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SPREADING SPEEDS AND TRAVELING WAVES FOR NON-COOPERATIVE INTEGRO-DIFFERENCE SYSTEMS

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Abstract. The study of spatially explicit integro-difference systems when the local population dynamics are given in terms of discrete-time generations models has gained considerable attention over the past two decades. These nonlinear systems arise naturally in the study of the spatial dispersal of organisms. The brunt of the *mathematical* research on these systems, particularly, when dealing with *cooperative* systems, has focused on the study of the existence of traveling wave solutions and the characterization of their spreading speed. Here, we characterize the minimum propagation (spreading) speed, via the convergence of initial data to wave solutions, for a large class of *non cooperative* nonlinear systems of integro-difference equations. The spreading speed turns out to be the slowest speed from a family of non-constant traveling wave solutions. The applicability of these theoretical results is illustrated through the explicit study of an integro-difference system with *local* population dynamics governed by Hassell and Comins' non-cooperative competition model (1976). The corresponding integro-difference nonlinear systems that results from the redistribution of individuals via a dispersal kernel is shown to satisfy conditions that guarantee the existence of minimum speeds and traveling waves. This paper is dedicated to Avner Friedman as we celebrate his immense contributions to the fields of partial differential equations, integral equations, mathematical biology, industrial mathematics and applied mathematics in general. His leadership in the mathematical sciences and his mentorship of students and friends over several decades has made a huge difference in the personal and professional lives of many, including both of us.

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1. Introduction.

Finding and developing macroscopic descriptions for the dynamics and behavior of heterogeneous large ensembles of individuals subject to ecological forces like dispersal continues to provide challenges and opportunities for mathematical and biological scientists. Over the past century, particular attention has been placed on the study of the role played by dispersal in shaping plant communities, in helping understand biological invasions, in assisting in the quantification and control of the spread of infectious disease, or in disentangling the dynamics of marine open-ocean and intertidal systems, to name but a few examples. The work of pioneers like Aronson [1, 2], Fisher [7], Hadeler [8, 9, 10], Kolmogorov [16], Levin [19], Okubo [20], Skellam [29], Slobodkin [15], Weinberger [35] and the subsequent cadre of *distinguished* mathematicians and theoreticians across the world who have worked at this interface, set not only the foundation of an important and fertile area of interdisciplinary research (ecology, mathematics, and evolutionary biology) but in the process it has inspired novel mathematical research while being re-energized by unsolved questions in emerging fields like urban ecology and sustainability and the challenges and opportunities posed by the growing body of research on the co-evolving dynamics of socio-biological systems [5] [18].

Early models for the dispersal of invasive species used nonlinear reaction-diffusion equations, with the prototype provided by Fisher's Equation [7]. In 1937, Fisher [7] studied the nonlinear parabolic equation

$$u_t = du_{xx} + ru(1 - \frac{u}{K}). \tag{1}$$

Here, $u(x,t)$ represents the population density at location x and time t, r is the intrinsic rate of population increase, K is the environmental carrying capacity, and D is the diffusion coefficient. for the spatial spread of an advantageous gene in a population and conjectured that $c^* = 2\sqrt{rd}$ is the asymptotic speed of propagation of an advantageous gene. Special solutions, traveling wave fronts, are of interest since they enable us to better understand how a population propagates. Traveling wave fronts are solutions to partial differential equations, which have a fixed shape and translate at a constant speed c as time evolves. Fisher's results show that (1) has a traveling wave solution of the form $w(x+ct)$ if and only if $|c| \geq c^*$. Kolmogorov, Petrowski, and Piscounov [16] proved the similar results with more general model that the minimum speed of propagation for (2)

$$u_t = du_{xx} + f(u) \tag{2}$$

is

$$c^* = 2\sqrt{f'(0)d}$$

if $f(0) = f(1) = 0$ and $f(u) \leq f'(0)x$. This pioneering research together with the paper by Aronson and Weinberger [1, 2] confirmed the conjecture of Fisher, and established the speeding spreads for nonlinear parabolic equations. This basic formula $c^* = 2\sqrt{f'(0)d}$ indicates that the rate of spread is a linear function of time and that it can be predicted quantitatively as a function of measurable life history parameters.

However, it has been observed that *empirically* measured rates of dispersal when combined with Model (2) do not accurately predict the rates of range expansion in invasions (Hastings et al. 2005[12]). The inability of the model to explain the data is usually justified or explained away as the kind of discrepancies generated by the inability of the model to capture the effect of rare long-distance dispersal events.

Model (2) allows for diffusive movement, and in fact, it assumes that the distribution of dispersal distances is normal. Model (2) ignores the role of population structure, including age structure while assuming that reproduction and movement occur randomly over the lifetime of an individual, conditions, that of course, are rarely met by populations. In fact, there are a wide variety of measured distributions, peaking around their mode, with fatter tails than a normal distribution and the same variance.

Evidence that integro-difference equations can effectively model biological dispersal processes has been published (see Kot 1992 [17], Hastings et al. 2005 [12] and references therein). In the case, a single population composed of identical individuals, all distributed along an infinite one-dimensional habitat, the process of dispersal, using re-distribution kernels can be modeled by

$$w_{n+1}(x) = \int_{-\infty}^{\infty} k(x-y)g(w_n(y))dy \tag{3}$$

where w_n representing the population density at time n. The change of population density from w_n from n to $n+1$ is reflected in two sub-processes: population growth g and dispersal [via a kernel $k(x-y)$]. It is assumed that the probability of moving from point x to point y depends only on the relative locations of the two points. The change of population density w_n from n to $n+1$ is reflected in two processes: population growth and dispersal. Under a monotonicity (local dynamics) and additional assumptions, it is shown (e.g. Weinberger [1, 2]) that the minimum speed of propagation for Model (3) is

$$c^* = \min_{\lambda>0} \frac{1}{\lambda} \ln\left(\int_{-\infty}^{\infty} g'(0)k(s)e^{\mu s}ds\right)$$

The *theme* of finding *mathematical* macroscopic descriptions for the spatial dynamics of heterogeneous large-ensembles of populations was set in "motion" by the fundamental ecological contributions of Skellam [29], Kierstad and Slobodkin [15], Levin and Paine [19], Okubo [20], and others. The study of integro-difference equations dispersal models in the mathematical literature has its origins in the study of the coupled spatial dynamics of organisms with discrete *primarily* non-overlapping (but see [30]) local dynamics with dispersal processes modeled via re-distribution kernels [1, 2]. Weinberger [35] and Lui [25] research expanded the mathematical foundation for the theory of spreading speeds and traveling waves, through their analysis of traveling waves via the convergence of initial data to wave solutions, in the context of *cooperative* operators. Recently, Weinberger, Lewis and Li made additional contributions [33, 21, 22, 34]. The mathematical analyses of integro-difference spatially explicit systems enhances the understanding of the dynamics of introduced species like weeds or pests in terrestrial systems, or the study of the impact of dominant alien species in freshwaters while generating additional challenges and opportunities to mathematicians, whose interests, are driven by the study of challenging dynamical systems.

The pervasiveness of overcompensation in biological systems implies that integro-difference equations models are in general *non-cooperative*, and therefore, existing theoretical work has yet to address effectively the mathematical consequences of *non-cooperative* local dynamics on dispersal. In other words, the incorporation of biological forces/mechanisms that drive population overcompensation leads to mathematical models whose dynamics have yet to be satisfactorily teased out in the context of relevant biological settings. Deep mathematical challenges remain

[17]. The research in this manuscript does not start in the vacuum since relevant mathematical work for non-cooperative systems has been carried out by several researchers. Thieme [28] showed, in the context of a general model with non-monotone growth functions, that the asymptotic spreading speed could still be obtained with the aid of carefully constructed monotone functions. Hsu and Zhao [14] and Li, Lewis and Weinberger [23] just extended the theory of spreading speeds in the context of non-monotone integro-difference equations. Their extensions relied on two methods: the construction of two monotone operators (with appropriate properties) and the application of fixed point theorems in Banach spaces–an approach also used in Ma [27] and Wang [31] to establish the existence of traveling wave solutions of reaction-diffusion equations. The results in this manuscript on the speed of propagation for non-cooperative systems in the context of integro-difference equations rely on the spreading results for monotone systems in Weinberger et al. [33].

In a recent paper, one of the authors [32] has established the minimum speed and the existence of traveling solutions for a class of non-cooperative systems of reaction-diffusion equations.

$$u_t = Du_{xx} + f(u) \text{ for } x \in \mathbb{R},\ t \geq 0.$$

where $u = (u^i),\ D = \text{diag}(d_1, d_2, ..., d_N), d_i > 0$ for $i = 1, ..., N$

$$f(u) = (f_1(u), f_2(u), ..., f_N(u))$$

The assumptions in [32] are similar to the assumptions (H1-H3) in this paper for integro-difference equations. Many relevant results hold for both systems of cooperative reaction-diffusion equations and integro-difference equations. Indeed, [33, 22] and several others studied minimum speeds with a more abstract discrete-time recursion systems which include both reaction-diffusion equations and integro-difference equations. However, for non-cooperative systems, as we shall see, there are many differences in proofs between systems of reaction-diffusion equations and integro-difference equations. In particular, the versifications of upper and lower solutions are completely different. Further, with more concrete models some sharper results (Proposition 1) than those in [25, 33] can be obtained.

We highlight our results in the context of a two-dimensional nonlinear discrete system describing the local nonlinear dynamics of two competing species with discrete reproduction cycles [11]. The model focuses on the growth and spread of these competing species with their population densities at generation n and spatial location x being tracked by the state variables $X_n(x)$ and $Y_n(x)$, respectively. The system is a natural extension of the classical single population "scramble" competition model of Ricker [3]. Specifically, the non-spatial interference-competition model of Hassell and Comins is given by the following system of coupled nonlinear difference equations:

$$\begin{aligned} X_{n+1}(x) &= X_n(x)e^{r_1 - X_n(x) - \sigma_1 Y_n(x)} \\ Y_{n+1}(x) &= Y_n(x)e^{r_2 - Y_n(x) - \sigma_2 X_n(x)} \end{aligned} \tag{4}$$

where $r_1, r_2, \sigma_1, \sigma_2$ are all positive constants.

The possibility that individuals in the above two populations may disperse to different sites is modeled with a redistribution kernel $k_i(y)$. Hence, a discrete-time model, where individuals interact locally according to Model (4), can be naturally formulated via a system of coupled nonlinear integro-difference equations. Hence, we have that

$$\begin{aligned} X_{n+1}(x) &= \int_{\mathbb{R}} k_1(x-y)X_n(y)e^{r_1-X_n(y)-\sigma_1 Y_n(y)}dy \\ Y_{n+1}(x) &= \int_{\mathbb{R}} k_2(x-y)Y_n(y)e^{r_2-Y_n(y)-\sigma_2 X_n(y)}dy \end{aligned} \tag{5}$$

where the dispersal of the i-species is modeled by a redistribution kernel $k_i, i = 1, 2$ that depends just on the signed distance $x-y$, connecting the "birth" y location and the "settlement" location x. In other words, $k_i(y)$ is a homogenous "probability" kernel that satisfies $\int_{-\infty}^{\infty} k_i(y)dy = 1$.

Since the above system is *non-cooperative* in general, it is in such a context that new results will be formulated, and illustrated but first, we introduce the notation that will be used for the explicit mathematical formulation of the dynamics of two-interacting, *dispersing*, and competing populations. Consequently, $\beta, \beta^{\pm}, F, F^{\pm}, r, u, v$ are used to denote vectors in $\mathbb{R}^N$ or N-vector valued functions while x, y, ξ are used to denote variables in $\mathbb{R}$. The use of $u = (u^i)$ and $v = (v^i) \in \mathbb{R}^N$ allow us to define $u \geq v$ whenever $u^i \geq v^i$ for all i; and $u \gg v$ whenever $u^i > v^i$ for all i. We further define for any $r = (r^i) \gg 0, r \in \mathbb{R}^N$ the R^N-interval

$$[0, r] = \{u : 0 \leq u \leq r, u \in \mathbb{R}^N\} \subseteq \mathbb{R}^N$$

and

$$\mathcal{C}_r = \{u = (u^1, ..., u^N) : u^i \in C(\mathbb{R}, \mathbb{R}), 0 \leq u^i(x) \leq r^i, x \in \mathbb{R},\ i = 1, ..., N\},$$

where $C(\mathbb{R}, \mathbb{R})$ is the set of all continuous functions from $\mathbb{R}$ to $\mathbb{R}$. Our focus will be on the set $\mathcal{C}_{\beta+}, \beta^+ \gg 0$.

Specifically, we consider the system of integro-difference equations

$$u_{n+1} = \mathcal{Q}[F(u_n)]; \tag{6}$$

where $u_n = (u_n^i) \in \mathcal{C}_{\beta+},\ F(u) = (f_i(u))$;

$$\mathcal{Q}[F(u)] = (\mathcal{Q}^i[F(u)]);$$

$$\mathcal{Q}^i[F(u)](x) = \int_{\mathbb{R}} k_i(x-y) f_i\big(u(y)\big)dy;$$

$u_n(x)$ is the density of individuals at point x and time/generation n; $F(u)$ is the density-dependent fecundity (local growth rate); and $k_i(x-y)$ (dispersal kernel) models the dispersal of the ith species. It is assumed to depend only on the signed distance $x-y$ between the location of "birth" y and the "settlement" or "landing" location x. As noted before, $k_i(x-y)$ can be viewed as a probability kernel since $\int_{-\infty}^{\infty} k_i(x)dx = 1$. The notation $\mathcal{Q}[F(u_n)]$ is slightly different from those used in [14, 23, 25, 33] and hence individuals wishing to compare results must account for this since no F (as defined here) can be found in the standard literature notation for integro-difference systems. Here, F is included since it is needed to carry out the proofs involving non-monotone systems effectively.

The integro-difference system (6) models the reproduction and dispersal of a time-synchronized species where all individuals first undergo reproduction, then redistribute their offspring, and proceed to reproduce again. The goal here is to carry out the characterization of the spreading speed, in a system involving a rather general non-cooperative system (6), as the slowest speed of a family of non-constant traveling wave solutions of (6).

2. **Non-cooperative systems' results.** Since the focus is on the characterization of the speeds of propagation for (6) when the system is non-cooperative, we make use of prior results, as is typical in mathematics, whenever possible of established results for *cooperative* systems ([33]). The existence of two additional monotone functions $F^{\pm}$ with the properties that the first lies above F and the second below F is required by our method of proof. The use of this approach is motivated by prior work on non-monotone equations [28, 14, 23, 27, 37, 31]. Specifically, we observe that $F^{\pm}$ can be "constructed" via piecewise functions made up of "monotone pieces" of F and the incorporation of appropriate constants. If F happens to be monotone, then naturally $F^{\pm} = F$. We introduce additional technical assumptions below. These assumptions are critical since the feasibility of the mathematical analysis depends on whether or not the components of our problem meet them:

(H1) For $i = 1, ..., N$, $k_i(\tau) \geq 0$ is integrable on $\mathbb{R}$, $k_i(\tau) = k_i(-\tau), \tau \in \mathbb{R}$, and $\int_{\mathbb{R}} k_i(\tau)d\tau = 1, \int_{\mathbb{R}} k_i(\tau)e^{\lambda\tau}d\tau < +\infty$, for all $\lambda > 0$.

(H2) (i) Let $0 \ll \beta^- = (\beta_i^-) \leq \beta = (\beta_i) \leq \beta^+ = (\beta_i^+)$. Assume that $F : [0, \beta^+] \to [0, \beta^+]$ is a continuous, twice piecewise continuous differentiable function, and that there exist continuous, twice piecewise continuous differentiable functions $F^{\pm} = (f_i^{\pm}) : [0, \beta^+] \to [0, \beta^+]$ such that for $u \in [0, \beta^+]$,

$$F^-(u) \leq F(u) \leq F^+(u).$$

(ii) $F(0) = 0, F(\beta) = \beta$ and there is no other positive equilibrium of $\mathcal{Q}[F]$ between 0 and β (that is, there is no constant $v \neq \beta$ such that $F(v) = v, 0 \ll v \leq \beta$). $F^{\pm}(0) = 0, F^{\pm}(\beta^{\pm}) = \beta^{\pm}$ and there is no other positive equilibrium of $\mathcal{Q}[F^{\pm}]$ between 0 and $\beta^{\pm}$. F has a finite number of equilibria in $[0, \beta^+]$.

(iii) $F^{\pm}$ are nondecreasing functions on $[0, \beta^+]$ and $F^{\pm}(u)$ and $F(u)$ have the same Jacobian at 0.

Assumptions (H1-H2) do not suffice if the goal is to characterize the speeds of propagation for (6). The assumption (H3), which includes the requirement that the operator grows less than its linearization along the particular function $\nu_\mu e^{-\mu x}$, is essential since it implies that the operator $\mathcal{Q}$ does not display an Allee effect for this particular function (see [33]). Assumption (H3), explicitly formulated below, is satisfied by several *biological systems* of interest; this will be highlighted in our example. Assumption (H3), hence does not severely handicap the usefulness of the results in this manuscript.

The need for Frobenius' theorem stating that any nonzero irreducible matrix with nonnegative entries has a unique principal positive eigenvalue with a corresponding principal eigenvector "made up" of strictly positive coordinates is implicit in Assumption (H3). The formulation of (H3) depends on the concept of irreducibility. A matrix is irreducible if it is not similar to a lower triangular matrix with two blocks via a permutation (See [13, 33]). By reordering the coordinates, one can put any matrix into a block lower triangular form, then we say that the matrix is in *Frobenius form* if all the diagonal blocks are irreducible (an irreducible matrix consists of the single diagonal block which is the matrix itself). Here, we use the definition of *Frobenius form* found in Weinberger et al. [33]. Following the approach in [33], we conclude that for each $\mu > 0$, the $N \times N$ matrix B_μ is given by

$$B_\mu = (b_\mu^{i,j}) = \big(\partial_j f_i(0) \int_{\mathbb{R}} k_i(s)e^{\mu s}ds\big), \tag{7}$$

where $b_\mu^{i,j}$ is the (i,j) entry of the matrix, is in *Frobenius form* ([33]). In other words, it is assumed that the needed reordering has been carried out for B_μ ([33]) so that it is in Frobenius form. If $\lambda(\mu)$ denotes the principal eigenvalue of the first diagonal blocks, then the formulation required by Assumption (H3) can be explicitly stated as:

(H3) (i) Assume that B_μ is in Frobenius form and that the principal eigenvalue, $\lambda(\mu)$, of the first diagonal block is strictly larger than the principal eigenvalues of other diagonal blocks. Further, let's assume that B_μ has a positive eigenvector $\nu_\mu = (\nu_\mu^i) \gg 0$ corresponding to $\lambda(\mu)$ with the additional requirement that $\lambda(0) > 1$.

(ii) For each $\mu > 0$ and $\alpha > 0$, we let $v^\pm = (v_i^\pm) = (\min\{\beta_i^\pm, \nu_\mu^i \alpha\})$, and assume that

$$F^\pm(v^\pm) \leq B_0 v^\pm.$$

(iii) For every sufficiently large positive integer k, there is a small constant vector $\omega = (\omega^i) \gg 0$ such that

$$F^\pm(u) \geq (1 - \frac{1}{k}) B_0 u, \quad u \in [0, \omega],$$

Remark 1. If B_0 is in Frobenius form, then B_μ is also in Frobenius form. Because all the B_μ have the same zero entries, it follows that all the matrices B_μ are in Frobenius form [33].

It follows from (H1) that $\lambda(\mu)$ is an even function. In fact, Lui showed ([25]) that $\ln \lambda(\mu)$ is a convex function and therefore, $\ln \lambda(\mu)$ achieves its minimum at $\mu = 0$. Therefore the assumption that $\lambda(0) > 1$ implies that $\ln \lambda(\mu) > 0$. The statement in Proposition 1 below, which is critical to the rest of analysis that leads to the main result, involves the following function of the largest principal eigenvalue $\lambda(\mu)$

$$\Phi(\mu) = \frac{1}{\mu} \ln \lambda(\mu) > 0.$$

Part (5) of Proposition 1 highlights the use of this function in the construction of lower solutions and estimates of the traveling wave solutions.

Proposition 1. *Assume that* $(H1) - (H3)$ *hold. Then*

1 $\Phi(\mu) \to \infty$ *as* $\mu \to 0$;
2 $\Phi(\mu)$ *is decreasing near* $\mu = 0$ *and* $\mu > 0$;
3 $\Phi'(\mu)$ *changes sign at most once on* $(0, \infty)$;
4 $\Phi(\mu)$ *has a minimum* $c^* > 0$.
5 For each $c > c^*$, *there exist* $\Lambda_c > 0$ *and* $\gamma \in (1, 2)$ *such that*

$$\Phi(\Lambda_c) = c, \quad \Phi(\gamma \Lambda_c) < c.$$

Parts (1)-(4) of Proposition 1 are essentially due to Lui [25]. However, Lui's results only guarantee that $c^* \geq 0$. The proof of the strict inequality, that is, that $c^* > 0$, is found in the Appendix. This is also briefly discussed in a remark in [33, pp. 197]. Since $\lambda(\mu)$ is a simple root of the characteristic equation of an irreducible block, it can be shown that $\lambda(\mu)$ is twice continuously differentiable on $\mathbb{R}$. Part (5) is a direct consequence of the results stated in Parts (1)-(4).

A traveling wave solution u_n of (6) is defined as a solution of the form $u_n(\xi) = u(\xi - cn), u \in C(\mathbb{R}, \mathbb{R}^N)$. The theorems that guarantee the existence of traveling wave solutions for cooperative systems have already been established (e.g. [22]). It also has been established that the asymptotic spreading speed, for such systems, can be characterized as the speed of the slowest non-constant traveling wave solution for monotone operators [22] and for scalar equations [36, 35, 14, 23].

We start with the statement of Theorem 2.1, the main theorem, which *generalizes* results previously established for cooperative systems to non-cooperative systems. Some parts of Theorem 2.1 such as the asymptotic behavior of traveling waves are new even for cooperative systems. The new information about cooperative systems are, in fact, required to be able to carry out the proofs of the results for non-cooperative systems. The details associated with the proof of the *main* result are included in a series of lemmas and theorems all collected in the following sections.

The two major new contributions in this paper are: 1) for a large class of non-monotone systems (6), the question of the existence of the minimum speed of propagation is settled (Theorem 2.1(i-ii)) and this speed is characterized as the speed of the slowest non-constant traveling wave solution (Theorem 2.1(iii-v)); and 2) in the case of *competition* models, a direct application of the main theorem helps identify simple and meaningful conditions that turned out to be needed for the proofs of the existence of traveling waves with the *minimum* speed of propagation (Theorem 5.1). That is, what must be required to guarantee the success of a biological invasion. It is worth re-iterating that the application of the results in this manuscript to the study of relevant monotone operators case [22, 35] does give additional information. In fact, these results help explicitly characterize the asymptotic behavior of traveling waves via the careful analysis of eigenvalues and upper-lower solutions. This analysis was not done before [22, 35] most likely because the focus was exclusively in establishing the existence of traveling waves. The results and analysis for the n-dimensional case is typically harder. Our approach works because the analysis of the n dimensional case is closely related to the structure of the eigenvalues and corresponding eigenvectors, an analysis that is embedded in our study of the relevant monotone operators.

The following theorem summarizes the main results.

Theorem 2.1. *Assume $(H1)-(H3)$ hold, then the following statements are valid:*

(i) For any $u_0 \in \mathcal{C}_\beta$ with compact support and $0 \le u_0 \ll \beta$, the solution u_n of (6) satisfies

$$\lim_{n\to\infty} \sup_{|x|\ge nc} u_n(x) = 0, \text{ for } c > c^*$$

(ii) For any strictly positive vector $\omega \in \mathbb{R}^N$, there is a positive R_ω with the property that if $u_0 \in \mathcal{C}_\beta$ and $u_0 \ge \omega$ on an interval of length $2R_\omega$, then the solution $u_n(x)$ of (6) satisfies

$$\beta^- \le \liminf_{n\to\infty} \inf_{|x|\le nc} u_n(x) \le \beta^+, \text{ for } 0 < c < c^*$$

(iii) For each $c > c^*$ (6) admits a traveling wave solution $u(\xi - cn) = (u^i(\xi - cn))$ such that $0 \ll u(\xi) \le \beta^+, \xi \in \mathbb{R}$,

$$\beta^- \le \liminf_{\xi\to-\infty} u(\xi) \le \limsup_{\xi\to-\infty} u(\xi) \le \beta^+$$

$\lim_{\xi\to\infty} u(\xi) = 0$ and

$$\lim_{\xi\to\infty} u(\xi)e^{\Lambda_c \xi} = \nu_{\Lambda_c}. \tag{8}$$

If, in addition, F is non-decreasing on $\mathcal{C}_\beta$, then u is non-increasing on $\mathbb{R}$.

(iv) For $c = c^*$ (6) admits a non-constant traveling wave solution $u(\xi - cn) = (u^i(\xi - cn))$ such that $0 \le u(\xi) \le \beta^+, \xi \in \mathbb{R}$.

(v) *For* $0 < c < c^*$ *(6) does not admit a traveling wave solution* $u_n(\xi) = u(\xi - cn)$ *such that* $u \in \mathcal{C}_{\beta^+}$ *with* $\liminf_{\xi\to-\infty} u(\xi) \gg 0$ *and* $u(+\infty) = 0$.

Remark 2. When F is monotone, $F^{\pm} = F, \beta^{\pm} = \beta$.

Remark 3. The assumption that F has a finite number of equilibria in $[0, \beta^+]$ is only used in the proof of Theorem 2.1 (iv) and can be further relaxed. In fact, as long as for some component i and a sufficiently small positive number δ, $u = (u^i) \geq 0$ with $u^i = \delta$ are not equilibria of F, it can be verified that the conclusion is still valid from the proof.

We shall establish Theorem 2.1 in Sections 3 and 4.

3. Spreading speeds.

Our results on the speed of propagation for non-cooperative systems make use of Theorem 3.1 below which collects the properties of the spreading speed c^* for monotone systems as established in Weinberger, Lewis and Li [33]. Theorem 3.1 extends the related spreading results in Lui [25] to systems of monotone recursive operators with more than two equilibria. The operator at the center of this manuscript may support more than two equilibria with one lying at the boundary as in [33] (see Section 5).

Theorem 3.1. *(Weinberger, Lewis and Li [33] [Lemma 2.2, Theorem 3.1]) Assume* $(H1)-(H3)$ *hold. Further assume that* $f^i(x), i = 1, ..., N$ *is **non-decreasing**. Then the following statements are valid:*

(i) *For any* $u_0 \in \mathcal{C}_\beta$ *with compact support and* $0 \leq u_0 \ll \beta$, *the solution* $u_n(x)$ *of (6) satisfies*
$$\lim_{n\to\infty} \sup_{|x|\geq nc} u_n(x) = 0, \text{ for } c > c^*$$

(ii) *For any strictly positive vector* $\omega \in \mathbb{R}^N$, *there is a positive* R_ω *with the property that if* $u_0 \in \mathcal{C}_\beta$ *and* $u_0 \geq \omega$ *on an interval of length* $2R_\omega$, *then the solution* $u_n(x)$ *of (6) satisfies*
$$\liminf_{n\to\infty} \inf_{|x|\leq nc} u_n(x) = \beta, \text{ for } 0 < c < c^*$$

It is clear that $\mathcal{Q}[F^{\pm}]$ are monotone (order preserving) on $\mathcal{C}_{\beta^+}$. That is, if $u, v \in \mathcal{C}_{\beta^+}$ and $u(x) \leq v(x), x \in \mathbb{R}$, then
$$\mathcal{Q}[F^{\pm}(u)](x) \leq \mathcal{Q}[F^{\pm}(v)](x),\ x \in \mathbb{R}.$$
Further, for $u = (u^i) \in \mathcal{C}_{\beta^+}$ and $x \in \mathbb{R}$, we have
$$f_i^-\big(u(x)\big) \leq f_i\big(u(x)\big) \leq f_i^+\big(u(x)\big), i = 1, ..., N.$$
and therefore
$$\mathcal{Q}[F^-(u)](x) \leq \mathcal{Q}[F(u)](x) \leq \mathcal{Q}[F^+(u)](x),\ x \in \mathbb{R}.$$

We are now able to establish Part (i) and (ii) of Theorem 2.1 by following essentially the method of proof for the scalar cases found in [14, 23].

Proof of Parts (i) and (ii) of Theorem 2.1. Part (i). For a given $u_0 \in \mathcal{C}_\beta$ with compact support, let u_n be the n-th iteration of $\mathcal{Q}[F]$ starting from u_0 and let u_n^+ be the n-th iteration of $\mathcal{Q}[F^+]$ starting from u_0. By (H2), we have
$$0 \leq u_n(x) \leq u_n^+(x), x \in \mathbb{R}, n > 0.$$

Thus for any $c > c^*$, it follows from Theorem 3.1 (i) that

$$\lim_{n\to\infty} \sup_{|x|\geq nc} u_n^+(x) = 0,$$

and hence

$$\lim_{n\to\infty} \sup_{|x|\geq nc} |u_n(x)| = 0,$$

Part (ii). Let u_n, u_n^+ be the n-th iteration of $\mathcal{Q}[F], \mathcal{Q}[F^+]$ starting from u_0 respectively. Let $v_0^i = \min\{u_0^i, \beta_i^-\}, i = 1, ..., N$. Then $v_0 = (v_0^i) \in \mathcal{C}_{\beta^-}$. Letting u_n^- denote the n-th iteration of $\mathcal{Q}[F^-]$ starting from v_0 and observing that $v_0 \leq u_0$ and $\beta^- \leq \beta \leq \beta^+$, from (H2), we have that

$$u_n^-(x) \leq u_n(x) \leq u_n^+(x), x \in \mathbb{R}, n > 0.$$

Theorem 3.1 (ii) states that for any strictly positive constant ω, there is a positive R_ω (choose the larger one between the R_ω for F^+ and the R_ω for F^-) with the property that if $u_0 \geq \omega$ on an interval of length $2R_\omega$. Hence, it follows that the solutions $u_n^\pm(x)$ satisfy

$$\liminf_{t\to\infty} \inf_{|x|\leq tc} u^\pm(x) = \beta^\pm, \text{ for } 0 < c < c^*.$$

Thus for any $c < c^*$, it follows from Theorem 3.1 (ii) that

$$\liminf_{n\to\infty} \inf_{|x|\leq nc} u_n^\pm(x) = \beta^\pm,$$

and consequently, that

$$\beta^- \leq \liminf_{n\to\infty} \inf_{|x|\geq nc} u_n(x) \leq \beta^+.$$

□

4. **Characterization of c^* as the slowest speeds of traveling waves.** A non-constant solution of (6) is a traveling wave of speed c provided that it has the form $u_n(x) = u(x - cn)$, where $u \in C(\mathbb{R}, \mathbb{R}^N)$ and, of course, if it satisfies (6). By substituting this form into (6), it follows that $u(\xi)$ must satisfy the following system of equations.

$$u(\xi) = \mathcal{Q}_c[F(u)](\xi) = (\mathcal{Q}_c^i[F(u)](\xi)) := \mathcal{Q}[F(u)](\xi + c) \tag{9}$$

In the rest of this section we complete the proof of Theorem 2.1 (iii), (iv) and (v), that is, the portion of our main result that characterizes the spread speed c^* as *the speed* of the slowest member of a family of non-constant traveling wave solutions. This is an extension of prior results for monotone operators [22] and for scalar equations [36, 35, 14, 23].

4.1. **Upper and lower solutions.** In this subsection, we verify that ϕ^+ and ϕ^- defined below are the upper and lower solutions of (9) respectively. These solutions are only continuous on $\mathbb{R}$. Upper and lower solutions of this type have been frequently used in the literature (see Diekmann [6], Weinberger [36], Lui [25], Weinberger, Lewis and Li [33], Rass and Radcliffe [26], Weng and Zhao [38], more recently by Ma [27] and Wang [31]). In particular, the explicit use of upper vector-valued solutions can be traced to the work in [25, 33, 26, 38]; for lower vector-valued solutions, in the context of multi-type epidemic models, to the work in [26]; and in [38] in the context of multi-type SIS epidemic models. Our construction of ϕ^+ and ϕ^-, the upper and lower solutions of (9), is motivated by the research in these references.

Our verification of the lower and upper solutions for n-dimensional systems is new and different from the above mentioned references. The details follow below.

Let $c > c*$, $1 < \gamma < 2$, $q > 1$ and recall the definitions of Λ_c and $\gamma\Lambda_c$ as utilized in Proposition 1. The corresponding positive eigenvectors ν_{Λ_c} and $\nu_{\gamma\Lambda_c}$ of B_μ for the eigenvalues λ_μ when $\mu = \Lambda_c, \gamma\Lambda_c$ can therefore be identified.

Define

$$\phi^+(\xi) = (\phi_i^+),$$

where

$$\phi_i^+ = \min\{\beta_i, \nu^i_{\Lambda_c} e^{-\Lambda_c \xi}\},\ \xi \in \mathbb{R};$$

and

$$\phi^-(\xi) = (\phi_i^-),$$

where

$$\phi_i^- = \max\{0, \nu^i_{\Lambda_c} e^{-\Lambda_c \xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c \xi}\},\ \xi \in \mathbb{R}.$$

It is clear that if $\xi \leq \frac{\ln \frac{\beta_i}{\nu^i_{\Lambda_c}}}{-\Lambda_c}$ then $\phi_i^+(\xi) = \beta_i$; and if $\xi > \frac{\ln \frac{\beta_i}{\nu^i_{\Lambda_c}}}{-\Lambda_c}$ then $\phi_i^+(\xi) = \nu^i_{\Lambda_c} e^{-\Lambda_c \xi}$. Similarly, if $\xi \leq \ln(q\frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})\frac{1}{(\gamma-1)\Lambda_c}$ then $\phi_i^-(\xi) = 0$; and if $\xi > \ln(q\frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})\frac{1}{(\gamma-1)\Lambda_c}$ then $\phi_i^-(\xi) = \nu^i_{\Lambda_c} e^{-\Lambda_c \xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c \xi}$.

We choose $q > 1$ large enough so that

$$\frac{\ln(q\frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})}{(\gamma-1)\Lambda_c} > \frac{\ln \frac{\beta_i}{\nu^i_{\Lambda_c}}}{-\Lambda_c}$$

and therefore

$$\phi_i^+(\xi) > \phi_i^-(\xi), \xi \in \mathbb{R}.$$

We verify in the two lemmas below that ϕ^+ and ϕ^- are upper and lower solutions of (9) respectively. Since it is assumed that F is monotone in Lemma 4.1, then $F^\pm = F, \beta^\pm = \beta$.

Lemma 4.1. *Assume F is monotone and $(H1)-(H3)$ hold. For any $c > c^*$, then ϕ^+ is an upper solution of $\mathcal{Q}_c[F]$. That is*

$$\mathcal{Q}_c[F(\phi^+)](\xi) \leq \phi^+(\xi), \xi \in \mathbb{R}.$$

Proof. Let $\xi_i^* = \frac{\ln \frac{\beta_i}{\nu^i_{\Lambda_c}}}{\Lambda_c}$. Then $\phi_i^+(\xi) = \beta_i$ if $\xi \leq \xi_i^*$, and $\phi_i^+(\xi) = \nu^i_{\Lambda_c} e^{-\Lambda_c \xi}$ if $\xi > \xi_i^*$. Note that $\phi_i^+(\xi) \leq \nu^i_{\Lambda_c} e^{-\Lambda_c \xi}, \xi \in \mathbb{R}$.

In view of (H3) we have, for $\xi \in \mathbb{R}$

$$f_i(\phi^+(\xi)) \leq \sum_{j=1}^N \partial_j f_i(0) \phi_i^+(\xi) \leq \sum_{j=1}^N \partial_j f_i(0) \nu^j_{\Lambda_c} e^{-\Lambda_c \xi}$$

Thus, for $\xi \in \mathbb{R}$, in view of (7), (H3), Proposition 1, we obtain that

$$\begin{aligned} \mathcal{Q}^i[F(\phi^+)](\xi+c) &\leq e^{-\Lambda_c(\xi+c)} \sum_{j=1}^{N} \nu^j_{\Lambda_c} b^{i,j}_{\Lambda_c} \\ &= e^{-\Lambda_c(\xi+c)} \lambda(\Lambda_c) \nu^i_{\Lambda_c} \\ &= e^{-\Lambda_c(\xi+c)} e^{\Lambda_c \Phi(\Lambda_c)} \nu^i_{\Lambda_c} \\ &= \nu^i_{\Lambda_c} e^{-\Lambda_c(\xi+c)} e^{\Lambda_c c} \\ &= \nu^i_{\Lambda_c} e^{-\Lambda_c \xi}. \end{aligned} \tag{10}$$

On the other hand, since $\phi_i^+(\xi) \leq \beta_i, i = 1, ..., N$, we have for $\xi \in \mathbb{R}$

$$\mathcal{Q}^i[F(\phi^+)](\xi+c) \leq \beta_i. \tag{11}$$

Thus, we have for $\xi \in \mathbb{R}$

$$\mathcal{Q}^i_c[F(\phi^+)](\xi) = \mathcal{Q}^i[F(\phi^+)](\xi+c) \leq \phi_i^+(\xi). \tag{12}$$

This completes the proof of Lemma 4.1.

□

In order to verify that ϕ^- is the lower solution, the following estimate for F is needed. For $N = 1, 2$, Lemma 4.2 can be found in [31].

Lemma 4.2. *Assume* $(H1 - H2)$ *hold. There exist positive constants* $D_i, i = 1, ..., N$ *such that*

$$f_i(u) \geq \sum_{j=1}^{N} \partial_j f_i(0) u^j - D_i \sum_{j=1}^{N} (u^j)^2, \ \ u = (u^j), u \in [0, \beta^+], i = 1, ..., N.$$

Proof. In a sufficiently small neighborhood of the origin, since F is twice continuously differentiable. From the Taylor's Theorem for multi-variable functions, for u sufficiently small.

$$f_i(u) = \sum_{j=1}^{N} \partial_j f_i(0) u^j + O(\sum_{j=1}^{N} (u^j)^2), \ \ u = (u^j), u \in [0, \beta^+], i = 1, ..., N.$$

There exist small $\epsilon > 0$ and $D'_i > 0$ such that for $\sum_{j=1}^{n} (u^j)^2 < \epsilon$

$$f_i(u) \geq \sum_{j=1}^{N} \partial_j f_i(0) u^j - D'_i \sum_{j=1}^{N} (u^j)^2, \ \ u = (u^j), u \in [0, \beta^+], i = 1, ..., N.$$

For $u \in [0, \beta]$ and $\sum_{j=1}^{n} (u^j)^2 \geq \epsilon$, noting that $f_i(u), \sum_{j=1}^{N} \partial_j f_i(0) u^j$ are bounded, we always choose a sufficiently large constant $D''_i > 0$ such that

$$f_i(u) \geq \sum_{j=1}^{N} \partial_j f_i(0) u^j - D''_i \sum_{j=1}^{N} (u^j)^2.$$

Thus if we let $D_i = \max\{D'_i, D''_i\}$, then Lemma 4.2 is proved. □

Lemma 4.3. *Assume* $(H1) - (H3)$ *hold. For any* $c > c^*$ *if* q *is sufficiently large,* ϕ^- *is a lower solution of* $\mathcal{Q}_c[F]$. *That is*

$$\mathcal{Q}_c[F(\phi^-)](\xi) \geq \phi^-(\xi), \ \ \xi \in \mathbb{R}.$$

Proof. Again let $\xi_i^* = \ln(q\frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})\frac{1}{(\gamma-1)\Lambda_c}$. Hence if $\xi \le \xi_i^*$ then $\phi_i^-(\xi) = 0$; while if $\xi > \xi_i^*$ then $\phi_i^-(\xi) = \nu^i_{\Lambda_c} e^{-\Lambda_c\xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi}$. It is easy to see that

$$\nu^i_{\Lambda_c} e^{-\Lambda_c\xi} \ge \phi^-(\xi) \ge \nu^i_{\Lambda_c} e^{-\Lambda_c\xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi}, \quad \xi \in \mathbb{R}, i = 1, ..., N. \tag{13}$$

For $\xi \in \mathbb{R}$, in view of Lemma 4.2, we have, for $\xi \in \mathbb{R}, i = 1, ..., N$,

$$\begin{aligned} f^i(\phi^-(\xi)) &\ge \sum_{j=1}^N \partial_j f_i(0)\phi_j^-(\xi) - D_i \sum_{j=1}^N (\phi_j^-(\xi))^2 \\ &\ge \sum_{j=1}^N \partial_j f_i(0)\nu^j_{\Lambda_c} e^{-\Lambda_c\xi} - q\sum_{j=1}^N \partial_j f_i(0)\nu^j_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi} - \widehat{M}_i e^{-2\Lambda_c\xi} \end{aligned} \tag{14}$$

where $\widehat{M}_i = D_i \sum_{j=1}^N (\nu^j_{\Lambda_c})^2 > 0$. Now we are able to estimate $\mathcal{Q}[F(\phi^-)]$ for $\xi \ge \min_i \xi_i^*, i = 1, ..., N$ as in (10)

$$\begin{aligned} \mathcal{Q}^i[F(\phi^-)](\xi + c) &\ge e^{-\Lambda_c(\xi+c)} \sum_{j=1}^N \nu^j_{\Lambda_c} b^{i,j}_{\Lambda_c} - qe^{-\gamma\Lambda_c(\xi+c)} \sum_{j=1}^N \nu^j_{\gamma\Lambda_c} b^{i,j}_{\gamma\Lambda_c} \\ &\quad - \widehat{M}_i e^{-2\Lambda_c(\xi+c)} \int_{\mathbb{R}} k_i(y) e^{2\Lambda_c y} dy \\ &= \nu^i_{\Lambda_c} e^{-\Lambda_c(\xi+c)} e^{\Lambda_c\Phi(\Lambda_c)} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c(\xi+c)} e^{\gamma\Lambda_c\Phi(\gamma\Lambda_c)} \\ &\quad - \widehat{M}_i e^{-2\Lambda_c(\xi+c)} \int_{\mathbb{R}} k_i(y) e^{2\Lambda_c y} dy \\ &= \nu^i_{\Lambda_c} e^{-\Lambda_c\xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi} e^{\gamma\Lambda_c(\Phi(\gamma\Lambda_c)-c)} \\ &\quad - \widehat{M}_i e^{-2\Lambda_c(\xi+c)} \int_{\mathbb{R}} k_i(y) e^{2\Lambda_c y} dy \\ &= \nu^i_{\Lambda_c} e^{-\Lambda_c\xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi} \\ &\quad + q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi} e^{\gamma\Lambda_c(\Phi(\gamma\Lambda_c)-c)} \\ &\quad - \widehat{M}_i e^{-2\Lambda_c(\xi+c)} \int_{\mathbb{R}} k_i(y) e^{2\Lambda_c y} dy \\ &= \phi_i^-(\xi) + e^{-\gamma\Lambda_c\xi}\Big(q\nu^i_{\gamma\Lambda_c}\big(1 - e^{\gamma\Lambda_c(\Phi(\gamma\Lambda_c)-c)}\big) \\ &\quad - \widehat{M}_i e^{(\gamma-2)\Lambda_c\xi} e^{-2\Lambda_c c} \int_{\mathbb{R}} k_i(y) e^{2\Lambda_c y} dy\Big) \end{aligned} \tag{15}$$

For $\xi \ge \min_i \xi_i^*$, $e^{(\gamma-2)\Lambda_c\xi}$ is bounded above. Finally, from (15) and the fact that $\Phi(\gamma\Lambda_c) < c$, we conclude that there exists $q > 0$, which is independent of ξ, such that, for $\xi \ge \xi_i^*$

$$\mathcal{Q}^i[F(\phi^-)](\xi + c) \ge \nu^i_{\Lambda_c} e^{-\Lambda_c\xi} - q\nu^i_{\gamma\Lambda_c} e^{-\gamma\Lambda_c\xi}. \tag{16}$$

And since $\phi_i^-(\xi) = 0$ for $\xi < \xi_i^*$, $i = 1, ..., N$

$$\mathcal{Q}_c^i[F(\phi^-)](\xi) = \mathcal{Q}^i[F(\phi^-)](\xi + c) \ge \phi_i^-(\xi), \quad \xi \in \mathbb{R}.$$

This completes the proof. $\square$

4.2. **Proof of Theorem 2.1 (iii) with monotonicity of F.** Theorems that guarantee the existence of traveling wave solutions for cooperative systems have been established (e.g. [22, 35]). In this section, it is assumed that F is non-decreasing on $[0, \beta]$ and from this assumption, we proceed to establish Theorem 2.1.

As stated in Section 2, even for the case of monotone operators, the results and analysis in this manuscript are different from those found in [22, 35]. In fact, we are able to characterize explicitly the asymptotic behavior of traveling waves through the careful analysis of eigenvalues and upper-lower solutions (an analysis not provided in [22, 35]). The analysis of the asymptotic behavior of traveling wave solutions for monotone operators enable us also *to prove the existence of traveling wave solutions for non monotone operators.*

In order to complete the last step, the following Banach space is required,

$$\mathcal{B}_\rho = \{u = (u^i) : u^i \in C(\mathbb{R}), \quad \sup_{\xi\in\mathbb{R}} |u^i(\xi)|e^{\rho\xi} < \infty, i = 1, ..., N\},$$

equipped with the weighted norm

$$\|u\|_\rho = \sum_{i=1}^{N} \sup_{\xi\in\mathbb{R}} |u^i(\xi)|e^{\rho\xi},$$

where $C(\mathbb{R})$ denotes the set of all continuous functions on $\mathbb{R}$, and where ρ is a positive constant such that $\rho < \Lambda_c$. It follows that $\phi^+ \in \mathcal{B}_\rho$ and $\phi^- \in \mathcal{B}_\rho$. Finally, the following set is required (domain of the operator of interest):

$$\mathcal{A}_\rho = \{u : u \in \mathcal{B}_\rho, \phi^-(\xi) \leq u(\xi) \leq \phi^+(\xi), \xi \in \mathbb{R}\}$$

It is clear that $\mathcal{A}_\rho \subseteq \mathcal{C}_\beta$. By the use of standard procedures (see [27, 14, 31]), it can be shown that $\mathcal{Q}_c[F]$ is a continuous map of the bounded set $\mathcal{A}_\rho$ into a compact set. We state this result.

Lemma 4.4. *Assume $(H1) - (H3)$ hold. Then $\mathcal{Q}_c[F] : \mathcal{A}_\rho \to \mathcal{A}_\rho$ is continuous with the weighted norm $\|.\|_\rho$ and relatively compact in $\mathcal{B}_\rho$.*

Now we are in a position to prove Theorem 2.1 when F is monotone. Define the following iteration

$$u_1 = (u_1^i) = \mathcal{Q}_c[F(\phi^+)], \quad u_{n+1} = (u_n^i) = \mathcal{Q}_c[F(u_n)], n \geq 1. \tag{17}$$

From Lemmas 4.1, 4.3, and the fact that F is non-decreasing, u_n is non-increasing on $\mathbb{R}$, it follows that

$$\phi_i^-(\xi) \leq u_{n+1}^i(\xi) \leq u_n^i(\xi) \leq \phi_i^+(\xi), \xi \in \mathbb{R}, \; n \geq 1, i = 1, ..., N.$$

By Lemma 4.4 and the monotonicity of (u_n), we conclude that there is $u \in \mathcal{A}_\rho$ such that $\lim_{n\to\infty} \|u_n - u\|_\rho = 0$. Lemma 4.4 then implies that $\mathcal{Q}[u] = u$. Furthermore, since u is non-increasing, it is clear that $\lim_{\xi\to\infty} u^i(\xi) = 0, i = 1, ..., N$. Now we assume that $\lim_{\xi\to-\infty} u_i(\xi) = \hat{k^i}, i = 1, ..., N$ $\hat{k^i} > 0, i = 1, ..., N$ because of $u \in \mathcal{A}_\rho$. Applying the dominated convergence theorem, we get $\hat{k_i} = f_i(\hat{k})$. By (H2), $\hat{k} = \beta$. Finally, since

$$\nu_{\Lambda_c}^i(e^{-\Lambda_c\xi} - q\epsilon^{-\gamma\Lambda_c\xi}) \leq u^i(\xi) \leq \nu_{\Lambda_c}^i e^{-\Lambda_c\xi}, \xi \in \mathbb{R}$$

we conclude that

$$\lim_{\xi\to\infty} u^i(\xi)e^{\Lambda_c\xi} = \nu_{\Lambda_c}^i, i = 1, ..., N. \tag{18}$$

This completes the proof of Theorem 2.1 when F is monotone.

4.3. **Proof of Theorem 2.1 (iii).** We proceed to characterize traveling wave solutions when the assumption that F is monotone is *dropped*. We observe that our treatment is different even for the scalar case ($N = 1$). The key mathematical ideas used can be found in the literature with some differences. Specifically, our use of the Schauder Fixed Point Theorem and the construction of the bounded set $\mathcal{D}_\rho$ are different from those found in [14, 23]. We observe that as noted in Section 4, both $\mathcal{Q}_c[F^+]$ and $\mathcal{Q}_c[F^-]$ are monotone. We further observer that F, F^+, F^- have the same linearization at the origin. In view of the results in Section 4, there exists a non-increasing fixed point $u_- = (u_-^i) \in \mathcal{C}_{\beta^-}$ of $\mathcal{Q}_c[F^-]$ such that

$$\mathcal{Q}_c[F^-(u_-)] = u_-$$

and $\lim_{\xi\to-\infty} u_-^i(\xi) = \beta_i^-, i = 1, ..., N$, and $\lim_{\xi\to\infty} u_-^i(\xi) = 0, i = 1, ..., N$. Furthermore, $\lim_{\xi\to\infty} u_-^i(\xi)e^{\Lambda_c\xi} = \nu_{\Lambda_c}^i, i = 1, ..., N$. If we let

$$\widetilde{\phi^+}(\xi) = (\widetilde{\phi_i^+}),$$

where

$$\widetilde{\phi_i^+} = \min\{\beta_i^+, \nu_{\Lambda_c}^i e^{-\Lambda_c\xi}\},\ \xi \in \mathbb{R}, i = 1, ..., N,$$

then according to Lemma 4.1, $\widetilde{\phi^+}$ is an upper solution of $\mathcal{Q}_c[F^+]$. Also if β^+ is replaced with β^-, then $\widetilde{\phi^+}(\xi)$ is an upper solution of $\mathcal{Q}_c[F^-]$. By the construction of $u_-^i(\xi)$, it follows that

$$u_-(\xi) \le \widetilde{\phi^+}(\xi), \xi \in \mathbb{R}$$

In order to complete our argument we must reintroduce the following set:

$$\mathcal{D}_\rho = \{u : u = (u^i) \in \mathcal{B}_\rho, u_-^i(\xi) \le u^i(\xi) \le \widetilde{\phi_i^+}(\xi), \xi \in (-\infty, \infty), i = 1, ..., N\},$$

where $\mathcal{B}_\rho$ is defined in Section 4.2. It is clear that $\mathcal{D}_\rho$ is a bounded nonempty closed convex subset in $\mathcal{B}_\rho$. Furthermore, we have, for any $u = (u^i) \in \mathcal{D}$

$$u_- = \mathcal{Q}_c[F^-(u_-)] \le \mathcal{Q}_c[F^-(u)] \le \mathcal{Q}_c[F(u)] \le \mathcal{Q}_c[F^+(u)] \le \mathcal{Q}_c[F^+(\widetilde{\phi^+})] \le \widetilde{\phi^+}.$$

Therefore, $\mathcal{Q}_c[F] : \mathcal{D}_\rho \to \mathcal{D}_\rho$. Since the proof of Lemmas 4.4 does not need the monotonicity of F^-, in the same way it can be shown that $\mathcal{Q}_c[F^-] : \mathcal{D}_\rho \to \mathcal{B}_\rho$ is continuous and maps bounded sets into compact sets. Therefore, the Schauder Fixed Point Theorem guarantees that the operator $\mathcal{Q}_c[F]$ has a fixed point u in $\mathcal{D}_\rho$, a traveling wave solution of (6) for $c > c^*$. Since $u_-^i(\xi) \le u^i(\xi) \le \widetilde{\phi_i^+}(\xi), \xi \in (-\infty, \infty), i = 1, ..., N$, it is easy to see that for $i = 1, ..., N$, $\lim_{\xi\to\infty} u^i(\xi) = 0$, $\lim_{\xi\to\infty} u^i(\xi)e^{\Lambda_c\xi} = \nu_{\Lambda_c}^i$,

$$\beta_i^- \le \liminf_{\xi\to-\infty} u^i(\xi) \le \limsup_{\xi\to-\infty} u^i(\xi) \le \beta_i^+$$

and $0 < u_-^i(\xi) \le u^i(\xi) \le \beta_i^+, \xi \in (-\infty, \infty)$. □

4.4. **Proof of Theorem 2.1 (iv).** *Proof.* The proof in this subsection follows the approach found in [4, 14]. We make use of the results in Theorem 2.1 (iii). Hence, for each $m \in \mathbb{N}$, we choose $c_m > c^*$ such that $\lim_{m\to\infty} c_m = c^*$. According to Theorem 2.1 (iii), for each c_m there is a traveling wave solution $u_m = (u_m^i)$ of (6) such that

$$u_m = \mathcal{Q}[F(u_m)](\xi + c_m).$$

and

$$\lim_{\xi\to\infty} u^i(\xi) = 0,\ \beta_i^- \le \liminf_{\xi\to-\infty} u_m^i(\xi) \le \limsup_{\xi\to-\infty} u_m^i(\xi) \le \beta_i^+, i = 1, ..., N.$$

The use of standard procedures (see [27, 14, 31]) guarantees that (u_m) is equicontinuous and uniformly bounded on $\mathbb{R}$. Hence, the Ascoli's theorem implies that there is a vector valued continuous function $u = (u^i)$ on $\mathbb{R}$ and a subsequence (u_{m_k}) of (u_m), such that

$$\lim_{k\to\infty} u_{m_k}(\xi) = u(\xi)$$

uniformly in ξ on any compact interval of $\mathbb{R}$. Further, the use of the dominated convergence theorem guarantees that we have

$$u = \mathcal{Q}[F(u)](\xi + c^*)$$

Because of the translation invariance of u_m, we can always assume that the first component $u_m^1(0)$ equals to a sufficiently small positive number $\sigma > 0$ for all m. Since there is only a finite number of equilibria, we can choose σ in such a way that it is not the first component of any nontrivial equilibrium. Consequently, u is a nonconstant traveling solution of (6) for $c = c^*$. □

4.5. **Proof of Theorem 2.1 (v).** The proof of the key result in this subsection follows the approach in [14, 23]. Suppose, by contradiction, that for some $c \in (0, c^*)$, (6) has a traveling wave $u_n(x) = u(x - cn)$ such that $u \in \mathcal{C}_\beta$ with $\liminf_{x\to-\infty} u(x) \gg 0$ and $u(+\infty) = 0$. Thus $u(x)$ can be larger than a positive vector with arbitrary length. It follows from Theorem 2.1 (ii)

$$\liminf_{n\to\infty} \inf_{|x|\le nc} u_n(x) \ge \beta^-, \text{ for } 0 < c < c^*$$

If we now let $\hat{c} \in (c, c^*)$ and $x = \hat{c}n$, then

$$\lim_{n\to\infty} u\big((\hat{c} - c)n\big) = \lim_{n\to\infty} u_n(\hat{c}n) \ge \liminf_{n\to\infty} \inf_{|x|\le n\hat{c}} u_n(x) \ge \beta^-,$$

but since $\lim_{n\to\infty} u\big((\hat{c} - c)n\big) = u(\infty) = 0$, we have reached a contradiction. □

5. Minimum speeds and traveling waves for a competition model.

Hassell and Comins' model of the growth and spread of two population densities at time n and location x under an interference competition regime is used to highlight the applicability of the mathematical results established in this manuscript. We make use of the local analysis (no spatial) results of their model as reported in [11]. The inclusion of the possibility of dispersal via the re-distribution kernel $k_i(x - y)$ leads to Model (5). If the two spatially-explicit densities are denoted by $X_n(x)$ and $Y_n(x)$ then the model is still given locally by the set of nonlinear coupled difference equations (4); with the addition of dispersal leads to (5). The following results highlight the application of the main theorem. It highlights its contribution towards increasing our understanding of the role of dispersal, in the context of local competitive systems. There has been some additional contributions. In particular we observe at this juncture that Li [24] has also investigated the minimum speed of (5).

Model (5) can support four constant equilibria: the unpopulated state $(0, 0)$; the second-species monoculture state $(0, r_2)$; the first monculture state $(r_1, 0)$; and

$(\frac{r_1-\sigma_1 r_2}{1-\sigma_1\sigma_2}, \frac{r_2-\sigma_2 r_1}{1-\sigma_1\sigma_2})$. The change of variables $p = X, q = r_2 - Y$ allows to convert system (5) into the following equivalent coupled system of integro-difference equations

$$\begin{aligned} p_{n+1}(x) &= \int_{\mathbb{R}} k_1(x-y) f(p_n(y), q_n(y)) dy \\ q_{n+1}(x) &= \int_{\mathbb{R}} k_2(x-y) g(p_n(y), q_n(y)) dy \end{aligned} \tag{19}$$

where

$$\begin{aligned} f(p,q) &= h(p) e^{r_1 - \sigma_1 r_2 + \sigma_1 q} \\ g(p,q) &= r_2 - \big(r_2 - q\big) e^{q - \sigma_2 p} \\ h(p) &= p e^{-p} \end{aligned}$$

It is clear that (5) and (19) are not monotone systems. A straightforward calculation shows that (19) has the four explicit equilibria $(0,0), (0,r_2), (r_1,r_2)$ and

$$\Big(\frac{r_1-\sigma_1 r_2}{1-\sigma_1\sigma_2}, \sigma_2 \frac{r_1-\sigma_1 r_2}{1-\sigma_1\sigma_2}\Big).$$

Under the conditions of Theorem 5.1, we show in the Appendix that there are no positive equilibrium of (19) between $(0,0)$ and (r_1,r_2). Theorem 2.1 is used to guarantee the existence of a spreading speed and traveling wave solutions of the nonmonotone system (19)(with accompanying results on the speed of propagation). We summarize the results obtained in the context of this example in Theorem 5.1. Its proof is outlined in the Appendix.

Theorem 5.1. *Let* $0 < r_2 < 1 < r_1$, $0 < \sigma_1 < 1 < \sigma_2, \sigma_1\sigma_2 < 1$, *and*

$$r_2 < \sigma_2 e^{r_1 - 1 - e^{r_1 - 1}}$$

and

$$\sigma_1 r_2 < e^{r_1 - 1 - e^{r_1 - 1}}.$$

Assume that k_1, k_2 *satisfy (H1) and* $\int_{\mathbb{R}} k_1(s) e^{\mu s} ds \geq \int_{\mathbb{R}} k_2(s) e^{\mu s} ds$ *for* $\mu > 0$. *Then the conclusions of Theorem 2.1 hold for (19).*

The biological interpretation of the conditions in Theorem 5.1 in the context of this application are straightforward. For an invasion to be successful, the overall dispersal of the invader (X) is relatively larger than the overall dispersal of the out-competed resident (Y). Further competition favors the invader whenever σ_1 is sufficiently small (invader less affected by competition) and σ_2 is sufficiently large (a relatively fragile resident, that is, the resident is more susceptible to interference competition). Under these conditions, there exist traveling wave solutions of (19) "loosely" connecting its two equilibria $(0,0)$ and (r_1,r_2). Equivalently, there are traveling wave solutions of (5) "loosely" connecting its two boundary states $(0,r_2)$ and $(r_1,0)$. Here the term "loosely" means the traveling waves may oscillate around the equilibria since they are not necessarily monotone. For specific k_i, the exact value of c^* can be computed and compared to experimental data as it has been done by Kot, Lewis, others and their collaborators (see past cited references).

6. **Conclusions.** Integro-difference systems arise naturally in the study of the dispersal of populations, including interacting populations, composed of organisms that reproduce locally via discrete generations and compete for resources, before dispersing . The brunt of the *mathematical* research has focused on the the study of the existence of traveling wave solutions and characterizations of the spreading

speed in the context of cooperative systems. In this paper, we characterize the spreading speed for a large class of *non cooperative systems*, formulated in terms of integro-difference equations, via the convergence of initial data to wave solutions. The spreading speed is characterized as the slowest speed of a family of non-constant traveling wave solutions. The results are applied to a spatially explicit version of *non-cooperative* local competitive system proposed by Hassell and Comins (1976) [11]. We are in the process of applying these results to additional ecological and epidemiological systems where the local population dynamics are naturally non-cooperative. One of our goals is to increase our understanding of the role of dispersal in communities where the local dynamics are richer, a possible more realistic, than those previously supported by the mathematical theory.

Appendix. Proof of Proposition 1 (4). The conclusion is also briefly discussed in a remark in [33, pp. 197]. If $\Phi(\mu) = \frac{1}{\mu}\ln\lambda(\mu)$ achieves its minimum at a finite μ, then $c^* = \min_{\mu>0}\Phi(\mu) > 0$. Now let $c^* = \lim_{\mu\to\infty}\frac{1}{\mu}\ln\lambda(\mu)$. We recall that $\lambda(\mu)$ is an eigenvalue of B_μ with a positive eigenvector. Thus there exists a positive constant $\delta > 0$ and a positive integer $i \le N$ such that $\lambda(\mu) \ge \delta\int_{\mathbb{R}} k_i(x)e^{\mu x}dx$. Thus

$$c^* \ge \lim_{\mu\to\infty}\frac{1}{\mu}\ln\big(\delta\int_{\mathbb{R}} k_i(x)e^{\mu x}dx\big).$$

Let $\Psi(\mu) = \frac{\int_{\mathbb{R}} xk_i(x)e^{\mu x}dx}{\int_{\mathbb{R}} k_i(x)e^{\mu x}dx}, \quad \mu \ge 0$. Then by the L'Hopital's rule we have $c^* \ge \lim_{\mu\to\infty}\Psi(\mu)$. Differentiation of Ψ and rearrangement of terms show

$$\Psi'(\mu) = \frac{\int_{\mathbb{R}}\big(x-\Psi(\mu)\big)^2 k_i(x)e^{\mu x}dx}{\int_{\mathbb{R}} k_i(x)e^{\mu x}dx} > 0, \mu \ge 0,$$

also see Weinberger [36]. Note that $\Psi(0) = 0$ and therefore, $c^* \ge \lim_{\mu\to\infty}\Psi(\mu) > 0$. □

Proof of Theorem 5.1. We verify that the conditions (H1-H3) hold for (19). From the assumptions of Theorem 5.1, (H1) holds for (19). We proceed to verify (H2) for (19) which, as we had noticed earlier, has four equilibria $(0,0),(0,r_2),(r_1,r_2)$ and

$$\Big(\frac{r_1-\sigma_1 r_2}{1-\sigma_1\sigma_2}, \sigma_2\frac{r_1-\sigma_1 r_2}{1-\sigma_1\sigma_2}\Big). \tag{20}$$

If it is further assumed that $r_1 > 1, r_2 < 1$, and $\sigma_1 < 1, \sigma_2 > 1, \sigma_1\sigma_2 < 1$ then

$$\Big(\frac{r_1-\sigma_1 r_2}{1-\sigma_1\sigma_2}, \sigma_2\frac{r_1-\sigma_1 r_2}{1-\sigma_1\sigma_2}\Big) \gg (r_1, r_2). \tag{21}$$

Thus (19) has no other positive equilibrium $(\underline{p},\underline{q})$ between $(0,0)$ and (r_1,r_2) with $\underline{p} > 0$ and $\underline{q} > 0$. Observe that 1 is the maximum point of $h(p)$, that is, $h(p)$ is not monotone on $[0,r_1]$. Further simple calculations show that $g_p(p,q) = \sigma_2(r_2 - q)e^{q-\sigma_2 p} \ge 0$, for $q \in [0,r_2]$, $g_q(p,q) = (1-r_2+q)e^{q-\sigma_2 p} \ge 0$.

In order to use Theorem 2.1, we define the upper monotone function

$$h^+(p) = \begin{cases} h(p), & 0 \le p \le 1, \\ h(1) = e^{-1}, & 1 \le p. \end{cases}$$

and corresponding monotone systems with h^+

$$\begin{aligned} p_{n+1}(x) &= \int_{\mathbb{R}} k_1(x-y) f^+(p_n(y), q_n(y)) dy \\ q_{n+1}(x) &= \int_{\mathbb{R}} k_2(x-y) g(p_n(y), q_n(y)) dy. \end{aligned} \tag{22}$$

where $f^+(p,q) = h^+(p) e^{r_1 - \sigma_1 r_2 + \sigma_1 q}$.

The origin, $(0,0)$ is an equilibrium of (22) and $g(p,q) = q$ has only two possible solutions $q^* = r_2$ and $q^* = \sigma_2 p^*$. Thus for $q^* = r_2$, Equation (22) has two equilibria $(0, r_2), (e^{r_1-1}, r_2)$. The second equilibrium (e^{r_1-1}, r_2) comes from the fact that $p^* > 1$ and therefore $h^+(p^*) = e^{-1}$. (If $0 < p^* \leq 1$, then $h^+(p^*) = h(p^*)$ and $(p^*, q^*) = (r_1, r_2)$; however, $r_1 > 1$, which is a contradiction). In order for Equation (22) to have another positive equilibrium (p^*, q^*), when $q^* = \sigma_2 p^*$, it must satisfy $p^* > 1$ (otherwise, $p^* \leq 1$ and (p^*, q^*) is (20) which means that (21) implies that $p^* > 1$, a contradiction) and therefore

$$\begin{aligned} e^{r_1 - \sigma_1 r_2 + \sigma_1 \sigma_2 p^* - 1} &= p^* \\ q^* &= \sigma_2 p^*. \end{aligned} \tag{23}$$

We will use the inequality, $e^x \geq x + 1$, $x \in \mathbb{R}$ to estimate e^x. Thus $p^* = e^{r_1 - \sigma_1 r_2 + \sigma_1 \sigma_2 p^* - 1} \geq r_1 - \sigma_1 r_2 + \sigma_1 \sigma_2 p^*$ and $p^* \geq \frac{r_1 - \sigma_1 r_2}{1 - \sigma_1 \sigma_2} > r_1$, which implies that $p^* > e^{r_1 - 1}$, from the first equation of (23) and $\sigma_2 r_1 > r_2$. Again since $\sigma_2 r_1 > r_2$, we also have $q^* = \sigma_2 p^* > r_2$ and thus Equation (22) has no positive equilibrium between $(0,0)$ and (e^{r_1-1}, r_2).

There is a $t_0 \in (0,1)$ such that $h(t_0) = h(e^{r_1-1})$ and define

$$h^-(p) = \begin{cases} h(p), & 0 \leq p \leq t_0, \\ h(t_0), & t_0 \leq p \leq e^{r_1-1}. \end{cases}$$

and corresponding lower monotone system

$$\begin{aligned} p_{n+1}(x) &= \int_{\mathbb{R}} k_1(x-y) f^-(p_n(y), q_n(y)) dy \\ q_{n+1}(x) &= \int_{\mathbb{R}} k_2(x-y) g(p_n(y), q_n(y)) dy. \end{aligned} \tag{24}$$

where $f^-(p,q) = h^-(p) e^{r_1 - \sigma_1 r_2 + \sigma_1 q}$. Then

$$0 < h^-(p) \leq h(p) \leq h^+(p) \leq h'(0)p, p \in (0, e^{r_1-1}]$$

$h^-(0) = h^+(0) = 0$, $h^{\pm}(p), h(p)$ have the same derivative at 0.

Since $g(p,q) = q$ has only two possible solutions $q = r_2$ and $q = \sigma_2 p$ and $h(t_0) = t_0 e^{-t_0} = h(e^{r_1-1}) = e^{r_1-1} e^{-e^{r_1-1}}$, we can therefore calculate that (24) has three equilibria $(0,0), (0, r_2)$ and (t_1, r_2) where $t_1 = e^{2r_1 - 1 - e^{r_1-1}}$. Again (t_1, r_2) comes from the fact that $t_1 \geq t_0$ and $h(t_1) = h(t_0)$. (The same argument applied to (22) implies that $t_1 < t_0$ is a contradiction.) We will now show that

$$t_1 < r_1. \tag{25}$$

Indeed, since Expression (25) is equivalent to $2r_1 - 1 - e^{r_1-1} < \ln r_1$, we let $l(x) = 2x - 1 - e^{x-1} - \ln x$ and therefore $l(1) = 0$ and

$$l'(x) = 2 - e^{x-1} - \frac{1}{x} \leq 2 - x - \frac{1}{x} < 0, \text{ for } x > 1,$$

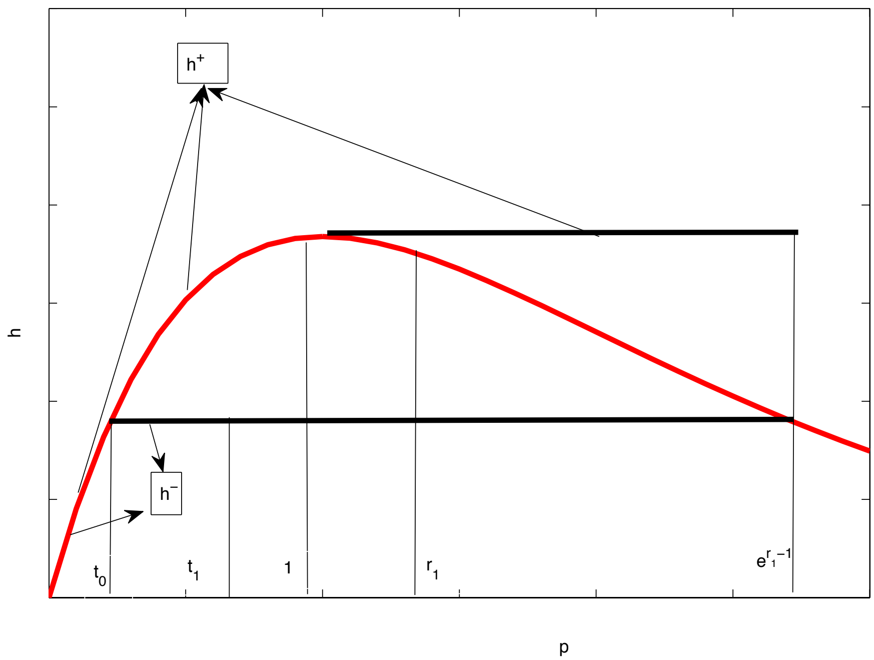

FIGURE 1. The construction of h^+ and h^-. The red curve is h. t_1 is always less than r_1.

and this verifies (25). Since $0 < t_0 < 1 < r_1$, the following inequality holds

$$0 < e^{r_1-1-e^{r_1-1}} < t_0 = e^{t_0}e^{r_1-1}e^{-e^{r_1-1}} < e^{2r_1-1-e^{r_1-1}} = t_1. \tag{26}$$

If (p^*, q^*) is a another positive equilibrium of (24) when $q^* = \sigma_2 p^*$, then it must satisfy $p^* > t_0$ (otherwise, $p^* \le t_0$ and (p^*, q^*) is (20) and from (21) we have that $p^* > 1 > t_0$, a contradiction) and therefore

$$\begin{aligned} e^{r_1-1}e^{-e^{r_1-1}}e^{r_1-\sigma_1 r_2+\sigma_1\sigma_2 p^*} &= p^* \\ q^* &= \sigma_2 p^*. \end{aligned} \tag{27}$$

Since $r_1 > \sigma_1 r_2$ and $p^* > 0$, we have $p^* > e^{r_1-1-e^{r_1-1}}$. In view of the assumption, $\sigma_2 e^{r_1-1-e^{r_1-1}} > r_2$ and System (27), we have $q^* > r_2$. Again from (27), we have $p^* > e^{2r_1-1-e^{r_1-1}} = t_1$. Thus (24) has no other positive equilibrium between $(0,0)$ and (t_1, r_2) and

$$(0,0) \ll (t_1, r_2) \le (r_1, r_2) \le (e^{r_1-1}, r_2).$$

See Fig. 6 for the construction of h^+ and h^-. Let $\beta^- = (t_1, r_2)$ and $\beta^+ = (e^{r_1-1}, r_2)$ and we have verified (H2) for (19).

We now proceed to verify (H3) for (19). The matrix in (7) for (19) is

$$B_\mu = (b_\mu^{i,j}) = \begin{pmatrix} e^{r_1-\sigma_1 r_2}\int_{\mathbb{R}} k_1(s)e^{\mu s}ds & 0 \\ r_2\sigma_2\int_{\mathbb{R}} k_2(s)e^{\mu s}ds & (1-r_2)\int_{\mathbb{R}} k_2(s)e^{\mu s}ds \end{pmatrix} \tag{28}$$

Since $e^{r_1-\sigma_1 r_2} > 1 > 1-r_2$, the principal eigenvalue for the matrix is

$$\lambda(\mu) = e^{r_1-\sigma_1 r_2}\int_{\mathbb{R}} k_1(s)e^{\mu s}ds$$

and the corresponding positive eigenvector

$$\eta_\mu = \begin{pmatrix} \nu_\mu^{(1)} \\ \nu_\mu^{(2)} \end{pmatrix} = \begin{pmatrix} \frac{e^{r_1-\sigma_1 r_2}\int_{\mathbb{R}} k_1(s)e^{\mu s}ds-(1-r_2)\int_{\mathbb{R}} k_2(s)e^{\mu s}ds}{r_2\sigma_2\int_{\mathbb{R}} k_2(s)e^{\mu s}ds} \\ 1 \end{pmatrix}. \tag{29}$$

Because $\int_{\mathbb{R}} k_2(s)e^{\mu s}ds \le \int_{\mathbb{R}} k_1(s)e^{\mu s}ds$, canceling $\int_{\mathbb{R}} k_2(s)e^{\mu s}ds$ in $\nu_\mu^{(1)}$ leads to

$$\nu_\mu^{(1)} \ge \frac{e^{r_1-\sigma_1 r_2}-(1-r_2)}{r_2\sigma_2} \ge \frac{1}{\sigma_2} + \frac{e^{r_1-\sigma_1 r_2}-1}{r_2\sigma_2} \ge \frac{1}{\sigma_2} \tag{30}$$

It is clear now that (H3)(i) holds. We can proceed to verify (H3)(ii) for (22). Let

$$(p,q) = (\min\{e^{r_1-1}, \nu_\mu^{(1)}\alpha\}, \min\{r_2,\alpha\}), \alpha > 0.$$

Since $e^{q-\sigma_2 p} \ge 1+q-\sigma_2 p$, we need to show that

$$\begin{aligned} h^+(p)e^{r_1-\sigma_1 r_2+\sigma_1 q} &\le e^{r_1-\sigma_1 r_2}p \\ r_2 - (r_2-q)e^{q-\sigma_2 p} &\le r_2\sigma_2 p + (1-r_2)q + q(q-\sigma_2 p) \\ &\le r_2\sigma_2 p + (1-r_2)q \end{aligned} \tag{31}$$

Therefore, it is easy to see that we only need to verify that

$$q \le \sigma_2 p \tag{32}$$

and

$$\frac{h^+(p)}{p} \le e^{-\sigma_1 q} \tag{33}$$

For (32), we need to consider the two cases: $p = e^{r_1-1}$ and $p = \nu_\mu^{(1)}\alpha$. If $p = e^{r_1-1}$, then

$$q \le r_2 \le \sigma_2 e^{r_1-1} \tag{34}$$

which is true by the assumption ($r_2 < \sigma_2 e^{r_1-1-e^{r_1-1}}$). If $p = \nu_\mu^{(1)}\alpha$, then $q \le \alpha \le \sigma_2\nu_\mu^{(1)}\alpha$, which is true because of (30).

In order to verify (33), first assume that $p \in (0,1)$, then $h^+(p) = pe^{-p}$ and $p = \nu_\mu^{(1)}\alpha$ since $e^{r_1-1} > 1$. Since $e^{-\sigma_1\alpha} \le e^{-\sigma_1 q}$, it suffices to verify that $e^{-\nu_\mu^{(1)}\alpha} \le e^{-\sigma_1\alpha}$, which is true because of (30) and $\sigma_2\sigma_1 < 1$. For the case $p \ge 1$ we have $h^+(p) = e^{-1}$. Again since

$$e^{-r_2} \le e^{-\sigma_1 r_2} \le e^{-\sigma_1 q}, \tag{35}$$

it suffices to verify $\frac{e^{-1}}{p} \le e^{-1} \le e^{-r_2}$, which holds because $r_2 < 1$.

It remains to verify (H3)(ii) for (24). Let

$$(p,q) = (\min\{t_1, \nu_\mu^{(1)}\alpha\}, \min\{r_2,\alpha\}), \alpha > 0.$$

For (32), we need to consider the two cases: $p = t_1$ and $p = \nu_\mu^{(1)}\alpha$. If $p = t_1$, from the assumptions, we have

$$q \le r_2 \le \sigma_2 e^{r_1-1-e^{r_1-1}} < \sigma_2 e^{2r_1-1-e^{r_1-1}} = \sigma_2 t_1 = \sigma_2 p \tag{36}$$

and then (32) holds. If $p = \nu_\mu^{(1)}\alpha$, then $q \le \alpha \le \sigma_2\nu_\mu^{(1)}\alpha$, which is true because of (30).

We must verify (33) (with h^+ being replaced by h^-) for (24). If $0 < p < t_0$, then $h^-(p) = pe^{-p}$ and $p = \nu_\mu^{(1)}\alpha$ because of (26). Since $e^{-\sigma_1\alpha} \le e^{-\sigma_1 q}$, it suffices to verify that $e^{-\nu_\mu^{(1)}\alpha} \le e^{-\sigma_1\alpha}$, which is true because of (30) and $\sigma_2\sigma_1 < 1$. For the case that $p \ge t_0$, then $h^-(p) = h(t_0)$. From the definition of h^- and (35) we see that it suffices to verify that

$$\frac{h^-(p)}{p} \le \frac{h(t_0)}{t_0} = e^{-t_0} \le e^{-\sigma_1 r_2} \tag{37}$$

holds, which follows from Expression (26) and the assumption,

$$e^{-t_0} \le e^{-e^{r_1-1-e^{r_1-1}}} \le e^{-\sigma_1 r_2}. \tag{38}$$

We observe here that the assumption $\sigma_1 r_2 < e^{r_1-1-e^{r_1-1}}$ can be relaxed as long as (37)($t_0 \ge \sigma_1 r_2$) holds.

To verify (H3)(iii), we note that $h^-(p) = h^+(p) = h(p)$ for p small, and conclude from Lemma 4.2, for sufficiently larger k, there is a small $\omega \gg 0$, if $0 \le (p,q) \le \omega$, $f(p,q) \ge f(p,0) \ge (1-\frac{1}{k})e^{r_1-\sigma_1 r_2}p$ and $g(p,q) \ge (1-\frac{1}{k})r_2\sigma_2 p + (1-\frac{1}{k})(1-r_2)q$.

This concludes the proof of Theorem 5.1 since the conditions (H1-H3) have been verified. □

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