Numerical Analysis of Crowding Effects in Competing Species

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Abstract. In recent decades, scientists have observed that the mortality rate of some competing species increases superlinearly as populations grow to unsustainable levels. This is modeled by terms representing *crowding effects* in a system of nonlinear differential equations that describes population growth of two species competing for resources under the effects of crowding. After applying nondimensionalization to reduce parameters in the system, the stability of the steady state solutions of the system is examined. A semi-implicit numerical scheme is proposed which guarantees the positivity of the solutions. The long term behavior of the numerical solutions is studied. The error estimate between the numerical solution and the true solution is given.

Key words. crowding effects, long term behavior, error estimate

1 Introduction

Competition is a fundamental component of interaction between species. Species survival in a bounded ecological system is influenced by limited resources and the ensuing competition for them [3]. Many models in differential equations for either competing species or even cooperating species use as a reference point the classical Lotka-Volterra (LV) system [4, 5, 6], which has been referred to as the basic equation of ecology [7]. The LV system is a widely studied model of competition between species, but requires variation to account for many other factors observed in nature, such as seasonal reproduction, seasonal food availability, and density and crowding. For a general overview of these scenarios and multiple references in which they have been considered, see [8] and [9] and the excellent references therein related to LV limitations and uses related to capelin in the Barents Sea. In these references, density or crowding are considered and shown to have significant impact on survival.

Crowding effects, or high density counts of species are considered here separately with a standard LV model as a factor that can drive species to additional competition for resources, in this case intra-specific competition. This crowding effect can take several different forms, such as the consumption of resources that are available to the members of the ecosystem, or possibly an adverse affect of two members of the species encountering each other [10]. While these crowding effects have been studied by applying numerical methods [11], very little has been done to analyze the stability of steady states of these systems. That is the purpose of this paper, to present a method to approximate a solution to the LV model with competition and study under what conditions coexistence is predicted based on stability of the numerical scheme.

This paper will proceed as follows: In Section 2, we introduce the LV system, modified to include crowding effects, and reduce its parameters to prepare for numerical approximation. In Section 3 we investigate stability of its steady states. In Section 4 we introduce a nonstandard numerical scheme to approximate solutions to the system and prove stability of the numerical scheme. In Section 5 we show that the numerical scheme converges to the true, theoretical solution of the system. Finally, we present some numerical experiments in Section 6.

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2 LV Model with Crowding Effects

The modified LV model we use as given in [11] is

$$\begin{cases} x' = \beta_1 x(1 - x - \alpha_{12} y) - (m_{10} + d_1 x^\delta)x, \\ y' = \beta_2 y(1 - y - \alpha_{21} x) - (m_{20} + d_2 y^\delta)y. \end{cases} \tag{1}$$

In this model, note that both population densities will be represented by numbers between zero and one, and that the carrying capacities of both species have been set to 1. Here, the variables and constants are interpreted as follows. In the system, each is nonnegative.

x	population density/biomass of Species 1,
y	population density/biomass of Species 2,
β_i	birth rate of Species i,
m_{i0}	death rate of Species i,
d_i	density-dependent factor for the death rate of Species i,
α_{ij}	the effect of Species j on Species i,
δ	a measure of the degree of species crowding,

and where, as per [11], $m_{i0} + d_i \in [0, 1]$.

We apply the nondimensionalization [14] to system (1) to significantly reduce the number of parameters. This is accomplished by first assuming that $\beta_1 > m_{10}$ and $\beta_2 > m_{20}$ and setting $c_1 = \beta_1 - m_{10}$ and $c_2 = \beta_2 - m_{20}$, giving

$$\begin{cases} x' = c_1 x - \beta_1 x^2 - \alpha_{12}\beta_1 xy - d_1 x^{\delta+1}, \\ y' = c_2 y - \beta_2 y^2 - \alpha_{21}\beta_2 xy - d_2 y^{\delta+1}. \end{cases}$$

Setting $\beta_1 = \frac{c_1}{e_1}$ and $\beta_2 = \frac{c_2}{e_2}$,

$$\begin{cases} x' = \frac{c_1}{e_1} x(e_1 - x - \alpha_{12} y - d_1 \frac{e_1}{c_1} x^\delta), \\ y' = \frac{c_2}{e_2} y(e_2 - y - \alpha_{21} x - d_2 \frac{e_2}{c_2} y^\delta). \end{cases}$$

Then if $u = \frac{x}{e_1}$ and $v = \frac{y}{e_2}$ is followed by $x = e_1 u, x' = e_1 u', y = e_2 v, y' = e_2 v'$, $\tau = c_1 t$, and $u'(t) = u'(\tau)\frac{d\tau}{dt} = u'(\tau) \cdot c_1$, we arrive at

$$\begin{cases} u' = u(1 - u - \frac{\alpha_{12} e_2}{e_1} v - d_1 \frac{e_1^\delta}{c_1} u^\delta), \\ v' = \frac{c_2}{c_1} v(1 - v - \frac{\alpha_{21} e_1}{e_2} v - d_2 \frac{e_2^\delta}{c_2} v^\delta). \end{cases}$$

Finally, renaming $\frac{\alpha_{12} e_2}{e_1} = a_1, d_1 \frac{e_1^\delta}{c_1} = b_1, \frac{\alpha_{21} e_1}{e_2} = a_2, d_2 \frac{e_2^\delta}{c_2} = b_2$, and $\rho = \frac{c_2}{c_1}$, followed by τ being replaced again by t, we have the nonparametrized version of the LV system with crowding effects

$$\begin{cases} u' = u(1 - u - a_1 v - b_1 u^\delta), \\ v' = \rho v(1 - v - a_2 u - b_2 v^\delta). \end{cases}$$

Even with the reduction from eight to five parameters, detailed study of the stability of steady states and applying a numerical method to this system for general $\delta > 1$ is highly technical and will be saved for future work. In fact, since our goal is to show a stable and convergent numerical scheme for a particular LV system with crowding, we will choose $\delta = 2$. Therefore, the specific case that will be studied throughout this paper is

$$\begin{cases} u' = u(1 - u - a_1 v - b_1 u^2), \\ v' = \rho v(1 - v - a_2 u - b_2 v^2). \end{cases} \tag{2}$$

3 Steady States and Stability

In the analysis of Sections 4-5, we show that numerical solutions using the nonstandard discretization proposed reflects the same behavior as true solutions to (2); for this purpose, in this section we will consider the stability of its steady state solutions. This will show that when convergence behavior of the numerical scheme is discussed under appropriate conditions on the parameters, we can be sure it accurately reflects convergence of true solutions to these steady states. The system of interest (2) has four steady state solutions, clearly, $(u_1, v_1) = (0, 0)$ is a steady state. The other three steady states are given by

$$\begin{cases} u_2 = 0 \\ 1 - v_2 - a_2 u_2 - b_2 v_2^2 = 0 \end{cases} \tag{3}$$

$$\begin{cases} 1 - u_3 - a_1 v_3 - b_1 u_3^2 = 0 \\ v_3 = 0 \end{cases} \tag{4}$$

$$\begin{cases} 1 - u_4 - a_1 v_4 - b_1 u_4^2 = 0 \\ 1 - v_4 - a_2 u_4 - b_2 v_4^2 = 0. \end{cases} \tag{5}$$

For the second steady state (u_2, v_2) in (3), we set $u_2 = 0$ and find the positive solution of $0 = 1 - v_2 - a_2 u_2 - b_2 v_2^2 = 1 - v_2 - b_2 v_2^2$, which is

$$v_2 = \frac{\sqrt{1 + 4b_2} - 1}{2b_2}.$$

Similarly, for the third steady state (u_3, v_3) in (4), we set $v_3 = 0$ and find the positive solution of $0 = 1 - u_3 - a_1 v_3 - b_1 u_3^2 = 1 - u_3 - b_1 u_3^2$, which is

$$u_3 = \frac{\sqrt{1 + 4b_1} - 1}{2b_1}.$$

The final steady state (u_4, v_4) in (5) is complicated due to the large number of parameters. However, if we make the choice $a_1 = b_1 = a_2 = b_2 = 1$, then we have the unique positive solution $u_4 = v_4 = \sqrt{2} - 1$. Thus the steady states of (2) are given by

$$(u_1, v_1) = (0, 0) \tag{6}$$

$$(u_2, v_2) = \left(0, \frac{\sqrt{1 + 4b_2} - 1}{2b_2}\right) \tag{7}$$

$$(u_3, v_3) = \left(\frac{\sqrt{1 + 4b_1} - 1}{2b_1}, 0\right) \tag{8}$$

$$(u_4, v_4) = (\sqrt{2} - 1, \sqrt{2} - 1) \tag{9}$$

where (9) holds if $a_1 = b_1 = a_2 = b_2 = 1$. We will now analyze the stability of these steady states. To do this, we set

$$f(u, v) = u(1 - u - a_1 v - b_1 u^2) \text{ and } g(u, v) = \rho v(1 - v - a_2 u - b_2 v^2)$$

and compute the Jacobian, which yields

$$J(u, v) = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix} = \begin{pmatrix} 1 - 2u - a_1 v - 3b_1 u^2 & -a_1 u \\ -a_2 \rho v & \rho - 2\rho v - \rho a_2 u - 3b_2 \rho v^2 \end{pmatrix}. \tag{10}$$

Evaluating J at any of the steady states from (6)-(9), we have that each steady state is stable if and only if the determinant $\det(J(u_i, v_i))$ is positive and its trace $\mathrm{tr}(J(u_i, v_i))$ is negative. We will now determine the stability of each steady state by analyzing the determinant and trace of the above matrix.

For the zero steady state $(u_1, v_1) = (0, 0)$,

$$J(u_1, v_1) = J(0, 0) = \begin{bmatrix} 1 & 0 \\ 0 & \rho \end{bmatrix},$$

for which $\det(J(u_1, v_1)) = \rho > 0$ and $\text{tr}(J(u_1, v_1)) = \rho + 1 > 0$, so the zero steady state is unstable. This agrees with expectation in that if either species has a nonzero population or biomass initially, it will exhibit growth on some level under nonzero conditions for the constant coefficients in (2). So we investigate next what happens to a species' biomass when there is indeed nonzero population of at least one species as the more important cases.

For the second steady state (u_2, v_2) in (7), analyzing signs of $\det(J(u_2, v_2))$ and $\text{tr}(J(u_2, v_2))$ to ensure stability, after a considerable amount of algebra and given that all constants must be nonnegative, we come to the condition

$$(u_2, v_2) \text{ is stable if and only if } a_1 > 1 \text{ and } b_2 < a_1^2 - a_1.$$

Similarly, for the third steady state (u_3, v_3) in (8), again analyzing signs of $\det(J(u_3, v_3))$ and $\text{tr}(J(u_3, v_3))$, the condition for (u_3, v_3) being a stable steady state becomes what we would expect from the symmetry of the system equations, namely

$$(u_3, v_3) \text{ is stable if and only if } a_2 > 1 \text{ and } b_1 < a_2^2 - a_2.$$

The stability of the fourth steady state (9) is easily verified by again analyzing the trace and determinant of $J(u_4, v_4)$. Evaluating general conditions on steady states for arbitrary constants is technical and more than will be treated here, but this positive steady state suggests that there are conditions under which there is a stable solution with both $u, v > 0$.

Hence, there are some reasonable conditions that, if enforced and considered together with initial conditions, assure convergence of the true solution of (2) to the three nonzero steady states. These will be applied and it will be shown numerically, as well as proven, that the method introduced next provides numerical approximations $(u(t_k), v(t_k))$ that converge to the same steady state as $k \to \infty$ obtained for true solutions as $t \to \infty$.

4 Nonstandard Discretization Scheme

Euler's method may be used to approximate this system with the following system of equations

$$\begin{aligned} u_{n+1} &= u_n + \Delta t u_n(1 - u_n - a_1 v_n - b_1 u_n^2), \\ v_{n+1} &= v_n + \rho \Delta t v_n(1 - v_n - a_2 u_n - b_2 v_n^2). \end{aligned}$$

However, too large a choice for Δt may fail to reflect the properties of the true solutions. For example, it is not difficult to come up with examples where one of the population densities eventually becomes negative. It is unclear what Δt should be chosen and, in fact, it cannot be stated how close an Euler solution is to the true solution depending on the size of Δt.

Inspired by the methods in [1, 2, 12] and [13], we introduce the nonstandard discretization

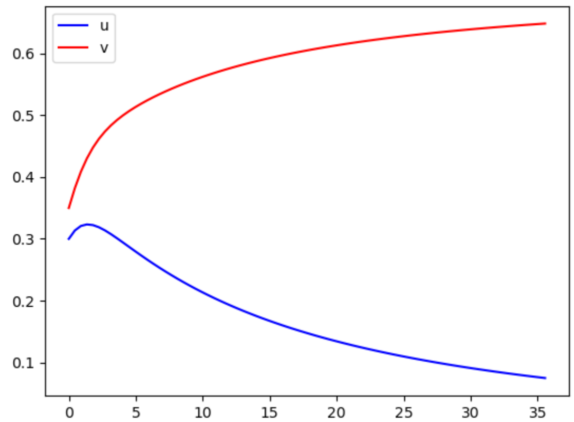
$$\begin{aligned} u_{n+1} &= u_n + \Delta t u_n - \Delta t u_n u_{n+1} - \Delta t a_1 u_{n+1} v_n - \Delta t b_1 u_{n+1} u_n^2 \\ v_{n+1} &= v_n + \rho \Delta t v_n - \rho \Delta t v_{n+1} v_n - \rho \Delta t a_2 v_{n+1} u_n - \rho \Delta t b_2 v_{n+1} v_n^2 \end{aligned}$$

as the numerical scheme and discuss the advantages of using the proposed method. Solving for u_{n+1} and v_{n+1}, the new iterative scheme becomes

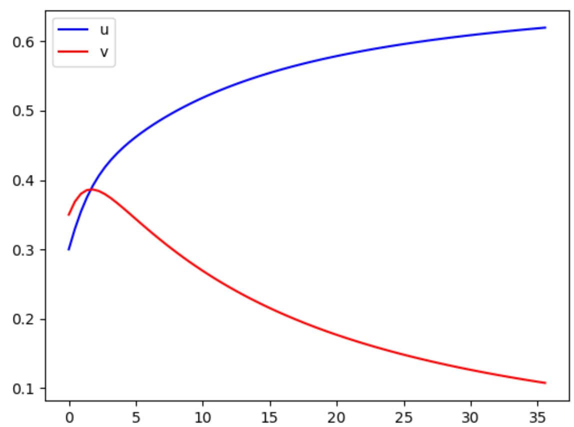
$$u_{n+1} = \frac{u_n(1 + \Delta t)}{1 + \Delta t(u_n + a_1 v_n + b_1 u_n^2)} \tag{11}$$

$$v_{n+1} = \frac{v_n(1 + \rho \Delta t)}{1 + \rho \Delta t(v_n + a_2 u_n + b_2 v_n^2)}. \tag{12}$$

As stated previously, throughout the following sequence of results related to the system (2) all constant coefficients a_1, a_2, b_1, b_2 and ρ are positive. Inductive reasoning applies directly to show that for initial conditions $u_0 > 0$ and $v_0 > 0$ in (11)-(12), all iterates remain positive. Hence we have already gained one advantage over Euler's method for the system.



(a) Numerical results under Steady State 2, where $a_1 = 1.5$, $a_2 = 1$, $b_1 = 0.4$, and $b_2 = 0.65$. These parameters were chosen to ensure convergence of the system to (u_2, v_2), which in this case is $(0, 0.682)$.



(b) Numerical results under Steady State 3, where $a_1 = 1$, $a_2 = 1.5$, $b_1 = 0.7$, and $b_2 = .3$. Parameters where chosen to ensure convergence to (u_3, v_3), which, under these parameters, is $(0.678, 0)$.

Figure 1

Together with this positivity of u_n and v_n for all $n \in \mathbb{N}$, we claim there are upper bounds on iterates for the nonstandard method (11)-(12). These will be shown in the following three theorems.

Theorem 4.1 *If* $0 < u_0 < 1$ *and* $v_0 > 0$*, then* $0 < u_n < 1$ *for all* $n \in \mathbb{N} \cup \{0\}$*.*

Proof. Let $0 < u_0 < 1$. Then, as observed in previous comments, $u_n > 0$ for all $n \in \mathbb{N} \cup \{0\}$. Now assume that for some $n \in \mathbb{N}$ that $u_n < 1$. Then

$$u_{n+1} = \frac{u_n(1+\Delta t)}{1 + \Delta t(u_n + a_1 v_n + b_1 u_n^2)} < \frac{u_n(1+\Delta t)}{1 + \Delta t u_n} < \frac{u_n(1+\Delta t)}{u_n(1+\Delta t)} = 1.$$

So by mathematical induction, $u_n < 1$ for all $n \in \mathbb{N} \cup \{0\}$. Thus we have that $0 < u_n < 1$ for all $n \in \mathbb{N} \cup \{0\}$. A similar result holds for v_n. ■

Theorem 4.2 *If $0 < v_0 < 1$ and $u_0 > 0$, then $0 < v_n < 1$ for all $n \in \mathbb{N} \cup \{0\}$.*

Proof. Let $0 < v_0 < 1$. Then it follows that $v_n > 0$ for all $n \in \mathbb{N} \cup \{0\}$. Now assume that for some $n \in \mathbb{N}$ that $v_n < 1$. Then

$$v_{n+1} = \frac{v_n(1+\rho\Delta t)}{1+\rho\Delta t(v_n + a_2 u_n + b_2 v_n^2)} < \frac{v_n(1+\rho\Delta t)}{1+\rho\Delta t v_n} < \frac{v_n(1+\Delta t)}{v_n(1+\Delta t)} = 1.$$

Hence by induction, we conclude that $v_n < 1$ for all $n \in \mathbb{N} \cup \{0\}$. ■

Under this nonstandard scheme, the desirable property that both u_n and v_n are bounded sequences follows. We prove this in the next theorem.

Theorem 4.3 *If $u_0, v_0 > 0$, then $u_n \le \max\{1, u_0\}$ and $v_n \le \max\{1, v_0\}$ for all $n \in \mathbb{N}$.*

Proof. By the previous two theorems, if $u_0 < 1$, then $u_n < 1$ for all $n \in \mathbb{N} \cup \{0\}$, and the result follows. Similarly, if $v_0 < 1$, then $v_n < 1$ for all $n \in \mathbb{N} \cup \{0\}$. Now assume that $u_0 > 1$. Since $u_0 \le u_0$, following induction we assume that $u_n \le u_0$ for some $n \in \mathbb{N}$. Then it is clear that

$$u_n + \Delta t u_n \le u_0 + \Delta t u_n u_0$$

since $u_0 > 1$. Thus

$$\frac{u_n(1+\Delta t)}{1+\Delta t u_n} \le u_0.$$

Consider now u_{n+1}. Applying again (11),

$$u_{n+1} = \frac{u_n(1+\Delta t)}{1+\Delta t(u_n + a_1 v_n + b_1 u_n^2)} < \frac{u_n(1+\Delta t)}{1+\Delta t u_n} \le u_0.$$

Also, since $v_0 \le v_0$, using the inductive hypothesis again,

$$v_n + \rho\Delta t v_n \le v_0 + \rho\Delta t v_n v_0,$$

which gives

$$\frac{v_n(1+\rho\Delta t)}{1+\rho\Delta t v_n} \le v_0.$$

Therefore,

$$v_{n+1} = \frac{v_n(1+\rho\Delta t)}{1+\rho\Delta t(v_n + a_2 u_n + b_2 v_n^2)} < \frac{v_n(1+\rho\Delta t)}{1+\rho\Delta t v_n} \le v_0.$$

Thus by induction, if $u_0, v_0 > 1$, then $u_n \le u_0,\ v_n \le v_0$. Hence, $u_n \le \max\{1, u_0\}$ and $v_n \le \max\{1, v_0\}$ for all $n \in \mathbb{N} \cup \{0\}$. ■

We now turn our attention to proving that under certain conditions the nonstandard scheme (11)-(12), must converge. We have already shown that the sequences $\{u_n\}$ and $\{v_n\}$ are bounded, so if it can be shown also that they are monotonic, the Monotone Sequence Theorem will yield the convergence result for $\{u_n\}$ and $\{v_n\}$ from (11)-(12). First follows a technical lemma necessary for the final result.

Lemma 4.4 *If $0 < b_1 < 1$, $a_1 = a_2 = b_2 = 1$, $1 - u_0 - v_0 - b_1 u_0^2 < 0$ and $1 - u_0 - v_0 - v_0^2 > 0$, then $1 - u_n - v_n - b_1 u_n^2 < 0$ for all $n \in \mathbb{N}$. If, in addition, $u_0 + b_1 u_0^2 \le 1$, then $1 - u_n - v_n - v_n^2 > 0$ for all $n \in N$.*

Proof. We will first show under the given conditions that $1 - u_1 - v_1 - v_1^2 > 0$. If $1 - v_0 - v_0^2 - u_0 > 0$ and $1 - u_0 - b_1 u_0^2 - v_0 < 0$, then applying the definitions (11)-(12),

$$1 - u_1 - v_1 - v_1^2 = \frac{1 - v_0 - u_0 - v_0^2 + A\Delta t + B\Delta t^2 + C\Delta t^3}{(1 + \Delta t u_0 + B_1 u_0^2 + \Delta t v_0)(1 + \Delta t u_0 + \Delta t v_0 + \Delta t v_0^2)^2}$$

where

$$
\begin{aligned}
A &= (1 - u_0 - v_0^2 - v_0)(3u_0 + b_1 u_0^2 + 2v_0) - (u_0 - u_0^2 - b_1 u_0^3 - u_0 v_0),\\
B &= (1 - u_0 - v_0^2 - v_0)(2u_0 + u_0^2 + 2u_0 v_0 + b_1 u_0^2 v_0 + u_0 v_0^2) - (2u_0 - 2u_0^2 - 2b_1 u_0^3 - 2u_0 v_0), \text{ and}\\
C &= (1 - u_0 - v_0 - v_0^2)(u_0 - b_1 u_0^3 - b_1 u_0^2 v_0^2 - v_0^3) - (u_0 - u_0^2 - b_1 u_0^3 - u_0 v_0).
\end{aligned}
$$

By assumption, we know that both $1 - v_0 - v_0^2 - u_0 > 0$, and $1 - u_0 - b_1 u_0 - v_0 < 0$, and since $u_0 > 0$,

$$u_0 - u_0^2 - b_1 u_0^3 - u_0 v_0 < 0.$$

Noting also that $u_0, v_0, b_1 > 0$, it follows that $A > 0$.

Similarly, since both $1 - v_0 - v_0^2 - u_0 > 0$ and $1 - u_0 - v_0^2 - v_0 < 0$, and $2u_0 > 0$, we have that

$$2u_0 - 2u_0^2 - 2b_1 u_0^3 - 2u_0 v_0 < 0.$$

And thus since $u_0, v_0, b_1 > 0$, we must have that $B > 0$.

Finally, since $1 - u_0 - b_1 u_0^2 - v_0 < 0$ and $u_0 > 0$, we must have that

$$u_0 - u_0^2 - b_1 u_0^3 - u_0 v_0 < 0.$$

We can also see that from $1 - u_0 - v_0 - v_0^2 > 0$, that we must have that $u_0 < 1$, then $b_1 < 1$, from which we obtain

$$u_0 - b_1 u_0^2 > 0.$$

By previous result we have that $b_1 u_0^2 > v_0^2$. Then $-b_1 u_0^2 v_0 < -v_0^3$, and thus

$$
\begin{aligned}
u_0 - b_1 u_0^3 - b_1 u_0^2 v_0^2 - v_0^3 &> u_0 - b_1 u_0^3 - b_1 u_0^2 v_0^2 - b_1 u_0^2 v_0\\
&= u_0 - b_1 u_0^2 + (b_1 u_0^2 - b_1 u_0^3 - b_1 u_0^2 v_0 - b_1 u_0^2 v_0^2)\\
&> 0
\end{aligned}
$$

since $1 - u_0 - v_0 - v_0^2 > 0$ and $b_1 u_0^2 > 0$. Thus if $0 < b_1 < 1$, then $C > 0$, as desired. We conclude that each coefficient of the expression above is positive, from which

$$1 - u_1 - v_1 - v_1^2 > 0,$$

follows, as desired. A similar inductive argument shows that

$$1 - u_n - v_n - v_n^2 > 0$$

for all $n \in \mathbb{N}$.

Now assume that, in addition to the previous conditions, $u_0 > 0$ satisfies $u_0 + b_1 u_0^2 \leq 1$. Then it follows that

$$1 - u_1 - b_1 u_1^2 - v_1 = \frac{1 - u_0 - b_1 u_0^2 - v_0 + A_1 \Delta t + B_1 \Delta t^2 + C_1 \Delta t^3}{(1 + \Delta t u_0 + b_1 \Delta t u_0^2 + \Delta t v_0)^2 (1 + \Delta t u_0 + \Delta t v_0 + \Delta t v_0^2)},$$

where A_1, B_1 and C_1 are defined by

$$
\begin{aligned}
A_1 &= 2u_0 - 2u_0^2 - 2b_1 u_0^3 + 2v_0 - 4u_0 v_0 - 3b_1 u_0^2 v_0 - v_0^2 - b_1 u_0^2 v_0^2 - u_0 v_0^2\\
B_1 &= u_0^2 - b_1 u_0^2 - u_0^3 + b_1 u_0^3 - b_1 u_0^4 + b_1^2 u_0^4 + 2u_0 v_0 - 3u_0^2 v_0 - 3b_1 u_0^3 v_0 - b_1^2 u_0^4 v_0 + v_0^2\\
&\quad - 2u_0 v_0^2 - u_0^2 v_0^2 - 2b_1 u_0^2 v_0^2 - b_1 u_0^3 v_0^2 + v_0^3 - u_0 v_0^3\\
C_1 &= -b_1 u_0^3 + b_1 u_0^4 + b_1^2 u_0^5 - b_1 u_0^2 v_0 + b_1 u_0^3 v_0 - b_1 u_0^2 v_0^2 + b_1 u_0^3 v_0^2 + b_1^2 u_0^4 v_0^2 + u_0 v_0^3 + 2b_1 u_0^2 v_0^3 + v_0^4.
\end{aligned}
$$

We claim that under the given conditions, A_1, B_1, and C_1 are all negative. To this end, we define constants $D_p > 0$ and $D_n < 0$ by

$$D_p = 1 - u_0 - v_0 - v_0^2 \quad \text{and} \quad D_n = 1 - u_0 - b_1 u_0^2 - v_0.$$

Dividing A_1, B_1 and C_1 by D_pD_n and applying partial fraction decomposition,

$$\frac{A_1}{D_pD_n} = \frac{-1+u_0+b_1u_0^2}{D_n} + \frac{1+u_0+2v_0}{D_p}, \tag{13}$$

$$\frac{B_1}{D_pD_n} = 1-u_0+\frac{-2+2u_0+2b_1u_0^2}{D_n} + \frac{1-b_1u_0^2+v_0+u_0v_0+b_1u_0^2v_0}{D_p}, \tag{14}$$

$$\frac{C_1}{D_pD_n} = b_1u_0^2+v_0+\frac{-1+u_0+b_1u_0^2}{D_n} + \frac{1-u_0-b_1u_0^2-v_0+u_0v_0+b_1u_0^2v_0}{D_p}, \tag{15}$$

since $D_pD_n < 0$ by assumption, if we can show that each of the preceding decompositions is positive, we can conclude that each of A_1, B_1 and C_1 is negative.

For (13), since $u_0 + b_1u_0^2 \leq 1$, the first numerator must be negative, so dividing by $D_n < 0$ gives us a positive value for the first fraction in this expression. Since the second fraction is positive, (13) is likewise positive.

Given that $1 - u_0 > 0$, applying similar reasoning we know that the first fraction in (14) is positive. Applying again the additional assumption $u_0 + b_1u_0^2 \leq 1$ to the second fraction, $1 - b_1u_0^2 \geq u_0$, so the last fraction is also positive.

Finally, for (15), since

$$1-b_1u_0^2-u_0+u_0v_0+b_1u_0^2v_0 \geq u_0-u_0+u_0v_0+b_1u_0^2v_0 = u_0v_0(1-b_1u_0) > 0,$$

all three fractions are positive, establishing the negativity of A_1, B_1 and C_1. This completes the proof that $1 - u_1 - b_1u_1^2 - v_1 < 0$.

A similar argument gives us that

$$1-u_n-b_1u_n^2-v_n<0$$

for all $n \in \mathbb{N}$. ■

Theorem 4.5 *If* $0 < b_1 < 1$ $a_1 = a_2 = b_2 = 1$, $1 - u_0 - b_1u_0^2 - v_0 < 0$, *and* $1 - u_0 - v_0 - v_0^2 > 0$, *then the sequence* $\{u_n\}$ *is monotone decreasing. If, in addition,* $u_0 + b_1u_0^2 \leq 1$, *then* $\{v_n\}$ *is monotone increasing.*

Proof. By the previous theorem, if $0 < b_1 < 1$ then

$$1 < u_n + v_n + b_1u_n^2$$

for all $n \in \mathbb{N}$, so that

$$u_{n+1} = \frac{u_n(1+\Delta t)}{1+\Delta t(u_n+v_n+b_1u_n^2)} \leq \frac{u_n(1+\Delta t)}{1+\Delta t} = u_n.$$

A similar application of the previous theorem gives that

$$1 > u_n + v_n + v_n^2,$$

from which it follows that

$$v_{n+1} = \frac{v_n(1+\rho\Delta t)}{1+\rho\Delta t(v_n+u_n+v_n^2)} \geq \frac{v_n(1+\rho\Delta t)}{1+\rho\Delta t} = v_n,$$

as desired. ■

The conditions stated in Theorem 4.5 are not without meaning for the biological system introduced in Section 2. Recalling the definitions of the constants in equations (2), we now analyze what these assumptions tell us about the constants in (1). We have that

$$b_1 = d_1\frac{e_1^\delta}{c_1}.$$

Now, since $\beta_1 = \frac{c_1}{e_1}$, and $c_1 = \beta_1 - m_{10}$, this becomes

$$b_1 = d_1 \beta_1^{-1} e_1^{\delta - 1}.$$

Since we have assumed that $\delta = 2$, this can be rearranged to become

$$\beta_1 = d_1 e_1 b_1^{-1}.$$

The assumption that $0 < b_1 < 1$, then permits us to write

$$\beta_1 = d_1 e_1 b_1^{-1} > d_1 e_1.$$

Now, since $e_1 = \frac{c_1}{\beta_1} = \frac{\beta_1 - m_{10}}{\beta_1}$, this becomes

$$\beta_1 > d_1 \left(\frac{\beta_1 - m_{10}}{\beta_1} \right).$$

Thus the condition that $0 < b_1 < 1$ becomes this relation between the birth and death rates of species 1, as well as the density-dependent factor for the death rate of species 1. This can be interpreted as meaning the density-dependent factor must not be so great that this inequality fails. Now let us consider the condition $a_1 = 1$. Recall that in section 2, we set

$$a_1 = \frac{\alpha_{12} e_2}{e_1}, \qquad e_1 = \frac{c_1}{\beta_1},$$
$$e_2 = \frac{c_2}{\beta_2}, \qquad c_1 = \beta_1 - m_{10},$$

and

$$c_2 = \beta_2 - m_{20}.$$

This gives us that

$$1 = a_1 = \frac{\alpha_{12} e_2}{e_1} = \frac{\alpha_{12} \beta_1 c_2}{\beta_2 c_1} = \frac{\alpha_{12} \beta_1 (\beta_2 - m_{20})}{\beta_2 (\beta_1 - m_{10})}.$$

Simlarly, we calculate that

$$1 = a_2 = \frac{\alpha_{21} \beta_2 (\beta_1 - m_{10})}{\beta_1 (\beta_2 - m_{20})}.$$

Finally, let us consider the condition that $b_2 = 1$. Since

$$1 = b_2 = \frac{d_2 e_2^{\delta}}{c_2},$$

we can use the definitions of e_2 and c_2 to write this as

$$1 = b_2 = d_2 (\beta_2 - m_{20})^{\delta - 1} \beta_2^{-\delta}.$$

Now, since $\delta = 2$, this can be written as

$$1 = b_2 = \frac{d_2 (\beta_2 - m_{20})}{\beta_2^2}.$$

So, the condition that $b_2 = 1$ becomes

$$\frac{d_2 (\beta_2 - m_{20})}{\beta_2^2} = 1.$$

These results are summarized in the following table, where the conditions on the parameters of the nondimensionalized system are on the left, and what those conditions imply about the parameters of the original system are on the right.

$$a_1 = 1 \quad \rightarrow \quad \frac{\alpha_{12} \beta_1 (\beta_2 - m_{20})}{\beta_2 (\beta_1 - m_{10})} = 1$$
$$a_2 = 1 \quad \rightarrow \quad \frac{\alpha_{21} \beta_2 (\beta_1 - m_{10})}{\beta_1 (\beta_2 - m_{20})} = 1$$
$$b_2 = 1 \quad \rightarrow \quad \frac{d_2 (\beta_2 - m_{20})}{\beta_2^2} = 1.$$

Under the assumptions of Theorem 4.5, and applying the Monotone Sequence Theorem, the sequences $\{u_n\}$ and $\{v_n\}$ defined in (11)-(12) converge. We study more about this convergence and its accuracy next.

5 Convergence to the True Solution

Let $U_n = u(t_n)$ and $V_n = v(t_n)$ represent the theoretical solutions to (2). Then it follows that

$$\frac{U_{n+1}-U_n}{\Delta t} = U_n(1-U_n-a_1V_n-b_1U_n^2)+O(\Delta t),$$
$$\frac{V_{n+1}-V_n}{\Delta t} = \rho V_n(1-V_n-a_2U_n-b_2V_n^2)+O(\Delta t).$$

Define the difference between true solutions to (2) and (11)-(12) by $X_n = U_n - u_n$ and $Y_n = V_n - v_n$. Then

$$\begin{aligned}
|X_{n+1}-X_n| &= |U_{n+1}-U_n-(u_{n+1}-u_n)| \\
&= |\Delta t U_n(1-U_n-a_1V_n-b_1U_n^2)+O(\Delta t^2) \\
&\qquad -\Delta t(u_n-u_nu_{n+1}-a_1v_nu_{n+1}-b_1u_n^2u_{n+1})|+O(\Delta t^2) \\
&= |\Delta t(U_n-u_n)+\Delta t(u_nu_{n+1}-U_n^2)+\Delta t b_1(u_n^2u_{n+1}-U_n^3) \\
&\qquad +\Delta t a_1(v_nu_{n+1}-U_nV_n)|+O(\Delta t^2) \\
&\leq \Delta t|U_n-u_n|+\Delta t|u_nu_{n+1}-U_n^2|+\Delta t b_1|u_n^2u_{n+1}-U_n^3| \\
&\qquad +\Delta t a_1|v_nu_{n+1}-U_nV_n|+O(\Delta t^2).
\end{aligned} \tag{16}$$

Now

$$\begin{aligned}
u_nu_{n+1}-U_n^2 &= u_nu_{n+1}-u_nU_n+u_nU_n-U_n^2 \\
&= u_n(u_{n+1}-U_n)+U_n(u_n-U_n) \\
&= u_n(u_{n+1}-u_n+u_n-U_n)+U_n(u_n-U_n) \\
&= u_n(O(\Delta t)-X_n)-U_nX_n
\end{aligned}$$

and

$$\begin{aligned}
u_n^2u_{n+1}-U_n^3 &= u_n^2u_{n+1}-u_nU_n^2+u_nU_n^2-U_n^3 \\
&= u_n(u_nu_{n+1}-U_n^2)+U_n^2(u_n-U_n) \\
&= u_n(u_nu_{n+1}-u_{n+1}U_n-U_n^2)-U_n^2X_n \\
&= u_n(-u_{n+1}X_n+U_n(u_{n+1}-U_n))-U_n^2X_n \\
&= u_n(-u_{n+1}X_n+U_n(O(\Delta t)-X_n))-U_n^2X_n.
\end{aligned}$$

Finally,

$$\begin{aligned}
v_nu_{n+1}-U_nV_n &= v_nu_{n+1}-u_{n+1}V_n+u_{n+1}V_n-U_nV_n \\
&= u_{n+1}(v_n-V_n)+V_n(u_{n+1}-U_n) \\
&= -u_{n+1}Y_n+V_n(O(\Delta t)-X_n).
\end{aligned}$$

These three preceding equalities together with (16) yield the result

$$\begin{aligned}
|X_{n+1}-X_n| &\leq \Delta t|U_n-u_n|+\Delta t|u_nu_{n+1}-U_n^2| \\
&\qquad +\Delta t b_1|u_n^2u_{n+1}-U_n^3|+\Delta t a_1|v_nu_{n+1}-U_nV_n|+O(\Delta t^2) \\
&\leq \Delta t|X_n|+\Delta t|u_n(O(\Delta t)-X_n)-U_nX_n| \\
&\qquad +\Delta t b_1|u_n(-u_{n+1}X_n+U_n(O(\Delta t)-X_n))-U_n^2X_n| \\
&\qquad +\Delta t a_1|-u_{n+1}Y_n+V_n(O(\Delta t)-X_n)|+O(\Delta t^2).
\end{aligned}$$

Which, after expanding and collecting like terms, gives

$$\begin{aligned}|X_{n+1}-X_n| &\leq \Delta t(1+|u_n|+|U_n|+b_1|u_nu_{n+1}|+b_1|u_nU_n|+b_1U_n^2+a_1|V_n|)|X_n| \\ &\quad +\Delta t a_1|u_{n+1}||Y|+O(\Delta t^2).\end{aligned}$$

Now, since u_n, v_n, U_n, and V_n are all bounded above, define constants C_1 and C_2 by

$$\begin{aligned}&C_1 = 1+|u_n|+|U_n|+b_1|u_nu_{n+1}|+b_1|u_nU_n|+b_1U_n^2+a_1|V_n|,\\ &C_2 = a_1u_{n+1}.\end{aligned}$$

Then

$$|X_{n+1}-X_n| \leq \Delta t C_1|X_n|+\Delta t C_2|Y_n|+O(\Delta t^2).$$

Now, applying the triangle inequality,

$$\begin{aligned}|X_{n+1}| &\leq |X_{n+1}-X_n|+|X_n| \\ &\leq (1+\Delta t C_1)|X_n|+\Delta t C_2|Y_n|+O(\Delta t^2).\end{aligned}$$

We follow a similar procedure to measure $|Y_{n+1}-Y_n|$.

$$\begin{aligned}|Y_{n+1}-Y_n| &= |V_{n+1}-V_n-(v_{n+1}-v_n)| \\ &= |\rho\Delta t V_n(1-V_n-a_2U_n-b_2V_n^2)+O(\Delta t^2) \\ &\quad -\Delta t(\rho v_n-\rho v_nv_{n+}-\rho a_2u_nv_{n+1}-\rho b_2v_n^2v_{n+1})| \\ &= |\rho\Delta t(V_n-v_n)+\rho\Delta t(v_nv_{n+1}-V_n^2) \\ &\quad +\rho\Delta t a_2(u_nv_{n+1}-U_nV_n)+\rho\Delta t b_2(v_n^2v_{n+1}-V_n^3)| \\ &\leq \rho\Delta t|V_n-v_n|+\rho\Delta t|v_nv_{n+1}-V_n^2|+\rho\Delta t a_2|u_nv_{n+1}-U_nV_n| \\ &\quad +\rho\Delta t b_2|v_n^2v_{n+1}-V_n^3|.\end{aligned}$$

Since

$$\begin{aligned}v_nv_{n+1}-V_n^2 &= v_nv_{n+1}-v_{n+1}V_n+v_{n+1}V_n-V_n^2 \\ &= -v_{n+1}Y_n+V_n(v_{n+1}-v_n+v_n-V_n) \\ &= -v_{n+1}Y_n+V_n(O(\Delta t)-Y_n),\end{aligned}$$

$$\begin{aligned}u_nv_{n+1}-U_nV_n &= u_nv_{n+1}-u_nV_n+u_nV_n-U_nV_n \\ &= u_n(v_{n+1}-V_n)-V_nX_n \\ &= u_n(O(\Delta t)-Y_n)-V_nX_n,\end{aligned}$$

and

$$\begin{aligned}v_n^2v_{n+1}-V_n^3 &= v_n^2v_{n+1}-v_nV_n^2+v_nV_n^2-V_n^3 \\ &= v_n(v_nv_{n+1}-V_n^2)-V_n^2Y_n \\ &= v_n(v_nv_{n+1}-v_nV_n+v_nV_n-V_n^2)-V_n^2Y_n \\ &= v_n(v_n(O(\Delta t)-Y_n)-V_nY_n)-V_n^2Y_n,\end{aligned}$$

it follows that

$$\begin{aligned}|Y_{n+1}-Y_n| &\leq \rho\Delta t|V_n-v_n|+\rho\Delta t|v_nv_{n+1}-V_n^2|+\rho\Delta t a_2|u_nv_{n+1}-U_nV_n| \\ &\quad +\rho\Delta t b_2|v_n^2v_{n+1}-V_n^3|+O(\Delta t^2) \\ &= \rho\Delta t|Y_n|+\rho\Delta t|-v_{n+1}Y_n+V_n(O(\Delta t)-Y_n)|+\rho\Delta t a_2|u_n(O(\Delta t)-Y_n)-V_nX_n| \\ &\quad +\rho\Delta t b_2|v_n(v_n(O(\Delta t)-Y_n)-V_nY_n)-V_n^2Y_n|+O(\Delta t^2).\end{aligned}$$

Expanding and collecting like terms again,

$$\begin{aligned} |Y_{n+1} - Y_n| &\leq \rho\Delta t(1 + |v_{n+1}| + |V_n| + a_2|u_n| + b_2|v_n| + b_2|V_n| + b_2V_n^2)|Y_n| \\ &\quad + \rho\Delta t a_2|V_n||X_n| + O(\Delta t^2). \end{aligned}$$

Similarly, since u_n, v_n, U_n, and V_n are all bounded above, define constants C_3 and C_4 by

$$\begin{aligned} C_3 &= 1 + |v_{n+1}| + |V_n| + a_2|u_n| + b_2|v_n| + b_2|V_n| + b_2V_n^2 \\ C_4 &= a_2|V_n|. \end{aligned}$$

Then

$$|Y_{n+1} - Y_n| \leq \rho\Delta t C_3|Y_n| + \rho\Delta t C_4|X_n| + O(\Delta t^2).$$

By reasoning to that as for the error term X_n,

$$|Y_{n+1}| \leq (1 + \rho\Delta t C_3)|Y_n| + \rho\Delta t C_4|X_n| + O(\Delta t^2).$$

For the final error terms and analysis, define $|W_n| = |X_n| + |Y_n|$. Then by the preceding analysis,

$$|W_{n+1}| = |X_{n+1}| + |Y_{n+1}| \leq (1 + \Delta t(C_1 + \rho C_4))|X_n| + (1 + \Delta t(C_2 + \rho C_3))|Y_n| + O(\Delta t^2).$$

Let $C = \max\{C_1 + \rho C_4, C_2 + \rho C_3\}$, then it follows that

$$\begin{aligned} |W_{n+1}| = |X_{n+1}| + |Y_{n+1}| &\leq (1 + \Delta t C)|X_n| + (1 + \Delta t C)|Y_n| + O(\Delta t^2) \\ &= (1 + \Delta t C)(|X_n| + |Y_n|) + O(\Delta t^2), \end{aligned}$$

which finally yields

$$W_{n+1} \leq (1 + \Delta t C)W_n + O(\Delta t^2).$$

This analysis leads to a theorem with a uniform bound on the error term W_n over a finite time interval. The next result gives us an upper bound for the error at any point in the nonstandard numerical method.

Theorem 5.1 *For all $n \in \mathbb{N} \cup \{0\}$,*

$$W_n \leq \sum_{i=0}^{n} O(\Delta t^2)(1 + C\Delta t)^i.$$

Proof. Since $W_0 = 0$, the result is true for $n = 0$. Now assume that for some $k \in \mathbb{N} \cup \{0\}$, that

$$W_k \leq \sum_{i=0}^{k} O(\Delta t^2)(1 + C\Delta t)^i.$$

Then we have that

$$\begin{aligned} W_{k+1} &\leq (1 + \Delta t C)W_n + O(\Delta t^2) \\ &\leq (1 + \Delta t C)\sum_{i=0}^{k} O(\Delta t^2)(1 + C\Delta t)^i + O(\Delta t^2) \\ &= \sum_{i=0}^{k} O(\Delta t^2)(1 + C\Delta t)^{i+1} + O(\Delta t^2) \\ &= \sum_{i=0}^{k+1} O(\Delta t^2)(1 + C\Delta t)^i. \end{aligned}$$

This completes the proof. ■

If we consider the interval $[0, T]$, where $T \in \mathbb{R}$ such that $T > 0$, and let

$$\frac{T}{n} = \Delta t.$$

Then we can write

$$\begin{aligned} W_n &\leq \sum_{i=0}^{n} O(\Delta t^2)(1 + C\Delta t)^i \\ &= \sum_{i=0}^{n} O(\Delta t^2)\left(1 + \frac{TC}{n}\right)^i \\ &= \frac{O(\Delta t^2)\left(\left(1 + \frac{TC}{n}\right)^{n+1} - 1\right)}{\left(1 + \frac{TC}{n}\right) - 1} \\ &= O(\Delta t^2)\frac{n}{TC}\left(\left(1 + \frac{TC}{n}\right)^{n+1} - 1\right) \\ &= O(\Delta t)\left(\left(1 + \frac{TC}{n}\right)^{n+1} - 1\right). \end{aligned}$$

Now, since we have that

$$\lim_{n\to\infty}\left(1 + \frac{TC}{n}\right)^{n+1} - 1 = e^{TC} - 1,$$

we must have that it is bounded, since the sequence converges. Let M be an upper bound for this sequence, then we have that

$$W_n \leq O(\Delta t)\left(\left(1 + \frac{TC}{n}\right)^{n+1} - 1\right) \leq O(\Delta t)M = O(\Delta t).$$

Thus, as we increase the number of subdivisions of the interval $[0, T]$, our numerical scheme converges uniformly to the true solution of the differential equations (2). This is summarized in the following theorem.

Theorem 5.2 *The numerical scheme given in (11)-(12) converges to the solution of equations (2), uniformly on the interval* $[0, T]$*, as* $n \to \infty$.

6 Numerical Experiments

In this section, we present some results of computational experiments to show that the proposed difference scheme is stable and gives reasonable solutions.

In Figure 2, we have chosen $a_1 = 4$, $b_1 = 1$, $a_2 = 1$, $b_2 = 2$, $\rho = 1$, $\Delta t = 0.01$, $u_0 = 0.8$, and $v_0 = 0.9$. These constants yield the steady state $(0, 0.5)$, which is a steady state of type (3). Note that in section 3, for steady steady state 2, $(0, 0.5)$ is a stable steady state. Convergence is demonstrated in the figure.

For Figure 3, we chose $a_1 = 1$, $b_1 = 0.85$, $a_2 = 1$, $b_2 = 1$, $\rho = 1$, $\Delta t = 0.01$, $u_0 = 0.5$, and $v_0 = 0.3$. So that

$$\begin{aligned} 1 - u_0 - b_1u_0^2 - v_0 = -0.0125 < 0 \qquad \text{and} \\ 1 - vu_0 - v_0 - v_0^2 = 0.11 > 0, \end{aligned}$$

and thus we can use Theorem 4.5, to say that $\{u_n\}$ is monotone decreasing. In addition, since $u_0 + b_1u_0^2 = 0.7125 \leq 1$, we also have that $\{v_n\}$ is monotone increasing. The graph in Figure 3 shows the predicted behaviour of both $\{u_n\}$ and $\{v_n\}$. In this figure, (u_n, v_n) approaches $(0.44, 0.4)$ by Theorem 5.2.

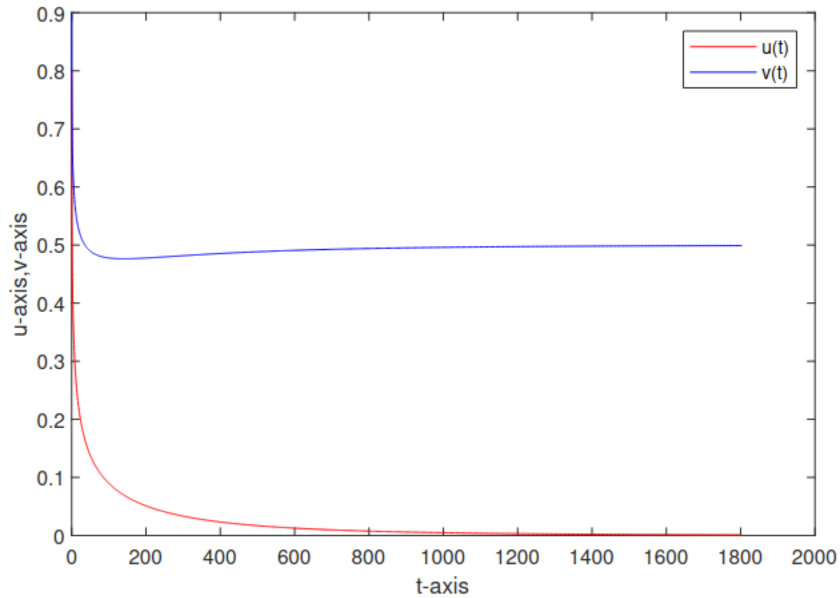


Figure 2

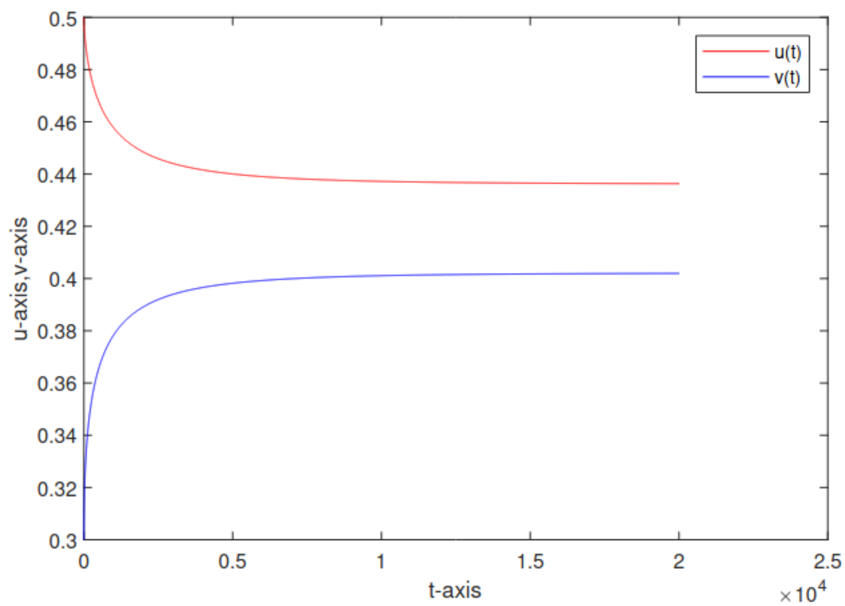


Figure 3

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