REVERSIBLE FLEMING-VIOT PROCESSES

BYRON SCHMULAND
UNIVERSITY OF ALBERTA, CANADA

Markov Processes and Related Topics
Beijing Normal University
August 19 2002

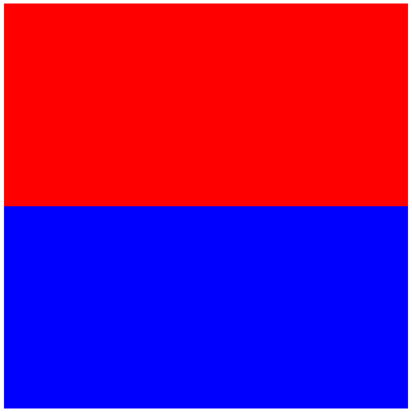
Which Fleming-Viot processes are reversible?

1. Wright-Fisher model
2. Fleming-Viot model
3. Which mutation operators give reversibility?
4. Reversible = Quasi-invariant
5. Cocycle identity implies mutation is uniform.

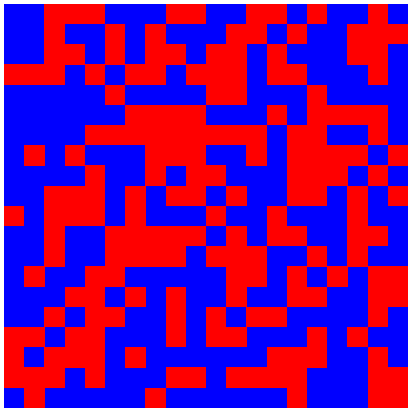
Wright-Fisher model

Imagine a population of fixed size N, that has two types of individuals; blue 🟦 and red 🟥. At time $t > 0$, every individual independently chooses a parent from the population at time $t - 1$, and adopts the parent's genetic type (🟦 or 🟥).

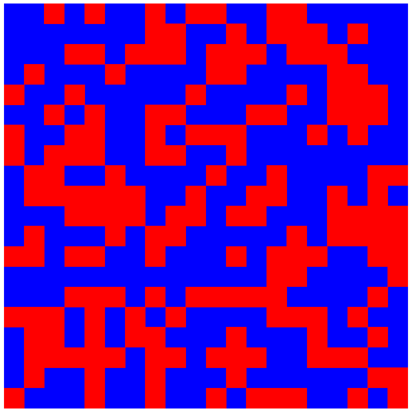
The old generation dies, and the new generation takes its place, keeping the population size fixed at N. This process repeats itself in every generation.



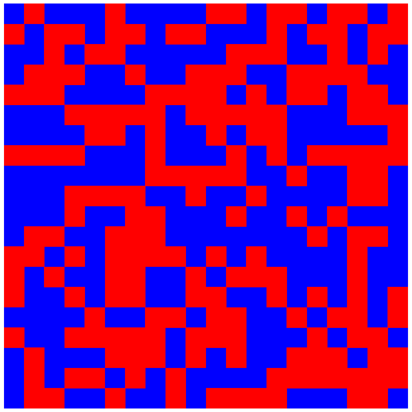
$t = 0$



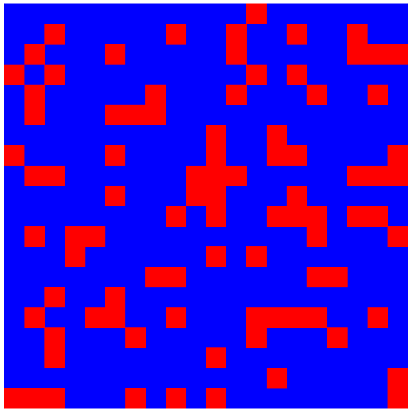
$t = 1$



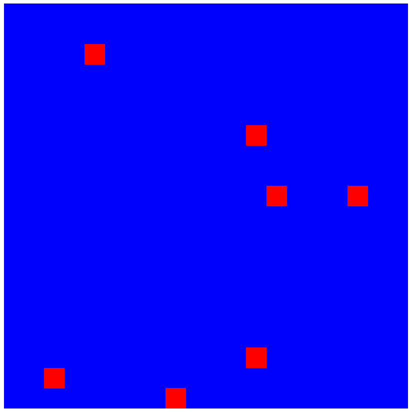
$t = 2$



$t = 100$



$t = 200$

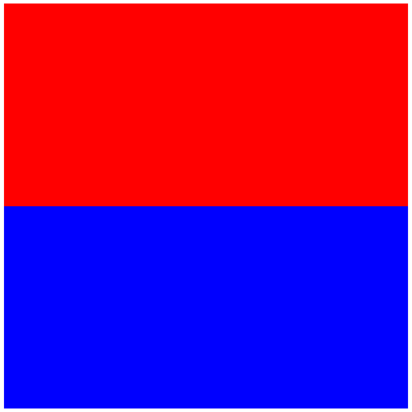


$t = 300$

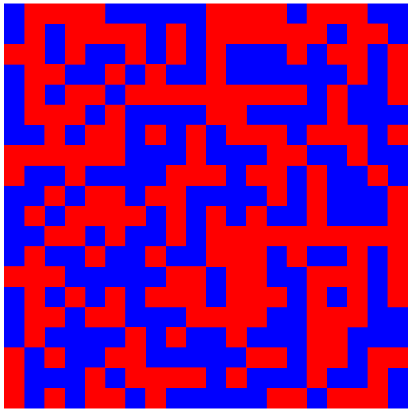
The population will always end up all 🟥 or all 🟦, i.e., in one of the absorbing states.

To preserve genetic diversity in the population, we must add other mechanisms for change. For example, suppose that with probability p an offspring *mutates*.

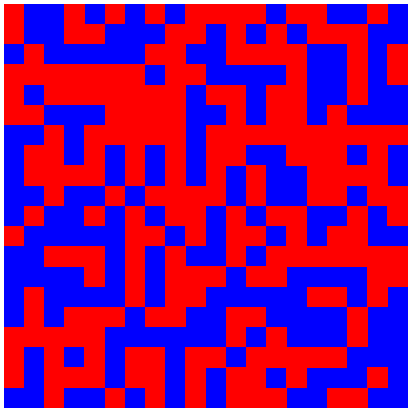
Mutation means the offspring doesn’t just adopt its parent’s type, but uses some other rule.



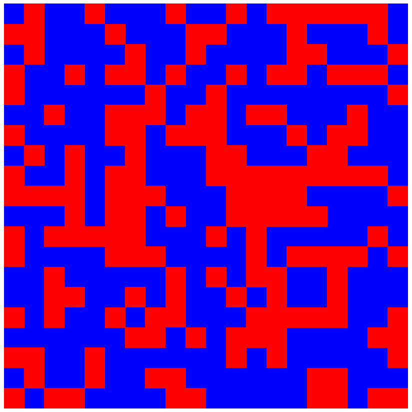
$t = 0$



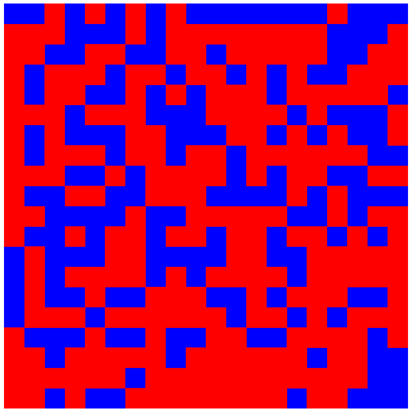
$t = 1$



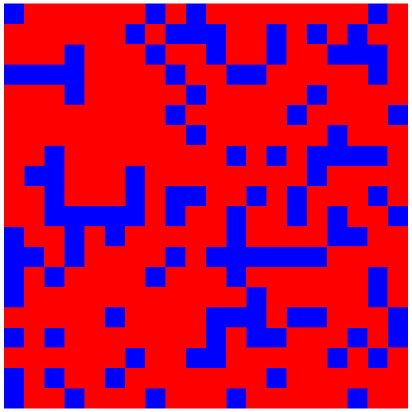
$t = 2$



$t = 100$



$t = 200$



$t = 300$

In this example, the chance of mutation is $p = 1/100$, and a mutant is equally likely to be 🟥 or 🟦.

The Markov chain is ergodic, and has a unique limiting distribution Π.

Since p is small, the distribution Π puts more weight on states that are almost all 🟥 or all 🟦.

As $p \longrightarrow 1$, the distribution Π puts more and more weight on states that are about half 🟥 and half 🟦.

In this model, the spatial information is irrelevant, and to keep track of the evolution of the population, we only need the number of 🟦's and the number of 🟥's.

We define X_t, the state of the population at time t, to be the empirical probability measure on the set of types.

The state space can be identified with $\mathcal{M}_1(E)$ where $E = \{\text{🟦}, \text{🟥}\}$.

Fleming-Viot model

This is the analogue of the Wright-Fisher model. Each individual in the population has a genetic type belonging to the type space E, and X_t denotes the empirical distribution of types at time t. The process X_t lives on the space $\mathcal{M}_1(E)$ of probability measures on E.

Here the time parameter t is continuous, and the type space E is arbitrary.

The changes to this population come from two opposing sources; *genetic drift* which encourages conformity by favoring individuals with dominant type and *mutation* which continually adds fresh variation.

Other mechanisms such as *selection* and *recombination* can be added to the model for more realism.

- Stationary: $P_\Pi(X_t \in B) = P_\Pi(X_0 \in B) = \Pi(B)$.
- Reversible:
  $P_\Pi(X_0 \in A, X_t \in B) = P_\Pi(X_t \in A, X_0 \in B)$.

If the starting point is randomly chosen using Π then the genetic forces are in perfect balance and X_t is stationary, i.e., in equilibrium.

As with all Markov processes, it is of great interest whether the limiting distribution Π makes the process reversible in time.

These conditions can be rewritten using the *generator* $\mathcal{L}$ of the process.

- Stationary: $\int \mathcal{L}\Phi \, d\Pi = 0$.
- Reversible: $\int \mathcal{L}\Phi\Psi \, d\Pi = \int \mathcal{L}\Psi\Phi \, d\Pi$.

$$\begin{aligned}\mathcal{L}\Phi(\mu) &= \underbrace{\frac{1}{2}\langle \delta_y(dx)\mu(dy) - \mu(dx)\mu(dy), \frac{\delta^2\Phi(\mu)}{\delta\mu(x)\delta\mu(y)}\rangle}_{\text{genetic drift}} \\ &+ \underbrace{\langle \mu, A\frac{\delta\Phi(\mu)}{\delta\mu(\cdot)}\rangle}_{\text{mutation}}\end{aligned}$$

Calculus for functions on $\mathcal{M}_1(E)$

$$\Phi(\mu) = F(\langle \mu, f_1\rangle, \ldots, \langle \mu, f_n\rangle)$$

$$\frac{\delta \Phi(\mu)}{\delta \mu(x)} = \frac{d}{d\epsilon}\Phi(\mu + \epsilon\delta_x)|_{\epsilon=0}$$

$$\frac{\delta^2 \Phi(\mu)}{\delta \mu(x)\delta\mu(y)} = \frac{\partial^2}{\partial\epsilon_1\partial\epsilon_2}\Phi(\mu + \epsilon_1\delta_x + \epsilon_2\delta_y)|_{\epsilon_1=\epsilon_2=0}$$

$$\mathcal{L}\Phi(\mu) = \frac{1}{2}\langle \delta_y(dx)\mu(dy) - \mu(dx)\mu(dy), \frac{\delta^2\Phi(\mu)}{\delta\mu(x)\delta\mu(y)}\rangle + \langle \mu, A\frac{\delta\Phi(\mu)}{\delta\mu(\cdot)}\rangle$$

Which operators A give a reversible process?

- It has long been known that if A is *uniform*, i.e.

  $$Af(x) = \frac{\theta}{2} \int_E (f(x) - f(y))\, \nu(dy),$$

  then the Fleming-Viot process is reversible.
- In 1999, Li, Shiga, and Yao proved the converse using moment calculations.
- In 2002, Handa re-proved this result using cocycles.

Reversible = Quasi-invariant

Define a “shifted” probability measure

$$S_f\mu(dx) := \frac{e^{f(x)}\mu(dx)}{\langle e^f, \mu\rangle}; \quad f \in C(E), \mu \in \mathcal{M}_1(E).$$

$(S_f)_{f\in C(E)}$ forms a transformation group on $\mathcal{M}_1(E)$ since $S_{f+g} = S_f(S_g)$.

A nice property of this flow: $\dfrac{d}{dt}\langle f, S_{tg}\mu\rangle = \mathrm{cov}_{S_{tg}\mu}(f, g)$.

Definition: $\Pi \in \mathcal{M}_1(\mathcal{M}_1(E))$ is called *quasi-invariant* with cocycle Λ if

$$\Pi \circ (S_{-f})^{-1}(d\mu) = e^{\Lambda(f,\mu)}\,\Pi(d\mu).$$

Implies: $\Lambda(f+g,\mu) = \Lambda(f, S_g\mu) + \Lambda(g,\mu), \quad \Pi\text{-a.s.}$

Theorem: (Handa) $\Pi \in \mathcal{M}_1(\mathcal{M}_1(E))$ is reversible for $\mathcal{L}$ if and only if Π is quasi-invariant with cocycle

$$\Lambda(f, \mu) := 2 \int_0^1 \langle Af, S_{uf}\mu \rangle \, du.$$

Let $(A, D(A))$ be a densely defined linear operator on $C(E)$, and define for $f \in D(A)$

$$\Lambda(f, \mu) := \int_0^1 \langle Af, S_{uf}\mu \rangle \, du. \tag{1}$$

We assume that the *cocycle identity* holds for all $f, g \in D(A)$ and $\mu \in \mathcal{M}_1(E)$:

$$\Lambda(f + g, \mu) = \Lambda(f, S_g\mu) + \Lambda(g, \mu). \tag{2}$$

The cocycle identity implies that A is uniform.

Lemma 1. If $\mathrm{Var}_\mu(f) = 0$, then $\mathrm{Var}_\mu(Af) = 0$.

Proof. Choose $f \in D(A)$ with $\mathrm{Var}_\mu(f) = 0$. Then $S_{uf}\mu = \mu$ for all $0 \leq u \leq 1$ so $\Lambda(f, S_h\mu) = \langle Af, S_h\mu\rangle$ for any $h \in C(E)$. The cocycle identity implies

$$\Lambda(f, S_g\mu) + \Lambda(g, \mu) \quad = \quad \Lambda(g, S_f\mu) + \Lambda(f, \mu),$$

or

$$\langle Af, S_g\mu\rangle \quad = \quad \langle Af, \mu\rangle.$$

Setting $g = t(Af)$ and differentiating gives $0 = \frac{d}{dt}\Big|_{t=0} \langle Af, S_{t(Af)}\mu\rangle = \mathrm{cov}_\mu(Af, Af)$. $\square$

Proposition 1. If $(A, D(A))$ is a closed operator satisfying the cocycle identity (2), then A must be of the form

$$Af(x) = \alpha f(x) + \langle f, \nu \rangle, \quad f \in C(E),$$

for some $\alpha \in \mathbb{R}$ and some finite signed measure ν.

Proof. Let $x \neq y \in E$ and $f, g \in D(A)$, and define the function

$$F = [g(x) - g(y)]f + [f(y) - f(x)]g.$$

Since $F(x) = F(y)$, we can apply Lemma 1 at $\mu = (\delta_x + \delta_y)/2$ and conclude that $AF(x) = AF(y)$.

This can be rearranged to read

$$[g(x)-g(y)][Af(x)-Af(y)] = [f(x)-f(y)][Ag(x)-Ag(y)].$$

Since $D(A)$ is dense in $C(E)$ we may choose $g \in D(A)$ with $g(x) \neq g(y)$ and define

$$\alpha_{xy} = [Ag(x) - Ag(y)]/[g(x) - g(y)],$$

so that for all $f \in D(A)$,

$$Af(x) - Af(y) = \alpha_{xy}[f(x) - f(y)].$$

If $f(z) \neq f(x)$, then

$$\begin{aligned} \alpha_{zx} &= \frac{Af(z) - Af(x)}{f(z) - f(x)} \\ &= \frac{Af(z) - Af(y)}{f(z) - f(x)} + \frac{Af(y) - Af(x)}{f(z) - f(x)} \\ &= \alpha_{zy} \frac{f(z) - f(y)}{f(z) - f(x)} + \alpha_{yx} \left(1 - \frac{f(z) - f(y)}{f(z) - f(x)} \right) . \end{aligned}$$

Since f is arbitrary, we conclude that $\alpha_{zy} = \alpha_{yx}$. Thus, all the α's are the same and for all $x, y \in E$ and $f \in D(A)$, we have

$$Af(x) - \alpha f(x) = Af(y) - \alpha f(y).$$

Thus $f \to (A - \alpha I)f(x)$ is a continuous linear functional on $D(A)$ and can be extended continuously to $C(E)$ where it is represented by a finite signed measure ν. For $f \in D(A)$ we have

$$(A - \alpha I)f(x) = \langle f, \nu \rangle.$$

The right hand side is continuous and A is closed so $D(A) = C(E)$ and

$$Af(x) = \alpha f(x) + \langle f, \nu \rangle. \qquad \square$$

Unfortunately, quasi-invariance gives the cocycle identity only for Π-almost every μ.

However, if A generates an irreducible Markov semigroup on E, Proposition 3.1 of Handa's paper says that Π-almost every μ has full support on E.

It is an easy exercise to show that Π has full support on $\mathcal{M}_1(E)$, so by continuity the cocycle identity extends to all of $\mathcal{M}_1(E)$.

References

Kenji Handa: Quasi-invariance and reversibility in the Fleming-Viot process. *Probability Theory and Related Fields* **122**, 545–566, 2002.

Zenghu Li, Tokuzo Shiga, and Lihua Yao: A reversibility problem for Fleming-Viot processes. *Electronic Communications in Probability* **4**, 65–76, 1999.

Byron Schmuland and Wei Sun: A cocycle proof that reversible Fleming Viot processes have uniform mutation. To appear in *Comptes Rendus Mathematical Reports, Royal Society of Canada.*