

Λ colescent and look-down model with selection

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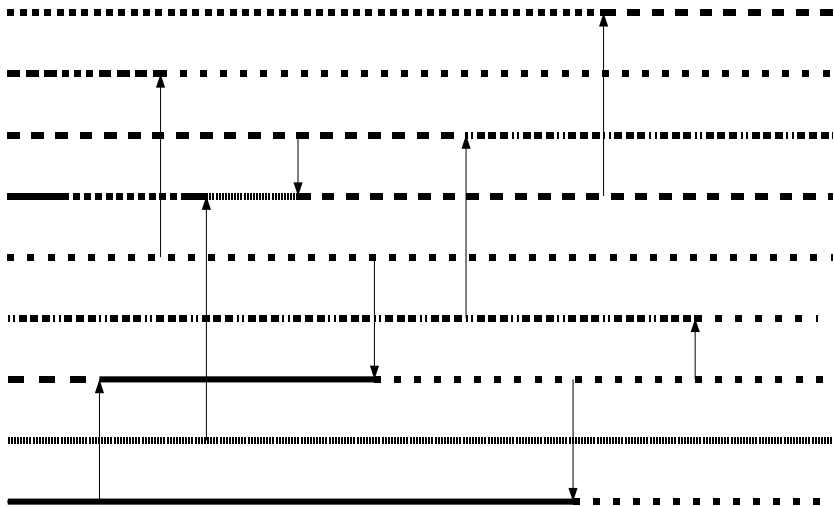
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- 1 The Moran and the lookdown models
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- 3 The equation for the evolution of X_t
- 4 Large time behavior of X_t

The Moran and the lockdown models

- Consider a population of fixed size N . Put at time $t = 0$ each individual on a distinct level between 1 and N . The population evolves as follows : for any ordered pair (i, j) ($i \neq j$), at rate $1/2$, we throw an arrow from i to j . At that time, a daughter of the individual sitting on level i replaces the individual sitting on level j .
- If we reverse time, we find an instance of Kingman's N -coalescent when following the genealogy of all the individuals in the population.

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The lockdown model, Donnelly and Kurtz '96, '99

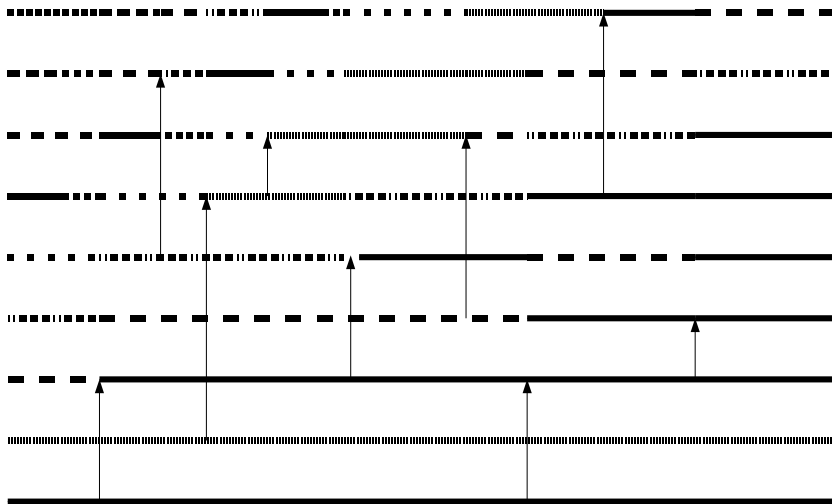
- The (original) lockdown model is obtained by reversing the downwards arrows in the Moran model, so as to have arrow from i to j at rate 1 for all $1 \leq i < j \leq N$. Note that the genealogy remains unchanged, and provided the initial different individuals are displayed on the various sites in an exchangeable manner, the population remains exchangeable at all times > 0 .
- The *modified* lockdown model is the following variant of the initial lockdown model : whenever a newborn is placed on level j at time t , the individual who was sitting on any level $j \leq k \leq N - 1$ at time t^- is shifted to the level $k + 1$; the individual who was sitting on site N at time t^- dies. The exchangeability property is still valid.
- The huge difference with the Moran model is that it is easy to define the lockdown model in case $N = +\infty$ (which is impossible for the Moran model).

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Λ look down with selection

Λ look down without selection

- Consider an countably infinite population made of individuals of two types, b and B .
- The type b individuals are coded by 1, and the type B individuals by 0. We assume that the individuals are placed at time 0 on levels $1, 2, \dots$, each one being, independently from the others, 1 with probability x , 0 with probability $1 - x$, for some $0 < x < 1$.
- For each $i \geq 1$ and $t \geq 0$, let $\eta_t(i) \in \{0, 1\}$ denote the type of the individual sitting on level i at time t . We now describe the evolution of $(\eta_t(i))_{i \geq 1}$ for $t > 0$.
- Consider a finite measure Λ on $[0, 1]$ with $\Lambda(\{0\}) = \Lambda(\{1\}) = 0$, and a Poisson Point Process

$$m = \sum_{i=1}^{\infty} \delta_{t_i, p_i}$$

on $\mathbb{R}_+ \times (0, 1)$ with intensity measure $dt \times \nu(dp)$, where $\nu(dp) = p^{-2} \Lambda(dp)$.

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- Each atom (t, ρ) of the Poisson point process m corresponds to a birth event. To each $(t, \rho) \in m$, we associate a sequence of i.i.d. Bernoulli random variables $(Z_i, i \geq 1)$ with parameter ρ . Let

$$l_{t,\rho} = \{i \geq 1 : Z_i = 1\} \text{ and } \ell_{t,\rho} = \inf\{i \in l_{t,\rho} : i > \min l_{t,\rho}\}.$$

At time t , each level in $l_{t,\rho}$ immediately adopts the type of the smallest level participating in this birth event. For the remaining levels, we reassign the types so that their relative order immediately prior to this birth event is preserved.

- More precisely

$$\eta_t(i) = \begin{cases} \eta_{t^-}(i), & \text{if } i < \ell_{t,\rho}; \\ \eta_{t^-}(\min l_{t,\rho}), & \text{if } i \in l_{t,\rho} \setminus \{\min l_{t,\rho}\}; \\ \eta_{t^-}(i - (\#\{l_{t,\rho} \cap [1, \dots, i]\} - 1)), & \text{otherwise.} \end{cases}$$

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Λ lockdown with selection

- We now introduce selection, which favors the type B individuals, i.e. the 0's.
- We do that by introducing *deaths*. Each type 1 individual dies at rate $\alpha > 0$, her vacant level being occupied by her neighbor who sits immediately above her, who herself is replaced by her neighbor above, etc.
- In other words, independently of the above arrows, crosses are placed on all levels according to mutually independent rate α Poisson processes. Suppose there is a cross at level i at time t . If $\eta_{t-}(i) = 0$, nothing happens. If $\eta_{t-}(i) = 1$, then

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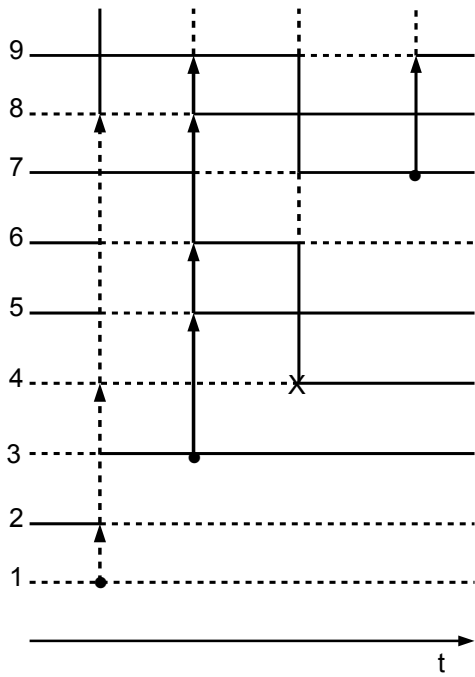
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Construction of the lockdown 1

- Without selection, there is no difficulty in defining our process. Indeed, for each finite size N , the model is easily defined (individuals who are pushed above level N die). This is because there are finitely many birth events on any finite time interval. Indeed

$$\#\{i, (t_i, p_i) \in m, t_i \leq t \text{ and } |I_{t_i, p_i} \cap [1, \dots, N]| \geq 2\} < \infty.$$

- Indeed the probability that an atom (t, p) affects at least 2 individuals among N is

$$1 - (1-p)^N - Np(1-p)^{N-1} \leq \binom{N}{2} p^2, \text{ and } \int_0^1 p^2 \nu(dp) = \int_0^1 \Lambda(dp) < \infty.$$

- If $N < M$, the N -model is a restriction of the M -model. Hence the infinite population model is defined by a projective limit argument.
- The same is not true for the model with selection : who will occupy site i at time t does not depend only upon what happens on sites $\{1, 2, \dots, i\}$ between time 0 and time t . Indeed, at a death event individuals go down.

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Construction of the lockdown 2

- Imagine that the model with selection has been defined. Consider a type B individual (i.e. a 0) sitting on some level i at time 0, and assume that this individual, who never dies, remains at a finite level forever.
- The behavior of the individuals who sit below that individual is independent of what happens above that individual. Hence we can define the “true” evolution of all individuals who are below that 0 individual, including him.
- Let now K_t denote the lowest level occupied by a type 0 individual at time t . There is no problem at defining the evolution of K_t , as well as that of all individuals who sit below K_t at time t .
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Construction of the lockdown 3

- In case K_t hits the lowest level 1 at some finite time τ , after that time the type 0 individuals invade all levels. Then one can show that for any $N > 1$, there exists a level $\psi(N)$ (which also depends upon τ) such that any individual located at time 0 on a level $\geq \psi(N)$ will never get below level N . Hence we can construct our model on levels 1 up to N , for each $N \geq 1$, and we are done.
- If $K_t \rightarrow \infty$ as $t \rightarrow \infty$, then we can construct our model below K_t , hence also below the trajectory of the second lowest 0 at time $t = 0$, the third,.. which allows one to define the whole model.

Some care is needed to treat the case where one of those trajectories reaches infinity in finite time.

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Exchangeability

- It is essential to show that, once the initial condition $\{\eta_i(0), i \geq 1\}$ is an exchangeable sequence (i.e. the $\eta_i(0)$'s are i.i.d., 1 with probability x , 0 with probability $1 - x$), then for any $t > 0$, the collection of r.v.'s $\{\eta_i(t), i \geq 1\}$ is exchangeable.
- Essentially the proof argues that if the sequence is exchangeable just before a birth or death event, then it remains exchangeable after the event.
- One important consequence of this result is that, as a consequence of de Finetti's theorem, if we define

$$X_t^N = \frac{1}{N} \sum_{i=1}^N \eta_i(t),$$

then for any $t > 0$, $X_t^N \rightarrow X_t$ a.s. as $N \rightarrow \infty$, where X_t is the proportion of type b individuals in the whole population.

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The equation for the evolution of X_t

The equation for the evolution of X^N

- We have

$$X_t^N = X_0^N + \int_{[0,t] \times [0,1]^4} \Psi^N(X_{s^-}^N, u, p, v, w) M_0(ds, du, dp, dv, dw) - \frac{1}{N} \int_{[0,t] \times [0,1]} \mathbf{1}_{u \leq X_{s^-}^N} \mathbf{1}_{\eta_{s^-} = (N+1)=0} M_1^N(ds, du),$$

- where M_0 and M_1^N are two independent Poisson Point Processes, with intensity resp.

$$\mu(ds, du, dp, dv, dw) = ds du p^{-2} \Lambda(dp) dv dw, \quad \alpha N ds du,$$

- and

$$\Psi^N(r, u, p, v, w) = \frac{1}{N} \mathbf{1}_{F_p^N(v) \geq 2} \left[\mathbf{1}_{u \leq r} \left(F_p^N(v) - 1 - G_{N, F_p^N(v), r}(w) \right) - \mathbf{1}_{u > r} \overline{G}_{N, F_p^N(v), r}(w) \right],$$

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with

$F_p^N = 1 -$ the distribution function of the $B(N, p)$ law;

$G_{N,n,r} = 1 -$ the d. f. of the hypergeometric law $(N - 1, n - 1, \frac{Nr - 1}{N - 1})$;

$\bar{G}_{N,n,r} = 1 -$ the d. f. of the hypergeometric law $(N - 1, n - 1, \frac{Nr}{N - 1})$.

- One has that

$$\int_{[0,1]^2} \Psi^N(r, u, p, v, w) dudw = 0.$$

- If we denote by \bar{M}_0 and \bar{M}_1^N the respective compensated PPPs, we have that

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Tightness and convergence as $N \rightarrow \infty$

- It not too hard to deduce from Aldous' criterion that the sequence of processes $\{X^N, t \geq 0\}_{N \geq 1}$ is tight in $D([0, +\infty))$ equipped with the Skorohod topology.
- Under the condition that $\Lambda([0, 1]) = +1$, we show that the limit, which is the asymptotic ratio of 1's in the population, solves the SDE

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The classical WF SDE

- Had we started with $\Lambda = c\delta_0$ (Kingman's coalescent), we would have obtained the classical Wright–Fisher SDE, where the stochastic integral is $\int_0^t \sqrt{cX_s(1-X_s)}dW_s$. In case of a general measure Λ , but with $0 < \Lambda(0) < \Lambda([0, 1])$, we have an SDE with both the Poisson and the Brownian stochastic integrals.
- Note that we can rewrite the continuous martingale $M_t = \int_0^t \sqrt{cX_s(1-X_s)}dW_s$ in the form $M'_t = \sqrt{c} \int_{[0,t] \times [0,1]} \Psi(u, X_s)W(ds, du)$,
- where $W(ds, du)$ is a space–time white noise, and again $\Psi(u, r) = \mathbf{1}_{u \leq r} - r$. Indeed the two continuous martingales satisfy $\langle M \rangle_t = \langle M' \rangle_t$, since

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Large time behavior of X_t

- Recall that the Λ coalescent comes down from infinity (in this case we shall write $\Lambda \in CDI$) iff (Schweinsberg '00)

$$\sum_{n=2}^{\infty} \phi^{-1}(n) < \infty,$$

where $\phi(n) = \int_0^1 [np - 1 + (1-p)^n] \nu(dp)$.

- Our process X_t is a positive supermartingale, so $X_t \rightarrow X_\infty$ a.s., as $t \rightarrow \infty$. It is not hard to show that while $X_t \in [0, 1]$, $X_\infty \in \{0, 1\}$.
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If $\Lambda \in CDI$, then $\exists \zeta < \infty$ a.s. such that $X_\zeta = X_\infty$ (one of the two types fixates in finite time).

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- Could we have $X_\infty = 0$ a. s. when fixation takes an infinite time?
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Let $\mu = \int_0^1 [\rho(1-\rho)]^{-1} \Lambda(d\rho)$. If $\mu < \alpha$, then $X_\infty = 0$ a. s.

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and moreover $\frac{\Phi(n)}{n} \rightarrow \mu$ as $n \rightarrow \infty$.

- Then the above theorem is intuitively clear : call again K_t the level of the lowest individual of type 0. When K_t is large, his mean speed is negative, hence K_t comes down, and will eventually reach the level 1.

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If $\alpha < \alpha^*$, then $\mathbb{P}(X_\infty = 1) > 0$. If $\alpha \geq \alpha^*$, then $\mathbb{P}(X_\infty = 1) = 0$.

$$\text{Here } \alpha^* = - \int_0^1 \log(1-p) \frac{\Lambda(dp)}{p^2} (< \mu).$$

- Consider the \mathbb{N} -valued Markov process R_t with generator

$$\mathcal{L}g(n) = \sum_{k=2}^n \binom{n}{k} \lambda_{n,k} [g(n-k+1) - g(n)] + \alpha n [g(n+1) - g(n)],$$

where $\lambda_{n,k} = \int_0^1 x^k (1-x)^{n-k} x^{-2} \Lambda(dx)$.

- R_t is in duality with X_t in the sense that

$$\mathbb{E}[X_t^n | X_0 = x] = \mathbb{E}[x^{R_t} | R_0 = n].$$

- Now

$$\begin{aligned} \mathbb{E}[X_\infty | X_0 = x] &= \lim_{t \rightarrow \infty} \mathbb{E}[X_t | X_0 = x] \\ &= \lim_{t \rightarrow \infty} \mathbb{E}[x^{R_t} | R_0 = 1] \\ &\begin{cases} > 0, & \text{if } R_t \text{ is positive recurrent;} \\ = 0, & \text{if } R_t \text{ is transient or null recurrent.} \end{cases} \end{aligned}$$

- Finally, Foucart shows that R_t is positive recurrent if $\alpha < \alpha^*$, transient if $\alpha > \alpha^*$. It is null recurrent if $\alpha = \alpha^*$.

- Consider the \mathbb{N} -valued Markov process R_t with generator

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