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Yuan Lou
Ohio State University, lou@math.ohio-state.edu

Daniel Munther
Cleveland State University, D.MUNTHER@csuohio.edu

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DYNAMICS OF A THREE SPECIES COMPETITION MODEL

Yuan Lou

Daniel Munther

Abstract. We investigate the dynamics of a three species competition model, in which all species have the same population dynamics but distinct dispersal strategies. Gejji et al. [15] introduced a general dispersal strategy for two species, termed as an ideal free pair in this paper, which can result in the ideal free distributions of two competing species at equilibrium. We show that if one of the three species adopts a dispersal strategy which produces the ideal free distribution, then none of the other two species can persist if they do not form an ideal free pair. We also show that if two species form an ideal free pair, then the third species in general can not invade. When none of the three species is adopting a dispersal strategy which can produce the ideal free distribution, we find some class of resource functions such that three species competing for the same resource can be ecologically permanent by using distinct dispersal strategies.

1. **Introduction.** Understanding the dynamics of interacting species has always been an important subject in population dynamics. For systems consisting of multiple competing species, of great interest are issues that concern competitive exclusion and the coexistence of species. In recent years many studies have considered the role of spatial movement of organisms on the persistence of interacting species [6, 26, 27, 30, 32]. In this article we shall address the following question of Chris Cosner [9]: in a spatially heterogeneous environment, can three competing species with the same population dynamics coexist, via different dispersal strategies? In order to give some context for Cosner's question, we provide a brief review of previous works on two competing species, starting with the work of Dockery et al. [12], in which they considered the following model for two competing species:

$$\begin{cases} u_t = \mu\Delta u + u(m-u-v) & \text{in } \Omega\times(0,\infty), \\ v_t = \nu\Delta v + v(m-u-v) & \text{in } \Omega\times(0,\infty), \\ \nabla u\cdot n = \nabla v\cdot n = 0 & \text{on } \partial\Omega\times(0,\infty). \end{cases} \tag{1.1}$$

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Here $u(x,t)$ and $v(x,t)$ account for the densities of two competing species at location x and time t, μ, ν correspond to their random diffusion rates, and $\Delta := \sum_{i=1}^{N} \frac{\partial^2}{\partial x_i^2}$ denotes the Laplace operator in the Euclidean space $\mathbb{R}^N$. The function $m(x)$ represents the intrinsic growth rate of both species at location x and is always assumed to be non-constant to reflect the spatial heterogeneity of the habitat (e.g., heterogeneous spatial distribution of resources and predation rates). The habitat Ω is a bounded domain in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$. The vector n denotes the outward unit normal vector on $\partial\Omega$, and the boundary conditions in (1.1) mean that there is no net flux of population across the boundary.

Dockery et al. [12] showed that if both species disperse by random diffusion, then the slower diffusing species will drive the faster diffusing species to extinction. In terms of the persistence theory, this result implies that in a spatially varying but temporally constant environment, two competing species with the same population dynamics but different random diffusion rates cannot coexist. Hastings [19] suggested that environmental cues can have important effect on the evolution of dispersal strategy for species. Following the work of Belgacem and Cosner [3], Cantrell et al. [7] extended model (1.1) by adding an advection term for species u as follows:

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u(m-u-v) & \text{in } \Omega \times (0,\infty), \\ v_t = \nu \Delta v + v(m-u-v) & \text{in } \Omega \times (0,\infty), \\ [\mu \nabla u - \alpha u \nabla m] \cdot n = \nabla v \cdot n = 0 & \text{on } \partial\Omega \times (0,\infty), \end{cases} \tag{1.2}$$

where $\alpha > 0$ is the advection rate of species u, which measures the tendency of the species u to move upward along the gradient of m. The following result is proved in [7]:

Theorem 1.1. [7] *Suppose that $m \in C^2(\bar{\Omega})$, $\int_\Omega m > 0$, the set of critical points of m has Lebesque measure zero, and m has at least one isolated global maximum. Then for every $\mu > 0$ and $\nu > 0$, there exists some positive constant α^* such that for $\alpha \geq \alpha^*$, system (1.2) has at least one stable positive steady state.*

Theorem 1.1 says that as long as species u has sufficiently large advection, both species can persist within the habitat. Cantrell et al. [7] suggested that such a coexistence result is possible because species u concentrates primarily on the local maxima of m, leaving enough resources in other locations for the species v to utilize. Chen and Lou [10] demonstrated that for appropriate m with a unique local maximum in $\bar{\Omega}$, species u with large advection is concentrated at this maximum as a Gaussian distribution. When m has multiple local maxima, Lam and Ni [24] and Lam [22, 23] recently completely determined the profiles of all positive steady states of (1.2). These works illustrate a general mechanism for the coexistence of two competing species with the same population dynamics but different dispersal strategies.

In another closely related direction, Cantrell et al. [8] observed that the influence of spatial resource variability on the competition of species is linked to the fact that diffusion generally produces a mismatch between population density and the quality of the environment. Is it possible to find dispersal mechanisms that can produce a perfect match of the population density with the environment? To this end, they generalized model (1.2) as

$$\begin{cases} u_t = \mu\nabla\cdot[\nabla u - u\nabla P] + u(m-u-v) & \text{in} \quad \Omega\times(0,\infty), \\ v_t = \nu\nabla\cdot[\nabla v - v\nabla Q] + v(m-u-v) & \text{in} \quad \Omega\times(0,\infty), \\ [\nabla u - u\nabla P]\cdot n = [\nabla v - v\nabla Q]\cdot n = 0 & \text{on} \quad \partial\Omega\times(0,\infty). \end{cases} \tag{1.3}$$

Here $P(x)$, $Q(x) \in C^2(\bar{\Omega})$ provide advective directions for the respective species as well as regulate their speeds in such directions. This generalization allows for the possibility that populations can "match environmental quality perfectly". In particular, consider the single species equation for u in (1.3) (i.e. set $v = 0$), if $P = \ln m$, then $u^* = m$ is always a positive steady state. Note that the net flux for species u satisfies $\nabla u^* - u^*\nabla(\ln m) = 0$ in Ω and the fitness of species u is equilibrated throughout Ω: $m/u^* \equiv 1$. A population exhibiting such a spatial distribution is said to have an ideal free distribution [13]. That is, the density of species u at any location $x \in \Omega$ is proportional to the habitat quality $m(x)$. In this context, we shall refer $P = \ln m$ as an ideal free dispersal strategy. Furthermore, Cantrell et al. [8] demonstrated that selection favors this ideal free dispersal strategy as it can beat any other "nearby" strategy. In [8] they conjectured that the ideal free dispersal strategy should be a global evolutionary stable strategy. Averill et al. [1] recently proved this conjecture in the following result.

Theorem 1.2. [1] *Suppose that m is a positive, non-constant function and $m \in C^2(\bar{\Omega})$. If $P = \ln m$ and $Q - \ln m$ is non-constant, then $(m, 0)$ is a globally asymptotically stable steady state of (1.3) among initial data that are nonnegative and not identically zero.*

Theorem 1.2 says that if species u plays the ideal free strategy and species v does not play an ideal free dispersal strategy, then species u always drives v to extinction. This means that if one of $P - \ln m$ and $Q - \ln m$ is a constant function, then we cannot expect the coexistence of these two species. Is coexistence possible if neither $P - \ln m$ nor $Q - \ln m$ is constant? To address this question, we consider the case that $P = \ln m + \alpha R$ and $Q = \ln m + \beta R$, where $R(x) \in C^2(\bar{\Omega})$ and $\alpha, \beta \in \mathbb{R}$. Note that $\alpha = 0$ and $\beta = 0$ correspond to ideal free dispersal strategies for species u and v, respectively. With such assumptions on P and Q, Cantrell et al. [8] showed that as long as $\alpha\beta < 0$, coexistence is always possible provided that $\mu = \nu$, Ω is an interval and $R_x \neq 0$ in Ω. Recently Averill et al. [1] generalized this result of Cantrell et al. as follows:

Theorem 1.3. [1] *Suppose that $P(x) = \ln m + \alpha R$, $Q(x) = \ln m + \beta R$, and $R \in C^2(\bar{\Omega})$ is non-constant. If $\alpha\beta < 0$, then system (1.3) has at least one stable positive steady state.*

Note that in Theorem 1.3 neither species plays the ideal free dispersal strategy because $\alpha \neq 0$ and $\beta \neq 0$. The spirit of Theorem 1.3 is the same as that of Theorem 1.1. Consider Fig. 1. We call species v in Fig. 1 a specialist as it pursues resources near the maxima of the resource function. In contrast, we call species u in Fig. 1 a generalist since it also makes use of resources away from such maxima. Theorem 1.3 demonstrates that generalist and specialist can persist together.

Can two generalists or two specialists coexist? If both species act as generalists or specialists, when the resource function is monotone, the following result of Cantrell et al. [8] suggests that they can not coexist. Let $(u^*, 0)$ and $(0, v^*)$ denote the two semi-trivial steady states of system (1.3).

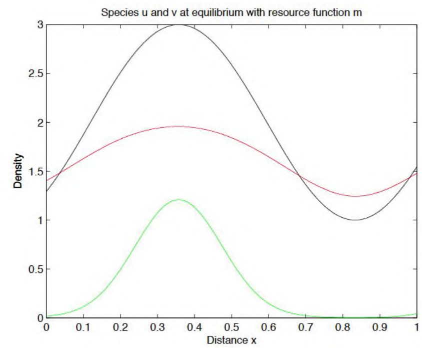

FIGURE 1. Illustration of Theorem 1.3: $R = \ln m$, Graphs of $m = \sin(2.1\pi x - \pi/4) + 2$ (black) and both species at equilibrium: u (red), v (green), $\mu = \nu = 1$, $\alpha = -0.5$, $\beta = 4$.

Theorem 1.4. [8] *Suppose that $\mu = \nu$, $P(x) = \ln m + \alpha R$, $Q(x) = \ln m + \beta R$, $\Omega = (0,1)$, and $R_x \neq 0$ in $[0,1]$. If $\alpha < \beta < 0$ or $0 < \beta < \alpha$, then $(u^*, 0)$ is unstable and $(0, v^*)$ is stable. Moreover, given any $\eta > 0$, there exists $\kappa > 0$ such that if either (i) $\alpha, \beta \in [-\eta, 0]$ and $0 < \beta - \alpha < \kappa$ or (ii) $\alpha, \beta \in [0, \eta]$ and $-\kappa < \beta - \alpha < 0$, then $(0, v^*)$ is globally asymptotically stable.*

Theorem 1.4 as well as results in [15] (Theorems 4, 7, 8 and numerical results there) indicate that when species use similar strategies (i.e. α and β are close to each other), system (1.3) generally exhibits competitive exclusion. Surprisingly, Theorem 1.4 fails for some non-monotone function R. For any function $m > 0$ in $\bar{\Omega}$, we place the following condition on R:

(A1) There exists some $x_0 \in \bar{\Omega}$ such that x_0 is local maximum of $R(x)$ and $R(x_0) < \int_\Omega m^2 R / \int_\Omega m^2$.

Since $\int_\Omega m^2 R / \int_\Omega m^2 \leq \max_{\bar{\Omega}} R$, we see that x_0 in assumption (A1) can not be a global maximum of R. This implies that any function R satisfying (A1) has at least two local maxima.

Theorem 1.5. [1] *Suppose that R satisfies assumption (A1) and all critical points of R are non-degenerate. Assume $P(x) = \ln m + \alpha R$ and $Q(x) = \ln m + \beta R$. Then there exists some $\alpha_0 > 0$ such that for every $\alpha \in (0, \alpha_0)$, we can find some $\mu_0 > 0$ such that if $\mu > \mu_0$, then given any $\nu > 0$, both $(u^*, 0)$ and $(0, v^*)$ are unstable for sufficiently large β and system (1.3) has at least one stable positive steady state.*

Theorem 1.5 demonstrates that for this new range of α and β both species act as specialists and they both can persist. While this seems to contradict the principle of competitive exclusion, as both species tend to purse locally the most favorable resources, Averill et al. [1] proposed that "if resource functions have two or more local maxima, the resident species at equilibrium may undermatch its resource at some local maximum of the resource, which makes it vulnerable to invasion by other species near such local maxima." Numerical simulations in [15] have indicated that this in effect leads to the species with the larger advection concentrating at some local (but not the global) maximum while the species with less advection concentrates at the global maximum. Biologically, this can be regarded as niche differentiation or niche separation as each species carves out a niche near different maximum of the resource. It seems a bit mysterious that it is the species with less advection, not the one with the larger advection, which concentrates at the global maximum of m.

To summarize the parameter ranges of α and β for the coexistence of two species, we see two possibilities:

1. for any resource $R \in C^2(\bar{\Omega})$, when $\alpha\beta < 0$ (generalist vs. specialist)
2. for R satisfying (A1), with α positive small and β sufficiently large (specialist vs. specialist).

It is an open problem whether two generalists can coexist with each other.

2. **Main results.** We now move into the three species realm. Can we establish results for three competing species similar to those for two species? For example, can two specialists and one generalist persist? If one of the species adopting ideal free dispersal strategy while other species do not, do we expect to see competitive exclusion? To address these questions, one serious mathematical difficulty immediately emerges. It is well known that systems of three competing species, unlike the two species competition model, are not monotone dynamical systems. To overcome this difficulty, we rely on two different methods, namely, the Lyapunov functional method (for competition exclusion) and "practical persistence" (for permanence) as described in [5].

We consider the following three species model:

$$\begin{cases} u_t = \mu\nabla\cdot[\nabla u - u\nabla P] + u(m-u-v-w) & \text{in} \quad \Omega\times(0,\infty),\\ v_t = \nu\nabla\cdot[\nabla v - v\nabla Q] + v(m-u-v-w) & \text{in} \quad \Omega\times(0,\infty),\\ w_t = \gamma\nabla\cdot[\nabla w - w\nabla L] + w(m-u-v-w) & \text{in} \quad \Omega\times(0,\infty),\\ [\nabla u - u\nabla P]\cdot n = [\nabla v - v\nabla Q]\cdot n = [\nabla w - w\nabla L]\cdot n = 0 \text{ on } \partial\Omega\times(0,\infty), \end{cases} \tag{2.1}$$

where species w has diffusion rate $\gamma > 0$, and $L(x) \in C^2(\bar{\Omega})$.

First, we aim to generalize Theorem 1.2 to (2.1). In view of Theorem 1.2, it is tempting to propose the following:

Conjecture. If $P - \ln m$ is constant, $Q - \ln m$ is non-constant, and $L - \ln m$ is non-constant, the steady state $(m, 0, 0)$ of system (2.1) is globally asymptotically stable for initial data that are non-negative and not identically zero.

It turns out that this conjecture is false. To see this, assume that $P = \ln m$. Let r be any constant in $(0, 1)$ and let Q be any function satisfying $(1-r)m > e^Q$, and $Q - \ln m$ is non-constant in $\bar{\Omega}$. Set $L = \ln[(1-r)m - e^Q]$, i.e., $(1-r)m = e^Q + e^L$ in Ω. Then $(u, v, w) = (rm, e^Q, e^L)$ is always a positive steady state of (2.1). In particular, the steady state $(m, 0, 0)$ of system (2.1) cannot be globally stable. This example implies that the conjecture needs to be modified. In this connection, we first define an *ideal free pair* for species v and w as follows:

Definition 2.1. We say that Q and L form an ideal free pair if there exist non-negative constants τ and η such that $\tau e^{Q(x)} + \eta e^{L(x)} = m(x)$ in Ω.

Note that if Q and L form an ideal free pair, then $(u, v, w) = (0, \tau e^{Q(x)}, \eta e^{L(x)})$ is a non-negative and non-trivial steady state of (2.1) such that $m-u-v-w \equiv 0$ in Ω. Furthermore, the net fluxes for both species v and w at this equilibrium are equal to zero. In other words, a consequence of an ideal free pair for two competing species is that the spatial distributions of both species at equilibrium are ideal free; See [15]. If one of the two coefficients τ and η is equal to zero, say $\tau = 0$, then $L - \ln m$

is equal to some constant. Hence, an ideal free pair is a natural generalization of the ideal free distribution from a single species to two species.

We now generalize Theorem 1.2 to system (2.1).

Theorem 2.2. *Suppose that m is positive in $\bar{\Omega}$ and non-constant, $P - \ln m$ is constant, and Q and L do not form an ideal free pair. Then $u(x,t) \to m(x)$, $v(x,t) \to 0$ and $w(x,t) \to 0$ in $L^\infty(\Omega)$ as $t \to \infty$.*

Theorem 2.2 says that the species playing the ideal free dispersal strategy (i.e., $P = \ln m$ up to a constant) will be the sole winner as long as the other two species do not form an ideal free pair. Continuing along this line of thought, we ask: suppose that two species adopt an ideal free pair dispersal strategy, can a third species invade? The answer in general is no, as shown by the following result.

Theorem 2.3. *Suppose that m is positive and non-constant, and P and Q form an ideal free pair such that $\tau e^{P(x)} + \eta e^{Q(x)} = m(x)$ in Ω for some positive constants τ, η. If neither P and L nor Q and L form an ideal free pair, then $(u,v,w) \to (\tau e^{P(x)}, \eta e^{Q(x)}, 0)$ in $L^\infty(\Omega)$ as $t \to \infty$.*

Biologically, Theorem 2.3 implies that species w will be driven to extinction by species u and v.

Summarizing these results for three species, we see that under the hypotheses of Theorems 2.2 and 2.3, three species cannot coexist. For two species we see that one generalist and one specialist can always coexist, and for some non-monotone resource functions, two specialists can also coexist. Is it possible for two specialists and one generalist to coexist? Interestingly, we can show that this is possible. To this end, we consider the following three species model:

$$
\begin{cases}
u_t = \mu \nabla \cdot [\nabla u - \alpha u \nabla \ln m] + u(m - u - v - w) \quad \text{in} \quad \Omega \times (0,\infty), \\
v_t = \nu \nabla \cdot [\nabla v - \beta v \nabla \ln m] + v(m - u - v - w) \quad \text{in} \quad \Omega \times (0,\infty), \\
w_t = \gamma \Delta w + w(m - u - v - w) \quad \text{in} \quad \Omega \times (0,\infty), \\
[\nabla u - \alpha u \nabla \ln m] \cdot n = [\nabla v - \beta v \nabla \ln m] \cdot n = \nabla w \cdot n = 0 \text{ on } \partial\Omega \times (0,\infty).
\end{cases}
\tag{2.2}
$$

Here we only study the case that the third competitor w moves via random diffusion. For species u and v, we assume that $R = \ln m$, so that $P = \ln m + \alpha R$ and $Q = \ln m + \beta R$ become $P = (1+\alpha)\ln m$ and $Q = (1+\beta)\ln m$, respectively. Replacing $1+\alpha$ and $1+\beta$ with α and β, respectively, we obtain the advective strategies, $P = \alpha \ln m$ and $Q = \beta \ln m$.

As R is now a function of m, our goal is to find resource functions m and movement parameters $(\mu, \alpha, \nu, \beta, \gamma)$ such that the permanence of three species is possible. In [6], Cantrell and Cosner describe permanence as "a *qualitative* criterion for addressing the qualitative issue of whether a model for interacting biological species predicts the coexistence of all the species in question." Practically, they say that "permanence in a model system for the densities of a collection of interacting species means the system possesses both an asymptotic 'ceiling' and a positive asymptotic 'floor' on the densities of all the species in question, the 'heights' of which are independent of the initial state of the system so long as each component is positive" [6]. Working from such a description, we utilize the following definition of ecological permanence as presented in [6].

Definition 2.4. The system (2.2) is ecologically permanent, if there exist numbers $K, k > 0$ with $k < K$ such that if $(u(x,t), v(x,t), w(x,t))$ is a solution to (2.2) with nonnegative and not identically zero initial data, then there is a $T_0 > 0$ which depends only on the initial condition such that $k \le u(x,t) \le K$, $k \le v(x,t) \le K$, and $k \le w(x,t) \le K$ for all $x \in \Omega$ and all $t \ge T_0$.

To establish the permanence of system (2.2), we rely on the following crucial assumption on m:

(A2) There exists some $x_0 \in \bar{\Omega}$ such that x_0 is local maximum of $m(x)$ and

$$\ln \frac{\int_\Omega m^2}{\int_\Omega m} < \ln m(x_0) < \frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}. \tag{2.3}$$

We shall give some intuitive interpretation of (2.3) after the statement of the following result on the permanence of three competing species:

Theorem 2.5. *Suppose that $m > 0$, $m \in C^2(\bar{\Omega})$, all critical points of m are non-degenerate, and it satisfies* (A2). *There exists some sufficiently large constant $\bar{\mu}$ such that for any $\mu > \bar{\mu}$, there exists some constant $\bar{\alpha} > 1$ and close to 1 such that for every $1 < \alpha < \bar{\alpha}$ and $\nu, \gamma > 0$, there exists some sufficiently large constant $\bar{\beta}$ such that if $\beta > \bar{\beta}$, system* (2.2) *is ecologically permanent. Furthermore, system* (2.2) *has at least one positive steady state.*

From Theorem 1.3 we see that if $\alpha > 1$, system (2.2) always has a steady state of the form $(u, 0, w)$, where u and w are positive in $\bar{\Omega}$. In order for the species v to invade when rare, since species v has a strong tendency to concentrate at the local maxima of m, it is crucial that the growth rate of v, given by $m - u - w$, is strictly positive at some local maximum of m. If the inequalities in (2.3) are violated at each local maximum of m, it might cause $m - u - w$ to be negative at each local maximum of m and thus prevent the species v to invade when rare. Biologically, species u and v both have an established niche as u concentrates near the global maximum of m and v concentrates near some local maximum of m. Species w, on the other hand, has a more evenly spread distribution. In short, we may say that u pursues the "best" resource, v pursues the "second best" resource, and w goes after the "rest" of the resource (see Figure 2).

The rest of the paper is organized as follows: In Sect. 3 we establish Theorems 2.2 and 2.3. Sections 4-6 are devoted to the proofs of the uniform lower bounds of three species, respectively, among which the lower bound of species v is the most technical and is thus postponed to Sect. 6. The proof of Theorem 2.5 will be completed in Sect. 7.

3. **Competitive exclusion.** We first briefly discuss the well-posedness of the reaction-diffusion-advection model (2.1). We rewrite (2.1) as

$$\begin{cases} \tilde{u}_t = \mu e^{-P}\nabla \cdot [e^P \nabla \tilde{u}] + \tilde{u}(m - e^P\tilde{u} - e^Q\tilde{v} - e^L\tilde{w}) & \text{in} \quad \Omega \times (0,\infty), \\ \tilde{v}_t = \nu e^{-Q}\nabla \cdot [e^Q \nabla \tilde{v}] + \tilde{v}(m - e^P\tilde{u} - e^Q\tilde{v} - e^L\tilde{w}) & \text{in} \quad \Omega \times (0,\infty), \\ \tilde{w}_t = \gamma e^{-L}\nabla \cdot [e^L \nabla \tilde{w}] + \tilde{w}(m - e^P\tilde{u} - e^Q\tilde{v} - e^L\tilde{w}) & \text{in} \quad \Omega \times (0,\infty), \\ \nabla\tilde{u}\cdot n = \nabla\tilde{v}\cdot n = \nabla\tilde{w}\cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0,\infty), \end{cases} \tag{3.1}$$

where $\tilde{u} = ue^{-P}$, $\tilde{v} = ve^{-Q}$ and $\tilde{w} = we^{-L}$ in Ω. By the maximum principle for parabolic equations [28], if the initial data $(u(x,0), v(x,0), w(x,0))$ of (2.1) are nonnegative and not identically zero, then $\tilde{u}(x,t), \tilde{v}(x,t), \tilde{w}(x,t) > 0$ for every $x \in \bar{\Omega}$ and $t > 0$. Hence, $u(x,t), v(x,t), w(x,t) > 0$ for every $x \in \bar{\Omega}$ and $t > 0$. Similarly by the maximum principle we can show *a priori* that u, v, and w are uniformly bounded

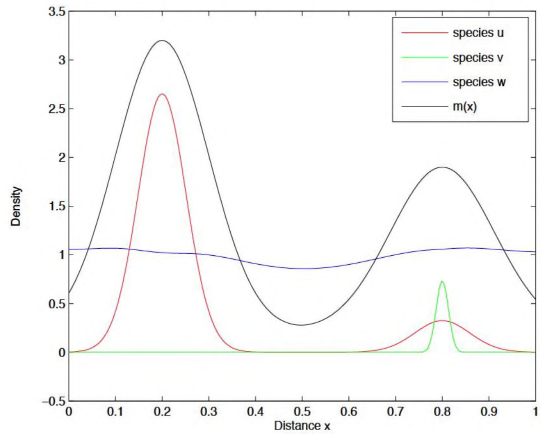

FIGURE 2. Illustration of Theorem 2.5: Graphs of $m = 3e^{-50(x-.2)^2} + 1.7e^{-40(x-.8)^2} + .2$ (black) and three species at equilibrium: u (red), v (green), w (blue), $\mu = 1000$, $\nu = 10$, $\alpha = 4$, $\beta = 80$, $\gamma = .05$.

in $L^\infty(\Omega)$ norm for all $t > 0$. By the regularity theory of parabolic partial differential equations [14], u, v, and w exist for all time and belong to $C^{2,1}(\bar{\Omega} \times (0, \infty))$. Using the theory of analytic semi-groups and parabolic partial differential equations, we can recast system (2.1) as a dynamical system $\Pi[(u^0, v^0, w^0), t]$ defined on the space $[C(\bar{\Omega})]^3$, where $\Pi[(u^0, v^0, w^0), t]$ denotes the unique solution $(u(x,t), v(x,t), w(x,t))$ to (2.1) such that $(u(x,0), v(x,0), w(x,0)) = (u^0, v^0, w^0)$ [6].

3.1. **LaSalle's invariance principle.** Let (B, ρ) be a complete metric space and $\{S(t), t \geq 0\} : B \to B$ be a dynamical system on B. For any $x \in B$, the positive trajectory of x is defined as $\gamma(x) := \{S(t)x | t \geq 0\}$. We say that x is a ω-limit point of $\gamma(x_0)$ if there exist $t_n > 0, t_n \to \infty$ as $n \to \infty$ such that $\lim_{n\to\infty} \rho(S(t_n)x_0, x) = 0$. We say that V is a Lyapunov functional on a set G in B if V is continuous in $\bar{G}$ (the closure of $\bar{G}$) and for every $x \in G$,

$$\limsup_{t \to 0} \frac{V(S(t)x) - V(x)}{t} \leq 0.$$

We denote

$$\dot{V}(x) := \limsup_{t \to 0} \frac{V(S(t)x) - V(x)}{t}.$$

We will make use of the following version of LaSalle's invariance principle for infinite dimensional systems [17].

Theorem 3.1. *Let V be a Lyapunov function in G, where G is a subset of B. Define $\mathcal{M} := \{x | x \in \bar{G}, \dot{V}(x) = 0\}$. Let $\mathcal{M}'$ be the maximal invariant subset of $\mathcal{M}$ (i.e., $\mathcal{M}'$ is the union of all invariant subsets of $\mathcal{M}$). Suppose that $x_0 \in G$, $\gamma(x_0)$ belongs to G and is contained in a compact subset of B. Then, the set of ω-limit points of x_0 is contained in $\mathcal{M}'$ and $\rho(S(t)x_0, \mathcal{M}') \to 0$ as $t \to \infty$.*

3.2. **Proof of Theorem 2.2.** Set $B := [C(\bar{\Omega})]^3$. For any $(u, v, w) \in B$ with $u > 0$ in $\bar{\Omega}$, define $E : B \to \mathbb{R}$ as

$$E(u, v, w) = \int_\Omega (u + v + w) - \int_\Omega m \ln u. \tag{3.2}$$

We first establish some *a priori* estimates for positive solutions of (2.1).

Lemma 3.2. *For any solution $(u(x,t), v(x,t), w(x,t))$ of (2.1), if $P - \ln m$ is constant, then*

$$\frac{d}{dt}E(u(\cdot,t), v(\cdot,t), w(\cdot,t)) = -\int_\Omega [m(x) - u - v - w]^2 - \mu \int_\Omega m \left|\nabla\left(\ln\frac{u}{m}\right)\right|^2 \leq 0. \tag{3.3}$$

Proof. Integrating the equations of u, v, and w in Ω and then summing up the results, we get

$$\frac{d}{dt}\int_\Omega (u + v + w) = \int_\Omega (u + v + w)(m - u - v - w).$$

Next,

$$\frac{d}{dt}\int_\Omega m \ln u = \mu \int_\Omega \frac{m}{u}\nabla \cdot [\nabla u - u\nabla(\ln m)] + \int_\Omega m(m - u - v - w).$$

Integrating by parts, we see that

$$\mu \int_\Omega \frac{m}{u}\nabla \cdot [\nabla u - u\nabla(\ln m)] = \mu \int_\Omega \frac{m}{u}\nabla \cdot \left[m\nabla\left(\frac{u}{m}\right)\right] = \mu \int_\Omega m \left|\nabla\left(\ln\frac{u}{m}\right)\right|^2. \tag{3.4}$$

Hence, we have our result. □

Next we show that u has a positive uniform lower bound in Ω.

Lemma 3.3. *There exists some positive constant C, depending only on m, Ω, N, $||u(\cdot,0)||_{L^\infty(\Omega)}$, $||v(\cdot,0)||_{L^\infty(\Omega)}$, and $||w(\cdot,0)||_{L^\infty(\Omega)}$, such that $\inf_\Omega u(x,t) \geq C$ for all $t \geq 1$.*

Proof. By Lemma 3.2, $E(u(x,t), v(x,t), w(x,t)) \leq E(u(x,0), v(x,0), w(x,0))$ for all $t \geq 0$. By the maximum principle, we know that u, v, and w are strictly positive and also uniformly bounded above for any $t \geq 0$ and $x \in \bar{\Omega}$. Hence,

$$\int_\Omega m \ln u(x,t) \geq -C_1 \tag{3.5}$$

for some constant C_1 and $t \geq 0$. Therefore for any $t \geq 0$,

$$\max_{\bar{\Omega}} u(\cdot,t) \geq e^{-\frac{C_1}{\int_\Omega m}}. \tag{3.6}$$

Set $u(x,t) = m\psi(x,t)$. Then ψ satisfies

$$\psi_t = \mu\Delta\psi + \mu\nabla(\ln m)\cdot\nabla\psi + c(x,t)\psi \quad \text{in } \Omega \times (0,\infty), \quad \nabla\psi \cdot n|_{\partial\Omega} = 0, \tag{3.7}$$

where $c(x,t) = m - (u + v + w)$ is uniformly bounded for x and $t \geq 0$. By Theorem 2.5 in [21], we have that $\inf_{x\in\Omega}\psi(x,t) \geq C_2 \sup_{x\in\Omega}\psi(x,t)$ for $t \geq 1$, where C_2 is a positive constant. Hence, $\inf_{x\in\Omega} u(x,t) \geq C_3 \sup_{x\in\Omega} u(x,t)$ for $t \geq 1$, where $C_3 = C_2 \min_{\bar{\Omega}} m / \max_{\bar{\Omega}} m$. This together with (3.6) imply that $\min_{\bar{\Omega}} u(x,t) \geq C_4$ for $t \geq 1$ and some constant $C_4 > 0$. □

For any $\chi > 0$, set $G = \{(u,v,w) \in B : u > 0 \text{ in } \bar{\Omega},\ \ E(u,v,w) \le E(m,0,0) + \chi\}$. For any $(u(x,0), v(x,0), w(x,0)) \in G$, by Lemma 3.2, $E(u(x,t), v(x,t), w(x,t)) \le E(u(x,0), v(x,0), w(x,0))$. Hence, $(u(x,t), v(x,t), w(x,t)) \in G$ for any $t > 0$. Define $S(t)(u(x,0), v(x,0), w(x,0)) := (u(x,t), v(x,t), w(x,t))$. Lemmas 3.2 and 3.3 allow us to conclude that E is a Lyapunov function on G. Next, we establish that the largest invariant subset of $\mathcal{M}$ is a singleton.

Lemma 3.4. *Suppose that $m(x)$ is positive in $\bar{\Omega}$ and non-constant, $P - \ln m$ is constant, and Q and L do not form an ideal free pair. Then the largest invariant subset $\mathcal{M}'$ consists of only $\{(m, 0, 0)\}$.*

Proof. Note that $\frac{d}{dt}E(u(\cdot,t_0), v(\cdot,t_0), w(\cdot,t_0)) = 0$ for some t_0 if and only if $\frac{u(x,t_0)}{m(x)}$ is constant and $m(x) = u(x,t_0) + v(x,t_0) + w(x,t_0)$ on Ω. Hence, $\mathcal{M}$ is given by $\mathcal{M} := \{(u,v,w) \in \bar{G} : u = \kappa m, u + v + w \equiv m\}$. Suppose that $(u(x,0), v(x,0), w(x,0)) \in \mathcal{M}'$. Then, $(u(x,t), v(x,t), w(x,t)) \in \mathcal{M}$ for every $t > 0$, i.e., $u(x,t) = \kappa(t)m(x)$ and $u(x,t) + v(x,t) + w(x,t) \equiv m(x)$. Since $u(x,t) + v(x,t) + w(x,t) \equiv m(x)$, we see that (u,v,w) satisfies

$$
\begin{cases}
u_t = \mu\nabla\cdot[\nabla u - u\nabla P] & \text{in} \quad \Omega\times(0,\infty), \\
v_t = \nu\nabla\cdot[\nabla v - v\nabla Q] & \text{in} \quad \Omega\times(0,\infty), \\
w_t = \gamma\nabla\cdot[\nabla w - w\nabla L] & \text{in} \quad \Omega\times(0,\infty), \\
[\nabla u - u\nabla P]\cdot n = [\nabla v - v\nabla Q]\cdot n = [\nabla w - w\nabla L]\cdot n = 0 & \text{on } \partial\Omega\times(0,\infty).
\end{cases}
\tag{3.8}
$$

Substituting $u(x,t) = \kappa(t)m(x)$ into the first equation of (3.8), by $P = \ln m$ we find $\kappa'(t) = 0$. Hence, κ is a constant. It is easy to see that $(v(x,t), w(x,t)) \to (c_2e^{Q(x)}, c_3e^{L(x)})$ as $t \to \infty$ for some non-negative constants c_2, c_3. Passing to the limit in $m(x) = u(x,t) + v(x,t) + w(x,t)$, we get $c_2e^{Q(x)} + c_3e^{L(x)} = (1-\kappa)m(x)$. As Q and L do not form an ideal free pair, it must be the case that $\kappa = 1$ and $c_2 = c_3 = 0$. Therefore, $u(x,t) = m(x)$. Since $m(x) = u(x,t) + v(x,t) + w(x,t)$ and v and w are non-negative, $v = w = 0$. Thus, $(u(x,t), v(x,t), w(x,t)) = (m(x), 0, 0)$. ☐

Proof of Theorem 2.2. In order to apply Theorem 3.1, we need to show that the solution trajectories of (2.1) are pre-compact in B. Given any $\delta > 0$, there exists constants $\tau \in (0,1)$ and $C^* > 0$ such that

$$\sup_{t\ge\delta} ||u_i(\cdot,t)||_{C^{2,\tau}(\bar{\Omega})} \le C^*$$

where $u_i = u, v$ and w, respectively (See [29]). Since $\chi > 0$ is arbitrary, Theorem 2.2 thus follows from Theorem 3.1. ☐

3.3. **Proof of Theorem 2.3.** For any $(u,v,w) \in B$ with $u > 0$ and $v > 0$ in $\bar{\Omega}$, define

$$E(u,v,w) = \int_\Omega (u + v + w) - \int_\Omega \tau e^P \ln u - \int_\Omega \eta e^Q \ln v. \tag{3.9}$$

For any $\chi > 0$, set

$$G = \{(u,v,w) \in B : u > 0, v > 0 \text{ in } \bar{\Omega},\ \ E(u,v,w) \le E(\tau e^P, \eta e^Q, 0) + \chi\}.$$

We first show that $\frac{d}{dt}E \le 0$ along solution trajectories.

Lemma 3.5. *For any solution $(u(x,t), v(x,t), w(x,t))$ of (2.1), if P and Q form an ideal free pair, then*

$$\begin{aligned}\frac{d}{dt}E(u(\cdot,t), v(\cdot,t), w(\cdot,t)) = &-\int_\Omega [m-u-v-w]^2 \\ &-\mu\tau\int_\Omega \frac{e^{3P}\left|\nabla\left(\frac{u}{e^P}\right)\right|^2}{u^2} - \nu\eta\int_\Omega \frac{e^{3Q}\left|\nabla\left(\frac{v}{e^Q}\right)\right|^2}{v^2} \le 0.\end{aligned} \tag{3.10}$$

Proof. Integrating the equations of u, v, and w and then summing gives

$$\frac{d}{dt}\int_\Omega (u+v+w) = \int_\Omega (u+v+w)(m-u-v-w). \tag{3.11}$$

Next, using integration by parts, we see that

$$\frac{d}{dt}\tau\int_\Omega e^P \ln u = \mu\tau\int_\Omega \frac{e^{3P}\left|\nabla\left(\frac{u}{e^P}\right)\right|^2}{u^2} + \int_\Omega \tau e^P(m-u-v-w), \tag{3.12}$$

and

$$\frac{d}{dt}\eta\int_\Omega e^Q \ln v = \nu\eta\int_\Omega \frac{e^{3Q}\left|\nabla\left(\frac{v}{e^Q}\right)\right|^2}{v^2} + \int_\Omega \eta e^Q(m-u-v-w). \tag{3.13}$$

Combining equations (3.11), (3.12), and (3.13) and using the fact that P and Q form an ideal free pair, i.e., $\tau e^P + \eta e^Q = m(x)$, we obtain the desired result. □

Next, we demonstrate that both u and v have uniform positive lower bounds.

Lemma 3.6. *There exists some positive constant D, depending only on $m(x)$, $P(x)$, $Q(x)$, Ω, N, $||u(\cdot,0)||_{L^\infty(\Omega)}$, $||v(\cdot,0)||_{L^\infty(\Omega)}$, and $||w(\cdot,0)||_{L^\infty(\Omega)}$, such that $\inf_\Omega u(x,t) \ge D$ for all $t \ge 1$.*

Proof. Lemma 3.5 implies that $E(u(x,t), v(x,t), w(x,t)) \le E(u(x,0), v(x,0), w(x,0))$ for all $t \ge 0$. By the maximum principle, we know that u, v, and w are uniformly bounded above, which means that

$$\int_\Omega \tau e^P \ln u(x,t) + \int_\Omega \eta e^Q \ln v(x,t) \ge -D_1 \tag{3.14}$$

for some constant D_1 and $t \ge 0$. Again, since v is uniformly bounded above,

$$\max_\Omega u \ge e^{-\frac{D_2}{\int_\Omega \tau e^P}}, \tag{3.15}$$

for some constant D_2. Now set $u = \psi e^P$. Then ψ satisfies

$$\psi_t = \mu\Delta\psi + \mu\nabla P\cdot\nabla\psi + c(x,t)\psi \quad \text{in } \Omega\times(0,\infty), \quad \nabla\psi\cdot n|_{\partial\Omega} = 0, \tag{3.16}$$

where $c(x,t) = e^P[m-u-v-w]$ is uniformly bounded for x and $t \ge 0$. By Theorem 2.5 in [21], we have that $\inf_{x\in\Omega}\psi(x,t) \ge D_3\sup_{x\in\Omega}\psi(x,t)$ for $t \ge 1$, where D_3 is a positive constant. Hence, $\inf_{x\in\Omega} u(x,t) \ge D_4 \sup_{x\in\Omega} u(x,t)$ for $t \ge 1$, where $D_4 = D_3 \min_{\bar\Omega} e^P / \max_{\bar\Omega} e^P$. This together with (3.15) implies that $\min_{\bar\Omega} u(x,t) \ge D_4$ for $t \ge 1$ and some constant $D_4 > 0$. □

Lemma 3.7. *There exists some positive constant D^*, depending only on $m(x)$, $P(x)$, $Q(x)$, Ω, N, $||u(\cdot,0)||_{L^\infty(\Omega)}$, $||v(\cdot,0)||_{L^\infty(\Omega)}$, and $||w(\cdot,0)||_{L^\infty(\Omega)}$, such that $\inf_\Omega v(x,t) \ge D^*$ for all $t \ge 1$.*

Proof. Similar to the proof of Lemma 3.6. □

Lemma 3.8. *Suppose that m is positive and non-constant in Ω, (P, Q) form an ideal free pair such that $\tau e^{P(x)} + \eta e^{Q(x)} = m(x)$ in Ω for some positive constants τ, η, and either $P - \ln m$ or $Q - \ln m$ is non-constant. Also suppose that (P, L) do not form an ideal free pair and (Q, L) do not form an ideal free pair. Then the largest invariant subset $\mathcal{M}'$ consists of only $\{(\tau e^P, \eta e^Q, 0)\}$.*

Proof. Note that $\frac{d}{dt}E(u(\cdot, t_0), v(\cdot, t_0), w(\cdot, t_0)) = 0$ for some t_0 if and only if $u(x, t_0)e^{-P}$ is constant, $v(x, t_0)e^{-Q}$ is constant and $m(x) = u(x, t_0)+v(x, t_0)+w(x, t_0)$ on Ω. Hence, the set $\mathcal{M}$ is given by $\mathcal{M} := \{(u, v, w) \in \bar{G} : u = \tau_1 e^P, v = \eta_1 e^Q, m \equiv u+v+w\}$. Suppose that $(u(x, 0), v(x, 0), w(x, 0)) \in \mathcal{M}'$. Then $(u(x, t), v(x, t), w(x, t)) \in \mathcal{M}$, i.e. $u(x, t) = \tau_1(t)e^{P(x)}$, $v(x, t) = \eta_1(t)e^{Q(x)}$, $m(x) = u(x, t) + v(x, t) + w(x, t)$. Substituting these equations into the equation for u we get $\tau_1'(t) = 0$, i.e., τ_1 is a constant. Similarly, we see that η_1 must also be a nonnegative constant. Because $m(x) = u(x, t) + v(x, t) + w(x, t)$ and $w \to c_3 e^L$ for some non-negative constant c_3 as $t \to \infty$, we have that $m(x) = \tau_1 e^P + \eta_1 e^Q + c_3 e^L$.

We aim to show that $\tau_1 = \tau, \eta_1 = \eta$ and $c_3 = 0$. To do this, we first suppose that $\tau_1, \eta_1, c_3 > 0$. Using the fact that $\tau e^P + \eta e^Q = m(x)$, we have

$$(\tau - \tau_1)e^P + (\eta - \eta_1)e^Q = c_3 e^L. \tag{3.17}$$

We claim that $\tau_1 \neq \tau$ and $\eta_1 \neq \eta$. First we show that $\tau_1 \neq \tau$, arguing by contradiction. If not, suppose that $\tau_1 = \tau$. Then $(\eta - \eta_1)e^Q = c_3 e^L$. Since $(\eta - \eta_1)$ must be positive as $c_3 > 0$, $e^Q = c_3/(\eta - \eta_1)e^L$. Substituting this into $\tau e^P + \eta e^Q = m(x)$, we have $\tau e^P + \eta c_3/(\eta - \eta_1)e^L = m(x)$. However, this contradicts our assumption that (P, L) do not form an ideal free pair. Thus, $\tau_1 \neq \tau$. Similarly, we can show that $\eta_1 \neq \eta$.

By (3.17), we have

$$e^P = -(\eta - \eta_1)/(\tau - \tau_1)e^Q + c_3/(\tau - \tau_1)e^L.$$

Substituting this expression into $\tau e^P + \eta e^Q = m(x)$ yields

$$m = \frac{\tau\eta_1 - \tau_1\eta}{\tau - \tau_1}e^Q + \frac{\tau c_3}{\tau - \tau_1}e^L. \tag{3.18}$$

Since (Q, L) is not an ideal free pair, we have either $\tau - \tau_1 < 0$ or $(\tau\eta_1 - \tau_1\eta)(\tau - \tau_1) < 0$. Note that $\tau\eta_1 - \tau_1\eta \neq 0$: if it is, then from (3.18) we see that (Q, L) is an ideal free pair. Therefore, there are two possibilities: (i) $\tau - \tau_1 < 0$ or (ii) $\tau\eta_1 - \tau_1\eta < 0$ and $\tau - \tau_1 > 0$.

Similarly, we have

$$m(x) = \frac{\eta\tau_1 - \eta_1\tau}{\eta - \eta_1}e^P + \frac{\eta c_3}{\eta - \eta_1}e^L. \tag{3.19}$$

Because (P, L) is not an ideal free pair, as above, we see that there are two possibilities: (iii) $\eta - \eta_1 < 0$ or (iv) $\eta\tau_1 - \eta_1\tau < 0$ and $\eta - \eta_1 > 0$.

In summary, we must rule out four cases:

Case 1: (i) and (iii) hold. $\tau - \tau_1 < 0$ and $\eta - \eta_1 < 0$. From (3.17) we see this is not possible.

Case 2: (i) and (iv) hold. $\tau - \tau_1 < 0$, $\eta\tau_1 - \eta_1\tau < 0$ and $\eta - \eta_1 > 0$. But $\tau - \tau_1 < 0$ and $\eta - \eta_1 > 0$, imply that $\eta\tau_1 > \eta_1\tau$ which is a contradiction.

Case 3: (ii) and (iii) hold. $\tau\eta_1 - \tau_1\eta < 0$, $\tau - \tau_1 > 0$ and $\eta - \eta_1 < 0$. By $\tau - \tau_1 > 0$ and $\eta - \eta_1 < 0$, we see that $\tau\eta_1 - \tau_1\eta > 0$, which is a contradiction.

Case 4: (ii) and (iv) hold. Again this is a contradiction since $\eta\tau_1 - \eta_1\tau < 0$ and $\tau\eta_1 - \tau_1\eta < 0$ cannot hold simultaneously.

Thus, we see that at least one of τ_1, η_1 and c_3 must be zero. If $\tau_1 = 0$, then because $m(x) = \tau_1 e^P + \eta_1 e^Q + c_3 e^L$ we see that (Q, L) form an ideal free pair contrary to our assumptions. If $\eta_1 = 0$, then we see that (P, L) form an ideal free pair which contradicts our assumptions. Therefore, it must be the case that $c_3 = 0$, and both $\tau_1, \eta_1 > 0$. With this in mind, (3.17) becomes $(\tau - \tau_1)e^P + (\eta - \eta_1)e^Q = 0$. Suppose that $\tau - \tau_1 \neq 0$. Then we have $e^P = (\eta_1 - \eta)/(\tau - \tau_1)e^Q$. Substituting the expression for e^P into $m(x) = \tau e^P + \eta e^Q$, gives us $m(x) = \kappa_1 e^Q$, where $\kappa_1 = \tau(\eta_1 - \eta)/(\tau - \tau_1) + \eta > 0$. Thus, $Q - \ln m$ is a constant. This fact together with $m(x) = \tau e^P + \eta e^Q$ implies that $P - \ln m$ is also constant. But this contradicts our assumptions on P and Q. Therefore, $\tau = \tau_1$. Similarly, we show that $\eta = \eta_1$. Putting our results together gives us that $u(x,t) = \tau e^P$ and $v(x,t) = \eta e^Q$. Since $m(x) = u(x,t) + v(x,t) + w(x,t)$ and $w(x,t)$ is nonnegative, $w(x,t) = 0$. Thus we have that $(u(x,t), v(x,t), w(x,t)) = (\tau e^P, \eta e^Q, 0)$. □

As in the proof of Theorem 2.2, the solution trajectories of (2.1) are pre-compact. Combining the lemmas in this subsection allows us to apply Theorem 3.1 and complete the proof of Theorem 2.3.

4. **Lower bound for species w.** The goal of this section is to establish

Theorem 4.1. *Let w be the last component of any positive solution (u, v, w) of (2.2). Suppose that the set of critical points of m has Lebesgue measure zero. Then for any μ, ν, $\gamma > 0$ and any $\alpha > 1$, there is some β_1 such that for all $\beta > \beta_1$, we can find some $\delta_1 > 0$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} w(x,t) \geq \delta_1$.*

Let u^* denote the unique positive solution of

$$\begin{cases} \mu\nabla \cdot [\nabla u - \alpha u \nabla \ln m] + u(m-u) = 0 \quad \text{in} \quad \Omega, \\ [\nabla u - \alpha u \nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{4.1}$$

The existence and uniqueness of u^* is well-known as we are assuming $m > 0$ on $\bar{\Omega}$ [6]. Clearly, when $\alpha = 1$, then $u^* = m$. The following result illustrates some interesting properties of u^* when $\alpha \neq 1$.

Lemma 4.2. *Suppose that m is strictly positive in $\bar{\Omega}$ and nonconstant. Then for every $\alpha > 1$, $\int_\Omega u^* < \int_\Omega m$; for every $\alpha \in [0,1)$, $\int_\Omega u^* > \int_\Omega m$.*

Proof. Rewrite the equation of u^* as

$$\begin{cases} \mu\nabla \cdot \left[m^\alpha \nabla \left(\dfrac{u^*}{m^\alpha}\right)\right] + u^*(m - u^*) = 0 \text{ in } \Omega, \\ \nabla \left(\dfrac{u^*}{m^\alpha}\right) \cdot n = 0 \text{ on } \partial\Omega. \end{cases} \tag{4.2}$$

Multiplying (4.2) by $\left(\frac{u^*}{m^\alpha}\right)^{1/(\alpha-1)}$ and integrating the result in Ω we have

$$\int_\Omega \left(\frac{u^*}{m}\right)^{\alpha/(\alpha-1)} (m - u^*) = \frac{\mu}{\alpha - 1} \int_\Omega m^\alpha \left(\frac{u^*}{m^\alpha}\right)^{(2-\alpha)/(\alpha-1)} \left|\nabla \left(\frac{u^*}{m^\alpha}\right)\right|^2.$$

Hence,

$$\begin{aligned}
&\int_\Omega (m-u^*)\\
&= \left[\int_\Omega (m-u^*) - \int_\Omega \left(\frac{u^*}{m}\right)^{\alpha/(\alpha-1)}(m-u^*)\right] + \int_\Omega \left(\frac{u^*}{m}\right)^{\alpha/(\alpha-1)}(m-u^*)\\
&= \int_\Omega (m-u^*)\frac{m^{\alpha/(\alpha-1)} - (u^*)^{\alpha/(\alpha-1)}}{m^{\alpha/(\alpha-1)}}\\
&\quad + \frac{\mu}{\alpha-1}\int_\Omega m^\alpha \left(\frac{u^*}{m^\alpha}\right)^{(2-\alpha)/(\alpha-1)} \left|\nabla\left(\frac{u^*}{m^\alpha}\right)\right|^2. \qquad (4.3)
\end{aligned}$$

We first claim that if $\alpha \neq 1$,

$$\int_\Omega m^\alpha \left(\frac{u^*}{m^\alpha}\right)^{(2-\alpha)/(\alpha-1)} \left|\nabla\left(\frac{u^*}{m^\alpha}\right)\right|^2 > 0. \tag{4.4}$$

It suffices to show that u^*/m^α is non-constant. We argue by contradiction. Suppose that u^*/m^α is constant, then from (4.2), we see that $u^* = m$. This implies that m/m^α is a constant. Since $\alpha \neq 1$ we must have that m is constant, which is a contradiction.

To complete the proof, we consider two cases:

Case 1. $\alpha > 1$. For this case, $(m-u^*)[m^{\alpha/(\alpha-1)} - (u^*)^{\alpha/(\alpha-1)}] \geq 0$ in Ω. This together with (4.3) and (4.4) imply that if $\alpha > 1$, then $\int_\Omega (m-u^*) > 0$.

Case 2. $\alpha < 1$. For this case, $(m-u^*)[m^{\alpha/(\alpha-1)} - (u^*)^{\alpha/(\alpha-1)}] \leq 0$ in Ω. This together with (4.3) and (4.4) imply that $\int_\Omega (m-u^*) < 0$, as long as $\alpha < 1$. □

Remark 1. For $\alpha = 0$, it was shown in [25] that $\int_\Omega u^* > \int_\Omega m$. Lemma 4.2 is a generalization of this earlier result.

Lemma 4.3. *Let $\tilde{u}$ be a positive solution of*

$$\begin{cases} u_t = \mu\nabla\cdot[\nabla u - \alpha u \nabla \ln m] + u(m-u) & in \quad \Omega\times(0,\infty),\\ [\nabla u - \alpha u\nabla \ln m]\cdot n = 0 \quad on \quad \partial\Omega\times(0,\infty). \end{cases} \tag{4.5}$$

Then $\tilde{u}(x,t) \to u^*(x)$ uniformly as $t \to \infty$, where u^* satisfies (4.1).

Proof. See [6] for details. □

Similarly, we have the following result.

Lemma 4.4. *Let $\tilde{v}$ be a positive solution of*

$$\begin{cases} v_t = \nu\nabla\cdot[\nabla v - \beta v \nabla \ln m] + v(m-v) & in \quad \Omega\times(0,\infty),\\ [\nabla v - \beta v\nabla \ln m]\cdot n = 0 \quad on \quad \partial\Omega\times(0,\infty). \end{cases} \tag{4.6}$$

Then $\tilde{v}(x,t) \to v^*(x)$ uniformly as $t \to \infty$, where v^* is the unique positive steady state of (4.6).

Using Lemmas 4.3, 4.4, and comparison of solutions, we state the following inequalities.

Corollary 1. *Let (u,v,w) be any positive solution of (2.2). Then $\limsup_{t\to\infty} u(x,t) \leq u^*$ and $\limsup_{t\to\infty} v(x,t) \leq v^*$. In particular, for each β, there is a $T := T(\beta) > 0$ such that if $t \geq T$, $u(x,t) \leq u^* + 1/\beta$ and $v(x,t) \leq v^* + 1/\beta$ on Ω.*

Proof of Theorem 4.1. From (2.2) we see that w is a super-solution to the following equation:

$$\begin{cases} \tilde{w}_t = \gamma\Delta\tilde{w} + \tilde{w}(m - u^* - v^* - 2/\beta - \tilde{w}) & \text{in} \quad \Omega \times (T(\beta), \infty), \\ \nabla\tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (T(\beta), \infty), \\ \tilde{w}(x, T(\beta)) = w(x, T(\beta)) \quad \text{in} \quad \bar{\Omega}, \end{cases} \tag{4.7}$$

where $\beta > 0$ will be chosen larger later. By Lemma 4.2, if we assume $\alpha > 1$, then $\int_\Omega u^* < \int_\Omega m$. By Theorem 3.5 in [7] we see that as $\beta \to \infty$, $\int_\Omega v^* \to 0$. Hence, we can choose $\beta > \beta_1$ such that

$$\int_\Omega (m - u^* - v^* - 2/\beta) > 0.$$

We claim $\tilde{w} \to w^*$ uniformly as $t \to \infty$, where w^* is the unique positive solution of the equation

$$\begin{cases} \gamma\Delta w^* + w^*(m - u^* - v^* - 2/\beta - w^*) = 0 \quad \text{in} \quad \Omega, \\ \nabla w^* \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{4.8}$$

Since $\int_\Omega (m - u^* - v^* - 2/\beta) > 0$, the zero steady state of (4.8) is unstable, thus w^* exists for all γ, and $\tilde{w} \to w^*$ uniformly as $t \to \infty$ [6]. By Corollary 1, w is super-solution of (4.7), that is, for all $t \geq T(\beta)$, $w(x,t) \geq \tilde{w}(x,t)$ on Ω. Finally, because $\tilde{w} \to w^*$ uniformly, we can choose $\delta_1 = \min_{\bar{\Omega}} w^*$ to conclude that for all $x \in \Omega$, $\liminf_{t\to\infty} w(x,t) \geq \delta_1 > 0$. □

5. Lower bound for species u.

The goal of this section is to establish

Theorem 5.1. *Suppose that m is positive and the set $\{x \in \bar{\Omega} : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. Let u be the first component of any positive solution (u, v, w) of (2.2). Then for any μ, ν, and $\gamma > 0$ and for any $\alpha > 1$, there exists a β_2 such that for all $\beta > \beta_2$, there is a $\delta_2 > 0$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} u(x,t) \geq \delta_2$.*

Proof. To show this, we consider the following equations of u and w (coming from (2.2)):

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - \alpha u \nabla \ln m] + u(m - u - v - w) \quad \text{in} \quad \Omega \times (0, \infty), \\ w_t = \gamma\Delta w + w(m - u - v - w) \quad \text{in} \quad \Omega \times (0, \infty), \\ [\nabla u - \alpha u \nabla \ln m] \cdot n = \nabla w \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty). \end{cases} \tag{5.1}$$

By Corollary 1, $v(x,t) \leq v^*(x) + 1/\beta$ for $t \geq T(\beta)$. Hence we see that

$$\begin{cases} u_t \geq \mu\nabla \cdot [\nabla u - \alpha u \nabla \ln m] + u(m - u - (v^* + 1/\beta) - w) \quad \text{in} \quad \Omega \times (T(\beta), \infty), \\ w_t \leq \gamma\Delta w + w(m - u - w) \quad \text{in} \quad \Omega \times (T(\beta), \infty), \\ [\nabla u - \alpha u \nabla \ln m] \cdot n = \nabla w \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (T(\beta), \infty). \end{cases} \tag{5.2}$$

Thus we are led to consider the following system:

$$\begin{cases} \bar{u}_t = \mu\nabla \cdot [\nabla \bar{u} - \alpha \bar{u} \nabla \ln m] + \bar{u}(m - \bar{u} - (v^* + 1/\beta) - \bar{w}) \quad \text{in} \quad \Omega \times (T(\beta), \infty), \\ \bar{w}_t = \gamma\Delta \bar{w} + \bar{w}(m - \bar{u} - \bar{w}) \quad \text{in} \quad \Omega \times (T(\beta), \infty), \\ [\nabla \bar{u} - \alpha \bar{u} \nabla \ln m] \cdot n = \nabla \bar{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (T(\beta), \infty), \\ \bar{u}(x, T(\beta)) = u(x, T(\beta)), \ \bar{w}(x, T(\beta)) = w(x, T(\beta)) \text{ in } \bar{\Omega}. \end{cases} \tag{5.3}$$

Put $y = (\bar{u}/m^\alpha)$. Then (5.3) becomes

$$
\begin{cases}
y_t = \mu m^{-\alpha}\nabla\cdot[m^\alpha \nabla y] + y(m - m^\alpha y - (v^* + 1/\beta) - \bar{w}) \quad \text{in} \quad \Omega\times(T(\beta),\infty),\\
\bar{w}_t = \gamma\Delta\bar{w} + \bar{w}(m - m^\alpha y - \bar{w}) \quad \text{in} \quad \Omega\times(T(\beta),\infty),\\
\nabla y\cdot n = \nabla\bar{w}\cdot n = 0 \quad \text{on} \quad \partial\Omega\times(T(\beta),\infty),\\
y(x,T(\beta)) = \bar{u}(x,T(\beta))/m^\alpha, \ \ \bar{w}(x,T(\beta)) = w(x,T(\beta)) \ \text{in} \ \bar{\Omega}.
\end{cases}
\tag{5.4}
$$

We first note that (5.4) is a strongly monotone dynamical system (by Theorem 1.20 in [6] and the strong maximum principle). We claim that the semi-trivial steady state $(0,\bar{w}^*)$ of (5.4) is unstable. Upon showing this, by the monotone dynamical system theory [20, 31], any solution with nonnegative initial data will either be attracted to $(y^*,0)$, where $y^*>0$ in Ω, or an order interval bounded above and below by positive equilibria of (5.4). In any case, there exists a $\bar{\delta}>0$ such that for all $x\in\Omega$ and $t>T_2$, where T_2 depends on the initial conditions and β, $y(x,t)\geq\bar{\delta}>0$. Since $y=\bar{u}/m^\alpha$ and $\inf_\Omega m^\alpha>0$, there exists a $\delta_2>0$ such that for all $x\in\Omega$ and $t>T_2$, $\bar{u}(x,t)\geq\delta_2$. Since $u(x,t)\geq\bar{u}(x,t)$ on Ω and for $t>T_2$, we see that $\liminf_{t\to\infty}u(x,t)\geq\delta_2>0$.

To show that $(0,\bar{w}^*)$ is unstable, we consider the following eigenvalue problem:

$$
\begin{cases}
\mu\nabla\cdot[m^\alpha\nabla\psi] + \psi m^\alpha(m-(v^*+1/\beta)-\bar{w}^*) = -\lambda_1\psi m^\alpha \quad \text{in} \quad \Omega,\\
\nabla\psi\cdot n = 0 \quad \text{on} \quad \partial\Omega,
\end{cases}
\tag{5.5}
$$

where λ_1 denotes the smallest eigenvalue of (5.5) and ψ is a positive eigenfunction associated to λ_1. Dividing (5.5) by ψ and integrating the resulting equation over Ω, we obtain

$$
\mu\int_\Omega m^\alpha\frac{|\nabla\psi|^2}{\psi^2} + \int_\Omega m^\alpha(m-\bar{w}^*) - \int_\Omega m^\alpha(v^*+1/\beta) = -\lambda_1\int_\Omega m^\alpha. \tag{5.6}
$$

Also note that $\bar{w}^*$ satisfies

$$
\begin{cases}
\gamma\Delta\bar{w}^* + \bar{w}^*(m-\bar{w}^*) = 0 \quad \text{in} \quad \Omega,\\
\nabla\bar{w}^*\cdot n = 0 \quad \text{on} \quad \partial\Omega.
\end{cases}
\tag{5.7}
$$

If we multiply (5.7) by $(\bar{w}^*)^{\alpha-1}$ and integrate the resulting equation over Ω we have that

$$
0 = \gamma(\alpha-1)\int_\Omega(\bar{w}^*)^{\alpha-2}|\nabla\bar{w}^*|^2 - \int_\Omega(\bar{w}^*)^\alpha(m-\bar{w}^*). \tag{5.8}
$$

Combining (5.6) and (5.8), we get

$$
\begin{aligned}
&\gamma(\alpha-1)\int_\Omega(\bar{w}^*)^{\alpha-2}|\nabla\bar{w}^*|^2 + \mu\int_\Omega m^\alpha\frac{|\nabla\psi|^2}{\psi^2} \\
&+ \int_\Omega[m^\alpha-(\bar{w}^*)^\alpha](m-\bar{w}^*) - \int_\Omega m^\alpha(v^*+1/\beta) = -\lambda_1\int_\Omega m^\alpha.
\end{aligned}
\tag{5.9}
$$

Since $\gamma>0$, $\alpha>1$, and $\bar{w}^*>0$ on Ω, we notice that

$$
-\lambda_1\int_\Omega m^\alpha \geq \int_\Omega[m^\alpha-(\bar{w}^*)^\alpha](m-\bar{w}^*) - \int_\Omega m^\alpha(v^*+1/\beta), \tag{5.10}
$$

where equality holds if and only if both $\bar{w}^*$ and ψ are constant functions. Now notice that $[m^\alpha-(\bar{w}^*)^\alpha](m-\bar{w}^*)\geq0$ in Ω with equality if and only if $m=\bar{w}^*$. Hence $\int_\Omega[m^\alpha-(\bar{w}^*)^\alpha](m-\bar{w}^*)=0$ if and only if $m\equiv\bar{w}^*$ in Ω. We claim that $\int_\Omega[m^\alpha-(\bar{w}^*)^\alpha](m-\bar{w}^*)>0$. To see this, suppose that $m\equiv\bar{w}^*$ in Ω. Then m must satisfy equation (5.7) and by the maximum principle, $m\equiv$ constant in Ω. This is a contradiction and thus $\int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m - \bar{w}^*) > 0$. By Theorem 3.5 in [7] we know that as $\beta \to \infty$, $\int_\Omega v^* \to 0$. Hence for large enough β,

$$-\lambda_1 \int_\Omega m^\alpha \geq \int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m - \bar{w}^*) - \int_\Omega m^\alpha (v^* + 1/\beta) \tag{5.11}$$
$$\geq \int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m - \bar{w}^*) - ||m^\alpha||_{L^\infty} \left(\int_\Omega v^* + (1/\beta)|\Omega| \right) > 0.$$

From (5.11) we have that $\lambda_1 < 0$, proving that $(0, \bar{w}^*)$ is unstable. □

6. **Lower bound for species v.** This is the most technical part of the paper. As we mentioned earlier, we work with non-monotone functions m that satisfy assumption (A2), looking for parameter values that cause species u to concentrate at the global maximum of m, species v to concentrate at the local maximum of m at x_0, and species w to pursue resources away from these maxima. However, for v to be able to concentrate at some x_0 and persist, its growth rate (2.2) near x_0 needs to be positive. That is, we need $m(x) - \tilde{u}(x) - \tilde{w}(x) > 0$ in a neighborhood of x_0, where $(\tilde{u}, 0, \tilde{w})$ is a steady state of the three species model (2.2) with $\tilde{u} > 0$ and $\tilde{w} > 0$ in Ω. So we first seek to understand the structure of the solution set $(\tilde{u}, \tilde{w})$ as we vary the advection parameter α near $\alpha = 1$.

6.1. **Structure of positive steady states for two species model.** Consider the following two species model (this is steady state problem for system (2.2) with $v = 0$ and $\alpha = 1 + \epsilon$):

$$\begin{cases} \mu \nabla \cdot [\nabla \tilde{u} - (1+\epsilon)\tilde{u} \nabla \ln m] + \tilde{u}(m - \tilde{u} - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma \Delta \tilde{w} + \tilde{w}(m - \tilde{u} - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ [\nabla \tilde{u} - (1+\epsilon)\tilde{u} \nabla \ln m] \cdot n = \nabla \tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{6.1}$$

We note that for $\alpha > 1$, there exists at least one steady state $(\tilde{u}, \tilde{w})$ of system (6.1) where both $\tilde{u}$ and $\tilde{w}$ are positive in Ω (see Theorem 1.4 in [1]). We also know that when $\alpha = 1$ that $(m, 0)$ is a solution of (6.1). Essentially, we will show that for α slightly larger than 1, system (6.1) has a unique branch of positive steady states bifurcating from $(m, 0)$ at $\alpha = 1$.

Let $u = \frac{\tilde{u}}{m^{1+\epsilon}}$. Then $(u, \tilde{w})$ satisfies

$$\begin{cases} \mu \nabla \cdot [m^{1+\epsilon} \nabla u] + m^{1+\epsilon} u (m - m^{1+\epsilon} u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma \Delta \tilde{w} + \tilde{w}(m - m^{1+\epsilon} u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \nabla u \cdot n = \nabla \tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{6.2}$$

Note that (6.2) can be written as

$$\begin{cases} \mu \Delta u + \mu \nabla \ln(m^{1+\epsilon}) \nabla u + u(m - m^{1+\epsilon} u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma \Delta \tilde{w} + \tilde{w}(m - m^{1+\epsilon} u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \nabla u \cdot n = \nabla \tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{6.3}$$

We begin by defining a map $\hat{\mathbf{F}} : (-r, r) \times C^{2,\tau}_n(\bar{\Omega}) \times C^{2,\tau}_n(\bar{\Omega}) \to C^\tau(\bar{\Omega}) \times C^\tau(\bar{\Omega})$ for some $\tau \in (0,1)$ and $r > 0$, where $C^{2,\tau}_n(\bar{\Omega}) = \{f \in C^{2,\tau}(\bar{\Omega}) : \nabla f \cdot n|_{\partial\Omega} = 0\}$, by

$$\hat{\mathbf{F}}(\epsilon, u, \tilde{w}) = \begin{pmatrix} \mu \Delta u + \mu \nabla \ln(m^{1+\epsilon}) \nabla u + u(m - m^{1+\epsilon} u - \tilde{w}) \\ \gamma \Delta \tilde{w} + \tilde{w}(m - m^{1+\epsilon} u - \tilde{w}) \end{pmatrix}$$

Now $\hat{\mathbf{F}}(\epsilon, u_\epsilon, 0) = 0$, where $(u_\epsilon, 0)$ satisfies (6.3). In particular, note that $u_0 = 1$, so $\hat{\mathbf{F}}(0,1,0) = 0$. Next define a map $\mathbf{F}$ with the same domain and target spaces as $\hat{\mathbf{F}}$ but with formula

$$\mathbf{F}(\epsilon, u, \tilde{w}) = \hat{\mathbf{F}}(\epsilon, u + u_\epsilon, \tilde{w}). \tag{6.4}$$

Then $\mathbf{F}(\epsilon, 0, 0) = 0$ for $\epsilon \in (-r, r)$ and we note that

$$\begin{aligned}&\mathbf{F}(\epsilon, u, \tilde{w})\\ &= \begin{pmatrix} \mu\Delta(u+u_\epsilon) + \mu\nabla\ln(m^{1+\epsilon})\nabla(u+u_\epsilon) + (u+u_\epsilon)[m - m^{1+\epsilon}(u+u_\epsilon) - \tilde{w}] \\ \gamma\Delta\tilde{w} + \tilde{w}[m - m^{1+\epsilon}(u+u_\epsilon) - \tilde{w}] \end{pmatrix}\end{aligned}$$

Because we want to understand the solution structure of $\mathbf{F}(\epsilon, u, \tilde{w}) = 0$ near $(0,0,0)$, we make use of the following result from the bifurcation theory.

Theorem 6.1. [11] *Suppose that $\mathbf{F}(\epsilon, 0) = 0$ for all $\epsilon \in \mathbb{R}$, dim $Ker(\mathbf{F}_y(\epsilon_0, 0)) =$ codim $Range(\mathbf{F}_y(\epsilon_0, 0)) = 1$, $\mathbf{F} \in C^2(V \times U)$, where $0 \in U$ is an open set of a Banach space and $\epsilon_0 \in V$ is an open set of $\mathbb{R}$, $Ker(\mathbf{F}_y|_{(\epsilon_0,0)}) =$ span $\{v_0\}$, and $\mathbf{F}_{y\epsilon}(\epsilon_0, 0)v_0 \notin Range(\mathbf{F}_y(\epsilon_0, 0))$. Then there is a non-trivial continuously differentiable curve through $(\epsilon_0, 0)$, $\{(\epsilon(s), x(s)) : s \in (-\delta, \delta), (\epsilon(0), x(0)) = (\epsilon_0, 0)\}$, such that $\mathbf{F}(\epsilon(s), x(s)) = 0$ for $s \in (-\delta, \delta)$, and all solutions of $\mathbf{F}(\epsilon, x) = 0$ in a neighborhood of $(\epsilon_0, 0)$ are on the trivial solution line or on the curve $(\epsilon(s), x(s))$.*

We establish several lemmas which show that $\mathbf{F}$ as defined in (6.4) satisfies the hypotheses of Theorem 6.1. Differentiating $\mathbf{F}$ with respect to $(u, \tilde{w})$ and evaluating the derivative at $(\epsilon, 0, 0)$ gives us

$$\begin{aligned}&\mathcal{L}_\epsilon\\ &= D_{(u,\tilde{w})}\mathbf{F}|_{(\epsilon,0,0)} = \begin{pmatrix} \mu\Delta + \mu\nabla\ln(m^{1+\epsilon})\nabla + m - 2m^{1+\epsilon}u_\epsilon & -u_\epsilon \\ 0 & \gamma\Delta + m - m^{1+\epsilon}u_\epsilon \end{pmatrix}.\end{aligned}$$

Recall $u_0 = 1$ and let $\mathcal{L}_\epsilon = \mathcal{L}$ when $\epsilon = 0$. Put $\mathbf{X} = C_n^{2,\tau}(\bar{\Omega}) \times C_n^{2,\tau}(\bar{\Omega})$. Given any vector $(\varphi, \psi) \in \mathbf{X}$ we have

$$\mathcal{L}\begin{pmatrix}\varphi \\ \psi\end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi + \mu\nabla\ln m\nabla\varphi - m\varphi - \psi \\ \gamma\Delta\psi \end{pmatrix}$$

Lemma 6.2. *$Ker(\mathcal{L}) =$ span $(\bar{\varphi}, 1)$, where $\bar{\varphi}$ is the unique solution of*

$$\begin{cases} \mu\Delta\bar{\varphi} + \mu\nabla\ln m\nabla\bar{\varphi} - m\bar{\varphi} - 1 = 0 & in \quad \Omega, \\ \nabla\bar{\varphi}\cdot n = 0 & on \quad \partial\Omega. \end{cases} \tag{6.5}$$

Proof. Let $(\varphi, \psi) \in \mathrm{Ker}(\mathcal{L})$. Then $\gamma\Delta\psi = 0$ in Ω with $\nabla\psi\cdot n|_{\partial\Omega} = 0$. Hence, $\psi \equiv$ constant in Ω. Note that if $\psi = 0$ in Ω, then $\varphi = 0$ as well. To see this, we multiply the equation of φ by $m\varphi$ and integrate by parts to obtain

$$\mu\int_\Omega |\nabla\varphi|^2 m + \int_\Omega m^2\varphi^2 = 0. \tag{6.6}$$

This implies that $\varphi \equiv 0$ in Ω. Hence, ψ is a non-zero constant. Normalizing ψ, substituting it into the equation for φ (from the definition of $\mathcal{L}$) and multiplying by m we have

$$\mu\nabla\cdot[m\nabla\varphi] - m^2\varphi = m \quad \text{in } \Omega, \quad \nabla\varphi\cdot n|_{\partial\Omega} = 0. \tag{6.7}$$

We claim that the operator $S : C_n^{2,\tau}(\bar{\Omega}) \to C_n^{\tau}(\bar{\Omega})$, defined by $S(\varphi) = \mu\nabla\cdot[m\nabla\varphi] - m^2\varphi$ is invertible. To prove this, we note that the principal eigenvalue λ

of S satisfies $\mu\nabla\cdot[m\nabla\phi]-m^2\phi=-\lambda\phi$ in Ω where $\nabla\phi\cdot n|_{\partial\Omega}=0$ and $\phi>0$ in Ω. Multiplying the equation of ϕ by ϕ and integrating by parts, we see that λ satisfies

$$\mu\int_\Omega|\nabla\phi|^2m+\int_\Omega m^2\phi^2=\lambda\int_\Omega\phi^2. \tag{6.8}$$

Thus we have that $\lambda>0$, indicating that S is invertible. Taking $\bar\varphi=S^{-1}(m)$ we complete the proof. □

Lemma 6.3. *Range*($\mathcal{L}$) $=\left\{(f,g)\in C^\tau(\bar\Omega)\times C^\tau(\bar\Omega):\int_\Omega g=0\right\}$ *and hence is of co-dimension 1 in* $C^\tau(\bar\Omega)\times C^\tau(\bar\Omega)$.

Proof. It is well-known that $\gamma\Delta\psi=g$ has a solution $\psi\in W^{1,2}(\Omega)$ where $\nabla\psi\cdot n|_{\partial\Omega}=0$ if and only if $\int_\Omega g=0$. By elliptic regularity and the Sobolev embedding theorem [16], we see that $\psi\in C^{2,\tau}(\Omega)$. Using a similar argument as in the proof of Lemma 6.2, namely the invertibility of S, we justify the existence of $\varphi\in C^{2,\tau}(\bar\Omega)$, such that $\mu\Delta\varphi+\mu\nabla\ln m\nabla\varphi-m\varphi-\psi=f$ in Ω with $\nabla\varphi\cdot n|_{\partial\Omega}=0$. To see that Range($\mathcal{L}$) is of co-dimension 1, we note that $(f,g)=\left(f,g-\frac{1}{|\Omega|}\int_\Omega g\right)+\left(0,\frac{1}{|\Omega|}\int_\Omega g\right)$. □

Note that by the implicit function theorem u_ϵ is a differentiable function of ϵ near 0 (see Section 3.4 in [6]). Using this fact, we can justify the computation that

$$D_\epsilon\mathcal{L}_\epsilon=\begin{pmatrix}\mu\nabla\ln m\nabla-2[m^{1+\epsilon}\ln mu_\epsilon+m^{1+\epsilon}u'_\epsilon] & -u'_\epsilon\\ 0 & -[m^{1+\epsilon}(\ln m)u_\epsilon+m^{1+\epsilon}u'_\epsilon]\end{pmatrix}$$

where $u'_\epsilon=\frac{d}{d\epsilon}(u_\epsilon)$. Evaluating at $\epsilon=0$, we have

$$D_\epsilon\mathcal{L}=\begin{pmatrix}\mu\nabla\ln m\nabla-2[m\ln m+mu'_0] & -u'_0\\ 0 & -[m\ln m+mu'_0]\end{pmatrix}.$$

Since the kernel of $\mathcal{L}$ is spanned by one vector, we want to show that $D_\epsilon\mathcal{L}(\bar\varphi,1)\notin$ Range($\mathcal{L}$). Since

$$D_\epsilon\mathcal{L}\begin{pmatrix}\bar\varphi\\1\end{pmatrix}=\begin{pmatrix}\mu\nabla\ln m\nabla\bar\varphi-2[m\ln m+mu'_0]\bar\varphi-u'_0\\ -[m\ln m+mu'_0]\end{pmatrix},$$

we want that

$$\int_\Omega(m\ln m+mu'_0)\neq 0.$$

To check this integral, we first need an expression for u'_0. Because u is a differentiable function of ϵ, we consider its first order expansion at 0, i.e., $u_\epsilon=1+\epsilon u'_0+O(\epsilon^2)$. Plugging in such an expression into system (6.3) (here $\tilde w=0$), we have that u'_0 satisfies:

$$\begin{cases}\mu\Delta u'_0+\mu\nabla\ln m\nabla u'_0-[mu'_0+m\ln m]=0 & \text{in}\quad\Omega,\\ \nabla u'_0\cdot n=0\quad\text{on}\quad\partial\Omega.\end{cases} \tag{6.9}$$

We have the following result.

Lemma 6.4. *Let u_1 denote the unique solution of*

$$\begin{cases}\mu\nabla\cdot[m\nabla u_1-\nabla m]-m^2u_1=0 & \text{in}\quad\Omega,\\ [m\nabla u_1-\nabla m]\cdot n=0 & \text{on}\quad\partial\Omega.\end{cases} \tag{6.10}$$

Suppose m is nonconstant. Then $\int_\Omega mu_1<0$.

Proof. We first show that $\int_\Omega m u_1 e^{u_1} < 0$. Notice that if we multiply (6.10) by e^{u_1}/m and integrate the resulting equation in Ω, we see that

$$\begin{aligned}\int_\Omega m u_1 e^{u_1} &= \mu \int_\Omega \nabla \cdot [m\nabla u_1 - \nabla m] \cdot \frac{e^{u_1}}{m} \\ &= -\mu \int_\Omega [m\nabla u_1 - \nabla m] \cdot \nabla \left(\frac{e^{u_1}}{m}\right) \\ &= -\mu \int_\Omega m\nabla(u_1 - \ln m) \cdot \nabla(e^{u_1 - \ln m}) \\ &= -\mu \int_\Omega e^{u_1} |\nabla(u_1 - \ln m)|^2 < 0,\end{aligned}$$

where the last inequality is strict since $u_1 - \ln m$ is nonconstant as m is nonconstant. To complete the proof of the lemma, it suffices to show that $\int_\Omega m u_1 \leq \int_\Omega m u_1 e^{u_1}$. To this end, for every $p \in \mathbb{R}$, define

$$h(p) = \int_\Omega m u_1 e^{p u_1}.$$

Since $h'(p) = \int_\Omega m u_1^2 e^{p u_1} \geq 0$, we see that $h(1) \geq h(0)$. This completes the proof. □

We notice that $u_0' = u_1 - \ln m$. Hence, Lemma 6.4 gives us that

$$\int_\Omega (m \ln m + m u_0') < 0$$

and we see that $D_\epsilon \mathcal{L}(\bar{\varphi}, 1) \notin \mathrm{Range}(\mathcal{L})$, allowing us to use Theorem 6.1. We can then parameterize u, $\tilde{w}$, and ϵ for small s by the following:

$$\begin{cases} u(s) = s\bar{\varphi} + \psi(s), \\ \tilde{w}(s) = s + \tau(s), \\ \epsilon(s) = \lambda(s), \end{cases} \tag{6.11}$$

where both ψ and τ are at least of order s^2. Recall that $\mathrm{Ker}(\mathcal{L})$ is spanned by $(\bar{\varphi}, 1)$. We claim that ϵ and s are of the same order and sign. We proceed to show this by first expanding $\epsilon(s) = \lambda(0) + s\lambda'(0) + O(s^2) = s\lambda'(0) + O(s^2)$ (here $\lambda(0) = 0$ since $\epsilon(0) = 0$). Now we substitute the expressions in (6.11) and the expansion for ϵ in terms of s, back into the equation $\mathbf{F} = 0$ and calculate the first and second order terms in s. Doing so gives us the following equation in Ω

$$\begin{aligned}&\gamma\Delta(s + \tau(s)) + (s + \tau(s))[m - \\ &(m + s\lambda'(0) m \ln m + O(s^2))(s\bar{\varphi} + 1 + s\lambda'(0) u_0' + O(s^2)) - (s + \tau(s))] = 0.\end{aligned} \tag{6.12}$$

From (6.12) we have the following equation:

$$\gamma\Delta\left(\frac{\tau(s)}{s^2}\right) - m\bar{\varphi} - m\lambda'(0) u_0' - \lambda'(0) m \ln m - 1 = O(s) \quad \text{in} \quad \Omega. \tag{6.13}$$

Thus if we integrate both sides of (6.13), letting $s \to 0$ and using the fact that $\nabla\tilde{w} \cdot n|_{\partial\Omega} = 0$, we obtain

$$\lambda'(0) = \frac{-\int_\Omega (m\bar{\varphi} + 1)}{\int_\Omega (m u_0' + m \ln m)}. \tag{6.14}$$

By Lemma 6.4 we see that the denominator of (6.14) must be negative. We claim that the numerator of (6.14) is negative as well.

Lemma 6.5. *For any* $\mu > 0$, $\int_\Omega (m\bar{\varphi} + 1) > 0$.

Proof. To see this, recall that $\bar{\varphi}$ satisfies (6.5). If we multiply (6.5) by $m\bar{\varphi}$ and integrate the result in Ω, we have

$$\mu \int_\Omega m|\nabla\bar{\varphi}|^2 + \int_\Omega m\bar{\varphi}(m\bar{\varphi}+1) = 0.$$

So, we have that

$$\begin{aligned}\int_\Omega (m\bar{\varphi}+1) &= \int_\Omega (m\bar{\varphi}+1)^2 - \int_\Omega m\bar{\varphi}(m\bar{\varphi}+1) \\ &= \int_\Omega (m\bar{\varphi}+1)^2 + \mu\int_\Omega m|\nabla\bar{\varphi}|^2 > 0,\end{aligned}$$

where strict inequality holds as $\bar{\varphi}$ is nonconstant. □

By Lemmas 6.4 and 6.5 we see that both the numerator and the denominator of (6.14) must be negative. Hence, $\lambda'(0) > 0$ and for both s and ϵ small,

$$s = \frac{\epsilon}{\lambda'(0)} + O(\epsilon^2). \tag{6.15}$$

Noticing that $\tilde{u} = m^{1+\epsilon}(u + u_\epsilon)$, we have demonstrated that we can parameterize the positive solution $(\tilde{u}, \tilde{w})$ of system (6.1) in terms of ϵ as follows:

Theorem 6.6. *Let* $(\tilde{u}, \tilde{w})$ *be a positive solution pair of system* (6.1). *Then for sufficiently small* ϵ,

$$\begin{cases} \tilde{u} = m + \epsilon m[\Lambda\bar{\varphi} + \ln m + u_0'] + O(\epsilon^2), \\ \tilde{w} = \epsilon\Lambda + O(\epsilon^2), \end{cases} \tag{6.16}$$

where $\Lambda = 1/\lambda'(0)$.

The next two results establish the fact that for α slightly larger than 1, the only positive solutions $(\tilde{u}, \tilde{w})$ of (6.1) are on the solution branch bifurcating from $(m, 0)$ as described by Theorem 6.1. This completes the global picture for positive solutions of (6.1) for α slightly larger than 1. In fact, (6.1) has no positive solutions for $\alpha \le 1$ and close to 1.

Lemma 6.7. *Consider a positive solution* $(\tilde{u}, \tilde{w})$ *to* (6.1). *Then* $\lim_{\epsilon\to 0^+}(\hat{u}, \tilde{w}) = (m, 0)$.

Proof. By elliptic regularity and the Sobolev embedding theorem, for $0 < \epsilon \ll 1$, $(\hat{u}, \tilde{w})$ is uniformly bounded in $C^{2,\tau}(\bar{\Omega})$ for some $\tau \in (0,1)$ [16]. If we let $\epsilon \to 0^+$, passing to a subsequence if necessary, then by the Ascoli-Arzelá lemma, we see that $(\tilde{u}, \tilde{w})$ converges to $(\hat{u}, \hat{w})$ in $C^2(\bar{\Omega})$, where $(\hat{u}, \hat{w})$ satisfies

$$\begin{cases} \mu\nabla\cdot[\nabla\hat{u} - \hat{u}\nabla\ln m] + \hat{u}(m - \hat{u} - \hat{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma\Delta\hat{w} + \hat{w}(m - \hat{u} - \hat{w}) = 0 \quad \text{in} \quad \Omega, \\ [\nabla\hat{u} - \hat{u}\nabla\ln m]\cdot n|_{\partial\Omega} = \nabla\hat{w}\cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.17}$$

By Theorem 2 of [1], we know that (6.17) has no strictly positive steady states, rather it has a two semi-trivial steady states $(m, 0)$ and $(0, \hat{w}^*)$. Thus $(\hat{u}, \hat{w}) = (0, 0)$, or $(0, \hat{w}^*)$, or $(m, 0)$.

Suppose that $(\hat{u}, \hat{w}) = (0, 0)$. Set $u = \tilde{u}/||\hat{u}||_\infty$. By elliptic regularity and the equation of $\tilde{u}$ we see that $u \to u_1$ in $C^2(\bar{\Omega})$ for some $u_1 \geq 0$ in Ω, which satisfies $||u_1||_\infty = 1$ and

$$\begin{cases} \mu\nabla \cdot [\nabla u_1 - u_1 \nabla \ln m] + u_1 m = 0 \quad \text{in} \quad \Omega, \\ [\nabla u_1 - u_1 \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.18}$$

Integrating both sides of equation (6.18) over Ω and using the boundary condition, we see that

$$\int_\Omega u_1 m = 0.$$

But this is a contradiction since $m > 0$ and $u_1 \geq 0$, $u_1 \not\equiv 0$ on Ω.

Now suppose $(\hat{u}, \hat{w}) = (0, \hat{w}^*)$. Again we set $u = \tilde{u}/||\tilde{u}||_\infty$ and see that by elliptic regularity and the equation of $\tilde{u}$ we see that $u \to u_1$ in $C^2(\bar{\Omega})$ for some $u_1 \geq 0$ in Ω, which satisfies $||u_1||_\infty = 1$ and

$$\begin{cases} \mu\nabla \cdot [\nabla u_1 - u_1 \nabla \ln m] + u_1(m - \hat{w}^*) = 0 \quad \text{in} \quad \Omega, \\ [\nabla u_1 - u_1 \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.19}$$

Since $u_1 \geq 0$, $u_1 \not\equiv 0$, we see 0 is the principal eigenvalue for the eigenvalue problem

$$\begin{cases} \mu\nabla \cdot [\nabla \phi - \phi \nabla \ln m] + \phi(m - \hat{w}^*) = -\lambda\phi \quad \text{in} \quad \Omega, \\ [\nabla \phi - \phi \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.20}$$

But this contradicts the result in Theorem 2 of [1] which says that the above eigenvalue problem has a negative principal eigenvalue. Hence, we must have that $(\hat{u}, \hat{w}) = (m, 0)$. □

Lemma 6.8. *There exists $\epsilon_0 > 0$ such that for all ϵ with $0 < \epsilon < \epsilon_0$, $(\tilde{u}^*, \tilde{w}^*)$ is the unique steady state of (6.1) and is linearly stable.*

Proof. Note for suitably small ϵ the uniqueness of $(\tilde{u}^*, \tilde{w}^*)$ as the steady state of (6.1) follows from Lemma 6.7 and Theorem 6.1.

Consider the following system

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - (1+\epsilon) u \nabla \ln m] + u(m - u - w) \quad \text{in} \quad \Omega, \\ w_t = \gamma \Delta w + w(m - u - w) \quad \text{in} \quad \Omega, \\ [\nabla u - (1+\epsilon) u \nabla \ln m] \cdot n = \nabla w \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{6.21}$$

Linearizing and then perturbing the above system about $(\tilde{u}^*, \tilde{w}^*)$, we put $u = \tilde{u}^* + \delta\phi e^{-\eta t} + O(\delta^2)$ and $w = \tilde{w}^* + \delta\psi e^{-\eta t} + O(\delta^2)$, substitute these expressions into (6.21), divide by $\delta e^{-\eta t}$ and let $\delta \to 0$ to obtain the following eigenvalue problem

$$\begin{cases} -\eta\phi = \mu\nabla \cdot [\nabla \phi - (1+\epsilon)\phi \nabla \ln m] - \tilde{u}^*(\phi + \psi) + \phi(m - \tilde{u}^* - \tilde{w}^*) \quad \text{in} \quad \Omega, \\ -\eta\psi = \gamma\Delta\psi + \psi(m - \tilde{u}^* - \tilde{w}^*) - \tilde{w}^*(\psi + \phi) \quad \text{in} \quad \Omega, \\ [\nabla \phi - (1+\epsilon)\phi \nabla \ln m] \cdot n|_{\partial\Omega} = \nabla\psi \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.22}$$

By Lemma 6.7, we know that when $\epsilon = 0$, $\tilde{u}^* = m$, $\tilde{w}^* = 0$, $\eta = 0$ (here 0 is the principal eigenvalue), $\phi = m\bar{\varphi}$ (where $\bar{\varphi}$ satisfies (6.5)), and $\psi = 1$, after suitable scaling. Using the implicit function theorem, we know that the principal eigenvalue η and corresponding eigenfunctions ϕ and ψ are smooth functions of ϵ (see Lemma 3.3.1 of [2]). Hence, we can write $\eta = 0 + \epsilon\eta_1 + O(\epsilon^2)$, $\phi = m\bar{\varphi} + \epsilon m\phi_1 + O(\epsilon^2)$, and $\psi = 1 + \epsilon\psi_1 + O(\epsilon^2)$, after suitable scaling. Recall that $\tilde{u}^* = m^{1+\epsilon}(u + u_\epsilon)$.

Using this and the fact that $s = \epsilon\Lambda$, where $\Lambda = 1/\lambda'(0)$ we can write $\tilde{u}^* = (m + \epsilon m \ln m)(\Lambda\epsilon\bar{\varphi} + 1 + \epsilon u_0') + O(\epsilon^2)$ and $\tilde{w}^* = \epsilon\Lambda + O(\epsilon^2)$. Substituting these expansions into the second equation of (6.22) we obtain the following equation in Ω

$$\begin{aligned} -\epsilon\eta_1 &= \gamma\Delta(1+\epsilon\psi_1) + (1+\epsilon\psi_1)[m - (\epsilon\Lambda m\bar{\varphi} + m + \epsilon m \ln m + \epsilon m u_0') - \epsilon\Lambda] \\ &\quad - \epsilon\Lambda(m\bar{\varphi} + \epsilon m\phi_1 + 1 + \epsilon\psi_1) + O(\epsilon^2), \end{aligned} \tag{6.23}$$

and $\nabla\psi_1 \cdot n|_{\partial\Omega} = 0$. Dividing both sides by ϵ and letting $\epsilon \to 0$, we see that

$$-\eta_1 = \gamma\Delta\psi_1 - 2\Lambda(m\bar{\varphi} + 1) - mu_0' - m\ln m \ \text{ in } \Omega, \quad \nabla\psi_1 \cdot n|_{\partial\Omega} = 0. \tag{6.24}$$

Thus if we integrate both sides of (6.24), using the boundary condition and the definition of Λ,

$$\eta_1 = -\frac{1}{|\Omega|}\int_\Omega (mu_0' + m\ln m) > 0. \tag{6.25}$$

Because $\eta_1 > 0$, we conclude that for sufficiently small positive ϵ, $\eta > 0$. □

6.2. **Bounds on solutions of the three species system.** Given a solution $(u(x,t), v(x,t), w(x,t))$ of system (2.2), we aim to establish upper bounds on $u(x,t)$ and $w(x,t)$ in $\Omega \times (T, \infty)$ for some T which depends on the nonnegative, not identically zero initial data of the solution (u, v, w). The main result of this section is

Theorem 6.9. *Let (u, v, w) be any positive solution of (2.2) with $\alpha = 1+\epsilon$. Assume that the set $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. Then there exists an $\epsilon_0 > 0$ such that for every $0 < \epsilon < \epsilon_0$, there exists $\tilde{\Gamma}$ such that for all $\beta > \tilde{\Gamma}$, there exists a $T > 0$ such that $u(x,t) \le \tilde{u}^*(x) + 1/\beta$ and $w(x,t) \le \tilde{w}^*(x) + 1/\beta$ on $\Omega \times (T, \infty)$, where $(\tilde{u}^*, \tilde{w}^*)$ is the unique positive steady state of (6.1).*

To establish this result, we make use of appropriate "sub/super" systems as follows.

Lemma 6.10. *Consider the system*

$$\begin{cases} \check{u}_t = \mu\nabla\cdot[\nabla\check{u} - (1+\epsilon)\check{u}\nabla\ln m] + \check{u}(m - \check{u} - \hat{w} - (v^* + 1/\beta)) \ \text{in } \Omega \times (T(\beta), \infty), \\ \hat{w}_t = \gamma\Delta\hat{w} + \hat{w}(m - \check{u} - \hat{w}) \quad \text{in} \quad \Omega \times (T(\beta), \infty), \\ [\nabla\check{u} - (1+\epsilon)\check{u}\nabla\ln m]\cdot n = \nabla\hat{w}\cdot n = 0 \quad \text{on} \quad \partial\Omega \times (T(\beta), \infty), \\ \check{u}(x, T(\beta)) = u(x, T(\beta)), \quad \hat{w}(x, T(\beta)) = w(x, T(\beta)) \quad \text{in} \quad \Omega, \end{cases} \tag{6.26}$$

where v^* is the unique positive steady state of (4.6). Let $(\check{u}^*_\beta, \hat{w}^*_\beta)$ be a positive steady state of (6.26). Let $\epsilon_0 > 0$ be as in Lemma 6.8. Then for all ϵ with $0 < \epsilon < \epsilon_0$, there exists $\bar{\beta}(\epsilon)$ such that if $\beta > \bar{\beta}(\epsilon)$, $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is linearly stable.

Proof. We know that for each $\beta > 0$, the system linearized at $(\check{u}^*_\beta, \hat{w}^*_\beta)$ has principal eigenfunctions (f, g) in $C^2(\bar{\Omega})$ such that f and g are of opposite signs on Ω, $||f||^2_{L^2} + ||g||^2_{L^2} = 1$ and

$$\begin{cases} -\eta f = \mu\nabla\cdot[\nabla f - (1+\epsilon)f\nabla\ln m] - \check{u}^*_\beta(f+g) \\ \qquad\qquad + f(m - \check{u}^*_\beta - \hat{w}^*_\beta - (v^* + 1/\beta)) \quad \text{in} \quad \Omega, \\ -\eta g = \gamma\Delta g - \hat{w}^*_\beta(f+g) + g(m - \check{u}^*_\beta - \hat{w}^*_\beta) \quad \text{in} \quad \Omega, \\ [\nabla f - (1+\epsilon)f\nabla\ln m]\cdot n = \nabla g\cdot n = 0 \quad \text{on} \quad \partial\Omega, \end{cases} \tag{6.27}$$

where η is the associated principal eigenvalue. By elliptic regularity and Sobolev embedding theorem [16], this sequence is uniformly bounded in $C^{1,\tau}(\bar{\Omega})$ for some

$\tau \in (0,1)$. Thus passing to a subsequence if necessary, we see that as $\beta \to \infty$, (f,g) converges to a limit (f^*, g^*) in $C^1(\bar{\Omega})$ where either $f^* \geq 0$ and $g^* \leq 0$ or $f^* \leq 0$ and $g^* \geq 0$, $||f^*||^2_{L^2} + ||g^*||^2_{L^2} = 1$, and

$$\begin{cases} -\eta^* f^* = \mu\nabla \cdot [\nabla f^* - (1+\epsilon) f^* \nabla \ln m] - \tilde{u}^*(f^* + g^*) \\ \qquad\qquad + f^*(m - \tilde{u}^* - \tilde{w}^*) \quad \text{in} \quad \Omega, \\ -\eta^* g^* = \gamma \Delta g^* - \tilde{w}^*(f+g) + g^*(m - \tilde{u}^* - \tilde{w}^*) \quad \text{in} \quad \Omega, \\ [\nabla f^* - (1+\epsilon) f^* \nabla \ln m] \cdot n = \nabla g^* \cdot n = 0 \quad \text{on} \quad \partial\Omega, \end{cases} \tag{6.28}$$

where $(\tilde{u}^*, \tilde{w}^*)$ is as in Lemma 6.8. Note that for small enough positive ϵ, as $\beta \to \infty$, $(\tilde{u}^*_\beta, \tilde{w}^*_\beta)$ converges to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$. To see this notice that by elliptic regularity and Sobolev embedding theorem [16], a subsequence of $(\tilde{u}^*_\beta, \tilde{w}^*_\beta)$ converges to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$. For sufficiently small positive ϵ, the positive steady state of (6.1) is uniquely determined by Lemma 6.8. Thus, we see that convergence is independent of the subsequence.

Now we establish the uniqueness of the limit (f^*, g^*). Since $\tilde{u}^*, \tilde{w}^* > 0$ in Ω, we must have that neither f^* nor g^* is zero in Ω. Thus, we see that the triple (f^*, g^*, η^*) satisfies the eigenvalue problem in equation (6.22) and because f^* and g^* have opposite signs, η^* must be the principal eigenvalue. Note η^* is simple and since $||f^*||^2_{L^2} + ||g^*||^2_{L^2} = 1$, it must be that the triple (f^*, g^*, η^*) is uniquely determined. This proves that convergence is independent of the subsequence.

By Lemma 6.8, we know then that for $0 < \epsilon < \epsilon_0$, $\eta^* > 0$. Hence for $\beta > \bar{\beta}(\epsilon)$, the principal eigenvalue η associated to $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is positive. $\square$

Lemma 6.11. *Consider the system*

$$\begin{cases} \hat{u}_t = \mu\nabla \cdot [\nabla \hat{u} - (1+\epsilon)\hat{u}\nabla \ln m] + \hat{u}(m - \hat{u} - \check{w}) \quad \textit{in} \quad \Omega \times (T(\beta), \infty), \\ \check{w}_t = \gamma \Delta \check{w} + \check{w}(m - \hat{u} - \check{w} - (v^* + 1/\beta)) \quad \textit{in} \quad \Omega \times (T(\beta), \infty), \\ [\nabla \hat{u} - (1+\epsilon)\hat{u}\nabla \ln m] \cdot n = \nabla \check{w} \cdot n = 0 \quad \textit{on} \quad \partial\Omega \times (T(\beta), \infty), \\ \hat{u}(x, T(\beta)) = u(x, T(\beta)), \;\; \check{w}(x, T(\beta)) = w(x, T(\beta)) \quad \textit{in} \quad \Omega, \end{cases} \tag{6.29}$$

where v^* is the unique positive steady state of (4.6). Let $(\hat{u}^*_\beta, \check{w}^*_\beta)$ be a positive steady state of (6.29). Let $\epsilon_0 > 0$ be as in Lemma 6.8. Then for ϵ with $0 < \epsilon < \epsilon_0$, there exists $\bar{\beta}(\epsilon)$ such that if $\beta > \bar{\beta}(\epsilon)$, $(\hat{u}^*_\beta, \check{w}^*_\beta)$ is linearly stable.

Proof. The proof is similar to that of Lemma 6.10. $\square$

Lemma 6.12. *Assume that the set $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. There exists β_s such that for all $\beta > \beta_s$ the semi-trivial steady states, $(\tilde{u}^*, 0)$ and $(0, \tilde{w}^*)$, of system (6.26) are unstable.*

Proof. To show that $(\check{u}^*, 0)$ is unstable, we must show that the principal eigenvalue λ, satisfying the following eigenvalue problem, is negative:

$$\begin{cases} \gamma \Delta \phi + \phi(m - \check{u}^*) = -\lambda \phi \quad \text{in} \quad \Omega, \\ \nabla \phi \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.30}$$

Note that in equation (6.30) we can choose the principal eigenfunction ϕ so that $\phi > 0$ in $\bar{\Omega}$. Dividing the equation of ϕ by ϕ, integrating the resulting equation over Ω and using the boundary conditions, we have

$$-\lambda|\Omega| = \gamma \int_\Omega \frac{|\nabla \phi|^2}{\phi^2} + \int_\Omega (m - \check{u}^*). \tag{6.31}$$

By the comparison principle, $\check{u}^* \le u^*$, where u^* is the unique positive solution of (4.1). By Lemma 4.2, if $\alpha > 1$, $\int_\Omega u^* < \int_\Omega m$. Hence, $\int_\Omega \check{u}^* < \int_\Omega m$. This together with (6.31) implies that $\lambda < 0$ for all β.

Next, we want to prove that $(0, \hat{w}^*)$ is unstable. The proof is almost identical to that of Theorem 5.1. Working through the corresponding eigenvalue problem for system (6.26), we finally arrive at the following expression for the principal eigenvalue λ:

$$-\lambda \int_\Omega m^{1+\epsilon} \ge \int_\Omega [m^{1+\epsilon} - (\hat{w}^*)^{1+\epsilon}](m - \hat{w}^*) - \int_\Omega m^{1+\epsilon}(v^* + 1/\beta). \tag{6.32}$$

As in the proof of Theorem 5.1, we cannot have $m = \hat{w}^*$ in Ω. Thus, $\int_\Omega [m^{1+\epsilon} - (\hat{w}^*)^{1+\epsilon}](m - \hat{w}^*) > 0$. Also, we know that as $\beta \to \infty$, $\int_\Omega v^* \to 0$ and $1/\beta \to 0$. Thus because $||m^{1+\epsilon}||_{L^\infty} < \infty$, there exists a β_s such that if $\beta > \beta_s$ then right hand side of (6.32) will be positive. Hence, $\lambda < 0$, proving that $(0, \hat{w}^*)$ is unstable. □

Lemma 6.13. *Assume that the set $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. There exists β_p such that for all $\beta > \beta_p$ the semi-trivial steady states, $(\hat{u}^*, 0)$ and $(0, \check{w}^*)$, of system (6.29) are unstable.*

Proof. The proof is similar to that of the previous Lemma. □

Theorem 6.14. *Assume that the set $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. Let $\epsilon_0 > 0$ be as in Lemma 6.8. Then for all ϵ with $0 < \epsilon < \epsilon_0$, there exists a Γ_ϵ, such that for all $\beta > \Gamma_\epsilon$, both systems (6.26) and (6.29) have unique positive steady states, denoted as $(\check{u}^*_\beta, \hat{w}^*_\beta)$ and $(\hat{u}^*_\beta, \check{w}^*_\beta)$, respectively. Furthermore, as $\beta \to \infty$, both $(\check{u}^*_\beta, \hat{w}^*_\beta)$ and $(\hat{u}^*_\beta, \check{w}^*_\beta)$ converge to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$, where $(\tilde{u}^*, \tilde{w}^*)$ is as in Lemma 6.8.*

Proof. Let $\epsilon \in (0, \epsilon_0)$. If $\beta > \bar{\beta}(\epsilon)$, then by Lemma 6.10, any positive steady state $(\check{u}^*_\beta, \hat{w}^*_\beta)$ of (6.26) has a corresponding positive principal eigenvalue. This means that $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is locally stable. From Lemma 6.12 we know that for $\beta > \beta_s$, both semi-trivial steady states of system (6.26) are unstable. Thus because system (6.26) is strongly monotone, for $\beta > \max\{\bar{\beta}(\epsilon), \beta_s\}$, by the monotone dynamical system theory [31], system (6.26) must have only one positive steady state, denoted by $(\check{u}^*_\beta, \hat{w}^*_\beta)$, which is globally asymptotically stable.

Similarly, by Lemma 6.11, $(\hat{u}^*_\beta, \check{w}^*_\beta)$ has a corresponding positive principal eigenvalue for $\beta > \tilde{\beta}(\epsilon)$. From Lemma 6.13 we have that for $\beta > \beta_p$, both semi-trivial steady states of system (6.29) are unstable. Again, by the monotone dynamical system theory [31], since (6.29) is a strongly monotone system, for $\beta > \max\{\tilde{\beta}(\epsilon), \beta_p\}$, system (6.29) has a unique positive steady state, denoted by $(\hat{u}^*_\beta, \check{w}^*_\beta)$, which is globally asymptotically stable.

Therefore, if we let $\Gamma_\epsilon = \max\{\beta_s, \beta_p, \bar{\beta}(\epsilon), \tilde{\beta}(\epsilon)\}$, then for $\beta > \Gamma_\epsilon$, both positive steady states are unique for their respective systems. Finally, we reference the proof of Lemma 6.10 for justification of the result that as $\beta \to \infty$, both $(\check{u}^*_\beta, \hat{w}^*_\beta)$ and $(\hat{u}^*_\beta, \check{w}^*_\beta)$ converge to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$, where $(\tilde{u}^*, \tilde{w}^*)$ is as in Lemma 6.8. □

Corollary 2. *Assume that the set $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. For all ϵ with $0 < \epsilon < \epsilon_0$, there exists $\tilde{\Gamma}$ such that for all $\beta > \tilde{\Gamma}$, there exists a $T_\beta > 0$ such that $\hat{u}(x,t) \le \tilde{u}^*(x) + 1/\beta$ and $\hat{w}(x,t) \le \tilde{w}^*(x) + 1/\beta$ on $\Omega \times (T_\beta, \infty)$. (Note: $\hat{u}$ comes from the solution pair $(\hat{u}, \check{w})$ satisfying (6.29) and $\hat{w}$ comes from the solution pair $(\check{u}, \hat{w})$ satisfying (6.26).)*

Proof. Let $\epsilon \in (0, \epsilon_0)$ and let $\beta > \Gamma_\epsilon$. Then from Theorem 6.14, $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is a globally asymptotically stable positive steady state for system (6.26) and $(\hat{u}^*_\beta, \check{w}^*_\beta)$ is a globally asymptotically stable steady state for system (6.29). Thus for a solution $(\check{u}, \hat{w})$ to system (6.26) with prescribed nonnegative initial data, there exists a $T_w > 0$ such that if $t > T_w$, $\hat{w}(x,t) \le \hat{w}^*_\beta(x) + 1/(2\beta)$ in Ω. Similarly, for a solution $(\hat{u}, \check{w})$ to system (6.29), there exists a $T_u > 0$ such that if $t > T_u$, $\hat{u}(x,t) \le \hat{u}^*_\beta(x) + 1/(2\beta)$ in Ω. By Theorem 6.14, as $\beta \to \infty$, both $(\check{u}^*_\beta, \hat{w}^*_\beta)$ and $(\hat{u}^*_\beta, \check{w}^*_\beta) \to (\hat{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$. Hence, there exists Γ_1 such that if $\beta > \Gamma_1$, $\hat{w}^*_\beta(x) \le \tilde{w}^* + 1/(2\beta)$ in Ω and $\hat{u}^*_\beta(x) \le \tilde{u}^* + 1/(2\beta)$ in Ω. Thus if we let $\beta > \tilde{\Gamma} = \max\{\Gamma_\epsilon, \Gamma_1\}$ and then put $T_\beta = \max\{T_u, T_w\}$, we obtain our result. ☐

To prove Theorem 6.9, we simply apply Corollary 2 and $u \le \hat{u}$ and $w \le \hat{w}$ on $\Omega \times (T, \infty)$ for some $T > 0$.

6.3. **A key estimate and instability of** $(\tilde{u}^*, 0, \tilde{w}^*)$. We begin this section with a useful result concerning u_0' for large μ.

Lemma 6.15. *The following holds:*

$$\lim_{\mu\to\infty} \int_\Omega (m u_0' + m \ln m) < 0,$$

where u_0' is the unique solution satisfying (6.9).

Proof. Consider equation (6.9). If we let $\mu \to \infty$, then

$$u_0' \to -\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}$$

uniformly in Ω. Thus,

$$\lim_{\mu\to\infty} \int_\Omega (m u_0' + m \ln m) = -\left(\int_\Omega m\right)\left(\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2} - \frac{\int_\Omega m \ln m}{\int_\Omega m}\right).$$

It suffices to show that

$$\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2} > \frac{\int_\Omega m \ln m}{\int_\Omega m}.$$

Define f as

$$f(p) = \frac{\int_\Omega m^p \ln m}{\int_\Omega m^p}, \quad p > 0.$$

Then

$$f'(p) = \frac{\int_\Omega m^p (\ln m)^2 \int_\Omega m^p - (\int_\Omega m^p \ln m)^2}{(\int_\Omega m^p)^2} > 0,$$

where the numerator of $f'(p)$ is positive by Hölder's inequality. Thus, f is a strictly increasing function of p and our result follows. ☐

The following version of Jensen's inequality can be found in [18].

Lemma 6.16. [18] *Let E be a measurable subset of $\mathbb{R}^N$. Suppose that $a \le f \le b$, where a and b are in $\mathbb{R}$, and that f is almost never equal to a and b; that p, the "weight function", is finite and positive everywhere in E, and integrable over E. Further, suppose that $\phi''(t)$ is positive and finite for $a < t < b$. Then*

$$\phi\left(\frac{\int_E fp}{\int_E p}\right) \le \frac{\int_E \phi(f) p}{\int_E p},$$

whenever the right-hand side exists and is finite. Also, note that equality holds when f is effectively constant.

Lemma 6.17. *For $m > 0$, nonconstant and $m \in C(\bar{\Omega})$,*

$$\frac{\int_\Omega m^2}{\int_\Omega m} < e^{\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}}.$$

Proof. We apply Lemma 6.16 by choosing $\phi(t) = t \ln t$, $p = m$, $f = m$ and $E = \Omega$. □

Using the inequality in Lemma 6.17, we are now ready to establish our "key estimate" on the size of $m(x_0)$. As we discussed in section 6, this result is fundamental to establishing the instability of $(\tilde{u}, 0, \tilde{w})$ and the lower bound for v.

Lemma 6.18. *Suppose that $m > 0$, nonconstant and $m \in C^2(\bar{\Omega})$. Furthermore, suppose that*

$$\ln\left(\frac{\int_\Omega m^2}{\int_\Omega m}\right) < \ln(m(x_0)) < \frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}$$

for $x_0 \in \Omega$, where x_0 is a local maximum of m. Then there exists some $\bar{\mu}$ such that for all $\mu > \bar{\mu}$, there exists an $\bar{\epsilon} > 0$ such that for all $0 < \epsilon < \bar{\epsilon}$,

$$\tilde{u}^*(x_0) + \tilde{w}^*(x_0) - m(x_0) < 0,$$

where $(\tilde{u}^*, \tilde{w}^*)$ is the unique positive steady state of (6.1) as shown by Lemma 6.8.

Proof. Using our expansions (6.16), for $0 < \epsilon < \epsilon_0$,

$$\begin{cases} \tilde{u}^* = m + \epsilon m[\Lambda\bar{\varphi} + u_0' + \ln m] + O(\epsilon^2), \\ \tilde{w}^* = \epsilon\Lambda + O(\epsilon^2), \end{cases} \tag{6.33}$$

which gives us

$$\begin{aligned} \tilde{u}^* + \tilde{w}^* - m &= \epsilon\Lambda[m\bar{\varphi} + 1] + \epsilon[m \ln m + u_0' m] + O(\epsilon^2) \\ &= \epsilon B + O(\epsilon^2), \end{aligned} \tag{6.34}$$

where $\Lambda = 1/\lambda'(0) > 0$, $B = \Lambda[m\bar{\varphi} + 1] + [m \ln m + u_0' m]$. Let $\mu \to \infty$. Then we know that $\bar{\varphi} \to \frac{-\int_\Omega m}{\int_\Omega m^2}$ and $u_0' \to \frac{-\int_\Omega m^2 \ln m}{\int_\Omega m^2}$. Hence, as $\mu \to \infty$

$$\begin{aligned} \Lambda \to & \frac{\int_\Omega [m \ln m + \left(\frac{-\int_\Omega m^2 \ln m}{\int_\Omega m^2}\right) m]}{-\int_\Omega [m\left(\frac{-\int_\Omega m}{\int_\Omega m^2}\right) + 1]} \\ = & \frac{\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m}{\left(\int_\Omega m\right)^2 - |\Omega| \int_\Omega m^2}. \end{aligned} \tag{6.35}$$

If we use our expression in (6.35) for Λ, then as $\mu \to \infty$

$$\begin{aligned}B \to &\left(\frac{\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m}{\left(\int_\Omega m\right)^2 - |\Omega| \int_\Omega m^2}\right) \left[m\left(\frac{-\int_\Omega m}{\int_\Omega m^2}\right) + 1\right] \\ &+ \left[m \ln m + m\left(\frac{-\int_\Omega m^2 \ln m}{\int_\Omega m^2}\right)\right] \\ &= \frac{(\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m)(-m\int_\Omega m + \int_\Omega m^2)}{(\int_\Omega m^2)((\int_\Omega m)^2 - |\Omega| \int_\Omega m^2)} \\ &+ \frac{(m \ln m \int_\Omega m^2 - m\int_\Omega m^2 \ln m)((\int_\Omega m)^2 - |\Omega| \int_\Omega m^2)}{(\int_\Omega m^2)((\int_\Omega m)^2 - |\Omega| \int_\Omega m^2)}.\end{aligned}$$

Put $A = (\int_\Omega m^2)\left((\int_\Omega m)^2 - |\Omega| \int_\Omega m^2\right) < 0$, then $B \to \frac{D}{A}$ as $\mu \to \infty$, where

$$\begin{aligned}D = &\left(\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m\right)\left(-m\int_\Omega m + \int_\Omega m^2\right) \\ &+ \left(m \ln m \int_\Omega m^2 - m\int_\Omega m^2 \ln m\right)\left(\left(\int_\Omega m\right)^2 - |\Omega| \int_\Omega m^2\right).\end{aligned}$$

Note that by our assumption on m, at x_0, $m \ln m \int_\Omega m^2 - m\int_\Omega m^2 \ln m < 0$. Also, by Lemma 6.15, we see that $\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m < 0$. Now if we want $D > 0$ (evaluated at x_0), then rearranging the above expression for D gives us

$$\begin{aligned}D(x_0) =&m(x_0)\int_\Omega m\left(-\int_\Omega m^2 \int_\Omega m \ln m + \int_\Omega m \int_\Omega m^2 \ln m\right) \\ &+m(x_0)\left(\ln m(x_0)\int_\Omega m^2 - \int_\Omega m^2 \ln m\right)\left(\left(\int_\Omega m\right)^2 - |\Omega| \int_\Omega m^2\right) \\ &-\left(-\int_\Omega m^2 \int_\Omega m \ln m + \int_\Omega m \int_\Omega m^2 \ln m\right)\int_\Omega m^2.\end{aligned}$$

Manipulating the above expression gives us that $D(x_0) > 0$ is equivalent to

$$m(x_0) > \frac{\int_\Omega m^2}{\int_\Omega m + \frac{ST}{C}}, \tag{6.36}$$

where $S = -\ln m(x_0)\int_\Omega m^2 + \int_\Omega m^2 \ln m > 0$, $T = \frac{-A}{\int_\Omega m^2} > 0$ and

$$C = -\int_\Omega m^2 \int_\Omega m \ln m + \int_\Omega m \int_\Omega m^2 \ln m > 0.$$

Since $\frac{ST}{C} > 0$, (6.36) follows from assumption $m(x_0) > \frac{\int_\Omega m^2}{\int_\Omega m}$. Hence for large enough μ and small enough ϵ, $\tilde{u}^* + \tilde{w}^* - m < 0$ at x_0. □

Theorem 6.19. *Suppose that $m > 0$, $m \in C^2(\bar{\Omega})$, and all critical points of m are nondegenerate. Furthermore, suppose that*

$$\ln\left(\frac{\int_\Omega m^2}{\int_\Omega m}\right) < \ln(m(x_0)) < \frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}$$

for some $x_0 \in \Omega$, where x_0 is a local maximum of m. Then there exists $\bar{\mu} > 0$ such that for all $\mu > \bar{\mu}$, there exists $\bar{\epsilon} > 0$ (from the previous Lemma) such that if $1 < \alpha < 1 + \bar{\epsilon}$, for all $\gamma > 0$, $\nu > 0$, there exists a $\bar{\beta}(\mu, \epsilon, \gamma, \nu)$ such that for any

$\beta > \bar{\beta}$ the positive solution of $\mathbf{F}(\epsilon, u, \tilde{w}) = 0$ bifurcating from the trivial solution is unstable in the three species system (2.2). In other words, $(\tilde{u}^*, 0, \tilde{w}^*)$ is unstable.

Proof. We consider the following eigenvalue problem:

$$\begin{cases} \nu\nabla \cdot [\nabla\phi - \beta\phi\nabla \ln m] + \phi(m - \tilde{u}^* - \tilde{w}^*) = -\lambda\phi \quad \text{in} \quad \Omega, \\ \nabla[\nabla\phi - \beta\phi\nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega, \end{cases} \tag{6.37}$$

where $\tilde{u}^*$ and $\tilde{w}^*$ satisfy (6.1) for $0 < \epsilon < \epsilon_0$. Set $\zeta = e^{-\beta \ln m}\phi$. Then ζ satisfies

$$\begin{cases} \nu\nabla \cdot [e^{\beta \ln m}\nabla\zeta] + e^{\beta \ln m}\zeta(m - \tilde{u}^* - \tilde{w}^*) = -\lambda e^{\beta \ln m}\zeta \quad \text{in} \quad \Omega, \\ \nabla\zeta \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{6.38}$$

Simplifying the expression in (6.38), we see that ζ satisfies

$$-\nu\Delta\zeta - \nu\beta\nabla \ln m\nabla\zeta + (\tilde{u}^* + \tilde{w}^* - m)\zeta = \lambda\zeta \quad \text{in} \quad \Omega, \quad \nabla\zeta \cdot n|_{\partial\Omega} = 0. \tag{6.39}$$

Let λ^* denote the principal eigenvalue of equation (6.37). Then from Theorem 1 of [10], we have

$$\lim_{\beta\to\infty} \lambda^* = \min_{\mathcal{M}}(\tilde{u}^* + \tilde{w}^* - m), \tag{6.40}$$

where $\mathcal{M}$ denotes the set of local maxima of m. From Lemma 6.18, we know that for small enough ϵ, $\tilde{u}^*(x_0) + \tilde{w}^*(x_0) - m(x_0) < 0$. Thus for large enough β, we see that $\lambda^* < 0$. This completes the proof. □

6.4. **Proof of lower bound for species v.**

Lemma 6.20. *Consider the problem*

$$\begin{cases} \check{v}_t = \nu\nabla \cdot [\nabla\check{v} - \beta\check{v}\nabla \ln m] + \check{v}(m - \tilde{u}^* - \tilde{w}^* - 2/\beta - \check{v}) \quad \text{in} \quad \Omega \times (T, \infty), \\ [\nabla\check{v} - \beta\check{v}\nabla \ln m] \cdot n = 0 \ \text{on} \ \partial\Omega \times (T, \infty), \\ \check{v}(x, T) = v(x, T) \quad \text{in} \quad \bar{\Omega}. \end{cases} \tag{6.41}$$

Suppose that m satisfies assumption (A2) and that all critical points of m are non-degenerate. Then there exists $\bar{\mu} > 0$ such that for all $\mu > \bar{\mu}$, there exists $\bar{\epsilon} > 0$ such that for $0 < \epsilon < \bar{\epsilon}$ and for all $\gamma > 0$, $\nu > 0$, there exists $\hat{\beta} := \hat{\beta}(\epsilon, \mu, \gamma, \nu)$ such that if $\beta > \hat{\beta}$, the zero steady state solution of (6.41) is unstable. (Note: $\bar{\epsilon} > 0$ and $\bar{\mu} > 0$ are as in Theorem 6.19.)

Proof. To show that zero solution is unstable, we must show that the principle eigenvalue λ of the following eigenvalue problem is negative:

$$\begin{cases} \nu\nabla \cdot [\nabla\varphi - \beta\varphi\nabla \ln m] + \varphi(m - \tilde{u}^* - \tilde{w}^* - 2/\beta) = -\lambda\varphi \quad \text{in} \quad \Omega, \\ [\nabla\varphi - \beta\varphi\nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.42}$$

Note that we can choose φ, the corresponding eigenfunction of λ, to be positive in Ω. If we let $\phi = \varphi/m^\beta$, then (6.42) becomes

$$\begin{cases} \nu\nabla \cdot [m^\beta\nabla\phi] + \phi m^\beta(m - \tilde{u}^* - \tilde{w}^* - 2/\beta) = -\lambda m^\beta\phi \quad \text{in} \quad \Omega, \\ \nabla\phi \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{6.43}$$

Expanding and simplifying (6.43), we have

$$\begin{cases} -\nu\Delta\phi - \nu\beta\nabla \ln m\nabla\phi + (\tilde{u}^* + \tilde{w}^* + 2/\beta - m)\phi = \lambda\phi \quad \text{in} \quad \Omega, \\ \nabla\phi \cdot n|_{\partial\Omega} = 0. \end{cases}$$

Now let $\delta_l > 0$ be any constant. Choose $\beta_l \gg 1$ such that $2/\beta \leq \delta_l$ for all $\beta \geq \beta_l$. Consider the eigenvalue problem

$$\begin{cases} -\nu\Delta\phi_l - \nu\beta\nabla \ln m\nabla\phi_l + (\tilde{u}^* + \tilde{w}^* + \delta_l - m)\phi = \lambda_1\phi_l & \text{in} \quad \Omega, \\ \nabla\phi_l \cdot n|_{\partial\Omega} = 0, \end{cases}$$

where λ_l is the principal eigenvalue. By Theorem 1 of [10],

$$\lim_{\beta\to\infty} \lambda_l = \min_{\mathcal{M}}(\tilde{u}^* + \tilde{w}^* + \delta_l - m), \tag{6.44}$$

where $\mathcal{M}$ denotes the set of local maxima of m. Choosing

$$\delta_l = \frac{1}{2}\left[m(x_0) - \tilde{u}^*(x_0) - \tilde{w}^*(x_0)\right] > 0,$$

we see that by the choice of δ_l and Lemma 6.18,

$$\min_{\mathcal{M}}(\tilde{u}^* + \tilde{w}^* + \delta_l - m) \leq \frac{1}{2}\left[\tilde{u}^*(x_0) + \tilde{w}^*(x_0) - m(x_0)\right] < 0.$$

Hence, $\lambda_l < 0$ for $\beta \gg 1$. By the comparison principle, $\lambda_l \geq \lambda$ for $\beta \geq \beta_l$. Therefore, for $\beta \geq \beta_l$, $\lambda < 0$. ☐

Finally, we can state and prove the lower bound result for species v.

Theorem 6.21. *Let m satisfy assumption* (A2). *Assume that all the critical points of m are nondegenerate. Let v be the second component of any positive solution (u, v, w) of* (2.2). *Let $\bar{\mu} > 0$ be as in Theorem 6.19. Then for all $\mu > \bar{\mu}$, there exists $0 < \bar{\epsilon}$ (where $\bar{\epsilon}$ is as above and is less than ϵ_0) such that for all $1 < \alpha < 1 + \bar{\epsilon}$, and for all $\gamma > 0$, $\nu > 0$, there exists an $\beta_3 = \max\{\bar{\Gamma}, \hat{\beta}\}$ (where $\bar{\Gamma}$ is from Corollary 2 and $\hat{\beta}$ is from Lemma 6.20), such that for all $\beta > \beta_3$, there exists a $\delta_3 > 0$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} v(x, t) \geq \delta_3 > 0$.*

Proof. Comparing system (6.26) and system (6.29) to system (2.2) and using Corollary 2, we see that v is a super solution to (6.41) for $t > T_\beta$ where T_β is as in Corollary 2. That is, for all $x \in \Omega$ and for all $t > T_\beta$, $v(x, t) \geq \bar{v}(x, t)$. By Lemma 6.20, we know that zero is unstable for system (6.41) which implies that $\bar{v}(x, t)$ tends to a unique positive equilibrium of (6.41) as $t \to \infty$. Hence we see that there exists a $\delta_3 > 0$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} v(x, t) \geq \delta_3 > 0$. ☐

7. **Permanence of three species.** Putting the results of Theorems 4.1, 5.1, and 6.21 together, we demonstrate that for appropriate parameters, any solution of (2.2), with nonnegative and not identically zero initial data, eventually has a positive lower bound which is independent of the initial conditions. More precisely, we have shown

Theorem 7.1. *Suppose that $m > 0$, it satisfies assumption* (A2), *and all the critical points of m are nondegenerate. There exists $\bar{\mu} > 0$ (as in Theorem 6.19) such that for all $\mu > \bar{\mu}$, there exists $\bar{\epsilon} > 0$ (where $\bar{\epsilon}$ is as in Theorem 6.21) such that for all $1 < \alpha < 1 + \bar{\epsilon}$, and for all $\gamma > 0$, $\nu > 0$, there exists some $\beta_4 = \max\{\beta_1, \beta_2, \beta_3\}$ such that for all $\beta > \beta_4$, there exists some $k = \min\{\delta_1, \delta_2, \delta_3\} > 0$ such that for any solution (u, v, w) of* (2.2) *with nonnegative and not identically zero initial data, $\liminf_{t\to\infty} u(x, t)$, $\liminf_{t\to\infty} v(x, t)$, $\liminf_{t\to\infty} w(x, t) \geq k > 0$, for all $x \in \Omega$.*

As the hard work has been completed, we turn to the upper bound result:

Lemma 7.2. *Given any positive solution (u, v, w) of system (2.2), for $m > 0$ and nonconstant, if we let*

$$K = \max\{\sup_{\Omega} u^*(x), \sup_{\Omega} v^*(x), \sup_{\Omega} w^*(x)\} + 1,$$

where $(u^*, 0, 0)$, $(0, v^*, 0)$ and $(0, 0, w^*)$ are the steady states of (2.2) when only one species is present. Then $\limsup_{t\to\infty} u(x,t)$, $\limsup_{t\to\infty} v(x,t)$, $\limsup_{t\to\infty} w(x,t)$ $< K$.

Proof. Let (u, v, w) be a positive solution of (2.2). From Corollary 1 we know that $\limsup_{t\to\infty} u(x,t) \le u^*$ and $\limsup_{t\to\infty} v(x,t) \le v^*$ in Ω. Examining the single species equation for w, i.e. the equation for w in (2.2) when $u = v = 0$, we obtain a similar result for $w(x,t)$. That is, $\limsup_{t\to\infty} w(x,t) \le w^*$. Putting these results together we complete the proof. ◻

In order to demonstrate that our permanence result implies the existence of a componentwise positive steady state for the three species model (2.2), we first rewrite (2.2) as follows

$$\begin{cases} \tilde{u}_t = \mu m^{-\alpha}\nabla\cdot[m^\alpha \nabla \tilde{u}] + \tilde{u}(m - m^\alpha \tilde{u} - m^\beta \tilde{v} - w) & \text{in} \quad \Omega\times(0,\infty), \\ \tilde{v}_t = \nu m^{-\beta}\nabla\cdot[m^\beta \nabla \tilde{v}] + \tilde{v}(m - m^\alpha \tilde{u} - m^\beta \tilde{v} - w) & \text{in} \quad \Omega\times(0,\infty), \\ w_t = \gamma\Delta w + w(m - u - v - w) \quad \text{in} \quad \Omega\times(0,\infty), \\ \nabla\tilde{u}\cdot n = \nabla\tilde{v}\cdot n = \nabla w\cdot n = 0 \quad \text{on} \quad \partial\Omega\times(0,\infty), \end{cases} \tag{7.1}$$

where $\tilde{u} = um^{-\alpha}$ and $\tilde{v} = vm^{-\beta}$ in Ω. Using the theory of analytic semi-groups and parabolic partial differential equations, we can recast system (7.1) as a semi-dynamical system $\Pi[(\tilde{u}^0, \tilde{v}^0, w^0), t]$ defined on the space $[C(\bar{\Omega})]^3$, where $\Pi[(\tilde{u}^0, \tilde{v}^0, w^0), t]$ denotes the unique solution of (7.1) such that $(\tilde{u}(x,0), \tilde{v}(x,0), w(x,0)) = (\tilde{u}^0, \tilde{v}^0, w^0)$ [6]. As we are interested in nonnegative solutions of (7.1), we restrict Π to the cone V of $[C(\bar{\Omega})]^3$ where each of the components of an element of V are nonnegative. Note that V is a closed subspace of $[C(\bar{\Omega})]^3$ and hence is a Banach space. Also, by the maximum principle [28], V has nonempty interior. Note that from Theorem 7.2 and reaction-diffusion system theory, $\Pi[(\cdot,\cdot),t] : V \to V$ for any $t > 0$ is compact.

For the remainder of this section, we fix m and parameters $\mu, \alpha, \nu, \beta, \gamma$ such that the hypotheses of Theorem 7.1 and Lemma 7.2 are satisfied. So, there exists positive numbers k and K, such that if (u, v, w) is a solution of (2.2) with nonnegative initial data, there exists a $T_0 > 0$ such that $k < u < K$, $k < v < K$, and $k < w < K$ in $\Omega\times[T_0,\infty)$. In light of system (7.1), we have $k < \tilde{u}m^\alpha < K$, $k < \tilde{v}m^\beta < K$, and $k < w < K$ in $\Omega\times[T_0,\infty)$. Because m^α and m^β are bounded above and below by positive constants, there are positive constants b and B such that $b < \tilde{u} < B$, $b < \tilde{v} < B$, and $b < w < B$ in $\Omega\times[T_0,\infty)$.

Define $W^* = \{f : f \in [C(\bar{\Omega})]^3, f = (f_1, f_2, f_3) \text{ where } b < f_i < B \text{ in } \Omega\}$. Clearly, W^* is a nonempty, open, bounded, and convex subset of $[C(\bar{\Omega})]^3$. Following [6], we note that the proof of the existence of a positive steady state for (7.1) and hence for (2.2) depends on showing that for any $t > 0$, $\Pi[\cdot, t]$ has a fixed point in W^*. To show this, we rely on the Asymptotic Schauder Fixed Point Theorem which is stated as follows:

Theorem 7.3. [33] *Let G be a nonempty bounded open convex set in a Banach space X. Let the operator $A : X \to X$ be compact and suppose for some prime $p \ge 2$ we have that $A^k(\bar{G}) \subseteq G$ where $k = p, p+1$. Then A has a fixed point in G.*

Consider the following result.

Lemma 7.4. *Let $t^* > 0$. There exists an integer $n_0 > 0$ such that $\Pi[\bar{W}^*, nt^*] \subseteq W^*$ for all $n \geq n_0$.*

Proof. See [6]. □

Note that Lemma 7.4 allows us to apply Theorem 7.3 to Π acting on $\bar{W}^*$ and hence we have shown that for any $t > 0$, $\Pi[\cdot, t]$ has a fixed point in W^*. It follows then that system (7.1) has a steady state in W^* (see Lemma 3.7 in [4]). By definition of W^* this steady state is positive in each component. It is clear then that system (2.2) also has a positive steady state. We summarize our result as follows:

Theorem 7.5. *Under the assumptions of Theorem 7.1, (2.2) has a positive steady state $(u_e(x), v_e(x), w_e(x))$.*

By Theorem 7.1, Lemma 7.2 and Theorem 7.5, the proof of Theorem 2.5 is complete.

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