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Stability Analysis of Food Webs: An Introduction to Local Stability of Dynamical Systems

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Stability Analysis of Food Webs

An Introduction to Local Stability of Dynamical Systems

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Outline

A simple dynamical system

We can describe the dynamics of a population through time by means of an autonomous ordinary differential equation:

One Population

$$\frac{dX(t)}{dt} = f\left(X(t)\right) \tag{1}$$

Where:

- $X(t) \rightarrow$ density (or biomass) of population X at time t.
- $f\left(X(t)\right) \rightarrow$ function of $X(t)$.
- $\frac{dX(t)}{dt} \rightarrow$ rate of change.

In the remainder of the talk we will write X for $X(t)$.

Equilibrium

The population reaches a fixed point when:

Equilibrium

$$\frac{dX}{dt} = 0 = f(X) \tag{2}$$

We will indicate with X^* the solution of the equation above.

- If $X^* > 0 \rightarrow$ **feasible** equilibrium.
- If $X^* = 0 \rightarrow$ **extinction**.
- If $X^* < 0 \rightarrow$ **unfeasible** equilibrium.

We are typically interested in feasible equilibria only.

Stability

Say that the population is at a fixed point X^*. What happens if we perturb it (i.e. we move the population to $X^* + x(t)$? Does the system recover from the perturbation?

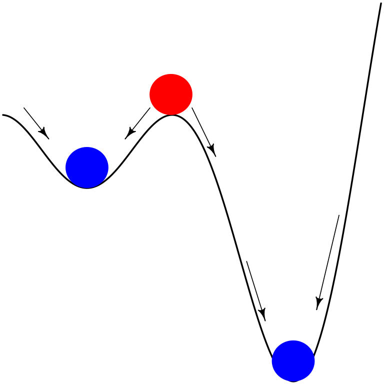


Figure adapted from Soetaert and Herman, 2009

Stability: graphical methods

$$\frac{dX}{dt} = rX\left(1 - \frac{X}{K}\right) - \theta\frac{X}{X+h} \tag{3}$$

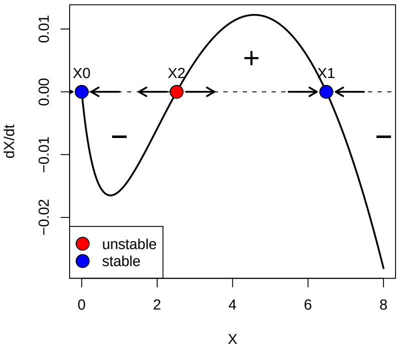


Figure adapted from Soetaert and Herman, 2009

Stability: two populations

$$\frac{dX}{dt} = f_X(X, Y)$$
$$\frac{dY}{dt} = f_Y(X, Y)$$

Simple predator-prey system

- X is the prey
- Y is the predator

$$\frac{dX}{dt} = (b - d)X\left(1 - \frac{X}{K}\right) - \alpha XY$$
$$\frac{dY}{dt} = \alpha\epsilon XY - mY$$

Stability: two populations

Simple predator-prey system

$$\frac{dX}{dt} = (b-d)X\left(1-\frac{X}{K}\right) - \alpha XY$$

$$\frac{dY}{dt} = \alpha\epsilon XY - mY$$

- b is the birth and d the death rate for the prey.
- K is the carrying capacity for the prey (max. possible level).
- α is the interaction term, modeling the probability of "effective encounters".
- ϵ is the efficiency of the predator.
- m is the death rate for the predator.

When there is no predator

$$\frac{dX}{dt} = (b-d)X\left(1-\frac{X}{K}\right)$$

The equilibrium values are:

$$0 = (b-d)X\left(1-\frac{X}{K}\right) \rightarrow X^* = 0,\ X^* = K$$

When predators are present

$$\frac{dX}{dt} = (b-d)X\left(1-\frac{X}{K}\right) - \alpha XY$$

The equilibrium values are:

$$\begin{aligned} 0 = (b-d)X\left(1-\frac{X}{K}\right) - \alpha XY \rightarrow \\ X^* = 0, \\ Y = \frac{b-d}{\alpha}\left(1-\frac{X^*}{K}\right) \end{aligned}$$

This is called the zero isocline for X.

Isocline for the predator

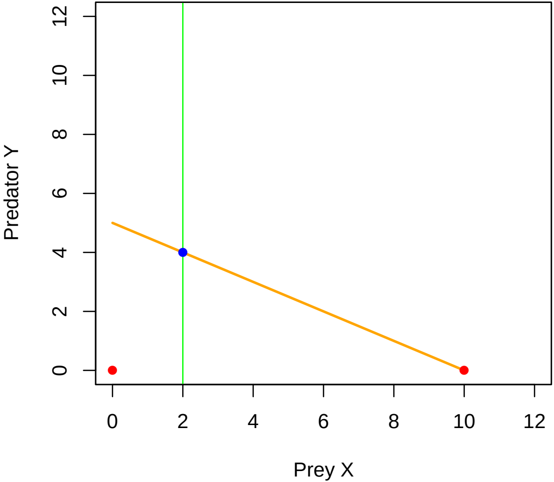
$$\frac{dY}{dt} = \alpha\epsilon XY - mY$$

The equilibrium values are:

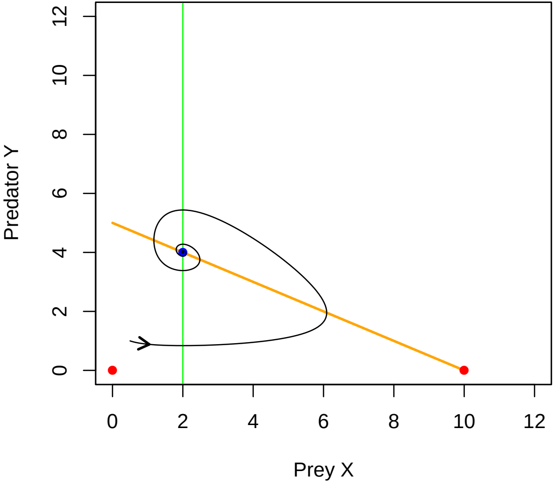
$$\begin{aligned} 0 &= \alpha\epsilon XY - mY \\ Y^* &= 0, \\ X &= \frac{m}{\epsilon\alpha} \end{aligned}$$

This is called the zero isocline for Y.

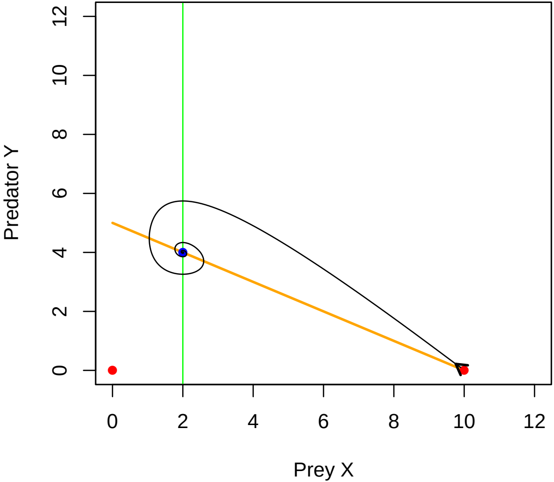
Phase Plane



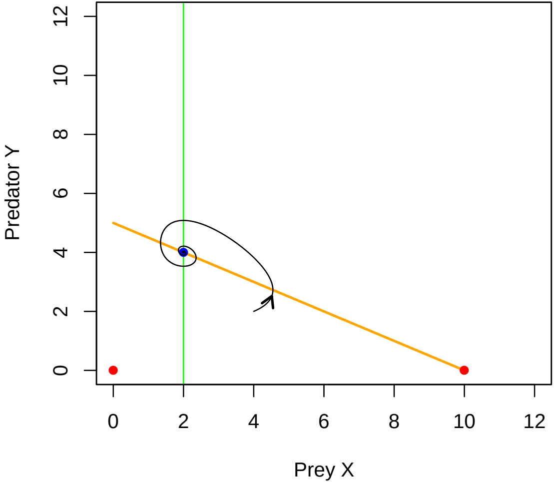
Trajectories



Trajectories



Trajectories



Stability in multiple species communities

$$\frac{dX_i}{dt} = f_i(X_1, \ldots, X_n)$$

Feasible Equilibrium:

$$f_i(X_1, \ldots, X_n) = 0 \ \forall i$$

$$X_i^* > 0 \ \forall i$$

How to evaluate stability of equilibria?

Perturbation

$$X_i(t) = X_i^* + x_i(t)$$

We want to study if the perturbation x_i grows or tends to zero. We can write the change in the growth rate of x (using Taylor expansion):

$$\frac{dx_i}{dt} = \sum_j \alpha_{ij} x_j \tag{4}$$

We can rewrite the system in matrix form:

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\mathbf{x} \tag{5}$$

Community matrix

$$\frac{d\mathbf{x}}{dt} = \mathbf{A}\mathbf{x}$$

A is the community matrix for the system. **A** is defined as:

$$\mathbf{A}\left[\alpha_{ij}\right] = \left.\frac{\partial f_i}{\partial X_j}\right|_{X_1^*,\ldots,X_n^*}$$

We can rewrite the effects of a perturbation studying the **eigenvalues** of the community matrix:

$$\frac{dx_i}{dt} = \sum_j \gamma_{ij} e^{\lambda_j t} \tag{6}$$

Depending on the sign of the eigenvalues we can classify the equilibrium.

Eigenvalues

Eigenvalues can have real and imaginary parts $\lambda_j = r_j \pm i c_j$. We can classify systems behavior after a perturbation according to the signs of eigenvalues.

r_j	c_j	System Behavior after Perturbation
$< 0,\ \forall j$	$0,\ \forall j$	Stable: returns to the fixed point monotonically.
$< 0,\ \forall j$	$\neq 0,\ \exists j$	Stable: returns to the fixed point with damped oscillations.
$= 0,\ \forall j$	$0,\ \forall j$	Neutrally stable: moves to a new fixed point.
$= 0,\ \forall j$	$\neq 0,\ \exists j$	Neutrally stable: sustained oscillations.
$> 0,\ \forall j$	$0,\ \forall j$	Unstable: moves monotonically away from the fixed point.
$> 0,\ \forall j$	$\neq 0,\ \exists j$	Unstable: moves away with increasing oscillations.

If the eigenvalues of matrix **A** λ_i all have negative real parts, $Re(\lambda_i) < 0\ \forall i$, then the equilibrium X^* is Lyapunov stable: the system will return to the fixed point when perturbed.

A simple example

$$\begin{cases} \frac{dX}{dt} = X\left(1 - \frac{X}{K}\right) - pXY \\ \frac{dY}{dt} = pXY - mY \end{cases}$$

Equilibria

$$\begin{cases} X^* = 0 \\ Y^* = 0 \end{cases} \quad \begin{cases} X^* = K \\ Y^* = 0 \end{cases} \quad \begin{cases} X^* = \frac{m}{p} \\ Y^* = \frac{1}{p}\left(1 - \frac{m}{Kp}\right) \end{cases}$$

A simple example

$$\begin{cases} \frac{dX}{dt} = X\left(1 - \frac{X}{K}\right) - pXY \\ \frac{dY}{dt} = pXY - mY \end{cases}$$

Jacobian

$$\frac{\partial \frac{dX}{dt}}{\partial X} = 1 - \frac{2X}{K} - pY$$

$$\frac{\partial \frac{dX}{dt}}{\partial Y} = -pX$$

$$\frac{\partial \frac{dY}{dt}}{\partial X} = pY$$

$$\frac{\partial \frac{dY}{dt}}{\partial Y} = pX - m$$

A simple example

Jacobian

$$\frac{\partial \frac{dX}{dt}}{\partial X} = 1 - \frac{2X}{K} - pY\bigg|_{X^*,Y^*} = -\frac{m}{Kp}$$

$$\frac{\partial \frac{dX}{dt}}{\partial Y} = -pX\bigg|_{X^*,Y^*} = -m$$

$$\frac{\partial \frac{dY}{dt}}{\partial X} = pY\bigg|_{X^*,Y^*} = 1 - \frac{m}{Kp}$$

$$\frac{\partial \frac{dY}{dt}}{\partial Y} = pX - m\bigg|_{X^*,Y^*} = 0$$

A simple example

Community Matrix

$$\mathbf{C} = \begin{bmatrix} -\frac{m}{Kp} & -m \\ 1-\frac{m}{Kp} & 0 \end{bmatrix}$$

Char Poly

$$Det(\mathbf{C} - \lambda \mathbf{I}) = 0 = \begin{vmatrix} -\frac{m}{Kp} - \lambda & -m \\ 1-\frac{m}{Kp} & -\lambda \end{vmatrix}$$

Char Poly

$$Det(\mathbf{C} - \lambda \mathbf{I}) = 0 = \lambda^2 + \lambda \frac{m}{Kp} + m\left(1 - \frac{m}{Kp}\right)$$

A simple example

Char Poly

$$Det(\mathbf{C} - \lambda \mathbf{I}) = 0 = \begin{vmatrix} -\frac{m}{Kp} - \lambda & -m \\ 1 - \frac{m}{Kp} & -\lambda \end{vmatrix}$$

Char Poly

$$Det(\mathbf{C} - \lambda \mathbf{I}) = 0 = \lambda^2 + \lambda \frac{m}{Kp} + m\left(1 - \frac{m}{Kp}\right)$$

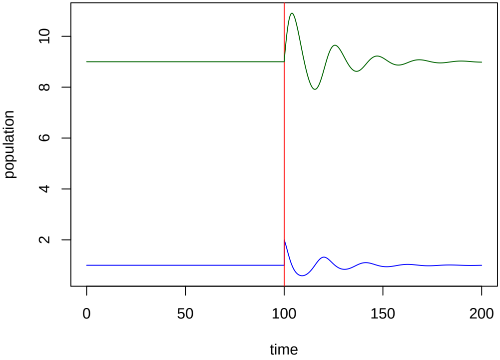
Eigenvalue

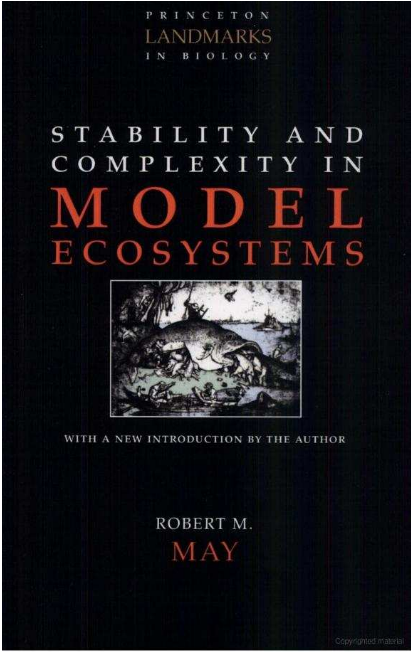
$$\lambda_{1,2} = \frac{-m \pm \sqrt{m^2 + 4Kmp - 4K^2p^2m}}{2Kp}$$

Example: K=10, m=0.1, p=0.1

Eigenvalue

$$\lambda_{1,2} = -0.05 \pm 0.947i$$





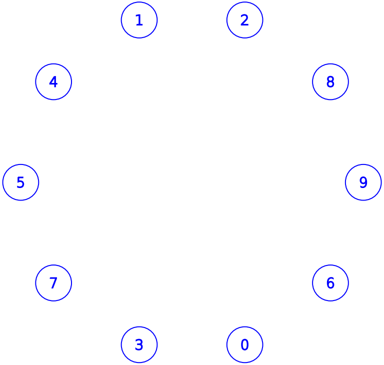
PRINCETON
LANDMARKS
IN BIOLOGY

STABILITY AND
COMPLEXITY IN
MODEL
ECOSYSTEMS

WITH A NEW INTRODUCTION BY THE AUTHOR

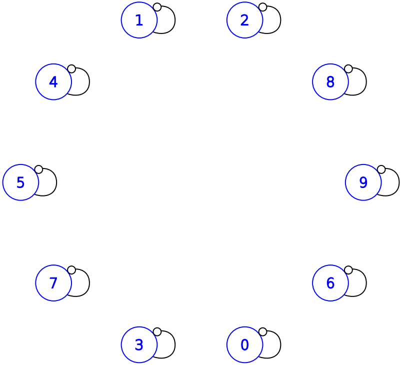
ROBERT M.
MAY

May Argument: Networks



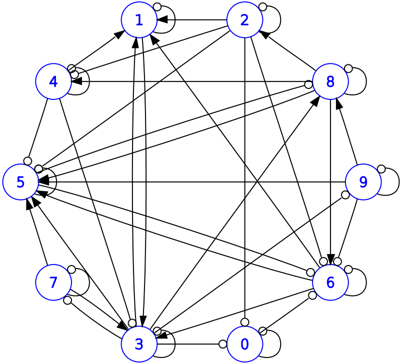
S Species

May Argument: Networks



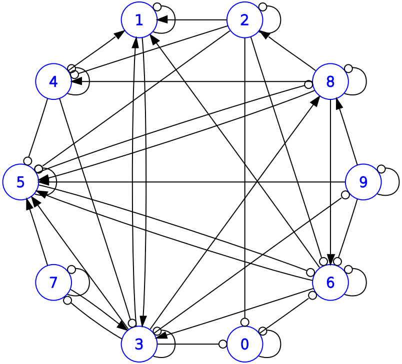
Self Limitation ($m_{ii} < 0$). Dots stand for negative coefficients.
Arrows for positive coefficients.

May Argument: Networks



Two species interact with probability C (Connectance).

May Argument: Networks



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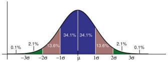


The signs of interaction and interaction strengths are random (Standard Normal Distribution)

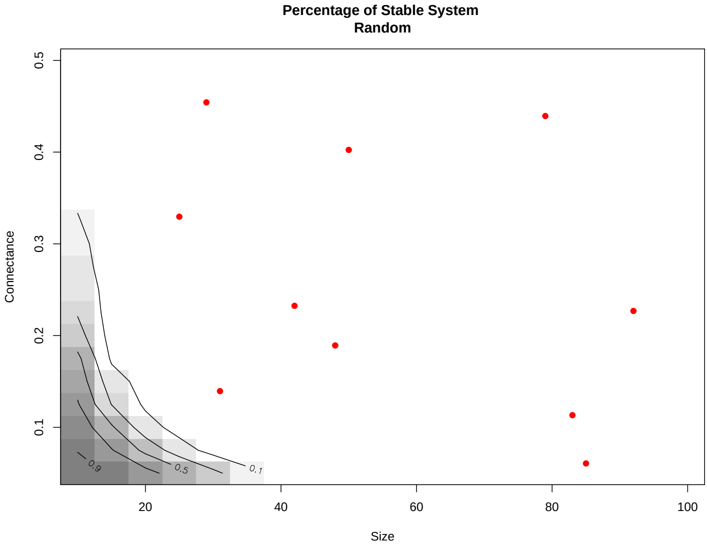
May Argument: Main Result

- Probability of stability → 0 (for large communities) when:

$$\sigma^2\sqrt{SC} > 1$$

- This relation tells us that the probability of stability, for a given variance, tends to 0 when the richness or the connectance of the system are large enough.
- Therefore, according to this argument, we would not expect to observe rich, highly interconnected ecosystems.

May Argument: Main Result - Numeric Simulations



May Argument: Consequences

- This is one of the most influential articles in theoretical ecology.
- The statement that complex, rich systems are unstable has been attacked from different angles (functional responses, persistence, other types of stability).
- Although this work was published in 1972, it is still important for recent papers.

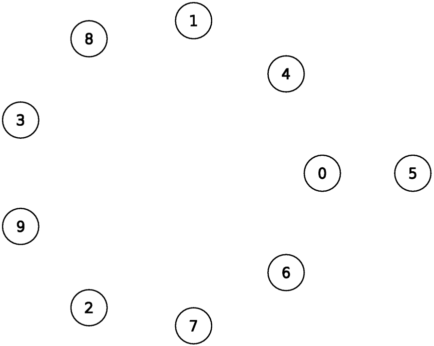
Theor Ecol (2008) 1:55–64
DOI 10.1007/s12080-007-0007-8

ORIGINAL PAPER

Network structure, predator–prey modules, and stability in large food webs

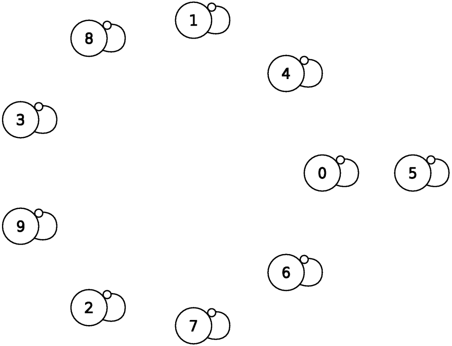
Stefano Allesina · Mercedes Pascual

Predator-Prey: Networks



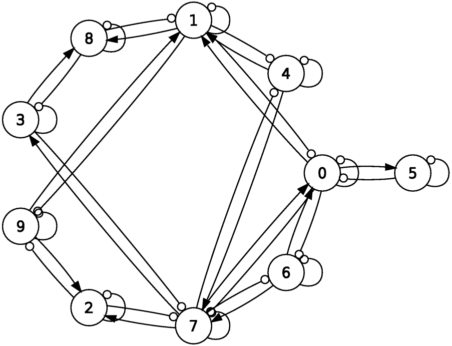
S Species

Predator-Prey: Networks



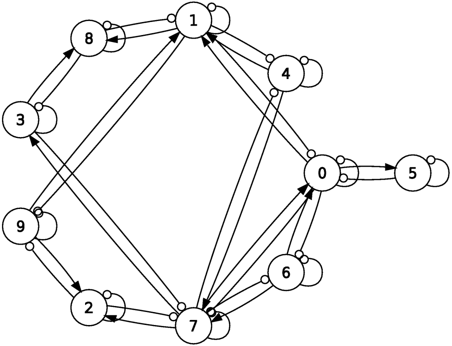
Self Limitation ($m_{ii} < 0$). Dots stand for negative coefficients. Arrows for positive coefficients.

Predator-Prey: Networks

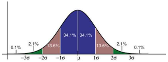


Two species interact with probability $C/2$. The interaction is always predator-prey (+/-). The Connectance is therefore C.

Predator-Prey: Networks

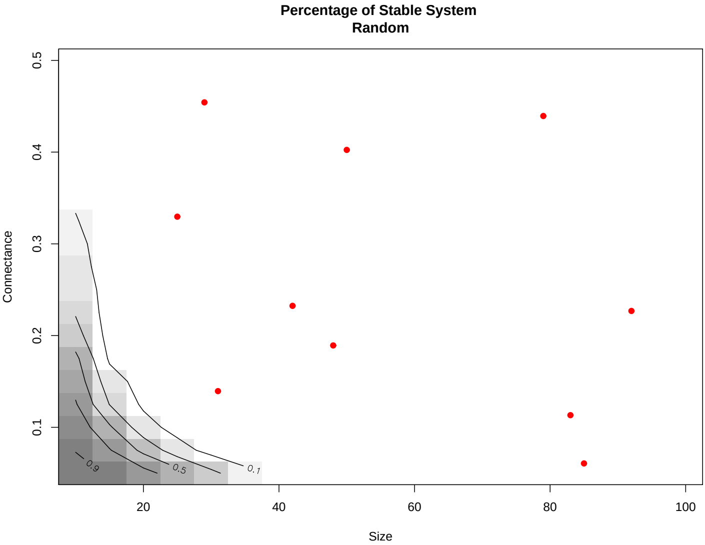


Two species interact with probability $C/2$. The interaction is always predator-prey (+/-). The Connectance is therefore C.

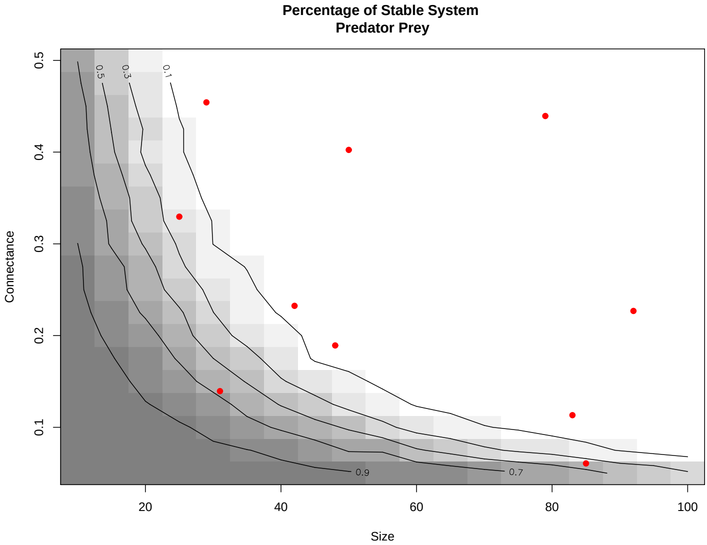


The signs of interaction are fixed, but interaction strengths are random (Standard Normal Distribution).

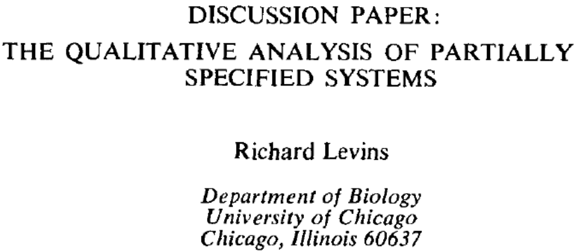
May Argument: Main Result - Numeric Simulations



Predator-Prey - Numeric Simulations



Qualitative Stability



DISCUSSION PAPER:

THE QUALITATIVE ANALYSIS OF PARTIALLY SPECIFIED SYSTEMS

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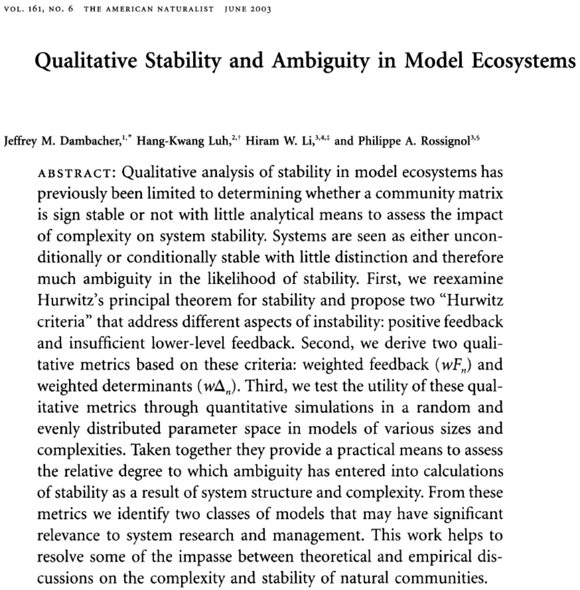
Chicago, Illinois 60637

Qualitative Stability



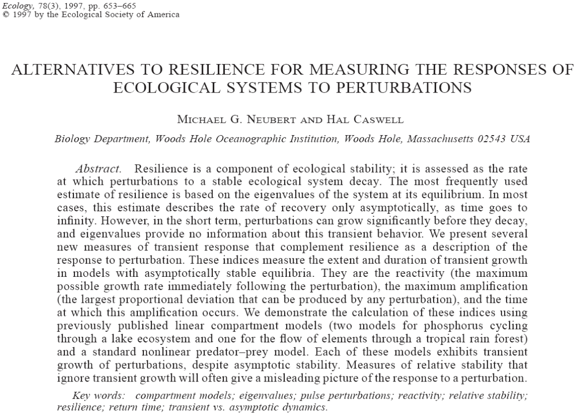
VOL. 161, NO. 6 THE AMERICAN NATURALIST JUNE 2003

Qualitative Stability and Ambiguity in Model Ecosystems

Jeffrey M. Dambacher,[1,*] Hang-Kwang Luh,[2,†] Hiram W. Li,[3,4,‡] and Philippe A. Rossignol[3,§]

ABSTRACT: Qualitative analysis of stability in model ecosystems has previously been limited to determining whether a community matrix is sign stable or not with little analytical means to assess the impact of complexity on system stability. Systems are seen as either unconditionally or conditionally stable with little distinction and therefore much ambiguity in the likelihood of stability. First, we reexamine Hurwitz's principal theorem for stability and propose two "Hurwitz criteria" that address different aspects of instability: positive feedback and insufficient lower-level feedback. Second, we derive two qualitative metrics based on these criteria: weighted feedback (wF_n) and weighted determinants ($w\Delta_n$). Third, we test the utility of these qualitative metrics through quantitative simulations in a random and evenly distributed parameter space in models of various sizes and complexities. Taken together they provide a practical means to assess the relative degree to which ambiguity has entered into calculations of stability as a result of system structure and complexity. From these metrics we identify two classes of models that may have significant relevance to system research and management. This work helps to resolve some of the impasse between theoretical and empirical discussions on the complexity and stability of natural communities.

Alternatives to dominant eigenvalue



Ecology, 78(3), 1997, pp. 653–665

ALTERNATIVES TO RESILIENCE FOR MEASURING THE RESPONSES OF ECOLOGICAL SYSTEMS TO PERTURBATIONS

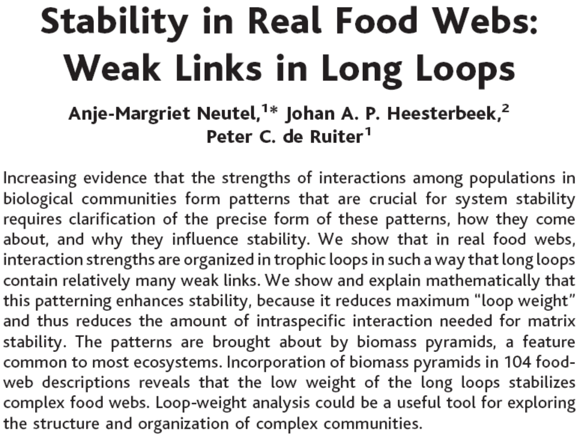
Michael G. Neubert and Hal Caswell

Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 USA

Abstract. Resilience is a component of ecological stability; it is assessed as the rate at which perturbations to a stable ecological system decay. The most frequently used estimate of resilience is based on the eigenvalues of the system at its equilibrium. In most cases, this estimate describes the rate of recovery only asymptotically, as time goes to infinity. However, in the short term, perturbations can grow significantly before they decay, and eigenvalues provide no information about this transient behavior. We present several new measures of transient response that complement resilience as a description of the response to perturbation. These indices measure the extent and duration of transient growth in models with asymptotically stable equilibria. They are the reactivity (the maximum possible growth rate immediately following the perturbation), the maximum amplification (the largest proportional deviation that can be produced by any perturbation), and the time at which this amplification occurs. We demonstrate the calculation of these indices using previously published linear compartment models (two models for phosphorus cycling through a lake ecosystem and one for the flow of elements through a tropical rain forest) and a standard nonlinear predator–prey model. Each of these models exhibits transient growth of perturbations, despite asymptotic stability. Measures of relative stability that ignore transient growth will often give a misleading picture of the response to a perturbation.

Key words: compartment models; eigenvalues; pulse perturbations; reactivity; relative stability; resilience; return time; transient vs. asymptotic dynamics.

Weak interactions



Stability in Real Food Webs: Weak Links in Long Loops

Anje-Margriet Neutel,[1]* Johan A. P. Heesterbeek,[2]
Peter C. de Ruiter[1]

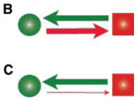
Increasing evidence that the strengths of interactions among populations in biological communities form patterns that are crucial for system stability requires clarification of the precise form of these patterns, how they come about, and why they influence stability. We show that in real food webs, interaction strengths are organized in trophic loops in such a way that long loops contain relatively many weak links. We show and explain mathematically that this patterning enhances stability, because it reduces maximum "loop weight" and thus reduces the amount of intraspecific interaction needed for matrix stability. The patterns are brought about by biomass pyramids, a feature common to most ecosystems. Incorporation of biomass pyramids in 104 food-web descriptions reveals that the low weight of the long loops stabilizes complex food webs. Loop-weight analysis could be a useful tool for exploring the structure and organization of complex communities.

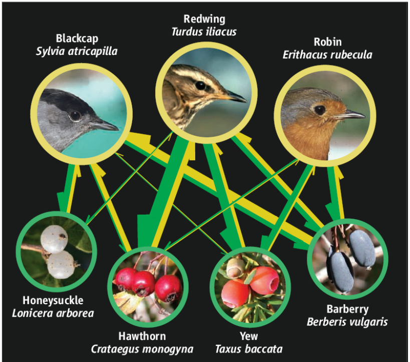
Asymmetric interactions

Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance

Jordi Bascompte,[1]* Pedro Jordano,[1] Jens M. Olesen[2]

The mutualistic interactions between plants and their pollinators or seed dispersers have played a major role in the maintenance of Earth's biodiversity. To investigate how coevolutionary interactions are shaped within species-rich communities, we characterized the architecture of an array of quantitative, mutualistic networks spanning a broad geographic range. These coevolutionary networks are highly asymmetric, so that if a plant species depends strongly on an animal species, the animal depends weakly on the plant. By using a simple dynamical model, we showed that asymmetries inherent in coevolutionary networks may enhance long-term coexistence and facilitate biodiversity maintenance.





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