

# A comparison of spatial interactions at different scales

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# Spatial Ecology

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*Theory in spatial ecology has to steer a narrow and challenging course between the Scylla of oversimplification and the Charybdis of intractability.*

– U. Dieckmann and R. Law

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In: The Geometry of Ecological Interactions: Simplifying Spatial Complexity, eds. Dieckmann U, Law R & Metz JAJ, pp. 412–455. Cambridge University Press.



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**Example.** Obtain  $\Pi_{m+1}$  from  $\Pi_m$  by sub-dividing every patch  $X \in \Pi_m$ .

# Ancestors and Descendants

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Let  $(\Omega, \Pi_\bullet)$  be fixed.

For every  $X \in \Pi_m$  there exist unique **ancestors**  $X_0, X_1, X_2, \dots, X_{m-1}$  and non-unique **descendants**  $X_{m+1}, X_{m+2}, \dots$  of  $X$  such that  $X_k \in \Pi_k$  and

$$X_0 \supseteq X_1 \supseteq X_2 \supseteq \cdots X_{m-1} \supseteq X \supseteq X_{m+1} \supseteq X_{m+2} \supseteq \cdots .$$

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$$X_0 \supseteq X_1 \supseteq X_2 \supseteq \dots X_{m-1} \supseteq X \supseteq X_{m+1} \supseteq X_{m+2} \supseteq \dots .$$

If  $Y$  is a descendant of  $Y$  then we write  $Y < X$ .

For  $X \in \Pi_m$  and  $k \geq 0$ , define

$$X[m, k] = \{Y \in \Pi_{m+k} : Y < X\}$$

to be the collection of  $X$ 's  $k$ -descendants.

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An infinite sequence of real-valued functions  $\Phi_\bullet$  is **a chain of functions defined** on  $\Pi_\bullet$  if  $\Phi_m$  is defined on  $\Pi_m$  for all  $m$ .

# Intensive and Extensive

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Let  $(\Omega, \Pi_\bullet, \Phi_\bullet)$  be fixed.

$\Phi_\bullet$  is an **extensive** (**intensive**) chain of functions defined on  $\Pi_\bullet$  if the value of  $\Phi_m$  on any patch  $X \in \Pi_m$  is the **sum** (**average**) of the respective daughter function defined on any complete set of  $k$ -descendents of  $X$ . Formally,

$$\Phi_m(X) = \begin{cases} \sum_{Y \in X[m,k]} \Phi_{m+k}(Y), & \text{(extensive)} \\ \frac{\sum_{Y \in X[m,k]} \Phi_{m+k}(Y)h(Y)}{\sum_{Y \in X[m,k]} h(Y)}, & \text{(intensive)} \end{cases}$$

for all  $m, k \geq 0$  and  $X \in \Pi_m$ .

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for all  $m, k \geq 0$  and  $X \in \Pi_m$ .

**Example.** (extensive) The number of animals in a patch  $X \in \Pi_m$ .

**Example.** (intensive) The quality of a patch  $X \in \Pi_m$ .

# Kernels and Convolutions

---

Let  $(\Omega, \Pi_\bullet, \Phi_\bullet)$  be fixed.

Let  $I = \{x : x \geq 0\}$  and let  $h(X)$  be the area of a patch  $X \in \Pi_m$ .

Define  $K_m : \Pi_m \times \Pi_m \rightarrow I$  to be a (discrete) **kernel** for  $\Pi_m$  if

$$\sum_{Y \in \Pi_m} K_m(X, Y) h(Y) = 1, \quad \text{for all } X \in \Pi_m.$$

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Define the (discrete) **convolution** of  $K_m$  with  $\Phi_m$  at  $X \in \Pi_m$  to be

$$(K_m \circledast \Phi_m)(X) = \sum_{Y \in \Pi_m} K_m(Y, X)\Phi_m(Y)h(Y).$$

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A **chain of kernels** for  $\Pi_\bullet$  is an infinite sequence of kernels  $K_\bullet$  such that  $K_m$  is a kernel for  $\Pi_m$  for all  $m$ .



# Transition Rules

---

Fix  $(\Omega, \Pi_\bullet)$  and  $m \geq 0$ . Let  $N(X, t, m) \in \{0, 1, 2, \dots\}$  be the number of individuals in patch  $X \in \Pi_m$  at time  $t \geq 0$ , and let  $N(X, 0, m)$  be given. Let  $\Delta t > 0$ .

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Assume the following transition rules:

event	effect ( $\Delta N$ )	$p(\text{event})$
seed dispersal	+1	$fh(D_m \circledast N)(X) \Delta t + o(\Delta t)$
density-independent mortality	-1	$h(H_m \circledast \mu)(X)N(X) \Delta t + o(\Delta t)$
density-dependent mortality	-1	$\alpha(U_m \circledast N)(X)N(X) \Delta t + o(\Delta t)$

Here,  $f$  is the fecundity of an individual,  $h$  is the uniform mesh of  $\Pi_m$ ,  $\mu(X)$  represents mortality due to the environment,  $\alpha$  represents mortality due to crowding, and  $D_m$ ,  $H_m$ , and  $U_m$  are discrete and radially symmetric kernels for  $\Pi_m$ .

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Q. Rigorous reason for presence or absence of  $h$ ?

Q. Are the transition rules compatible for different  $m$ ?

# Master Equation

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$$\frac{\overline{\Delta N(X, t, m)}}{\Delta t} = fh(D_m \circledast N)(X) - N(X, t, m) \left[ h(H_m \circledast \mu)(X) + \alpha(U_m \circledast N)(X) \right],$$

where  $\overline{\Delta N(X, t, m)}$  (a continuous quantity) denotes the expected change in  $N(X, t, m)$  over a short time step  $\Delta t$  with a fixed configuration.

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seed dispersal	+1	$fh(D_m \otimes N)(X) \Delta t + o(\Delta t)$
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Q. Are the master equations compatible for different  $m$ ?

Q. Can the master equation **really** determine  $\overline{N(X, k\Delta t, m)}$ ?

# Central Equation

---

Letting

$$n(x, t) = \lim_{m \rightarrow \infty} \frac{N(X, t, m)}{h}$$

in the master equation

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we obtain a continuous space ( $h \rightarrow 0$ ) and time ( $\Delta t \rightarrow 0$ ) **central equation** (lots of hand-waving)

$$\frac{\partial n(x, t)}{\partial t} = f(D * n)(x) - n(x, t) \left[ (H * \mu)(x) + \alpha(U * n)(x) \right]$$

Here, the kernels  $D$ ,  $H$ , and  $U$  are the limits of  $D_m$ ,  $H_m$ , and  $U_m$  as  $m \rightarrow \infty$  and they integrate to 1 on  $\Omega$ .

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Q. Under what circumstances do all these limits exist?

Q. Should the LHS have a line over it?

# A Question

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How do short-range dispersal and local mortality in the central equation

$$\frac{\partial n(x, t)}{\partial t} = f(D * n)(x) - n(x, t) \left[ (H * \mu)(x) + \alpha(U * n)(x) \right]$$

give rise to a spatial logistic equation with diffusion?



# Short-Range Dispersal

---

Suppose that  $D$  is narrow. Given  $x, y \in \Omega$ , we write  $y = x + (a, b)$  where  $a, b \in \mathbb{R}$ . Then

$$(D*n)(x) \approx \int_{\Omega} D(y-x) \underbrace{\left[ n(x) + n_a(x)a + n_b(x)b + n_{aa}(x)\frac{a^2}{2} + n_{ab}(x)ab + n_{bb}(x)\frac{b^2}{2} \right]}_{n(y)} dy$$

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Since  $D$  is radially symmetric, its first moments vanish, as does its mixed second moment. Let

$$\sigma^2 = \int_{\Omega} D(y-x)a^2 dy = \int_{\Omega} D(y-x)b^2 dy$$

be the second moment of  $D$  in each of the  $a$ - and  $b$ -directions (these moments are equal by radial symmetry).

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be the second moment of  $D$  in each of the  $a$ - and  $b$ -directions (these moments are equal by radial symmetry). Then

$$\begin{aligned} (D * n)(x) &= n(x) + \frac{\sigma^2}{2} \left[ n_{aa}(x) + n_{bb}(x) \right] \\ &= n(x) + \frac{\sigma^2}{2} \Delta n(x). \end{aligned}$$

# A Spatial Logistic Equation with Diffusion

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So let dispersal be short-range

$$(D * n)(x) = n(x) + \frac{\sigma^2}{2} \Delta n(x).$$

And let landscape-induced mortality and crowding be local interactions

$$H(y - x) = U(y - x) = \delta(y - x).$$

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Then the central equation

$$\frac{\partial n(x, t)}{\partial t} = f(D * n)(x) - n(x, t) \left[ (H * \mu)(x) + \alpha(U * n)(x) \right]$$

becomes a spatial logistic equation with diffusion

$$\frac{\partial n(x, t)}{\partial t} = \frac{f\sigma^2}{2} \Delta n(x, t) + n(x, t) \left[ f - \mu(x) - \alpha n(x, t) \right].$$



# Reaction-Diffusion Model

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- Connect habitat-related fluctuations to population-related fluctuations for the special case in which dispersal is short-range and both forms of mortality are local.
- Population fluctuations around a spatially homogenous equilibrium solution.
- Spatial associations between these fluctuations and habitat mortality.
- Spatial associations among the population fluctuations themselves.

# Spatially-Homogeneous Equilibrium Solution

---

Let  $\bar{n}(x)$  be the equilibrium solution of the spatial logistic equation with diffusion

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when  $\mu(x) \equiv \bar{\mu}$ , where  $\bar{\mu}$  is a positive constant, and suppose that fluctuations  $\hat{\mu}(x)$  in the habitat are small with mean zero, i.e.,  $0 \leq |\hat{\mu}(x)| \leq \epsilon$  for all  $x \in \Omega$  and  $\int_{\Omega} \hat{\mu}(x) dx = 0$ .

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Let  $A$  and  $B$  be two functions defined on  $\Omega$ .

The **cross-correlation** of  $A$  and  $B$  is

$$C_{AB}(x - y) = \langle A(x)B(y) \rangle - \bar{A}\bar{B}$$

and the **auto-correlation** of  $A$  is

$$C_{AA}(x - y) = \langle A(x)A(y) \rangle - \bar{A}^2 - \delta(x - y)\bar{A},$$

# Fluctuations around the Equilibrium

---

## Theorem

Let  $n(x, t) = \bar{n} + \hat{n}(x, t)$  be the solution of the spatial logistic equation with diffusion

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The equilibrium  $\bar{n}(x)$  is positive, spatially homogeneous, and satisfies

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The population fluctuation  $\hat{n}(x, t)$  satisfies

$$\frac{\partial \hat{n}}{\partial t} = \frac{f\sigma^2}{2} \Delta \hat{n} - \bar{n}(\hat{\mu} + \alpha \hat{n}) + \mathcal{O}(\epsilon),$$

The *deterministic equation for the fluctuation around the mean.*

# Associations Between Fluctuations

---

## Theorem

The correlations  $C_{\hat{\mu}\hat{n}} = C_{\hat{\mu}\hat{n}}(x - y, t)$  and  $C_{\hat{n}\hat{n}} = C_{\hat{n}\hat{n}}(x - y, t)$  satisfy

$$\begin{aligned}\frac{\partial C_{\hat{\mu}\hat{n}}}{\partial t} &= \frac{f\sigma^2}{2} \Delta C_{\hat{\mu}\hat{n}} - (f - \bar{\mu})C_{\hat{\mu}\hat{n}} - \bar{n}C_{\hat{\mu}\hat{\mu}} + \mathcal{O}(\epsilon), \\ \frac{1}{2} \frac{\partial C_{\hat{n}\hat{n}}}{\partial t} &= \frac{f\sigma^2}{2} \Delta C_{\hat{n}\hat{n}} - (f - \bar{\mu})C_{\hat{n}\hat{n}} - \bar{n}C_{\hat{\mu}\hat{n}} + \mathcal{O}(\epsilon).\end{aligned}$$

The *deterministic cross-correlation* and *auto-correlation equations*.

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The *deterministic cross-correlation* and *auto-correlation equations*.

The mortality associated auto-correlation  $C_{\hat{\mu}\hat{\mu}} = C_{\hat{\mu}\hat{\mu}}(x - y)$  is treated as a model parameter.



# Pattern for the Mean

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## Theorem

Let  $n(x, t)$  be the solution of the central equation

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$$\frac{\partial n(x, t)}{\partial t} = f(D * n)(x) - n(x, t) \left[ (H * \mu)(x) + \alpha(U * n)(x) \right]$$

Then the population mean  $\bar{n}(t) = \langle n(x, t) \rangle$  satisfies

$$\frac{d\bar{n}}{dt} = \bar{n}(f - \bar{\mu} - \alpha\bar{n}) - (H * C_{\mu n})(0) - \alpha(U * C_{nn})(0) - \alpha\bar{n}U(0) + \mathcal{O}(\epsilon).$$

The *stochastic equation for the mean*.

# Associations

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## Theorem

Let  $n(x, t)$  be the solution of the central equation

$$\frac{\partial n(x, t)}{\partial t} = f(D * n)(x) - n(x, t) \left[ (H * \mu)(x) + \alpha(U * n)(x) \right]$$

The correlations  $C_{\mu n} = C_{\mu n}(x - y, t)$  and  $C_{nn} = C_{nn}(x - y, t)$  satisfy

$$\begin{aligned} \frac{\partial C_{\mu n}}{\partial t} &= [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{\mu n} - \bar{n}(H * C_{\mu\mu}) + \mathcal{O}(\epsilon), \\ \frac{1}{2} \frac{\partial C_{nn}}{\partial t} &= [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{nn} - \bar{n}(H * C_{\mu n}) + \bar{n}(fD - \alpha \bar{n}U) + \mathcal{O}(\epsilon). \end{aligned}$$

The *stochastic cross-correlation* and *auto-correlation* equations.

# Comments

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The stochastic equation for the mean

$$\frac{d\bar{n}}{dt} = \bar{n}(f - \bar{\mu} - \alpha\bar{n}) - (H * C_{\mu n})(0) - \alpha(U * C_{nn})(0) - \alpha\bar{n}U(0) + \mathcal{O}(\epsilon).$$

and the stochastic correlation equations

$$\begin{aligned}\frac{\partial C_{\mu n}}{\partial t} &= [fD - \bar{\mu} - \alpha\bar{n}(U + 1)] * C_{\mu n} - \bar{n}(H * C_{\mu\mu}) + \mathcal{O}(\epsilon), \\ \frac{1}{2} \frac{\partial C_{nn}}{\partial t} &= [fD - \bar{\mu} - \alpha\bar{n}(U + 1)] * C_{nn} - \bar{n}(H * C_{\mu n}) + \bar{n}(fD - \alpha\bar{n}U) + \mathcal{O}(\epsilon).\end{aligned}$$

Mortality associated auto-correlation  $C_{\mu\mu} = C_{\mu\mu}(x - y)$  is treated as a model parameter. The expressions  $H * C_{\mu\mu}$  and  $H * C_{\mu n}$  denote habitat associated mortality due to site quality, and  $U * C_{\mu n}$  and  $U * C_{nn}$  denote habitat associated mortality due to crowding. It can be shown that  $H * C_{\mu n}$  has a fixed sign, whereas  $U * C_{nn}$  can be either positive or negative.

# Stochastic and Deterministic Correlation equations

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$$\frac{\partial C_{\mu n}}{\partial t} = [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{\mu n} - \bar{n}(H * C_{\mu\mu}) + \mathcal{O}(\epsilon),$$

$$\frac{1}{2} \frac{\partial C_{nn}}{\partial t} = [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{nn} - \bar{n}(H * C_{\mu n}) + \bar{n}(fD - \alpha \bar{n}U) + \mathcal{O}(\epsilon).$$

Replacing  $(\mu, n)$  with  $(\hat{\mu}, \hat{n})$ , the stochastic correlation equations (above) reduce to the deterministic correlation equations (below) under suitable assumptions on the kernels, i.e., short-range dispersal and local mortality:  $D * K = \left(1 + \frac{\sigma^2}{2} \Delta\right) K + \mathcal{O}(\epsilon)$  and  $H(x) = U(x) = \delta(x)$

$$\frac{\partial C_{\hat{\mu}\hat{n}}}{\partial t} = \frac{f\sigma^2}{2} \Delta C_{\hat{\mu}\hat{n}} - (f - \bar{\mu})C_{\hat{\mu}\hat{n}} - \bar{n}C_{\hat{\mu}\hat{\mu}} + \mathcal{O}(\epsilon),$$

$$\frac{1}{2} \frac{\partial C_{\hat{n}\hat{n}}}{\partial t} = \frac{f\sigma^2}{2} \Delta C_{\hat{n}\hat{n}} - (f - \bar{\mu})C_{\hat{n}\hat{n}} - \bar{n}C_{\hat{\mu}\hat{n}} + \mathcal{O}(\epsilon).$$



# Initial behavior of solutions

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Recall the stochastic correlation equations

$$\frac{\partial C_{\mu n}}{\partial t} = [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{\mu n} - \bar{n}(H * C_{\mu\mu}) + \mathcal{O}(\epsilon),$$

$$\frac{1}{2} \frac{\partial C_{nn}}{\partial t} = [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{nn} - \bar{n}(H * C_{\mu n}) + \bar{n}(fD - \alpha \bar{n}U) + \mathcal{O}(\epsilon).$$

Recall that if  $C_{\mu n} < 0$  then individuals situated at  $x$  are located favorably with respect to the quality of the habitat at site  $y$ , if  $C_{\mu n} = 0$  then the relationship is neutral, and if  $C_{\mu n} > 0$  then the relationship is unfavorable.

# Initial behavior of solutions

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Recall the stochastic correlation equations

$$\frac{\partial C_{\mu n}}{\partial t} = [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{\mu n} - \bar{n}(H * C_{\mu\mu}) + \mathcal{O}(\epsilon),$$
$$\frac{1}{2} \frac{\partial C_{nn}}{\partial t} = [fD - \bar{\mu} - \alpha \bar{n}(U + 1)] * C_{nn} - \bar{n}(H * C_{\mu n}) + \bar{n}(fD - \alpha \bar{n}U) + \mathcal{O}(\epsilon).$$

Recall that if  $C_{\mu n} < 0$  then individuals situated at  $x$  are located favorably with respect to the quality of the habitat at site  $y$ , if  $C_{\mu n} = 0$  then the relationship is neutral, and if  $C_{\mu n} > 0$  then the relationship is unfavorable.

If individuals everywhere are initially randomly situated with respect to the quality of the landscape ( $C_{\mu n} = 0$ ), then

$$\frac{\partial C_{\mu n}}{\partial t} = -\bar{n}(H * C_{\mu\mu}).$$

It follows that if the habitat-related mortality clusters then  $C_{\mu n}$  will initially decrease.

# Stability of Equilibrium Patterns

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The stability and parameter dependence of equilibrium patterns can be examined using Fourier-transformed correlation equations (with  $\mathcal{F}[\partial/\partial x] = i\omega$ )

$$\begin{aligned}\frac{\partial \tilde{C}_{\hat{\mu}\hat{n}}}{\partial t} &= -\frac{f\sigma^2}{2}\omega^2 \tilde{C}_{\hat{\mu}\hat{n}} - (f - \bar{\mu})\tilde{C}_{\hat{\mu}\hat{n}} - \bar{n}\tilde{C}_{\hat{\mu}\hat{\mu}} \\ \frac{1}{2} \frac{\partial \tilde{C}_{\hat{n}\hat{n}}}{\partial t} &= -\frac{f\sigma^2}{2}\omega^2 \tilde{C}_{\hat{n}\hat{n}} - (f - \bar{\mu})\tilde{C}_{\hat{n}\hat{n}} - \bar{n}\tilde{C}_{\hat{\mu}\hat{n}}.\end{aligned}$$

This linear system can be written as

$$\frac{\partial \mathbf{x}}{\partial t} = \mathbf{M}(\mathbf{A}\mathbf{x} - \mathbf{b})$$

where

$$\mathbf{x}(\omega, t) = \begin{bmatrix} \tilde{C}_{\hat{\mu}\hat{n}} \\ \tilde{C}_{\hat{n}\hat{n}} \end{bmatrix}, \quad \mathbf{M} = \begin{bmatrix} 1 & 0 \\ 0 & 2 \end{bmatrix}, \quad \mathbf{A}(\omega) = \begin{bmatrix} k(\omega) & 0 \\ -\bar{n} & k(\omega) \end{bmatrix}, \quad \mathbf{b}(\omega) = \begin{bmatrix} \bar{n}\tilde{C}_{\hat{\mu}\hat{\mu}} \\ 0 \end{bmatrix},$$

and

$$k(\omega) = \bar{\mu} - (1 + \sigma^2\omega^2/2)f.$$

The forcing term  $\mathbf{b}(\omega)$  explicitly contains environmental stochasticity but not demographic stochasticity. However,  $\bar{n}$  does depend on demographic stochasticity.

# Stability of Equilibrium Patterns

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An equilibrium pattern arises by setting the derivative equal to  $\mathbf{0}$ ,

$$\mathbf{x}^* = \mathbf{A}^{-1}\mathbf{b} = \frac{\bar{n}}{k(\omega)^2} \begin{bmatrix} k(\omega) \\ \bar{n} \end{bmatrix} \tilde{C}_{\hat{\mu}\hat{\mu}},$$

where  $\mathbf{x}^* = \mathbf{x}^*(\omega)$ . The expression multiplying  $\tilde{C}_{\hat{\mu}\hat{\mu}}$  on the right-hand side is a transfer function.

The assumption  $f > \bar{\mu}$  implies that the double eigenvalue  $k(\omega)$  of  $\mathbf{A}(\omega)$  is negative for all  $\omega \in (-\infty, \infty)$ . Therefore,  $\mathbf{x}^*$  is stable for all  $\omega \in (-\infty, \infty)$ .

# What do Mathematicians Want?

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- Clear ecological Qs that produce interesting mathematical Qs
- Clear sets of model assumptions
- Make connections between mathematics and biology
- Really new mathematics would be nice (but not necessary)
- Promotion (existence, uniqueness, behavior, stability, persistence, bifurcation, asymptotics, ...)
- Good ecological data (!)
- Biological intuition (invite us to visit your field sites)
- ...