Invasion speed and LTRE analysis in stochastic environments

Hal Caswell[1] Michael Neubert[1]

[1]Biology Department
Woods Hole Oceanographic Institution

Everything Disperses to Miami

Invasion speed

Environment	Scalar populations	Structured populations
Constant	$c^* = \min_s \left\{ \frac{1}{s} \log \lambda M(s) \right\}$	$c^* = \min_s \left\{ \frac{1}{s} \log \rho_1 \left[\mathbf{H}(s) \right] \right\}$
Periodic	$\bar{c}^* = \frac{1}{p} \min_s \left\{ \frac{1}{s} \log \left(\prod_{i=1}^{p} \lambda_i m_i(s) \right) \right\}$	$\bar{c}^* = \frac{1}{p} \min_s \left\{ \frac{1}{s} \log \rho_{\text{per}} \left[\mathbf{H}_p(s) \cdots \mathbf{H}_1(s) \right] \right\}$
Stochastic	$\bar{c}^* = \min_s \left\{ \frac{1}{s} E \left[\log \left(\lambda m(s) \right) \right] \right\}$	$\bar{c}^* = \min_s \left(\frac{1}{s} \log \rho_{\text{stoch}} \right) = \min_s \left\{ \frac{1}{s} \lim_{T \to \infty} \frac{1}{T} \log \left\| \mathbf{H}_T(s) \cdots \mathbf{H}_1(s) \mathbf{w} \right\| \right\}$

Structured integrodifference equation

$$\mathbf{n}(x, t+1) = \int_{-\infty}^{\infty} \left(\mathbf{K}_t(x-y) \circ \mathbf{B}_t[\mathbf{n}(y,t)] \right) \mathbf{n}(y,t)\, dy,$$

and its linearization

$$\mathbf{n}(x, t+1) = \int_{-\infty}^{\infty} \left(\mathbf{K}_t(x-y) \circ \mathbf{A}_t \right) \mathbf{n}(y,t)\, dy.$$

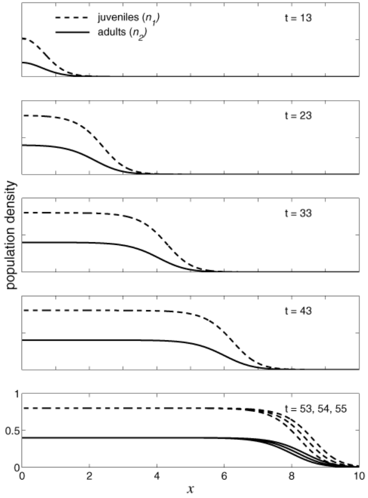
Invasion speed

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

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

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

Invasion speed: constant environments



Neubert and Caswell 2000

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

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

Define:

$$\begin{aligned} \mathbf{A} &= \mathbf{B}(0) \\ \mathbf{H}(s) &= \mathbf{A} \circ \mathbf{M}(s) \\ \rho(s) &= \text{largest eigenvalue of } \mathbf{H}(s) \end{aligned}$$

Invasion speed:

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

Invasion speed

Environment	Scalar populations	Structured populations
Constant	$c^* = \min_s \left\{ \frac{1}{s} \log \lambda M(s) \right\}$	$c^* = \min_s \left\{ \frac{1}{s} \log \rho_1 \left[\mathbf{H}(s) \right] \right\}$
Periodic	$\bar{c}^* = \frac{1}{p} \min_s \left\{ \frac{1}{s} \log \left(\prod_{i=1}^{p} \lambda_i m_i(s) \right) \right\}$	$\bar{c}^* = \frac{1}{p} \min_s \left\{ \frac{1}{s} \log \rho_{\text{per}} \left[\mathbf{H}_p(s) \cdots \mathbf{H}_1(s) \right] \right\}$
Stochastic	$\bar{c}^* = \min_s \left\{ \frac{1}{s} E \left[\log \left(\lambda m(s) \right) \right] \right\}$	$\bar{c}^* = \min_s \left(\frac{1}{s} \log \rho_{\text{stoch}} \right) = \min_s \left\{ \frac{1}{s} \lim_{T \to \infty} \frac{1}{T} \log \lVert \mathbf{H}_T(s) \cdots \mathbf{H}_1(s) \mathbf{w} \rVert \right\}$

Stochastic invasion references

- H. Caswell, M. G. Neubert, and C.M. Hunter. 2011. Demography and dispersal: invasion speeds and sensitivity analysis in periodic and stochastic environments.
  Theoretical Ecology 4:407–421
- S. J. Schreiber & M. E. Ryan. 2011.
  Invasion speeds for structured populations in fluctuating environments.
  Theoretical Ecology 4:423–434.
- S.P. Ellner and S.J. Schreiber. Temporally variable dispersal and demography can accelerate the spread of invading species. Theoretical Population Biology.

Sensitivity analysis: general

Let

$$\boldsymbol{\theta} = \text{parameter vector}$$

Sensitivity of c^*

$$\frac{dc^*}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{1}{s^*} \frac{d \log \rho}{d\boldsymbol{\theta}^{\mathsf{T}}}.$$

Elasticity of c^*

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

where $\mathcal{D}(\boldsymbol{\theta})$ is a matrix with $\boldsymbol{\theta}$ on the diagonal

Sensitivity analysis: constant environment

$$\rho(s^*) = \max \operatorname{eig} \mathbf{H}(s^*)$$

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

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

$$\frac{d\text{vec}\, \mathbf{H}(s^*)}{d\boldsymbol{\theta}^{\mathsf{T}}} = \mathcal{D}(\text{vec}\, \mathbf{A}) \frac{d\text{vec}\, \mathbf{M}(s^*)}{d\boldsymbol{\theta}^{\mathsf{T}}} + \mathcal{D}(\text{vec}\, \mathbf{M}(s^*)) \frac{d\text{vec}\, \mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}}.$$

Sensitivity analysis: periodic environment

$$\begin{aligned} c^* &= \min_s \left(\frac{1}{s} \log \rho_{\text{per}}(s) \right) \\ \rho_{\text{per}} &= \max \operatorname{eig} \left(\mathbf{H}_p \cdots \mathbf{H}_1 \right) \end{aligned}$$

$$\frac{d \log \rho_{\text{per}}}{d\boldsymbol{\theta}^\mathsf{T}} = \left(\frac{\mathbf{w}^\mathsf{T} \otimes \mathbf{v}^\mathsf{T}}{\rho_{\text{per}}} \right) \sum_{i=1}^{p} \frac{\partial \text{vec}\, \mathbf{H}}{\partial \text{vec}^\mathsf{T} \mathbf{H}_i} \left. \frac{d \text{vec}\, \mathbf{H}_i}{d\boldsymbol{\theta}^\mathsf{T}} \right|_{\boldsymbol{\theta}=\boldsymbol{\theta}_i},$$

with

$$\frac{\partial \text{vec}\, \mathbf{H}}{\partial \text{vec}^\mathsf{T} \mathbf{H}_i} = \begin{cases} \mathbf{I} \otimes (\mathbf{H}_p \cdots \mathbf{H}_2) & i = 1 \\ (\mathbf{H}_{i-1} \cdots \mathbf{H}_1)^\mathsf{T} \otimes (\mathbf{H}_p \cdots \mathbf{H}_{i+1}) & 1 < i < p \\ (\mathbf{H}_{p-1} \cdots \mathbf{H}_1)^\mathsf{T} \otimes \mathbf{I} & i = p \end{cases}$$

Sensitivity analysis: stochastic environment

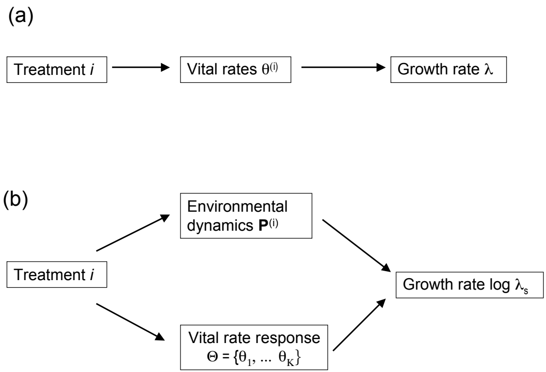
$$\log \rho_{\text{stoch}} = \lim_{T \to \infty} \frac{1}{T} \log \|\mathbf{H}_{T-1}(s) \cdots \mathbf{H}_0(s)\mathbf{w}\|$$

Tuljapurkar's formula

$$\frac{d \log \rho_{\text{stoch}}}{d\boldsymbol{\theta}^{\mathsf{T}}} = \frac{1}{T} \sum_{i=0}^{T-1} \frac{\left[\mathbf{w}^{\mathsf{T}}(i) \otimes \mathbf{v}^{\mathsf{T}}(i+1)\right]}{R_i \mathbf{v}^{\mathsf{T}}(i+1)\mathbf{w}(i+1)} \frac{d\text{vec}\,\mathbf{H}_i}{d\boldsymbol{\theta}^{\mathsf{T}}} \qquad (1)$$

Retrospective perturbation analysis

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



Aust. N. Z. J. Stat. **47**(1), 2005, 75–85

SENSITIVITY ANALYSIS OF THE STOCHASTIC GROWTH RATE: THREE EXTENSIONS[†]

Hal Caswell[1]

Woods Hole Oceanographic Institution, Massachusetts

Theor Ecol
DOI 10.1007/s12080-010-0091-z

ORIGINAL PAPER

Demography and dispersal: invasion speeds and sensitivity analysis in periodic and stochastic environments

Hal Caswell · Michael G. Neubert · Christine M. Hunter

Journal of Ecology

British Ecological Society

Journal of Ecology 2010, **98**, 324–333 doi: 10.1111/j.1365-2745.2009.01627.x

SPECIAL FEATURE

ADVANCES IN PLANT DEMOGRAPHY USING MATRIX MODELS

Life table response experiment analysis of the stochastic growth rate

Hal Caswell*

Determinants of invasion speed

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

$$\mathbf{P} = \text{Pr}\left(u(t+1) = i | u(t) = j\right)$$

- demographic responses

$$\mathbf{A}_1, \ldots, \mathbf{A}_k$$

- dispersal responses

$$\alpha_1, \ldots, \alpha_k$$

Decomposing differences

$$\text{treatment 1}: \quad \left.\begin{array}{c} \mathbf{P}^{(1)} \\ \mathbf{A}_1^{(1)}, \ldots, \mathbf{A}_k^{(1)} \\ \alpha_1^{(1)}, \ldots, \alpha_k^{(1)} \end{array}\right\} \longrightarrow \quad c^{*(1)}$$

$$\text{treatment 2}: \quad \left.\begin{array}{c} \mathbf{P}^{(2)} \\ \mathbf{A}_1^{(2)}, \ldots, \mathbf{A}_k^{(2)} \\ \alpha_1^{(2)}, \ldots, \alpha_k^{(2)} \end{array}\right\} \longrightarrow \quad c^{*(2)}$$

LTRE: the basic idea

$$\begin{aligned} y_1 &= y(\boldsymbol{\theta}_1) \\ y_2 &= y(\boldsymbol{\theta}_2) \end{aligned}$$

Then

$$y_2 - y_1 \approx \frac{dy}{d\boldsymbol{\theta}^{\mathsf{T}}} (\boldsymbol{\theta}_2 - \boldsymbol{\theta}_1)$$

Contributions:

$$C(\boldsymbol{\theta}) = \left(\frac{dy}{d\boldsymbol{\theta}^{\mathsf{T}}} \right)^{\mathsf{T}} \circ (\boldsymbol{\theta}_2 - \boldsymbol{\theta}_1)$$

Environment-specific sensitivity

Indicator variable

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

$$\begin{aligned} \left.\frac{dc^*}{d\boldsymbol{\theta}^\mathsf{T}}\right|_{u=h} &= \frac{1}{s^*} \left.\frac{d \log \rho_{\text{stoch}}}{d\boldsymbol{\theta}^\mathsf{T}}\right|_{u=h} \\ &= \frac{1}{s^*} \frac{1}{T} \sum_{i=0}^{T-1} \frac{J_i(h) \left[\mathbf{w}^\mathsf{T}(i) \otimes \mathbf{v}^\mathsf{T}(i+1)\right]}{R_i \mathbf{v}^\mathsf{T}(i+1)\mathbf{w}(i+1)} \frac{d\text{vec}\, \mathbf{H}_i}{d\boldsymbol{\theta}^\mathsf{T}} \end{aligned}$$

Environment-specific sensitivities

Use this to get

$$\left.\frac{dc^*}{d\text{vec}^{\mathsf{T}}\mathbf{A}}\right|_{u=h} \qquad \text{and} \qquad \left.\frac{dc^*}{d\boldsymbol{\alpha}^{\mathsf{T}}}\right|_{u=h}$$

for $h = 1, \ldots, k$.

But what about contributions from the environment ($\mathbf{P}$)?

Kitagawa-Keyfitz demcomposition

Suppose

$$
\begin{aligned}
c^{*(1)} &= c^*[a, b] \\
c^{*(2)} &= c^*[A, B].
\end{aligned}
$$

Then

$$
\begin{aligned}
C(A - a) &= (1/2)\left(c^*[A, B] - c^*[a, B]\right) \\
&\quad + (1/2)\left(c^*[A, b] - c^*[a, b]\right) \\
C(B - b) &= (1/2)\left(c^*[A, B] - c^*[A, b]\right) \\
&\quad + (1/2)\left(c^*[a, B] - c^*[a, b]\right).
\end{aligned}
$$

Decomposition of effect of environmental dynamics

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

Kitigawa-Keyfitz decomposition

$$\begin{aligned} C(\mathbf{P}) &= 0.5\left(c^*\left[\mathbf{P}^{(2)}, \mathbf{\Theta}^{(1)}\right] - c^*\left[\mathbf{P}^{(1)}, \mathbf{\Theta}^{(1)}\right]\right. \\ &\quad \left. + \left[\mathbf{P}^{(2)}, \mathbf{\Theta}^{(2)}\right] - c^*\left[\mathbf{P}^{(1)}, \mathbf{\Theta}^{(2)}\right]\right) \end{aligned}$$

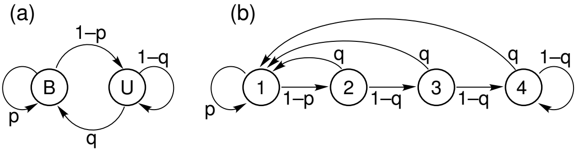
Decompose into contributions from the *frequency* differences and the effects of *autocorrelation*

$$C(\mathbf{P}) = C(\mathbf{Q}) + C(\mathbf{R})$$

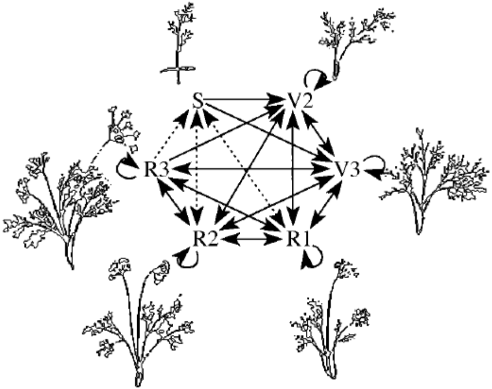
Lomatium bradshawii

Caswell, H. and T. Kaye. Stochastic demography and conservation of Lomatium bradshawii in a dynamic fire regime. Advances in Ecological Research 32:1-51

Environment



Demography



Dispersal

A made-up example

Demography

$$\mathbf{A}_1, \ldots, \mathbf{A}_4 = \text{Fisher Butte with extra fertility}$$
$$\mathbf{A}_1, \ldots, \mathbf{A}_4 = \text{Rose Prairie}$$

Dispersal

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

Environment

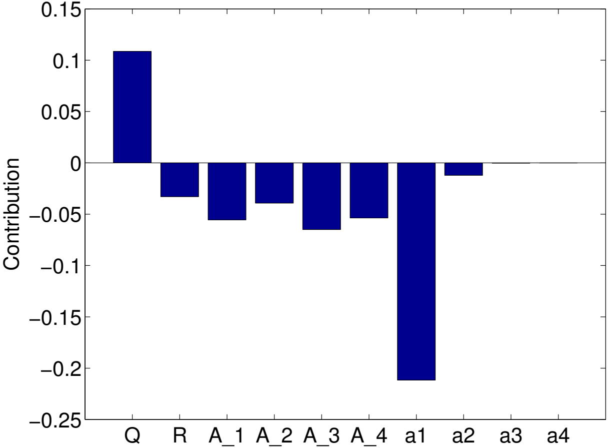
frequency	0.5	0.7
autocorrelation	−0.3	0

Invasion speed

$$c^{*(1)} = 0.57 \qquad c^{*(2)} = 0.18 \qquad \Delta c^* = -0.4$$

Contributions

$$c^{*(2)} - c^{*(1)} = -0.4$$



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!