

LINEAR AND NONLINEAR STABILITY IN A DIFFUSIONAL ECOTOXICOLOGICAL MODEL WITH TIME DELAYS

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ABSTRACT. We propose a reaction-diffusion extension of a two species ecotoxicological model with time-delays proposed by Chattopadhyay *et al* (1997). Each species has the capacity to produce a substance toxic to its competitor, and a distributed time-delay is incorporated to model lags in the production of toxin. Additionally, nonlocal spatial effects are present because of the combination of delay and diffusion.

The stability of the various uniform equilibria of the model are studied by using linearised analysis, on an infinite spatial domain. It is shown that simple exponentially decaying delay kernels cannot destabilise the coexistence equilibrium state.

In the case of a finite spatial domain, with purely temporal delays, a nonlinear convergence result is proved using ideas of Lyapunov functionals together with invariant set theory. The result is also applicable to the purely temporal system studied by other investigators and, in fact, extends their results.

1. Introduction. In the ecological community there is considerable interest in ecotoxicological problems, as is evidenced by the many experimental studies which have been carried out on the effects of toxicants on ecosystems (see, for example, [5,12,13,14]). In contrast, there have been relatively few studies on the mathematical modelling of such problems, even though relatively simple one or two species models have proved to be both ecologically insightful and mathematically interesting and non-trivial (see, for example, [9,10,1,11]).

There have been a few papers in which investigators have modified the classic two-species Lotka-Volterra competition system to include extra terms which model the production of toxins. Maynard-Smith [10] proposed the model

$$\begin{aligned}dN_1/dt &= \varepsilon_1 N_1 [1 - N_1/K_1 - \beta_{12} N_2 - \gamma_1], \\dN_2/dt &= \varepsilon_2 N_2 [1 - N_2/K_2 - \beta_{21} N_1 - \gamma_2],\end{aligned}$$

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where the γ_i are the rates of production of toxic substances, and Chattopadhyay [3] proposed

$$\begin{aligned} dN_1/dt &= \varepsilon_1 N_1 [1 - N_1/K_1 - \beta_{12} N_2 - \gamma_1 N_1 N_2], \\ dN_2/dt &= \varepsilon_2 N_2 [1 - N_2/K_2 - \beta_{21} N_1 - \gamma_2 N_1 N_2], \end{aligned} \quad (1)$$

as a model for the case when each species produces a substance toxic to the other, but only when the other is present. Later, Chattopadhyay, Beretta and Solimano [4] incorporated time delays into the $\gamma_i N_1 N_2$ terms of (1) to allow the possibility that the production of a toxin may take some time. In fact, they studied systems of the form

$$\begin{aligned} dN_1/dt &= \varepsilon_1 N_1 \left[1 - N_1/K_1 - \beta_1 N_2 - \gamma_1 \int_0^\infty f(\tau) N_1(t-\tau) N_2(t-\tau) d\tau \right], \\ dN_2/dt &= \varepsilon_2 N_2 \left[1 - N_2/K_2 - \beta_2 N_1 - \gamma_2 \int_0^\infty f(\tau) N_1(t-\tau) N_2(t-\tau) d\tau \right], \end{aligned} \quad (2)$$

and the system to be studied in the present paper (system (3) below) is an extension of the above system.

Let us explain the ecological reasoning that led the above investigators to propose system (2). The toxin terms are those with the γ_i factors. It is assumed that the individuals of a particular species will initiate toxin production at a rate proportional to the number of members of the other species present at that same time. However, the toxin takes time to produce and become potent. The amount of the substance toxic to N_1 at time t is therefore proportional not only to the numbers of the competing species N_2 that were present at earlier times to produce it, but also to the numbers of the species N_1 that were around at these earlier times, since their numbers determined the rate at which each N_2 member produced toxin. This leads to the integral $\gamma_1 \int_0^\infty f(\tau) N_1(t-\tau) N_2(t-\tau) d\tau$ representing the amount present at time t of the substance toxic to N_1 , and the per-capita death rate of N_1 due to poisoning is taken as proportional to this.

It is possible to include time delays in other terms of the model also. Stage structured population models often include a delay in the births (or, more precisely, adult recruitment) terms, and one can argue that in certain circumstances the intra- or inter-specific competition terms should involve time-delays. However, because of the algebraic and technical difficulties involved with the inclusion of further delays, we shall restrict attention to having delays in the toxic terms only.

It should be stressed that there are alternatives to the classic Lotka Volterra approach to modelling ecological competition. One problem with the Lotka-Volterra models is that it is difficult to measure the parameters without actually growing the species together in competition. Another approach involves the use of resource-based models, in which the dynamics of the resources are explicitly considered as well the species. These models tend to be harder to analyse but have the important advantage that the parameters can be measured on species grown alone. See, for example, Li and Smith [8].

The present paper considers a reaction-diffusion extension of these previously studied models, to model movement of the individuals in the population. The diffusion will be taken to be Fickian, represented in the equations by Laplacian terms, which assumes the individuals in the population are moving at random. The time delays will appear in the equations by the use of spatio-temporal convolution terms allowing the various types of time-delays commonly seen in the literature on delay equations, and also nonlocal spatial effects which model the movement of individuals to their present positions from their possible positions at previous times [2].

There are situations where spatial averaging can be present in the equations for other ecological reasons unrelated to time delays. Equations in which the various terms are not all evaluated at the same point in space are called non-local equations. Quite often the nonlocal term, as in the present paper, involves some weighted integral of one or more of the state variables over the whole spatial domain. Such weighted averaging in space, to allow for individuals having been moving about in the duration of a time lag, arises very naturally in the modelling of any scenario where both time-lags and spatial diffusion are important.

We shall let $N_1(\mathbf{x}, t)$ and $N_2(\mathbf{x}, t)$ denote the population densities of two competing species at time $t \geq 0$ and position $\mathbf{x} \in \mathbf{R}^n$. The equations we shall study are:

$$\begin{aligned} \partial N_1 / \partial t &= \varepsilon_1 N_1 [1 - N_1 / K_1 - \beta_1 N_2 - \gamma_1 f_1 ** (N_1 N_2)] + d_1 \nabla^2 N_1, \\ \partial N_2 / \partial t &= \varepsilon_2 N_2 [1 - N_2 / K_2 - \beta_2 N_1 - \gamma_2 f_2 ** (N_1 N_2)] + d_2 \nabla^2 N_2, \end{aligned} \tag{3}$$

for $\mathbf{x} \in \mathbf{R}^n, t > 0$, with $f_i ** (N_1 N_2)$ defined to be the spatio-temporal convolution

$$[f_i ** (N_1 N_2)](\mathbf{x}, t) = \int_{\mathbf{R}^n} \int_{-\infty}^t f_i(\mathbf{x} - \mathbf{y}, t - \tau) N_1(\mathbf{y}, \tau) N_2(\mathbf{y}, \tau) d\tau d\mathbf{y}. \tag{4}$$

For $i, j = 1, 2 (i \neq j)$, the various parameters have the following ecological interpretations:

- K_i : carrying capacity of species i ;
- ε_i : intrinsic growth rate of species i ;
- β_i : competition feedback of species j on species i ;
- γ_i : toxic response of species j against species i ;
- d_i : diffusivity of species i ;

all of which are strictly positive, and

- $f_i(\mathbf{x}, t)$: temporal delay in and/or spatial averaging of the production of toxin by species j against species i .

The $f_i(\mathbf{x}, t)$ are non-negative functions of \mathbf{x} and t in $L^1(\mathbf{R}^n \times [0, \infty))$ satisfying

$$f_i ** (1) = \int_{\mathbf{R}^n} \int_0^\infty f_i(\mathbf{y}, \tau) d\tau d\mathbf{y} = 1. \tag{5}$$

In other words, we are assuming that the delay kernels $f_i(\mathbf{x}, t)$ are normalised such that the spatially uniform equilibria of the model remain unchanged by the incorporation of the time lags and spatial averaging.

The initial conditions for this problem will have the form

$$(N_1(\mathbf{x}, \tau), N_2(\mathbf{x}, \tau)) = (\psi_1(\mathbf{x}, \tau), \psi_2(\mathbf{x}, \tau)), \quad -\infty < \tau \leq 0, \quad \mathbf{x} \in \mathbf{R}^n, \tag{6}$$

where the $\psi_i (i = 1, 2)$ are prescribed non-negative functions.

The paper consists of five parts. In the next section we restate the existence results for the spatially uniform equilibria from [4]. We shall then establish sharp linear asymptotic stability criteria for each of these equilibria. These results hold for general $f_i(\mathbf{x}, t)$, except those concerning the interior equilibrium (the equilibrium (N_1^*, N_2^*) mentioned in Propositions 2.1, 2.3 and 2.4 below). For the latter equilibrium, it is in practice necessary to specify the kernels f_i in order to be able to carry out the analysis and obtain useful results, and for this purpose we shall concentrate on one spatial dimension ($n = 1$) and take

$$f_i(x, t) = f(x, t) = \frac{\theta \alpha}{2} e^{-\alpha|x| - \theta t}, \quad \alpha, \theta > 0, \quad i = 1, 2, \tag{7}$$

although the methods we shall use do not depend heavily on the kernel having this specific functional form and will apply to many other kernels as well. With this choice of the kernel the delay and spatial averaging increase with decreasing θ and α respectively and in this sense we can regard $1/\theta$ as a measure of the delay, and $1/\alpha$ as a measure of the spatial averaging.

In section 4 we shall establish a nonlinear convergence result for the interior equilibrium of (3) in the case when the general spatio-temporal convolution terms degenerate to purely temporal convolutions without any spatial averaging present. In section 4 (only), the model will be considered on the *finite* spatial domain $\Omega \subset \mathbf{R}^n$, with homogeneous Neumann boundary conditions

$$(\mathbf{n} \cdot \nabla) \begin{pmatrix} N_1 \\ N_2 \end{pmatrix} = 0, \quad \mathbf{x} \in \partial\Omega \quad (8)$$

where \mathbf{n} is an outward pointing normal to the boundary. A purely temporal convolution arises as a particular case of the general spatio-temporal convolution when a kernel f_i assumes the form $f_i(\mathbf{x}, t) = \delta(\mathbf{x})f(t)$ where δ denotes Dirac's delta function, so that

$$[f_i ** (N_1 N_2)](\mathbf{x}, t) = \int_{-\infty}^t f(t - \tau) N_1(\mathbf{x}, \tau) N_2(\mathbf{x}, \tau) d\tau, \quad i = 1, 2.$$

Note that it is only for purely temporal convolutions that our model formulation makes sense on a finite spatial domain. Kernels of the form (7), for example, are not appropriate for finite domains as is fairly easily seen. Also, such a kernel would fail to satisfy the normalisation condition (5) if the space integral were taken over a finite domain instead of \mathbf{R}^n . However, the normalisation condition can certainly be satisfied by a kernel of the form $f_i(\mathbf{x}, t) = \delta(\mathbf{x})f(t)$ provided it is assumed that

$$\int_0^\infty f(t) dt = 1.$$

In section 5 we present the results of some numerical simulations which confirm the analytical results. In section 6 we discuss what conclusions may be drawn.

2. Spatially uniform equilibria. In this and the next section we study the model equations (3) on the whole of \mathbf{R}^n . Since the kernels f_i are normalised the spatially uniform equilibria remain unchanged by their presence. Therefore, seeking such solutions amounts to finding non-negative solutions (N_1, N_2) of

$$\varepsilon_1 N_1 [1 - N_1/K_1 - \beta_1 N_2 - \gamma_1 N_1 N_2] = 0,$$

$$\varepsilon_2 N_2 [1 - N_2/K_2 - \beta_2 N_1 - \gamma_2 N_1 N_2] = 0,$$

and, from [4], we have:

PROPOSITION 2.1. *The system (3) has the following possible uniform equilibria:*

$$E^0 = (0, 0), \quad E^1 = (K_1, 0), \quad E^2 = (0, K_2), \quad E^* = (N_1^*, N_2^*), \quad (N_1^*, N_2^* \neq 0).$$

PROPOSITION 2.2. *The trivial equilibrium E^0 and the boundary equilibria E^1, E^2 always exist.*

PROPOSITION 2.3. *A positive equilibrium E^* exists iff there exist $N_1^* > 0, N_2^* > 0$ such that*

$$N_1^* = \frac{K_2 - N_2^*}{K_2(\beta_2 + \gamma_2 N_2^*)}, \quad N_2^* = \frac{K_1 - N_1^*}{K_1(\beta_1 + \gamma_1 N_1^*)}. \quad (9)$$

In general we may have none, one or two distinct positive equilibria. Note that the components of any positive equilibrium must satisfy $N_1^* < K_1$ and $N_2^* < K_2$.

PROPOSITION 2.4. *Sufficient (but not necessary) conditions for the existence of a unique positive equilibrium E^* are (i) $K_1\beta_2 < 1$ and $K_2\beta_1 < 1$, or (ii) $K_1\beta_2 > 1$ and $K_2\beta_1 > 1$.*

3. **Linear stability.** Let us first remark that, in the complete absence of time-delays and spatial averaging, which arises when we set $f_i(\mathbf{x}, t) = \delta(\mathbf{x})\delta(t)$, $i = 1, 2$, giving $f_i * * (N_1 N_2) = N_1 N_2$, instability of a uniform state cannot arise via the well known Turing mechanism of diffusion driven instability. This is because our model is a competition model, and not a predator-prey or “activator-inhibitor” type model which would be a necessary prerequisite for diffusion-driven instability to occur. This section will show that time delays and nonlocal averaging of the purely exponentially decaying kind are not sufficient to destabilise a positive (interior) equilibrium E^* , so that no spatial or spatio-temporal patterning is to be expected. More precisely, we shall show that, if the delay kernels are given by (7), then as long as the two boundary equilibria E^1 and E^2 are unstable (which implies the existence of an interior equilibrium E^* as shown below) then the interior equilibrium must remain linearly stable, independently of the delay/spatial averaging parameters θ and α in (7). For the trivial equilibrium $(0, 0)$ and boundary equilibria E^1, E^2 , the stability analysis is very similar to the spatially independent case studied in [4] since the linearised equations about these equilibria do not involve convolution terms.

We let $(N_1, N_2) = E + (n_1, n_2)$, where E is any of the equilibria mentioned in Proposition 2.1, and look for solutions of the linearised equations of the form

$$(n_1, n_2) = (c_1, c_2) \exp(\lambda t + i\mathbf{k} \cdot \mathbf{x}) \tag{10}$$

where \mathbf{k} denotes the wave vector of the perturbation. Furthermore, we denote $k = |\mathbf{k}|$. If $\text{Re } \lambda < 0$ for all $k^2 \geq 0$ then the equilibrium is linearly stable, and if $\text{Re } \lambda > 0$ for some k^2 then it is unstable. Since this section of the paper assumes the spatial domain is all of \mathbf{R}^n , we have to consider all $k^2 \geq 0$.

PROPOSITION 3.1. *The trivial equilibrium $E^0 = (0, 0)$ is unstable.*

Indeed, the linearised equations about the trivial equilibrium E^0 have solutions of the form (10) when λ satisfies a characteristic equation having roots

$$\lambda_i(k^2) = \varepsilon_i - d_i k^2, \quad i = 1, 2, \tag{11}$$

both of which are strictly positive for sufficiently small $k^2 \geq 0$.

PROPOSITION 3.2. *The boundary equilibrium $E^1 = (K_1, 0)$ is*

- (i) *linearly asymptotically stable iff $K_1\beta_2 > 1$;*
- (ii) *unstable to general perturbations if $K_1\beta_2 < 1$.*

Indeed, linearising (3) about $(N_1, N_2) = (K_1, 0)$, we obtain this time a characteristic equation for λ having roots

$$\lambda_1(k^2) = -\varepsilon_1 - d_1 k^2, \quad \lambda_2(k^2) = -\varepsilon_2 (K_1\beta_2 - 1) - d_2 k^2. \tag{12}$$

The statements (i) and (ii) of the proposition follow immediately.

In a similar way, we have:

PROPOSITION 3.3. *The boundary equilibrium $E^2 = (0, K_2)$ is*

- (i) *linearly asymptotically stable iff $K_2\beta_1 > 1$;*
- (ii) *unstable to general perturbations if $K_2\beta_1 < 1$.*

A consequence of Propositions 2.4, 3.2 and 3.3 is that

PROPOSITION 3.4. *If E^1 and E^2 are both linearly asymptotically stable, then there exists a unique positive equilibrium E^* ,*

and

PROPOSITION 3.5. *If E^1 and E^2 are both linearly unstable, then there exists a unique positive equilibrium E^* .*

Note that none of the above results, or those of section 2, depend on the choices made for the non-local delay kernels $f_1(\mathbf{x}, t)$ and $f_2(\mathbf{x}, t)$.

The linearised stability analysis about the positive (interior) equilibrium E^* is algebraically much more complicated. Therefore, for simplicity in the exposition we shall concentrate on one spatial dimension and consider the particular case when the kernels are given by (7).

PROPOSITION 3.6. *Let the spatial dimension $n = 1$ and assume the delay kernels f_i are both given by*

$$f_i(x, t) = f(x, t) = \frac{\theta\alpha}{2}e^{-\alpha|x|-\theta t}, \quad \alpha, \theta > 0, \quad i = 1, 2,$$

and assume that

$$K_1\beta_2 < 1 \quad \text{and} \quad K_2\beta_1 < 1 \tag{13}$$

(so that the boundary equilibria are both unstable). Then the positive equilibrium E^* is linearly asymptotically stable, independently of θ and α .

Proof

We set $N_i = N_i^* + n_i$, $i = 1, 2$, and linearise about E^* . The $n_i(x, t)$ satisfy

$$\begin{aligned} \frac{\partial}{\partial t} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} - \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix} \nabla^2 \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} &= \begin{pmatrix} -\varepsilon_1 N_1^*/K_1 & -\varepsilon_1 \beta_1 N_1^* \\ -\varepsilon_2 \beta_2 N_2^* & -\varepsilon_2 N_2^*/K_2 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} \\ &+ \begin{pmatrix} -\varepsilon_1 N_1^* N_2^* \gamma_1 & -\varepsilon_1 N_1^{*2} \gamma_1 \\ -\varepsilon_2 N_2^{*2} \gamma_2 & -\varepsilon_2 N_1^* N_2^* \gamma_2 \end{pmatrix} \begin{pmatrix} f^{**} n_1 \\ f^{**} n_2 \end{pmatrix} \end{aligned} \tag{14}$$

where $f(x, t)$ is given by (7). We seek solutions of the form $(n_1, n_2) = (c_1, c_2)e^{\lambda t + ikx}$ and note that, since f is of the form $f(x, t) = g(x)h(t)$, it follows that

$$f^{**} n_i = \hat{g}(k) \bar{h}(\lambda) n_i, \quad i = 1, 2,$$

where \hat{g} and \bar{h} denote the Fourier transform of g and the Laplace transform of h respectively. In fact,

$$g(x) = \frac{\alpha}{2}e^{-\alpha|x|} \quad \text{and} \quad h(t) = \theta e^{-\theta t},$$

so that

$$f^{**} n_i = \frac{\theta}{\theta + \lambda} \frac{\alpha^2}{\alpha^2 + k^2} n_i, \quad i = 1, 2.$$

Therefore, the characteristic equation of the linearisation about E^* is $\Delta(\lambda) = 0$ where

$$\Delta(\lambda) = \begin{vmatrix} \Delta_{11}(\lambda) & \Delta_{12}(\lambda) \\ \Delta_{21}(\lambda) & \Delta_{22}(\lambda) \end{vmatrix}$$

and

$$\begin{aligned} \Delta_{11}(\lambda) &= \lambda + d_1 k^2 + \frac{\varepsilon_1 N_1^*}{K_1} + \varepsilon_1 \gamma_1 N_1^* N_2^* \frac{\theta}{\theta + \lambda} \frac{\alpha^2}{\alpha^2 + k^2}, \\ \Delta_{12}(\lambda) &= \varepsilon_1 \beta_1 N_1^* + \varepsilon_1 \gamma_1 N_1^{*2} \frac{\theta}{\theta + \lambda} \frac{\alpha^2}{\alpha^2 + k^2}, \end{aligned}$$

$$\Delta_{21}(\lambda) = \varepsilon_2\beta_2N_2^* + \varepsilon_2\gamma_2N_2^{*2} \frac{\theta}{\theta + \lambda} \frac{\alpha^2}{\alpha^2 + k^2},$$

$$\Delta_{22}(\lambda) = \lambda + d_2k^2 + \frac{\varepsilon_2N_2^*}{K_2} + \varepsilon_2\gamma_2N_1^*N_2^* \frac{\theta}{\theta + \lambda} \frac{\alpha^2}{\alpha^2 + k^2}.$$

In the complete absence of delay/spatial averaging (a particular case obtained by formally setting $\theta = \alpha = \infty$) it is straightforward to see that the characteristic equation $\Delta(\lambda) = 0$ is a quadratic equation in λ in which the coefficients of λ^2 and of λ are trivially positive. The constant term is positive too, but less trivially so (the proof of this fact is similar to the analysis we are about to present for finite θ, α and is thus omitted). By the Routh-Hurwitz conditions (see, for example, Murray [11]) the equilibrium E^* is linearly stable in the absence of delay/spatial averaging.

To complete the proof we need to show that, under assumption (13), no stability switches can occur as any parameters are varied. This will be achieved by showing that neither zero, nor any pair of complex conjugate purely imaginary roots $\lambda = i\omega$, can satisfy $\Delta(\lambda) = 0$. We shall prove the former first, by showing that

$$\Delta(0) > 0. \tag{15}$$

Now, $\Delta(0)$ is clearly larger than the corresponding determinant without the d_1k^2, d_2k^2 terms, and thus

$$\Delta(0) \geq \varepsilon_1\varepsilon_2N_1^*N_2^* \left[\left(\frac{1}{K_1} + \gamma_1N_2^* \frac{\alpha^2}{\alpha^2 + k^2} \right) \left(\frac{1}{K_2} + \gamma_2N_1^* \frac{\alpha^2}{\alpha^2 + k^2} \right) - \left(\beta_1 + \gamma_1N_1^* \frac{\alpha^2}{\alpha^2 + k^2} \right) \left(\beta_2 + \gamma_2N_2^* \frac{\alpha^2}{\alpha^2 + k^2} \right) \right]$$

so that

$$\frac{\Delta(0)}{\varepsilon_1\varepsilon_2N_1^*N_2^*} \geq \underbrace{\frac{1}{K_1K_2} - \beta_1\beta_2}_{>0} + \frac{\alpha^2}{\alpha^2 + k^2} \left[N_1^* \left(\frac{\gamma_2}{K_1} - \gamma_1\beta_2 \right) + N_2^* \left(\frac{\gamma_1}{K_2} - \gamma_2\beta_1 \right) \right]. \tag{16}$$

The strict positivity of the underbraced term is a consequence of assumption (13). If the square bracketed term in (16) is positive then we have shown $\Delta(0) > 0$ as desired. So it remains to consider the possibility that this term is negative. If this is so then, as far as proving $\Delta(0) > 0$ is concerned, the worst case scenario is when $k^2 = 0$, and so we can say

$$\frac{\Delta(0)}{\varepsilon_1\varepsilon_2N_1^*N_2^*} \geq \frac{1}{K_1K_2} - \beta_1\beta_2 + N_1^* \left(\frac{\gamma_2}{K_1} - \gamma_1\beta_2 \right) + N_2^* \left(\frac{\gamma_1}{K_2} - \gamma_2\beta_1 \right). \tag{17}$$

Now, if we eliminate N_2^* in (9) we obtain a quadratic equation for N_1^* , from which it follows that

$$N_1^* \left(\frac{\gamma_2}{K_1} - \gamma_1\beta_2 \right) = \frac{\beta_1\beta_2K_1K_2 - 1}{K_1K_2} + \gamma_2 - \gamma_1 + \frac{1 - \beta_1K_2}{K_2N_1^*}.$$

In a similar way, we can show that

$$N_2^* \left(\frac{\gamma_1}{K_2} - \gamma_2\beta_1 \right) = \frac{\beta_1\beta_2K_1K_2 - 1}{K_1K_2} + \gamma_1 - \gamma_2 + \frac{1 - \beta_2K_1}{K_1N_2^*}.$$

Therefore,

$$\frac{\Delta(0)}{\varepsilon_1\varepsilon_2N_1^*N_2^*} \geq \frac{\beta_1\beta_2K_1K_2 - 1}{K_1K_2} + \frac{1 - \beta_1K_2}{K_2N_1^*} + \frac{1 - \beta_2K_1}{K_1N_2^*}. \tag{18}$$

But $N_1^* < K_1$ and $N_2^* < K_2$. Recalling also (13), we now have

$$\begin{aligned} \frac{\Delta(0)}{\varepsilon_1 \varepsilon_2 N_1^* N_2^*} &\geq \frac{\beta_1 \beta_2 K_1 K_2 - 1}{K_1 K_2} + \frac{1 - \beta_1 K_2}{K_2 K_1} + \frac{1 - \beta_2 K_1}{K_1 K_2} \\ &= \frac{(1 - \beta_1 K_2)(1 - \beta_2 K_1)}{K_1 K_2} \\ &> 0 \end{aligned}$$

so that $\Delta(0) > 0$.

Proving that $\Delta(\lambda) = 0$ has no purely imaginary roots under the assumption (13) is algebraically extremely complicated, and we shall not include the details here, but we will summarise how we carried out the calculation. First note that, if the determinant defining $\Delta(\lambda)$ is expanded out then the $(\theta + \lambda)^{-2}$ terms cancel out. If one then multiplies the expanded out determinant by $\theta + \lambda$, one sees that the characteristic equation $\Delta(\lambda) = 0$ can be rewritten as a cubic equation in λ , in which the coefficient of λ^3 is 1. Now, for a general cubic equation

$$\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0$$

the conditions to have a pair of purely imaginary roots $\lambda = \pm i\omega$ are

$$a_1 a_2 = a_3, \quad a_2 > 0.$$

Applied to our situation, $a_1 a_2 - a_3 = 0$ generates a quadratic equation in θ (with extremely long and complicated coefficients). The aim is to show that this quadratic has no real *positive* roots, and in this regard an obvious strategy is to show that all of its coefficients are positive. Those of θ^2 and θ are easily seen to be so, but the constant term is a (still very complicated) quartic expression in k^2 . Examining each of its coefficients in turn shows that they are all positive and, in doing so, one repeatedly makes use of assumption (13). The proof of the proposition is complete.

4. Nonlinear stability of E^* . In this section we consider the case where both species have the same *purely temporal* delay kernel, so that the f_i have the form

$$f_i(\mathbf{x}, t) = \delta(\mathbf{x})f(t), \quad i = 1, 2, \quad \text{with} \quad \int_0^\infty f(t) dt = 1. \quad (19)$$

Any $f(t)$ satisfying (19) is allowed; there is no restriction to the exponential case in this section.

The Dirac delta function has the effect of suppressing the spatial averaging so that the convolution terms in (3) become purely temporal convolutions

$$\int_{-\infty}^t f(t - \tau) N_1(\mathbf{x}, \tau) N_2(\mathbf{x}, \tau) d\tau.$$

Ideally the delay term should be a convolution in space as well as in time, to allow for motion of the species or chemical during the time lag period. However, the methods we use in this section appear to work only for purely temporal convolutions. In some situations (e.g. in the case of a non-diffusing toxin) the use of a purely temporal delay without spatial averaging should be a good approximation.

The following gives conditions under which all solutions in a specified region will converge to the positive equilibrium E^* . Existence of such an equilibrium is ensured by condition (21) below, together with Proposition 2.4. In this section

the problem is considered on a finite spatial domain $\Omega \subset \mathbf{R}^n$ with homogeneous Neumann boundary conditions

$$(\mathbf{n} \cdot \nabla) \begin{pmatrix} N_1 \\ N_2 \end{pmatrix} = 0, \quad \mathbf{x} \in \partial\Omega.$$

THEOREM 4.1. *Suppose that (19) holds. If*

$$0 < N_1^{*2} < \frac{4\beta_1}{3K_2\gamma_1\gamma_2} \left(1 - K_2\beta_1 \frac{\gamma_2}{\gamma_1} \right), \quad 0 < N_2^{*2} < \frac{4\beta_2}{3K_1\gamma_1\gamma_2} \left(1 - K_1\beta_2 \frac{\gamma_1}{\gamma_2} \right), \tag{20}$$

$$K_2\beta_1 \leq 1 - \gamma_1 K_1 K_2, \quad K_1\beta_2 \leq 1 - \gamma_2 K_1 K_2, \tag{21}$$

and also

$$\begin{aligned} \max \{ K_1 - N_1^*, N_1^* - K_1(1 - \beta_1 K_2 - \gamma_1 K_1 K_2) + \delta_1 \} &< \sqrt{2} \left[\frac{4\beta_1}{3K_2\gamma_1\gamma_2} \left(1 - K_2\beta_1 \frac{\gamma_2}{\gamma_1} \right) - N_1^{*2} \right]^{\frac{1}{2}} \\ \max \{ K_2 - N_2^*, N_2^* - K_2(1 - \beta_2 K_1 - \gamma_2 K_1 K_2) + \delta_2 \} &< \sqrt{2} \left[\frac{4\beta_2}{3K_1\gamma_1\gamma_2} \left(1 - K_1\beta_2 \frac{\gamma_1}{\gamma_2} \right) - N_2^{*2} \right]^{\frac{1}{2}} \end{aligned} \tag{22}$$

for some δ_1, δ_2 such that $0 < \delta_i < K_i(1 - \beta_i K_j - \gamma_i K_1 K_2)$, $i = 1, 2$, $i \neq j$, then the set

$$B = \{ (N_1, N_2) : K_i(1 - \beta_i K_j - \gamma_i K_1 K_2) - \delta_i < N_i < K_i, \quad i, j = 1, 2, \quad i \neq j \} \tag{23}$$

is a basin of attraction for the positive equilibrium E^* in the sense that any solution $(N_1(\mathbf{x}, t), N_2(\mathbf{x}, t))$ with initial conditions (ψ_1, ψ_2) such that

$$K_i(1 - \beta_i K_j - \gamma_i K_1 K_2) - \delta_i < \psi_i(\mathbf{x}, t) < K_i, \quad \mathbf{x} \in \Omega, \quad t \in (-\infty, 0], \quad i, j = 1, 2, \quad i \neq j, \tag{24}$$

will satisfy

$$\lim_{t \rightarrow \infty} (N_1(\mathbf{x}, t), N_2(\mathbf{x}, t)) = (N_1^*, N_2^*).$$

Remark. Note that (21) implies $K_2\beta_1 < 1$ and $K_1\beta_2 < 1$, the conditions for instability of the boundary equilibria E^1 and E^2 (Propositions 3.2 and 3.3), for existence of a unique E^* (Proposition 3.5) and for linear asymptotic stability of E^* for exponentially decaying kernels (Proposition 3.6).

The proof of Theorem 4.1 is in three parts, comprising the bringing together of the three lemmas stated below. We define the following, for ease of notation in the calculations. Let

$$n_i^{(l)} = K_i(1 - \beta_i K_j - \gamma_i K_1 K_2) - \delta_i, \quad n_i^{(u)} = K_i, \quad i, j = 1, 2, \quad i \neq j,$$

then we can write B as $B = [n_1^{(l)}, n_1^{(u)}] \times [n_2^{(l)}, n_2^{(u)}]$.

Let

$$n_i^* = \sqrt{2} \left[\frac{4\beta_i}{3K_j\gamma_1\gamma_2} \left(1 - K_j\beta_i \frac{\gamma_j}{\gamma_i} \right) - N_i^{*2} \right]^{\frac{1}{2}} \quad i, j = 1, 2, \quad (i \neq j), \tag{25}$$

which we know to be real by (20), and define the set \mathcal{B} as

$$\mathcal{B} = \{ (N_1, N_2) : |N_i - N_i^*| < n_i^*, \quad i = 1, 2 \}.$$

Finally, let

$$N_i^{(l)} = N_i^* - n_i^*, \quad N_i^{(u)} = N_i^* + n_i^*, \quad i, j = 1, 2, \quad (i \neq j),$$

so that $\mathcal{B} = [N_1^{(l)}, N_1^{(u)}] \times [N_2^{(l)}, N_2^{(u)}]$.

LEMMA 4.1. *If condition (20) holds, then E^* is attracting for all (N_1, N_2) such that $(N_1, N_2) \in \mathcal{B}$ for all $\mathbf{x} \in \Omega, t \in \mathbf{R}$.*

LEMMA 4.2. *If condition (21) holds, then B is an invariant set.*

LEMMA 4.3. *If condition (22) holds, then $B \subseteq \mathcal{B}$.*

Proof of Lemma 4.1. Let $N_i = N_i^*(1 + n_i), i = 1, 2$, so that we centre our equations (3) about the equilibrium. Then we need to show that the origin is attracting for (n_1, n_2) such that

$$\begin{aligned} \frac{\partial n_1}{\partial t} &= d_1 \nabla^2 n_1 - \varepsilon_1 (1 + n_1) \left[\frac{N_1^*}{K_1} n_1 + N_2^* \beta_1 n_2 \right. \\ &\quad \left. + N_1^* N_2^* \gamma_1 \int_0^\infty f(\tau) (n_2(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) n_2(\mathbf{x}, t - \tau)) d\tau \right], \\ \frac{\partial n_2}{\partial t} &= d_2 \nabla^2 n_2 - \varepsilon_2 (1 + n_2) \left[\frac{N_2^*}{K_2} n_2 + N_1^* \beta_2 n_1 \right. \\ &\quad \left. + N_1^* N_2^* \gamma_2 \int_0^\infty f(\tau) (n_2(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) n_2(\mathbf{x}, t - \tau)) d\tau \right]. \end{aligned} \tag{26}$$

Consider the Lyapunov function

$$V(n_1, n_2) = \int_\Omega (\omega_1 (n_1 - \log(1 + n_1)) + \omega_2 (n_2 - \log(1 + n_2))) dx, \tag{27}$$

with ω_1 and ω_2 being positive constants to be determined later. Note that $V(n_1, n_2) \geq 0$ for all $n_i, i = 1, 2$, and $V(n_1, n_2) = 0$ iff $(n_1, n_2) = (0, 0)$. Now

$$\frac{dV}{dt} = \int_\Omega \left(\omega_1 \left(\frac{n_1}{1 + n_1} \right) \frac{\partial n_1}{\partial t} + \omega_2 \left(\frac{n_2}{1 + n_2} \right) \frac{\partial n_2}{\partial t} \right) dx,$$

so that, along solutions of (26),

$$\begin{aligned} \frac{dV}{dt} &= \int_\Omega dx \left\{ \omega_1 d_1 \left(\frac{n_1}{1 + n_1} \right) \nabla^2 n_1 - \omega_1 \varepsilon_1 n_1 \left[\frac{N_1^*}{K_1} n_1 + N_2^* \beta_1 n_2 \right. \right. \\ &\quad \left. \left. + N_1^* N_2^* \gamma_1 \int_0^\infty f(\tau) (n_2(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) n_2(\mathbf{x}, t - \tau)) d\tau \right] \right. \\ &\quad \left. + \omega_2 d_2 \left(\frac{n_2}{1 + n_2} \right) \nabla^2 n_2 - \omega_2 \varepsilon_2 n_2 \left[\frac{N_2^*}{K_2} n_2 + N_1^* \beta_2 n_1 \right. \right. \\ &\quad \left. \left. + N_1^* N_2^* \gamma_2 \int_0^\infty f(\tau) (n_2(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) n_2(\mathbf{x}, t - \tau)) d\tau \right] \right\}. \end{aligned} \tag{28}$$

Now

$$\begin{aligned} \int_\Omega \left(\frac{n_i}{1 + n_i} \right) \nabla^2 n_i dx &= \int_{\partial\Omega} \left(\frac{n_i}{1 + n_i} \right) \frac{\partial n_i}{\partial \nu} dS - \int_\Omega |\nabla n_i|^2 \frac{\partial}{\partial n_i} \left(\frac{n_i}{1 + n_i} \right) dx \\ &= - \int_\Omega \left(\frac{|\nabla n_i|}{1 + n_i} \right)^2 dx \leq 0, \quad i, j = 1, 2, \end{aligned}$$

since $\partial n_i / \partial \nu = 0$ along $\partial \Omega$ by (8). Hence, from (28), we have

$$\begin{aligned} \frac{dV}{dt} \leq & \int_{\Omega} \left\{ -\omega_1 \varepsilon_1 n_1 \left(\frac{N_1^*}{K_1} n_1 + N_2^* \beta_1 n_2 \right) - \omega_2 \varepsilon_2 n_2 \left(\frac{N_2^*}{K_2} n_2 + N_1^* \beta_2 n_1 \right) \right. \\ & \left. - N_1^* N_2^* (\omega_1 \varepsilon_1 \gamma_1 n_1 + \omega_2 \varepsilon_2 \gamma_2 n_2) \cdot \int_0^\infty f(\tau) [n_2(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) + n_1(\mathbf{x}, t - \tau) n_2(\mathbf{x}, t - \tau)] d\tau \right\} d\mathbf{x}. \end{aligned} \tag{29}$$

Using ideas similar to [4] we can show that when $\omega_i = \omega_i^*$, where

$$\omega_1^* = \frac{2\beta_2}{3N_2^* \varepsilon_1 \gamma_1 \gamma_2}, \quad \omega_2^* = \frac{2\beta_1}{3N_1^* \varepsilon_2 \gamma_1 \gamma_2},$$

the positive definite functional

$$\begin{aligned} U(n_1, n_2) = & V(n_1, n_2) + \int_{\Omega} \left[\frac{N_1^* N_2^*}{2} \int_0^\infty f(\tau) \left(\int_{t-\tau}^t n_1^2(\mathbf{x}, \mu) d\mu \right. \right. \\ & \left. \left. + \int_{t-\tau}^t n_2^2(\mathbf{x}, \mu) d\mu + \int_{t-\tau}^t n_1^2(\mathbf{x}, \mu) n_2^2(\mathbf{x}, \mu) d\mu \right) d\tau \right] d\mathbf{x}, \end{aligned} \tag{30}$$

satisfies

$$\begin{aligned} \frac{dU}{dt} \leq & \int_{\Omega} \left\{ -\left(\omega_1^* \varepsilon_1 N_1^* \left(\frac{1}{K_1} - \beta_2 \frac{\gamma_1}{\gamma_2} \right) - \frac{N_1^* N_2^*}{2} \right) n_1^2 \right. \\ & \left. - \left(\omega_2^* \varepsilon_2 N_2^* \left(\frac{1}{K_2} - \beta_1 \frac{\gamma_2}{\gamma_1} \right) - \frac{N_1^* N_2^*}{2} \right) n_2^2 + \frac{N_1^* N_2^*}{2} n_1^2 n_2^2 \right\} d\mathbf{x}. \end{aligned} \tag{31}$$

We can rewrite (31) as

$$\begin{aligned} \frac{dU}{dt} \leq & -\frac{N_1^* N_2^*}{4} \int_{\Omega} \left\{ \frac{1}{N_1^{*2}} \left(2 \left[\frac{4\beta_1}{3K_2 \gamma_1 \gamma_2} \left(1 - K_2 \beta_1 \frac{\gamma_2}{\gamma_1} \right) - N_1^{*2} \right] - N_1^{*2} n_1^2 \right) n_2^2 \right. \\ & \left. + \frac{1}{N_2^{*2}} \left(2 \left[\frac{4\beta_2}{3K_1 \gamma_1 \gamma_2} \left(1 - K_1 \beta_2 \frac{\gamma_1}{\gamma_2} \right) - N_2^{*2} \right] - N_2^{*2} n_2^2 \right) n_1^2 \right\} d\mathbf{x}, \end{aligned} \tag{32}$$

and note that (20) implies that the terms in the square brackets are positive. Finally we use the definition (25) and return to the original variables;

$$\frac{dU}{dt} \leq -\frac{N_1^* N_2^*}{4} \int_{\Omega} \left\{ [n_1^{*2} - (N_1 - N_1^*)^2] \left(\frac{n_2}{N_1^*} \right)^2 + [n_2^{*2} - (N_2 - N_2^*)^2] \left(\frac{n_1}{N_2^*} \right)^2 \right\} d\mathbf{x}, \tag{33}$$

so that sufficient conditions for U to satisfy $dU/dt < 0$ (and be a Lyapunov function for E^*) are $(N_1, N_2) \in \mathcal{B}$ for all $\mathbf{x} \in \Omega, t \in \mathbf{R}$.

Proof of Lemma 4.2. Here we are effectively generalising ideas of positively invariant regions (see for example [7] and references therein) to equations with temporal delay.

We claim that the solution $(N_1(\mathbf{x}, t), N_2(\mathbf{x}, t))$ satisfies

$$n_i^{(l)} \leq N_i(\mathbf{x}, t) \leq n_i^{(u)}, \quad i = 1, 2, \quad \forall t \in \mathbf{R}. \tag{34}$$

Since this is certainly true for all $t \leq 0$ by our initial condition (24), we suppose that, for a contradiction, there is a first time $t^* > 0$ (and corresponding point $\mathbf{x}^* \in \Omega$) such that (N_1, N_2) leaves the set $[n_1^{(l)}, n_1^{(u)}] \times [n_2^{(l)}, n_2^{(u)}]$.

Suppose that (without loss of generality) it is N_1 that leaves, and that it does so through the lower bound $n_1^{(l)}$. Since the solution is leaving the lower boundary at time t^* ,

$$\frac{\partial N_1}{\partial t}(\mathbf{x}^*, t^*) \leq 0,$$

and the solution is locally minimal (with respect to position \mathbf{x}), so that

$$\nabla^2 N_1(\mathbf{x}^*, t^*) \geq 0.$$

The first equation of system (3) then yields

$$\varepsilon_1 N_1 \left[1 - \frac{N_1}{K_1} - \beta_1 N_2 - \gamma_1 \int_0^\infty f(\tau) N_1(\mathbf{x}, t - \tau) N_2(\mathbf{x}, t - \tau) d\tau \right] \Big|_{t=t^*, \mathbf{x}=\mathbf{x}^*} \leq 0. \tag{35}$$

Now, since t^* is the first time this happens,

$$n_i^{(l)} \leq N_i(\mathbf{x}, t) \leq n_i^{(u)} = K_i, \quad i = 1, 2, \quad \forall t \leq t^*.$$

Also at (\mathbf{x}^*, t^*) we have $N_1 = n_1^{(l)}$ and, recalling that

$$n_1^{(l)} = K_1(1 - \beta_1 K_2 - \gamma_1 K_1 K_2) - \delta_1,$$

we obtain

$$\begin{aligned} & \varepsilon_1 N_1 \left[1 - \frac{N_1}{K_1} - \beta_1 N_2 - \gamma_1 \int_0^\infty f(\tau) N_1(\mathbf{x}, t - \tau) N_2(\mathbf{x}, t - \tau) d\tau \right] \Big|_{t=t^*, \mathbf{x}=\mathbf{x}^*} \\ &= \varepsilon_1 n_1^{(l)} \left[\delta_1 + \beta_1 (K_2 - N_2) + \gamma_1 \left(K_1 K_2 - \int_0^\infty f(\tau) N_1(\mathbf{x}^*, t^* - \tau) N_2(\mathbf{x}^*, t^* - \tau) d\tau \right) \right] \\ &\geq \varepsilon_1 n_1^{(l)} \left[\delta_1 + \gamma_1 \left(K_1 K_2 - K_1 n_2 \int_0^\infty f(\tau) d\tau \right) \right] \\ &= \varepsilon_1 n_1^{(l)} \delta_1 > 0, \end{aligned}$$

and this contradicts (35).

Now imagine that N_1 leaves through the upper bound $n_1^{(u)}$ at time t^* and point \mathbf{x}^* . Then in this case the first equation of (3) implies that

$$\varepsilon_1 N_1 \left[1 - \frac{N_1}{K_1} - \beta_1 N_2 - \gamma_1 \int_0^\infty f(\tau) N_1(\mathbf{x}, t - \tau) N_2(\mathbf{x}, t - \tau) d\tau \right] \Big|_{t=t^*, \mathbf{x}=\mathbf{x}^*} \geq 0.$$

But also, at (\mathbf{x}^*, t^*) ,

$$\begin{aligned} & \varepsilon_1 N_1 \left[1 - \frac{N_1}{K_1} - \beta_1 N_2 - \gamma_1 \int_0^\infty f(\tau) N_1(\mathbf{x}, t - \tau) N_2(\mathbf{x}, t - \tau) d\tau \right] \\ &= -\varepsilon_1 K_1 \left[\beta_1 N_2 + \gamma_1 \int_0^\infty f(\tau) N_1(\mathbf{x}^*, t^* - \tau) N_2(\mathbf{x}^*, t^* - \tau) d\tau \right] < 0, \end{aligned}$$

a contradiction. Similar ideas hold for N_2 .

Proof of Lemma 4.3. A direct consequence of condition (22) is that

$$N_i^{(l)} \leq n_i^{(l)}, \quad n_i^{(u)} \leq N_i^{(u)}, \quad i = 1, 2,$$

i.e. $B \subseteq \mathcal{B}$.

Proof of Theorem 4.1. Let the initial conditions (ψ_1, ψ_2) satisfy (24). By Lemma 4.2 the solution never leaves B . Therefore, by Lemma 4.3, the solution

has values in \mathcal{B} for all (\mathbf{x}, t) . Hence, by Lemma 4.1, the solution tends asymptotically to the positive equilibrium N^* . Thus, it is the combination of all three lemmas which gives the result.

5. Numerical simulations. The conditions of Theorem 4.1 would appear to be quite stringent. In this section we aim to demonstrate that, not only are there parameter values for which all the hypotheses are satisfied, but in fact that the stability basin of attractivity can be quite large and, in some cases, larger than the predictions of other investigators who were only concerned with the ODE model for the spatially uniform dynamics.

As an example, let

$$K_1 = 1, \quad K_2 = 1, \quad \beta_1 = 0.4, \quad \beta_2 = 0.3, \quad \gamma_1 = 0.5, \quad \gamma_2 = 0.4. \quad (36)$$

In the absence of competition, each population is expected to evolve such as to be bounded by its carrying capacity in the long term. Therefore, let us take initial data satisfying $0 \leq \psi_i(\mathbf{x}, t) \leq K_i, i = 1, 2$. Substituting the values (36) into the conditions (20), (21) and (22), we see that Theorem 4.1 holds for all δ_1, δ_2 such that $\delta_1 < 0.1, \delta_2 < 0.3$.

Therefore, our theorem furnishes the set

$$B = (0, 1] \times (0, 1]$$

as a basin of attraction for the unique positive equilibrium E^* , the components of which are given by (9) as

$$E^* = (0.538, 0.690).$$

The equilibrium will attract all initial data with values in this set B for all $\mathbf{x} \in \Omega$ and $t \leq 0$. Of course, this requires $\psi_i, i = 1, 2$, to be strictly positive for all such \mathbf{x}, t . However, numerical simulations suggest that it is sufficient only to have $\psi_i > 0 (i = 1, 2)$ on some subset of Ω . Before we present the results of some numerical work, note that an advantage of having results which do not depend on the diffusivities is that our theorem is immediately applicable to the ODEs governing the evolution of the spatially uniform solutions. In addition, unlike the asymptotic stability basin derived in [4] (Theorem 5.3, p43), our result is independent of both the strength of the delay $f(t)$, as measured by the quantity T defined by

$$T = \int_0^\infty \tau f(\tau) d\tau,$$

and the intrinsic growth rates $\varepsilon_i, i = 1, 2$. Looking at the result of [4], with the parameter values (36), then the stability basin given by Theorem 5.3 in [4] is

$$B_\delta = \{(N_1, N_2) : |\psi_i - N_i^*| < \delta, i = 1, 2\}$$

with

$$\delta \approx 17.3 \left(\frac{\min(1.45 \varepsilon_1^{-1}, 2.48 \varepsilon_2^{-1}) \varepsilon_1 \varepsilon_2}{7240 \varepsilon_2 + 12300 \varepsilon_1 + 3340 T \varepsilon_1 \varepsilon_2} \right)^{\frac{1}{2}}.$$

It is simple to show that δ is bounded above by 0.175 for all $\varepsilon_i > 0 (i = 1, 2)$ even when there is no delay (i.e., when T defined above is zero), so that, in this case, the attractive basin B_δ is always a subset of

$$(0.363, 0.714) \times (0.514, 0.865).$$

Hence, *for some parameter values at least*, Theorem 4.1 of the present paper is a stronger result than Theorem 5.3 of [4].

The analytical results described in this paper are confirmed by computer simulations. We carried out a numerical simulation of the full model (3), on the one-dimensional spatial domain $x \in [0, 20]$, with the parameter values (36) and the kernels f_i both given by

$$f_i(x, t) = \frac{1}{2} \alpha e^{-\alpha|x|} \theta e^{-\theta t}.$$

In this case, by defining

$$N_3(x, t) = \int_{-\infty}^t \theta e^{-\theta(t-\tau)} N_1(x, \tau) N_2(x, \tau) d\tau$$

and

$$N_4(x, t) = \int_{-\infty}^{\infty} \frac{1}{2} \alpha e^{-\alpha|x-y|} N_3(y, t) dy$$

it is easily seen that the system (3) is equivalent to

$$\begin{aligned} \partial N_1 / \partial t &= \varepsilon_1 N_1 [1 - N_1 / K_1 - \beta_1 N_2 - \gamma_1 N_4] + d_1 \partial^2 N_1 / \partial x^2, \\ \partial N_2 / \partial t &= \varepsilon_2 N_2 [1 - N_2 / K_2 - \beta_2 N_1 - \gamma_2 N_4] + d_2 \partial^2 N_2 / \partial x^2, \\ \partial N_3 / \partial t &= \theta (N_1 N_2 - N_3), \\ 0 &= \alpha^2 (N_3 - N_4) + \partial^2 N_4 / \partial x^2. \end{aligned} \quad (37)$$

In addition, we let

$$\varepsilon_1 = 1, \quad \varepsilon_2 = 0.8, \quad d_1 = 10^{-1}, \quad d_2 = 1.5 \times 10^{-1}, \quad \theta = 0.1, \quad \alpha = 0.5. \quad (38)$$

The results of a numerical simulation of the system (37), carried out using the NAG library routine D03PCF, are shown in Fig. 1. The number of spatial grid points used was 1000, but problems of file storage led us to plot the computed solution at only 100 grid points. The number of time steps was also somewhat larger than the figure suggests. Convergence to the equilibrium is rapid, but non-monotone. The initial conditions were $(N_1(x, 0), N_2(x, 0)) = (0, 1)$ in the first quarter of the domain and $(N_1(x, 0), N_2(x, 0)) = (1, 0)$ in the last quarter, with values for $(N_1(x, 0), N_2(x, 0))$ in the remaining half consisting of random numbers uniformly distributed across $(0, 1)$. The fact that part of the initial conditions is on the boundary of the stability basin does not seem to affect the dynamics.

6. Discussion. We have proposed and studied a reaction-diffusion extension of the ecotoxicological model proposed in [4], in which we allow for linear diffusion and nonlocal spatial effects, as well as time delays. As far as the linear stability of the equilibrium states is concerned, the introduction of the diffusion and nonlocal averaging does not seem to affect the stability of the equilibria, although of course our investigation of the linear stability of the positive equilibrium E^* was confined to the case of exponentially decaying kernels.

For the case of a purely temporal convolution we have also established nonlinear convergence to the positive equilibrium under certain conditions on the parameters and the initial data. The result is also applicable to the corresponding spatially homogeneous model studied in [4] and, furthermore, we have demonstrated that, for certain parameter values at least, our theorem is an improvement on the corresponding result in [4]. The techniques we have used to establish nonlinear stability appear to work well only for purely temporal delays; nonlocal ecological models on finite domains are more recent (see, for example, Gourley & So [6]). However, our nonlinear convergence result is for general temporal delay kernels.

It is of interest to look at the particular case of our model (3) when the interspecific competition terms are switched off (i.e., when we set $\beta_1 = \beta_2 = 0$ in (3)).

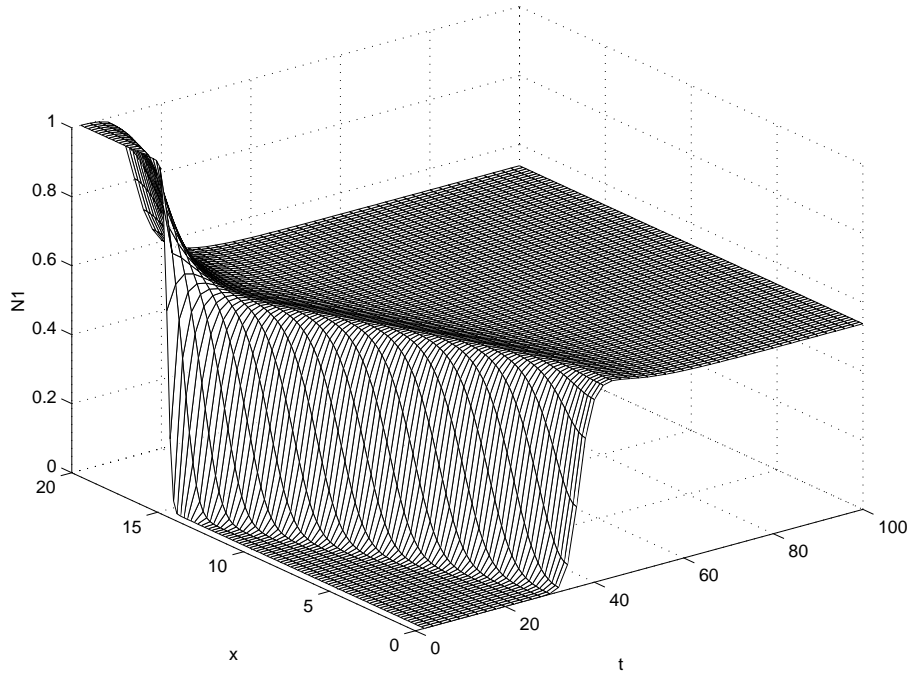


FIGURE 1. Numerical simulation of system (37) under homogeneous Neumann boundary conditions, with parameter values and initial conditions as described in the text. Only the solution for the population N_1 is plotted; that for N_2 is similar. Convergence to the equilibrium is rapid, but non-monotone. Since N_3 and N_4 are the temporal and spatial averages of the quantities of interest, these are not plotted. Note that our problem is really on the whole real line $x \in (-\infty, \infty)$; this is why the domain was taken to be reasonably large. However, a function satisfying homogeneous Neumann boundary conditions on the finite subdomain $[0, 20]$ of $(-\infty, \infty)$ can be extended to an even function on $[-20, 20]$ and then periodically over all of $(-\infty, \infty)$ (note that N_4 is periodic in x whenever N_3 is).

The species are still in competition with each other, because of the toxins secreted by each species. In this case, the boundary equilibria are still the same (they do not depend on the β_i), but they are now always unstable. The positive (coexistence) equilibrium E^* exists, is unique, and (by Proposition 3.6) is automatically linearly stable for exponentially decaying kernels. Thus, the species can coexist in the presence of the toxins. This is in accordance with the findings of Chattopadhyay et al. [4]. Unfortunately our nonlinear stability theorem (Theorem 4.1) cannot be applied if either of the β_i is zero, and thus it is an open problem to investigate nonlinear stability in this case.

In our view, the most interesting and worthwhile extensions to the model concern the modelling of the production of the toxins. We have assumed that each individual of one species will produce toxin at a rate proportional to the number of members of the other species present. Such an assumption will be reasonable only if the

numbers of the opposing species are relatively small. In practice, there will be a maximum possible rate at which each individual can produce its toxic substance, regardless of how many of the competitor are present. The toxin term in the first equation of (3) would be replaced by

$$-\gamma_1 \int_{\mathbf{R}^n} \int_{-\infty}^t f_1(\mathbf{x} - \mathbf{y}, t - \tau) p_1(N_1(\mathbf{y}, \tau)) N_2(\mathbf{y}, \tau) d\tau d\mathbf{y}$$

while that of the second equation would become

$$-\gamma_2 \int_{\mathbf{R}^n} \int_{-\infty}^t f_2(\mathbf{x} - \mathbf{y}, t - \tau) N_1(\mathbf{y}, \tau) p_2(N_2(\mathbf{y}, \tau)) d\tau d\mathbf{y}$$

where the functions $p_i(N)$ are linear in N for small N but level off for large N . Functions of the form $p_i(N) = A_i N / (1 + B_i N)$ would be appropriate simple choices. We leave these considerations for future work.

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