

Applying mathematical insights on transient dynamics to ecology, what can we learn about how plant populations respond to disturbance in a changing world?



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Introduction and Aims

- This interdisciplinary project aimed to explore the intersection between mathematics and ecology, focusing on the mathematical modelling of transient population dynamics of plant species.
- Matrix models are mainly used to analyse dynamics of plant populations over long periods of time, using matrix eigenvalues to calculate the asymptotic rate of convergence to the stable long-term population distribution. However, with the effects of global change increasing due to climate change, there is an urgent need to better understand the short-term dynamics of populations during periods of recovery or decline.
- There were two fundamental questions – with significance for both mathematics and ecology – that I prioritised in my research:
 - 1. What happens before the stabilisation of the population? Can we make a mathematical prediction about what will happen and when?
 - 2. The Special Case- When there are multiple stable states, (i) can we make a prediction? And (ii) what does this mean scientifically?

Background Reading

There was a significant amount of background reading involved in this project in order to become familiar with the current literature in the area.

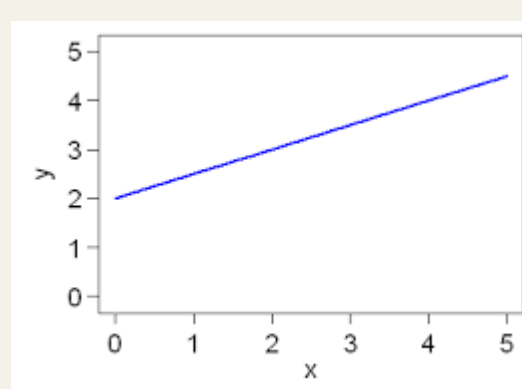
1. Variability (towards stability) is not necessarily an inherent property of systems because it typically also depends on external factors that act as perturbations. However, this paper views stability as an inherent ability of a dynamical system to endure perturbations. Variability may be caused by a particular perturbation regime, so a different regime could lead to a different value of variability. Stronger perturbations will generate larger fluctuations, and the way a perturbation's intensity is distributed and correlated across species is also critical. Variability is an inherently multidimensional notion, reflecting the multidimensionality of an ecosystem's responses to perturbation.
2. Recovery in a population is the norm but remains incomplete. In this research, the degree of recovery was higher if resistance or resilience were high, whereas between resistance and resilience a strong negative correlation emerged. Stability aspects differed between systems, organisms and experimental approaches. Results indicate that functions can be restored even in the absence of compositional recovery because functional redundancy can allow a different community to perform almost the exact same functions.
3. This paper concludes that we can expect that legacy effects of disturbances on communities, triggered by repeated pulse disturbances affecting all species in a similar way, are more likely to be correlated with an increase in the intensity of extreme events rather than an increase in the frequency of small to intermediate disturbances.
4. The relationship between different stability components can vary with disturbance type so it is vital to consider multiple measures of stability simultaneously without combining them to a single measure.
5. This study showed that unusual environmental events may be the number one environmental triggers of community collapses. The most abundant species are sensitive to environmental events and they start to decline immediately as a response to the environmental event. The decline of the pre-collapse dominant species could be an important secondary cause of collapses. In this study, the combined indicator of the total change of pre-collapse and collapse dominant species proved to be an effective indicator of small-scale and large-scale collapse. The paper concludes that small-scale signals should be involved in studies because they can be earlier than large-scale trend changes of collapse indicators.

Research Methodology

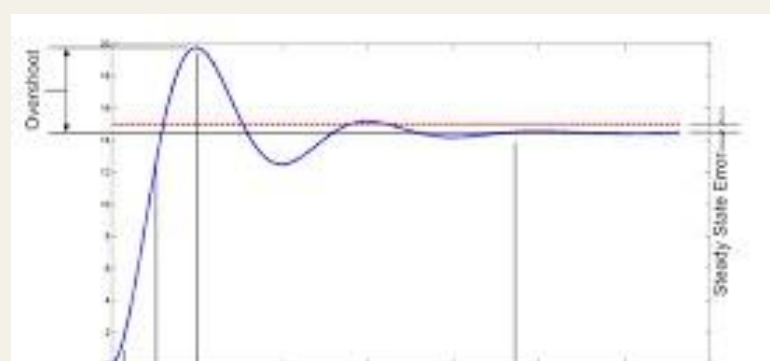
Using a combination of R, MATLAB and 'by-hand' techniques, I analysed the properties of the matrices. Since these matrices are triangular, certain structural properties could be exploited – for example, we already knew their eigenvalues.

Much of this project focused on looking at the two ways that plant populations approach their stable state. For the sake of simplicity, throughout the course of this project I have referred to these two ways of reaching the stable state as Pattern A and Pattern B.

Pattern A is the standard direct approach to the stable state, where the population incrementally approaches the stable state in a straight line.



Pattern B refers to the more unusual (and interesting) case where the population initially appears to move away from approaching its stable state before coming back and achieving convergence



Of course, there is also the case where the plant population never reaches a stable state, but we could not begin to examine that until Pattern A and Pattern B were more deeply understood.

As there are relatively few real-life examples of Pattern B, I artificially created matrices that would replicate the path of a Pattern B matrix in order to be able to spot patterns and properties more easily.

MATLAB was particularly useful for running simulations, as it allowed the paths to be drawn with each stage marked, which made spotting the changes in direction for Pattern B much easier. I also looked at how Pattern B matrices would have to be manipulated in order to behave like Pattern A. This was examined both mathematically and computationally but required such comprehensive change that it did not seem that there would be a formulaic way to apply this to every matrix as an analysis method.

My methodology also looked at the most basic case – a 2x2 matrix – in order to spot more fundamental relationships. It was this methodology that revealed that the positioning of the eigenvectors was significant in revealing the pattern the matrix would follow. After finding out that this was significant, I manipulated my matrices in order to ensure they had specific eigenvectors that I knew would plot at certain positions and angles, focusing on the most basic 2x2 case.

The two boundary cases I considered were when the two eigenvectors were almost orthogonal or when they were almost in line, and then considered increments in between.

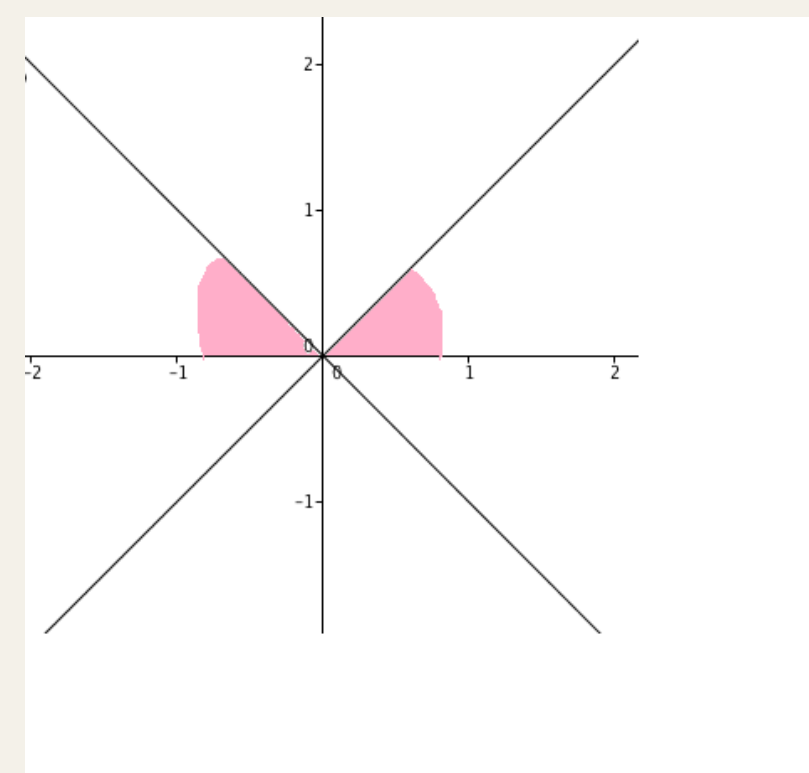
Although it was difficult to artificially create matrices that followed both the pattern I wanted them to and had the eigenvector properties I required, I was able to construct enough to come to some interesting results. However, the ability to construct more matrices with the desired properties would provide more rigorous grounds for my results and would help to draw deeper and more nuanced conclusions regarding the significance of the positioning of eigenvectors in the pattern of a population matrix.

Now find the eigenvectors. Solve $(A - \lambda I)x = 0$ separately for $\lambda_1 = 0$ and $\lambda_2 = 5$:

$$(A - 0I)x = \begin{bmatrix} 1 & 2 \\ 2 & 4 \end{bmatrix} \begin{bmatrix} y \\ z \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \text{ yields an eigenvector } \begin{bmatrix} y \\ z \end{bmatrix} = \begin{bmatrix} 2 \\ -1 \end{bmatrix} \text{ for } \lambda_1 = 0$$
$$(A - 5I)x = \begin{bmatrix} -4 & 2 \\ 2 & -1 \end{bmatrix} \begin{bmatrix} y \\ z \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \text{ yields an eigenvector } \begin{bmatrix} y \\ z \end{bmatrix} = \begin{bmatrix} 1 \\ 2 \end{bmatrix} \text{ for } \lambda_2 = 5.$$

Results

An interesting result obtained from my research was finding that in all the populations I used and constructed that followed Pattern B, the starting population vector was located between the x-axis and the eigenvector closest to it. I initially did this in the 2*2 case and then scaled up to 3*3, 4*4 and 5*5, and the results remained consistent.



Most interestingly, it seemed that the position of this starting vector was the vital part of this – when artificially creating starting vectors in order to sport patterns, the same population matrix which sent a starting vector located between x-axis and eigenvector to follow Pattern B would send a starting vector outside this region to follow Pattern A.

This indicates that it is the relationship between the starting vector and matrix which is most important to consider when trying to predict whether a population will follow Pattern A or Pattern B rather than any inherent properties of the matrix itself.

These results remained consistent when I artificially constructed matrices that had eigenvectors that were almost in line with the x axis and placed the starting population inside it and continued to increase this till the eigenvectors were almost orthonormal.

Further Questions

Although the results are interesting and significant, they raise a number of further questions and areas for study:

- The most pressing question raised by the above results is obviously: what are the exact properties of the relationship between the eigenvectors of the matrix and the starting vector of the population that make these susceptible to following Pattern B?
- Consider the 'worst case scenario'. What is the most deviation from asymptotic convergence that can occur?
- From a structural standpoint, what structures put the population away from ever converging if they keep happening?
- Consider the return times for Pattern B – in practice, how long does it typically take the plant populations to return to stability?
- Do the other eigenvectors (ie the ones that are not closest to the x-axis) in matrices larger than 2x2 have any relevance to the pattern the population follows or its return time to the stable state? Why or why not?

References

1. Arnoldi, J., Loreau, M. and Haegeman, B., 2019. The inherent multidimensionality of temporal variability: how common and rare species shape stability patterns. *Ecology Letters*, 22(10), pp.1557-1567.
2. Hillebrand, H. and Kunze, C., 2020. Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters*, 23(3), pp.575-585.
3. Jacquet, C. and Altermatt, F., 2020. The ghost of disturbance past: long-term effects of pulse disturbances on community biomass and composition. *Proceedings of the Royal Society B: Biological Sciences*, 287(1930), p.20200678.
4. White, H., Gaul, W., Sadykova, D., León-Sánchez, L., Caplat, P., Emmerson, M. and Yearsley, J., 2020. Quantifying large-scale ecosystem stability with remote sensing data. *Remote Sensing in Ecology and Conservation*, 6(3), pp.354-365.
5. Pálinkás, M. and Hufnagel, L., 2020. The collapse indicators of the dominant species outperform community-level critical slowing down indicators.

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