Lecture 16 – Press perturbations

Concepts:

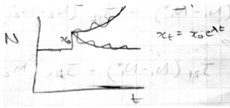
- Formalize pulse vs. press perturbations
- Community matrix vs. Interaction matrix
- Net Effects matrix (direct, indirect, vs. net effects)

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 $\frac{dN}{dt}$

e.g., change in abundance of focal species (held to new abundance)

No complete species removals!

Will assume:

(1) Fixed point 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.:

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

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 $h.o.t.$...

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

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:

$$F_2(N_1 + x, N_2 + y) \approx A_{21}(N_1 - N_1^*) + A_{22}(N_2 - N_2^*)$$

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:

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

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

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**

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

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

$$F_1(\vec{N}^{**} + (\vec{N}^* - \vec{N}^{**})) \approx \cancelto{0}{F_1(N^{**})} + P_1 + A_{11}(N_1^* - N_1^{**}) + A_{12}(N_2^* - N_2^{**})$$

= 0 assuming new system is at steady state

Therefore, rearranging and generalizing to include S species:

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

In matrix form,

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

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

Want to know how much i^{th} species N_2 changes given a press perturbation P_j to species $j = 1$?

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!

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

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

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

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 and a perturbation p_j of any kind:

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

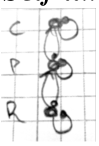
Example in 3-spp. system:

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

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...

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

Trophic Cascade - Build some intuition for what's going on.
Self-limitation in all species



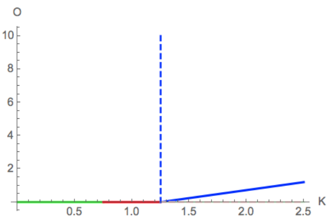
Predict perturbation to $\Rightarrow$ will cause:

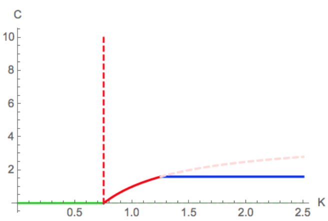
$$\begin{array}{cccc} & R & P & C\\ R & \Rightarrow\uparrow & \downarrow & \uparrow\\ P & \uparrow & \Rightarrow\uparrow & \downarrow\\ C & \uparrow & \uparrow & \Rightarrow\uparrow\end{array}$$

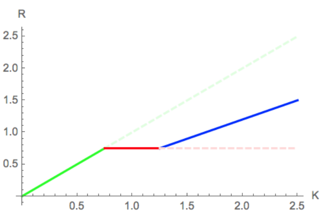
$\Rightarrow$ Mathematica

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

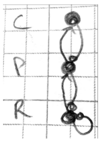
But what did we observe in class last time as a function of K?







Self-limitation in basal species only



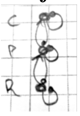
⇒ Mathematica

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

Symbolic Inverse of Trophic chain

Look at how net effects emerge from pairwise direct effects

Self-limitation in all species



⇒ Mathematica

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

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

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

Thus

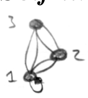
$$-\mathbf{A}^{-1} = -\frac{adj(\mathbf{A})}{det(\mathbf{A})}$$

Things to notice:
Determinant is common to all elements of $\mathbf{A}^{-1}$ ⇒ 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 $A_{12} \times A_{33}$.
Resource will affect Consumer only if Top Predator doesn't increase in abundance and eat more Consumers!
e.g., How Resource responds to positive press of itself is affected by self-limitation of both predators!

Symbolic Inverse of IGP

Self-limitation basal species



⇒ Mathematica

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

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

Things to notice:
Responses of Omnivore to IConsumer, and of IConsumer 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)

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

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.

Press perturbation of *per capita* growth rate starts with:

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

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

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