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Numerical examination of competitive and predatory behaviour for the Lotka-Volterra equations with diffusion based on the maximum-minimum theorem and the one-sided maximum principle.

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Abstract: Understanding the spatial behaviour of populations is a crucial element for gaining a cohesive picture of the overall dynamics of a model and should be explored in conjunction with analytical techniques. As an example, when considering vegetation process modelling of ecosystems, the inclusion of spatial components is critical for accurate modelling results (Jörgensen, 2008). However, through the inclusion of additional components, models often tend to be complex and it becomes increasingly more difficult to analyse the overall system. Techniques then turn to numerical methods (Mickens, 2003); with applications in (Jesse, 1999).

The problem considered in this paper originates from population growth modeling of several groups of marine phytoplankton, and algae species in Australian coastal lagoons. A simplified version of a diffusion, growth, competition/predator system of P.D.E.'s is considered in order to model the population dynamics. More specifically, this work is concerned with the maximum-minimum theorem and the one-sided maximum principle for the diffusive Lotka-Volterra type equations, with populations of $N = 1$ and 2 species (u and v), under imposed von Neumann boundary conditions. The predator-prey and competition systems with two-dimensional diffusion are explored.

The analytically proven theorem indicates that in the case of equal diffusion coefficients a certain function of u and v has no maximum inside the bounding rectangle, $0 < x < l$ and $0 < t < T$, and on the external boundary $t \leq T$ and therefore attains its maximum on the base $t = 0$ or on the vertical sides $x = 0$ and $x = l$. It is also shown that proportionally larger initial populations with higher growth rates will maintain a competitive advantage over their counterparts in the competition equations.

Numerical computations have been implemented to examine the system's behaviour for the case when $N = 2$ with simplified lagoon geometry when two-dimensional diffusion is considered. The results of numerical experiments illustrate that the system's behaviour are consistent with the analytic conclusions obtained for the one-dimensional case.

Keywords: *Competition, Diffusion, Lotka-Volterra, Population Modelling, Predation*

1. INTRODUCTION

The Lotka-Volterra equations for modelling species interactions, also termed the predator-prey and competition equations, have been widely analysed. The competition-diffusion system has been the focus of several analytic works: for two species (Leung et al., 2008), for three species (Mimura and Fife, 1986), for n-species (Rothe, 1976). In this study, analytical techniques have been implemented to give general results for the maximum-minimum theorem for the Lotka-Volterra predator-prey equations, and the one-sided maximum principle for the Lotka-Volterra competition equations, both with one-dimensional diffusion. The analytical results are then extended and compared to numerical simulations for two-dimensional diffusion. The systems are examined under varying diffusive rates and different initial conditions in order to provide an overall picture of the system dynamics.

The application used for the numerical simulations originates from population growth modeling of several groups of marine phytoplankton and algae species in Australian coastal lagoons. To avoid complexities the lagoon geometry is simplified to a dimensionless 1 x 1 bounding square with von Neumann boundary conditions. Numerical simulations are carried out using a finite element approach.

2. PREDATOR-PREY INTERACTIONS

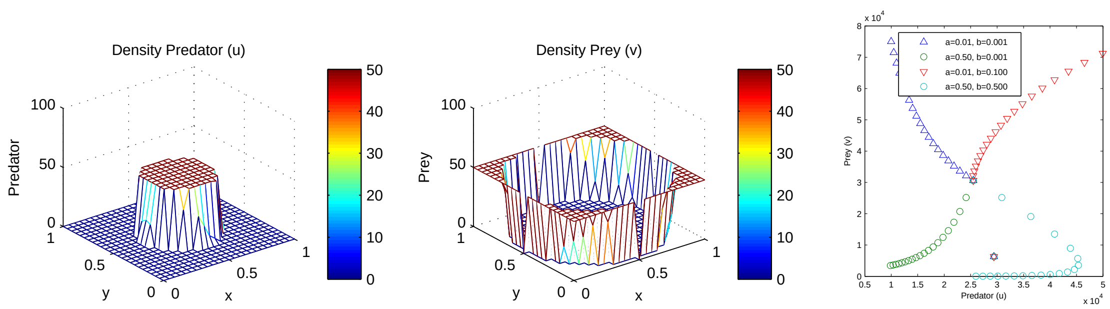
Introducing one-dimensional diffusion terms to the 1D Lotka-Volterra Predator Prey equations and assuming diffusion coefficients are equal to one, the system of equations is given by:

$$\begin{aligned} Lu &= \frac{\partial u}{\partial t} - \frac{\partial^2 u}{\partial x^2} = u(v-\beta) \qquad \text{in} \quad (0,l)\times[0,T] \\ Lv &= \frac{\partial v}{\partial t} - \frac{\partial^2 v}{\partial x^2} = v(\alpha-u) \\ &\frac{\partial u}{\partial x}\Big|_{x=0} = 0 \quad \frac{\partial v}{\partial x}\Big|_{x=0} = 0 \quad \frac{\partial u}{\partial x}\Big|_{x=l} = 0 \quad \frac{\partial v}{\partial x}\Big|_{x=l} = 0. \end{aligned} \tag{1}$$

For this case, we can prove the following statement (the proof is omitted here, but provided in the full paper which is in preparation):

Lemma 2.1: In max $L\phi \geq 0$ and $\frac{\partial \phi}{\partial t} \geq 0$ and $\frac{\partial^2 \phi}{\partial x^2} \leq 0$ there is no maximum inside the bounding rectangle, $0 < x < l$ and $0 < t \leq T$, and the maximum can only be assumed on the base $t = 0$ or on the vertical sides $x = 0$ and $x = l$.

2.1 Numerical Simulations: Numerically, we wish to examine the predator-prey equations with two-dimensional diffusion to see Lemma 2.1 holds for a 1x1 bounding rectangle. The initial conditions for the predator (u) and the Prey (v) are given in Figure 1(a) and 1(b) with initial results given in Figure 1(c).



(a) Initial Condition: Predator u **(b)** Initial Condition: Prey v **(c)** Predator-Prey numerical results.

Figure 1: The predator-prey equations: IC and results.

It is hard to describe the maximum in terms of two dimensional space when diffusion, d, is considered at such a large rate ($d = 1$). Over this time step ($t = 1$), diffusive rates as large as these tend to result in total diffusion within a short space of time and so diffusion in the FEM is only considered in the initial time step. The final results, then become completely dependant on the Lotka-Volterra interaction terms. The maximum is therefore dependant on the initial conditions at time ($t = 0$), where if diffusion is large, the maximum will be within the initial condition or dependant on the initial populations (also at $t = 0$) and the scale of the interaction coefficients.

Figure 1(c) demonstrates that proportionally larger α leads to initial decline in predator numbers with dominance of prey. Large β tends to an initial dominance of prey before the species levels out due to no predation. Equal α and β shows an initial die-off of prey which results in the decline of predators due to a shortage of resources. This however is linked to the initial condition of the predator which is significantly larger than the prey species. In all simulations it is noted that diffusive terms dominate the initial time-steps.

3. COMPETITION INTERACTIONS

The competitive Lotka-Volterra equations for species who contend for the same resource, without diffusion are:

$$\frac{du}{dt} = u(\beta - v)$$
$$\frac{dv}{dt} = v(\alpha - u) \tag{2}$$

In a manner similar to the operations in Section 2.1, the trajectories are level lines of the function

$$\psi = -v + \beta ln(v) + u - \alpha ln(u) \tag{3}$$

and are given by the equation $\psi = C$, where C is some constant.

The point (α,β) corresponds to $\psi_u = 0$ and $\psi_v = 0$ but is not a minimum but a "mountain pass" point for ψ. The equation for the level line passing through (α, β) is

$$u - \alpha ln(u) - v + \beta ln(v) = \alpha - \alpha ln(\alpha) - \beta + \beta ln(\beta) \tag{4}$$

For System (2) with diffusion and diffusive rates equal to 1, we can obtain an equation for ψ. An attempt is now made to obtain a single equation for the function $\psi_1 = f(\psi)$. The equation for $\frac{\partial \psi_1}{\partial t}$ is

$$\frac{\partial \psi_1}{\partial t} = \psi_{1u}\frac{\partial^2 u}{\partial x^2} + \psi_{1v}\frac{\partial^2 v}{\partial x^2} \tag{5}$$

If the R.H.S. of System (2) are multiplied by ψ_u and ψ_v correspondingly and summed, the following equality arises:

$$\psi_u u(\beta - v) + \psi_v v(\alpha - u) = 0 \tag{6}$$

It follows that

$$L\psi = -(\psi_{uu}u_x^2 + 2\psi_{uv}u_x v_x + \psi_{vv}v_x^2) \tag{7}$$

for any function $\psi(u, v)$. Consider $\psi_1 = f(\psi)$, where ψ is given by (3), the question is, can ψ_1 be convex "locally"? To answer this, consider

$$\begin{aligned}
\psi_{1u} &= f'(\psi)\psi_u \\
\psi_{1v} &= f'(\psi)\psi_v \\
\psi_{1uu} &= f''(\psi)\psi_u^2 + f'(\psi)\psi_{uu} \\
\psi_{1vv} &= f''(\psi)\psi_v^2 + f'(\psi)\psi_{vv} \\
\psi_{1uv} = \psi_{1vu} &= f''(\psi)\psi_u\psi_v + f'(\psi)\psi_{uv}
\end{aligned} \tag{8}$$

Substitution of the equations from System (8) into the conditions for convexity:

$$\begin{aligned}
\psi_{1uu}\psi_{1vv} - \psi_{1uv}^2 &= (f''(\psi)\psi_u^2 + f'(\psi)\psi_{uu})(f''(\psi)\psi_v^2 + f'(\psi)\psi_{vv}) - (f''(\psi)\psi_u\psi_v \\
&\quad + f'(\psi)\psi_{uv})^2 \\
&= f'^2(\psi)(\psi_{uu}\psi_{vv} - \psi_{uv}^2) + f'(\psi)f''(\psi)(\psi_{uu}\psi_v^2 - 2\psi_{uv}\psi_u\psi_v + \psi_{vv}\psi_u^2) \\
&\quad +(f''^2(\psi_u^2\psi_v^2 - \psi_u^2\psi_v^2)
\end{aligned}$$

Defining $f(\psi)$ by letting $f(\psi) = e^{\psi}$ and $\psi = -v + \beta ln(v) + u - \alpha ln(u)$ gives

$$\psi_u = 1 - \frac{\alpha}{u}, \quad \psi_{uu} = \frac{\alpha}{u^2}, \quad \psi_v = -1 + \frac{\beta}{v}, \quad \psi_{vv} = -\frac{\beta}{v^2} \tag{9}$$

and

$$\psi_{1uu}\psi_{1vv} - \psi_{1uv}^2 = e^{2\psi}\left(\frac{-\alpha\beta + \alpha(v-\beta)^2 - \beta(u-\alpha)^2}{u^2v^2}\right) \tag{10}$$

Expression (10) is positive when

$$\alpha(v-\beta)^2 - \beta(u-\alpha)^2 > \alpha\beta \tag{11}$$

The points $(\alpha, \beta + \sqrt{\beta})$, $(\alpha, \beta - \sqrt{\beta})$ lie on the boundary of the domain determined by inequality (11):

$$\alpha(v-\beta)^2 - \beta(u-\alpha)^2 = \alpha\beta \tag{12}$$

The domain (11), is such that in it either $v < \beta - \sqrt{\beta}$ (lower part) or $v < \beta + \sqrt{\beta}$ (upper part). The lower part has intersection with $\{u > 0, v > 0\}$ only for $\beta > 1$. Substituting the equations from System (9) into the conditions for convexity gives:

$$\begin{aligned}
\psi_{1uu} &= e^{\psi}\left((1 - \frac{\alpha}{u})^2 + \frac{\alpha}{u^2}\right) && > 0 \\
\psi_{1vv} &= e^{\psi}\left((1 - \frac{\beta}{v})^2 - \frac{\beta}{v^2}\right) && > 0 \\
&= e^{\psi}\frac{(v - \beta - \sqrt{\beta})(v - \beta + \sqrt{\beta})}{v^2} && > 0
\end{aligned}$$

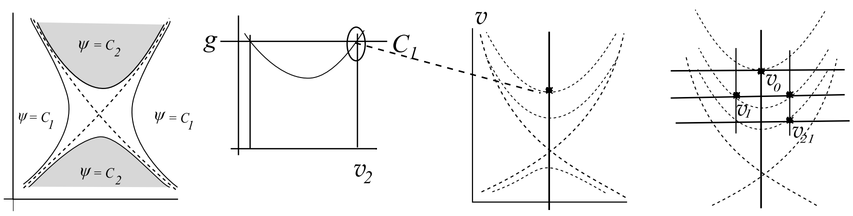
which holds for either the upper or lower value of v, $v < \beta - \sqrt{\beta}$ or $v > \beta + \sqrt{\beta}$. This implies that ψ_1 is convex in domain (11), and a one-sided maximum principle is valid. Hence, in the domain (11) $L\psi_1 < 0$ and ψ_1 has no maximum in $[0,l] \times (0,T]$ as long as u, v remain in the domain (11). The same is true for ψ since ψ_1 is monotonically increasing with respect to ψ. Thus if $(u,\ v)\ \epsilon\ (11)$,

$$\psi \leq \max_{x \epsilon [0,l]} \psi(u_0(x), v_0(x)) = C \tag{13}$$

Figure () illustrates the curves $\psi = C$. Refer to Equation (4) for the equation of the curve containing (α, β) which corresponds to

$$C = C_o = \alpha - \alpha ln(\alpha) - \beta + \beta ln(\beta) \tag{14}$$

The left and right branch curves correspond to $C > C_0$. The curves with upper and lower branches correspond to $C < C_0$. In the case when $C < C_0$ the domain $\psi \leq C$ is shaded.



(a) Curves $\psi = C$.

(b) The bordering curve of the convexity domain.

Figure 2: $\psi = C$ and the bordering curve of the convexity domain.

Figure (2(b)) illustrates the bordering curve of the convexity domain, a hyperbola with asymptotes:

$$\frac{v - \beta}{u - \alpha} = \pm\sqrt{\frac{\beta}{\alpha}} \tag{15}$$

The question now is: Does the inequality (13) make the values of $(u,\ v)$ remain in the domain (11)? To answer this, consider now the upper parts of the domains given by (11) and (13) using notations (11) and (13) for those upper parts. Consider the right hand and upper branch of the curve $\psi = C$, that is, $C < C_0$ given by:

$$v - \beta ln(v) - u + \alpha ln(u) = -C \tag{16}$$

and

$$\frac{dv}{du} = \frac{1 - \frac{\alpha}{u}}{1 - \frac{\beta}{v}} \tag{17}$$

For $u > 2\alpha$, $v > 0$, we can estimate $\frac{du}{dv}$ from below:

$$1 - \frac{\alpha}{u} > \frac{1}{2}, \quad 1 - \frac{\beta}{v} < 1 \tag{18}$$

and therefore

$$\frac{du}{dv} > \frac{1}{2} \quad \text{for} \quad u > 2\alpha, \quad v > 0 \tag{19}$$

This means that $v \to \infty$ as $u \to \infty$, and Equation (16) gives $\frac{v}{u} \to 1$ as $u \to \infty$. Indeed:

$$\begin{aligned} v\left(1 - \beta\frac{ln(v)}{v}\right) &= u\left(1 - \alpha\frac{ln(u)}{u}\right) - C \\ \frac{v}{u} &= \frac{(1 - \alpha\frac{ln(u)}{u})}{(1 - \beta\frac{ln(v)}{v})} = \frac{C}{u(1 - \beta\frac{ln(v)}{v})} \\ v &= u(1 + \varepsilon(u)), \quad \varepsilon(u) \to 0 \quad \text{as} \quad u \to \infty \end{aligned} \tag{20}$$

For the hyperbola (Equation (12)):

$$v = \sqrt{\frac{\beta}{\alpha}} \quad u(1 + \varepsilon_1(u)), \quad \varepsilon_1(u) \to 0 \quad \text{as} \quad u \to \infty \tag{21}$$

For $\alpha > \beta$ and for large u, the curve (20) lies higher than (21). The rest of the curve (16) lies higher than (12) for sufficiently large C. The curve (10) intersects the line $u = 0$ at $v = \beta + \sqrt{\beta(1+\alpha)}$ and the whole line for $u < \alpha$ lies lower than $\beta + \sqrt{\beta(1+\alpha)}$.

On the curve the minimal value of v is assumed for $u = \alpha$ and is defined by

$$v - \beta ln(v) = \alpha - \alpha ln(\alpha) - C \tag{22}$$

and if $v > 1$

$$v > -C + \alpha - ln(\alpha) = v_0 \tag{23}$$

It follows that for negative C large in absolute value, v is also large and the whole curve (16) is situated higher than (12). Therefore Equation (13) implies Equation (11). The result is as expected, given that α and β are the reproductive coefficients for v and u in the absence of other species. If v has a large advantage for $t = 0$ and reproduces quicker than u, it is natural that it keeps the advantage.

Corollary: If for the hyperbola, Figure (2(b)), $\frac{u}{v} < 1$, the curve $\psi = -C$ will be situated higher than the domain or the set which is bounded within $\psi = -C$. Therefore ψ_1 is convex in this set and hence, ψ_1 does not have a maximum and $\psi_1 \leq \max_{t=0} \psi_1$. Because ψ_1 is monotonically increasing then $\psi_{\leq} \max_{t=0} \psi$ and v will be above the curve.

For large C, the domain, $\psi \leq -C$:

$$v - \beta ln(v) - u + \alpha ln(u) \geq C$$

belongs to the domain of large, positive v (because it also exists in the lower part of v closer to zero). Indeed the curve:

$$v - \beta ln(v) - u + \alpha ln(u) = C \tag{24}$$

has a minimum for

$$1 - \frac{\alpha}{u} = 0 \tag{25}$$

i.e. for $u = \alpha$. Then

$$v - \beta ln(v) = C_1 = C + \alpha - \alpha ln(\alpha) \tag{26}$$

For large C, C_1 is also large and the graph of the L.H.S. of (26) has a shape indicated in Figure (2(b)) and horizontal straight lines $g(v) = C$ intersecting (26) at two points. For $v \to \infty$ the curve $\psi = -C$ lies higher than the corresponding branch of the hyperbola (12). Suppose that this is true for $v > v_1$. Now is it possible to choose C so large that the rest if the curve $\psi = -C$ lies higher than the remaining part of the hyperbola. The function *v(u)*, defined by $\psi = -C$ has a minimum at $u = \alpha$, and this minimum tends to infinity as $C \to \infty$. If C is so large that $v_0 > v_1$, $v_0 > \beta + \sqrt{\beta(1+\alpha)}$, and the whole curve $\psi = -C$ lies over the hyperbola (where v_0 is defined in (23). Indeed for $u \geq u_1(\varepsilon)$, $v \geq u(1-\varepsilon)$ for the hyperbola $v \leq \sqrt{\frac{\beta}{\alpha}u}$, where $\frac{\beta}{\alpha} < 1$.

For $0 < u < u_1(\varepsilon)$ and (12), $v \leq v_1$ and all of the curve (24) is located as far as necessary above for large enough C.

These conclusions only relate to the upper part of the domain, $\psi = -C$. Therefore the initial conditions have to belong to the upper domain $v(0) \geq \beta + \sqrt{\beta}$.

3.1 Numerical Simulations: The most interesting question is how v keeps its advantage mentioned in the paragraph above: does it eliminate u or does u keep non-zero equilibrium less than values of v. Figure illustrates the different simulations. Included in the simulations of the diffusive competition equations are the intraspecific competition terms for each species. Hence the equations for simulation in 2D are:

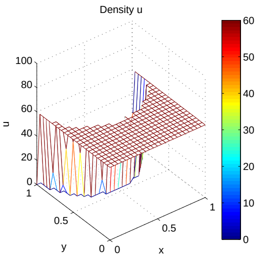
$$\begin{aligned}
&\frac{\partial u}{\partial t} - d_1\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) = u(r_1 - \alpha_{11}u - \alpha_{12}v) \qquad \text{in} \quad (0,l) \times [0,T]\\
&\frac{\partial v}{\partial t} - d_2\left(\frac{\partial^2 y}{\partial x^2} + \frac{\partial^2 v}{\partial y^2}\right) = v(r_2 - \alpha_{21}u - \alpha_{22}v)\\
&\tfrac{\partial u}{\partial x}|_{x=0} = 0 \quad \tfrac{\partial v}{\partial x}|_{x=0} = 0 \qquad \tfrac{\partial u}{\partial x}|_{x=1} = 0 \quad \tfrac{\partial v}{\partial x}|_{x=1} = 0\\
&u(0,x,y) = u_0 \qquad v(0,x,y) = v_0.
\end{aligned} \tag{27}$$

In System (27) d_i are the coefficients of diffusion and α_{ii} and α_{ij} represent intraspecific and interspecific competition respectively with $i = 1, 2$ and $j = 1, 2$. The simulations are initialized with a much larger v for $t = 0$ and the system is observed under different diffusive and growth rates. The initial conditions for u and v are presented in Figures 3(a) and 3(b). The graphical results are also presented in Figure 3.

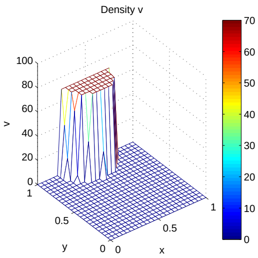
If v has a large advantage for $t = 0$ and reproduces quicker than u, it is natural that it keeps the advantage. The result is as expected, given that α and β are the reproductive coefficients for v and u in the absence of other species. This is given subject to the condition that the intraspecific competition rates are reasonable, i.e. there are abundant resources to sustain species v. When the intraspecific rates are zero with equal growth we see a dominance of species v as is also the case with a larger growth rate for v, Figures 3(i and j). The diffusive rates maintain the same property as that of the predator-prey system.

4. CONCLUSIONS AND FUTURE WORK

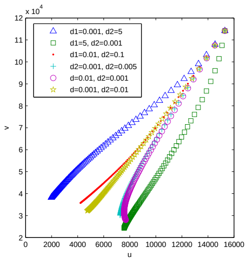
We provide analytical quantification of population dynamics described by predator-prey equations with diffusion for one the dimensional case, $0 \leq x \leq l$ and $0 \leq t \leq T$. We also implemented numerical simulations for the two spatial dimensional case. The simulation was implemented for a rectangular spatial domain with von Neumann boundary conditions. The results of the simulation confirmed the conclusion obtained for the one dimensional analytical case. Future work includes writing a program for the numerical solution of the von Neumann problem for the diffusive Lotka-Volterra equations when the spatial domain has a sophisticated geometry reflecting the real shape of estuarine lakes.



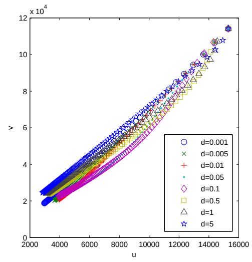
(a) Initial Condition: Competitive u



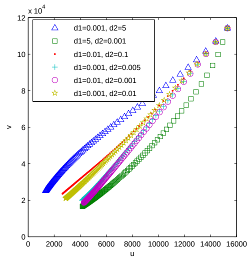
(b) Initial Condition: Competitive v



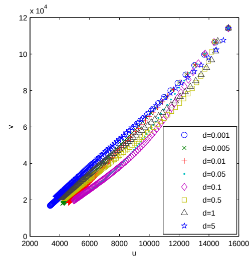
(c) Var.Diff.: $\alpha_{11} = \alpha_{22} = \alpha_{12} = \alpha_{21} = 0.1$, $r_1 = r_2 = 1.1$



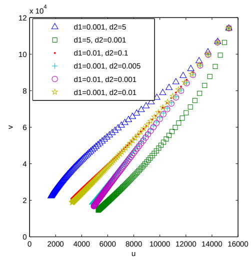
(d) Eq.Diff.: $\alpha_{11} = \alpha_{22} = \alpha_{12} = \alpha_{21} = 0.1$, $r_1 = 0.2$, $r_2 = 0.4$



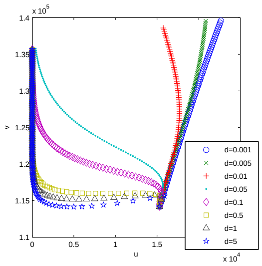
(e) Var.Diff.: $\alpha_{11} = \alpha_{22} = \alpha_{12} = \alpha_{21} = 0.1$, $r_1 = 0.2$, $r_2 = 0.4$



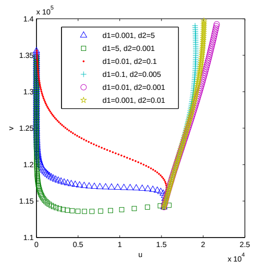
(f) Eq.Diff.: $\alpha_{11} = \alpha_{22} = \alpha_{12} = \alpha_{21} = 0.1$, $r_1 = r_2 = 0.4$



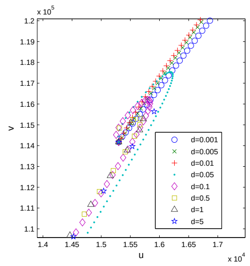
(g) Var.Diff.: $\alpha_{11} = \alpha_{22} = \alpha_{12} = \alpha_{21} = 0.1$, $r_1 = r_2 = 0.2$



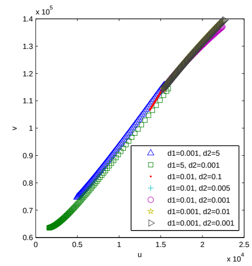
(h) Eq.Diff.: $\alpha_{11} = \alpha_{22} = \alpha_{12} = \alpha_{21} = 0.1$, $r_1 = r_2 = 1.1$



(i) Var.Diff.: $\alpha_{11} = \alpha_{22} = 0$, $\alpha_{12} = 0.4$, $\alpha_{21} = 0.1$, $r_1 = r_2 = 1.1$



(j) Eq.Diff.: $\alpha_{11} = \alpha_{22} = 0$, $\alpha_{12} = 0.1$, $\alpha_{21} = r_1 = 0.4$, $r_2 = 0.2$



(k) Var.Diff.: $\alpha_{11} = \alpha_{22} = 0$, $\alpha_{12} = 0.1$, $\alpha_{21} = r_1 = 0.4$, $r_2 = 0.2$

Figure 3: Competition equations: IC and results.

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