RESIDENT-INVADER DYNAMICS IN INFINITE DIMENSIONAL SYSTEMS

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ABSTRACT. Motivated by evolutionary biology, we study general infinite-dimensional dynamical systems involving two species - the resident and the invader. Sufficient conditions for competition exclusion phenomena are given when the two species plays similar strategies. Those conditions are based on invasibility criteria, for instance, evolutionarily stable strategies in the framework of adaptive dynamics.

These type of questions is first proposed and studied by [S. Geritz et al., J. Math. Biol., 2002] and [S. Geritz, J. Math. Biol., 2005] for a class of ordinary differential equations. We extend and generalize previous works in two directions. First, we consider analytic semiflows in infinite-dimensional spaces. Secondly, we device an argument based on Hadamard's graph transform method that do not depend on the monotonicity of the two-species system. Our results are applicable to a wide class of reaction-diffusion models as well as models with nonlocal diffusion operators.

1. INTRODUCTION

An important issue in evolutionary theory is what happens when an established population employing a given strategy relative to some trait is invaded by a second population that is identical in all respects except for its strategy relative to this trait. There are three basic possible outcomes of the encounter. The resident population could effectively resist invasion so that the second population does not become established. If such is not the case and the

invader establishes itself, then there are two possibilities. Either the two populations coexist or the invader replaces the resident and then becomes the resident itself.

Geritz and Geritz et al. [21, 22] considered resident-invader dynamics when the strategy of the invader is close to that of an established resident. When the strategies are identical, the resident-invader dynamics are somewhat special and then the family of equilibria $\Gamma = \{(s\theta, (1-s)\theta) : 0 \leq s \leq 1\}$ is attracting, where θ denotes the equilibrium density of the resident. The focus of Geritz and Geritz et al. is what happens if the invader strategy is close to, but not identical to that of the resident, and the configuration of the resident and invader is close to Γ. What they found was that if the resident's strategy is far from being evolutionarily singular, then successful invasion always implies replacement. However, near an evolutionarily singular strategy, invasion may or may not imply replacement. In either case, they observed that during the invasion process the sum of the densities of the resident and the invader remain near the heretofore established resident equilibrium density θ. Consequently the pair of population densities may be envisioned as lying in a tube in two dimensions about the set Γ, a phenomenon that has come to be called the Tube Theorem. See Figure 1.

The results in [21, 22] were set in the context of systems of two ordinary differential equations. Recently, there has been considerable interest in questions related to evolution of dispersal in spatially explicit and spatially implicit models. Such models include general finite dimensional systems such as discrete diffusion systems, but also models which are realized as infinite dimensional dynamical systems, including reaction-diffusion models and integro-differential models. The purpose of this paper is to extend the results of Geritz and Geritz et al. to such models. This requires considering infinite dimensional dynamical systems. To this end, we employ the semi-group theory of unbounded operators, chiefly the infinite dimensional version of the variation of parameters formula. With these tools, we obtain a version of the Tube Theorem that is applicable in particular to systems of reaction-diffusion equations wherein strategies may incorporate second order derivatives.

In [21, 22], the fact that they are considering two dimensional systems of ordinary differential equations allows them to employ the Poincare-Bendixson Theorem to prove convergence to equilibria. Such arguments do not carry over even to higher dimensional finite dimensional systems let alone infinite dimensional ones. Imposing monotonicity of the dynamical systems is one way of generalizing the resident-invader dynamics results of [21, 22] to infinite dimensions. However, this imposes some restriction to the applicability of the results. Consequently, we have adapted the Graph Transform of Hadamard to obtain a satisfactory description of the resident-invader dynamics that does not require the dynamical systems to be monotone. However, in the application of these results to reaction-diffusion systems, we can only allow strategies that depend on at most first order derivatives.

The notions of adaptive dynamics are inherently local. Nevertheless, some of our results have global implications. For instance, if the invader employs a strategy that both is evolutionarily and convergent stable, then it invades and replaces resident with any nearby

strategy regardless of initial configuration (Theorem 5.2). In particular, it does not have to start near Γ.

The remainder of this paper is organized as follows. In Section 2, we introduce the modeling framework of single and two species systems. In Section 3, we establish an infinite dimensional version of the Tube Theorem. In Section 4, we adapt the Graph Transform of Hadamard to obtain the existence of a one dimensional invariant manifold for the flow within the tube. This construction enables us to get good properties related to convergence to equilibrium. The consequences of these results and their connection to notions from adaptive dynamics are discussed in Sections 5 and 6. Applications to reaction-diffusion systems are given in Sections 7 and 8. In Section 9, we present applications to integro-differential models. In this context, it has been necessary to further develop the spectral theory of integro-differential operators, and we collect those results in the Appendix. Finally, we wish to thank Professors Odo Diekmann and Amy Hurford for raising the questions that prompted the research for this paper.

2. Modeling Framework

2.1. **Modeling of a Single Species.** Suppose a species has a continuous trait $\alpha \in S$ where S is an open interval in $\mathbb{R}^1$. The habitat of the species is represented by a smooth bounded domain $\bar{\Omega} \subset \mathbb{R}_N$. Let $\theta = \theta(x,t)$ denote the population density of species with trait α, with its dynamics governed by

$$(2.1) \qquad \begin{cases} \theta_t = A(\alpha)\theta + F(\alpha, G(\alpha)\theta)\theta, \\ \theta\big|_{t=0} = \theta_0 \in X := C(\bar{\Omega}). \end{cases}$$

Here for each α, $A(\alpha)$ is a sectorial operator defined on a dense subset $D(A)$ of $X = C(\bar{\Omega})$ which is independent of $\alpha \in S$ (see, e.g. [25, P.18]); i.e. $A(\alpha)$ is closed, linear, and densely defined operator such that, for some $\eta \in (0, \pi/2)$ and some $M \geq 1$ and $a \in \mathbb{R}$, the sector

$$S_{a,\eta} = \{\lambda \in \mathbb{C} : 0 \leq |\mathrm{Re}\,(\lambda - a)| \leq \pi - \eta, \text{ and } \lambda \neq a\}$$

is in the resolvent set of $A(\alpha)$, and

$$\left\|(\lambda - A(\alpha))^{-1}\right\| \leq \frac{M}{|\lambda - a|} \qquad \text{for all } \lambda \in S_{\eta,a}.$$

We assume that $A(\alpha)$ is smooth in α in the sense that for each $\lambda \notin \sigma(A(\alpha))$, $R(\lambda, A(\alpha)) = (\lambda - A(\alpha))^{-1}$ is smooth in α as a linear operator from X to X. Moreover, $F(\alpha, w) : S \times X \to X$, $G(\alpha) : S \to X$ are smooth functions. (Here we make use of the fact that $C(\bar{\Omega})$ is a Banach algebra.) By standard theory, $A(\alpha) + w$ is sectorial for each $w \in X$, and generates an analytic semigroup. We will also assume that $A(\alpha)$ is a positive operator or has a positive resolvent.

2.2. **Modeling for Two Competing Species.** Consider the following system, which models the competition of two phenotypes of the same species, with traits α and β in S respectively.

(2.2)
$$\begin{cases} u_t = A(\alpha)u + F(\alpha, G(\alpha)u + G(\beta)v)u \\ v_t = A(\beta)v + F(\beta, G(\alpha)u + G(\beta)v)v \\ u\big|_{t=0} = u_0 \in X_+, \quad v\big|_{t=0} = v_0 \in X_+. \end{cases}$$

Here we denote $X_+ = \{w \in C(\bar{\Omega}) : w \geq 0 \text{ in } \bar{\Omega}\}$ and $\text{Int } X = \{w \in C(\bar{\Omega}) : w > 0 \text{ in } \bar{\Omega}\}$. It is well-known that (2.2) is invariant in $X_+ \times X_+$ under our assumptions on $A(\alpha)$ and $A(\beta)$.

It is also well known that (2.2) generates an analytic semiflow $\{\Phi^t\}_{t>0}$ on $X_+ \times X_+$. In fact, if $u_0, v_0 \in X_+$ are both non-trivial, then $(u, v) \in \text{Int } X_+ \times \text{Int } X_+$ for all $t > 0$. We assume in this paper that (2.2) is dissipative, i.e. for all $\mu \in (0, 1)$ and $p \in [1, \infty]$, forward orbits satisfy

(2.3) $\|(u, v)\|_{[X]^2} \leq C, \quad \|(u, v)\|_{[D(A)]^2} \leq C(1 + t^{-1}), \quad \|(u, v)\|_{[D_A(\mu,p)]^2} \leq C(1 + t^{-\mu})$

where C depends only on $\|(u_0, v_0)\|_{[X]^2}$, $D_A(\mu, p)$ denotes the real interpolation space between X and $D(A)$. For example, if $A(\alpha) = \alpha\Delta$ for $\alpha > 0$ complemented by Neumann boundary condition, then by [36, Corollary 3.1.24(ii)]

$$D(A) = \left\{ u \in \cap_{p \geq 1} W^{2,p}_{loc}(\Omega) : u, \Delta u \in C(\bar{\Omega}), \frac{\partial u}{\partial n}\bigg|_{\partial\Omega} = 0 \right\}.$$

and by [36, Theorem 3.1.30],

$$D_A(\mu, \infty) = \begin{cases} C^{2\mu}(\bar{\Omega}) & \text{when } \mu \in (0, 1/2), \\ \{w \in C^{2\mu}(\bar{\Omega}) : \frac{\partial w}{\partial n}\big|_{\partial\Omega} = 0\} & \text{when } \mu \in (1/2, 1). \end{cases}$$

In the following, we denote $D_A(\mu, \infty)$ by X^μ for $\mu \in (0, 1)$.

3. Tube Theorem

Suppose a single species with trait any $\alpha \in S$ always sustains a linearly stable equilibrium; i.e.

(T1): (Existence of linearly stable steady state θ_α) For each $\alpha \in S$, (2.1) has a strictly positive steady state $\theta_\alpha \in D(A)$ which is a hyperbolic attractor; that is, if we define the linear operator A_0 by

$$A_0 z := A(\alpha)z + F(\alpha, G(\alpha)\theta_\alpha)z + \theta_\alpha F_w(\alpha, G(\alpha)\theta_\alpha)[G(\alpha)z]$$

then there exists $a_0 > 0$ such that the spectrum $\sigma(A_0)$ satisfies

$$\text{Re}(\sigma(A_0)) \leq -a_0 < 0.$$

(T2): (Regularity of Perturbation in α) There exists a positive smooth function $g : S \to (0, \infty)$ and a constant $\mu \in (0, 1)$, such that $\left(\frac{1}{g(\alpha)}A(\alpha) - \frac{1}{g(\beta)}A(\beta)\right) A(\alpha)^{-\mu}$ is bounded on X, where $A(\alpha)^{-\mu}$ is the fractional power of $A(\alpha)$. Moreover, $\epsilon_{\alpha,\beta} = \|(\frac{1}{g(\alpha)}A(\alpha) - \frac{1}{g(\beta)}A(\beta))A(\alpha)^{-\mu}\|$ tends to zero as $|\beta - \alpha| \to 0$.

Remark 3.1. *(T2) is satisfied for instance if* (i) *$A(\alpha)$ is a bounded operator that depends continuously on α, or if* (ii) *$A(\alpha)$ is a second order elliptic operator subject to a Robin or Neumann boundary condition such that for some positive smooth function $g : S \to (0, \infty)$,*

$$A(\alpha) = g(\alpha) \sum_{ij} a_{ij} D_{ij} + \sum_j b_j(\alpha) D_j + c(\alpha),$$

where a_{ij} is continuous in $x \in \bar{\Omega}$ and satisfies $\sum_{ij} a_{ij}(x)\xi_i\xi_j \geq \nu|\xi|^2$ for some $\nu > 0$ and for all $x \in \bar{\Omega}$ and $\xi \in \mathbb{R}^N$; $b_j(\alpha)$ and $c(\alpha)$ are continuous in x and smooth in α. Precisely, for $\mu \in (1/2, 1)$, $A(\alpha)^{-\mu}$ is a bounded operator from X to $D(A^\mu) \subset D_A(\mu, \infty) = \{w \in C^{2\mu}(\bar{\Omega}) : \mathcal{B}w\big|_{\partial\Omega} = 0\}$ (see [36, Proposition 2.2.15]), and $\frac{1}{g(\alpha)}A(\alpha) - \frac{1}{g(\beta)}A(\beta)$ is a bounded operator from $\{w \in C^{2\mu}(\bar{\Omega}) : \mathcal{B}w\big|_{\partial\Omega} = 0\}$ to X.

The tube theorem says that if u and v are phenotypes of the same species with similar traits $\alpha \approx \beta$, then the total population of the two will be approximately the total population of a single species, i.e. $u + v \approx \theta_\alpha$. If we assume in addition stronger spectral properties, which follows, e.g. if $A(\alpha)$ has a compact, strongly positive resolvent, then we can obtain a stronger form of the Tube Theorem in infinite dimensions.

(T3): (Compact, Strongly Positive Resolvent) For each α, $R(\lambda, A(\alpha)) = (\lambda - A(\alpha))^{-1}$ exists for all sufficiently large $\lambda > 0$, and is compact and strongly positive.

Theorem 3.1. *Assume (T1) and (T2) hold. For each $\epsilon > 0$ and $\alpha \in S$, there exists $\delta > 0$ such that if $\beta \in (\alpha - \delta, \alpha + \delta)$ and $\|u_0 + v_0 - \theta_\alpha\| < \delta$, then (u, v) exists globally in time, and $\|u + v - \theta_\alpha\| < \epsilon$ for all $t \geq 0$. Assume in addition that (T3) holds, then*

$$\Phi^t\left(V^\delta\Gamma_\alpha\right) \subset V^\epsilon\Gamma_\alpha,$$

where $\Gamma_\alpha = \{(s\theta_\alpha, (1-s)\theta_\alpha) : s \in [0,1]\}$ and $V^\delta\Gamma_\alpha$ and $V^\epsilon\Gamma_\alpha$ denote the $\delta-$ and $\epsilon-$ neighborhood of Γ_α in $X \times X$ respectively.

Proof of Theorem 3.1. From now on denote $\|\cdot\| = \|\cdot\|_X$ or $\|\cdot\|_{X \times X}$ depending on context. We may assume without loss of generality that $\|u_0 + v_0 - \theta_\alpha\| < 1$.

  Step 1: For all ϵ, there exists $\delta > 0$ such that if

$$\|u_0 + v_0 - \theta_\alpha\| < \delta, \quad \text{then} \quad \|u + v - \theta_\alpha\| < \epsilon \text{ for all } t \geq 0.$$

Let $w = u + v$. Then w satisfies

(3.1)
$$\begin{cases} w_t = A(\alpha)w + F(\alpha, G(\alpha)w)w + [A(\beta) - A(\alpha)]v + \eta_{\alpha,\beta} \\ w(t) \in D(A) \subset X \quad \text{for } t > 0, \end{cases}$$

where
(3.2)
$$\eta_{\alpha,\beta} = [F(\alpha, G(\alpha)u + G(\beta)v) - F(\alpha, G(\alpha)w)]w + [F(\beta, G(\alpha)u + G(\beta)v) - F(\alpha, G(\alpha)u + G(\beta)v)]v.$$

Then $[A(\beta) - A(\alpha)]v(t)$ will be estimated by (T2), and for some constant $C = C(\|(u_0, v_0)\|) > 0$, we have
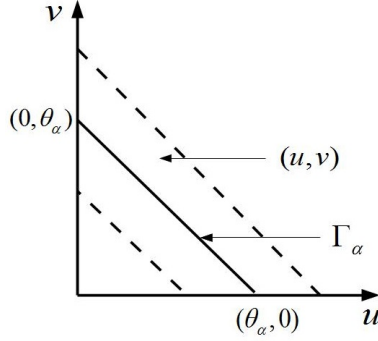
(3.3)
$$\|\eta_{\alpha,\beta}\| \leq C|\beta - \alpha|.$$

FIGURE 1. Dynamics of (2.2) when β is close to α. The distance to Γ_α of points (u, v) along a trajectory of (2.2) starting at (u_0, v_0), defined by $\mathrm{dist}((u, v), \Gamma_\alpha) = \inf_{0 \leq s \leq 1} \|(u, v), (s\theta_\alpha, (1 - s)\theta_\alpha)\|$, has the property that for any $\epsilon > 0$ there exists a $\delta > 0$ such that $\mathrm{dist}((u, v), \Gamma_\alpha) < \epsilon$ if $\mathrm{dist}((u_0, v_0), \Gamma_\alpha) < \delta$. Moreover, $\|u + v - \theta_\alpha\|_X < \epsilon$ for all $t \geq 0$.

Set $z = w - \theta_\alpha = u + v - \theta_\alpha$. As long as $\|w - \theta_\alpha\| = \|z\| < 1$, z satisfies

$$
\begin{aligned}
z_t &= A(\alpha)z + F(\alpha, G(\alpha)\theta_\alpha)z + [F(\alpha, G(\alpha)w) - F(\alpha, G(\alpha)\theta_\alpha)]\, w + [A(\beta) - A(\alpha)]v + \eta_{\alpha,\beta} \\
&= A(\alpha)z + F(\alpha, G(\alpha)\theta_\alpha)z + \big[F_w(\alpha, G(\alpha)\theta_\alpha)[G(\alpha)z] + O(\|z\|^2)\big]\, w + [A(\beta) - A(\alpha)]v + \eta_{\alpha,\beta} \\
&= A(\alpha)z + F(\alpha, G(\alpha)\theta_\alpha)z + F_w(\alpha, G(\alpha)\theta_\alpha)[G(\alpha)z]\theta_\alpha + F_w(\alpha, G(\alpha)\theta_\alpha)[G(\alpha)z]z + O(\|z\|^2)w \\
&\quad + [A(\beta) - A(\alpha)]v + \eta_{\alpha,\beta} \\
&= \{A(\alpha)z + F(\alpha, G(\alpha)\theta_\alpha)z + F_w(\alpha, G(\alpha)\theta_\alpha)[G(\alpha)z]\theta_\alpha\} + f(z) + [A(\beta) - A(\alpha)]v + \eta(t) \\
&= A_0 z + f(z) + [A(\beta) - A(\alpha)]v + \eta_{\alpha,\beta}
\end{aligned}
$$

where $f(z) = F_w(\alpha, G(\alpha)\theta_\alpha)[G(\alpha)z]z + O(\|z\|^2)w$ and we used the fact that X is a Banach algebra in the second equality to get the $O(\|z\|^2)$ term. By the assumption that $\|z\| = \|w - \theta_\alpha\| = \|u + v - \theta_\alpha\| < 1$,

$$
\tag{3.4} \|f(z)\| \leq C\|z\|^2.
$$

Since $A(\alpha)$ is sectorial and F and F_w are bounded, A_0 is sectorial and generates an analytic semigroup. By (T1), there exists $a_0 > 0$ such that $\sigma(A_0) \subset \{z \in \mathbb{C} : \mathrm{Re}\, z < -a_0\}$. Hence there exists $C_1 \geq 1$ depending only on A_0 and a_0 such that (see, e.g. [25, Theorem 1.3.4])

$$
\tag{3.5} \|e^{tA_0}w\| \leq C_1 e^{-a_0 t}\|w\|, \quad t \geq 0.
$$

Also, by the variation of parameters formula (see, e.g. [25, P. 52], [36, P. 124, Proposition 2.4.1]),

$$
\tag{3.6} z = e^{tA_0}z_0 + \int_0^t e^{(t-s)A_0}\big(f(z(s)) + [A(\beta) - A(\alpha)]v + \eta_{\alpha,\beta}(s)\big)\, ds.
$$

Next we estimate the integral term in the variation of parameters formula. We begin with

$$\left\| \int_0^t e^{(t-s)A_0} f(z(s)) + \eta_{\alpha,\beta}\, ds \right\|$$

$$\leq C_1 \int_0^t e^{-a_0(t-s)} \left[\|f(z(s)\| + \|\eta_{\alpha,\beta}(s)\| \right] ds \quad \text{by (3.5)}$$

$$\leq C_2 \int_0^t e^{-a_0(t-s)} \left[\|z(s)\|^2 + |\beta - \alpha| \right] ds \quad \text{by (3.3) and (3.4),}$$

$$\leq C_3 \left(\sup_{[0,t]} \|z(s)\|^2 + |\beta - \alpha| \right),$$

as long as $\|z\| < 1$ in $[0, t]$. Here C_2, C_3 are positive constants independent of the particular solution (u, v).

Claim 1. $\left\| \int_0^t e^{(t-s)A_0}(A(\beta) - A(\alpha))v\, ds \right\| \leq C \tilde{\epsilon}_{\alpha,\beta}$, *where* $\tilde{\epsilon}_{\alpha,\beta} \to 0$ *as* $|\alpha - \beta| \to 0$ *independently of* $t > 0$.

To show the Claim 1, we note that $A(\alpha) = A_0 + B(\alpha)$ for some bounded linear operator $B(\alpha)$ from X to X, and

$$(3.7) \qquad A(\beta) - A(\alpha) = \left(A(\beta) - \frac{g(\beta)}{g(\alpha)} A(\alpha) \right) + \left(\frac{g(\beta)}{g(\alpha)} - 1 \right) (A_0 + B(\alpha)).$$

Hence

$$\int_0^t e^{A_0(t-s)}(A(\beta) - A(\alpha))v(s)\, ds$$

$$= g(\beta) \int_0^t e^{A_0(t-s)} \left(\frac{A(\beta)}{g(\beta)} - \frac{A(\alpha)}{g(\alpha)} \right) A(\alpha)^{-\mu} A(\alpha)^\mu v(s)\, ds + \left(\frac{g(\beta)}{g(\alpha)} - 1 \right) \int_0^t e^{A_0(t-s)}(A_0 + B(\alpha))v(s)\, ds$$

$$= I + II$$

First we estimate I:

$$\|I\| \leq C \epsilon_{\alpha,\beta} \int_0^t \left\| e^{A_0(t-s)} \right\| \|A(\alpha)^\mu v(s)\|\, ds \leq C \epsilon_{\alpha,\beta} \int_0^t e^{-a_0(t-s)}(1 + s^{-\mu})\, ds \leq C \epsilon_{\alpha,\beta},$$

where we have used (T2) and the dissipativity of the system (2.2) in the first and second inequalities respectively. Next, we estimate II:

$$\|II\| \leq \left| \frac{g(\beta)}{g(\alpha)} - 1 \right| \left[\int_0^t \left\| e^{A_0(t-s)} A_0^{\frac{1}{2}} \right\| \left\| A_0^{\frac{1}{2}} v(s) \right\| ds + \int_0^t \left\| e^{A_0(t-s)} B(s) v(s) \right\| ds \right]$$

$$\leq C \left| \frac{g(\beta)}{g(\alpha)} - 1 \right| \left[\int_0^t (t-s)^{-\frac{1}{2}} e^{-a_0(t-s)} \|v(s)\|_{D_A(\frac{1}{2}, 1)} ds + \int_0^t e^{-a_0(t-s)} ds \right]$$

$$\leq C \left| \frac{g(\beta)}{g(\alpha)} - 1 \right| \left[\int_0^t (t-s)^{-\frac{1}{2}} e^{-a_0(t-s)} (1 + s^{-\frac{1}{2}}) ds + \frac{1}{a_0} (1 - e^{-\delta t}) \right]$$

$$\leq C \left| \frac{g(\beta)}{g(\alpha)} - 1 \right|$$

where we have again used dissipativity in the third inequality. This finishes the proof of Claim 1.

By Claim 1, we may deduce from (3.5), (3.6) and the calculation preceeding Claim 1 that

$$(3.8) \qquad \|z(t)\| \leq C_1 \|z_0\| + \tilde{\epsilon}_{\alpha,\beta} + C_3 \left(\sup_{[0,t]} \|z(s)\|^2 + |\beta - \alpha| \right)$$

as long as $\sup_{[0,t]} \|z(s)\| \leq 1$. Now fix any $\epsilon < \min\left\{ 1, \frac{1}{3C_3} \right\}$ and choose $|z_0|$ and $|\beta - \alpha|$ small enough that

$$\tilde{\epsilon}_{\alpha,\beta} < \frac{\epsilon}{3}, \quad \text{and} \quad C_1 \|z_0\| + C_3 |\beta - \alpha| < \frac{\epsilon}{\max\{2C_1, 3\}}.$$

Then $\|z_0\| \leq \epsilon/3 < 1/3$ as $C_1 \geq 1$. Therefore $\|z\| < \epsilon < 1$ for all small positive $t > 0$ and the above argument holds. We claim that $\|z(t)\| < \epsilon$ for all $t \geq 0$. To see the claim, let us suppose to the contrary that $\{t > 0 : \|z(t)\| \geq \epsilon\}$ is non-empty, and let $t_* = \inf\{t > 0 : \|z(t)\| \geq \epsilon\}$. By $\epsilon < 1/(3C_3)$, (3.6) and definition of t_*, for all $t \in [0, t_*]$,

$$\|z(t)\| \leq C_1 \|z_0\| + \tilde{\epsilon}_{\alpha,\beta} + C_3 \left(\sup_{[0,t]} \|z(s)\|^2 + |\beta - \alpha| \right) < 2\epsilon/3 + C_3 \epsilon^2 < \epsilon.$$

Hence $\sup_{t \in [0,t_*]} \|z(t)\| < \epsilon$. This contradicts the finiteness of t_* and finishes Step 1.

Step 2: It remains to show that $\mathrm{dist}(u, \mathrm{span}\{\theta_\alpha\})$ remains small, in such event

$$\mathrm{dist}(v, \mathrm{span}\{\theta_\alpha\}) \leq \mathrm{dist}(u + v, \mathrm{span}\{\theta_\alpha\}) + \mathrm{dist}(u, \mathrm{span}\{\theta_\alpha\})$$

also remains small (by Step 1, $\|u + v - \theta_\alpha\|$ is small). Now,

$$u_t = A(\alpha)u + F(\alpha, G(\alpha)u + G(\beta)v)u$$
$$= [A(\alpha) + F(\alpha, G(\alpha)\theta_\alpha)]u + \bar{\eta}(t)$$

for some

$$\bar{\eta}(t) = [F(\alpha, G(\alpha)u + G(\beta)v) - F(\alpha, G(\alpha)\theta_\alpha)]u = O(\|z\| + |\beta - \alpha|).$$

By Step 1, we have $\sup_{t>0} \|\bar{\eta}(t)\| = O(\epsilon)$.

Next, we recall the following spectral decomposition result.

Theorem 3.2. [25, Theorem 1.5.2] *Suppose A is a closed linear operator in X (with domain $D(A) \subset X$) with spectrum $\sigma(A) = \{\lambda_1\} \cup \hat{\sigma}$ such that $\hat{\sigma} \cup \{\infty\}$ is closed in the compactified complex plane. Let*

$$E_1 := \frac{1}{2\pi i} \int_{\partial B_\epsilon(\lambda_1)} (\lambda - A)^{-1} \, d\lambda, \quad E_2 := \frac{1}{2\pi i} \int_\Gamma (\lambda - A)^{-1} \, d\lambda$$

where Γ is a positively oriented smooth curve with $\arg \lambda \to \pm\Theta$ as $|\lambda| \to \infty$ for some $\Theta \in (\pi/2, \pi)$, and having $\hat{\sigma}$ in the interior and λ_1 in the exterior. Then E_1, E_2 are the spectral projections associated with the spectral sets $\{\lambda_1\}$ and $\hat{\sigma}$. Define $X_j = E_j(X)$ $(j = 1, 2)$, then $X = X_1 \oplus X_2$ and X_j $(j = 1, 2)$ are invariant under A. Moreover, if A_j is the restriction of A to X_j, then

$$A_1 : X_1 \to X_1 \quad \text{is bounded,} \quad \sigma(A_1) = \{\lambda_1\},$$

while

$$D(A_2) = D(A) \cap X_2 \quad \text{and} \quad \sigma(A_2) = \hat{\sigma}.$$

Proof. See [16, Chapter 7] or [43, Theorem 5.7 A,B]. □

Take $\bar{A} = A(\alpha) + F(\alpha, G(\alpha)\theta_\alpha)$, then since $\bar{A}$ is sectorial, $\sigma(\bar{A}) \cup \{\infty\}$ is closed in $\mathbb{C}$. We recall the spectral properties of linear operators with strongly positive, compact resolvent, see, e.g. [34].

Proposition 3.3. *If $A : D(A) \to X$ has a strongly positive, compact resolvent, then A has a principal eigenvalue μ_1 which* (i) *is real and simple,* (ii) *has an eigenfunction $\phi_1 \in \text{Int } X_+$, and is such that* (iii) *$\sigma(A) \setminus \{\mu_1\} \subset \{z \in \mathbb{C} : \text{Re } z < \mu_1 - a_0\}$ for some $a_0 > 0$. Moreover, if μ is an eigenvalue of A with an eigenfunction $\phi \in X_+ \setminus \{0\}$, then $\mu = \mu_1$.*

Therefore, by (T3), 0 is a simple eigenvalue of $\bar{A}$ with eigenfunction θ_α, and $\sigma(\bar{A})$ can be decomposed into the closed sets $\{0\}$ and $\sigma(\bar{A}) \setminus \{0\}$, and $\sigma(\bar{A}) \setminus \{0\} \subset \{z \in \mathbb{C} : \text{Re } z < -a_0\}$. Therefore, by Theorem 3.2,

$$u = E_1 u + E_2 u = u_1 + u_2,$$

and

$$\bar{A}_2 = \bar{A}\big|_{E_2(X)=X_2} : X_2 \to X_2.$$

Then

$$\frac{d}{dt} u_2 = \bar{A}_2 u_2 + E_2 \bar{\eta}(t).$$

Hence $u_2 = e^{t\bar{A}_2} u_2(0) + \int_0^t e^{(t-s)\bar{A}_2} E_2 \bar{\eta}(s) \, ds$, so that

$$\|u_2(t)\| \leq C_1 e^{-a_0 t} \|u_2(0)\| + C_2 \sup_{[0,t]} \|E_2 \eta(s)\| \leq C_3 (e^{-a_0 t} \|u_2(0)\| + \epsilon).$$

Hence

$$\text{dist}(u, \text{span}\{\theta_\alpha\}) = \|u_2(t)\| \leq C_3 (\epsilon + \|u_2(0)\|) \quad \text{for all } t \geq 0.$$

Now, if we choose the initial data $(u(0), v(0))$ close to Γ_α so that $\|u_2(0)\| < \epsilon$, then we can deduce that

$$\text{dist}(u, \text{span}\{\theta_\alpha\}) \leq 2C_3 \epsilon \quad \text{for all } t \geq 0.$$

This completes the proof of Theorem 3.1.   □

Remark 3.2. *In fact, Theorem* 3.1 *continues to hold if the compactness and positivity assumption in* (T3) *is weakened to*

> **(T3′):** (*Spectral Property I*) *In addition to* (*T*1), *assume* 0 *is a simple eigenvalue of the operator* $A_\alpha := A(\alpha) + F(\alpha, G(\alpha)\theta_\alpha)$, *and that* $\sigma(A_\alpha) \setminus \{0\} \subset \{z \in \mathbb{C} : \operatorname{Re} z < -a_0\}$ *for some positive constant* $a_0 > 0$.

4. Graph Transform

The most general theory of compact, normally hyperbolic, invariant manifolds for finite-dimensional dynamical systems was independently obtained by Hirsch, Pugh, and Shub [28] and Fenichel [20]. Since then, the theory has been generalized to the infinite-dimensional setting.

For semiflows in a Banach space, the Hadamard method has been successfully applied in the contexts of (i) invariant manifolds without boundary [2]; or (ii) invariant manifolds with boundary that is either overflowing or inflowing [3].

In this section, we apply the Hadamard graph transform technique [23] to prove the persistence of a one-dimensional invariant manifold of equilibria with respect to a semiflow in a Banach space. The methods we use to construct the inertial manifolds are adaptations of the arguments in the study of center manifolds in finite-dimensional spaces [11].

In our settings, the boundary of our invariant manifold lies on two invariant subspaces $X_+ \times \{0\}$ and $\{0\} \times X_+$ of the flow, i.e. it is neither overflowing nor inflowing. As a consequence, the graphs we are working on do not have a common domain. For this purpose, we develop a generalized distance function (to which there is no triangle inequality) and prove the existence of a fixed point via a modified contraction mapping argument.

Beside the Hadamard graph transformation, another important technique that is frequently being used in the classical center manifold theory is the Lyapunov-Perron method [37, 39]. See, e.g. [10] This method relies on the variation of constant formula and allows us to obtain optimal estimates. For our purposes, the Hadamard method is more appropriate as it respects the invariant manifolds $X_+ \times \{0\}$ and $\{0\} \times X_+$ to which the boundary of our invariant manifold belongs.

When $\alpha = \beta$, it can be shown that (2.2) has a one-dimensional manifold of steady states, $\Gamma_\alpha = \{(s\theta_\alpha, (1-s)\theta_\alpha) : s \in [0, 1]\}$ that is an exponential attractor. The tube theorem asserts that for β sufficiently close to α, any trajectory of (2.2) that starts close to Γ_α remains close to Γ_α for all time.

In this section, we assume the following condition which implies **(T2)**.

> **(T2′):** There exist constants $C > 0$ and $\mu \in (0, 1)$ such that $\|[A(\beta) - A(\alpha)]A(\alpha)^{-\mu}\| \le C|\beta - \alpha|$ for all $\alpha, \beta \in \mathcal{S}$.

We shall apply the method of *Graph transform* due to [23] to show that for β close to α, (2.2) has a one-dimensional invariant manifold that is exponentially attracting and that connects the two semi-trivial steady states $(\theta_\alpha, 0)$ and $(0, \theta_\beta)$. Although the proof is

inspired by the arguments of [11], new methods are introduced due to the fact that the flow is generated by an unbounded operator and our invariant manifold has boundary. In particular, we develop a contraction mapping principle for a generalized distance function where the triangle inequality fails to hold.

Theorem 4.1. *Suppose* (T1), (T2′), (T3) *hold and let* $\alpha \in S$. *There exists a constant* $\delta > 0$ *such that for all* $\beta \in (\alpha - \delta, \alpha + \delta)$, *there is a closed one-dimensional invariant manifold* $\Gamma^* \subset V^\delta \Gamma_\alpha$ *with respect to the semiflow* $\Phi_{\alpha,\beta}^t$ *that can be expressed as the graph of a Lipchitz continuous function over* Γ_α, *connecting the semi-trivial steady states* $(\theta_\alpha, 0)$ *and* $(0, \theta_\beta)$. *Moreover,* Γ^* *attracts all trajectories starting in* $V^\delta \Gamma_\alpha$.

4.1. **The equations for** p, z, U**.** We make the transformation $X^\mu \times X^\mu \to \mathbb{R} \times (X^\mu \times E_2 X^\mu)$: $(u, v) \mapsto (p, q) = (p, z, U)$ given by

$$p = (E_1 u)/\theta_\alpha, \quad z = u + v - \theta_\alpha, \quad U = E_2 u,$$

with the inverse transformation $(\hat{u}(p, q), \hat{v}(p, q)) : \mathbb{R} \times (X^\mu \times E_2 X^\mu) \to X^\mu \times X^\mu$ defined by

(4.1) $$u = \hat{u}(p, q) = p\theta_\alpha + U, \quad v = \hat{v}(p, q) = z - (p\theta_\alpha + U) + \theta_\alpha,$$

where E_i, $X_i^\mu = E_i X^\mu$ are the spectral projection and subspaces given by Theorem 3.2 applied to $\bar{A}\big|_{X^\mu}$.
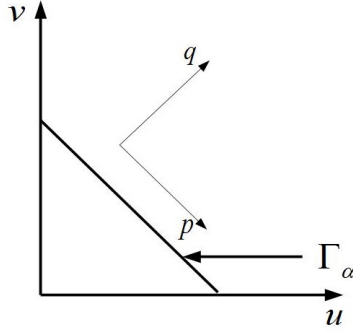

FIGURE 2. A caricature of the coordinate change from (u, v) to $(p, q) = (p, z, U)$ which underlies the graph transform. Here $(u, v) = (\hat{u}(p, q), \hat{v}(p, q))$, and $\hat{u} = p\theta_\alpha + U$, $\hat{v} = (1 - p)\theta_\alpha + z - U$, where $p \in \mathbb{R}$ is now the independent variable.

Now, (p, z, U) satisfies

(4.2) $$\begin{cases} p_t &= E_1[(F(\alpha, G(\alpha)u + G(\beta)v) - F(\alpha, G(\alpha)\theta_\alpha))(U + p\theta_\alpha)]/\theta_\alpha \\ z_t &= A_0 z + f(z) + [A(\beta) - A(\alpha)]v + \eta_{\alpha,\beta} \\ U_t &= \bar{A}_2 U + E_2[(F(\alpha, G(\alpha)u + G(\beta)v) - F(\alpha, G(\alpha)\theta_\alpha))(U + p\theta_\alpha)] \end{cases}$$

where $\eta_{\alpha,\beta} = \eta_{\alpha,\beta}(p, z, U) = \eta_{\alpha,\beta}(u, v)$ satisfies (3.2); $\bar{A} = A(\alpha) + F(\alpha, G(\alpha)\theta_\alpha)$ with spectral projections $\bar{A}_i$ with respect to the spectral spaces X_i $(i = 1, 2)$.

Let (p_i, z_i, U_i) $(i = 1, 2)$ be two solutions of (4.2), and denote $\tilde{p} = p_2 - p_1$, $\tilde{z} = z_2 - z_1$, and $\tilde{U} = U_2 - U_1$, then

(4.3) $\tilde{z}_t = A_0\tilde{z} + f(z_2) - f(z_1) + [A(\beta) - A(\alpha)](\tilde{z} - \tilde{U} - \tilde{p}\theta_\alpha) + \eta_{\alpha,\beta}(p_2, z_2, U_2) - \eta_{\alpha,\beta}(p_1, z_1, U_1),$

where $\|f(z)\| \leq o(\|z\|)$ and $\|\eta_{\alpha,\beta}\| \leq C|\beta - \alpha|$. For $\tilde{U}$, we compute

$$\tilde{U}_t - \bar{A}_2\tilde{U} = E_2[F(\alpha, G(\alpha)u_2 + G(\beta)v_2)u_2 - F(\alpha, G(\alpha)u_1 + G(\beta)v_1)u_1 - F(\alpha, G(\alpha)\theta_\alpha)(\tilde{U} + \tilde{p}\theta_\alpha)]$$
$$= E_2\big[F(\alpha, G(\alpha)u_2 + G(\beta)v_2)(\tilde{U} + \tilde{p}\theta_\alpha) + F_w(\alpha, G(\alpha)u_1 + G(\beta)v_1)[G(\alpha)(\tilde{U} + \tilde{p}\theta_\alpha)$$
$$+ G(\beta)(\tilde{z} - \tilde{U} - \tilde{p}\theta_\alpha)]u_1 - F(\alpha, G(\alpha)\theta_\alpha)(\tilde{U} + \tilde{p}\theta_\alpha) + h.o.t.\big]$$

Here $\|h.o.t.\| \leq o(|\tilde{p}| + \|\tilde{z}\| + \|\tilde{U}\|)$. Therefore, $\tilde{U}$ satisfies

(4.4) $$\tilde{U}_t = \bar{A}_2\tilde{U} + E_2[F_w(\alpha, G(\alpha)\theta_\alpha)[G(\beta)\tilde{z}]p_1\theta_\alpha] + E_2\tilde{F}_1$$

where

(4.5)
$$\tilde{F}_1 = (F(\alpha, G(\alpha)u_2 + G(\beta)v_2) - F(\alpha, G(\alpha)\theta_\alpha))(\tilde{U} + \tilde{p}\theta_\alpha)$$
$$+ F_w(\alpha, G(\alpha)u_1 + G(\beta)v_1)[(G(\alpha) - G(\beta))(\tilde{U} + \tilde{p}\theta_\alpha)]u_1 + F_w(\alpha, G(\alpha)u_1 + G(\beta)v_1)[G(\beta)\tilde{z}]U_1$$
$$+ (F_w(\alpha, G(\alpha)u_1 + G(\beta)v_1) - F_w(\alpha, G(\alpha)\theta_\alpha))[G(\beta)\tilde{z}]p_1\theta_\alpha + h.o.t.$$

satisfies

(4.6) $$\|\tilde{F}_1\| \leq \epsilon|\tilde{p}| + C_0(\|\tilde{z}\| + \|\tilde{U}\|),$$

where ϵ is some arbitrarily some small constant in the application of tube theorem, provided $|\beta - \alpha|$ and $\text{dist}((p_u, z_i, U_i), \{(p, z, U) : z = 0 \text{ and } U = 0\})$ are chosen small. Finally, we compute the equation for $\tilde{p}$, which follows directly from the computations for $\tilde{U}$, but with projection operator E_1 instead of E_2.

(4.7) $$\tilde{p}_t = E_1[F_w(\alpha, G(\alpha)\theta_\alpha)[G(\beta)\tilde{z}]p_1\theta_\alpha] + E_1\tilde{F}_1.$$

4.2. **Linear operator of** (z, U). For each given continuous $p(t) : [0, \infty) \to \mathbb{R}$ such that $\sup_{t>0} |p(t)| \leq 2$, we define the non-autonomous operator $L(t) : D(A) \times E_2(D(A)) \to X \times X_2$ by

$$L(t)\begin{pmatrix} z \\ U \end{pmatrix} = \begin{pmatrix} A_0z \\ \bar{A}_2U + E_2[F_w(\alpha, G(\alpha)\theta_\alpha)[G(\beta)z]p(t)\theta_\alpha] \end{pmatrix},$$

where A_0 is the sectorial operator given in assumption **(T1)**. Then it is well-known [25, Chapter 7] that the linear non-autonomous problem

$$\frac{d}{dt}\begin{pmatrix} z(t) \\ U(t) \end{pmatrix} = L(t)\begin{pmatrix} z(t) \\ U(t) \end{pmatrix}$$

generates a family of *evolution operators* $\Psi(t, \tau)$ (for $0 \leq \tau \leq t$) defined by

$$\begin{pmatrix} z(t) \\ U(t) \end{pmatrix} = \Psi(t, \tau)\begin{pmatrix} z(\tau) \\ U(\tau) \end{pmatrix}$$
$$= \begin{pmatrix} e^{A_0(t-\tau)}z(\tau) \\ e^{\bar{A}_2(t-\tau)}U(\tau) + \int_\tau^t e^{\bar{A}_2(t-s)}E_2[F_w(\alpha, G(\alpha)\theta_\alpha)[G(\beta)e^{A_0(s-\tau)}z(\tau)]p(t)\theta_\alpha] \end{pmatrix}$$

Next, define $q = (z, U)$ and $\|q\|_\mu = \|z\|_\mu + \|U\|_\mu$. Suppose there exists $\gamma > 0$ such that for each $0 \le \nu \le \mu \le 1$, there exists $C_{\mu,\nu}$ such that $\|e^{A_0 t} z_0\|_\mu \le C_{\mu,\nu} e^{-\gamma t} t^{-(\mu-\nu)} \|z_0\|_\nu$ and $\|e^{\bar{A}_2 t} U_0\|_\mu \le C_{\mu,\nu} e^{-\gamma t} t^{-(\mu-\nu)} \|U_0\|_\nu$. (This will hold, for example, for sectorial operators satisfying (3.5).) Then there exists $\delta \in (0, \delta_0)$ such that for each $\mu, \nu \in [0, 1]$, there exists $C'_{\mu,\nu}$ (independent of $p(t)$ as long as $\sup |p| \le 2$) such that

$$(4.8) \qquad \|q(t)\|_\mu = \|\Psi(t, \tau) q(\tau)\|_\mu \le C'_{\mu,\nu} e^{-\gamma(t-\tau)} (t - \tau)^{-(\mu-\nu)} \|q(\tau)\|_\nu$$

for all $0 \le \tau < t$. (Here $\| \cdot \|_\mu = \|(A_0 - I)^\mu \cdot \|$.) Note that

$$(4.9) \qquad \lim_{t \to 0} \|\Psi(t, 0)\|_{\mu,\mu} = 1,$$

where $\|\Psi(t, 0)\|_{\mu,\mu}$ denotes the norm of $\Psi(t, 0)$ regarded as an operator from $X^\mu \times X_2^\mu$ to $X^\mu \times X_2^\mu$.

4.3. **Estimates relating to exponential dichotomy.**

Suppose $(p_i, z_i, U_i) = (p_i, q_i)$ ($i = 1, 2$) are two solutions of (4.2). By the tube theorem, we may take β sufficiently close to α and assume that $\|q_i\|$ is arbitrarily close to 0 for all $t \ge 0$.

Proposition 4.2. *Let μ be as in **(T2$'$)**. For each fixed $T > 0$, there exists a constant $C(T)$ such that for each $\epsilon > 0$, there exists $\delta > 0$ such that if $|\beta - \alpha| < \delta$ then any solution (p_i, q_i) ($i = 1, 2$) of (4.2) satisfying $\sup_{[0,T]} \|q_i(t)\|_\mu < \delta$, $\sup_{[0,T]} |p_i(t)| \le 2$ also satisfy*
(4.10)
$$\|q_2(t) - q_1(t)\|_\mu \le (\|\Psi(t, 0)\|_{\mu,\mu} + C(T)\epsilon) \|q_2(0) - q_1(0)\|_\mu + C(T)\epsilon |p_2(0) - p_1(0)| \quad \text{for } t \in [0, T],$$
and
(4.11)
$$|p_2(t) - p_1(t)| \ge e^{-C(T)\epsilon} (1 - C(T)\epsilon) |p_2(0) - p_1(0)| - C_0 (e^{C(T)\epsilon} + C(T)\epsilon) \|q_2(0) - q_1(0)\|_\mu \quad \text{for } t \in [0, T]$$
where $\|\Psi(t, 0)\|_{\mu,\mu}$ is the norm of $\Psi(t, 0)$, defined in Subsection 4.2 by taking $p = p_1$, as a function from $X^\mu \times X_2^\mu$ to $X^\mu \times X_2^\mu$; C_0 is a constant independent of T and ϵ. In particular, by (4.8),
(4.12)
$$\|q_2(t) - q_1(t)\|_\mu \le (C'_{\mu,\mu} e^{-\gamma t + C(T)\epsilon} + C(T)\epsilon) \|q_2(0) - q_1(0)\|_\mu + C(T)\epsilon |p_2(0) - p_1(0)| \quad \text{for } t \in [0, T].$$

Proof. Let $(p_i, q_i)(p_i, z_i, U_i)$ ($i = 1, 2$) be two solutions of (4.2). Let $\tilde{q} = q_2 - q_1$ and $\tilde{q}_0 = q_2(0) - q_1(0)$. By definition of $\Psi(t, \tau)$ in Subsection 4.2 with $p = p_1$, we have by (4.3) and (4.4),

$$\tilde{q}(t) = \Psi(t, 0) \tilde{q}_0$$
$$+ \int_0^t \Psi(t, \tau) \begin{pmatrix} f(z_2) - f(z_1) + [A(\beta) - A(\alpha)](\tilde{z} - \tilde{U} - \tilde{p}\theta_\alpha + \eta_{\alpha,\beta}(z_2, U_2, p_2) - \eta_{\alpha,\beta}(z_1, U_1, p_1) \\ E_2 \tilde{F}_1 \end{pmatrix} d\tau,$$

where $\tilde{F}_1$ is given by (4.5). For each $\epsilon > 0$, choose $\delta > 0$ such that if $\beta \in (\alpha - \delta, \alpha + \delta)$, and $\sup_{[0,T]} \|q_i(t)\|_\mu < \delta$, then for all $t \in [0, T]$,

$$(4.13) \qquad \begin{aligned} \|\tilde{q}(t)\|_\mu &\le \|\Psi(t, 0)\|_{\mu,\mu} \|\tilde{q}_0\|_\mu + \epsilon \int_0^t \|\Psi(t, s)\|_{0,\mu} (\|\tilde{q}(s)\|_\mu + |\tilde{p}(s)|) \, ds \\ &\le \|\Psi(t, 0)\|_{\mu,\mu} \|\tilde{q}_0\|_\mu + C_0 \epsilon \int_0^t e^{-\gamma(t-s)} (t - s)^{-\mu} (\|\tilde{q}(s)\|_\mu + |\tilde{p}(s)|) \, ds, \end{aligned}$$

By (4.6) and (4.7), we have (provided $|\alpha - \beta| \ll 1$ and $\|q_i\|_\mu \ll 1$)

$$|\tilde{p}_t| \leq C_0(\|\tilde{z}\|_\mu + \|\tilde{U}\|_\mu) + \epsilon|\tilde{p}| = C_0\|\tilde{q}\|_\mu + \epsilon|\tilde{p}|.$$

By integration, we have

(4.14)
$$|\tilde{p}(t)| \leq e^{\epsilon t}|\tilde{p}_0| + C_0 \int_0^t e^{\epsilon(t-\tau)}\|\tilde{q}(\tau)\|_\mu \, d\tau.$$

Substitute (4.14) into (4.13). We have

$$\|\tilde{q}(t)\|_\mu \leq \|\Psi(t,0)\|_{\mu,\mu}\|\tilde{q}_0\|_\mu + C_0\epsilon \int_0^t e^{-\gamma(t-\tau)}(t-\tau)^{-\mu}\|\tilde{q}(\tau)\|_\mu d\tau$$

$$+ C_0\epsilon \int_0^t e^{-\gamma(t-s)}(t-s)^{-\mu}\left[e^{\epsilon s}|\tilde{p}_0| + C_0 \int_0^s e^{\epsilon(s-\tau)}\|\tilde{q}(\tau)\|_\mu \, d\tau\right] ds$$

$$\leq \|\Psi(t,0)\|_{\mu,\mu}\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0| + C(T)\epsilon \int_0^t (t-\tau)^{-\mu}\|\tilde{q}(\tau)\|_\mu \, d\tau.$$

By applying Gronwall's inequality [Henry, Lemma 7.1.1], we deduce that

$$\|\tilde{q}(t)\|_\mu \leq \|\Psi(t,0)\|_{\mu,\mu}\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0| + C(T)\epsilon \int_0^t (t-\tau)^{-\mu}\left[\|\Psi(\tau,0)\|_{\mu,\mu}\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0|\right] d\tau$$

$$\leq (\|\Psi(t,0)\|_{\mu,\mu} + C(T)\epsilon)\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0|.$$

This proves (4.10). Note that substituting the previous line, (4.8) into (4.14), one may conclude that for some C_0 independent of ϵ and T,

(4.15)
$$|p_2(T) - p_1(T)| = |\tilde{p}(T)|$$
$$\leq e^{\epsilon T}|\tilde{p}_0| + C_0 \int_0^T e^{\epsilon(T-\tau)}\left[(\|\Psi(\tau,0)\|_{\mu,\mu} + C(T)\epsilon)\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0|\right] d\tau$$
$$\leq (e^{C(T)\epsilon} + C(T)\epsilon)(|\tilde{p}_0| + C_0\|\tilde{q}_0\|_\mu)$$

To show (4.11), we deduce similarly from (4.7) that

$$|\tilde{p}_t| \geq -\epsilon|\tilde{p}| - C_0\|\tilde{q}\|_\mu.$$

By substituting (4.10) into the previous line, we have

$$|\tilde{p}_t| + \epsilon|\tilde{p}| \geq -C_0\left[(\|\Psi(t,0)\|_{\mu,\mu} + C(T)\epsilon)\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0|\right]$$
$$\geq -C_0\left[(e^{-\gamma t} + C(T)\epsilon)\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0|\right],$$

where we used (4.8). Integrating, we obtain

$$e^{t\epsilon}|\tilde{p}(t)| \geq |\tilde{p}_0| - C_0\left[(e^{C(T)\epsilon} + C(T)\epsilon)\|\tilde{q}_0\|_\mu + C(T)\epsilon|\tilde{p}_0|\right]$$

for all $t \in [0,T]$. This proves (4.11). $\qquad\square$

4.4. **Main Results.** We introduce a function space to which the Graph Transform will apply. We consider the collection of functions $h = (h_z, h_U) : I_h \to X^\mu \times E_2(X^\mu)$ whose graphs over an interval $I_h = (a_h, b_h)$ (depending on h) lies in $V^\delta \Gamma_\alpha$, with the endpoints corresponding to a semi-trivial state, i.e. $(\hat{u}, \hat{v})(a_h, h(a_h)) \in \{0\} \times X_+$ and $(\hat{u}, \hat{v})(b_h, h(b_h)) \in X_+ \times \{0\}$. Precisely, if we recall the notations introduced in (4.1), that amounts to

$$(4.16) \qquad h_U(a_h) + a_h \theta_\alpha = 0 \quad \text{and} \quad h_z(b_h) - (h_U(b_h) + b_h \theta_\alpha) + \theta_\alpha = 0.$$

This motivates us to define

$$\Xi := \{h = (h_z, h_U) : (a_h, b_h) \to X^\mu \times E_2(X^\mu) : \sup \|h\|_\mu < \delta \text{ and } (4.16) \text{ holds.}\}$$

where δ is the constant in the statement of Proposition 4.2, so that $\text{Graph}(h) \subset V^\delta \Gamma_\alpha$ for all $h \in \Xi$. Next, we define

$$(4.17) \qquad \Xi_\rho := \left\{ h \in \Xi : \frac{\|h(p_2) - h(p_1)\|_\mu}{|p_2 - p_1|} \le \rho \text{ for all } p_2, p_1 \in (a_h, b_h) \right\}.$$

We consider small values of ρ so that

$$(4.18) \qquad \frac{1}{2} \theta_\alpha - q' > 0 \quad \text{for all } q' \in X^\mu \text{ with } \|q'\|_\mu < \rho,$$

(which is possible since $\theta_\alpha \in \text{Int } X_+$) and $\cap_{h \in \Xi_\rho} I_h \ne \emptyset$, e.g. $\left[\frac{1}{3}, \frac{2}{3} \right] \subset I_h$ for all $h \in \Xi_\rho$. Moreover, for each $h \in \Xi_\rho$, $(\hat{u}, \hat{v})(p, h(p)) \in (\{0\} \times X_+) \cup (X_+ \times \{0\})$ if and only if $p = a_h$ or $p = b_h$. We define the generalized distance function

$$d(h, h') = \sup_{I_h \cap I_{h'}} \|h(p) - h'(p)\|,$$

which satisfies $d(h, h') \ge 0$ for all $h, h' \in \Xi_\rho$ and equality holds if and only if $I_h = I_{h'}$ and $h = h'$. Although the triangle inequality fails to hold for d, the generalized distance function d suffices for our purpose of locating a fixed point of a contraction mapping.

We first characterize the topology of Ξ_ρ induced by the generalized metric d.

Lemma 4.1. *Suppose* $h_n, h^* \in \Xi_\rho$, *then* $d(h_n, h^*) \to 0$ *if and only if* $a_{h_n} \to a_{h^*}$, $b_{h_n} \to b_{h^*}$ *and for each* $\epsilon > 0$,

$$\sup_{[a_{h^*}+\epsilon, b_{h^*}-\epsilon]} \|h_n - h^*\|_\mu \to 0.$$

Proof. For convenience of notation, we denote

$$a_n := a_{h_n}, \quad b_n := b_{h_n}, \quad a^* := a_{h^*}, \quad b^* := b_{h^*}.$$

First, we assume $a_n \to a^*$, $b_n \to b^*$ and for each given $\epsilon > 0$, $\sup_{[a^*+\epsilon, b^*-\epsilon]} \|h_n - h^*\|_\mu \to 0$. We can then choose N such that for all $n \ge N$,

$$\max\{|a_n - a^*|, |b_n - b^*|\} < \epsilon \quad \text{and} \quad \sup_{[a^*+\epsilon, b^*-\epsilon]} \|h_n - h^*\|_\mu < \epsilon.$$
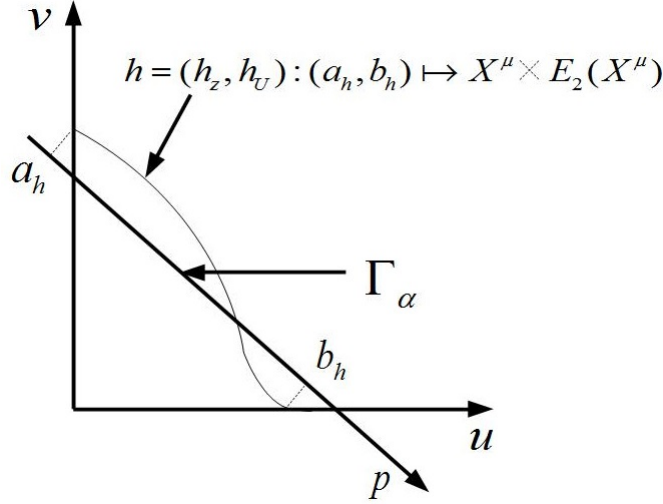
FIGURE 3. Illustration of the graph of $h \in \Xi_\rho$ with domain (a_h, b_h). Here $h(p) = (h_z(p), h_U(p)) \in X^\mu \times E_2(X^\mu)$ for $a_h < p < b_h$.

For each $p \in [a_n, b_n] \cap [a^*, b^*]$, there exists $p_0 \in [a^* + \epsilon, b^* - \epsilon]$ such that $|p - p_0| < 2\epsilon$, hence by the fact that $h_n, h^* \in \Xi_\rho$, i.e. uniform Lipschitz property, we deduce

$$\|h_n(p) - h^*(p)\|_\mu \leq \|h_n(p) - h_n(p_0)\|_\mu + \|h_n(p_0) - h^*(p_0)\|_\mu + \|h^*(p_0) - h^*(p)\|_\mu$$
$$\leq \sup_{[a^* + \epsilon, b^* - \epsilon]} \|h_n - h^*\|_\mu + 4\rho\epsilon$$
$$< (4\rho + 1)\epsilon.$$

This shows that $d(h_n, h^*) < (4\rho + 1)\epsilon$ for all $n \geq N$.

Conversely, assume $d(h_n, h^*) \to 0$. Define

$$\hat{a} = \max\{\limsup_{n\to\infty} a_n, a^*\}, \quad \text{and} \quad \hat{b} = \min\{\liminf_{n\to\infty} b_n, b^*\}.$$

Then it follows from definition that for each $\epsilon > 0$, $\sup_{[\hat{a}+\epsilon, \hat{b}-\epsilon]} \|h_n - h^*\|_\mu \to 0$.

It remains to show that

(4.19) $$\lim_{n\to\infty} a_n = a^* \quad \text{and} \quad \lim_{n\to\infty} b_n = b^*,$$

which implies that $\hat{a} = a^*$ and $\hat{b} = b^*$. We will show (4.19) with two claims.

Claim 2. $\limsup_{n\to\infty} a_n \leq a^*$ *and* $\liminf_{n\to\infty} b_n \geq b^*$.

Suppose there is a subsequence $\{n'\}$ so that $a_0 = \lim_{n'\to\infty} a_{n'} > a^*$. Then by uniform Lipschitz continuity, $h_{n'}(a_{n'}) \to h^*(a_0)$. Thus, by taking limit in $(h_{n'})_U(a_{n'}) + a_{n'}\theta_\alpha = 0$ (the first relation of (4.16)), we obtain

(4.20) $$(h^*)_U(a_0) + a_0\theta_\alpha = 0.$$

Since $h^* \in \Xi_\rho$, we also have

(4.21)
$$(h^*)_U(a^*) + a^*\theta_\alpha = 0.$$

Subtracting (4.21) from (4.20), we deduce that

$$(a_0 - a^*)\left[\theta_\alpha + \frac{(h^*)_U(a_0) - (h^*)_U(a^*)}{a_0 - a^*}\right] = 0,$$

which contradicts the fact that $a_0 > a^*$ and the expression in the square bracket is non-zero (by (4.18)). This shows $\limsup_{n\to\infty} a_n \leq a^*$. The proof for $\liminf_{n\to\infty} b_n \geq b^*$ is analogous. This shows Claim 2.

Claim 3. $\liminf_{n\to\infty} a_n \geq a^*$ and $\limsup_{n\to\infty} b_n \leq b^*$.

Suppose $\liminf_{n\to\infty} a_n < a^*$, then there is a subsequence $\{n'\}$ such that $a_0 := \lim_{n'\to\infty} a_{n'} < a^*$. Then $a^* \in [a_{n'}, b_{n'}]$ for all sufficiently large n', and $d(h_n, h^*) \to 0$ implies that

(4.22)
$$(h_{n'})_U(a^*) + a^*\theta_\alpha \to (h^*)_U(a^*) + a^*\theta_\alpha = 0,$$

as $n' \to \infty$. Here we used $h^* \in \Xi_\rho$ and the first relation of (4.16) in the last equality. Subtracting

(4.23)
$$(h_{n'})_U(a_{n'}) + a_{n'}\theta_\alpha = 0$$

from (4.22), we deduce

$$
\begin{aligned}
0 &= \lim_{n'\to\infty}(a^* - a_{n'})\left[\theta_\alpha + \frac{(h_{n'})_U(a^*) - (h_{n'})_U(a_{n'})}{a^* - a_{n'}}\right] \\
&\geq \lim_{n'\to\infty}(a^* - a_{n'})\frac{\theta_\alpha}{2} \\
&= (a^* - a_0)\frac{\theta_\alpha}{2} > 0.
\end{aligned}
$$

This contradiction establishes $\liminf_{n\to\infty} a_n \geq a^*$. The proof of $\limsup_{n\to\infty} b_n \leq b^*$ is analogous and is omitted. This proves Claim 3 and the proof of Lemma 4.1 is completed. □

Proposition 4.3. *If T^* is a contraction mapping from Ξ_ρ into Ξ_ρ, i.e. there exists $\kappa \in (0,1)$ such that $d(T^*h, T^*h') \leq \kappa d(h, h')$ for all $h, h' \in \Xi_\rho$, then there exists a unique $h^* \in \Xi_\rho$ such that $T^*h^* = h^*$.*

Proof. Suppose ρ is chosen sufficiently small such that $I_0 = \cap_{h\in\Xi_\rho}I_h \neq \emptyset$ and (4.18) holds. Take a particular $h_0 \in \Xi_\rho$, and let $h_n = (T^*)^n h_0$. We are going to show that there exists $h^* \in \Xi_\rho$ such that $\lim_{n\to\infty} d(h_n, h^*) = 0$ and ultimately $h^* = T^*h^*$.

By the standard Contraction Mapping Theorem and the uniform Lipschitz continuity of the sequence, h_n converges uniformly on

$$\liminf_{n\to\infty} I_{h_n} = [\limsup a_{h_n}, \liminf b_{h_n}] := [a^*, b^*]$$

to some h^*. Recall the notations

$$a_n := a_{h_n} \quad \text{and} \quad b_n := b_{h_n}.$$

Let $\{n'\}$ be a subsequence so that $a_{n'} \to a^*$ and $b_{n'} \to b^*$.

Claim 4. $\lim\limits_{n' \to \infty} h_n(a_{n'}) = h^*(a^*)$ *and* $\lim\limits_{n \to \infty} h_n(b_{n'}) = h^*(b^*)$.

Given arbitrary $\epsilon_0 > 0$, then $a^* + \epsilon_0 \in [a_{n'}, b_{n'}]$ for all large n'. Hence,

$$\|h_n(a_{n'}) - h^*(a^*)\|_\mu \leq \|h_n(a_{n'}) - h_n(a^* + \epsilon_0)\|_\mu + \|h_n(a^* + \epsilon_0) - h^*(a^*)\|_\mu.$$

Since $|a_{n'} - a^*| < \epsilon_0$ for all sufficiently large n', we let $n' \to \infty$ to get

$$\limsup_{n' \to \infty} \|h_n(a_{n'}) - h^*(a^*)\|_\mu \leq 2\rho\epsilon_0 + \|h^*(a^* + \epsilon_0) - h^*(a^*)\|_\mu$$

for all $\epsilon_0 > 0$. Letting $\epsilon_0 \to 0$, and using the (Lipschitz) continuity of h^*, we have shown $\lim_{n' \to \infty} h_n(a_{n'}) = h^*(a^*)$. The proof for $\lim_{n' \to \infty} h_n(b_{n'}) = h^*(b^*)$ is analogous. This proves Claim 4.

By Claim 4, we deduce, by passing to the limit in

$$(h_{n'})_U(a_{n'}) + a_{n'}\theta_\alpha = 0 \quad \text{and} \quad (h_{n'})_z(b_{n'}) - ((h_{n'})_U(b_{n'}) + b_{n'}\theta_\alpha) + \theta_\alpha = 0$$

that

$$(h^*)_U(a^*) + a^*\theta_\alpha = 0 \quad \text{and } (h^*)_z(b^*) - ((h^*)_U(b^*) + b^*\theta_\alpha) + \theta_\alpha = 0.$$

This shows that $h^* \in \Xi$, with $\text{Dom}(h^*) = [a^*, b^*]$. Since uniform convergence preserves Lipschitz continuity, we conclude that $h^* \in \Xi_\rho$. In fact, we can show that the full sequences $a_n \to a^*$ and $b_n \to a^*$. By Lemma 4.1, this implies $d(h_n, h^*) \to 0$.

Claim 5. *If* $d(h_n, h^*) \to 0$, *then* $d(h_{n+1}, T^*h^*) \to 0$.

Claim 5 follows easily from the fact that T^* is a contraction, so that

$$d(h_{n+1}, T^*h^*) = d(T^*h_n, T^*h^*) \leq \kappa d(h_n, h^*) \to 0.$$

By the characterization in Lemma 4.1, the limit of $\{h_n\}$ and $\{h_{n+1}\}$ in Ξ_ρ is the same, this gives $h^* = T^*h^*$, which proves the existence of a fixed point in Ξ_ρ.

For uniqueness, suppose h_i^* ($i = 1, 2$) are fixed points of T^* in Ξ_ρ, then $d(h_1^*, h_2^*) = d(T^*h_1^*, T^*h_2^*) \leq \kappa d(h_1^*, h_2^*)$, which implies that $d(h_1^*, h_2^*) = 0$, i.e. $h_1^* = h_2^*$. $\square$

For each $h \in \Xi_\rho$, the Graph of h is given by $\text{Graph}(h) := \{(p, h(p)) : p \in I_h\}$. Now, we define our Graph transform T^*.

Let Ξ_ρ (ρ is a positive constant to be chosen) be as before, and let ϵ, T be some positive constants to be chosen. Let $\Phi^T : X_+ \times X_+ \to X_+ \times X_+$ denote the time T map of the semiflow (4.2). Define the *Graph transform*

$$T^* : \Xi_\rho \to \Xi_\rho \text{ by } T^*h = H, \text{ where } \text{Graph}(H) = \Phi^T(\text{Graph}(h)).$$

The existence of an exponentially attracting, one-dimensional invariant manifold for the system (4.2) is an immediate consequence of the following proposition.

Proposition 4.4. *Fix $\alpha \in S$. There exists $\rho \in (0,1)$, $T > 0$ and $\delta > 0$ sufficiently small such that for all $\beta \in (\alpha - \delta, \alpha + \delta)$, the following holds.*

(i) *The Graph transform $T^* : \Xi_\rho \to \Xi_\rho$ is well-defined.*

(ii) *$T^* : \Xi_\rho \to \Xi_\rho$ is a contraction mapping with respect to the generalized distance function d.*

(iii) *Let $h^* \in \Xi_\rho$ be the fixed point of T^*. Then $\mathrm{Graph}(h^*)$ is an invariant Lipschitz manifold of (4.2). i.e. $\Phi^t(\mathrm{Graph}(h^*)) = \mathrm{Graph}(h^*)$ for all $t > 0$.*

Proof. We will first fix the constants T, ρ and then fix ϵ. Let γ be given in Subsection 4.2, which will be independent of T, ϵ. Choose $T > 0$ large enough so that

$$(4.24) \qquad \max\{C'_{\mu,\mu}, C_0\}e^{-\gamma T/3} < \frac{2}{9} \quad \text{and} \quad C'_{\mu,\mu}e^{-4\gamma T/3} \cdot 3C_0 + C'_{\mu,\mu}e^{-\gamma T} < 1$$

where $C'_{\mu,\mu}$ is given by (4.8) and C_0 is the maximum of those appearing in (4.11) and (4.15). Then choose

$$(4.25) \qquad \rho = e^{-\gamma T/3}.$$

Lemma 4.2. *If $T > 0$ is such that (4.24) holds, we may choose $\epsilon = \epsilon(T)$ sufficiently small so that (4.26) - (4.30) in the following hold:*

$$(4.26) \qquad \frac{e^{C(T)\epsilon} + C(T)\epsilon}{e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3}} < \frac{3}{2},$$

$$(4.27) \qquad \frac{C(T)\epsilon}{e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3}} < \frac{e^{-\gamma T/3}}{2},$$

$$(4.28) \qquad \frac{(C'_{\mu,\mu}e^{-\gamma T/3} + C(T)\epsilon)e^{-\gamma T/3} + C(T)\epsilon}{e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3}} < \frac{e^{-\gamma T/3}}{3},$$

(4.29)

$$e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3} > \frac{2}{3} \quad \text{and} \quad (e^{C(T)\epsilon} + C(T)\epsilon)(1 + C_0 e^{-\gamma T/3}) < \frac{4}{3},$$

and

$(4.30) \ \left[(C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)e^{-\gamma T/3} + C(T)\epsilon\right] \cdot 3(e^{C(T)\epsilon} + C(T)\epsilon)C_0 + (C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon) < 1,$

where $C(T)$ is as in Proposition 4.2.

Proof. By first inequality of (4.24), $C_0 e^{-\gamma T/3} < \frac{1}{3}$, hence (4.26) and (4.29) are satisfied for all ϵ sufficiently small. Also, (4.27) is satisfied by all small ϵ. By the first inequality in (4.24), $C'_{\mu,\mu}e^{-2\gamma T/3} < \frac{e^{-\gamma T/3}}{3}$ and hence (4.28) is satisfied for small ϵ. Finally, (4.30) follows from the second inequality in (4.24). $\square$

Now we begin the proof of part (i) of Proposition 4.4. Let $h \in \Xi_\rho$. We wish to show that $T^*h \in \Xi_\rho$. To show that $\Phi^T(\mathrm{Graph}(h))$ can be represented as the graph of a Lipschitz function H from a subset of $\mathbb{R}$ to the $q = (z, U)$ space (which is a subset of $X^\mu \times X_2^\mu$), it is equivalent to show that, for any $(p'_i, q'_i) \in \Phi^T(\mathrm{Graph}(h))$ $(i = 1, 2)$, we have $\frac{\|q'_2 - q'_1\|_\mu}{|p'_2 - p'_1|} \le \rho$.

Let $(p_i', q_i') \in \Phi^T(\mathrm{Graph}(h))$ $(i = 1, 2)$ be given. By definition, there exists $(p_i, q_i) \in$ Graph(h) $(i = 1, 2)$ such that $(p_i', q_i') = (p_i(T), q_i(T)) := \Phi^T(p_i, q_i)$. We proceed to estimate the Lipschitz coefficient of the resulting graph. By (4.10) and (4.11), for any $t \in [0, T]$,

$$\frac{\|q_2(t) - q_1(t)\|_\mu}{|p_2(t) - p_1(t)|} \leq \frac{(\|\Psi(t, 0)\|_{\mu,\mu} + C(T)\epsilon)\|q_2(0) - q_1(0)\|_\mu + C(T)\epsilon|p_2(0) - p_1(0)|}{e^{-C(T)\epsilon}(1 - C(T)\epsilon)|p_2(0) - p_1(0)| - C_0(e^{C(T)\epsilon} + C(T)\epsilon)\|q_2(0) - q_1(0)\|_\mu}$$

$$\leq \frac{(\|\Psi(t, 0)\|_{\mu,\mu} + C(T)\epsilon)\|q_2(0) - q_1(0)\|_\mu + C(T)\epsilon|p_2(0) - p_1(0)|}{[e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3}]|p_2(0) - p_1(0)|} \qquad (*)$$

where the second inequality follows from the fact that $(p_i(0), q_i(0)) \in \mathrm{Graph}(h)$ for some $h \in \Xi_\rho$ (so that $\|q_2(0) - q_1(0)\|_\mu / |p_2(0) - p_1(0)| \leq \rho$) and that $\rho = e^{-\gamma T/3}$ (by (4.25)). It follows that at $t = T$,

$$\frac{\|q_2' - q_1'\|_\mu}{|p_2' - p_2'|} = \frac{\|q_2(T) - q_1(T)\|_\mu}{|p_2(T) - p_1(T)|}$$

$$\leq \frac{(C_{\mu,\mu}' e^{-\gamma T/3} + C(T)\epsilon)e^{-\gamma T/3} + C(T)\epsilon}{e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3}}$$

$$< e^{-\gamma T/3}/3 = \rho/3.$$

where we have used (4.8) for the inequality and (4.28) for the strict inequality. We may then conclude:

Claim 6. $\Phi^T(Graph(h))$ *is the Graph of some function* H *with Lipschitz constant* strictly less than $\rho/3$.

Given $h \in \Xi_\rho$, let $\mathrm{Dom}(h) = [a_h, b_h]$. By connectedness and previous step, $\mathrm{Dom}(H) = [a_H, b_H]$ and $(a_H, H(a_H)) = \Phi^T(a_h, h(a_h))$ and $(b_H, H(b_H)) = \Phi^T(b_h, h(b_h))$. By the invariance of $X_+ \times \{0\}$, $\{0\} \times X_+$ and $\mathrm{Int}\,(X_+ \times X_+)$ with respect to the flow (2.2), we see that (4.16) is satisfied at $(a_H, H(a_H))$ and $(b_H, H(b_H))$. This shows that $H \in \Xi_\rho$, i.e. (i) is proved.

We now make an observation which will be used at the end of this subsection.

Remark 4.1. *By (4.26) and (4.9), there exists a small positive constant τ_0 such that for all* $\tau \in [0, \tau_0]$,

$$\frac{\|\Psi(\tau, 0)\|_{\mu,\mu} + C(T)\epsilon}{e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3}} < \frac{3}{2}.$$

By applying the previous line and (4.27) to $(*)$, one deduces that for all $\tau \in [0, \tau_0]$, and $\hat{h} \in \Xi_{\rho/3}$,

$$(4.31) \qquad \frac{\|q_2(\tau) - q_1(\tau)\|_\mu}{|p_2(\tau) - p_1(\tau)|} < \frac{3}{2}\frac{\|q_2(0) - q_1(0)\|_\mu}{|p_2(0) - p_1(0)|} + \frac{\rho}{2} \leq \rho.$$

In particular, for any $\hat{h} \in \Xi_{\rho/3}$, $\Phi^\tau(\mathrm{Graph}(\hat{h}))$ is the Graph of a function $\hat{H}$ with Lipschitz constant less than or equal to ρ. Together with the invariance of $\{0\} \times X_+$, $X_+ \times \{0\}$ and $\mathrm{Int}\,(X_+ \times X_+)$, we conclude that if $\hat{h} \in \Xi_{\rho/3}$ then for all $\tau \in [0, \tau_0]$, $\Phi^\tau(\mathrm{Graph}(h))$ can be represented as the Graph of some $\hat{H} \in \Xi_\rho$. Note here that this contrasts with Proposition 4.4(i) where $\hat{H} \in \Xi_\rho$ when $\hat{h} \in \Xi_\rho$.

Next, we prove part (ii) of Proposition 4.4. Let $h_1, h_2 \in \Xi_\rho$ and denote $H_i = T^*(h_i)$, for $i = 1, 2$. For any $p \in I_{H_1} \cap I_{H_2}$, we choose p_1, p_2 such that $\Phi^T(p_i, h_i(p_i)) = (p, H_i(p))$. Next, choose p_3 between p_1, p_2 (i.e. $|p_1 - p_3| + |p_3 - p_2| = |p_1 - p_2|$) such that $p_3 \in I_{h_1} \cap I_{h_2}$ and

$$(4.32) \qquad 5|p_1 - p_3| \leq |p_2 - p_3| \quad \text{or} \quad 5|p_2 - p_3| \leq |p_1 - p_3|,$$

which is possible if ρ is chosen small enough so that $|I_h|/|\cap_{\Xi_\rho} I_{h'}| \leq 6/5$. Suppose for definiteness that $5|p_1 - p_3| \leq |p_2 - p_3|$, for the other case can be treated in a similar way. Then, (denoting the projections $\pi_1(p, q) = p$ and $\pi_2(p, q) = q$)

$$(4.33) \qquad \begin{aligned} \|H_2(p) - H_1(p)\|_\mu &= \|\pi_2\Phi^T(p_2, h_2(p_2)) - \pi_2\Phi^T(p_1, h_1(p_1))\|_\mu \\ &\leq \|\pi_2\Phi^T(p_2, h_2(p_2)) - \pi_2\Phi^T(p_3, h_2(p_3))\|_\mu \\ &\quad + \|\pi_2\Phi^T(p_3, h_2(p_3)) - \pi_2\Phi^T(p_3, h_1(p_3))\|_\mu \\ &\quad + \|\pi_2\Phi^T(p_3, h_1(p_3)) - \pi_2\Phi^T(p_1, h_1(p_1))\|_\mu \end{aligned}$$

By (4.12) and (4.8),

$$(4.34) \qquad \begin{aligned} &\|\pi_2\Phi^T(p_3, h_2(p_3)) - \pi_2\Phi^T(p_3, h_1(p_3))\|_\mu \\ &\leq (C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)\|h_2(p_3) - h_1(p_3)\|_\mu \\ &\leq (C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)d(h_2, h_1), \end{aligned}$$

and (since $h \in \Xi_\rho$ and $\rho = e^{-\gamma T/3}$)

$$(4.35) \qquad \begin{aligned} &\|\pi_2\Phi^T(p_2, h_2(p_2)) - \pi_2\Phi^T(p_3, h_2(p_3))\|_\mu \\ &\leq (C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)\|h_2(p_2) - h_2(p_3)\|_\mu + C(T)\epsilon|p_2 - p_3| \\ &\leq [(C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)e^{-\gamma T/3} + C(T)\epsilon]|p_2 - p_3|, \end{aligned}$$

Similarly,

$$(4.36) \quad \|\pi_2\Phi^T(p_3, h_1(p_3)) - \pi_2\Phi^T(p_1, h_1(p_1))\|_\mu \leq [(C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)e^{-\gamma T/3} + C(T)\epsilon]|p_3 - p_1|,$$

Substituting (4.34), (4.35) and (4.36) in (4.33), we see that (since p_3 is between p_1 and p_2)

$$(4.37)$$
$$\begin{aligned} &\|H_2(p) - H_1(p)\|_\mu \\ &\leq [(C'_{\mu,\mu}e^{-\gamma T + C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3} + C(T)\epsilon]|p_1 - p_2| + (C'_{\mu,\mu}e^{-\gamma T + C(T)\epsilon} + C(T)\epsilon)d(h_1, h_2). \end{aligned}$$

Next, we estimate $|p_1 - p_2|$ in terms of $d(h_1, h_2)$. Since $\pi_1\Phi^T(p_1, h_1(p_1)) = \pi_1\Phi^T(p_2, h_2(p_2)) = p$, we have

$$\begin{aligned} &-[\pi_1\Phi^T(p_3, h_2(p_3)) - \pi_1\Phi^T(p_3, h_1(p_3))] \\ &= [\pi_1\Phi^T(p_2, h_2(p_2)) - \pi_1\Phi^T(p_3, h_2(p_3))] + [\pi_1\Phi^T(p_3, h_1(p_3)) - \pi_1\Phi^T(p_1, h_1(p_1))] \end{aligned}$$

and hence

$$(4.38) \qquad \begin{aligned} &|\pi_1\Phi^T(p_3, h_2(p_3)) - \pi_1\Phi^T(p_3, h_1(p_3))| \\ &\geq |\pi_1\Phi^T(p_2, h_2(p_2)) - \pi_1\Phi^T(p_3, h_2(p_3))| - |\pi_1\Phi^T(p_3, h_1(p_3)) - \pi_1\Phi^T(p_1, h_1(p_1))|. \end{aligned}$$

By (4.11) and (4.29),

$$(4.39) \qquad \begin{aligned} &|\pi_1\Phi^T(p_2, h_2(p_2)) - \pi_1\Phi^T(p_3, h_2(p_3))| \\ &\geq e^{-C(T)\epsilon}(1 - C(T)\epsilon)|p_2 - p_3| - C_0(e^{C(T)\epsilon} + C(T)\epsilon\|h_2(p_2) - h_2(p_3)\|_\mu \\ &\geq [e^{-C(T)\epsilon}(1 - C(T)\epsilon) - C_0(e^{C(T)\epsilon} + C(T)\epsilon)e^{-\gamma T/3}]|p_2 - p_3| \\ &\geq \tfrac{2}{3}|p_2 - p_3|. \end{aligned}$$

By (4.15) and (4.29),

(4.40)
$$\begin{aligned}
|\pi_1\Phi^T(p_3, h_1(p_3)) - \pi_1\Phi^T(p_1, h_1(p_1))| &\le (e^{C(T)\epsilon} + C(T)\epsilon)(|p_1 - p_3| + C_0\|h_1(p_3) - h_1(p_1)\|_\mu) \\
&\le (e^{C(T)\epsilon} + C(T)\epsilon)(1 + C_0 e^{-\gamma T/3})|p_1 - p_3| \\
&\le \tfrac{4}{3}|p_1 - p_3|.
\end{aligned}$$

If we subtract (4.40) from (4.39), we deduce

(4.41)
$$\begin{aligned}
&|\pi_1\Phi^T(p_2, h_2(p_2)) - \pi_1\Phi^T(p_3, h_2(p_3))| - |\pi_1\Phi^T(p_3, h_1(p_3)) - \pi_1\Phi^T(p_1, h_1(p_1))| \\
&\ge \tfrac{2}{3}|p_3 - p_2| - \tfrac{4}{3}|p_1 - p_3| \\
&\ge \tfrac{2}{3}|p_3 - p_2| - \tfrac{1}{3}|p_3 - p_2| + \tfrac{5}{3}|p_1 - p_3| - \tfrac{4}{3}|p_1 - p_3| \\
&= \tfrac{1}{3}(|p_3 - p_2| + |p_1 - p_3|) = \tfrac{1}{3}|p_1 - p_2|
\end{aligned}$$

where we used $5|p_1 - p_3| \le |p_2 - p_3|$ in the second inequality.

By (4.38), (4.41) and (4.15), we may estimate $|p_2 - p_1|$ in terms of $d(h_1, h_2)$.

(4.42)
$$\begin{aligned}
\tfrac{1}{3}|p_2 - p_1| &\le |\pi_1\Phi^T(p_3, h_2(p_3)) - \pi_1\Phi^T(p_3, h_1(p_3))| \\
&\le (e^{C(T)\epsilon} + C(T)\epsilon)C_0\|h_2(p_3) - h_1(p_3)\|_\mu \\
&\le (e^{C(T)\epsilon} + C(T)\epsilon)C_0 d(h_1, h_2).
\end{aligned}$$

Substituting (4.42) into (4.37), we have estimated $\|H_2(p) - H_1(p)\|_\mu$ in terms of $d(h_1, h_2)$.

$$\begin{aligned}
\|H_2(p) - H_1(p)\|_\mu \le &\{[C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)e^{-\gamma T/3} + C(T)\epsilon] \cdot 3(e^{C(T)\epsilon} + C(T)\epsilon)C_0 \\
&+ (C'_{\mu,\mu}e^{-\gamma T} + C(T)\epsilon)\}d(h_1, h_2)
\end{aligned}$$

Let κ denote the coefficient of $d(h_2, h_1)$ in the above. By (4.30), it is clear that $\kappa \in (0, 1)$. This implies (ii).

To prove (iii), we apply Proposition 4.3 such that T^* has a unique fixed point h^* in Ξ_ρ. By Claim 6, h^* has Lipschitz constant strictly smaller than $\rho/3$. By Remark 4.1, we can fix a small number $\tau_0 > 0$ such that for $0 \le \tau \le \tau_0$, $\Phi^\tau(\text{Graph}(h^*))$ can be represented as the Graph of a function $H_\tau \in \Xi_\rho$. Then

$$\Phi^T\Phi^\tau(\text{Graph}(h^*)) = \Phi^\tau\Phi^T(\text{Graph}(h^*)) = \Phi^\tau(\text{Graph}(h^*))$$

which implies, by uniqueness of the fixed point in Ξ_ρ, that $\Phi^\tau(\text{Graph}(h^*)) = \text{Graph}(h^*)$. Now for any t, we write $t = \left[\frac{t}{\tau_0}\right]\tau_0 + \tau$ for some $0 \le \tau < \tau_0$. Then

$$\Phi^t(\text{Graph}(h^*)) = \Phi^{\left[\frac{t}{\tau_0}\right]\tau_0 + \tau}(\text{Graph}(h^*)) = \Phi^\tau(\Phi^{\tau_0})^{\left[\frac{t}{\tau_0}\right]}(\text{Graph}(h^*)) = \Phi^\tau(\text{Graph}(h^*)) = \text{Graph}(h^*),$$

i.e., $\text{Graph}(h^*)$ is invariant to (4.2). This proves (iii).

Finally, we note that the invariant manifold given by $\text{Graph}(h*))$ is exponentially attracting follows from the fact that it is the fixed point of the T^* map (representing the forward time T map Φ^T), which is a contraction. $\square$

5. Invasion Implies Fixation

We now define the notion of invasion.

Definition 1. *For each $\beta \in S$ and $w \in X$, define $\tilde{\lambda}(\beta, w)$ by*

$$\tilde{\lambda}(\beta, w) = \inf\{\lambda' \in \mathbb{R} : A(\beta)\phi + F(\beta, w)\phi \leq \lambda'\phi \text{ for some } \phi \in D(A) \text{ such that } \phi > 0 \text{ in } \bar{\Omega}\}.$$

An important special case of the above is the invasion exponent $\lambda(\alpha, \beta)$ which gives the rate of exponential growth/death as a rare phenotype β attempts to invade the steady state population θ_α of phenotype α; i.e.

$$\lambda(\alpha, \beta) = \tilde{\lambda}(\beta, G(\alpha)\theta_\alpha).$$

In view of (T3), one may deduce (see, e.g. [1, P.130, Corollary 1.14]) that $\tilde{\lambda}(\beta, w)$ (resp. $\lambda(\alpha, \beta)$) is the principal eigenvalue, in the sense of Proposition 3.3, of

$$A(\beta)\phi + F(\beta, w)\phi = \lambda\phi \qquad (\text{resp.} \quad A(\beta)\phi + F(\beta, G(\alpha)\theta_\alpha)\phi = \lambda\phi).$$

In particular, if (T3) holds, then $\tilde{\lambda}(\beta, w)$ and $\lambda(\alpha, \beta)$ are both simple eigenvalues. We summarize two useful consequences of this fact.

(C1): $\tilde{\lambda}$ is smooth in $\beta \in S$ and $w \in X$, and λ is smooth in $\alpha, \beta \in S$.

(C2): If for some $\beta \in S$ and $w \in X$, λ' is an eigenvalue of $A(\beta) + F(\beta, w)$ with non-negative eigenfunction φ', then necessarily $\tilde{\lambda}(\beta, w) = \lambda'$ and $\varphi' \in \text{Int } X_+$. In particular, if λ' is an eigenvalue of $A(\beta) + F(\beta, G(\alpha)\theta_\alpha)$ with nonnegative eigenfunction φ', then necessarily $\lambda(\alpha, \beta) = \lambda'$ and $\varphi' \in \text{Int } X_+$.

Suppose (T1), (T2$'$), (T3) hold. By Theorem 4.1, there exists $\delta > 0$ such that if $|\beta - \alpha| < \delta$, then there is a one-dimensional invariant manifold $\Gamma^* \subset V^\delta\Gamma_\alpha$ connecting $(\theta_\alpha, 0)$ and $(0, \theta_\beta)$. Moreover, Γ^* attracts all trajectories starting in $V^\delta\Gamma_\alpha$. Suppose $\frac{\partial\lambda}{\partial\beta}(\alpha_0, \alpha_0) > 0$, then there exists $\delta > 0$ such that for all α, β such that $\alpha_0 - \delta < \alpha < \beta < \alpha_0 + \delta$, we have $\lambda(\alpha, \beta) > 0 > \lambda(\beta, \alpha)$, i.e. phenotype v can invade phenotype u, but not vice versa. We shall see that such an invasion by a population with an advantageous trait will cause that trait to go to fixation, i.e. v will oust u to the point of extinction.

Theorem 5.1. *Assume that* (T1), (T2$'$), (T3) *hold and $\epsilon > 0$ is given. Suppose*

$$(5.1) \qquad \frac{\partial\lambda}{\partial\beta}(\alpha_0, \alpha_0) > 0,$$

then there exists $\delta > 0$ such that for all $\alpha_0 - \delta < \alpha < \beta < \alpha_0 + \delta$, all solutions to (2.2) *initiating in $V^\delta\Gamma_\alpha$ converge to $(0, \theta_\beta)$, i.e. $\omega(V^\delta\Gamma_\alpha) = \{(0, \theta_\beta)\}$.*

A global version of Theorem 5.1 is available if we make additional assumptions regarding the global dynamics of (2.1).

(T4): (Persistence and Uniqueness of θ_α) For all $\alpha \in S$, (2.1) has a globally asymptotically stable steady state $\theta_\alpha \in \text{Int } X_+$.

(T5): (Dissipativity) There exists $\epsilon_0 > 0$ such that for all trajectories (u, v),

$$\epsilon_0 \leq \limsup_{t\to\infty} \|(u, v)\| \leq 1/\epsilon_0.$$

Theorem 5.2. *Suppose* (T1), (T2′), (T3) - (T5) *hold. If* (5.1) *holds, then there exists* $\delta > 0$ *such that if* $\alpha_0 - \delta < \alpha < \beta < \alpha_0 + \delta$, *then* $(0, \theta_\beta)$ *is globally asymptotically stable among all initial conditions* $(u_0, v_0) \in X^+$ *such that* $u_0 \neq 0$ *and* $v_0 \neq 0$.

Remark 5.1. *By the same proof, the symmetric conclusion holds when* $\frac{\partial \lambda}{\partial \beta}(\alpha_0, \alpha_0) < 0$; *i.e. when* $\alpha_0 - \delta < \alpha < \beta < \alpha_0 + \delta$, *then phenotype* u *with lower trait* α *has the advantage.*

Lemma 5.1. *Suppose* (T1), (T3) *and that* $\frac{\partial \lambda}{\partial \beta}(\alpha_0, \alpha_0) \neq 0$. *Then there exists* $\delta > 0$ *such that if* $\alpha, \beta \in (\alpha_0 - \delta, \alpha_0 + \delta)$ *and* $\alpha \neq \beta$, *then* (2.2) *has no positive steady states in* $V^\delta \Gamma_\alpha$.

Proof. Suppose to the contrary that for some sequences $\alpha_k \neq \beta_k$ converging to α_0, (2.2) has positive steady states (u_k, v_k) in $V^{\delta_k} \Gamma_{\alpha_k}$ such that $(u_k, v_k) \to (s_0 \theta_{\alpha_0}, (1 - s_0)\theta_{\alpha_0})$ for some $s_0 \in [0, 1]$. Then by (C2)

$$\tilde{\lambda}(\beta_k, G(\alpha_k)u_k + G(\beta_k)v_k) = 0 = \tilde{\lambda}(\alpha_k, G(\alpha_k)u_k + G(\beta_k)v_k).$$

Subtracting and dividing by $\beta_k - \alpha_k$, we have

$$0 = \left[\tilde{\lambda}(\beta_k, G(\alpha_k)u_k + G(\beta_k)v_k) - \tilde{\lambda}(\alpha_k, G(\alpha_k)u_k + G(\beta_k)v_k) \right] / (\beta_k - \alpha_k)$$

$$= \frac{\partial \tilde{\lambda}}{\partial \beta}(\gamma_k, G(\alpha_k)u_k + G(\beta_k)v_k)$$

for some γ_k between β_k and α_k. By continuity, we may let $k \to \infty$ to conclude that

$$\frac{\partial \lambda}{\partial \beta}(\alpha_0, \alpha_0) = \frac{\partial \tilde{\lambda}}{\partial \beta}(\alpha_0, G(\alpha_0)\theta_{\alpha_0}) = 0.$$

This is in contradiction to (5.1). □

Remark 5.2. (T3) *is needed in Lemma* 5.1 *only to ensure the validity of* (C2).

By considering the restriction of the semiflow $\Phi_{\alpha,\beta}^t$ on the one-dimensional invariant manifold Γ^* (guaranteed by Theorem 4.1), the non-existence of steady states implies that one of the endpoints of Γ^* attracts all trajectories in Γ^*. We omit the proof of the following statement.

Lemma 5.2. *Let* Γ^* *be a one-dimensional invariant manifold of the semiflow* $\Phi_{\alpha,\beta}^t$ *connecting* $(\theta_\alpha, 0)$ *and* $(0, \theta_\beta)$. *Suppose* (2.2) *has no positive steady states on* Γ^*.

- *If* $\lambda(\alpha, \beta) > 0$, *then* $(0, \theta_\beta)$ *is globally asymptotically stable on* $\Gamma^* \setminus \{(\theta_\alpha, 0)\}$;
- *If* $\lambda(\beta, \alpha) > 0$, *then* $(\theta_\alpha, 0)$ *is globally asymptotically stable on* $\Gamma^* \setminus \{(0, \theta_\beta)\}$.

Since the set Γ^* is a local attractor, the steady state $(0, \theta_\beta)$ actually attracts all trajectories in $V^\delta \Gamma_\alpha$ if $\lambda(\alpha, \beta) > 0$, and analogously for $(\theta_\alpha, 0)$ if If $\lambda(\beta, \alpha) > 0$.

Lemma 5.3. *Suppose* (T1), (T2′), (T3) *hold, so that there is a one-dimensional invariant manifold* Γ^* *of the semiflow* $\Phi_{\alpha,\beta}^t$ *connecting* $(\theta_\alpha, 0)$ *and* $(0, \theta_\beta)$, *which is an attractor in* $V^\delta \Gamma_\alpha$. *Suppose* (2.2) *has no positive steady states on* Γ^*.

- *If* $\lambda(\alpha, \beta) > 0$, *then* $(0, \theta_\beta)$ *is globally asymptotically stable on* $V^\delta \Gamma_\alpha \setminus \{(\theta_\alpha, 0)\}$;

• If $\lambda(\beta, \alpha) > 0$, then $(\theta_\alpha, 0)$ is globally asymptotically stable on $V^\delta \Gamma_\alpha \setminus \{(0, \theta_\beta)\}$.

Proof. Since $\Gamma^* \subset V^\delta \Gamma_\alpha$ and $(0, \theta_\beta)$ attracts all trajectories in $\Gamma^* \setminus \{(\theta_\alpha, 0)\}$, it suffices to show that no trajectories starting in Int $V^\delta \Gamma_\alpha$ converge to $(\theta_\alpha, 0)$. Suppose for contradiction that there is $(u, v) \to (\theta_\alpha, 0)$ as $t \to \infty$. First, by $\lambda(\alpha, \beta) > 0$, we can choose $\epsilon_0 > 0$ and $\phi_0 \in \text{Int } X^+$ such that

$$A(\beta)\phi_0 + F(\beta, G(\alpha)u + G(\beta)v)\phi_0 \geq \epsilon_0 \phi_0 \quad \text{for all } t \geq t_0.$$

Let $\delta_0 = \sup\{\delta > 0 : \delta\phi_0 \leq u(t_0)\}$. By (T3), we may deduce by method of upper and lower solutions that

$$v(t) \geq \delta_0 e^{\epsilon_0(t-t_0)}\phi_0 \quad \text{for all } t \geq t_0.$$

But this implies that $v \not\to 0$, which is a contradiction to $(u, v) \to (\theta_\alpha, 0)$. □

Proof of Theorem 5.1. Choose $\delta_1 > 0$ by Lemma 5.1 so that for all $\alpha, \beta \in (\alpha_0 - \delta_1, \alpha_0 + \delta_1)$ with $\alpha \neq \beta$, (2.2) does not have any steady states in $V^{\delta_1}\Gamma_\alpha$. Let $\delta_2 \in (0, \delta_1)$ be chosen small so that for all $\alpha, \beta \in (\alpha_0 - \delta_2, \alpha_0 + \delta_2)$, Theorem 4.1 guarantees the existence of a one-dimensional invariant manifold $\Gamma^* \subset V^{\delta_2}\Gamma_\alpha$ connecting $(\theta_\alpha, 0)$ and $(0, \theta_\beta)$, which attracts all trajectories starting in $V^{\delta_2}\Gamma_\alpha$. Let $\alpha_0 - \delta_2 < \alpha < \beta < \alpha_0 + \delta_2$. Then $\lambda(\alpha, \beta) > 0$, so that by Lemma 5.3, $(0, \theta_\beta)$ is globally asymptotically stable in $V_1^\delta \Gamma_\alpha$. □

Proof of Theorem 5.2. In view of Theorem 5.1, it is enough to show that given $\delta > 0$, provided β is sufficiently close to α, then for all $(u_0, v_0) \neq (0, 0)$, there exists $T > 0$ such that $\Phi^T(u_0, v_0) \in V^\delta \Gamma_\alpha$.

First, we observe that by (T5), there exists $\epsilon_0 > 0$ such that for each $\alpha, \beta \in S$, $\epsilon_0 \leq \limsup_{t\to\infty} \|\Phi^t(u_0, v_0)\| < 1/\epsilon_0$. By the variation of constants formula, one may deduce that for each $\mu \in (0, 1)$, there exists some $C' = C'(\epsilon_0)$ (independent of α and β close to α_0) such that $\limsup_{t\to\infty} \|\Phi^t(u_0, v_0)\|_\mu < C'$.

We now define

$$K = \{(u_0, v_0) \in X_+ \times X_+ : \|(u_0, v_0)\|_\mu \leq C' \quad \text{and} \quad \|(u_0, v_0)\| \geq \epsilon_0\}.$$

It is easy to see that K, being bounded in $X^\mu \times X^\mu$ for some $\mu \in (0, 1)$, is compact in $X \times X$. Also, $(0, 0) \notin K$ by definition.

Claim 7. *Let $\beta = \alpha$. For each $\delta_1 > 0$, there exists $T_1 > 0$ such that $\Phi^{T_1}(K) \subset V_{\delta_1}\Gamma_\alpha$.*

We now prove Claim 7. Let $\beta = \alpha$ and $(u, v) = \Phi^t(u_0, v_0)$ for some $(u_0, v_0) \neq (0, 0)$. By setting $\alpha = \beta$ in the proof of Theorem 3.1, we see that $u + v$ satisfies (2.1) and deduce that $u + v \to \theta_\alpha$ and then $\text{dist}((u, v), \Gamma_\alpha) \to 0$. That is, for each $(u_0, v_0) \neq (0, 0)$ there exists $t_0 > 0$ such that $\Phi^{t_0}(u_0, v_0) \in V^{\delta_1}\Gamma_\alpha$. Claim 7 thus follows from compactness of K and continuous dependence of initial data.

Claim 8. *There exists $\delta_2 > 0$ such that if $\beta \in (\alpha - \delta_2, \alpha + \delta_2)$, then $\Phi^{T_1}(K) \subset V^{\delta_1}\Gamma_\alpha$, where T_1 is given in Claim 7.*

Claim 8 follows from continuous dependence of the semiflow Φ on α and β.

Finally, fix $\beta \in (\alpha - \delta_2, \alpha + \delta_2)$ and let $(u_0, v_0) \neq (0, 0)$ be given. By (T5), and the discussion at the beginning of the proof, $\limsup_{t \to \infty} \|\Phi^t(u_0, v_0)\|_\mu < C'$. Since also $\limsup_{t \to \infty} \|\Phi^t(u_0, v_0)\| > \epsilon_0$, we deduce that there exists $T_2 > 0$ such that $\Phi^{T_2}(u_0, v_0) \in K$. Then by Claim 8, $\Phi^{T_1 + T_2}(u_0, v_0) \in V^{\delta_1} \Gamma_\alpha$. This completes the proof. $\square$

6. Neighborhood Invader Strategy

A strategy $\hat{\alpha} \in S$ is a local Evolutionarily Stable Strategy [Maynard Smith and Price] if there is $\delta > 0$ such that $\lambda(\hat{\alpha}, \beta) < 0$ for all $\beta \in (\hat{\alpha} - \delta, \hat{\alpha} + \delta) \setminus \{\hat{\alpha}\}$. A closely related concept is that of a local Convergence Stable Strategy, which refers to those $\hat{\alpha} \in S$ such that for some $\delta > 0$.

$$(6.1) \qquad \frac{\partial \lambda}{\partial \beta}(\alpha, \alpha) = \begin{cases} > 0 & \text{if } \alpha \in (\hat{\alpha} - \delta, \hat{\alpha}), \\ < 0 & \text{if } \alpha \in (\hat{\alpha}, \hat{\alpha} + \delta). \end{cases}$$

A strategy $\hat{\alpha}$ is a Continuously Stable Strategy [19, 18] if it is both a local Evolutionarily Stable Strategy, and a local Convergence Stable Strategy. We introduce a sufficient condition for $\hat{\alpha} \in S$ to be continuously stable:

(CSS): $\frac{\partial \lambda}{\partial \beta}(\hat{\alpha}, \hat{\alpha}) = 0, \quad \frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) < 0 \quad$ and $\quad \frac{\partial^2 \lambda}{\partial \alpha^2}(\hat{\alpha}, \hat{\alpha}) > 0.$

It is elementary to see that $\frac{\partial \lambda}{\partial \beta}(\hat{\alpha}, \hat{\alpha}) = 0$ together with $\frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) < 0$ implies evolutionary stability. As illustrated in the following lemma, if two traits α and β are both greater, or both less than $\hat{\alpha}$, the trait closer to $\hat{\alpha}$ has the advantage.

Lemma 6.1. *Suppose* (CSS) *holds, then there exists $\delta > 0$ such that*

$$\frac{\partial \lambda}{\partial \beta}(\alpha, \alpha) = \begin{cases} > 0 & \text{if } \alpha \in (\hat{\alpha} - \delta, \hat{\alpha}), \\ < 0 & \text{if } \alpha \in (\hat{\alpha}, \hat{\alpha} + \delta). \end{cases}$$

Proof.

$$\frac{\partial}{\partial t}\left[\frac{\partial \lambda}{\partial \beta}(t, t)\right]\bigg|_{t = \hat{\alpha}} = \frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) + \frac{\partial^2 \lambda}{\partial \alpha \partial \beta}(\hat{\alpha}, \hat{\alpha}).$$

Since $\lambda(t, t) \equiv 0$ for all $t > 0$, we have

$$(6.2) \qquad \frac{\partial^2 \lambda}{\partial \alpha^2}(t, t) + 2\frac{\partial^2 \lambda}{\partial \alpha \partial \beta}(t, t) + \frac{\partial^2 \lambda}{\partial \beta^2}(t, t) = 0.$$

It follows that

$$\frac{\partial}{\partial t}\left[\frac{\partial \lambda}{\partial \beta}(t, t)\right]\bigg|_{t = \hat{\alpha}} = \frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) - \frac{1}{2}\left[\frac{\partial^2 \lambda}{\partial \alpha^2}(\hat{\alpha}, \hat{\alpha}) + \frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha})\right] = \frac{1}{2}\left[\frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) - \frac{\partial^2 \lambda}{\partial \alpha^2}(\hat{\alpha}, \hat{\alpha})\right] < 0.$$

$\square$

In fact, if we assume (CSS), then there exists $\delta > 0$ such that

$$(6.3) \qquad \lambda(\alpha, \beta) = \begin{cases} > 0 & \text{if } \hat{\alpha} \leq \beta < \alpha < \hat{\alpha} + \delta \quad \text{or} \quad \hat{\alpha} - \delta < \alpha < \beta \leq \hat{\alpha}, \\ < 0 & \text{if } \hat{\alpha} \leq \alpha < \beta < \hat{\alpha} + \delta \quad \text{or} \quad \hat{\alpha} - \delta < \beta < \alpha \leq \hat{\alpha}. \end{cases}$$

i.e. the phenotype closer to $\hat{\alpha}$ always invades the phenotype further away from $\hat{\alpha}$, while the reverse invasion always fails, hence the name *local convergence stable strategy*. Suppose the strategy $\hat{\alpha}$ satisfies (CSS), then the following result determines the global dynamics of (2.2) completely, whenever (i) one of α, β equals $\hat{\alpha}$, or (ii) both of them are larger than $\hat{\alpha}$, or (iii) both of them are less than $\hat{\alpha}$.

Theorem 6.1. *Suppose* (T1) - (T3) *and* (CSS) *hold. Then there exists $\delta > 0$ such that if* (i) $\hat{\alpha} \leq \beta < \alpha < \hat{\alpha} + \delta$ *or* (ii) $\hat{\alpha} - \delta \leq \alpha < \beta < \hat{\alpha}$, *then all solutions to* (2.2) *initiating in* $V^\delta \Gamma_\alpha$ *converge to* $(0, \theta_\beta)$, *i.e.* $\omega(V^\delta \Gamma_\alpha) = \{(0, \theta_\beta)\}$.

Theorem 6.2. *Suppose* (T1) - (T5) *and* (CSS) *hold, then there exists $\delta > 0$ such that if* (i) $\hat{\alpha} \leq \beta < \alpha < \hat{\alpha} + \delta$ *or* (ii) $\hat{\alpha} - \delta \leq \alpha < \beta < \hat{\alpha}$, *then* $(0, \theta_\beta)$ *is globally asymptotically stable.*
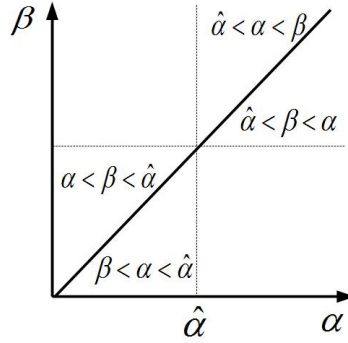

FIGURE 4. Illustration of the range of parameters (α, β) where Theorems 6.1 and 6.2 apply.

The key to the proofs of Theorems 6.1 and 6.2 lies in the following result.

Proposition 6.3. *Suppose* (T1) - (T3), *and* (CSS) *hold. There exist some $\delta > 0$ such that whenever $\beta, \alpha \in (\hat{\alpha} - \delta, \hat{\alpha}]$ or $\beta, \alpha \in [\hat{\alpha}, \hat{\alpha} + \delta)$, then* (2.2) *has a positive steady state in $V^\delta \Gamma_{\hat{\alpha}}$ if and only if $\alpha = \beta$.*

Proof. Suppose to the contrary that the conclusion of the proposition is false and there exists a sequence $\beta_k, \alpha_k \to \hat{\alpha}$, such that either

    (I) $\hat{\alpha} \leq \alpha_k < \beta_k$, or
    (II) $\beta_k < \alpha_k \leq \hat{\alpha}$

and positive steady states (u_k, v_k) of (2.2) corresponding to (α_k, β_k) satisfying

$$(u_k, v_k) \to (s_0 \theta_{\hat{\alpha}}, (1 - s_0) \theta_{\hat{\alpha}}) \quad \text{for some } s_0 \in [0, 1].$$

We have the following technical lemma.

Lemma 6.2. *Let $\epsilon_k = \beta_k - \alpha_k$. Then*

$$\frac{1}{\epsilon_k} (u_k + v_k - \theta_{\alpha_k}) \to (1 - s_0) \frac{\partial}{\partial \alpha} \theta_\alpha \big|_{\alpha = \hat{\alpha}} \quad \text{as } k \to \infty.$$

Proof. Choose $\lambda_0 > 0$ large such that the resolvent $R(\lambda_0, A(\alpha))$ exists for all α in a neighborhood of $\hat{\alpha}$. For simplicity we suppress the subscript k, and write

$$u = u_k, \quad v = v_k, \quad \alpha = \alpha_k, \quad \beta = \beta_k, \quad R_\alpha = R(\lambda_0, \alpha_k), \quad R_\beta = R(\lambda_0, \beta_k)$$

and that

$$\theta = \theta_\alpha, \quad \hat{\theta} = \theta_{\hat{\alpha}}, \quad \hat{R} = R(\lambda_0, \hat{\alpha}).$$

Now, u and v satisfy

$$u = R_\alpha[\lambda_0 u + F(\alpha, G(\alpha)u + G(\beta)v)u], \quad \text{and} \quad v = R_\beta[\lambda_0 v + F(\beta, G(\alpha)u + G(\beta)v)v].$$

Let $w = u + v$, and rewrite the preceding as

(6.4) $\quad u = R_\alpha[\lambda_0 u + F(\alpha, G(\alpha)w)u] + R_\alpha[F(\alpha, G(\alpha)u + G(\beta)v)u - F(\alpha, G(\alpha)w)u]$

and

(6.5)
$$\begin{aligned}
v = \ & R_\alpha[\lambda_0 v + F(\alpha, G(\alpha)w)v] + R_\alpha[F(\alpha, G(\alpha)u + G(\beta)v)v - F(\alpha, G(\alpha)w)v] \\
& + R_\alpha[F(\beta, G(\alpha)u + G(\beta)v)v - F(\alpha, G(\alpha)u + G(\beta)v)v] \\
& + (R_\beta - R_\alpha)[\lambda_0 v + F(\beta, G(\alpha)u + G(\beta)v)v].
\end{aligned}$$

Recall that $\theta = \theta_\alpha$ satisfies

(6.6) $\quad \theta = R_\alpha[\lambda_0 \theta + F(\alpha, G(\alpha)w)\theta] - R_\alpha[F(\alpha, G(\alpha)w)\theta - F(\alpha, G(\alpha)\theta)\theta].$

Let $z = u + v - \theta = w - \theta$ and $\epsilon = \beta - \alpha$, then $z \to 0$ and satisfies

(6.7) $$z = I + II + III + IV + V.$$

Here

(6.8) $\quad I = R_\alpha[\lambda_0 z + F(\alpha, G(\alpha)w)z] = \hat{R}[\lambda_0 z + F(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})z] + T_1 z,$

and

(6.9) $II = R_\alpha[F(\alpha, G(\alpha)w)\theta - F(\alpha, G(\alpha)\theta)\theta] = \hat{R}\left[F_w(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})[G(\hat{\alpha})z]\hat{\theta}\right] + T_2 z + o(\|z\|)$

where $\|T_1\|, \|T_2\| \to 0$ in operator norm,

(6.10)
$$\begin{aligned}
III \ & = R_\alpha[F(\alpha, G(\alpha)u + G(\beta)v)w - F(\alpha, G(\alpha)w)w] \\
& = \epsilon\{\hat{R}\left[F_w(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})[G'(\hat{\alpha})(1 - s_0)\hat{\theta}]\hat{\theta} + o(1),
\end{aligned}$$

(6.11)
$$\begin{aligned}
IV \ & = R_\alpha[F(\beta, G(\alpha)u + G(\beta)v)v - F(\alpha, G(\alpha)u + G(\beta)v)v] \\
& = \epsilon\left\{\hat{R}[F_\alpha(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})(1 - s_0)\hat{\theta}] + o(1)\right\},
\end{aligned}$$

and

(6.12)
$$\begin{aligned}
V \ & = (R_\beta - R_\alpha)[\lambda_0 v + F(\beta, G(\alpha)u + G(\beta)v)v] \\
& = \epsilon\left\{\frac{\partial}{\partial \alpha}R_\alpha\big|_{\alpha=\hat{\alpha}}[\lambda_0(1 - s_0)\hat{\theta} + F(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})(1 - s_0)\hat{\theta}] + o(1)\right\}
\end{aligned}$$

From the equations (6.7) to (6.12) we deduce that

(6.13) $$Tz - T_1 z - T_2 z + o(\|z\|) = \epsilon[(1 - s)K + o(1)]$$

where

$$Tz = z - \hat{R}\left[\lambda_0 z + F(\hat{\alpha}, G(\alpha)\hat{\theta})z + F_w(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})[G(\hat{\alpha})z]\hat{\theta}\right]$$

and

$$K = \hat{R}\left[F_\alpha(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})\hat{\theta} + F_w(\hat{\alpha}, G(\hat{\alpha})[G'(\hat{\alpha})\hat{\theta}]\hat{\theta}\right] + \left.\frac{\partial}{\partial\alpha}R_\alpha\right|_{\alpha=\hat{\alpha}}\left[\lambda_0\hat{\theta} + F(\hat{\alpha}, G(\hat{\alpha})\hat{\theta}\right].$$

By the spectral assumption in (T1), $T : X \to X$ is an invertible linear operator. Since $\|T_i\| \to 0$ in operator norm, $T - T_1 - T_2$ is also invertible, provided $\alpha = \alpha_k$ is sufficiently close to $\hat{\alpha}$. Since $\epsilon \to 0$ and $z \to 0$, we may apply the Implicit Function Theorem to (6.13) to deduce that

(6.14) $$\|z\| = O(\epsilon).$$

Dividing (6.13) by ϵ, and using (6.14), and that $\|T_i\| \to 0$, we see that $\tilde{z} = z/\epsilon$ satisfies $(T - T_1 - T_2)\tilde{z} = K + o(1)$. Since $\|T_i\| \to 0$, this implies

$$\lim \tilde{z} = (1 - s_0)T^{-1}K.$$

Now, differentiating (6.6), we can show that $\hat{\theta}' = \left.\frac{\partial}{\partial\alpha}\theta_\alpha\right|_{\alpha=\hat{\alpha}}$ satisfies

$$\hat{\theta}' = \left.\frac{\partial}{\partial\alpha}R_\alpha\right|_{\alpha=\hat{\alpha}}[\lambda_0\hat{\alpha} + F(\hat{\alpha}, G(\hat{\alpha})\hat{\alpha})\hat{\alpha}]$$
$$+ \hat{R}\left[\lambda_0\hat{\theta}' + F(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})\hat{\theta}' + F_\alpha(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})\hat{\theta} + F_w(\hat{\alpha}, G(\hat{\alpha})\hat{\theta})[G'(\hat{\alpha})\hat{\theta} + G(\hat{\alpha})\hat{\theta}']\hat{\theta}\right],$$

which is equivalent to $T\hat{\theta}' = K$. Hence $\lim \tilde{z} = (1 - s_0)T^{-1}K = (1 - s_0)\hat{\theta}'$. This proves the lemma. $\qquad\square$

Now we are in position to finish the proof of Proposition 6.3. Suppose $\beta_k > \alpha_k \geq \hat{\alpha}$ or $\hat{\alpha} \geq \alpha_k > \beta_k$. By the equation satisfied by u_k, v_k respectively, and denoting $\epsilon_k := \beta_k - \alpha_k$,

$$0 = \tilde{\lambda}(\alpha_k + \epsilon_k, G(\alpha_k)u_k + G(\beta_k)v_k) - \tilde{\lambda}(\alpha_k, G(\alpha_k)u_k + G(\beta_k)v_k)$$
$$= \epsilon_k\frac{\partial\tilde{\lambda}}{\partial\beta}(\alpha_k, G(\alpha_k)u_k + G(\beta_k)v_k) + \frac{\epsilon_k^2}{2}\frac{\partial^2\tilde{\lambda}}{\partial\beta^2}(\gamma_k, G(\alpha_k)u_k + G(\beta_k)v_k)$$

for some γ_k between α_k and $\alpha_k + \epsilon_k$, so that

$$\leq \epsilon_k\left[\frac{\partial\tilde{\lambda}}{\partial\beta}(\alpha_k, G(\alpha_k)u_k + G(\beta_k)v_k) - \frac{\partial\tilde{\lambda}}{\partial\beta}(\alpha_k, G(\alpha_k)\theta_{\alpha_k})\right] + \frac{\epsilon_k^2}{2}\left[\frac{\partial^2\tilde{\lambda}}{\partial\beta^2}(\hat{\alpha}, G(\hat{\alpha})\theta_{\hat{\alpha}}) + o(1)\right].$$

The last inequality follows from the fact that

$$\frac{\partial\lambda}{\partial\beta}(\alpha, \alpha) = \frac{\partial\tilde{\lambda}}{\partial\beta}(\alpha, G(\alpha)\theta_\alpha) = \begin{cases} > 0 & \text{if } \alpha \in (\hat{\alpha} - \delta, \hat{\alpha}), \\ < 0 & \text{if } \alpha \in (\hat{\alpha}, \hat{\alpha} + \delta). \end{cases}$$

Hence by Taylor's expansion again,

$$
0 \leq \epsilon_k \left\{ \frac{\partial^2 \tilde{\lambda}}{\partial w \partial \beta}(\alpha_k, G(\alpha_k)\theta_{\alpha_k}) \left[G(\alpha_k)(u_k + v_k - \theta_{\alpha_k}) + (G(\beta_k) - G(\alpha_k))v_k \right] \right.
$$

$$
\left. + o\left(\| G(\alpha_k)(u_k + v_k - \theta_{\alpha_k}) + (G(\beta_k) - G(\alpha_k))v_k \| \right) \right\} + \frac{\epsilon_k^2}{2}\left[\frac{\partial^2 \tilde{\lambda}}{\partial \beta^2}(\hat{\alpha}, G(\hat{\alpha})\theta_{\hat{\alpha}}) + o(1) \right]
$$

$$
= \epsilon_k^2 \left\{ \frac{\partial^2 \tilde{\lambda}}{\partial w \partial \beta}(\alpha_k, G(\alpha_k)\theta_{\alpha_k}) \left[G(\alpha_k)\frac{u_k + v_k - \theta_{\alpha_k}}{\epsilon_k} + \frac{G(\beta_k) - G(\alpha_k)}{\beta_k - \alpha_k}v_k \right] \right.
$$

$$
\left. + o\left(\left\| G(\alpha_k)\frac{u_k + v_k - \theta_{\alpha_k}}{\epsilon_k} + \frac{G(\beta_k) - G(\alpha_k)}{\epsilon_k}v_k \right\| \right) + \frac{1}{2}\frac{\partial^2 \tilde{\lambda}}{\partial \beta^2}(\hat{\alpha}, G(\hat{\alpha})\theta_{\hat{\alpha}}) + o(1) \right\}.
$$

Now, apply Lemma 6.2 and the identities

$$
\begin{cases}
\frac{\partial^2 \lambda}{\partial \alpha \partial \beta}(\alpha, \beta) = \frac{\partial}{\partial \alpha}\left[\frac{\partial \tilde{\lambda}}{\partial \beta}(\beta, G(\alpha)\theta_{\alpha}) \right] = \frac{\partial^2 \tilde{\lambda}}{\partial \beta \partial w}(\beta, G(\alpha)\theta_{\alpha})\left(G'(\alpha)\theta_{\alpha} + G(\alpha)\frac{\partial \theta_{\alpha}}{\partial \alpha} \right), \\
\frac{\partial \tilde{\lambda}}{\partial \beta}(\beta, G(\alpha)\theta_{\alpha}) = \frac{\partial \lambda}{\partial \beta}(\alpha, \beta) \quad \text{and} \quad \frac{\partial^2 \tilde{\lambda}}{\partial \beta^2}(\beta, G(\alpha)\theta_{\alpha}) = \frac{\partial^2 \lambda}{\partial \beta^2}(\alpha, \beta).
\end{cases}
$$

Continue the above calculation and to get

$$
0 \leq \epsilon_k^2 \left\{ \frac{\partial^2 \tilde{\lambda}}{\partial w \partial \beta}(\hat{\alpha}, G(\hat{\alpha})\theta_{\hat{\alpha}}) \left[G(\hat{\alpha})(1 - s_0)\frac{\partial}{\partial \alpha}\theta_{\alpha}\big|_{\alpha=\hat{\alpha}} + G'(\hat{\alpha})(1 - s_0)\theta_{\hat{\alpha}} \right] + \frac{1}{2}\frac{\partial^2 \tilde{\lambda}}{\partial \beta^2}(\hat{\alpha}, G(\hat{\alpha})\theta_{\hat{\alpha}}) + o(1) \right\}
$$

$$
= \epsilon_k^2 \left\{ (1 - s_0)\frac{\partial^2 \lambda}{\partial \alpha \partial \beta}(\hat{\alpha}, \hat{\alpha}) + \frac{1}{2}\frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) + o(1) \right\}.
$$

Recalling the identity (6.2), we have

$$
0 \leq \epsilon_k^2 \left\{ -\frac{1 - s_0}{2}\left(\frac{\partial^2 \lambda}{\partial \alpha^2}(\hat{\alpha}, \hat{\alpha}) + \frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) \right) + \frac{1}{2}\frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) + o(1) \right\}
$$

$$
= \frac{\epsilon_k^2}{2} \left\{ -(1 - s_0)\frac{\partial^2 \lambda}{\partial \alpha^2}(\hat{\alpha}, \hat{\alpha}) + s_0 \frac{\partial^2 \lambda}{\partial \beta^2}(\hat{\alpha}, \hat{\alpha}) + o(1) \right\}.
$$

The last line is always negative, by our assumptions. This is a contradiction and proves Proposition 6.3. □

Finally, Theorems 6.1 and 6.2 follow by repeating the proofs of Theorems 5.1 and 5.2, using the local stability criterion (6.3) and the non-existence of positive steady states (Proposition 6.3).

7. APPLICATION 1: TUBE THEOREM

In this section, we consider a reaction-diffusion-advection model. In the case of a single species, the model supports more than one stable steady state. Let Ω be a smooth bounded

domain in $\mathbb{R}^N$. Consider

(7.1)
$$\begin{cases} \bar{u}_t = \nabla \cdot (d\nabla \bar{u} - \alpha \bar{u} \nabla m) + g(x, \bar{u} + \bar{v})\bar{u} & \text{in } \Omega \times (0, \infty), \\ \bar{v}_t = \nabla \cdot (d\nabla \bar{v} - \beta \bar{v} \nabla m) + g(x, \bar{u} + \bar{v})\bar{v} & \text{in } \Omega \times (0, \infty), \\ d\frac{\partial \bar{u}}{\partial n} - \alpha \bar{u} \frac{\partial m}{\partial n} = d\frac{\partial \bar{v}}{\partial n} - \beta \bar{v} \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

where $g(x, s)$ is a smooth function satisfying

$$g(x, s) = \begin{cases} (m(x) - s) & \text{for } s \geq \min_{\bar{\Omega}} m, \\ \frac{s-a}{\min_{\bar{\Omega}} m - a}(m(x) - s) & \text{for } s \leq (a + \min_{\bar{\Omega}} m)/2, \end{cases}$$

$a \in (0, \min_{\bar{\Omega}} m)$ is a positive constant, $m(x)$ is a smooth positive function such that

$$\frac{a + \max_{\bar{\Omega}} m}{\min_{\bar{\Omega}} m} < 2.$$

The main result in this section is the following extension of a result in [7], which indicates the selection of advective movement. We will prove the result by applying Theorems 3.1 and 5.1.

Theorem 7.1. *Suppose Ω is convex. There exists $\delta > 0$ such that for all $0 \leq \alpha < \beta < \delta$, every trajectory of (7.1) starting in $V^\delta \Gamma_\alpha$ converges to $(0, \theta_\beta)$ as $t \to \infty$.*

To apply the abstract results proved in the previous sections, we transform the equation by $u = e^{\alpha m/d}\bar{u}$ and $v = e^{\beta m/d}\bar{v}$, so that

(7.2)
$$\begin{cases} u_t = d\Delta u + \alpha\nabla m \cdot \nabla u + g(x, e^{-\alpha m/d}u + e^{-\beta m/d}v)u & \text{in } \Omega \times (0, \infty), \\ v_t = d\Delta v + \beta\nabla m \cdot \nabla v + g(x, e^{-\alpha m/d}u + e^{-\beta m/d}v)v & \text{in } \Omega \times (0, \infty), \\ \frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

Let $A(\alpha) = d\Delta + \alpha\nabla m \cdot \nabla$ subject to a homogeneous Neumann boundary condition. Then by [36, p. 107], $A(\alpha)$ is sectorial, with compact, strongly positive resolvent, and generates an analytic semigroup in $C(\bar{\Omega})$. This verifies (T3). As a result, (7.2) generates an analytic semiflow in $X_+ = \{(u', v') \in C(\bar{\Omega}) \times C(\bar{\Omega}) : u', v' \geq 0\}$. In particular, the Neumann boundary condition is satisfied by the solution for all $t > 0$. We shall check that (T1) and (T2') are also satisfied by the reaction-diffusion-advection system (7.2).

To verify (T1), we first observe some facts about the steady states of the single species case, which are given by the positive solutions of

(7.3)
$$\begin{cases} d\Delta\theta + \alpha\nabla m \cdot \nabla\theta + g(x, e^{-\alpha m/d}\theta)\theta = 0 & \text{in } \Omega, \\ \frac{\partial \theta}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

The following result says that for sufficiently small α, (7.3) has at least two stable solutions. (This is a version of what ecologists call an Allee effect.)

Lemma 7.1. *$\theta \equiv 0$ is a linearly stable solution to (7.3). In addition, there exists $\alpha_1 > 0$ such that for all $\alpha \in [0, \alpha_1)$, (7.3) has a linearly stable positive solution θ_α.*

Proof. It is easy to see that $\theta \equiv 0$ is a solution to (7.3), and the linear stability of which is determined by the principal eigenvalue μ_1 of

$$\begin{cases} d\Delta\varphi + \alpha\nabla m \cdot \nabla\varphi + g(x,0)\varphi = \mu\varphi & \text{in } \Omega, \\ \frac{\partial\varphi}{\partial n} = 0 & \text{on } \partial\Omega, \end{cases}$$

which can be written as

$$d\nabla \cdot [e^{\alpha m/d}\nabla\varphi] + g(x,0)e^{\alpha m/d}\varphi = \mu e^{\alpha m/d}\varphi.$$

By variational characterization, using the fact that $g(x,0) = \frac{-am(x)}{\min_{\bar{\Omega}} m - a} < 0$,

$$\mu_1 = \max_{\varphi \in H^1(\Omega)\setminus\{0\}} \left\{ \frac{\int e^{\alpha m/d}[-d|\nabla\varphi|^2 + g(x,0)\varphi^2]}{\int e^{\alpha m/d}\varphi^2} \right\} < 0.$$

This proves that $\theta \equiv 0$ is linearly stable.

Next, we show the existence of another stable solution θ_α. Let θ_α be the unique positive solution of (see [5])

(7.4)
$$\begin{cases} d\Delta\theta + \alpha\nabla m \cdot \nabla\theta + (m - e^{-\alpha m/d}\theta)\theta = 0 & \text{in } \Omega, \\ \frac{\partial\theta}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

By the maximum principle, one can deduce that when $\alpha = 0$, $\min_{\bar{\Omega}} m < \theta_0 < \max_{\bar{\Omega}} m$. By continuity, there exists $\alpha_1 > 0$ such that for all $\alpha \in [0, \alpha_1)$,

(7.5)
$$\min_{\bar{\Omega}} m < e^{-\alpha m/d}\theta_\alpha < \max_{\bar{\Omega}} m \quad \text{in } \bar{\Omega}.$$

Hence θ_α is a positive solution of (7.3) for all $\alpha \in [0, \alpha_1)$. By (7.4), 0 is the principal eigenvalue of

(7.6)
$$\begin{cases} d\Delta\varphi + \alpha\nabla m \cdot \nabla\varphi + (m - e^{-\alpha m/d}\theta_\alpha)\varphi = \mu\varphi & \text{in } \Omega, \\ \frac{\partial\varphi}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Hence appealing again to a variational characterization,

(7.7)
$$\inf_{\varphi \in H^1\setminus\{0\}} \left\{ \frac{\int_\Omega e^{\alpha m/d}[d|\nabla\varphi|^2 + (\theta_\alpha - m)\varphi^2]}{\int_\Omega e^{\alpha m/d}\varphi^2} \right\} = 0.$$

Finally, by (7.5), the linear stability of θ_α is determined by the principal eigenvalue of

(7.8)
$$\begin{cases} \nabla \cdot (d\nabla\varphi - \alpha\varphi\nabla m) + (m - 2\theta_\alpha)\varphi = \mu\varphi & \text{in } \Omega, \\ d\frac{\partial\varphi}{\partial n} - \alpha\varphi\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Let φ be a principal eigenfunction corresponding to the eigenvalue $\mu = \mu_1$. Multiply (7.8) by $e^{\alpha m/d}\varphi_1$ and integrate by parts. We have

$$\mu_1 = -\frac{\int_\Omega e^{\alpha m/d}[d|\nabla\varphi_1|^2 + (2\theta_\alpha - m)\varphi_1^2]}{\int_\Omega e^{\alpha m/d}\varphi_1^2} < 0 \quad \text{by (7.7)}.$$

i.e., θ_α is linearly stable steady state of (7.3) for all small α.   □

For (T2$'$), we simply observe that $A(\beta) - A(\alpha) = (\beta - \alpha)\nabla m \cdot \nabla$ does not have any second derivative terms. Hence $[A(\beta) - A(\alpha)]A(\alpha)^{-\gamma}$ is bounded in X for each $\gamma \in (1/2, 1)$, and its norm goes to zero as $|\beta - \alpha| \to 0$.

In order to apply Theorem 5.1, we need to determine the sign of $\frac{\partial \lambda}{\partial \beta}(0, 0)$, where $\lambda = \lambda(\alpha, \beta)$ is the principal eigenvalue of

$$(7.9) \qquad \begin{cases} d\Delta\varphi + \beta\nabla m \cdot \nabla\varphi + g(x, e^{-\alpha m/d}\theta_\alpha)\varphi = \lambda\varphi & \text{in } \Omega, \\ \frac{\partial\varphi}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Lemma 7.2. *Suppose Ω is convex. Then $\frac{\partial\lambda}{\partial\beta}(0,0) > 0$.*

Proof. By (7.5), for $\alpha \in [0, \alpha_1)$ (α_1 given by Lemma 7.1) (7.9) becomes

$$(7.10) \qquad \begin{cases} d\Delta\varphi + \beta\nabla m \cdot \nabla\varphi + (m - e^{-\alpha m/d}\theta_\alpha)\varphi = \lambda\varphi & \text{in } \Omega, \\ \frac{\partial\varphi}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Now normalize the principal eigenfunction by $\int_\Omega \varphi^2 = \int_\Omega \theta_\alpha^2$, so that $\beta = \alpha$ implies $\varphi = \theta_\alpha$. Differentiate (7.10) in β, and set $\beta = \alpha$, we have $\lambda = 0$ and (denoting $\varphi' = \frac{\partial}{\partial\beta}\varphi$ and $\lambda' = \frac{\partial\lambda}{\partial\beta}$)

$$\begin{cases} d\Delta\varphi' + \alpha\nabla m \cdot \nabla\varphi' + (m - e^{-\alpha m/d}\theta_\alpha)\varphi' = \lambda'\theta_\alpha - \nabla m \cdot \nabla\theta_\alpha & \text{in } \Omega, \\ \frac{\partial\varphi'}{\partial n} = 0 \quad \text{on } \partial\Omega, \quad \text{and} \quad \int_\Omega \varphi\varphi' = 0. \end{cases}$$

Next, multiply by $e^{\alpha m/d}\theta_\alpha$ and integrate by parts. The left-hand side vanishes and the boundary terms cancel. Hence, we have

$$0 = \lambda' \int_\Omega e^{\alpha m/d}\theta_\alpha^2 - \int_\Omega e^{\alpha m/d}\theta_\alpha\nabla m \cdot \nabla\theta_\alpha.$$

This means

$$\frac{\partial\lambda}{\partial\beta}(\alpha, \alpha) = \frac{\int_\Omega e^{\alpha m/d}\theta_\alpha\nabla m \cdot \nabla\theta_\alpha}{\int_\Omega e^{\alpha m/d}\theta_\alpha^2}.$$

When $\alpha = 0$, we have

$$\frac{\partial\lambda}{\partial\beta}(0, 0) = \frac{\int_\Omega \theta_0\nabla m \cdot \nabla\theta_0}{\int_\Omega \theta_0^2} > 0,$$

where the inequality follows from [6, Lemma 3.3]. $\qquad\square$

Finally, a direct application of Theorem 5.1 yields Theorem 7.1.

8. Application 2: Neighborhood Invader Strategy

The following model, which studies the evolution of a directed dispersal trait, was introduced in [9].

$$(8.1) \qquad \begin{cases} \tilde{u}_t = \nabla \cdot (d\nabla\tilde{u} - \alpha\tilde{u}\nabla m) + (m - \tilde{u} - \tilde{v})\tilde{u} & \text{in } \Omega \times (0, \infty), \\ \tilde{v}_t = \nabla \cdot (d\nabla\tilde{v} - \beta\tilde{v}\nabla m) + (m - \tilde{u} - \tilde{v})\tilde{v} & \text{in } \Omega \times (0, \infty), \\ d\frac{\partial\tilde{u}}{\partial n} - \alpha\tilde{u}\frac{\partial m}{\partial n} = d\frac{\partial\tilde{v}}{\partial n} - \beta\tilde{v}\frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

In this model, u and v represent the population densities of two phenotypes of the same species that differ only by their directed dispersal rates, α and β. Again, if we transform (8.1) by $u = e^{-\alpha m/d}\tilde{u}$ and $v = e^{-\beta m/d}\tilde{v}$, then we obtain

$$
(8.2) \quad
\begin{cases}
u_t = d\Delta u + \alpha\nabla m \cdot \nabla u + (m - e^{\alpha m/d}u - e^{\beta m/d}v)u & \text{in } \Omega \times (0,\infty), \\
v_t = d\Delta v + \beta\nabla m \cdot \nabla v + (m - e^{\alpha m/d}u - e^{\beta m/d}v)v & \text{in } \Omega \times (0,\infty), \\
\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty).
\end{cases}
$$

It is straightforward to check that (T1), (T2′), (T3) - (T5) hold. (See [5, 6] for details.) System (8.1) has two semitrivial steady states $(\theta_\alpha, 0)$ and $(0, \theta_\beta)$, where θ_α is the unique positive steady state of (7.4).

By the proof in [24, Theorem 3.2], we have:

Theorem 8.1. *Suppose $\Omega = (0,1)$ and $m, m_x > 0$ in $[0,1]$. Then*

$$
\frac{\partial\lambda}{\partial\beta}(\alpha,\alpha) =
\begin{cases}
> 0 & \text{if } \alpha \in [0, d/\max_{\bar\Omega} m), \\
< 0 & \text{if } \alpha \in (d/\min_{\bar\Omega} m, \infty).
\end{cases}
$$

Hence by Theorem 5.2, any strategy $\alpha \notin [d/\max_{\bar\Omega} m, d/\min_{\bar\Omega} m]$ can be invaded by strategies closer to the set $[d/\max_{\bar\Omega} m, d/\min_{\bar\Omega} m]$. This suggests that if one is to look for evolutionarily singular strategies (i.e. values of α where $\lambda_\beta(\alpha,\alpha) = 0$) in (8.1) (a necessary condition for ESS), one should focus on $\alpha \in [d/\max_{\bar\Omega} m, d/\min_{\bar\Omega} m]$.

Next, let Ω be a smooth and bounded domain in $\mathbb{R}^N$. The following theorem gives a sufficient condition for the existence of a unique evolutionarily singular strategy in $[d/\max_{\bar\Omega} m, d/\min_{\bar\Omega}]$.

Theorem 8.2 ([31, Theorem 2.2]). *Suppose $\frac{\max_{\bar\Omega} m}{\min_{\bar\Omega} m} \le 3 + 2\sqrt{2}$. For all $\Lambda > 1/\min_{\bar\Omega} m$, there exists $d_0 > 0$ such that for all $d \in (0, d_0)$, there exists a unique $\hat\alpha = \hat\alpha(d) \in [d/\max_{\bar\Omega} m, d/\min_{\bar\Omega} m]$ such that*

$$
\frac{\partial\lambda}{\partial\beta}(\alpha,\alpha) =
\begin{cases}
> 0 & \text{if } \alpha \in [0, \hat\alpha), \\
= 0 & \text{if } \alpha = \hat\alpha, \\
< 0 & \text{if } \alpha \in (\hat\alpha, d\Lambda).
\end{cases}
$$

Theorem 8.2 gives a sufficient condition for $\hat\alpha$ to be an evolutionarily singular strategy in (8.1). By refining the assumptions on Ω and m it is possible to show that $\hat\alpha$ is actually a continuously stable strategy, i.e. $\hat\alpha$ satisfies (CSS), as in the following result.

Theorem 8.3. *Suppose Ω is convex with diameter D and $D\|\nabla\ln m\|_{L^\infty(\Omega)} \le \beta_0$, where $\beta_0 \approx 0.814$ is the unique positive root of the function $t \mapsto 4t + e^{-t} + 2\ln t - 1 - 2\ln\pi$. Then for all d sufficiently small,*

$$
\frac{\partial\lambda}{\partial\beta}(\hat\alpha,\hat\alpha) = 0 \quad \frac{\partial^2\lambda}{\partial\beta^2}(\hat\alpha,\hat\alpha) < 0 \quad \text{and} \quad \frac{\partial^2\lambda}{\partial\alpha^2}(\hat\alpha,\hat\alpha) > 0.
$$

Here $\hat\alpha$ is given in Theorem 8.2.

Proof. The first two inequalities follow from the proof of [31, Theorems 2.5]. The third inequality can be proved by following the arguments in [32, Section 6] for a related model. □

We may now apply Theorem 6.2 to obtain the following result, which says that $\hat{\alpha}$ is a neighborhood invader strategy.

Theorem 8.4. *Under the assumptions in Theorem 8.3, there exists $\delta > 0$ such that if $\hat{\alpha} - \delta < \beta < \alpha \le \hat{\alpha}$ or $\hat{\alpha} \le \alpha < \beta < \hat{\alpha} + \delta$, then $(\theta_\alpha, 0)$ is globally asymptotically stable.*

9. Problems involving Nonlocal Operators

In this section, we would like to show that the results can be applied to problems involving nonlocal operators, even though they do not satisfy the compactness assumption (T3).

9.1. Modeling. The following model has been considered in [8, 27].

$$(9.1) \quad \begin{cases} u_t = \int_\Omega [k(x,y;\alpha)u(y,t) - k(y,x;\alpha)u(x,t)]\, dy + g(x, u+v)u & \text{in } \Omega \times (0,\infty), \\ v_t = \int_\Omega [k(x,y;\beta)v(y,t) - k(y,x;\beta)v(x,t)]\, dy + g(x, u+v)v & \text{in } \Omega \times (0,\infty), \\ u(x,0) = u_0(x) \ge 0 \quad \text{and} \quad v(x,0) = v_0(x) \ge 0 & \text{in } \Omega, \end{cases}$$

where $k(x,y;\alpha), g(x,w)$ are smooth functions, and $k(x,y;\alpha) > 0$ for all $x, y \in \bar{\Omega}$ and $\alpha \in \mathcal{S}$.

Definition 2.　　(i) *For each $\alpha \in \mathcal{S}$, let $A(\alpha)$ be the linear operator defined by $A(\alpha)[\phi] = \int_\Omega k(x,y;\alpha)\phi(y)\, dy - \int_\Omega k(y,x;\alpha)\phi(x)\, dy$.*
　(ii) *For each $\beta \in \mathcal{S}$ and $w \in C(\bar{\Omega})$ let $\tilde{\lambda}(\beta, w)$ be the spectral point of the operator $\phi \mapsto A(\beta)[\phi] + g(x,w)\phi$.*
　Then $A(\alpha)$ can be expressed as $\mathcal{L}$ in (A.1) with $h = -\int_\Omega k(y,x;\alpha)\, dy$.

In this section, we assume

(N1): $g_w(x,w) < 0$ for all $x \in \bar{\Omega}$, $\sup_\Omega g(x,M) < 0$ for some $M > 0$.
(N2): $\tilde{\lambda}(\alpha, g(\cdot, 0)) > 0$ for all $\alpha \in \mathcal{S}$.

Condition (N1) gives an apriori L^∞ bound for solutions to (9.1), while (N2) implies the persistence of a single species. Together, (N1) and (N2) give a sufficient condition for the existence of a globally asymptotically stable steady state θ_α, for each $\alpha \in \mathcal{S}$.

Theorem 9.1 ([4, 12, 30, 41, 42]). *Assume* **(N1)** *and* **(N2)**. *For each $\alpha \in \mathcal{S}$, the equation*

$$(9.2) \quad \begin{cases} \theta_t = A(\alpha)[\theta] + g(x,\theta)\theta & \text{in } \Omega \times (0,\infty), \\ \theta(x,0) = \theta_0(x). \end{cases}$$

has a unique positive equilibrium θ_α. Moreover, θ_α is globally asymptotically stable among all non-negative, non-trivial solutions.

Theorem 9.1 implies the following result concerning the competition system (9.1).

Proposition 9.2. *$(\theta_\alpha, 0)$ and $(0, \theta_\beta)$ are the global attractors in $(X_+ \setminus \{0\}) \times \{0\}$ and $\{0\} \times (X_+ \setminus \{0\})$ respectively.*

Define the partial orders $\leq_K$ and $\ll_K$ of $C(\bar{\Omega}) \times C(\bar{\Omega})$ by

$$(u_1, v_1) \leq_K (u_2, v_2) \quad \Leftrightarrow \quad u_1 \leq u_2 \text{ and } v_1 \geq v_2 \text{ in } \Omega.$$

and

$$(u_1, v_1) \ll_K (u_2, v_2) \quad \Leftrightarrow \quad u_1 < u_2 \text{ and } v_1 > v_2 \text{ in } \bar{\Omega}.$$

Then (9.1) is strongly positive with respect to the partial order $\leq_K$ in the sense that if (u_i, v_i) $(i = 1, 2)$ are solutions to (9.1), then (see [27])

$$(u_1, v_1)\big|_{t=0} <_K (u_2, v_2)\big|_{t=0} \quad \Leftrightarrow \quad (u_1, v_1) \ll_K (u_2, v_2) \text{ for all } t > 0.$$

Proposition 9.3. *There exists an open set $\tilde{U}$ in $\mathcal{S} \times C(\bar{\Omega})$ that contains $\{(\alpha, \theta_\alpha) : \alpha \in \mathcal{S}\}$, such that for all $(\beta, w) \in \tilde{U}$, $\tilde{\lambda}(\beta, w)$ is a simple eigenvalue of $A(\beta) + g(x, w)$ with a positive eigenfunction. In particular, $\tilde{\lambda}(\beta, w)$ is a smooth function in $\tilde{U}$.*

Proof. First, we observe that for all $\alpha \in \mathcal{S}$, $\tilde{\lambda}(\alpha, \theta_\alpha)$ is an eigenvalue of $A(\alpha) + g(x, \theta_\alpha)$ with positive eigenfunction θ_α. It follows from Theorem A.2 that

$$(9.3) \qquad \sup_{x \in \Omega} \left[g(x, \theta_\alpha(x)) - \int_\Omega k(y, x; \alpha)\, dy \right] < \tilde{\lambda}(\alpha, \theta_\alpha) \quad \text{for all } \alpha \in \mathcal{S}.$$

By continuity of $\tilde{\lambda}$ (Lemma A.4), the continuity of g in x, w, and the continuity of k in x, y, α we deduce that

$$\tilde{U} := \left\{ (\beta, w) : \sup_{x \in \Omega} \left[g(x, w) - \int_\Omega k(y, x; \beta)\, dy \right] < \tilde{\lambda}(\beta, w) \right\}$$

is an open set in $S \times X$ that contains $\{(\alpha, \theta_\alpha) : \alpha \in \mathcal{S}\}$. The conclusion of the theorem thus follows from Theorem A.2 and standard arguments based on the implicit function theorem. $\qquad \square$

Corollary 9.1. *There exists an open set U in $\mathcal{S} \times \mathcal{S}$ that contains $\{(\alpha, \alpha) : \alpha \in \mathcal{S}\}$, such that for all $(\alpha, \beta) \in U$, $\lambda(\alpha, \beta)$ is a simple eigenvalue of $A(\beta) + g(x, \theta_\alpha)$ with a positive eigenfunction. In particular, $\lambda(\alpha, \beta)$ is a smooth function in U.*

9.2. **Tube Theorem.** By Remark 3.2, Theorem 3.1 is applicable to (9.1), which yields the following result.

Theorem 9.4. *For each $\alpha \in \mathcal{S}$, and each $\epsilon > 0$, there exists $\delta > 0$ such that if $\beta \in (\alpha - \delta, \alpha + \delta)$ and $(u_0, v_0) \in V^\delta \Gamma_\alpha$, then $(u, v) \in V^\epsilon \Gamma_\alpha$ for all $t \geq 0$.*

Proof. In view of Theorem 3.1 and Remark 3.2, it is enough to verify conditions (T1), (T2) and (T3′). Let $\alpha \in S$ be given. First, the existence of θ_α is guaranteed by Theorem 9.1. By Corollary 9.1, 0 is a principal eigenvalue of $A(\alpha) + g(x, \theta_\alpha)$. Hence (T3′) is a consequence of Proposition A.3. By comparison (Lemma A.4), we deduce that the spectral point λ_p of $A(\alpha) + g(x, \theta_\alpha) + g_w(x, \theta)$ is strictly negative, as $g_w < 0$. Hence (T1) is also verified. Finally, (T2) is a consequence of continuity of k.

$\qquad \square$

9.3. **Invasion Implies Fixation.** We first prove a regularity result for positive steady states of (9.1). We say that (u, v) is a positive steady state of (9.1) if (u, v) is a solution of (9.1) that is independent of t, and if both u and v are non-negative and not identically zero. (See also [Bates and Zhao, JMAA, 2007] for related results for a single species model.)

Proposition 9.5. *Let $(u, v) \in L^\infty(\Omega) \times L^\infty(\Omega)$ be a positive steady state of* (9.1). *Then $(u, v) \in C(\bar{\Omega})$. Moreover, $0 \le u \le \theta_\alpha$ and $0 \le v \le \theta_\beta$ in $\bar{\Omega}$.*

Proof. Suppose (u, v) is a bounded measurable positive steady state of (9.1). By (N1), for all $M > 1$,

$$(9.4) \qquad A(\alpha)M\theta_\alpha + g(x, M\theta_\alpha)M\theta_\alpha < 0, \quad \text{and} \quad A(\beta)M\theta_\beta + g(x, M\theta_\beta)M\theta_\beta < 0.$$

Claim 9. *$u \le \theta_\alpha$ and $v \le \theta_\beta$ a.e. in Ω. In particular, the set of all positive steady states is uniformly bounded in $L^\infty(\Omega) \times L^\infty(\Omega)$.*

Let $M_1 = \inf\{M > 1 : u \le M\theta_\alpha$ a.e. in $\Omega\}$. Suppose to the contrary that $M_1 > 1$, then by continuity $w = M_1\theta_\alpha - u \ge 0$ a.e. in Ω, and $\text{essinf}_\Omega w = 0$. By (9.4) and the fact that $g_w < 0$, w satisfies

$$-\int_\Omega k(x, y; \alpha)w(y)\,dy \ge -\int_\Omega k(y, x; \alpha)\,dy\,w(x) + g(x, M_1\theta_\alpha)M_1\theta_\alpha - g(x, u + v)u$$

$$\ge -\int_\Omega k(y, x; \alpha)\,dy\,w(x) + g(x, M_1\theta_\alpha)M_1\theta_\alpha - g(x, u)u = \Phi w$$

for some $\Phi \in L^\infty$. Here both inequalities are strict on a set of positive measure. If w is non-negative and not identically zero, then since the left-hand side is continuous and has strictly negative essential supremum in Ω, the same is true for the right-hand side. By non-negativity of w, we deduce that $\text{esssup}_\Omega \Phi < 0$ and $\text{essinf}_\Omega w > 0$. This contradicts our choice of M_1. Hence $w \equiv 0$, i.e. $u = M_1\theta_\alpha$. But then by (N1),

$$0 \le A(\alpha)u + g(x, u)u = A(\alpha)M_1\theta_\alpha + g(x, M_1\theta_\alpha)M_1\theta_\alpha \le M_1\left[A(\alpha)\theta_\alpha + g(x, \theta_\alpha)\theta_\alpha\right] = 0.$$

We again obtain a contradiction, as the last inequality is strict on a set of positive measure. This contradiction shows $u \le \theta_\alpha$. Similarly, $v \le \theta_\beta$. This completes the proof of Claim 9.

Now, $\int_\Omega k(y, x; \alpha)\,dy - g(x, u + v)$ and u are both L^∞ bounded in Ω, and

$$(9.5) \qquad \left(\int_\Omega k(y, x; \alpha)\,dy - g(x, u + v)\right)u(x) = \int_\Omega k(x, y; \alpha)u(y)\,dy$$

where the left-hand side is a strictly positive continuous function in $\bar{\Omega}$ (since $u > 0$ on a set of positive measure implies the right-hand side is positive on $\bar{\Omega}$). It follows that

$$(9.6) \qquad \text{essinf}_\Omega u > 0 \quad \text{and} \quad \text{essinf}_\Omega \left(\int_\Omega k(y, x; \alpha)\,dy - g(x, u + v)\right) > 0.$$

By repeating the argument for

$$(9.7) \qquad \left(\int_\Omega k(y, x; \beta)\,dy - g(x, u + v)\right)v(x) = \int_\Omega k(x, y; \beta)v(y)\,dy$$

we similarly deduce that

$$(9.8) \qquad \text{essinf}_\Omega v > 0 \quad \text{and} \quad \text{essinf}_\Omega \left(\int_\Omega k(y,x;\beta)\,dy - g(x,u+v) \right) > 0.$$

Now, suppose to the contrary that u or v is not continuous. By symmetry, we may assume without loss of generality that u is not continuous at some $x_0 \in \bar\Omega$. Hence, there exist two sequences $\{x_n\}$ and $\{y_n\}$ converging to x_0, such that, after passing to subsequences, (by (9.6) and Claim 9)

$$(9.9) \qquad 0 < \lim_{n\to\infty} u(x_n) < \lim_{n\to\infty} u(y_n) < +\infty.$$

By (9.8) and boundedness of v, we may pass into further subsequences and deduce that $\lim_{n\to\infty} v(x_n)$ and $\lim_{n\to\infty} v(y_n)$ exist and are positive, and that

$$\lim_{n\to\infty} \left(\int_\Omega k(y,x;\alpha)\,dy - g(x,u+v) \right) \Big|_{x=x_n} > \lim_{n\to\infty} \left(\int_\Omega k(y,x;\alpha)\,dy - g(x,u+v) \right) \Big|_{x=y_n}.$$

Since $\int_\Omega k(y,x;\alpha)\,dy \in C(\bar\Omega)$, we have

$$(9.10) \qquad \lim_{n\to\infty} g(x,u+v)|_{x=x_n} < \lim_{n\to\infty} g(x,u+v)|_{x=y_n}.$$

This in turn implies, by $\int_\Omega k(y,x;\beta)\,dy \in C(\bar\Omega)$, that

$$\lim_{n\to\infty} \left(\int_\Omega k(y,x;\beta)\,dy - g(x,u+v) \right) \Big|_{x=x_n} > \lim_{n\to\infty} \left(\int_\Omega k(y,x;\beta)\,dy - g(x,u+v) \right) \Big|_{x=y_n},$$

which, in view of (9.7), implies that

$$(9.11) \qquad 0 < \lim_{n\to\infty} v(x_n) < \lim_{n\to\infty} v(y_n) < +\infty.$$

However, the assumption $g_w < 0$, (9.9) and (9.11) together imply that

$$\lim_{n\to\infty} g(x,u+v)|_{x=x_n} > \lim_{n\to\infty} g(x,u+v)|_{x=y_n},$$

which is in contradiction with (9.10). This completes the proof. $\qquad\square$

Here is the main result of this subsection.

Theorem 9.6. *If $\frac{\partial \lambda}{\partial \beta}(\alpha_0,\alpha_0) > 0$ (resp. < 0), then there exists $\delta > 0$ such that if $\alpha_0 - \delta < \alpha < \beta < \alpha_0 + \delta$, then $(0,\theta_\beta)$ (resp. $(\theta_\alpha,0)$) is globally asymptotically stable.*

We prepare for the proof of Theorem 9.6 with two lemmas. Fix $\alpha_0 \in \mathcal{S}$. By Proposition 9.3, we have that the spectral point $\tilde\lambda(\beta,w)$ of $A(\beta) + g(x,w)$ is a smooth function in (β,w) is some neighborhood of $(\alpha_0, \theta_{\alpha_0})$, and that (C1) and (C2) hold.

Lemma 9.2. *Suppose $\frac{\partial \lambda}{\partial \beta}(\alpha_0,\alpha_0) \neq 0$, then for some $\delta > 0$, (2.2) has no positive steady states in $\{(u,v) \in C(\bar\Omega) \times C(\bar\Omega) : u \geq 0 \text{ and } v \geq 0 \text{ in } \Omega\}$, whenever $\alpha, \beta \in (\alpha_0 - \delta, \alpha_0 + \delta)$ and $\alpha \neq \beta$.*

Proof. Suppose to the contrary that there are two sequences $\{\alpha_j\}$, $\{\beta_j\}$ converging to α_0 such that $\alpha_j \neq \beta_j$ for all k.

Lemma 9.3. *Suppose for each j, (9.1) has a positive (u_j, v_j) corresponding to $\alpha = \alpha_j$ and $\beta = \beta_j$. If $\alpha_j, \beta_j \to \alpha_0$, then $\mathrm{dist}((u_j, v_j), \Gamma_{\alpha_0}) \to 0$.*

Proof. We first prove that $w_j = u_j + v_j \to \theta_{\alpha_0}$ as $j \to \infty$. From here on we denote $\theta_j = \theta_{\alpha_j}$ for simplicity. Let $\epsilon > 0$ be given. It suffices to show that $(1 - \epsilon)\theta_j < w_j < (1 + \epsilon)\theta_j$ in Ω for all j sufficiently large.

First, (u_j, v_j) satisfies

$$(9.12) \qquad A(\alpha_j)u_j + g(x, w_j)u_j = 0 \quad \text{and} \quad A(\beta_j)v_j + g(x, w_j)v_j = 0.$$

We observe that u, v, being non-negative and non-trivial, must be strictly positive. For, suppose $u(x_0) = 0$ for some x_0, then at x_0,

$$A(\alpha_j)u_j(x_0) + g(x_0, w_j(x_0))u_j(x_0) = \int_\Omega k(x_0, y; \alpha)u_j(y)\, dy > 0,$$

which is a contradiction. Similarly, $v > 0$ in $\bar{\Omega}$. Adding the two equations in (9.12), we deduce that w_j satisfies

$$(9.13) \qquad A(\alpha_j)w_j + g(x, w_j)w_j = f_j,$$

where $f_j := A(\alpha_j)v_j - A(\beta_j)v_j \to 0$ in $C(\bar{\Omega})$ as $j \to \infty$.

Given $0 < \epsilon < 1$, we have

$$A(\alpha_j)[(1 \pm \epsilon)\theta_j] + g(x, (1 \pm \epsilon)\theta_j)[(1 \pm \epsilon)\theta_j] = (1 \pm \epsilon)[g(x, (1 \pm \epsilon)\theta_j) - g(x, \theta_j)].$$

Using the fact that $\theta_j \to \theta_{\alpha_0}$ as $j \to \infty$, we deduce that for each given ϵ, there exists a positive constant $a_1 > 0$ and integer j_0 such that for all $j \geq j_0$ and all $x \in \bar{\Omega}$,

$$(9.14) \qquad \begin{cases} A(\alpha_j)(1 + \epsilon)\theta_j + g(x, (1 + \epsilon)\theta_j)(1 + \epsilon)\theta_j < -a_1 \\ A(\alpha_j)(1 - \epsilon)\theta_j + g(x, (1 - \epsilon)\theta_j)(1 - \epsilon)\theta_j > a_1. \end{cases}$$

Now we fix $j \geq j_0$ sufficiently large so that $\|f_j\| < a_1$, then $z = (1 + \epsilon)\theta_j - w_j$ satisfies

$$(9.15) \qquad A(\alpha_j)z + [g(x, w_j) + \omega(x, w_j)]z < -a_1 - f_j < 0 \quad \text{in } \bar{\Omega},$$

where (using $g_w < 0$)

$$\omega(x, w_j) = \frac{g(x, (1 + \epsilon)\theta_j) - g(x, w_j)}{(1 + \epsilon)\theta_j - w_j}(1 + \epsilon)\theta_j < 0.$$

By (9.12), we also have

$$(9.16) \qquad u_j > 0 \quad \text{and} \quad A(\alpha_j)u_j + [g(x, w_j) + \omega(x, w_j)]u_j = \omega(x, w_j)u_j < 0 \text{ in } \bar{\Omega}.$$

We claim that $z \geq 0$. Suppose to the contrary that $z < 0$ somewhere, then by applying Lemma A.1 to (9.15) and (9.16), we deduce that $z = -\beta u_j$ for some $\beta > 0$. But this is impossible since both the inequalities of (9.15) and (9.16) are strict. Hence $z \geq 0$, i.e. $w_j \leq (1 + \epsilon)\theta_j$.

Similarly, set $\tilde{z} = w_j - (1 - \epsilon)\theta_j$, then

$$(9.17) \qquad A(\alpha_j)z + [g(x, w_j) + \tilde{\omega}(x, w_j)]z < -a_1 + f_j < 0 \quad \text{in } \bar{\Omega},$$

where (using $g_w < 0$)

$$\tilde{\omega}(x, w_j) = \frac{g(x, w_j) - g(x, (1 - \epsilon)\theta_j)}{w_j - (1 - \epsilon)\theta_j}(1 - \epsilon)\theta_j < 0.$$

We also have

(9.18) $u_j > 0$ and $A(\alpha_j)u_j + [g(x, w_j) + \tilde{\omega}(x, w_j)]u_j = \tilde{\omega}(x, w_j)u_j < 0$ in $\bar{\Omega}$.

It follows by Lemma A.1 applied to (9.17) and (9.18) that $\tilde{z} \geq 0$, i.e. $w_j \geq (1 - \epsilon)\theta_j$. This shows that $w_j \to \theta_{\alpha_0}$ as $j \to \infty$.

Now for each j, u_j is principal eigenfunction of $A(\alpha_j) + g(x, w_j)$ such that $\sup_j\{\|u_j\|\} < +\infty$. By writing

$$u_j = \frac{\int_\Omega k(x, y; \alpha_j)u_j(y)\, dy}{\int_\Omega k(y, x; \alpha_j)\, dy - g(x, w_j)}$$

and noticing that by the convergence of $\alpha_j \to \alpha_0$ and $w_j \to \theta_{\alpha_0}$,

$$\inf_j \left[\inf_\Omega \int_\Omega k(y, x; \alpha_j)\, dy - g(x, w_j)\right] > 0,$$

we can deduce by compactness that u_j converges to the one-dimensional space spanned by the principal eigenfunction θ_{α_0} of $L(\alpha_0) + g(x, \theta_{\alpha_0})$. i.e. $\mathrm{dist}(u_j, \mathrm{span}\{\theta_{\alpha_0}\}) \to 0$. Since also $u_j + v_j \to \theta_{\alpha_0}$, we have $\mathrm{dist}((u_j, v_j), \Gamma_{\alpha_0}) \to 0$. $\square$

By Lemma 9.3, we may repeat the arguments in Lemma 5.1 to finish the proof. $\square$

The following argument is inspired by [27].

Proof of Theorem 9.6. By Lemma 9.2, we may fix $\alpha < \beta$ close enough to α_0 such that (9.1) has no positive steady states in $C(\bar{\Omega})$. Since $\frac{\partial\lambda}{\partial\beta}(\alpha_0, \alpha_0) > 0$, we also have $\lambda(\alpha, \beta) > 0$. By Corollary 9.1, for all β close to α, there exists a $\hat{\phi} \in C(\bar{\Omega})$, $\hat{\phi} > 0$ in $\bar{\Omega}$ such that

$$A(\beta)\hat{\phi} + g(x, \theta_\alpha)\hat{\phi} = \lambda(\alpha, \beta)\hat{\phi}.$$

We claim that there exists $\epsilon_0 > 0$ such that for all $\epsilon_1 \in (0, \epsilon_0]$ and $\epsilon_2 \in (0, \epsilon_0]$,

(9.19) $\begin{cases} A(\alpha)[(1 + \epsilon_1)\theta_\alpha] + g(x, (1 + \epsilon_1)\theta_\alpha + \epsilon_2\hat{\phi})((1 + \epsilon_1)\theta_\alpha) < 0 & \text{in } \bar{\Omega}, \\ A(\beta)[\epsilon_2\hat{\phi}] + g(x, (1 + \epsilon_1)\theta_\alpha + \epsilon_2\hat{\phi})(\epsilon_2\hat{\phi}) > 0 & \text{in } \bar{\Omega}, \end{cases}$

To prove the claim, we observe that for all $\epsilon_1, \epsilon_2 > 0$, it follows by definition of θ_α and $g_w < 0$ that

$$A(\alpha)\theta_\alpha + g(x, (1 + \epsilon_1)\theta_\alpha + \epsilon_2\hat{\phi})\theta_\alpha < A(\alpha)\theta_\alpha + g(x, \theta_\alpha) = 0.$$

For the second inequality in (9.19), we have

$$A(\beta)[\epsilon_2\hat{\phi}] + g(x, (1 + \epsilon_1)\theta_\alpha + \epsilon_2\hat{\phi})(\epsilon_2\hat{\phi}) = \epsilon_2\hat{\phi}[\lambda(\alpha, \beta) + g(x, (1 + \epsilon_1)\theta_\alpha + \epsilon_2\hat{\phi}) - g(x, \theta_\alpha)]$$
$$= \epsilon_2\hat{\phi}[\lambda(\alpha, \beta) + O(\epsilon_1 + \epsilon_2)] > 0.$$

Denote the solution of (9.1) with initial condition $(u_0, v_0) = ((1 + \epsilon_1)\theta_\alpha, \epsilon_2\hat{\phi})$ by $(\overline{u}, \underline{v})$. We claim that $(\overline{u}, \underline{v})$ converges to $(0, \theta_\beta)$ as $t \to \infty$. First, it follows by monotonicity that for all $0 \leq t_1 < t_2$, (see [27])

$$(\overline{u}, \underline{v})|_{t=t_2} \ll_K (\overline{u}, \underline{v})|_{t=t_1}.$$

Therefore, we deduce that $\lim_{t\to\infty}(\overline{u}, \underline{v}) = (\hat{u}, \hat{v})$ exists in $L^\infty(\Omega)$, and that $\hat{v} > 0$ in $\bar{\Omega}$. By passing to the limit in the variation of parameters formula, $(\hat{u}, \hat{v})$ is either a positive steady state in $L^\infty(\Omega)$ or $(\hat{u}, \hat{v}) = (0, \theta_\beta)$. By Proposition 9.5, $(\hat{u}, \hat{v}) \in C(\bar{\Omega}) \times C(\bar{\Omega})$. Since there are no positive steady states by our choice of α and β, we necessarily have $(\hat{u}, \hat{v}) = (0, \theta_\beta)$. i.e.

$$(9.20) \qquad\qquad \lim_{t\to\infty}(\overline{u}, \underline{v}) = (0, \theta_\beta).$$

Next, let an arbitrary initial condition (u_0, v_0) where both components are non-negative, non-trivial be given. Let (u, v), $(\tilde{u}, 0)$ and $(0, \tilde{v})$ be the solutions to (9.1) with initial conditions (u_0, v_0) and $(u_0, 0)$ and $(0, v_0)$ respectively. By comparison, we have

$$(0, \tilde{v}) \leq_K (u, v) \leq_K (\tilde{u}, 0) \quad \text{for all } t \geq 0.$$

Let ϵ_0 be as given above. By the global asymptotic stability of $(\theta_\alpha, 0)$ and $(0, \theta_\beta)$ in $\{(u', 0) \in C(\bar{\Omega}) \times C(\bar{\Omega}) : u' \geq 0 \text{ and } u' \not\equiv 0\}$ and $\{(0, v') \in C(\bar{\Omega}) \times C(\bar{\Omega}) : v' \geq 0 \text{ and } v' \not\equiv 0\}$, we have $\tilde{u} \to \theta_\alpha$ and $\tilde{v} \to \theta_\beta$. Hence, we may deduce that there exists $T > 0$ such that $u \leq \tilde{u} < (1 + \epsilon_0)\theta_\alpha$ when $t = T$. Now, take $\epsilon_1 = \epsilon_0$ and $\epsilon_2 \in (0, \epsilon_0]$ small enough so that $(u, v) \leq_K ((1 + \epsilon_1)\theta_\alpha, \epsilon_2\hat{\phi})$, we deduce that

$$(0, \tilde{v}) \leq_K (u, v) \leq_K (\overline{u}, \underline{v}) \quad \text{for all } t \geq T.$$

Since $(0, \tilde{v}) \to (0, \theta_\beta)$ and $(\overline{u}, \underline{v}) \to (0, \theta_\beta)$, the same holds true for (u, v). This proves the global asymptotic stability of $(0, \theta_\beta)$ among non-negative, non-trivial data. $\qquad\square$

9.4. **Neighborhood Invader Strategy.**

Theorem 9.7. *Assume for some $\hat{\alpha} \in \mathcal{S}$, (CSS) holds. Then there exists $\delta > 0$ such that if either (i) $\hat{\alpha} \leq \alpha < \beta < \hat{\alpha}+\delta$ or (ii) $\hat{\alpha}-\delta < \beta < \alpha \leq \hat{\alpha}$, then $(\theta_\alpha, 0)$ is globally asymptotically stable.*

Proof. We first claim that there exists $\delta_1 > 0$ such that if (i) $\hat{\alpha} \leq \alpha < \beta < \hat{\alpha} + \delta_1$ or (ii) $\hat{\alpha} - \delta < \beta < \alpha \leq \hat{\alpha}$, then (9.1) does not have any positive steady states. We only deal with the case (i), as the other can be proved in a similar manner. Suppose to the contrary that for each k, there exists $\hat{\alpha} \leq \alpha_k < \beta_k$ such that (9.1) has a positive steady state (u_k, v_k) and that $\alpha_k, \beta_k \to \hat{\alpha}$. By Lemma 9.3, we may assume that by passing to a subsequence,

$$(9.21) \qquad\qquad (u_k, v_k) \to (s_0\theta_{\hat{\alpha}}, (1 - s_0)\theta_{\hat{\alpha}}) \quad \text{for some } s_0 \in [0, 1].$$

Then, we may apply Proposition 6.3(ii) to finish the proof. Here we observe that the compactness assumption is only needed to deduce (9.21), and the smoothness of $\tilde{\lambda}(\beta, w)$ and $\lambda(\alpha, \beta)$ for all α, β close to $\hat{\alpha}$ and w near $\theta_{\hat{\alpha}}$, which holds in view of Proposition 9.3. $\qquad\square$

Appendix A. Spectral Properties of Nonlocal Operators in $C(\bar{\Omega})$

In this section, we collect and develop some spectral properties for nonlocal operators that is needed for our purposes. We refer the interested readers to the recent work in [35] for a more comprehensive treatment. For each $k \in C(\bar{\Omega} \times \bar{\Omega})$, $h \in C(\bar{\Omega})$ such that $k > 0$ in $\bar{\Omega} \times \bar{\Omega}$, define

$$(A.1) \qquad \mathcal{L}\phi := \int_{\Omega} k(\cdot, y)\phi(y)\, dy + h\phi.$$

The idea of the following comparison lemma can be traced back to [44].

Lemma A.1. *Suppose there are $u, v \in C(\bar{\Omega})$ such that*

$$\mathcal{L}u \leq 0, \quad \mathcal{L}v \leq 0 \quad \text{and} \quad v > 0 \quad \text{in } \bar{\Omega}.$$

If u is negative somewhere in $\bar{\Omega}$, then $u = -\beta v$ for some positive constant β. In particular, if either of the two inequalities is strict for some $x_0 \in \bar{\Omega}$, then $u \geq 0$ in $\bar{\Omega}$.

Proof. Let $\beta = \inf\{\mu \in \mathbb{R} : u + \mu v \geq 0 \text{ in } \Omega\}$. If u is negative somewhere in $\bar{\Omega}$, then $\beta > 0$, $w = u + \beta v \geq 0$ in $\bar{\Omega}$ and

$$\int_{\Omega} k(x, y)w(y)\, dy + h(x)w(x) \leq 0.$$

Either $w \equiv 0$ (in which case $u = -\beta v$) or $w(x_0) > 0$ for some $x_0 \in \bar{\Omega}$. In the second case,

$$0 < \int_{\Omega} k(x, y)w(y)\, dy \leq -h(x)w(x).$$

In this event, $w(x) \neq 0$ for all $x \in \bar{\Omega}$. Then $w(x) > 0$ in $\bar{\Omega}$. Hence

$$u + (\beta - \epsilon)v \geq 0$$

in $\bar{\Omega}$ for some $\epsilon > 0$, a contradiction to the definition of β. So if u is negative somewhere in $\bar{\Omega}$, $u = -\beta v$ and $\mathcal{L}u(x) = -\beta\mathcal{L}v(x)$ for all $x \in \bar{\Omega}$. Since $\mathcal{L}u \leq 0$ and $\mathcal{L}v \leq 0$, it must be the case that $\mathcal{L}u \equiv 0$ and $\mathcal{L}v \equiv 0$ if u is negative somewhere in $\bar{\Omega}$. Consequently, in particular, if for some $x \in \bar{\Omega}$, we have either $\mathcal{L}u < 0$ or $\mathcal{L}v < 0$, then $u \geq 0$ in $\bar{\Omega}$. $\qquad\square$

Next, define the spectral point $\lambda_p = \lambda_p(\mathcal{L})$ of the operator $\mathcal{L} : C(\bar{\Omega}) \to C(\bar{\Omega})$ (defined in (A.1)) by

$$\lambda_p = \inf\{\lambda \in \mathbb{R} : \mathcal{L}\phi - \lambda\phi \leq 0 \text{ for some positive } \phi \in C(\bar{\Omega})\}.$$

The spectral properties of $\mathcal{L} + cI$ for a real constant c are equivalent to those of $\mathcal{L}$. Hence we may assume that $h \geq 0$, which makes $\mathcal{L}$ a strongly positive operator in $X = C(\bar{\Omega})$. First, we note that λ_p gives the spectral radius $|\sigma(\mathcal{L})|$ of $\mathcal{L}$.

Proposition A.1. *If $h \geq 0$, then $\lambda_p = |\sigma(\mathcal{L})|$, where $|\sigma(\mathcal{L})| = \sup\{|\lambda| : \lambda \in \sigma(\mathcal{L})\}$.*

Proof. First, it follows from $h \geq 0$ that $\lambda_p \geq 0$. Next, it is easy to see that

$$(\lambda_p, \infty) \subset \{\lambda \in \mathbb{R} : \mathcal{L}\phi - \lambda\phi \leq 0 \text{ in } \bar{\Omega} \text{ for some } \phi \in C(\bar{\Omega}) \text{ such that } \phi > 0 \text{ in } \bar{\Omega}\}.$$

Hence for each $\tilde{\lambda} > \lambda_p$, there exists $\tilde{\phi} \in C(\bar{\Omega})$ such that $\tilde{\phi} > 0$ in $\bar{\Omega}$, and

$$(A.2) \qquad\qquad \mathcal{L}\tilde{\phi} - \tilde{\lambda}\tilde{\phi} \leq 0.$$

By positivity, we deduce that $\mathcal{L}^n\tilde{\phi} \leq \tilde{\lambda}^n\tilde{\phi}$ for all n. By a property of positive operators (see for example [40]) , $|\sigma(\mathcal{L})| = \lim_{n\to\infty} \|\mathcal{L}^n\tilde{\phi}\|^{1/n}$. We also have

$$\|\mathcal{L}^n\tilde{\phi}\| = \sup_{\bar{\Omega}} |\mathcal{L}^n\tilde{\phi}| \leq \tilde{\lambda}^n \max_{\bar{\Omega}} \tilde{\phi} \quad \text{for all } n,$$

which implies that $|\sigma(\mathcal{L})| \leq \tilde{\lambda}$. Letting $\tilde{\lambda} \searrow \lambda_p$, we deduce $|\sigma(\mathcal{L})| \leq \lambda_p$.

Next, for $\tilde{\lambda} \in \rho(\mathcal{L})$, let $\tilde{u} = (\tilde{\lambda} - \mathcal{L})^{-1}1$.

Claim 10. *For all $\tilde{\lambda} > \lambda_p$, $\tilde{u} > 0$ in $\bar{\Omega}$.*

By definition $\tilde{\lambda} > \lambda_p \geq |\sigma(\mathcal{L})|$, so $(\tilde{\lambda} - \mathcal{L})^{-1}$ exists. Next, we claim that $(\tilde{\lambda} - \mathcal{L})^{-1}$ is strongly positive. To show the claim, suppose $\mathcal{L}u - \tilde{\lambda}u \leq 0$, where the inequality is strict somewhere, then together with (A.2), we may apply Lemma A.1 to conclude that $u \geq 0$ in $\bar{\Omega}$. It remains to show that $u > 0$ in $\bar{\Omega}$. Suppose to the contrary that $u(x_0) = 0$ for some $x_0 \in \bar{\Omega}$, then at $x = x_0$,

$$0 \leq \int_\Omega k(x_0, y)u(y)\, dy = \mathcal{L}u - \tilde{\lambda}u \leq 0,$$

which is a contradiction to the fact that the last inequality is strict somewhere. So $u > 0$ in $\bar{\Omega}$. This proves the claim. In particular, $\tilde{u} = (\tilde{\lambda} - \mathcal{L})^{-1}1 > 0$ in $\bar{\Omega}$.

Claim 11. *For all $\tilde{\lambda} > |\sigma(\mathcal{L})|$, $\tilde{u} > 0$ in $\bar{\Omega}$.*

Suppose to the contrary that

$$\tilde{\lambda}_0 = \inf\{\lambda' \in (|\sigma(\mathcal{L})|, \infty) : \tilde{u} = (\tilde{\lambda} - \mathcal{L})^{-1}1 > 0 \text{ in } \bar{\Omega} \text{ for all } \tilde{\lambda} \in (\lambda', \infty)\} > |\sigma(\mathcal{L})|.$$

Then by continuity of $(\tilde{\lambda} - \mathcal{L})^{-1}$ in $\tilde{\lambda} \in \rho(\mathcal{L})$, $\tilde{u}_0 = (\tilde{\lambda}_0 - \mathcal{L})^{-1}1$ satisfies $\tilde{u}_0 \geq 0$ and $\tilde{u}_0(x_0) = 0$ for some $x_0 \in \bar{\Omega}$. But then at $x = x_0$,

$$0 \leq \int_\Omega k(x_0, y)\tilde{u}_0(y)\, dy = \mathcal{L}\tilde{u}_0 - \tilde{\lambda}_0\tilde{u}_0 = -1 < 0,$$

which is a contradiction. Hence for all $\tilde{\lambda} > |\sigma(\mathcal{L})|$, there exists $\tilde{u} \in C(\bar{\Omega})$ such that $\tilde{u} > 0$ in $\bar{\Omega}$ and $\mathcal{L}\tilde{u} - \tilde{\lambda}\tilde{u} = -1 \leq 0$. i.e. $\tilde{\lambda} \geq \lambda_p$. Letting $\tilde{\lambda} \searrow |\sigma(\mathcal{L})|$, we obtain $|\sigma(\mathcal{L})| \geq \lambda_p$. $\qquad\square$

λ_p may or may not be an eigenvalue of $\mathcal{L}$ [14]. One may observe that, by definition of λ_p,

$$\lambda_p \geq \sup_\Omega h.$$

A precise characterization is given by the following result in [15].

Theorem A.2. *There exists a positive continuous eigenfunction associated with λ_p if and only if $\lambda_p > \sup_\Omega h$.*

Here we collect the properties which characterize λ_p as a principal eigenvalue of $\mathcal{L}$.

Proposition A.3. *Suppose λ_0 is an eigenvalue of L with a positive continuous eigenfunction. Then $\lambda_p = \lambda_0$, and the following hold:*

    (i) *λ_p is a simple eigenvalue.*
    (ii) *There exists $\delta > 0$ such that $\mathrm{Re}\,\lambda < \lambda_p - \delta$ for all $\lambda \in \sigma(\mathcal{L}) \setminus \{\lambda_p\}$.*

    By replacing $\mathcal{L}$ by $\mathcal{L}+cI$ for some real constant c, we may assume without loss of generality that $h > 0$ in $\bar{\Omega}$. In particular, this makes $\mathcal{L}$ into a bounded, strongly positive operator.

    Before proving Proposition A.3, we start with a few useful lemmas.

Lemma A.2. *Let $\mathcal{L} : C(\bar{\Omega}) \to C(\bar{\Omega})$ be a bounded, linear, strongly positive operator. If $\mathcal{L}$ has an eigenvalue λ_1 with a a positive eigenfuntion in $C(\bar{\Omega})$, then λ_1 is simple, $\lambda_1 = |\sigma(\mathcal{L})|$, and $\lambda_1 > |\lambda|$ for any other eigenvalue λ of $\mathcal{L}$.*

Proof. First, we claim that if λ is an eigenvalue corresponding to a positive eigenfunction ϕ (which implies right away that $\lambda \in \mathbb{R}_+$), then necessarily $\lambda = \lambda_p$. By definition, $\lambda \geq \lambda_p$. Suppose to the contrary that $\lambda > \lambda_p$, then there exists $\lambda' \in (\lambda_p, \lambda)$ and $\phi' > 0$ such that

$$(A.3) \qquad\qquad \mathcal{L}\phi - \lambda\phi' \leq (\lambda' - \lambda)\phi' < 0.$$

With the last inequality being strict, Lemma A.1 implies that $-\phi$ satisfying

$$(A.4) \qquad\qquad \mathcal{L}(-\phi) - \lambda(-\phi) = 0,$$

can never be negative anywhere (otherwise $-\phi$ is a multiple of ϕ' and equality cannot hold in (A.4)). Hence $-\phi \geq 0$, which is a contradiction. Therefore, if λ is an eigenvalue corresponding to a positive eigenfunction ϕ, then $\lambda = \lambda_p$. In fact, by Proposition A.1, we have shown $\lambda = \lambda_p = |\sigma(\mathcal{L})|$.

    To show that λ_p is simple, let ϕ_1 be a positive eigenfunction and let ϕ_2 be another eigenfunction. Then one of ϕ_2 or $-\phi_2$ is negative somewhere. So Lemma A.1 implies that ϕ_2 is a constant multiple of ϕ_1.

    Finally, if $\lambda' \in \sigma(\mathcal{L})$, then $|\lambda'| \leq |\sigma(\mathcal{L})|$. From the arguments in [34, p. 253-255], the equality can hold only if $\lambda = |\sigma(\mathcal{L})|$ (line 22 p. 254 to line 2 p.255), i.e. $\lambda' \neq |\sigma(\mathcal{L})|$ implies $|\lambda'| < |\sigma(\mathcal{L})|$. Hence, Lemma A.2 follows. $\qquad\square$

    The next lemma shows that if $\lambda_p > \sup_\Omega h = |h|_{L^\infty(\Omega)}$, then the part of the spectrum

$$\{\lambda \in \sigma(\mathcal{L}) : |\lambda| > |h|_{L^\infty(\Omega)}\}$$

behaves like that of a compact operator.

Lemma A.3. *Suppose $\lambda_p > \sup_\Omega h$, then for each constant $\lambda_0 \in (\sup_\Omega h, \lambda_p)$,*

$$\{\lambda \in \sigma(\mathcal{L}) : |\lambda| > \lambda_0\}$$

consists of finitely many eigenvalues of $\mathcal{L}$ with finite multiplicities.

Proof. Let $(K\phi)(x) := \int_\Omega k(x, y)\phi(y)\,dy$ and $(H\phi)(x) := h(x)\phi(x)$, then $\mathcal{L} = K + H$, such that K is a compact linear operator in $C(\bar{\Omega})$, and H is a bounded linear operator in $C(\bar{\Omega})$. First, for all $\lambda \in \mathbb{C}$ such that $|\lambda| > \sup_\Omega h = |h|_{L^\infty(\Omega)}$, $\lambda I - H : C(\bar{\Omega}) \to C(\bar{\Omega})$ is invertible.

Hence $\lambda I - \mathcal{L} = (\lambda - H) - K$, being a compact perturbation of an invertible map, is Fredholm of index zero. This shows that each $\lambda \in \sigma(\mathcal{L})$ such that $|\lambda| > \sup_\Omega h$ is an eigenvalue of finite multiplicity.

It remains to show that for each constant $\lambda_0 \in (\sup_\Omega h, \lambda_p)$, $\{\lambda \in \sigma(\mathcal{L}) : |\lambda| > \lambda_0\}$ is a finite set. Suppose to the contrary that there is a sequence of distinct λ_k such that $\lambda_k \in \sigma(\mathcal{L})$ and $\inf_k\{|\lambda_k|\} \geq \lambda_0$. By the above argument, for each k, there exist $\phi_k \in C(\bar{\Omega})$ such that $\mathcal{L}\phi_k = \lambda_k \phi_k$. Fix a positive integer N such that

$$(A.5) \qquad (\lambda_0)^N > 6|h|_{C(\bar{\Omega})}^N.$$

Then $\tilde{\mathcal{L}} := \mathcal{L}^N = \tilde{K} + \tilde{H}$, where $\tilde{H} = H^N$ is a bounded operator such that $\|H\| = \|h\|_{L^\infty(\Omega)}^N$ and $\tilde{K} = \tilde{\mathcal{L}} - \tilde{H}$ is a compact operator. (The operator $\tilde{K}$ has the form $\tilde{K} = K(\mathcal{L}^{N-1}) + K_1$ where K_1 is a finite sum of finite compositions of the operators H and K with the form $H^m \circ K \circ \ldots$ where $1 \leq m \leq N - 1$.) Moreover, for each k, $\tilde{\lambda}_k := \lambda_k^N$ is an eigenvalue of $\tilde{\mathcal{L}}$ for all k, with the same eigenfunction. By (A.5), we have

$$(A.6) \qquad |\tilde{\lambda}_k| > 6\|H\|.$$

For each m, define Y_m to be the subspace spanned by $\phi_1, ..., \phi_m$. Since eigenfunctions pertaining to distinct eigenvalues are linearly independent, ϕ_k, being eigenfunctions of distinct eigenvalues of $\mathcal{L}$, are linearly independent. Choose, for each $n \geq 2$, $y_n \in Y_n$ such that $\|y_n\|_{C(\bar{\Omega})} = 1$ and $\text{dist}(y_n, Y_{n-1}) > 1/2$ for all $n \geq 2$. Now we claim that $\|\tilde{K}y_m - \tilde{K}y_n\|_{C(\bar{\Omega})} \geq \|H\| > 0$ for all $m > n \geq 2$, which contradicts the compactness of $\tilde{K}$. Since, for $m > n \geq 2$,

$$\tilde{K}y_m - \tilde{K}y_n = \tilde{\mathcal{L}}y_m - \tilde{\mathcal{L}}y_n - \tilde{H}y_m + \tilde{H}y_n = (\tilde{\lambda}_m y_m - y') - (\tilde{H}y_m - \tilde{H}y_n)$$

for some $y' \in Y_{m-1}$. Hence by (A.6),

$$\|\tilde{K}y_m - \tilde{K}y_n\|_{C(\bar{\Omega})} \geq |\tilde{\lambda}_m|\text{dist}(y_m, Y_{m-1}) - 2\|H\|_{C(\bar{\Omega})} > \frac{|\tilde{\lambda}_m|}{2} - 2\|H\|_{C(\bar{\Omega})} > \|H\| > 0.$$

for all $m > n \geq 2$. This contradicts the compactness of $\tilde{K}$, which completes the proof. $\square$

Proof of Proposition A.3. Let λ_0 be an eigenvalue of $\mathcal{L}$ with a positive eigenfunction. Then by Proposition A.1 and Lemma A.2,

$$(A.7) \qquad \lambda_0 = |\sigma(\mathcal{L})| = \lambda_p,$$

and it is a simple eigenvalue. Hence (i) follows. Next, by Theorem A.2,

$$(A.8) \qquad \lambda_p > \sup_\Omega h.$$

Claim 12. $|\lambda| < \lambda_p$ *for all* $\lambda \in \sigma(\mathcal{L}) \setminus \{\lambda_p\}$.

Let $\lambda \in \sigma(\mathcal{L})$, if $|\lambda| \leq \sup_\Omega h$, then $|\lambda| < \lambda_p$, by (A.8). Otherwise $|\lambda| > \sup_\Omega h$, and λ is an eigenvalue of $\mathcal{L}$ (Lemma A.3) and hence $|\lambda| < \lambda_p$, by Lemma A.2. This proves the claim.

Finally, the spectral gap follows from Claim 12 and the fact that $\{\lambda \in \sigma(\mathcal{L}) : |\lambda| > (\sup_\Omega h + \lambda_p)/2\}$ is a finite set (Lemma A.3). Therefore,

$$\sup\{|\lambda| : \lambda \in \sigma(\mathcal{L}) \setminus \{\lambda_p\}\} < \lambda_p.$$

This completes the proof of Proposition A.3. □

Next, we state a comparison lemma which follows from the definition of spectral point for nonlocal operators. This in particular implies the continuity of λ_p with respect to $h \in C(\bar\Omega)$ and positive functions $k \in C(\bar\Omega \times \bar\Omega)$.

Lemma A.4. *Let $k_1(x,y), k_2(x,y) > 0$, and $a_1(x), a_2(x)$ be continuous. Define*

$$\lambda_{1,1} := \sup\{\lambda \in \mathbb{R} : \exists \phi > 0 \text{ such that } k_1(x,\cdot) * \phi + a_1\phi + \lambda\phi \le 0.\}$$
$$\lambda_{1,2} := \sup\{\lambda \in \mathbb{R} : \exists \phi > 0 \text{ such that } k_1(x,\cdot) * \phi + a_2\phi + \lambda\phi \le 0.\}$$
$$\lambda_{2,1} := \sup\{\lambda \in \mathbb{R} : \exists \phi > 0 \text{ such that } k_2(x,\cdot) * \phi + a_1\phi + \lambda\phi \le 0.\},$$

then we have

$$\min(a_2 - a_1) \le \lambda_{1,1} - \lambda_{1,2} \le \max(a_2 - a_1)$$
$$\lambda_{1,1} - \min(k_1/k_2)\lambda_{2,1} \le |\min(k_1/k_2) - 1| \max|a_1|$$
$$\lambda_{2,1} - \min(k_2/k_1)\lambda_{1,1} \le |\min(k_2/k_1) - 1| \max|a_1|.$$

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