The effects of adaptive predator movement on coexistence of prey species in a spatially varying environment

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and

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Plan of the talk

- An approach to spatial dynamics: scale transition theory
- Predation-competition interactions in space
- Coexistence mechanisms arising from spatial dynamics
- The effects of optimal predator movement on species coexistence

Scale transition theory

- Discrete or continuous time
- Discrete or continuous space

λ_{ixt} : fitness in discrete-time

$\lambda_{ixt} N_{ixt}$: output of spatial location, x

x : point in continuous space (any dimension), a lattice point or patch

r_{ixt} : fitness in continuous time

Example: annual plants

$$\lambda_{jxt} = s_j(1 - g_{jxt}) + g_{jxt} Y_{jxt} e^{-C_{xt} - A_{xt}}$$

$$A_{xt} \; : \; \text{"apparent competition"}$$

$$\text{example: } A_{xt} = a_j P_{xt}$$

$$C_{xt} \; : \; \text{"competition"}$$

$$\text{examples: } C_{xt} = \sum_l \alpha_l g_{lxt} N_{lxt}$$

$$C_{xt} = \ln\left(1 + \sum_l \alpha_l g_{lxt} N_{lxt}\right)$$

Dynamics at different scales

"Output" of a spatial location

$$\lambda_{jxt} N_{jxt} \neq N_{jx,t+1}$$

However

$$\sum_x \lambda_{jxt} N_{jxt} = \sum_x N_{jx,t+1}$$

Landscape-level dynamics

$$\bar{N}_{t+1} = \tilde{\lambda}_t \bar{N}_t$$

Landscape-level fitness: “individual-average fitness”

$$\tilde{\lambda}_t = \frac{\bar{N}_{t+1}}{\bar{N}_t} = \frac{\sum_x N_{x,t+1}}{\sum_x N_{xt}} = \frac{\sum_x \lambda_{xt} N_{xt}}{\sum_x N_{xt}}$$

$$= \frac{\overline{\lambda_{xt} N_{xt}}^{x}}{\overline{N_{xt}}^{x}} = \overline{\lambda_{xt} N_{xt} / \bar{N}_t}^{x} = \overline{\lambda_{xt} \nu_{xt}}^{x}$$

ν_{xt} : "relative density at location x"

Individual average, spatial average, fitness-density covariance

$$\tilde{\lambda}_t = \overline{\lambda_{xt}\nu_{xt}}^{\,x} = \bar{\lambda}_t \cdot \bar{\nu}_t + \mathrm{cov}_x(\lambda_{xt}, \nu_{xt})$$

$$= \bar{\lambda}_t + \mathrm{cov}_x(\lambda_{xt}, \nu_{xt})$$

$$\bar{\lambda}_t = \text{"spatial average fitness"}$$

$$\mathrm{cov}(\lambda_t, \nu_t) = \text{"fitness-density covariance"}$$

Why does spatial structure matter to regional dynamics?

Spatial structure:

ν_{xt} varies with x

Fitness factors, $\mathbf{W}_x$ (e.g. C_{xt}, A_{xt} and E_{xt})

vary with x

$$\lambda_{xt} = f(\mathbf{W}_x)$$

Why does spatial structure matter to regional dynamics?

Regional dynamics determined by

$$\tilde{\lambda}_t = \bar{\lambda}_t + \mathrm{cov}(\lambda_t, \nu_t)$$

$\mathrm{cov}_x(\lambda_{xt}, \nu_{xt}) \neq 0$ (different fractions of the population have different fitnesses)

$$\bar{\lambda}_t = \overline{f(\mathbf{W}_x)}^x \neq f(\bar{\mathbf{W}})$$

because f is nonlinear

Predation competition-interactions in space

$\lambda_{jxt} = f(\mathbf{W}_x) = G_j(E_{jxt}, D_{jxt})$ for prey species j

E_{jxt} : environmental response

$D_{jxt} = C_{jxt} + A_{jxt}$: multispecies density-dependent response

e.g., $G_j(E_{jxt}, D_{jxt}) = s_j(1 - g_{jxt}) + g_{jxt} Y_j e^{-D_{xt}}$

Transforming the responses to simplify the equation

$$\lambda_{jxt} - 1 \approx \mathsf{E}_{jxt} - \mathsf{D}_{jxt} + \gamma_j \mathsf{E}_{jxt} \mathsf{D}_{jxt}$$

$$\mathsf{E}_{jxt} = G_j(E_{jxt}, D_j^*) - 1$$

$$\mathsf{D}_{jxt} = 1 - G_j(E_j^*, D_{jxt})$$

$$\tilde{\lambda}_{jt} - 1 \approx \overline{\mathsf{E}}_{jt} - \overline{\mathsf{D}}_{jt} + \gamma_j \operatorname{cov}(\mathsf{E}_{jt}, \mathsf{D}_{jt}) + \operatorname{cov}(\mathsf{E}_{jt} - \mathsf{D}_{jt}, \nu_{jt})$$

Coexistence by invasion analysis

$$\tilde{\lambda}_i \approx \tilde{\lambda}_i' - \Delta N + \Delta I + \Delta \kappa$$

$\tilde{\lambda}_i'$: nonspatial mechanisms

ΔN : relative nonlinearity

ΔI : the storage effect

$\Delta \kappa$: fitness-density covariance

Making it simple: seed bank model

$$\tilde{\lambda}_i \approx \tilde{\lambda}_i' - \Delta N + \Delta I + \Delta\kappa$$

$$(\tilde{\lambda}_i' - 1)/\beta_i = \overline{\mathsf{E}}_i/\beta_i - \overline{\overline{\mathsf{E}}_r/\beta_r}^{r\neq i}$$ Average fitness comparison

$$\Delta N = 0$$ Relative nonlinearity

$$\Delta I/\beta_i = \mathrm{cov}(\overline{E}_r^{r\neq i}, D^{\{-i\}}) - \mathrm{cov}(E_i, D^{\{-i\}})$$ The storage effect

$$\Delta\kappa/\beta_i = \mathrm{cov}\left(\mathsf{E}_i/\beta_i, \nu_i\right) - \overline{\mathrm{cov}\left(\mathsf{E}_r/\beta_r, \nu_r\right)}^{r\neq i}$$

$$+\,\mathrm{cov}\left(D^{\{-i\}}, \overline{\nu_r}^{r\neq i} - \nu_i\right)$$

Fitness-density covariance

$$\beta_j = \left(\frac{\partial\lambda_{jxt}}{\partial D_{xt}}\right)^*$$: rate of response to d.d.

$$G_j(E_{jxt}, D_{xt}) = a_j(E_{jxt}) + b_j(E_{jxt})c(D_{xt})$$

Making it simpler: spatio-temporal variation, two prey species

$$\frac{\tilde{\lambda}_i - 1}{\beta_i} \approx \overline{E}_i / \beta_i - \overline{E}_r / \beta_r$$

Storage effect

Fitness-density covariance

$$+ \left(\frac{\overline{C}'_r}{\overline{C}'_r - 1} + \theta_r \right) \left(\sigma_{E_r E_r} - \sigma_{E_i E_r} + \sigma_{\nu_r \nu_r} - \sigma_{\nu_i \nu_r} \right)$$

$\overline{C}'_r$: magnitude of competition

θ_r: response of predators to local abundance

$$\sigma_{E_j E_k} = \mathrm{cov}(E_j, E_k)$$

$$\sigma_{\nu_j \nu_k} = \mathrm{cov}(\nu_j, \nu_k)$$

How to get θ_r

Need an equation for predator dynamics

$$\lambda_{\mathrm{P}xt} = Y_r g_{rxt} e^{-C_{xt}} N_{rxt} \left(1 - e^{-aP_{xt}}\right) / P_{xt}$$

Assuming an idea free distribution, this equals 1 in every spatial location.

Hence
$$P_{xt} = f_r(\ln N_{rxt} + E_{rxt})$$
$$\theta_r = f_r'(\ln \bar{N}_r + E_r^*)$$

Making it simpler: spatio-temporal variation, two prey species

$$\frac{\tilde{\lambda}_i - 1}{\beta_i} \approx \bar{E}_i / \beta_i - \bar{E}_r / \beta_r$$

Storage effect

Fitness-density covariance

$$+\left(\frac{\bar{C}'_r}{\bar{C}'_r - 1} + \theta_r\right)\left(\sigma_{E_r E_r} - \sigma_{E_i E_r} + \sigma_{\nu_r \nu_r} - \sigma_{\nu_i \nu_r}\right)$$

$\bar{C}'_r$: magnitude of competition

θ_r: response of predators to local abundance

$$\sigma_{E_j E_k} = \mathrm{cov}(E_j, E_k)$$

$$\sigma_{\nu_j \nu_k} = \mathrm{cov}(\nu_j, \nu_k)$$

Effects of Predation

- Predation weakens competition by lowering prey (plant) densities
  - This weakens competition-based coexistence mechanisms and undermines coexistence
- With adaptive predator movement
  - predation-based mechanisms appear
    - Storage-effect due to apparent competition
    - Fitness-density covariance due to apparent competition
  - These may compensate for the reduction in competition-based mechanisms

The simple case: spatio-temporal variation, two prey species

$$\frac{\tilde{\lambda}_i - 1}{\beta_i} \approx \bar{E}_i / \beta_i - \bar{E}_r / \beta_r$$

$$+\left(\frac{\bar{C}_r'}{\bar{C}_r' - 1} + \theta_r\right)\left(\sigma_{E_r E_r} - \sigma_{E_i E_r} + \sigma_{\nu_r \nu_r} - \sigma_{\nu_i \nu_r}\right)$$

$\bar{C}_r'$: magnitude of competition

θ_r: reponse of predators to local abundance

$$\sigma_{E_j E_k} = \mathrm{cov}(E_j, E_k)$$

$$\sigma_{\nu_j \nu_k} = \mathrm{cov}(\nu_j, \nu_k)$$

Arbitrary spatial variation: spatio-temporal + pure spatial variation

$$\frac{\tilde{\lambda}_i - 1}{\beta_i} \approx \overline{\mathrm{E}_i} / \beta_i - \overline{\mathrm{E}_r} / \beta_r$$

$$+ \left(\frac{\overline{C}_r'}{\overline{C}_r' - 1} + \theta_r \right) \left(\sigma_{E_r E_r} - \sigma_{E_i E_r} + \sigma_{E_r \nu_r} - \sigma_{E_r \nu_i} \right)$$

Storage effect

$$+ \left(\frac{\overline{C}_r'}{\overline{C}_r' - 1} + \theta_r \right) \left(\sigma_{\nu_r \nu_r} - \sigma_{\nu_r \nu_i} + \sigma_{E_r \nu_r} - \sigma_{E_r \nu_i} \right)$$

Fitness-density covariance

$$+ \frac{1 - s_i}{\beta_i} \sigma_{E_i \nu_i} - \frac{1 - s_r}{\beta_r} \sigma_{E_r \nu_r}$$

Variable parameter	Type of Environmental variation	Type of dispersal	Covariance between Environment and competition		Covariance between fitness and density	
			resident	invader	resident	invader
V	spatio-temporal (st)	wide-spread (w)	+	0	0	0
	st	local retention (l)	+	0	-	+
	Pure spatial (ps)	w	+	0	0	0
	ps	l	+	0	+	+
G	st	w	+	0	-	+
		l	+	0	-	?
	ps	w	+	0	-	-
		l	+	0	?	?
YU	st	w	0	0	0	0
		l	0	0	-	+
	ps	w	0	0	0	0
		l	+	0	+	+

$$\lambda_{jx}(t) = s_j(1-g_j) + V_j Y_j g_j e^{-C_x - A_x}$$