# Spatial Moran Models with Local Interactions

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#### **Chapter 1: Spatial Moran Models**

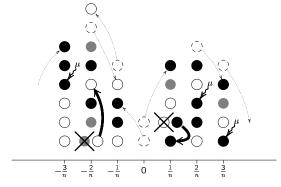
- Construct a stepping stone Moran model;
- Derive limiting system of interacting Brownian motions.

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#### Stepping Stone Model

- one-dimensional lattice  $n^{-1}\mathbb{Z}$  of sites:
- initially distributed iid Poisson mean  $n^{-1}K$  at each site;
- random walk migration (rate  $\theta n^2$ );
- mutation of types;
- Moran dynamics at each site.



#### The Generator

For  $\mathbf{x} \in (n^{-1}\mathbb{Z})^{\infty}$  and  $\mathbf{z} \in E^{\infty}$ :

$$egin{aligned} ilde{A}_n f(\mathbf{x}, \mathbf{z}) &:= \sum_j B_{n,j}^{ heta} f(\mathbf{x}, \mathbf{z}) + \sum_j B_j^{\mu} f(\mathbf{x}, \mathbf{z}) \ &+ \sum_{\substack{i 
eq j \ x_i = x_j}} \left( \lambda/2 + \sigma(z_i, z_j) 
ight) \left( f ig( \mathbf{x}, \eta_j(\mathbf{z}|z_i) ig) - f(\mathbf{x}, \mathbf{z}) ig) \end{aligned}$$

with  $\eta_j(\mathbf{z}|z_0) := (z_1, z_2, \dots, z_{j-1}, z_0, z_{j+1}, \cdots)$  and

$$\begin{split} B_{n,j}^{\theta}f(\mathbf{x},\mathbf{z}) &:= \theta n^2 \bigg( \frac{1}{2} f \big( \eta_j(\mathbf{x} \mid x_j + 1/n), \mathbf{z} \big) \\ &+ \frac{1}{2} f \big( \eta_j(\mathbf{x} \mid x_j - 1/n), \mathbf{z} \big) - f(\mathbf{x}, \mathbf{z}) \bigg) \end{split}$$

and something like

$$B_j^\mu f(\mathbf{x},\mathbf{z}) \coloneqq \int_E ig(f(\mathbf{x},\eta_j(\mathbf{z}|z_0)) - f(\mathbf{x},\mathbf{z})ig)\mu(z_j,dz_0)$$

#### **Explicit Construction**

We will construct a solution  $(\mathbf{X}^{(n)}, \tilde{\mathbf{Z}}^{(n)})$  as follows. Define location processes:

$$X_j^{(n)}(t) := X_j^{(n)}(0) + \frac{1}{n} W_j^{\mathbb{Z}}(\theta n^2 t)$$

and define pairwise interaction counting processes:

$$\tilde{V}_{ij}^{(n),\lambda}(t) := N_{ij}^{\lambda} \left( \frac{\lambda}{2} \int_{0}^{t} 1_{\{X_{i}^{(n)}(s) = X_{j}^{(n)}(s)\}} ds \right) 
\bar{V}_{ij}^{(n),\sigma}(t) := \bar{N}_{ij}^{\sigma} \left( \bar{\sigma} \int_{0}^{t} 1_{\{X_{i}^{(n)}(s) = X_{j}^{(n)}(s)\}} ds \right)$$

to count when j (maybe) copies i's type.

(Where we've assumed  $0 \le \sigma(\cdot, \cdot) \le \overline{\sigma}$ .)

### Defining the Type Process

Order all random times when j (maybe) copies someone's type:

$$0 \equiv \tilde{\tau}_{j,0} < \tilde{\tau}_{j,1} < \tilde{\tau}_{j,2} < \tilde{\tau}_{j,3} < \dots$$

Let  $ilde{Z}_{j}^{(n)}$  be such that

$$\tilde{Z}_{j}^{(n)}(t) = Y_{jk} \left( \tilde{Z}_{j}^{(n)}(\tilde{\tau}_{jk}), t - \tilde{\tau}_{jk} \right),$$
$$\tilde{\tau}_{jk} \le t < \tilde{\tau}_{j,k+1}, \ k \in \mathbb{Z}^{+}$$

where  $Y_{jk}(y,\cdot)$  are independent copies of the mutation process started at y.

Now, we need only define all  $ilde{Z}_{j}^{(n)}( ilde{ au}_{jk})$  .

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#### Defining the Type Process (cont.)

For  $k \in \mathbb{N}$ , time  $\tilde{\tau}_{jk}$  is an interaction of j with a specific particle i.

If potential selective, event becomes *actual* selective with probability:

$$\bar{\sigma}^{-1}\sigma\left(\tilde{Z}_{i}^{(n)}(\tilde{ au}_{jk}-),\tilde{Z}_{j}^{(n)}(\tilde{ au}_{jk}-)\right)$$

If neutral, event is always "actual."

Take new type of j to be:

$$ilde{Z}_{j}^{(n)}( ilde{ au}_{jk}) = egin{cases} ilde{Z}_{i}^{(n)}( ilde{ au}_{jk}-), & ext{if event is actual;} \ ilde{Z}_{j}^{(n)}( ilde{ au}_{jk}-), & ext{otherwise.} \end{cases}$$

#### Potential vs. Actual

Potential selective events  $ar{V}_{ij}^{(n),\sigma}$  take place at time change

$$\bar{\sigma} \int_0^t \mathbf{1}_{\{X_i^{(n)}(s) = X_j^{(n)}(s)\}} ds$$

and are filtered according to

$$ar{\sigma}^{-1}\sigma\left( ilde{Z}_i^{(n)}(s-), ilde{Z}_j^{(n)}(s-)
ight)$$

so actual selective events  $\tilde{V}_{ij}^{(n),\sigma}$  take place at time change

$$\int_0^t \sigma\left(\tilde{Z}_i^{(n)}(s), \tilde{Z}_j^{(n)}(s)\right) 1_{\{X_i^{(n)}(s) = X_j^{(n)}(s)\}} ds$$

#### **Brownian Limit**

As  $n \to \infty$ , location processes converge:

$$X_i^{(n)} \Rightarrow X_i := X_i(0) + \sqrt{\theta}W_i$$

and (scaled) interaction integrals converge:

$$n \int_{0}^{1} \{X_{i}^{(n)}(s) = X_{j}^{(n)}(s)\}^{ds}$$
  
$$\Rightarrow (2\theta)^{-1} L_{t}^{0}(X_{i} - X_{j})$$

#### **Brownian Model**

- particles live on  $\mathbb{R}$ ;
- initially distributed  $Poisson(K\ell_{\mathbb{R}})$ ;
- Brownian migration;
- mutation of types;
- pairwise Moran interactions driven by local times.

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#### **Explicit Construction**

Define location processes:

$$X_j(t) := X_j(0) + \sqrt{\theta}W_j(t)$$

and define pairwise interaction counting processes:

$$\tilde{V}_{ij}^{\lambda}(t) := N_{ij}^{\lambda} \left( \frac{\lambda}{4\theta} L^{0}(X_{i} - X_{j}) \right)$$

$$\bar{V}_{ij}^{\sigma}(t) := \bar{N}_{ij}^{\sigma} \left( \frac{\bar{\sigma}}{2\theta} L^{0}(X_{i} - X_{j}) \right)$$

to count when j (maybe) copies i's type.

Create a type process as before:

- mutate between interactions  $Y_{jk}(y,\cdot)$ ;
- at interaction, copy if "actual" event.

## Chapter 2: Infinite-Density Stepping Stone Model

- Construct an ordered stepping stone model;
- Couple Moran and ordered models (generator argument);
- Construct an infinite-density neutral model embedding the finite-density neutral models.

#### Ordering the Model

Assign iid uniform levels to particles, independent of location and type.

Neutral interactions only occur in one direction. Only the higher-level particle changes its type.

#### **Comparison of Generators**

For  $\mathbf{x} \in (n^{-1}\mathbb{Z})^{\infty}$  and  $\mathbf{z} \in E^{\infty}$ :

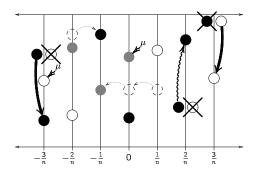
$$egin{aligned} ilde{A}_n f(\mathbf{x}, \mathbf{z}) &:= \sum_j B_{n,j}^{ heta} f(\mathbf{x}, \mathbf{z}) + \sum_j B_j^{\mu} f(\mathbf{x}, \mathbf{z}) \ &+ \sum_{\substack{i 
eq j \ x_i = x_j}} \left( \lambda/2 + \sigma(z_i, z_j) 
ight) \left( f ig( \mathbf{x}, \eta_j(\mathbf{z}|z_i) ig) - f(\mathbf{x}, \mathbf{z}) ig) \end{aligned}$$

versus (for  $\mathbf{u} \in [0, 1]^{\infty}$ )

$$egin{aligned} A_n f(\mathbf{x}, \mathbf{z}, \mathbf{u}) &:= \sum_j B_{n,j}^{ heta} f(\mathbf{x}, \mathbf{z}, \mathbf{u}) + \sum_j B_j^{\mu} f(\mathbf{x}, \mathbf{z}, \mathbf{u}) \ &+ \sum_{\substack{i \neq j \ x = r_i, \ x = r_i}} \left( \mathbb{1}_{\{u_i < u_j\}} \lambda + \sigma(z_i, z_j) 
ight) \left( f\left(\mathbf{x}, \eta_j(\mathbf{z}|z_i) 
ight) - f\left(\mathbf{x}, \mathbf{z} 
ight) 
ight) \end{aligned}$$

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#### Ordered Model in Action



#### **Coupling via Generators**

If  $V_{ij}^{(n),\lambda}$  is the counting process of (ordered) neutral interactions:

$$V_{ij}^{(n),\lambda}(t) := 1_{\{U_i < U_j\}} N_{ij}^{\lambda} \left( \lambda \int_0^t 1_{\{X_i^{(n)}(s) = X_j^{(n)}(s)\}} ds \right)$$

then let Φ be such that

$$\Phi_j(t) = j + \sum_{i \neq j} \int_0^t \left( \Phi_i(s-) - \Phi_j(s-) \right)$$
$$\hat{V}_{\Phi_i(s-), \Phi_j(s-)}(ds)$$

where

$$\widehat{V}_{ij}(t) := \sum_{l=1}^{V_{ij}^{(n),\lambda}(t)} \xi_{ijl}$$

for  $\xi_{ijl}$  iid fair coin flips.

Note  $j\mapsto \Phi_j(t)$  is a permutation of indices  $\mathbb{N}$ .

#### Coupling via Generators (cont.)

Using filtered martingale problem machinery, we show that

$$(\mathbf{X}_{\Phi}^{(n)}, \mathbf{Z}_{\Phi}^{(n)}) = d(\mathbf{X}^{(n)}, \tilde{\mathbf{Z}}^{(n)})$$

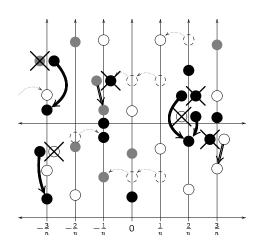
where  $\mathbf{X}_{\Phi}^{(n)}$  means:

$$\left(X_{\Phi_1(\cdot)}^{(n)}(\cdot),X_{\Phi_2(\cdot)}^{(n)}(\cdot),\ldots\right)$$

Since  $\Phi$  is permutation-valued, it follows that

$$\sum_{j} \delta_{(X_{j}^{(n)}(\cdot), \tilde{Z}_{j}^{(n)}(\cdot))} =^{d} \sum_{j} \delta_{(X_{j}^{(n)}(\cdot), Z_{j}^{(n)}(\cdot))}$$

#### Infinite-Density, Neutral Model



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## Chapter 3 (first half): Infinite-Density Brownian Model

- Construct a (finite-density) ordered system of interacting Brownian motions;
- Study selection mechanism in limit to construct an infinite-density ordered model with selection;
- Couple Moran and ordered models (level-flipping argument):
  - Couple finite-density Moran and ordered models:
  - Couple infinite-density ordered model to "hybrid" model.

#### Finite-Density Ordered Model

Define location processes:

$$X_j(t) := X_j(0) + \sqrt{\theta}W_j(t)$$

and define pairwise interaction counting processes:

$$V_{ij}^{\lambda}(t) := 1_{\{U_i < U_j\}} N_{ij}^{\lambda} \left( \frac{\lambda}{2\theta} L^0(X_i - X_j) \right)$$
  
$$\bar{V}_{ij}^{\sigma}(t) := \bar{N}_{ij}^{\sigma} \left( \frac{\bar{\sigma}}{2\theta} L^0(X_i - X_j) \right)$$

to count when j (maybe) copies i's type.

Create a type process as before:

- mutate between interactions  $Y_{jk}(y,\cdot)$ ;
- at interaction, copy if "actual" event.

#### **Limiting Selection**

Define

$$ar{V}_j^\sigma := \sum_{i \neq j} ar{V}_{ij}^\sigma$$

counting all potential selective events affecting particle j.

Then

$$ar{V}_j^\sigma = ar{N}_j^\sigma \left(rac{ar{\sigma}}{2 heta}\sum_{i 
eq j} L_{ij}(\cdot)
ight)$$

and, for each fixed j,

$$\frac{\bar{\sigma}_0}{2\theta K} \sum_{i \neq j} L_{ij}(t) \xrightarrow[K \to \infty]{L^2} \bar{\sigma}_0 t$$

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#### **Infinite-Density Ordered Model**

Define location processes:

$$X_j(t) := X_j(0) + \sqrt{\theta}W_j(t)$$

Define pairwise neutral counting processes:

$$V_{ij}^{\lambda}(t) := 1_{\{U_i < U_j\}} N_{ij}^{\lambda} \left(\frac{\lambda}{2\theta} L^{0}(X_i - X_j)\right)$$

to count when j copies i's type

Define per-particle potential selective event counting processes:

$$\bar{V}_i^{\sigma}(t) := \bar{N}_i^{\sigma}(\bar{\sigma}t)$$

to count when j (maybe) copies the type of a "nearby" particle.

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#### **Selective Events**

Create a type process almost as before:

- mutate between interactions  $Y_{ik}(y,\cdot)$ ;
- at interaction, copy if "actual" event.

But, what do we copy for a selective event?

For now, suppose

$$Z_0 = \psi \left( \sum_{i} \delta_{(X_i(s-), Z_i(s-), U_i)}, X_j(s-), \eta \right)$$

gives us a candidate type when  $\eta \sim U[0,1].$  As before, potential becomes actual with probability

$$\bar{\sigma}^{-1}\sigma(Z_0,Z_j(s-))$$

#### Coupling via Level-Flipping

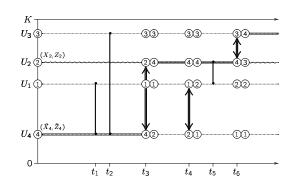
Create a finite-density intermediate model:

- particles start with iid uniform levels;
- neutral events are ordered (high copies low);
- immediately after a neutral event, particles swap levels half the time.

Ignore levels and follow indices, and you "see" the symmetric model.

Ignore indices and follow levels, and you "see" the ordered model.

#### **Intermediate Model**



Consequence:  $\sum_{j} \delta_{(\tilde{X}_{j}(\cdot), \tilde{Z}_{j}(\cdot))} = \sum_{j} \delta_{(X_{j}(\cdot), Z_{j}(\cdot))}$ 

#### Coupling via Level-Flipping (cont.)

Also can create an infinite-density hybrid model:

- below level K, looks like symmetric;
- ullet above level K, looks like ordered.

As a consequence, the infinite-density model can be broken in two at any level, and you can "ignore the levels" of the bottom part.

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## Chapter 3 (second half): Infinite-Density Brownian Model

- Define infinite-density location/type measure-valued process (via backwards martingales "in level space");
- Establish conditional Poisson structure of particle system;
- Characterize the measure-valued process with martingales using:
  - "hybrid" model symmetry;
  - backwards martingale convergence;
  - Poisson structure.

#### Location/Type Measure

Write

$$\left\langle u_t^K,h\right\rangle :=\sum_{U_j\leq K}h\left(X_j(t),Z_j(t)\right)$$

Note that  $\frac{1}{K}\left\langle u_{t}^{K},h\right\rangle$  is the average "h-ness" of all particles below level K.

If limits

$$\langle u_t, h 
angle := \lim_{K o \infty} rac{1}{K} \left\langle u_t^K, h 
ight
angle$$

exist, they will characterize the location/type distribution of the infinite-density process.

#### Location/Type Measure (cont.)

Define filtrations

$$\mathfrak{F}_t^K := \sigma \left\{ \sum_{U_j \le K} \delta_{(X_j(r), Z_j(r))}, \\ \sum_{U_j > K} \delta_{(X_j(r), Z_j(r), U_j)}, r \le t \right\}$$

and  $\mathfrak{F}^\infty_t = \cap_{K>0} \, \mathfrak{F}^K_t$ 

By the hybrid model coupling:

$$\mathsf{E}\left[\left\langle u_t^1,h
ight
angle \, \left|\, \mathfrak{F}_t^K
ight] = rac{1}{K} \left\langle u_t^K,h
ight
angle$$

and by backwards martingale convergence:

$$\mathsf{E}\left[\left\langle u_{t}^{1},h\right\rangle \bigm| \mathfrak{F}_{t}^{K}\right] \underset{K\rightarrow\infty}{\longrightarrow} \mathsf{E}\left[\left\langle u_{t}^{1},h\right\rangle \bigm| \mathfrak{F}_{t}^{\infty}\right]$$

#### **Poisson Structure**

Assume Poisson starting conditions.

For every  $t \geq 0$ , conditioned on  $\mathfrak{F}_t^{\infty}$ ,

$$\xi_t := \sum_j \delta_{\left(X_j(t), Z_j(t), U_j
ight)} \sim \mathit{Poisson}(
u_t imes \ell_{\mathbb{R}^+})$$

where

$$\nu_t(A \times B) := \langle u_t, 1_{A \times B} \rangle$$

Also,  $\nu_t(\cdot \times E) = \ell_{\mathbb{R}}$ .

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#### **Selection Revisited**

There exists  $\hat{\nu}$  such that

$$u_t(C) = \int_{\mathbb{R}} \int_E 1_C(x,z) \widehat{\nu}_t(x,dz) dx$$

for all  $C \in \mathfrak{B}(\mathbb{R} \times E)$ .

So,  $\hat{\nu}_t(x,\cdot)$  is rather like the probability distribution of types "at" point x.

Wouldn't it be nice if, conditioned on  $\mathfrak{F}_t^{\mathbf{X},\mathbf{Z},\mathbf{U}}$ , the candidate type

$$Z_0 = \psi\left(\xi_{s-}, X_i(s-), \eta\right)$$

had distribution  $\widehat{\nu}_t(X_j(s-),\cdot)$ ?

#### Martingale Characterization

All this machinery allows us to show that, for  $f \in C^2_c(\mathbb{R})$  and  $g \in \mathfrak{D}(B^{\mu})$ ,

$$M_t := \langle u_t, fg \rangle - \langle u_0, fg \rangle - \int_0^t \langle u_s, \frac{\theta}{2} f''g + fB^{\mu}g + h_s^{\sigma} \rangle ds$$

is an  $\{\mathfrak{F}_t^\infty\}$ -martingale where

$$h_s^{\sigma}(x, z, \omega) := f(x) \int_0^1 \sigma(\psi(\xi_{s-}(\omega), x, \eta), z) \left(g(\psi(\xi_{s-}(\omega), x, \eta)) - g(z)\right) d\eta$$

#### **Quadratic Variation**

Using the same machinery, we can establish that

$$\langle M^K \rangle_t \xrightarrow[K \to \infty]{L^1} \langle M \rangle_t$$

where

$$egin{aligned} M^K_t &:= rac{1}{K} igg( igg\langle u^K_t, fg igg
angle - igg\langle u^K_0, rac{ heta}{2} f''g + f B^\mu g + h^\sigma_s igg
angle \, ds igg) \end{aligned}$$

#### **Quadratic Variation (cont.)**

Using a physically painful analysis argument, we can establish that

$$\langle M \rangle = \theta \lambda \int_0^{\cdot} ds \int_{\mathbb{R}} dx \int_{E \times E} \widehat{\nu}_s(x, dz) \widehat{\nu}_s(x, dz')$$

$$\left( f(x)g(z) - f(x)g(z') \right)^2$$

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#### **Tightness**

Using another involved argument, we can establish that  $\left(\frac{1}{K}\left\langle u_{\cdot}^{K},fg\right\rangle \right)_{K}$  and  $\left(M^{K}\right)_{K}$  are tight.

A consequence of this, since the maximum jump size goes to zero, is that the limits are pathwise continuous. (And the angle-brackets process of M is also its quadratic variation.)

#### **Complete Martingale Problem**

For  $f \in C^2_c(\mathbb{R})$  and  $g \in \mathfrak{D}(B^\mu)$ ,

$$egin{aligned} M_t &:= \langle u_t, fg 
angle - \langle u_0, fg 
angle \ &- \int_0^t \! \left\langle u_s, rac{ heta}{2} f''g + f B^\mu g + h_s^\sigma 
ight
angle \, ds \end{aligned}$$

is an  $\{\mathfrak{F}_t^\infty\}$ -martingale with quadratic variation

$$[M^K] = heta \lambda \int_0^{\cdot} ds \int_{\mathbb{R}} dx \int_{E \times E} \widehat{\nu}_s(x, dz) \widehat{\nu}_s(x, dz') \\ \left( f(x) g(z) - f(x) g(z') \right)^2$$

#### Mueller-Tribe SPDE

- Two types  $E = \{0, 1\};$
- No mutation;

Then, for  $g=\delta_1$  and  $u(s,x)=\widehat{\nu}_s(x,\delta_1)$ , we have

$$egin{aligned} \int_{\mathbb{R}}f(x)u(t,x)dx &- \int_{\mathbb{R}}f(x)u(0,x)dx \ &- \int_{0}^{t}\int_{\mathbb{R}}\Bigl(rac{ heta}{2}f''(x)u(s,x) \ &+ ar{\sigma}u(s,x)(1-u(s,x))\Bigr)dx\,ds \end{aligned}$$

a martingale with quadratic variation

$$2 heta\lambda\int_0^t\!\!\int_{\mathbb{R}}f^2(x)u(s,x)(1-u(s,x))dx\,ds$$

Thus, u is a weak solution of:

$$\dot{u} = \frac{\theta}{2}\Delta u + \bar{\sigma}u(1-u) + \sqrt{2\theta\lambda u(1-u)}\dot{W}$$