Invasion speed and LTRE analysis in stochastic environments

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Everything Disperses to Miami
## Invasion speed

<table>
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<th>Structured populations</th>
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\[
\bar{c}^* = \min_s \left\{ \frac{1}{s} \lim_{T \to \infty} \frac{1}{T} \log \|H_T(s) \cdots H_1(s)w\| \right\} \]
Structured integrodifference equation

\[
n(x, t + 1) = \int_{-\infty}^{\infty} \left( K_t(x - y) \circ B_t[n(y, t)] \right) n(y, t) \, dy,
\]

and its linearization

\[
n(x, t + 1) = \int_{-\infty}^{\infty} \left( K_t(x - y) \circ A_t \right) n(y, t) \, dy.
\]
Invasion speed

\[ c^* = \min_{s > 0} \left( \frac{1}{s} \log \rho(s) \right) \]

where \( \rho(s) \) is a growth-rate, based on both demographic and dispersal information.

\[ H(s) = A \circ M(s) \]
Invasion speed: constant environments

Moment-generating matrix $\mathbf{M}(s)$:

$$m_{ij}(s) = \int_{-\infty}^{\infty} k_{ij}(x) e^{sx} \, dx$$

Define:

$$\mathbf{A} = \mathbf{B}(0)$$

$$\mathbf{H}(s) = \mathbf{A} \circ \mathbf{M}(s)$$

$$\rho(s) = \text{largest eigenvalue of } \mathbf{H}(s)$$

Invasion speed:

$$c^* = \min_s \left\{ \frac{1}{s} \ln \rho(s) \right\}$$

Neubert and Caswell 2000
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= \min_s \left\{ \frac{1}{s} \lim_{T \to \infty} \frac{1}{T} \log \|H_T(s) \cdots H_1(s)w\| \right\}$ |


Sensitivity analysis: general

Let

\[ \theta = \text{parameter vector} \]

Sensitivity of \( c^* \)

\[
\frac{dc^*}{d\theta^T} = \frac{1}{s^*} \frac{d\log \rho}{d\theta^T}.
\]

Elasticity of \( c^* \)

\[
\frac{\epsilon c^*}{\epsilon \theta^T} = \left( \frac{1}{c^*} \right) \frac{dc^*}{d\theta^T} \mathcal{D}(\theta)
\]

where \( \mathcal{D}(\theta) \) is a matrix with \( \theta \) on the diagonal
Sensitivity analysis: constant environment

\[ \rho(s^*) = \max \text{eig} \mathbf{H}(s^*) \]

Let \( \mathbf{w} \) and \( \mathbf{v} \) be the right and left eigenvectors of \( \mathbf{H}(s^*) \)

\[
\frac{d \log \rho}{d \theta^T} = \frac{1}{\rho} \left( \mathbf{w}^T \otimes \mathbf{v}^T \right) \frac{d \text{vec} \mathbf{H}(s^*)}{d \theta^T}
\]

\[
\frac{d \text{vec} \mathbf{H}(s^*)}{d \theta^T} = \mathcal{D}(\text{vec} \mathbf{A}) \frac{d \text{vec} \mathbf{M}(s^*)}{d \theta^T} + \mathcal{D}(\text{vec} \mathbf{M}(s^*)) \frac{d \text{vec} \mathbf{A}}{d \theta^T}
\]
Sensitivity analysis: periodic environment

\[ c^* = \min_s \left( \frac{1}{s} \log \rho_{\text{per}}(s) \right) \]

\[ \rho_{\text{per}} = \max \text{ eig} \left( H_p \cdots H_1 \right) \]

\[ \frac{d \log \rho_{\text{per}}}{d \theta^T} = \left( \frac{w^T \otimes v^T}{\rho_{\text{per}}} \right) \sum_{i=1}^{p} \frac{\partial \text{ vec } H}{\partial \text{ vec }^T H_i} \left. \frac{d \text{ vec } H_i}{d \theta^T} \right|_{\theta=\theta_i}, \]

with

\[ \frac{\partial \text{ vec } H}{\partial \text{ vec }^T H_i} = \begin{cases} I \otimes (H_p \cdots H_2) & i = 1 \\ (H_{i-1} \cdots H_1)^T \otimes (H_p \cdots H_{i+1}) & 1 < i < p \\ (H_{p-1} \cdots H_1)^T \otimes I & i = p \end{cases} \]
Sensitivity analysis: stochastic environment

\[
\log \rho_{\text{stoch}} = \lim_{T \to \infty} \frac{1}{T} \log \| H_{T-1}(s) \cdots H_0(s) w \|
\]

Tuljapurkar’s formula

\[
\frac{d \log \rho_{\text{stoch}}}{d \theta^T} = \frac{1}{T} \sum_{i=0}^{T-1} \frac{[w^T(i) \otimes v^T(i+1)]}{R_i v^T(i+1) w(i+1)} \frac{d \text{vec} H_i}{d \theta^T}
\] (1)
Retrospective perturbation analysis

Goal: to decompose differences among “treatments” into contributions from effects on each of the parameters defining the problem.

(a)

Treatment $i$\rightarrow Vital rates $\theta^{(i)}$\rightarrow Growth rate $\lambda$

(b)

Treatment $i$\rightarrow Environmental dynamics $P^{(i)}$\rightarrow Growth rate log $\lambda_s$

\begin{align*}
\text{Vital rate response } & \Theta = \{\theta_1, \ldots, \theta_k\} \\
\end{align*}
SENSITIVITY ANALYSIS OF THE STOCHASTIC GROWTH RATE: THREE EXTENSIONS

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Determinants of invasion speed

- environmental states $1, \ldots, k$
- environmental state dynamics

\[ P = \Pr (u(t + 1) = i | u(t) = j) \]

- demographic responses

\[ A_1, \ldots, A_k \]

- dispersal responses

\[ \alpha_1, \ldots, \alpha_k \]
Decomposing differences

\[
\begin{align*}
\text{treatment 1:} & \quad \{ \mathbf{P}^{(1)}, \mathbf{A}_1^{(1)}, \ldots, \mathbf{A}_k^{(1)}, \alpha_1^{(1)}, \ldots, \alpha_k^{(1)} \} \quad \rightarrow \quad c^{*(1)} \\
\text{treatment 2:} & \quad \{ \mathbf{P}^{(2)}, \mathbf{A}_1^{(2)}, \ldots, \mathbf{A}_k^{(2)}, \alpha_1^{(2)}, \ldots, \alpha_k^{(2)} \} \quad \rightarrow \quad c^{*(2)}
\end{align*}
\]
LTRE: the basic idea

\[ y_1 = y(\theta_1) \]
\[ y_2 = y(\theta_2) \]

Then

\[ y_2 - y_1 \approx \frac{dy}{d\theta^\intercal} (\theta_2 - \theta_1) \]

Contributions:

\[ C(\theta) = \left( \frac{dy}{d\theta^\intercal} \right)^\intercal \circ (\theta_2 - \theta_1) \]
Environment-specific sensitivity

Indicator variable

\[ J_t(h) = \begin{cases} 
1 & u(t) = h \\
0 & \text{otherwise} 
\end{cases} \]

\[
\left. \frac{dc^*}{d\theta^T} \right|_{u=h} = \frac{1}{s^*} \left. \frac{d \log \rho_{\text{stoch}}}{d\theta^T} \right|_{u=h}
\]

\[ = \frac{1}{s^*} \sum_{i=0}^{T-1} J_i(h) \left[ w^T(i) \otimes v^T(i + 1) \right] \frac{d \text{vec} H_i}{d\theta^T} \]
Environment-specific sensitivities

Use this to get

\[
\frac{dc^*}{d\text{vec}^\top A} \bigg|_{u=h} \quad \text{and} \quad \frac{dc^*}{d\alpha^\top} \bigg|_{u=h}
\]

for \( h = 1, \ldots, k \).

But what about contributions from the environment \((P)\)?
Suppose

\[ c^{*}(1) = c^{*}[a, b] \]
\[ c^{*}(2) = c^{*}[A, B]. \]

Then

\[ C(A - a) = \frac{1}{2} (c^{*}[A, B] - c^{*}[a, B]) \]
\[ + \frac{1}{2} (c^{*}[A, b] - c^{*}[a, b]) \]

\[ C(B - b) = \frac{1}{2} (c^{*}[A, B] - c^{*}[A, b]) \]
\[ + \frac{1}{2} (c^{*}[a, B] - c^{*}[a, b]). \]
Decomposition of effect of environmental dynamics

Let $\Theta$ be the combination of demographic and dispersal parameters.

Kitigawa-Keyfitz decomposition

$$C(P) = 0.5 \left( c^* \left[ P^{(2)}, \Theta^{(1)} \right] - c^* \left[ P^{(1)}, \Theta^{(1)} \right] \ight.$$  

$$+ \left[ P^{(2)}, \Theta^{(2)} \right] - c^* \left[ P^{(1)}, \Theta^{(2)} \right] \right)$$

Decompose into contributions from the *frequency* differences and the effects of *autocorrelation*

$$C(P) = C(Q) + C(R)$$
Lomatium bradshawii

Environment

(a) B U

1–p

1–q

3

q

p

(b) 1 2 3 4

1–p

1–q

1–q

p

q

q

1–q
Demography
Dispersal
A made-up example

Demography

\[ A_1, \ldots, A_4 = \text{Fisher Butte with extra fertility} \]
\[ A_1, \ldots, A_4 = \text{Rose Prairie} \]

Dispersal

\[ \alpha^{(1)} = \begin{pmatrix} 2 & 1 & .4 & .2 \end{pmatrix} \]
\[ \alpha^{(2)} = \begin{pmatrix} 1 & .5 & .2 & .1 \end{pmatrix} \]

Environment

frequency 0.5 0.7
autocorrelation −0.3 0

Invasion speed

\[ c^{*(1)} = 0.57 \quad c^{*(2)} = 0.18 \quad \Delta c^* = −0.4 \]
贡献

$$c^{(2)} - c^{(1)} = -0.4$$
Step by step

1. Decompose environmental differences using the Kitagawa-Keyfitz decomposition.
2. Compute contributions of the aggregate demography and dispersal differences using Kitagawa-Keyfitz.
3. Use environment-specific derivatives of $c^*$ to get contributions from each demographic parameter and each dispersal parameter in each environment.
Data requirements

In each environmental state, under two or more “treatments”, need data on:

1. Markovian environmental dynamics
2. stage-structured demography
3. stage-specific dispersal kernels
Thank you!