PROCEEDINGS A

royalsocietypublishing.org/journal/rspa

Research

Cite this article: Adimy M, Calero M, Chekroun A, Pujo-Menjouet L. 2026 Travelling waves for delayed reaction–diffusion systems with semi-mixed quasi-monotonicity: a prion disease model. *Proc. R. Soc. A* **482**: 20250630. https://doi.org/10.1098/rspa.2025.0630

Received: 17 July 2025
Accepted: 9 January 2026

Subject Areas:
applied mathematics, mathematical modelling

Keywords:
delayed reaction–diffusion systems, travelling waves, non-quasi-monotonicity, contracting rectangles, prion disease modelling

Author for correspondence:
M. Adimy
e-mail: mostafa.adimy@inria.fr

Travelling waves for delayed reaction–diffusion systems with semi-mixed quasi-monotonicity: a prion disease model

M. Adimy[1], M. Calero[2], A. Chekroun[3] and L. Pujo-Menjouet[2]

[1]Inria, Univ Lyon, Universite Claude Bernard Lyon 1, CNRS UMR 5208, Institut Camille Jordan, F-69603 Villeurbanne, France
[2]Universite Claude Bernard Lyon 1, CNRS, Centrale Lyon, INSA Lyon, Université Jean Monnet, ICJ UMR5208, Inria, 69622 Villeurbanne, France
[3]Laboratoire d'Analyse Nonlinéaire et Mathématiques Appliquées, University of Tlemcen, Tlemcen 13000, Algeria

MA, 0000-0003-2732-3830

In this paper, we study the existence of travelling wave solutions in a system of delayed reaction–diffusion equations (DRDEs) satisfying the semi-mixed quasi-monotonicity condition. As an application, we analyse a mathematical model of a prion disease, whose reaction terms fall within the framework of our approach. Under biologically motivated assumptions, we construct appropriate upper and lower solutions and apply an existence theorem tailored to such systems. We then use the contracting rectangle method to describe the asymptotic behaviour of the solutions as they converge to a non-trivial positive equilibrium. The paper concludes with numerical simulations.

1. Introduction

It is well established that travelling waves play a crucial role in the dynamics of many biological processes; see, for example, the book by Winfree [1]. As highlighted by Murray [2], wave-like phenomena

THE ROYAL SOCIETY PUBLISHING

are frequently observed in biology and, thus, warrant detailed investigation. The earliest studies on travelling wave solutions can be traced back to the seminal works of Kolmogorov *et al.* [3] and Fisher [4]. Since then, the literature has grown substantially, especially within the context of reaction–diffusion equations.

On one hand, numerous studies have focused on reaction–diffusion equations without delay, examining the existence of travelling wave solutions using various techniques [5–12]. For scalar equations, phase plane analysis has been particularly effective [2], while for systems of equations, methods such as the Conley index and degree theory have been employed; see, for instance, [7,8,12].

On the other hand, owing to their relevance in biological applications [13], the existence of travelling wave solutions in delayed reaction–diffusion equations (DRDEs) has also been extensively studied. Schaaf [14] was the first to establish the existence of travelling wave solutions for scalar DRDEs using techniques such as the maximum principle, phase plane arguments and the sub- and super-solution approach, inspired by Atkinson & Reuter [15]. Later, Wu [16] proved the existence and stability of wavefronts for the delayed Fisher equation [4] using the maximum principle and for the delayed Hodgkin–Huxley equation [17] via phase plane technique. These results extended early works by Cohen [5], Nagumo *et al.* [18] and Aronson & Weinberger [19].

In the same period, Wu [16] as well as Wu & Zou [20] initiated the study the existence of travelling wave for systems of DRDEs with monostable nonlinearities. Their approach relied on monotone iteration schemes [21,22], basing their choice of upper and lower solutions on the work of Volpert *et al.* [12] for systems of reaction–diffusion equations without delay. Later on, Wu & Zou [23] developed a new iteration scheme for which the authors provided a convergence result when the reaction term is either monotone with respect to the time delay (also called quasi-monotone (QM)) or non-monotone (also called exponential monotone (QM*)). The main differences between these cases lie in the initial function of the iteration, which is more restrictive for the non-monotone case, but also by the additional use of a non-standard ordering of the profile set. It is worth noting that the convergence results of Wu & Zou [23] require the initial function used in the iteration to be an upper solution belonging to a specific profile set defined in their paper. The authors then applied their results to further investigate the existence of travelling wave solutions for the delayed Fisher-KPP equation with a non-monotone delayed reaction term, as well as for a delayed system modelling the Belousov–Zhabotinsky reaction, thereby extending the existence results obtained by Troy [6], Ye & Wang [9], Kanel [10] and Kapel [11].

Subsequently, by using Schauder's fixed point theorem, Ma [24] studied the existence of travelling wave solutions in DRDEs under the condition of QM for the reaction term. More specifically, the author reduced the existence of a travelling wavefront to the existence of a pair of upper and lower solutions verifying conditions less restrictive than in [23]. Notably, unlike Wu & Zou [23], the upper solution is not required to converge to a wave system's trivial solution. Ma [24] applied this approach to investigate the existence of travelling wave solutions for a delayed predator–prey model with diffusion and for the delayed system of the Belousov-Zhabotinskii reaction model. In addition, based on the work of Ma [24], several authors examined the existence of travelling waves when the reaction term satisfies conditions other than QM, and more particularly the QM* condition [25], the weak QM (WQM) and weak QM* conditions (WQM*) [26], the partial QM (PQM) and PQM conditions (PQM*) [27] and the mixed QM (MQM) and exponentially mixed QM conditions (EMQM) or (MQM*) [28,29].

Note that the MQM condition (respectively, EMQM) introduced in [28] differs from the mixed QM condition (respectively, MQM*) mentioned in [29]. For example, unlike Lin *et al.* [28], the mixed QM condition of [29] includes the MQM-1 condition introduced by Wang & Zhou [30]. For clarity, we illustrate the relationships among these conditions with an Euler figure 1.

As a result, the general framework developed by these authors has enabled the analysis of various classes of DRDEs; see [31–46].

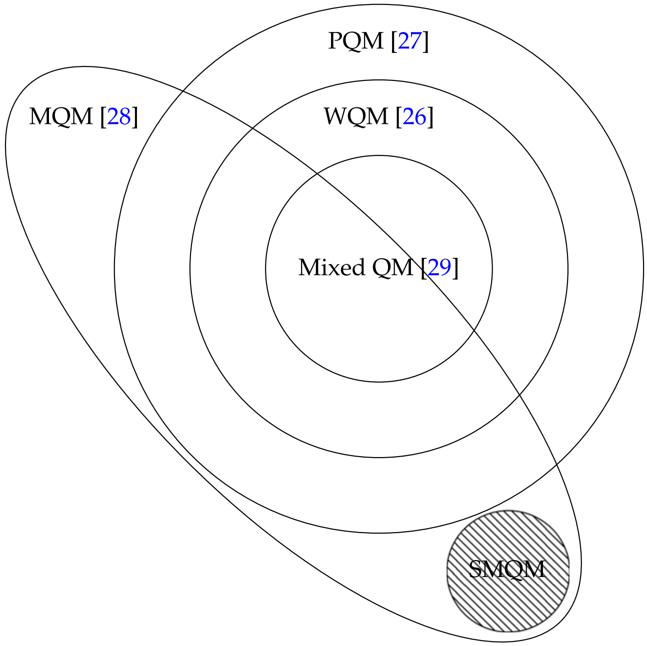

Figure 1. Euler diagram which illustrating relations between the different conditions for the reaction term when considering a system of DRDEs. The hatched circle represents a new condition (SMQM) introduced in the present paper.

Finally, although beyond the scope of the present work, we mention that travelling waves in non-local reaction–diffusion systems have also been widely studied; see, for instance, [47–62] and references therein.

In this paper, we are concerned with existence of travelling wave solutions of the following general two delayed reaction–diffusion system,

$$\left.\begin{aligned} &\frac{\partial u}{\partial t}(x,t)=\delta_1\Delta u(x,t)+f_1(u_t(x),\mathrm{v}_t(x))\\ \text{and}\qquad &\frac{\partial \mathrm{v}}{\partial t}(x,t)=\delta_2\Delta \mathrm{v}(x,t)+f_2(u_t(x),\mathrm{v}_t(x)),\end{aligned}\right\}\tag{1.1}$$

where $x\in\mathbb{R}^n$, $t>0$, $\delta_1>0$ and $\delta_2>0$. The functions $u_t(x),\mathrm{v}_t(x)\in\mathcal{C}([-T,0],\mathbb{R})$, with $T>0$, are defined, for $t>0$, $s\in[-T,0]$ and $x\in\mathbb{R}^n$, by

$$u_t(x)(s)=u(x,t+s)\quad\text{and}\quad \mathrm{v}_t(x)(s)=\mathrm{v}(x,t+s).\tag{1.2}$$

Furthermore, we assume that function $f=(f_1,f_2):\mathcal{C}([-T,0],\mathbb{R}^2)\longrightarrow\mathbb{R}^2$ is continuous and satisfies the following condition:

$$f_1(0,0)=f_1(k_1,k_2)=f_2(0,0)=f_2(k_1,k_2)=0,\quad \text{with } k_1>0,\ \ k_2>0.\tag{1.3}$$

Without loss of clarity, we denote by (k_1,k_2) the constant function in $\mathcal{C}([-T,0],\mathbb{R}^2)$. In other words, the above condition indicates that f has two steady states, namely, the trivial one $\mathbf{0}:=(0,0)$ and a positive one $\mathbf{K}:=(k_1,k_2)$ with $k_1>0$ and $k_2>0$. As explained by Lin *et al.* [28], in order to avoid issues that may arise when only considering the region $[0,k_1]\times[0,k_2]$ for the existence of travelling wave solutions, we assume the existence of $M_1\geq k_1$ and $M_2\geq k_2$ such that $[0,M_1]\times[0,M_2]$ corresponds to the minimal invariant set of the corresponding ODEs of system (1.1). In addition, we assume that there exist two positive constants L_1,L_2 such that

$$|f_1(\phi_1,\phi_2)-f_1(\psi_1,\psi_2)|\leq L_1||\Phi-\Psi||\quad\text{and}\quad |f_2(\phi_1,\phi_2)-f_2(\psi_1,\psi_2)|\leq L_2||\Phi-\Psi||,\tag{1.4}$$

for $\Phi = (\phi_1, \phi_2), \Psi = (\psi_1, \psi_2) \in \mathcal{C}([-T, 0], \mathbb{R}^2)$, with

$$0 \le \phi_1(s), \psi_1(s) \le M_1, \quad 0 \le \phi_2(s), \psi_2(s) \le M_2, \ \ s \in [-T, 0]. \tag{1.5}$$

In the above condition, the symbol $|\,.\,|$ denotes the Euclidean norm, whereas $||\,.\,||$ corresponds to the supremum norm in $\mathcal{C}([-T, 0], \mathbb{R}^2)$.

Furthermore, as explained above, by applying Schauder's fixed point theorem, we aim to reduce the study of travelling wave solution existence for system (1.1) to the construction of an admissible pair of upper and lower solutions under suitable conditions on the reaction term f. Typically, such a construction can be achieved with relative ease; see, for example, [29]. In this work, we propose a new condition on the reaction term, referred to as the semi-mixed QM (SMQM) condition, which can be viewed as a subset of the MQM framework introduced by Lin *et al.* [28], as illustrated in figure 1. This condition consequently led to a new definition of upper and lower solutions adapted to the SMQM framework. As further demonstrated through a practical application to a neurodegenerative prion disease model, and in contrast to previous studies, the SMQM condition may present specific challenges in the construction of a suitable pair of upper and lower solutions. Accordingly, the present paper aims to provide a replicable and general framework for establishing the existence of travelling wave solutions for systems of DRDEs under the SMQM condition.

The paper is organized as follows. Section 2 introduces the notations and definitions necessary for the analysis. In §3, we investigate the existence of travelling wave solutions for systems of DRDEs under the SMQM condition. Section 4 is devoted to a mathematical model of a neurodegenerative prion disease, whose reaction term satisfies the SMQM condition. After stating biologically motivated assumptions, we construct suitable upper and lower solutions and apply the existence result from §3. The paper concludes with a brief summary.

2. Preliminaries

Definition 2.1. A travelling wave solution of system (1.1) is a solution of the form

$$(u(x,t), \mathrm{v}(x,t)) = (\phi_1(x_j + ct), \phi_2(x_j + ct)), \tag{2.1}$$

where $\phi_1, \phi_2 \in \mathcal{C}^2(\mathbb{R}, \mathbb{R})$ and $c > 0$ is a constant representing the wave speed. Also, $z_j := x_j + ct$ denotes the wave variable with $x_j := x \cdot e_j$ corresponding to the jth coordinate in the canonical basis of $\mathbb{R}^n$. For example, and without loss of generality, we can take $j = 1$ so that $z_j = z_1 = x_1 + ct$. In the remainder of the paper, z_j is denoted by z for the sake of clarity.

Let $z \in \mathbb{R}$. By virtue of equation (2.1), substituting $(\phi_1(z), \phi_2(z))$ into system (1.1) leads to the so-called *wave system*,

$$\left.\begin{aligned} \delta_1\phi_1''(z) - c\phi_1'(z) + f_1^c(\phi_{1_z}, \phi_{2_z}) = 0 \\ \text{and} \qquad \delta_2\phi_2''(z) - c\phi_2'(z) + f_2^c(\phi_{1_z}, \phi_{2_z}) = 0, \end{aligned}\right\} \tag{2.2}$$

where $f^c = (f_1^c, f_2^c) : \mathcal{C}([-cT, 0], \mathbb{R}^2) \longrightarrow \mathbb{R}^2$ is given by

$$f_i^c(\phi_{1_z}, \phi_{2_z}) = f_i(\phi_{1_z}^c, \phi_{2_z}^c), \quad \phi_{i_z}^c(s) = \phi_i(z + cs), \ \ s \in [-T, 0], \ i = 1, 2. \tag{2.3}$$

In addition, as is common practice, we are looking for travelling wave solutions possibly satisfying the following asymptotic boundary conditions:

$$\lim_{z \to -\infty} (\phi_1(z), \phi_2(z)) = (0, 0) \quad \text{and} \quad \lim_{z \to +\infty} (\phi_1(z), \phi_2(z)) = (k_1, k_2). \tag{2.4}$$

As mentioned in §1, we assume throughout this work that the reaction term f satisfies the SMQM condition. To the best of our knowledge, this condition has never been explicitly addressed in the literature, except as a special case within the general MQM framework introduced by [28]. Accordingly, we provide its definition below.

Definition 2.2. The SMQM condition holds for $f=(f_1,f_2)$ if and only if there exist two positive constants β_1, β_2, such that

$$\left.\begin{aligned}&f_1(\phi_1,\phi_2)-f_1(\psi_1,\phi_2)+\beta_1(\phi_1(0)-\psi_1(0))\ge 0,\\ &f_1(\phi_1,\phi_2)-f_1(\phi_1,\psi_2)\ge 0,\\ &f_2(\phi_1,\phi_2)-f_2(\phi_1,\psi_2)+\beta_2(\phi_2(0)-\psi_2(0))\ge 0\\ \text{and}\quad &f_2(\phi_1,\phi_2)-f_2(\psi_1,\phi_2)\le 0,\end{aligned}\right\}\tag{2.5}$$

for ϕ_1, ϕ_2, ψ_1, $\psi_2\in\mathcal{C}([-T,0],\mathbb{R})$, with

$$0\le\psi_1(s)\le\phi_1(s)\le M_1,\quad 0\le\psi_2(s)\le\phi_2(s)\le M_2,\ \ s\in[-T,0].\tag{2.6}$$

The originality of reaction terms satisfying the SMQM condition equation (2.5) lies in their structure, which imposes distinct monotonicity requirements on each component: f_1 is non-decreasing with respect to its second argument, while f_2 is non-increasing with respect to its first argument. An illustrative example related to prion dynamics in neurodegenerative disorders will be presented in §4; similar models can also be applied to ecological systems involving interacting populations.

Definition 2.3. The set $\mathcal{C}_{[\mathbf{0},\mathbf{M}]}(\mathbb{R},\mathbb{R}^2)$ is given by

$$\mathcal{C}_{[\mathbf{0},\mathbf{M}]}(\mathbb{R},\mathbb{R}^2):=\{(\phi_1,\phi_2)\in\mathcal{C}(\mathbb{R},\mathbb{R}^2):0\le\phi_i(z)\le M_i,\quad i=1,2,\ \ z\in\mathbb{R}\}.$$

Next, we define the function $H=(H_1,H_2):\mathcal{C}_{[\mathbf{0},\mathbf{M}]}(\mathbb{R},\mathbb{R}^2)\longrightarrow\mathcal{C}(\mathbb{R},\mathbb{R}^2)$ by

$$H_1(\phi_1,\phi_2)(z)=f_1^c(\phi_{1_z},\phi_{2_z})+\beta_1\phi_1(z)\quad\text{and}\quad H_2(\phi_1,\phi_2)(z)=f_2^c(\phi_{1_z},\phi_{2_z})+\beta_2\phi_2(z),$$

for all $z\in\mathbb{R}$, where β_1 and β_2 are given in condition (2.5). Let $z\in\mathbb{R}$, then the wave system (2.2) can be rewritten as follows:

$$\left.\begin{aligned}&\delta_1\phi_1''(z)-c\phi_1'(z)-\beta_1\phi_1(z)+H_1(\phi_1,\phi_2)(z)=0\\ \text{and}\quad &\delta_2\phi_2''(z)-c\phi_2'(z)-\beta_2\phi_2(z)+H_2(\phi_1,\phi_2)(z)=0.\end{aligned}\right\}\tag{2.7}$$

Further, we consider the operator $F=(F_1,F_2):\mathcal{C}_{[\mathbf{0},\mathbf{M}]}(\mathbb{R},\mathbb{R}^2)\longrightarrow\mathcal{C}(\mathbb{R},\mathbb{R}^2)$, with

$$\left.\begin{aligned}&F_1(\phi_1,\phi_2)(z)=\frac{1}{\delta_1(\kappa_{12}-\kappa_{11})}\left[\int_{-\infty}^{z}e^{\kappa_{11}(z-s)}H_1(\phi_1,\phi_2)(s)\,ds+\int_{z}^{+\infty}e^{\kappa_{12}(z-s)}H_1(\phi_1,\phi_2)(s)\,ds\right]\\ \text{and}\quad &F_2(\phi_1,\phi_2)(z)=\frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{-\infty}^{z}e^{\kappa_{21}(z-s)}H_2(\phi_1,\phi_2)(s)\,ds+\int_{z}^{+\infty}e^{\kappa_{22}(z-s)}H_2(\phi_1,\phi_2)(s)\,ds\right],\end{aligned}\right\}\tag{2.8}$$

where $z\in\mathbb{R}$, $\kappa_{11}<0<\kappa_{12}$ and $\kappa_{21}<0<\kappa_{22}$ are given by

$$\kappa_{11}=\frac{c-\sqrt{c^2+4\delta_1\beta_1}}{2\delta_1},\quad\kappa_{12}=\frac{c+\sqrt{c^2+4\delta_1\beta_1}}{2\delta_1},\quad\kappa_{21}=\frac{c-\sqrt{c^2+4\delta_2\beta_2}}{2\delta_2},\quad\kappa_{22}=\frac{c+\sqrt{c^2+4\delta_2\beta_2}}{2\delta_2}.$$

In particular, κ_{11} and κ_{12} (respectively, κ_{21} and κ_{22}) have been chosen so that they are the roots of the first (respectively, second) quadratic equation below:

$$\delta_1\kappa^2-c\kappa-\beta_1=0\quad\text{and}\quad\delta_2\kappa^2-c\kappa-\beta_2=0.\tag{2.9}$$

It is straightforward to notice that the operator F is well defined. Also, by using the second lemma established by Boumenir & Nguyen [63], F satisfies, for all $z\in\mathbb{R}$,

$$\left.\begin{aligned}&\delta_1(F_1(\phi_1,\phi_2))''(z)-c(F_1(\phi_1,\phi_2))'(z)-\beta_1F_1(\phi_1,\phi_2)(z)+H_1(\phi_1,\phi_2)(z)=0\\ \text{and}\quad &\delta_2(F_2(\phi_1,\phi_2))''(z)-c(F_2(\phi_1,\phi_2))'(z)-\beta_2F_2(\phi_1,\phi_2)(z)+H_2(\phi_1,\phi_2)(z)=0.\end{aligned}\right\}\tag{2.10}$$

Therefore, by virtue of system (2.10), any fixed point of F is a solution of the wave system (2.2) and, thus, a travelling wave solution of system (1.1). Moreover, owing to the possible asymptotic boundary conditions equations (2.4), the travelling wave solution connects the trivial equilibrium $\mathbf{0}:=(0,0)$ with the positive one $\mathbf{K}:=(k_1,k_2)$. Accordingly, in what follows, we show the existence of such a fixed point by applying Schauder's fixed point theorem.

3. Existence of travelling wave solutions under SMQM

The strategy for proving the existence of travelling wave solutions follows an approach similar to that described, for example, in [29]. In particular, the first step consists in properly defining the upper and lower solutions so that their definition takes into account SMQM for the reaction term f. Indeed, the conditions imposed for f have direct consequences on the properties of the operators H and F. Herein, under SMQM, we have the following proposition.

Proposition 3.1. *Let* (ϕ_1,ϕ_2) *and* $(\psi_1,\psi_2)\in C_{[\mathbf{0},\mathbf{M}]}(\mathbb{R},\mathbb{R}^2)$ *such that* $\phi_1(z)\geq\psi_1(z)$ *and* $\phi_2(z)\geq\psi_2(z)$ *for all* $z\in\mathbb{R}$. *Then, under SMQM, we have for all* $z\in\mathbb{R}$,

$$H_1(\phi_1,\phi_2)(z)\geq H_1(\psi_1,\phi_2)(z),\quad F_1(\phi_1,\phi_2)(z)\geq F_1(\psi_1,\phi_2)(z),$$
$$H_1(\phi_1,\phi_2)(z)\geq H_1(\phi_1,\psi_2)(z),\quad F_1(\phi_1,\phi_2)(z)\geq F_1(\phi_1,\psi_2)(z),$$
$$H_2(\phi_1,\phi_2)(z)\geq H_2(\phi_1,\psi_2)(z),\quad F_2(\phi_1,\phi_2)(z)\geq F_2(\phi_1,\psi_2)(z)$$

and

$$H_2(\phi_1,\phi_2)(z)\leq H_2(\psi_1,\phi_2)(z),\quad F_2(\phi_1,\phi_2)(z)\leq F_2(\psi_1,\phi_2)(z).$$

Proof. Let $z\in\mathbb{R}$. Then, we have

$$\begin{aligned}H_1(\phi_1,\phi_2)(z)-H_1(\psi_1,\phi_2)(z)&=f_1^c(\phi_{1_z},\phi_{2_z})-f_1^c(\psi_{1_z},\phi_{2_z})+\beta_1(\phi_1(z)-\psi_1(z)),\\&\geq-\beta_1(\phi_1(z)-\psi_1(z))+\beta_1(\phi_1(z)-\psi_1(z))\geq 0,\\H_1(\phi_1,\phi_2)(z)-H_1(\phi_1,\psi_2)(z)&=f_1^c(\phi_{1_z},\phi_{2_z})+\beta_1\phi_1(z)-f_1^c(\phi_{1_z},\psi_{2_z})-\beta_1\phi_1(z),\\&=f_1^c(\phi_{1_z},\phi_{2_z})-f_1^c(\phi_{1_z},\psi_{2_z})\geq 0,\\H_2(\phi_1,\phi_2)(z)-H_2(\phi_1,\psi_2)(z)&=f_2^c(\phi_{1_z},\phi_{2_z})-f_2^c(\phi_{1_z},\psi_{2_z})+\beta_2(\phi_2(z)-\psi_2(z)),\\&\geq-\beta_2(\phi_2(z)-\psi_2(z))+\beta_2(\phi_2(z)-\psi_2(z))\geq 0\end{aligned}$$

and

$$\begin{aligned}H_2(\phi_1,\phi_2)(z)-H_2(\psi_1,\phi_2)(z)&=f_2^c(\phi_{1_z},\phi_{2_z})+\beta_2\phi_2(z)-f_2^c(\psi_{1_z},\phi_{2_z})-\beta_2\phi_2(z),\\&=f_2^c(\phi_{1_z},\phi_{2_z})-f_2^c(\psi_{1_z},\phi_{2_z})\leq 0.\end{aligned}$$

By construction of the operator F in system (2.8) and owing to the above results, the proof of the last four inequalities is straightforward and, thus, left to the reader. ∎

Next, we introduce below the corresponding super-solutions and sub-solutions which are needed to construct the appropriate upper and lower solutions.

Definition 3.2. Let us assume that SMQM holds. A quadruple $(\phi_1^-,\phi_2^-,\phi_1^+,\phi_2^+)$ is called a coupled system of sub- and super-solutions of the wave system (2.2) if

(i) $(\phi_1^-,\phi_2^-,\phi_1^+,\phi_2^+)\in C_{[\mathbf{0},\mathbf{M}]}(\mathbb{R},\mathbb{R}^2)^2$ with $\phi_1^-\leq\phi_1^+$ and $\phi_2^-\leq\phi_2^+$.

(ii) The first and second derivatives of ϕ_1^-, ϕ_2^-, ϕ_1^+, ϕ_2^+ exist almost everywhere and are essentially bounded on $\mathbb{R}$.

(iii) $(\phi_1^-,\phi_2^-,\phi_1^+,\phi_2^+)$ satisfies

$$\left.\begin{aligned}&\delta_1(\phi_1^-)''(z)-c(\phi_1^-)'(z)-\beta_1\phi_1^-(z)+H_1(\phi_1^-,\phi_2^-)(z)\geq 0,\\&\delta_2(\phi_2^-)''(z)-c(\phi_2^-)'(z)-\beta_2\phi_2^-(z)+H_2(\phi_1^+,\phi_2^-)(z)\geq 0,\\&\delta_1(\phi_1^+)''(z)-c(\phi_1^+)'(z)-\beta_1\phi_1^+(z)+H_1(\phi_1^+,\phi_2^+)(z)\leq 0\\\text{and}\quad&\delta_2(\phi_2^+)''(z)-c(\phi_2^+)'(z)-\beta_2\phi_2^+(z)+H_2(\phi_1^-,\phi_2^+)(z)\leq 0.\end{aligned}\right\}\ \text{a.e. on }\mathbb{R}.$$

(vi) Let $\widetilde{y_1}$, $\widetilde{y_2}$, $\widetilde{z_1}$ and $\widetilde{z_2}$ be points of discontinuity of the first derivatives of ϕ_1^-, ϕ_2^-, ϕ_1^+ and ϕ_2^+, respectively. Then, we have

$$(\phi_1^-)'(\widetilde{y_{1+}})>(\phi_1^-)'(\widetilde{y_{1-}}),\quad(\phi_2^-)'(\widetilde{y_{2+}})>(\phi_2^-)'(\widetilde{y_{2-}})$$

and

$$(\phi_1^+)'(\widetilde{z_{1+}})<(\phi_1^+)'(\widetilde{z_{1-}}),\quad(\phi_2^+)'(\widetilde{z_{2+}})<(\phi_2^+)'(\widetilde{z_{2-}}).$$

In the above definition, we allow the first derivatives of the functions ϕ_i^-, ϕ_i^+ to be discontinuous on a discrete set of points, easing the future construction of the pair of upper and lower solutions. In order to avoid any issues that may arise owing to those discontinuities, we have added in the definition the condition (iv). It should be mentioned that this approach has already been employed in the past via the notion of *weak upper and lower solutions*; see, for example, definition 3 and lemma 3.5 in [29] for additional details. Notably, as proved in [29], the appropriate upper and lower solutions are obtained through the composition of the sub-, super-solutions and the operator F. More specifically, we have the following proposition whose proof is similar to that in lemma 3.5 in [29].

Proposition 3.3. *Let us assume that SMQM holds with* (ϕ_1^+,ϕ_2^+) *and* (ϕ_1^-,ϕ_2^-) *a super- and sub-solution of the wave system (2.2) as defined in definition 3.2. Then,* $\Phi^- := (F_1(\phi_1^-,\phi_2^-), F_2(\phi_1^+,\phi_2^-))$ *and* $\Phi^+ := (F_1(\phi_1^+,\phi_2^+), F_2(\phi_1^-,\phi_2^+))$ *are also, respectively, a sub- and super-solution of the wave system (2.2). Moreover,* Φ^- *and* Φ^+ *are twice differentiable on* $\mathbb{R}$.

Further, we consider in the remainder of this section that such sub- and super-solutions exist in order to apply the fixed point approach. Accordingly, we define now the profile set of travelling wavefronts Θ as

$$\Theta := \{\Phi = (\phi_1,\phi_2) \in \mathcal{C}_{[\mathbf{0},\mathbf{M}]}(\mathbb{R},\mathbb{R}^2) : \text{ for all } z \in \mathbb{R}, \phi_i^-(z) \le \phi_i(z) \le \phi_i^+(z),\ i = 1,2\}.$$

To apply Schauder's fixed point theorem, it is necessary to verify that the profile set Θ is a non-empty, convex and closed subset of a suitable Banach space. Let $\nu > 0$. In what follows, and in line with common practice, we work within the Banach space $B_\nu(\mathbb{R},\mathbb{R}^2)$ and the exponential decay norm $|\,.\,|_\nu$ defined as follows:

$$B_\nu(\mathbb{R},\mathbb{R}^2) := \left\{\Phi \in \mathcal{C}(\mathbb{R},\mathbb{R}^2) : \sup_{z\in\mathbb{R}} |\,\Phi(z)\,|\, e^{-\nu|z|} < \infty\right\} \quad \text{and} \quad |\,\Phi\,|_\nu = \sup_{z\in\mathbb{R}} |\,\Phi(z)\,|\, e^{-\nu|z|}.$$

Next, we provide below the first lemma needed to apply the Schauder fixed-point theorem. In particular, it ensures the existence of fixed points for the operator F in the profile set Θ. Before doing so, we establish the following proposition that is used in the proof of the first lemma.

Proposition 3.4. *Let* $\Phi = (\phi_1,\phi_2) \in \Theta$ *and* $z \in \mathbb{R}$*. Then, under SMQM, we have*

$$H_1(\phi_1^-,\phi_2^-)(z) \le H_1(\phi_1,\phi_2)(z) \le H_1(\phi_1^+,\phi_2^+)(z),$$
$$H_2(\phi_1^+,\phi_2^-)(z) \le H_2(\phi_1,\phi_2)(z) \le H_2(\phi_1^-,\phi_2^+)(z)$$

and

$$F_1(\phi_1^-,\phi_2^-)(z) \le F_1(\phi_1,\phi_2)(z) \le F_1(\phi_1^+,\phi_2^+)(z),$$
$$F_2(\phi_1^+,\phi_2^-)(z) \le F_2(\phi_1,\phi_2)(z) \le F_2(\phi_1^-,\phi_2^+)(z).$$

Proof. Let $(\phi_1,\phi_2) \in \Theta$. If SMQM holds, then by virtue of proposition 3.1, we have for all $z \in \mathbb{R}$

$$H_1(\phi_1,\phi_2)(z) \ge H_1(\phi_1^-,\phi_2)(z) \ge H_1(\phi_1^-,\phi_2^-)(z),$$
$$H_1(\phi_1,\phi_2)(z) \le H_1(\phi_1^+,\phi_2)(z) \le H_1(\phi_1^+,\phi_2^+)(z),$$
$$H_2(\phi_1,\phi_2)(z) \ge H_2(\phi_1,\phi_2^-)(z) \ge H_2(\phi_1^+,\phi_2^-)(z)$$

and

$$H_2(\phi_1,\phi_2)(z) \le H_2(\phi_1^-,\phi_2)(z) \le H_2(\phi_1^-,\phi_2^+)(z).$$

The proof for F is similar and, thus, left to the reader. ■

Lemma 3.5.

1. *The set Θ is non-empty, bounded, closed and convex in $(B_\nu(\mathbb{R},\mathbb{R}^2), |\,.\,|_\nu)$.*
2. *The operator F maps Θ into Θ.*

Proof. The proof of the first point is straightforward and is, thus, omitted. With regard to the second point, we take an arbitrary $\Phi = (\phi_1, \phi_2) \in \Theta$. The objective consists in proving that $F(\Phi)$ is also in Θ. More specifically, we aim to show that for all $z \in \mathbb{R}$, we have

$$\phi_1^-(z) \le F_1(\phi_1,\phi_2)(z) \le \phi_1^+(z) \quad \text{and} \quad \phi_2^-(z) \le F_2(\phi_1,\phi_2)(z) \le \phi_2^+(z).$$

Owing to proposition 3.4, the above condition can be reduced to prove that, for all $z \in \mathbb{R}$, we have

$$\phi_1^-(z) \le F_1(\phi_1^-,\phi_2^-)(z), \quad F_1(\phi_1^+,\phi_2^+)(z) \le \phi_1^+(z)$$

and

$$\phi_2^-(z) \le F_2(\phi_1^+,\phi_2^-)(z), \quad F_2(\phi_1^-,\phi_2^+)(z) \le \phi_2^+(z).$$

Each inequality is studied in a similar way. For convenience, in what follows, we only provide the proof of the last inequality, namely, $F_2(\phi_1^-,\phi_2^+)(z) \le \phi_2^+(z)$ for all $z \in \mathbb{R}$.

Owing to the definition of super- and sub-solutions, as pointed out above, it may be possible that the first derivative of ϕ_2^- has certain discontinuities. Herein, for simplicity, we consider only one point of discontinuity, denoted by $\widetilde{z_2}$. Please note that the proof below can be generalized for a fixed number of discontinuities in a straightforward manner.

On the one hand, let $z \in \mathbb{R}$ such that $z < \widetilde{z_2}$. Then, by employing partial integration, making use of equations (2.9) and point (iv) of definition 3.2, we have

$$\begin{aligned}
F_2(\phi_1^-,\phi_2^+)(z) &= \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{-\infty}^{z} e^{\kappa_{21}(z-s)} H_2(\phi_1^-,\phi_2^+)(s)\,\mathrm{d}s\right] \\
&\quad + \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{z}^{\widetilde{z_2}} e^{\kappa_{22}(z-s)} H_2(\phi_1^-,\phi_2^+)(s)\,\mathrm{d}s + \int_{\widetilde{z_2}}^{+\infty} e^{\kappa_{22}(z-s)} H_2(\phi_1^-,\phi_2^+)(s)\,\mathrm{d}s\right], \\
&\le \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{-\infty}^{z} e^{\kappa_{21}(z-s)} (-\delta_2(\phi_2^+)''(s) + c(\phi_2^+)'(s) + \beta_2\phi_2^+(s))\,\mathrm{d}s\right] \\
&\quad + \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{z}^{\widetilde{z_2}} e^{\kappa_{22}(z-s)} (-\delta_2(\phi_2^+)''(s) + c(\phi_2^+)'(s) + \beta_2\phi_2^+(s))\,\mathrm{d}s\right] \\
&\quad + \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{\widetilde{z_2}}^{+\infty} e^{\kappa_{22}(z-s)} (-\delta_2(\phi_2^+)''(s) + c(\phi_2^+)'(s) + \beta_2\phi_2^+(s))\,\mathrm{d}s\right].
\end{aligned}$$

We obtain

$$\begin{aligned}
F_2(\phi_1^-,\phi_2^+)(z) &\le \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{-\infty}^{z} e^{\kappa_{21}(z-s)} \phi_2^+(s)(-\delta_2\kappa_{21}^2 + c\kappa_{21} + \beta_2)\,\mathrm{d}s\right] \\
&\quad + \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{z}^{+\infty} e^{\kappa_{22}(z-s)} \phi_2^+(s)(-\delta_2\kappa_{22}^2 + c\kappa_{22} + \beta_2)\,\mathrm{d}s\right] \\
&\quad + \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}[\delta_2\phi_2^+(z)(\kappa_{22}-\kappa_{21}) + \delta_2 e^{\kappa_{22}(z-\widetilde{z_2})}((\phi_2^+)'(\widetilde{z_{2+}}) - (\phi_2^+)'(\widetilde{z_{2-}}))], \\
&\le \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}[\delta_2\phi_2^+(z)(\kappa_{22}-\kappa_{21}) + \delta_2 e^{\kappa_{22}(z-\widetilde{z_2})}((\phi_2^+)'(\widetilde{z_{2+}}) - (\phi_2^+)'(\widetilde{z_{2-}}))], \\
&< \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}[\delta_2\phi_2^+(z)(\kappa_{22}-\kappa_{21})] = \phi_2^+(z).
\end{aligned}$$

On the other hand, let $z \in \mathbb{R}$ such that $z \geq \widetilde{z_2}$. Then, by employing the same arguments as above, we obtain

$$\begin{aligned} F_2(\phi_1^-,\phi_2^+)(z) \leq & \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{-\infty}^{z} e^{\kappa_{21}(z-s)}\phi_2^+(s)(-\delta_2\kappa_{21}^2+c\kappa_{21}+\beta_2)\,\mathrm{d}s\right] \\ & + \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}\left[\int_{z}^{+\infty} e^{\kappa_{22}(z-s)}\phi_2^+(s)(-\delta_2\kappa_{22}^2+c\kappa_{22}+\beta_2)\,\mathrm{d}s\right] \\ & + \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}[\delta_2\phi_2^+(z)(\kappa_{22}-\kappa_{21})+\delta_2 e^{\kappa_{21}(z-\widetilde{z_2})}((\phi_2^+)'(\widetilde{z_{2+}})-(\phi_2^+)'(\widetilde{z_{2-}}))]. \end{aligned}$$

Therefore,

$$\begin{aligned} F_2(\phi_1^-,\phi_2^+)(z) \leq & \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}[\delta_2\phi_2^+(z)(\kappa_{22}-\kappa_{21})+\delta_2 e^{\kappa_{21}(z-\widetilde{z_2})}((\phi_2^+)'(\widetilde{z_{2+}})-(\phi_2^+)'(\widetilde{z_{2-}}))], \\ & < \frac{1}{\delta_2(\kappa_{22}-\kappa_{21})}[\delta_2\phi_2^+(z)(\kappa_{22}-\kappa_{21})] = \phi_2^+(z). \end{aligned}$$

As mentioned above, we can show in a similar manner, the three others inequalities. Consequently, the second point of the lemma is proved, thus ending the proof. ∎

Further, we establish in the following lemma, the last two conditions required to apply Schauder's fixed-point theorem, namely, the compactness and continuity of the operator F. The proof of this result has already been given in previous works for a suitable choice of ν and is, therefore, omitted here; see, for example, [27] for details. The main ingredients are standard: for any bounded set in $B_\nu(\mathbb{R},\mathbb{R}^2)$, the image under F is uniformly bounded owing to the exponential decay of the kernels and the boundedness of the nonlinearities, and it is equicontinuous because of the regularizing effect of the integral terms. By the Arzelà–Ascoli theorem, these properties imply that F is compact. The continuity of F follows from the continuity of the nonlinear terms and the dominated convergence theorem.

Lemma 3.6.

1. *The operator F is continuous with respect to the norm $|\,.\,|_\nu$ in $B_\nu(\mathbb{R},\mathbb{R}^2)$.*
2. *The operator F is compact with respect to the norm $|\,.\,|_\nu$ in $B_\nu(\mathbb{R},\mathbb{R}^2)$.*

The main theorem can now be stated and proved.

Theorem 3.7. *Let us assume that the conditions (1.3)–(1.4) are satisfied and SMQM holds. If the wave system (2.2) has a pair of super- and sub-solutions as given in definition 3.2, then system (1.1) has a travelling wave solution. Moreover, if the super- and sub-solutions satisfy the asymptotic boundary conditions equations (2.4) (or at least one of them), then such solution connects $\mathbf{0} := (0,0)$ to the positive equilibrium $\mathbf{K} := (k_1, k_2)$, namely, satisfying equations (2.4) (or just one of them).*

Proof. By virtue of lemmas 3.5–3.6 and Schauder's fixed point theorem, there exists a fixed point of the operator F, denoted by $(\phi_1^*,\phi_2^*) \in \Theta$. In addition, owing to system (2.10) and as stated in proposition 3.3, (ϕ_1^*,ϕ_2^*) is a solution of the wave system (2.2) and, therefore, a travelling wave solution of system (1.1). Moreover, if we suppose additionally that the upper and lower solutions satisfy the asymptotic boundary conditions equations (2.4), then since $(\phi_1^*,\phi_2^*) \in \Theta$, we have that (ϕ_1^*,ϕ_2^*) also satisfies equations (2.4) by applying the squeeze theorem. Thus, in this case, the travelling wave solution (ϕ_1^*,ϕ_2^*) connects $\mathbf{0} := (0,0)$ to the positive equilibrium $\mathbf{K} := (k_1, k_2)$. ∎

4. Practical application in biology

(a) Presentation of the model and simplifying assumptions

In this section, we use theorem 3.7 to analyse a system of DRDEs involving two given populations, denoted by u and v. It is stated as follows:

$$\frac{\partial u}{\partial t}(x,t) = \underbrace{\delta_1 \Delta u(x,t)}_{\text{Diffusion}} \underbrace{-\mu_1 u(x,t)}_{\text{Death}} \underbrace{-\rho \frac{u(x,t)\mathrm{v}(x,t)}{u(x,t)+\mathrm{v}(x,t)}}_{\text{Recruitment}} + \underbrace{h(\mathrm{v}(x,t-T))}_{\text{Production}} \tag{4.1}$$

and

$$\frac{\partial \mathrm{v}}{\partial t}(x,t) = \underbrace{\delta_2 \Delta \mathrm{v}(x,t)}_{\text{Diffusion}} \underbrace{-\mu_2 \mathrm{v}(x,t)}_{\text{Death}} + \underbrace{\rho \frac{u(x,t)\mathrm{v}(x,t)}{u(x,t)+\mathrm{v}(x,t)}}_{\text{Recruitment}}, \tag{4.2}$$

where $t > 0$ denotes time, $x \in \mathbb{R}^n$ represents the spatial position and δ_1, δ_2, μ_1, μ_2, ρ, and T are positive constants. The derivation of this system is based on the following biological assumptions.

The first terms on the right-hand side of equations (4.1)–(4.2) indicate that both populations are spatially mobile and diffuse throughout the domain with constant diffusion rates δ_1 and δ_2, respectively. The second terms represent natural death, occurring at constant rates μ_1 and μ_2 for the respective populations. Furthermore, we assume that the second population, v, can recruit (or capture) individuals from the first population, u. This recruitment process depends on a constant rate $\rho > 0$, referred to as the capturing rate, and on the concentrations of both populations. Notably, the recruitment is more likely to occur when the concentrations of u and v are high, although it is biologically reasonable to assume that this effect saturates at high densities. In particular, in the absence of v, the recruitment of u does not take place. These biological interactions are modelled by the third terms on the right-hand side of equations (4.1)–(4.2).

Furthermore, the last term on the right-hand side of equation (4.1) represents the production of the population u, which depends on v. Specifically, we assume that the presence of the second population exerts stress on the production of the u-species, potentially leading to a reduction or even a complete shutdown of production. In addition, the production process is not assumed to be instantaneous, but rather to involve a processing delay of duration T, as is typically observed in various classes of biological processes [2].

Such a model can be applied to the ecological description of interacting populations, for instance either within a single species (juveniles and adults) exhibiting self-regulatory behaviour or in a specific predator–pray interaction. However, our primary motivation stems from modelling the dynamics of prion proteins in the brain.

Recall that prions are proteins implicated in neurodegenerative disorders, notably the transmissible spongiform encephalopathies, such as scrapie in sheep, bovine spongiform encephalopathy (also known as mad cow disease) in cattle, and Creutzfeldt–Jakob disease in humans [64,65]. This protein, produced by cells in its normal conformation, is referred to as PrP^C (for prion protein cellular) and appears to have a protective function [65]. However, when it undergoes a structural change, it becomes pathogenic and fatal. This misfolded, disease-causing form, known as PrP^{Sc} (for prion protein scrapie), can be acquired either through transmission—as was the case during the mad cow disease outbreak in the 1990s—or spontaneously, typically in individuals over 75 years of age [66].

Despite extensive research in recent decades, the precise mechanism by which this protein leads to neuronal death remains unclear. Nonetheless, recent discoveries offer potential explanations and point to new therapeutic avenues. One such mechanism, known as the unfolded protein response (UPR) [67–71], can be described as follows. When prion proteins, either owing to overexpression of PrP^C or impaired diffusion, accumulate near a neuron, the neuron detects this buildup. In response to the stress, it shuts down nearly all of its functions, maintaining only those necessary for survival.

This global shutdown, triggered by a high concentration of PrP^{Sc} in the neuronal environment, leads the neuron to cease production of PrP^{C}, which is not essential for its immediate survival. The halt in protein production persists until the accumulated proteins dissipate via diffusion or degradation. Once the local concentration is reduced, the neuron resumes protein synthesis, continuing the cycle until the next stress episode.

Although the detailed mechanisms underlying the UPR are still under active investigation [72], they have yet to be fully elucidated.

First, when produced by the cell, the PrP^{C} protein remain anchored to its membrane, unless misfolded PrP^{Sc} in the extracellular matrix forces it to set it free and to join the pathological cohort. It is important to remember here that, by contact, a PrP^{Sc} protein allows the normal form PrP^{C} to change its conformation and to become misconformed. Once in this state, the proteins have the ability to polymerize, that is, to tie together. They can easily reach very large sizes, stay in the neighbourhood of the cell or diffuse in the extracellular matrix to seed other neurons. This biological feature is incorporated into the model through the function h in equation (4.1), defined as follows:

$$h(\mathrm{v}) = \frac{a}{1 + (\mathrm{v}/\mathrm{v}_c)^m}, \tag{4.3}$$

where $a > 0$ is a constant and $\mathrm{v}_c > 0$ corresponds to the threshold density of the v-species over which the production becomes low. Taking the biological example mentioned above, the constant $m \geq 1$ could denote for example the UPR sensitivity to an overload of oligomers as explained by [73]. For this reason, we consider that this m is large enough to have a negligible production term when the v-species exceeds v_c. Finally, with regard to simplifying assumptions, we note the following.

(H1) We consider that the diffusion rate of the first population is bigger than that of the second one, namely, $\delta_1 \geq \delta_2$. We can explain it biologically by a non-negligible difference of size between both populations as is typically the case between monomers and oligomers, for example.

(H2) To ensure the survival of the v-species, we consider that the difference between the capturing rate ρ and the death rate μ_2 is controlled as $\mu_2 < \rho \leq 2\mu_2$.

Further assumptions, namely, (H3) and (H4), will be introduced later when required for the construction of travelling waves.

(b) Steady states and change of variables

Herein, we propose adequate changes to systems (4.1)–(4.2) in order to apply later on the theorem of existence established in §3. First, we look for steady states of systems (4.1)–(4.2). Hence, such a point should verify the following conditions:

$$\overline{u}\left(\mu_1 + \frac{\rho\overline{\mathrm{v}}}{\overline{u} + \overline{\mathrm{v}}}\right) = h(\overline{\mathrm{v}}) \quad \text{and} \quad \overline{\mathrm{v}}\left(\frac{\rho\overline{u}}{\overline{u} + \overline{\mathrm{v}}} - \mu_2\right) = 0. \tag{4.4}$$

Then, system (4.4) admits at least one steady state $(\overline{u_1}, \overline{\mathrm{v}_1})$, corresponding to the case in which only the u-species is present, which can be assimilated to either the *disease-free equilibrium* or the *prey-only state*. It reads

$$\overline{u_1} = \frac{h(0)}{\mu_1} := \frac{a}{\mu_1} \quad \text{and} \quad \overline{\mathrm{v}_1} = 0. \tag{4.5}$$

On the other hand, when $\overline{\mathrm{v}} \neq 0$, system (4.4) admits another solution if and only if $\rho > \mu_2$. Owing to (H2), we consider that this conditions holds. In this case, the second equilibrium of systems (4.1)–(4.2), denoted as $(\overline{u_2}, \overline{v_2})$, is given by

$$\overline{u_2} = \frac{\mu_2 \overline{v_2}}{\rho - \mu_2} \quad \text{and} \quad h(\overline{v_2}) = \mu_2 \overline{v_2}\left(1 + \frac{\mu_1}{\rho - \mu_2}\right). \tag{4.6}$$

As a result, systems (4.1)–(4.2) admit two steady states, namely, $(\overline{u_1}, \overline{v_1})$ and $(\overline{u_2}, \overline{v_2})$, defined above. Further, by comparing equations (4.5) with equations (4.6), we notice that for the associated ODE, $\overline{v_2} > \overline{v_1}$ whereas $\overline{u_1} > \overline{u_2}$. Indeed, we have

$$\overline{u_2} = \frac{\mu_2 \overline{v_2}}{\rho - \mu_2} = \frac{h(\overline{v_2})}{\rho - \mu_2 + \mu_1} < \frac{h(\overline{v_2})}{\mu_1} < \frac{a}{\mu_1} := \overline{u_1}.$$

In order to have the same monotony between the two equilibria and notably to verify equation (1.3), we operate a change of variables. For practical purposes, this change concerns the variable u with $\widetilde{u} := \overline{u_1} - u$. Therefore, the new system of equations reads, for $x \in \mathbb{R}^n$ and $t > 0$,

$$\left.\begin{aligned} &\frac{\partial \widetilde{u}}{\partial t}(x,t) = \delta_1 \Delta \widetilde{u}(x,t) - \mu_1 \widetilde{u}(x,t) + \frac{\rho\left(\frac{a}{\mu_1} - \widetilde{u}(x,t)\right) v(x,t)}{\frac{a}{\mu_1} - \widetilde{u}(x,t) + v(x,t)} + a - h(v(x,t-T)) \\ \text{and} \quad &\frac{\partial v}{\partial t}(x,t) = \delta_2 \Delta v(x,t) - \mu_2 v(x,t) + \frac{\rho\left(\frac{a}{\mu_1} - \widetilde{u}(x,t)\right) v(x,t)}{\frac{a}{\mu_1} - \widetilde{u}(x,t) + v(x,t)}. \end{aligned}\right\} \tag{4.7}$$

In particular, the above system can be rewritten in a similar fashion to system (1.1) by using the following reaction term $f := (f_1, f_2)$:

$$\left.\begin{aligned} &f_1(u_t(x), v_t(x)) = -\mu_1 u(x,t) + \frac{\rho\left(\frac{a}{\mu_1} - u(x,t)\right) v(x,t)}{\frac{a}{\mu_1} - u(x,t) + v(x,t)} + a - h(v(x,t-T)) \\ \text{and} \quad &f_2(u_t(x), v_t(x)) = -\mu_2 v(x,t) + \frac{\rho\left(\frac{a}{\mu_1} - u(x,t)\right) v(x,t)}{\frac{a}{\mu_1} - u(x,t) + v(x,t)}. \end{aligned}\right\} \tag{4.8}$$

Accordingly, f satisfies equation (1.3) with (0,0) and (k_1, k_2) as steady states where $k_1 = a/\mu_1 - \mu_2 k_2/\rho - \mu_2 > 0$ and k_2 is given by

$$h(k_2) = \mu_2 k_2 \left(1 + \frac{\mu_1}{\rho - \mu_2}\right). \tag{4.9}$$

Lemma 4.1. *Let $\Phi = (\phi_1, \phi_2)$, $\Psi = (\psi_1, \psi_2) \in \mathcal{C}([-T, 0], \mathbb{R}^2)$ such as $M_1 = a/\mu_1$ and $M_2 \geq k_2$ arbitrary, for instance, we choose $M_2 = a(\rho - \mu_2)/\mu_1\mu_2$. Then, the reaction term defined in equations (4.8) satisfies condition condition (1.4).*

Proof. Let $\Phi = (\phi_1, \phi_2)$, $\Psi = (\psi_1, \psi_2) \in \mathcal{C}([-T, 0], \mathbb{R}^2)$ such as equation (1.5) holds, with $M_1 = a/\mu_1$. Then, we have

$$\begin{aligned} |f_1(\phi_1, \phi_2) - f_1(\psi_1, \psi_2)| = &| - \mu_1(\phi_1(0) - \psi_1(0)) + h(\psi_2(-T)) - h(\phi_2(-T)) \\ &+ \frac{\rho(\phi_2(0) - \psi_2(0))(\frac{a}{\mu_1} - \phi_1(0))(\frac{a}{\mu_1} - \psi_1(0))}{(\frac{a}{\mu_1} - \phi_1(0) + \phi_2(0))(\frac{a}{\mu_1} - \psi_1(0) + \psi_2(0))} \\ &+ \frac{\rho(\psi_1(0) - \phi_1(0))\phi_2(0)\psi_2(0)}{(\frac{a}{\mu_1} - \phi_1(0) + \phi_2(0))(\frac{a}{\mu_1} - \psi_1(0) + \psi_2(0))}|, \\ \leq &\mu_1|(\phi_1(0) - \psi_1(0))| + K|\psi_2(-T) - \phi_2(-T)| \\ &+ \rho|\phi_2(0) - \psi_2(0)| + \rho|\phi_1(0) - \psi_1(0)|, \\ \leq &L_1 \,||\Phi - \Psi||, \end{aligned}$$

where $K := am/v_c(M_2/v_c)^{m-1}$ and $L_1 := 2\rho + \mu_1 + K$. Similarly, we also have

$$|f_2(\phi_1, \phi_2) - f_2(\psi_1, \psi_2)| \le (\mu_2 + \rho)|\phi_2(0) - \psi_2(0)| + \rho|\phi_1(0) - \psi_1(0)| \le L_2||\Phi - \Psi||,$$

where $L_2 := 2\rho + \mu_2$. The lemma is, thus, proved. ■

Lemma 4.2. *The reaction term f defined in equations (4.8) satisfies the SMQM condition equations (2.5).*

Proof. Let $\Phi = (\phi_1, \phi_2)$, $\Psi = (\psi_1, \psi_2) \in \mathcal{C}([-T, 0], \mathbb{R}^2)$ such as equations (2.6) holds. On the one hand, we have

$$\begin{aligned} f_1(\phi_1, \phi_2) - f_1(\psi_1, \phi_2) &= -\mu_1(\phi_1(0) - \psi_1(0)) \\ &\quad - \frac{\rho\phi_2(0)^2(\phi_1(0) - \psi_1(0))}{(\frac{a}{\mu_1} - \phi_1(0) + \phi_2(0))(\frac{a}{\mu_1} - \psi_1(0) + \phi_2(0))}, \\ &\ge -(\phi_1(0) - \psi_1(0))(\mu_1 + \rho). \end{aligned}$$

By taking $b_1 := \mu_1 + \rho$, the first condition of equations (2.5) is verified. On the other hand, we have

$$\begin{aligned} f_1(\phi_1, \phi_2) - f_1(\phi_1, \psi_2) &= h(\psi_2(-T)) - h(\phi_2(-T)) \\ &\quad + \frac{\rho(\phi_2(0) - \psi_2(0))(\frac{a}{\mu_1} - \phi_1(0))^2}{(\frac{a}{\mu_1} - \phi_1(0) + \phi_2(0))(\frac{a}{\mu_1} - \phi_1(0) + \psi_2(0))}, \\ &\ge 0. \end{aligned}$$

The second condition of equations (2.5) is, thus, proved. Further, we have

$$\begin{aligned} f_2(\phi_1, \phi_2) - f_2(\phi_1, \psi_2) &= -\mu_2(\phi_2(0) - \psi_2(0)) \\ &\quad + \frac{\rho(\phi_2(0) - \psi_2(0))(\frac{a}{\mu_1} - \phi_1(0))^2}{(\frac{a}{\mu_1} - \phi_1(0) + \phi_2(0))(\frac{a}{\mu_1} - \phi_1(0) + \psi_2(0))}, \\ &\ge -\mu_2(\phi_2(0) - \psi_2(0)). \end{aligned}$$

By taking $b_2 := \mu_2$, the third condition of equations (2.5) is proved. Furthermore, we have

$$\begin{aligned} f_2(\phi_1, \phi_2) - f_2(\psi_1, \phi_2) &= -\frac{\rho\phi_2(0)^2(\phi_1(0) - \psi_1(0))}{(\frac{a}{\mu_1} - \phi_1(0) + \phi_2(0))(\frac{a}{\mu_1} - \psi_1(0) + \phi_2(0))}, \\ &\le 0. \end{aligned}$$

Therefore, the fourth condition of equations (2.5) is verified, thus implying that f satisfies SMQM. ■

Hence, by virtue of theorem 3.7, the existence of travelling wave solutions for systems (4.1)–(4.2) is reduced to show the existence of upper and lower solutions.

(c) Construction of adequate upper and lower solutions

In this section, under stated conditions, we prove the existence of an adequate pair of super- and sub-solutions for the wave system considered herein, i.e., wave system (2.2) with f defined in equations (4.8). In other words, we show that there exist (ϕ_1^+, ϕ_2^+) and (ϕ_1^-, ϕ_2^-) satisfying definition 3.2. Typically, and as mentioned in §1, their existence is obtained in a straightforward manner when the reaction term f satisfies the QM, MQM or WQM condition; see, for example, [26–29]. Herein, owing to the SMQM condition, the construction of such solutions can be challenging and requires a specific attention. In particular, we find necessary for the super-solutions ϕ_i^+ to exceed the equilibrium value k_i. As a result, these specific aspects have led us

royalsocietypublishing.org/journal/rspa Proc. R. Soc. A 482: 20250630

to look for solutions with the following forms:

$$\left.\begin{aligned} &\phi_1^+(z)=\begin{cases}\dfrac{a}{\mu_1}e^{\lambda_1 z} & \text{if } z\le 0,\\ \dfrac{a}{\mu_1} & \text{if } z>0,\end{cases} \qquad \phi_1^-(z)=0 \\ \text{and}\quad &\phi_2^+(z)=\begin{cases}\dfrac{a(\rho-\mu_2)}{\mu_1\mu_2}e^{\lambda_2 z} & \text{if } z\le 0,\\ \dfrac{a(\rho-\mu_2)}{\mu_1\mu_2} & \text{if } z>0,\end{cases} \qquad \phi_2^-(z)=\begin{cases}\dfrac{a(\rho-\mu_2)}{\mu_1\mu_2}(e^{\lambda_2 z}-\sigma e^{\eta\lambda_2 z}) & \text{if } z\le \tilde{z},\\ 0 & \text{if } z>\tilde{z},\end{cases}\end{aligned}\right\} \tag{4.10}$$

with

$$k_1<\frac{a}{\mu_1},\quad k_2<\frac{a(\rho-\mu_2)}{\mu_1\mu_2},\quad \tilde{z}=\frac{1}{(\eta-1)\lambda_2}\ln\left(\frac{1}{\sigma}\right)<0,$$

and the constants $\lambda_1,\lambda_2,\eta,\sigma$ are positive and assigned below. We notice that $\eta,\sigma>1$. Despite $\phi_1^-\equiv 0$, the desired solution is not trivial. This can be checked directly from the system. It is only sufficient to consider that ϕ_2^- is not identically zero. Clearly, we have

$$\lim_{z\to-\infty}(\phi_1^-(z),\phi_2^-(z))=\lim_{z\to-\infty}(\phi_1^+(z),\phi_2^+(z))=(0,0).$$

Figure 2 shows the shape of these functions. We choose $\lambda_1:=c-\sqrt{c^2-4\delta_1\xi_1}/2\delta_1$ and $\lambda_2:=c-\sqrt{c^2-4\delta_2\xi_2}/2\delta_2$, with

$$\xi_1:=-\mu_1+\left(\rho+m\left(\frac{a}{\mathrm{v}_c}\right)^m\left(\frac{\rho-\mu_2}{\mu_1\mu_2}\right)^{m-1}\right)\frac{\rho-\mu_2}{\mu_2},\quad \xi_2:=\rho-\mu_2, \tag{4.11}$$

where v_c is the threshold value for the v-species defined in equations (4.3) and the wave speed c verifying,

$$c>c^*:=2\max\{\sqrt{\delta_1\xi_1},\sqrt{\delta_2\xi_2}\},\quad \text{if } \xi_1>0.$$

So, we have

$$\left.\begin{aligned} &\delta_1\lambda_1^2-c\lambda_1+\xi_1=0\\ \text{and}\qquad &\delta_2\lambda_2^2-c\lambda_2+\xi_2=0.\end{aligned}\right\} \tag{4.12}$$

About the choice of σ and η, we shall see that σ is chosen large enough and η is chosen such that

$$1<\eta<\frac{1}{\lambda_2}\min\left\{\lambda_1+\lambda_2,\frac{c+\sqrt{c^2-4\delta_2\xi_2}}{2\delta_2}\right\}. \tag{4.13}$$

We need the following additive hypothesis:

(H3) We assume the following inequality: $0\le\delta_1\xi_1\le\delta_2\xi_2$. In order to satisfy (H1) as well, it is necessary that $0<\xi_1\le\xi_2$.

We seek conditions ensuring simultaneously (H1), (H2) and (H3). Define

$$A:=\frac{\rho}{\mu_2}-\frac{\delta_2}{\delta_1}>0,\quad B:=m\left(\frac{a}{\mathrm{v}_c}\right)^m\left(\frac{\xi_2}{\mu_2}\right)^m,\quad C:=A\xi_2+\frac{B}{(A\xi_2)^{m-1}},\quad D:=\frac{\rho}{\mu_2}\xi_2,$$

where ξ_1, ξ_2 are given by equation (4.11). Consider the interval $I:=[C,D)$. It is non-empty if and only

$$A\xi_2+\frac{B}{(A\xi_2)^{m-1}}<\frac{\rho}{\mu_2}\xi_2\Longleftrightarrow B<\frac{\delta_2}{\delta_1}A^{m-1}\xi_2^m.$$

Equivalently, this gives the positive upper bound

$$\frac{a}{\mathrm{v}_c}<\bar{\rho}:=\mu_2\left(\frac{\delta_2}{m\delta_1}\right)^{1/m}\left(\frac{\rho}{\mu_2}-\frac{\delta_2}{\delta_1}\right)^{m-1/m}. \tag{4.14}$$

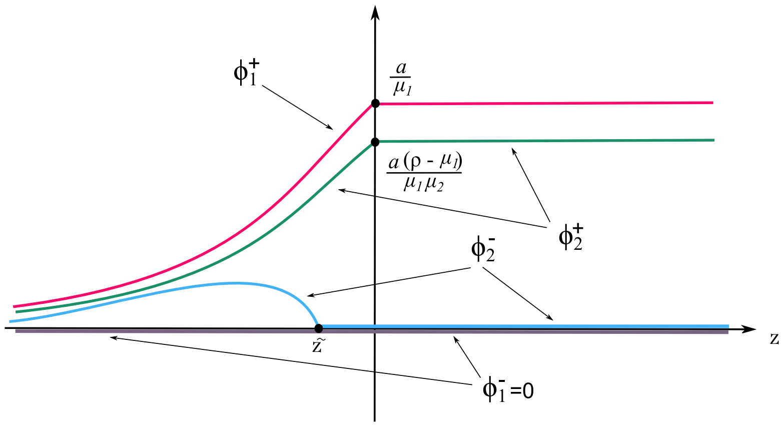

Figure 2. The curves of the functions ϕ_1^-, ϕ_2^-, ϕ_1^+ and ϕ_2^+ are represented for illustration.

The following verification establishes (H3). Let $\mu_1 \in [C, D)$. It is not difficult to see that

$$\xi_1 \geq -\mu_1 + \rho\frac{\xi_2}{\mu_2} = -\mu_1 + D > 0.$$

Hence, $\xi_1 > 0$. Next, the inequality $\delta_1\xi_1 \leq \delta_2\xi_2$ is equivalent to

$$-\mu_1 + A\xi_2 + \frac{B}{\mu_1^{m-1}} \leq 0 \Longleftrightarrow \mu_1^m - (A\xi_2)\mu_1^{m-1} - B \geq 0.$$

Since $\mu_1 \geq C$, we have both

$$\mu_1 - A\xi_2 \geq \frac{B}{(A\xi_2)^{m-1}} \quad \text{and} \quad \mu_1 > A\xi_2,$$

and, thus,

$$\mu_1^m - (A\xi_2)\mu_1^{m-1} = \mu_1^{m-1}(\mu_1 - A\xi_2) \geq (A\xi_2)^{m-1}\frac{B}{(A\xi_2)^{m-1}} = B.$$

Hence, under the condition equation (4.14) and $\mu_1 \in [C, D)$, we get $\xi_1 > 0$ and $\delta_1\xi_1 \leq \delta_2\xi_2$. Finally, from (H1), we have $\delta_1 \geq \delta_2$, so

$$\delta_1\xi_1 \leq \delta_2\xi_2 \Rightarrow \xi_1 \leq \frac{\delta_2}{\delta_1}\xi_2 \leq \xi_2.$$

Combining with $\xi_1 > 0$ yields $0 < \xi_1 \leq \xi_2$, and, therefore, (H3) holds.

Now, we are interested in identifying a simple sufficient condition under which $\mu_2 < C$, which ensures that $\mu_2 < \mu_1$ for every admissible μ_1. A sufficient condition is $\mu_2 < A\xi_2$, where $A = \rho/\mu_2 - \delta_2/\delta_1$ and $\xi_2 = \rho - \mu_2 = \mu_2(\frac{\rho}{\mu_2} - 1)$. Therefore,

$$\mu_2 < A\xi_2 = \left(\frac{\rho}{\mu_2} - \frac{\delta_2}{\delta_1}\right)\mu_2\left(\frac{\rho}{\mu_2} - 1\right) = \mu_2\left(\frac{\rho}{\mu_2} - \frac{\delta_2}{\delta_1}\right)\left(\frac{\rho}{\mu_2} - 1\right)$$

is equivalent to

$$\left(\frac{\rho}{\mu_2} - \frac{\delta_2}{\delta_1}\right)\left(\frac{\rho}{\mu_2} - 1\right) > 1. \tag{4.15}$$

This implies $\mu_2 < C$, and hence $\mu_2 < C \leq \mu_1$ for all $\mu_1 \in [C, D)$. Condition (4.15) depends only on the ratios $\rho/\mu_2 \in (1, 2]$ and $\delta := 1 - \delta_2/\delta_1 \in [0, 1)$. Equivalently, it can be checked by

$$\frac{\rho}{\mu_2} > 1 + \frac{-\delta + \sqrt{\delta^2 + 4}}{2}. \tag{4.16}$$

In the context of the model, this may be interpreted as assuming that the degradation rate of monomers, denoted by μ_1, is larger than that of polymers, μ_2. To the best of our knowledge, this assumption is consistent with biological evidence: monomers are generally more fragile and degrade more easily than polymers, which tend to form more stable and resistant structures.

Owing to the hypothesis (H1) and (H3), we affirm that $\lambda_1 \leq \lambda_2$. In this case, the wave speed is

$$c > c^* := 2\max\left\{\sqrt{\delta_1\xi_1}, \sqrt{\delta_2\xi_2}\right\} = 2\sqrt{\delta_2\xi_2}. \tag{4.17}$$

Now, we can establish the second theorem of this paper.

Theorem 4.3. *Let $c > c^*$ defined in equation (4.17). Then, wave system (2.2) admits a solution satisfying*

$$\lim_{z\to-\infty}(\phi_1(z), \phi_2(z)) = (0, 0)$$

and

$$0 \leq \liminf_{z\to+\infty}\phi_1(z) \leq \limsup_{z\to+\infty}\phi_1(z) \leq \frac{a}{\mu_1}, \quad \textit{with } k_1 < \frac{a}{\mu_1},$$

$$0 \leq \liminf_{z\to+\infty}\phi_2(z) \leq \limsup_{z\to+\infty}\phi_2(z) \leq \frac{a(\rho-\mu_2)}{\mu_1\mu_2}, \quad \textit{with } k_2 < \frac{a(\rho-\mu_2)}{\mu_1\mu_2}.$$

Proof. First, since the reaction term f satisfies SMQM and conditions (1.3)–(1.4), we apply theorem 3.7 to reduce the proof to the existence of an admissible pair of super- and sub-solutions. For that, we make use of ϕ_i^- and ϕ_i^+ in system (4.10) with the adequate constants. Then, by construction, the conditions mentioned by the points (i), (ii) and (iv) in definition 3.2 are easily corroborated and, thus, omitted. Therefore, it remains to show that the point (iii) of definition 3.2 is verified. To this end, we split the proof into four parts.

Step 1: Prove that the first two conditions of (iii) in definition 3.2 are satisfied.

On the one hand, let $z > 0$. We have

$$\phi_1^+(z) = \frac{a}{\mu_1}, \quad z > 0.$$

Then, we obtain

$$\delta_1(\phi_1^+)''(z) - c(\phi_1^+)'(z) + f_1^c(\phi_{1_z}^+, \phi_{2_z}^+) = f_1^c(\phi_{1_z}^+, \phi_{2_z}^+) = -h(\phi_2^+(z - cT)) \leq 0.$$

On the other hand, let $z < 0$. We have

$$\phi_1^+(z) = \frac{a}{\mu_1}e^{\lambda_1 z}, \quad \phi_2^+(z) = \frac{a(\rho-\mu_2)}{\mu_1\mu_2}e^{\lambda_2 z}, \quad z < 0.$$

Therefore, by applying the mean value theorem to h, we obtain

$$\begin{aligned} f_1^c(\phi_{1_z}^+, \phi_{2_z}^+) &= -\mu_1\phi_1^+(z) + \frac{\rho(\frac{a}{\mu_1} - \phi_1^+(z))\phi_2^+(z)}{\frac{a}{\mu_1} - \phi_1^+(z) + \phi_2^+(z)} + a - h(\phi_2^+(z - cT)), \\ &\leq -\mu_1\phi_1^+(z) + \rho\phi_2^+(z) + a - h(\phi_2^+(z - cT)), \\ &\leq -\mu_1\phi_1^+(z) + \rho\phi_2^+(z) + m\left(\frac{a}{v_c}\right)^m\left(\frac{\rho-\mu_2}{\mu_1\mu_2}\right)^{m-1}\phi_2^+(z - cT). \end{aligned}$$

Again, using the fact that $\lambda_1 \leq \lambda_2$, we obtain

$$\begin{aligned} f_1^c(\phi_{1_z}^+, \phi_{2_z}^+) &\leq -\mu_1\phi_1^+(z) + \left(\rho + m\left(\frac{a}{v_c}\right)^m\left(\frac{\rho-\mu_2}{\mu_1\mu_2}\right)^{m-1}\right)\phi_2^+(z), \\ &\leq -\mu_1\phi_1^+(z) + \left(\rho + m\left(\frac{a}{v_c}\right)^m\left(\frac{\rho-\mu_2}{\mu_1\mu_2}\right)^{m-1}\right)\frac{\rho-\mu_2}{\mu_2}\phi_1^+(z) = \xi_1\phi_1^+(z). \end{aligned}$$

royalsocietypublishing.org/journal/rspa Proc. R. Soc. A 482: 20250630

Then, we get

$$\delta_1(\phi_1^+)''(z) - c(\phi_1^+)'(z) + f_1^c(\phi_{1_z}^+, \phi_{2_z}^+) \le \delta_1(\phi_1^+)''(z) - c(\phi_1^+)'(z) + \xi_1\phi_1^+(z),$$
$$\le \phi_1^+(z)(\delta_1(\lambda_1)^2 - c\lambda_1 + \xi_1) = 0.$$

Step 2: Prove that the last two conditions of (iii) in definition 3.2 are satisfied.

On the one hand, let $z > 0$. In this case, we get

$$\phi_2^+(z) = \frac{a(\rho - \mu_2)}{\mu_1\mu_2}, \quad z > 0.$$

Then, we have

$$\delta_2(\phi_2^+)''(z) - c(\phi_2^+)'(z) + f_2^c(\phi_{1_z}^-, \phi_{2_z}^+) = f_2^c(\phi_{1_z}^-, \phi_{2_z}^+),$$
$$= \frac{(\rho - \mu_2)}{\rho}\left(-\mu_2\frac{\rho a}{\mu_1\mu_2} + \frac{\rho a}{\mu_1}\right) = 0.$$

On the other hand, let $z < 0$. In this case, we get

$$\phi_2^+(z) = \frac{a(\rho - \mu_2)}{\mu_1\mu_2}e^{\lambda_2 z}, \quad z < 0.$$

Then, we have

$$\delta_2(\phi_2^+)''(z) - c(\phi_2^+)'(z) + f_2^c(\phi_{1_z}^-, \phi_{2_z}^+) \le \phi_2^+(z)(\delta_2(\lambda_2)^2 - c\lambda_2 + \rho - \mu_2) = 0.$$

Step 3: Prove that the first two conditions of (iii) in definition 3.2 are satisfied.

Let $z \in \mathbb{R}$. We have $\phi_1^- \equiv 0$ and the proof is straightforward. In fact, we get

$$\delta_1(\phi_1^-)''(z) - c(\phi_1^-)'(z) + f_1^c(\phi_{1_z}^-, \phi_{2_z}^-) \ge \frac{\rho(a/\mu_1)\phi_2^-(z)}{\frac{a}{\mu_1} + \phi_2^-(z)} + a - h(\phi_2^-(z - cT)) \ge 0.$$

Step 4: Prove that the last two conditions of (iii) in definition 3.2 are satisfied.

Let $z < \tilde{z}$. Then, we have, for $z < \tilde{z}$,

$$\phi_1^+(z) = \frac{a}{\mu_1}e^{\lambda_1 z} \quad \text{and} \quad \phi_2^-(z) = \frac{a(\rho - \mu_2)}{\mu_1\mu_2}(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z}).$$

We use the following notations:

$$\rho_1 := \frac{a}{\mu_1} \quad \text{and} \quad \rho_2 := \frac{a(\rho - \mu_2)}{\mu_1\mu_2}.$$

Therefore, we obtain

$$\begin{aligned}
&\delta_2(\phi_2^-)''(z) - c(\phi_2^-)'(z) + f_2^c(\phi_{1_z}^+, \phi_{2_z}^-) \\
&\quad = \rho_2 e^{\lambda_2 z}(\delta_2\lambda_2^2 - c\lambda_2 - \mu_2) - \rho_2\sigma e^{\eta\lambda_2 z}(\delta_2(\eta\lambda_2)^2 - c(\eta\lambda_2) - \mu_2) \\
&\qquad + \frac{\rho\rho_1\rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}{\rho_1 - \rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})} - \frac{\rho\rho_1 e^{\lambda_1 z}\rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}{\rho_1 - \rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}.
\end{aligned}$$

Under the assumption that $\rho \le 2\mu_2$, we have that $\rho_2 \le \rho_1$ and we get

$$-\rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z}) \le 0, \quad z < \tilde{z}.$$

royalsocietypublishing.org/journal/rspa *Proc. R. Soc. A* **482**: 20250630

Thus, we get

$$\begin{aligned}
&\delta_2(\phi_2^-)''(z) - c(\phi_2^-)'(z) + f_2^c(\phi_{1_z}^+, \phi_{2_z}^-) \\
&\quad \geq \rho_2 e^{\lambda_2 z}(\delta_2\lambda_2^2 - c\lambda_2 - \mu_2) - \rho_2\sigma e^{\eta\lambda_2 z}(\delta_2(\eta\lambda_2)^2 - c(\eta\lambda_2) - \mu_2) \\
&\qquad + \rho\rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z}) - \frac{\rho\rho_1 e^{\lambda_1 z}\rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}{\rho_1 - \rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}, \\
&\quad = \rho_2 e^{\lambda_2 z}(\delta_2\lambda_2^2 - c\lambda_2 - \mu_2 + \rho) - \rho_2\sigma e^{\eta\lambda_2 z}(\delta_2(\eta\lambda_2)^2 - c(\eta\lambda_2) - \mu_2 + \rho) \\
&\qquad - \frac{\rho\rho_1\rho_2 e^{(\lambda_1+\lambda_2)z}}{\rho_1 - \rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})} + \frac{\rho\rho_1\rho_2\sigma e^{(\lambda_1+\eta\lambda_2)z}}{\rho_1 - \rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}.
\end{aligned}$$

Taking into account equation (4.13), we obtain

$$\begin{aligned}
&\delta_2(\phi_2^-)''(z) - c(\phi_2^-)'(z) + f_2^c(\phi_{1_z}^+, \phi_{2_z}^-) \\
&\quad \geq \rho_2 e^{\eta\lambda_2 z}\left[\sigma(-\delta_2(\eta\lambda_2)^2 + c(\eta\lambda_2) + \mu_2 - \rho) - \frac{\rho\rho_1}{\rho_1 - \rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}\right].
\end{aligned}$$

We denote by

$$\zeta(\sigma) := \sup_{z\in(-\infty,\tilde{z}]}\left[\frac{\rho\rho_1}{\rho_1 - \rho_1 e^{\lambda_1 z} + \rho_2(e^{\lambda_2 z} - \sigma e^{\eta\lambda_2 z})}\right] < +\infty.$$

We can choose

$$\sigma \geq \frac{\zeta(\sigma)}{-\delta_2(\eta\lambda_2)^2 + c(\eta\lambda_2) + \mu_2 - \rho}.$$

This leads to

$$\delta_2(\phi_2^-)''(z) - c(\phi_2^-)'(z) + f_2^c(\phi_{1_z}^+, \phi_{2_z}^-) \geq 0.$$

In addition, when $z > \tilde{z}$, we have that $\phi_2^- \equiv 0$, implying that the proof is straightforward. Furthermore, it is worth adding that ϕ_2^- remains non-negative while the condition (iv) of definition 3.2 is also satisfied. All the points are verified, thus proving that ϕ_i^- and ϕ_i^+ are indeed a pair of super- and sub-solutions, as stated in definition 3.2. Therefore, by virtue of theorem 3.7, the system (4.1)–(4.2) admits a travelling wave solution connecting $\mathbf{0} := (0, 0)$ to a certain possible point. Thus, the theorem is proved. ■

To complete the above result, we use the technique of contracting rectangles to determine the asymptotic behaviour of travelling waves; see [74]. It is a well-known qualitative technique originally developed for delay differential equations, see theorem 2.5 on page 84 of [75], and later in [74] extended to delayed reaction–diffusion systems. This method provides a way to prove global convergence toward an equilibrium without constructing an explicit Lyapunov function. The idea is to construct a family of ordered invariant rectangles that gradually shrink under the flow, forcing all trajectories to converge toward the equilibrium. Let us define $\underline{E} = (0, 0)$ and $\overline{E} = (\rho_1, \rho_2)$, where

$$\rho_1 := \frac{a}{\mu_1} \quad \text{and} \quad \rho_2 := \frac{a(\rho - \mu_2)}{\mu_1\mu_2}.$$

It is easy to verify that $[\underline{E}, \overline{E}]$ is a positively invariant ordered interval (see page 83 of [75] for the definition of this notion) for the following system:

$$\left.\begin{aligned}
&\frac{\mathrm{d}u}{\mathrm{d}t}(t) = -\mu_1 u(t) + \frac{\rho(\frac{a}{\mu_1} - u(t))\mathrm{v}(t)}{\frac{a}{\mu_1} - u(t) + \mathrm{v}(t)} + a - h(\mathrm{v}(t - T)) \\
\text{and}\quad &\frac{\mathrm{d}\mathrm{v}}{\mathrm{d}t}(t) = -\mu_2\mathrm{v}(t) + \frac{\rho(\frac{a}{\mu_1} - u(t))\mathrm{v}(t)}{\frac{a}{\mu_1} - u(t) + \mathrm{v}(t)}.
\end{aligned}\right\} \tag{4.18}$$

We assume the following inequality:

(H4) $\rho\rho_1\rho_2 + a < \mu_1 k_1 + h(\rho_2)$.

With this additional condition, it remains to check that the set of parameters satisfying (H1)–(H4) is non-empty. Using the expressions of k_1 and $h(k_2)$, equation (4.9), we see that (H4) is equivalent to

$$\frac{\rho a^2 \xi_2}{\mu_1^2 \mu_2} < h(\rho_2) - \frac{\mu_1}{\mu_1 + \xi_2} h(k_2). \tag{4.19}$$

Define

$$\ell(x) := \mu_2 x \left(1 + \frac{\mu_1}{\xi_2}\right) - h(x), \quad x \geq 0.$$

It is clear that ℓ is increasing and the equation $\ell(x) = 0$ has a unique positive solution $x = k_2$. Evaluating ℓ at $x = \rho_2$ gives

$$\ell(\rho_2) = \mu_2 \rho_2 \left(1 + \frac{\mu_1}{\xi_2}\right) - h(\rho_2) = a\left(1 + \frac{\xi_2}{\mu_1}\right) - h(\rho_2) > a - h(\rho_2) \geq 0.$$

Hence, $\rho_2 > k_2$ and, since h is decreasing, $h(\rho_2) < h(k_2)$. Substituting this into equation (4.19) yields the sufficient condition,

$$\frac{\rho a^2 \xi_2}{\mu_1^2 \mu_2} < h(\rho_2)\left(1 - \frac{\mu_1}{\mu_1 + \xi_2}\right) = h(\rho_2)\frac{\xi_2}{\mu_1 + \xi_2}. \tag{4.20}$$

To get a clean lower estimate on $h(\rho_2)$, assume $\rho_2 \leq \mathrm{v}_c$. Then, $h(\rho_2) \geq a/2$. The condition $\rho_2 \leq \mathrm{v}_c$ is equivalent to

$$\mu_1 \geq \frac{a}{\mathrm{v}_c}\frac{\xi_2}{\mu_2}.$$

Under this bound, equation (4.20) is implied by $\mu_2 \mu_1^2 - 2\rho a \mu_1 - 2\rho a \xi_2 > 0$, which holds as soon as

$$\mu_1 > \mu_1^{(+)} := \frac{\rho a + \sqrt{(\rho a)^2 + 2\mu_2 \rho a \xi_2}}{\mu_2}.$$

Set

$$\bar{C} := \max\left\{C, \frac{a\xi_2}{\mathrm{v}_c \mu_2}, \mu_1^{(+)}\right\},$$

where C is the lower endpoint of the interval I, defined just after (H3), and let $\bar{I} := (\bar{C}, D)$, where D is the upper endpoint of I, defined just after (H3). To satisfy all the assumptions (H1)–(H4) with some $\mu_1 \in \bar{I} \subset I$, it remains first to ensure that $\bar{I}$ is non-empty. A sufficient condition for $a\xi_2/\mathrm{v}_c\mu_2 < D$ is

$$\frac{a}{\mathrm{v}_c} < \rho, \tag{4.21}$$

and a sufficient condition for $\mu_1^{(+)} < D$ is

$$a < \frac{\rho \xi_2}{2(\rho + \mu_2)}. \tag{4.22}$$

Combining equations (4.14) (the smallness assumption, $a/\mathrm{v}_c < \bar{\rho}$, used to make $C < D$ in (H3)), (4.21) and (4.22), we conclude that for

$$\frac{a}{\mathrm{v}_c} < \min\{\rho, \bar{\rho}\} \quad \text{and} \quad a < \frac{\rho(\rho - \mu_2)}{2(\rho + \mu_2)}, \tag{4.23}$$

the interval $\bar{I}$ is non-empty. Moreover, if (H1)–(H2) hold, then (H3)–(H4) are satisfied for any $\mu_1 \in \bar{I} \subset I$. Under these assumptions, $\bar{\rho} \leq \rho$, and condition (4.16) (ensuring $\mu_1 > \mu_2$) remains compatible with equations (4.23).

Define

$$\hat{E}^* = (k_1, k_2), \quad \hat{\rho} = (\rho_1, \rho_2) \quad \text{and} \quad \hat{\epsilon}(s) = (-s(\rho_1 - k_1)\epsilon_1, \epsilon_2),$$

with $0 < \epsilon_1, \epsilon_2 \ll 1$ sufficiently small (e.g. $\epsilon_1 < \rho_1/(\rho_1 - k_1)$). For any $0 < s < 1$, we shall show that the one-parameter family of ordered intervals defined by

$$\Sigma(s) = [s\hat{E}^*, s\hat{E}^* + (1 - s)(\hat{\rho} + \hat{\epsilon}(s))]$$

forms a strict contracting rectangle for the functional differential system (4.18).

First, we notice that $s\hat{E}^* \le \hat{E}^* \le s\hat{E}^* + (1-s)(\hat{\rho} + \hat{\epsilon}(s))$ for any $0 \le s \le 1$. We check easily that $s \to sk_1 + (1-s)(\rho_1 - s(\rho_1 - k_1)\epsilon_1)$ and $s \to sk_2 + (1-s)(\rho_2 + \epsilon_2)$ are decreasing. Now, we assume that $s \in (0,1)$ and $(u, \mathrm{v}) \in \Sigma(s)$. If $\mathrm{v}(0) = sk_2$, then

$$-\mu_2 \mathrm{v}(0) + \frac{\rho(\frac{a}{\mu_1} - u(0))\mathrm{v}(0)}{\frac{a}{\mu_1} - u(0) + \mathrm{v}(0)} = sk_2 \left(-\mu_2 + \frac{\rho(\rho_1 - u(0))}{\rho_1 - u(0) + sk_2} \right).$$

Since $sk_1 \le u(0) \le sk_1 + (1-s)(\rho_1 - s(\rho_1 - k_1)\epsilon_1)$, then $\rho_1 - u(0) \ge s(\rho_1 - k_1)(1 + (1-s)\epsilon_1)$. Recall that positive equilibrium satisfies

$$-\mu_2 + \frac{\rho(\rho_1 - k_1)}{(\rho_1 - k_1) + k_2} = 0.$$

Therefore, we get

$$\begin{aligned} -\mu_2 \mathrm{v}(0) + \frac{\rho(\frac{a}{\mu_1} - u(0))\mathrm{v}(0)}{\frac{a}{\mu_1} - u(0) + \mathrm{v}(0)} &\ge sk_2 \left(-\mu_2 + \frac{\rho(\rho_1 - k_1)(1 + (1-s)\epsilon_1)}{(\rho_1 - k_1)(1 + (1-s)\epsilon_1) + k_2} \right), \\ &> sk_2 \left(-\mu_2 + \frac{\rho(\rho_1 - k_1)}{\rho_1 - k_1 + k_2} \right) = 0. \end{aligned}$$

We define the following function:

$$g_{\epsilon_2}(s) := \frac{\rho(\frac{a}{\mu_1} - sk_1)}{\frac{a}{\mu_1} - sk_1 + sk_2 + (1-s)(\rho_2 + \epsilon_2)}, \quad s \in [0,1], \ \ \epsilon_2 > 0$$

and recall that

$$k_1 = \frac{a}{\mu_1} - \frac{\mu_2 k_2}{\rho - \mu_2} \quad \text{and} \quad \rho_2 := \frac{a(\rho - \mu_2)}{\mu_1 \mu_2}.$$

It can be verified that $g_0'(s) = 0$ for all $s \in [0,1]$; hence, $g_0(s)$ is constant. Moreover, we have $g_0(0) = g_0(1) = \mu_2$. If $\mathrm{v}(0) = sk_2 + (1-s)(\rho_2 + \epsilon_2)$, then, since $g_{\epsilon_2}(s) < \mu_2$ for all $s \in [0,1]$, we obtain

$$\begin{aligned} &-\mu_2 \mathrm{v}(0) + \frac{\rho(\frac{a}{\mu_1} - u(0))\mathrm{v}(0)}{\dfrac{a}{\mu_1} - u(0) + \mathrm{v}(0)} \\ &\quad \le (sk_2 + (1-s)(\rho_2 + \epsilon_2)) \left[-\mu_2 + \frac{\rho(\frac{a}{\mu_1} - sk_1)}{\frac{a}{\mu_1} - sk_1 + sk_2 + (1-s)(\rho_2 + \epsilon_2)} \right] < 0, \end{aligned}$$

because

$$g_0(s) := \frac{\rho(\frac{a}{\mu_1} - sk_1)}{\frac{a}{\mu_1} - sk_1 + sk_2 + (1-s)\rho_2} = \mu_2, \quad s \in [0,1].$$

If $u(0) = sk_1$ and $sk_2 \le \mathrm{v}(0)$, $\mathrm{v}(-T) \le sk_2 + (1-s)(\rho_2 + \epsilon_2)$, then

$$-\mu_1 sk_1 + \frac{\rho(\frac{a}{\mu_1} - sk_1)\mathrm{v}(0)}{\frac{a}{\mu_1} - sk_1 + \mathrm{v}(0)} + a - h(\mathrm{v}(-T)) \ge -\mu_1 sk_1 + \frac{\rho(\rho_1 - k_1)sk_2}{\rho_1 - k_1 + sk_2} + a - h(sk_2) =: S_1(s).$$

Clearly, $S_1(0) = S_1(1) = 0$. Moreover, we have

$$S_1'(s) = -\mu_1 k_1 + \frac{\rho(\rho_1 - k_1)^2 k_2}{(\rho_1 - k_1 + sk_2)^2} + \frac{ma\frac{k_2}{\mathrm{v}_c}(sk_2/\mathrm{v}_c)^{m-1}}{(1 + (sk_2/\mathrm{v}_c)^m)^2}, \quad s \in (0,1).$$

It is easy to observe that $S_1''(s) < 0$ for $s \in (0,1)$ when $m = 1$. This implies that $S_1(s) > 0$ for $s \in (0,1)$. Although providing a rigorous analytical proof of the inequality $S_1(s) > 0$ for $s \in (0,1)$ when $m \neq 1$ is challenging owing to the complexity of the expressions involved, we present numerical evidence supporting its validity. These numerical investigations indicate that the inequality

royalsocietypublishing.org/journal/rspa Proc. R. Soc. A **482**: 20250630

indeed holds. If $u(0) = sk_1 + (1-s)(\rho_1 - s(\rho_1 - k_1)\epsilon_1)$, we have

$$\begin{aligned}&-\mu_1(sk_1 + (1-s)(\rho_1 - s(\rho_1-k_1)\epsilon_1))\\ &\quad + \frac{\rho(\frac{a}{\mu_1} - sk_1 - (1-s)(\rho_1 - s(\rho_1-k_1)\epsilon_1))\mathrm{v}(0)}{\frac{a}{\mu_1} - sk_1 - (1-s)(\rho_1 - s(\rho_1-k_1)\epsilon_1) + \mathrm{v}(0)} + a - h(\mathrm{v}(-T))\\ &\le -\mu_1(sk_1 + (1-s)(\rho_1 - s(\rho_1-k_1)\epsilon_1))\\ &\quad + \frac{\rho(\frac{a}{\mu_1} - sk_1 - (1-s)(\rho_1 - s(\rho_1-k_1)\epsilon_1))(sk_2 + (1-s)(\rho_2+\epsilon_2))}{\frac{a}{\mu_1} - sk_1 - (1-s)(\rho_1 - s(\rho_1-k_1)\epsilon_1) + (sk_2 + (1-s)(\rho_2+\epsilon_2))}\\ &\quad + a - h(sk_2 + (1-s)(\rho_2+\epsilon_2)) =: S_2(s).\end{aligned}$$

We obtain again, using (H4),

$$\begin{aligned}S_2(s) &< -\mu_1(sk_1 + (1-s)(\rho_1 - s(\rho_1-k_1)\epsilon_1))\\ &\quad + \frac{\rho(\frac{a}{\mu_1} - sk_1)(sk_2 + (1-s)(\rho_2+\epsilon_2))}{\frac{a}{\mu_1} - sk_1 + sk_2 + (1-s)(\rho_2+\epsilon_2)} + a - h(\rho_2+\epsilon_2)),\\ &< -\mu_1 k_1 + \rho\rho_1(\rho_2+\epsilon_2) + a - h(\rho_2+\epsilon_2) < 0, \quad \epsilon_2 \ll 1.\end{aligned}$$

To complete this part, we state the following lemma.

Lemma 4.4. *Assume that (H1)–(H4) hold. Then, the solution of wave system (2.2) obtained in theorem* 4.3 *satisfies*

$$0 \ll \liminf_{z\to+\infty}\phi_1(z) \le \limsup_{z\to+\infty}\phi_1(z) \ll \rho_1 \quad \text{and} \quad 0 \ll \liminf_{z\to+\infty}\phi_2(z) \le \limsup_{z\to+\infty}\phi_2(z) \ll \rho_2.$$

Proof. The solution (ϕ_1, ϕ_2) is a special classical bounded solution of the following initial value problem

$$\left.\begin{aligned}&\frac{\partial\tilde{u}}{\partial t}(x,t) = \delta_1\Delta\tilde{u}(x,t) - \mu_1\tilde{u}(x,t) + \frac{\rho(\frac{a}{\mu_1} - \tilde{u}(x,t))\mathrm{v}(x,t)}{\frac{a}{\mu_1} - \tilde{u}(x,t) + \mathrm{v}(x,t)} + a - h(\mathrm{v}(x,t-T))\\ \text{and}\quad &\frac{\partial\mathrm{v}}{\partial t}(x,t) = \delta_2\Delta\mathrm{v}(x,t) - \mu_2\mathrm{v}(x,t) + \frac{\rho(\frac{a}{\mu_1} - \tilde{u}(x,t))\mathrm{v}(x,t)}{\frac{a}{\mu_1} - \tilde{u}(x,t) + \mathrm{v}(x,t)}\end{aligned}\right\} \tag{4.24}$$

and

$$\tilde{u}(x,\theta) = \phi_1(x\cdot e_1 + c\theta) \quad \text{and} \quad \tilde{v}(x,\theta) = \phi_2(x\cdot e_1 + c\theta), \tag{4.25}$$

for $x \in \mathbb{R}^n$ and $\theta \in [-T, 0]$. From the first equation, we have

$$\frac{\partial\tilde{u}}{\partial t}(x,t) < \delta_1\Delta\tilde{u}(x,t) - \mu_1\tilde{u}(x,t) + \rho(\rho_1 - \tilde{u}(x,t)) + a - h(\mathrm{v}(x,t-T)).$$

At the same time, for any $\varepsilon > 0$, there exists t_ε large enough such that

$$\frac{\partial\tilde{u}}{\partial t}(x,t) \le \delta_1\Delta\tilde{u}(x,t) - \mu_1\tilde{u}(x,t) + \rho(\rho_1 - \tilde{u}(x,t)) + a - h(\rho_2 + \varepsilon), \quad t \ge t_\varepsilon.$$

Using (H4) and for a sufficiently small ε, we obtain

$$\frac{\partial\tilde{u}}{\partial t}(x,t) \le \delta_1\Delta\tilde{u}(x,t) - \mu_1\tilde{u}(x,t) + \rho(\rho_1 - \tilde{u}(x,t)) + \mu_1 k_1 - \rho\rho_1\rho_2, \quad t \ge t_\varepsilon.$$

The asymptotic behaviour of the partial differential system (4.24)–(4.25) satisfies

$$\limsup_{t\to+\infty}\tilde{u}(x,t) < l^\infty := \frac{\rho\rho_1 + \mu_1 k_1 - \rho\rho_1\rho_2}{\rho + \mu_1} < \rho_1.$$

Here, we used the fact that

$$k_1 = \frac{a}{\mu_1} - \frac{\mu_2 k_2}{\rho - \mu_2}.$$

The boundedness and smoothness of $\phi_2(x \cdot e_1 + ct)$ implies that it is an upper solution for a large time of the following equation with a non-degenerate monostable nonlinearity (see, e.g. [12]),

$$\frac{\partial \mathrm{v}}{\partial t}(x,t) = \delta_2 \Delta \mathrm{v}(x,t) - \mu_2 \mathrm{v}(x,t) + \frac{\rho(\frac{a}{\mu_1} - l^\infty)\mathrm{v}(x,t)}{\frac{a}{\mu_1} - l^\infty + \mathrm{v}(x,t)}.$$

For the same threshold velocity $c^* = 2\sqrt{\delta_2 \xi_2}$, the above equation admits a non-trivial travelling wave connecting zero to the positive equilibrium (monostable equation). Then, the asymptotic behaviour of the partial differential system (4.24)–(4.25) satisfies

$$\liminf_{t\to+\infty} \mathrm{v}(x,t) > \tilde{l}_\infty > 0, \quad \text{with } \tilde{l}_\infty < \rho_2.$$

Using the last point, we can show easily that

$$\liminf_{t\to+\infty} \widetilde{u}(x,t) > l_\infty > 0.$$

Again, for a large time, $\phi_2(x \cdot e_1 + ct)$ is a lower solution of

$$\frac{\partial \mathrm{v}}{\partial t}(x,t) = \delta_2 \Delta \mathrm{v}(x,t) - \mu_2 \mathrm{v}(x,t) + \frac{\rho(\frac{a}{\mu_1} - l_\infty)\mathrm{v}(x,t)}{\frac{a}{\mu_1} - l_\infty + \mathrm{v}(x,t)}.$$

For $c > c^* = 2\sqrt{\delta_2 \xi_2}$, the above equation admits a non-trivial travelling wave connecting zero to the positive equilibrium. Then, the solution of system (4.24)–(4.25) satisfies

$$\limsup_{t\to+\infty} \mathrm{v}(x,t) < \tilde{l}^\infty < \rho_2.$$

This completes the proof. ∎

We can now state the following conclusion which is based on the result in theorem 3.2 of [74].

Theorem 4.5. *Let $c > c^*$ defined in equation (4.17). Assume that (H1)–(H4) hold. Then, wave system (2.2) admits a solution satisfying:*

$$\lim_{z\to-\infty} (\phi_1(z), \phi_2(z)) = (0,0) \quad \text{and} \quad \lim_{z\to+\infty} (\phi_1(z), \phi_2(z)) =; (k_1, k_2).$$

We finish this part by carrying out a numerical simulation to observe the existence of a wave connecting the two equilibria: from the trivial steady state to the positive steady state. We consider the following parameter values:

$$a = 0.005, \quad v_c = 1, \; m = 2, \quad \mu_1 = 0.1, \quad \mu_2 = 0.109, \quad \rho = 0.209, \quad \tau = 15, \quad \delta_1 = 0.51, \quad \delta_2 = 0.49.$$

Considering these values, we obtain $(\overline{u_2}, \overline{\mathrm{v}_2}) = (0.025, 0.0229)$ and we have

$$\xi_1 = 0.0917 > 0 \quad \text{and} \quad \delta_2\xi_2 - \delta_1\xi_1 = 0.002 > 0.$$

Moreover, we have

$$-\mu_1 k_1 - h(\rho_2) + \rho\rho_1\rho_2 + a = -0.0020 < 0.$$

We notice that our choice suggests that $S_1(s) > 0$ for $s \in (0,1)$, see figure 3, which illustrates the desired behaviour, for a sufficiently large time, that the solution of system (4.1)–(4.2) takes the form of a travelling wave propagating from right to left. The system also generates non-monotone wave-type solutions, and both the delay and the diffusion coefficients clearly affect the wave amplitude (see figure 5). In this figure, we vary only the delay since variations in the diffusion coefficients induce qualitatively similar effects on the wave amplitude (figure 4).

Throughout the present study, we have investigated the existence of travelling wave solutions for delayed reaction–diffusion systems under the SMQM condition. In the first part, we have elaborated on the development of the appropriate general framework. In particular, we have introduced the notion of SMQM which in turn required a new definition for the upper and lower solutions that are in adequacy with SMQM. In the second part, we have applied the existence result to a general model that aims to describe several biological phenomena such as the

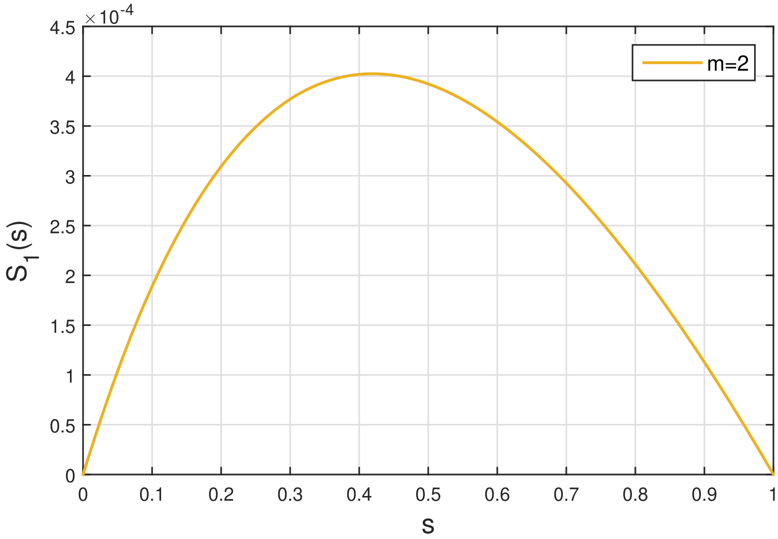

Figure 3. The curve of the function S_1 is drawn for $s \in [0, 1]$. We see that $S_1(s) > 0$, for $s \in (0, 1)$.

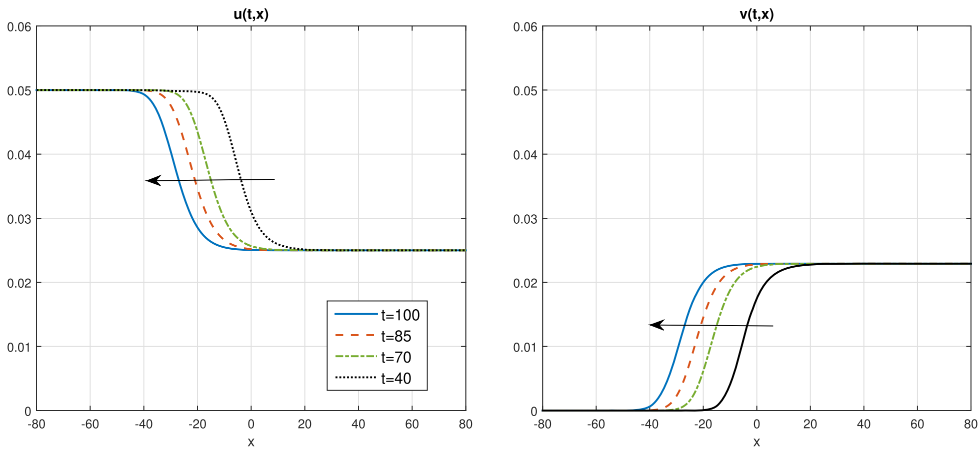

Figure 4. For the parameter values considered, we observe the emergence of a monotonic wave in both components u and v. As expected, the equilibrium $(\overline{u_2}, \overline{v_2})$ invades equilibrium $(\overline{u_1}, 0)$.

spatiotemporal dynamics of the UPR by looking at the dynamics of prion proteins. Accordingly, we have shown that under certain hypotheses on the model explicitly stated, travelling wave solutions can exist.

With regard to future perspectives, we note the following. First, future studies could aim at reproducing the present work when the reaction term satisfies the exponential SMQM condition which can be assimilated as the equivalent for SMQM as EQM is for QM. On another note, future research should consider extending the present study for non-local reaction–diffusion systems when the reaction term satisfies SMQM. In this case, we could, for example, replace the production term in the biological model with a new term derived from an age-structured model equation. The latter could have the advantage of considering the diffusion of the v-species since they are not likely to be at the same point in space at two different times. Finally, one avenue for future work could be the investigation of the different hypotheses established for the biological

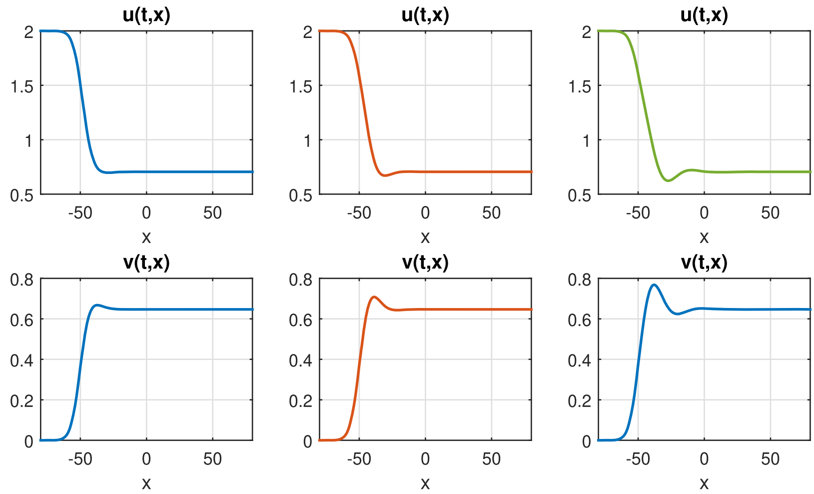

Figure 5. Non-monotone wave patterns also arise in the system, with the delay playing a key role in shaping the amplitude of the wave. The values of the delay τ are 0.5, 10 and 20 from left to the right, with $a = 0.2$.

model in order to know if less restrictive conditions can be applied, notably on both the minimal wave speed and the production term.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. M.A.: conceptualization, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; M.C.: conceptualization, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; A.C.: conceptualization, formal analysis, investigation, methodology, writing—original draft, writing—review and editing; L.P.-M.: conceptualization, formal analysis, investigation, methodology, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. No funding has been received for this article.

References

1. Winfree A. 2000 *The geometry of biological time*, 2nd edn. Berlin-Heidelberg-New York: Springer-Verlag.
2. Murray J. 2002 *Mathematical biology: I. An introduction. Interdisciplinary applied mathematics*. Mathematical Biology, 17. Springer.
3. Kolmogorov A, Petrovskii I, Piskunov N. 1937 Study of a diffusion equation that is related to the growth of a quality of matter, and its application to a biological problem. *Byul. Mosk. Gos. Univ. Ser. A. Mat. Mekh.* **1**, 1–26.
4. Fisher R. 1937 The wave of advance of advantageous genes. *Ann. Eugen.* **7**, 355–369. (doi:10.1111/ahg.1937.7.issue-4)
5. Cohen H. 1971 Non-linear diffusion problems. *Math. Assoc. Am.* **7**, 27–64.
6. Troy W. 1980 The existence of traveling wave front solutions of a model of the Belousov-Zhabotinskii reaction. *J. Differ. Equ.* **36**, 89–98. (doi:10.1016/0022-0396(80)90078-9)
7. Gardner R. 1982 Existence and stability of traveling wave solutions of competition models: a degree theoretic approach. *J. Differ. Equ.* **44**, 343–364. (doi:10.1016/0022-0396(82)90001-8)
8. Gardner R. 1984 Existence of travelling wave solutions of predator-prey systems via the connection index. *Siam. J. Appl. Math.* **44**, 56–79. (doi:10.1137/0144006)
9. Ye Q, Wang M. 1987 Traveling wave front solutions of Noyes-Field System for Belousov-Zhabotinskii reaction. *Nonlin. Anal. TMA* **11**, 1289–1302. (doi:10.1016/0362-546X(87)90046-0)

10. Kanel Y. 1990 Existence of a traveling-wave solution of the Belousov-Zhabotinskii system. *Diiferetsial'nye Uravneniya* **26**, 652–660.
11. Kapel A. 1991 Existence of traveling-wave type solutions for the Belousov-Zhabotinskii system equations. *Sibirskii, Math. Zh.* **32**, 47–59.
12. Volpert A, Volpert V, Volpert V. 1994 *Traveling wave solutions of parabolic systems*, vol. 140. Providence, RI: American Mathematical Society.
13. Baker C, Paul C, Wille D. 1995 A bibliography on the numerical solution of delay differential equations. Numerical Analysis Report. University of Manchester.
14. Schaaf K. 1987 Asymptotic behavior and traveling wave solutions for parabolic functional differential equations. *Trans. Am. Math. Soc.* **302**, 587–615.
15. Atkinson C, Reuter G. 1976 Deterministic epidemic waves. In *Mathematical Proceedings of the Cambridge Philosophical Society*, vol. 80, pp. 315–330. Cambridge University Press.
16. Wu J. 1996 *Theory and applications of partial functional differential equations*, 1st edn. New York: Springer.
17. Hodgkin A, Huxlev A. 1952 A quantitative description of membrane current and its application to conduction and excitation in nerve. *J. Physiol.* **117**, 500–544. (doi:10.1113/jphysiol.1952.sp004764)
18. Nagumo J, Arimoto S, Yoshizawa S. 1962 An active pulse transmission line simulating nerve axon. *Proc. lnst. Radio Eng.* **50**, 2061–2071.
19. Aronson DG, Weinberger HF. 1975 Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. In *Partial Differential Equations and Related Topics*, pp. 5–49. Berlin, Heidelberg: Springer Berlin Heidelberg.
20. Zou X, Wu J. 1997 Existence of traveling wave fronts in delayed reaction–diffusion systems via the monotone iteration method. *Proc. Am. Math. Soc.* **125**, 2589–2598. (doi:10.1090/proc/1997-125-09)
21. Leung A. 1989 *Systems of Nonlinear Partial Differential Equations with Applications to Biology and Engineering*, 1989th edn. New York: Springer.
22. Pao C. 1992 *Nonlinear parabolic and elliptic equations*, 1st edn. New York: Springer.
23. Wu J, Zou X. 2001 Traveling wave fronts of reaction-diffusion systems with delay. *J. Dyn. Differ. Equ.* **13**, 651–687. (doi:10.1023/A:1016690424892)
24. Ma S. 2001 Traveling wavefronts for delayed reaction–diffusion systems via a fixed point theorem. *J. Differ. Equ.* **171**, 294–314. (doi:10.1006/jdeq.2000.3846)
25. Huang J, Zou X. 2003 Existence of traveling wavefronts of delayed reaction–diffusion systems without monotonicity. *Discrete Cont. Dyn. Syst.* **9**, 925–936. (doi:10.3934/dcds.2003.9.925)
26. Li W, Lin G, Ruan S. 2006 Existence of travelling wave solutions in delayed reaction–diffusion systems with applications to diffusion–competition systems. *Nonlinearity* **19**, 1253–1273. (doi:10.1088/0951-7715/19/6/003)
27. Huang J, Zou X. 2006 Travelling wave solutions in delayed reaction diffusion systems with partial monotonicity. *Acta Math. Appl. Sin.* **22**, 243–256. (doi:10.1007/s10255-006-0300-0)
28. Lin G, Li W, Ma M. 2010 Traveling wave solutions in delayed reaction diffusion systems with applications to multi-species models. *Discrete Contin. Dyn. Syst. Ser. B* **13**, 393–414.
29. Lin Y, Wang Q, Zhou K. 2013 Traveling wave solutions in n-dimensional delayed reaction-diffusion systems with mixed monotonicity. *J. Comput. Appl. Math.* **243**, 16–27. (doi:10.1016/j.cam.2012.11.007)
30. Wang Q, Zhou K. 2010 Traveling wave solutions in delayed reaction–diffusion systems with mixed monotonicity. *J. Comput. Appl. Math.* **233**, 2549–2562. (doi:10.1016/j.cam.2009.11.002)
31. Ruan S, Zhao X. 1999 Persistence and extinction in two species reaction–diffusion systems with delays. *J. Differ. Equ.* **156**, 71–92. (doi:10.1006/jdeq.1998.3599)
32. Huang J, Zou X. 2002 Traveling wavefronts in diffusive and cooperative Lotka–Volterra system with delays. *J. Math. Anal. Appl.* **271**, 455–466. (doi:10.1016/S0022-247X(02)00135-X)
33. Zhao X. 2003 *Dynamical systems in population biology*, vol. 16. New York: Springer.
34. Zhou X, Xiao D. 2006 The asymptotic speed of spread and traveling waves for a vector disease model. *J. Dyn. Differ. Equ.* **18**, 1001–1019. (doi:10.1007/s10884-006-9044-z)
35. Wang Q, Zhao X. 2006 Spreading speed and traveling waves for the diffusive logistic equation with a sedentary compartment. *Dyn. Contin. Discrete Impuls. Syst. A: Math. Anal.* **13**, 231.
36. Zhang K, Zhao X. 2007 Asymptotic behaviour of a reaction–diffusion model with a quiescent stage. *Proc. R. Soc. A* **463**, 1029–1043. (doi:10.1098/rspa.2006.1806)
37. Liang X, Zhao X. 2007a Asymptotic speeds of spread and traveling waves for monotone semiflows with applications. *Commun. Pure Appl. Math.* **60**, 1–40. (doi:10.1002/cpa.v60:1)

38. Liang X, Zhao X. 2007b Erratum: Asymptotic speeds of spread and traveling waves for monotone semiflows with applications. *Commun. Pure Appl. Math.* **61**, 137–138. (doi:10.1002/cpa.v61:1)
39. Webb GF. 2008 *Population models structured by age, size, and spatial position*, pp. 1–49. Berlin Heidelberg: Springer.
40. Kwong M, Ou C. 2010 Existence and nonexistence of monotone traveling waves for the delayed Fisher equation. *J. Differ. Equ.* **249**, 728–745. (doi:10.1016/j.jde.2010.04.017)
41. Zhang P, Li W. 2010 Monotonicity and uniqueness of traveling waves for a reaction–diffusion model with a quiescent stage. *Nonlinear. Anal. Theory Methods Appl.* **72**, 2178–2189. (doi:10.1016/j.na.2009.10.016)
42. Wu S, Zhao H. 2011 Traveling fronts for a delayed reaction–diffusion system with a quiescent stage. *Commun. Nonlinear. Sci. Numer. Simul.* **16**, 3610–3621. (doi:10.1016/j.cnsns.2011.01.012)
43. Zhou K, Wang Q. 2014 Existence of traveling waves for a delayed SIRS epidemic diffusion model with saturation incidence rate. *Abstr. Appl. Anal.* **214**, 369072.
44. Lin Y, Wang Q. 2015 Spreading speed and traveling wave solutions in impulvise reaction-diffusion models. *Commun. Nonlinear. Sci. Numer. Simulat.* **23**, 185–191. (doi:10.1016/j.cnsns.2014.11.006)
45. Polyanin A. 2019 Generalized traveling-wave solutions of nonlinear reaction–diffusion equations with delay and variable coefficients. *Appl. Math. Lett.* **90**, 49–53. (doi:10.1016/j.aml.2018.10.012)
46. Wang K, Zhao H, Wang H, Zhang R. 2023 Traveling wave of a reaction–diffusion vector-borne disease model with nonlocal effects and distributed delay. *J. Dyn. Differ. Equ.* **35**, 3149–3185. (doi:10.1007/s10884-021-10062-w)
47. Gourley S. 2000 Travelling front solutions of a nonlocal Fisher equation. *J. Math. Biol.* **41**, 272–284. (doi:10.1007/s002850000047)
48. So J, Wu J, Zou X. 2001 A reaction–diffusion model for a single species with age structure. I Travelling wavefronts on unbounded domains. *Proc. R. Soc. A* **457**, 1841–1853. (doi:10.1098/rspa.2001.0789)
49. So J, Zou X. 2001 Traveling waves for the diffusive Nicholson's blowfies equation. *Appl. Math. Comput.* **122**, 385–392. (doi:10.1016/S0096-3003(00)00055-2)
50. Gourley S. 2001 Wave front solutions of a diffusive delay model for populations of Daphnia magna. *Comput. Math. Appl.* **42**, 1421–1430. (doi:10.1016/S0898-1221(01)00251-6)
51. Ashwin P, Bartuccelli M, Bridges T, Gourly S. 2002 Travelling fronts for the KPP equation with spatio-temporal delay. *Z. Angew. Math. Phys.* **53**, 103–122. (doi:10.1007/s00033-002-8145-8)
52. Al-Omari J, Gourly S. 2002 Monotone traveling fronts in age-structured reaction–diffusion model of a single species. *J. Math. Biol.* **45**, 294–312. (doi:10.1007/s002850200159)
53. Billingham J. 2004 Dynamics of a strongly nonlocal reaction–diffusion population model. *Nonlinearity* **17**, 313–346. (doi:10.1088/0951-7715/17/1/018)
54. Wang Z, Li W, Ruan S. 2006 Traveling wave fronts in reaction–diffusion systems with spatio-temporal delays. *J. Differ. Equ.* **222**, 185–232. (doi:10.1016/j.jde.2005.08.010)
55. Lan K, Wu J. 2003 Traveling wavefronts of reaction–diffusion equations with and without delays. *Nonlinear Anal. RWA* **4**, 173–188. (doi:10.1016/S1468-1218(02)00020-2)
56. Li W, Ruan S, Wang Z. 2007 On the diffusive Nicholson's blowflies equation with nonlocal delay. *J. Nonlinear. Sci.* **17**, 505–525. (doi:10.1007/s00332-007-9003-9)
57. Fenichel N. 1979 Geometric singular perturbation theory for ordinary differential equations. *J. Differ. Equ.* **31**, 53–98. (doi:10.1016/0022-0396(79)90152-9)
58. Zhou K, Wang Q. 2010 Traveling wave solutions in delayed nonlocal diffusion systems with mixed monotonicity. *J. Math. Anal. Appl.* **372**, 598–610. (doi:10.1016/j.jmaa.2010.07.032)
59. Wang Z, Wu J. 2010 Traveling waves of a diffusive Kermack-McKendrick epidemic model with non-local delayed transmission. *Proc. R. Soc. A* **466**, 237–261. (doi:10.1098/rspa.2009.0377)
60. Zhou K, Lin Y, Wang Q. 2013 Existence and asymptotics of traveling wave fronts for a delayed nonlocal diffusion model with a quiescent stage. *Commun. Nonlinear. Sci. Numer. Simulat.* **18**, 3006–3013. (doi:10.1016/j.cnsns.2013.04.025)
61. Adimy M, Chekroun A, Kazmierczak B. 2022a Traveling waves for reaction-diffusion PDE coupled to difference equation with nonlocal dispersal term and time delay. *Math. Model. Nat. Phenom* **17**, 17–31. (doi:10.1051/mmnp/2022021)
62. Adimy M, Chekroun A, Kuniya T. 2022b Traveling waves of a differential-difference diffusive Kermack-McKendrick epidemic model with age-structured protection phase. *J. Math. Anal. Appl.* **505**, 125464. (doi:10.1016/j.jmaa.2021.125464)

63. Boumenir A, Nguyen V. 2008 Perron theorem in the monotone iteration method for traveling waves in delayed reaction–diffusion equations. *J. Differ. Equ.* **244**, 1551–1570. (doi:10.1016/j.jde.2008.01.004)
64. Prusiner SB, Scott MR, DeArmond SJ, Cohen FE. 1998 Prion protein biology. *Cell* **93**, 337–348. (doi:10.1016/S0092-8674(00)81163-0)
65. Roucou X, LeBlanc AC. 2005 Cellular prion protein neuroprotective function: implications in prion diseases. *J. Mol. Med.* **83**, 3–11. (doi:10.1007/s00109-004-0605-5)
66. Prusiner SB. 1998 Prions. *Proc. Natl Acad. Sci. USA* **95**, 13 363–13 383. (doi:10.1073/pnas.95.23.13363)
67. Genereux JC, Wiseman RL. 2015 Regulating extracellular proteostasis capacity through the unfolded protein response. *Prion* **9**, 10–21. (doi:10.1080/19336896.2015.1011887)
68. Hetz C, Mollereau B. 2014 Disturbance of endoplasmic reticulum proteostasis in neurodegenerative diseases. *Nat. Rev. Neurosci.* **15**, 233–249. (doi:10.1038/nrn3689)
69. Hetz C, Saxena S. 2017 ER stress and the unfolded protein response in neurodegeneration. *Nature Rev. Neurol.* **13**, 477–491. (doi:10.1038/nrneurol.2017.99)
70. Hetz C, Zhang K, Kaufman RJ. 2020 Mechanisms, regulation and functions of the unfolded protein response. *Nat. Rev. Mol. Cell Biol.* **21**, 421–438. (doi:10.1038/s41580-020-0250-z)
71. Smith HL, Mallucci GR. 2016 The unfolded protein response: mechanisms and therapy of neurodegeneration. *Brain* **139**, 2113–2121. (doi:10.1093/brain/aww101)
72. Adimy M, Chekroun A, Pujo-Menjouet L, Sensi M. 2024 A multigroup approach to delayed prion production. *Discrete Contin. Dyn. Syst. Ser. B.* **29**, 2972–2998. (doi:10.3934/dcdsb.2023209)
73. Adimy M, Babin L, Pujo-Menjouet L. 2022 Neuron scale modeling of prion production with the unfolded protein response. *SIADS* **21**, 2487–2517. (doi:10.1137/21M1443157)
74. Lin G, Ruan S. 2014 Traveling wave solutions for delayed reaction–diffusion systems and applications to diffusive Lotka–Volterra competition models with distributed delays. *J. Dyn. Differ. Equ.* **26**, 583–605. (doi:10.1007/s10884-014-9355-4)
75. Smith H. 1995 *Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems*. Providence, RI: American Mathematical Society.