

# Kallenberg Symposium 2013

# Evolution of genealogies in populations

A. Greven

Universität Erlangen-Nürnberg

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## Joint work with

- Anita Winter (Essen)
- Andrej Depperschmidt (Freiburg)  
Peter Pfaffelhuber (Freiburg)
- Patric Glöde (Erlangen)  
Thomas Rippl (Erlangen)
- Chiranjib Mukherjee (München)

## Goal

Present framework for modelling of genealogical information of a stochastically evolving population as a strong Markov process, i.e. the *forward* picture is described.

Apply this to obtain properties of process, equilibria, parameter dependence, path properties.

## Content

- 1 Population models
- 2 Description of genealogies
- 3 Topologies on genealogies
- 4 Martingale problems for genealogical processes and applications

- 1 Population models
  - Moran model (with migration)
  - Logistic branching random walk
  - Diffusion models
- 2 Description of genealogies: Basics
  - Genealogy
  - Moran model size- $N$  genealogies
  - Logistic branching genealogies: extended up-space
  - Population with types and locations: marked up-space
  - Extension to infinite populations
- 3 Topologies on genealogies: Analytic aspects
  - Polynomials
  - Topology
- 4 Martingale problems for genealogical processes and applications
  - Martingale problems
  - Applications

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## Moran dynamics

- $N$ -individuals with types, type space  $\mathbb{K}$
- ( $N$ -individuals at each of the sites of  $\mathbb{G}$ )
- pairs of individuals resample if at same site
- (Each individual performs independently continuous time rate  $a(\cdot, \cdot)$  random walks on  $\mathbb{G}$ .)
- We can add mutation and selection.
- We could work with Cannings models.



## Logistic branching random walk

- particles give at rate  $b$  birth to two or 0 particles and die
- particles give birth at rate  $s$  to a new particle
- particles die at rate  $d(k)$ , if we have  $k$  particles at the site
- migration of individuals according to independent continuous time rate  $a(\cdot, \cdot)$  random walks

Assumption:  $x \rightarrow F(x) = sx - d(x)x$  , concave,  $F(x) < 0$  for  $x \geq K$ .

One wants to take the number of individuals (per site) to infinity and obtain in suitable scalings:

*Diffusion* processes of type-frequencies, respectively masses  
examples:

$$dy_t = \sqrt{y_t(1 - y_t)}dB_t \quad \text{Fisher-Wright}$$

$$dx_t = F(x_t)dt + \sqrt{bx_t}dB_t \quad \text{Logistic branching}$$

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## The genealogical tree

Birth event

$$\iota \longrightarrow \iota', \iota''$$

$\iota', \iota''$  are the descendents of  $\iota$ ,  $\iota$  is ancestor of  $\iota', \iota''$ .

This defines:

- (1) a "genealogical tree", a rooted labelled tree.
- (2) Genealogical distance:  $2 \cdot$  time to MRCA

Of interest is a structure abstracting from labels.

*We are interested to model the stochastic evolution of the genealogical structure as solution to a **martingale problem** on a **Polish space**, in particular for the diffusion limit.*

Our model for a Moran population genealogy:

$$\mathcal{U} = \overline{(U, r, \mu)},$$

$U$  = set of individuals

$r : U \times U \rightarrow [0, \infty)$ , quasi ultrametric

$r(\iota, \iota') =$  genealogical distance of  $\iota$  and  $\iota' =$  twice time to MRCA

$\mu = \frac{1}{|U|} \cdot \sum_{\iota \in U} \delta_{\iota} \in \mathcal{M}_1(U)$ , sampling measure

— : equivalence class under isometries and measure-preserving maps of  $\text{supp}(\mu) : \mathcal{U}$ .

$\mathcal{U}$  is called an *ultrametric probability space*

$\mathbb{U} := \{\mathcal{U} \mid \mathcal{U} \text{ is um-space}\}$

$\mathbb{U}$  is a **Polish** space for topology introduced later.

Our model for a logistic branching genealogy with *varying population size* requires  $\mu \in \mathcal{M}_{\text{fin}}(U)$ .

$$\mathcal{U} = (\bar{\mu}, (\overline{(U, r, \hat{\mu})}),$$

$$\hat{\mu} \in \mathcal{M}_1(U), \quad \bar{\mu} \in \mathbb{R}^+,$$

$$\mu = \sum_{\iota \in U} \delta_{\iota} \quad , \quad \bar{\mu} = \mu(U) \quad , \quad \hat{\mu}(\cdot) = \frac{\mu(\cdot)}{\mu(U)}.$$

$\mathbb{U}^* = \mathbb{R}^+ \times \mathbb{U}$  (extended ultrametric probability measures)

$\mathbb{U}^*$  is a **Polish** space

Individuals with types and locations require:

$V = \mathbb{K} \times \mathbb{G}$ ,  $\mathbb{K}$  = type space,  $\mathbb{G}$  = geographic space.

Assume that  $\mathbb{K}$  is a compact Polish space,  $\mathbb{G}$  finite or compact.

Mark function is added to description  $\kappa : U \rightarrow V$ .

Consider  $(U, r, \kappa, \mu)$ .

Form equivalence class including mark preservation.

Obtain (extended)  $V$ -marked ultrametric probability measure spaces:

$$\mathcal{U} = \overline{(U, r, \kappa, \mu)}$$

Allow  $\kappa$  : kernel  $U \times V$ ,  $\nu = \mu \otimes \kappa : (U, r, \nu)$

State space:  $\mathbb{U}_V$ , respectively  $\mathbb{U}_V^*$  ultrametric probability measure spaces.

$\mathbb{U}_V, \mathbb{U}_V^*$  are Polish spaces.

It is necessary to consider spaces  $\mathbb{G}$  which are infinite and allow infinite total population size, populations which are only "locally" finite.

Assume:  $\mathbb{G}$  is a metric (Polish) space.  $\mathbb{G} = \mathbb{Z}^d, \mathbb{R}^d$  etc.



Infinite populations are modelled as:

$$\mathcal{U} = (\bar{\nu}, \overline{(U, r, \hat{\nu})})$$

$$\bar{\nu}(\cdot) = \nu(U \times (\mathbb{K} \times \{\cdot\})), \quad \bar{\nu} \in \mathcal{M}(\mathbb{G})$$

$$\hat{\nu}(\cdot \times A) = \sum_{i \in A} \hat{\nu}_i(\cdot) \quad , \quad \hat{\nu}_i(\cdot) = \frac{\nu(\cdot \times \{i\})}{\nu(U \times \mathbb{K} \times \{i\})}, \quad \forall i \in \mathbb{G}, \quad \hat{\nu}_i \in \mathcal{M}_1(U \times \mathbb{K}).$$

Gives as set of all isomorphy classes:

$$\mathcal{U}_{\mathcal{V}}^* \quad (\text{Polish space})$$

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**Polynomials** are functions of the form:

$$\Phi : U \longrightarrow \mathbb{R}, \quad U^* \longrightarrow \mathbb{R}, \quad U_V^* \longrightarrow \mathbb{R}$$

$$(1) \quad \Phi(U) = \int_{U^n} \varphi((r(u_i, u_j))_{1 \leq i < j \leq n}) \mu(du_1) \cdots \mu(du_n)$$

$$\varphi \in C_b^1((\mathbb{R})^{\binom{n}{2}}, \mathbb{R}) \quad , \quad \mu \in \mathcal{M}_1(U).$$

$$(2) \quad \Phi(\mathcal{U}) = \bar{\Phi}(\bar{\mu}) \hat{\Phi}((U, r, \hat{\mu})) \quad , \quad \bar{\Phi} \in C_b(\mathbb{R}, \mathbb{R})$$

(3)

$$\Phi(\mathcal{U}) = \bar{\Phi}(\bar{\nu}) \int_{(U \times V)^n} \varphi((r(u_i, u_j))_{1 \leq i < j \leq n}) \chi((v_1, v_2, \dots, v_n)) \hat{\nu}^{\otimes n}(d(\underline{u}, \underline{v}))$$

$$\nu = \mu \otimes \kappa$$

$$\chi \in C_b(V, \mathbb{R}) (\chi \in C_{bb}(V, \mathbb{R}))$$

We call the generated algebra of functions by  $\Pi, \Pi^*, \Pi_V$ .

Define topology via convergence of sequences.

*Idea:* Convergence  $\longleftrightarrow$  convergence of sampled (marked) subtrees and population sizes.

$\mathcal{U}_n \implies \mathcal{U}$  as  $n \rightarrow \infty$  iff

$$\Phi(\mathcal{U}_n) \xrightarrow[n \rightarrow \infty]{} \Phi(\mathcal{U}), \quad \forall \Phi \in \Pi \text{ resp. } \Pi^*, \Pi_V, \Pi_V^*.$$

In particular polynomials are bounded continuous functions on :

$$\mathbb{U}, \mathbb{U}_V, \mathbb{U}^*, \mathbb{U}_V^*.$$

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Consider a linear operator  $L$  on  $C_b(E, \mathbb{R})$ , for  $E = \mathbb{U}, \mathbb{U}_V, \dots$  with domain a subalgebra of  $\Pi$  ( resp.  $(\Pi_V, \Pi_V^*)$  ) of smooth functions and the

$(L, \Pi, \delta_{\mathcal{U}})$ -martingale problem

for a  $\mathbb{U}_V^*$ -valued *diffusion process* ( $\mathbb{U}_V$  resp.  $\mathbb{U}$ ).

## Key operator

$$L_{\text{res}} \widehat{\Phi}(\mathcal{U}) = \sum_{\substack{k, \ell=1 \\ k < \ell}}^n (\varphi \circ \theta_{k, \ell}(\underline{r}(\underline{u})) - \varphi(\underline{r}(\underline{u}))) \mu^{\otimes n}(d\underline{u})$$

$$\underline{r} = (r(u_i, u_j))_{1 \leq i < j \leq n}, \quad \underline{u} = (u_1, \dots, u_n)$$

$$\theta_{k, \ell}(\underline{r}(\underline{u})) = \underline{r}(\underline{u}_{k, \ell}),$$

$$\underline{u}_{k, \ell} = (u_1, \dots, u_{\ell-1}, u_k, u_{\ell+1}, \dots, u_n).$$



In case of varying population size:

*product rule form*

$$L(\bar{\Phi}\hat{\Phi}) = (L^{\text{mass}}\bar{\Phi})\hat{\Phi} + \bar{\Phi} \cdot L^{\text{gen}}(\hat{\Phi})$$

Connects with fixed mass case (Fleming-Viot).

$L^{\text{gen}}$ : time-inhomogeneous resampling/migration operators.

Conditional duality: time-inhomogeneous coalescent.

We get

- wellposed martingale problems.
- Genealogical diffusion models arise as many individual per site limits.
- Convergence into equilibrium states, equilibrium genealogy.
- Duality theory, conditioned duality.
- Coalescent representation of equilibria.
- Spatial continuum limit of genealogy processes.
- Almost sure path properties for qualitative features.

Example of path property:

Consider the number of covering balls of radius  $2\varepsilon$  of  $U_t$ :

$$N_t^\varepsilon.$$

Then in path space

$$\left(\frac{\varepsilon}{2} N_t^\varepsilon\right)_{t>0} \implies (1)_{t>0}, \quad \text{as } \varepsilon \rightarrow 0.$$

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