Generational spreading speed

and the

dynamics of ecological invasions

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Bateman, A.W., Neubert, M.G., Krkošek, M., Lewis, M.A. (2015) Generational spreading speed and the dynamics of ecological invasions. *American Naturalist* 186(3): 362-375

Generational spreading speed
and the
dynamics of ecological invasions

Andrew Bateman

Mike Neubert

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(Spatial) Demography

- In many cases, simple quantities can characterise changes in population size or density:
  - λ: (annual) rate of population growth
  - R_0: net reproductive number (generational population growth)

- Versions of R_0, in particular, are used across ecology and epidemiology

"…$\boldsymbol{R_0}$ **is arguably the most important quantity in the study of epidemics**…"

Heesterbeek, J. (2002). *Acta Biotheoretica*, *50*, 189–204.

Spreading speed

- Integrodifference equations (IDEs) can represent both scalar and stage-structured (age, size, maturity) populations growing and spreading in space

- Can be used to calculate theoretical *spreading speed* for a population (re)colonising empty habitat
  - applies to both scalar (Kot *et al.* 1996) and stage-structured (Neubert & Caswell 2000) demography

- These measures of spreading speed are analogous to the population growth rate, λ, in discrete-time population dynamics models

- **A measure of generational spread analogous to R_0 is missing**

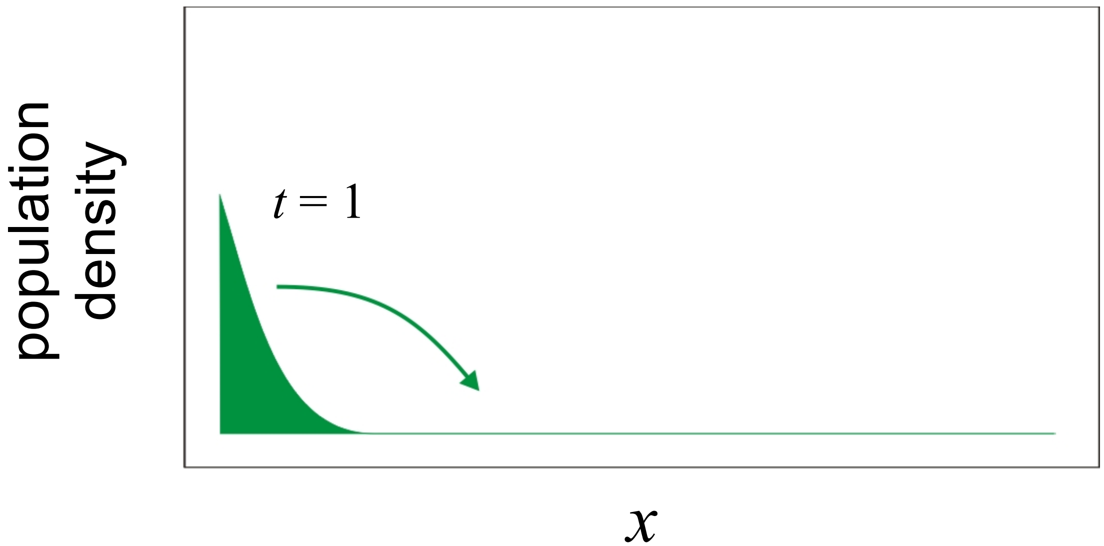
Kot, M., Lewis, M., & van den Driessche, P. (1996). *Ecology*, *77*(7), 2027–2042.
Neubert, M., & Caswell, H. (2000). *Ecology*, *81*(6), 1613–1628.

Outline

- Background: IDEs, annual spreading speed
- Next-generation matrix, R_0, and motivation
- Generational spreading speed
- Example

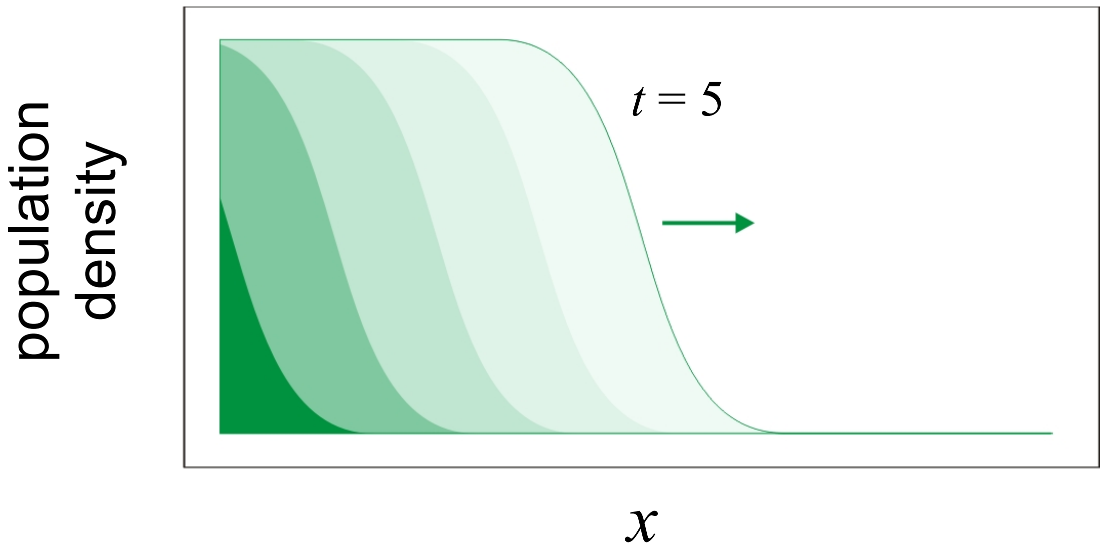
Spatial spread

- Consider an invasion in a single continuous spatial dimension, x



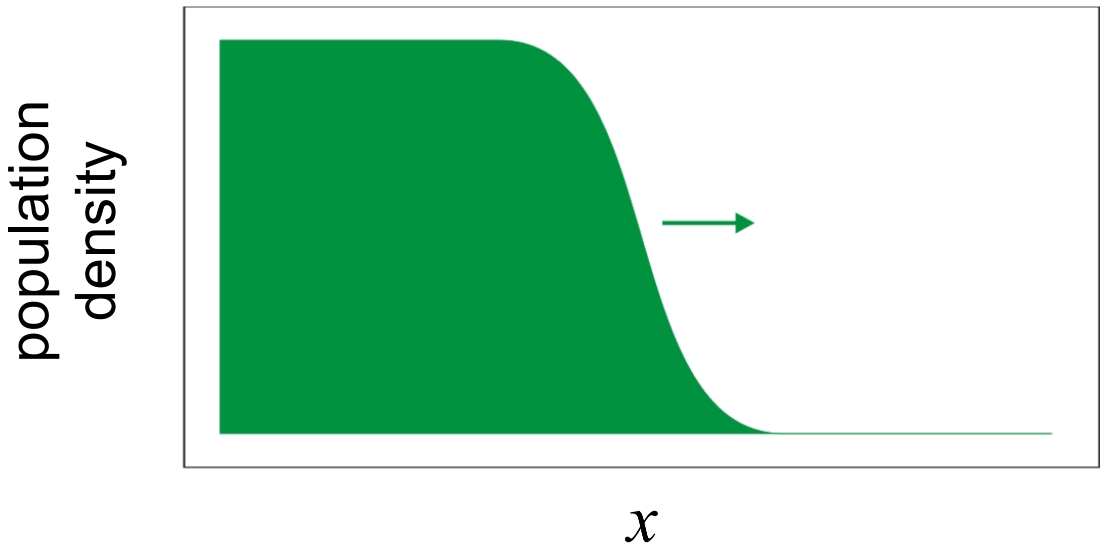
Spatial spread

- Consider an invasion in a single continuous spatial dimension, x



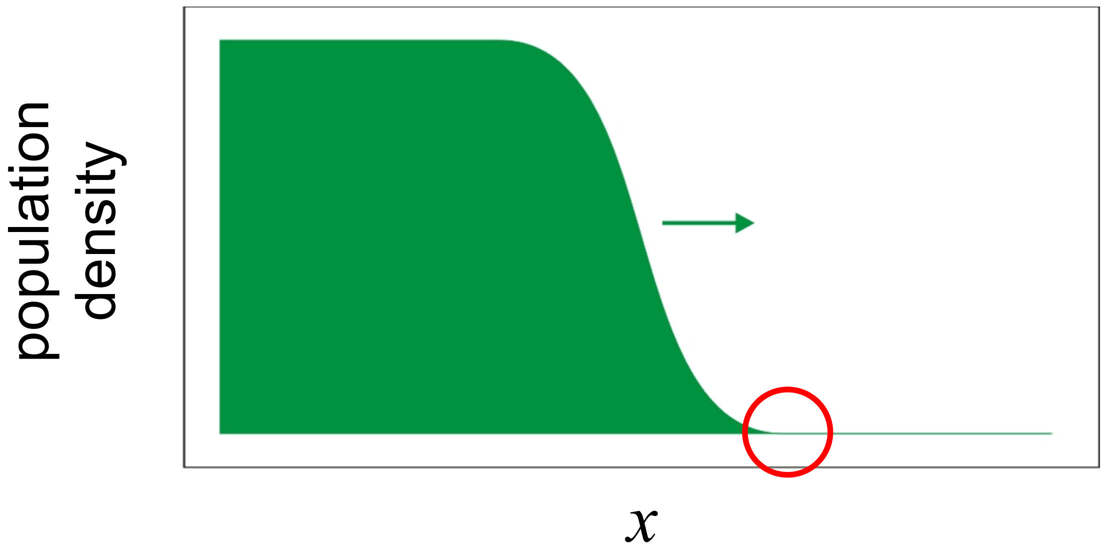
Spatial spread

- Population density will level off as density dependence takes effect behind the invasion front



Spatial spread

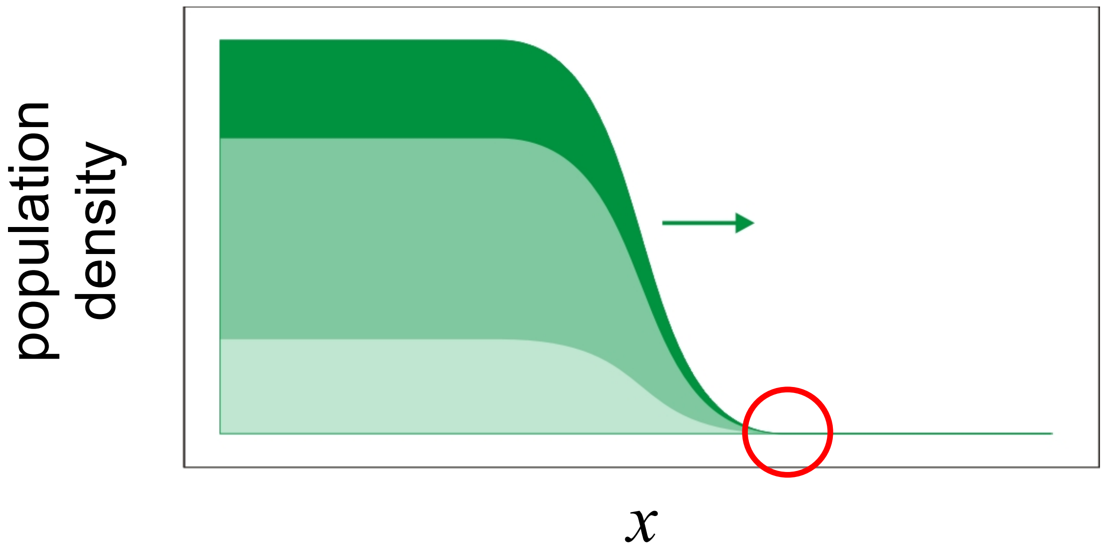
- In many cases, it is possible to derive the spreading speed of the advancing population by considering dynamics at the invasion front



- When this occurs we say the spreading speed is *linearly determined*
- It is this case that we focus upon

Spatial spread

- Here, we consider the case of a stage-structured population:



Stage-structured IDEs

- Model:

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

  - **A** is a population projection matrix
  - **K**(x,y) is a matrix of dispersal kernels, with entries $k_{ij}(x,y)$ describing movement to x of a stage-*i* individual, produced at y by a stage-*j* individual
  - $\circ$ is the Hadamard (elementwise) product

Example: wild teasel

- Native to Eurasia, wild teasel (*Dispacus fullonum*) is now an invasive of increasing concern in eastern North America

- Teasel rosettes develop into plants that put up tall flower stalks and finally drop seed

Growth and dispersal matricies for teasel

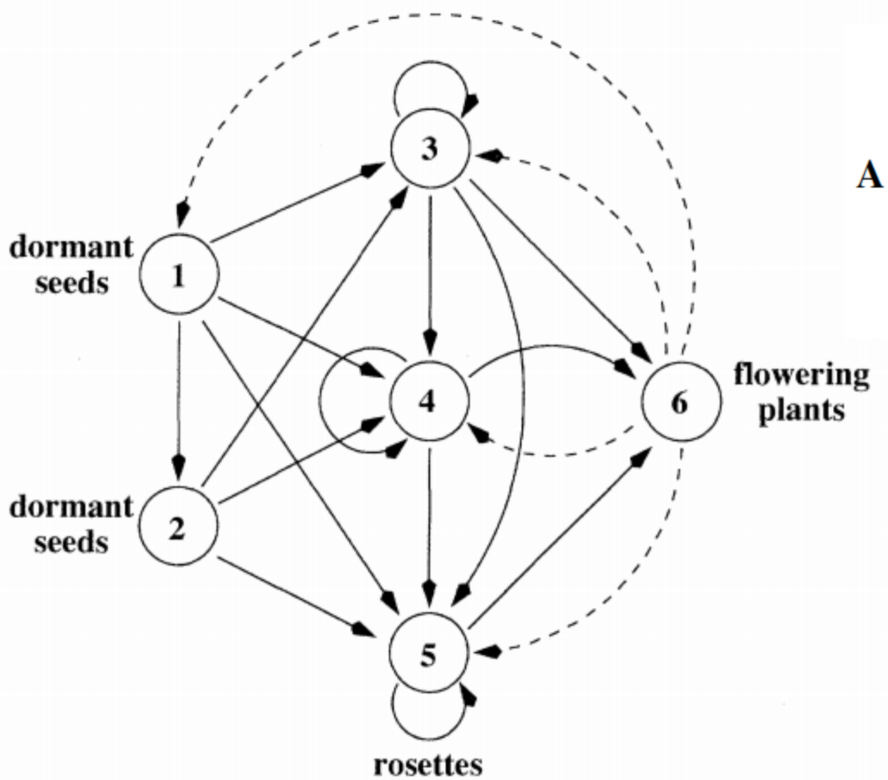


FIG. 6. The life cycle of teasel (*Dipsacus sylvestris*). Dashed lines represent transitions during which dispersal occurs.

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 402.59 \\ 0.974 & 0 & 0 & 0 & 0 & 0 \\ 0.017 & 0.011 & 0 & 0 & 0 & 8.255 \\ 0.004 & 0.002 & 0.077 & 0.212 & 0 & 69.215 \\ 0.003 & 0 & 0.038 & 0.218 & 0 & 3.810 \\ 0 & 0 & 0 & 0.063 & 1.000 & 0 \end{pmatrix}$$

$$k_{i6}(x-y) = \frac{1}{2\alpha} \exp\left(\frac{-|x-y|}{\alpha}\right)$$

$$k_{ij}(x-y) = \delta(x-y), \qquad j \neq 6$$

Spreading speed

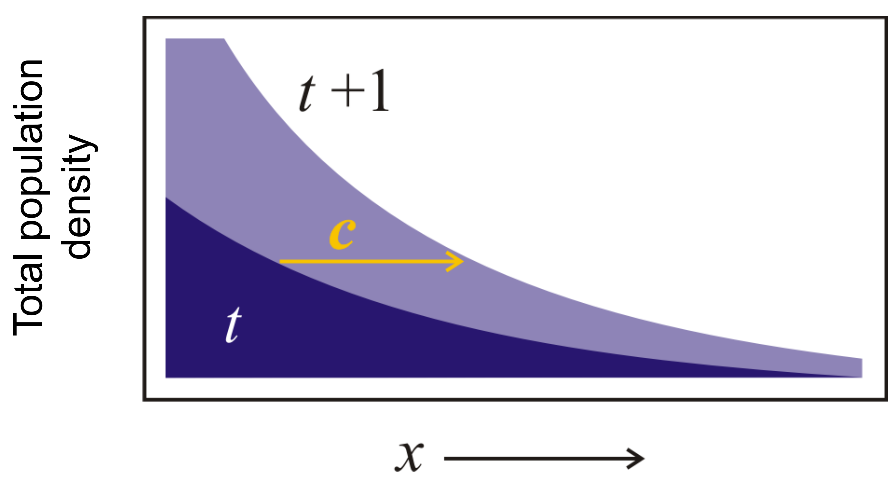
- Model:

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

- Assume $\mathbf{K}(x,y) = \mathbf{K}(x\text{-}y)$ and consider solutions of the form:

$$\mathbf{n}(x,t) = \mathbf{w}e^{-s(x-ct)}$$

  – s determines the shape of the low-density wave front
  – $\mathbf{w}$ gives the relative stage abundances in the wave
  – $c > 0$ is the wave speed



Neubert, M., & Caswell, H. (2000). *Ecology*, *81*, 1613–1628.

Spreading speed

- Rearrangement and change of variables yields

$$\mathbf{w}e^{sc} = \mathbf{H}(s)\mathbf{w}$$

where $\mathbf{H}(\mathrm{s}) = \mathbf{M}(\mathrm{s}) \circ \mathbf{A}$, and $\mathbf{M}(\mathrm{s})$ is the matrix of moment-generating functions,

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

corresponding to the dispersal kernels

Neubert, M., & Caswell, H. (2000). *Ecology*, *81*, 1613–1628.

Spreading speed

- From $\mathbf{w}e^{sc} = \mathbf{H}(s)\mathbf{w}$ we can equate e^{sc} to the dominant eigenvalue of $\mathbf{H}(s)$, with eigenvector $\mathbf{w}$, to give:

$$c(s) = \frac{1}{s} \ln\Big(\rho_1[\mathbf{H}(s)]\Big),$$

where $\rho_1[\cdot]$ denotes the dominant eigenvalue of a matrix

- The *asymptotic spreading speed* for the invading population is

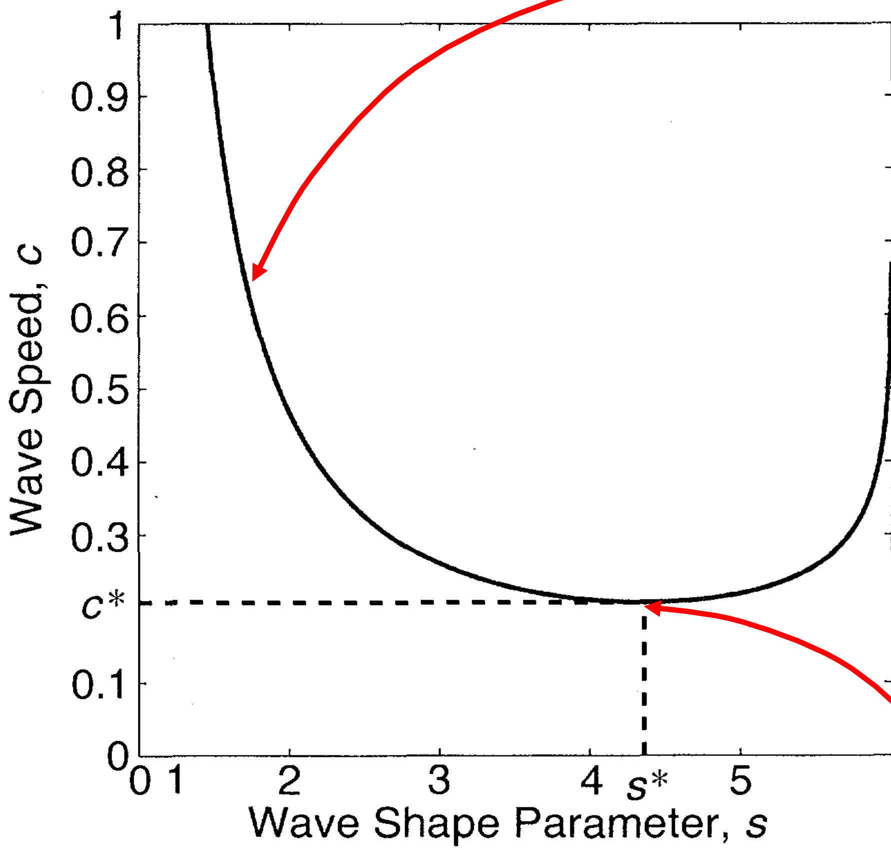
$$c^* = \inf_{s \in \Omega} \left[\frac{1}{s} \ln\Big(\rho_1[\mathbf{H}(s)]\Big) \right]$$

where Ω is the domain of existence for $\mathbf{M}(s)$

Lui, R. (1989). *Math. Biosci.*, 93, 269–295.
Neubert, M., & Caswell, H. (2000). *Ecology*, *81*, 1613–1628.

Spreading speed

$$c(s) = \frac{1}{s} \ln\Big(\rho_1[\mathbf{H}(s)]\Big)$$



$$c^* = \inf_{s \in \Omega} \left[\frac{1}{s} \ln\Big(\rho_1[\mathbf{H}(s)]\Big) \right]$$

Neubert, M., & Caswell, H. (2000). *Ecology*, *81*, 1613–1628.

Spreading speed for teasel

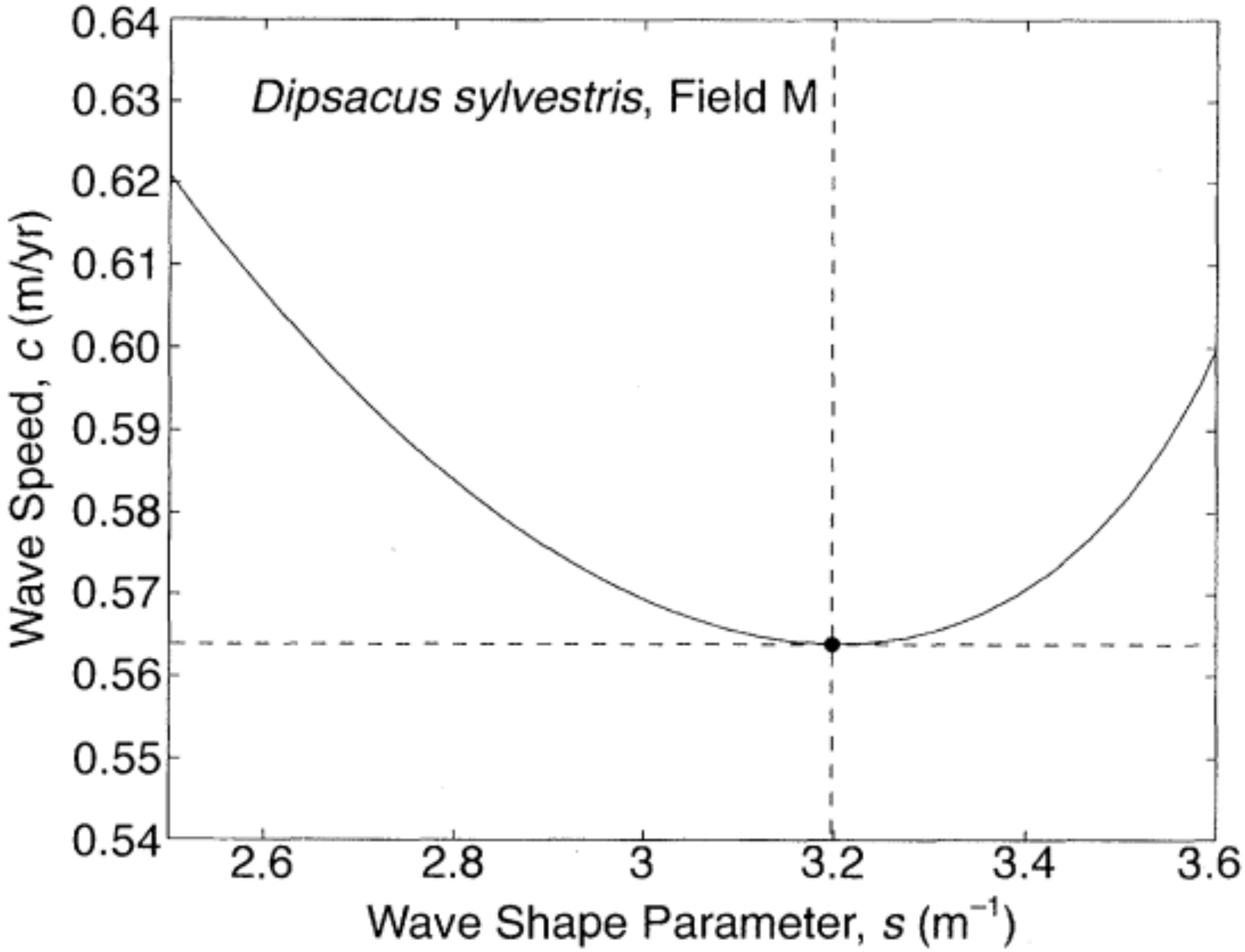


FIG. 7. Invasion speed c as a function of the spatial decay rate s for teasel (Field M).

Stage-structured invasion

- So, we can calculate a theoretical invasion speed, given descriptions of life history and dispersal

- Can also calculate sensitivity of wave speed to parameters (Neubert & Caswell 2000)

BUT…

- For complicated life-histories, calculations are numerical (eigenvalue of an NxN matrix involves solving an N^{th}-order polynomial)

- Any other way to gain analytical insight?

Neubert, M., & Caswell, H. (2000). *Ecology*, *81*, 1613–1628.

Generational demography

- Each generation produces the next as it ages, reproduces, and dies

- Consider the processes that go into demographic change:

$$\mathbf{A} = \mathbf{F} + \mathbf{T}$$

$\mathbf{T}$ is the *transition* matrix – survival and maturation

$\mathbf{F}$ is the *fecundity* matrix – reproduction

Generational demography

- If we start with a (stage-structured) vector, $\mathbf{u}(\mathrm{g})$, of population density in generation g

- then:

$$\begin{aligned}\mathbf{u}(\mathrm{g}+1) &= \mathbf{F}\mathbf{u}(\mathrm{g}) + \mathbf{F}\mathbf{T}\mathbf{u}(\mathrm{g}) + \mathbf{F}\mathbf{T}^2\mathbf{u}(\mathrm{g}) + \mathbf{F}\mathbf{T}^3\mathbf{u}(\mathrm{g}) + \ldots \\ &= \mathbf{F}[\mathbf{I} + \mathbf{T} + \mathbf{T}^2 + \mathbf{T}^3 + \ldots]\mathbf{u}(\mathrm{g}) \\ &= \mathbf{F}[\mathbf{I} - \mathbf{T}]^{-1}\mathbf{u}(\mathrm{g})\end{aligned}$$

- $\mathbf{Q} = \mathbf{F}[\mathbf{I} - \mathbf{T}]^{-1}$ is the *next-generation matrix*

Generational demography

- λ, the asymptotic annual population growth rate is $\rho_1[\mathbf{A}]$

- $\rho_1[\mathbf{Q}]$ is the asymptotic *generational population growth* rate (or net reproductive number), R_0

- Calculation of λ, like c^*, commonly involves solving an N^{th}-order polynomial

- $\mathbf{Q} = \mathbf{F}[\mathbf{I} - \mathbf{T}]^{-1}$, however, is typically of rank one because of its direct dependence on the fecundity matrix, $\mathbf{F}$, and all reproduction commonly passes through a single stage (*e.g.* adults, seeds)

Generational demography

- Also, $R_0 - 1$ and $\lambda - 1$ have the same sign (Cushing & Yicang 1994), so that both R_0 and λ indicate:

  population decline ____________ $R_0, \lambda < 1$
  population stability ____________ $R_0, \lambda = 1$
  population growth ____________ $R_0, \lambda > 1$

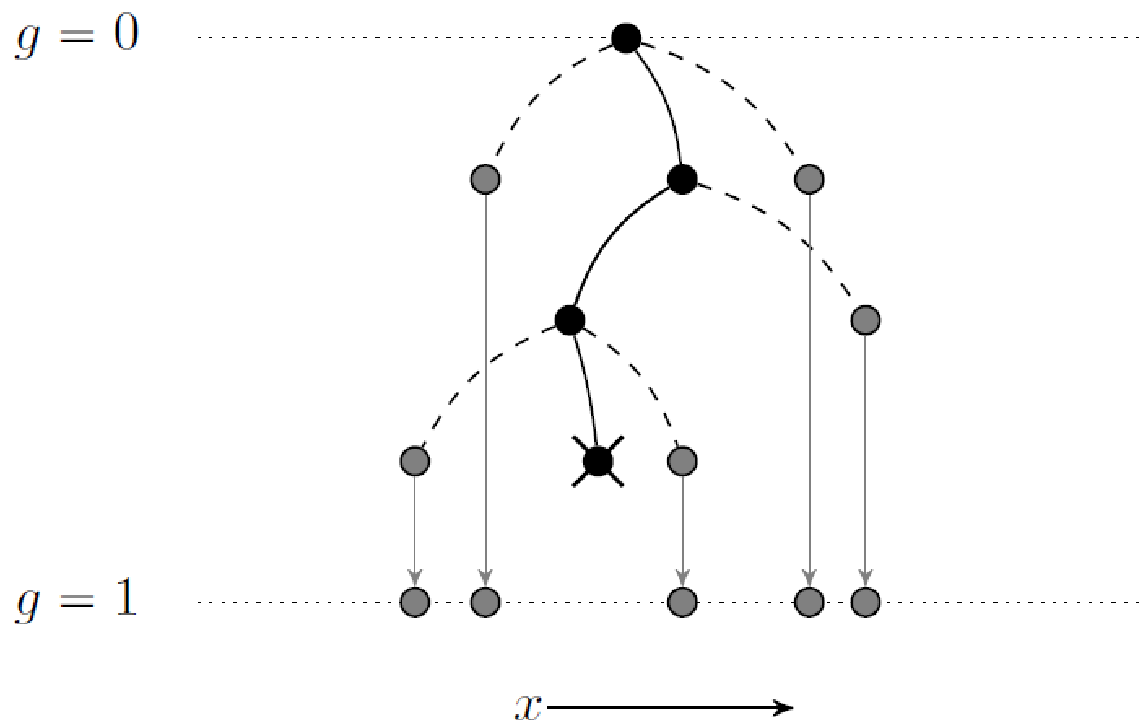
- Analytical insight gained about changes to R_0 can carry information about population growth more generally

- Motivated by potential for similar insight into process of spatial spread

Cushing, J. & Yicang, Z. (1994). *Nat. Resour. Model.*, 8, 297–333.

Generational spread

- Consider the process of generational spread:



Generational spread

- To begin, we decompose the linearised IDE into spatiopemporal transition and fecundity operators:

$$\mathbf{n}(x,t+1) = \int_{-\infty}^{\infty} \big[\mathbf{K}(x-y)\circ(\mathbf{F}+\mathbf{T})\big]\,\mathbf{n}(y,t)\,dy$$

$$= \underbrace{\int_{-\infty}^{\infty} [\mathbf{K}(x-y)\circ\mathbf{F}]\,\mathbf{n}(y,t)\,dy}_{\mathscr{L}_F\mathbf{n}(x,t)} + \underbrace{\int_{-\infty}^{\infty} [\mathbf{K}(x-y)\circ\mathbf{T}]\,\mathbf{n}(y,t)\,dy}_{\mathscr{L}_T\mathbf{n}(x,t)}$$

- The dispersal-dependent next generation in space is:

$$\mathbf{u}(x,g+1) = \mathscr{L}_G\mathbf{u}(x,g) = \mathscr{L}_F\mathbf{u}(x,g) + \mathscr{L}_F\mathscr{L}_T\mathbf{u}(x,g) + \mathscr{L}_F\mathscr{L}_T\mathscr{L}_T\mathbf{u}(x,g) + \ldots$$

$$= \underbrace{\mathscr{L}_F[\mathbf{I} + \mathscr{L}_T + \mathscr{L}_T^2 + \ldots]}_{\text{next-generation operator}}\mathbf{u}(x,g).$$

Generational spread

- We look for exponential-form solutions

$$\mathbf{u}(x,g) = \mathbf{w}_G e^{-s_G(x - c_G g)}$$

with wave speed c_G and wave shape s_G,

- and we define $\mathbf{H}_F(s)$ and $\mathbf{H}_T(s)$ so that

$$\begin{aligned}\mathbf{H}(s_G) &= \mathbf{M}(s_G) \circ \mathbf{A} = \mathbf{M}(s_G) \circ [\mathbf{F} + \mathbf{T}] \\ &= \underbrace{\mathbf{M}(s_G) \circ \mathbf{F}}_{H_F(s_G)} + \underbrace{\mathbf{M}(s_G) \circ \mathbf{T}}_{H_T(s_G)}\end{aligned}$$

Generational spread

- We can show that:

$$\mathbf{w}_G e^{s_G c_G} = \mathbf{H}_F(s_G)[\mathbf{I} - \mathbf{H}_T(s_G)]^{-1}\mathbf{w}_G$$

under the condition that $\rho_1[\mathbf{H}_T(s_G)] < 1$.

- Here, $\mathbf{H}_F(s_G)[I - \mathbf{H}_T(s_G)]^{-1} = \mathbf{H}_G(s_G)$ is the spatiodemographic analogue of the purely demographic next-generation matrix, $\mathbf{Q}$.

Generational spread

- We get a dispersion relation for the linearised system:

$$c_G(s_G) = \frac{1}{s_G} \ln\Big(\rho_1[\mathbf{H}_G(s_G)]\Big)$$

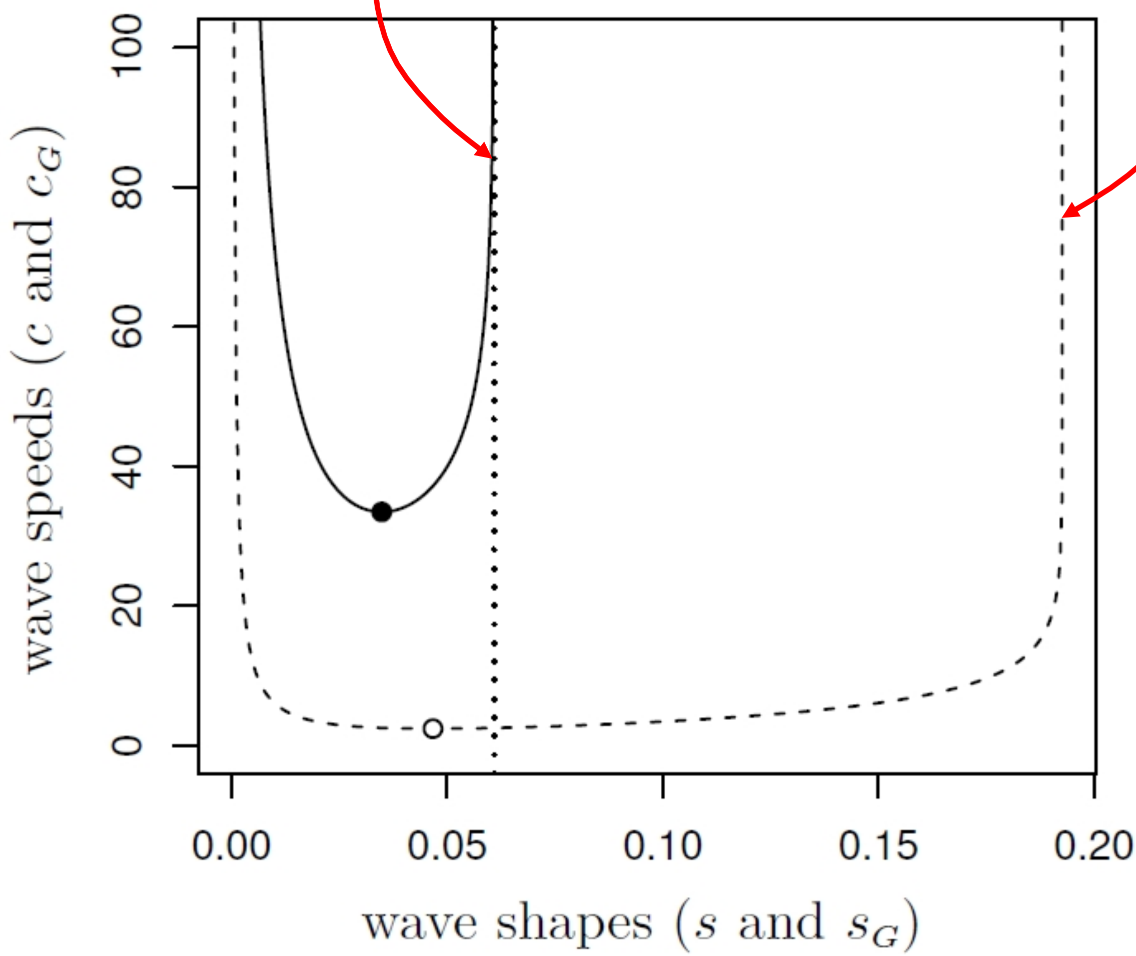
- the *generational spreading speed* is:

$$\boxed{c_G^* = \inf_{s_G \in \Omega_G} \left[\frac{1}{s_G} \ln\Big(\rho_1[\mathbf{H}_G(s_G)]\Big) \right]}$$

where Ω_G incorporates the condition $\rho_1[\mathbf{H}_T(s_G)] < 1$; $\Omega_G \subseteq \Omega$

Generational spreading speed

$$c_G(s_G) = \frac{1}{s_G} \ln\Big(\rho_1[\mathbf{H}_G(s_G)]\Big) \qquad c(s) = \frac{1}{s} \ln\Big(\rho_1[\mathbf{H}(s)]\Big)$$



Generational spreading speed

- We can also show that the following holds:

$$c_G^* < 0 \iff c^* < 0,$$

$$c_G^* = 0 \iff c^* = 0, \text{ or}$$

$$c_G^* > 0 \iff c^* > 0.$$

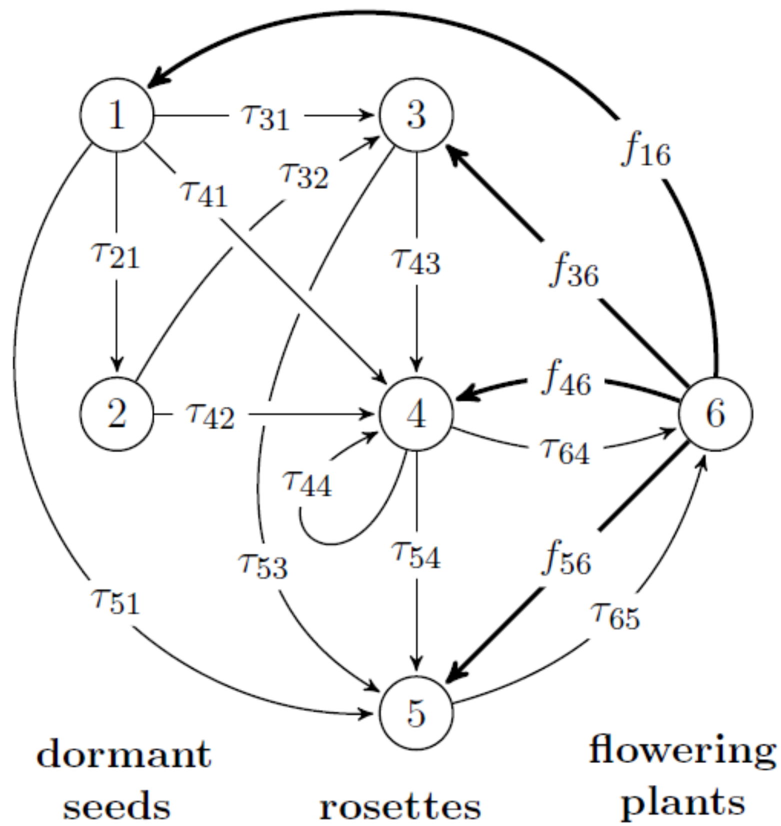
→ generational spreading speed, c_G^*, carries information about c^* comparable to that which R_0 carries about λ.

Population-change statistics

	annual	generational
demographic	$\lambda = \rho_1[\mathbf{A}]$	$R_0 = \rho_1[\mathbf{Q}]$
spatiodemographic	$c^* = \inf_{s \in \Omega} \left[\frac{1}{s} \ln\Big(\rho_1[\mathbf{H}(s)] \Big) \right]$	$c_G^* = \inf_{s_G \in \Omega_G} \left[\frac{1}{s_G} \ln\Big(\rho_1[\mathbf{H}_G(s_G)] \Big) \right]$

Example: wild teasel

- Recall the lifecycle is complex, with multiple dormant seed and rosette stages as well as adult plants



Example: wild teasel

- Estimates for transition and fecundity parameters result in corresponding matrices (Werner & Caswell 1977):

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 402.59 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 8.255 \\ 0 & 0 & 0 & 0 & 0 & 69.215 \\ 0 & 0 & 0 & 0 & 0 & 3.810 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} \text{ and } \mathbf{T} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0.974 & 0 & 0 & 0 & 0 & 0 \\ 0.017 & 0.011 & 0 & 0 & 0 & 0 \\ 0.004 & 0.002 & 0.077 & 0.212 & 0 & 0 \\ 0.003 & 0 & 0.038 & 0.281 & 0 & 0 \\ 0 & 0 & 0 & 0.063 & 1.000 & 0 \end{bmatrix}.$$

Werner, P. & Caswell, H. (1977). *Ecology*, 58, 1103–1111.

Example: wild teasel

- When seeds are mature, they drop a short distance from their parent plants.
- Seed dispersal can be characterised by a Laplace distribution with a mean dispersal distance of $\alpha = 0.257$ m (Werner 1975):

$$k_{i6}(x-y) = \frac{1}{2\alpha}\exp\left(\frac{-|x-y|}{\alpha}\right)$$

- The wave-speed function can be simplified:

$$c_G(s_G) = \frac{1}{s_G}\ln[m(s_G)R_0]$$

- where $m(s_G)=1/(1-\alpha^2 s_G^2)$ is the moment-generating function associated with seed dispersal

Werner, P. (1975). *Can. J. Bot.*, 53, 810–813.

Example: wild teasel

- We can solve for R_0 algebraically (Rueffler & Metz 2013) or using graph reduction (de-Camino-Beck & Lewis 2007):

$$R_0 = \left[\left(\frac{(\tau_{64} + \tau_{65}\tau_{54})[\tau_{41} + \tau_{42}\tau_{21} + \tau_{43}(\tau_{31} + \tau_{32}\tau_{21})]}{1 - \tau_{44}} + \tau_{65}[\tau_{51} + \tau_{53}(\tau_{31} + \tau_{32}\tau_{21})] \right) f_{16} \right.$$
$$\left. + \left(\frac{(\tau_{64} + \tau_{65}\tau_{54})\tau_{43}}{1 - \tau_{44}} + \tau_{65}\tau_{53} \right) f_{36} + \frac{(\tau_{64} + \tau_{65}\tau_{54})}{1 - \tau_{44}} f_{46} + \tau_{65} f_{56} \right],$$

- Then the spreading speed is given by

$$c_G^* = \min_{s_G \in \Omega_G} \left(\frac{1}{s_G} \ln[m(s_G) R_0] \right)$$

Rueffler, C. & Metz, J. (2013). *J. Math. Biol.*, 66, 1099–1122.
de-Camino-Beck, T. & Lewis, M. (2007). *Bull. Math. Biol.*, 69, 1341–1354.

Example: wild teasel

- Although we cannot find a closed form for the generational spreading speed in this case, due to the non-normal dispersal kernel, we can use an approximation (Lutscher 2007):

$$\tilde{c}_G^* = 2\sigma\sqrt{\frac{\ln(R_0)}{2}} + \frac{\sigma}{3}\left(\sqrt{\frac{\ln(R_0)}{2}}\right)^3\gamma$$

  where σ is the standard deviation and γ is the excess kurtosis, relative to the normal distribution, of the moment-generating function

- This gives

$$\tilde{c}_G^* = 0.514\sqrt{\ln(R_0)} + 0.1285\left(\sqrt{\ln(R_0)}\right)^3,$$

- Compare to the case of normal dispersal:

$$c_G^* = 2\sigma\sqrt{\frac{\ln(R_0)}{2}}$$

Lutscher, F. (2007). *Bull. Math. Biol.*, 69, 1615–1630.

Summary

- We can calculate generational wave speed, a spatiotemporal R_0–analogue, for stage-structured populations growing and spreading in space
- This quantity completes a set of four statistics to assess the potential for population growth and spread
- Generational spreading speed can be easier to calculate and offer greater analytical insight than often-numerical calculations of annual spreading speed.
- However, we have been unable to find a simple way to connect c_G* to c* via the mean generation time or something similar.

$\lambda = \rho_1[\mathbf{A}]$	$R_0 = \rho_1[\mathbf{Q}]$
$c^* = \inf\limits_{s\in\Omega}\left[\frac{1}{s}\ln\Big(\rho_1[\mathbf{H}(s)]\Big)\right]$	$\boxed{c_G^* = \inf\limits_{s_G\in\Omega_G}\left[\frac{1}{s_G}\ln\Big(\rho_1[\mathbf{H}_G(s_G)]\Big)\right]}$

Thank You

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CRSNG

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$$\mathbf{w}_G\, e^{s_G c_G} = \mathbf{H}_F(s_G)\left[\mathbf{I} - \mathbf{H}_T(s_G)\right]^{-1} \mathbf{w}_G$$

$$c_G{}^* = \inf_{s_G \in \Omega_G} \left(\frac{1}{s_G} \ln\left[\rho_1\left(\mathbf{H}_F(s_G)\left[\mathbf{I} - \mathbf{H}_T(s_G)\right]^{-1} \right) \right] \right)$$

Example: wild teasel

- Teasel rosettes develop into flowering plants that drop seeds