Some mathematical models from population genetics

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with thanks to numerous collaborators

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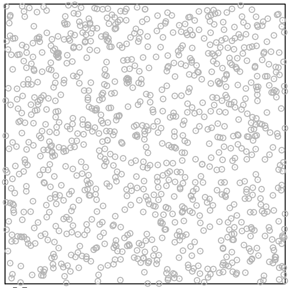
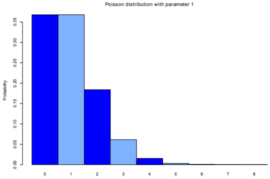
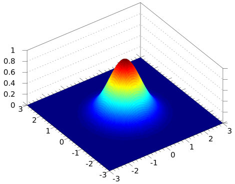
Recap: the Wright-Malécot model



$N = 1000$

- Individuals are scattered across a two-dimensional space.
- In each generation, each individual produces a Poisson number of offspring (average one).
- Offspring are scattered in a Gaussian distribution around their parent.





Mitch Gooding
Jerome Kelleher

Modelling populations in which population density changes

Recall the pain in the torus.

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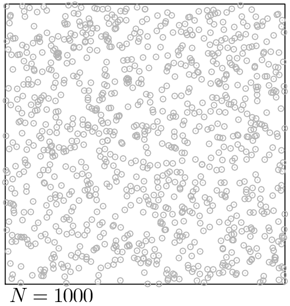
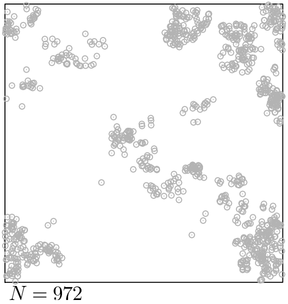
$t = 0$



$t = 10$



Modelling populations in which population density changes

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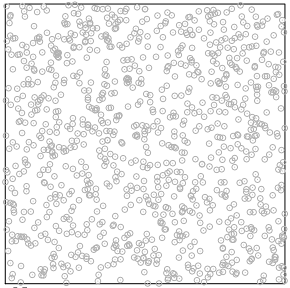
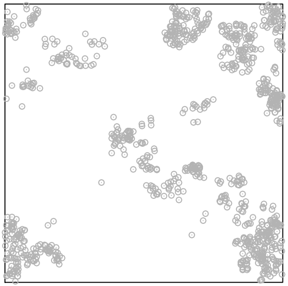


$t = 0$ $N = 1000$



$t = 10$ $N = 972$

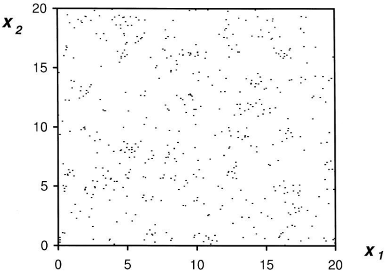
- In $d = 1, 2$, independent reproduction $\implies$ clumping;

Modifying Wright-Malécot (à la Bolker-Pacala)

Think of population as a (purely atomic) measure X.

- Expected number offspring of individual at x in generation t,
  $\Big(1 + \varepsilon(M - \langle h(x,y), X(t,y)\rangle)\Big)_+$ ($\langle\cdot,\cdot\rangle$ integration)

(Small in crowded regions, big in sparsely populated regions)



For suitable M, h and dispersal kernel, the population is stable.

Roughly, individuals must disperse sufficiently quickly relative to the range of interaction induced by density dependent regulation.

Sometimes easier to consider scaling limits.

For our modified Wright-Malécot model, can obtain (stochastic non-local) Fisher-KPP equation in the limit of high population intensity.

Informally:

$$dX_s(x) = \sigma \Delta X_s(x) ds + (M - \langle h(x,y), X_s(y) \rangle) X_s(x) ds \\ + \sqrt{\gamma X_s(x)} W(ds, dx)$$

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More rigorously

$$\langle \phi, X_t \rangle - \langle \phi, X_0 \rangle - \int_0^t \langle \sigma \Delta \phi, X_s \rangle ds$$
$$- \int_0^t \langle \Big(M - \langle h(x,y), X_s(dy) \rangle \rangle \Big) \phi, X_s(dx) \rangle ds$$

is a martingale with quadratic variation

$$\int_0^t \langle \gamma \phi^2, X_s \rangle ds.$$

$h(x,y) = h(\|x-y\|)$. Define X^θ by

$$\langle \phi, X_t^\theta \rangle = \langle \frac{1}{\theta^2}\phi\Big(\frac{x}{\theta}\Big), X_{\theta^2 t}(dx)\rangle$$

and $h^\theta(r) = \theta^2 h(\theta r)$.

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Survival/extinction $d = 2,\ X_0$ Lebesgue

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$$\int_0^t \langle \gamma\phi^2, X_s^\theta\rangle ds.$$

If $r^2 h(r) \to \infty$ as $r \to \infty$ expect extinction.

Ancestral lineages?

The lineage of a bit of modern genome is

$$L_t = \text{(location of the genetic ancestor at time } t \text{ ago)}$$

Key quantity, effective dispersal rate σ_e of ancestral lineages.

Sample individual from the population in steady state.

- Wright-Malécot assumed ancestry described by random walk with jumps determined by the forwards in time Gaussian dispersion kernel. Over large spatial and temporal scales approximately Brownian motion;
- (Numerically) in modified model, over large spatial and temporal scales approximately Brownian motion, but with *larger* variance than suggested by forwards in time kernel.

Compare to stepping stone model.

Is this behaviour generic?

Some problems with models so far

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- **Stepping stone model:** subdivided population, population size in each deme exogenously specified;
- **Wright-Malécot model:** inconsistent assumptions, clumping/extinction (the pain in the torus);
- **Wright-Malécot with local regulation:** overcomes clumping, but no known expressions for ancestral lineages;

The world is not homogeneous

How we model it

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What are we missing?

The path to survival

$\eta(x) =$ 'population density at x'

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- A juvenile is born

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$\eta(x) =$ 'population density at x'

- A juvenile is born per capita rate $\gamma(x, \eta(x))$
- Dispersal distribution $q(x, dy)$ (Gaussian)
- Establishment probability $r(y, \eta(y))$

The path to survival

$\eta(x)$ = 'population density at x'

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- Death of mature individuals

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- Death of mature individuals rate $\mu(x, \eta(x))$

Assume maturity reached instantly
We only track mature individuals

A cautionary tale

Simulations by Gilia Patterson, using SLiM

- death: $\mu = 0.3$ per generation
- establishment: $r = 0.7$
- dispersal: Gaussian with SD σ
- local density: in circles radius $\epsilon = 1$
- reproduction with $K = 2$, $\lambda = 3$,

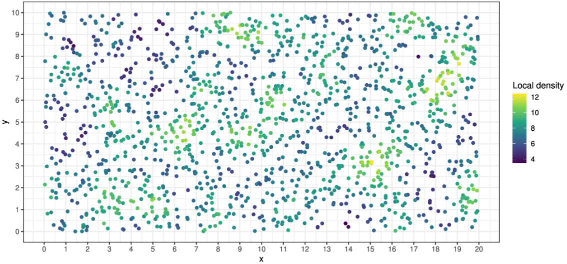
$$\gamma = \frac{\lambda}{1 + (\text{local density})/K}$$

- non-spatial equilibrium density:

$$K\left(\frac{\lambda}{1-r} - 1\right)$$

Large dispersal distance

- dispersal distance $\sigma = 3$
- interaction distance $\epsilon = 1$
- mean number offspring $\propto \left(1 + (\text{density})/K\right)^{-1}$



Small dispersal distance

- dispersal distance $\sigma = 0.2$
- interaction distance $\epsilon = 1$
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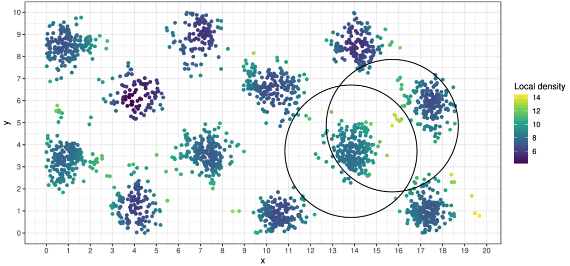

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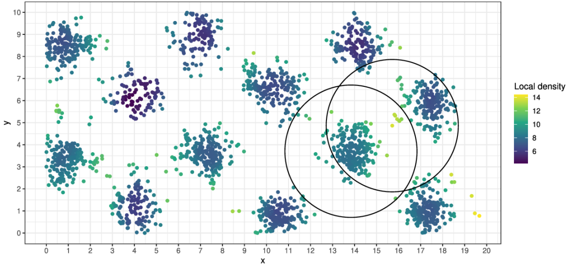

Low dispersal distance compared to distance over which negatively influenced by presence of neighbours can lead to strong clumping.

c.f., e.g., Spatial structures and periodic travelling waves in an integro-differential reaction-diffusion population model, N Britton, SIAM J. Appl. Math. 1990.

Characterising the model

Birth-death process with dynamics:

- A juvenile is born per capita rate $\gamma(x, \eta(x))$
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Think of population as a point measure, with atoms of mass $1/N$. Write

$$\langle f, \eta \rangle = \frac{1}{N} \sum f(X_i) = \int f(x)\eta(dx)$$

Unpacking the notation:

$$\gamma(x, \eta(x)) = \gamma\big(x, \rho_\gamma * \eta(x)\big); \qquad \rho_\gamma * \eta(x) = \int \rho_\gamma(x-y)\eta(dy)$$

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ρ_r need not be the same as ρ_γ

Scaling the model

Parameters N, θ

Birth-death process with dynamics:

- A juvenile is born per capita rate $\theta\gamma(x, \eta(x))$
- Dispersal distribution $q_\theta(x, dz)$ (Gaussian mean and variance order $1/\theta$))
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Assume: Typically $\mathcal{B} = \Delta$

$$\int \theta\Big(r(z,\eta)f(z) - r(x,\eta)f(x)\Big)q_\theta(x, dz) \quad \xrightarrow{\theta\to\infty} \quad \mathcal{B}\big(r(\cdot,\eta)f(\cdot)\big)(x)$$

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$$\theta\Big(r(x,\eta)\gamma(x,\eta) - \mu_\theta(x,\eta)\Big) = F(x,\eta)$$

Mean measure

- Individual at x gives birth to single mature offspring at z rate $\theta\gamma(x,\eta)r(z,\eta)q_\theta(x,dz)$ increment $\langle f,\eta\rangle = \frac{1}{N}f(z)$

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$$= \lim_{\delta t \downarrow 0} \frac{1}{\delta t}\mathbb{E}\Big[\langle f,\eta_{\delta t}\rangle - \langle f,\eta\rangle \Big| \eta_0 = \eta\Big]$$

$$= \theta \int\int f(z)r(z,\eta)q_\theta(x,dz)\gamma(x,\eta)\eta(dx) - \theta\int f(x)\mu_\theta(x,\eta)\eta(dx).$$

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$$= \int\left(\int \theta\left(f(z)r(z,\eta)-f(x)r(x,\eta)\right)q_\theta(x,dz)\right)\gamma(x,\eta)\eta(dx)$$

$$+\int\int f(x)\theta\Big(r(x,\eta)\gamma(x,\eta)-\mu_\theta(x,\eta)\Big)\eta(dx).$$

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$$= \int\left(\int \theta\left(f(z)r(z,\eta) - f(x)r(x,\eta)\right)q_\theta(x,dz)\right)\gamma(x,\eta)\eta(dx)$$

$$+ \int\int f(x)\theta\Big(r(x,\eta)\gamma(x,\eta) - \mu_\theta(x,\eta)\Big)\eta(dx).$$

$$\overset{\theta\to\infty}{\longrightarrow} \quad \int \gamma(x,\eta)\mathcal{B}\big(f(\cdot)r(\cdot,\eta)\big)(x)\eta(dx) + \int f(x)F(x,\eta)\eta(dx)$$

Squared increments (angle bracket process)

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$$
\begin{aligned}
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&\qquad\qquad + \Big\langle\frac{1}{N^2}f^2(x)\mu_\theta(x,\eta),\eta(dx)\Big\rangle\Big\} \\
&= \frac{\theta}{N}\langle\gamma(x,\eta)\int f^2(z)r(z,\eta)q_\theta(x,dz) + f^2(x)\mu_\theta(x,\eta),\eta(dx)\rangle
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$$=\frac{\theta}{N}\langle\gamma(x,\eta)\int f^2(z)r(z,\eta)q_\theta(x,dz)+f^2(x)\mu_\theta(x,\eta),\eta(dx)\rangle$$

$$\int f^2(z)r(z,\eta)q_\theta(x,dz)\to f^2(x)r(x,\eta), \quad \mu_\theta = r\gamma-\frac{1}{\theta}F\to r\gamma$$

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$$\xrightarrow{\theta\to\infty} \quad \frac{\theta}{N}\langle 2r(x,\eta)\gamma(x,\eta)f^2(x),\eta(dx)\rangle \qquad \alpha := \lim\frac{\theta}{N}$$

Martingale characterisation of limit

$$\langle f(x), \eta_t(dx)\rangle - \langle f(x), \eta_0(dx)\rangle \\ - \int_0^t \Big\langle \gamma(x, \eta_s)\mathcal{B}\big(f(\cdot)r(\cdot, \eta_s)\big)(x) + F(x, \eta_s)f(x), \eta_s(dx)\Big\rangle ds$$

is a martingale, $M_f(\cdot)$, with

$$\langle M_f\rangle_t = \alpha \int_0^t \Big\langle 2r(x, \eta_s)\gamma(x, \eta_s)f^2(x), \eta_s(x)\Big\rangle ds$$

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- $\alpha > 0$, nonlinear superprocess

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e.g. $\gamma \equiv 1, r \equiv 1, F = 1 - h * \eta$, diffusion limit of Bolker-Pacala model: spatial branching process; reproductive successs decreases in crowded regions.

What is needed to make this rigorous?

$\mathcal{D}([0,\infty),S)$ càdlàg paths in S

Theorem (S,d) complete and separable. $\{X^N\}_{N\geq 1}$ family of processes with sample paths in $\mathcal{D}([0,\infty),S)$. Suppose

- For every $\varepsilon > 0$, and $T > 0$, $\exists$ compact $\Gamma_{\varepsilon,T}$ s.t.

$$\inf_N \mathbb{P}\Big[X_t^N \in \Gamma_{\varepsilon,T} \quad \text{for } 0 \leq t \leq T\Big] \geq 1-\varepsilon$$

- For Θ a dense subset of the set of bounded continuous functions in topology of uniform convergence on compacts, for each $f \in \Theta$, $\{f(X_\cdot^N)\}_{N\geq 1}$ is relatively compact as family of processes in $\mathcal{D}([0,\infty),\mathbb{R})$.

Then $\{X_\cdot^N\}_{N\geq 1}$ is relatively compact.

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Then $\{X_\cdot^N\}_{N\geq 1}$ is relatively compact.
Any infinite subsequence has a convergent subsequence.

What is needed to make this rigorous?

$\mathcal{D}([0,\infty),S)$ càdlàg paths in S

Theorem (S,d) complete and separable. $\{X^N\}_{N\geq 1}$ family of processes with sample paths in $\mathcal{D}([0,\infty),S)$. Suppose

- For every $\varepsilon > 0$, and $T > 0$, $\exists$ compact $\Gamma_{\varepsilon,T}$ s.t.

$$\inf_N \mathbb{P}\Big[X_t^N \in \Gamma_{\varepsilon,T} \quad \text{for } 0 \leq t \leq T\Big] \geq 1 - \varepsilon$$

- For Θ a dense subset of the set of bounded continuous functions in topology of uniform convergence on compacts, for each $f \in \Theta$, $\{f(X_\cdot^N)\}_{N\geq 1}$ is relatively compact as family of processes in $\mathcal{D}([0,\infty),\mathbb{R})$.

Then $\{X_\cdot^N\}_{N\geq 1}$ is relatively compact.

Any infinite subsequence has a convergent subsequence.

If limit point unique have convergence.

Application to $\{\eta_\cdot^N\}_{N\geq 1}$

$\{\eta_\cdot^N\}_{N\geq 1}$ sequence of $D\big([0,\infty),\mathcal{M}_F(\mathbb{R}^d)\big)$-valued processes.

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- Take $\overline{\mathbb{R}^d}$, the one-point compactification of $\mathbb{R}^d$
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(We have already done the work in identifying the limit points)

Conditions on our parameters?

$$\langle f(x), \eta_t^N(dx)\rangle - \langle f(x), \eta_0^N(dx)\rangle$$
$$- \int_0^t \Big\langle \gamma(x,\eta_s)\Big(\theta \int \big(f(z)r(z,\eta_s) - f(x)r(x,\eta_s)\big) q_\theta(x,dz)\Big)$$
$$+ F(x,\eta_s)f(x), \eta_s(dx)\Big\rangle ds$$

is a martingale, $M_f^N(\cdot)$, with

$$\langle M_f^N \rangle_t = \frac{\theta}{N}\int_0^t \Big\langle \gamma(x,\eta_s)\int f^2(y)r(y,\eta_s)q_\theta(x,dy)$$
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- γ bounded above
- F bounded above *but not necessarily below, c.f. Bolker-Pacala example*

Compact containment of $\{\eta_\cdot^N\}_{N\geq 1}$

$$\begin{aligned}\langle 1, \eta_t^N(dx)\rangle &= \langle 1, \eta_0^N(dx)\rangle \\ &\quad + \int_0^t \Big\langle \gamma(x,\eta_s)\Big(\theta \int \big(r(z,\eta_s) - r(x,\eta_s)\big) q_\theta(x,dz)\Big) \\ &\qquad\qquad + F(x,\eta_s), \eta_s(dx)\Big\rangle ds + M_1^N(t) \\ &\qquad\qquad\qquad \leq \langle 1, \eta_0^N\rangle + C\int_0^t \langle 1, \eta_s^N\rangle ds + M_1^N(t)\end{aligned}$$

Grönwall's inequality $\implies$ for all $t \in [0,T]$,

$$\mathbb{E}\big[\langle 1, \eta_t^N\rangle\big] \leq C_T \mathbb{E}\big[\langle 1, \eta_0^N\rangle\big]$$

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For compact containment we'd like to bound $\mathbb{E}\big[\sup_{0\leq t\leq T}\langle 1, \eta_t^N\rangle\big]$.

Taking suprema above, need to control $\sup_{0\leq t\leq T} M_1^N(t)$

A useful trick

$$\langle M_1^N \rangle_t = \frac{\theta}{N} \int_0^t \Big\langle \gamma(x, \eta_s) \int r(y, \eta_s) q_\theta(x, dy) + \Big(r(x, \eta_s)\gamma(x, \eta_s) - \frac{1}{\theta} F(x, \eta_s) \Big), \eta_s(x) \Big\rangle ds$$

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Problem: F not bounded below
Solution: Rearrange equation for $\langle 1, \eta_t^N \rangle$

$$- \int_0^t \big\langle F(x,\eta_s), \eta_s(dx) \big\rangle ds = \langle 1, \eta_0^N(dx) \rangle - \langle 1, \eta_t^N(dx) \rangle + \int_0^t \Big\langle \gamma(x,\eta_s) \Big(\theta \int \big(r(z,\eta_s) - r(x,\eta_s) \big) q_\theta(x,dz) \Big) ds + M_1^N(t) \leq \langle 1, \eta_0^N \rangle + C \int_0^t \langle 1, \eta_s^N \rangle ds + M_1^N(t)$$

Compact containment of $\{\eta_\cdot^N\}_{N\geq 1}$

Combining boundedness of $\mathbb{E}\big[\langle 1, \eta_t^N\rangle\big]$ and the calculation above, $\mathbb{E}[\langle M_1^N\rangle_T] < C'_T$

- Burkholder-Davis-Gundy $\implies \mathbb{E}\big[\sup_{0\leq t\leq T} M_1^N(t)\big] < C''_T$

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- Markov inequality $\leadsto$ compact containment of $\{\eta_{\cdot}^N\}_{N\geq 1}$

Still need to show that for suitable test functions, the sequence of *real-valued* processes $\{f(\eta_{\cdot}^N)\}_{N\geq 1}$ is relatively compact

The Aldous-Rebolledo criterion

For each $T > 0$, for each fixed $0 \le t \le T$, the sequence $\{\langle f, \eta_t^N \rangle\}_{N \ge 1}$ is tight, and for any sequence of stopping times τ_N bounded by T, and each $\nu > 0$, there exist $\delta > 0$, $N_0 > 0$ s.t.

$$\sup_{N > N_0} \sup_{t \in [0,\delta]} \mathbb{P}\Big\{ \Big| \int_\tau^{\tau+t} \int_{\mathbb{R}^d} \{\gamma(x, \eta_s^N) B_f(x, \eta_s^N) \\ + f(x) F(x, \eta_s^N)\} \eta_s^N(dx) ds \Big| > \nu \Big\} < \nu,$$

and $$\sup_{N > N_0} \sup_{t \in [0,\delta]} \mathbb{P}\left\{ \left| \langle M^N(f) \rangle_{\tau+t} - \langle M^N(f) \rangle_\tau \right| > \nu \right\} < \nu.$$

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Follow easily from our calculations above

- When limit points deterministic, can scale again to get classical pde
- Can also go direct to deterministic pde in some circumstances

Ancestral lineages: heuristics

Recall $L_t =$ (location of the genetic ancestor at time t ago)
New individual establishes at y from parent at x rate

$$\theta N \eta_t^N(dx)\gamma(x, \eta_t^N) q_\theta(x, dy) r(y, \eta_t^N).$$

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Suppose that η^N had a density (it does not), $\eta_t^N(dx) = \varphi_t^N(x)dx$.

$$\mathbb{P}\big[L_{t+dt} = x | L_t = y\big] = \frac{\theta\gamma(x, \eta_t^N)r(y, \eta_t^N)\varphi_t^N(x)}{\varphi_t^N(y)} \frac{q_\theta(x, dy)}{dy} dxdt.$$

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$$\mathbb{E}[f(L_{s+ds}^N) - f(y) \mid L_s^N = y]$$
$$= ds\,\theta \int (f(x) - f(y))\,\frac{\varphi_{T-s}^N(x)\gamma(x,\eta_{T-s}^N)r(y,\eta_{T-s}^N)}{\varphi_{T-s}^N(y)}q_\theta(x,y)dx.$$

(Note that this integral is with respect to x.)

Generator ancestral lineage

$$\mathcal{L}_s^\theta f(y) = \lim_{ds\to 0} \frac{1}{ds}\mathbb{E}[f(L_{s+ds}^N) - f(y) \mid L_s^N = y]$$

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Set $g = \varphi_{T-s}\gamma$,

$$\mathcal{L}_s f = \frac{r}{\varphi_{T-s}}\{\mathcal{B}^*(\gamma\varphi_{T-s}f) - f\mathcal{B}^*(\gamma\varphi_{T-s})\}$$

Example: $\mathcal{B} = \Delta$

$$\mathcal{L}_s f = \frac{r}{\varphi_{T-s}} \left\{ \mathcal{B}^*(\gamma \varphi_{T-s} f) - f \mathcal{B}^*(\gamma \varphi_{T-s}) \right\}$$

$$\begin{aligned} \mathcal{L}_s f = \frac{r}{\varphi_{T-s}} \left\{ \Delta(\gamma \varphi_{T-s} f) - f \Delta(\gamma \varphi_{T-s}) \right\} \\ = r\gamma \Delta f + 2r\gamma \nabla \log(\gamma \varphi) \cdot \nabla f \end{aligned}$$

Generator of a time inhomogeneous diffusion process

Ancestral lineages

Suppose population has a stationary density $w(x)$ say,

$$dL_t = 2r(L_t)\gamma(L_t)\nabla \log(w\gamma)(L_t)dt + \sqrt{2r(L_t)\gamma(L_t)}dB_t$$

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Lineage motion not uniquely determined by population density

$$r\Delta(\gamma w) + (r\gamma - \mu)w = 0.$$

Multiply r and μ by λ.

- Same stationary density.
- Lineages spend more time where $\lambda < 1$ - so those areas have higher reproductive value.

Some remarks about our model

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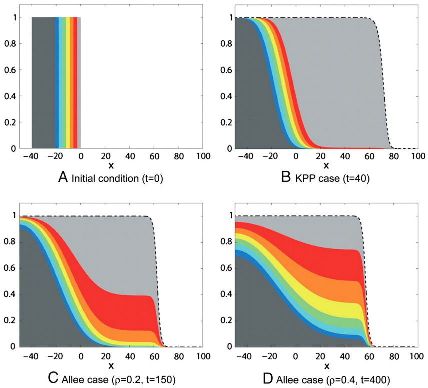
For the purpose of this talk, work in classical PDE limit

Reaction diffusion equations and range expansion ($d = 1$)

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u\ (1 - u)$$



Roques et al. PNAS (2012)

Individuals in front descended from individuals in front at previous time

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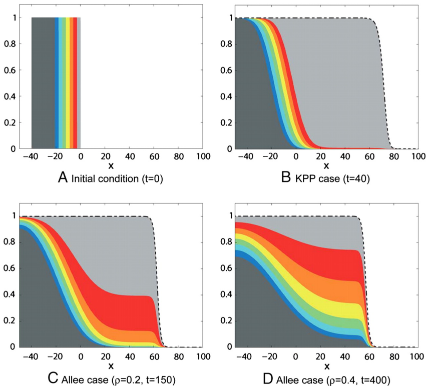

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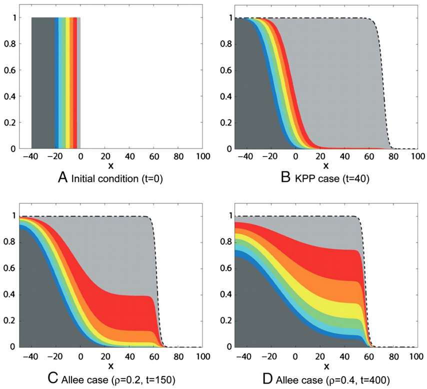

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Individuals in front can be descended from individuals in bulk.

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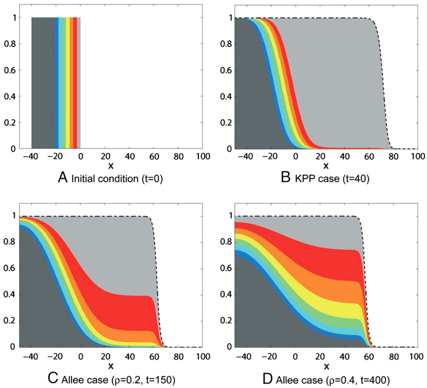

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Individuals in front can be descended from individuals in bulk.

When add noise, $\rightsquigarrow$ different genealogies (c.f. E-Penington 2022)

A less classical example $\gamma \propto$ pop density, logistic control

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}(u^2) + u(1-u),$$

'Effective' density dependent dispersal

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$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}(u^2) + u(1-u), \quad u(t,x) = \left(1 - \exp\left(\frac{1}{2}(x-t)\right)\right)_+$$

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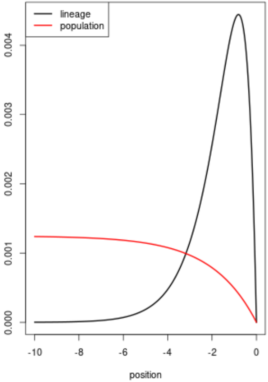

Ancestral lineage has stationary distribution $\pi(x) \propto e^x \left(1 - e^{x/2}\right)$ for $x < 0$ ..., in contrast to the Fisher-KPP equation

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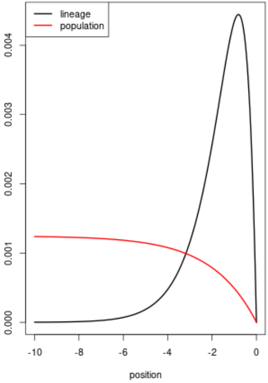
'Effective' density dependent dispersal



Ancestral lineage has stationary distribution $\pi(x) \propto e^x \left(1 - e^{x/2}\right)$ for $x < 0$ ..., in contrast to the Fisher-KPP equation

$\leadsto$ When add noise can expect genealogy to be quite different from that under Fisher-KPP,

$\sim$ Allee effect

Take-home messages from these lectures

- Noise matters
- Space matters
  - The dimension of the space
  - The geometry of the space
- Local interactions matter, even over large scales

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THANK YOU FOR YOUR ATTENTION