# Lecture 16 – Press perturbations

**Concepts:**

- Formalize pulse vs. press perturbations
- Community matrix vs. Interaction matrix
- Net Effects matrix (direct, indirect, vs. net effects)

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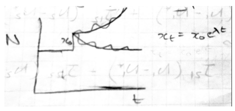
So far dealing explicitly with pulse perturbations:

Q was: How will system respond?

*Pulse* - 'instantaneous', one-time acute change in population size (or factor affecting growth rates)

Watched how system, including perturbed spp., responded.



⇒ Empirically relevant for invasibility or pulse-like disturbances

(Note importance of spp. generation time)

**Today:** *Press* perturbations

(Often-misused term by empiricists)

Chronic, sustained change in growth rate or abundance

e.g., continuous addition/removal of individuals at a constant rate

e.g., change in parameters contributing to $\frac{dN}{dt}$

Not species removal!

Will assume:

(1) Equilibrium coexistence before and after

(2) No species goes extinct

(3) No bifurcations crossed (e.g., no Hopf bifurcation to limit cycles)

⇒ Sufficiently small perturbations between nearby fixed point equilibria

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**Review Jacobian and Taylor expansion**

For 1-sp.:

$$\frac{dN}{dt} = F(N) = N \cdot f(N) \qquad f \text{ can be highly nonlinear}$$

Approximate $F(N)$ with 1st-order Taylor expansion around $N^*$.

$$F(N^* + x_0) = F(N^* + (N - N^*)) = F(N^*) + \frac{F'(N^*)}{1!}(N - N^*) + h.o.t.$$

Since by definition $F(N^*) = 0$ & ignoring $h.o.t.$...

$$\approx F'(N^*)(N - N^*) = F'(N^*)x_0 = \left.\frac{d\frac{dN}{dt}}{dN}\right|_{N^*} \cdot x_0 = \lambda x_0$$

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For 2-spp.:

$$\frac{dN_1}{dt} = F_1(N_1, N_2) \qquad \frac{dN_2}{dt} = F_2(N_1, N_2)$$

Taylor expansion around $(N_1^*, N_2^*)$...

$$\begin{aligned} F_1(N_1 + x, N_2 + y) = \cancelto{0}{F_1(N_1^*, N_2^*)} &+ F_1'(N_1^*)(N_1 - N_1^*) + ... \\ &... + F_1'(N_2^*)(N_2 - N_2^*) + h.o.t. \\ &\approx \underbrace{\left.\frac{\partial F_1}{\partial N_1}\right|_{(N_1^*, N_2^*)}}_{A_{11}}(N_1 - N_1^*) + \underbrace{\left.\frac{\partial F_1}{\partial N_2}\right|_{(N_1^*, N_2^*)}}_{A_{12}}(N_2 - N_2^*) \\ &\approx A_{11}(N_1 - N_1^*) + A_{12}(N_2 - N_2^*) \end{aligned}$$

Similarly for 2nd species:

$$F_1(N_1 + x, N_2 + y) \approx A_{21}(N_1 - N_1^*) + A_{22}(N_2 - N_2^*)$$

Thus in general for $S$ species:

$$F_i(\vec{N} + \vec{n}) \approx \sum_{k=1}^{S} A_{ik}(N_k - N_k^*)$$

And in matrix form:

$$F(\vec{N} + \vec{n}) \approx \mathbf{A}\vec{n} \qquad \text{where } \vec{n_i} = N_i - N_i^*$$

Vector $\vec{n}$ = pulse perturbations - one-time additions/subtractions
$\Rightarrow$ eigenvalues, trace, determinant $\Rightarrow$ *asymptotic stability* etc.

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**Press perturbations**
Assume we're starting at fixed-point coexistence steady state $\vec{N}^*$ and add chronic perturbation to $N_1$:

$$\frac{dN_1}{dt} = F_1(\vec{N}^*) + P_1 \qquad \frac{dN_2}{dt} = F_2(\vec{N}^*)$$

$P_1$ = adding $P$ individuals of $N_1$ **per time**
(will show later that parameters of $F_1(\vec{N})$ can also be changed)

Assume system will come to a new steady state, $N^{**}$

$\Rightarrow$ Taylor expand $F_1(\vec{N}^*)$ around $N^{**}$

$$F_1(\vec{N}^{**} + (\vec{N}^* - \vec{N}^{**})) \approx \cancelto{0}{F_1(N^{**})} + P_1 + A_{21}(N_1^* - N_1^{**}) + A_{22}(N_2^* - N_2^{**})$$

= 0 assuming new system is at steady state

Therefore, rearranging:

$$-P_1 = \sum_{k=1}^{S} A_{ik}(N_k^* - N_k^{**})$$

In matrix form, adding $P_i$ for each $i^{th}$ species:

$$-\mathbf{I} \cdot \vec{P} = \mathbf{A} \cdot \vec{n}^*$$

$$-\begin{bmatrix} P_1 & 0 \\ 0 & P_2 \end{bmatrix} = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix} \underbrace{\begin{bmatrix} N_1^* - N_1^{**} \\ N_2^* - N_2^{**} \end{bmatrix}}_{\text{Our interest}}$$

Want to know how much $i^{th}$ species $N_i^*$ change given a press perturbation $P_j$ to species $j$?

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Can't divide by a matrix. Use **Matrix inverse**!
By def., $\mathbf{A} \cdot \mathbf{A}^{-1} = \mathbf{I}$ Example:

$$\begin{bmatrix} 7 & 8 \\ 6 & 7 \end{bmatrix} \cdot \begin{bmatrix} ? & ? \\ ? & ? \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

$$\begin{bmatrix} 7 & 8 \\ 6 & 7 \end{bmatrix} \cdot \begin{bmatrix} w & x \\ y & z \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

Corresponds to 4 equations with 4 unknowns. $\Rightarrow$ solvable!

$$7w + 8y = 1$$
$$7x + 8z = 0$$
$$6w + 7y = 0$$
$$6x + 7z = 1$$

$$\begin{bmatrix} 7 & 8 \\ 6 & 7 \end{bmatrix} \cdot \begin{bmatrix} 7 & -8 \\ -6 & 7 \end{bmatrix} = \begin{bmatrix} 49 - 48 & 56 - 56 \\ 42 - 42 & -48 + 49 \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$$

In **R**: *solve*(A) or *ginv*(A) from MASS package
In Mathematica: *Inverse*[A] or use *Solve*

Thus rewrite:

$$\begin{aligned}
\mathbf{A} \cdot \vec{n}^* &= -\mathbf{I} \cdot \vec{P} \\
\mathbf{A} \cdot \vec{n}^* &= -\mathbf{A}^{-1}\mathbf{A} \cdot \vec{P} \\
\vec{n}^* &= -(\mathbf{A}^{-1}) \cdot \vec{P}
\end{aligned}$$

$$n_i^* = -\sum_{k=1}^{S} (\mathbf{A}^{-1})_{ik} \cdot P_j$$

Or derived in terms of derivatives

$$\frac{\partial N_i^*}{\partial p_j} = -\sum_{k=1}^{S} (\mathbf{A}^{-1})_{ik} \cdot \frac{\partial F_k}{\partial p_j}$$

Example in 3-spp. system:

$$\frac{\Delta N_1^*}{P_2} = -\underbrace{\begin{bmatrix} A_{11}^{(-1)} & A_{12}^{(-1)} & A_{13}^{(-1)} \\ \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot \end{bmatrix}}_{\mathbf{A}^{-1}} \cdot \begin{bmatrix} O \\ P_2 \\ 0 \end{bmatrix} = -\mathbf{A}_{12}^{(-1)} \cdot P_2$$

Elements of $-(\mathbf{A}^{-1})$ specify the **Net effect** resulting from all direct and indirect effect pathways.
Net effect of column $j$ on row $i$. Contrast to Jacobian.
Multiple perturbations at once: Add columns...

$$\frac{\Delta N_1^*}{P_2 \text{ and } P_3} = -\mathbf{A}_{12}^{(-1)} \cdot P_2 \; + \; -\mathbf{A}_{13}^{(-1)} \cdot P_3$$

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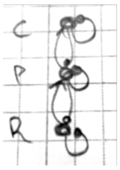
**Trophic Cascade**
Build some intuition for what's going on.

***Self-limitation in all species***



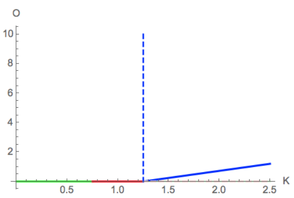

Predict perturbation to $\Rightarrow$ will cause:

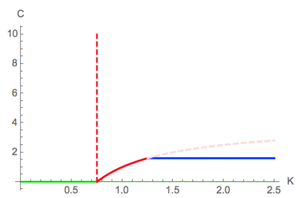
$$\begin{array}{cccc}
 & R & P & C \\
R & \Rightarrow\uparrow & \downarrow & \uparrow \\
P & \uparrow & \Rightarrow\uparrow & \downarrow \\
C & \uparrow & \uparrow & \Rightarrow\uparrow
\end{array}$$

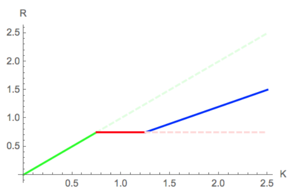
$\Rightarrow$ Mathematica

$$\mathbf{A} = \begin{bmatrix} -1 & -1 & 0 \\ 1 & -1 & -1 \\ 0 & 1 & -1 \end{bmatrix} \quad \Rightarrow \quad -\mathbf{A}^{-1} = \begin{bmatrix} 2/3 & -1/3 & 1/3 \\ 1/3 & 1/3 & -1/3 \\ 1/3 & 1/3 & 2/3 \end{bmatrix}$$ matches all predictions!

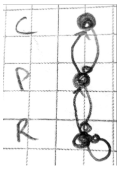
But what did we observe in class last time as a function of $K$?



***Self-limitation in basal species only***




$\Rightarrow$ Mathematica

$$\mathbf{A} = \begin{bmatrix} -1 & -1 & 0 \\ 1 & 0 & -1 \\ 0 & 1 & 0 \end{bmatrix} \qquad \Rightarrow \qquad -\mathbf{A^{-1}} = \begin{bmatrix} 1 & 0 & 1 \\ 0 & 0 & -1 \\ 1 & 1 & 1 \end{bmatrix} \qquad \text{matches all predictions!}$$

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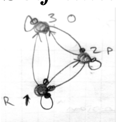
**Symbolic Inverse of Trophic chain**

Look at how net effects emerge from pairwise direct effects

***Self-limitation in all species***




$\Rightarrow$ Mathematica

$$\mathbf{A} = \begin{bmatrix} -A_{11} & -A_{12} & 0 \\ A_{21} & -A_{22} & -A_{23} \\ 0 & A_{32} & -A_{33} \end{bmatrix} \qquad \Rightarrow$$

$$\mathbf{A^{-1}} = \begin{bmatrix} \frac{A_{23}A_{32}+A_{22}A_{33}}{det(\mathbf{A})} & -\frac{A_{12}A_{33}}{det(\mathbf{A})} & \frac{A_{12}A_{23}}{det(\mathbf{A})} \\ \frac{A_{21}A_{33}}{det(\mathbf{A})} & \frac{A_{11}A_{33}}{det(\mathbf{A})} & -\frac{A_{11}A_{23}}{det(\mathbf{A})} \\ \frac{A_{21}A_{32}}{det(\mathbf{A})} & \frac{A_{11}A_{32}}{det(\mathbf{A})} & \frac{A_{12}A_{21}+A_{11}A_{22}}{det(\mathbf{A})} \end{bmatrix}$$

$$det(\mathbf{A}) = -A_{11}A_{23}A_{32} - A_{12}A_{21}A_{33} - A_{11}A_{22}A_{33}$$

Thus

$$-\mathbf{A}^{-1} = \frac{adj(\mathbf{A})}{-det(\mathbf{A})}$$

Things to notice:

- **Determinant** is common to all elements of $\mathbf{A}^{-1}$ $\Rightarrow$ measure of community sensitivity
- **Classical adjoint matrix** reflects *magnitude and direction* of species-specific responses.
- Species responses depend on both *inter-* and *intra-* specific direct effects.

e.g., How Resource responds to Intermediate consumer depends on $A_{12}$ *times* $A_{33}$.

Sp2 will affect Sp1 only if Sp3 doesn't increase in abundance and eat more of Sp2!

e.g., How Resource responds to positive press of itself is affected by self-limitation of both consumers.

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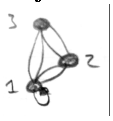
**Symbolic Inverse of IGP**

***Self-limitation basal species***




$\Rightarrow$ Mathematica

$$\mathbf{A} = \begin{bmatrix} -A_{11} & -A_{12} & -A_{13} \\ A_{21} & 0 & -A_{23} \\ A_{31} & A_{23} & 0 \end{bmatrix} \qquad \Rightarrow$$

$$adj(\mathbf{A}) = \begin{bmatrix} A_{23}A_{23} & -A_{13}A_{23} & A_{12}A_{23} \\ -A_{23}A_{31} & A_{13}A_{31} & \boxed{-A_{13}A_{21} - A_{11}A_{23}} \\ A_{21}A_{23} & \boxed{A_{11}A_{23} - A_{12}A_{31}} & A_{12}A_{21} \end{bmatrix}$$

Things to notice:

- Responses of Omnivore to IGPrey, and of IGPrey to Omnivore are **qualitatively indeterminate**.

...depend on quantitative interaction strength values.

...in particular the strength of *intraspecific self-limitation in the* ***Resource!***

Net effects matrix is potentially very powerful if we can estimate *'interaction strengths'*.
Gonna skip lecture on 'Interaction strengths' to talk about 'Tipping points & Early-warning signals',
but do want to clear up confusion that's pervasive in the literature regarding three common terms:

$$\text{'The Jacobian'} \quad \Leftrightarrow \quad \text{'The Community Matrix'}$$
$$\text{'The Community Matrix'} \quad \Leftrightarrow \quad \text{'The Interaction Matrix'}$$

Using LV-pred prey model as example

**Population growth rates**

$$\frac{dR}{dt} = F_R = R(b - aC)$$
$$\frac{dC}{dt} = F_C = C(eaR - d)$$
$$\mathbf{A}_{ij} = \frac{\partial F_i}{\partial N_j}$$

**Community matrix**
(is a Jacobian)

$$= \begin{bmatrix} b - aC^* & -aR^* \\ eaC^* & eaR^* - d \end{bmatrix}$$
$$= \begin{bmatrix} 0 & -aR^* \\ eaC^* & 0 \end{bmatrix}$$

Use this for stability analysis.
Remember: $F_R(R^*, C^*) = F_C(R^*, C^*) = 0$
...making rest of analysis possible.

$-\mathbf{A}^{-1} \Rightarrow$ perturbation of popn growth rates.

**Per capita growth rates**

$$\frac{1}{R}\frac{dR}{dt} = f_R = b - aC$$
$$\frac{1}{C}\frac{dC}{dt} = f_C = eaR - d$$
$$\mathbf{A}_{ij} = \frac{\partial f_i}{\partial N_j}$$

**Interaction matrix**
(is a Jacobian)

$$= \begin{bmatrix} 0 & -a \\ ea & 0 \end{bmatrix}$$

Doesn't have same stability properties.
But, if 'D-Stable'$\Rightarrow$ Community matrix also stable.

$-\mathbf{A}^{-1} \Rightarrow$ perturb of per capita growth rates.

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Press perturbation (Perturbation of per capita growth rate):

$$\frac{1}{N_1}\frac{dN_1}{dt} = f_1(\vec{N}^*) + p_1 \qquad \frac{1}{N_2}\frac{dN_2}{dt} = f_2(\vec{N}^*)$$

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Press perturbation of population sizes!
$\Rightarrow$ *Normalized Net Effects matrix*

$$\hat{\mathbf{A}}^{-1} = \frac{A_{ij}^{(-1)}}{A_{ii}^{(-1})} = \frac{\frac{\partial N_i^*}{\partial p_j}}{\frac{\partial N_j^*}{\partial p_j}} = \frac{\partial N_i^*}{\partial N_j^*}$$

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