Lecture 13 – Eigenvalues

Concepts:

- n-spp. stability
- eigenvalues & complex numbers
- Determinant, Traces & Routh-Hurwitz criteria
- Touch on Complexity vs. Stability debate

Matrix Algebra & Conventions

$\mathbf{A}$ - matrix (bold) $\quad$ $\vec{w}$ - vector (italicized) $\quad$ A_{ij} or w_i - scalars

$\begin{bmatrix} a \\ b \end{bmatrix}$ - column vector $\quad$ $\begin{bmatrix} a & b \end{bmatrix}$ - row vector

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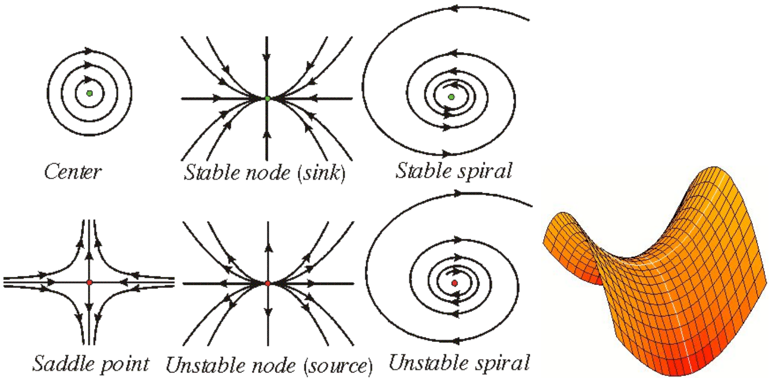
Why do eigenvalues indicate stability properties?

Eigenvalues (λ_i)	**Interpretation**
$Re(\lambda_i) < 0$ for all i	Stable point attractor
$Re(\lambda_i) < 0$ for some i	Saddle node (repellor-attractor) ('unstable')
$Re(\lambda_i) > 0$ for all i	Unstable point repellor
$Re(\lambda_i) = 0$ for all i	Neutrally stable
$Im(\lambda_i) = 0$ for all i	No oscillations
$Im(\lambda_i) \neq 0$ for some i	Oscillations



Recall:

$$f_1(u_1^* + x, u_2^* + y) \approx \underbrace{\left.\frac{\partial f_1}{\partial u_1}\right|_{u_1^*,u_2^*}}_{A_{11}} \cdot x + \underbrace{\left.\frac{\partial f_1}{\partial u_2}\right|_{u_1^*,u_2^*}}_{A_{12}} \cdot y$$

and

$$f_2(u_1^* + x, u_2^* + y) \approx \underbrace{\left.\frac{\partial f_2}{\partial u_1}\right|_{u_1^*,u_2^*}}_{A_{21}} \cdot x + \underbrace{\left.\frac{\partial f_2}{\partial u_2}\right|_{u_1^*,u_2^*}}_{A_{22}} \cdot y$$

Therefore, if x and y are small, can approximate dynamics of perturbation as:

$$\frac{dx}{dt} = A_{11} \cdot x + A_{12} \cdot y$$
$$\frac{dy}{dt} = A_{21} \cdot x + A_{22} \cdot y$$

In matrix form:

$$\underbrace{\begin{bmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{bmatrix}}_{\frac{d\vec{n}}{dt}} = \underbrace{\begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix}}_{\mathbf{A}} \cdot \underbrace{\begin{bmatrix} x \\ y \end{bmatrix}}_{\vec{n}}$$

or equivalently

$$\frac{d\vec{n}}{dt} = \mathbf{A} \cdot \vec{n}$$

Side note:
Matrix addition:

$$\begin{bmatrix} a & b \\ c & d \end{bmatrix} + \begin{bmatrix} e & f \\ g & h \end{bmatrix} = \begin{bmatrix} a+e & b+f \\ c+g & d+h \end{bmatrix}$$

Matrix multiplication:

$$\begin{bmatrix} a & b \\ c & d \end{bmatrix} \cdot \begin{bmatrix} e & f \\ g & h \end{bmatrix} = \begin{bmatrix} a \cdot e + b \cdot g & a \cdot f + b \cdot h \\ c \cdot e + d \cdot g & c \cdot f + d \cdot h \end{bmatrix}$$

In ***R*** use **A % * % B** for matrix multiplication (i.e. dot product).

The default is element-wise multiplication (Hadmard product).

Recall integration of single-spp exponential growth model:

$$\frac{dN}{dt} = rN \qquad \Rightarrow \qquad N(t) = \int_0^t \frac{dN}{dt} dt = N(0)\, e^{rt}$$

$r < 0 \Rightarrow$ decay.
$r > 0 \Rightarrow$ increase.

Represent dynamics of perturbation is same way.
For i^{th} perturbation:

$$\frac{dn_i}{dt} = A_{i\cdot} \cdot n_i \qquad \Rightarrow \qquad n_i(t) = n_i(0)\, e^{A_{i\cdot} t}$$

... or for both perturbations:

$$\vec{n}_t = \vec{n}_0\, e^{\mathbf{A}t}$$

But $e^{\mathbf{A}}$ is e^{matrix} which is not possible!

But what if we could replace matrix **A** with some constant – call it λ.
That would require that:

$$\boxed{\mathbf{A}\vec{w} = \lambda\vec{w}}$$

Vector $\vec{w}$ the **right eigenvector** of **A**.
$\vec{w}$ is a column vector.

Side-note (since we won't actually use this fact)
The **left eigenvector** comes from:

$$\vec{v}\mathbf{A} = \vec{v}\lambda$$

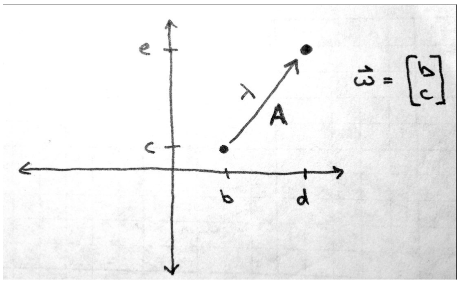
$\vec{v}$ is a row vector.

What is an eigenvalue?

Can think of both any matrix A and its associated eigenvalues λ as equivalent transformation operations,

...like a multiplication by a 'slope' or 'direction'.

For example,



That is, if we let $\mathbf{A} = \begin{bmatrix} a_1 & a_2 \\ a_3 & a_4 \end{bmatrix}$ and $\vec{w} = \begin{bmatrix} b \\ c \end{bmatrix}$.

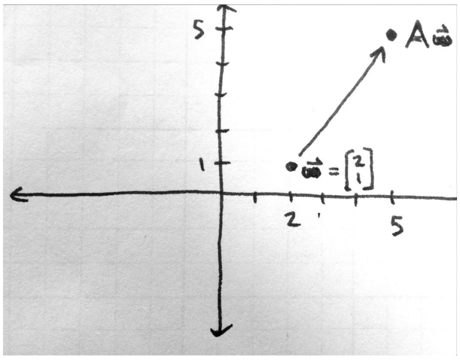
Then:

$$\mathbf{A}\vec{w} = \begin{bmatrix} a_1 & a_2 \\ a_3 & a_4 \end{bmatrix} \cdot \begin{bmatrix} b \\ c \end{bmatrix} = \begin{bmatrix} a_1 b + a_2 c \\ a_3 b + a_4 c \end{bmatrix} = \begin{bmatrix} d \\ e \end{bmatrix}$$

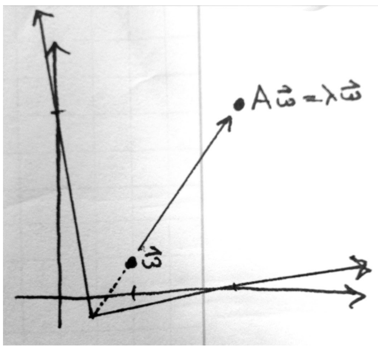
$$\lambda\vec{w} = \lambda \begin{bmatrix} b \\ c \end{bmatrix} = \begin{bmatrix} \lambda b \\ \lambda c \end{bmatrix} = \begin{bmatrix} d \\ e \end{bmatrix}$$

Numerical example:

Start at $\vec{w} = \begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} 2 \\ 1 \end{bmatrix}$ and $\mathbf{A} = \begin{bmatrix} 2 & 1 \\ 1 & 3 \end{bmatrix}$ $\Rightarrow$ $\begin{bmatrix} 2 & 1 \\ 1 & 3 \end{bmatrix} \cdot \begin{bmatrix} 2 \\ 1 \end{bmatrix} = \begin{bmatrix} 4+1 \\ 2+3 \end{bmatrix} = \begin{bmatrix} 5 \\ 5 \end{bmatrix}$



We can do the same thing with λ by defining a new coordinate system:



How do we determine what λ is?
Need to solve:

$$\mathbf{A}\vec{w} = \lambda\vec{w} \qquad \Rightarrow \qquad \mathbf{A}\vec{w} - \lambda\vec{w} = 0$$

First we have to write λ in matrix form using **Identity matrix**:

$$\lambda\mathbf{I} = \lambda \cdot \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} = \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix}$$

Thus:

$$\begin{aligned} \mathbf{A}\vec{w} - \lambda\vec{w} &= 0 \\ (\mathbf{A} - \lambda\mathbf{I})\vec{w} &= 0 \end{aligned}$$

Thus the solution is either

$$\vec{w} = 0 \qquad \text{or} \qquad (\mathbf{A} - \lambda\mathbf{I}) = 0$$

Not interested in $\vec{w} = 0$, but solving $(\mathbf{A} - \lambda\mathbf{I}) = 0$ isn't any easier than what we started with!
However,

$$det(\mathbf{A} - \lambda\mathbf{I}) = 0$$

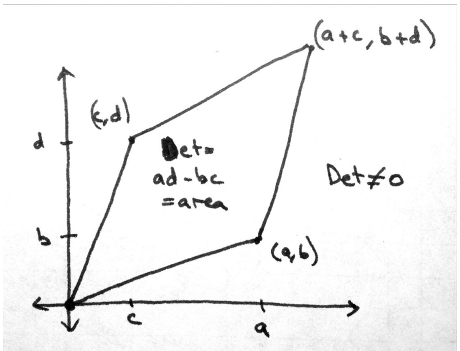
gives us a way to solve it.

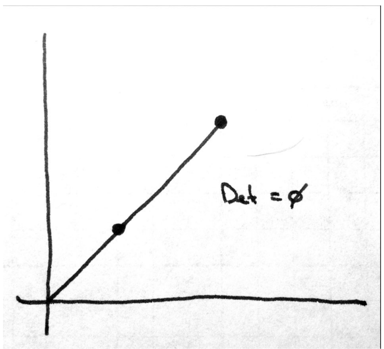
What is a matrix determinant?

$$det\left(\begin{bmatrix} a & b \\ c & d \end{bmatrix}\right) = ad - bc$$

$$det\left(\begin{bmatrix} a & b & c \\ d & e & f \\ g & h & i \end{bmatrix}\right) = aei + bfg + cdh - ceg - fha - ibd$$

Graphical interpretation of the determinant is as a *volume* (or *area* for 2x2 matrices):





$$det\left(\begin{bmatrix} 2 & 1 \\ 1 & 3 \end{bmatrix}\right) = 2 \cdot 3 - 1 \cdot 1 = 5 \qquad det\left(\begin{bmatrix} 2 & 1 \\ 4 & 2 \end{bmatrix}\right) = 2 \cdot 2 - 4 \cdot 1 = 0$$

Back to solving for eigenvalues
If λ is just a scaling factor, then the volume of $\mathbf{A} - \lambda\mathbf{I}$ must equal 0.

$$\begin{aligned} 0 &= det(\mathbf{A} - \lambda\mathbf{I}) \\ &= det\left(\begin{bmatrix} A_{11} - \lambda & A_{12} \\ A_{21} & A_{22} - \lambda \end{bmatrix}\right) \\ &= (A_{11} - \lambda)(A_{22} - \lambda) - A_{12}A_{12} \\ &= \underbrace{\lambda^2 - (A_{11} + A_{22})\lambda + A_{11}A_{22} - A_{12}A_{21}}_{\text{Characteristic equation}} \end{aligned}$$

$\Rightarrow$ Solve for λ_i's by solving the **characteristic equation**.

Solve for λ using quadratic formula:

$$ax^2 + bx + c = 0 \qquad \Rightarrow \qquad x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

By defining... (*yes, this is confusing, but it's how it's done in the literature*)

$$\lambda^2 - \underbrace{(A_{11} + A_{22})}_{\mathrm{A}_1}\lambda + \underbrace{A_{11}A_{22} - A_{12}A_{21}}_{\mathrm{A}_2}$$

That is: $\mathrm{A}_1 = A_{11} + A_{22}$ and $\mathrm{A}_2 = A_{11}A_{22} - A_{12}A_{21}$

...we have $a = 1$, $b = -\mathrm{A}_1$ and $c = \mathrm{A}_2$.

$$1 \cdot \lambda^2 + (-\mathrm{A}_1)\lambda + \mathrm{A}_2 = 0 \qquad \Rightarrow \qquad \begin{cases} \lambda_1 = \frac{\mathrm{A}_1 + \sqrt{(-\mathrm{A}_1)^2 - 4\mathrm{A}_2}}{2} \\ \lambda_2 = \frac{\mathrm{A}_1 - \sqrt{(-\mathrm{A}_1)^2 - 4\mathrm{A}_2}}{2} \end{cases}$$

The two solutions to λ are called a **complex conjugate pair**, or **complex conjugate roots** (=soltns.).

Compare to single-sp. model

For 1-sp. model we used the sign of the slope $\frac{d\,f(N)}{dN}$ to infer stability:

$$\frac{d\,f(N)}{dN} < 0 \quad \Rightarrow \quad \text{stable} \qquad \text{vs.} \qquad \frac{d\,f(N)}{dN} > 0 \quad \Rightarrow \quad \text{unstable}$$

Now we're saying that it's the eigenvalues of $\mathbf{A}$ that matter, not the slopes themselves.
But remember that the eigenvalues reflect the partial derivative slopes $\frac{\partial\, f_i(\vec{N})}{\partial N_j}$.
They reflect the same transformation of the perturbation.

In fact, for a 1-sp. model they are exactly the same:

$$\mathbf{A}\vec{w} = \lambda\vec{w} \qquad \Leftrightarrow \qquad \frac{d\,f(N)}{dN} \cdot w = \lambda \cdot w \qquad \Rightarrow \qquad \frac{d\,f(N)}{dN} = \lambda$$

How do Complex numbers arise?

$$\lambda = \frac{\mathrm{A}_1 \pm \sqrt{(-\mathrm{A}_1)^2 - 4\mathrm{A}_2}}{2}$$

When $(-\mathrm{A}_1)^2 < 4\mathrm{A}_2 \quad \Rightarrow \quad \frac{1}{2}(\mathrm{A}_1 \pm \sqrt{\text{negative}})$
But how do we take the $\sqrt{\ }$ of a negative number?
$\Rightarrow$ Imaginary unit i.

$$\boxed{\text{Define } i^2 = -1}$$

$$\begin{aligned} &\sqrt{-\#} &= \sqrt{-1 \cdot \#} &= \sqrt{i^2\#} &= i\sqrt{\#} & \\ \text{e.g.,}\quad &\sqrt{-4} &= \sqrt{-1 \cdot 4} &= \sqrt{i^2 4} &= i\sqrt{4} &= 2i \end{aligned}$$

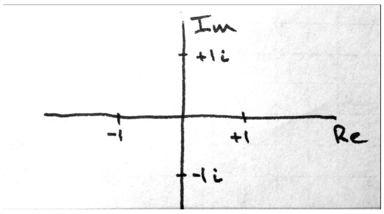
$$\lambda = \underbrace{\tfrac{1}{2}\mathrm{A}_1}_{\text{Real}} \pm \underbrace{\tfrac{1}{2}\sqrt{(-\mathrm{A}_1)^2 - 4\mathrm{A}_2}\; i}_{\text{imaginary}}$$

There is nothing 'imaginary' about imaginary numbers! They're as 'real' as negative numbers!
Real numbers are just counts or fractional counts
(= easy to think about as an amount of something).
Can you imagine how much an amount of -10 is? No!
Negative counts don't exist. They're a mathematical convenience to subtract amounts.
Imaginary numbers exist as much as negative numbers do!
They're a mathematical convenience to allow taking roots of negative numbers.

In order to solve... we invented...

$$\begin{aligned} x-5=0 &\quad\Rightarrow\quad \text{Integers (Real numbers)} \\ x+5=0 &\quad\Rightarrow\quad \text{Negative integers (Real numbers)} \\ 2x=1 &\quad\Rightarrow\quad \text{Rational numbers (fractions, quotients of integers)} \\ x^2=2 &\quad\Rightarrow\quad \text{Irrational numbers (can't be expressed as fractions, e.g., } \sqrt{2}, \pi, e) \\ x^2=-1 &\quad\Rightarrow\quad \text{Imaginary numbers.} \end{aligned}$$

Think about imaginary numbers as representing a different number dimension:



Why do imaginary parts indicate oscillations?
Remember that λ represents dynamics of the perturbation:

$$\vec{n}_t = \vec{n}_0 e^{\lambda t}$$

With a complex part:

$$\vec{n}_t = \vec{n}_0 e^{(a \pm bi)t} = e^{at} \cdot e^{ibt}$$

From the theory of complex numbers:

$$\begin{aligned} e^{i\Theta} &= \cos\Theta + i\sin\Theta \\ e^{-i\Theta} &= \cos\Theta - i\sin\Theta \end{aligned}$$

Thinking of bt as Θ gives:

$$e^{ibt} = \cos(bt) + \sin(bt)$$

Thus:

$$e^{(a \pm bi)t} = e^{at} \cdot [\cos(bt) \pm \sin(bt)]$$

Therefore, a controls stability

$$\begin{aligned} a<0 \Rightarrow &\quad \text{oscillations will dampen} \\ a>0 \Rightarrow &\quad \text{oscillations will amplify} \\ a=0 \Rightarrow &\quad \text{neutral stability with cycles} \end{aligned}$$

And b controls the *frequency* of the oscillations.

Back to Biology: Classifying steady states
For 2x2 system:

$$\lambda^2 - \underbrace{(A_{11} + A_{22})}_{\mathrm{A}_1}\lambda + \underbrace{A_{11}A_{22} - A_{12}A_{21}}_{\mathrm{A}_2}$$

For nxn-species system:

$$\lambda^n - \mathrm{A}_1\lambda^{n-1} + ... + (-1)\mathrm{A}_n = 0$$

For 3x3: $\mathrm{A}_n = \mathrm{A}_3$. That is, there's a conjugate pair and a 3rd λ.

For 2x2:

$$\begin{aligned} \mathrm{A}_1 = A_{11} + A_{22} &\quad=\quad \textbf{Trace} \quad=\quad \sum A_{ii} \\ \mathrm{A}_2 = A_{11}\cdot A_{22} - A_{12}\cdot A_{21} &\quad=\quad \textbf{Determinant} \quad=\quad Det(\mathbf{A}) \end{aligned}$$

Therefore, we could either evaluate all the λ's (i.e. if $\lambda_i < 0\ \forall i$) $\Rightarrow$ stable system or use **Routh-Hurwitz stabiliy criteria**

Provide *biological insight* (not possible using just λ's)

Trace($\mathbf{A}$) $< 0 \quad \Rightarrow \quad A_{11} + A_{22} < 0$ is necessary for stability

$\Rightarrow$ *At least some species must be strongly self-limiting for stability* $\Leftarrow$

Det($\mathbf{A}$) $> 0 \quad \Rightarrow \quad A_{11}A_{22} - A_{12}A_{21} > 0$ is necessary for stability

$\Rightarrow$ *Overall self-limitation must be stronger then interspecific effects for stability* $\Leftarrow$

$\Rightarrow$ *Intra ¿ inter-specific effects* $\Leftarrow$

Each condition by itself is *necessary, but not sufficient.*

$$\lambda = \frac{1}{2}\mathrm{Tr}(\mathbf{A}) \pm \frac{1}{2}\sqrt{(-\mathrm{Tr}(\mathbf{A}))^2 - 4 \cdot \mathrm{Det}(\mathbf{A})}\; i$$

Whichever parts of $\sqrt{\ }$ is bigger determines with or without oscillations.
Bifurcation occurs at $(-\mathrm{Tr}(\mathbf{A}))^2 = 4 \cdot \mathrm{Det}(\mathbf{A})$.