

Robert May and the Stability of Ecological Delayed Dynamics

Department of Mathematics, University of York

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In his 1973 monograph, *Stability and Complexity in Model Ecosystems* [May73], Robert May showed that ecological stability was not inevitable. This challenged the assumed consensus at the time: that when simple systems were embedded in complex ecosystems, stability would eventually emerge. Although, May's model considered a variety of different factors, theoretical ecologists have since discovered additional parameters that contribute to the stability of ecological communities. In this review report we will address how May's ideas have been challenged and revised in the 21st century, specifically drawing attention to the recent developments that arise from delayed differential equations.

A first approach to large complex ecosystems

It is a worth a very thorough discussion in May's initial investigations as these ideas are still fundamental to the modern research in this area. We will begin with some basic ODE theory; consider a system of ODEs

$$\frac{dx_i}{dt} = f_i(x_i)$$

and suppose $\frac{dx}{dt} = \mathbf{f}(\mathbf{x}^*) = \mathbf{0}$, where \mathbf{x}^* is referred to as a fixed point. Then by introducing $\boldsymbol{\xi}(t) = \mathbf{x}(t) - \mathbf{x}^*$ and expanding through a multivariate Taylor series, we obtain

$$\frac{d\boldsymbol{\xi}(t)}{dt} = \mathbf{J}\boldsymbol{\xi}(t) \quad (1)$$

where $J_{ij} = \frac{\partial f_i}{\partial x_j}$ evaluated at \mathbf{x}^* is the corresponding Jacobian matrix. Thus, we have constructed a method for linearizing a non-linear system of ODEs about a fixed point. Robert May used this result by assuming that the Jacobian matrix represented an ecological dynamical system. We rename this Jacobian to be A and notice that the a_{ij} entry would describes how species j affects species i . The entries a_{ii} are referred to as self-limiting terms and describes the species i in the absence of the other species. In order to gain further insight, May assumed that the self-limiting terms were all a negative constant $-d_0$ and that the rest of the entries sampled from a normal distribution $\mathcal{N}(0, \sigma^2)$, with a probability of $(1 - C)$ to be 0. One may immediately notice that does not accurately model a real ecological system. This will be addressed later, however this will make our current model easier to work with.

It is known for a linear system of ODEs $\dot{\mathbf{x}} = \mathbf{M}\mathbf{x}$, has solutions of the form

$$\mathbf{x}(t) = \sum_{i=1}^S c_i \mathbf{v}_i e^{\lambda_i t}, \quad (2)$$

where the system is asymptotically stable if all the eigenvalues have a negative real part, $\Re(\lambda_i) < 0 \forall i$. This fact is also

true for our linear approximation. Hence, we compute the eigenvalues of an interaction matrix of size $S \times S$ in Figure 1 to evaluate the stability of the system.

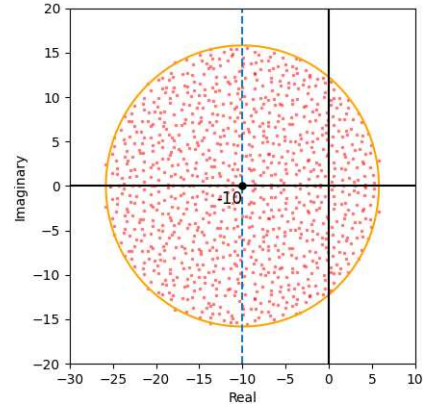


Figure 1: Eigenvalues of A , with May's simplifications, where $d_0 = 10$, $\sigma = 1$, $C = 0.25$ and the number of species or system size S is 1,000.

The immediate follow-up question is why the eigenvalues of A generate this circular shape? This is due to the Gershgorin circle theorem, in which every eigenvalue of A lies within at least one of the Gershgorin discs $D(a_{ii}, R_i)$, where R_i is the sum of the absolute values of the non-diagonal entries in the i -th row. In fact a theoretical physicist, Eugene Wigner, was able to show that the distribution of eigenvalues converges to a uniform disc with centre $(-d_0, 0)$ and radius $\sigma\sqrt{SC}$, which would later be named complexity. This gives us a tool for comparing the stability of other models. For May's random model, we can combine this with the previous result to deduce that, for stable systems, the whole of the circle is contained in the left half of the plane. Thus the stability criterion of a random model is if the complexity of the system is less than its self-limiting terms, $\sigma\sqrt{SC} < d_0$, as the circle is centred on $(-d_0, 0)$.

Limitations of the May Model

Robert May's model provided much insight into theoretical ecology however there were certainly holes in his approach that deserve consideration. Firstly, we consider the classic model for a deterministic one-predator-one prey system with continuous growth: the Generalized Lotka-Volterra (GLV) equations

$$\frac{dx_i}{dt} = x_i \left(r_i + \sum_{j=1}^S A_{ij} x_j \right) \quad (3)$$

where \mathbf{r} is the intrinsic birth or death rate and A is the interaction matrix. The matrix A is the same interaction matrix

we previously defined. According to May the Jacobian of these ODEs should have a similar structure to A , thus a good question to ask is whether the Jacobian of the GLV equations and A are indeed the same matrix. The Jacobian of the GLV equations J can be found [LCP22] and it satisfies

$$\begin{aligned} \mathbf{x}^* &= -A^{-1}\mathbf{r}, \\ J &= \mathbf{x}^* A. \end{aligned} \quad (4)$$

It is clear that the Jacobian is not the same as the interaction matrix, as it depends on the fixed point \mathbf{x}^* . Thus, May's matrix does not accurately represent the dynamics of the GLV model.

We can further investigate the limitations of May's model with another approach- by modelling the interaction matrix as a network, with the species as nodes and edges between them if there is an interaction. This is simply done setting $d_0 = 0$ and letting the non-zero entries be 1, for our Jacobian, which creates an augmented matrix to generate a graph from.

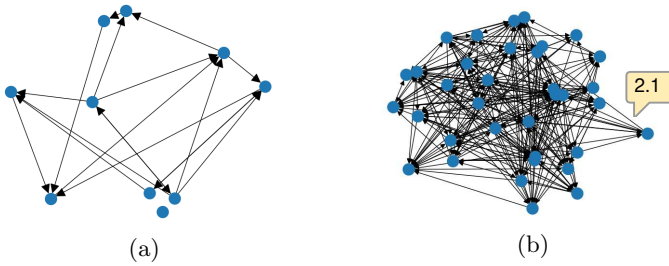


Figure 2: Directed network representations of May's model sampled from $\mathcal{N}(0, 1)$, where $d_0 = 0, C = 0.25$ with system size $S = 10$ (a) and $S = 35$ (b). If $A_{ij} \neq 0$, then we illustrate this with an arrow from node i to node j .

It is now more clear that May's Model fails for small system sizes. As shown in Figure 2a, there is a species that does interact with any other species, which does not happen in the real world, unless you were to consider a species in a faraway ecosystem. Additionally there are species that interact one-way but not the other, which is not possible. Figure 2b also

shows another inaccuracy in the model, however this easier to see with the histograms in Figure 3.

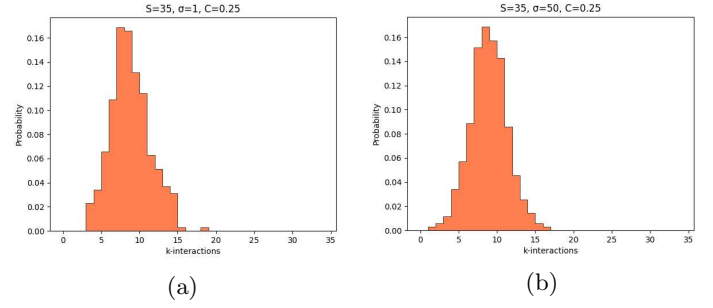


Figure 3: Numerical simulations of May's Model represented by histograms at $S = 120, C = 0.25$ with 10 iterations. The probability is plotted against the probability that a species has k -interactions, which represents the node degree of the network. (a) and (c) differ by their sigma value of $\sigma = 1$ and $\sigma = 50$ respectively.

The histograms represent the number of interactions a species has with other species in their environment, with the corresponding probabilities relating to the the number of interactions a species has. The distribution of the graphs follows a bell curve, which does not align with the empirical evidence. From empirical evidence it seems that species that interact feebly with others do so with a great number of other species. Conversely, species with strong interactions are often part of a system with a small number of species... [Mar68]. This statement is clearly contrasted by Figure 3a and 3b, as the interaction strength σ does not have an impact on the number of interactions a species will have.

Stability of Real Ecological Networks

We have now addressed some of the problems with May's model and we see that it has limited applicability. In the pursuit of a more accurate model, we will now investigate the stability of different types of interactions. Much of this discussion will be surmising results by Allesina and Tang [AT12].

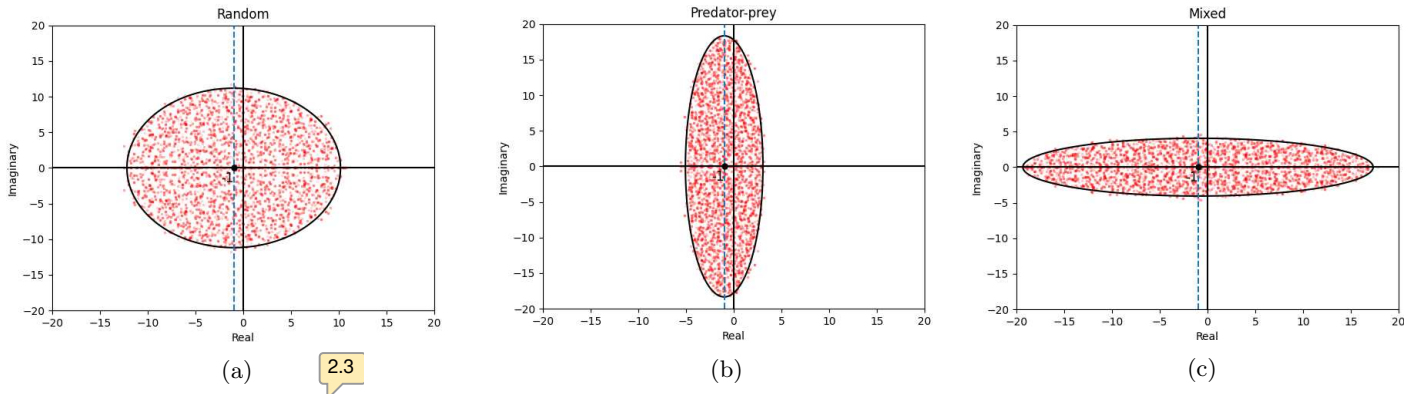


Figure 4: Eigenvalue distribution of various ecological models, with $S = 250, C = 0.5, d_0 = -1, \sigma = 1$, each with 10 iterations. As mentioned previously, the radius of (a) is $\sigma\sqrt{SC}$ so the stability criterion is $\sigma\sqrt{SC} < d$. The horizontal and vertical radius for (b) are $\sigma\sqrt{SC} (1 - \mathbb{E}^2(|X|)/\sigma^2)$ and $\sigma\sqrt{SC} (1 + \mathbb{E}^2(|X|)/\sigma^2)$, hence the stability criterion is $\sigma\sqrt{SC} < d / (1 - \mathbb{E}^2(|X|)/\sigma^2)$. The ellipse in (c) has the the opposite corresponding horizontal and vertical radius, hence the stability criterion is $\sigma\sqrt{SC} < d / (1 + \mathbb{E}^2(|X|)/\sigma^2)$. Note that the expectation value of a half normal distribution is $\mathbb{E}(|X|) = \sigma\sqrt{2}/\sqrt{\pi}$.

3.1

Firstly we will consider a predator-prey model and notice that interactions must come in pairs, i.e. whenever $A_{ij} < 0$, then $A_{ji} > 0$. To generate the matrix, we sample one interaction, with probability $(1 - C)$, from the half normal distribution of $|\mathcal{N}(0, \sigma)|$ and the other from $-\mathcal{N}(0, \sigma^2)$, otherwise the entries are both 0, i.e. the probability both are 0 is $(1 - C)$. We emphasize that it is not required that upper or lower diagonals of A must be entirely positive or negative. Interestingly, the eigenvalue distribution does not actually depend whether we sample from half normal distributions, a bivariate normal distribution or uniform distribution [AT15]. Now we consider the case for mutualism and competitive interactions, we shall call these mixed interactions. The corresponding matrix will be constructed in the same way as the predator-prey matrix, except M_{ij} and M_{ji} will be constrained to have the same sign. Now we easily recreate the findings by Allesina and Tang by computing the eigenvalues for these models, shown in Figure 4.

Even though the stability criterion for the models have been explicitly stated, we can comment on model stability from immediate inspection of the graphs. We can infer that the predator-prey interactions offer the most stability, as it has less eigenvalues on the right side of the plane and the mixed interactions thus offer the least stability. However, this contradicts the popularity of mixed interactions in the real world. It is only natural that we attempt another approach to improving May's model.

Delay Effects in Ecological Stability

We will now introduce another approach to evaluating the stability of an ecological community, by expanding on our previous model. This will use concepts used in delay differential equations (DDEs), which are differential equations that depend on past history. We will also be basing this section from the paper by Pigani et al. [Pig+22]. The motivation behind this approach is that the empirical evidence of species' interactions typically occur after a time lag [Nel05]. Recall that we considered linearizing a non-linear system of ODEs about a fixed point in Equation 1. Similarly for a discrete positive time delay τ , we can linearise a system of DDEs from a fixed point, which has the form

$$\dot{\xi}_i(t) = \sum_{j=1}^S A_{ij} \xi_j(t) + \sum_{j=1}^S B_{ij} \xi_j(t - \tau), \quad (5)$$

where $A_{ij} = \frac{\partial f_i}{\partial x_j(t)}$ and $B_{ij} = \frac{\partial f_i}{\partial x_j(t-\tau)}$ both evaluated at \mathbf{x}^* , are the interaction matrices that describe current and delayed coupling strengths. The corresponding eigenvalues (with commutable A and B) for the system are given by

$$\lambda = a_i + b_i e^{-\lambda_i \tau}, \quad (6)$$

where a_i and b_i are the eigenvalues for A and B respectively. Similar to our Jacobian in Equation 1, the system is asymptotically stable if $\Re(\lambda_i) < 0 \forall i$. Solving λ in terms of a_i , b_i and τ yields

$$\lambda_i = a_i + \frac{\mathcal{W}(b_i \tau e^{-a_i \tau})}{\tau}, \quad (7)$$

where \mathcal{W} is the Lambert \mathcal{W} function, defined implicitly by $\mathcal{W}(z)e^{\mathcal{W}(z)} = z$. We have omitted the analytical details of these equations for the sake of simplicity, however Pignani et al. discusses these ideas in more rigour. Now we try to uncover the geometric profile of the eigenspectrum, by considering the simple case where $A = -d_A I$ with $d_A \geq 0$, which

3.2

ensures commutativity of A and B . We also assume that B is in the form of May's random matrix as defined previously, with diagonal elements of $-d_B \leq 0$. The physical importance of these assumptions is that we are focusing on systems with two components; intraspecies terms that are self-stabilizing and coupling terms in the past that affect the current growth rate. Letting $r_B = \sigma\sqrt{SC}$, the geometric profile of the eigenvalues follow the curve

$$d_B^2 + 2d_B e^{\tau\Lambda} [(d_A + \Lambda) \cos(\tau\omega) - \omega \sin(\tau\omega)] + e^{2\tau\Lambda} [(d_A + \Lambda)^2 + \omega^2] = r_B^2, \quad (8)$$

where $\Lambda \equiv \Re(\lambda)$ and $\omega \equiv \Im(\lambda)$. Plotting the eigenvalues reveals a wing-like structure.

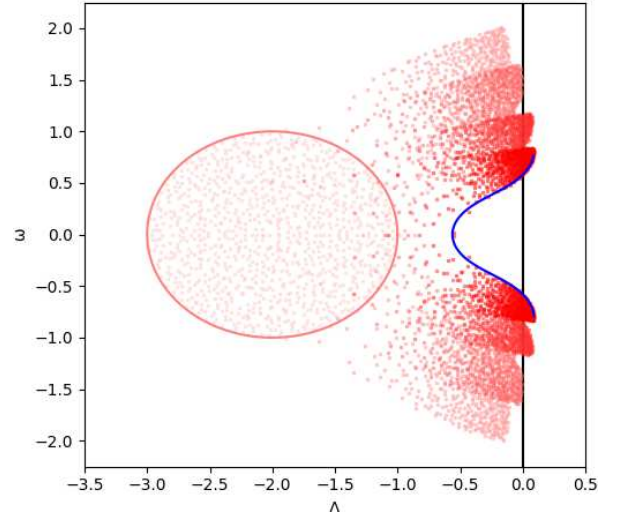


Figure 5: Eigenvalues of the linearised system of DDEs plotted on Argand diagram, for $d_A = 1.1$, $d_B = 0.9$, $C = 0.1$, $\sigma = 0.1$ and $S = 1,000$. From darkest to lightest shade of red, τ is varied for $\tau = 0, 1, 2$ and 3 . The curve in blue is described by Equation 8 at $\tau = 3$ for $\Lambda \in [-1, \frac{1}{2}]$ and $\omega \in [-0.8, 0.8]$.

As expected the circle law is apparent for $\tau = 0$, centered on $(-(d_A + d_B), 0)$. Additionally, the graph also shows that if the system is unstable for $\tau = 0$, then the delay is unable to stabilize the system. It would be useful to know the maximum τ^* delay before the system becomes unstable, for an already unstable system we shall say $\tau^* = 0$. From Equation 8 it is actually possible to determine equations that determine τ^* and ω^* - the critical frequency.

$$d_B^2 + d_A^2 + (\omega^*)^2 + d_B [d_A \cos(\omega^* \tau^*) - \omega^* \sin(\omega^* \tau^*)] = r_B^2, \quad (9)$$

$$(1 + d_A \tau^*) d_B \sin(\omega^* \tau^*) + d_B \omega^* \tau^* \cos(\omega^* \tau^*) = \omega^*. \quad (10)$$

These equations are satisfied if and only if $\omega = 0$ and $r_B = d_A$, which implies that the stability does not depend on our choice of τ when $r_B < d_A$ ($\tau^* = \infty$) so May's bound for stability is not affected by the delay.

In the paper only the random matrix for B is considered. Using the models in the previous section, it becomes easy to adapt this model for other interactions Figure 6, namely the predator-prey and mixed interactions we discussed in the previous section.

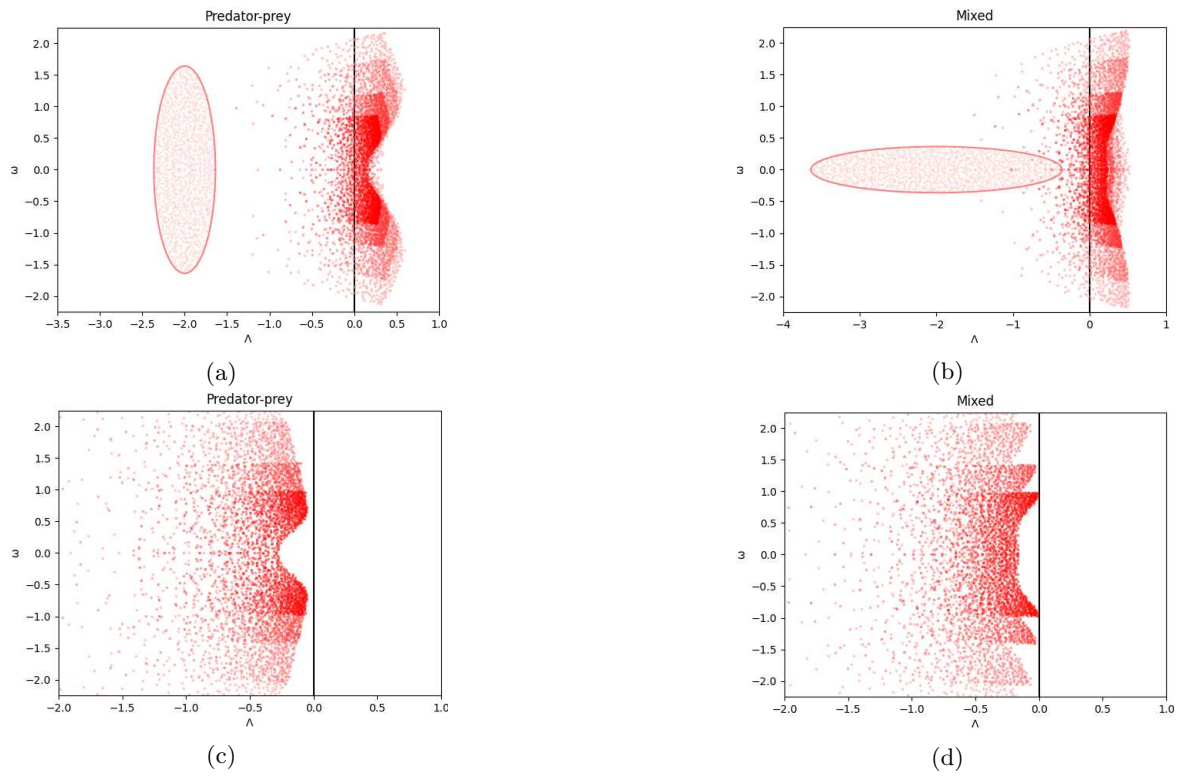


Figure 6: Eigenvalues of delayed models for different interactions, with same parameters as Figure 5 except for (c) and (d) which have their d_A value increased to 4.5. As expected we see ellipses in (a) and (b) for $\tau = 0$, where they have the same radii from Figure 4, but instead centred on $-(d_A + d_B, 0)$.

Similar to the random case, the stability criterion for these models seem to involve the value of d_A . Without deriving this criterion, we see that these interactions will need a much higher current self-limiting factor for stability so it is worth exploring if one could derive this criterion analytically and why the d_A value needed is so much greater compared to the mixed case, however we will not do this here. Additionally, we see that the stability is not affected by our choice of τ once we have chosen a suitable d_A , similar to the mixed case. Figure 5 and 6 also implies that mixed interactions offer the most stability when time-delay effects are taken into account, which is not the case when not considering the time-delay.

Conclusion

In this paper we have explored Robert May’s ideas on the stability of ecological communities. We then discuss the limitations of May’s Model of modelling real complex systems, but we still see its usefulness as a foundational theory in the following sections. Different types of interaction models have been considered and we have applied ideas from delay differential equations by invoking a discrete time delay τ . We have provided some original computation and have shown that the question of ecological stability is not as trivial as May’s model made it to be and hence many different approaches must be considered to accurately model complex ecosystems.

References

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Index of comments

- 1.1 missing subscript
- 1.2 Avoid unclear antecedents - notice that the term "this" refers to two different things here.
- 1.3 would have perhaps made sense to stick to λ_i here (consistent with the linear system in Eq.(1))
- 1.4 terms need defining.

- 2.1 Use `` rather than " to open quotation marks in LaTeX
- 2.2 of systems with different types of interactions (interactions on their own don't have stability)
- 2.3 discussed in test (see Eq.(xx) OR see Section XX) - Cross referencing helps the reader navigate the text, especially as you move towards your thesis.

- 3.1 Would have been useful to specify i is prey and j predator in this example
- 3.2 Consistent and clear notation
- 3.3 emphasise
- 3.4 ;
- 3.5 fewer
- 3.6 Really great flow
- 3.7 Making connections between the sections and approaches
- 3.8 Good attention to detail
- 3.9 ... and pitched at exactly the right level.