Asymptotic genealogies of non-neutral populations

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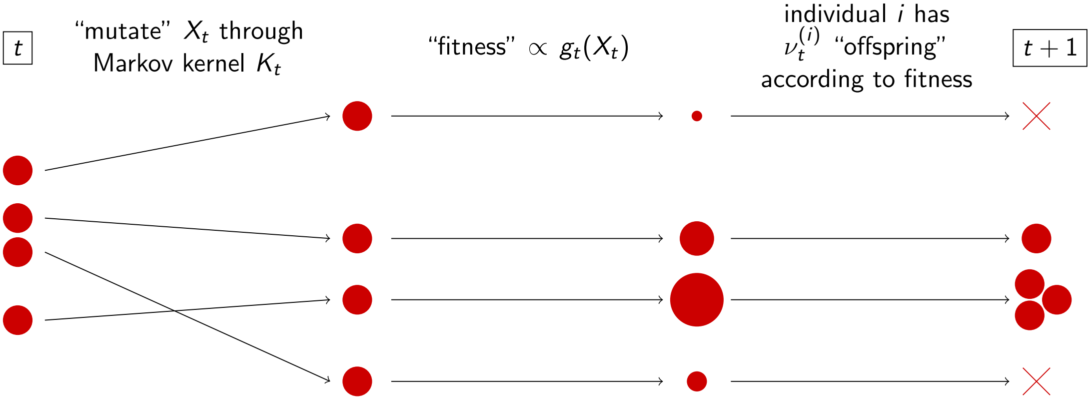
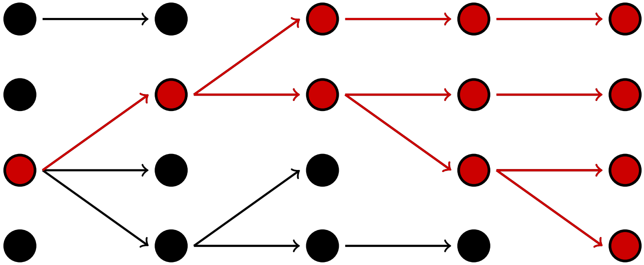
Interacting particle system

- Constant population size N
- "Genotype" $X_t^{(i)} \in \mathcal{X} \subseteq \mathbb{R}^d$
- Initial genotypes $X_0 \sim \mu$

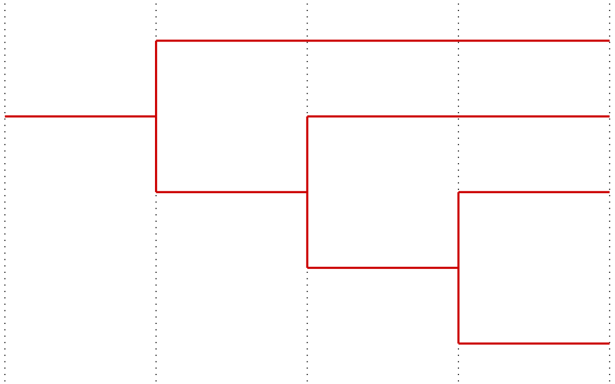
Interacting particle system



Genealogies

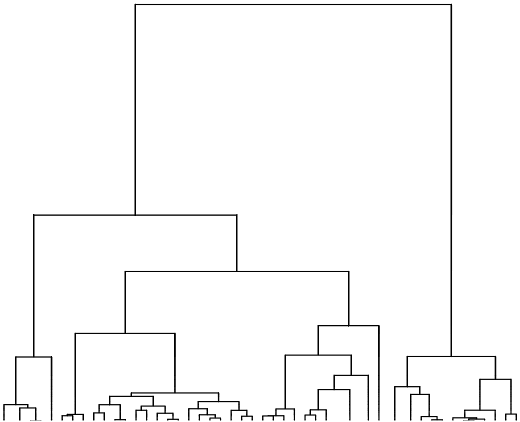


Genealogies



Kingman's n-coalescent

- Continuous-time Markov chain on the space of partitions of $\{1, \ldots, n\}$
- Single pair mergers only
- Each pair merges independently at rate 1 (total merge rate $\binom{k}{2}$ while there are k distinct lineages)



Scenario

- Population size N
- Discrete generations
- Sample $n \leq N$ individuals from the terminal generation
- Rescale time appropriately
- Let $N \to \infty$

Sufficient conditions, neutral case

Theorem (Kingman 1982)

- *Individuals are exchangeable*
- *Offspring counts $\nu^{(1:N)}$ are i.i.d. across generations*
- $\mathrm{Var}[\nu^{(1)}] = \sigma_N^2 \longrightarrow \sigma^2 \in (0, \infty)$
- $\sup_N \mathbb{E}[(\nu^{(1)})^k] < \infty$ *for all* $k \geq 3$

Then the rescaled genealogy of n individuals converges weakly to the n-coalescent as $N \to \infty$.

Sufficient conditions, neutral case

- Exchangeability $=$ neutrality (genotype does not affect number of offspring)
- System completely specified by distribution of $\nu^{(1:N)}$
- **Wright-Fisher model:** $\nu^{(1:N)} \sim \text{Multinomial}(N, (\frac{1}{N}, \dots, \frac{1}{N}))$
- **Moran model:** $\nu^{(1:N)}$ uniform over permutations of $(2, 0, 1, \dots, 1)$
- Since $\sum \nu^{(i)} = N$ and individuals are exchangeable, $\mathbb{E}[\nu^{(i)}] = 1$.
- Case $\sigma^2 = 0$ would mean no coalescences in the limit

Necessary and sufficient conditions, neutral case

Theorem (Möhle Sagitov 2001, 2003)

- *Individuals are exchangeable*
- *Offspring counts* $\nu^{(1:N)}$ *are i.i.d. across generations*
- $c_N > 0$ *for all* $N < \infty$
- $c_N \longrightarrow 0$
- $d_N / c_N \longrightarrow 0$

If and only if the rescaled genealogy of n individuals converges weakly to the n-coalescent as $N \to \infty$.

$$d_N := \frac{N\mathbb{E}[(\nu^{(1)})_3]}{(N)_3}, \qquad c_N := \frac{N\mathbb{E}[(\nu^{(1)})_2]}{(N)_2}$$

Necessary and sufficient conditions, neutral case

- The condition $c_N > 0$ plays the same role as Kingman's condition $\sigma^2 > 0$
- $c_N = \frac{\mathrm{Var}[\nu^{(1)}]}{N-1}$, so $c_N \to 0$ is less restrictive than Kingman's condition $\mathrm{Var}[\nu^{(1)}] \to \sigma^2$
- Only requires control up to 3rd moment, cf. Kingman requires *all* moments finite

Sufficient conditions, non-neutral case

Theorem (B Koskela Jenkins Johansen 2021)

- *Given* $\nu_t^{(1:N)}$*, assignment of offspring to parents is uniform over all valid assignments*
- *Time scale is almost surely finite*
- $\exists$ *deterministic sequence* $b_N \to 0$ *such that* $\forall N, t$

$$\frac{1}{(N)_3} \sum_{i=1}^{N} \mathbb{E}_t[(\nu_t^{(i)})_3] \leq b_N \frac{1}{(N)_2} \sum_{i=1}^{N} \mathbb{E}_t[(\nu_t^{(i)})_2]$$

Then the rescaled genealogy of n *individuals converges weakly to the* n*-coalescent as* $N \to \infty$*.*

Open questions

- Are the conditions necessary and sufficient in the non-neutral case?
- What does the random time scale look like?
- Rate of convergence?
- Can the conditions be verified for some interesting population genetic models?

References

1. JFC Kingman (1982) *The coalescent*. Stochastic Processes and Their Applications 13:235–248.
2. JFC Kingman (1982) *On the genealogy of large populations*. Journal of Applied Probability 19A:27–43.
3. M Möhle, S Sagitov (2001) *A classification of coalescent processes for haploid exchangeable population models*. The Annals of Probability 29(4):1547–1562.
4. M Möhle, S Sagitov (2003) *Coalescent patterns in diploid exchangeable population models*. Journal of Mathematical Biology 47(4):337–352.
5. S Brown, PA Jenkins, AM Johansen, J Koskela (2021) *Simple conditions for convergence of sequential Monte Carlo genealogies with applications*. Electronic Journal of Probability 26:1–22.