Some mathematical models from population genetics

4: Spatial models

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Lessons learned so far

The key message of our balancing selection example is that if we want to study the genealogy of a sample from a structured population, then fluctuations in background frequencies matter.

A central question then is how should we model fluctuations of spatially distributed populations.

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If $\left\{\frac{Z_0}{N}\right\}_{N \geq 1}$ converges, so does $\left\{\frac{Z_{\lfloor Nt \rfloor}}{N}\right\}_{N \geq 1}$.

Limit process: $dX_t = aX_t dt + \sqrt{\gamma X_t} dB_t.$

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Feller rescaling: individual represented by atom of mass $\frac{1}{N}$, time in units of size N.

The limiting processes

The Dawson-Watanabe superprocess:

For positive, twice differentiable test functions ϕ,

$$\langle \phi, X_t \rangle - \langle \phi, X_0 \rangle - \int_0^t \langle D\Delta\phi, X_s \rangle ds - \int_0^t \langle a\phi, X_s \rangle ds$$

is a martingale with quadratic variation $\int_0^t \langle \gamma\phi^2, X_s \rangle ds$.

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Super-random walk:

$$dX_i(t) = \sum_j m_{ij} \left(X_j(t) - X_i(t) \right) dt + aX_i(t)dt + \sqrt{\gamma X_i(t)} dW_i(t), \quad i \in \mathbb{Z}^d,$$

where $\{W_i(t), t \geq 0\}_{i \in \mathbb{Z}^d}$ is a collection of independent Brownian motions and $X_i(t)$ is the size of the population in deme i at time t.

Clumping and extinction.

$$\mathbb{E}\left[\langle \phi, X_t \rangle\right] = e^{at} \langle T_t \phi, X_0 \rangle,$$

Take $a = 0$.

$$var\left(\langle \phi, X_t \rangle\right) = \int_0^t \langle \gamma T_{t-s}\left((T_s \phi)^2 \right), X_0 \rangle ds.$$

In one and two dimensions grows without bound.

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Exogenously specify total population size $\rightsquigarrow$ **Fleming-Viot superprocess**.

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Populations should be regulated by local rules.

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Populations should be regulated by local rules.

Individuals living in locally crowded regions will have a lower reproductive success than those living in sparsely populated regions.

Locally regulated populations

$$a(s,x) = \alpha\big(M - \langle h(x,y), X_s(dy)\rangle\big).$$

For simplicity $h(x,y) = h(\|x-y\|)$.

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The stepping-stone version of the Bolker-Pacala model: In the super-random walk setting the corresponding model is

$$dX_t(i) = \sum_j m_{ij}\left(X_t(j) - X_t(i)\right)dt + \alpha\left(M - \sum_j \lambda_{ij} X_t(j)\right) X_t(i)dt$$
$$+ \sqrt{\gamma X_t(i)}\, dB_t^{(i)}.$$

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Note that moment equations not closed.

Survival and Extinction

Theorem

For each fixed interaction kernel h and $\gamma, K > 0$ there exists $\alpha_0 = \alpha_0(K, \gamma, h)$ such that for $\alpha > \alpha_0$, the superprocess version of the Bolker-Pacala model with parameters $(h, K/\alpha, \alpha, \gamma)$ started from any finite initial measure dies out in finite time. If h also satisfies $\int h(r)r^{d-1}dr < \infty$, then when started from any tempered initial measure (with $p > d$) the process with these parameters suffers local extinction.

Let $\alpha > 0$ be fixed.

- If $r^{2-\delta}h(r)$ is unbounded for some $\delta > 0$, then for each fixed $\gamma > 0$, there is an $M_0 > 0$ such that for $M < M_0$ the superprocess version of the Bolker-Pacala model with parameters (h, M, α, γ) started from any finite initial measure dies out in finite time. If also $\int h(r)r^{d-1}dr < \infty$, so that in particular $d = 1$, then when started from any tempered initial measure (with $p > 1$) the process with these parameters suffers local extinction.

- Suppose that the population $\{X_t(i)\}_{i\in\mathbb{Z}^d, t\geq 0}$ evolves according to the stepping stone version of the Bolker-Pacala model, then if $m_{ij} > c\lambda_{ij}$, for some $c > 0$, then there exists $M_1 > 0$ such that for $M > M_1$ the process survives for all time with (strictly) positive probability (started from any non-trivial initial condition).

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Hutzenthaler & Wakolbinger prove an ergodic theorem and also show that if M is too small, the process dies out.

Rescaling:

Take $d = 2$. Define X^θ by

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

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

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$$\langle \phi, X_t^\theta \rangle - \langle \phi, X_0^\theta \rangle - \int_0^t \langle D\Delta\phi, X_s^\theta \rangle ds$$
$$- \int_0^t \left\langle \theta^2 \alpha \left(M - \langle h^\theta(\|x - y\|), X_s^\theta(dy) \rangle \right) \phi(x), X_s^\theta(dx) \right\rangle ds$$

a martingale with quadratic variation

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

Notes:

If $r^2h(r) \to \infty$ as $r \to \infty$, then h^θ grows without bound as $\theta \to \infty$, suggesting extinction.

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In $d = 2$, for classical Dawson-Watanabe superprocess, if x is typical point in support of X_t, then

$$\lim_{r \downarrow 0} \mathbb{E}^{(x)} \left[\frac{\langle \chi_{B(x,r)}, X_t \rangle}{r^2 \log(1/r)} \right] = k$$

for a constant k (independent of x and t).

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$$\langle h^\theta(\|x - y\|), X_s(dy) \rangle \sim \log \theta.$$

Survival in two dimensions reflects successful eradication of clumping.

Competing species

Strategies for survival:

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Strategies for survival:

- colonise relatively unpopulated areas quickly,
- quickly exploit resources in those areas,
- tolerate local competition.

Model I

$$
\begin{aligned}
dX_i(t) &= \sum_{j\in\mathbb{Z}^d} m_{ij}\left(X_j(t)-X_i(t)\right)dt \\
&+\alpha\left(M-\sum_{j\in\mathbb{Z}^d}\lambda_{ij}X_j(t)-\sum_{j\in\mathbb{Z}^d}\gamma_{ij}Y_j(t)\right)X_i(t)dt+\sqrt{X_i(t)}dB_i(t),
\end{aligned}
$$

Model I

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$$+\,\alpha\left(M - \sum_{j\in\mathbb{Z}^d} \lambda_{ij} X_j(t) - \sum_{j\in\mathbb{Z}^d} \gamma_{ij} Y_j(t)\right) X_i(t)dt + \sqrt{X_i(t)}dB_i(t),$$

$$dY_i(t) = \sum_{j\in\mathbb{Z}^d} m'_{ij}\left(Y_j(t) - Y_i(t)\right) dt$$

$$+\,\alpha'\left(M' - \sum_{j\in\mathbb{Z}^d} \lambda'_{ij} Y_j(t) - \sum_{j\in\mathbb{Z}^d} \gamma'_{ij} X_j(t)\right) Y_i(t)dt + \sqrt{Y_i(t)}d\tilde{B}_i(t).$$

Model II

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Write

$$p_i(t) = \frac{X_i(t)}{(X_i(t) + Y_i(t))} = \frac{X_i(t)}{N}.$$

$$dp_i(t) = \sum_{j \in \mathbb{Z}^d} m_{ij}\left(p_j(t) - p_i(t)\right) dt$$

$$+ s p_i(t)\left(1 - p_i(t)\right)\left(1 - \mu p_i(t)\right) dt + \sqrt{\frac{1}{N} p_i(t)\left(1 - p_i(t)\right)}\, dW_i(t),$$

where

$$s = \alpha M - \alpha' M' + \left(\alpha' \lambda'_{ii} - \alpha \gamma_{ii}\right) N,$$

$$\mu = \frac{\left(\alpha' \lambda'_{ii} - \alpha \gamma_{ii}\right) N + \left(\alpha \lambda_{ii} - \alpha' \gamma'_{ii}\right) N}{\alpha M - \alpha' M' + \left(\alpha' \lambda'_{ii} - \alpha \gamma_{ii}\right) N}$$

$$dp_i(t) = \sum_{j\in\mathbb{Z}^d} m_{ij}\,(p_j(t) - p_i(t))\,dt$$

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‘Selection in favour of heterozygosity’ when $\mu > 1$, $s > 0$,

$(\alpha\lambda_{ii} - \alpha'\gamma'_{ii})\,N > \alpha M - \alpha' M'$, and $(\alpha'\lambda'_{ii} - \alpha\gamma_{ii})\,N > \alpha' M' - \alpha M$.

The symmetric case

In the case when the two populations evolve symmetrically, Model II reduces to

$$dp_i(t) = \sum_j m_{ij} \left(p_j(t) - p_i(t)\right) dt$$

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For general s there is no convenient moment dual, but we find an alternative duality with a system of *branching annihilating random walks*.

Branching annihilating random walk

The Markov process $\{n_i(t), i \in \mathbb{Z}^d\}_{t\geq 0}$, in which $n_i(t) \in \mathbb{Z}_+$, with dynamics

$$\begin{array}{ll} \left\{\begin{array}{l} n_i \mapsto n_i - 1, \\ n_j \mapsto n_j + 1 \end{array}\right. & \text{at rate } n_i m_{ij} \\ n_i \mapsto n_i + m & \text{at rate } s n_i \\ n_i \mapsto n_i - 2 & \text{at rate } \frac{1}{2} n_i (n_i - 1) \end{array}$$

is called a *branching annihilating random walk with offspring number* m *and branching rate* s.

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$$n_i \mapsto n_i + m \qquad \text{at rate } s n_i$$

$$n_i \mapsto n_i - 2 \qquad \text{at rate } \tfrac{1}{2} n_i (n_i - 1)$$

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Duality: Set $w_i = 1 - 2p_i$ and let $\underline{n}_t$ be branching annihilating random walk with offspring number two, then for $s > 0$

$$\mathbb{E}\left[\underline{w}(t)^{\underline{n}(0)}\right] = \mathbb{E}\left[\underline{w}(0)^{\underline{n}(t)}\right].$$

Conjectures for Model II

Based on results of Cardy and Täuber, we conjecture:

For Model II with $\mu = 2$

- In $d = 1$, there is a critical value $s_0 > 0$ such that the populations will both persist for all time with positive probability if and only if $s > s_0$,
- In $d = 2$, there is positive probability that both populations will persist for all time if and only if $s > 0$,
- In $d \geq 3$, this probability is positive if and only if $s \geq 0$.

It would be odd if the case $\mu = 2$ were pathological.

Conjectures for Model I

Let $m_{ij} = m'_{ij}$, $\alpha = \alpha'$, $M = M'$ fixed, and $\lambda_{ij} = \lambda'_{ij}, \gamma_{ij} = \gamma'_{ij}$. Parameters such that each population can survive in absence of the other.

1. If $\lambda_{ij} < \gamma_{ij}$ for all j, then eventually only one population will be present.
2. If $\lambda_{ij} > \gamma_{ij}$ for all j, then if $d \geq 2$, with positive probability both populations will exihibit longterm coexistence.
   In one dimension the same result will hold true provided that $\lambda_{ij} - \gamma_{ij}$ is sufficiently large.
3. If $\lambda_{ij} = \gamma_{ij}$ and $d \geq 3$ positive probability coexistence.
   If $d \leq 2$ then with probability one, one population will die out.

Heteromyopia

Does space promote coexistence?

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- Overall strength of interspecific and intraspecific competition is the same ($\sum_j \lambda_{ij} = \sum_j \gamma_{ij}$) but distance over which sense heterospecific neighbours (competitors) is shorter than that over which sense conspecific neighbours.

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- Analogue in our setting: symmetric version of Model I with $\lambda_{ij} = \lambda\left(\|i-j\|\right)$, $\gamma_{ij} = \gamma\left(\|i-j\|\right)$, where the functions λ and γ are monotone decreasing and $\sum_j \lambda_{ij} = \sum_j \gamma_{ij}$, but the range of λ_{ij} is greater than that of γ_{ij}.

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Small scales $\rightsquigarrow$ homozygous advantage.

Larger scales $\rightsquigarrow$ heterozygous advantage.

What about genetics?

Recall from 1st lecture that for a neutral subdivided population with allelic types a, A, the proportion of type a alleles is

$$dp_i(t) = \sum_j \frac{N_j}{N_i} m_{ij} \left(p_j(t) - p_i(t)\right) dt + \sqrt{\frac{\gamma}{N_i} p_i(t) \left(1 - p_i(t)\right)} dW_i(t).$$

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Hidden assumption: the population size in each deme is large.

An approach of Malécot

Discrete time:
Infinite alleles model, write $F(y)$ for the probability of identity in state of two genes separated by y.

- Ancestral lineages follow independent Brownian motions,
- *local population density*, δ, a constant,
- probability two lineages currently at separation y (a vector in $\mathbb{R}^2$ in the most interesting setting) have a common ancestor in the previous generation is $\frac{1}{\delta}\int g_1(y-z)g_1(z)dz$, where g_1 is a Gaussian density.

A recursion for identity

Writing k for the mutation probability

$$F(y) = (1-k)^2 \Big(\frac{1-F(0)}{\delta} \int g_1(y-z) g_1(z) dz \\ + \int g_1(x) g_1(x') F(y+x'-x) dx dx' \Big).$$

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Continuous time

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Problem: There is no consistent forwards in time population model.

- No sampling consistency

Fourier transform

$$F(y) = (1-k)^2\Big(\frac{1-F(0)}{\delta}\int g_1(y-z)g_1(z)dz$$
$$+\int g_1(x)g_1(x')F(y+x'-x)dxdx'.$$

Writing $f(y)=\frac{1-F(0)}{\delta}\int g_1(y-z)g_1(z)dz$,

$$\tilde{F}(\tilde{y}) = \frac{1}{2\pi}\int e^{iy.\tilde{y}}F(y)dy.$$

$$\tilde{F}(\tilde{y}) = (1-k)^2\Big(\tilde{f}(\tilde{y}) + (2\pi)^2\tilde{g}_1(-\tilde{y})\tilde{g}_1(\tilde{y})\tilde{F}(\tilde{y})\Big)$$

Rearranging,

$$\tilde{F}(\tilde{y}) = \frac{(1-k)^2\tilde{f}(\tilde{y})}{1-(1-k)^2(2\pi)^2\tilde{g}_1(\tilde{y})\tilde{g}_1(-\tilde{y})}.$$

For $y \neq 0$

$$F(y) = \frac{(1-F(0))}{\delta}\int_0^\infty \frac{1}{4\pi\sigma^2 t}(1-k)^{2t}e^{-\|y\|^2/(4\sigma^2 t)}dt,$$

where σ^2 is the variance of the dispersal distribution g_1.

Write $(1-k) = e^{-\mu}$. Since

$$\int_0^\infty e^{-pt} t^{\nu-1} e^{-\frac{\alpha}{4t}} dt \;=\; 2\left(\frac{1}{4}\frac{\alpha}{p}\right)^{\nu/2} K_\nu(\sqrt{\alpha p}), Re\alpha \;>\; 0, Rep \;>\; 0,$$

$$F(y) = \frac{(1-F(0))}{\delta 2\pi\sigma^2} K_0\left(\frac{\|y\|}{\sigma}\sqrt{2\mu}\right).$$

Now assume a local scale κ over which $F(\kappa) \approx F(0)$. Using $K_0(z) \sim \log(1/z)$ as $z \to 0$

$$F(y) \approx \frac{1}{\mathcal{N} + \log(\sigma/\kappa\sqrt{2\mu})} K_0(\sqrt{2\mu}\|y\|/\sigma), \quad \|y\| > \kappa.$$

$\mathcal{N} = 2\pi\delta\sigma^2$ is Wright’s *neighbourhood size*.

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- For large timesteps, temporal correlations are negligible.
- For well separated lineages:
  - the chances of coancestry are negligible,
  - movements of lineages uncorrelated,

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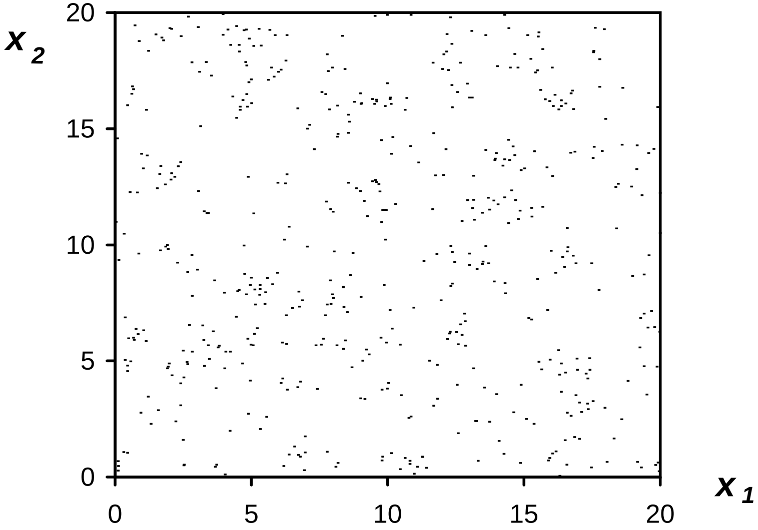
- For well separated lineages:
  - the chances of coancestry are negligible,
  - movements of lineages uncorrelated,

Then over all but small scales, Malécot’s formula remains valid if parameters replaced by *effective* parameters (dispersal rate, neighbourhood size and local scale).

Some comments

Effective parameters may be hard to find.



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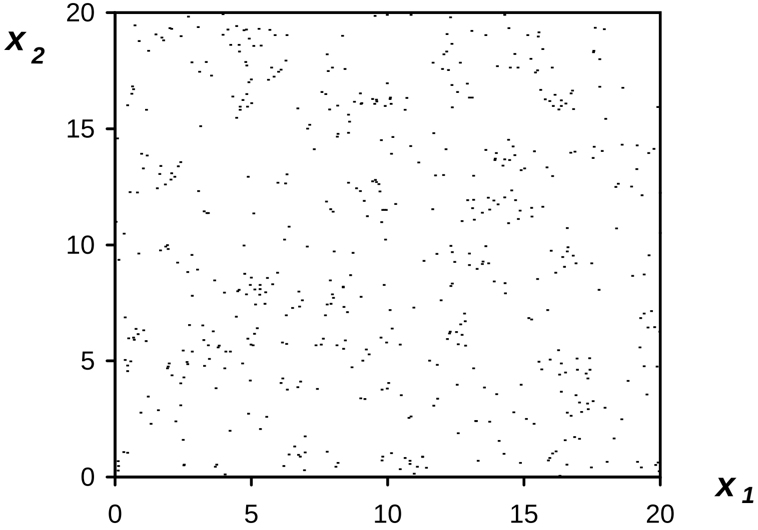

No explicit models for which we can calculate the parameters.

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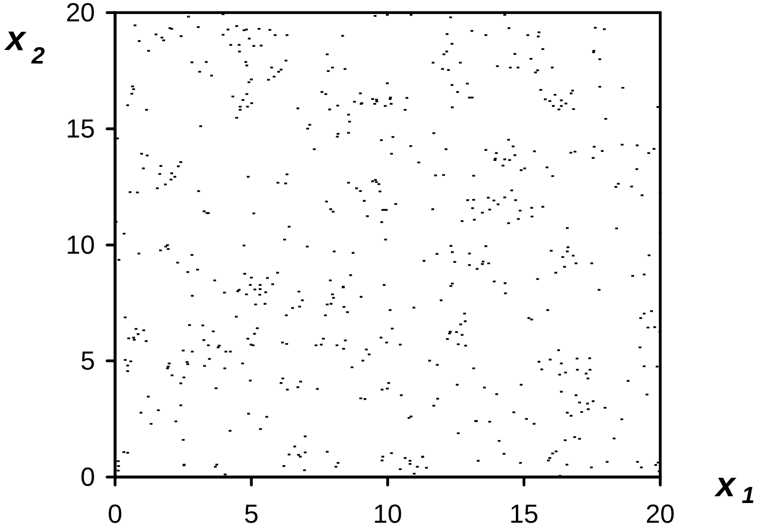

No explicit models for which we can calculate the parameters.

No extension to a sample of size $n > 2$.

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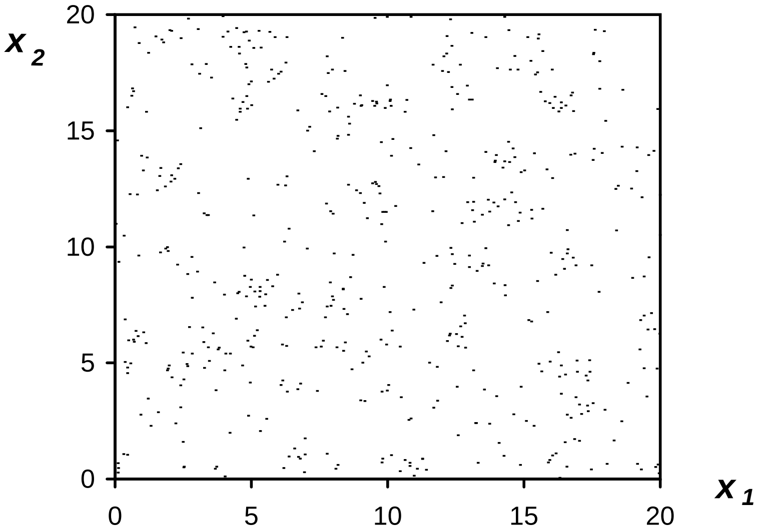

No explicit models for which we can calculate the parameters.
No extension to a sample of size $n > 2$.

... but anyway in a spatial continuum, neighbourhood size could be small and then pairwise coalescences may not dominate.