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Demographic stochasticity versus spatial variation in the competition between fast and slow dispersers

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Outline

- Elements of population dynamics
- Birth-death processes & fluctuations
- Competition & evolutionary dynamics
- Spatial inhomogeneities & mobility
- Modeling, analysis & conclusions

Elements of population dynamics

Malthusian growth: population $u(t)$ satisfies

$$\frac{du}{dt} = \gamma u$$

$$\Downarrow$$

$$u(t) = u(0)\, e^{\gamma t}$$

Elements of population dynamics

Logistic growth : growth rate *decreases* with u

$$\frac{du}{dt} = \left(\gamma - \frac{u}{n}\right)u$$

$$\Downarrow$$

$$u(t) \to n\gamma \text{ as } t \to \infty$$

Birth-death processes & fluctuations

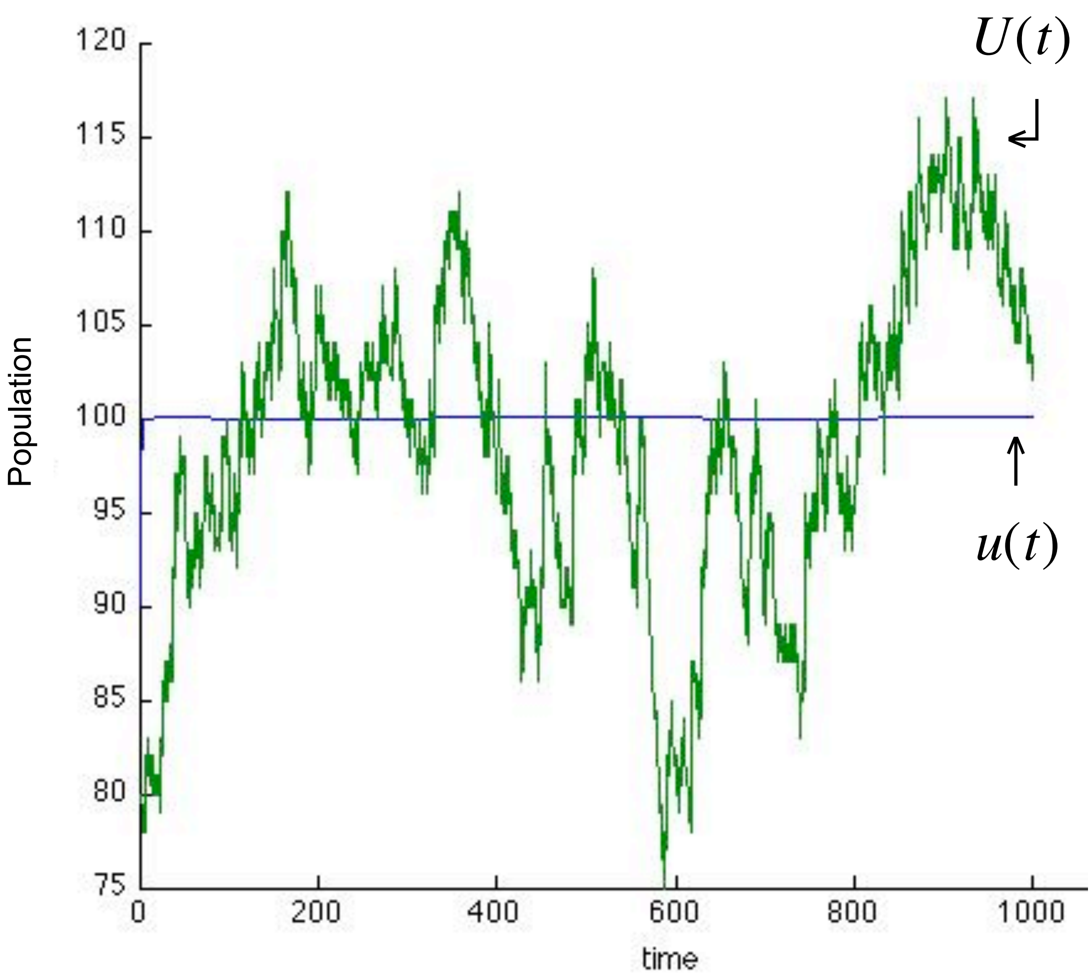
$$U(t) = \text{population at time } t$$

$$p_N(t) \ = \ \mathrm{P}\{U(t) = N\}$$

$$\textit{Master Equation}:$$

$$\frac{dp_N}{dt} = \gamma(N-1)\,p_{N-1} - \gamma N p_N + \frac{(N+1)^2}{n}\,p_{N+1} - \frac{N^2}{n}\,p_N$$

Birth-death processes & fluctuations



Growth rate

$\gamma = 1$

Capacity

$n = 100$

Birth-death processes & fluctuations

$$\text{Defining } u(t) = \mathrm{E}\{U(t)\} = \sum_{N=1}^{\infty} N p_N(t)$$

$$\Downarrow$$

$$\frac{du}{dt} = \left(\gamma - \frac{u}{n}\right) u - \frac{\mathrm{Var}\{U\}}{n}$$

$$\textit{Variance}\ \ \mathrm{Var}\{U\} \equiv \mathrm{E}\{U^2\} - \mathrm{E}\{U\}^2 > 0$$

$$\approx O(u) \text{ in quasistationary state}$$

Competition & evolutionary dynamics

Competing species with populations $u_1(t)$ & $u_2(t)$:

$$\frac{du_1}{dt} = \left(\gamma_1 - \frac{\alpha_1 u_1 + \beta_1 u_2}{n}\right) u_1$$

$$\frac{du_2}{dt} = \left(\gamma_2 - \frac{\alpha_2 u_1 + \beta_2 u_2}{n}\right) u_2$$

Principle of *competetive exclusion* :

generally one or the other prevails …

Spatial inhomogeneities & mobility

- ***Faster*** dispersers or ***slower*** dispersers may have an advantage in inhomogeneous environments…

- … which in turn would affect whether dispersal rates evolve toward faster or slower values.

- Examples: spatio-temporal variability in the environment tends to ***increase*** dispersal rates …

- … but spatial variability alone may ***reduce*** dispersal rates.

Mathematical modeling & analysis

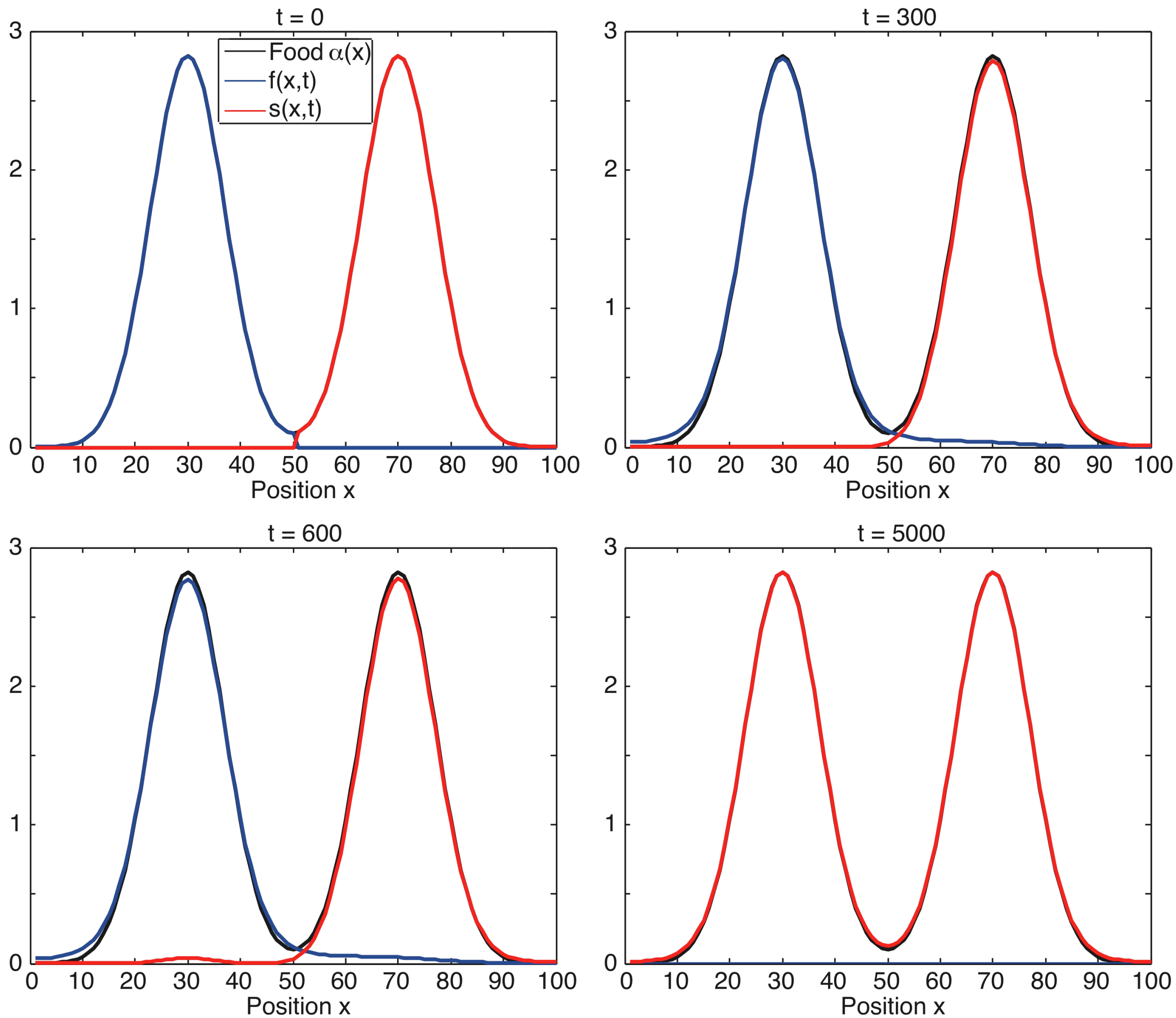
- Hastings (*Th. Pop. Bio.* 1983) and Dockery, Hutson, Mischaikow & Pernarowski, (*J. Math. Bio.* 1998): ***deterministic***, ***continuous population***, ***continuous space*** models of N species in inhomogenous environment:

$$\frac{\partial u_i}{\partial t} = D_i \nabla^2 u_i + u_i \left(\gamma(x) - \frac{1}{n} \sum_{i=1}^{N} u_i \right)$$

where $u_i(x,t)$ = population of i^{th} species, D_i = dispersal rate of i^{th} species, and $n\gamma(x)$ = heterogeneous carrying capacity.

- **Theorem:** in ***pairwise*** competition the ***slower*** dispersing species always drives a competing species to extinction.

Direct numerical simulations



- Dockery *et al* conjectured that the "victory" of the slower competitor generalizes beyond pair-wise competitions suggesting that dispersal rates tend to evolve towards zero in environments with any spatial variation.

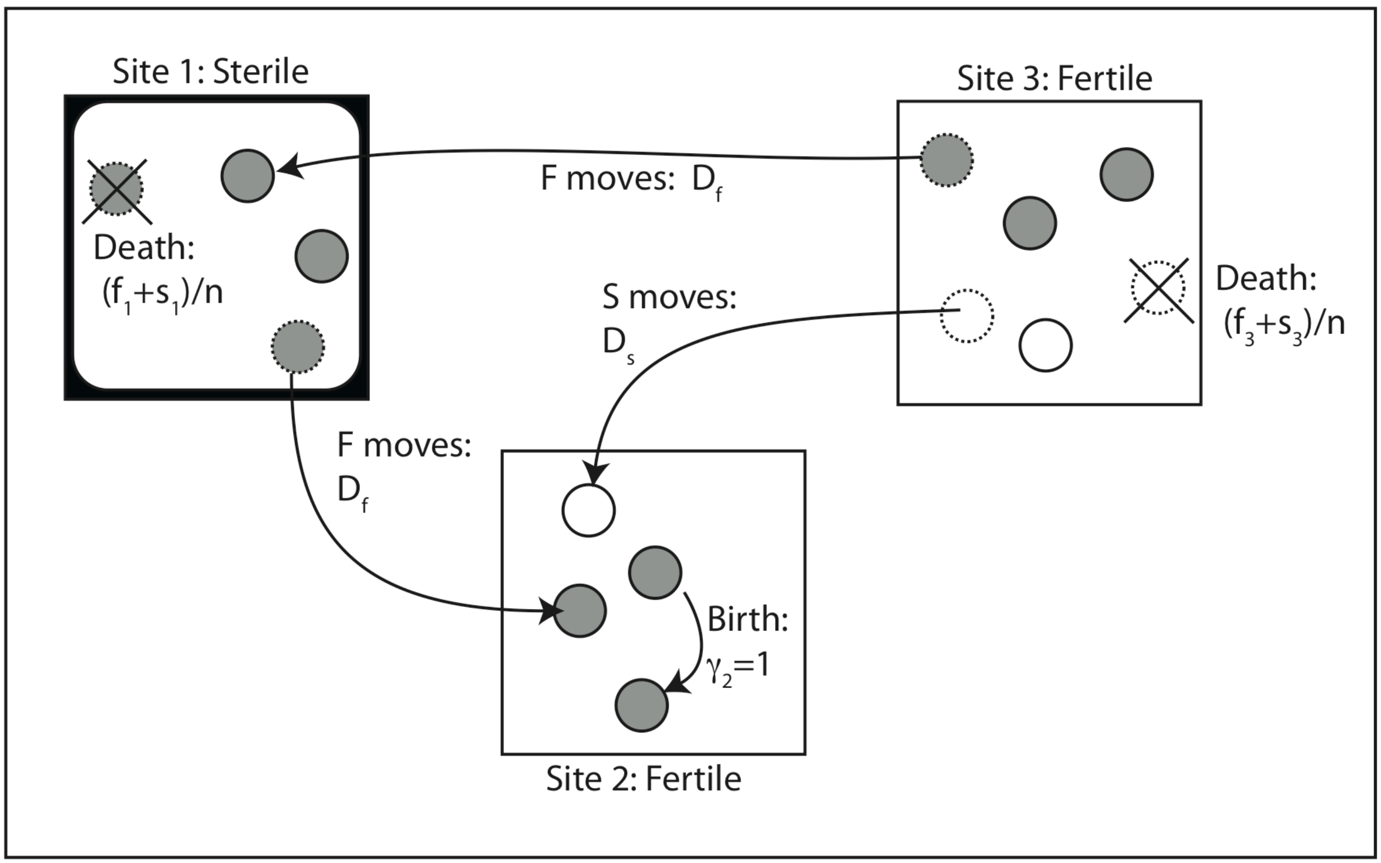
- ***Question***: how much does this qualitative conclusion depend on the ***continuous population*** assumption?

- …. is the conclusion robust under the inclusion of ***demographic fluctuations***, a.k.a., birth-death noise?

- Kessler & Sander *Physical Review E* (2009) performed Monte-Carlo simulations of discrete population version of the reaction-diffusion model suggesting the answer ….

- … ***no***.

- L = spatial sites ($1 \leq i \leq L$) with γ_i = growth rate at site i
- F_i = number of fast-dispersers, hopping rate D_f, at site i
- S_i = number of slow-dispersers, hopping rate D_s, at site i
- n = population scale … carrying capacity at a site i is $n\gamma_i$



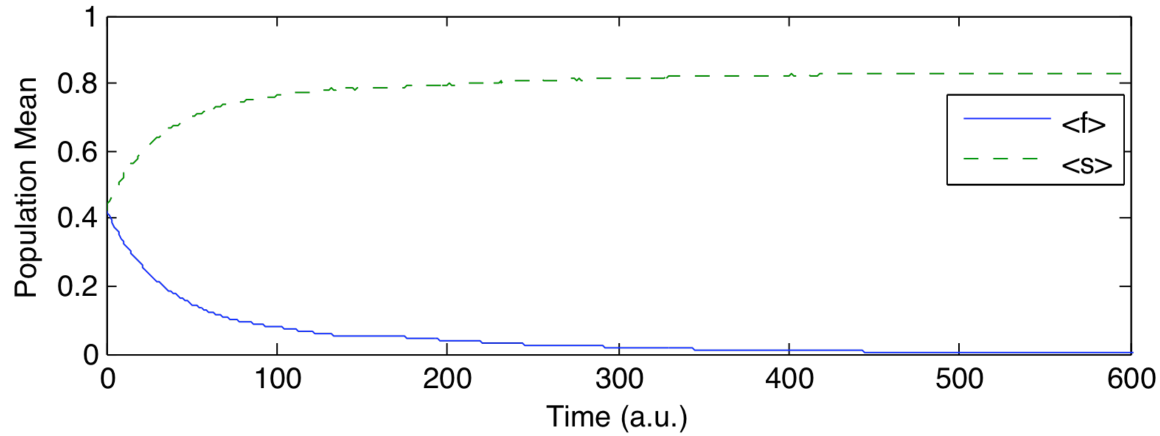
Moments:

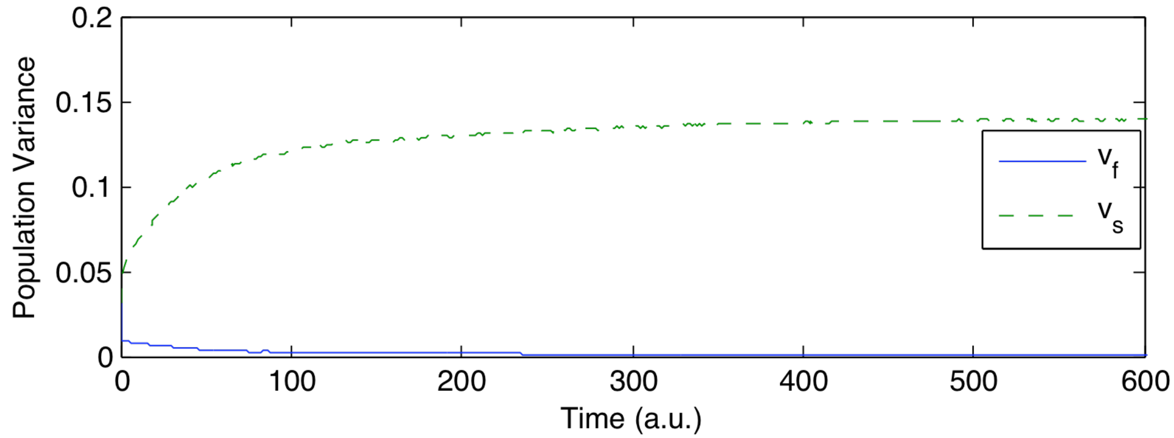
$$\langle f \rangle = \mathrm{E}\left\{ \lim_{L \to \infty} \frac{1}{L} \sum_{i=1}^{L} \frac{F_i}{n} \right\}$$

$$v_f = \langle f^2 \rangle - \langle f \rangle^2 = \mathrm{E}\left\{ \lim_{L \to \infty} \frac{1}{L} \sum_{i=1}^{L} \left(\frac{F_i}{n} - \langle f \rangle \right)^2 \right\}$$

Et cetera …

Direct (Monte-Carlo) simulations



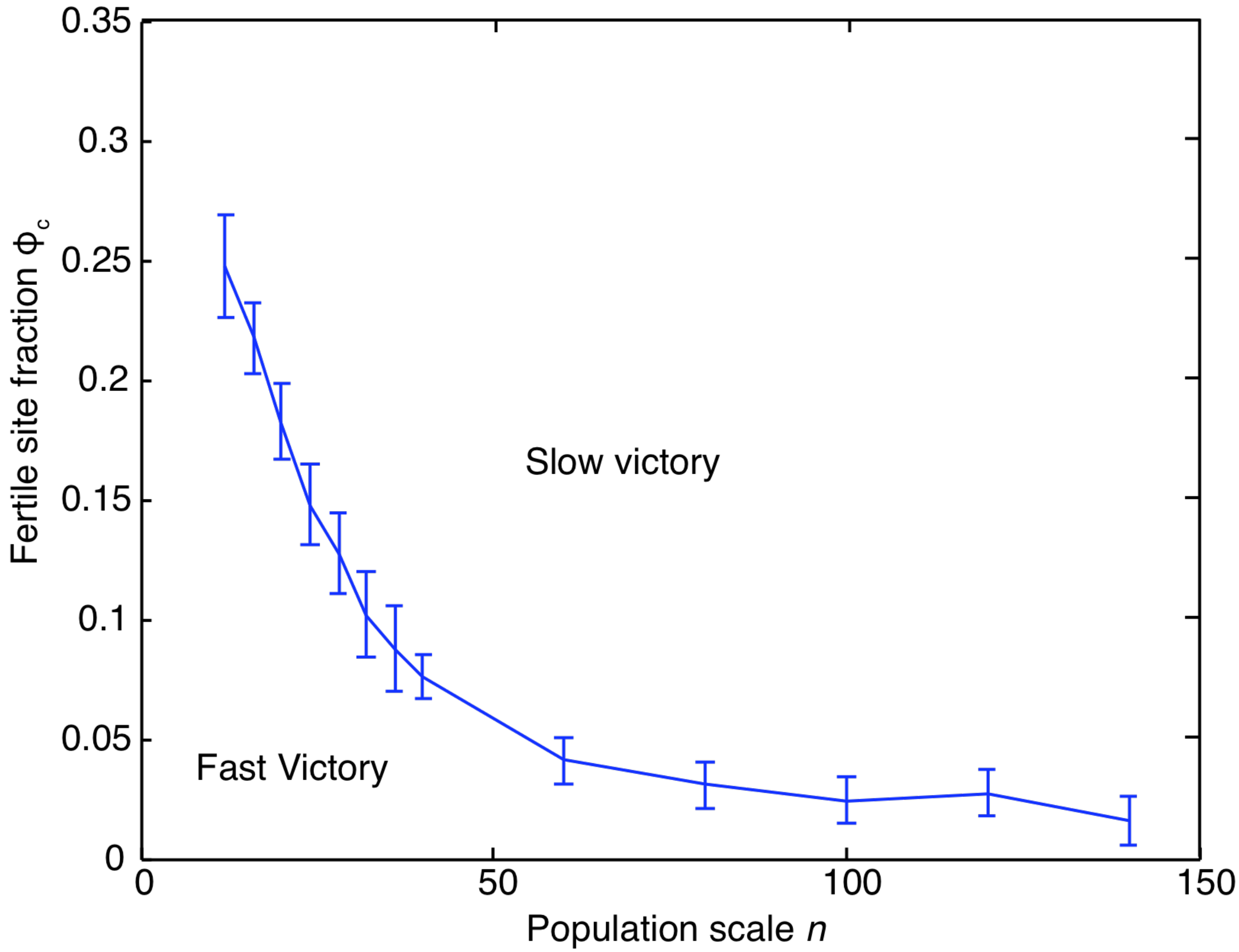


In these simulations $\gamma = 0$ or 1 with $\phi = \mathrm{E}\{\gamma\} = 0.85$

$n = 50$, $D_f = 10$, and $D_s = 0$.

(Averaged over $L = 100$ sites and 100 realizations.)

Direct (Monte-Carlo) simulations



$D_f = 10$, and $D_s = 0$.

Moment evolution equations

NO CLOSURE!

$$\frac{d\langle f\rangle}{dt} = \langle \gamma f\rangle - \langle fs\rangle - \langle f\rangle^2 - v_f$$

$$\frac{dv_f}{dt} = -\,2D_f\left(v_f - \frac{\langle f\rangle}{n}\right) + \frac{\langle \gamma f\rangle + \langle f\rangle^2 + v_f + \langle fs\rangle}{n} +$$

$$+\;2\left(\langle \gamma f^2\rangle - \langle \gamma f\rangle\langle f\rangle + \langle f\rangle^3 + \langle f\rangle v_f - \langle f^3\rangle + \langle f\rangle\langle fs\rangle - \langle f^2 s\rangle\right)$$

Et cetera …

Simplifying limits and closure …

- Let $\gamma_i = 0$ or 1 …

  … and define $\phi = \mathrm{E}\{\gamma\}$ so $\phi(1-\phi) = \mathrm{Var}\{\gamma\}$

- Let $D_f \to \infty$ …

  … then $v_f \to \langle f\rangle / n$

  … and $\langle \gamma f\rangle \to \phi\langle f\rangle$

  … and $\langle fs\rangle \to \langle f\rangle\langle s\rangle$, etc.

- Let $D_s \to 0$ …

  … then (for compatible initial data) $\langle \gamma s\rangle = \langle s\rangle$.

Exact reduced system

$$p(t) \equiv \frac{\langle s \rangle}{\phi} \qquad v_p(t) \equiv \frac{v_s(t)}{\phi} - p(t)^2(1-\phi) \qquad q(t) \equiv \frac{\langle f \rangle}{\phi}$$

$$\frac{dq}{dt} = \phi\left(1 - q - p - \frac{1}{n\phi}\right)q$$

$$\xi = \frac{\left\langle \left(s_i - \langle s \rangle\right)^3 \right\rangle}{\phi^3}$$

$$\frac{dp}{dt} = \left(1 - \phi q - p - \frac{v_p}{p}\right)p$$

$$\downarrow$$

$$\downarrow$$

$$\frac{dv_p}{dt} = 2\left(1 - \phi q - 2p + \frac{1}{2n}\right)v_p + \frac{(1 + p + \phi q)p}{n} - 2\xi$$

Approximate

~~Exact~~ reduced system

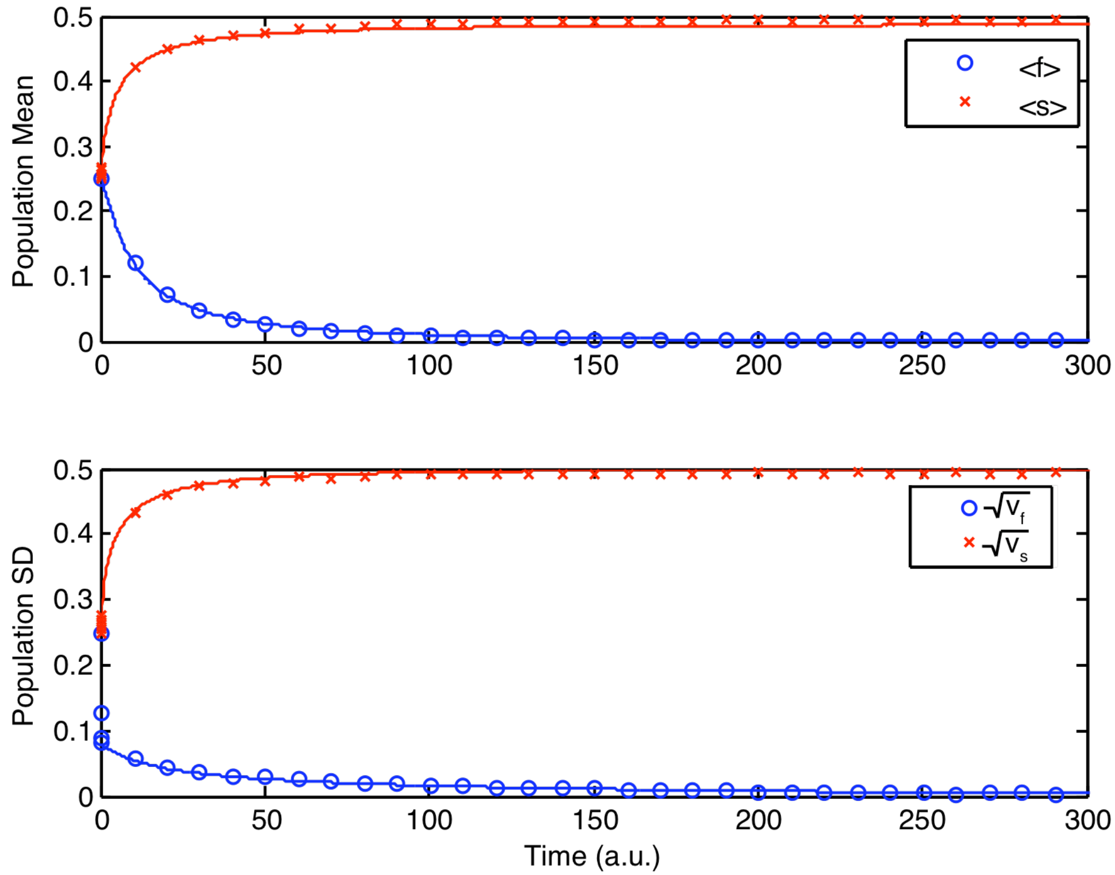
$$p(t) \equiv \frac{\langle s \rangle}{\phi} \qquad v_p(t) \equiv \frac{v_s(t)}{\phi} - p(t)^2 (1-\phi) \qquad q(t) \equiv \frac{\langle f \rangle}{\phi}$$

$$\frac{dq}{dt} = \phi \left(1 - q - p - \frac{1}{n\phi} \right) q$$

$$\frac{dp}{dt} = \left(1 - \phi q - p - \frac{v_p}{p} \right) p$$

$$\frac{dv_p}{dt} = 2 \left(1 - \phi q - 2p + \frac{1}{2n} \right) v_p + \frac{(1 + p + \phi q) p}{n} - \cancel{2\xi}$$

Theory versus simulations

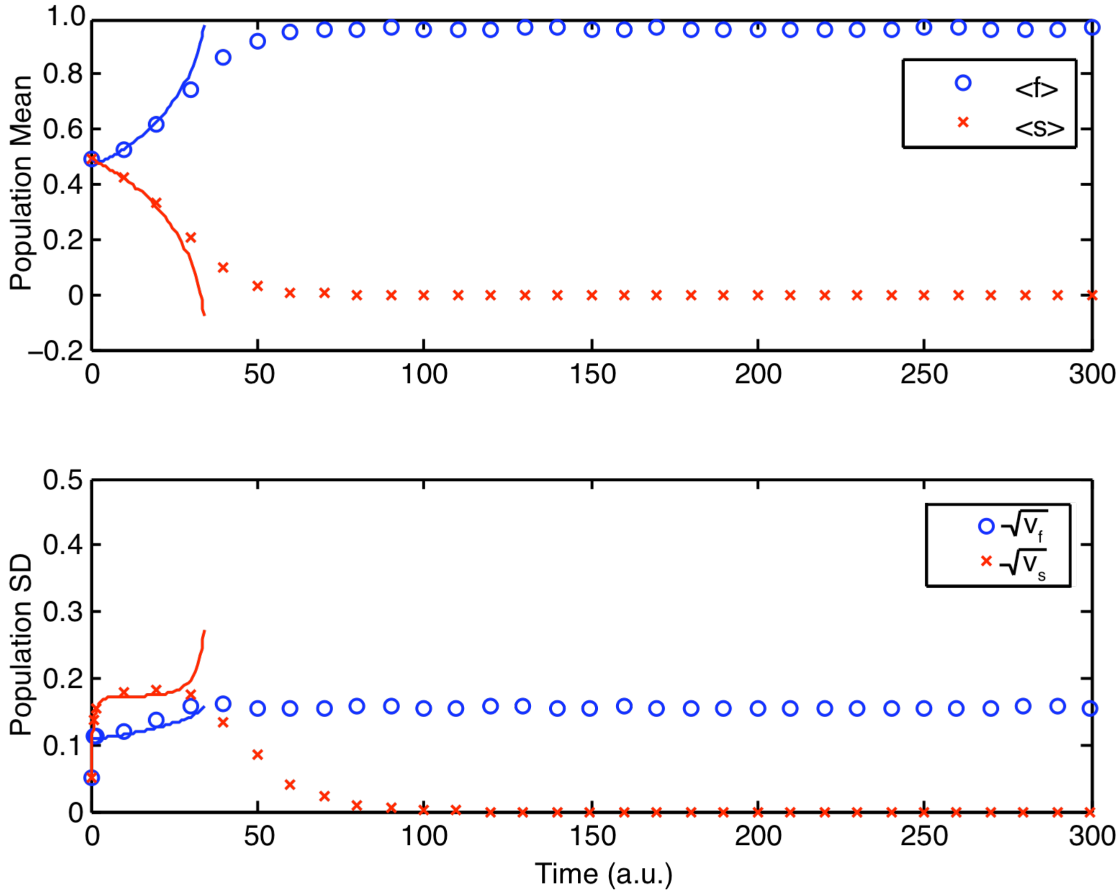


Solid lines: ODEs setting $\xi = 0$, Circles & crosses: simulations.

Here $\phi = E\{\gamma\} = 0.50$, $n = 40$, $D_f = 10$, and $D_s = 0.001$

(Averaged over $L = 100$ sites and 100 realizations.)

Theory versus simulations

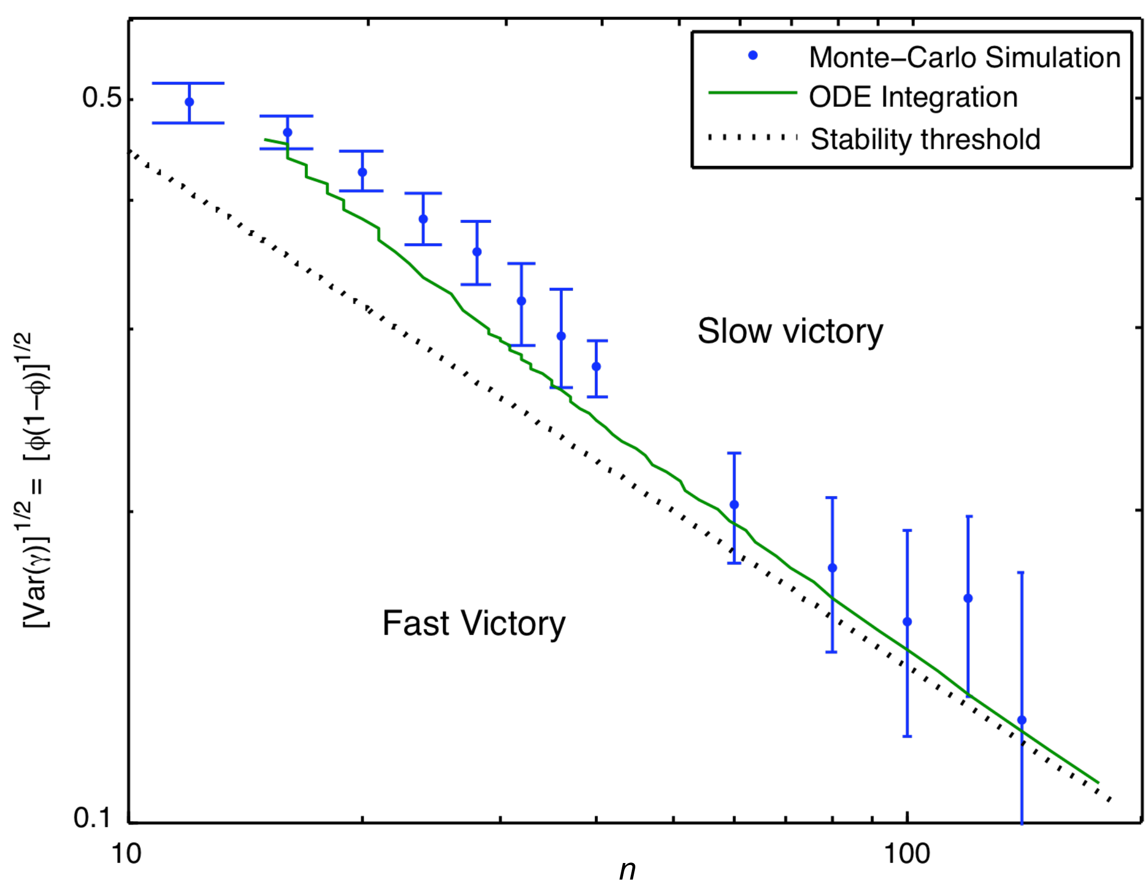


Solid lines: ODEs setting $\xi = 0$, Circles & crosses: simulations.

Here $\phi = \mathrm{E}\{\gamma\} = 0.99$, $n = 40$, $D_f = 10$, and $D_s = 0.001$

(Averaged over $L = 100$ sites and 100 realizations.)

Theory versus simulations



— threshold from ODEs setting $\xi = 0$: Slow wins ***or*** ODEs ***break down***!

(Simulations: $D_f = 10$ & $D_s = 0$, averaged over $L = 100$ sites and 100 realizations.)

Approximate

~~Exact~~ reduced system

$$p(t) \equiv \frac{\langle s \rangle}{\phi} \qquad v_p(t) \equiv \frac{v_s(t)}{\phi} - p(t)^2 (1 - \phi) \qquad q(t) \equiv \frac{\langle f \rangle}{\phi}$$

$$\frac{dq}{dt} = \phi \left(1 - q - p - \frac{1}{n\phi} \right) q$$

$$\frac{dp}{dt} = \left(1 - \phi q - p - \frac{v_p}{p} \right) p$$

$$\frac{dv_p}{dt} = 2\left(1 - \phi q - 2p + \frac{1}{2n} \right) v_p + \frac{(1 + p + \phi q)p}{n} - \cancel{2\xi}$$

Slow species' stability/sensitivity:

Fixed points of the $\xi \equiv 0$ system (for $n \geq 8$): $\left(q,p,v_p\right) =$

$$\left(0,0,0\right) \quad \rightarrow \textit{All extinct}$$

$$\left(1-\frac{1}{n\phi},\ 0,\ 0\right) \quad \rightarrow \textit{Fast wins}$$

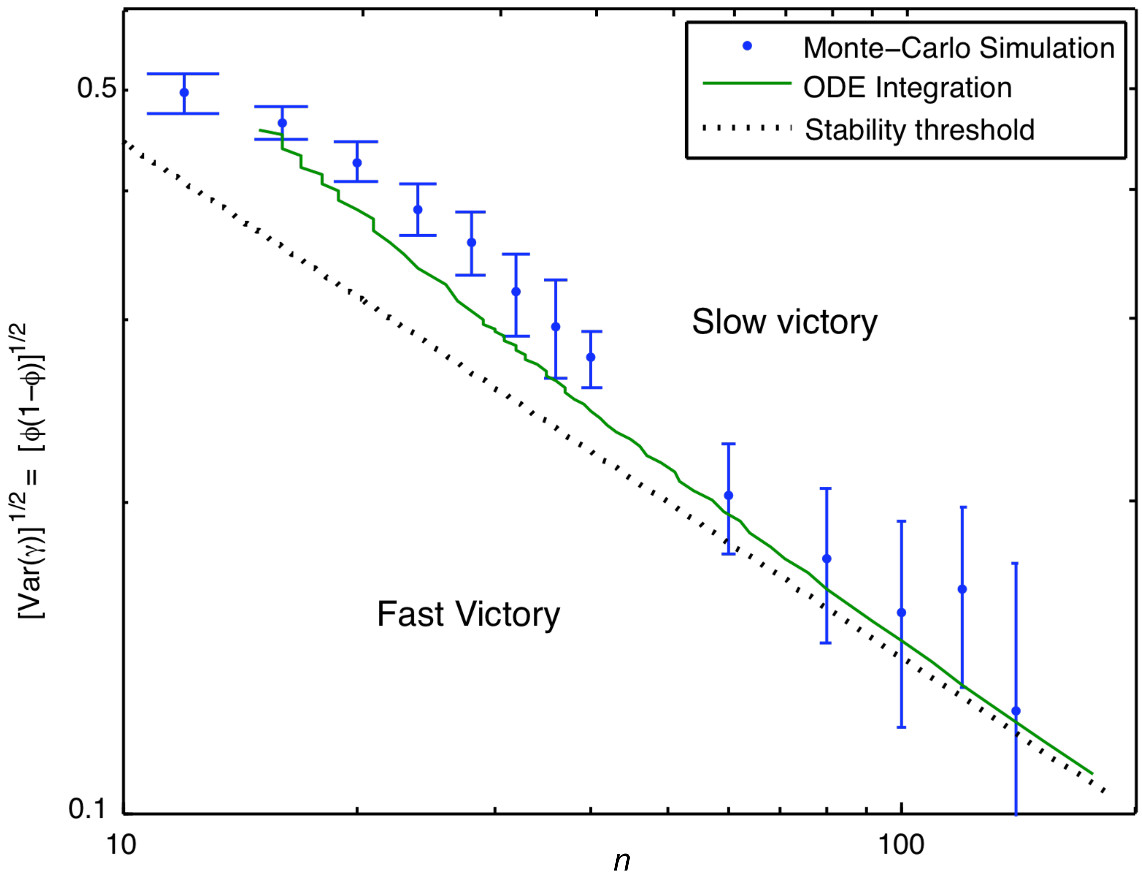
$$\left(0,\ \frac{3}{4}+\sqrt{\frac{n-8}{16n}},\ \frac{1}{8}-\sqrt{\frac{n-8}{64n}}+\frac{1}{2n}\right) \quad \rightarrow \textit{Slow wins}$$

$$\left(0,\ \frac{3}{4}-\sqrt{\frac{n-8}{16n}},\ \frac{1}{8}+\sqrt{\frac{n-8}{64n}}+\frac{1}{2n}\right) \quad \rightarrow \textit{Slow's viability boundary}$$

Slow wins fixed point is stable (against invasion by *Fast*) when

$$n > \frac{2}{\phi(1-\phi)} = \frac{2}{\mathrm{Var}\{\gamma\}}$$

Theory versus simulations



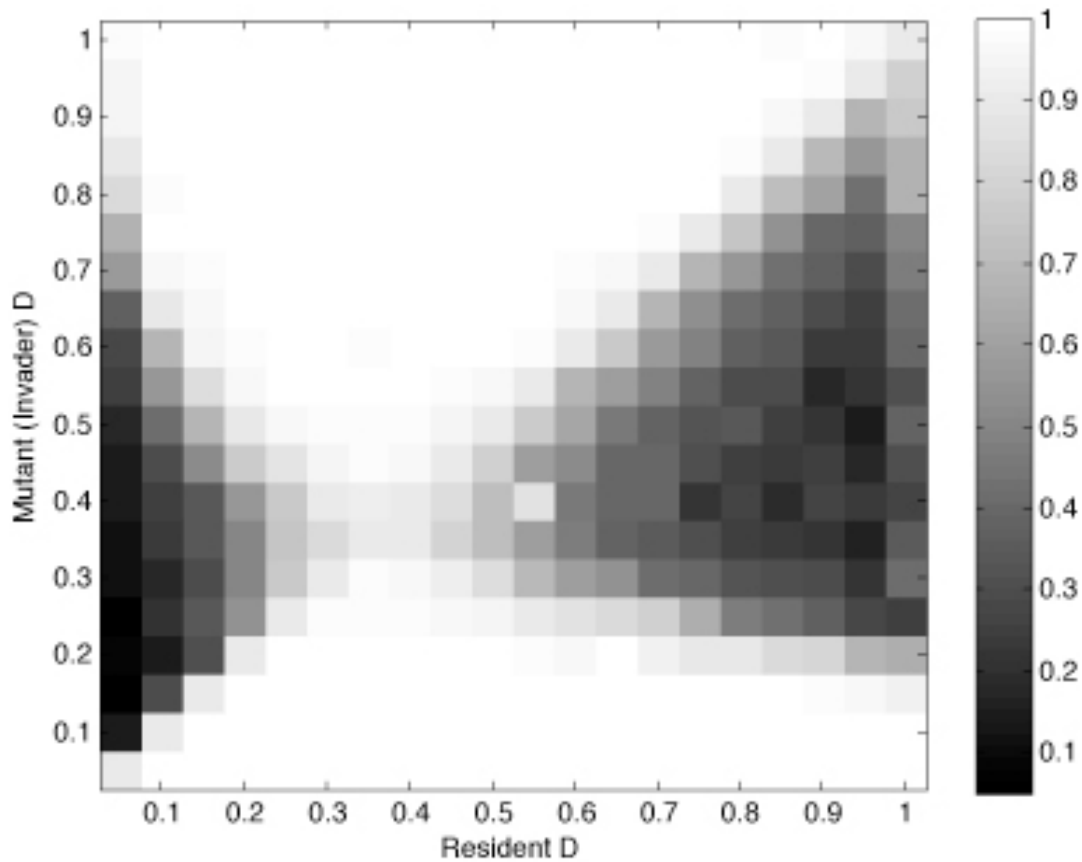
·········· *Slow wins* fixed point of ODEs marginally stable to *Fast* invasion!

(Simulations: $D_f = 10$ & $D_s = 0$, averaged over $L = 100$ sites and 100 realizations.)

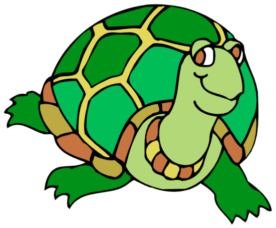
Conclusions & remarks

- Wanderlust may be ***advantageous*** despite it's risks …
- … ability to ***exploit*** occasional random opportunities!
- Moment dynamics may ***succeed*** in predicting victors …
- … sometimes useful information in a model's ***failure***!
- $\mathrm{Var}\{\gamma\} = 2/n$ analytical ***Slow wins*** boundary agrees quantitatively w/Kessler-Sander simulations for 1-d, simple diffusion & "mild" environmental fluctuations.
- ***Major question*: given environment with given level of demographic fluctuations, is there ***optimal*** mobility?
- Seems so!

Variable mobility competition



Pairwise invasibility plot. Resident species begins at carrying capacity on each fecund site, mutant begins with one individual on each site. Grey scale represents fraction of trials where invader goes extinct in 100 runs with n=10, L=500, ϕ=0.5.



Thanks for your attention!