assume that $m \in C_T^{\alpha,\alpha/2}(\bar{\Omega} \times \mathbb{R})$ and m > 0 on $\bar{\Omega} \times [0,T]$. Then

$$\lim_{d \to \infty} \|\theta_d - \xi\|_{C(\bar{\Omega} \times [0,T])} = 0,$$

where $\xi(t)$ is the unique positive solution to

$$\begin{cases} \xi_t = \xi(\bar{m} - \xi), & t \in \mathbb{R}, \\ \xi \text{ is } T\text{-periodic in } t. \end{cases}$$
(4.15)

The above lemma can be proved by similar arguments to those in the proof of [23, Lemma 3.7] and hence we omit the details.

5. Proofs of Theorems 2.2 and 2.3

In this section, we first prove Theorem 2.3 under condition (M1).

Proof of Theorem 2.3. We will only prove the theorem for $d_1 < d_2$, as the case $d_2 > d_1$ follows by symmetry. Throughout the proof, we assume that condition (M1) holds.

Claim 5.1. Assume that (M1) holds. There exists a constant D > 0 depending only on m such that the following hold:

(i) Any coexistence T-periodic solution (U, V) of system (1.1) with $d_1, d_2 > D$, if it exists, satisfies

$$\frac{\partial \mu_1(d, m - U - V)}{\partial d} > 0 \quad \forall d > D. \tag{5.1}$$

(ii) For i = 1, 2,

$$\frac{\partial \mu_1(d, m - \theta_{d_i})}{\partial d} > 0 \quad \forall d, d_i > D. \tag{5.2}$$

To prove Claim 5.1, we first show there exists D > 0 depending only on m such that any coexistence T-periodic solution (U, V) of system (1.1) with $d_1, d_2 > D$, if it exists, satisfies

$$\|\nabla \Gamma_{m-U-V}\|_{L^{2}((0,T),L^{2}(\Omega))} \ge \frac{1}{2} \|\nabla \Gamma_{m}\|_{L^{2}((0,T),L^{2}(\Omega))} > 0.$$
 (5.3)

To see this, it is easy to observe that $\Gamma_{m-U-V} = \Gamma_m - \Gamma_U - \Gamma_V$. Therefore

$$\|\nabla\Gamma_{m-U-V}\|_{L^{2}((0,T),L^{2}(\Omega))} \ge \|\nabla\Gamma_{m}\|_{L^{2}((0,T),L^{2}(\Omega))} - \|\nabla\Gamma_{V}\|_{L^{2}((0,T),L^{2}(\Omega))} - \|\nabla\Gamma_{V}\|_{L^{2}((0,T),L^{2}(\Omega))}.$$
(5.4)

Multiplying both sides of the equation for Γ_U by Γ_U and integrating over $\Omega \times (0, T)$, as $\overline{\Gamma_U}(t) \equiv 0$, by Hölder's inequality and Poincaré's inequality, we obtain

$$\int_{0}^{T} \int_{\Omega} |\nabla \Gamma_{U}|^{2} = \int_{0}^{T} \int_{\Omega} \Gamma_{U}(U - \bar{U}) \leq \varepsilon \int_{0}^{T} \int_{\Omega} \Gamma_{U}^{2} + C(\varepsilon) \int_{0}^{T} \int_{\Omega} (U - \bar{U})^{2}$$

$$\leq \frac{1}{2} \int_{0}^{T} \int_{\Omega} |\nabla \Gamma_{U}|^{2} + C(\varepsilon) \int_{0}^{T} \int_{\Omega} (U - \bar{U})^{2}, \tag{5.5}$$

where the last inequality follows by choosing ε sufficiently small. Multiplying both sides of the equation for U by U and integrating over $\Omega \times (0, T)$, we obtain

$$d_1 \int_0^T \int_{\Omega} |\nabla U|^2 = \int_0^T \int_{\Omega} U^2(m - U - V).$$

By Lemma 4.4 and Poincaré's inequality, we see that

$$\int_0^T \int_{\Omega} (U - \overline{U})^2 \le C \int_0^T \int_{\Omega} |\nabla U|^2 \le \frac{C}{d_1},$$

where C is a constant depending only on m and Ω and may change from place to place. This combined with (5.5) implies that $\|\nabla \Gamma_U\|_{L^2((0,T),L^2(\Omega))} \leq C/\sqrt{d_1}$. Similarly, we can show that $\|\nabla \Gamma_V\|_{L^2((0,T),L^2(\Omega))} \leq C/\sqrt{d_2}$. Therefore, (5.3) follows from (5.4) by choosing D sufficiently large.

By similar arguments, we can show that for i = 1, 2,

$$\|\nabla\Gamma_{m-\theta_{d_i}}\|_{L^2((0,T),L^2(\Omega))} \ge \frac{1}{2}\|\nabla\Gamma_m\|_{L^2((0,T),L^2(\Omega))} > 0 \quad \forall d_i > D.$$
 (5.6)

Hence, Claim 5.1 follows directly from (5.3), (5.6), Lemma 4.4 and Proposition 3.2, by choosing D even larger if necessary.

Claim 5.2. Assume that (M1) holds. If $(d_1, d_2) \in (D, \infty) \times (D, \infty)$ and $0 < d_1 < d_2$, then $(\theta_{d_1}, 0)$ is globally asymptotically stable for system (1.1).

To prove Claim 5.2, we first show that for any $(d_1,d_2) \in (D,\infty) \times (D,\infty)$ with $d_2 > d_1$, system (1.1) has no coexistence periodic solution. Assume for contradiction that (U,V) is a coexistence T-periodic solution. Then we see from the equations satisfied by U and V that $\mu_1(d_1,m-U-V)=\mu_1(d_2,m-U-V)=0$, which contradicts (5.1). Moreover, it is easy to see from (5.2) that $\mu_1(d_2,m-\theta_{d_1})>\mu_1(d_1,m-\theta_{d_1})=0$ and $\mu_1(d_1,m-\theta_{d_2})<\mu_1(d_2,m-\theta_{d_2})=0$, Therefore, $(\theta_{d_1},0)$ is linearly stable and $(0,\theta_{d_2})$ is linearly unstable. Now, Claim 5.2 follows directly from the theory of monotone dynamical systems (see e.g. [20, Theorem 34.1]).

Claim 5.3. Assume that (M1) holds. For each $\varepsilon > 0$, there exists some $\hat{D}_{\varepsilon} > 0$ such that for all $(d_1, d_2) \in [\varepsilon, D] \times (\hat{D}_{\varepsilon}, \infty)$:

- (i) $(\theta_{d_1}, 0)$ is linearly stable;
- (ii) $(0, \theta_{d_2})$ is linearly unstable;
- (iii) system (1.1) has no coexistence periodic solution.

Consequently, $(\theta_{d_1}, 0)$ is globally asymptotically stable for all $(d_1, d_2) \in [\varepsilon, D) \times (\widehat{D}_{\varepsilon}, \infty)$.

To prove Claim 5.3, note that parts (i)–(iii) follow by a standard perturbation argument from the proofs of Lemma 3.3 (c), Lemma 3.6 (c) and Theorem 5.3 (a) in [23] respectively (see also [23, Remark 1]). Note that it is sufficient to assume that $\nabla m \not\equiv 0$ in their proofs. Hence, we omit the proofs of (i)–(iii). Now for each $(d_1,d_2) \in [\varepsilon,D] \times (\widehat{D}_\varepsilon,\infty)$ fixed, we may apply [20, Theorem 34.1] to conclude that $(\theta_{d_1},0)$ is globally asymptotically stable. This finishes the proof of Claim 5.3.

Theorem 2.3 now follows directly from Claims 5.2 and 5.3 by setting $D_{\varepsilon} := \max\{D, \widehat{D}_{\varepsilon}\}.$

Next, we prove Theorem 2.2, which characterizes the stability properties of the two semitrivial periodic solutions $(0, \theta_{d_1})$ and $(\theta_{d_2}, 0)$ when d_2 is sufficiently large.

Proof of Theorem 2.2. We divide the proof into several claims.

Claim 5.4. Assume that (M1)–(M3) hold. There exist constants $\varepsilon_1 > 0$ small and $\widetilde{D}_{\varepsilon_1} \geq \widehat{D}_{\varepsilon_1}$ large such that for each $d_2 > \widetilde{D}_{\varepsilon_1}$ fixed, $\mu_1(d_2, m - \theta_{d_1})$ is strictly increasing in $d_1 \in (0, \varepsilon_1)$. Moreover, there exists a unique continuously differentiable function $\check{d}_1 : (\widetilde{D}_{\varepsilon_1}, \infty) \to (0, \varepsilon_1)$ such that for $(d_1, d_2) \in (0, \varepsilon_1) \times (\widetilde{D}_{\varepsilon_1}, \infty)$,

$$\mu_1(d_2, m - \theta_{\check{d}_1(d_2)}) = 0 \iff d_1 = \check{d}_1(d_2).$$
 (5.7)

To prove Claim 5.4, for each $\varepsilon > 0$, let $\widehat{D}_{\varepsilon}$ be as in Claim 5.3. For each $d_2 > \widehat{D}_{\varepsilon}$ fixed, it follows from [23, Lemma 3.4] and (M1)–(M3) that $(\theta_{d_1}, 0)$ is linearly unstable for all d_1 sufficiently small. By Claim 5.3, $(\theta_{d_1}, 0)$ is linearly stable for all $d_1 \in [\varepsilon, D]$. Therefore, $\mu_1(d_2, m - \theta_{d_1})$ must change sign at least once when d_1 increases from 0 to ε .

Now, to show the existence and uniqueness of the function \check{d}_1 in Claim 5.4, it suffices to show that there exist $\varepsilon_1 > 0$ small and $\widetilde{D}_{\varepsilon_1} \geq \widehat{D}_{\varepsilon_1}$ large such that for each $d_2 \in (\widetilde{D}_{\varepsilon_1}, \infty)$ fixed, $\mu_1(d_2, m - \theta_{d_1})$ is strictly increasing in $d_1 \in (0, \varepsilon_1)$. Indeed, let φ and ψ be the principal eigenfunction and the principal adjoint eigenfunction corresponding to $\mu_1(d_2, m - \theta_{d_1})$ respectively, normalized so that

$$\|\varphi\|_{L^2((0,T),L^2(\Omega))} = \|\psi\|_{L^2((0,T),L^2(\Omega))} = 1.$$

In other words, φ and ψ are positive and satisfy the following equations respectively:

$$\begin{cases} \varphi_t - d_2 \Delta \varphi = (m - \theta_{d_1}) \varphi + \mu_1(d_2, m - \theta_{d_1}) \varphi & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \varphi = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \varphi \text{ is } T\text{-periodic in } t, \end{cases}$$
 (5.8)

and

$$\begin{cases} -\psi_t - d_2 \Delta \psi = (m - \theta_{d_1}) \psi + \mu_1 (d_2, m - \theta_{d_1}) \psi & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \psi = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \psi & \text{is } T\text{-periodic in } t. \end{cases}$$
(5.9)

Differentiating the equation for φ in (5.8) with respect to d_1 , denoting $\mu_1 := \mu_1(d_2, m - \theta_{d_1})$ and $d' = \frac{\partial}{\partial d_1}$ for simplicity, we obtain

$$\begin{cases} \partial_t \varphi' - d_2 \Delta \varphi' = \varphi'(m - \theta_{d_1}) - \varphi \theta'_{d_1} + \mu_1 \varphi' + \mu'_1 \varphi & \text{in } \Omega \times \mathbb{R}, \\ \partial_\nu \varphi' = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \varphi' & \text{is } T\text{-periodic in } t. \end{cases}$$

Multiplying the equation for φ' by ψ and the equation for ψ by φ' , integrating over $\Omega \times (0, T)$ and subtracting, we obtain

$$\mu_1' \int_0^T \int_{\Omega} \varphi \psi = \int_0^T \int_{\Omega} \varphi \psi \theta_{d_1}'. \tag{5.10}$$

Differentiating the equation for θ_{d_1} with respect to d_1 , we see that

$$\begin{cases} \partial_t \theta'_{d_1} - d_1 \Delta \theta'_{d_1} = \theta'_{d_1} (m - 2\theta_{d_1}) + \Delta \theta_{d_1} & \text{in } \Omega \times \mathbb{R}, \\ \partial_\nu \theta'_{d_1} = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \theta'_{d_1} & \text{is T-periodic in t.} \end{cases}$$

Then it follows from Lemmas 4.2 and 4.6 that

$$\lim_{d_1 \to 0} \|\theta'_{d_1} - w\|_{\infty} = 0, \tag{5.11}$$

where w is the unique solution to the ODE (4.3). Dividing the equation for w by p and integrating over (0, T), we see that

$$\int_0^T \frac{w(m-2p)}{p} + \int_0^T \frac{\Delta p}{p} = \int_0^T \frac{w_t}{p} = \int_0^T \frac{wp_t}{p^2} = \int_0^T \frac{w(m-p)}{p},$$

which implies that

$$\int_0^T w = \int_0^T \frac{\Delta p}{p}.$$
 (5.12)

Integrating the above identity over Ω and using the divergence theorem, we obtain

$$\int_{0}^{T} \int_{\Omega} w = \int_{0}^{T} \int_{\Omega} \frac{|\nabla p|^{2}}{p^{2}} > 0.$$
 (5.13)

It is easy to see from (M3) that m - p is spatially heterogeneous. Therefore, by Lemma 4.6, we have

$$\|\nabla\Gamma_{m-\theta_{d_1}}\|_{L^2((0,T),L^2(\Omega))} \ge \frac{1}{2}\|\nabla\Gamma_{m-p}\|_{L^2((0,T),L^2(\Omega))} > 0 \quad \forall d_1 \text{ small.}$$
 (5.14)

Moreover, by Lemmas 4.4 and 4.6, $\|m-\theta_{d_1}\|_{L^{\infty}(\Omega\times(0,T))}$ and $\|m_t-\partial_t\theta_{d_1}\|_{L^2((0,T),L^2(\Omega))}$ are uniformly bounded for all d_1 small. Consequently, by Proposition 3.2 and (3.18), there exists a constant C>0 such that for all d_1 small and d_2 sufficiently large,

$$\begin{split} \varphi(x,t) &= \overline{\varphi}(t) + \frac{\overline{\varphi}(t)\Gamma_{m-\theta_{d_1}}(x,t)}{d_2} + \frac{\varphi_2(x,t)}{d_2^2}, \\ \psi(x,t) &= \overline{\psi}(t) + \frac{\overline{\psi}(t)\Gamma_{m-\theta_{d_1}}(x,t)}{d_2} + \frac{\psi_2(x,t)}{d_2^2}, \end{split}$$

where

$$\begin{split} \overline{\varphi}(t) &= \overline{\varphi}(0) \exp\biggl(\int_0^t \left(\overline{m - \theta_{d_1}}(s) + \mu_1\right) ds\biggr) + \tau(t), \\ \overline{\psi}(t) &= \overline{\psi}(0) \exp\biggl(-\int_0^t \left(\overline{m - \theta_{d_1}}(s) + \mu_1\right) ds\biggr) + \tilde{\tau}(t), \\ \|\varphi_2\|_{L^2((0,T),H^1(\Omega))} &\leq C, \quad \|\psi_2\|_{L^2((0,T),H^1(\Omega))} \leq C, \\ \tau(t) &= O\biggl(\frac{1}{\sqrt{d_2}}\biggr), \quad \tilde{\tau}(t) &= O\biggl(\frac{1}{\sqrt{d_2}}\biggr) \quad \text{and} \quad \frac{1}{C} \leq \overline{\varphi}(t), \overline{\psi}(t) \leq C \quad \forall t \in [0,T]. \end{split}$$

Plugging the above estimates into (5.10), we deduce from (5.13) that

$$\mu_1' \int_0^T \int_{\Omega} \varphi \psi = \int_0^T \int_{\Omega} \varphi \psi \theta_{d_1}' = \int_0^T \int_{\Omega} \varphi \psi w + \int_0^T \int_{\Omega} \varphi \psi (\theta_{d_1}' - w)$$

$$= \overline{\varphi}(0) \overline{\psi}(0) \int_0^T \int_{\Omega} w + O\left(\frac{1}{\sqrt{d_2}}\right) + \alpha(d_1)$$

$$= \overline{\varphi}(0) \overline{\psi}(0) \int_0^T \int_{\Omega} \frac{|\nabla p|^2}{p^2} + O\left(\frac{1}{\sqrt{d_2}}\right) + \alpha(d_1),$$

where $\alpha(d_1) := \int_0^T \int_\Omega \varphi \psi(\theta'_{d_1} - w) = o(1)$ as $d_1 \to 0$ by (5.11). Therefore, there exist $\varepsilon_1 > 0$ small and $\widetilde{D}_{\varepsilon_1} \ge \widehat{D}_{\varepsilon_1}$ large such that $\mu'_1 > 0$ for all $(d_1, d_2) \in (0, \varepsilon_1) \times (\widetilde{D}_{\varepsilon_1}, \infty)$. Hence, the existence and uniqueness of the function $\check{d}_1(d_2) : (\widetilde{D}_{\varepsilon_1}, \infty) \to (0, \varepsilon_1)$ are proved. Moreover, $\check{d}_1(d_2)$ is continuously differentiable by the implicit function theorem. This finishes the proof of Claim 5.4.

Claim 5.5. The function $\check{d}_1: (\widetilde{D}_{\varepsilon_1}, \infty) \to (0, \varepsilon_1)$ defined in Claim 5.4 is strictly decreasing and satisfies

$$\check{d}_1(d_2) = O\left(\frac{1}{d_2}\right) \quad as \ d_2 \to \infty.$$

To prove Claim 5.5, we first show that

$$\check{d}_1(d_2) \to 0 \quad \text{as } d_2 \to \infty.$$
(5.15)

Assume for contradiction that $\limsup_{d_2\to\infty}\check{d}_1(d_2)=d_1^\star\in(0,\varepsilon_1].$ Then there exists a sequence $\{d_2^{(n)}\}_{n=1}^\infty\subset(\widetilde{D}_{\varepsilon_1},\infty)$ such that $d_2^{(n)}\to\infty$ and $\check{d}_1(d_2^{(n)})\to d_1^\star$ as $n\to\infty$. Therefore, there exists some $N^\star\in\mathbb{N}$ such that $\check{d}_1(d_2^{(n)})>d_1^\star/2$ for all $n>N^\star$. It follows from Claim 5.4 that $\mu_1(d_2^{(n)},m-\theta_{d_1})<0$ for all $n>N^\star$ and $d_1\leq d_1^\star/2<\check{d}_1(d_2^{(n)}).$ On the other hand, choosing $\varepsilon=d_1^\star/4$ in Claim 5.3, we see that $(\theta_{d_1},0)$ is globally asymptotically stable for all $(d_1,d_2)\in[d_1^\star/4,D]\times(\widehat{D}_{d_1^\star/4},\infty)$, which is a contradiction since $(d_1^\star/2,d_2^{(n)})$ belongs to that set for all n sufficiently large such that $d_2^{(n)}>\widehat{D}_{d_1^\star/4}$, while $\mu_1(d_2^{(n)},m-\theta_{d_1^\star/2})<0$. This finishes the proof of (5.15).

To finish the proof of the claim, it suffices to show that

$$\check{d}_1'(d_2) = O\left(\frac{1}{d_2^2}\right) \quad \forall d_2 > \widetilde{D}_{\varepsilon_1}. \tag{5.16}$$

To see this, let $\check{\phi}$ and $\check{\psi}$ be the principal eigenfunction and principal adjoint eigenfunction of (5.8) and (5.9) respectively with d_1 replaced by $\check{d}_1(d_2)$ and $\mu_1(d_2, m - \theta_{\check{d}_1(d_2)}) = 0$ normalized so that $\|\check{\phi}\|_{L^2((0,T),L^2(\Omega))} = \|\check{\psi}\|_{L^2((0,T),L^2(\Omega))} = 1$. Differentiating the equation for $\check{\phi}$ with respect to d_2 , multiplying the equation for $\frac{\partial \check{\phi}}{\partial d_2}$ by $\check{\psi}$ and the equation for $\check{\psi}$ by $\frac{\partial \check{\phi}}{\partial d_2}$, integrating over $\Omega \times (0,T)$ and subtracting, we obtain

$$\check{d}_{1}'(d_{2}) \int_{0}^{T} \int_{\Omega} \check{\varphi} \check{\psi} \frac{\partial \theta_{d}}{\partial d} \bigg|_{d=\check{d}_{1}(d_{2})} = -\int_{0}^{T} \int_{\Omega} \nabla \check{\varphi} \cdot \nabla \check{\psi}.$$
(5.17)

By a similar calculation to that in the proof of Claim 5.4, we can show that for all d_2 in $(\tilde{D}_{\varepsilon_1}, \infty)$,

$$\int_{0}^{T} \int_{\Omega} \check{\phi} \check{\psi} \frac{\partial \theta_{d}}{\partial d} \bigg|_{d=\check{d}_{1}(d_{2})} = \int_{0}^{T} \int_{\Omega} \check{\phi} \check{\psi} w + \int_{0}^{T} \int_{\Omega} \check{\phi} \check{\psi} \left(\frac{\partial \theta_{d}}{\partial d} \bigg|_{d=\check{d}_{1}(d_{2})} - w \right) \\
= \overline{\check{\phi}}(0) \overline{\check{\psi}}(0) \int_{0}^{T} \int_{\Omega} \frac{|\nabla p|^{2}}{p^{2}} + O\left(\frac{1}{\sqrt{d_{2}}}\right) + \check{\alpha}(d_{2}), \quad (5.18)$$

where

$$\check{\alpha}(d_2) := \int_0^T \int_{\Omega} \check{\varphi} \check{\psi} \left(\frac{\partial \theta_d}{\partial d} \bigg|_{d = \check{d}_1(d_2)} - w \right) = o(1) \quad \text{as } d_2 \to \infty$$

by (5.11) and (5.15). By similar arguments to the proof of (5.14) and calculation as in the proof of Claim 5.4, we can show that

$$\int_{0}^{T} \int_{\Omega} \nabla \check{\varphi} \cdot \nabla \check{\psi} = \frac{1}{d_{2}^{2}} \int_{0}^{T} \overline{\check{\varphi}}(t) \overline{\check{\psi}}(t) \int_{\Omega} |\nabla \Gamma_{m-\theta_{\check{d}_{1}}(d_{2})}|^{2} + O\left(\frac{1}{d_{2}^{3}}\right)$$

$$\geq \frac{1}{2C^{2}d_{2}^{2}} \int_{0}^{T} \int_{\Omega} |\nabla \Gamma_{m-p}|^{2} + O\left(\frac{1}{d_{2}^{3}}\right). \tag{5.19}$$

Now, (5.16) follows from (5.17)–(5.19). This finishes the proof of Claim 5.5.

Now we are ready to finish the proof of Theorem 2.2 (i). Let ε_1 be as in Claim 5.4. Then for all $d_2 > D_{\varepsilon_1}$, where D_{ε_1} is defined as in Theorem 2.3, it follows from the proof of Theorem 2.3 that $(\theta_{d_1}, 0)$ is linearly stable for all $d_2 > D_{\varepsilon_1}$. Now setting $D_2 := \max\{D_{\varepsilon_1}, \widetilde{D}_{\varepsilon_1}\}$, we can deduce Theorem 2.2 (i) from Claims 5.4 and 5.5.

It only remains to prove Theorem 2.2 (ii).

Claim 5.6. Assume that (**M1**) holds and $\hat{m} \not\equiv \text{const on } \bar{\Omega}$. Then there exist $\varepsilon_2 > 0$ small and $D_2 > 0$ large such that $(0, \theta_{d_2})$ is linearly unstable for all $(d_1, d_2) \in (0, \varepsilon_2) \times (D_2, \infty)$.

To prove this, note that since $\hat{m} \neq \text{const}$ on $\bar{\Omega}$, there exist some $x_0 \in \Omega$ and a constant $\eta_1 > 0$ such that $\hat{m}(x_0) - \hat{\bar{m}} = \eta_1 > 0$. By Lemma 4.8,

$$\lim_{d_2 \to \infty} \|\theta_{d_2} - \xi\|_{C(\bar{\Omega} \times [0, T])} = 0.$$

Therefore, choosing D_2 sufficiently large, we see that for all $d_2 > D_2$,

$$m - \theta_{d_2} > m - \xi - \eta_1/2$$
 on $\bar{\Omega} \times \mathbb{R}$. (5.20)

By Lemma 3.1 (ii) and the fact that $\hat{\xi} = \hat{m}$, we see that

$$\lim_{d_1 \to 0} \mu_1(d_1, m - \xi - \eta_1/2) = -\max_{x \in \bar{\Omega}} (\hat{m} - \hat{m} - \eta_1/2) \le -(\hat{m}(x_0) - \hat{m}) + \eta_1/2 < 0.$$
(5.21)

By [20, Lemma 15.5], $\mu_1(d_1, m - \theta_{d_2}) < \mu_1(d_1, m - \xi - \eta_1/2)$. Therefore, by choosing $\varepsilon_2 > 0$ sufficiently small, we see that $\mu_1(d_1, m - \theta_{d_2}) < 0$ for all $(d_1, d_2) \in (0, \varepsilon_2) \times (D_2, \infty)$. This finishes the proof of the claim.

Let ε_2 and D_2 be as in Claim 5.6. Then choosing D_2 even larger such that $D_2 \ge \widehat{D}_{\varepsilon_2}$, where $\widehat{D}_{\varepsilon_2}$ is as in Claim 5.3, we deduce Theorem 2.2 (ii).

By Lemma 4.5, the linear stability of $(\theta_{d_1}, 0)$ is determined by the sign of $\mu_1(d_2, m - \theta_{d_1})$. To end this section, we prove the following result which will be used in Section 6.

Lemma 5.7. Assume that (M1) holds. Then there exists a constant D > 0 depending only on m such that

$$\frac{\partial \mu_1(d_2, m - \theta_{d_1})}{\partial d_2} \bigg|_{d_2 = d_1} > 0 \quad \forall d_1 > D.$$
 (5.22)

If further (M2) holds, then

$$\lim_{d_1 \to 0} \frac{\partial \mu_1(d_2, m - \theta_{d_1})}{\partial d_2} \bigg|_{d_2 = d_1} = -\frac{I(p)}{T \int_{\Omega} \exp(\frac{1}{T} \int_0^T \ln p^2 \, dt)}.$$
 (5.23)

Proof. Note that (5.22) is a special case of (5.2). Hence it only remains to prove (5.23). Let φ and ψ be the principal eigenfunction and principal adjoint eigenfunction satisfying (5.8) and (5.9) respectively, normalized so that $\|\varphi\psi\|_{L^2((0,T),L^2(\Omega))} = 1$. Differentiating the equation for φ with respect to d_2 , denoting $\mu_1 = \mu_1(d_2, m - \theta_{d_1})$ and $' = \frac{\partial}{\partial d_2}$ for simplicity, we obtain

$$\begin{cases} \partial_t \varphi' - d_2 \Delta \varphi' = \varphi'(m - \theta_{d_1}) + \mu_1 \varphi' + \Delta \varphi + \mu_1' \varphi & \text{in } \Omega \times \mathbb{R}, \\ \partial_\nu \varphi' = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \varphi' \text{ is } T\text{-periodic in } t. \end{cases}$$

Multiplying the equation for φ' by ψ and the equation for ψ by φ' , integrating over $\Omega \times (0, T)$ and subtracting, we obtain

$$\mu_1' \int_0^T \int_{\Omega} \varphi \psi = -\int_0^T \int_{\Omega} \psi \Delta \varphi = -\int_0^T \int_{\Omega} \varphi \psi \frac{\Delta \varphi}{\varphi}.$$
 (5.24)

When $d_2 = d_1$, we know that $\mu_1(d_2, m - \theta_{d_1}) = 0$ with φ being a constant multiplier of θ_{d_1} . It follows from Corollary 3.6 and Lemma 4.6 that

$$\varphi \psi \to c_p \exp\left(\frac{1}{T} \int_0^T \ln p^2 dt\right)$$
 in $L^2((0,T), H^1(\Omega))$ when $d_2 = d_1$ and $d_1 \to 0$,

where the constant $c_p > 0$ is uniquely determined such that $||c_p \exp(\frac{1}{T} \int_0^T \ln p^2 dt)||_{L^2(\Omega)} = 1/\sqrt{T}$. Plugging the above estimates into (5.24), we obtain

$$\mu_1'T \int_{\Omega} \exp\left(\frac{1}{T} \int_0^T \ln p^2 dt\right) = -\int_{\Omega} \left[\exp\left(\frac{1}{T} \int_0^T \ln p^2 dt\right) \int_0^T \frac{\Delta p}{p} dt \right].$$

This finishes the proof of (5.23).

6. Local stability of semitrivial periodic solutions for small dispersal rates

In this section, we characterize the stability properties of the two semitrivial periodic solutions $(0, \theta_{d_1})$ and $(\theta_{d_2}, 0)$ of system (1.1) when both d_1 and d_2 are sufficiently small. Throughout this section, we always assume that m satisfies conditions (M1) and (M2).

Recall that p is the unique positive periodic solution to (2.2). We consider the following indefinite-weight eigenvalue problem:

$$\begin{cases} \Delta \Phi + \frac{1}{T} \int_0^T \nabla \ln p^2 \, dt \cdot \nabla \Phi - \Lambda(p) \left(\frac{1}{T} \int_0^T \frac{\Delta p}{p} \, dt \right) \Phi = 0 & \text{in } \Omega, \\ \partial_{\nu} \Phi = 0 & \text{on } \partial \Omega. \end{cases}$$
(6.1)

We say that $\Lambda(p)$ is a *principal eigenvalue* of (6.1) if (6.1) has a positive solution. The adjoint eigenvalue problem of (6.1) is

$$\begin{cases} \nabla \cdot \left(\nabla \Psi - \frac{\Psi}{T} \int_0^T \nabla \ln p^2 \, dt \right) - \Lambda(p) \left(\frac{1}{T} \int_0^T \frac{\Delta p}{p} \, dt \right) \Psi = 0 & \text{in } \Omega, \\ \partial_{\nu} \Psi = 0 & \text{on } \partial \Omega. \end{cases}$$
(6.2)

Notice that 0 is always a principal eigenvalue of (6.1) and (6.2) with principal eigenfunctions \mathbb{I} and $\exp(\frac{1}{T}\int_0^T \ln p^2 dt)$ respectively.

Recall that I(p) is defined in (2.3). The following result can be easily obtained from [40].

Lemma 6.1. Problem (6.1) has a nonzero principal eigenvalue, denoted by $\Lambda_1(p)$, if and only if $\int_0^T \frac{\Delta p}{p} dt$ changes sign in Ω and $I(p) \neq 0$. Furthermore, when $\int_0^T \frac{\Delta p}{p} dt$ changes sign in Ω , the following hold:

- (i) if I(p) > 0, then $\Lambda_1(p) > 0$,
- (ii) if I(p) < 0, then $\Lambda_1(p) \in [-1, 0)$ with

$$\Lambda_1(p) = -1 \iff p(x,t) = e^{\int_0^t b(s) \, ds} a(x) \text{ for some } b(t) \text{ satisfying}$$

$$\hat{b} = 0 \text{ and } a(x) > 0 \text{ on } \bar{\Omega}. \tag{6.3}$$

Proof. Except for (ii), the lemma follows from [40, Theorem 2]. We now show that $\Lambda_1(p) \ge -1$ if I(p) < 0. To see this, denote by Ψ the principal eigenfunction of (6.2) corresponding to $\Lambda_1(p)$. Dividing the equation for Ψ by Ψ and integrating over Ω , we obtain

$$\Lambda_{1}(p) \int_{0}^{T} \int_{\Omega} \frac{|\nabla p|^{2}}{p^{2}} = T \int_{\Omega} \frac{|\nabla \Psi|^{2}}{\Psi^{2}} - 2 \int_{\Omega} \int_{0}^{T} \frac{\nabla p}{p} \cdot \frac{\nabla \Psi}{\Psi}$$

$$\geq -\int_{0}^{T} \int_{\Omega} \frac{|\nabla p|^{2}}{p^{2}}.$$
(6.4)

Therefore, $\Lambda_1(p) > -1$.

Assume that $p(x,t) = e^{\int_0^t b(s) \, ds} a(x)$ for some b(t) satisfying $\hat{b} = 0$ and a(x) > 0 on $\bar{\Omega}$. It is easy to check that $\Lambda_1(p) = -1$ and $\Psi = a$. Now, we assume that $\Lambda_1(p) = -1$. Then it follows from (6.4) that

$$\int_0^T \int_{\Omega} \left(\frac{\nabla \Psi}{\Psi} - \frac{\nabla p}{p} \right)^2 = 0.$$

Therefore, $\nabla \ln p(x,t) \equiv \nabla \ln \Psi(x)$ on $\bar{\Omega} \times [0,T]$, which implies that there exists b(t) with $\int_0^T b(t) dt = 0$ such that $p(x,t) = e^{\int_0^t b(s) ds} \Psi(x)$. This finishes the proof of (6.3) and the lemma.

Remark 6.2. Since p is the unique positive periodic solution to (2.2), it is easy to check that $p(x,t) = e^{\int_0^t b(s) ds} a(x)$ if and only if $m(x,t) = e^{\int_0^t b(s) ds} a(x) + b(t)$, where $\hat{b} = 0$ and a(x) > 0 on $\bar{\Omega}$. In other words, m satisfies condition (**M3**) if and only if $\Lambda_1(p) \neq -1$ by Lemma 6.1 (ii).

Now we are ready to prove Theorem 2.1. Note that since the dynamics of system (1.1) is symmetric with respect to the line $d_1 = d_2$ in $\mathcal{Q} = (0, \infty)^2$, we stated our results in Theorem 2.1 concerning the linear stability of both $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$ only in the region $(0, \varepsilon_0)^2 \cap \{(d_1, d_2) \mid d_1 < d_2\}$. Equivalently, we can also state our results concerning only the linear stability of $(\theta_{d_1}, 0)$ but in the region $(0, \varepsilon_0)^2$. In either case, the other half information which is not stated there can be inferred by exchanging d_1 and d_2 . Since it is smoother to conduct our proof in the latter form and to make things clear, we now state the following equivalent version of Theorem 2.1 and prove it.

Theorem 2.1'. Assume that (M1) and (M2) hold. Then there exists some $\varepsilon_0 > 0$ small such that for all $(d_1, d_2) \in (0, \varepsilon_0)^2$, the following statements hold on the linear stability of $(\theta_{d_1}, 0)$:

- (i) If I(p) > 0 and $\min_{x \in \bar{\Omega}} \int_0^T \frac{\Delta p}{p}(x,t) dt > 0$, then $(\theta_{d_1},0)$ is linearly unstable for all $d_1 < d_2$ and linearly stable for all $d_1 > d_2$.
- (ii) If I(p) > 0 and $\min_{x \in \bar{\Omega}} \int_0^T \frac{\Delta p}{p}(x,t) dt < 0$, then there exists a continuously differentiable function $\hat{d}_2 : (0, \varepsilon_0) \to (0, \varepsilon_0)$ with $\hat{d}_2(d_1) \in (0, d_1)$ such that $(\theta_{d_1}, 0)$ is linearly unstable for all $d_2 \in (0, \hat{d}_2(d_1)) \cup (d_1, \varepsilon_0)$ and linearly stable for all $d_2 \in (\hat{d}_2(d_1), d_1)$. Moreover, $\lim_{d_1 \to 0} \hat{d}_2(d_1), \hat{d}'_2(0)$ and $\lim_{d_1 \to 0} \hat{d}'_2(d_1)$ exist with

$$\lim_{d_1 \to 0} \hat{d}_2(d_1) = 0 \quad and \quad \lim_{d_1 \to 0} \hat{d}_2'(d_1) = \hat{d}_2'(0) = \frac{1}{1 + \Lambda_1(p)} \in (0, 1).$$

(iii) If I(p) < 0 and in addition (M3) holds, then there exists a continuously differentiable function $\tilde{d}_1: (0, \varepsilon_0) \to (0, \varepsilon_0)$ with $\tilde{d}_1(d_2) \in (0, d_2)$ such that $(\theta_{d_1}, 0)$ is linearly unstable for all $d_1 \in (0, \tilde{d}_1(d_2)) \cup (d_2, \varepsilon_0)$ and linearly stable for all $d_1 \in (\tilde{d}_1(d_2), d_2)$. Moreover, $\lim_{d_2 \to 0} \tilde{d}_1(d_2), \tilde{d}_1'(0)$ and $\lim_{d_2 \to 0} \tilde{d}_1'(d_2)$ exist with

$$\lim_{d_2 \to 0} \tilde{d}_1(d_2) = 0 \quad and \quad \lim_{d_2 \to 0} \tilde{d}_1'(d_2) = \tilde{d}_1'(0) = 1 + \Lambda_1(p) \in (0, 1).$$

Note that $\hat{d}_2 \equiv \hat{d}_1$ by symmetry, where \hat{d}_2 is defined in Theorem 2.1' (ii) and \hat{d}_1 is defined in Theorem 2.1 (ii).

Proof of Theorem 2.1'. Recall from Lemma 4.5 that the linear stability of $(\theta_{d_1}, 0)$ is determined by the sign of $\mu_1(d_2, m - \theta_{d_1})$: $(\theta_{d_1}, 0)$ is linearly stable if $\mu_1(d_2, m - \theta_{d_1}) > 0$ and linearly unstable if $\mu_1(d_2, m - \theta_{d_1}) < 0$. It is obvious that $\mu_1(d_2, m - \theta_{d_1}) = 0$

when $d_2=d_1$ with principal eigenfunction θ_{d_1} . Let ψ be the adjoint principal eigenfunction to $\mu_1(d_2,m-\theta_{d_1})$ defined in (5.9) and denote $v=\psi\theta_{d_1}$. By direct computation, we see that v satisfies

see that
$$v$$
 satisfies
$$\begin{cases} -v_t - d_2 \nabla \cdot (\nabla v - 2v \nabla \ln \theta_{d_1}) - (d_1 - d_2) \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} v = \mu_1(d_2, m - \theta_{d_1}) v & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} v = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ v \text{ is } T\text{-periodic in } t. \end{cases}$$

$$(6.5)$$

We now consider the following one-parameter family of eigenvalue problems (with parameter λ):

$$\begin{cases} -\phi_t - d_2 \nabla \cdot (\nabla \phi - 2\phi \nabla \ln \theta_{d_1}) - \lambda \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \phi = \chi(\lambda) \phi & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \phi = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \phi & \text{is } T\text{-periodic in } t \end{cases}$$
(6.6)

and the adjoint eigenvalue problem

$$\begin{cases} \rho_{t} - d_{2}\Delta\rho - 2d_{2}\nabla\rho \cdot \nabla \ln\theta_{d_{1}} - \lambda \frac{-\Delta\theta_{d_{1}}}{\theta_{d_{1}}}\rho = \chi(\lambda)\rho & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu}\rho = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \rho \text{ is } T\text{-periodic in } t. \end{cases}$$
(6.7)

Denote by $\chi_1(\lambda)$ the principal eigenvalue of both (6.6) and (6.7) with principal eigenfunctions ϕ_{λ} and ρ_{λ} respectively, normalized so that $\|\phi_{\lambda}\|_{L^2((0,T),L^2(\Omega))} = \|\rho_{\lambda}\|_{L^2((0,T),L^2(\Omega))} = 1$. Then it is easy to see that

$$\chi(0) = 0$$
 with $\rho_0 = 1/\sqrt{|\Omega|T}$ and $\phi_0 = c_{\theta_{d_1}} \exp\left(\frac{1}{T} \int_0^T \ln \theta_{d_1}^2 dt\right)$, (6.8)

where the constant $c_{\theta_{d_1}} > 0$ is uniquely determined such that $\|\phi_0\|_{L^2((0,T),L^2(\Omega))} = 1$. By Lemma 4.6, we easily obtain

$$\lim_{d_1, d_2 \to 0} \left\| \phi_0 - c_p \exp\left(\frac{1}{T} \int_0^T \ln p^2 \, dt \right) \right\|_{L^2((0,T), H^1(\Omega))} = 0, \tag{6.9}$$

where the constant $c_p > 0$ is uniquely determined such that $||c_p \exp(\frac{1}{T} \int_0^T \ln p^2 dt)||_{L^2(\Omega)} = 1/\sqrt{T}$.

Differentiating the equation for ϕ_{λ} in (6.6) with respect to λ , integrating over $\Omega \times (0, T)$ and evaluating at $\lambda = 0$, we see that

$$\frac{d\chi_1}{d\lambda}(0) = \int_0^T \int_{\Omega} \phi_0 \frac{\Delta \theta_{d_1}}{\theta_{d_1}}.$$

Hence, it follows from (6.9) and Lemma 4.6 that

$$\lim_{d_1, d_2 \to 0} \frac{d\chi_1}{d\lambda}(0) = c_p \int_{\Omega} \left[\exp\left(\frac{1}{T} \int_0^T \ln p^2 dt \right) \int_0^T \frac{\Delta p}{p} \right] = c_p I(p). \tag{6.10}$$

Since for each $t \in \mathbb{R}$, $\int_{\Omega} \Delta \theta_{d_1} = \int_{\partial \Omega} \nabla \theta_{d_1} \cdot \nu = 0$ and $\Delta \theta_{d_1} \neq 0$, it is obvious that

$$\int_0^T \biggl(\min_{x \in \tilde{\Omega}} \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \biggr) \, dt < 0 < \int_0^T \biggl(\max_{x \in \tilde{\Omega}} \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \biggr) \, dt \quad \forall d_1 > 0.$$

Therefore, the following claim follows from [20, Lemmas 15.2 & 15.5]:

Claim 6.3. The function $\chi_1(\lambda_1)$ is concave in λ . Moreover,

$$\lim_{\lambda \to \pm \infty} \chi_1(\lambda) = -\infty.$$

We now characterize the zeros of $\chi_1(\lambda)$ and consider the following indefinite-weight eigenvalue problem:

$$\begin{cases} \rho_{t} - d_{2}\Delta\rho - 2d_{2}\nabla\rho \cdot \nabla \ln\theta_{d_{1}} - \lambda \frac{-\Delta\theta_{d_{1}}}{\theta_{d_{1}}}\rho = 0 & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu}\rho = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \rho \text{ is } T\text{-periodic in } t. \end{cases}$$
(6.11)

By [20, Theorem 16.3], problem (6.11) has a unique nonzero principal eigenvalue $\lambda_1(d_1, d_2)$ for all $d_1, d_2 > 0$ if and only if $\frac{d\chi_1}{d\lambda}(0) \neq 0$. Moreover, if $\frac{d\chi_1}{d\lambda}(0) \neq 0$, we see from Claim 6.3 that

$$\chi_1(\lambda) = 0 \iff \lambda = 0 \text{ or } \lambda = \lambda_1(d_1, d_2).$$
(6.12)

We now assume that

$$I(p) \neq 0$$
.

Then by (6.10), there exists $\varepsilon_0 > 0$ small such that $\frac{d\chi_1}{d\lambda}(0)$ has the same sign as I(p) for all $(d_1,d_2) \in (0,\varepsilon_0)^2$. Therefore, to determine the sign of $\mu_1(d_2,m-\theta_{d_1})$, we see from (6.5) and (6.7) (or (6.6)), (6.12) and Claim 6.3 that it suffices to locate $\lambda_1(d_1,d_2)$ and then determine the sign of $\chi_1(\lambda)$ according to the relative positions of 0, $\lambda_1(d_1,d_2)$ and d_1-d_2 when $(d_1,d_2) \in (0,\varepsilon_0)^2$.

We now study the asymptotic behavior of $\lambda_1(d_1, d_2)$ when d_1 and d_2 are sufficiently small and consider the following two cases separately:

Case (i): I(p) > 0.

Case (ii): I(p) < 0.

We first treat Case (i). Then by (6.10), we see that $\frac{d\chi_1}{d\lambda}(0) > 0$ for all $(d_1, d_2) \in (0, \varepsilon_0)^2$, which implies by [20, Theorem 16.3] that

$$\lambda_1(d_1, d_2) > 0 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2.$$
 (6.13)

Since $\chi_1(0) = \chi_1(\lambda_1(d_1, d_2)) = 0$, it follows from Claim 6.3 that

$$\begin{cases} \chi_1(\lambda) > 0 & \text{for all } \lambda \in (0, \lambda_1(d_1, d_2)), \\ \chi_1(\lambda) < 0 & \text{for all } \lambda \in (-\infty, 0) \cup (\lambda_1(d_1, d_2), \infty). \end{cases}$$

$$(6.14)$$

We need to further consider the following two subcases:

Case (i)(a): $\min_{x \in \bar{\Omega}} \int_0^T \frac{\Delta p}{n}(x, t) dt > 0$.

Case (i)(b): $\min_{x \in \bar{\Omega}} \int_0^T \frac{\Delta p}{p}(x,t) dt < 0$, i.e., there exist $x^* \in \Omega$ and $\eta_2 > 0$ such that

$$\int_0^T \frac{\Delta p}{p}(x^*, t) dt =: -\eta_2 < 0.$$
 (6.15)

For simplicity of notation, we denote

$$\vartheta_{d_1} = \frac{-\Delta \theta_{d_1}}{\theta_{d_1}}$$

in the remainder of this proof.

For Case (i)(a), by Lemma 4.6, we see that $\hat{\vartheta}_{d_1} < 0$ on $\bar{\Omega}$ for all $d_1 \in (0, \varepsilon_0)$ by choosing ε_0 smaller if necessary. Fix $\lambda_0 > \varepsilon_0$. For each $d_1 \in (0, \varepsilon_0)$, by [23, Lemma 2.4(c)], the principal eigenvalue $\chi_1(\lambda)$ of (6.7) satisfies

$$\lim_{d_2 \to 0} \chi_1(\lambda_0) = -\max_{x \in \bar{\Omega}} \lambda_0 \hat{\vartheta}_{d_1}(x) > 0.$$

Therefore, choosing ε_0 smaller if necessary, we see from continuous dependence of $\chi_1(\lambda_0)$ on $d_1 \in (0, \varepsilon_0)$ and [20, Lemma 15.5] that

$$\lambda_1(d_1, d_2) > \lambda_0 > \varepsilon_0 > 0 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2.$$

In particular, this combined with (6.5), (6.7) and (6.14) implies that $\mu_1(d_2, m - \theta_{d_1}) > 0$ when $d_1 - d_2 \in (0, \varepsilon_0)$, while $\mu_1(d_2, m - \theta_{d_1}) < 0$ when $d_1 - d_2 < 0$. This finishes the proof of Theorem 2.1'(i).

For Case (i)(b), by Lemma 4.6 there exist $x^* \in \Omega$ and a constant r > 0 such that $\vartheta_{d_1}(t) := \min_{x \in \overline{\Omega}_0} \vartheta_{d_1}(x, t)$ satisfies

$$\int_{0}^{T} \mathfrak{Y}_{d_{1}}(t) > \eta_{2}/2 > 0 \quad \forall d_{1} \in (0, \varepsilon_{0}), \tag{6.16}$$

where $\Omega_0 := B(x^*, r) \subset\subset \Omega$ and $B(x^*, r)$ is the ball centered at x^* with radius r.

Claim 6.4. There exists a constant $C_1 > 0$ such that

$$0 < \frac{\lambda_1(d_1, d_2)}{d_2} \le C_1 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2. \tag{6.17}$$

To prove Claim 6.4, we consider the periodic-parabolic Dirichlet eigenvalue problem

$$\begin{cases} \partial_t \underline{w} - d_2 \Delta \underline{w} - 2d_2 \nabla \underline{w} \cdot \nabla \ln \theta_{d_1} - \lambda \underline{\vartheta}_{d_1} \underline{w} = \underline{\chi}(\lambda) \underline{w} & \text{in } \Omega_0 \times \mathbb{R}, \\ \underline{w} = 0 & \text{on } \partial \Omega_0 \times \mathbb{R}, \\ \underline{w} & \text{is } T\text{-periodic in } t. \end{cases}$$

$$(6.18)$$

Since \mathfrak{Y}_{d_1} is independent of $x \in \Omega_0$, it follows from [20, Lemma 15.3] that

$$\underline{\chi}(\lambda) = \underline{\chi}(0) - \frac{\lambda}{T} \int_0^T \underline{\vartheta}_{d_1}(s) \, ds.$$

We now claim that there exists a constant $C_2 > 0$ independent of d_1 and d_2 such that

$$0 < \chi(0) \le C_2 d_2 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2. \tag{6.19}$$

Indeed, the fact that $\chi(0) > 0$ follows from [20, Prop. 17.1], since it is obvious that 0 is the principal eigenvalue of (6.18) for $\lambda = 0$ with the Dirichlet boundary condition replaced by the Neumann boundary condition on $\partial \Omega_0 \times \mathbb{R}$. To show the second inequality in (6.19), we follow the idea in the proof of [2, Lemma 2.6] to construct a positive supersolution of (6.18) with $\lambda = 0$. For this purpose, let $\Theta > 0$ be the principal eigenfunction of $-\Delta$ with zero Dirichlet boundary condition on $\partial \Omega$ normalized so that $\|\Theta\|_{C(\bar{\Omega})} = 1$, i.e., $\Theta \in C^2(\bar{\Omega})$ satisfies

$$-\Delta\Theta = \lambda_1(\Omega)\Theta \text{ in } \Omega, \quad \Theta = 0 \text{ on } \partial\Omega, \tag{6.20}$$

where $\lambda_1(\Omega) > 0$ is the principal eigenvalue corresponding to Θ . Denote $\widetilde{\Theta} = \exp(\kappa\Theta) - 1$, where $\kappa > 0$ is constant to be determined. By a similar computation to the proof of [2, Lemma 2.6], we can show that there exists a sufficiently large κ depending only on Θ and $\sup_{d_1 \in (0, \kappa_0)} \|\nabla \ln \theta_{d_1}\|_{\infty}$ such that

$$\partial_t \widetilde{\Theta} - d_2 \Delta \widetilde{\Theta} - 2d_2 \nabla \widetilde{\Theta} \cdot \nabla \ln \theta_{d_1} \le d_2 C(\kappa, \|\Theta\|_{C^2(\bar{\Omega})}) \widetilde{\Theta}.$$

Then, by the comparison principle for time-periodic parabolic eigenvalue problems (see e.g. [2, Prop. 2.2]) and Lemma 4.6, there exists a constant $C_2 = C(\kappa, \|\Theta\|_{C^2(\bar{\Omega})})$ such that the second inequality in (6.19) holds.

Next we consider the periodic-parabolic Dirichlet eigenvalue problem

$$\begin{cases} \partial_t w - d_2 \Delta w - 2d_2 \nabla w \cdot \nabla \ln \theta_{d_1} - \lambda \vartheta_{d_1}(x, t) w = \underline{\chi}(\lambda) w & \text{in } \Omega_0 \times \mathbb{R}, \\ w = 0 & \text{on } \partial \Omega_0 \times \mathbb{R}, \\ w \text{ is } T\text{-periodic in } t, \end{cases}$$
(6.21)

where $\underline{\chi}(\lambda)$ is the principal eigenvalue of (6.21). Since $\vartheta_{d_1}(x,t) \geq \underline{\vartheta}_{d_1}(t)$ on $\overline{\Omega}_0 \times \mathbb{R}$, we see from [20, Lemma 15.5] that $\underline{\chi}(\lambda) \leq \underline{\chi}(\lambda)$. By [2, Corollary 4.2], we find that $\chi_1(\lambda) \leq \underline{\chi}(\lambda)$. Consequently,

$$\chi_1(\lambda) \leq \underline{\chi}(\lambda) \leq \underline{\chi}(\lambda) = \underline{\chi}(0) - \frac{\lambda}{T} \int_0^T \mathfrak{Y}_{d_1}(s) \, ds.$$

In particular, plugging $\lambda = \lambda_1(d_1, d_2)$ in the above inequality and using the fact that $\chi_1(\lambda_1(d_1, d_2)) = 0$, we find by (6.16) and (6.19) that

$$\frac{\lambda_1(d_1, d_2)}{d_2} \le \frac{\chi(0)}{d_2} \cdot \frac{T}{\int_0^T \psi_{d_1} ds} \le \frac{2C_2T}{\eta_2} =: C_1 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2.$$

This combined with (6.13) finishes the proof of (6.17) and hence Claim 6.4.

Claim 6.5.

$$\lim_{d_1, d_2 \to 0} \frac{\partial \lambda_1(d_1, d_2)}{\partial d_2} = \Lambda_1(p) > 0. \tag{6.22}$$

To prove Claim 6.5, denote by φ_1 the principal eigenfunction of (6.11) and ψ_1 the principal eigenfunction of its adjoint eigenvalue problem corresponding to the eigenvalue $\lambda_1(d_1, d_2)$ normalized so that

$$\|\varphi_1\|_{L^2((0,T),L^2(\Omega))} = \|\psi_1\|_{L^2((0,T),L^2(\Omega))} = 1.$$

In other words, φ_1 and ψ_1 satisfy respectively

$$\begin{cases} \partial_t \varphi_1 - d_2 \Delta \varphi_1 - 2 d_2 \nabla \varphi_1 \cdot \nabla \ln \theta_{d_1} - \lambda_1 (d_1, d_2) \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \varphi_1 = 0 & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \varphi_1 = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \varphi_1 \text{ is } T\text{-periodic in } t, \end{cases}$$

$$(6.23)$$

and

$$\begin{cases} -\partial_t \psi_1 - d_2 \nabla \cdot (\nabla \psi_1 - 2 \psi_1 \nabla \ln \theta_{d_1}) - \lambda_1 (d_1, d_2) \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \psi_1 = 0 & \text{in } \Omega \times \mathbb{R}, \\ \partial_\nu \psi_1 = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \psi_1 \text{ is } T\text{-periodic in } t. \end{cases}$$

Differentiating the equation for φ_1 with respect to d_2 and denoting $' = \frac{\partial}{\partial d_2}$, $\lambda_1 := \lambda_1(d_1, d_2)$, we obtain

$$\begin{cases} \partial_t \varphi_1' - d_2 \Delta \varphi_1' - 2d_2 \nabla \varphi_1' \cdot \nabla \ln \theta_{d_1} - (\Delta \varphi_1 + 2 \nabla \varphi_1 \cdot \nabla \ln \theta_{d_1}) \\ -\lambda_1' \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \varphi_1 - \lambda_1 \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \varphi_1' = 0 & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \varphi_1' = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \varphi_1' \text{ is } T\text{-periodic in } t. \end{cases}$$

Multiplying the equation for φ_1' by ψ_1 and the equation for ψ_1 by φ_1' , subtracting the resulting equations and integrating over $\Omega \times (0, T)$, we obtain

$$\frac{\partial \lambda_1(d_1, d_2)}{\partial d_2} = \frac{\int_0^T \int_{\Omega} (\nabla \varphi_1 - 2\psi_1 \nabla \ln \theta_{d_1}) \cdot \nabla \psi_1}{\int_0^T \int_{\Omega} \frac{-\Delta \theta_{d_1}}{\theta_{d_1}} \varphi_1 \psi_1}.$$
 (6.25)

By Proposition 3.4, Lemma 4.8 and (6.17), we conclude that, passing to a subsequence of (d_1, d_2) if necessary,

$$\varphi_1 \to \Phi_1, \psi_1 \to \Psi_1 \quad \text{in } L^2((0,T), H^1(\Omega)), \\ \lambda_1(d_1, d_2)/d_2 \to \Lambda \in [0, C_1], \quad \text{as } d_1, d_2 \to 0,$$
 (6.26)

where $\Phi_1, \Psi_1 \in H^1(\Omega)$ are the principal eigenfunctions to (6.1) and (6.2) respectively, with Λ being the corresponding principal eigenvalue, satisfying

$$\|\Phi_1\|_{L^2(\Omega)} = \|\Psi_1\|_{L^2(\Omega)} = 1/\sqrt{T}.$$

Since $\int_0^T \int_\Omega \frac{\Delta p}{p} \, dt = \int_0^T \int_\Omega \frac{|\nabla p|^2}{p^2} \, dt > 0$, we see from (6.15) that $\int_0^T \frac{\Delta p}{p} \, dt$ changes sign in Ω . Hence, it follows from Lemma 6.1 that $\Lambda_1(p)$, the nonzero principal eigenvalue

of (6.1), exists and $\Lambda_1(p) > 0$. Therefore, we have either $\Lambda = 0$ or $\Lambda = \Lambda_1(p)$. We now claim that $\Lambda \neq 0$. Assume for contradiction that $\Lambda = 0$. Then it is easy to check that $\Psi_1 = c_p \exp(\frac{1}{T} \int_0^T \ln p^2 \, dt)$. However, integrating the equation for ψ_1 over $\Omega \times (0,T)$, we see that

$$\lambda_1(d_1, d_2) \int_0^T \int_{\Omega} \frac{\Delta \theta_{d_1}}{\theta_{d_1}} \psi_1 = 0.$$

Since $\lambda_1(d_1, d_2) > 0$, letting $d_1, d_2 \to 0$ we deduce from (6.26) and Lemma 4.6 that

$$0 = \lim_{d_1, d_2 \to 0} \int_0^T \int_{\Omega} \frac{\Delta \theta_{d_1}}{\theta_{d_1}} \psi_1 = c_p \int_0^T \int_{\Omega} \exp\left(\frac{1}{T} \int_0^T \ln p^2 dt\right) \frac{\Delta p}{p} = c_p I(p) > 0,$$

which is a contradiction. Hence $\Lambda \neq 0$ and thus we must have $\Lambda = \Lambda_1(p)$. Multiplying the equation for Φ_1 by Ψ_1 and integrating over Ω , we obtain

$$\Lambda_1(p) = \frac{\int_{\Omega} (T \nabla \Phi_1 - 2\Psi_1 \int_0^T \nabla \ln p) \cdot \nabla \Psi_1}{\int_0^T \int_{\Omega} \frac{-\Delta p}{p} \Phi_1 \Psi_1}.$$
 (6.27)

Letting $d_1, d_2 \to 0$ in (6.25), and then combining the result with (6.26) and (6.27), we derive (6.22). This finishes the proof of the claim.

Claim 6.6. There exists a unique continuously differentiable function $\hat{d}_2:(0,\varepsilon_0)\to (0,\infty)$ with $\hat{d}_2(d_1)< d_1$ such that for $(d_1,d_2)\in (0,\varepsilon_0)^2$,

$$\lambda_1(d_1, d_2) = d_1 - d_2 \iff d_2 = \hat{d}_2(d_1).$$

Moreover,

$$\lim_{d_1 \to 0} \hat{d}_2(d_1) = 0, \quad \hat{d}'_2(0) = \frac{1}{1 + \Lambda_1(p)} \in (0, 1), \quad \lim_{d_1 \to 0} \hat{d}'_2(d_1) = \frac{1}{1 + \Lambda_1(p)} \in (0, 1). \tag{6.28}$$

To prove Claim 6.6, note that by (6.17) and (6.22), we may extend the definitions of $\lambda_1(d_1, d_2)$ and $\frac{\partial \lambda_1(d_1, d_2)}{\partial d_2}$ so that

$$\lambda_1(\cdot,0) = 0 \text{ in } [0,\varepsilon_0) \quad \text{and} \quad \frac{\partial \lambda_1(0,0)}{\partial d_2} = \Lambda_1(p) > 0.$$
 (6.29)

Choosing ε_0 smaller if necessary, we may assume that $\frac{\partial \lambda_1(d_1,d_2)}{\partial d_2} > 0$ for all $(d_1,d_2) \in (0,\varepsilon_0)^2$. Therefore,

$$\frac{\partial[\lambda_1(d_1, d_2) - d_1 + d_2]}{\partial d_2} > 1 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2.$$
 (6.30)

Now for each $d_1 \in (0, \varepsilon_0)$ fixed, by (6.13) and (6.29) we see that $\lambda_1(d_1, 0) - d_1 + 0 = -d_1 < 0$ and $\lambda_1(d_1, d_1) - d_1 + d_1 > 0$. Hence, by the intermediate value theorem and (6.30), for each $d_1 \in (0, \varepsilon_0)$ there exists a unique $d_2 = \hat{d}_2(d_1) \in (0, d_1)$ such that $\lambda_1(d_1, d_2) - d_1 + d_2 = 0$ if and only if $d_2 = \hat{d}_2(d_1)$. It is obvious that $\lim_{d_1 \to 0} \hat{d}_2(d_1) = 0$. Since $\lambda_1(d_1, d_2)$ is analytic, $\hat{d}_2(d_1)$ is actually analytic in $d_1 \in (0, \varepsilon_0)$.

It only remains to prove the last two identities in (6.28). Dividing both sides of the equation $d_1 - \hat{d}_2(d_1) = \lambda_1(d_1, \hat{d}_2(d_1))$ by $\hat{d}_2(d_1)$ and letting $d_1 \to 0$, since $\lim_{d_1 \to 0} \hat{d}_2(d_1) = 0$ we see by (6.22) and (6.29) that

$$\lim_{d_1 \to 0} \frac{d_1 - \hat{d}_2(d_1)}{\hat{d}_2(d_1)} = \lim_{d_1 \to 0} \frac{\lambda_1(d_1, \hat{d}_2(d_1))}{\hat{d}_2(d_1)} = \lim_{d_1 \to 0} \frac{\lambda_1(d_1, \hat{d}_2(d_1)) - \lambda_1(d_1, 0)}{\hat{d}_2(d_1) - 0} = \Lambda_1(p).$$
(6.31)

From this, we deduce the second identity in (6.28). Since $d_1 - \hat{d}_2(d_1) = \lambda_1(d_1, \hat{d}_2(d_1))$, by (6.5)–(6.7) and (6.12) we see that $\mu_1(\hat{d}_2(d_1), m - \theta_{d_1}) = 0$. Denote by $\tilde{\varphi}$ and $\tilde{\psi}$ the principal eigenfunction and adjoint principal eigenfunction corresponding to $\mu_1(\hat{d}_2(d_1), m - \theta_{d_1}) = 0$ respectively normalized so that

$$\|\tilde{\varphi}/\theta_{d_1}\|_{L^2(\Omega\times(0,T))} = \|\tilde{\psi}\theta_{d_1}\|_{L^2(\Omega\times(0,T))} = 1. \tag{6.32}$$

In other words, $\tilde{\varphi}$ and $\tilde{\psi}$ are positive and satisfy respectively

$$\begin{cases} \tilde{\varphi}_t - \hat{d}_2(d_1)\Delta \tilde{\varphi} = (m - \theta_{d_1})\tilde{\varphi} & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \tilde{\varphi} = 0 & \text{on } \partial \Omega \times \mathbb{R}, \\ \tilde{\varphi} \text{ is } T\text{-periodic in } t, \end{cases}$$

and

$$\begin{cases} -\tilde{\psi}_t - \hat{d}_2(d_1)\Delta\tilde{\psi} = (m-\theta_{d_1})\tilde{\psi} & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu}\tilde{\psi} = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \tilde{\psi} \text{ is } T\text{-periodic in } t. \end{cases}$$

Differentiating the equation for $\tilde{\varphi}$ with respect to d_1 and denoting $' = \frac{\partial}{\partial d_1}$, we obtain

$$\begin{cases} \tilde{\varphi}_t' = \hat{d}_2(d_1)\Delta\tilde{\varphi}' + (m-\theta_{d_1})\tilde{\varphi}' + \hat{d}_2'(d_1)\Delta\tilde{\varphi} - \theta_{d_1}'\tilde{\varphi} & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu}\tilde{\varphi}' = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ \tilde{\varphi}' \text{ is } T\text{-periodic in } t. \end{cases}$$

Multiplying the above equation by $\tilde{\psi}$ and the equation for $\tilde{\psi}$ by $\tilde{\varphi}'$, integrating over $\Omega \times (0,T)$ and subtracting the resulting equations, we deduce from the divergence theorem that

$$\hat{d}_{2}'(d_{1}) = -\frac{\int_{0}^{T} \int_{\Omega} \theta_{d_{1}}' \tilde{\psi} \tilde{\varphi}}{\int_{0}^{T} \int_{\Omega} \nabla \tilde{\psi} \cdot \nabla \tilde{\varphi}}.$$
(6.33)

Let $\tilde{v} = \tilde{\varphi}/\theta_{d_1}$. By direct computation, we see that \tilde{v} satisfies

$$\begin{cases} \tilde{v}_t = \hat{d}_2(d_1)[\Delta \tilde{v} + \nabla \ln \theta_{d_1}^2 \cdot \nabla \tilde{v}] - \hat{d}_2(d_1) \cdot \frac{d_1 - \hat{d}_2(d_1)}{\hat{d}_2(d_1)} \cdot \frac{\Delta \theta_{d_1}}{\theta_{d_1}} \tilde{v} & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} \tilde{v} = 0 & \text{on } \partial \Omega \times \mathbb{R} \\ \tilde{v} \text{ is } T\text{-periodic in } t. \end{cases}$$

Therefore, by Proposition 3.4, Lemma 4.6, (6.31) and (6.32), we conclude that

$$\tilde{v} = \tilde{\varphi}/\theta_{d_1} \to \Phi_1 \quad \text{in } L^2((0,T), H^1(\Omega)) \text{ as } d_1 \to 0,$$
 (6.34)

where $\Phi_1 > 0$ on $\bar{\Omega}$ is the principal eigenfunction of (6.1) corresponding to $\Lambda_1(p) > 0$ and satisfying $\|\Phi_1\|_{L^2(\Omega)} = 1/\sqrt{T}$. Similarly, we can prove that

$$\tilde{\psi}\theta_{d_1} \to \Psi_1 \text{ in } L^2((0,T), H^1(\Omega)) \text{ as } d_1 \to 0,$$
 (6.35)

where $\Psi_1 > 0$ on $\bar{\Omega}$ is the principal eigenfunctions to (6.2) corresponding to $\Lambda_1(p) > 0$ and satisfying $\|\Psi_1\|_{L^2(\Omega)} = 1/\sqrt{T}$. By Lemma 4.6, (6.34) and (6.35), we obtain

$$\tilde{\varphi} \to p\Phi_1$$
 and $\tilde{\psi} \to \Psi_1/p$ in $L^2((0,T), H^1(\Omega))$ as $d_1 \to 0$.

Consequently, as $d_1 \rightarrow 0$,

$$\int_0^T \int_{\Omega} \nabla \tilde{\psi} \cdot \nabla \tilde{\varphi} \to \int_0^T \int_{\Omega} \nabla \Psi_1 \cdot \nabla \Phi_1 - 2 \int_0^T \int_{\Omega} \Phi_1 \frac{\nabla p}{p} \cdot \nabla \Psi_1 + \int_0^T \int_{\Omega} \frac{\Delta p}{p} \Phi_1 \Psi_1,$$

and

$$\int_0^T \int_\Omega \theta'_{d_1} \tilde{\psi} \tilde{\varphi} \to \int_0^T \int_\Omega \frac{\Delta p}{p} \Phi_1 \Psi_1,$$

where in the last limit we have used (5.11) and (5.12). Now letting $d_1 \to 0$ in (6.33), the last identity in (6.28) follows from the above two limits and (6.27). This finishes the proof of Claim 6.6.

We now finish the proof for Case (i)(b). Since $\lambda_1(d_1, d_2) - (d_1 - d_2)$ is strictly increasing in $d_2 \in (0, \varepsilon_0)$ by (6.30), we see from Claim 6.6 that

$$\begin{cases} d_1 - d_2 \in (\lambda_1(d_1, d_2), \infty) & \text{for all } d_1 \in (0, \varepsilon_0) \text{ and } d_2 \in (0, \hat{d}_2(d_1)), \\ d_1 - d_2 \in (0, \lambda_1(d_1, d_2)) & \text{for all } d_1 \in (0, \varepsilon_0) \text{ and } d_2 \in (\hat{d}_2(d_1), d_1), \\ d_1 - d_2 \in (-\infty, 0) & \text{for all } d_1 \in (0, \varepsilon_0) \text{ and } d_2 \in (d_1, \varepsilon_0). \end{cases}$$
(6.36)

This combined with (6.5), (6.7) and (6.14) finishes the proof for Case (i)(b) and hence the proof for Theorem 2.1' (ii).

Finally, we deal with Case (ii) and assume that I(p) < 0. Then by (6.10), we see that $\frac{d\chi_1}{d\lambda}(0) < 0$ for all $(d_1, d_2) \in (0, \varepsilon_0)^2$, which implies by [20, Theorem 16.3] that

$$\lambda_1(d_1, d_2) < 0 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2.$$
 (6.37)

Since $\chi_1(0) = \chi_1(\lambda_1(d_1, d_2)) = 0$, it follows from Claim 6.3 that

$$\begin{cases} \chi_1(\lambda) > 0 & \text{for all } \lambda \in (\lambda_1(d_1, d_2), 0), \\ \chi_1(\lambda) < 0 & \text{for all } \lambda \in (-\infty, \lambda_1(d_1, d_2)) \cup (0, \infty). \end{cases}$$

$$(6.38)$$

Claim 6.7.

$$-1 \le \frac{\lambda_1(d_1, d_2)}{d_2} < 0 \quad \forall d_1, d_2 > 0. \tag{6.39}$$

To prove Claim 6.7, recall that φ_1 is the principal eigenfunction of (6.23) corresponding to $\lambda_1(d_1, d_2)$, normalized so that $\|\varphi_1\|_{L^2((0,T),L^2(\Omega))} = 1$. Dividing both sides of the equation for φ_1 by φ_1 and integrating over $\Omega \times (0,T)$, we obtain

$$\begin{split} \frac{\lambda_1(d_1,d_2)}{d_2} \int_0^T \int_{\Omega} \frac{|\nabla \theta_{d_1}|^2}{\theta_{d_1}^2} &= \int_0^T \int_{\Omega} \frac{|\nabla \varphi_1|^2}{\varphi_1^2} + 2 \int_0^T \int_{\Omega} \frac{\nabla \varphi_1}{\varphi_1} \cdot \frac{\nabla \theta_{d_1}}{\theta_{d_1}} \\ &\geq - \int_0^T \int_{\Omega} \frac{|\nabla \theta_{d_1}|^2}{\theta_{d_1}^2}. \end{split}$$

This combined with (6.37) finishes the proof of (6.39) and hence of Claim 6.7.

Claim 6.8. Assume that m additionally satisfies condition (M3). Then

$$\lim_{d_1, d_2 \to 0} \frac{\partial \lambda_1(d_1, d_2)}{\partial d_2} = \Lambda_1(p) \in (-1, 0). \tag{6.40}$$

To prove Claim 6.8, recall that φ_1 and ψ_1 are the principal eigenfunction and the principal adjoint eigenfunction satisfying (6.23) and (6.24) respectively, normalized so that

$$\|\varphi_1\|_{L^2((0,T),L^2(\Omega))} = \|\psi_1\|_{L^2((0,T),L^2(\Omega))} = 1.$$

By (6.39) and similar arguments to the proof of Claim 6.5, passing to subsequences of (d_1, d_2) if necessary, we see that

$$\varphi_1 \to \Phi_1, \psi_1 \to \Psi_1 \quad \text{in } L^2((0, T), H^1(\Omega)),
\lambda_1(d_1, d_2)/d_2 \to \Lambda^* \in [-1, 0], \quad \text{as } d_1, d_2 \to 0,$$
(6.41)

where $\Phi_1, \Psi_1 \in H^1(\Omega)$ are the principal eigenfunctions to (6.1) and (6.2) respectively with Λ^* being the corresponding principal eigenvalue and

$$\|\Phi_1\|_{L^2(\Omega)} = \|\Psi_1\|_{L^2(\Omega)} = 1/\sqrt{T}.$$

Since I(p)<0 and $\int_0^T \int_\Omega \frac{\Delta p}{p} \, dt = \int_0^T \int_\Omega \frac{|\nabla p|^2}{p^2} \, dt > 0$, we see from (2.3) that $\int_0^T \frac{\Delta p}{p} \, dt$ changes sign in Ω . Hence, it follows from Lemma 6.1 that $\Lambda_1(p)$ exists and $\Lambda_1(p) \in (-1,0)$, where $\Lambda_1(p) \neq -1$ follows from (M3) and Remark 6.2. By similar arguments to the proof of Claim 6.5, we can show that $\Lambda^* \neq 0$ and hence we must have $\Lambda^* = \Lambda_1(p) \in (-1,0)$. Similarly to the proof of Claim 6.5, letting $d_1, d_2 \to 0$ in (6.25), and then combining the result with (6.41) and (6.27), we derive (6.40). This finishes the proof of the claim.

Claim 6.9. Let

$$\bar{\varepsilon} = \bar{\varepsilon}(\varepsilon_0, p) := \frac{1 + \Lambda_1(p)}{2} \varepsilon_0 \in (0, \varepsilon_0/2).$$

There exists a unique continuously differentiable function $\bar{d}_2:(0,\bar{\varepsilon})\to(0,\infty)$ with $\bar{d}_2(d_1)\in(d_1,\varepsilon_0)$ such that for $(d_1,d_2)\in(0,\bar{\varepsilon})\times(0,\varepsilon_0)$,

$$\lambda_1(d_1, d_2) = d_1 - d_2 \iff d_2 = \bar{d}_2(d_1).$$

Moreover,

$$\lim_{d_1 \to 0} \bar{d}_2(d_1) = 0, \quad \bar{d}_2'(0) = \frac{1}{1 + \Lambda_1(p)} > 1, \quad \lim_{d_1 \to 0} \bar{d}_2'(d_1) = \frac{1}{1 + \Lambda_1(p)} > 1. \quad (6.42)$$

We now prove Claim 6.9. By (6.39) and (6.40), we may extend the definitions of $\lambda_1(d_1, d_2)$ and $\frac{\partial \lambda_1(d_1, d_2)}{\partial d_2}$ so that

$$\lambda_1(\cdot, 0) = 0 \text{ in } [0, \varepsilon_0) \quad \text{and} \quad \frac{\partial \lambda_1(0, 0)}{\partial d_2} = \Lambda_1(p) \in (-1, 0).$$
 (6.43)

For notational convenience, denote

$$F(d_1, d_2) := \lambda_1(d_1, d_2) - d_1 + d_2.$$

We see from (6.43) that $\frac{\partial F(d_1,d_2)}{\partial d_2}\Big|_{(d_1,d_1)=(0,0)} = 1 + \Lambda_1(p) > 0$. Choosing ε_0 smaller if necessary, we may assume that

$$\frac{\partial F(d_1, d_2)}{\partial d_2} > \frac{1 + \Lambda_1(p)}{2} > 0 \quad \forall (d_1, d_2) \in (0, \varepsilon_0)^2. \tag{6.44}$$

Then for each $d_1 \in (0, \bar{\varepsilon})$, by (6.37) and (6.43) we see that

$$F(d_1, d_1) = \lambda_1(d_1, d_1) - d_1 + d_1 < 0$$

and there exists $\xi \in (0, 1)$ such that

$$F(d_1, \varepsilon_0) = F(d_1, 0) + \varepsilon_0 \frac{\partial F(d_1, d_2)}{\partial d_2} \bigg|_{d_2 = \varepsilon_0 \tilde{\varepsilon}} > -d_1 + \frac{1 + \Lambda_1(p)}{2} \varepsilon_0 = -d_1 + \bar{\varepsilon} > 0,$$

Hence, by the intermediate value theorem and (6.44), for each $d_1 \in (0, \bar{\varepsilon})$, there exists a unique $d_2 = \bar{d}_2(d_1) \in (d_1, \varepsilon_0)$ such that $\lambda_1(d_1, d_2) - d_1 + d_2 = 0$ if and only if $d_2 = \bar{d}_2(d_1)$. For each $d_1 \in (0, \bar{\varepsilon})$, there exists some $\xi' \in (0, 1)$ such that

$$\begin{split} d_1 &= \lambda_1(d_1, \bar{d}_2(d_1)) + \bar{d}_2(d_1) \\ &= \left[\lambda_1(d_1, \bar{d}_2(d_1)) - d_1 + \bar{d}_2(d_1) \right] - \left[\lambda_1(d_1, 0) - d_1 + 0 \right] \\ &= \left. \bar{d}_2(d_1) \frac{\partial F(d_1, d_2)}{\partial d_2} \right|_{d_2 = \xi' \bar{d}_2(d_1)} > \frac{1 + \Lambda_1(p)}{2} \bar{d}_2(d_1), \end{split}$$

where we use (6.44) in the last inequality. Consequently, $\lim_{d_1\to 0} \bar{d}_2(d_1) = 0$. Since $\lambda_1(d_1,d_2)$ is analytic, $\bar{d}_2(d_1)$ is actually analytic in $d_1\in(0,\bar{\varepsilon})$. The proof of (6.42) now follows from similar arguments to those for (6.28) and hence is omitted. This finishes the proof for Claim 6.9.

Choosing ε_0 even smaller if necessary, we see from (6.42) that $\bar{d}_2(d_1)$ is strictly increasing in $(0,\bar{\varepsilon})$. Now, replacing ε_0 by $\bar{d}_2(\bar{\varepsilon})$, we may define the inverse function of $\bar{d}_2(d_1)$ by $\tilde{d}_1:(0,\varepsilon_0)\to(0,\infty)$. To summarize, we have the following result:

Claim 6.10. There exists a unique continuously differentiable function $\tilde{d}_1:(0,\varepsilon_0)\to (0,\infty)$ with $\tilde{d}_1(d_2)\in(0,d_2)$ such that for $(d_1,d_2)\in(0,\varepsilon_0)^2$,

$$\lambda_1(d_1, d_2) = d_1 - d_2 \iff d_1 = \tilde{d}_1(d_2).$$

Moreover,

$$\lim_{d_2 \to 0} \tilde{d}_1(d_2) = 0, \quad \tilde{d}'_1(0) = 1 + \Lambda_1(p) \in (0, 1), \quad \lim_{d_2 \to 0} \tilde{d}'_1(d_2) = 1 + \Lambda_1(p) \in (0, 1).$$
(6.45)

We now finish the proof for Case (ii). Since $\lambda_1(d_1, d_2) - (d_1 - d_2)$ is strictly increasing in $d_2 \in (0, \varepsilon_0)$, we see from Claims 6.9 and 6.10 that

$$\begin{cases} d_1 - d_2 \in (0, +\infty) & \text{for all } d_2 \in (0, \varepsilon_0) \text{ and } d_1 \in (d_2, \varepsilon_0), \\ d_1 - d_2 \in (\lambda_1(d_1, d_2), 0) & \text{for all } d_2 \in (0, \varepsilon_0) \text{ and } d_1 \in (\tilde{d}_1(d_2), d_2), \\ d_1 - d_2 \in (-\infty, \lambda_1(d_1, d_2)) & \text{for all } d_2 \in (0, \varepsilon_0) \text{ and } d_1 \in (0, \tilde{d}_1(d_2)). \end{cases}$$
(6.46)

This combined with (6.5), (6.7) and (6.38) finishes the proof for Case (ii) and hence the proof of Theorem 2.1' (iii).

7. Miscellaneous remarks

In this section, we first construct explicit examples of m's such that the conditions in Theorem 2.1 (i, ii, iii) hold respectively. Recall that $0 < \Theta \in C^2(\bar{\Omega})$ is the principal eigenfunction of (6.20) normalized so that $\|\Theta\|_{C(\bar{\Omega})} = 1$, and $\lambda_1(\Omega) > 0$ is the corresponding principal eigenvalue. Define $\eta \in C^{\infty}(\mathbb{R})$ by

$$\eta(r) := \begin{cases} C \exp\left(\frac{1}{r^2 - 1}\right) & \text{if } |r| < 1, \\ 0 & \text{if } |r| \ge 1, \end{cases}$$

where the constant C > 0 is selected so that $\int_{\mathbb{R}^N} \eta \, dx = 1$.

Lemma 7.1. Let $h \in C_T^2(\mathbb{R})$ with $\min_{t \in [0,T]} h(t) = 0$ and $\max_{t \in [0,T]} h(t) = M > 0$. For each $\delta > 0$ and $\beta \in (1,2)$, set

$$\eta_{\beta,\delta}(x) := \delta^{\beta} \eta(|x|/\delta).$$

Then the following hold:

(i) Define

$$p(x,t) = kh(t - \xi \cdot x)\Theta(x)^2 + k\sigma, \tag{7.1}$$

where $0 \neq \xi \in \mathbb{R}^N$ and $0 < k \in \mathbb{R}$. Then for $\sigma > 0$ sufficiently small and k > 0 sufficiently large, $m = p_t/p + p$ satisfies conditions (**M1**) and (**M2**), and $(-\Delta p/p)^{\wedge} < 0$ on $\bar{\Omega}$, i.e., the conditions in Theorem 2.1 (i) hold.

(ii) Denote

$$S := \{0
$$and (-\Delta p/p)^{\wedge} < 0 \text{ on } \bar{\Omega}\}. \tag{7.2}$$$$

Let $p_1 \in S$, $x_0 \in \Omega$ and define

$$p(x,t) := p_1(x,t) + \eta_{\beta,\delta}(x-x_0).$$

Then for all $\delta > 0$ sufficiently small, $m = p_t/p + p$ satisfies (M1) and (M2), I(p) > 0 and $(-\Delta p/p)^{\wedge}(x_0) > 0$, i.e., the conditions in Theorem 2.1 (ii) hold.

(iii) Let

$$p(x,t) = a(x)(b(t) + k) + \sigma,$$

where $0 < a \in C^2(\bar{\Omega})$ satisfies $\partial_{\nu} a = 0$ on $\partial \Omega$, $b \in C^1_T(\mathbb{R})$ with $\min_{[0,T]} b > 0$, and $k, \sigma \in (0, \infty)$. Then for all $\sigma > 0$ sufficiently small and k > 0 sufficiently large, $m = p_t/p + p$ satisfies conditions (M1)–(M3) and I(p) < 0, i.e., the conditions in Theorem 2.1 (iii) hold.

Proof. We first prove part (i) of the lemma. By direct calculation, we see that

$$\Delta p = kh''(t - \xi \cdot x)\Theta^2 |\xi|^2 - 4kh'(t - \xi \cdot x)\Theta \xi \cdot \nabla \Theta + 2kh(t - \xi \cdot x)(\Theta \Delta \Theta + |\nabla \Theta|^2).$$

Therefore.

$$\int_0^T \frac{-\Delta p}{p} dt = J_1 + J_2 + J_3,\tag{7.3}$$

where

$$J_{1} := -\int_{0}^{T} \frac{h''(t - \xi \cdot x)\Theta^{2}|\xi|^{2}}{h(t - \xi \cdot x)\Theta^{2} + \sigma} dt = -|\xi|^{2} \int_{0}^{T} \left(\frac{h'(t - \xi \cdot x)\Theta^{2}}{h(t - \xi \cdot x)\Theta^{2} + \sigma} \right)^{2} dt$$

$$\leq -\frac{|\xi|^{2}}{T} \left(\int_{0}^{T} \left| \frac{h'(t - \xi \cdot x)\Theta^{2}}{h(t - \xi \cdot x)\Theta^{2} + \sigma} \right| dt \right)^{2} \leq -\frac{|\xi|^{2}}{T} \left(\int_{t_{1}^{x}}^{t_{2}^{x}} \left| \frac{h'(t - \xi \cdot x)\Theta^{2}}{h(t - \xi \cdot x)\Theta^{2} + \sigma} \right| dt \right)^{2}$$

$$= -\frac{|\xi|^{2}}{T} \left[\ln \left(\frac{M\Theta^{2}(x)}{\sigma} + 1 \right) \right]^{2} \leq 0,$$

$$J_{2} := 4 \int_{0}^{T} \frac{h'(t - \xi \cdot x)\Theta\xi \cdot \nabla\Theta}{h(t - \xi \cdot x)\Theta^{2} + \sigma} dt = 0,$$

$$J_{3} := -2(\Theta\Delta\Theta + |\nabla\Theta|^{2}) \int_{0}^{T} \frac{h(t - \xi \cdot x)}{h(t - \xi \cdot x)\Theta^{2} + \sigma} dt$$

$$= 2(\lambda_{1}(\Omega)\Theta^{2} - |\nabla\Theta|^{2}) \int_{0}^{T} \frac{h(t - \xi \cdot x)}{h(t - \xi \cdot x)\Theta^{2} + \sigma} dt.$$

Note that in the estimation of J_1 , t_1^x , $t_2^x \in [0, T]$ are chosen such that $h(t_1^x - \xi \cdot x) = \min_{t \in [0, T]} h(t) = 0$ and $h(t_2^x - \xi \cdot x) = \max_{t \in [0, T]} h(t) = M$. In the computation of J_3 , we have used the identity (6.20).

Let $\Omega_{\varepsilon} := \{x \in \Omega \mid \operatorname{dist}(x, \partial \Omega) > \varepsilon\}$. Then by the Hopf boundary lemma, there exists $\varepsilon' > 0$ small such that

$$\sigma_0 := \min_{\bar{\Omega} \setminus \Omega_{\epsilon'}} (|\nabla \Theta|^2 - \lambda_1(\Omega)\Theta^2) > 0 \quad \text{and} \quad \sigma_1 = \min_{\Omega_{\epsilon'}} \Theta > 0.$$

Since J_3 is uniformly bounded on $\bar{\Omega}_{\varepsilon'}$ with respect to $\sigma > 0$, for all $\sigma > 0$ sufficiently small we can guarantee that

$$\int_0^T \frac{-\Delta p}{p} \, dt = J_1 + J_2 + J_3 \le -\frac{|\xi|^2}{T} \left[\ln \left(\frac{M \sigma_1^2}{\sigma} + 1 \right) \right]^2 + J_3 < 0 \quad \text{on } \bar{\Omega}_{\varepsilon'}.$$

On $\bar{\Omega} \setminus \Omega_{\varepsilon'}$, it follows from the positivity of σ and the above estimations that

$$\int_0^T \frac{-\Delta p}{p} dt = J_1 + J_2 + J_3 \le J_3 \le -2\sigma_0 \int_0^T \frac{h(t - \xi \cdot x)}{h(t - \xi \cdot x)\Theta^2 + \sigma} dt < 0.$$

It is easy to check that $m = p_t/p + p > 0$ on $\bar{\Omega} \times \mathbb{R}$ by choosing k sufficiently large and m satisfies (M1) and (M2). Note that in the construction of p(x,t) in (7.1), we have chosen Θ^2 other than Θ to make sure that condition (M2) is satisfied. This finishes the proof of part (i) of the lemma.

We next prove part (ii). It follows from (i) that the set S defined by (7.2) is nonempty. Without loss of generality, we may assume that $0 \in \Omega$ and set $x_0 = 0$ in the rest of the proof. By direct calculation, we see that

$$\Delta \eta_{\beta,\delta}(x) = \delta^{\beta-2} \left[\eta'' \left(\frac{|x|}{\delta} \right) + (N-1) \frac{\delta}{|x|} \eta' \left(\frac{|x|}{\delta} \right) \right]. \tag{7.4}$$

Note that $\frac{\delta}{|x|}\eta'(\frac{|x|}{\delta})$ is uniformly bounded and continuous in $B_{\delta}(0)\setminus\{0\}$ and we can extend its definition to x=0. Since $\Delta\eta_{\beta,\delta}(0)=\delta^{\beta-2}N\eta''(0),\,\eta''(0)<0$ and $\beta\in(1,2)$, we can show that

$$\int_0^T \frac{-\Delta p}{p}(0,t) dt = \int_0^T \frac{-\Delta p_1(0,t) - \delta^{\beta-2} N \eta''(0)}{p_1(0,t) + C} dt \to +\infty \quad \text{as } \delta \to 0.$$

On the other hand,

$$\begin{split} I(p) &= \int_{\Omega \setminus B_{\delta}(0)} \left[\exp \left(\frac{1}{T} \int_0^T \ln p^2 \, dt \right) \int_0^T \frac{\Delta p}{p} \, dt \right] dx \\ &+ \int_{B_{\delta}(0)} \left[\exp \left(\frac{1}{T} \int_0^T \ln p^2 \, dt \right) \int_0^T \frac{\Delta p}{p} \, dt \right] dx =: I_1(p) + I_2(p). \end{split}$$

Since $p \equiv p_1$ on $\Omega \setminus B_{\delta}(0)$ and $p_1 \in S$, we see that $I_1(p) > 0$ and $I_1(p)$ is decreasing in $\delta > 0$. We now estimate $I_2(p)$. Let $K_1, K_2 > 0$ be chosen such that

$$K_1 \le p_1 \le K_2 \text{ on } \bar{\Omega} \times [0, T], \quad |\Delta p_1| \le K_2 \text{ on } \bar{\Omega} \times [0, T],$$

$$\left| \eta''(|x|) + (N - 1) \frac{\eta'(|x|)}{|x|} \right| \le K_2 \quad \text{in } B_1(0).$$

By direct computation, we have

$$\begin{split} |I_2(p)| &\leq \int_{B_{\delta}(0)} \left[\exp \left(\frac{1}{T} \int_0^T \ln p^2 \, dt \right) \int_0^T \left| \frac{\Delta p}{p} \right| dt \right] dx \\ &\leq (K_2 + C\delta^{\beta})^2 \int_{B_{\delta}(0)} \int_0^T \left| \frac{\Delta p_1 + \Delta \eta_{\beta,\delta}}{p_1 + \eta_{\beta,\delta}} \right| dt dx \\ &\leq (K_2 + C\delta^{\beta})^2 \omega_N \delta^N \frac{K_2 + \delta^{\beta - 2} K_2}{K_1 - \delta^{\beta}} \\ &\leq 8(K_2 + C)^3 \omega_N (\delta^N + \delta^{N + \beta - 2}) / K_1 \to 0 \quad \text{as } \delta \to 0, \end{split}$$

where ω_N is the volume of the unit ball $B_1(0)$ in \mathbb{R}^N . Consequently, I(p) > 0 for all $\delta > 0$ sufficiently small. This finishes the proof of (ii).

Finally, we prove (iii). By direct computation,

$$I(p-\sigma) = -T \exp\left(\frac{1}{T} \int_0^T \ln[(b+k)^2] dt\right) \int_{\Omega} |\nabla a|^2 dx < 0.$$

Therefore, choosing k > 0 sufficiently large first and then $\sigma > 0$ sufficiently small, we can make sure that I(p) < 0 and $m = p_t/p + p$ satisfies conditions (M1)–(M3).

For a general spatially heterogeneous and temporally periodic function m(x,t) satisfying conditions (M1) and (M2), we have shown in Theorem 2.3 that when the diffusion rates of both species are sufficiently large, the fast dispersal is selected against. On the other hand, when the two diffusion rates are sufficiently small and close, and in addition I(p) > 0, we know by Corollary 2.5 that the phenotype with the faster diffusion rate is selected for. Therefore, when I(p) > 0, it is interesting to know whether there exists an *optimal* dispersal rate in the sense that if the resident species U adopts such dispersal rate, then a small number of mutant or exotic species V using a different random dispersal rate can never successfully invade. Such an optimal dispersal rate is usually called a globally *evolutionarily stable strategy* (ESS), which is an important concept in adaptive dynamics introduced by Maynard Smith and Price [35]. See also [7,8,10,11] for the general approach of adaptive dynamics. We now recall the definition of local ESS for system (1.1) motivated from [25,26].

Definition 7.2. A strategy d_1^* is a *local ESS* if there exists $\delta > 0$ such that $\mu_1(d_2, m - \theta_{d_1^*}) > 0$ for all $d_2 \in (d_1^* - \delta, d_1^* + \delta) \setminus \{d_1^*\}$.

When $d_2 = d_1$, $\mu_1(d_2, m - \theta_{d_1}) = 0$ with θ_{d_1} being the corresponding eigenfunction. By Taylor's theorem,

$$\mu_1(d_2, m - \theta_{d_1}) = \frac{\partial \mu_1(d_2, m - \theta_{d_1})}{\partial d_2} \bigg|_{d_2 = d_1} (d_2 - d_1) + O((d_2 - d_1)^2).$$

Hence, if $\frac{\partial \mu_1(d_2,m-\theta_{d_1})}{\partial d_2}\big|_{d_2=d_1}$ is positive (resp. negative), then a rare mutant V with strategy d_2 slightly less than (resp. greater than) d_1 can invade the resident U successfully.

Therefore, it is important to first seek the existence of *evolutionarily singular strategies*, defined as follows:

Definition 7.3. We say that d_1^* is an evolutionarily singular strategy if

$$\left.\frac{\partial \mu_1(d_2,m-\theta_{d_1^*})}{\partial d_2}\right|_{d_2=d_1^*}=0.$$

Then Lemma 5.7 implies

Lemma 7.4. If I(p) > 0, there exists at least one evolutionarily singular strategy.

If there is a unique evolutionarily singular strategy, we suspect that it should be an ESS.

Appendix

In this appendix, we derive a global boundedness result for nonnegative classical solutions of quasilinear time-periodic parabolic equations by modifying the Moser–Alikakos iteration procedure [1]. We believe that this result will be of interest in its own right in the study of periodic-parabolic equations. As we could not find a precise reference with accurate dependence on all the parameters involved in the equation, and some major modifications to the original procedure are also necessary, we include a detailed proof here for the sake of completeness.

Consider the following periodic-parabolic equation:

$$\begin{cases} u_t = \nabla \cdot \mathbf{A}(x, t, u, \nabla u) + B(x, t, u, \nabla u) & \text{in } \Omega \times \mathbb{R}, \\ \mathbf{A}(x, u, \nabla u) \cdot v = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ u \text{ is } T\text{-periodic in } t, \end{cases}$$
(A.1)

where the functions $\mathbf{A}: \Omega \times \mathbb{R} \times \mathbb{R} \times \mathbb{R}^N \to \mathbb{R}^N$ and $\mathbf{B}: \Omega \times \mathbb{R} \times \mathbb{R} \times \mathbb{R}^N \to \mathbb{R}$ are measurable and T-periodic in t.

We assume that **A** and **B** satisfy the structure conditions

$$\mathbf{A}(x, t, u, \nabla u) \cdot \nabla u \ge \lambda |\nabla u|^2 - u\mathbf{a} \cdot \nabla u - \mathbf{f} \cdot \nabla u,$$

$$B(x, t, u, \nabla u) \le |\mathbf{b}| |\nabla u| + |du| + |g|,$$
(A.2)

where $\lambda > 0$ is a constant, $\mathbf{a} = (a^1, \dots, a^N)$, $\mathbf{b} = (b^1, \dots, b^N)$, $\mathbf{f} = (f^1, \dots, f^N)$, d and g are measurable functions and $a^i, b^i, f^i, d, g : \Omega \times \mathbb{R} \to \mathbb{R}$ are T-periodic in t for $i = 1, \dots, N$. To simplify the form of these inequalities, we write

$$\bar{u} = |u| + k, \quad \bar{b} = \lambda^{-2} (|\mathbf{a}|^2 + |\mathbf{b}|^2 + k^{-2}|\mathbf{f}|^2) + \lambda^{-1} (|d| + k^{-1}|g|)$$
 (A.3)

for some k > 0. Using the Schwarz inequality, we then obtain, for any $0 < \epsilon < 1$,

$$\mathbf{A}(x,t,u,\nabla u) \cdot \nabla u \ge \frac{\lambda}{2} (|\nabla u|^2 - 2\bar{b}\bar{u}^2),$$

$$B(x,t,u,\nabla u)\bar{u} \le \frac{\lambda}{2} \left(\epsilon |\nabla u|^2 + \frac{\bar{b}}{\epsilon}\bar{u}^2\right).$$
(A.4)

Lemma A.1. Let u be a nonnegative classical solution of (A.1) which is T-periodic in t and $u \in L^{\beta}((0,T), H^{\beta}(\Omega))$ for some $\beta \geq 1$. Let $\gamma > N$ and $\theta = \frac{\hat{N}(\gamma+2)}{\gamma(\hat{N}+2)} \in (0,1)$ be two given constants, where $\hat{N} = N$ for N > 2 and $2 < \hat{2} < \gamma$. Assume further that $a^i, b^i, f^i \in L^{2/(1-\theta)}((0,T), L^{\gamma}(\Omega))$, $i = 1, \ldots, N, d, g \in L^{1/(1-\theta)}((0,T), L^{\gamma/2}(\Omega))$. Then $u \in L^{\infty}((0,T), L^{\infty}(\Omega))$ and

$$\sup_{\Omega \times \mathbb{R}} u \leq \left(\frac{1}{T} + \lambda e^{\lambda T}\right)^{1/\beta} \exp\left(\frac{C\lambda H}{\beta}\right) C H^{1/\beta} \left[\|u\|_{L^{\beta}((0,T),L^{\beta}(\Omega))} + \frac{\bar{k}}{\lambda} \right], \quad (A.5)$$

where $C = C(N, \Omega, T, \gamma, \beta)$, \bar{b} is defined in (A.3),

$$\bar{k} := \|\mathbf{f}\|_{L^{\frac{2}{1-\theta}}((0,T),L^{\gamma}(\Omega))} + \|g\|_{L^{\frac{1}{1-\theta}}((0,T),L^{\gamma/2}(\Omega))}, \quad H = \int_{0}^{T} \left(\int_{\Omega} (\bar{b}+2)^{\frac{\gamma}{2}} \right)^{\frac{2}{\gamma(1-\theta)}}$$

Proof. Let w = u + k. For $\beta \ge 2$, multiplying (A.1) by $w^{\beta - 1}$ and integrating over Ω , using the structure (A.4) and taking $\epsilon = 1/2$, since $\nabla w = \nabla u$, we obtain

$$\begin{split} &\frac{1}{\lambda} \biggl(\int_{\Omega} w^{\beta} \biggr)_{t} = -\frac{\beta}{\lambda} \int_{\Omega} (\beta - 1) w^{\beta - 2} \mathbf{A} \cdot \nabla u + \frac{\beta}{\lambda} \int_{\Omega} B w^{\beta - 1} \\ & \leq -\frac{\beta - 1}{\beta} \int_{\Omega} |\nabla w^{\beta / 2}|^{2} + \beta^{2} \int_{\Omega} \bar{b} w^{\beta} \\ & \leq -\frac{(\beta - 1)}{\beta} \biggl(\int_{\Omega} |\nabla w^{\beta / 2}|^{2} + \int_{\Omega} w^{\beta} \biggr) - \beta^{2} \int_{\Omega} w^{\beta} + \int_{\Omega} \beta^{2} (\bar{b} + 2) w^{\beta} \\ & \leq -\frac{(\beta - 1)C_{1}}{\beta} \|w^{\beta / 2}\|_{L^{\frac{2\hat{N}}{\hat{N} - 2}}(\Omega)}^{2} - \beta^{2} \int_{\Omega} w^{\beta} + \beta^{2} \|\bar{b} + 2\|_{L^{\gamma / 2}(\Omega)} \|w^{\beta}\|_{L^{\frac{\gamma}{\gamma - 2}}(\Omega)}^{2} \\ & \leq -\frac{(\beta - 1)C_{1}}{\beta} \|w^{\beta / 2}\|_{L^{\frac{2\hat{N}}{\hat{N} - 2}}(\Omega)}^{2} \\ & \leq -\frac{(\beta - 1)C_{1}}{\beta} \|w^{\beta / 2}\|_{L^{\frac{2\hat{N}}{\hat{N} - 2}}(\Omega)}^{2} \\ & \leq -\frac{\beta^{2}}{\beta} \int_{\Omega} w^{\beta} + \beta^{2} \|\bar{b} + 2\|_{L^{\gamma / 2}(\Omega)} \|w^{\beta / 2}\|_{L^{\frac{2\hat{N}}{\hat{N} - 2}}(\Omega)}^{2\theta} \|w^{\beta / 2}\|_{L^{1}(\Omega)}^{2(1 - \theta)}, \end{split}$$

where $C_1 = C_1(N, \Omega)$ is a positive constant. It is clear that the structure (A.4) and consequently the above estimate continue to hold for k = 0 provided in (A.2) the terms involving \mathbf{f} and g are set equal to zero. Choosing k as in the statement of the lemma and using Young's inequality

$$\begin{split} \beta^2 \| \bar{b} + 2 \|_{L^{\gamma/2}(\Omega)} \| w^{\beta/2} \|_{L^{\frac{2\hat{N}}{\hat{N}-2}}(\Omega)}^{2\theta} \| w^{\beta/2} \|_{L^{1}(\Omega)}^{2(1-\theta)} \\ & \leq \frac{(\beta-1)C_1}{\beta} \| w^{\beta/2} \|_{L^{\frac{2\hat{N}}{\hat{N}-2}}(\Omega)}^{2} + \left(\frac{\beta}{(\beta-1)C_1} \right)^{\frac{\theta}{1-\theta}} \beta^{\frac{2}{1-\theta}} \| \bar{b} + 2 \|_{L^{\gamma/2}(\Omega)}^{\frac{1}{1-\theta}} \| w^{\beta/2} \|_{L^{1}(\Omega)}^{2}, \end{split}$$

we eventually get

$$\frac{1}{\lambda} \left(\int_{\Omega} w^{\beta} \right)_{t} \le - \int_{\Omega} w^{\beta} + C_{2} \beta^{\frac{2}{1-\theta}} \|\bar{b} + 2\|_{L^{\gamma/2}(\Omega)}^{\frac{1}{1-\theta}} \|w^{\beta/2}\|_{L^{1}(\Omega)}^{2}, \tag{A.6}$$

where $C_2 = C_2(N, \Omega, \gamma, \beta)$ and we have used the fact that $\beta \ge 2$. Denote

$$y(t) := \int_{\Omega} w^{\beta}, \quad h(t) := \|\bar{b} + 2\|_{L^{\gamma/2}(\Omega)}^{\frac{1}{1-\theta}}, \quad z(t) := \|w^{\beta/2}\|_{L^{1}(\Omega)}^{2}, \quad H := \int_{0}^{T} h(t) dt.$$

Then we can rewrite (A.6) as

$$y'(t) \le -\lambda y(t) + C_2 \lambda \beta^{\frac{2}{1-\theta}} h(t) z(t). \tag{A.7}$$

Let $s_0 \in \mathbb{R}$ be such that $y(s_0) = \inf_t y(t)$ and $t_0 \in [s_0, s_0 + T]$ such that $y(t_0) = \sup_t y(t)$. Integrating both sides of (A.6) from s_0 to $s_0 + T$, we see that

$$Ty(s_0) \le \int_{s_0}^{s_0+T} y(t) dt \le C_2 H \beta^{\frac{2}{1-\theta}} \sup_t z(t).$$
 (A.8)

On the other hand, applying the variation of constants formula to (A.7) and integrating from s_0 to t_0 , we obtain

$$y(t_0) \le e^{\lambda(t_0 - s_0)} y(t_0) \le y(s_0) + C_2 \lambda \beta^{\frac{2}{1 - \theta}} \int_{s_0}^{t_0} e^{\lambda(t - s_0)} h(t) z(t) dt$$

$$\le y(s_0) + \lambda e^{\lambda T} C_2 H \beta^{\frac{2}{1 - \theta}} \sup_{t} z(t).$$

Plugging (A.8) into the above inequalities, we see that

$$\sup_{t} y(t) \le \left(\frac{1}{T} + \lambda e^{\lambda T}\right) C_2 H \beta^{\frac{2}{1-\theta}} \sup_{t} z(t).$$

This implies that

$$\sup_{t} \|w\|_{L^{\beta}(\Omega)} \le C_3^{1/\beta} \beta^{\frac{1}{\beta} \cdot \frac{2}{1-\theta}} \sup_{t} \|w\|_{L^{\beta/2}(\Omega)}, \tag{A.9}$$

where $C_3 = (1/T + \lambda e^{\lambda T})C_2H$. Therefore, for any $\beta \geq 2$, the inclusion of $w \in L^{\infty}((0,T),L^{\beta/2}(\Omega))$ implies the stronger inclusion, $w \in L^{\infty}((0,T),L^{\beta}(\Omega))$. By iteration of the above estimate, we may assume that $w \in \bigcap_{1 \leq \beta < \infty} L^{\infty}((0,T),L^{\beta}(\Omega))$ and by (A.9),

$$\begin{split} \sup_{t} \|w\|_{L^{2}K_{\beta}(\Omega)} &\leq \Big(\prod_{m=1}^{K} C_{3}^{\frac{1}{2^{m}\beta}} (2^{m}\beta)^{\frac{2\theta}{(1-\theta)2^{m}\beta}}\Big) \sup_{t} \|w\|_{L^{\beta}(\Omega)} \\ &\leq C_{3}^{\sigma/\beta} \exp\left(\frac{2}{1-\theta} \cdot \frac{\ln\beta}{\beta} \cdot \sigma + \frac{2}{1-\theta} \cdot \frac{\ln2}{\beta} \cdot \kappa\right) \sup_{t} \|w\|_{L^{\beta}(\Omega)}, \end{split}$$

where $\sigma = \sum_{m=1}^{K} 2^{-m} < 1$ and $\kappa = \sum_{m=1}^{K} m 2^{-m}$. Letting $K \to \infty$ and denoting $\kappa_0 = \sum_{m=1}^{\infty} m 2^{-m}$, we obtain

$$\|w\|_{L^{\infty}((0,T),L^{\infty}(\Omega))} \le \left(\frac{1}{T} + \lambda e^{\lambda T}\right)^{1/\beta} H^{1/\beta} C_4 \|w\|_{L^{\infty}((0,T),L^{\beta}(\Omega))},$$
 (A.10)

where $\beta \geq 1$ and

$$C_4 = C_4(N, \Omega, \gamma, \beta) = C_2^{1/\beta} \exp\left(\frac{2}{1-\theta} \cdot \frac{\ln \beta}{\beta} + \frac{2}{1-\theta} \cdot \frac{\ln 2}{\beta} \cdot \kappa_0\right).$$

By (A.6) and Hölder's inequality, we see that

$$\left(\int_{\Omega} w^{\beta}\right)_t \leq C_5 \lambda h(t) \int_{\Omega} w^{\beta},$$

where $C_5 = C_5(N, \Omega, \gamma, \beta) = C_2 \beta^{\frac{2}{1-\theta}}$. Hence, for any $s, t \in [0, T]$ with $t \ge s$, it follows from the above inequality that

$$\int_{\Omega} w(x,t)^{\beta} dx \leq e^{C_5 \lambda \int_s^t h(\xi) d\xi} \int_{\Omega} w(x,s)^{\beta} dx \leq e^{C_5 \lambda H} \int_{\Omega} w(x,s)^{\beta} dx$$

and

$$\int_{\Omega} w(x,s)^{\beta} dx = \int_{\Omega} w(x,s+T)^{\beta} dx \le e^{C_5 \lambda \int_t^{s+T} h(\xi) d\xi} \int_{\Omega} w(x,t)^{\beta} dx$$
$$\le e^{C_5 \lambda H} \int_{\Omega} w(x,t)^{\beta} dx.$$

Thus, we have showed that for any $s, t \in [0, T]$,

$$e^{-C_5\lambda H/\beta} \|w(\cdot,s)\|_{L^{\beta}(\Omega)} \leq \|w(\cdot,t)\|_{L^{\beta}(\Omega)} \leq e^{C_5\lambda H/\beta} \|w(\cdot,s)\|_{L^{\beta}(\Omega)},$$

which implies that

$$||w||_{L^{\infty}((0,T),L^{\beta}(\Omega))} = \sup_{t} ||w(\cdot,t)||_{L^{\beta}(\Omega)} \le e^{C_{5}\lambda H/\beta} \inf_{t} ||w(\cdot,t)||_{L^{\beta}(\Omega)}$$
$$\le T^{-1/\beta} e^{C_{5}\lambda H/\beta} ||w||_{L^{\beta}((0,T),L^{\beta}(\Omega))}.$$

Combining the above estimate with (A.10), we obtain

$$||w||_{L^{\infty}((0,T),L^{\infty}(\Omega))} \leq \left(\frac{1}{T} + \lambda e^{\lambda T}\right)^{1/\beta} H^{1/\beta} e^{C_5 \lambda H/\beta} C_4 T^{-1/\beta} ||w||_{L^{\beta}((0,T),L^{\beta}(\Omega))}.$$
(A.11)

Now, letting $C(N, \Omega, T, \gamma, \beta) := \max\{C_5, C_4 T^{-1/\beta}\}$ and $k = \bar{k}/\lambda$, the desired estimate (A.5) follows from the definition w = u + k.

Proof of Lemma 3.3. By Proposition 3.2, for all d sufficiently large, there exist $\varphi_2(x,t;d)$ and $\psi_2(x,t;d)$ with $\|\varphi_2\|_{L^2((0,T),H^1(\Omega))}$ and $\|\psi_2\|_{L^2((0,T),H^1(\Omega))}$ uniformly bounded in d such that

$$\varphi(x,t) = \overline{\varphi}(t) + \frac{\overline{\varphi}(t)\Gamma_h(x,t)}{d} + \frac{\varphi_2(x,t)}{d^2},$$

$$\psi(x,t) = \overline{\psi}(t) + \frac{\overline{\psi}(t)\Gamma_h(x,t)}{d} + \frac{\psi_2(x,t)}{d^2},$$

where the dependence on d of all the functions involved is suppressed for notational convenience. Denote $\mu_1 := \mu_1(d, h)$ in the remainder of this proof. Integrating the equation for φ over Ω , we see that

$$\overline{\varphi}_t = \overline{\varphi}(\overline{h} + \mu_1) + \frac{1}{|\Omega|} \int_{\Omega} h(\varphi - \overline{\varphi}) = \overline{\varphi}(\overline{h} + \mu_1) + \overline{\varphi} \frac{1}{d|\Omega|} \int_{\Omega} h\Gamma_h + \frac{1}{d^2|\Omega|} \int_{\Omega} h\varphi_2.$$
(A.12)

Dividing the above equation by $\overline{\varphi}$ and integrating from 0 to T, we deduce from (3.7) that

$$0 = \hat{\bar{h}} + \mu_1 + \frac{1}{d} \widehat{h \Gamma_h} + O\left(\frac{1}{d^2}\right),$$

Multiplying the equation for Γ_h by Γ_h and integrating over Ω , we find that $\overline{h\Gamma_h} = \overline{|\nabla \Gamma_h|^2}$. Hence

$$\mu_1 = -\hat{\bar{h}} + \frac{1}{d} \widehat{|\nabla \Gamma_h|^2} + + O\left(\frac{1}{d^2}\right).$$

Plugging this back into (A.12), we see that

$$\overline{\varphi}_t = \overline{\varphi} \left[(\overline{h} - \hat{\overline{h}}) + \frac{1}{d} \left(|\overline{\nabla \Gamma_h}|^2 - \widehat{|\nabla \Gamma_h|^2} \right) \right] + O\left(\frac{1}{d^2}\right).$$

Therefore, using the variation of constants formula, we deduce the asymptotic expression for $\overline{\varphi}$. Similarly, we can deduce the asymptotic expression for $\overline{\psi}$.

Finally, we prove Lemmas 4.1, 4.2 and 4.7.

Proof of Lemma 4.1. First of all, for any $\delta > 0$, we can approximate f by $\tilde{f} \in C_T^{\infty}(\bar{\Omega} \times \mathbb{R})$ such that

$$\|\tilde{f} - f\|_{C(\bar{\Omega} \times [0,T])} < \delta/2.$$

Hence, it suffices to prove the lemma assuming that $f \in C^{\infty}_T(\bar{\Omega} \times \mathbb{R})$.

For each $x \in \Omega$, let $d(x) := \operatorname{dist}(x, \partial \Omega)$ and $\Omega_{\epsilon} := \{x \in \Omega \mid d(x) > \epsilon\}$. Since $\partial \Omega$ is smooth, there exists some $\epsilon_0 > 0$ small such that for each $\epsilon < \epsilon_0$ and any $x \in \partial \Omega_{\epsilon}$, there exists a unique nearest boundary point $y_x \in \partial \Omega$ such that $|x - y_x| = d(x)$. Moreover, the points x and y_x are related by

$$x = y_x - \nu(y_x)d(x),$$

where $v(y_x)$ is the unit outer normal to $\partial\Omega$ at y_x .

Now for $\epsilon < \epsilon_0/3$, define

$$\tilde{f}_{\epsilon}(x,\cdot) := \begin{cases} 0 & \text{in } \bar{\Omega}_{3\epsilon}, \\ f(y_x,\cdot) & \text{in } \bar{\Omega} \setminus \Omega_{3\epsilon}. \end{cases}$$

Then $\tilde{f}_{\epsilon}(\cdot,\cdot) \in C_T^{\infty}((\bar{\Omega} \setminus \Omega_{3\epsilon}) \times \mathbb{R})$ with $\partial_{\nu} \tilde{f}_{\epsilon} = 0$ on $\partial \Omega \times \mathbb{R}$. Moreover,

$$\|\tilde{f}_{\epsilon} - f\|_{C((\bar{\Omega} \setminus \Omega_{3\epsilon}) \times [0,T])} \le 3\epsilon \|f\|_{C^{1}((\bar{\Omega} \setminus \Omega_{3\epsilon}) \times [0,T])}.$$

Recall that $\eta \in C^{\infty}(\mathbb{R})$ is the standard mollifier defined at the beginning of Section 6. For each $\epsilon > 0$, set $\eta_{\epsilon}(x) := \eta(|x|/\epsilon)/\epsilon^N$. Let $\zeta := \chi_{\Omega_{3\epsilon/2}} * \eta_{\epsilon/2}$, where $\chi_{\Omega_{3\epsilon/2}}$ is the characteristic function of the set $\Omega_{3\epsilon/2}$. Extending ζ by setting $\zeta(x) = 0$ in $\bar{\Omega} \setminus \Omega_{\epsilon/2}$, it is easy to see that $\zeta \in C^{\infty}(\bar{\Omega})$ and that $\zeta \equiv 1$ in $\Omega_{2\epsilon}$ and $\zeta \equiv 0$ in $\Omega \setminus \bar{\Omega}_{\epsilon}$. Let $f_{\epsilon} = \zeta f + (1-\zeta)\tilde{f}_{\epsilon}$. Then it is easy to verify that $f_{\epsilon} \in C^{\infty}(\bar{\Omega} \times \mathbb{R})$ is T-periodic in t with $\partial_{\nu}f_{\epsilon} = 0$ on $\partial\Omega \times \mathbb{R}$ and

$$||f_{\epsilon} - f||_{C(\bar{\Omega} \times [0,T])} < \delta$$

for all ϵ sufficiently small.

Proof of Lemma 4.2. Since $\hat{h}_0 < 0$ on $\bar{\Omega}$, $\beta := -\max_{x \in \bar{\Omega}} \hat{h}_0(x) > 0$. For all d sufficiently small, we have

$$h_d < h_0 + \beta/2$$
 on $\bar{\Omega} \times [0, T]$.

Hence, it follows from [20, Lemma 15.5] that $\mu_1(d, h_d) > \mu_1(d, h_0 + \beta/2)$. By [23, Lemma 2.4],

$$\lim_{d \to 0} \mu_1(d, h_0 + \beta/2) = -\max_{x \in \bar{\Omega}} (\hat{h}_0(x) + \beta/2) = \beta/2 > 0.$$

Therefore, $\mu_1(d, h_d) > 0$ and hence by [33, Proposition 4.4.8], for all d sufficiently small equation (4.1) has a unique T-periodic strong solution u_d in the sense of [33, Definition 4.4.1].

Since $\hat{h}_0 < 0$ on $\bar{\Omega}$, we can show that for each $x \in \bar{\Omega}$, there is a unique T-periodic solution $u_0(x,\cdot)$ of the ODE (4.2). Indeed, by direct calculation, we see that

$$u_0(x,t) = e^{\int_0^t h_0(x,s) ds} \left[\frac{\int_0^T e^{-\int_0^\tau h_0(x,s) ds} f_0(x,\tau) d\tau}{e^{-\int_0^T h_0(x,s) ds} - 1} + \int_0^t e^{-\int_0^\tau h_0(x,s) ds} f_0(x,\tau) d\tau \right]. \tag{A.13}$$

For each $\varepsilon > 0$ small, let $u_0^{\varepsilon,\pm}$ be the unique strong solution of (4.2) with f_0 replaced by $f_0 \pm 2\varepsilon$. It follows from (A.13) that

$$\lim_{\varepsilon \to 0} \|u_0^{\varepsilon, \pm} - u_0\|_{C(\bar{\Omega} \times [0, T])} = 0. \tag{A.14}$$

Therefore, there is a constant C > 0 depending only on f_0 and h_0 such that for all $\varepsilon < 1$,

$$\|u_0^{\varepsilon,\pm}\|_{C(\bar{\Omega}\times[0,T])} \leq C.$$

By Lemma 4.1, for each $\varepsilon>0$ small, there exists $\tilde{u}_0^{\varepsilon,\pm}\in C^{2,1}_T(\bar{\Omega}\times\mathbb{R})$ such that

$$\|\tilde{u}_0^{\varepsilon,\pm} - u_0^{\varepsilon,\pm}\|_{C^{0.1}(\bar{\Omega} \times [0,T])} < \frac{\varepsilon}{2(\|h_0\|_{C(\bar{\Omega} \times [0,T])} + 1)}, \quad \partial_{\nu} \tilde{u}_0^{\varepsilon,\pm} = 0 \text{ on } \partial\Omega \times \mathbb{R}.$$
(A.15)

Moreover, there exists $d_{\varepsilon} > 0$ such that

$$\|f_d - f_0\|_{C(\bar{\Omega} \times [0,T])} \le \frac{\varepsilon}{2}$$
 and $\|h_d - h_0\|_{C(\bar{\Omega} \times [0,T])} \le \frac{\varepsilon}{2C}$ $\forall d < d_{\varepsilon}$.

Then by direct computation, we have

$$\begin{split} &\partial_t \tilde{u}_0^{\varepsilon,+} - d\Delta \tilde{u}_0^{\varepsilon,+} - h_d \tilde{u}_0^{\varepsilon,+} - f_d \\ &= (\partial_t \tilde{u}_0^{\varepsilon,+} - \partial_t u_0^{\varepsilon,+}) - d\Delta \tilde{u}_0^{\varepsilon,+} + u_0^{\varepsilon,+} (h_0 - h_d) + h_d (u_0^{\varepsilon,+} - \tilde{u}_0^{\varepsilon,+}) + (f_0 - f_d) + 2\varepsilon \\ &\geq -\varepsilon/2 - d\Delta \tilde{u}_0^{\varepsilon,+} - \varepsilon/2 - \varepsilon/2 + 2\varepsilon \\ &= \varepsilon/2 - d\Delta \tilde{u}_0^{\varepsilon,+}. \end{split}$$

Similarly, we can show that

$$\partial_t \tilde{u}_0^{\varepsilon,-} - d\Delta \tilde{u}_0^{\varepsilon,-} - h_d \tilde{u}_0^{\varepsilon,-} - f_d \le -\varepsilon/2 - d\Delta \tilde{u}_0^{\varepsilon,-}.$$

Therefore, by choosing $d_{\epsilon} > 0$ smaller if necessary, we see that for all $d < d_{\epsilon}$,

$$\partial_t \tilde{u}_0^{\varepsilon,-} - d\Delta \tilde{u}_0^{\varepsilon,-} - h_d \tilde{u}_0^{\varepsilon,-} - f_d < 0 < \partial_t \tilde{u}_0^{\varepsilon,+} - d\Delta \tilde{u}_0^{\varepsilon,+} - h_d \tilde{u}_0^{\varepsilon,+} - f_d.$$

Consequently, by the comparison principle for periodic-parabolic equations, we obtain

$$\tilde{u}_0^{\varepsilon,-} < u_d < \tilde{u}_0^{\varepsilon,+} \quad \forall d < d_{\epsilon}.$$

Hence, letting $d \to 0$, we see that

$$\liminf_{d\to 0} u_d \ge \tilde{u}_0^{\varepsilon,-} \quad \text{and} \quad \limsup_{d\to 0} u_d \le \tilde{u}_0^{\varepsilon,+}.$$

Finally, letting $\epsilon \to 0$, we see from (A.14) and (A.15) that

$$||u_d - u_0||_{C^{0,1}(\bar{\Omega} \times [0,T])} \to 0 \text{ as } d \to 0.$$

This finishes the proof of the lemma.

Proof of Lemma 4.7. By Lemma 4.1, for any $\epsilon > 0$, there exists $m_{\epsilon} \in C_T^{2,1}(\bar{\Omega} \times \mathbb{R})$ with $\partial_{\nu} m_{\epsilon} = 0$ on $\partial \Omega \times \mathbb{R}$ such that

$$||m_{\epsilon}-m||_{C^{0,1}(\bar{\Omega}\times\mathbb{R})}<\epsilon/2.$$

Define $m_{\epsilon}^{\pm} = m_{\epsilon} \pm \epsilon$. Then

$$m_{\epsilon}^{-} < m < m_{\epsilon}^{+}, \quad \epsilon/2 < \|m_{\epsilon}^{\pm} - m\|_{L^{\infty}(\bar{\Omega} \times \mathbb{R})} < 3\epsilon/2, \quad \|m_{\epsilon,t}^{\pm} - m_{t}\|_{L^{\infty}(\bar{\Omega} \times \mathbb{R})} < \epsilon/2.$$
(A.16)

Let $\theta_d^{\epsilon,\pm}$ be the unique positive T-periodic solution to

$$\begin{cases} u_t - d\Delta u = u(m_{\epsilon}^{\pm} - u) & \text{in } \Omega \times \mathbb{R}, \\ \partial_{\nu} u = 0 & \text{on } \partial\Omega \times \mathbb{R}, \\ u \text{ is } T\text{-periodic in } t. \end{cases}$$

Then it is easy to check that $\theta_d^{\epsilon,\pm}$ is a pair of sub- and supersolutions to (1.2) and that $0 < \theta_d^{\epsilon,-} < \theta_d^{\epsilon,+}$ for all ϵ sufficiently small. Therefore, by the sub- and supersolution method and uniqueness of a positive periodic solution to (1.2), we must have

$$\theta_d^{\epsilon,-} < \theta_d < \theta_d^{\epsilon,+}. \tag{A.17}$$

On the other hand, by Lemma 4.6 we have

$$\|\theta_d^{\epsilon,\pm} - p^{\epsilon,\pm}\|_{C^{0,1}(\Omega \times [0,T])} \to 0 \quad \text{as } d \to 0, \tag{A.18}$$

where $p^{\epsilon,\pm}$ is the unique positive solution to the ODE

$$p_t^{\epsilon,\pm} = p^{\epsilon,\pm} (m_{\epsilon}^{\pm} - p^{\epsilon,\pm}),$$

and it follows from (A.16) that

$$\|p^{\epsilon,\pm} - p\|_{C^{0,1}(\Omega \times [0,T])} \to 0 \quad \text{as } \epsilon \to 0.$$
 (A.19)

Therefore, letting $d \to 0$ in (A.17), we deduce from (A.18) that

$$\liminf_{d\to 0} \theta_d \ge p^{\epsilon,-} \quad \text{and} \quad \limsup_{d\to 0} \theta_d \le p^{\epsilon,+}.$$

Since $\epsilon > 0$ is arbitrary, letting $\epsilon \to 0$ we see from (A.19) that

$$\|\theta_d - p\|_{C(\bar{\Omega} \times [0,T])} \to 0 \quad \text{as } d \to 0.$$

By similar arguments to the proof of Lemma 4.6, we can show that

$$\|\theta_{d,t} - p_t\|_{C(\bar{\Omega} \times [0,T])} \to 0 \quad \text{as } d \to 0.$$

This finishes the proof of the lemma.

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