Classifying Equilibria With Unknown Parameters for a Dynamic Population Model

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***Abstract*— The goal is to use a mean field approximation to analyze a model for population dynamics introduced by Bolker and Pacala. After generating a system of ordinary differential equations for the mean field (MF) approximation with unspecified parameters - including birth, death, migration, and competition dynamics - we find the equilibrium points using *MATHEMATICA*. We then use the eigenvalue method to classify the stability of these equilibria and determine under what conditions on the given parameters, the population equilibria are stable and unstable. We find that for the *2-Box* model there is indeed a case with a stable equilibrium point.**
Key Words: Bolker-Pacala Model, Mean Field Approximation, Eigenvalue Method

I. INTRODUCTION

In 1998 Benjamin M. Bolker and Stephen W. Pacala wrote a paper called Spatial Moment Equations for Plant Competition: Understanding Spatial Strategies and the Advatages of Short Dispersal. In it they build on the classic competition-colonization trade-off model introduced by Levins and Culver (1971) and popularized by Hastings (1980) and Tilman (1994). The issue with the classic model was that it put an emphasis on colonization and competition. Bolker and Pacala however, saw that another factor was missing.

That factor is exploitation. They defined this term as "..exploitation of a habitat before a dominant competitor can take over" [1]. Including this new term, the three main factors that Bolker and Pacala talk about are colonization, competition, and exploitation. We will be considering Bolker and Pacala's model for this project as the addition of the factor "exploitation", gives more depth to the classic population dynamics model.

So our terms have an air of parallelism to them we will replace colonization, competition, and exploitation with migration rate, outer competition, and inner competition respectively. We will also consider the most natural factors of population dynamics, birth and death rates.

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II. THEORY

A. Necessary Definitions

1) Mean Field Approximation: In probability theory when a stochastic model is too complex we can understand it better by analyzing a simpler version of the same model. The idea is that any findings that apply to the simple model will hopefully apply to the complex model. This is called a mean field theory.

The Bolker and Pacala's *2-Box* model that we talk about later is a mean field approximation of a much more complex *n-Box* model that describes population dynamics between *n* locations each with its own population density.

2) Equilibrium Points: Equilibrium points are solutions to systems of equations in which the state of the system does not change due to small disturbances. The state of the system can be classified as stable or unstable.

3) Eigenvalue Method/Stability Check: The eigenvalue method helps us classify the state of equilibria as either stable of unstable. In the discrete-time case the method states that an equilibrium point is stable if every of its eigenvalues are absolute value less than one. In the continuous case the eigenvalue method states that an equilibrium point is stable if the real part of all the eigenvalues for that point are less than zero. We will be using the eigenvalue method for the continuous case.

B. Methodology

We will use a mean field approximation to figure out the domain for our unspecified parameters associated with stability. We will first generate and input a system of differential equations for a Bolker-Pacala *2-Box* model using *MATHEMATICA*.

We will then find the equilibrium points of the system by setting the system equal to zero and solving for the independent variables which will be the population densities. After, we will use the eigenvalue method for the continuous case to express our eigenvalues in terms of the unknown parameter - birth, death, migration, and two types of competition rates.

By hand we then figure out a simple way to express the domain for stability, if it exists, on each of the equilibria. With that we can rationalize under what conditions the system is stable or not stable. We complete this process for the *2-Box* model.

III. Analysis

This *2-Box* model that we will be using is shown in Figure [1]. From this representation we make our system of equations. The box of green dots represents the population densities or z_i where i is the number of the box. The boxes with b_i are the birth rates and u_i are the death rates of their corresponding z_i. The green arrows represents the particles migrating from one box to another. The orange arrows with an x represent a competition between particles of the two boxes where the x is the losing particle dying off. Lastly the red circle represents inner competition where that box's z_i population has a particle dying off.

From this box we can accurately make our system of equations. The general system generated from this representation is:

$$f1 = \frac{dz_1}{dt} = b_1 z_1 - u_1 z_1 - z_1^2 a_{11}^- - z_1 a_{12}^+ - z_1 z_2 a_{12}^- + z_2 a_{21}^+$$

$$f2 = \frac{dz_2}{dt} = b_2 z_2 - u_2 z_2 - z_2^2 a_{22}^- - z_2 a_{21}^+ - z_1 z_2 a_{21}^- + z_1 a_{12}^+$$

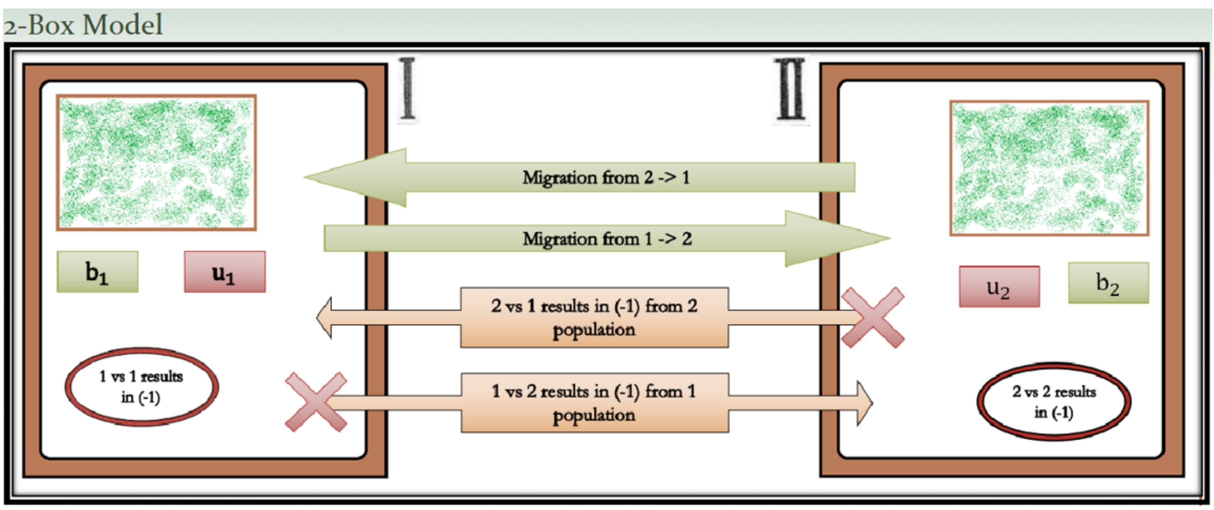

Fig. 1. Image of the *2-Box* model showing birth, death, migration, inner competition and outer competition.

The function g is the basic case of the *2-Box* model when each box has equal birth (b), death(u), inner(a_i), outer(a_o), and migration(a_m^+) rates. The function g is:

$$g1 = \frac{dz_1}{dt} = bz_1 - uz_1 - z_1^2 a_i^- - z_1 a_m^+ - z_1 z_2 a_o^- + z_2 a_m^+$$

$$g2 = \frac{dz_2}{dt} = bz_2 - uz_2 - z_2^2 a_i^- - z_2 a_m^+ - z_1 z_2 a_o^- + z_1 a_m^+$$

We will be using the function g to start off our analysis of the *2-Box* model.

Now that we have established the system we are going to use, we need to use *MATHEMATICA* to solve our system of equations. We do this by setting the system equal to zero. From that we obtain our four equilibrium points (z_1, z_2) shown in Figure [2]:

$$\left\{\{z1 \to 0,\ z2 \to 0\},\ \left\{z1 \to \frac{b-u}{a_i^- + a_o^-},\ z2 \to \frac{b-u}{a_i^- + a_o^-}\right\},\right.$$

$$\left\{z1 \to \frac{(b-u-2a_{12}^+)a_i^- - b a_o^- + u a_o^- + 2a_{12}^+ a_o^- + \sqrt{(b-u-2a_{12}^+)(a_i^- - a_o^-)((b-u+2a_{12}^+)a_i^- + (-b+u+2a_{12}^+)a_o^-)}}{2a_i^-(a_i^- - a_o^-)},\right.$$

$$\left. z2 \to -\frac{(-b+u+2a_{12}^+)a_i^- + b a_o^- - u a_o^- - 2a_{12}^+ a_o^- + \sqrt{(b-u-2a_{12}^+)(a_i^- - a_o^-)((b-u+2a_{12}^+)a_i^- + (-b+u+2a_{12}^+)a_o^-)}}{2a_i^-(a_i^- - a_o^-)}\right\},$$

$$\left\{z1 \to \frac{(b-u-2a_{12}^+)a_i^- - b a_o^- + u a_o^- + 2a_{12}^+ a_o^- - \sqrt{(b-u-2a_{12}^+)(a_i^- - a_o^-)((b-u+2a_{12}^+)a_i^- + (-b+u+2a_{12}^+)a_o^-)}}{2a_i^-(a_i^- - a_o^-)},\right.$$

$$\left.\left. z2 \to \frac{(b-u-2a_{12}^+)a_i^- - b a_o^- + u a_o^- + 2a_{12}^+ a_o^- + \sqrt{(b-u-2a_{12}^+)(a_i^- - a_o^-)((b-u+2a_{12}^+)a_i^- + (-b+u+2a_{12}^+)a_o^-)}}{2a_i^-(a_i^- - a_o^-)}\right\}\right\}$$

Fig. 2. The equilibrium points for the system g.

Before we continue we need to define a few general conditions. Those general conditions are:

$$b > u > 0$$

$$a_m^+ \geq 0, a_i \geq 0, a_o \geq 0$$

$$a_i \vee a_o > o$$

We need to do this so that when we define our unknown parameters as inequalities, they will make sense biologically. For example, if the death rate was greater than the birth rate the only equilibrium point will be (0,0), which tells us that both species will eventually die out. The other general conditions are obvious because you can't have negative rates.

Now that we have our four equilibrium points and general conditions, we must use the eigenvalue method. We do this by first finding the Jacobian matrix. Figure[3] shows the general definition of a 2x2 Jacobian matrix, and the Jacobian matrix for our system g.

$$J_g\,(Z_1, Z_2) = \begin{pmatrix} \frac{\partial g1}{\partial z_1} & \frac{\partial g1}{\partial z_2} \\ \frac{\partial g2}{\partial z_1} & \frac{\partial g2}{\partial z_2} \end{pmatrix}$$

$$J_g = \begin{pmatrix} b - u - a_{12}^{\dagger} - 2\,z1\,a_i^{-} - z2\,a_o^{-} & a_{12}^{\dagger} - z1\,a_o^{-} \\ a_{12}^{\dagger} - z2\,a_o^{-} & b - u - a_{12}^{\dagger} - 2\,z2\,a_i^{-} - z1\,a_o^{-} \end{pmatrix}$$

Fig. 3. The Jacobian matrix of the system g.

To find the eigenvalues in *MATHEMATICA* we input an equilibrium point as the values for z_1 and z_2, we then use the command *Eigenvalues[A]* where the matrix A is the Jacobian matrix of the system g. Figure[4] shows the code used for the equilibrium point (0,0) with the two eigenvalues highlighted, while Figure[5] and Figure[6] shows the rest of the eigenvalues for points 2,3 and 4 respectively. The eigenvalues for the third and fourth EQ point are luckily the same. This means that when we start to make inequalities for stability by hand we only need to do the work for three sets of eigenvalues.

```
z1 = 0;
z2 = 0;
MatrixForm[A]
Simplify[Eigenvalues[A]]
```

$$\begin{pmatrix} b - u - a_{12}^{\dagger} & a_{12}^{\dagger} \\ a_{12}^{\dagger} & b - u - a_{12}^{\dagger} \end{pmatrix}$$

$$\{b - u,\ b - u - 2\,a_{12}^{\dagger}\}$$

Fig. 4. The code for the Eigenvalues of the first equilibrium point (0,0) of the system g. With the eigenvalues outputted highlighted.

$$z1 = \frac{b-u}{a_i^{-} + a_o^{-}};\quad z2 = \frac{b-u}{a_i^{-} + a_o^{-}};$$

$$\left\{-b + u,\ \frac{1}{a_i^{-} + a_o^{-}}\left((-b + u - 2\,a_{12}^{\dagger})\,a_i^{-} + (b - u - 2\,a_{12}^{\dagger})\,a_o^{-}\right)\right\}$$

Fig. 5. The Eigenvalues of the second equilibrium point of the system g. With the eigenvalues outputted highlighted.

With our list of eigenvalues we start to see how complicated general inequalities will be. So we make several special cases that we will apply to each EQ point to further constrict the solution set for stability. Those cases are:

1) b, u, a_o, a_m^+, $a_i = 0$
   Which translates to the *2-Box* model having no inner competition.
2) b, u, a_i, a_m^+, $a_o = 0$
   Which translates to the *2-Box* model having no outer competition.
3) b, u, a_o, a_i, $a_m^+ = 0$
   Which translates to the *2-Box* model having no migration.

$$z1 = \frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\left((b - u - 2\,a_{12}^{\dagger})\,a_i^{-} - b\,a_o^{-} + u\,a_o^{-} + 2\,a_{12}^{\dagger}\,a_o^{-} + \sqrt{\left((b - u - 2\,a_{12}^{\dagger})\,(a_i^{-} - a_o^{-})\,\left((b - u + 2\,a_{12}^{\dagger})\,a_i^{-} + (-b + u + 2\,a_{12}^{\dagger})\,a_o^{-}\right)\right)}\right);$$

$$z2 = -\frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\left((-b + u + 2\,a_{12}^{\dagger})\,a_i^{-} + b\,a_o^{-} - u\,a_o^{-} - 2\,a_{12}^{\dagger}\,a_o^{-} + \sqrt{\left((b - u - 2\,a_{12}^{\dagger})\,(a_i^{-} - a_o^{-})\,\left((b - u + 2\,a_{12}^{\dagger})\,a_i^{-} + (-b + u + 2\,a_{12}^{\dagger})\,a_o^{-}\right)\right)}\right);$$

$$\Big\{-\frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\Big(b\,a_i^{-}\,a_o^{-} - u\,a_i^{-}\,a_o^{-} - b\,(a_o^{-})^2 + u\,(a_o^{-})^2 - 2\,a_{12}^{\dagger}\,\left((a_i^{-})^2 - (a_o^{-})^2\right) + \sqrt{\left((a_i^{-} - a_o^{-})^2\,\left(4\,\left((b - u)^2 - 3\,(a_{12}^{\dagger})^2\right)\,(a_i^{-})^2 - 4\,\left((b - u)^2 - 3\,(b - u)\,a_{12}^{\dagger} + 2\,(a_{12}^{\dagger})^2\right)\,a_i^{-}\,a_o^{-} + (-b + u + 2\,a_{12}^{\dagger})^2\,(a_o^{-})^2\right)\right)}\Big),$$
$$\frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\Big(-b\,a_i^{-}\,a_o^{-} + u\,a_i^{-}\,a_o^{-} + b\,(a_o^{-})^2 - u\,(a_o^{-})^2 + 2\,a_{12}^{\dagger}\,\left((a_i^{-})^2 - (a_o^{-})^2\right) + \sqrt{\left((a_i^{-} - a_o^{-})^2\,\left(4\,\left((b - u)^2 - 3\,(a_{12}^{\dagger})^2\right)\,(a_i^{-})^2 - 4\,\left((b - u)^2 - 3\,(b - u)\,a_{12}^{\dagger} + 2\,(a_{12}^{\dagger})^2\right)\,a_i^{-}\,a_o^{-} + (-b + u + 2\,a_{12}^{\dagger})^2\,(a_o^{-})^2\right)\right)}\Big)\Big\}$$

$$z1 = \frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\left((b - u - 2\,a_{12}^{\dagger})\,a_i^{-} - b\,a_o^{-} + u\,a_o^{-} + 2\,a_{12}^{\dagger}\,a_o^{-} - \sqrt{\left((b - u - 2\,a_{12}^{\dagger})\,(a_i^{-} - a_o^{-})\,\left((b - u + 2\,a_{12}^{\dagger})\,a_i^{-} + (-b + u + 2\,a_{12}^{\dagger})\,a_o^{-}\right)\right)}\right);$$

$$z2 = \frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\left((b - u - 2\,a_{12}^{\dagger})\,a_i^{-} - b\,a_o^{-} + u\,a_o^{-} + 2\,a_{12}^{\dagger}\,a_o^{-} + \sqrt{\left((b - u - 2\,a_{12}^{\dagger})\,(a_i^{-} - a_o^{-})\,\left((b - u + 2\,a_{12}^{\dagger})\,a_i^{-} + (-b + u + 2\,a_{12}^{\dagger})\,a_o^{-}\right)\right)}\right);$$

$$\Big\{-\frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\Big(b\,a_i^{-}\,a_o^{-} - u\,a_i^{-}\,a_o^{-} - b\,(a_o^{-})^2 + u\,(a_o^{-})^2 - 2\,a_{12}^{\dagger}\,\left((a_i^{-})^2 - (a_o^{-})^2\right) + \sqrt{\left((a_i^{-} - a_o^{-})^2\,\left(4\,\left((b - u)^2 - 3\,(a_{12}^{\dagger})^2\right)\,(a_i^{-})^2 - 4\,\left((b - u)^2 - 3\,(b - u)\,a_{12}^{\dagger} + 2\,(a_{12}^{\dagger})^2\right)\,a_i^{-}\,a_o^{-} + (-b + u + 2\,a_{12}^{\dagger})^2\,(a_o^{-})^2\right)\right)}\Big),$$
$$\frac{1}{2\,a_i^{-}\,(a_i^{-} - a_o^{-})}\Big(-b\,a_i^{-}\,a_o^{-} + u\,a_i^{-}\,a_o^{-} + b\,(a_o^{-})^2 - u\,(a_o^{-})^2 + 2\,a_{12}^{\dagger}\,\left((a_i^{-})^2 - (a_o^{-})^2\right) + \sqrt{\left((a_i^{-} - a_o^{-})^2\,\left(4\,\left((b - u)^2 - 3\,(a_{12}^{\dagger})^2\right)\,(a_i^{-})^2 - 4\,\left((b - u)^2 - 3\,(b - u)\,a_{12}^{\dagger} + 2\,(a_{12}^{\dagger})^2\right)\,a_i^{-}\,a_o^{-} + (-b + u + 2\,a_{12}^{\dagger})^2\,(a_o^{-})^2\right)\right)}\Big)\Big\}$$

Fig. 6. The Eigenvalues of the third and fourth equilibrium point of the system g. With the eigenvalues outputted highlighted.

Classification

Even without the special cases we can start to classify an equilibria. For example since the eigenvalue method requires all eigenvalues to be greater than zero we can see that the equilibrium point (0,0) is unstable. This is because it's first eigenvalue $(b-u)$ can never be negative since our general condition sets $b > u$.

After simplifying the eigenvalues by hand, we use this type of rationale and logic along with our special cases to finally classify all four of our equilibria as inequalities in terms of the unknown parameters.

IV. Results

After we dissect every eigenvalue we come up with a list of results of when our equilibria are stable and unstable.

- The first equilibrium point $(0, 0)$ is unstable in every special case.
- The second equilibrium point $(\frac{b-u}{a_i^- + a_o^-}, \frac{b-u}{a_i^- + a_o^-})$ is stable in these scenarios:
  1) When $a_i = 0$, if $(b - u - 2a_m^+) < 0$
  2) When $a_o = 0$, if $(-b + u - 2a_m^+) < 0$ [Always Stable]
  3) When a_i and $a_o > 0$, if $a_i > a_o$.
- The third and fourth equilibrium point have the same several scenarios:
  1) Is unstable when $a_i = 0$.
  2) Is stable when $a_o = 0$, if
  $$(a_m^+ - \frac{1}{2}a_i\sqrt{-4(b - u + 3a_i^2 - a_m^+)a_m^+ + (b - u)^2(1 + 4a_i^2)}$$
  $$< 0$$
  3) When $a_m^+ = 0$, if
  $$\frac{(-b + u)(a_o + \sqrt{1 - 4a_oa_i + 4a_i^2})}{2a_i} < 0$$

and if

$$\frac{-(b+u)a_i a_o - (b-u)a_o^2}{2a_i(a_i - a_o)} - \frac{(b-u)\sqrt{1 - 4a_o a_i + 4a_i^2}}{2a_i} < 0$$

V. CONCLUSIONS

We can see that the *2-Box* model has instances of stability. These instances show up when the inequalities mentioned in the *Results* section hold.

REFERENCES

[1] M. Bessonov, S. Molchanov, and J. Whitmeyer, *A Mean Field Approximation of The Bolker-Pacala Population Model.* Markov Processes and Related Fields, 20(2):329348, 2014.

[2] M. Bessonov, S. Molchanov, and J. Whitmeyer, *A Multi-Class Extension of the Mean Field Bolker-Pacala Population Model*, Under Review for Publication, 2016.

[3] B. M. Bolker, S. W. Pacala, *Spatial moment equations for plant competition: Understanding Spatial Strategies and The Advantages of Short Dispersal*, The American Naturalist, 153, (1999) 575-602.