

Competing Species

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- Competition amongst species is increasingly important to study in order to understand survival and extinction patterns. Mathematical models are a much-used technique for observing population dynamics as observing numerous species in the wild is difficult to do. The goal is to study coexistence and chaos amid these populations.

Introduction:

Coexistence and chaos amongst populations in the wild is an important topic that is widely researched today. It is important to study survival and extinction patterns in species in order to fully understand population dynamics. Simulating this using mathematical models is necessary because it is difficult, and expensive, to study trends of large numbers of species in their natural habitats. There are currently many models of population dynamics used, however; we chose to use a model done by J.C. Sprott because it includes adaptation, which helps to make the model accurate by modeling environmental stresses. Current work on the model is being done to more accurately reproduce chaos. In our project we are attempting to replicate the results of Sprott, as well as investigate the effects that changes in adaptation will have on population dynamics.

The paper, titled "Coexistence and chaos in complex ecologies," by J.C. Sprott, J.A. Vano, J.C. Wildenberg, J.C. Anderson, J.K. Noel, discusses competition between species, and the method used by the authors to model these patterns. It opens by discussing the differences between theoretical models and nature; the main difference being while theoretical models show instability and extinction, nature shows that complex ecologies are relatively stable. The flour beetle is given as an example of this dissimilarity, because in the lab there is chaos, however it is not seen in its natural environment. Most non-evolutionary models produce chaos, bounded on either side by extinction or stable behavior. On the contrary, the authors' model produces complex systems that coexist with weakly chaotic fluctuations. To model the competition of these species, a variant of the generalized Lotka-Volterra equation is used due to its simplicity. Chaos is not possible in competitive systems with fewer than four species. Coexisting chaotic

systems for larger numbers of species are more difficult to encounter in a random search because the conditions for coexistence and for chaos are mutually exclusive. In nature, ecologies are not chosen from random, but rather adaptation occurs to enhance survival rates. This adaptation factor is what makes Sprott's model more appealing than previous models of population dynamics.

The members of a population that is near extinction are the most fit, and therefore they are more likely to survive through alternative resources as well as being more capable of evading predators. The purpose of the adaptation factor is to account for these facts, assuring competition of species.

The parameters taken for the initial data in this model can be taken from real ecologies, random values, or by randomly choosing species of various types. The authors used random values to initialize the data. Enhanced competition is introduced into our model periodically in time. When a species population gets too small, (in this case 10^{-6} on a scale from 0 to 1) clamping occurs to keep a species population from becoming negative. For a higher number of species, the clamp size would have to be changed to eliminate the possibility of fractions of animals. For example, there could be $\frac{1}{2}$ of a bunny, which is not realistic. This also allows for species to coexist with optimal fitness.

We chose to use the paper, "Coexistence and chaos in complex ecologies" for a multitude of reasons, the first reason being that the model was relatively simple to reproduce. While some information (mostly in regards to initial conditions) was omitted, we found this was not crucial in our reproduction and we were still able to achieve similar results (refer to Fig. 2, 3, 5, and 6). Another reason for using this paper is that everything is fairly well explained and the paper was very inclusive. We did not need to reference other resources regarding population dynamics in

order to reproduce the results. The third reason for using the Sprott paper is because of the adaptation factor. This makes the Sprott model a relatively accurate representation of population dynamics.

Model:

Sprott's model is based off of the simple predator-prey equations known as the Lotka-Volterra equations which describe the interactions between two species. Let x be the number of prey and y be the number of predators. The Lotka-Volterra equations give the rate of change of the predator and prey population with respect to time.

$$\frac{dx}{dt} = x(\alpha - \beta y); \quad \frac{dy}{dt} = -y(\gamma - \delta x) \quad (1)$$

In this report, the authors modified the Lotka-Volterra equations to form the equation

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \sum_{j=1}^N a_{ij} x_j \right) \quad (2)$$

which produces complex systems where most species coexist with adaptation (without adaptation many species go extinct, causing low biodiversity). N number of competing species are used and population size is x_i for $i = 1$ to N . For simplicity, the growth rates, r_i , are equal to 1 for $1 \leq i, j \leq N$, and the matrix of species interactions, a_{ij} , are greater than or equal to 0 . Positive a_{ij} values indicate a competitive system and assures that the solutions are between 0 and 1 . Having exclusively positive a_{ij} values ignores the relationship between two species that both benefit from the relationship and the effect of varying prey on the predators, but a few negative a_{ij} values do not change the results dramatically. It also replicates chaotic tendencies which are independent of the initial conditions.

The article suggests that nature is not random but rather individual species adapt to their environment to ensure the highest survival rate. Therefore adaptation is added to model this characteristic. Most models assume that a species becomes extinct when the population drops too low. Rather than assume this, the authors assume that adaptation activates as a population drops to just above extinction levels. They support this by claiming that the survivors of a species that is close to extinction are the most fit and capable of continued existence. Therefore a change in the a_{ij} coefficients may occur due to the increase in the instability of the a_{ij} coefficients as x_i grows closer to zero.

Without adaptation, the model needs to be run for a time of $t = 10^6$ in dimensionless units for chaos to exist. With the adaptation term present, x_i is clamped at 10^{-6} and whenever x_i falls below 10^{-6} , the a_{ij} elements are replaced with $a_{ij}(1 - \varepsilon_1 x_j)$ for $j = 1$ to N and $j \neq i$. This prevents the particular x_i species population from going extinct, and also captures the improved fitness of the surviving members of the species. In order to reproduce general adaptation for all species over time, an additional $(1 + \varepsilon_2)$ is added to all the off-diagonal entries of the matrix every 20 time steps while the diagonal entries remain unchanged. The values of the $\varepsilon_1, \varepsilon_2$ variables are unimportant, so long as they are fairly small; in our model we used $\varepsilon_1 = 10^{-6}$ and $\varepsilon_2 = 10^{-4}$.

The parameters of these types of models can be taken in various ways. They can be chosen from real ecologies, species can be chosen at random and the values from the species chosen used, or random values could be used. In this model, the matrix of interactions is generated randomly because high-quality data for multiple species was not available. With the adaptation factor added at every 20 time steps and the clamping of species, the matrix of interactions evolves to resemble superior data. We are able to generate the initial matrices

randomly because there was not a significant change in the graphs when different initial values were used. However, for modeling the changes in adaptation we used the same initial matrix so that it was controlled (Fig. 10-17).

Reproduction of Results - Computer Simulation:

In order to analyze the modified Lotka-Volterra equations, it is necessary to employ the tools of numerical methods. A process is undertaken to transform the problem at hand from one which may only be considered analytically to one which can be solved numerically. Once a certain framework has been established, solutions can be developed and analyzed.

First it is necessary to discretize: to transform the equation from continuous time to discrete time. This is done in a multitude of cases in mathematics when equations must be analyzed using computers due to the system having a nature intractable to analytical methods. It is a generally accepted method among those who study population dynamics to work with difference equations when a numerical simulation is necessary.

Developing the difference equation, a discrete approximation of the governing differential equation, is the next step in the process. First, this was done using the Forward Euler Method, an iterative method that can be derived from the forward finite difference approximation of the derivative.

To begin, start with this estimation of the derivative,

$$\frac{dx}{dt} \approx \frac{x_n - x_{n-1}}{\Delta t} \quad (3)$$

Now, call the true derivative (from modified Lotka-Volterra) f and rearrange x_n to equal

$$x_n \approx x_{n-1} + f\Delta t. \quad (4)$$

In this case, x_{n-1} is the current population level of some species, x_n is the population level of the species at the next time step, f is the true derivative, and Δt , the time step, is a small unit of time.

The next step in implementing the numerical method is to clearly define the x_0 , or initial population levels of the N species in the model as well as f , the rate of change of those population levels with respect to time. The $N x_0$ values for each particular simulation are chosen from a uniform random distribution on the interval $(0,1)$ each time that the simulation was run. The function f was generated in the following manner (with reference to the modified Lotka-Volterra equation): the vector of growth rates, r , was set to unity for simplicity, while the competition matrix, a_{ij} , was drawn from an exponential random distribution of mean 1 each time that the simulation was run. Subsequently, the main diagonal elements of the competition matrix were set to 1 as a method of normalization; these terms are the self-interaction terms.

Clamping and adaptation were implemented in a straightforward manner after the calculation of the new population levels during each time step, as was explained in the “Model” section.

Another important consideration in implementing the numerical method in MATLAB is choice of the step size, Δt . We used a step size of $\Delta t = 0.1$. This was the largest time step (therefore shortest simulation time) that gave accurate results, i.e. convergence. One way to test for convergence is to cut the time step in half and see if the new results are qualitatively and quantitatively similar. The results for $\Delta t = 0.05$ were not substantially different from those for $\Delta t = 0.1$ thus we conclude $\Delta t = 0.1$ is sufficiently small to ensure convergence of the numerical method.

The Forward Euler Method was initially chosen for several reasons. First, it is the simplest to implement of all numerical methods. Second, it is computationally inexpensive, allowing simulations to be run in a reasonable amount of time even with fairly small step sizes. However, after further analysis, this method did not yield accurate enough results.

Therefore, it was necessary to employ a more powerful numerical method in order to achieve more reliable results. The Runge-Kutta fourth order method was chosen. It is similar to the Forward Euler method in that it is also of the general form

$$x_n \approx x_{n-1} + f\Delta t. \quad (5)$$

The difference is that the function f which is the rate of change of the modified Lotka-Volterra equation is computed as the weighted average of 4 different slopes: k_1 , k_2 , k_3 , and k_4 which are successive corrections for the derivative of the function. The general form is this:

$$\begin{aligned} k_1 &= hf(x_i, y_i) \\ k_2 &= hf(x_i + \frac{1}{2}h, y_i + \frac{1}{2}k_1) \\ k_3 &= hf(x_i + \frac{1}{2}h, y_i + \frac{1}{2}k_2) \\ k_4 &= hf(x_i + h, y_i + k_3) \\ y_{i+1} &= y_i + \frac{1}{6}(k_1 + 2k_2 + 2k_3 + k_4) \end{aligned} \quad (6)$$

Results:

Once the equation was implemented in MATLAB, we were able to model biomass and biodiversity. We were able to qualitatively replicate the authors' graphs. Population graphs were used for a small amount of species (refer to Fig. 1), but the population graphs with larger number of species are so complex and visually difficult to interpret, there are two different measures that the authors employed. First is biomass, given by the equation

$$M = \frac{1}{N} \sum_{i=1}^N x_i \quad (7)$$

where N is the number of species and x_i is the different populations. Biomass is the total mass of living organisms in a certain ecosystem divided by the total number of species, or the average population size. When biomass is high, the average population size is high, and when biomass is low the average population size is low.

Next, we looked at biodiversity, given by the equation

$$D = 1 - \frac{1}{2(N-1)} \sum_{i=1}^N \left| \frac{x_i}{M} - 1 \right| \quad (8)$$

Biodiversity is qualitatively the diversity of plant and animal life in a specific habitat. For example, biodiversity is high when a majority of the species is of a similar size, and it is low when many species are approaching extinction while others are flourishing.

Since initial values were not included in our source, we used a random number generator, which is one cause of deviations between our graphs and the authors. One place where this is evident is in the fluctuations in the population of individual species, which are much larger than in the total biomass. Our biomass graph (refer to Fig. 2) contains “flat” planes, or what appear to be gaps with no oscillations, which are not present in the authors. The gaps in the biomass graphs appear to be flat, however when inspected more closely (zoomed in), these lines are indeed fluctuating (refer to Fig. 2). The author describes these points as punctuated equilibria, which is when the biomass suddenly becomes stable for a short period of time. The biomass without adaptation graph (refer to Fig. 4) fluctuates for the first part of the graph, but at approximately **0.2** time units the graph starts to become stable. The biomass without adaptation graph (refer to Fig. 4) can be viewed as a slice of the dynamics from the biomass with adaptation graph (refer to Fig. 2) over a short time scale where adaptation is negligible. An obvious difference from the authors’ biomass graph and our biomass graph (refer to Fig. 2 and 3) is that ours fluctuates more

wildly. As stated early, this could be due to an averaging on the authors part, but as there was no explanation offered by Sprott, this is an assumption.

It is evident from the biomass graph that there are two distinct regions of oscillations. The first region appears to be a linear increasing function multiplied by an oscillating function. This is the region where the total biomass of the system is increasing due to competition and adaptation of the various species. In the second region, the biomass function appears to be oscillatory with a semi-static mean. This could be indicative of the entire ecosystem reaching a limited carrying capacity. Sprott's graph is much cleaner probably due to averaging or a different time-step (refer to Fig. 3); however, the authors do not say, so this is an assumption.

The biodiversity with adaptation graphs (refer to Fig. 5 and 6) increased through time to a certain point, which is an indication that the adaptation is working. The gaps in the biodiversity graphs are again suggestive of punctuated equilibria, which means at any given time the biodiversity graph suddenly becomes relatively stable. Qualitatively this could be a period when all resources are flourishing, therefore all populations remain at a large size, therefore there is no change in biodiversity for that time period. The biodiversity graph without adaptation (refer to Fig. 7) fluctuates at the beginning, but right before time unit **0.2**, the biodiversity starts to stabilize. Biodiversity without adaptation can be viewed as a slice of the dynamics from biodiversity with adaptation with a short time scale and where adaptation is negligible.

In a similar manner to the biomass graph, there are two disparate segments present. The first section represents a region of increasing biodiversity (with oscillations) due to the effects of adaptation. The second region depicts a leveling off of the oscillations as they settle around a mean value. It is evident that biodiversity can never reach a value of **1**, because a value of **1** would imply equal population levels for all species. This would be an extremely improbable

situation due to the random starting values of the populations and the different rates of change for each species. Our graph fluctuates upwards more often while their graph is cleaner probably due to averaging or different time-step (refer to Fig. 5 and 6); however again the author does not state this, so is an assumption.

The biodiversity versus biomass graphs (refer to Fig. 8 and 9) were a bit more complicated. The authors only showed this graph without adaptation and it was bounded in a certain region. When our group implemented this graph in MATLAB, our graph did not replicate their graph. When biodiversity versus biomass was graphed with adaptation, our graph was clustered in a certain region. As the authors did not show this graph with adaptation, we did not have a point of comparison. However, our graph with adaptation approximately resembles their graph without adaptation because they are both bounded in a certain region (refer to Fig. 8 and 9). But in lots of other ways they are quite different.

While the vast majority of the results of the Sprott paper were reproduced, there are several that were not. First of all, while it was not too difficult to qualitatively compare graphs, quantitative comparison was a bit more difficult due to the source not providing initial data. One graph that eluded reproduction was that of biodiversity versus biomass without adaptation (refer to Fig. 9). It is unclear how the source obtained the graph exactly; they merely mention that the graph shows part of a strange attractor. Attempts to obtain a similar graph without adaptation were unsuccessful, but a graph with adaptation that was made showed some similarities. Additionally, the rather complicated and computationally expensive process of determining the largest Lyapunov exponent over time for a simulation was not undertaken. This is one area which can be further explored.

One modification undertaken in order to get a better understanding of the role of adaptation is variation of the clamp size. The nominal clamp size of 10^{-6} was tuned to the values of 10^{-8} , 10^{-4} , 10^{-3} , and 10^{-2} . The biodiversity and biomass graphs for the clamp sizes of 10^{-8} , 10^{-6} , and 10^{-4} are very similar, probably due to the fact that these values are all still extremely small compared to the normal population levels of the various species (which are always in the interval [clamp size, 1]) (refer to Figs. 10-15). When the clamp size was increased to 10^{-2} and to a lesser degree 10^{-3} , noticeable differences were seen in the biodiversity graphs (refer to Fig. 16 and 17). In the graph of biodiversity for a clamp size of 10^{-2} , the effect of clamp size became quite evident (refer to Fig. 17). For smaller clamp sizes, biodiversity exhibits the following behavior: a sharp drop off in the first few time steps, followed by a period of linear increase with oscillations, and finally a near constant phase with oscillations. When the clamp size is large enough, however, the quick drop off of biodiversity in the first few time steps is replaced by a linear decreasing with oscillations phase. This could be due to an increased resistance of the populations to adjust to the conditions imposed by the competition matrix in the early time steps. Therefore, we concluded that the clamp size in effect limits the derivative of the governing equation.

The other modification from the original work of Sprott implemented was experimenting with different mutation rates. Originally, mutation occurred at every twentieth time step (refer to Figs. 3, 6). We ran different mutation rates at every 5, 10, and 40 time steps and observed the effects different mutation rates had. Higher mutation rates produced a lower biomass as well as a lower biodiversity. Fluctuations decreased as adaptation was simulated less frequently (refer to Figs. 18-23) Since this mutation models various environmental stressors, with higher mutation rates, each species is less likely to flourish and our results were as expected.

With further time and higher quality computers, we would be able to run additional simulations with smaller deltas and compare the error between the results due to different time steps. Doing so would yield an accurate guess as to an adequate time step to run these simulations. As error decreases between time steps, we become closer to obtaining a decent delta size. Another modification would be to write a better numerical method that produces more accurate results than the classical Runge-Kutta algorithm.

Results from this model could be used to study species life cycles and help to understand possible adaptation or mutation in certain species. It may also help to predict extinction patterns. This model can be applied to any evolution model which can be characterized by a matrix of interactions; it is not restricted to ecology. Networks involving competition of resources and those that can be prone to crashes can be modeled in this way. Examples of this include financial markets, the brain, the internet, and traffic flow. Just as the ecological models shifted towards a weakly chaotic system, so could all these other systems, thus making our model applicable to the real world.

This project was mentored by Sarah Mann, whose help is acknowledged with great appreciation, as well as Dr. Ildar Gabitov.

Appendix

Figure 1. Population Graph with 4 Species

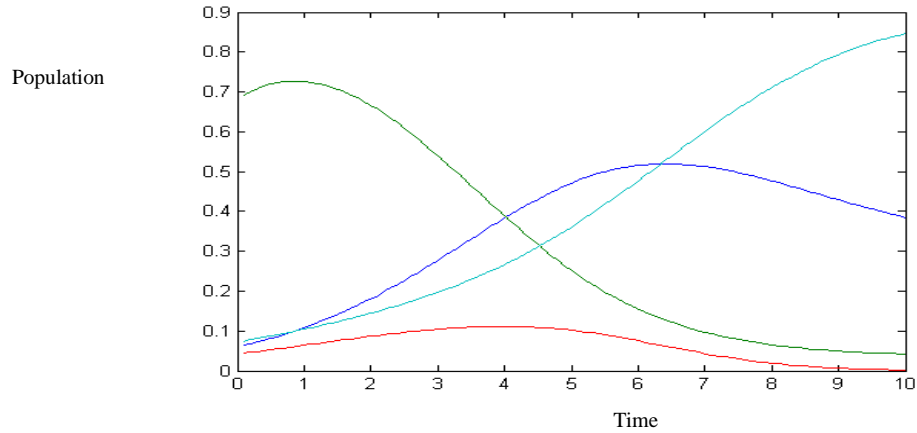


Figure 2. Biomass Graph with Adaptation (Our Model)

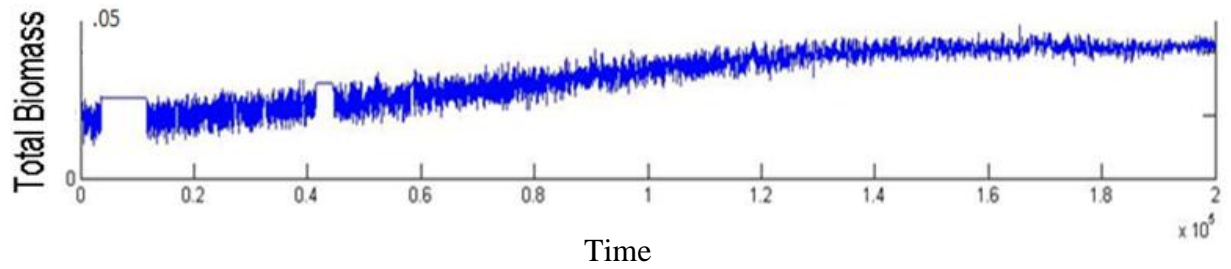


Figure 3. Biomass Graph with Adaptation (Spratt's Model)

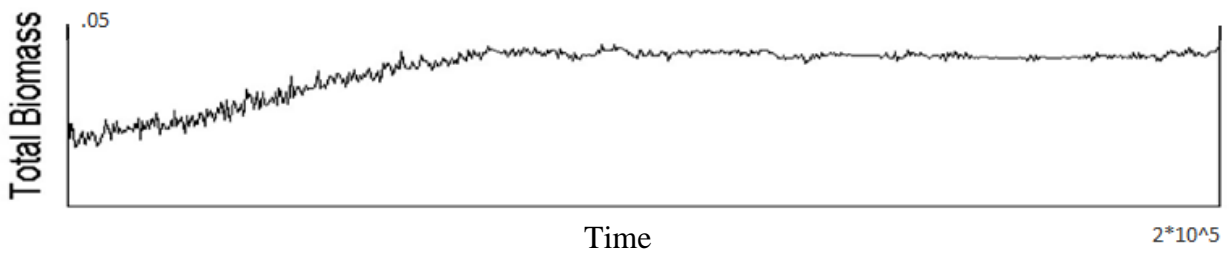
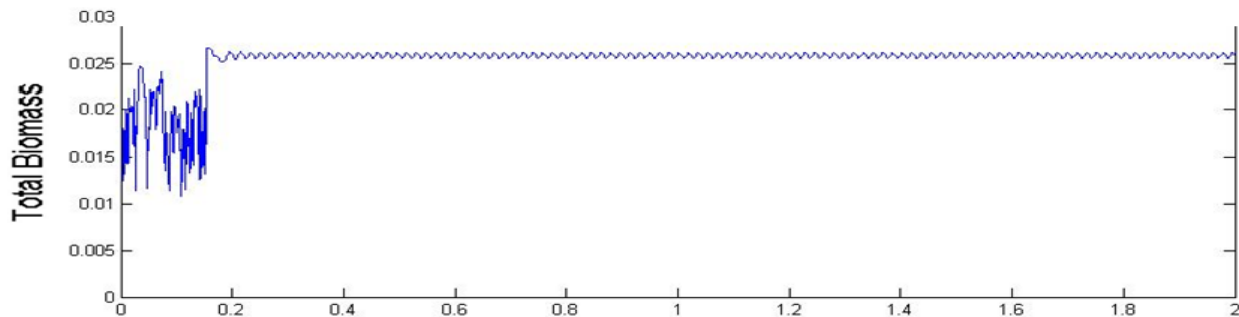


Figure 4. Biomass without Adaptation (Our Model)



Time

Figure 5. Biodiversity with Adaptation (Our Model)

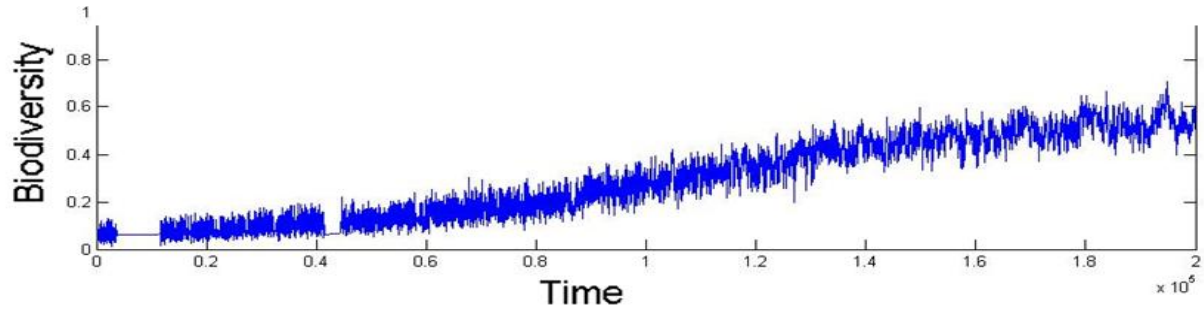


Figure 6. Biodiversity with Adaptation (Spratt's Model)

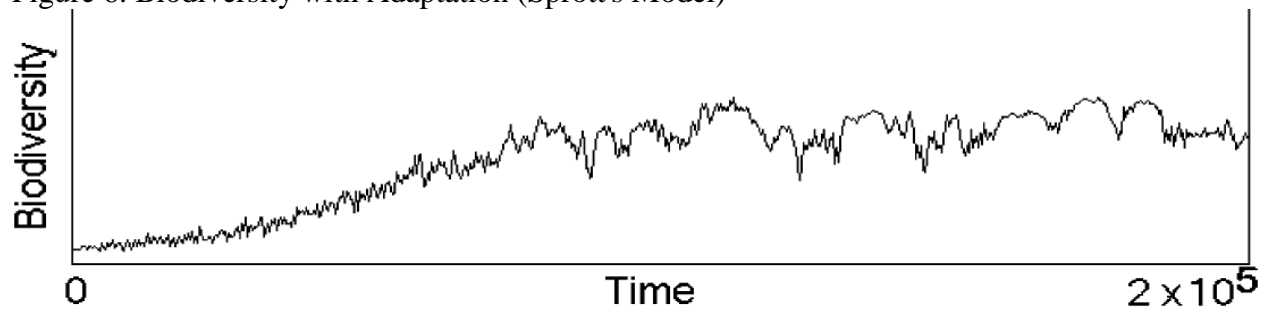


Figure 7. Biodiversity without Adaptation (Our Model)

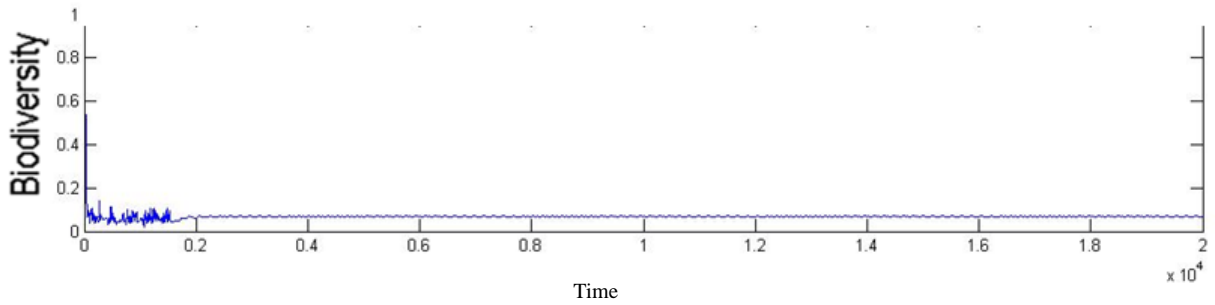


Figure 8. Biodiversity versus Biomass with Adaptation (Our Model)

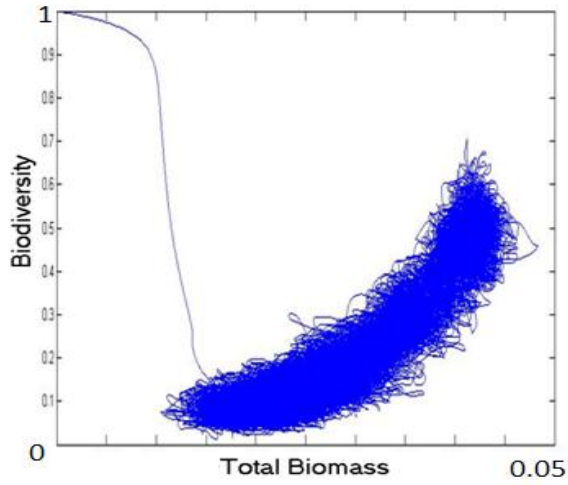


Figure 9. Biodiversity versus Biomass without Adaptation (Sprott's Model)

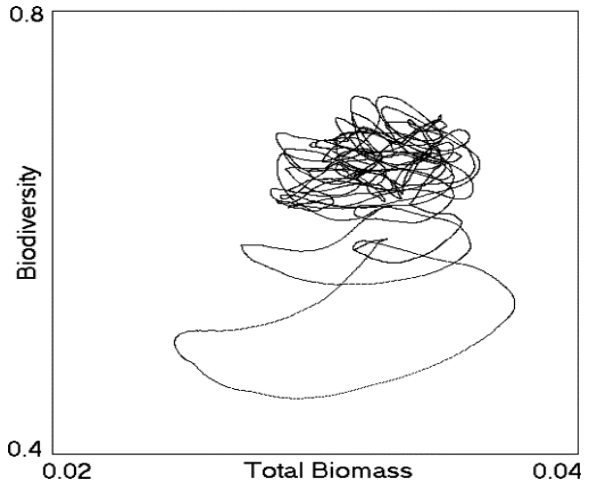


Figure 10. Biodiversity versus Time with (10^{-8} clamp)

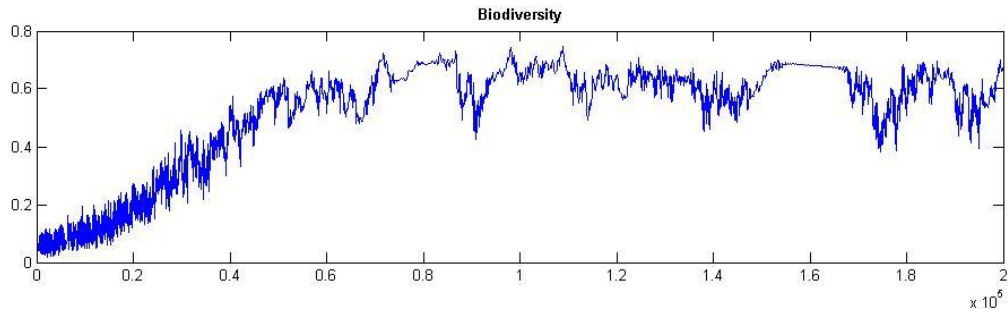


Figure 11. Biodiversity versus Time with (10^{-6} clamp)

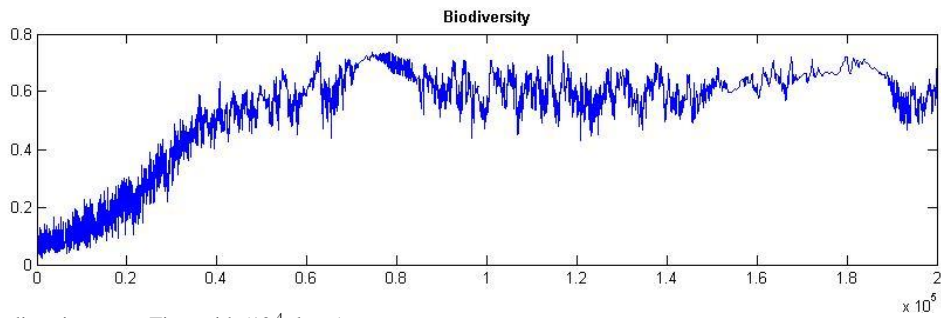


Figure 12. Biodiversity versus Time with (10^{-4} clamp)

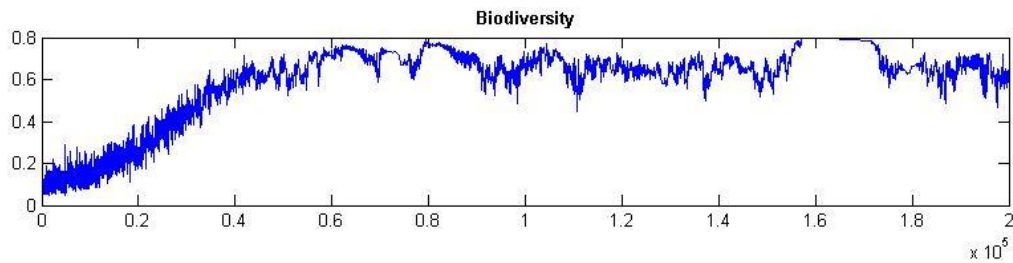


Figure 13. Biomass versus Time with (10^{-8} clamp)

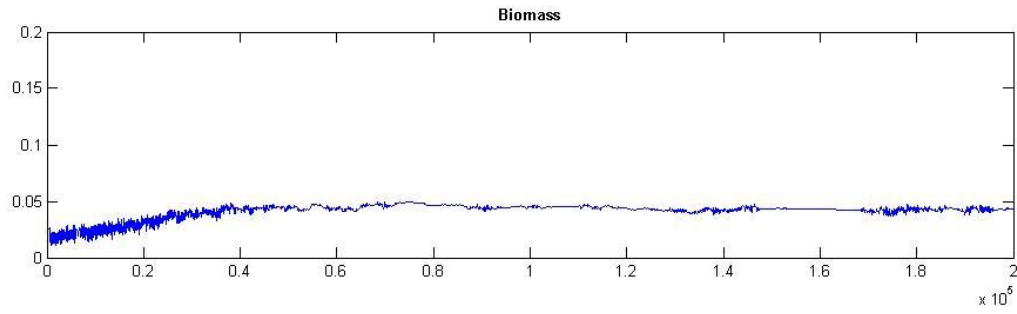


Figure 14. Biomass versus Time with (10^{-6} clamp)

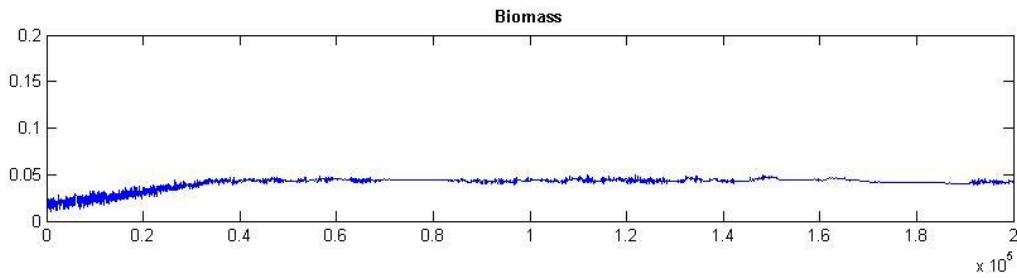


Figure 15. Biomass versus Time with (10^{-4} clamp)

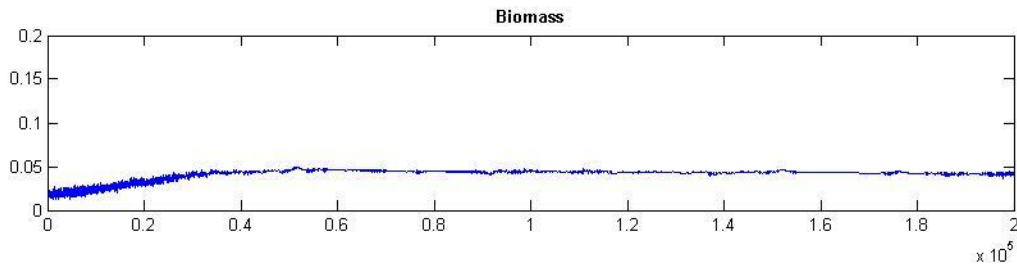


Figure 16. Biodiversity versus Time with (10^{-3} clamp)

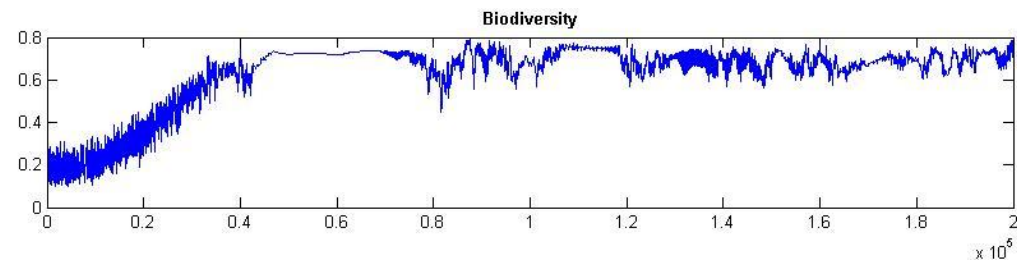


Figure 17. Biodiversity versus Time with (10^{-2} clamp)

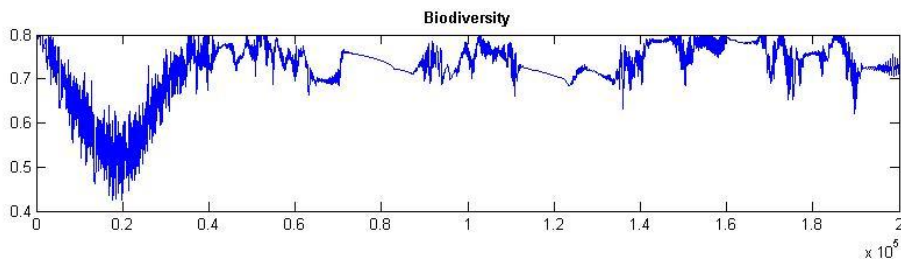


Figure 18. Biomass with mutation every 5 time steps:

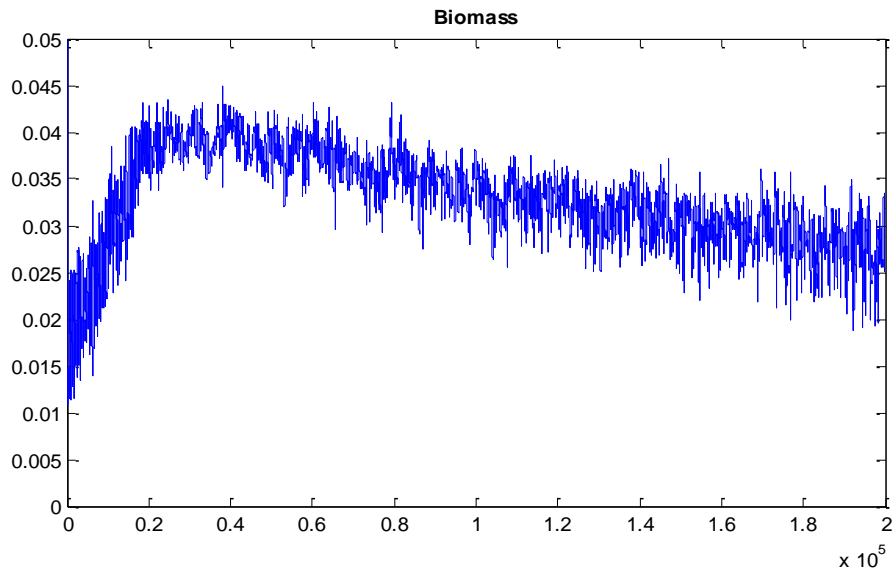


Figure 19. Biodiversity with mutatoin every 5 time steps:

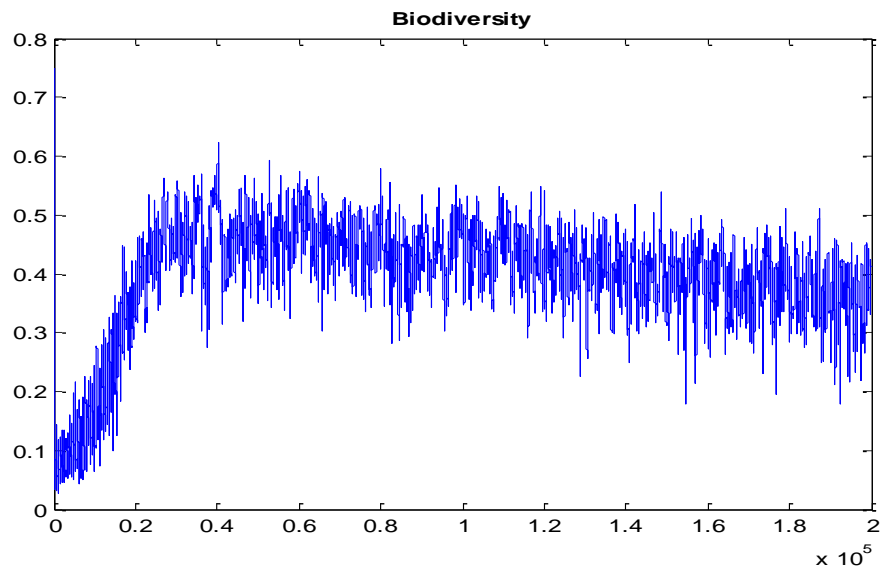


Figure 20. Biomass with mutation at every 10 time steps:

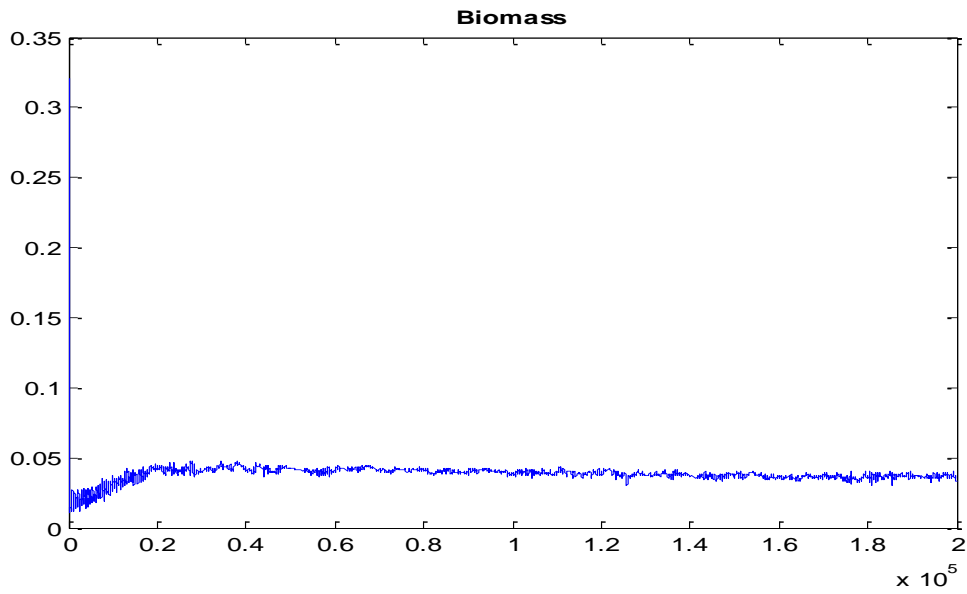


Figure 21. Biodiversity with mutation at every 10 time steps:

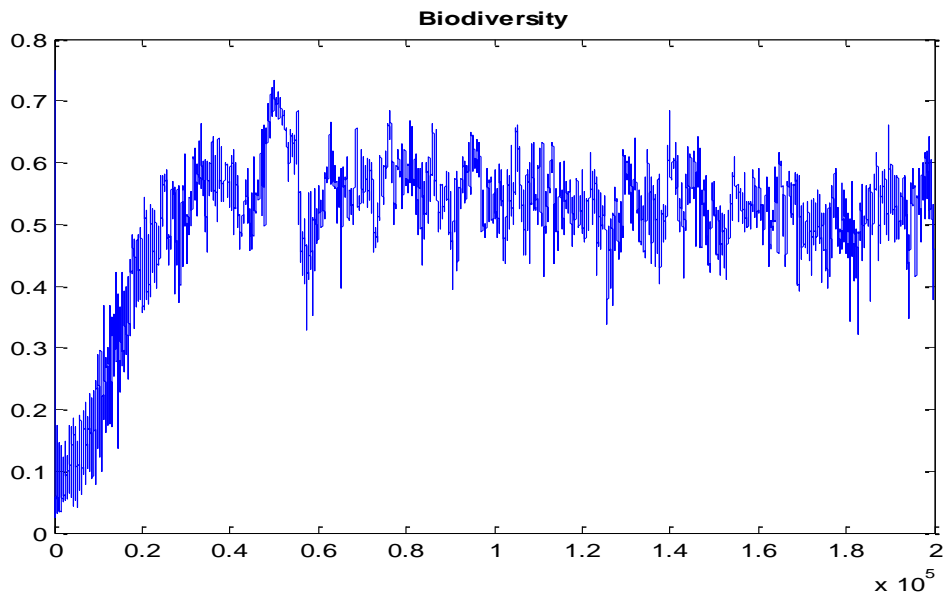


Figure 22: Biomass with mutation every 40 time steps:

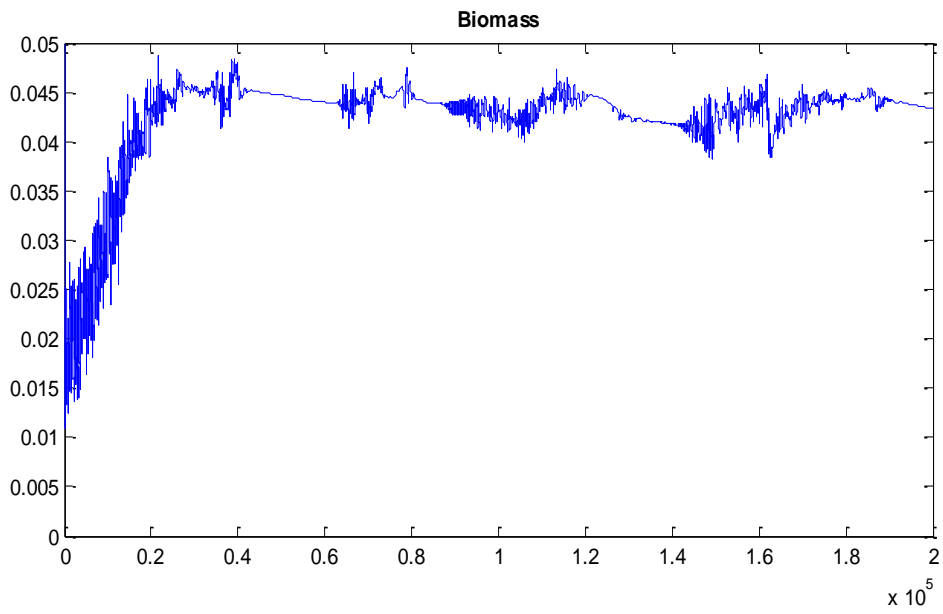
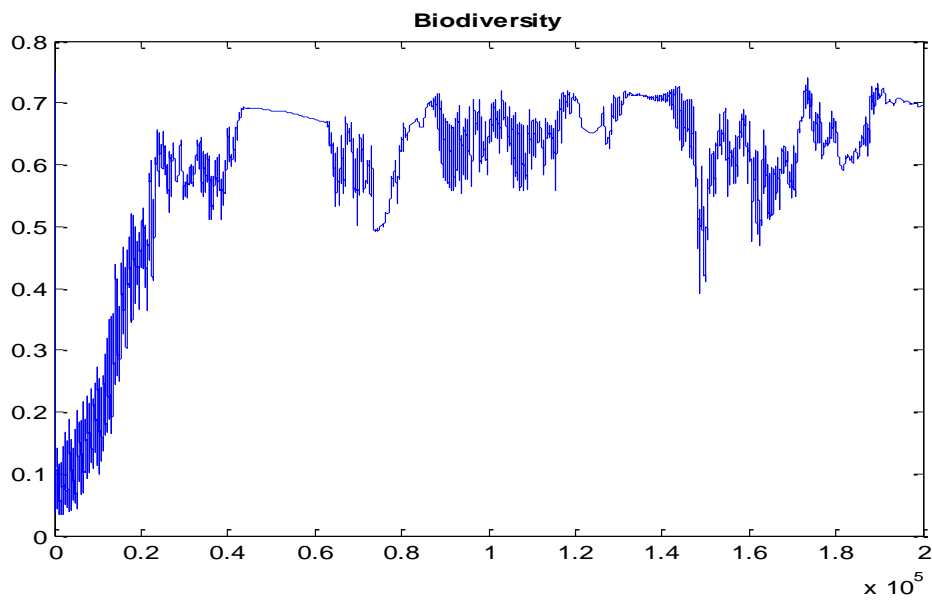


Figure 23. Biodiversity with mutation every 40 steps:



Works Cited

Sprott, J.C., J.A. Vano, J.C. Wildenberg, M.B. Anderson, and J.K. Noel. "Coexistence and chaos in complex ecologies." *Physics Letters A* 335.2 (2005): 207-12. *World Cat*. Web. 1 Feb. 2010.