# Coevolution of habitat use in stochastic environments

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In collaboration with Alex Hening (Tufts) and Dang Nguyen (University of Alabama)

February 13, 2020

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#### Can lead to...





4/20





## Fox & Eisenbach 1992

#### fertilized patches

Alternational Alternational

#### unfertilized patches







#### However, populations often aren't ideal...



However, populations often aren't ideal...



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Main questions: How should habitat selection of interacting species coevolve when environmental conditions vary in space and time? When is there selection for sink populations? What effect does spatio-temporal variation have on the ghost of competition past or enemy-free space?









Implicit space! Mass action!! Diffusion approximations!!!

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Assume

 $\mathbb{E}[x_i^\ell(t+\Delta t)-x_i^\ell(t)|x^\ell(t)]\approx x_i^\ell(t)\left(\sum_{j=1}^n a_{ij}^\ell x_j^\ell(t)+b_i^\ell\right)\Delta t,$ 

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and

 $\mathrm{Var}[x_i^\ell(t+\Delta t)-x_i^\ell(t)\mid x^\ell(t)]\approx \sigma_i^{\ell\ell}\left(x_i^\ell(t)\right)^2\Delta t$ 

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and

$$\operatorname{Var}[\mathrm{x}_{\mathrm{i}}^{\ell}(\mathrm{t} + \Delta \mathrm{t}) - \mathrm{x}_{\mathrm{i}}^{\ell}(\mathrm{t}) \mid \mathrm{x}^{\ell}(\mathrm{t})] \approx \sigma_{\mathrm{i}}^{\ell \ell} \left( \mathrm{x}_{\mathrm{i}}^{\ell}(\mathrm{t}) \right)^{2} \Delta \mathrm{t}$$

In limit  $\Delta t \downarrow 0$ , get the Itô stochastic differential equations (SDEs)

$$dx_i^{\ell}(t) = x_i^{\ell}(t) \left( \left( \sum_{j=1}^n a_{ij}^{\ell} x_j^{\ell}(t) + b_i^{\ell} \right) dt + dE_i^{\ell}(t) \right)$$

where  $E_i^{\ell}(t)$  is a Brownian motion with mean 0 and variance  $\sigma_i^{\ell\ell}t$ 

## Spatial coupling of patch dynamics

#### Assume

Assume  $Cov[x_i^{\ell}(t + \Delta t) - x_i^{\ell}(t), x_i^{m}(t + \Delta t) - x_i^{m}(t) | x(t)] \approx x_i^{\ell}(t) x_i^{m}(t) \sigma_i^{\ell m} \Delta t$ 

## Spatial coupling of patch dynamics

 $x_i(t) = \sum_{\ell=1}^k x_i^{\ell}(t)$  total density of species *i* 

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where  $E_i^{\ell}(t)$  are Brownian motions satisfying  $Cov[E_i^{\ell}(t), E_i^m(t)] = \sigma_i^{\ell m} t$ 

 $p_i^{\ell}$  fraction of species *i* in patch  $\ell$  where  $1 \leq i \leq n$  and  $1 \leq \ell \leq k$ 

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where  $B_i(t)$  are Brownian motions satisfying  $Var[B_i(t)] = t$ 





To persist or not to persist, that is the question

$$dx_i(t) = x_i(t) \left[ f_i(x(t)) dt + \sqrt{V_i(x(t))} dE_i(t) \right]$$

where  $E_i(t)$  a multivariate Brownian motion with  $Var[E_i(t)] = t$ .

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( $\bigstar$ ) is stochastically persistent if for all  $\varepsilon > 0$  there is  $\delta > 0$  s.t.

 $\limsup_{t\to\infty}\frac{\#\{1\leq\tau\leq t:\min_i x_i(t)\leq\delta\}}{t}\leq\varepsilon \text{ a.s. whenever }\min_i x_i(0)>0$ 

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When  $(\bigstar)$  compactly supported, Schreiber et al. [2011] introduced the sufficient condition:

$$\mathbb{E}\left[f_i(\widehat{x}) - \frac{V_i(\widehat{x})}{2}\right] \qquad (\clubsuit)$$

stationary  $\hat{x} = (\hat{x}_1, \dots, \hat{x}_n)$  s.t.  $\mathbb{P}[\min_i \hat{x}_i = 0] = 1$ .

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$$\max_{i} \mathbb{E}\left[f_{i}(\widehat{x}) - \frac{V_{i}(\widehat{x})}{2}\right] > 0$$

for all stationary  $\hat{x} = (\hat{x}_1, \dots, \hat{x}_n)$  s.t.  $\mathbb{P}[\min_i \hat{x}_i = 0] = 1$ .

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Hening and Nguyen [2018], Benaïm [2018] extended (\$) to non-compact domains (e.g. LV system) with additional condition to ensure tightness

 $(\bigstar)$ 

 $x(t) = (x_1(t), \ldots, x_n(t)) \le p_i^{\ell}$ 



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mutant  $y_{i'}(t)$  in spp  $i' \le q_{i'}^{\ell}$ 

$$x(t) = (x_1(t), \dots, x_n(t)) \text{ w/ } p_i^{\ell} \qquad \text{mutant } y_{i'}(t) \text{ in spp } i' \text{ w/ } q_{i'}^{\ell}$$
$$dx_i(t) = \sum_{\ell=1}^k p_i^{\ell} x_i(t) \left[ \left( \sum_{j=1}^n a_{ij}^{\ell} p_j^{\ell} x_j(t) + b_i^{\ell} \right) dt + dE_i^{\ell}(t) \right]$$

# $x(t) = (x_1(t), \dots, x_n(t)) \le p_i^{\ell}$ mutant $y_{i'}(t)$ in spp i' w/ $q_{i'}^{\ell}$ $dx_{i}(t) = \sum_{\ell=1}^{k} p_{i}^{\ell} x_{i}(t) \left[ \left( \sum_{j=1}^{n} a_{ij}^{\ell} p_{j}^{\ell} x_{j}(t) + a_{ii'} q_{i'}^{\ell} y_{i'}(t) + b_{i}^{\ell} \right) dt + dE_{i}^{\ell}(t) \right]$

$$\begin{aligned} x(t) &= (x_{1}(t), \dots, x_{n}(t)) \text{ w/ } p_{i}^{\ell} & \text{mutant } y_{i'}(t) \text{ in spp } i' \text{ w/ } q_{i}^{\ell} \\ dx_{i}(t) &= \sum_{\ell=1}^{k} p_{i}^{\ell} x_{i}(t) \left[ \left( \sum_{j=1}^{n} a_{ij}^{\ell} p_{j}^{\ell} x_{j}(t) + a_{ii'} q_{i'}^{\ell} y_{i'}(t) + b_{i}^{\ell} \right) dt + dE_{i}^{\ell}(t) \right] \\ dy_{i'}(t) &= \sum_{\ell=1}^{k} q_{i'}^{\ell} y_{i'}(t) \left[ \left( \sum_{j=1}^{n} a_{i'j}^{\ell} p_{j}^{\ell} x_{j}(t) + a_{i'i'}^{\ell} q_{i'}^{\ell} y_{i'}(t) + b_{i'}^{\ell} \right) dt + dE_{i'}^{\ell}(t) \right] \end{aligned}$$

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Theorem. Assume residents satisfy ( $\clubsuit$ ) (i.e. persistence) with a positive stationary distribution  $\hat{x} = (\hat{x}_1, \dots, \hat{x}_n)$ .

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$$\mathcal{I}(\boldsymbol{p},\boldsymbol{q}_{i'}) := \sum_{\ell} \boldsymbol{q}_{i'}^{\ell} \left( \sum_{j=1}^{n} a_{i'j}^{\ell} \boldsymbol{p}_{j}^{\ell} \mathbb{E}[\widehat{x}_{j}] + b_{i'}^{\ell} \right) - \frac{1}{2} \sum_{\ell,m=1}^{k} \boldsymbol{q}_{i'}^{\ell} \boldsymbol{q}_{i'}^{m} \sigma_{i'}^{\ell m} < 0$$

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then

$$\lim_{\delta\to 0} \mathbb{P}\left[\limsup_{t\to\infty} \frac{1}{t} \log y_{i'}(t) < 0 | y_{i'}(0) = \delta\right] = 1$$

unbeatable strategy [Hamilton, 1967] "This word was applied in just the same sense in which it could be applied to the 'minimax' strategy of a zero-sum two-person game.



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**Evolutionarily stable strategy** [Smith and Price, 1973] - a strategy that cannot be invaded by any other strategy that is initially rare



Invasion rates 
$$\mathcal{I}(p, q_i) := \sum_{\ell} q_i^{\ell} \left( \sum_{j=1}^n a_{ij}^{\ell} p_j^{\ell} \mathbb{E}[\hat{x}_j] + b_i^{\ell} \right) - \frac{1}{2} \underbrace{\sum_{j,\ell} q_i^{\ell} q_i^m \sigma_i^{\ell m}}_{j \in \mathcal{I}}$$

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Proposition. A necessary condition for p to be a coESS is: for all  $1 \le i \le n$   $f_i^{\ell}(p) - \sum_m p_i^m \sigma_i^{m\ell} = -\frac{1}{2}V_i(p)$  in patches  $\ell$  occupied by species iNote:  $f_i^{\ell}(p)$  are solutions to a system of linear equations

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imperfectly correlated fluctuations  $\Rightarrow$  local growth rate  $f_i^{\ell}(p) - \frac{\sigma_i^{\ell\ell}}{2} < 0$  in all occupied patches!!!!

# **Application: Competing species**

 $dx_{i}^{\ell}(t) = x_{i}^{\ell}(t) \left[ \left( r_{i}^{\ell} - x_{1}^{\ell}(t) - x_{2}^{\ell}(t) \right) dt + dE_{i}^{\ell}(t) \right] \qquad i = 1, 2$ 

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Now, spatially couple patches with  $X_i^{\ell} = p_i^{\ell} X_i \dots$ 



# **Application: Competing species** $dx_i(t) = x_i(t) \sum_{\ell} p_i^{\ell} \left[ \left( r_i^{\ell} - p_1^{\ell} x_1(t) - p_2^{\ell} x_2(t) \right) dt + dE_i^{\ell}(t) \right] \qquad i = 1, 2$







#### **Application:** Competing species $dx_{i}(t) = x_{i}(t) \sum_{i} p_{i}^{\ell} \left[ \left( r_{i}^{\ell} - p_{1}^{\ell} x_{1}(t) - p_{2}^{\ell} x_{2}(t) \right) dt + dE_{i}^{\ell}(t) \right]$ i = 1, 2 $r + \Delta r$ intrinsic growth rate $\Delta r > \frac{2v}{k} \Rightarrow$ ghost of competition past i.e. $p_1^{\ell} p_2^{\ell} = 0$ for all $\ell$ $\Delta r < \frac{2v}{k} \Rightarrow$ exorcism of the ghost species 1 species 2 i.e. $p_1^{\ell} p_2^{\ell} > 0$ for all $\ell$ 5 10 15 20 patch #





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You for listening! Questions?

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