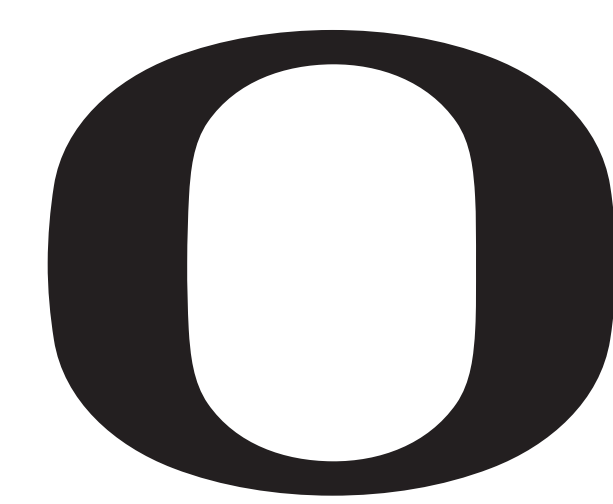


Spatial models in population genetics

Alison Etheridge[†], Tom Kurtz[§], Ian Letter[†], Gilia Patterson[‡], Peter Ralph[‡],
and Terence Tsui[†]. Code: github.com/petrelharp/probgen-2022-poster.

[‡] Mathematics and Biology, University of Oregon
[†] Department of Statistics, University of Oxford
[§] Departments of Mathematics and Statistics, University of Wisconsin - Madison



UNIVERSITY OF
OREGON

Spatial models

There's lots of ways space can enter a model, but the trickiest is through population regulation. Population dynamics must depend on the size somehow, or else the population will either die out or blow up, with certainty (no long-term stability). To do this, we can have:

1. reproduction rate, γ ,
2. establishment probability, r , or
3. deathrate, μ ,

depend on local population density, measured using a kernel density estimate (`sl.localPopulationDensity()` in SLiM).

The difference between (1) and (2) is that "local" means either (1) around the parent, or (2) around the child (after dispersal). Other spatial aspects of models are: **dispersal** of offspring, and/or **mate choice**.

Important quantities:

- N : equilibrium population density per unit area
- σ : dispersal distance
- ϵ , "interaction distance": width of the kernel used to measure population density
- $K = 4N\pi\epsilon^2$: size of interaction neighborhood
- $N_{\text{loc}} = 4N\pi\sigma^2$: Wright's neighborhood size

Debugging your model

It's easy to get populations that die out or quickly get too big. Here's a recipe to get what you want:

1. Pick functional forms so that $F(x) := r(x)\gamma(x) - \mu(x)$ has $F(x) > 0$ for $x < 1$ and $F(x) < 0$ for $x > 1$.
2. Pick a equilibrium density N , and at local density u , set establishment probability to $r(u/N)$, mean number of offspring to $\gamma(u/N)$, and probability of death to $\mu(u/N)$.
3. Ideally you'd be done, but there will be problems: for instance, discrete time steps. Adjust by multiplying μ by a constant α chosen so that a nonspatial population of size K is stable on average, by numerical simulation. Don't forget to look at plots of r , γ , μ , and F , and your non-spatial population dynamics!

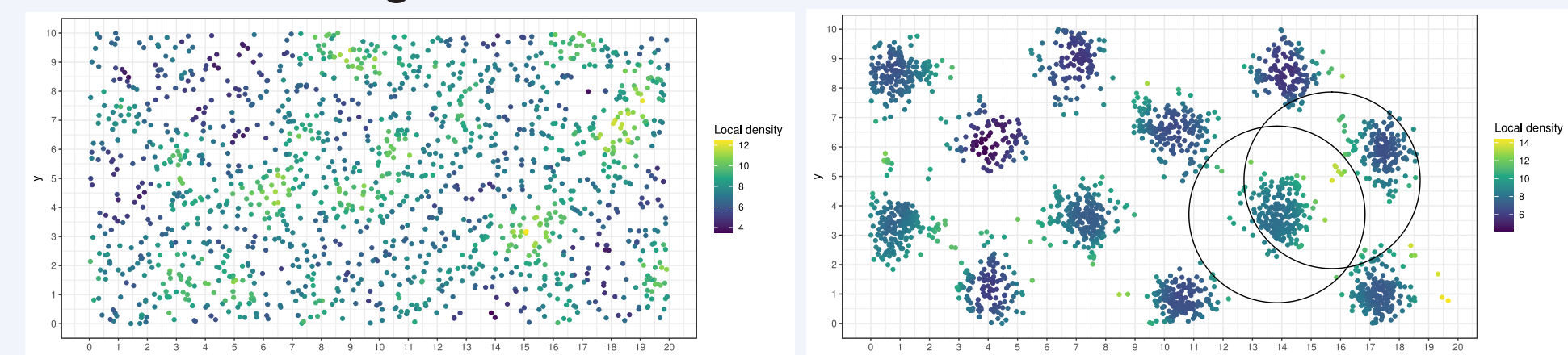
A note of caution

Here are screenshots from a straightforward spatial model, with death rate $\mu = 0.3$ per generation, establishment probability of $r = 0.7$, Gaussian dispersal with SD σ , local density measured in a circle of radius $\epsilon = 1$, and reproduction rate equal to

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

with $K = 2$ and $\lambda = 3$. SLiM code on github (URL above).

Left: $\sigma = 3$. Right: $\sigma = 0.2$.



What's going on? Imagine interactions are mediated by depletion of resources. The clumping pattern on the right is stable because areas between clumps have resources removed by more than one clump. There is always this tendency in a model, but we only see it if dispersal (σ) is less than the interaction distance (ϵ). See section 16.10 in the SLiM manual, or Sasaki (1997). *Note*: if you actually *want* clumps, you probably want an Allee effect, not this.

References

Simulations with SLiM (<https://messerlab.org/SLiM>) and msprime and tskit (<https://tskit.dev>)

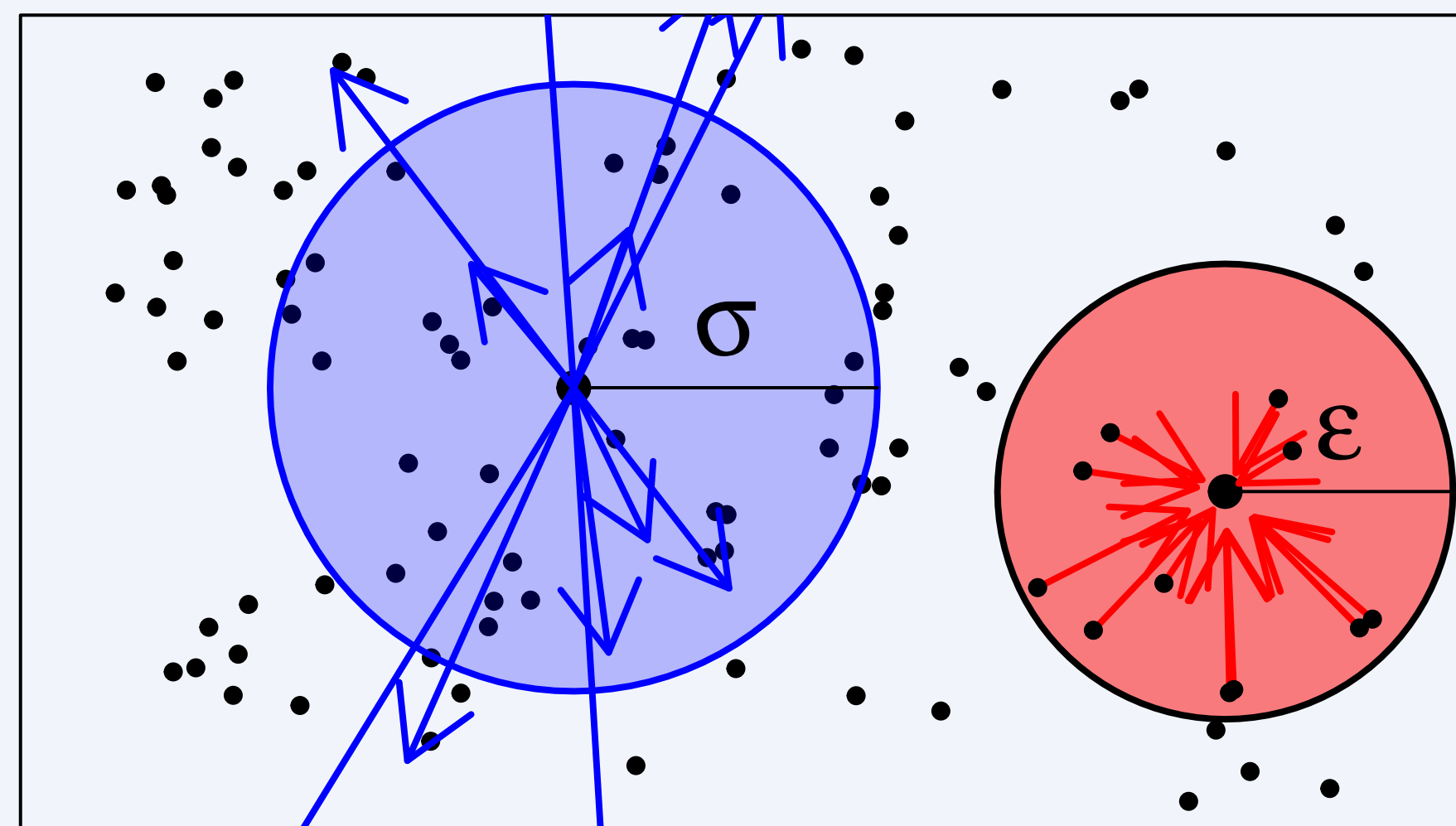
B. Bolker and S. W. Pacala. Using moment equations to understand stochastically driven spatial pattern formation in ecological systems. *Theoretical Population Biology*, 52(3): 179 – 197, 1997. ISSN 0040-5809.

A. M. Etheridge and T. G. Kurtz. Genealogical constructions of population models. *The Annals of Probability*, 47(4):1827–1910, July 2019.

T. G. Kurtz and E. R. Rodrigues. Poisson representations of branching Markov and measure-valued branching processes. *The Annals of Probability*, 39(3):939 – 984, 2011.

A. Sasaki. Clumped distribution by neighbourhood competition. *Journal of Theoretical Biology*, 186(4):415–430, June 1997.

Two sorts of spatial relations: offspring disperse (left) and nearby individuals interact (right), affecting each other's fitness:



A mathematical model

We're working on a formal description of the scaling limits of models like this, along with the model's lineages.

- N : scaling factor for density
- η_t : point measure with mass $1/N$ for each individual
- $\gamma(x, \eta_t)$: per capita birth rate at x
- $q(x, dy)$: probability a juvenile disperses to y
- $r(y, \eta_t)$: juvenile establishment probability at y
- $\mu(x, \eta_t)$: death rate at x

The (forwards) *dispersal distance* is:

$$\sigma^2 = \int |y - x|^2 q(x, dy).$$

Birth, establishment, and establishment rates depend on local population densities (like Bolker and Pacala (1997)):

- p_ϵ : the heat kernel at time ϵ^2
- $p_\epsilon * \eta_t(x)$: "local" population density at x
- ϵ : interaction distance

Scaling limits

We rescale

$$N \rightarrow \infty \quad (\text{local density})$$

and

$$\theta \rightarrow \infty \quad (\text{time scaling}).$$

To retain space:

$$\sigma \propto \frac{1}{\sqrt{\theta}} \quad (\text{dispersal distance}),$$

and to retain temporal dynamics:

$$\theta (r_\theta(x)\gamma_\theta(x) - \mu_\theta(x)) \rightarrow F(x) \quad (\text{net per capita replacement})$$

The limit, Ξ , "solves this PDE":

$$\dot{\Xi} = r\Delta(\gamma\Xi) + F\Xi$$

... but recall that the coefficients are "nonlocal": r may be a function of $p_\epsilon * \Xi$.

The governing equation(s)

The population η , encoded by putting mass $1/N$ on each individual, changes like

$$\begin{aligned} & \frac{1}{N} \times N\eta(y)\gamma(y, \eta) && (\text{birth at } y) \\ & \int q(y, dx)r(x, \eta) && (\text{dispersal to } x) \\ & - \frac{1}{N} \times N\eta(x)\mu(x, \eta) && (\text{death}) \end{aligned}$$

Suppose also the population measure converges, $\eta \rightarrow \Xi$ as $\theta, N \rightarrow \infty$. Then

$$\begin{aligned} & \lim_{t \searrow 0} \frac{1}{t} \mathbb{E} \left[\int f(x)\eta_t(dx) - \int f(x)\eta_0(dx) \mid \eta_0 = \eta \right] \Big|_{t=0} \\ & \rightarrow \int \left\{ \gamma(x, \Xi)\Delta(f(\cdot)r(\cdot, \Xi))(x) \right. \\ & \quad \left. + f(x)F(x, \Xi) \right\} \Xi(dx). \end{aligned}$$

Deterministic limit: $\theta/N \rightarrow 0$

If the limiting measure has density $\Xi_t(x)dx$, then it's a weak solution to

$$\frac{d}{dt}\Xi_t(x) = r(x, \Xi)\Delta(\gamma(\cdot, \Xi_t)\Xi_t(\cdot))(x) + F(x, \Xi_t)\Xi_t(x).$$

i.e.,

$$\dot{\Xi} = r\Delta(\gamma\Xi) + F\Xi.$$

This is an integro-differential equation – we can take the limit as $\epsilon \rightarrow 0$ in certain cases to get a PDE.

Lineages

Thanks to a lookdown construction, following Kurtz and Rodrigues (2011) and Etheridge and Kurtz (2019), we can take the limit while formally retaining lineages.

If a deterministic, local limit holds, with dispersal $N(m, \sigma^2 I)$, lineages should move in a stationary population density $n(x) = d\Xi/dx$ as

$$dL_t = r(L_t)\gamma(L_t) \left\{ (2\sigma^2 \nabla \log(n\gamma))(L_t) - m \right\} dt + \sigma dB_t.$$

i.e., as Brownian motion run at speed $\sigma r(y)\gamma(y)$ in the potential

$$n(y)\gamma(y)e^{-my/(2\sigma^2)},$$

... which has stationary distribution

$$\frac{n(y)}{r(y)} e^{-my/(2\sigma^2)}.$$

Consequence: if there is a bias m in migration then **genetic diversity is independent of range width**, if it is wider than σ^2/m .

Example: the Porus Medium Equation

If we take $r = 1$ and

$$\begin{aligned} \gamma(x) &= n(x) \\ \mu(x) &= (1 + 1/\theta)n(x) - 1/\theta, \end{aligned}$$

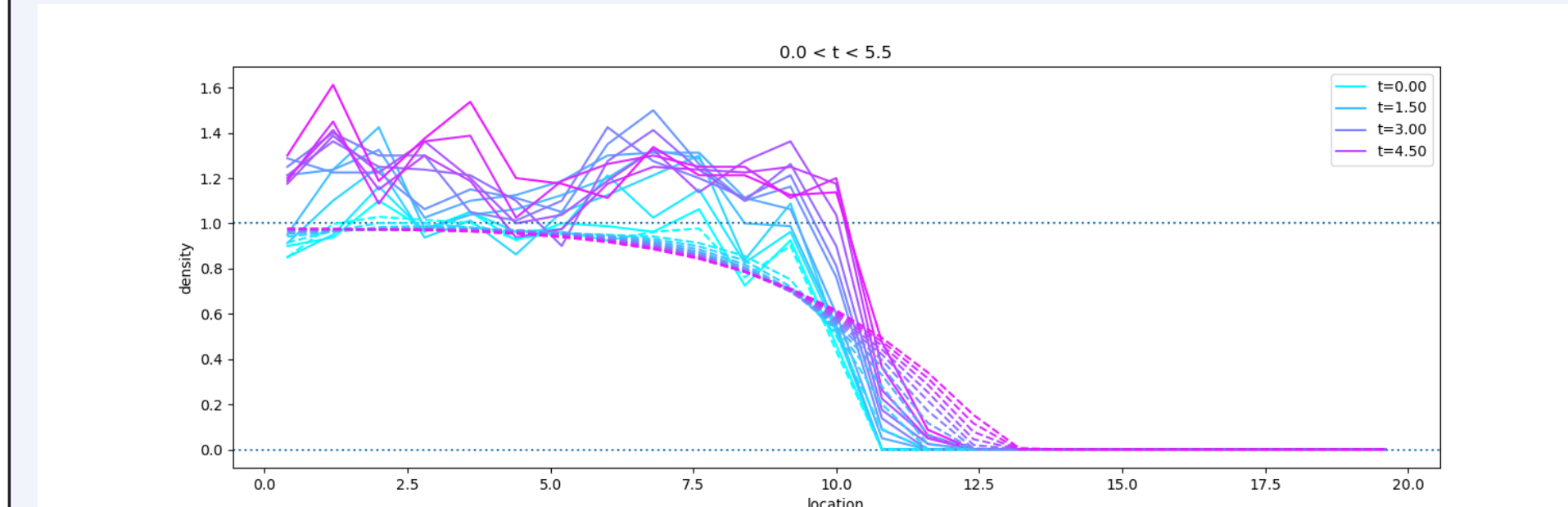
then the PDE we get is

$$\partial_t n_t(x) = \partial_x^2 n_t(x)^2 + n_t(x)(1 - n_t(x)) \quad (\text{PME}).$$

This has the traveling wave solution

$$n_t(x) = \left(1 - \exp\left(\frac{1}{2}(x - t)\right) \right)_+.$$

Population density in simulation, and a numerical solution:



A lineage in the stationary frame has generator

$$\phi \mapsto \left(1 - e^{x/2} \right) \phi_{xx} + \left(1 - 2e^{x/2} \right) \phi_x \quad \text{on } x < 0,$$

which has stationary distribution

$$\pi(x) \propto e^x \left(1 - e^{x/2} \right)$$

for $x < 0$. This is *different* than the Fisher-KPP behavior!

