# Pulses, Presses, and Nonlinear Response


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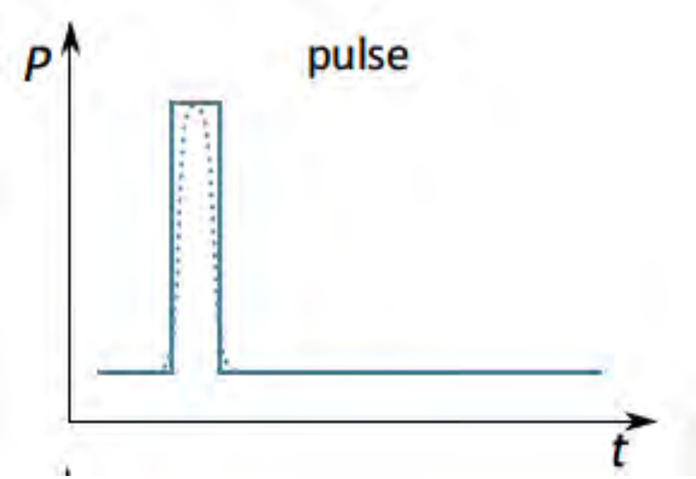


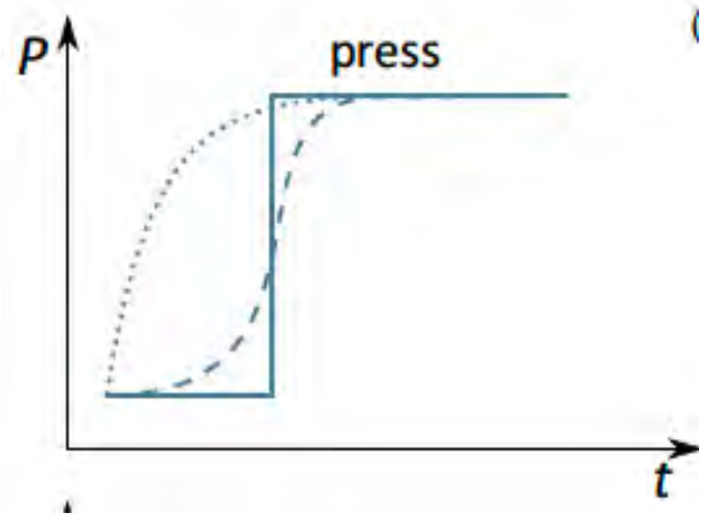



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RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES
Essay Review
Journal of Ecology


**Unifying the concepts of stability and resilience in ecology**


Koenraad Van Meerbeek[1,2,3] | Tommaso Jucker[4] | Jens-Christian Svenning[2,3]

# PRESS vs. PULSE ?

Simplest thing:

*A PRESS*

*IS JUST*

*A CONTINUED SERIES OF PULSES*

Structured Population Model (LINEAR!)

$$n(t+1) = B\,n(t)$$

Discrete time t
Population vector n(t)
Non-negative Matrix B

$u$ ***S***(table) ***S***(tage) ***D***(istribution)

$\lambda_0$ Long-run Growth Rate = Dominant Eigenvalue

$v$ ***S***(table) ***R***(eproductive) ***V***(alue)

$$B\,u = \lambda_0\,u$$

$$v^T\,B = \lambda_0\,v^T$$

NON-STABLE STAGE DISTRIBUTION $\widehat{u} \longrightarrow u$ SSD AS TIME GOES BY

$$Q_0 = u\,v^T$$

STABLE PART

UNSTABLE PART

$$Q_1 = \left(\frac{B}{\lambda_0} - Q_0\right)$$

$$\boxed{\left(\frac{B}{\lambda_0}\right) = Q_0 + Q_1}$$

*ADD!*

ANY NON-STABLE STAGE DISTRIBUTION CAN BE DECOMPOSED

Stable Bit

UNStable Bit

$$\widehat{u} = k\, u + u_{\perp},$$

$$Q_0\, u_{\perp} = [u\, v^T]\, u_{\perp} = 0$$

Perpendicular

$$\left(\frac{B^t}{\lambda_0^t}\right) \widehat{u} = ku + Q_1^t\, u_{\perp}$$

POPULATION DYNAMICS

TRANSIENT PART

PULSE!

START AT SSD,

PULSE AT t=0

ENDS AT t=1

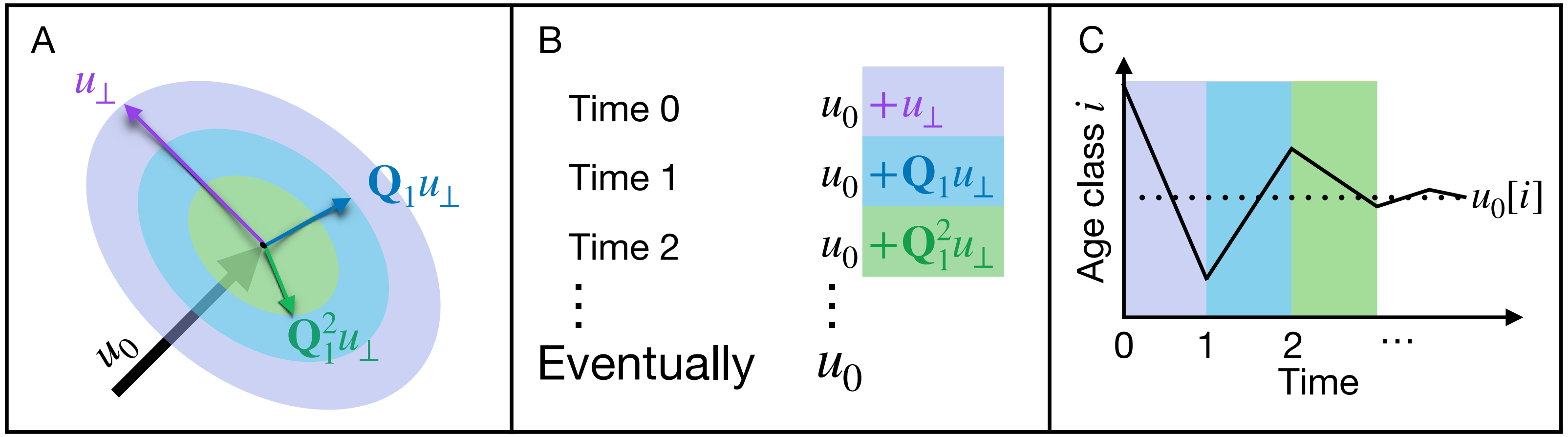
$$B \to B + D$$

ONLY for *one period*

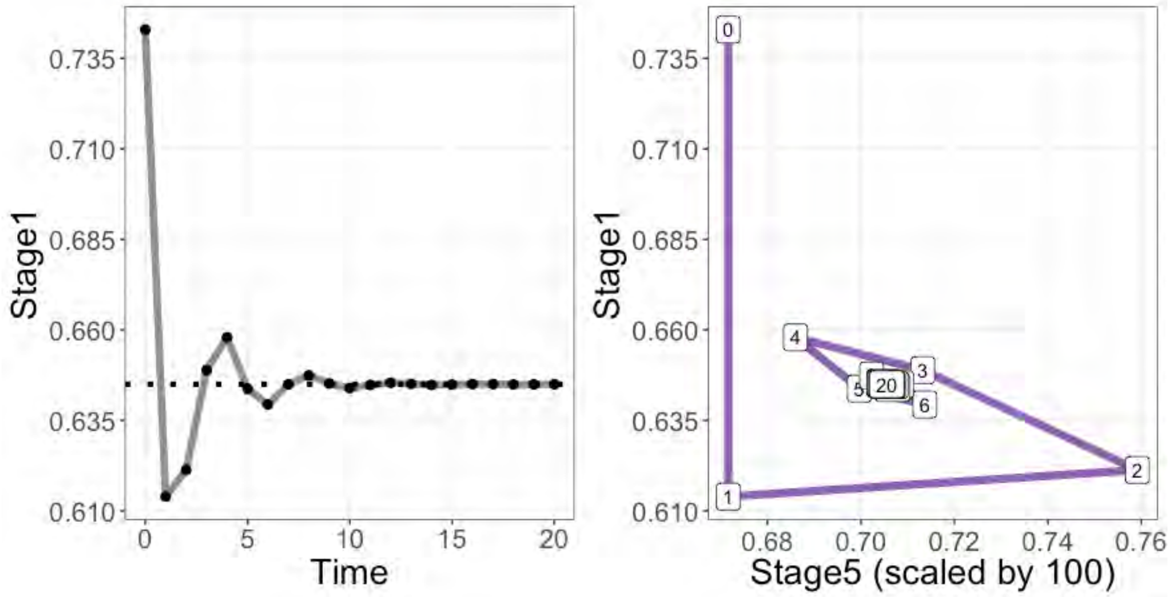
start with NOT-STABLE POPULATION AT t=1

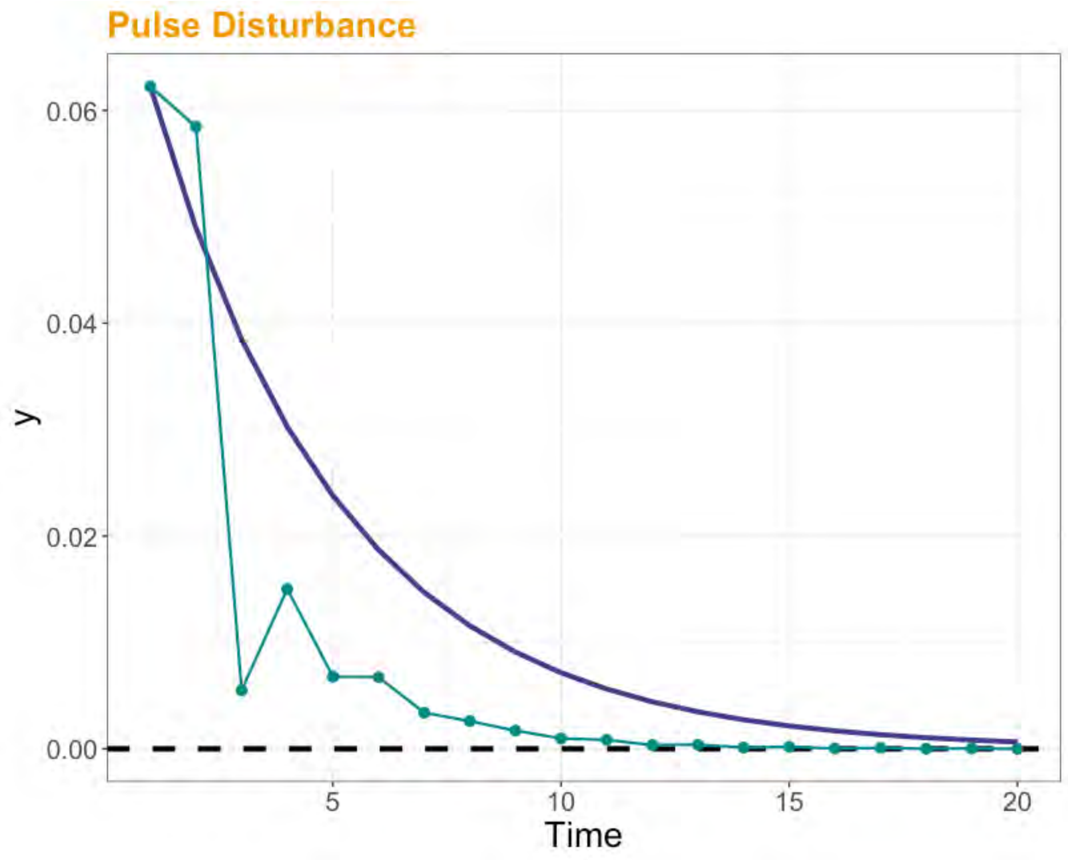
$$u(1) = k\,u + u_\perp$$

$$u(t+1) = k\,u + Q_1^t\,u_\perp$$


A
$u_\perp$
$\mathbf{Q}_1 u_\perp$
$\mathbf{Q}_1^2 u_\perp$
$u_0$
B
Time 0 $u_0 + u_\perp$
Time 1 $u_0 + \mathbf{Q}_1 u_\perp$
Time 2 $u_0 + \mathbf{Q}_1^2 u_\perp$
Eventually $u_0$
C
Age class $i$
$u_0[i]$
0
1
2
…
Time

## Pulse Disturbance




Pulse Disturbance
0.06
0.04
0.02
0.00
y
5
10
15
20
Time

PRESS!

START AT SSD,
PULSE AT t=0, 1, 2, ...
DOES NOT END

$$B \to B + \epsilon D$$

for *ever*

Known: long-run growth rate changes to

$$\mu = \lambda_0 + \epsilon \left(v^T D u\right)$$

Start with SSD at t=0

$$N(0) = u$$

A pulse at time t=0

$$\frac{N(1)}{\mu} = u + z^*$$

The added bit is PERPENDICULAR

$$z^* = (I - Q_0)\frac{D}{\lambda_0}u$$

Another pulse at time t=1

$$\frac{n(2)}{\mu^2} = u + z^* + Q_1\, z^*$$

and so on ...

Yet another pulse at time t-1

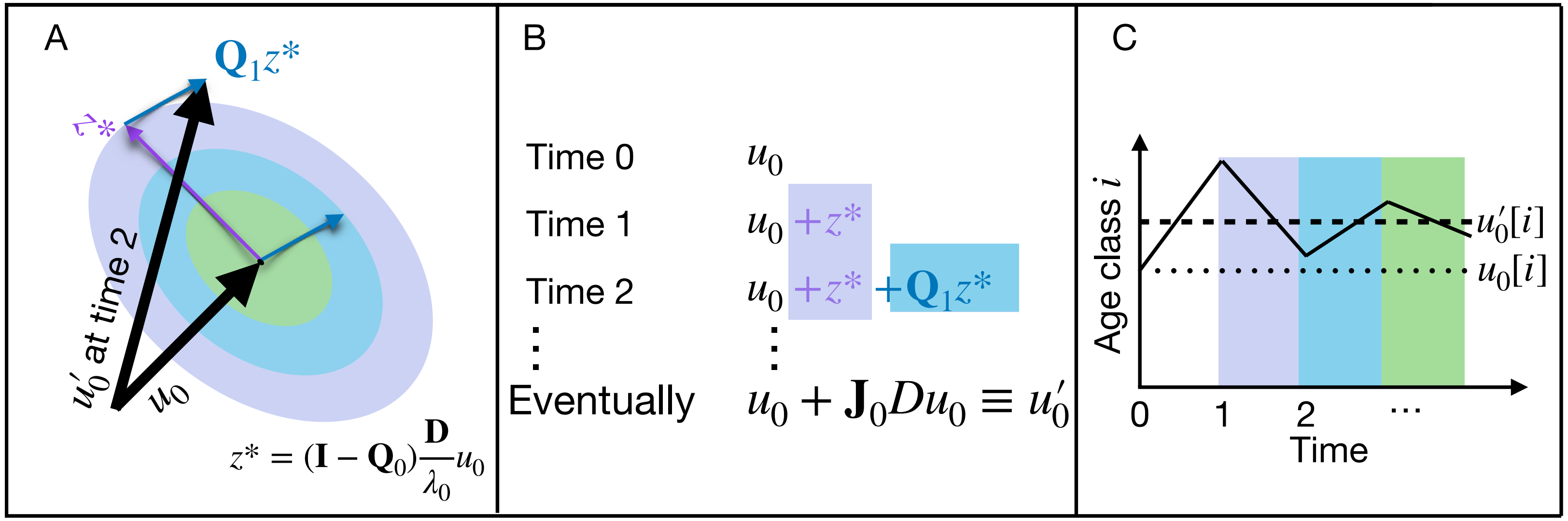
$$\frac{n(t)}{\mu^t} = u + z^* + Q_1\, z^* + \cdots + Q_1^{t-1}\, z^*$$

EFFECT OF PRESS = CUMULATIVE EFFECT OF REPEATED PULSES

$$J_0 = \frac{1}{\lambda_0} (I - Q_1)^{-1} (I - Q_0)$$

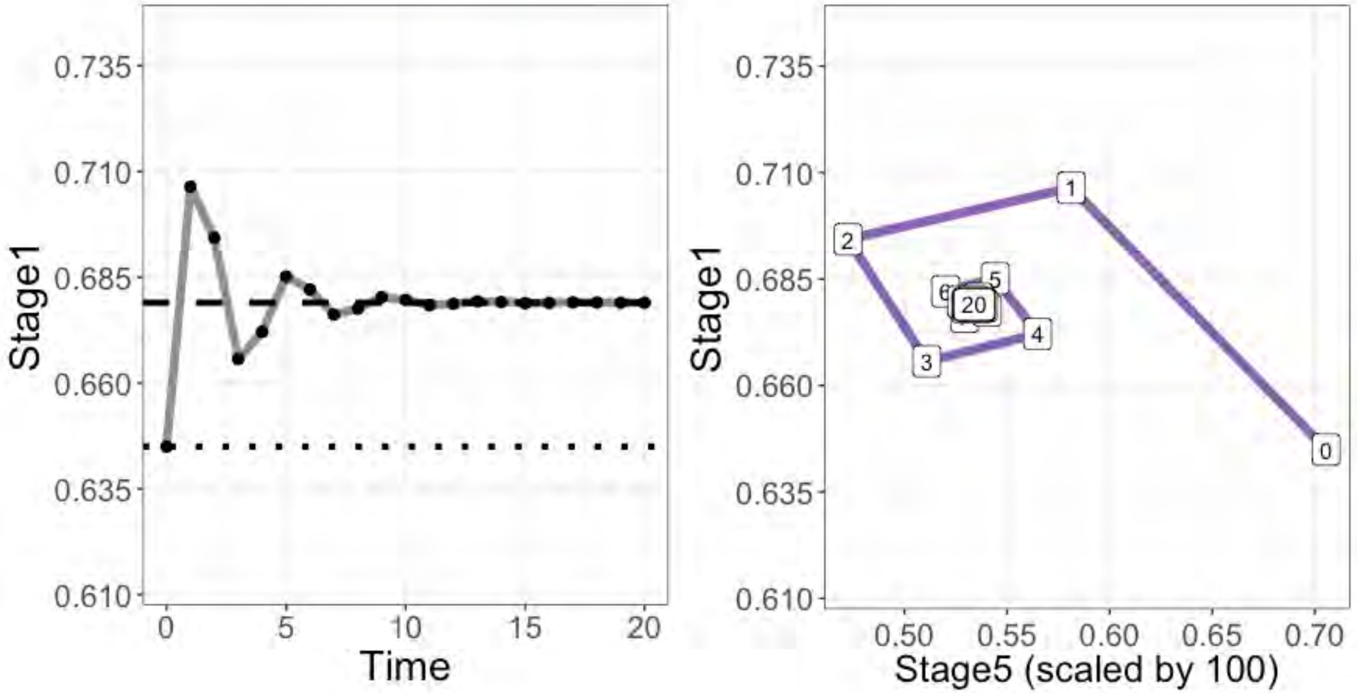
EFFECT OF PRESS: FINAL POPULATION STRUCTURE

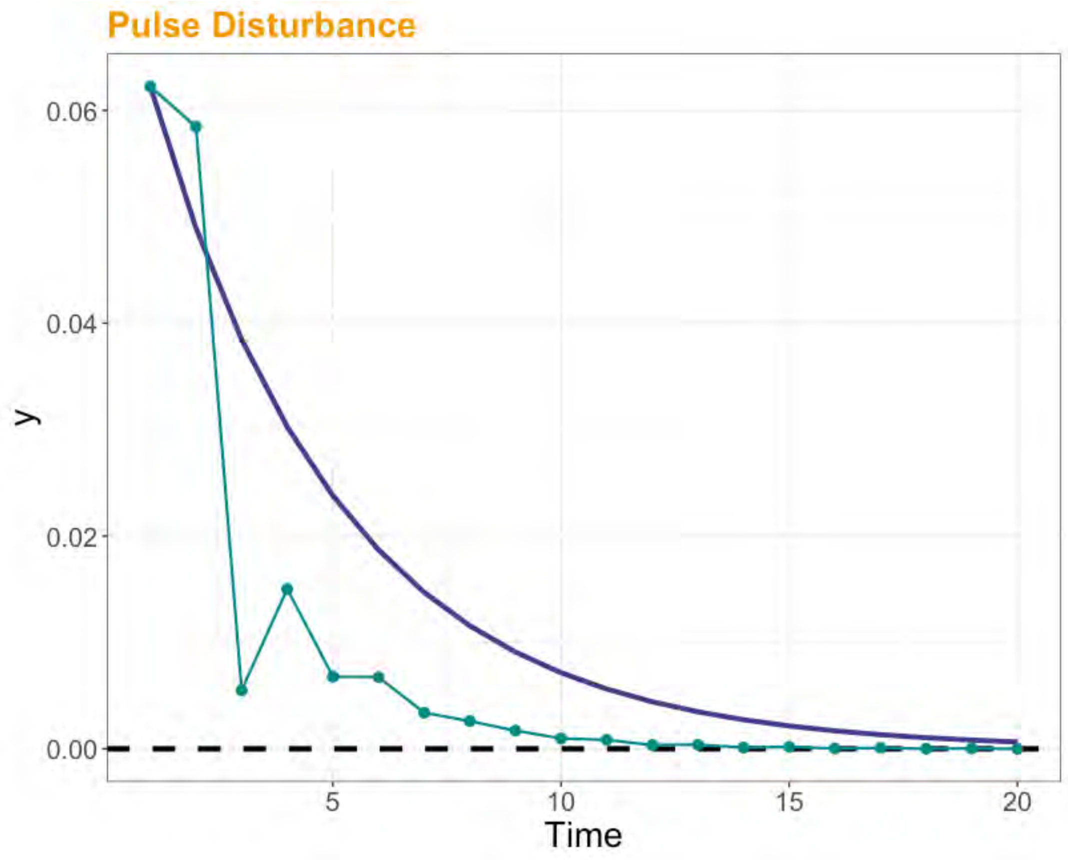
$$u + J_0 \, D \, u$$



A
$\mathbf{Q}_1 z^*$
$z^*$
$u_0'$ at time 2
$u_0$
$z^* = (\mathbf{I} - \mathbf{Q}_0)\frac{\mathbf{D}}{\lambda_0}u_0$
B
Time 0
Time 1
Time 2
Eventually
$u_0$
$u_0 + z^*$
$u_0 + z^* + \mathbf{Q}_1 z^*$
$u_0 + \mathbf{J}_0 D u_0 \equiv u_0'$
C
Age class $i$
$u_0'[i]$
$u_0[i]$
0
1
2
…
Time

# Press Disturbance




Pulse Disturbance
0.06
0.04
0.02
0.00
y
5
10
15
20
Time

DENSITY-DEPENDENT MODELS WITH ONE EQUILIBRIUM: ***ONE*** OR ***MANY*** SPECIES

MODEL

$$n(t+1) = A(\theta, n)\, n(t)$$

EQUILIBRUM

$$A(\theta, n^*) \equiv A^*$$
$$n^* = A^*\, n^*$$

LOCALLY STABLE

$$n(t) = n^* + \epsilon y(t)$$
$$y(t+1) = [A^* + \widehat{C}]\, y(t)$$

PULSE

$$\theta \;\to\; \theta + \epsilon\,\phi$$

NEW
EQUILIBRIUM

$$n^* + \epsilon x^*$$

$$x^* = \{I - [A + \widehat{C}]\}^{-1}\,\widetilde{C} n^*$$

Measures

$$P(t,n) = \int dm\, K(n|m)\, P(t-1,m)$$

$$P(t) = L[P(t-1)]$$

$$P^* = L[P^*]$$

P* IS LOCALLY STABLE!