Persistence of interacting structured populations in stochastic environments

Sebastian J. Schreiber
in collaboration with Gregory Roth

Department of Evolution and Ecology
and Center for Population Biology
University of California, Davis

December 14, 2012

Cantrell, Cosner, Hutson (1993) Proc. Royal Soc. Edinburgh, Dyn. Syst. Appl.

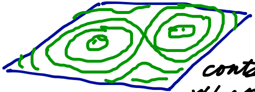
Considered reaction diffusion models of the form

$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i f_i(u, x)$$

conts. time → $\frac{\partial u_i}{\partial t}$

d_i: diffusion rate

$f_i(u,x)$: per-capita growth rate



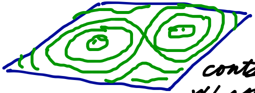
conts space w/ spatial heterog.

Cantrell, Cosner, Hutson (1993) Proc. Royal Soc. Edinburgh, Dyn. Syst. Appl.

Considered reaction diffusion models of the form

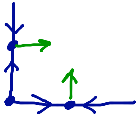
$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i f_i(u, x)$$

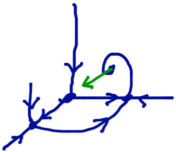
conts. time — diffusion rate — per-capita growth rate



conts space w/ spatial heterog.

Found sufficient conditions for coexistence (permanence)





Cantrell, Cosner, Hutson (1996) Rocky Mt. J. Math; Cantrell, Cosner (1998) JMB

- slow dispersers coexist if each can invade when rare somewhere
- competitors can coexist despite one being locally dominant everywhere.

Cantrell, Cosner, Hutson (1993) Proc. Royal Soc. Edinburgh, Dyn. Syst. Appl.

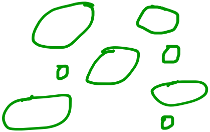
Considered reaction diffusion models of the form

$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i f_i(u, x)$$

~~conts.~~ discrete time → ∂t

d_i: diffusion rate

f_i: per-capita growth rate



~~conts space~~ discrete structure w/ spatial heterog.

Cantrell, Cosner, Hutson (1993) Proc. Royal Soc. Edinburgh, Dyn. Syst. Appl.

Considered reaction diffusion models of the form

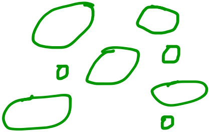
$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + u_i f_i(u,x)$$

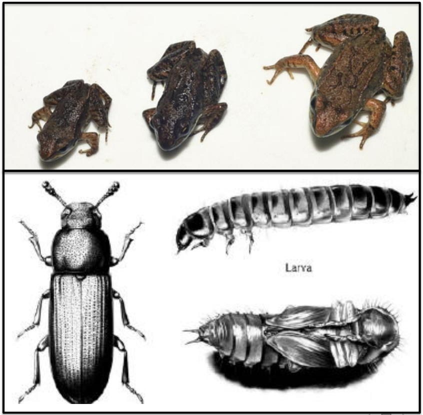
d_i: diffusion rate

$f_i(u,x)$: per-capita growth rate

∂t: discrete ~~conts.~~ time

discrete structure ~~conts space~~ w/ spatial heterog.

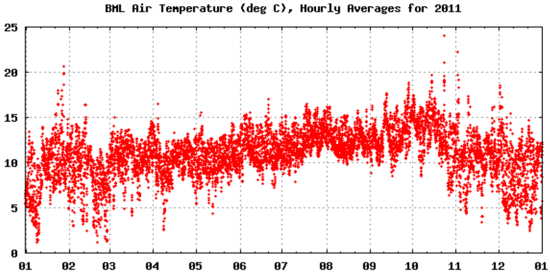




Environmental stochasticity

Lest men suspect your tale untrue, Keep probability in view. –John Gay

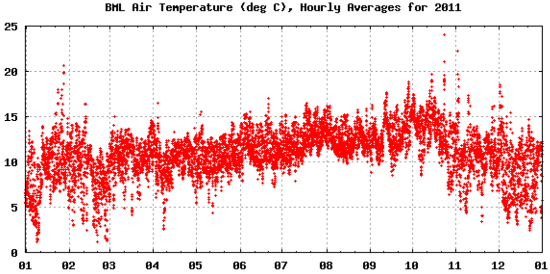
- fluctuations in temperature, precipitation, etc.

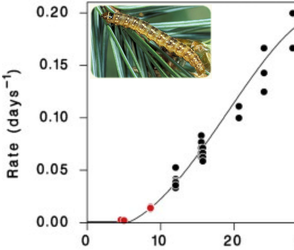


Environmental stochasticity

Lest men suspect your tale untrue, Keep probability in view. –John Gay

- fluctuations in temperature, precipitation, etc.
- demographic rates correlated to environmental conditions

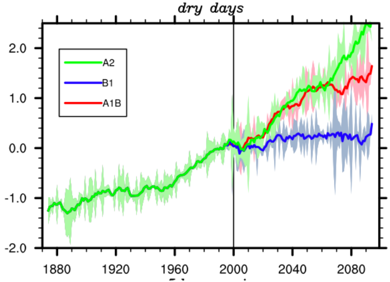




ENVIRONMENTAL STOCHASTICITY

Lest men suspect your tale untrue, Keep probability in view. –John Gay

- fluctuations in temperature, precipitation, etc.
- demographic rates correlated to environmental conditions
- variation predicted to increase in the next century

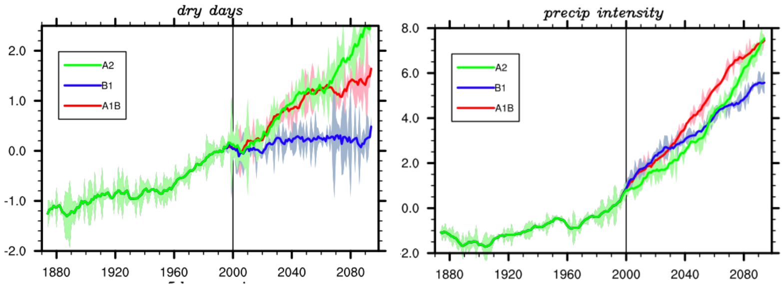


How do species interactions, population structure, and temporal fluctuations influence coexistence?

ENVIRONMENTAL STOCHASTICITY

Lest men suspect your tale untrue, Keep probability in view. –John Gay

- fluctuations in temperature, precipitation, etc.
- demographic rates correlated to environmental conditions
- variation predicted to increase in the next century



How do species interactions, population structure, and temporal fluctuations influence coexistence?

k interacting species

n_i individual states (e.g. size, age, location) for species i

$X^i = (X^{i1}, \ldots, X^{in_i})$ species i's abundances

$X = (X^1, \ldots, X^k)$ community state (stay in a compact set)

ξ environmental state (in a compact metric space)

$A_i(X, \xi)$ projection matrix for species i (continuous, primitive)

The environment-community dynamic:

$$\xi_1, \xi_2, \xi_3, \ldots \quad \text{ergodic, stationary sequence}$$

$$X^i_{t+1} = A_i(X_t, \xi_{t+1}) X^i_t \qquad i = 1, \ldots, k$$

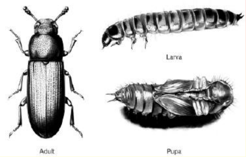
What ensures the long-term persistence of the community?

Prior work: Chesson (1982), Ellner (1982), Chesson & Ellner (1984), Ellner (1989), Hardin et al. (1988), Benaïm & S. (2009), S. et al. (2011), reviewed in S. (2012)

Examples

$$L_{t+1} = bA_t \exp(-\kappa_{el} L_t / V_{t+1} - \kappa_{ea} A_t / V_{t+1}) \exp(\xi_t^l)$$
$$P_{t+1} = (1 - \mu_l) L_t \exp(\xi_t^p)$$
$$A_{t+1} = (P_t \exp(-\kappa_{pa} A_t / V_{t+1}) + (1 - \mu_a) A_t) \exp(\xi_t^a)$$

Dennis et al. 1995, Constantino et al. 1997, Henson & Cushing 1997



Spatial Lottery Model:

$$X_{t+1}^{i\ell} = (1 - \varepsilon) X_t^{i\ell} + \varepsilon \frac{\sum_m d_{m\ell} \xi_{t+1}^{im} X_t^{im}}{\sum_{j,m} d_{m\ell} \xi_{t+1}^{jm} X_t^{jm}}$$

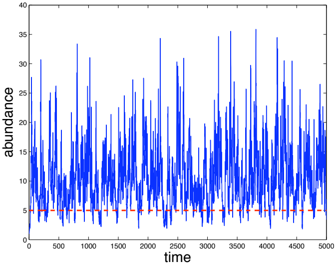
$$1 \le i \le k \quad 1 \le \ell \le n$$

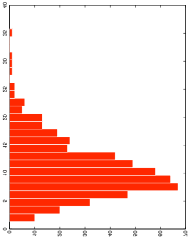
Chesson & Warner 1982, Chesson 1984, 2000
Muko & Iwasa 2000, 2008

The empirical measure for X_t given $X_0 = x$ is

$$\Pi_t^x = \frac{1}{t}\sum_{s=0}^{t-1} \delta_{X_s}$$

$\Pi_t^x(A)$ *is the fraction of time that* X *spends in the set* A *by time* $t-1$





The empirical measure for X_t given $X_0 = x$ is

$$\Pi_t^x = \frac{1}{t}\sum_{s=0}^{t-1} \delta_{X_s}$$

$\Pi_t^x(A)$ *is the fraction of time that* X *spends in the set* A *by time* $t-1$

The system is stochastically persistent if for all $\varepsilon > 0$ there exists $\delta > 0$ such that

$$\limsup_{t\to\infty} \Pi_t^x\left(\left\{\|X_t^i\| \le \delta \text{ for some } i\right\}\right) \le \varepsilon$$

with probability one.

An arbitrarily small fraction of time is spent below arbitrarily small densities

Main result

The (realized) per-capita growth rate of species i given $X_0 = x$ is

$$r_i(x) = \limsup_{t\to\infty} \frac{1}{t} \log \|A_i(X_{t-1}, \xi_t) \dots A_i(X_0, \xi_1)\|$$

$x^i > 0$ implies $r_i(x) \leq 0$ with probability one

$x^i = 0$ and $r_i(x) > 0$ implies that i increases when rare

Theorem(Roth & S.) If there exist weights $p_i > 0$ such that

$$\sum_i p_i r_i(x) > 0 \text{ with probability one}$$

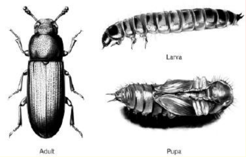
whenever $\prod_i \|x^i\| = 0$, then the system stochastically persists

If the community on average increases when rare, then it persists

Larvae-Pupae-Adult model

$$L_{t+1} = bA_t \exp(-\kappa_{el} L_t / V_{t+1} - \kappa_{ea} A_t / V_{t+1}) \exp(\xi_t^l)$$
$$P_{t+1} = (1-\mu_l) L_t \exp(\xi_t^p)$$
$$A_{t+1} = (P_t \exp(-\kappa_{pa} A_t / V_{t+1}) + (1-\mu_a) A_t) \exp(\xi_t^a)$$

Dennis et al. 1995, Constantino et al. 1997, Henson & Cushing 1997



Persistence requires that $r_1(0) > 0$

Theorem(Roth & S.) There exists a critical birth rate $b_{crit} > 0$ s.t.

Extinction: If $b < b_{crit}$, then $X_t = (L_t, P_t, A_t)$ converges almost surely to $(0,0,0)$ as $t \to \infty$.

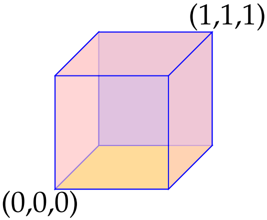
Stochastic persistence: If $b > b_{crit}$, then the LPA model stochastically persists

Spatial Lottery Model:

$$X_{t+1}^{i\ell} = (1-\varepsilon)X_t^{i\ell} + \varepsilon \frac{\sum_m d_{m\ell}\xi_{t+1}^{im}X_t^{im}}{\sum_{j,m} d_{m\ell}\xi_{t+1}^{jm}X_t^{jm}}$$

$$1 \le i \le k \quad 1 \le \ell \le n$$

Chesson & Warner 1982, Chesson 1984, 2000
Muko & Iwasa 2000, 2008



Say...2 species and 3 patches

persistent if $r_1(0,0,0) > 0$ and $r_2(1,1,1) > 0$

"mutual invasability"

Spatial Lottery Model:

$$X_{t+1}^{i\ell} = (1-\varepsilon)X_t^{i\ell} + \varepsilon \frac{\sum_m d_{m\ell}\xi_{t+1}^{im}X_t^{im}}{\sum_{j,m} d_{m\ell}\xi_{t+1}^{jm}X_t^{jm}}$$

$$1 \le i \le k \quad 1 \le \ell \le n$$

Chesson & Warner 1982, Chesson 1984, 2000
Muko & Iwasa 2000, 2008

slow dispersers: $r_1(0,\dots,0) = \max_\ell \mathbb{E}\left[\log\left((1-\varepsilon)+\varepsilon\frac{\xi_t^{1\ell}}{\xi_t^{2\ell}}\right)\right]$

"if each species has some region where it can locally coexist with or exclude the other, then for sufficiently low dispersal rates the population will coexist" – Cantrell, Cosner (1998) JMB

Spatial Lottery Model:

$$X_{t+1}^{i\ell} = (1-\varepsilon)X_t^{i\ell} + \varepsilon \frac{\sum_m d_{m\ell}\xi_{t+1}^{im}X_t^{im}}{\sum_{j,m} d_{m\ell}\xi_{t+1}^{jm}X_t^{jm}}$$

$$1 \le i \le k \quad 1 \le \ell \le n$$

Chesson & Warner 1982, Chesson 1984, 2000
Muko & Iwasa 2000, 2008

A slower disperser can coexist with a faster disperser that is competitively dominant everywhere –Cantrell, Cosner 1998

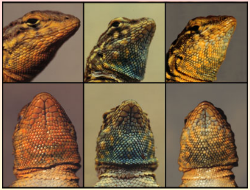
for a long-lived, slower disperser (species 1) occurs if

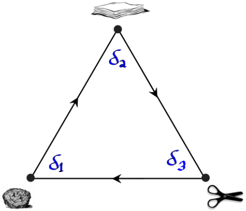
$$\mathbb{E}[\xi_t^{1\ell}] > \underbrace{\frac{1}{\mathbb{E}\left[\frac{1}{\frac{1}{k}\sum_m \xi_t^{2m}}\right]}}_{\text{Harmonic mean}} \qquad \text{for some } \ell$$

Rock-Paper-Scissor Lottery Model:

$$X_{t+1}^{ir} = (1-\varepsilon)X_t^{ir} + \varepsilon \frac{\sum_s d_{sr}\xi_{t+1}^{ij,s} X_t^{js} X_t^{is}}{\sum_{j,s} d_{sr}\xi_{t+1}^{j\ell,s} X_t^{js} X_t^{\ell s}}$$

$i = 1$ rock, $i = 2$ paper, $i = 3$ scissor





Each strategy has an equilibrium with
a positive stochastic growth rate r_i^+
a negative stochastic growth rate r_i^-

Persistence requires that $\prod_i r_i^+ > \prod_i |r_i^-|$

Product of invasion rates exceeds product of exclusion rates

Concluding Remarks

- For structured interacting populations in a fluctuating environment,

$$X^i_{t+1} = A_i(X_t, \xi_{t+1})X^i_t \qquad i = 1, \dots, k$$

there is a coexistence criterion:

$$\sum_i p_i r_i(x) > 0 \text{ with probability one when } \prod_i \|x^i\| = 0$$

If the community on average increases when rare, then the community persists

- This criterion applies to models with overcompensating density dependence, corresponds to *mutual invasibility* for two species models, and can be more subtle for higher dimensional communities.

FUTURE DIRECTIONS

- similar results for continuous-time processes e.g SDEs with Steve Evans, Alexandru Henning (Berkeley)
- exclusion criterion (with G. Roth)

$$\sum_i p_i r_i(x) < 0 \text{ with probability one if } \prod_i \|x^i\| = 0$$

If the community on average decreases when rare, then it is extinction prone

- "weak noise, weakly structured" approximations (ala Chesson, Tuljapurkar) of $r_i(x)$ to gain further analytical insights into the role of population structure and temporal fluctuations on coexistence.

FUTURE DIRECTIONS

- similar results for continuous-time processes e.g SDEs with Steve Evans, Alexandru Henning (Berkeley)
- exclusion criterion (with G. Roth)

$$\sum_i p_i r_i(x) < 0 \text{ with probability one if } \prod_i \|x^i\| = 0$$

If the community on average decreases when rare, then it is extinction prone

- "weak noise, weakly structured" approximations (ala Chesson, Tuljapurkar) of $r_i(x)$ to gain further analytical insights into the role of population structure and temporal fluctuations on coexistence.

a belated HAPPY B-DAY CHRIS!

Thank you for listening!
and NSF for funding