

# An Interspecies Competition Model with Multiscale Interpretations

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## Abstract

A method for simulating and analyzing the competition between similar species is presented here by first adapting a Gause type model that allows four fitting parameters [2]. From this deterministic model we derive conditions for the existence and stability of several equilibria, including multiple coexistence equilibria. An agent-based simulation is then created to model the biology of the species on the scale of individual interaction. Changes in the growth scale parameters for the deterministic model are then considered in order to try to replicate the behavior of the agent-based biology. This is done in an attempt to rationalize the growth scale parameters as a tool to capture all possible behaviors. In an effort to observe the dynamics on a different spatial scale, we implement a spatially structured stochastic simulation with parameters chosen to reflect the different outcomes of the agent-based model. This second simulation will track, on a larger scale, the interaction between groups or colonies of the species of interest. The multiscale method presented here allows for a broader interpretation of interspecies competition than is possible through deterministic analysis. For the purpose of an example, two species of ants will be considered (*Solenopsis invicta* and *S. geminata*).

**Keywords:** Agent-based modeling, competition, invasive species, pair-approximation.

# Introduction

Competition between similar species is a complex problem. In this paper, interference competition between two similar species of ants, *S. invicta* and *S. geminata*, is discussed and a framework for modeling and simulation is addressed. Primary to the idea of modeling is what aspects of the species should be considered when looking at competition.

In general, the size of an individual member of a species matters and affects several aspects of interspecific interference competition [7]. Ants display determinate growth patterns, that is, the adults of each class (worker, major, etc.) are about the same size [7]. We assume a larger ant will naturally dominate when it comes to individual physical confrontation with a smaller adversary. However, by intuition there must be a tradeoff with size. The larger a particular ant is the more food is likely required to sustain it self. While a species may be larger than its competitive counterpart, smaller ants may fight in packs or swarms and thus nullify any size advantage. It is assumed that an intrinsic carrying capacity for each species depending on the type of area it is inhabiting and its size. A larger ant species will have a lower carrying capacity than that made up of smaller ants. If the two species are competing for the same food source(s) in an area then their ability to persist in that area comes into question. For example, when several ant species locate a common food source, the species that find, carry, and alert others to the presence of the food more efficiently will have the advantage. These are some of the aspects deemed important while modeling *S. invicta* and *S. geminata*. These, however, are not the only considerations when constructing a simulation.

When simulating the movement of a species, aspects of sensory ability are considered (e.g. shortsightedness versus olfactory superiority) as well as their mobility. The ants considered here rely both on sight and smell to find food and communicate by leaving pheromone trails. Simulations may also take into account events which occur on different time scales into consideration. As an example, it is clear that the gathering of food and the rearing of an offspring do not happen on the same time scale and thus need to be accounted for accordingly. For instance, if one were to track the activities of an individual ant colony, care should be taken to consider the length of time the ants need to retrieve their food and convert it into biomass. However, if the interest is more in the large scale relationship of ant colonies, food can be considered arbitrarily close to a colony. Thus the concern is more over the distance between individual colonies.

It is known within the realm of interference competition models that outcomes may include competitive exclusion or coexistence. This paper is not an attempt to provide new insight into interference competition models, but rather offer tools to use in its analysis. Analysis of a deterministic model provides a theoretical background for the type of behavior searched for (e.g. coexistence, competitive exclusion). It is proposed that the growth scale parameters act as a control mechanism to force coexistence into a model with a parameter set that would not normally allow such a result. An agent-based model is an alternative to the formation of a traditional stochastic version of the deterministic model. Furthermore, the agent-based simulation offers a glimpse into the effects of small scale spatial relations between the individual ants. To observe interactions on a different spatial scale, that of interacting colonies, it is assumed that on the small scale the ants behave as the deterministic model portrays them. Thus a spatially structured multi-patch simu-

lation is offered as a tool to record interactions on the larger scale. First, we analyze the deterministic model.

## Deterministic Model

For the ants several ant characteristics, via model parameters, were considered: size as it relates to fighting and growth; ability to gather food as it relates to growth rates; and pheromone secretion. Once data has been found then parameters are fitted into these equations [2]:

$$\dot{x} = \mu_1 x \left( 1 - \left( \frac{x}{K_1} \right)^{\theta_1} - \frac{c_2 y}{\mu_1} \right), \quad (1)$$

$$\dot{y} = \mu_2 y \left( 1 - \left( \frac{y}{K_2} \right)^{\theta_2} - \frac{c_1 x}{\mu_2} \right). \quad (2)$$

This model was chosen because it is a traditional interference competition model which incorporates interference and the ability to control the speed of the logistic growth. Therefore the model is open to broader biological application. To better understand the model as given in Equations (1-2) a discussion of the parameters is required. We define  $\mathbf{P}$  to be the set of intervals for which our parameters have biological significance such that  $\mathbf{P} \subset \mathbb{R}_+^8$ .

Parameter	Interpretation
$\mu_i$	Intrinsic growth rate
$K_i$	Carrying capacity
$\theta_i$	Growth Scale
$c_i$	Competition Coefficient

Table 1: Parameters and Their Meaning for  $i = 1, 2$

It can be seen that without competition coefficients or growth scales (i.e.  $c_1 = c_2 = 0$  and  $\theta_1 = \theta_2 = 1$ ) Equations (1-2) form a standard two-dimensional Verhulst model, and each species will grow to its individual carrying capacity. Hence, the biological concepts of  $K_i$  and  $\mu_i$  do not change from the accepted interpretations from a standard Verhulst model, where subscript 1 and 2 refer to species  $x$  and  $y$  respectively. In the case of ants,  $\mu_i$  may be interpreted to depend on their ability to gather food which promotes colony growth. The addition of the growth scale parameters,  $\theta_i$ , allows a shift, with respect to population size, in the maximum rate of increase in the population. When  $\theta_i = 1$  the maximum increase is when the current population is  $\frac{1}{2}$  its carrying capacity. This is demonstrated in Figure 1.

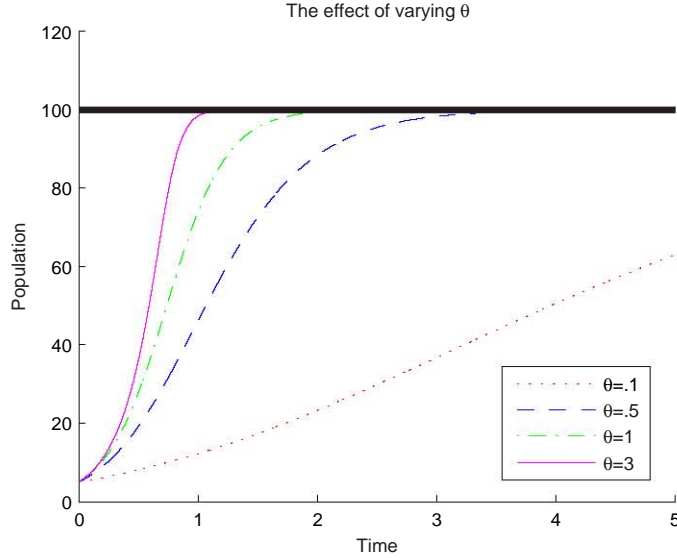


Figure 1: The effect of  $\theta$  on the population growth.

Here, the growth scales indicate how efficiently a species utilizes food to create population. Should a species be inefficient with the conversion of food to biomass then  $\theta$  would be particularly low. Finally,  $c_1xy$  and  $c_2xy$  reflect interspecific competition between species. The nature of this competition can be determined by the individual application.

## Analysis

### Stability of Boundary Equilibria: $E_0$ , $E_x$ , $E_y$

There are three boundary equilibria for the deterministic system, corresponding to competitive exclusion, in Equations (1-2). The extinction, “trivial”, equilibrium-  $E_0 = (x^*, y^*) = (0, 0)$ , and the boundary equilibria-  $E_y = (x^*, y^*) = (0, K_2)$  and  $E_x = (x^*, y^*) = (K_1, 0)$ . There is also a set of coexistence equilibria, **CE**. We denote this as a set because, as will be shown, there are conditions when zero, one, two or three interior coexistence equilibria, **CE**, may exist.

In order to determine the stability of the equilibria, the eigenvalues of the matrix

$$\mathbf{J} = \begin{pmatrix} \mu_1 - \frac{(\theta_1+1)\mu_1}{K_1^{\theta_1}}x^{\theta_1+1} - c_2y & -c_2x \\ -c_1y & \mu_2 - \frac{(\theta_2+1)\mu_2}{K_2^{\theta_2}}y^{\theta_2+1} - c_1x \end{pmatrix} \quad (3)$$

must be determined. Evaluating  $J$  at  $E_0$  yields eigenvalues  $\lambda_1 = \mu_1, \lambda_2 = \mu_2$ . This trivial equilibrium is always unstable because both of the eigenvalues are positive. Evaluating

the Jacobian at the boundary equilibria,  $E_x$  and  $E_y$ , results in the following matrices:

$$\mathbf{J}|_{E_y} = \begin{pmatrix} \mu_1 - c_2 K_2 & 0 \\ -c_1 K_2 & -\theta_2 \mu_2 \end{pmatrix} \quad (4)$$

$$\mathbf{J}|_{E_x} = \begin{pmatrix} -\theta_1 \mu_1 & -c_2 K_1 \\ 0 & \mu_2 - c_1 K_1 \end{pmatrix} \quad (5)$$

The eigenvalues of Matrix (4) are  $\lambda_1 = \mu_1 - c_2 K_2$  and  $\lambda_2 = -\theta_2 \mu_2$ . The value  $\lambda_2$  is always negative, so if  $\frac{\mu_1}{c_2} < K_2$  then  $E_y$  is a stable node. If  $\frac{\mu_1}{c_2} > K_2$  then  $E_y$  is a saddle point. A similar argument applies to  $E_x$  thus, the boundary equilibria are either stable or saddle nodes. This is illustrated in Figures (2-3).

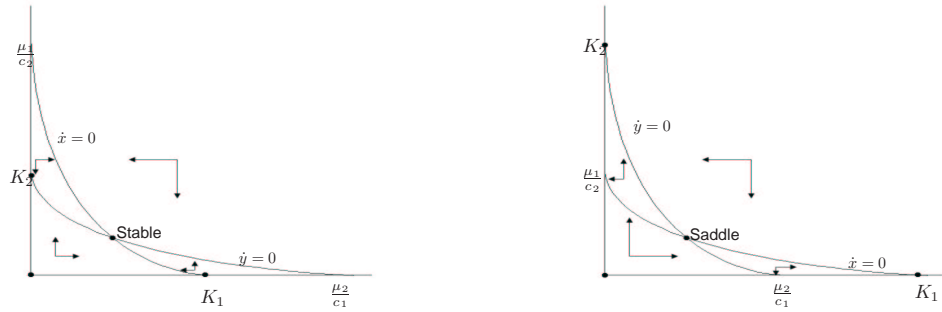


Figure 2: Dynamics when boundary equilibria are of the same type. On the left is species coexistence, on the right competitive exclusion dependant on initial conditions.

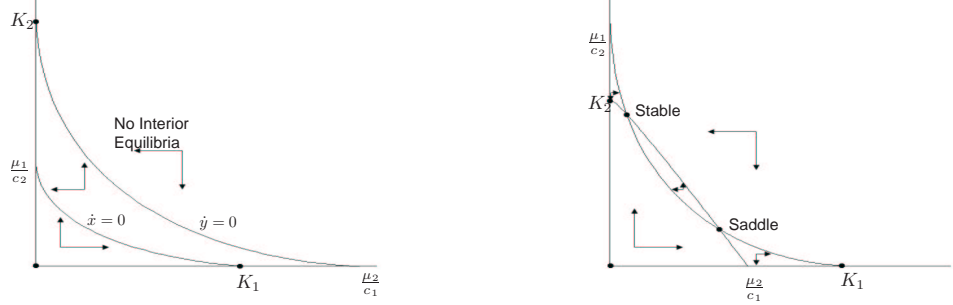


Figure 3: Dynamics when boundary equilibria are of different type. On the left is competitive exclusion with species  $y$  winning, on the right is coexistence or exclusion dependant on initial conditions.

Since the boundary equilibria were derived directly from the equations, the existence of the boundary equilibria is not dependant on system parameter. Thus it only remains to study the coexistence equilibria.

### Existence of the Coexistence Equilibria: CE

There is not a closed form expression for the coexistence equilibria, an explicit analysis of the eigenvalues of the Jacobian is not possible. Recall that coexistence equilibria will satisfy the equations:

$$1 - \left(\frac{x^*}{K_1}\right)^{\theta_1} = \frac{c_2 y^*}{\mu_1},$$

$$1 - \frac{c_1 x^*}{\mu_2} = \left(\frac{y^*}{K_2}\right)^{\theta_2}.$$

The nullclines for the system are obtained by solving for  $y^*$ , yielding two functions  $f, g : \mathbb{R}^+ \rightarrow \mathbb{R}^+$  such that  $\mathbb{R}^+ := (0, \infty)$  may be defined where:

$$f(x) := \frac{\mu_1}{c_2} \left(1 - \left(\frac{x}{K_1}\right)^{\theta_1}\right), \quad (6)$$

$$g(x) := K_2 \left(1 - \frac{c_1 x}{\mu_2}\right)^{\frac{1}{\theta_2}}. \quad (7)$$

From Equations (6-7), interior fixed points exist only if  $x \leq \omega := \min\left(\frac{\mu_2}{c_1}, K_1\right)$ , thus for the analysis, the domains of  $f$  and  $g$  are restricted to the interval  $[0, \omega]$ . It is assumed

that given  $P \in \mathbf{P}$   $f$  and  $g$  are not equivalent on  $P$ . If  $f$  and  $g$  are equivalent on  $P$  then the analysis is degenerate, having a curve which describes an infinite number of stable coexistence equilibria. The curve of  $f(x)$  has an x-intercept of  $(K_1, 0)$  and y-intercept of  $(0, \frac{\mu_1}{c_2})$ . The curve of  $g(x)$  has x-intercept of  $(\frac{\mu_2}{c_1}, 0)$  and y-intercept of  $(0, K_2)$ . Note that

$$\frac{df}{dx} = -\frac{\mu_1 \theta_1 x^{\theta_1 - 1}}{c_2 K_1^{\theta_1}} < 0, \text{ and}$$

$$\frac{dg}{dx} = -\frac{K_2 c_1}{\theta_2 (\mu_2 - c_1 x)} \left( \frac{\mu_2 - c_1 x}{\mu_2} \right)^{\frac{1}{\theta_2}} < 0.$$

Recall that the x-intercept for  $g$  is  $\frac{\mu_2}{c_1}$  and thus  $\mu_2 - c_1 x > 0$ . Therefore  $f$  and  $g$  are monotonically decreasing. To investigate the existence of elements of  $\mathbf{CE}$  the nature of the concavity of both  $f$  and  $g$  may be helpful.

Observe that

$$\frac{d^2 f}{dx^2} = \frac{\mu_1 \theta_1 (1 - \theta_1) x^{\theta_1 - 2}}{c_2 K_1^{\theta_1}} \quad (8)$$

then  $\frac{d^2 f}{dx^2} < 0$  if and only if  $\theta_1 > 1$  and  $\frac{d^2 f}{dx^2} > 0$  if and only if  $\theta_1 < 1$ . Similarly

$$\frac{d^2 g}{dx^2} = \frac{K_2 c_1^2 (1 - \theta_2)}{\theta_2^2 (\mu_2 - c_1 x)^2} \left( \frac{\mu_2 - c_1 x}{\mu_2} \right)^{\frac{1}{\theta_2}} \quad (9)$$

then  $\frac{d^2 g}{dx^2} < 0$  if and only if  $\theta_2 > 1$  and  $\frac{d^2 g}{dx^2} > 0$  if and only if  $\theta_2 < 1$ . Again if  $\theta_2 = 1$  then  $g$  is a linear function.

In other words for  $\theta_1, \theta_2 \neq 1$ , there are no inflection points for  $f$  and  $g$ .

**Proposition 0.1.** *Given that  $f$  is not equivalent to  $g$ .*

*If*

$$\left( \frac{\mu_1}{c_2} - K_2 \right) \left( \frac{\mu_2}{c_1} - K_1 \right) > 0, \quad (10)$$

*then there exists at least a point  $x^* \in \mathbb{R}^+$  such that  $f(x^*) = g(x^*)$ .*

*Proof.* Assume (10), and  $\omega$  as defined above, with both  $f$  and  $g$  continuous on the interval  $[0, \omega]$ . Further, without loss of generality let  $\frac{\mu_1}{c_2} > K_2$  (i.e.  $f(0) > g(0)$ ) and  $\frac{\mu_2}{c_1} > K_1$  (i.e.  $f(\omega) < g(\omega)$ ), then by the Intermediate Value Theorem there exists an  $\xi \in [0, \omega]$  such that  $f(\xi) = g(\xi)$ .  $\square$

Thus, if the relationship between the species is such that the carrying capacities,  $K_j$ , for each species are either both greater than or less than the ratio  $\frac{\mu_i}{c_j}$ , then there exists at least one coexistence equilibrium, i.e.  $\mathbf{CE} \neq \emptyset$ .

**Corollary 0.2.** *Given the same conditions as in Proposition 0.1,*

*if  $\theta_1, \theta_2 < 1$  and  $K_1 K_2 > \frac{\theta_1 \theta_2 \mu_1 \mu_2}{c_1 c_2}$  thus there exists a unique  $\xi$  such that  $(f(\xi) = g(\xi))$  and  $(\xi, f(\xi)) \in \mathbf{CE}$ .*

*Proof.* Due to the constant concavity and monotonic decrease we have  $\lim_{x \rightarrow 0} f' = -\infty$ ,  $f'(K_1) = -\frac{\mu_1 \theta_1}{c_2 K_1}$ ,  $g'(0) = -\frac{c_1 K_2}{\mu_2 \theta_2}$ , and  $g' \left( \frac{\mu_2}{c_1} \right) = 0$ . This is all shown in Figure 4. In the interval of consideration we have that  $g'$  attains a minimum of  $-\frac{c_1 K_2}{\mu_2 \theta_2}$  and we've demonstrated that the maximum of  $f'$  is  $-\frac{\mu_1 \theta_1}{c_2 K_1}$  thus  $f' > g'$ , and  $f - g$  is monotone therefore there exists a unique  $\xi \in (0, \omega)$  such that  $f(\xi) = g(\xi)$ .  $\square$

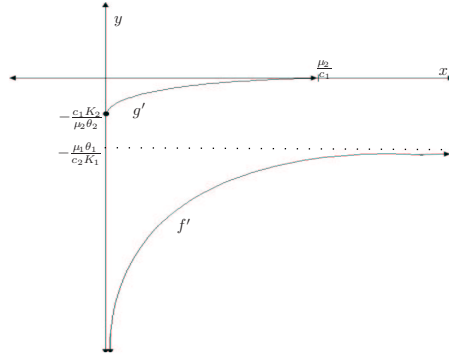


Figure 4: Illustration of the proof of Corollary 0.2.

Numerical results from a Latin Hypercube sampling, detailed in the Numerical Analysis section, have shown that 99.95% of parameter combinations found to produce an interior equilibrium, with each of the  $\theta_i < 1$  fit the criterion for uniqueness of that equilibrium. This reinforces the claim that  $\theta_i$  is the parameter that is producing the biologically significant results in the deterministic model. If one considers the inequality  $K_1 K_2 > \frac{\mu_1 \mu_2}{c_1 c_2}$ , in the case where both non-trivial boundary equilibria are saddle points, the inequality is false, refer to Equations (4-5). However, since it is a fact that the interior equilibrium must exist when  $E_x$  and  $E_y$  are both saddles and it must be stable, the introduction of the  $\theta_i$  terms is what curves the nullclines and introduces the coexistence equilibrium. There are also conditions where it can be shown that there exist at most two elements in **CE**.

**Proposition 0.3.** *Given  $f$  and  $g$  as defined in (6) and (7), without loss of generality, if  $\theta_1 > 1$  and  $\theta_2 \leq 1$  then  $f$  and  $g$  will have at most two intersections in  $\mathbb{R}_+^2$ .*

*Proof.* Let

$$h(x) = f(x) - g(x).$$

If the sign of  $\frac{d^2 h}{dx^2}$  does not change, then there exist at most two points,  $\tilde{x}_i, i = 1, 2$ , such that  $h(\tilde{x}_i) = 0$ , hence  $f(\tilde{x}_i) = g(\tilde{x}_i)$ .



Since

$$\frac{d^2 h}{dx^2} = \frac{d^2 f}{dx^2} - \frac{d^2 g}{dx^2},$$

$\theta_1 > 1 \Rightarrow \frac{d^2 f}{dx^2} < 0$ , and  $\theta_2 \leq 1 \Rightarrow \frac{d^2 g}{dx^2} \geq 0$ , it is the case that  $\frac{d^2 h}{dx^2} < 0$ . Thus there is no concavity change of  $h$ .  $\square$

Additionally, if  $\theta_1 \leq 1$  and  $\theta_2 > 1$  implies there are at most two elements in **CE**. Proposition 0.3 tells that if one of the curves is concave up and the other is either linear or concave down then there are at most two elements in **CE**. This is intuitive, and an extensive numerical search has shown that there are in fact no situations, with  $f$  and  $g$  as defined regardless of concavity, with more than two intersections within the biologically acceptable parameter range. The proof of this is outside the scope of this paper, but is numerically demonstrated in the Numerical Analysis section.

**Proposition 0.4.** *Given Equations (1-2) there are at most three intersections of  $f$  and  $g$  in  $\mathbb{R}_+^2$ .*

*Proof.* Making the following normalization:

$$\begin{aligned}\tilde{x} &= \frac{x}{K_1} \longrightarrow \dot{\tilde{x}} = \frac{1}{K_1} \dot{x}, \\ \tilde{y} &= \frac{y}{K_2} \longrightarrow \dot{\tilde{y}} = \frac{1}{K_2} \dot{y},\end{aligned}$$

and then substituting back into Equations (1-2) results in

$$\dot{\tilde{x}} = K_1 \mu_1 \tilde{x} \left( 1 - \tilde{x}^{\theta_1} - \frac{c_2 K_2}{\mu_1} \tilde{y} \right), \quad (11)$$

$$\dot{\tilde{y}} = K_2 \mu_2 \tilde{y} \left( 1 - \tilde{y}^{\theta_2} - \frac{c_1 K_1}{\mu_2} \tilde{x} \right). \quad (12)$$

Let  $A = \frac{c_2 K_2}{\mu_1}$  and  $B = \frac{c_1 K_1}{\mu_2}$ , and then solving for the nullclines of Equations (11-12) and disregarding the trivial solution yields:

$$1 - \tilde{x}^{\theta_1} - A\tilde{y} = 0, \quad (13)$$

$$1 - \tilde{y}^{\theta_2} - B\tilde{x} = 0. \quad (14)$$

Solving Equation (13) for  $\tilde{y}$  and then substituting into Equation (14) we get

$$1 - \left( \frac{1 - \tilde{x}^{\theta_1}}{A} \right)^{\theta_2} - B\tilde{x} = 0,$$

$$\text{thus, } A^{\theta_2} (1 - B\tilde{x}) = (1 - \tilde{x}^{\theta_1})^{\theta_2}.$$

We define  $\tilde{f} := (1 - \tilde{x}^{\theta_1})^{\theta_2}$  and  $\tilde{g} := A^{\theta_2} (1 - B\tilde{x})$ . The graph of  $\tilde{g}$  is linear so we consider  $\tilde{f}$ .

Observe,

$$\begin{aligned}\tilde{f}' &= \theta_2 (1 - \tilde{x}^{\theta_1})^{\theta_2-1} (-\theta_1 \tilde{x}^{\theta_1-1}), \\ \tilde{f}'' &= \theta_2 (\theta_2 - 1) (1 - \tilde{x}^{\theta_1})^{\theta_2-2} (-\theta_1 \tilde{x}^{\theta_1-1})^2 + \theta_2 (1 - \tilde{x}^{\theta_1})^{\theta_2-1} (\theta_1 - \theta_1^2) \tilde{x}^{\theta_1-2}.\end{aligned}\quad (15)$$

The zeros of Equation (15) are  $\tilde{x}_0 = 0, 1, \left(\frac{\theta_1-1}{\theta_1\theta_2-1}\right)^{\frac{1}{\theta_1}}$ . The values 0 and 1 are the boundaries of consideration, however  $\left(\frac{\theta_1-1}{\theta_1\theta_2-1}\right)^{\frac{1}{\theta_1}}$  may lie within  $(0, 1)$ . If it does not, then there are no inflection points for  $\tilde{f}$  and thus  $f$  and  $g$  intersect at most twice. However, should the inflection point lie within the interval then  $f$  and  $g$  have at most three intersections.  $\square$

## Limit Cycles

Now that some conditions are established for when  $\mathbf{CE} \neq \emptyset$  we will analyze the stability of the interior equilibria points. It is important at this juncture to rule out limit cycles to narrow the possible dynamics.

**Proposition 0.5.** *The system described by Equations (1-2) has no limit cycles.*

*Proof.* The proof is a standard application of Dulac's Criterion. Define a function

$$D(x, y) = \frac{1}{xy}.$$

Recall the system

$$\begin{aligned}\dot{x} &= \mu_1 x \left( 1 - \left( \frac{x}{K_1} \right)^{\theta_1} - \frac{c_2 y}{\mu_1} \right) := F, \\ \dot{y} &= \mu_2 y \left( 1 - \left( \frac{y}{K_2} \right)^{\theta_2} - \frac{c_1 x}{\mu_2} \right) := G,\end{aligned}$$

in which case

$$\frac{\partial(DF)}{\partial x} + \frac{\partial(DG)}{\partial y} = -\frac{\mu_1 \theta_1 x^{\theta_1-1}}{y K_1^{\theta_1}} - \frac{\mu_2 \theta_2 y^{\theta_2-1}}{x K_2^{\theta_2}} < 0. \quad (16)$$

Since Equation (16) is strictly negative on our parameter space  $\mathbf{P}$ , then by Dulac's Criterion there are no limit cycles.  $\square$

## Stability of Coexistence Equilibria

Now that limit cycles have been ruled out, consider the four possible combinations of the states of the non-trivial boundary equilibria. Consider the inequalities describing the stability of the points  $E_x$  and  $E_y$  respectively.

Recall Figures (2-3), and consider when both  $E_x$  and  $E_y$  are stable. According to Equations (4-5) and Proposition 0.1 this would imply that there is at least one element in  $\mathbf{CE}$ , which is a saddle point [2]. When  $E_x$  and  $E_y$  are saddles the element of  $\mathbf{CE}$  is a stable

node. By symmetry the dynamics of when  $E_x$  is stable and  $E_y$  is a saddle are equivalent to when  $E_x$  is saddle and  $E_y$  is stable.

For the case when  $E_x$  is stable and  $E_y$  is a saddle it is possible for  $\mathbf{CE} = \emptyset$ . However, there is also the chance that the function  $h$  has either one or two roots. A single root has been found to only occur if the functions  $f$  and  $g$  are of differing concavity. This is odd because there are no standard fixed points which will preserve the dynamics of the  $E_x$  and  $E_y$  in this case. Here the node has a stable manifold where the flow from the saddle point at  $E_x$  goes to the interior node, and on the other side of the manifold the flow is attracted by the stable point at  $E_y$  as in Figure 3. Past this bifurcation we are left with two coexistence equilibria: a saddle point and a stable point as in Figure 3. These points are arranged such that the stable coexistence equilibrium is nearest the saddle point boundary equilibrium, and the saddle point coexistence equilibrium is nearest the stable boundary equilibrium.

## Numerical Results

To garner more information from the equations an investigation of the numerics of the system is undertaken.

### Parameter Fitting

The work of Morrison [7] examines three different species of fire ants *S. invicta*, *S. geminata* and *S. geminata x xyloni*. To study their interfering competitive behavior, experiments were conducted using various combinations of pairs of the three species. For example, two ant species were put in the same environment with a common food source and the location and number of the dead ants were recorded relative to the location of their respected nests. The experiment was then repeated until each ant species was compared with all others and relative competition coefficients were extracted from these results.

Adams and Tschinkel [1] studied the biology of *S. invicta*, in particular their growth rates were analyzed. A time series of the population size was constructed over the course of six years which was used to fit parameters to Equations (1-2), see Figure 5.

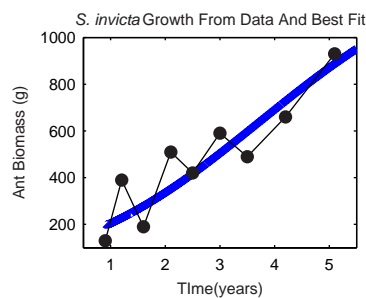


Figure 5: Least Squares fit of *S. invicta* over time

A Least Squares algorithm was used in the Berkeley Madonna software package to perform this fit. Due to the lack of many data points, the best fit parameters were combined with information from Morrison’s work to estimate new parameters to be used throughout this investigation 2. These parameters are considered as the base case for the numerical simulations presented here.

Parameter	Value
$\mu_1$	0.78
$\mu_2$	0.91
$c_1$	0.0089
$c_2$	0.01
$K_1$	1391
$K_2$	1000
$\theta_1$	0.61
$\theta_2$	0.55

Table 2: Least Squares fit of the parameters of Equations (1-2)

In some instances the dynamics of the system were inferred from the fit parameters but, for ease of simulation, different parameters were chosen from the appropriate parameter space. In this regard the dynamics were preserved while allowing for a more clear interpretation of the simulations as will be seen in the following sections, but first the interior equilibria are explored numerically as a function of the parameters.

## Parameter Sampling

While there are the propositions which assert the existence of interior equilibria there is not really a sense of how probable these combinations are of occurring. We employed Latin Hypercube Sampling on a parameter space of

$$\mathbf{P} = \{(.1, 2), (.1, 2), (1, 1500), (1, 1500), (.005, 2), (.005, 2), (.001, .1), (.001, .1)\}.$$

This sampling method has been shown to be not only more efficient but also a better method of obtaining a well stratified sample of random values versus Monte Carlo random sampling [6]. We ran a program sampling 2,000,000 different parameter sets from 10,000 striations of each parameter interval.

The sampling shows there were roughly 1.8 million parameter 8-tuples where there are only one interior equilibrium. Of these, none were found to be of the condition that the non-trivial boundary equilibria were of opposite type. Thus we conclude that the conditions that give the degenerate interior equilibria is a statistical improbability. There were 29,221 cases where there were two interior equilibria and merely 24 where there were three. Of the cases with three interior equilibria the carrying capacities were on the orders of 10 and  $10^2$ , while the competition coefficients were of the order  $10^{-3}$ . The intrinsic birthrates were also all greater than one. We view this as outside the realistic biological bounds.

## Deterministic Numerical Solutions

With the inability to solve the deterministic system in Equations (1-2) we turn to numerical solutions. Utilizing the numerical package `pplane7` within Matlab and numerical solutions to the ODE's we were able to replicate most of the situations stated above for the boundary and interior equilibria. The critical value for the degenerate saddle node has proved elusive, since no closed form for the critical parameter values has been found. To determine the outcome based on our real world parameters consider Figure 6 and then the phase plane in Figure 7.

It is apparent that with the parameters found by fitting the real world data that the only outcome is competitive exclusion. This agrees with G. F. Gause [2] who asserts competitive exclusion is the rule when it comes to two species in local competition over the same resources. The interesting aspect is that either ant species may prevail given different initial conditions. That being said, ant 2 being an individually inferior species, intuitively should never prevail over ant 1. However, with enough of an initial population advantage ant 2 will win. The separatrix of the saddle point in the interior divides the phase space in such a way that ant 2 has a higher probability of winning given random initial populations.

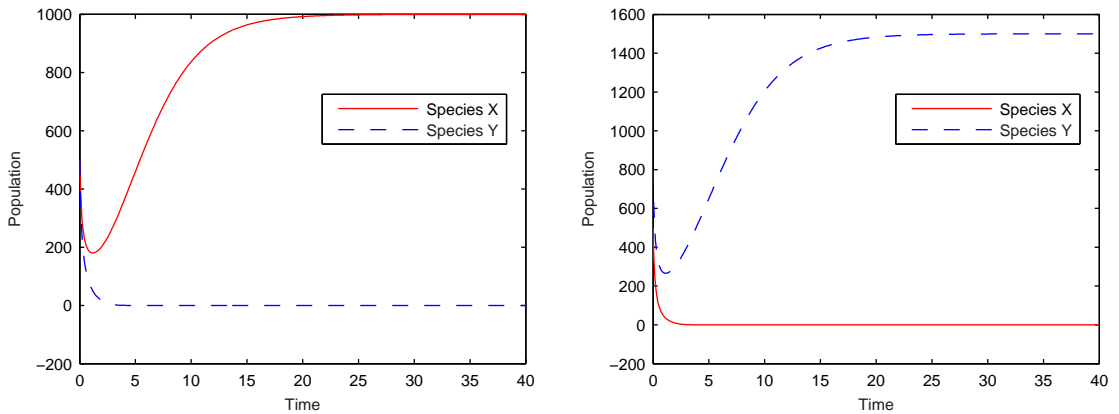


Figure 6: Competitive exclusion for real world data with  $(x(0), y(0)) = (500, 500)$  and  $(x(0), y(0)) = (500, 800)$ , and parameters  $\mu_1 = .8$ ,  $\mu_2 = .6$ ,  $K_1 = 1000$ ,  $K_2 = 1500$ ,  $\theta_1 = .4$ ,  $\theta_2 = .5$ ,  $c_1 = .01$ , and  $c_2 = .008$ .

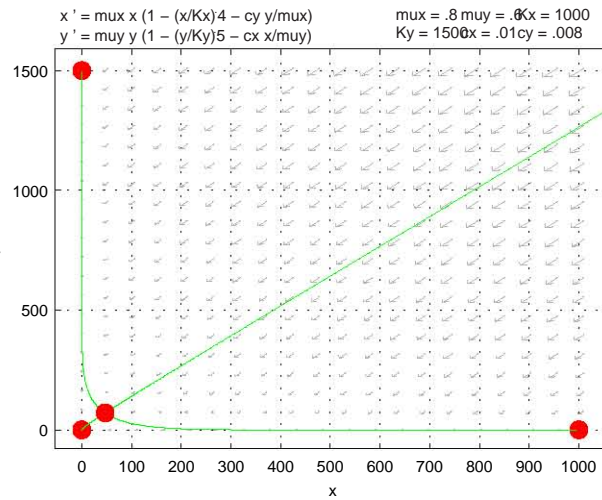


Figure 7: The stable and unstable manifolds of the saddle point are plotted here.

Numerics allow for a qualitative look at the expected results and support the stability analysis. While the quantity of data provided a poor fit, intuition supported the parameter's fit with little change. Sampling the parameter space via Latin Hyper Cube has provided a look into the expected number of interior equilibria. The conscientious reader has noticed that there is a high concentration on  $\theta_i < 1$ . What the Latin Hyper Cube sampling has demonstrated that out of 1.8 million parameter 8-tuples there were 471,636 which had the two  $\theta_i < 1$  and of those 471,417 fit the conditions presented in Corollary 0.2 for that intersection to be the unique one. Should an investigator use the deterministic model presented here and the  $\theta_i < 1$  inequality holds then they can be sure that competitive exclusion of each species are the dynamics to be expected, and it appears that *s. invicta* and *s. geminata* fall within this category. Numerics have also provided the information that given the real world parameters *s. geminata* is more likely to win.

One of the problems with the deterministic approach, and hence the numerics presented here, is that it is an "average" of behavior. It should also concern the reader that the deterministic model ignores any interactions on different spatial or temporal scales. If these are negligible then the deterministic model is reliable and can be used as a tool for modeling the competition. If the relationships are crucial to the interaction then other methods must be taken into account.

# Simulations

## Agent-Based

### Discrete Agent-Based Model

Unlike the deterministic model which is continuous, the agent-based model involves discrete individuals over a spatially explicit landscape. The agent-based model puts two species into competition in a bounded environment with limited resources where competition includes gathering limited food sources and interspecific death. While all the behavior seen in the deterministic model can be reproduced, the major advantage is each agent may behave independently and interact with other agents or the environment based on certain rules defined in the next section.

### Behavioral Rules

There are four major behaviors exhibited by the agents [1]:

- Each agent will leave the nest in search of a pheromone trail leading towards a food source. If one is found, it will follow the trail until it encounters the food. If no pheromone trail is found, then it will search in a random fashion until encounters a food source or a pheromone trail.
- If food is found, then the agent picks it up and returns home. As the agent returns home, it leaves a pheromone trail indicating that food has been found. It is assumed the pheromone evaporates at a constant rate.
- When two agents of different species contact each other (occupy the same space) then the agents may attack each other.
- The two species may grow as a function of the amount of food gathered.

There is a stochastic component to the movement of the agents which could cause them to deviate slightly from the “correct” path or in the worst case even head away. While an agent is searching for food, it can see in the neighboring areas, and can sense pheromone around itself. If food is found it heads home, otherwise it proceeds until a pheromone trail from its own species is found. The agent sets its heading (in degrees) towards the pheromone gradient with a small error. For the sake of argument the error was chosen to be normally distributed with mean 0 and variance 15 degrees. There is also some probability that the agent will ignore the pheromone gradient.

Once food is found, the agent will leave a constant amount of pheromone on each patch unless that patch already has some pheromone, in which case it will leave a fraction of its normal amount. If the pheromone trail already has too much pheromone, it will not lay down anything but simply head home.

If an agent encounters agents of a different species, then they immediately attempt to attack each other. Note several groups of agents may attack each other simultaneously, thus swarming behavior is possible. For simplicity it is assumed an agent dies only when successfully attacked and the probability of a successful attack is a random number taken

from a uniform distribution.

These rules incorporate mechanistic behavior, environmental factors and stochastic variability into an agent-based model while still preserving all the behavior seen from the deterministic model. This makes the model more realistic in the local scale between competing species and allows for a closer investigation of how the parameters affect the dynamics of the individuals. This information is precisely what is lost by the averaging inherent in the deterministic approach.

## Results from Agent-Based Model

In addition to verifying all the results from the deterministic model, the agent-based model provided some insight into the spatial component of interference competition. With parameters where coexistence was expected due to results from the deterministic model, both species were observed to exist at steady levels for long periods of time. It should be noted the only absorbing states are extinction of either species and thus one species will eventually die out, although this may take place only in the limit that time goes to infinity.

From parameters fit from data, see Table 2, the deterministic model predicted competitive exclusion as the only stable solution with a saddle point being the only interior equilibrium. This corresponds well with data since *S. invicta* has displaced other species of fire ants in much of the Southwestern United States. However, in the deterministic model there exists a separatrix of the interior saddle point that divides the basins of attraction for the two boundary equilibria. Hence initial conditions determine which boundary equilibrium solutions will tend to and it is not clear *S. invicta* should be as dominant as it has been. To illustrate the importance of initial conditions, parameter values were exaggerated to give species 1 a clear advantage. Initializing species 1 with the same number of agents as species 2 yields extinction of species 2 100% of the time in 150 trials. However, initializing species 2 with 4 times the number of agents as species 1 leads to extinction 83% of the time for species 1.

The next step is to see if the agent-based model can reproduce coexistence found in the deterministic model with the appropriate parameters, namely low competition coefficients and high birth rates proportional to the carrying capacities. It remains only to determine the criterion for coexistence. The end times were recorded in each of the previous sets of simulations and the set with the largest mean was chosen. The distribution of end times is examined with the hypothesis that it can be approximated by a log-normal distribution. Using a mean of 3.607 and standard deviation of .1415, the hypothesis is accepted with a p-value of  $> .150$ , see Figure 8. Since the  $\log_{10}$  of 10,000 is 4, which is well outside 2 standard deviation of the mean, with 95% confidence 10,000 is considered “long enough” such that we can talk about coexistence of our populations.

All populations survived past the 10,000 step threshold, but the population level of each species varied widely due to the stochastic nature of the simulations. A linear regression was applied to the data points from 10,000 to 10,500 steps and 11% were found to have a slope  $< |5 * 10^{-4}|$ . Thus we see coexistence and every dynamic of the deterministic model can be reproduced in the agent-based model. This offers some validation, but more insight



should be gained from this model for it to be useful.

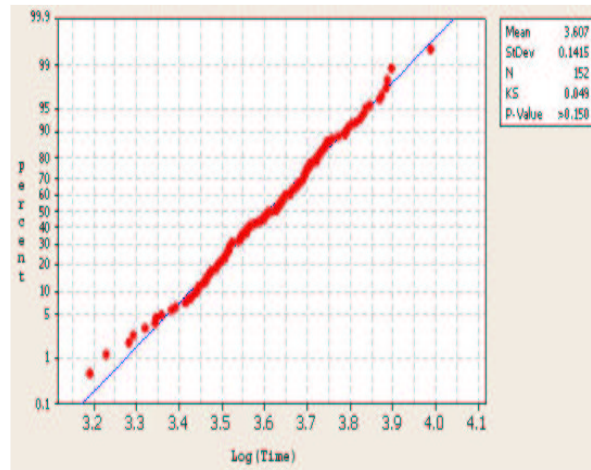


Figure 8: The probability distribution of the log of end times approximates a normal distribution.

In the agent-based model, a single food source placed between two nearby nests almost always leads to competitive exclusion. The results of Morrison support this since, although all of his experiments were on a short time scale, there was always a clear advantage to one of the species. This agrees well with the formulation of the deterministic model and competitive exclusion as defined by G.F. Gause [2].

Another interesting facet is the location of competitive interactions (death) in simulations where the parameters indicate one species should go extinct. According to Morrison the area near the food source always has a high number of dead of both species. Figure 9 demonstrates this phenomenon since the majority of the fighting, evidenced by the clustering of grey “X’s”, occurs around the food sources. Another subtle point is the prevalence of the blue pheromone trails connecting all the food sources to the nest in the upper left hand corner and the sparse red pheromone trails connecting the nest in the lower right hand corner to only a few of the food sources. This implies that species 2 dominates all the food sources and is out competing species 1 which fits well with the principle of competitive exclusion. Since both species are competing for the same resource and in the absence of limiting similarities (parameters yielding coexistence) we can consider them to occupy the same niche. Thus, we expect to see competitive exclusion. The location of the fighting and dominance of food sources are both results Morrison found experimentally when he paired *S. invicta* and *S. geminata* against each other, however the agent-based model is not without limitations.

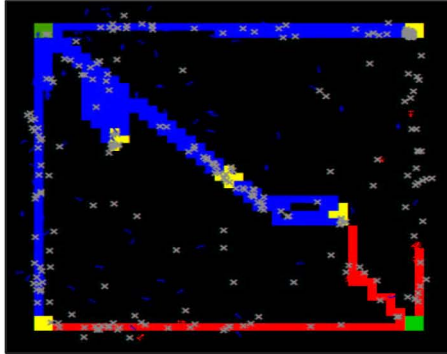


Figure 9: Distribution of dead agents “X’s”

## Agent-Based Discussion

While the agent-based model can reproduce all the dynamics of the deterministic model and shed some light into interactions among the individuals of the two species, analysis of the results is much more difficult. The model is inherently stochastic and has many parameters related to the behavioral rules. Nonetheless, the goal is to incorporate more realism on the individual level to understand the nature of local interactions and perhaps even global events. However care must be taken to avoid hasty generalizations of the results.

Looking at the individual level, *S. geminata* is a superior competitor, thus extrapolating individual level competition to colony level competition leads to the conclusion that *S. invicta* cannot invade. This is clearly not the case. Morrison notes, “A larger number of smaller workers (for the same overall biomass) appears to play a role in making *S. invicta* a superior competitor over *S. geminata*” and “*S. invicta* is able to reach higher densities faster than any of the other *Solenopsis* forms.” Initial conditions can drastically change the outcome, an event also predicted by the deterministic model.

Data from experiments yield parameters in our model which imply, locally, competitive exclusion is the rule (two stable border equilibria and an interior saddle point). In fact this is expected from the theory of niches in ecology. This reinforces our results and intuition: locally there can only be one species.

From data, however, it is clear that many species of fire ants exists simultaneously; *S. invicta* has been a successful invader in displacing many native species but has not completely eliminated *S. geminata*. The solution to this apparent contradiction may be revealed by an examination of the assumptions of the agent-based model: a closely connected and closed environment is assumed. In real life, there may be major land formations separating the colonies of different species. There may also be external factors like other competitors/prey, susceptibility to diseases and parasites, etc. An aspect we can explore,

however, is the role of initial conditions. Thus initial conditions (how many agents attempt to establish a new colony) and spatial flow between colonies may lead to more insight.

## Spatially Structured Simulation

While the agent-based model may be a good tool for tracking the individual behavior of the ants while they fight over a food source it may be necessary to view a species' growth on a larger scale. For this reason we developed a second simulation strategy which tracks the expansion of colonies, or groups, of the species in question as they disperse over territory. The idea is to have a lattice of susceptible sites where the species can live. Then after initializing the opposite edges of the lattice with the species we can track how they spread overland.

## Multi-Patch Simulation

This simulation puts the two species on a  $3 \times 3$  lattice and allows them to set up of colonies and expand over territory. In this simulation each site on the lattice may have one of four designators:  $\{[0, 0], [0, 1], [1, 0], [1, 1]\}$  The value of a lattice site is denoted  $[xval, yval]_{ij}$  where the  $ij^{th}$  site with only species  $x$  is denoted  $[1, 0]_{ij}$ , species  $y$  is denoted  $[0, 1]_{ij}$ , neither species as  $[0, 0]_{ij}$  and both species on a site as  $[1, 1]_{ij}$ . The lattice is considered finite, with no edge wrapping.

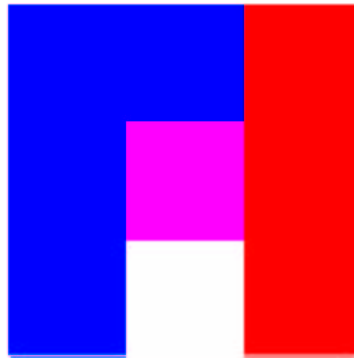


Figure 10: A snapshot of the Multi-Patch Simulation. Red-Species X, Blue-Species Y, Magenta-Both, White-Neither.

The lattice is initialized with the opposite vertical edges either saturated with a single species, or with some small population value (e.g. 500). Each site has its own version of the deterministic model running behind it to determine the growth or reduction of the species present. Each of the deterministic models have the same  $\mu_i, \theta_i, K_i,$  and  $c_i$  values.

However, an assumption is being made that once a site has attained 90% of its carrying capacity it sends out a small percentage of its population to a random neighbor in order to spread the colony. The behavior here should mirror the behavior found just running the deterministic model, with stochastic fluctuation, only on a different scale.

### Multi-Patch Results

The simulation was run 100 times with the following set of parameters, and each time with different initial conditions: The pairs of parameter values correspond to non-trivial

Trial	$(\mu_1, K_1, \theta_1, c_1)$	$(\mu_2, K_2, \theta_2, c_2)$	Initial Conditions $(x_0, y_0)$
1	(.8, 1000, .4, .01)	(.6, 1500, .5, .008)	(1000, 1500)
2	(.8, 1000, .4, .01)	(.6, 1500, .5, .008)	(500, 500)
3	(.8, 1000, .4, .0004)	(.6, 1500, .5, .008)	(1000, 1500)
4	(.8, 1000, .4, .0004)	(.6, 1500, .5, .008)	(500, 500)
5	(.8, 1000, .4, .01)	(.6, 1500, .5, .0004)	(1000, 1500)
6	(.8, 1000, .4, .01)	(.6, 1500, .5, .0004)	(500, 500)
7	(.8, 1000, .4, .0004)	(.6, 1500, .5, .0004)	(1000, 1500)
8	(.8, 1000, .4, .0004)	(.6, 1500, .5, .0004)	(500, 500)

Table 3: Parameter setups for Spatial Simulation.

boundary conditions of two stable points,  $E_x$  a saddle and  $E_y$  stable,  $E_x$  stable and  $E_y$  a saddle, and two saddle points respectively.

### Multi-Patch Results

The results are detailed in the following figure. The data show that the simulation does

Trial	Species X Wins	Species Y Wins	Coexistence
1	60	40	0
2	72	28	0
3	66	34	0
4	69	31	0
5	71	29	0
6	76	24	0
7	0	0	100
8	0	0	100

Table 4: Results from the Spatial Simulation.

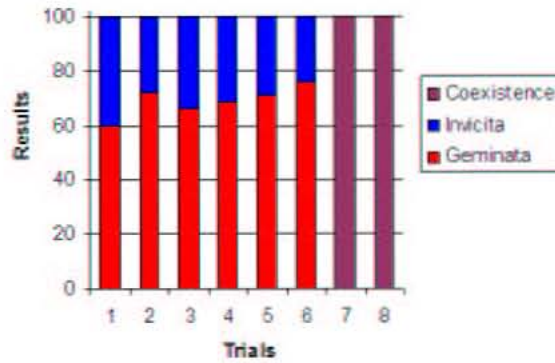


Figure 11: Results from the Spatial Simulation.

exactly support the deterministic model in the coexistence circumstances. With stochastic fluctuation there is also support of the other behaviors found in the deterministic model. This is due in part to the spatial component now being considered in the multi-patch simulation. There is an interesting aspect in the spatial structure of coexistence. The coexistence conditions are brought about by a parameter change that gives the two species of ants the same competition coefficients and other than that the parameters remain the same. Consider Figure 12 and observe that Species X is just barely alive. Their persistence is due to their ability to find and process food ,  $\mu_1$ .

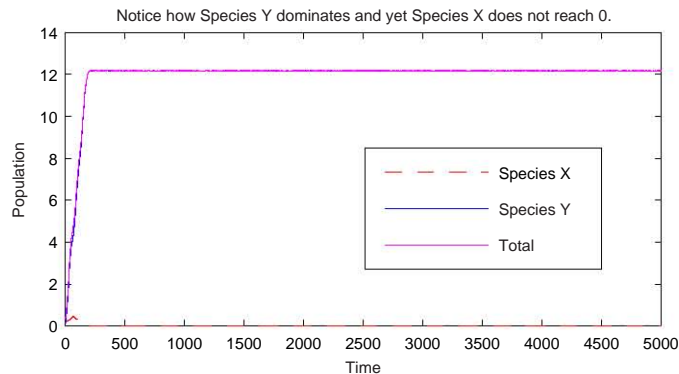


Figure 12: Coexistence is nearly Competitive Exclusion for the coexistence parameters.

The spatially structured model seems to exhibit very interesting and counterintuitive behavior. Even when a boundary equilibrium is unstable, if the other is stable, then we can get competitive exclusion of either species. At best a proposed reason for this can be expressed now. In the spatial simulation the dynamics aren't exactly like those of the deterministic model. There are both harvesting and stocking terms within the dynamics of each cell. These terms represent the number of ants sent forth to colonize other cells on the lattice as well as those who come to the current cell to settle. It is clear that analysis of this model is beyond the scope of this paper. However, it should be noted that simulation has shown that there are parallels in the results between this system and the deterministic model.

## Discussion

### General Results

Presented here has been an analysis, both numerical and classical, of the deterministic model. From this analysis it was concluded that there are at most three interior equilibria and that in any case there are at most one interior stable equilibrium. The Latin Hypercube Sampling has provided, within a set of potentially Biologically viable parameters a sense of the frequency of these conditions and what can be expected to be produced by biological systems.

The agent-based simulation proved to generate the same results as the deterministic model. It is important to state that it appears that with the amount of biology built into the agent-based simulation the deterministic equations do just as well at capturing what can happen given certain parameter values. However, the deterministic model cannot provide are insights into worst and best case scenarios, nor can it contain any spatial information on

the interaction of the species. It was found that with certain parameter sets, the agent-based model behaves much like a stochastic version of the model, capturing all possible behaviors, but some at a very low probability. Furthermore, the agent-based simulation provided an insight into where most ants come into conflict and to the nature of these individual processes.

The spatially structured, or multi-patch, simulation was crafted in an attempt to simulate the deterministic model on a larger scale. However, the spatial simulation captured a behavior, for certain coexistence parameters, that is counter intuitive. It was determined that the spatial correlations in this system drastically alter the outcomes as well as, it is hypothesized, the stability of the boundary equilibria.

The three approaches to modelling the competition between similar species each have pros and cons. The deterministic model is attractive due to its ease of solving and simulating. However, the deterministic model involves no spacial and very little temporal structure. The agent-based approach allows for a capturing of both of these structures missed in the deterministic model. The simulation may be formed in such a way to allow nearly all known biological considerations to have an effect. With this added realism comes the inability to form equations describing the interactions. This can be a problem if simply simulating the process is not enough. The spatially structured simulation has the ability to capture colony-level interactions at the price of complicating the equations which describe the dynamics. Furthermore the simulation is assuming that each colony is close enough to another to allow for interactions. The reason that this simulation does not match what is happening in the real world with the ants is that the ant colonies are, in some cases, of a distance too great from one another to facilitate direct competition.

It is stressed that each of these methods have the same richness. They can all replicate the same behavior within some interpretation and therefore each have merit when considering the outcomes. Further, each model addresses different questions and should therefore be utilized when appropriate.

## Future Extensions

The Latin Hypercube Sampling should be extended to a larger subset  $\mathbf{P} \subset \mathbb{R}_+^8$ . Further when situations of interest are found, three interior equilibria or two intersection with nullclines of same concavity, then a refinement of the sampling should be performed in expanding neighborhoods around the values of interest to find the subspaces where these parameter combinations give certain behavior.

The agent-based simulation should be run with a set collection of parameter values to determine a probability,  $\delta_i$ , that species  $i$  will exclude the existence of the other. This may also be done by considering the stable manifolds of the deterministic system and computing the probabilities over the acceptable phase space. Not only will these values be useful for comparison, analysis and prediction, but they can also be employed in a different version of the multi-patch model.

The multi-patch simulation can first be expanded upon by varying certain conditions between sites and thus introduce heterogeneity to the landscape. Furthermore the lattice can be expanded in size, so the simulation will not be affected as much by stochastic fluctuations, but take into account greater spatial structure. If one is to interpret the agent-based

simulation as the stochastic version of the deterministic model, then one may use the  $\delta_i$  described earlier to have the simulation decide what happens to sites. With this simplification it should be easy to construct ordinary pair approximation equations for analysis on how much impact the spatial structure has on the dynamics [4]. Finally equations truly describing the dynamics of the spatial simulation can be analyzed using traditional methods and analysis then done in a manner alternative to ordinary pair approximation.

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