Some mathematical models from population genetics
IV: Heterogeneous landscapes

Alison Etheridge
University of Oxford

with Tom Kurtz, Ian Letter, Peter Ralph, Terence Tsui

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What the world looks like

How we model it

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Justification: "homogenisation over the timescales of evolution"

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What are we missing?

Justification: "homogenisation over the timescales of evolution"

A model based on 'interacting branching processes'

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

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- Establishment probability $r(y, \eta(y))$

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- Death of mature individuals

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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 $K = 2$, $\lambda = 3$,

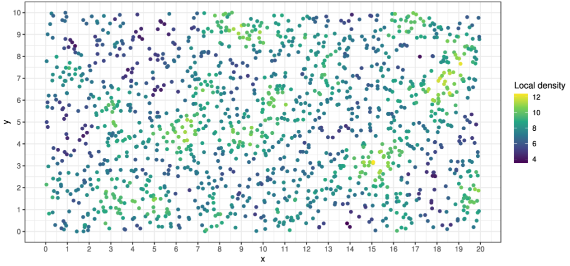
$$\gamma = \frac{\lambda}{1 + \text{(local density)}/K}$$

- 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 $\propto \left(1 + (\text{density})/K\right)^{-1}$



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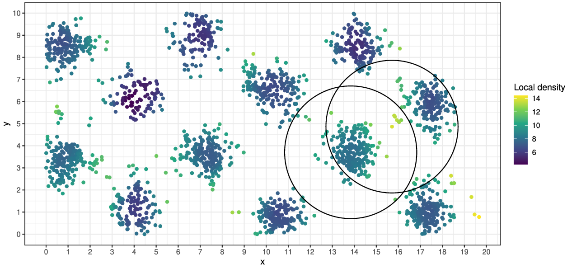

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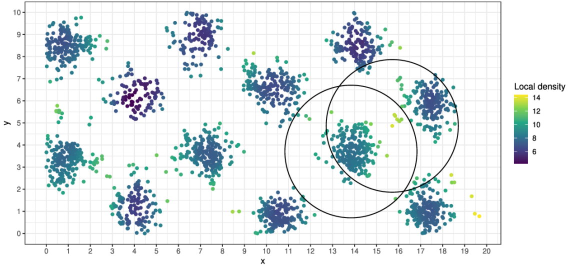

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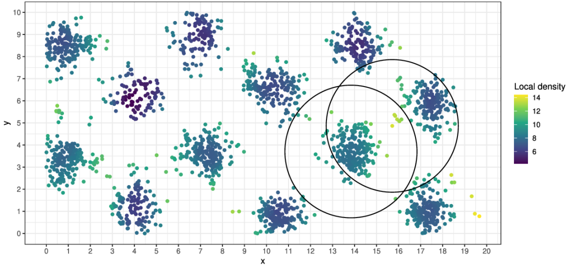

Low dispersal distance compared to distance over which negatively influenced by presence of neighbours can lead to strong clumping.
True even in corresponding deterministic model

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

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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Parameters N, θ

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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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(Roughly, r sufficiently smooth, and net per capita growth rate $\propto 1/\theta$)

Look for 'local characteristics'

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

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

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

Quadratic variation

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

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

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

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

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$$\partial_t \eta = r\mathcal{B}^*(\gamma\eta) + F\eta$$
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e.g. $\gamma \equiv 1, r \equiv 1, F = 1 - p_\epsilon * \eta$, 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 $\mathcal{D}([0,\infty), \mathbb{R})$.

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If limit point unique have convergence.

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

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- Prove relative compactness in $\mathcal{M}_F(\overline{\mathbb{R}^d})$
- Show 'no mass escaped to infinity', so limit points actually $D\big([0,\infty),\mathcal{M}_F(\mathbb{R}^d)\big)$-valued processes.

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(We have already done the work in identifying the limit points)

Conditions on our parameters?

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

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$$\langle M_f^N \rangle_t = \frac{\theta}{N} \int_0^t \langle \gamma(x, \eta_s) \int f^2(y) r(y, \eta_s) q_\theta(x, dy)$$
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$$+ f^2(x)\Big(r(x,\eta_s)\gamma(x,\eta_s) - \frac{1}{\theta}F(x,\eta_s)\Big), \eta_s(x)\Big\rangle ds$$

- γ bounded above
- F bounded above *but not necessarily below, c.f. Bolker-Pacala example*

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

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

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

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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 $\langle 1, \eta_t^N \rangle$

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

$$\leq \langle 1, \eta_0^N \rangle + C \int_0^t \langle 1, \eta_s^N \rangle ds + M_1^N(t)$$

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, $\mathbb{E}[\langle M_1^N\rangle_T] < C'_T$

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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 $0 \leq t \leq T$, the sequence $\{\langle f, \eta_t^N \rangle\}_{N \geq 1}$ 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

Some remarks about our model

- Classical models emerge as special cases of our scaling limits.

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

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

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Kolmogorov, Petrovskii, Piskunov (1937)

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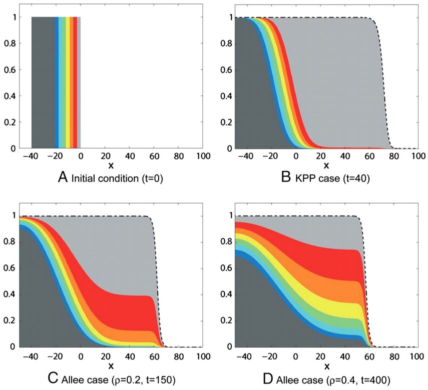
$$\frac{\partial u_k}{\partial t} = \frac{\partial^2 u_k}{\partial x^2} + u_k(1 - u)$$

$$u = \sum_k u_k$$



Individuals in front descended from individuals in front at previous time

Roques et al. PNAS (2012)

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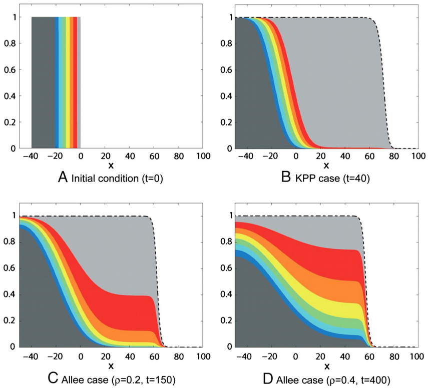

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Individuals in front can be descended from individuals in bulk.

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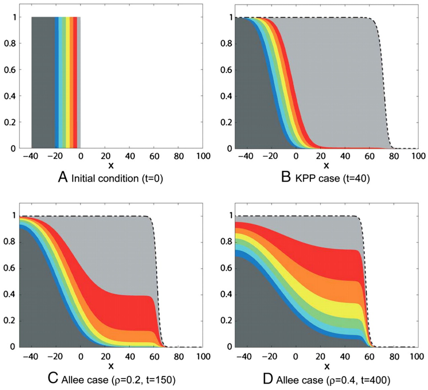

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Individuals in front can be descended from individuals in bulk.

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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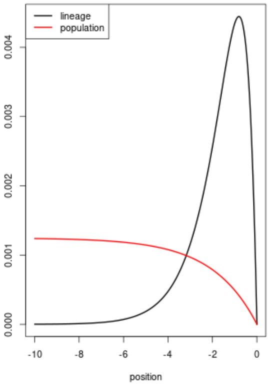

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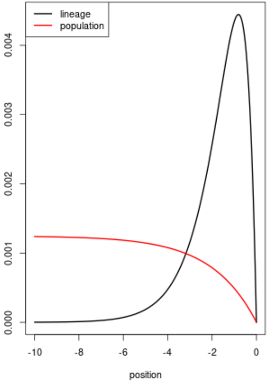

Ancestral lineage has stationary distribution $\pi(x) \propto e^x \left(1 - e^{x/2}\right)$ for $x < 0$ . . ., in contrast to the Fisher-KPP equation

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

$\sim$ Allee effect

Closing remarks

- In spite of complexity, some mathematical tractability;
- A trace of the two-step reproduction mechanism persists over large temporal and spatial scales;
- Readily simulated in SLiM;
- Readily extended (but the paper is already over 100 pages long);

Take-home messages from these lectures

- Noise matters
- Space matters
- Local interactions matter, even over large scales

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THANK YOU FOR YOUR ATTENTION