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The impact of different definitions of growth rate on cyclic dominance systems

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Abstract

In the study of cyclic dominance systems, there are typically two different definitions for the concept of 'growth rate'. These definitions have an influence on the behavior and final state of coexistence of the systems. In this paper, we investigated this influence using both analytical and numerical methods. We first found fixed points of the two-species and three-species systems, and performed a stability analysis to identify how systems with different definitions behave differently. We then used the method of finite difference on the partial differential equation systems to simulate two-species and three-species competitive systems in two-dimensions. Using MATLAB, we compared the different behavior of the systems with different definitions and obtained supporting numerical results for our analytical results. We also discovered that the final states of systems with different definitions responded differently to changing parameters. Therefore, we concluded that studies using different definitions of the growth rate may yield different, or even diametrically opposite results.

Keywords

Cyclic ecosystem, Growth rate, Partial differential equations, Stability analysis, Finite difference, Cyclic dominance, Three species competitive systems, Coexistance state, Birth term, Predator prey relationship.

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1. Introduction

In cyclic dominance systems, one species is dominated by another, and the chain of dominance forms a cycle (no hierarchical predatory chains) (1). The behavior of cyclic dominance systems is a widely studied topic. Kerr et. al. (1) showed that the stability and pattern of coexistence of a system consisting of colicin-producing bacteria, sensitive bacteria, and resistant bacteria depends on the size of neighboring area affecting each strain. Weber et. al. (2) explored the relationship between the final state of the same system and the growth rate, toxin effect range and the initial proportion of the different strains.

Research featuring this topic typically use one of the two distinct definitions of the 'growth rate' of bacteria: using a system consisting of two competing species u and v as an example, one definition of the growth rate of u would be $\frac{du}{dt} = ru\,(1 - u - \alpha v)$, and the other definition would be $\frac{du}{dt} = u(r - u - \alpha v)$. Researchers tend to adopt either one of those definitions, sometimes without clarification on which one they specifically used despite the real-world implications of using one definition over the other. For example, Weber et. al. (2) used the first definition, and Kerr et al. (1) used the second one, but neither one justified their choice.

In this paper, we investigate whether using the different definitions causes different results in problems involving cyclic dominance systems. Doing so will either support or challenge existing research in the field, and in doing so will add further rigor to future research.

In Section 2, we present the two definitions of growth rate. In Section 3, we use analytical methods to investigate properties about the definitions and identify differences in the two partial differential equation (PDE) systems' fixed points and their stability. In Section 4, we describe the numerical methods used to construct a mathematical model and simulate the two definitions. In Section 5, we present the result of the simulation and the qualitative conclusions. In Section 6, we comment on the study as a whole and discuss future directions.

2. The Two Definitions

The entire cyclic dominance system can be described by multiple differential equations. The growth rate of a certain species u refers to the derivative of its population with respect to time, or $\frac{du}{dt}$. The expression of each species' growth rate suffices to describe a system's behavior over time.

For cyclic dominance systems, the growth rates of a species is predominantly affected by its own population and by the population of the species that dominates it. The effects of other species' populations are usually too weak to cause qualitatively significant differences. Therefore a species' growth rate is predominantly determined by the former two attributes in mathematical models (3,4).

We present the two definitions of the growth rate used in existing researches most frequently.

2.1 Two Definitions of Growth Rate

For a cyclic dominance system consisting of n species $u_1, u_2, \cdots, u_n$, the first definition of growth rate of u_i is

$$\frac{du_i}{dt} = r_i u_i (1 - u_i - \alpha u_j), \tag{1}$$

and the second definition is

$$\frac{du_i}{dt} = u_i (r_i - u_i - \alpha u_j), \tag{2}$$

where $j = i + 1 \bmod n$ j = (i mod n) +1 in both cases (3).

The right hand side (RHS) of Equation (1) expands into the expression r_iu_i-$r_iu_i^2$-$\alpha r_1u_iu_j$, and the RHS of Equation (2) expands into the expression r_iu_i-u_i^2-αu_iu_j. These terms after expansion have real-life significance: r_iu_i represents the species' exponential growth, referred to as the *birth term*; -$r_iu_i^2$ in Equation (1) and -u_i^2 in Equation (2) represent the effect of resource shortage caused by overcrowding, referred to as the *intraspecies death terms*; αu_j-$\alpha r_1u_iu_j$ in Equation (1) and -αu_iu_j in Equation (2) represents the effect of either the direct predator-prey relationship or the interspecies competition on resources, referred to as *interspecies death terms* (4). The constant α represents the level of competition: the larger α is, the more intense the competition is. Apparently, the difference between the two definitions is whether the constants r_1, $r_2 \ldots r_n$ impact only the birth term, or influence all the terms.

The two systems of ordinary differential equations (ODEs) above only consider global effects. Since local dispersal has impact on the final state of the systems (1), we considered the local interactions in a two-dimensional space and converted the definitions into PDEs,

$$\frac{\partial u_i}{\partial t} = \frac{\partial^2 u_i}{\partial x^2} + \frac{\partial^2 u_i}{\partial y^2} + r_i u_i (1 - u_i - \alpha u_j) \tag{3}$$

$$\frac{\partial u_i}{\partial t} = \frac{\partial^2 u_i}{\partial x^2} + \frac{\partial^2 u_i}{\partial y^2} + u_i (r_i - u_i - \alpha u_j) . \tag{4}$$

2.2 Relationships between the Two Systems

Consider Equation (2):

$$\frac{du_i}{dt} = u_i (r_i - u_i - \alpha u_j) .$$

Let $u_i = u'_i r_i$ for all integers $1 \le i \le n$, then

$$r_i \frac{du'_i}{dt} = u'_i r_i (r_i - u'_i r_i - \alpha u'_j r_j) ,$$

$$\frac{du'_i}{dt} = u'_i r_i \left(1 - u'_i - \alpha u'_j \frac{r_j}{r_i}\right).$$

Let $\alpha'_i = \alpha \frac{r_j}{r_i}$, then

$$\frac{du'_i}{dt} = u'_i r_i (1 - u'_i - \alpha'_i u'_j). \quad (5)$$

Equation (5) is the result of a transformation that turns Equation (2) into one that has a similar structure to Equation (1). However, Equation (5) makes the value of α in each equation different. This technically means that Equation (1) and Equation (2) are isomorphic. However, existing research using different definitions does not assign the values of parameters in isomorphic ways. For example, existing research simply assigns the same values for α in each equation when the competition between species is even, whereas according to the transformation above, the system with the second definition would need a different value of α.

3. Analysis

We used analytical methods to derive properties about the two systems. We found the fixed points of the systems and performed a stability analysis.

For simplicity, u_1 and u_2 are referred to as u and v respectively in two-species systems, and u_1, u_2 and u_3 are referred to as u, v and w respectively in three-species systems.

3.1 Background: Stability Analysis

Solving certain systems of differential equations analytically can be tedious; if not impossible. However, using analytical methods, it is still possible to obtain certain properties of differential equation systems without an end result. *Stability analysis* is one such method that analyzes whether each fixed point of the system is a point of convergence, or a point of divergence.

To find the fixed points of the system, the value of each differential term is set to 0 such that the values do not change with respect to time. This turns the system into elementary equations that output fixed points in the system as solutions.

To perform the stability analysis, we first found the Jacobian matrix of the system, the $n \times n$ matrix where n is the total amount of variables and the term at ith row and jth column is the i th equation's partial derivative with respect to the jth variable.

To analyze the stability of a certain fixed point, the values of the variables at the points were substituted into the Jacobian matrix and the eigenvalues were computed. If all eigenvalues are negative, then the point was considered *stable*; conversely, if all eigenvalues were positive, the point was *unstable*; if both positive and negative eigenvalues existed, then the point was *semi-stable*. A stable fixed point is a point of convergence; implying that other points in the system tend to converge towards it over time; an unstable point is a point of divergence; implying that other points in the system tend to diverge from it over time; a semi-stable point is a point of convergence in certain dimensions and a point of divergence in

others, but it is usually considered simply as an unstable point (5).

According to Bayliss et al. (4), the fixed points and stabilities of the PDE system and the corresponding ODE system have negligible differences. Therefore, to simplify calculations, we analyzed the ODE system.

3.2 Stability Analysis: Two Species

Consider the two-species ODE system with the first definition Equation (1):

$$\frac{du}{dt} = r_1 u(1 - u - \alpha v) \quad \frac{dv}{dt} = r_2 v(1 - v - \alpha u) \tag{6a}$$

$$\frac{du}{dt} = r_1 u(1 - u - \alpha v) \quad \frac{dv}{dt} = r_2 v(1 - v - \alpha u) \,. \tag{6b}$$

The fixed points and their stabilities are:

1. (0,0), always unstable;
2. (1,0), (0,1), both semi-stable when $0 < \alpha < 1$ and both stable when $\alpha \geq 1$;
3. $(\frac{1}{\alpha + 1}, \frac{1}{\alpha + 1})$, always stable.

Consider the two-species ODE system with the second definition Equation (2):

$$\frac{du}{dt} = u(r_1 - u - \alpha v) \tag{7a}$$

$$\frac{dv}{dt} = v(r_2 - v - \alpha u) \,. \tag{7b}$$

The fixed points and their stabilities are:

1. (0,0), always unstable;
2. (r_1,0), semi-stable when $0 < \alpha < \frac{r_2}{r_1}$, and stable when $\alpha \geq \frac{r_2}{r_1}$;
3. (0,r_2), semi-stable when $0 < \alpha < \frac{r_1}{r_2}$, and stable when $\alpha \geq \frac{r_1}{r_2}$;
4. $(\frac{\alpha r_2 - r_1}{\alpha^2 - 1}, \frac{\alpha r_1 - r_2}{\alpha^2 - 1})$,

a) if $r_2 > r_1$, then the point is stable for $0 < \alpha \leq \frac{r_1}{r_2}$ or $1 \leq \alpha \leq \frac{r_2}{r_1}$ and is semi-stable for $\frac{r_1}{r_2} < \alpha < 1$ or $\alpha > \frac{r_2}{r_1}$;

b) if $r_1 > r_2$, then the point is stable for $0 < \alpha \leq \frac{r_2}{r_1}$ or $1 < \alpha \leq \frac{r_1}{r_2}$ and is semi-stable for $\frac{r_2}{r_1} < \alpha < 1$ or $\alpha > \frac{r_1}{r_2}$;

c) if $r_1 = r_2$, then the point is stable for $0 < \alpha \leq 1$ and semi-stable for $\alpha > 1$.

Using stability analysis, we find that Equation (6) and Equation (7) have different fixed points and different stability. Even the number of stable fixed points can be different. This means the two definitions are likely to impact the behavior of the systems.

It is worth noting that the stability of Equation (6) is not affected by the values of *r*s, whereas Equation (7) is.

3.3 Stability Analysis: Three Species

Consider the three-species ODE system with the first definition Equation (1):

$$\frac{du}{dt} = r_1 u(1 - u - \alpha v) \tag{8a}$$

$$\frac{dv}{dt} = r_2 v(1 - v - \alpha w) \tag{8b}$$

$$\frac{dw}{dt} = r_3 w(1 - w - \alpha u). \tag{8c}$$

The fixed points and their stabilities are:

1. (0,0,0), always unstable;
2. (0,0,1), (0,1,0), (1,0,0), always semi-stable;
3. $(0,1-\alpha,1),(1-\alpha,1,0),(1,0,1-\alpha)$, always semi-stable (Also notice that the cases where α is larger than 1 is not physically possible);
4. $(\frac{1}{\alpha+1}, \frac{1}{\alpha+1}, \frac{1}{\alpha+1})$, stable when $\alpha \leq 2$ and semi-stable when $\alpha > 2$.

Consider the three-species ODE system with the second definition Equation (2):

$$\frac{du}{dt} = u(r_1 - u - \alpha v) \tag{9a}$$

$$\frac{dv}{dt} = v(r_2 - v - \alpha w) \tag{9b}$$

$$\frac{dw}{dt} = w(r_3 - w - \alpha u). \tag{9c}$$

The fixed points and their stabilities are:

1. (0,0,0), always unstable;
2. $(0,0,r_3)$, $(0,r_2,0)$, $(r_1,0,0)$, always semi-stable;
3. $(0,r_2-\alpha r_3,r_3)$, $(r_1-\alpha r_2,r_2,0)$, $(r_1,0,r_3-\alpha r_1)$, , the point $(0,r_2-\alpha r_3,r_3)$ is stable when $\frac{r_2-\sqrt{r_2^2-4r_1r_3}}{2r_3}<\alpha<\frac{r_2+\sqrt{r_2^2-4r_1r_3}}{2r_3}$ and semi-stable otherwise, the other two points have symmetrical conditions for stability;
4. $(\frac{\alpha^2r_3-\alpha r_2+r_1}{(\alpha^2-\alpha+1)(\alpha+1)},\frac{\alpha^2r_1-\alpha r_3+r_2}{(\alpha^2-\alpha+1)(\alpha+1)},\frac{\alpha^2r_2-\alpha r_1+r_3}{(\alpha^2-\alpha+1)(\alpha+1)})$, stable when $\frac{r_1+r_2+r_3}{\alpha+1}\geq 1$ and semi-stable when $0<\frac{r_1+r_2+r_3}{\alpha+1}<1$ (4).

Similarly, we also identify large differences between the fixed points and stability of Equation (8) and Equation (9), indicating difference in behavior. The fact that the total number of stable fixed points may vary and that only the stability of Equation (9) depends on the values of *r*s resembles the conclusions from Section 3.2 and implies model consistency.

4. Simulation Methodology

Our objective was to answer the following questions using simulation:

1. Does our stability analysis accurately predict the behavior of the systems?
2. With fixed parameters, do the systems behave as predicted?
3. Is there an overall difference in the final pattern of coexistence between the systems?
4. Do systems with different definitions have different correlations with changing parameters?

We used finite differential equations to simulate the behavior of the PDE systems. We first simulated two-species systems in two-dimensional spaces to obtain direct evidence of difference between the two systems and to test our analytical results. We then simulated three-species systems in two-dimensional spaces to explore whether the final state of systems with different definitions responded differently to the value of growth rate and initial proportions of the species, identifying if the results of studies such as Weber et al. (2) were consistent with both definitions.

4.1 Background: Finite Differentials

Finite difference is a method used to approximate numerical solutions of differential equations. It uses the difference between function values over small ranges to approximate differentiation, transforming continuous functions into finite, discrete ones that can be approximated using computers.

Using the definition of derivatives, we can approximate first-order derivatives through the method of finite difference in the following way:

$$\frac{df(x)}{dx}=\lim_{h\to 0}\frac{f(x+h)-f(x)}{h}$$

Let $x=a$, then

$$f'(a) = \lim_{h \to 0} \frac{f(a+h) - f(a)}{h} \approx \frac{f(a+\Delta a) - f(a)}{\Delta a}, \quad (10)$$

where Δa takes a small value.

To approximate second-order derivatives, consider the Taylor series:

$$f(x) = \sum_{n=0}^{\infty} \frac{f^{(n)}(a)}{n!}(x-a)^n = f(a) + f'(a)(x-a) + \frac{f''(a)}{2}(x-a)^2 + O((x-a)^2).$$

$$f(x) = \sum_{n=0}^{\infty} \frac{f^{(n)}(a)}{n!}(x-a)^n = f(a) + f'(a)(x-a) + \frac{f''(a)}{2}(x-a)^2 + O(x^2)$$

*Let $x = a + \Delta a$ and $x = a - \Delta a$ respectively, where Δa takes a small value, we have

$$f(a+\Delta a) = f(a) + f'(a)\Delta a + \frac{f''(a)}{2}\Delta a^2 + O(\Delta a^2)$$
$$f(a-\Delta a) = f(a) - f'(a)\Delta a + \frac{f''(a)}{2}\Delta a^2 + O(\Delta a^2)$$

$$f(a+\Delta a) = f(a) + f'(a)\Delta a + \frac{f''(a)}{2}\Delta a^2 + O(a^2)$$

$$f(a-\Delta a) = f(a) - f'(a)\Delta a + \frac{f''(a)}{2}\Delta a^2 + O(a^2),$$

Thus

$$f(a+\Delta a) + f(a-\Delta a) = 2f(a) + f''(a)\Delta a^2 + O(\Delta a^2)$$

$$f(a+\Delta a) + f(a-\Delta a) = 2f(a) + f''(a)\Delta a^2 + O(a^2),$$

$$f''(a) \approx \frac{f(a+\Delta a) + f(a-\Delta a) - 2f(a)}{\Delta a^2}, \quad (11)$$

Although Δa is small, since it is still a finite value, we can use the method of finite difference to approximate first and second order differentiation. This method works for both ordinary and partial differentiation (6).

Dynamic systems can all be expressed as sets of functions of time and space $f(t, x, y, \ldots)$. With the method of finite difference, we break the time t into discrete *timesteps* Δt and the space into discrete *grids* with Δx, Δy, etc., denoting the coordinates (6). The value of timesteps and the length of grids are fixed, so a specific time can be denoted as "nth timestep," and a specific location can be written as coordinates. We use a superscript to denote the function's current timestep and a subscript to denote its coordinates in space.

4.2 The Model: Two Species

Using finite approximations, we turn the first system

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + r_1 u(1 - u - \alpha v)$$
$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} + r_2 v(1 - v - \alpha u)$$

into the following system of equations:

$$u_{j,k}^{n+1} = u_{j,k}^n + \Delta t\left(\frac{u_{j-1,k}^n + u_{j+1,k}^n - 2u_{j,k}^n}{\Delta x^2} + \frac{u_{j,k-1}^n + u_{j,k+1}^n - 2u_{j,k}^n}{\Delta y^2} + r_1 u_{j,k}^n\left(1 - u_{j,k}^n - \alpha v_{j,k}^n\right)\right) \quad (12a)$$

$$v_{j,k}^{n+1} = v_{j,k}^n + \Delta t\left(\frac{v_{j-1,k}^n + v_{j+1,k}^n - 2v_{j,k}^n}{\Delta x^2} + \frac{v_{j,k-1}^n + v_{j,k+1}^n - 2v_{j,k}^n}{\Delta y^2} + r_2 v_{j,k}^n\left(1 - v_{j,k}^n - \alpha u_{j,k}^n\right)\right) \quad (12b)$$

and we turn the second system

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} + u(r_1 - u - \alpha v)$$
$$\frac{\partial v}{\partial t} = \frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} + v(r_2 - v - \alpha u)$$

into the following system of equations:

$$u_{j,k}^{n+1} = u_{j,k}^n + \Delta t\left(\frac{u_{j-1,k}^n + u_{j+1,k}^n - 2u_{j,k}^n}{\Delta x^2} + \frac{u_{j,k-1}^n + u_{j,k+1}^n - 2u_{j,k}^n}{\Delta y^2} + u_{j,k}^n\left(r_1 - u_{j,k}^n - \alpha v_{j,k}^n\right)\right) \quad (13a)$$

$$v_{j,k}^{n+1} = v_{j,k}^n + \Delta t\left(\frac{v_{j-1,k}^n + v_{j+1,k}^n - 2v_{j,k}^n}{\Delta x^2} + \frac{v_{j,k-1}^n + v_{j,k+1}^n - 2v_{j,k}^n}{\Delta y^2} + v_{j,k}^n\left(r_2 - v_{j,k}^n - \alpha u_{j,k}^n\right)\right) \quad (13b)$$

Now we consider the boundary conditions. Since the grids on the border do not interact with the ones outside them, we use the no-flux boundary conditions (6), which fixed the normal derivatives at the borders at 0. Taking the left border in a two-dimensional space as an example and using center difference to approximate first order derivatives, we have $\frac{u_{2,k}^n - u_{0,k}^n}{2\Delta x} = 0,$ which means $u_{2,k}^n = u_{0,k}^n$. Therefore, the second order derivative of x on the left border is approximated using $\frac{2u_{2,k}^n - 2u_{1,k}^n}{\Delta x^2}$ (6).

We set Δt to 0.0001 and Δx and Δy to 0.05. For the two species systems, we set 9 testing groups, each with a set of parameters, as shown in Table 1.

Table 1: Parameters for Two-Species Simulation

Group	α	r_1	r_2
1	0.99	0.99	1.01
2	0.99	0.90	1.10
3	0.99	0.67	1.50
4	0.50	0.99	1.01
6	0.50	0.90	1.10
7	1.50	0.99	1.01
8	1.50	0.90	1.10
9	1.50	0.67	1.50

For each set of fixed parameters, we ran the simulation 100 times, each time with a random initial condition. To generate randomized initial condition, for each grid, we determined randomly, with equal possibility, if they initially contain species *u*, species *v*, or neither. We recorded the species fractions, $\frac{u}{u+v}$ and $\frac{v}{u+v}$, over time and the final state of coexistence at $t = 30$.

4.3 The Model: Three Species

The three-species model is derived in a similar way as in 4.2, using the method of finite difference to approximate the PDE systems:

$$u_{j,k}^{n+1} = u_{j,k}^{n} + \Delta t\left(\frac{u_{j-1,k}^{n} + u_{j+1,k}^{n} - 2u_{j,k}^{n}}{\Delta x^2} + \frac{u_{j,k-1}^{n} + u_{j,k+1}^{n} - 2u_{j,k}^{n}}{\Delta y^2} + r_1 u_{j,k}^{n}\left(1 - u_{j,k}^{n} - \alpha v_{j,k}^{n}\right)\right) \quad (14a)$$

$$v_{j,k}^{n+1} = v_{j,k}^{n} + \Delta t\left(\frac{v_{j-1,k}^{n} + v_{j+1,k}^{n} - 2v_{j,k}^{n}}{\Delta x^2} + \frac{v_{j,k-1}^{n} + v_{j,k+1}^{n} - 2v_{j,k}^{n}}{\Delta y^2} + r_2 v_{j,k}^{n}\left(1 - v_{j,k}^{n} - \beta w_{j,k}^{n}\right)\right) \quad (14b)$$

$$w_{j,k}^{n+1} = w_{j,k}^{n} + \Delta t\left(\frac{w_{j-1,k}^{n} + w_{j+1,k}^{n} - 2w_{j,k}^{n}}{\Delta x^2} + \frac{w_{j,k-1}^{n} + w_{j,k+1}^{n} - 2w_{j,k}^{n}}{\Delta y^2} + r_3 w_{j,k}^{n}\left(1 - w_{j,k}^{n} - \gamma u_{j,k}^{n}\right)\right) \quad (14c)$$

and

$$u_{j,k}^{n+1} = u_{j,k}^{n} + \Delta t\left(\frac{u_{j-1,k}^{n} + u_{j+1,k}^{n} - 2u_{j,k}^{n}}{\Delta x^2} + \frac{u_{j,k-1}^{n} + u_{j,k+1}^{n} - 2u_{j,k}^{n}}{\Delta y^2} + u_{j,k}^{n}\left(r_1 - u_{j,k}^{n} - \alpha v_{j,k}^{n}\right)\right) \quad (15a)$$

$$v_{j,k}^{n+1} = v_{j,k}^{n} + \Delta t\left(\frac{v_{j-1,k}^{n} + v_{j+1,k}^{n} - 2v_{j,k}^{n}}{\Delta x^2} + \frac{v_{j,k-1}^{n} + v_{j,k+1}^{n} - 2v_{j,k}^{n}}{\Delta y^2} + v_{j,k}^{n}\left(r_2 - v_{j,k}^{n} - \beta w_{j,k}^{n}\right)\right) \quad (15b)$$

$$w_{j,k}^{n+1} = w_{j,k}^{n} + \Delta t\left(\frac{w_{j-1,k}^{n} + w_{j+1,k}^{n} - 2w_{j,k}^{n}}{\Delta x^2} + \frac{w_{j,k-1}^{n} + w_{j,k+1}^{n} - 2w_{j,k}^{n}}{\Delta y^2} + w_{j,k}^{n}\left(r_3 - w_{j,k}^{n} - \gamma u_{j,k}^{n} \right) \right) \quad (15c)$$

Notice that we changed the competition intensity α into different values for each species. This is because typically in the actual experiments done in studies of rock-paper-scissors systems, the three species are respectively colocin-producing (emits toxin), resistant (not affected by toxin but less efficient at reproduction) and sensitive (is hindered by toxin) (1). Species affected by the toxin are facing different competition intensity.

Weber et al. (2) used the second definition Equation (4) to study how the final state of the system responded to different growth rate, toxin strength and initial proportion of the species. In our model, we let u be the toxic species, v be the resistant species and w be the sensitive species. Therefore, γ in Equation (14c, 15c) reflected the toxin's strength in hindering the growth of w. r_1, r_2 and r_3 were used to control growth rates, γ was used to control toxin strength, and the method of initial condition generation was modified to control the initial proportion. The other parameters and the boundary conditions remained the same as in the two-species model.

5. Results

5.1 Simulation Result for Two-Species Systems

Table 2: Qualitative Results of the Two-Species Simulation

Group	Definition 1			Definition 2		
	Coex	u Dom	v Dom	Coex	u Dom	v Dom
1	100	0	0	100	0	0
2	100	0	0	2	0	98
3	100	0	0	0	0	100
4	100	0	0	100	0	0
5	100	0	0	100	0	0
6	100	0	0	92	0	8
7	30	33	37	22	11	67
8	35	26	39	0	0	100
9	48	10	42	0	0	100

Table 2 presents the qualitative result of the simulation on Equation (12) and Equation (13). The column u Dom refers to instances of specie u dominance, meaning $\frac{\bar{u}}{\bar{v}} \geq 100$ in the final state, where $\bar{u}$ and $\bar{v}$ indicate the average value of u and v in the entire space respectively. The column v Dom is defined similarly. The column Coex refers to coexistence, which is any state between u Dom and v Dom.

The numerical results matched our analytical predictions. For Equation (12), when $\alpha < 1$, the

only stable fixed point is $(\frac{1}{\alpha+1}, \frac{1}{\alpha+1})$, which was verified by the coexistence ending state of Groups 1 to 6; when $\alpha \geq 1$, the points (0,1) and (1,0) were also stable fixed points, thus the systems usually converged to either one of those points, and due to symmetry, the probability of converging to each one was approximately equal. For Equation (13), $\alpha > \frac{r_1}{r_2}$ for Groups 1-3 and 6-9, and $\alpha > \frac{r_2}{r_1}$ only for Group 7, which meant that v dominance was stable in Groups 1-3, and 6-9 and u dominance was stable only in Group 7. In the simulation, Groups 2, 3, 6, 8, 9 ended at v dominance, and Group 7 ended at either u or v dominance as a result of having two stable fixed points. Although Group 1 ended at coexistence, v was found to increase and u was found to decrease rapidly by the time the final state was recorded. Group 1 would also reach v dominance if given more time steps, as shown in Figure 1. The graphs show the species fraction with respect to time, with the solid line indicating the systems modeled the first definition and the dashed line indicating the systems modeled with the second definition of the 'growth rate'.

The two-species model provided direct evidence of the two systems behaving differently under the same starting conditions.

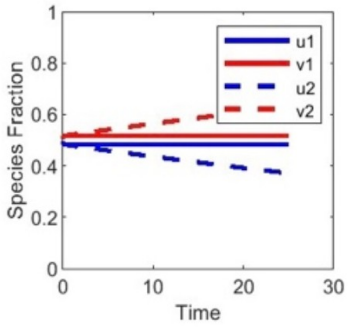

Figure 1: A typical result in group 1, where $\alpha = 0.99$, $r_1 = 0.99$, $r_2 = 1.0$. Although the system with the second definition reached a final state of coexistence, there existed a trend of u decreasing and v increasing, implying that the coexistance state was not stable.

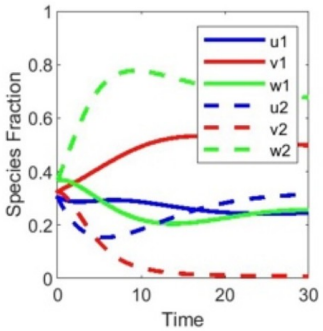

Figure 2: A typical result at r_1=0.25, r_2=0.50, r_3=0.75, α=β=0.99, γ=2.00. The system modeled using the first definition resulted in coexistence, whereas the one modeled using the second definition resulted in u-w dominance.

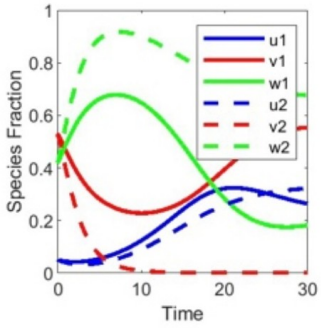

Figure 3: A result at r_1=0.25, r_2=0.50, r_3=0.75, α=β=0.99, γ=2.00 and u:v:w:empty = 0.1:1:1:1. This is an example of a system modeled using the second definition resulting in u-w dominance.

5.2 Simulation Result for Three-Species Systems

When $r_3 > r_2 > r_1$, Weber et al. (2) discovered that a strictly hierarchical interaction network would form. However, in our simulation, when $r_1 = 0.25, r_2 = 0.50, r_3 = 0.75, \alpha = \beta = 0.99, \gamma = 2.00$, a hierarchical relationship only occured in Equation (15), where the system ended in a u-w dominance. On the other hand, Equation (14) still retained stable coexistence as its final state, as shown in Figure 2.

Weber et al. (2) also claimed that changes of initial proportions of species and the toxin effect range affected the ending status. Our simulation confirmed the correlations. When the initial proportion $u : v : w$: empty changed to 0.1 : 1 : 1 : 1, instances of coexistence in Equation (15) seldom happened but were still possible. Out of 100 runs, we found 2 instances of coexistence, which - although significantly lesser when compared to the results by Weber et al. (2) - were still qualitatively consistent. However, the evolving process and quantitative ending states still differed using the two definitions. For example, more fluctuation was found in the evolving process when $u : v : w$: empty = 0.1 : 1 : 1 : 1, whereas the values remained relatively stable when $u : v : w$: empty = 1 : 1 : 1 : 1, as shown in Figure 3.

6. Discussion

We have shown that in problems associated with cyclic dominance systems, using different definitions of 'growth rate' affected the results. The two definitions lead to systems with different fixed points and different stability, indicating significantly different behaviors. Our simulation found that the parameters in the systems with different definitions influenced the final state of coexistence in different ways. We also found that existing studies such as Weber et al. (2) may have arrived at results that are inconsistent had they used a different definition of the growth rate. Our work shows that research in the field of cyclic dominance systems needs to be presented either with a clear definition of growth rate or be harmonized with respect to a standardized growth rate so that comparisons may be made between different studies. There is a need for future research in this area to pay particular attention to definitions and methods.

Regarding possible directions for further research, it is worth investigating whether our result is consistent with systems consisting of

more species. Systems with more than three species possess complicated behavior (3). While we expect that the use of one definition over the other will still cause qualitative differences in steady-state solutions, it may also be worth studying differences in the transient behavior of these systems.

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