MAY–LEONARD MODEL OF THREE SPECIES

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In natural ecosystems, species often compete for limited resources including food, water, and space. Often, when one competing population succeeds over the others, it will eventually be outcompeted by one of the others. This leads to oscillations between all competing populations due to the cyclic dependence on one another. A challenge that remains for mathematicians is finding a model that accurately describes the relationship between the different species.

The simplest one is the predator-prey equations.

$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \sigma xy - \gamma y$$

It shows the relationship between the predator such as a wolf and the prey such as a rabbit. The first equation described the growth rate of the prey. It not only depends on the population of the prey itself (x), but also the rate of interaction between the predator and prey(xy). The second equation described the growth rate of the predator. The number of prey would infect the number of predators. No food, no survival. Hence, you cannot talk about the population of prey without talking about predator or talking about predator without prey. They are interconnected.

In the natural world, the competition among the species would be more complicated than the simple predator-prey model. There might be dynamic competitive relations between many species. In our report, we will mainly focus on a 3 species competition model described by May and Leonard (1975).

1. Introduction

The May-Leonard equation was developed from the predator-prey equations, which describes the non-linear competition among three species. And the equations are different from predator-prey equations as seen by the cyclic dependence on one another (Phillipson et al., 1985).

$$\frac{dN_1}{dt} = N_1(1 - N_1 - \alpha N_2 - \beta N_3)$$
$$\frac{dN_2}{dt} = N_2(1 - \beta N_1 - N_2 - \alpha N_3)$$
$$\frac{dN_3}{dt} = N_3(1 - \alpha N_1 - \beta N_2 - N_3)$$

In these 3 equations, N is the population of each species. And $\frac{dN_1}{dt}, \frac{dN_2}{dt}, \frac{dN_3}{dt}$ represent the growth rate of the three different kinds of species. Two parameters α *and* β are the interaction coefficients between the species. From the 3 equations, it is clearly that the growth rate of N1 will be affected by N2 and N3, growth rate of N2 will be affected by N1 and N3, and growth rate ofN3 will be affected by N1and N2. Therefore, the population of these three species are mutually restrictive.

For our report, we are mainly concentrated on the analysis of equilibrium points and their stability.

2. Analysis

Fixed points

$$\frac{dN_1}{dt} = N_1(1 - N_1 - \alpha N_2 - \beta N_3)$$
$$\frac{dN_2}{dt} = N_2(1 - \beta N_1 - N_2 - \alpha N_3)$$
$$\frac{dN_3}{dt} = N_3(1 - \alpha N_1 - \beta N_2 - N_3)$$

We can see that the model is Nonlinear Multivariate Continuous Deterministic. Therefore, we can look for the equilibrium points by setting:

$$N_1(1 - N_1 - \alpha N_2 - \beta N_3) = 0$$
$$N_2(1 - \beta N_1 - N_2 - \alpha N_3) = 0$$
$$N_3(1 - \alpha N_1 - \beta N_2 - N_3) = 0$$

By solving the equations above, we got our fixed points which are:

1) (N1,N2,N3) = (0,0,0)
2) (N1,N2,N3) = (1,0,0) or (0,1,0) or (0,0,1)
3) $N_1 + N_2 + N_3 = 1$ when $\alpha = 1$ and $\beta = 1$
4) $(N_1, N_2, N_3) = (1,1,1)/(a + b + 1)$

Stability

To determine the stability of the system, we can create a 3X3 Jacobian matrix:

$$J = \begin{bmatrix} 1 - 2N_1 - \alpha N_2 - \beta N_3 & -\alpha N_1 & -\beta N_1 \\ -\beta N_2 & 1 - \beta N_1 - 2N_2 - \alpha N_3 & -\alpha N_2 \\ -\alpha N_3 & -\beta N_3 & 1 - \alpha N_1 - \beta N_2 - 2N_3 \end{bmatrix}$$

The fixed points are stable if and only if the real part of all the real part of eigenvalues from the above matrix are less than 0. (i.e. $\lambda_1 < 0$ and $\lambda_2 < 0$ and $\lambda_3 < 0$).

1) **For fixed points (0,0,0):**

$$J = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

We can easily see that the eigenvalues for this matrix are $\lambda_1 = \lambda_2 = \lambda_3 = 1$, which are all greater than 0. Hence, the fixed point is always **unstable.**

2) **For fixed points (1,0,0), (0,1,0) and (0,0,1):**

Fixed points (1,0,0), (0,1,0) and (0,0,1) will have the same stability. Because when we take these points into the Jacobian matrix, it only changes the order of rows, which does not affect the eigenvalues for a triangle matrix.

Therefore, we just need to look for the stability for (1,0,0):

$$J = \begin{bmatrix} -1 & -\alpha & -\beta \\ 0 & 1 - \beta & 0 \\ 0 & 0 & 1 - \alpha \end{bmatrix}$$

The eigenvalues for this matrix are: $\lambda_1 = -1, \lambda_2 = 1 - \beta, \lambda_3 = 1 - \alpha$.

Therefore, for these fixed points to be stable, $\boldsymbol{\alpha}$ **and** $\boldsymbol{\beta}$ **must be greater than 1**.

3) For fixed points $N_1 + N_2 + N_3 = 1$ when $\alpha = 1$ and $\beta = 1$:

$$J = \begin{bmatrix} 1 - 2N_1 - N_2 - N_3 & -N_1 & -N_1 \\ -N_2 & 1 - 2N_2 - N_1 - N_3 & -N_2 \\ -N_3 & -N_3 & 1 - 2N_3 - N_2 - N_1 \end{bmatrix}$$

The eigenvalues are:

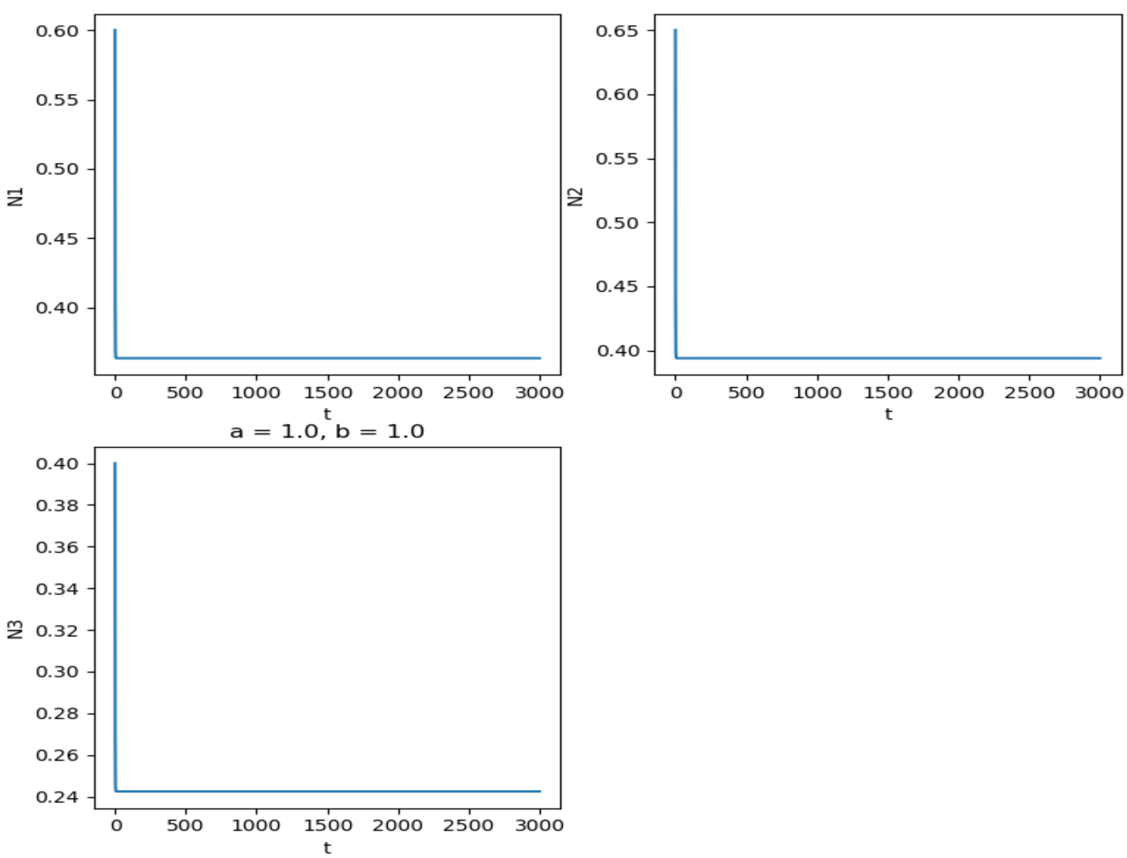
$$\lambda_1 = -(N_1 + N_2 + N_3 - 1)$$

$$\lambda_2 = -(N_1 + N_2 + N_3 - 1)$$

$$\lambda_3 = -(2N_1 + 2N_2 + 2N_3 - 1)$$

Then the fixed point is stable if $N_1 + N_2 + N_3 > 1$. However, $N_1 + N_2 + N_3 = 1$. Therefore, the fixed point is **unstable**.

To see the result more clearly, we can use Python to output the graph for $N_1, N_2, N_3, when\ \alpha = \beta = 1$ with initial point $(N_1, N_2, N_3) = (0.6, 0.65, 0.4)$:



We can identify that, as time t increases, the value of (N1, N2, N3) reaches the fixed points which is $(0.363636, 0.393939, 0.242424)$. Notice that $0.363636 + 0.393939 + 0.242424 = 1$. Which is exactly our fixed point: $N_1 + N_2 + N_3 = 1$ when $b = 1\ and\ a = 1$

4) For fixed points $(N_1, N_2, N_3) = (1, 1, 1)/(a + b + 1)$:

By letting $N_1 = N_2 = N_3 = \frac{1}{a+b+1} = c$, it is easier for us to compute. We then have the Jacobian matrix:

$$J = \begin{bmatrix} 1 - c(2 + \alpha + \beta) & -\alpha c & -\beta c \\ -\beta c & 1 - c(2 + \alpha + \beta) & -\alpha c \\ -\alpha c & -\beta c & 1 - c(2 + \alpha + \beta) \end{bmatrix}$$

Now recall that $c = \frac{1}{a+b+1}$, then we can change $1 - c(2 + \alpha + \beta)$ to $1 - c - 1$, so, the matrix can be written as:

$$J = \begin{bmatrix} -c & -\alpha c & -\beta c \\ -\beta c & -c & -\alpha c \\ -\alpha c & -\beta c & -c \end{bmatrix} = c \begin{bmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{bmatrix}$$

The eigenvalues are:

$$\lambda_1 = c(-1 - \alpha - \beta)$$

$$\lambda_2 = c(-1 + \frac{\alpha + \beta}{2} + i\left(\frac{\sqrt{3}}{2}\right)(\alpha - \beta))$$

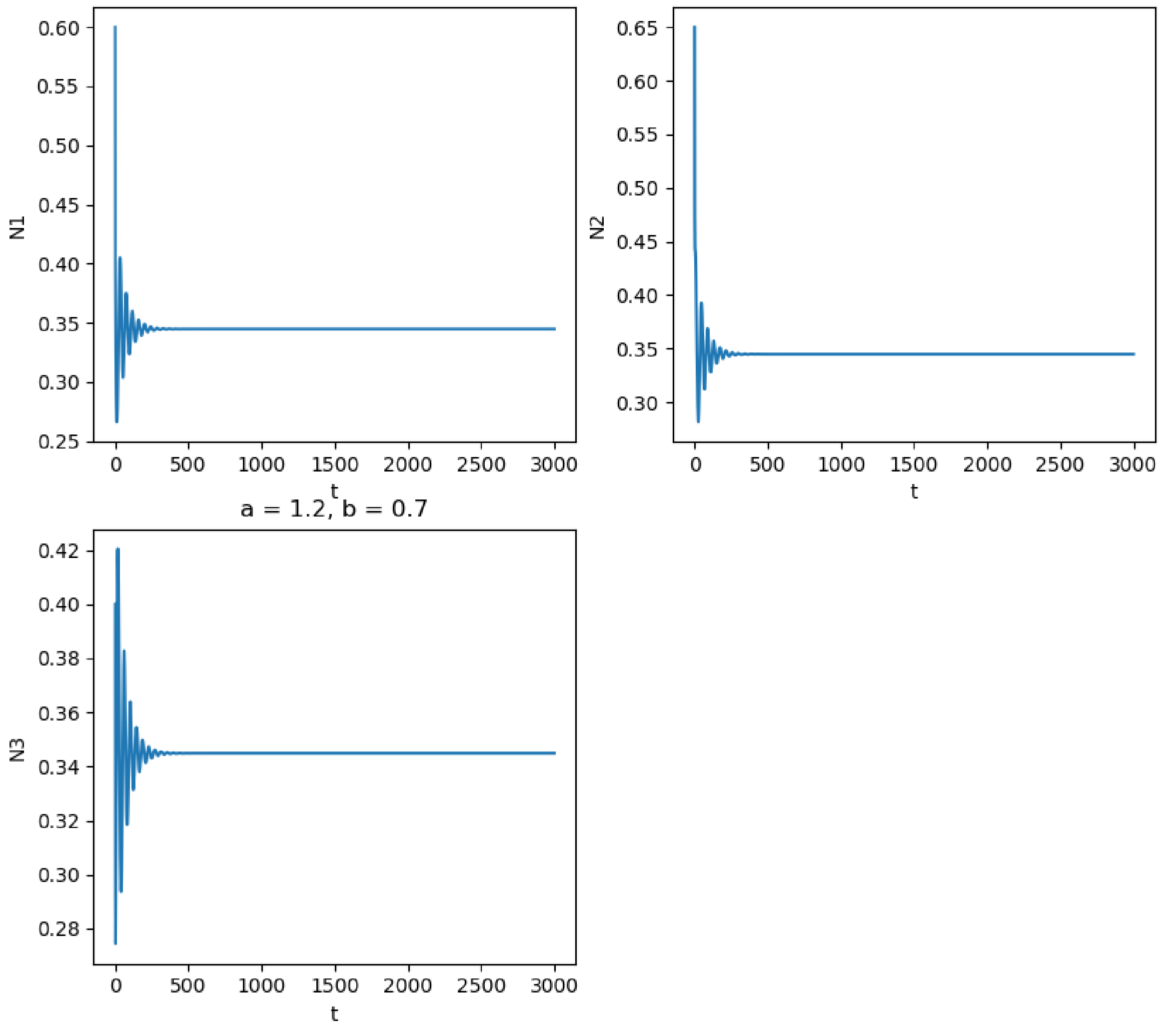
$$\lambda_3 = c(-1 + \frac{\alpha + \beta}{2} - i\left(\frac{\sqrt{3}}{2}\right)(\alpha - \beta))$$

We can ignore c in these eigenvalues because c is always greater than 0. λ_1 is always negative because $\alpha\ and\ \beta$ are both positive. For $\lambda_2\ and\ \lambda_3$, the real part $(-1 + \frac{\alpha+\beta}{2})$ is negative only if $\alpha + \beta < 2$.

Therefore, this fixed point is stable only if $\boldsymbol{\alpha + \beta < 2}$.

To see how the values of $\alpha\ and\ \beta$ can affect $N_1, N_2\ and\ N_3$, we can use Python to output the graph for $\alpha + \beta < 2$, $\alpha + \beta > 2$ and $\alpha + \beta = 2$.

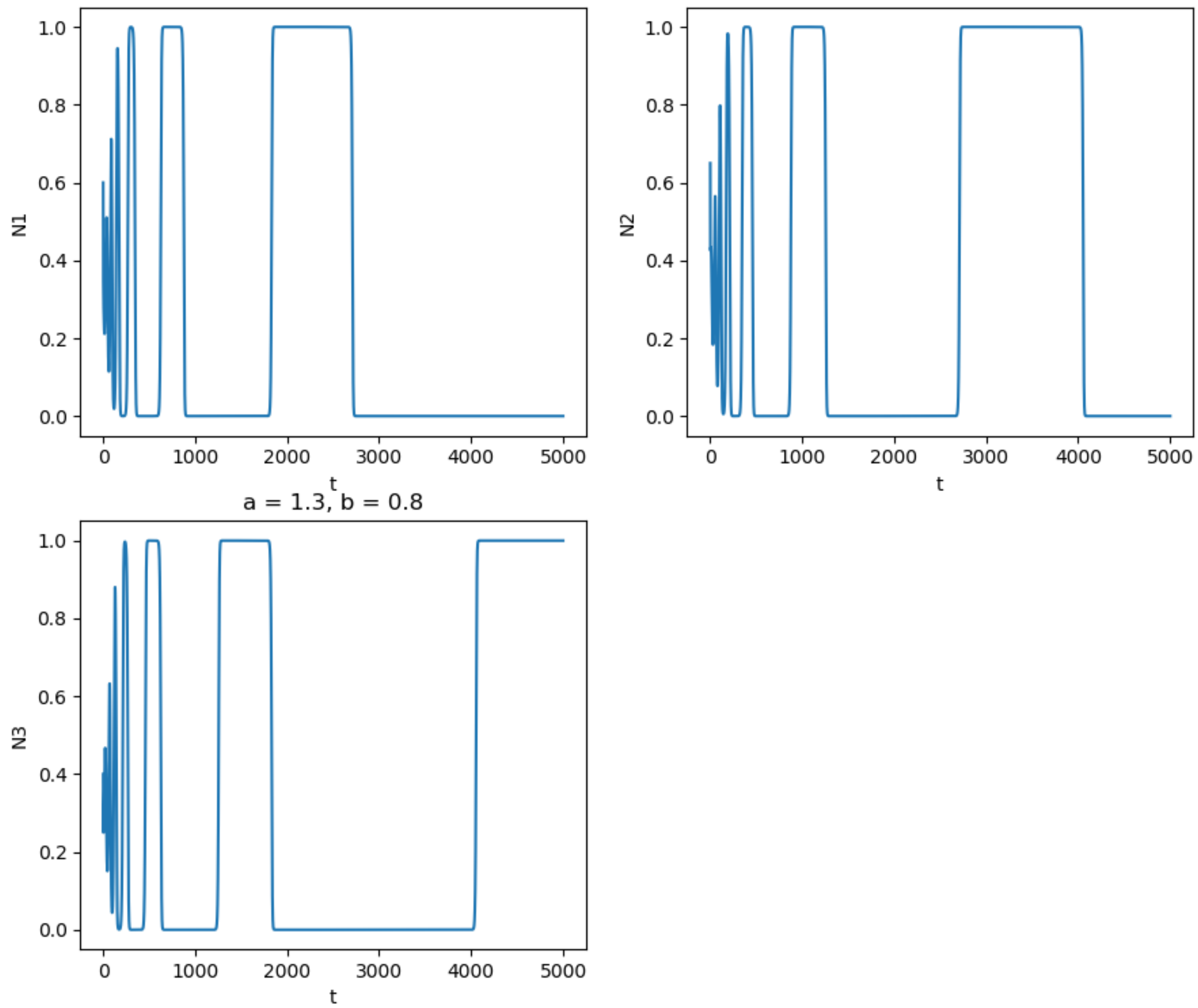
- For $\alpha + \beta < 2$, with initial point $(N_1, N_2, N_3) = (0.6, 0.65, 0.4)$:



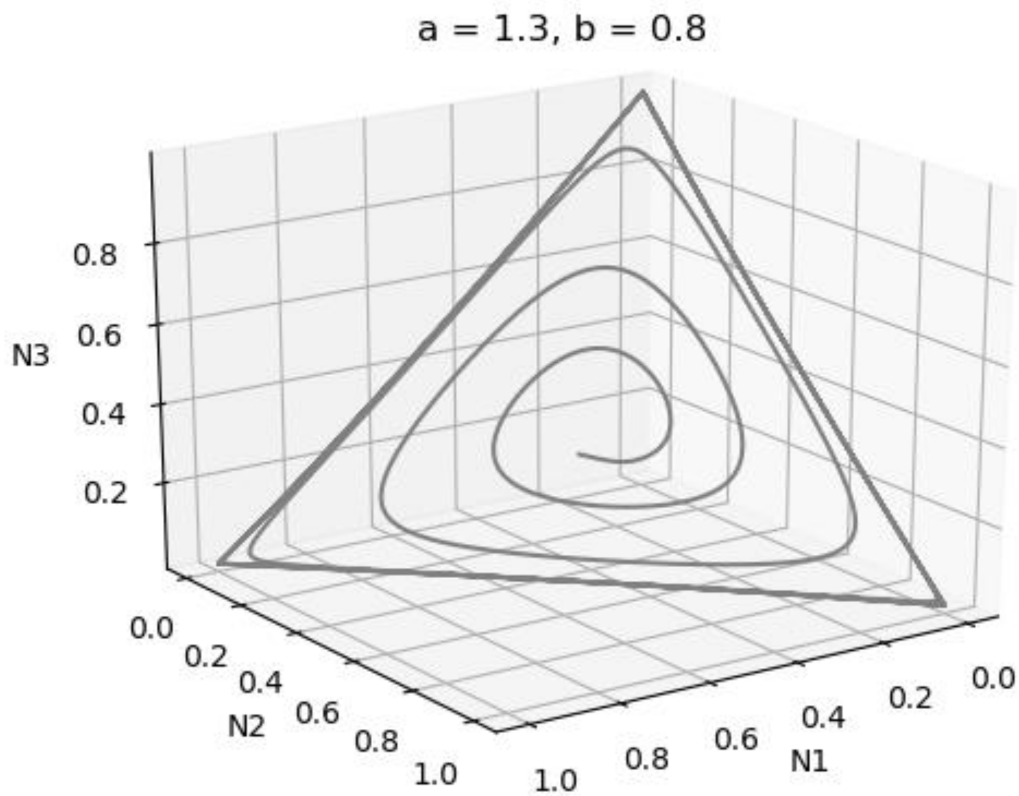
As we can see from the graph, all N_1, N_2 *and* N_3 convergent to $(0.34482759, 0.34482759, 0.34482759)$. Which is the fixed point we find:

$$(\boldsymbol{N_1}, \boldsymbol{N_2}, \boldsymbol{N_3}) = \frac{(\mathbf{1,1,1})}{\boldsymbol{a+b+1}} = \frac{(\mathbf{1,1,1})}{\mathbf{1.2+0.7+1}} = \frac{(\mathbf{1,1,1})}{\mathbf{2.9}} = (0.34482759, 0.34482759, 0.34482759)$$

- For $\alpha + \beta > 2$ with initial point $(N_1, N_2, N_3) = (0.6, 0.65, 0.4)$:

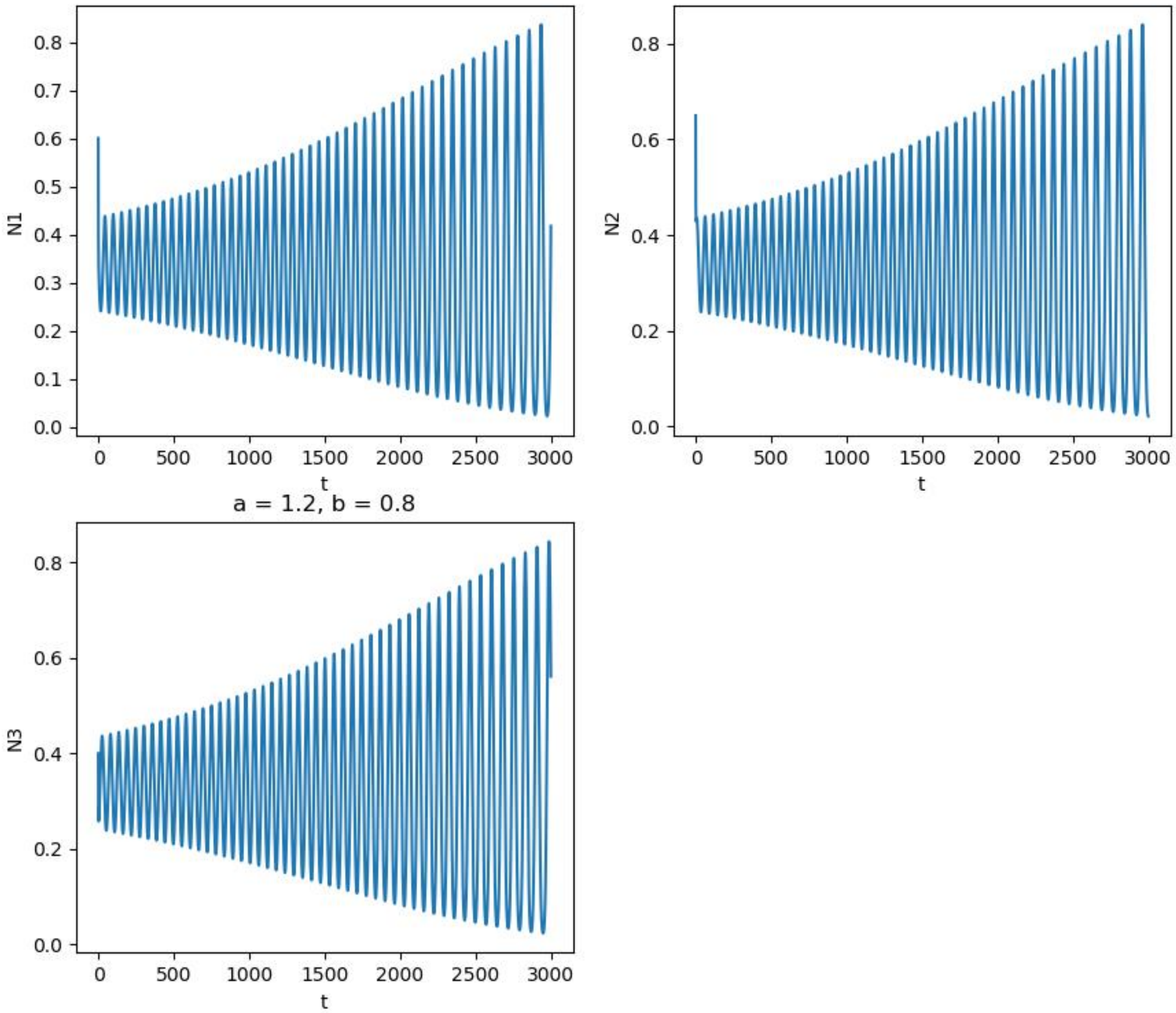


From the graph above, we can find that each of N_1, N_2 *and* N_3 increasing to 1 and then decreasing to 0, then go back to 1 from 0 again, in a not equaled period of time. And the model reaches the fixed points (1,0,0), (0,0,1), (0, 1, 0), however, since b < 1, then the fixed points are not stable. To get a better view of the system, a 3-D graph will be helpful:



From the 3-D graph, we can find that the behavior of the system is basically, in short, the population changes from wholly N_1 to wholly N_3, then from wholly N_3 to wholly N_2, then from wholly N_3 return to N_1.

- For $\alpha + \beta > 2$ with initial point $(N_1, N_2, N_3) = (0.6, 0.65, 0.4)$:



From the graph above we can discuss that the values of N_1, N_2 and N_3 are changing in an equaled period of time, like a sin function, but with an increasing amplitude. The maximum and minimum values are approaching fixed points: (1,0,0), (0,1,0), (0,0,1), (0,0,0).

3. Conclusion

The May-Leonard Model of Three Species is a nonlinear multivariable continuous model. The behavior of the system can be affected by different initial values. And most important, it can be affected by different values of α and β.

There are many fixed points in this model, which are:

1) (N1,N2,N3) = (0,0,0), which is an unstable fixed point
2) (N1,N2,N3) = (1,0,0) or (0,1,0) or (0,0,1). These fixed points are stable if $\alpha > 1$ and $\beta > 1$.
3) $N_1 + N_2 + N_3 = 1$ when $\alpha = 1$ and $\beta = 1$, this is an unstable fixed point.
4) $(N_1, N_2, N_3) = (1,1,1)/(a + b + 1)$, in this case, the fixed points are stable if $\alpha + \beta < 2$

Different value of α and β will influence the graph. For these 3 cases: $\alpha + \beta < 2$, $\alpha + \beta > 2$ and $\alpha + \beta = 2$, there is a huge difference between the graphs. But with the graph, the stability of each condition will be showed more clearly.

This 3-competitor models provides a more descriptive visualization of population dynamics seen in natural ecosystems. The extinction equilibrium (0,0,0) is unstable in all cases. If the interaction variables (a, b) are both greater than one, we see stability of the dominance equilibrium where only one species dominant the system. With full interaction, a = 1 and b = 1, the species show an unstable population dynamic. When the interaction sum is less than 2, we see stability for the coexistence equilibrium with all species fully equally expressed.

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