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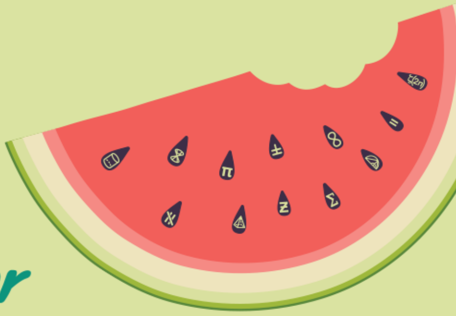

Investigating the Ecological Diversity-Stability Debate using Differential Equation Models and Statistical Sampling Techniques

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Abstract

The behaviour of Earth's large and complex ecosystems, like rain forests and coral reefs, seems to imply that ecosystem diversity leads to stability. We want to be able to model ecosystem behavior, specifically species populations over time, so we can predict the direct and indirect impacts of species reintroductions, invasive species management, habitat restoration, and predict how species behave when faced with natural events. The issue arises where mathematical theory struggles to capture and represent observations. In 2024, Hatton et al. released a new model, the sublinear growth model, for species population which was shown to capture the observed diversity-stability relationship. In testing their model, Hatton et al. assumed that species interactions are random, using random matrix theory and the cavity method to create distributions for sample parameters [6]. Interactions between species within complex ecosystems are not random. This investigation sought to validate the Sublinear growth model using random sampling approaches to check if parameter distributions of ecosystem network models that don't adhere to random matrix theory assumptions recover the same diversity-stability curves found by Hatton et al. Uniform distributions were used for parameter sampling as uniform distributions are the commonly assumed distribution when sampling to investigate the dynamics of ecosystems. The investigation found that when parameters were sampled from uniform distributions the sublinear growth model fails to return the diversity-stability relationship which Hatton et al. found. Theory is still unable to capture and represent behaviours of complex ecosystems which we observe.

Acknowledgement of Authorship This work was produced under the supervision of Dr Matthew Adams. The mathematical methods for solving the Generalised Lotka-Volterra model was replicated from literature cited within the report. All mathematical derivations for the sublinear growth model was derived for this investigation.

1 Introduction

Although there are many models which seek to predict the behavior of species populations in diverse ecosystems, none align to, or reflect, the observed natural trends that suggest that increased species diversity causes ecological stability [4]. One such model is the Generalized Lotka-Volterra (GLV) model which is a basic model of inter-specific competition based on the exponential growth model and sigmoid growth model for populations. The Generalized Lotka-Volterra Model is defined as follows [8]:

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = r_i n_i + \sum_{j=1}^{N} \alpha_{ij} n_i n_j \tag{1}$$

where n_i is the abundance of species i, r_i is the intrinsic growth rate, N is the number of species in the ecosystem and $\alpha_{i,j}$ is the interaction effect of species j on i. This model can be written in vector form as follows:

$$\frac{\mathrm{d}\mathbf{n}}{\mathrm{d}\mathbf{t}} = [\mathbf{r} + \alpha \mathbf{n}] \odot \mathbf{n} \tag{2}$$

where $\mathbf{n}$ is the vector of species abundance, $\mathbf{r}$ is vector of intrinsic growth rates and α is the interaction matrix of interaction strengths between species. $\odot$ is the element-wise product. The GLV model has been a major consideration for ecologists looking into species interaction for the last 100 years [10, 7].

A recent publication from Hatton et al. has proposed a sublinear population model as a means to predict growth and competitive coexistence across ecosystems [6]. Hatton et al. has claimed that the Sublinear Growth model (SLG) reflects the observations which suggest that diversity begets stability. The Sublinear Growth Model is defined as follows:

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = r_i n_i^k n_0^{1-k} - z_i n_i + \sum_{j \neq i}^{N} \alpha_{ij} n_i n_j \tag{3}$$

where n_i is the abundance of species i, r_i is the intrinsic growth rate, N is the number of species in the ecosystem, $\alpha_{i,j}$ is the interaction effect of species j on i, z_i is the death rate of species i, n_0 is the sublinear model constant, or the typical abundance of a species, and k is the subliearity of the intrinsic growth [6]. For this investigation, we set $k = 2/3$ and $n_0 = 1$.

In both models, the interaction matrix, α, is an $N \times N$ matrix of interaction strengths between species. For example, consider a simple three species ecosystem containing cats, birds and worms with the ecosystem diagram shown in Figure 1

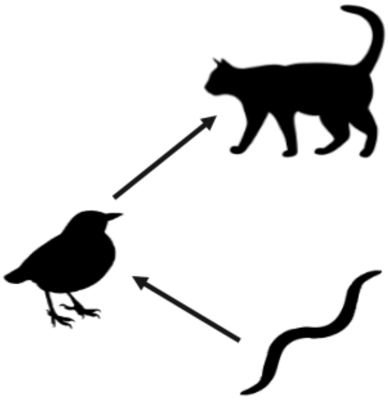

Figure 1: Simple 3 Species Ecosystem Network Diagram

Below are the signs of the interaction matrix for this ecosystem. In this matrix the impacting species are columns, and the impacted species are the rows. Interaction strengths are determined by the impact of one species on another. In this system, cats eat birds, which is a beneficial interaction for cats, so the impact of birds on cats, the element in the 1st row 2nd column, is positive. In contrast, the impact of cats on birds is negative. Cats and worms do not interact directly, therefore the interaction strength is 0. Intra-species interactions, a species impact on itself, are always assumed to be negative due to competition over resources. This information is important when considering parameter sampling which will be detailed later in the report.

$$\begin{array}{c c} & \begin{array}{ccc} \text{Cats} & \text{Birds} & \text{Worms} \end{array} \\ \begin{array}{c} \text{Cats} \\ \text{Birds} \\ \text{Worms} \end{array} & \begin{bmatrix} - & + & 0 \\ - & - & + \\ 0 & - & - \end{bmatrix} \end{array} \tag{4}$$

1.1 Ecological Constraints

Ecological models are constrained by feasibility and stability. A model is feasible when at equilibrium, $\frac{\mathrm{d}n_i}{\mathrm{d}t} = 0$ for all i, species abundance is positive for every species, $n_i > 0, \forall i$. A model is stable if the system recovers after small perturbations of species abundance away from equilibrium. A model must meet these constraints for acceptance [3]. For the calculation of equilibrium, n_i^* denotes the abundance of species i at equilibrium. Derivations for determining these ecological constraints for the Generalised Lotka-Volterra model have been demonstrated in previous publications [3]. When solving for feasibility, equilibrium occurs when $\frac{\mathrm{d}n_i}{\mathrm{d}t} = 0$ for all i, therefore:

$$0 = r_i n_i^* + \sum_{j=1}^{N} \alpha_{ij} n_i^* n_j^*$$

$$0 = n_i^* [r_i + \sum_{j=1}^{N} \alpha_{ij} n_j^*]$$

$$n_i^* \neq 0 \implies r_i + \sum_{j=1}^{N} \alpha_{ij} n_j^* = 0$$

This expression can be conveniently written in vector form:

$$\mathbf{r} + \alpha \mathbf{n}^* = 0 \tag{5}$$

Rearrangement of equation 5 yields:

$$\mathbf{n}^* = -\alpha^{-1} \mathbf{r} \tag{6}$$

where $\mathbf{n}^*$ is equilibrium population vector of all species. The model is feasible if all elements of $\mathbf{n}^*$ are positive.

The stability of the GLV model is determined by calculating the eigenvalues of the Jacobian matrix at the point n^*.The Jacobian matrix is an $N \times N$ matrix whose elements $J_{i,j}$ are given by,

$$J_{i,j} = \frac{\partial f_i}{\partial n_j} \tag{7}$$

where f_i is the rate of change of species abundance Following derivation, the elements of the Jacobian for the GLV model is defined:

$$J_{i,j} = \alpha_{ij} n_i^*, \forall i, j \tag{8}$$

The system is considered stable if the real parts of all the eigenvalues of the Jacobian matrix are negative.

The work published by Hatton et al. was reviewed by Aguade-Gorgorio et al. who found that the sublinear growth model has an unrealistic assumption where species growth rate diverges at low abundance, preventing species from ever going extinct and when you adjust this property to more realistic behaviour the model predicts that increasing diversity leads to species extinction [1].

This project aimed to investigate and review the Lokta-Volterra and the Sublinear models for ecosystem diversity to better understand the intricacies of the diversity-stability debate and make conclusions on whether the sublinear model is a viable solution to ecological predictions. The project explored the validity of the criticism of the sublinear model raised by Aguade-Gorgorio et al. through numerically solving and considering the behaviour of the SLG model. Following methods described above, ecological constraints for the Sublinear growth model were determined. Furthermore, random sampling and Bayesian approaches were used to check whether parameter distributions of ecosystem network models that do not adhere to random matrix theory assumptions recover the diversity-stability curves for the sublinear model and the generalized Lotka-Volterra model published by Hatton et al, shown in Figure 2 [6].

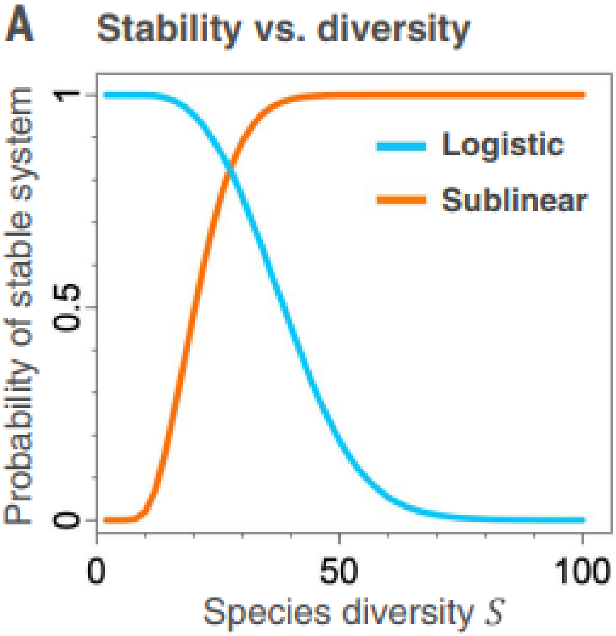

Figure 2: Results achieved by Hatton et al. when using Random Matrix Theory

2 Methods

The following section will outline the methods used to achieve the research objectives. Ecological constraint conditions for the SLG model will be determined and parameter sampling methods and model testing will be described in detail.

2.1 Sublinear Growth

2.1.1 Feasibility

Equilibrium of the Sublinear Growth model is found by setting $\frac{\mathrm{d}n_i}{\mathrm{d}t} = 0$ and solving for the steady state n_i^*.

$$0 = r_i n_i^k n_0^{1-k} - z_i n_i + \sum_{j \neq i}^{N} \alpha_{ij} n_i n_j$$

$$0 = n_i^* [r_i (n_i^*)^{k-1} n_0^{1-k} - z_i + \sum_{j \neq i}^{N} \alpha_{ij} n_j^*]$$

Following the same simplification applied to the GLV model leads to:

$$0 = r_i n_0^{1-k} (n_i^*)^{k-1} - z_i + \sum_{j \neq i}^{N} \alpha_{ij} n_j^* \tag{9}$$

Equation 9 is a nonlinear system of equations therefore a numerical root-finding method must be employed to solve for equilibrium. To solve for the equilibrium vector $\mathbf{n}^*$, we will use Newton's method due to the method's simplicity and convergence speed [5]. Newtons Method is defined as follows [9]:

$$\mathbf{n}_{m+1} = \mathbf{n}_m - J(\mathbf{n}_m)^{-1} f(\mathbf{n}_m) \tag{10}$$

where f is rate of change of species abundance and J is the Jacobian defined:

$$J_{i,j} = \frac{\partial f_i}{\partial n_j} \tag{11}$$

Where the entries of the Jacobian are:

$$\begin{cases} J_{i,j} = (k-1) r_i n_0^{1-k} (k-1) n_i^{k-2} & j = i \\ J_{i,j} = \alpha_{i,j} & j \neq i \end{cases} \tag{12}$$

The iteration was halted when the function reaches $n_{m+1} \approx n_m$ limited by an absolute tolerance of $1e-5$. An iteration limit was also added to the function to aid with model testing. The method terminates after 10000 iterations assuming that the system doesn't converge to a steady state after this point.

2.1.2 Stability

Stability is found following the same method for the Generalised Lotka-Volterra model. The stability of the solution, $\mathbf{n}^*$, is determined by investigating the eigenvalues of the Jacobian matrix solved at the point $\mathbf{n}^*$. The elements of the Jacobian are demonstrated in Eq.12.

2.2 Parameter Sampling for Model Testing

2.2.1 Parameter Sampling

The ability for a model to produce reliable and accurate system models is determined through parameter sampling and model testing. Model testing consists of randomly generating thousands of quantitative models, which are filtered to retain the models which uphold the ecological constraints of feasibility and stability [3].

To test their model, Hatton et al. used Random Matrix Theory and cavity method approaches for parameter sampling assuming random interactions between species. As such, the entries of the interaction matrix, α_{ij}, are independently distributed with an average μ, and a standard deviation σ and can be decomposed as:

$$\mu + \sigma A_{i,j} \tag{13}$$

where $A_{i,j} \sim \mathcal{N}(0,1)$, a normally distributed variable [6]. In the approach of Hatton et al, growth rates, r, and death rates z where extracted from distributions $P(r)$ and $P(z)$ respectively that do not appear to require explicit definition due to their usage of the cavity method [6]. This investigation took another approach to generating model parameters to verify the results of Hatton et al., assuming that interactions between species in ecosystems are not random, but instead occur in high-order combinations where the interactions between species are impacted by many other species [2]. Uniform distributions were used for sampling parameters as they are easy to sample and interpret when using sampling methods.

By observing ecosystems it is known which species are prey, which are predator, which species do not interact and the behaviour of intra-species interactions. The present investigation limited consideration to competitive networks. Educated by this knowledge in the interaction matrix the diagonals represent the intra-species interaction strength. Due to species competition over resources, the impact of intra-species interactions is negative. The off-diagonals represent all the other interactions within the ecosystem. The values of these elements were randomised between -1 and 1, to capture predator-prey interactions and 0 strength interactions. The distributions from which the interaction matrix is constructed from are thus defined:

$$\begin{aligned} \alpha_{i,i} &\sim \mathcal{U}(-5,-1) \\ \alpha_{i,j} &\sim \mathcal{U}(-1,1) \end{aligned}$$

Furthermore, death rates and growth rates are selected from similar uniform distributions which are also distributed based on observed information. Death rates were constrained between -1 and -3 and the growth rates between 0 and 1, represented by the following distributions:

$$\begin{aligned} z_i &\sim \mathcal{U}(-3,-1) \\ r_i &\sim \mathcal{U}(0,1) \end{aligned}$$

2.2.2 Model Testing

In this investigation, 99 ecosystems, with a number of species N increasing from 2 to 100 were modeled using both generalised Lotka-Volterra and Sublinear Growth model. For each ecosystem of size N, 1000 sets of parameters, r, z, and alpha, were generated and each set was tested to see if a feasible and stable model was produced. The parameter sets that passed were saved and the proportion of sets that passed for each ecosystem size N was then calculated.

3 Results

The aim of this investigation was to determine whether the sublinear growth model returned the same results that Hatton et al. found after changing the sampling technique. Shown in Figure 2, Hatton et al. found that when using random matrix theory and the cavity solution to construct distributions for parameter sampling, as ecosystem complexity increases, the sublinear growth model has a higher chance of returning acceptable results, whereas the probability for the Genearlised Lotka-Volterra model to return an acceptable model decreases as ecosystem complexity increases.

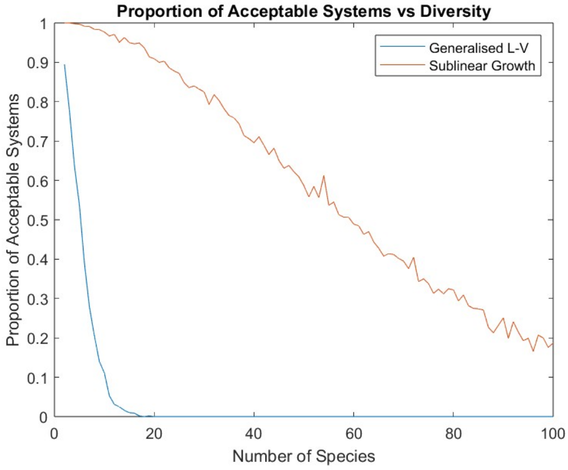

Figure 3: Results achieved when using sampling techniques

Figure 3 shows the results of the model analysis described in Section 2.2.2. This analysis shows that the Sublinear Growth Model does not imply a positive diversity-stability relation as Hatton et al. suggests [6], instead returning increasingly fewer acceptable systems as ecosystem complexity increases. Another feature of the graph is the jaggedness of the sublinear growth model plot compared to the Generalised Lotka-Volterra plot. To determine that this jagged feature was the result of using Newton's method and the number of iterations when testing the model and not an underlying mathematical problem, model testing was repeated with 10000 sets of parameters for each ecosystem size. The results of this testing are shown below in Figure 4. When the number of iterations are increased the graph smooths out showing that the jagged feature is due to the number of iterations not some underlying mathematical problem.

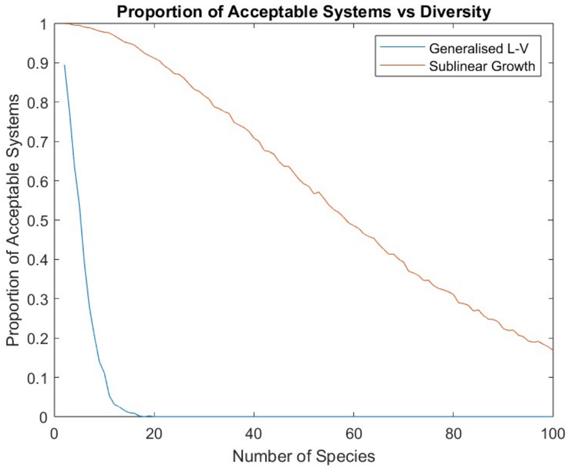

Figure 4: Results achieved when using sampling techniques with 10000 parameter sets per ecosystem size

For further analysis of results, the proportion of feasible and proportion of stable systems were determined separately, see Figure 5. As shown, the proportion of stable and feasible systems diverge as ecosystem complexity increases. This suggest that there are systems which achieve some steady state or equilibrium, but are not mathematically stable. This could be due to Newton's method finding a false point of convergence before the system behaves asymptotically. An example of such a system is displayed below, see Figure 6.

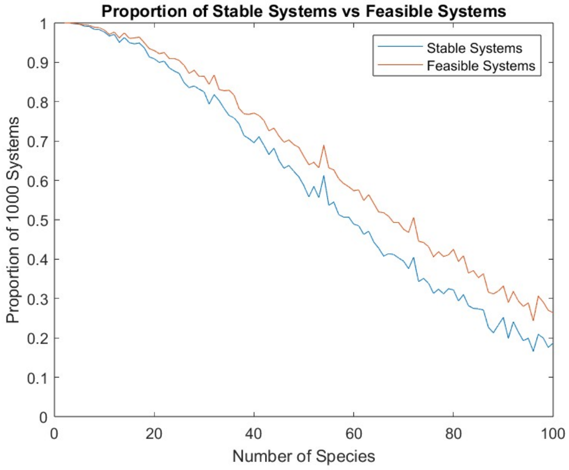

Figure 5: Proportion of feasible vs stable systems with 1000 parameter sets per ecosystem size

To appreciate this difference more, this analysis should be performed with 10000 parameter sets per ecosystem size to see of the proportions diverge to the same extent. Due to time constraints and computational duration for performing model testing with a large number of parameter sets, this was outside of the means of this investigation.

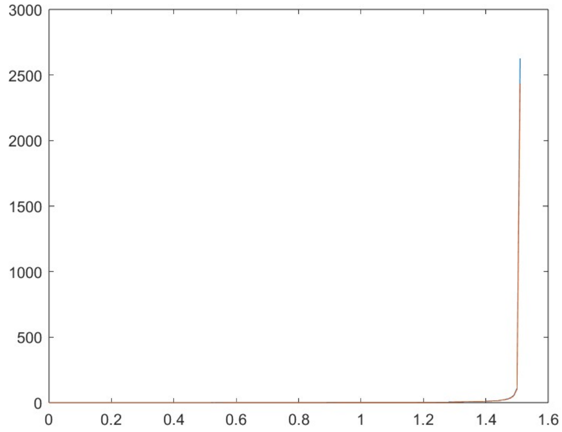

Figure 6: A false feasible system

From this analysis, it is determined that the Sublinear Growth model fails to capture observed ecosystem behaviour. Interestingly, this analysis does show that the Sublinear growth model performs better than the Generalized Lotka-Volterra model, indicating that it may be a useful model for ecosystem modelling over the Generalised Lotka-Volterra model.

4 Conclusion

At the conclusion of this investigation, it was determined that when parameter sampling is adjusted to reflect observable or expected ecosystem behaviour, the Sublinear Growth model doesn't imply a positive diversity-stability relation. Rather, the Sublinear Growth Model returns increasingly fewer acceptable systems as ecosystem complexity increases. Potential further research would be to construct distributions of parameters based on the parameter sets which yielded acceptable models. This would allow analysis of the parameter distributions giving further understanding of system dynamics. Conversely, further research could investigate the model improvement suggestions raised by Aguade-Gorgorio et al. to determine whether the sublinear model could be improved [1].

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