Stochastic evolution of genealogies of spatial populations: state description, characterization of dynamics and properties

A. Depperschmidt ¹, A. Greven²

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Abstract

We survey results on the description of stochastically evolving genealogies of populations and marked genealogies of multitype populations or spatial populations via tree-valued Markov processes on (marked) ultrametric measure spaces. In particular we explain the choice of state spaces and their topologies, describe the dynamics of genealogical Fleming-Viot and branching models by well-posed martingale problems, and formulate the typical results on the longtime behavior. Furthermore we discuss the basic techniques of proofs and sketch as two key tools of analysis the different forms of duality and the Girsanov transformation.

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1) Department Mathematik, Universität Erlangen-Nürnberg, Cauerstr. 11, D-91058 Erlangen, Germany, depperschmidt@math.fau.de

2) Department Mathematik, Universität Erlangen-Nürnberg, Cauerstr. 11, D-91058 Erlangen, Germany, greven@math.fau.de
1 Background

The aim of this contribution is to present the work of the authors and co-workers Peter Pfaffelhuber, Rongfeng Sun and Anita Winter, on evolving genealogies in spatial population models in a systematic way and to explain its role in the context of the field of tree-valued Markov processes which is a field with many facets which is developing in many directions and with many applications from population genetics to computer science. For reasons of consistency in this survey we deviate from the original notation at various points.

In the 1970s the study of spatial population models such as voter model, branching random walk, contact process began and the focus was on the understanding of the longtime behavior of these systems. In particular the occupation measures were studied, that is, the configurations of numbers of particles/types per site was viewed as a measure on geographic and/or types space. This process of occupation measures is a Markov process and can be studied as measure valued processes on infinite geographic spaces; see e.g. [AN72, Lig85, Dur88, Daw93]. Nevertheless inspired by the graphical construction often used, the results were interpreted in terms of genealogical information on individuals.

In this context tracing of ancestral paths of an individual from the current population backwards in time to its “ancestor” played an increasing role and was formalized by Dawson and Perkins in [DP91] via the so called historical process, i.e., a measure-valued process with measures on paths which were the ancestral paths of individuals currently alive. The approach worked well for branching random walks and the Dawson-Watanabe super processes. In the latter case these paths encoded indeed the genealogical distance between individuals using the information on location or type. However, the genealogies were not explicitly part of the state.

The techniques of treatment of historical processes used infinite divisibility. Conceptually the historical processes of the ancestral paths are also of importance in other population models as in the voter model, contact process or Moran and Fleming-Viot models, where results could be obtained using the technique of the hierarchical mean-field limit, see [DG95] or latter using ideas of the lookdown construction of Donnelly and Kurtz [DK99a] and particle system techniques of Liggett and Spitzer [LSS91] in [GLAV05]. In the Fleming-Viot model on \( \mathbb{Z}^1 \) the construction of the Brownian web [Arr81, NRS05, FINR04] can be used to obtain the processes of ancestral path, [GSW16]. The historical process can be combined with the coding of genealogical information as genealogical distances in quite some generality, even in case of branching processes and super random walks getting again (generalized) branching processes, provided that the genealogical information is coded suitably [GRG18]. We will discuss this coding later on.

The genealogical point of view gained more attention in the analysis of infinite particle systems which exhibit a regime of clustering in low dimensions. For example in the case of voter model there are growing clumps of a single opinion as time diverges, an opinion which originates from a single individual with that opinion. The formation of such clusters appears in Fleming-Viot models and in branching models as clumps of survivors in the sea of unpopulated sites. In many papers the growth in time and space of such “mono-ancestor” clumps was studied in detail starting from Cox and Griffeath [CG80] with [DG93, FG94, Kle96, Kle97, Win02]. In this series of works it became more and more apparent that the genealogy of the population and their evolution is behind all the effects.

At this point Aldous introduced in [Ald91a, Ald91b, Ald93] the continuum random tree which made the genealogical distances in a branching population explicit in the state description. The approach focused on all individuals ever alive and was working with metric trees. In this context the description of the genealogy based on an embedding of the genealogical trees in Brownian excursions, such as in [NP89, LG89] for example, gave an impulse to the ideas in the theory on continuum random trees. More systematically the concept of metric spaces, more precisely ultrametric spaces, was applied by Evans in [Eva03] to study the genealogy associated with the entrance law from an infinite population of the Kingman coalescent describing the individuals currently alive with their genealogy in a Fleming-Viot population. This was taken up by Le Gall in [LG93, LG99] in the work on the Brownian snake. Here the location marks on the path of descent are constructed as well. However, here also the population alive at some time was modeled as marked labeled tree.

The ideas of tracing ancestries and genealogical relations was a key point in the work of Donnelly and Kurtz [DK99a, DK99b]. In their lookdown construction the evolution of the population in,
for example a Fleming-Viot model, is represented by the evolution of a countably infinite ordered population. The state of the original population is obtained through the state of the ordered population and the latter is constructed by breaking the symmetry of the dynamics.

Also taking up the work of Donnelly and Kurtz \cite{DK99a, DK99b}, another method to code genealogical information of an evolving population was invented by Bertoin and Le Gall in \cite{BLG00, BLG03, BLG05}, generalized by Dawson and Li in \cite{DL12} and studied further in a number of concrete cases in \cite{Fon12, Lab14, Gu15}. This method leads to so called “flows of bridges” which might be seen as a specific technique to construct an explicit representation of a labeled tree which models the evolution of the genealogy of an evolving population.

In the program “Genealogies of interacting particle systems” in Singapore 2017 a learning session “Tree-valued Markov processes” (held by the authors of this contribution) was devoted to flows of bridges. Some other learning sessions where devoted to Aldous’ work on continuum random trees and variants of the lockdown construction of Donnelly and Kurtz. The approach via flows of bridges works extremely nicely in the case of non-spatial models whereas introducing space is a very difficult matter. We don’t have the space to spell out the details in this survey.

In 2009 Greven, Pfaffelhuber and Winter started to describe the evolution of genealogies of the individuals alive at the current time $t$ of populations in the large populations limit \cite{GP09, GPW13}. This was continued in a series of papers \cite{DG11, DG12, GSW16, GGR17, DG18}. This was motivated first of all by trying to understand some effects in the longtime behavior of spatially interacting systems and the growth in space of monotype clusters in such systems as time diverges, a phenomenon discussed above. Further motivation came from the interplay between the mechanisms of migration and selection in Fleming-Viot models. As these models are infinite population models, where also the representation by lockdown constructions gets a bit intransparent, we saw the necessity to work systematically in a framework with martingale problems on state spaces encoding the genealogies to an extent needed to obtain the observed effects. To understand the genealogy of voter models exhibiting the monotype clusters in the scaling limit on spatial scale $\sqrt{t}$ starting with \cite{Arr81, FINR04, SSS17}, went through a long struggle. We think that this model now can be treated best in the framework of processes with values in ultrametric measure spaces using the tools of the theory on the Brownian web \cite{Arr81, FINR04, NRS05, SSS17}; see \cite{GSW16}.

The description of the genealogy of a population and its dynamics is by means of well-posed martingale problems with values in the equivalence classes of ultrametric measure spaces respectively marked-ultrametric measures spaces in the case of multitype and/or spatial populations. Using methods of stochastic calculus path properties, longtime behavior and properties of equilibria could be proved for population models driven by Fleming-Viot resampling or Feller branching, i.e. in the case of two large classes of models which arise as limits of individual based models.

In the study of the evolution of genealogies of branching processes the idea of infinite divisibility plays also on the level of genealogies an important role, as it does for branching processes on $\mathbb{R}$. On $\mathbb{R}$ infinite divisibility was based on the concept of convolution and hence it makes use of the semigroup structure of $\mathbb{R}$, which is known to be sufficient to derive Lévy-Khintchine formulas. Thus, on the state space for the random genealogies one needs to have similar concepts and therefore we need here a binary operation with suitable algebraic properties, to be able to obtain the Lévy-Khintchine and Cox point process representations of the random genealogies in branching populations. Algebraic and topological methods play an important role since for the genealogies one can define semigroup operations, see here Evans and Molchanov \cite{EM17} respectively collections of such different operations introduced by Glöde, Greven and Ripl in \cite{GGR17, GGR18}, with the concatenation as binary operation of truncated trees, truncation generating a collection indexed in the truncation level, leading to a consistent structure of connected semigroups.

We will explain in this survey how states are modeled in the approaches mentioned in the last three paragraphs, introduce the martingale problems for the most basic processes and describe their properties. We consider tree-valued Fleming-Viot and tree-valued Feller diffusions and later the corresponding spatial versions. More precisely, we consider the genealogical processes associated with the following classical diffusion models for populations which are the many individuals/small mass limits of individual based models:

- the Fleming-Viot diffusion, cf. \cite{GPW13},
- the branching Feller diffusion, cf. \cite{DG18}. 


• the self-catalytic branching diffusion, cf. [Glö12],
• Fleming-Viot diffusion with selection and mutation, cf. [DGP12],
• interacting Fleming-Viot diffusions on countable geographic spaces, cf. [GSW16],
• interacting branching Feller diffusions, cf. [DG18], and interacting logistic Feller-branching diffusions, cf. [GM18].
• interacting Fleming-Viot diffusions on the continuum, i.e. \( \mathbb{R} \), cf. [GSW16].

The work in this direction continues; see [Löh13, KL15, LVW15, Guf18, ALW16]. Furthermore, the approach can be extended to genealogies of individuals ever alive up to the current time horizon. This leads to the study of the evolution of genealogies of fossils, cf. [GSW], [GRG18].

We choose here to outline two directions of our current research, namely first logistic branching processes to model populations in competition for limited resources and the effects on genealogies and second Fleming-Viot models with recombination. We will explain therefore at the end in Section 7 how infinitely divisible random genealogies can be studied and how the mechanism of recombination can be incorporated to give some perspectives.

We would like to mention that the field develops also in various other directions with further types of evolutions requiring new points of view. Recently Kliem and Winter [KW18] and Athreya, Löhr, Winter [ALW16, ALW17] have studied different types of evolution than in the list above which however we cannot discuss here in more detail.

2 State spaces

In the discussion of state spaces we start with the simplest case, pass then to refinements and finally come to some topological issues which will be needed later on.

2.1 Ultrametric probability measure spaces and random genealogies

The key problem in passing from individual based models and their genealogies to the “continuum” limit is the need to find a suitable Polish space which can serve as the state space for the evolution of random genealogies. We next describe the solution to that problem.

The state space \( \mathbb{U}_1 \) The first objective is to find a description of the essential features of the genealogy of the population of currently alive individuals of a population evolving in time and then to find a Polish space in which these states can be embedded. This will allow to apply the standard methods of the theory of stochastic processes, such as Markov process theory and martingale problems.

The key concept of the genealogical information is that of an ancestor. In particular the most recent common ancestor (MRCA) of two individuals allows to define the genealogical tree distance as twice the time back to the MRCA. Hence, our approach is to describe the genealogy by a pair \((\tilde{U}, r)\) where the set \(\tilde{U}\) labels the individuals of the population currently alive and \(r\) is the pseudo-ultrametric encoding the genealogical distance. Note that an individual having offspring generates individuals whose distance is zero at the time of their birth. Therefore it is convenient to declare them as equivalent points in \((\tilde{U}, r)\), obtaining an ultrametric measure space \((U, r)\) and encode the information, having here several individuals, by introducing a Borel probability measure on \((U, r)\) which is called the sampling measure. This measure allows to sample typical individuals from the population and is also useful in infinite populations to obtain observable data from the genealogy by drawing finite samples. Hence we obtain the ultrametric probability measure space

\[
(U, r, \mu)
\]

associated with the genealogy of the population of individuals currently alive. We do not want to keep the individual names as part of the description and therefore pass to equivalence classes of ultrametric probability measure spaces, which we denote by

\[
\mathcal{U} = [(U, r, \mu)]
\]
where two spaces \((U,r,\mu)\) and \((U',r',\mu')\) are said to be *equivalent* if there exists a bijective map
\[
\varphi : \text{supp}(\mu) \to \text{supp}(\mu'),
\]
with
\[
\varphi' (\varphi(x_1), \varphi(x_2)) = r(x_1, x_2), \quad \mu \text{- a.s., and } \varphi_* \mu = \mu'.
\]
Here \(\varphi_* \mu\) denotes the image measure of \(\mu\) under the map \(\varphi\). Note that for finite genealogical trees with sampling measure this equivalence relation means that any measure preserving renaming of the vertices gives a population with the same genealogy. We denote the set of all equivalence classes (to avoid set theoretic paradoxes, we require \(U \subseteq \mathbb{R}\) here, for example) by
\[
\mathbb{U}_1.
\]
This is the *state space* for the process of genealogies of the population alive at a given time \(t\).

In order to obtain a decent state space for stochastic processes, we have to equip \(\mathbb{U}_1\) with a topology \(\mathcal{G}\) so that the topological space \((\mathbb{U}_1, \mathcal{G})\) is Polish, and is therefore suitable to accommodate limits of sequences of finite trees. All populations we consider here arise as *limits of finite individual based* models.

We choose here the so called *Gromov weak topology*. The idea to define convergence, and thus \(\mathcal{G}\), is as follows. Suppose we consider for all \(U \in \mathbb{U}_1\) a sequence of *finite sampled trees*. Then we define the sequence \((U_n)_{n \in \mathbb{N}}\) as convergent to \(U_\infty\), if \(\mu \circ Z \to U_\infty\) - a.s. all sampled finite trees converge in the sense of finite graphs with a metric to the corresponding object in \(U_\infty\) in law. In other words the \((n \times n)\)-matrix of distances induces a family of distributions \(\left(\nu_m^{(n)}\right)_{m \in \mathbb{N}}\) on \(\left(\mathbb{R}^+\right)^{(2)}\) which converges weakly to \(\nu_\infty^{(n)}\):
\[
\nu_m^{(n)} \Rightarrow \nu_\infty^{(n)}, \text{ for all } n \in \{2, 3, \ldots\} \text{ as } m \to \infty.
\]
This convergence defines a topology, the *Gromov weak topology*, which has the following property.

**Theorem 2.1** (Polish state space \([\text{GPW09}]\)).
The space \(\mathbb{U}_1\) equipped with the Gromov-weak-topology is Polish.

**Remark 2.1** (Metric on \(\mathbb{U}_1\)). The metric can be introduced similarly to the Gromov-Hausdorff metric using the Prohorov metric of probability measures (instead of Hausdorff metric). More precisely, to compare \([U,r,\mu]\) and \([U',r',\mu']\) we consider isometric embeddings (of representatives) into a third metric space, say \((Z,r_Z)\)
\[
U \hookrightarrow Z, U' \hookrightarrow Z
\]
giving image probability measures \(\mu_Z^U, \mu_Z^{U'} \in \mathcal{P}(Z,r_Z)\) and then consider the Prohorov metric \(d_P(\mu_Z^U, \mu_Z^{U'})\). Then take the infimum over all such embeddings to define the distance. Since the quantity is independent of the choice of representatives of \([U,r,\mu]\) respectively \([U',r',\mu']\) this defines a metric on \(\mathbb{U}_1\). It can be shown that this metric generates the Gromov weak topology; see \([\text{GPW09}]\). △

**\(\mathbb{U}_1\)-valued random variables** Next we turn to random \(\mathbb{U}_1\)-valued variables, which we denote by
\[
\mathfrak{M}.
\]
The genealogy of a stochastically evolving population generates a \(\mathbb{U}_1\)-valued stochastic process, which we denote by
\[
\mathfrak{M} = (\mathfrak{M}_t)_{t \geq 0}
\]
slightly abusing the notation. The corresponding path spaces
\[
D([0,\infty), \mathbb{U}_1) \quad \text{and} \quad C([0,\infty), \mathbb{U}_1)
\]
are Polish.
are again Polish spaces and the theory of stochastic processes, Markov processes and martingale problems can be applied.

In order to study the $\mathbb{U}_1$-valued stochastic process by means of martingale problems or studying the longtime behavior we need a description via test functions on $\mathbb{U}_1$ whose expectations are law determining. The key idea is to draw finite samples of trees and then study these finite samples by test functions.

We consider therefore test functions of the following form: For $\mathcal{U} = [(U, r, \mu)] \in \mathbb{U}_1$ we set

$$
\Phi^n, \varphi(U) = \int_\mathcal{U} \varphi((r(x_i, x_j))_{1 \leq i < j \leq n}) \mu^\otimes n(dx_1, \ldots, dx_n), 
$$

where $\varphi \in C_b(\mathbb{R}^{(2)\times n}, \mathbb{R})$ for $n \geq 2$, and $\varphi$ constant function for $n = 1$. Alternatively, for $n \geq 2$ we could write

$$
\Phi^n, \varphi(U) = \langle \nu_{\mathcal{U}}^{(n)}, \varphi \rangle, 
$$

where $\nu^{(n)}(\mathcal{U})$ is the distance matrix distribution of order $n$ of $\mathcal{U}$. We refer to such test functions as polynomials. The set of all polynomials (together with the constant functions) will be denoted by

$$
\Pi. 
$$

This set forms an algebra of bounded continuous functions.

**Theorem 2.2** (Polynomials are law and convergence determining).

(i) The set $\Pi$ is separating on $\mathbb{U}_1$ and $\{E[F(\mathcal{U})], F \in \Pi\}$ is law determining.

(ii) The set $\Pi$ is convergence determining on the set of probability measures on $\mathbb{U}_1$.

For proofs of the above results see Theorem 5 in [DGP11] or Corollary 2.8 in [Löh13].

Now that we have introduced the polynomials let us note that the topology on $\mathbb{U}_1$, as defined in (2.6), could also be defined equivalently in terms of polynomials (see [GPP09]):

$$
\mathcal{U}_n \xrightarrow{n \to \infty} \mathcal{U} \text{ in } \mathbb{U}_1 \text{ iff } \Phi(\mathcal{U}_n) \xrightarrow{n \to \infty} \Phi(\mathcal{U}) \text{ for all } \Phi \in \Pi. 
$$

This will be used next for extending and enriching the state spaces.

### 2.2 Extensions: marks, finite and infinite populations, fossils

The concepts introduced in the previous section have to be extended in two ways. First to handle spatial and multitype populations we have to pass to marked genealogies. Second to incorporate varying population sizes we have to allow sampling measures which are not necessarily probability measures and which could even have infinite total mass, at least globally.

**Genealogies of multitype and spatial populations** If we have a multitype population which is spatially distributed we have to associate with the individuals types from some type set $\mathbb{I}$ and the types may influence the reproduction mechanism. Similarly we may have a geographic space $\mathbb{G}$ in which the individuals are located, i.e., we assign them geographic locations. We assume that the metric spaces $(\mathbb{I}, r_{\mathbb{I}})$ and $(\mathbb{G}, r_{\mathbb{G}})$ are complete and separable.

We incorporate this in our formalism by considering a measurable map

$$
\tilde{\kappa} : U \to \mathbb{V}, \quad \mathbb{V} = \mathbb{I} \times \mathbb{G}, 
$$

where $\mathbb{V}$ is the mark space and $\tilde{\kappa}(u)$ is the mark of individual $x \in U$. Here $\mathbb{V}$ equipped with the product metric $r_{\mathbb{V}}$ is also complete and separable. This results in the structure

$$
(U, r, \mu, \tilde{\kappa}) \quad (2.16)
$$
describing a $\mathbb{V}$-marked genealogy. We now introduce the Borel-measure $\nu$ on $(U \times \mathbb{V}, r \otimes r_\mathbb{V})$:
\[
\nu = \mu \otimes \kappa, \quad \kappa(x, dv) = \delta_{\pi(x)}(dv), \quad x \in U.
\]
\tag{2.17}

Then abstracting again from the individuals names (of course not their types or locations) we consider the equivalence classes of $\mathbb{V}$-marked ultrametric probability measures
\[
\{(U \times \mathbb{V}, r \otimes r_\mathbb{V}), \nu\},
\] where we say that $(U \times \mathbb{V}, r \otimes r_\mathbb{V}, \nu)$ and $(U' \times \mathbb{V}, r' \otimes r_\mathbb{V}, \nu')$ are equivalent if there is a map $\varphi : U \times \mathbb{V} \rightarrow U' \times \mathbb{V}$ such that (here $\pi_U$ and $\pi_\mathbb{V}$ are the projections on $U$ respectively $\mathbb{V}$)
\[
\pi_U \circ \varphi = \varphi_U \circ \varphi, \quad \varphi((x, v)) = ((\pi_U \varphi)(x, v), v) \quad \nu - \text{a.s., and}
\]
\[
\varphi_* \nu = \nu'.
\]
\tag{2.19}

To obtain later a complete space it is necessary to allow here instead of mark functions more generally mark kernels $\kappa$. Then we denote the set of all equivalence classes of $\mathbb{V}$-marked ultrametric probability measure spaces by
\[
\Pi^\mathbb{V},
\]
\tag{2.20}
which will be the state space for the marked genealogies.

On this space we introduce the $\mathbb{V}$-marked Gromov-weak topology as follows. Again we use the idea that finite samples converge as finite marked trees. Let
\[
\Pi^\mathbb{V}
\] be the set of polynomials of the form
\[
\Phi^{n, X}(\nu) = \Phi^n \varphi((x, v)) = \int_{(U \times \mathbb{V})^n} \varphi((x, v))^n \nu(dx_1, \ldots, dx_n),
\]
\tag{2.22}
where $\varphi \in C_b((0, \infty)^n, \mathbb{R})$, $\xi \in C_b(\mathbb{R}^n, \mathbb{R})$ and $n \in \mathbb{N}_0$. Using these polynomials we can again define convergence on $\Pi^\mathbb{V}$ by the requirement:
\[
U_n \xrightarrow{n \rightarrow \infty} U \text{ in } \Pi^\mathbb{V} \text{ iff } \Phi(U_n) \xrightarrow{n \rightarrow \infty} \Phi(U) \text{ for all } \Phi \in \Pi^\mathbb{V}.
\]
\tag{2.23}

The corresponding topology is called the $\mathbb{V}$-marked Gromov-weak topology and we obtain a Polish space as a state space for the random marked genealogies. It is metrizable by a metric which generalizes the one described in Remark 2.1; see [DGP11] for details.

**Theorem 2.3** (Polish state space).

The space $\Pi^\mathbb{V}$ equipped with the $\mathbb{V}$-marked Gromov-weak topology is a Polish space.

Now we can define evolving random genealogies $(U_t)_{t \geq 0}$ of spatial multitype populations as $\Pi^\mathbb{V}$-valued stochastic processes. Again for $\Pi^\mathbb{V}$ and $\Pi^\mathbb{V}$ the analogue of Theorem 2.2 holds; see [DGP11]. As a prototype we will discuss later the evolving genealogies of the spatial Fleming-Viot process with selection.

**Genealogies of populations with varying population sizes** If the population size of a population is fluctuating we have to incorporate this size explicitly in the state description, think of a multitype Feller diffusion for example. This means we consider now an element
\[
\mathcal{U} = (\bar{u}, \hat{u}), \quad \bar{u} \in \mathbb{R}, \hat{u} \in \mathbb{U}^1
\]
\tag{2.24}
where $\bar{u}$ describes the population size and $\hat{u}$ the $\mathbb{I}$-marked genealogy from above (without the spatial component). We note that now we consider the map
\[
\mathcal{U} = (\bar{u}, \hat{u}) \mapsto [(U \times \mathbb{I}, r \otimes r_\mathbb{I}, \bar{u} \nu)]
\]
\tag{2.25}
and we obtain the equivalence class of an ultrametric measure space where the measure on $U \times \mathbb{I}$ is now in $\mathcal{M}_{\text{fin}}((U \times \mathbb{I}), \mathcal{B}(U \times \mathbb{I}))$. We denote this set of states by

$$U_{\text{fin}}^\mathbb{I}.$$  \hfill (2.26)

Here we see that if we introduce a topology we have to settle, how we want to handle the elements $\{(0, \tilde{U}) : \tilde{U} \in U_{\text{fin}}^\mathbb{I}\}$. Without marks these are extinct populations where genealogy could at most make sense as a limiting object, genealogy at extinction. (In fact below we shall discuss also the role of extinct types.)

Consider first the case without marks. Then we could use on $U_{\text{fin}}^\mathbb{I}$ simply the topology based on the convergence of polynomials (we extend the definition of polynomials from (2.11) to $U_{\text{fin}}^\mathbb{I}$).

In this case a sequence of elements where the population sizes converge to zero is automatically converging to the 0-element and in particular all elements $\{(0, \tilde{U}) : \tilde{U} \in U_{\text{fin}}^\mathbb{I}\}$ are identified with the 0 element, i.e., give one object.

Alternatively we could define convergence for a sequence with total masses converging to zero as follows: the sequence $(\bar{U}_n, \tilde{U}_n)$ converges if $\bar{U}_n$ converges in $\mathbb{R}$ and $\tilde{U}_n$ converges in $U_{\text{fin}}^\mathbb{I}$. In the latter case we have the product topology of $[0, \infty) \times U_{\text{fin}}^\mathbb{I}$ and we distinguish elements $\{(0, \tilde{U}) : \tilde{U} \in U_{\text{fin}}^\mathbb{I}\}$ rather than identifying them all with the 0-element. On the set where $\bar{U} > 0$ both topologies agree.

We denote the two topological spaces by (cf. [DG18], [GRG18]) $U_{\text{fin}}^\mathbb{I}$ respectively $U_{\text{fin}}^{*, \mathbb{I}}$.  \hfill (2.27)

In $U_{\text{fin}}^{*, \mathbb{I}}$ we can study the behavior of a population at extinction more precisely.

In the case with marks a suitable description is more subtle. We assume in the following that the geographic space $\mathbb{G}$ is countable. The types could be extinct temporarily during the evolution, or geographic locations could be vacant during some time periods and may be recolonized again during the others. If we choose to define convergence by requiring that polynomials of the states converge we get (we extend the definition of polynomials from (2.22)):

$$U_{\text{fin}}^{\mathbb{G}, \mathbb{I}}.$$  \hfill (2.28)

However, in spatial models it is often of interest to study the genealogy on the way to extinction. What about the analogue of above (2.24) representation? We proceed as follows.

We consider the situation where for example the state at each site is given as a pair (population size, genealogy), i.e., an element in $\mathbb{R}_+ \times U_{\text{fin}}^\mathbb{I}$ and the complete system as a measure on the geographic space $\mathbb{V} = \mathbb{G}$ and the genealogy as an ultrametric measure space which is an element of $\left(\bigcup_{g \in \mathbb{G}} U_g, r, \sum_{g \in \mathbb{G}} \mu_g\right)$ so that we have pairs in $\mathcal{M}_{\text{fin}}(\mathbb{V}) \otimes U_{|\mathbb{V}|}$. Then the product topology is the generalization leading to the state space

$$U^{\mathbb{V}, \mathbb{I}}.$$  \hfill (2.29)

by choosing the product topology which is Polish.

In this situation of varying population sizes we obtain the random variables and stochastic processes

$$\mathbf{U} = (\bar{U}, \tilde{U}),$$  \hfill (2.30)

where we can distinguish population sizes and where $\tilde{U}$ is $[0, \infty)$-valued or $\mathcal{M}(\mathbb{V})$-valued where $\mathcal{M}$ denotes the set of Borel measures and genealogies $\tilde{U}$ of the evolving population.

**Theorem 2.4** (Polish state space).

In both constructions the spaces $U^{\mathbb{V}, \mathbb{I}}_{\text{fin}}$ and $U^{\mathbb{V}, \mathbb{I}}_{\text{fin}}^{*, \mathbb{I}}$ are Polish.

Again polynomials play an important role via moments even though now their expectations for stochastic processes do not exist in general or are not law determining, however in case we discuss later they will, see [Glö12] [DGPT18]. We have no space to explain the issues in further details here.
**Globally infinite locally finite population sizes** If we consider for example a population in an infinite geographic space as for example \( \mathbb{Z}^d \) or \( \mathbb{R}^d \) then it is often necessary to consider populations with an *overall infinite population size* which is however *locally finite*, that is, at single sites in \( \mathbb{Z}^d \) or in a compact subsets of \( \mathbb{R}^d \). We now modify our description of the genealogy to account for this possibility and distinguish a *measure-valued part* \( (\mathcal{U}_t)_{t \geq 0} \) describing occupation measures of the locations and \( (\mathcal{\tilde{U}}_t)_{t \geq 0} \) describing genealogies so that for example for \( G \) countable we may have a collection of ultrametric probability measure spaces and corresponding population sizes, which we view again as a measure on \( G \).

One important case is where this measure is always the counting measure (locally) fixed population as in Fleming-Viot models, while in super random walk these sizes fluctuate and we have to work with the full space of locally finite measures. In other words we consider sampling measures such that the projection on \( G \) satisfies:

\[
\nu_G(A) < \infty \text{ for all bonded Borel sets } A \subset \mathcal{V}. \tag{2.31}
\]

We denote this space by

\[
\mathcal{U}^\mathcal{V},\# . \tag{2.32}
\]

The topology is defined by considering the spaces corresponding to bounded and closed subsets of the geographic space \( G_n \subseteq G \) and \( G_n \uparrow G \). We say that a sequence of elements in \( \mathcal{U}^\mathcal{V},\# \) converges if all restrictions to \( G_n \) converge in the sense described before. This defines the *Gromov-weak-\#-topology* which is independent of the choice of the sequence \((G_n)_{n \in \mathbb{N}}\); see [GSW16].

**Theorem 2.5** (Polish state space). The space \( \mathcal{U}^\mathcal{V},\# \) equipped with the Gromov-weak-\#-topology is Polish.

This again means that we have a suitable state space also for *spatial* multitype populations with *infinite overall mass*.

**Genealogies including fossils** So far we have focused on the description of the genealogy of the population *currently alive*, leading to *ultra*-metric measure spaces. Sometimes however one is interested in the evolution in time \( t \) of the genealogy of the population alive up to time \( t \) which includes the individuals alive at *some time* \( s < t \) but which do not necessarily have descendants at time \( t \). In other words we include the *fossils* generated up to the present time \( t \) and see how this object now evolves as \( t \) increases.

This will then lead to equivalence classes of metric measure spaces denoted generically by \( \mathcal{M} \) whose projections on subspace of *leaves* gives the object \( \mathcal{U} \) we looked at above. Here \( \mathcal{U} \) denotes either \( U_t \) or \( U_{\text{fin}} \). The set \( \mathcal{M} \) equipped with the Gromov-weak topology is a Polish space which contains \( \mathcal{U} \) as a subspace (this holds also for the \( \mathcal{V} \)-marked case), see [GPW09, DCP11]. However in order to model the states of the genealogy in an evolving population of all the individual which have been alive up to the present time \( T \) (and for equilibrium considerations then also forever) it is useful to work with a subspace of \( \mathcal{M}^{\text{root}} \) of routed versions of \( \mathcal{M} \). By routed we mean that to the elements of the spaces a root is added as distinguished element which has to be preserved under forming of the equivalence classes. The root allows to pin down time \( 0 \) in the genealogy.

If \( T \geq 0 \) is the present time of the population, then the basic set of individuals is of the form

\[
M = \{(s,u) \mid u \in U_s, \ s \in [0,T]\} \cup \{\varrho\}, \tag{2.33}
\]

where \( \varrho = (0,\varrho^*) \) is the *root* used as reference point for time and \( U_s \) describes the population *alive at time* \( s \). Between the individuals alive at or before time \( t \) we have a *partial order* induced by the ancestor-descendant relation between any two elements of the set \( M \), which arise as children of children of children etc. of earlier living individuals. Such a structure arises in branching, Fleming-Viot models, in the contact process, the voter model and many more. We obtain in such a setup a metric measure space

\[
(M,\tilde{r},\tilde{\mu}), \tag{2.34}
\]

with \( \tilde{r}(i, i') \) being the genealogical distance of the individuals \( i \) and \( i' \) in \( M \), which is the sum of the times back to their MRCA and points in \( U_s \) have distance \( 2s \) to the root. The root allows to define
the position on the time axes uniquely. Further we think of the population alive at time \( s \), for each \( s \) as equipped with a sampling measure \( \tilde{\mu}_s \) on \( (U_s, r_s) \), where \( r_s \) is the genealogical distance restricted to \( U_s \times U_s \). We lift to a measure \( \tilde{\mu}_s \) on \( [0, T] \times U_s \) by extension. We note that with \( T \) denoting the present time the individuals \((i, T)\) with \( (i \in U_T) \) play a special role as population currently alive as the one driving the further evolution. Therefore the sampling measure of the whole structure \( M \) must be able to sample here a finite sample, whereas from the fossils, \((s, i)\) with \( s < T \) we should simply sample according to an aggregated (over time) sampling measure from \( \tilde{\mu}_s \), \( s \in [0, T] \) which are the measures allowing to sample from \( U_s \). Hence \( \tilde{\mu} \) is chosen of the form:

\[
\tilde{\mu} = \int_0^T \mu_s \, ds + \mu^{\text{top}}, \quad \mu_s \text{ is a measure on } [0, T] \times U_s
\]

and \( s \mapsto \mu_s \) is assumed measurable as a map \([0, T] \to \bigcup_{s \in [0, T]} [0, T] \times U_s \) supported on \([s] \times U_s \), \( s \in [0, T] \) and \( \mu^{\text{top}} \) on \( \{T\} \times UT \).

Then we consider again the equivalence classes of such rooted metric measure spaces w.r.t. measure preserving and root preserving isometries. We obtain for each \( T \) a Polish space and the union over all \( T \geq 0 \) gives

\[
\mathcal{M}_{(T, \varnothing)} \text{ and with marks } \mathcal{M}_{(T, \varnothing)}^Y.
\]

If we also introduce marks, we introduce the topology again via polynomials. This is being currently worked out in [GSGW], see also [GRG18].

This leads to stochastic processes describing the genealogy of a population up to time \( t \), where this structure evolves then with \( t \):

\[
(\mathbb{M}_t, \tilde{\mathbb{M}}_t)_{t \in [0, T]},
\]

which is a \( \mathcal{M}_{(T, \varnothing)}^Y \)-valued stochastic process.

This structure allows now to describe the genealogy of a population in time, which is an enrichment of the process \((U_t)_{t \geq 0} \) with states in \( U \), which now appear in the slices \([U_s, r_s, \mu_s] \) but include the additional information on genealogical relations between the individuals alive at different times before time \( T \).

Including now an infinite time horizon is possible, but needs some thought to deal with possibly infinite distances, if we try to take the closure of \( \bigcup_{T \geq 0} \mathcal{M}_{(T, \varnothing)} \).

# 3 Martingale problems for evolving genealogies

## 3.1 Concepts and examples

The processes of evolving genealogies are defined by well-posed martingale problems. First we recall the notion of martingale problems that we use here; see [EK86].

**Definition 3.1 (Martingale problem).**

Let \( E \) be a Polish space and let \( B(E) \) denote the space of bounded measurable functions on \( E \). Furthermore let \( P_0 \in \mathcal{M}_1(E), F \subseteq B(E) \) and let \( L \) be a linear operator on \( B(E) \) with domain \( F \). The law \( P \) of an \( E \)-valued stochastic process \( \mathcal{X} = (X_t)_{t \geq 0} \) is called a solution of the \((P_0, L, F)\)-martingale problem if \( X_0 \) has distribution \( P_0 \), \( \mathcal{X} \) has paths in the space \( \mathcal{D}_E([0, \infty)) \), \( P \)-almost surely, and for all \( F \in F \),

\[
(F(X_t) - \int_0^t L(F(X_s)) \, ds)_{t \geq 0}
\]

is a \( P \)-martingale with respect to the canonical filtration. Moreover, the \((P_0, L, F)\)-martingale problem is said to be well-posed if there is a unique solution \( P \).

To define a process by means of a martingale problem we need to define an operator \( L \) acting on an appropriate subset of the set of test functions \( F \). We do this in the following paragraphs for several examples of tree-valued processes by adding more and more evolutionary mechanisms to the processes.
The neutral tree-valued process without types

The most basic evolutionary mechanisms involving genealogies are

- aging, i.e., growth of genealogical distances with time;
- the splitting of a genealogical line in two due to resampling (i.e. birth) events.

Now the idea is to describe the evolution by describing the evolution of all finite samples drawn by the resampling measure. This means we consider the following test functions for the martingale problem.

For $U = [(U, r, \mu)] \in \mathbb{U}_1$ consider the polynomials

$$\Phi^n,\varphi(U) = \int_{U_n} \varphi(\underline{x}) \mu^{\otimes n}(d\underline{x})$$

with $\varphi : \mathbb{R}_+^n \to \mathbb{R}$ continuously differentiable,

where $\underline{x} = (x_1, \ldots, x_n) \in U^n$ and $\underline{r} := (r_{k,\ell})_{1 \leq k < \ell \leq n} = (r(x_k, x_\ell))_{1 \leq k < \ell \leq n}$.

Then the above mechanisms are described by the generator

$$\Omega = \Omega^{\text{grow}} + \Omega^{\text{res}}.$$ (3.3)

The growth operator acting on polynomials, see (3.2) is given by

$$\Omega^{\text{grow}} \Phi^n,\varphi(U) = 2 \int_{U_n} \mu^{\otimes n}(d\underline{x}) \sum_{1 \leq k < \ell \leq n} \frac{\partial}{\partial r_{k,\ell}} \varphi(\underline{r})$$

and the resampling generator by

$$\Omega^{\text{res}} \Phi^n,\varphi(U) = d \int_{U_n} \mu^{\otimes n}(d\underline{x}) \sum_{1 \leq k < \ell \leq n} (\varphi \circ \theta_{k,\ell} - \varphi)(\underline{r}).$$ (3.5)

Here, $d > 0$ is the resampling rate and the resampling operator $\theta_{k,\ell}$ replaces the distances of the $\ell$-th component by those of $k$-th. More precisely it is defined by $\theta_{k,\ell}(\underline{r}) = \tilde{\underline{r}}$ and

$$\tilde{r}_{i,j} := \begin{cases} r_{i,j}, & \text{if } i, j \neq \ell, \\ r_{i,k} \wedge r_{j,k}, & \text{if } j = \ell, \\ r_{j,k} \vee r_{j,k}, & \text{if } i = \ell. \end{cases}$$ (3.6)

The $\mathbb{U}_1$-valued process with generator consisting of the growth and resampling parts, the $\mathbb{U}_1$-valued Fleming-Viot processes $U^{\text{FV}}$, was constructed and studied in [GPW13]. The approach can be extended to Cannings processes or so called $A$-Fleming-Viot models, see [GKW18]. Mutation and selection have been included in [DGP12] leading to $\mathbb{U}_1$-valued processes. Spatial models giving $\mathbb{U}^{\mathbb{R}}$-valued Fleming-Viot processes were considered in [GSW16]. Both the latter are successively explained next in two paragraphs.

Similarly one can introduce on $\mathbb{U}_\text{fin}$ with these above two operators the process $U^{\text{Fel}}$ describing the evolution of the genealogies of the continuum state Feller branching diffusion and the self-catalytic branching diffusion; see [Glö12, GGR17, GRG18, DG18].

Tree-valued process with mutation and migration

Let the type of an individual be given by its genotype and its spatial location so that we may assume that the type space is $\mathcal{V} = \mathcal{G} \times \mathcal{I}$ with $\mathcal{G}$ being the geographical space and $\mathcal{I}$ the type space. Think for instance of $\mathcal{G}$ as a (finite) subset of $\mathbb{Z}^d$ and $\mathcal{I}$ as a compact space.

For $\mathbb{U}_\mathcal{V}$-valued processes we can take test functions of the following form: For $U = [(U \times \mathcal{V}, r \otimes \nu)]$ set

$$\Phi^{\nu,\psi,\eta}(U) = \int_{(U \times \mathcal{G} \times \mathbb{I})^n} \varphi(\underline{r}) \psi(\underline{g}) \eta(\underline{u}) \nu^{\otimes n}(d(\underline{x}, \underline{g}, \underline{u})).$$ (3.7)
with \( \varphi \) as in (5.2), \( \psi : \mathbb{G}^n \to \mathbb{R} \) and \( \eta : \mathbb{I}^n \to \mathbb{R} \), \( \underline{g} = (g_1, \ldots, g_n) \in \mathbb{G}^n \) and \( \underline{u} = (u_1, \ldots, u_n) \in \mathbb{I}^n \).

As in the basic case, due to aging the genealogical distances grow with time and do not affect the types or locations of individuals. Thus, the growth operator action on \( \Phi^{n,\varphi,\psi,\eta} \) is given by

\[
\Omega^{\text{grow}} \Phi^{n,\varphi,\psi,\eta}(\mathcal{U}) = 2 \int_{(U \times \mathbb{G} \times \mathbb{I})^n} \nu^{\otimes n}(d(\underline{x}, \underline{g}, \underline{u})) \psi(\underline{g}) \eta(\underline{u}) \sum_{1 \leq k < \ell \leq n} \frac{\partial}{\partial r_{k,\ell}} \varphi(r).
\]

(3.8)

The resampling generator does replace distances as before but now it also replaces the types of individuals but not their location. It is given by

\[
\Omega^{\text{res}} \Phi^{n,\varphi,\psi,\eta}(\mathcal{U}) = d \int_{(U \times \mathbb{G} \times \mathbb{I})^n} \nu^{\otimes n}(d(\underline{x}, \underline{g}, \underline{u})) \psi(\underline{g}) \prod_{1 \leq k < \ell \leq n} \mathbb{I}(g_k = g_{k'})(\varphi \otimes \eta)(\underline{x}, \underline{u}).
\]

(3.9)

Here, generalizing the resampling operator from (3.6), \( \theta_{k,\ell} \) is defined by \( \theta_{k,\ell}(\underline{x}, \underline{u}) = (\tilde{r}, \tilde{u}) \) with \( \tilde{r} \) as in (3.6) and

\[
\tilde{u}_i := \begin{cases} u_i & \text{if } i \neq \ell, \\ u_k & \text{if } i = \ell. \end{cases}
\]

(3.10)

For mutation, let \( \vartheta \geq 0 \) be the mutation rate and let \( \beta(\cdot, \cdot) \) be a Markov transition kernel on \( \mathbb{I} \times \mathbb{I} \) and set

\[
\Omega^{\text{mut}} \Phi^{n,\varphi,\psi,\eta}(\mathcal{U}) = \vartheta \int_{(U \times \mathbb{G} \times \mathbb{I})^n} \nu^{\otimes n}(d(\underline{x}, \underline{g}, \underline{u})) \varphi(\underline{x}) \psi(\underline{g}) \sum_{k=1}^n (\beta_k \eta - \eta)(\underline{u}).
\]

(3.11)

where

\[(\beta_k \eta)(\underline{u}) = \int \eta(\underline{u}^r_k) \beta(u_k, dv),\]

(3.12)

with \( \underline{u}^r_k = (u_1, \ldots, u_{k-1}, v, u_{k+1}, \ldots, u_n) \).

For migration let \( A \) be a transition kernel on \( \mathbb{G} \times \mathbb{G} \) and for \( \psi : \mathbb{G}^n \to \mathbb{R} \) we set

\[(M_{g_j, g'} \psi)(g_1, \ldots, g_n) = \psi(g_1, \ldots, g_{j-1}, g', g_{j+1}, \ldots, g_n).
\]

(3.13)

Then,

\[
\Omega^{\text{migr}} \Phi^{n,\varphi,\psi,\eta}(\mathcal{U}) = \int_{(U \times \mathbb{G} \times \mathbb{I})^n} \nu^{\otimes n}(d(\underline{x}, \underline{g}, \underline{u})) \varphi(\underline{x}) \psi(\underline{g}) \sum_{k=1}^n \sum_{g_j' \in \mathbb{G}} A(g_j, g_j')(M_{g_j, g_j'} \psi - \psi)(\underline{g}).
\]

(3.14)

Adding selection For selection let \( \alpha \geq 0 \) be the selection coefficient and let \( \chi : \mathbb{V} \to [0, 1] \) be a function that we refer to as fitness function. Then the selection operator is given by

\[
\Omega^{\text{sel}} \Phi^{n,\varphi,\psi,\eta}(\mathcal{U}) = \alpha \int_{(U \times \mathbb{G} \times \mathbb{I})^{n+1}} \nu^{\otimes (n+1)}(d(\underline{x}, \underline{g}, \underline{u})) \varphi(\underline{x}) \psi(\underline{g}) \sum_{k=1}^n \mathbb{I}(g_k = g_k)(\eta \cdot \chi_k - \eta \cdot \chi_{n+1})(\underline{u}).
\]

(3.15)

Here \( \chi_k(\underline{u}) = \chi(u_k) \). And the functions on \( \psi \) and \( g \) are extended to domains \( \mathbb{R}^{n+1} \) and \( \mathbb{G}^{n+1} \).

Note that it is possible to consider more general fitness functions to model diploid selection and kin selection, i.e. the fitness may depend on the distance of individuals involved in the selection event. We refer to Section 2.4. in [DGPT12] for background on selection that we have in mind here.
The branching world  Similarly to the above we can introduce $\mathbb{U}_{\text{fin}}$-valued branching diffusions, for example continuous state branching processes as $\mathbb{U}_{\text{fin}}$-valued Feller diffusion, or the spatial analog the $\mathbb{U}_{\text{G}}^2$-valued super random walk. Here one has as generator $\Omega_{\text{res}} + \Omega_{\text{grow}}$ and additionally $\Omega_{\text{migr}}$ in the spatial case acting now on polynomials arising by allowing for finite measures instead of probability measures in $\mathbb{U}_{\text{G}}^2$ and adding the functions $u \mapsto \bar{u}$ and $u \mapsto c$, where $c$ is a constant. As in the Fleming-Viot model we may consider drift terms, here of interest are sub/supercritical branching instead of just the critical case (which is the second order part) or we may consider the analog of selection which gives logistic branching with a competition term acting only on the total masses.

3.2 Results
In this section we state some general results concerning solutions of martingale problems and their basic properties in the case that the linear operator is given by the “full” generator

$$\Omega = \Omega_{\text{grow}} + \Omega_{\text{res}} + \Omega_{\text{out}} + \Omega_{\text{migr}} + \Omega_{\text{sel}}$$

acting on functions from $\Pi^V$ which are differentiable with respect to the distance part so that the action of $\Omega_{\text{grow}}$ in equation (3.16) is defined. Depending on the evolutionary forces to be included in the considered process one can of course omit some parts of the generator. In this case the set of polynomials $\Pi^V$ should also be modified accordingly. The corresponding proofs of Theorem 3.1 and Proposition 3.1 can be found in [GPW13], [DGP12] and [GSW16] and the proof in the case of “full” generator can be deduced by combination of the relevant results in the cited papers.

Theorem 3.1 (Martingale problem is well-posed).
For all $P_0 \in M_1(\mathbb{U}_{\text{fin}}^V)$, the $(P_0, \Omega, \Pi^V)$-martingale problem is well-posed.

A solution $P$ of the $(P_0, \Omega, \Pi^V)$ martingale problem from the above theorem is referred to as tree-valued Fleming-Viot dynamics with migration, mutation and selection and $\mathbb{U}_{\text{fin}}^V$-valued Fleming-Viot dynamics with initial distribution $P_0$ and has the following basic properties.

Proposition 3.1 (Properties of $\mathbb{U}_{\text{fin}}^V$-valued Fleming-Viot dynamics).
Let $\mathcal{U} = (\mathcal{U}_t)_{t \geq 0}$ be a $\mathbb{U}_{\text{fin}}^V$-valued Fleming-Viot dynamics with distribution $P$. Then the following properties hold:

(i) The sample paths of $\mathcal{U}$ are in $C_{\mathbb{U}_{\text{fin}}^V}([0, \infty))$, $P$-a.s.

(ii) For all $t > 0$ we have $\mathcal{U}_t \in \mathbb{U}_{\text{fin}}^{\text{comp}}$, $P$-a.s., where $\mathbb{U}_{\text{fin}}^{\text{comp}}$ refers to marked metric measure spaces in which the metric space components $(U, r)$ are compact.

(iii) The process $\mathcal{U}$ is a Feller and a strong Markov process.

The meaning of assertions (i) and (iii) in the above proposition is self explaining. Assertion (ii) states that all genealogies except maybe the initial one can be encoded by a compact ultrametric space. On the level of genealogies that means that for each $\varepsilon > 0$ the population at time $t > 0$ can be decomposed in finitely many families so that the time to MRCA of individuals within each of the families is bounded by $\varepsilon$. This should remind the reader of the “coming down from infinity”-property of some coalescent processes.

The same statements as above are or will be proven on $\mathbb{U}_{\text{fin}}$ respectively $\mathbb{U}^V_{\text{fin}}$ with $\mathbb{W} = \mathbb{G}$ and $\mathbb{G}$ a countable, i.e., mostly infinite, Abelian group for $\mathbb{U}_{\text{fin}}$-valued Feller diffusion and $\mathbb{U}_{\text{fin}}^V$-valued super random walk in [Goi12], [DGi18], [GRGi18] and in [GMi18] for logistic spatial branching.

Remark 3.1 (Existence of solutions). A standard method to construct a solution to the martingale problem, as for example the class in equation (3.16) is by approximations with individual based models. In a number of the models appearing in population genetics as in equation (3.16) the solution to such a martingale problem as in equation (3.16) can be obtained by graphical construction of the ancestral relations in time, see for example the Brownian web in [GSW16] or by lookdown constructions see [GLW05], [GFW13], [GLFW15], or by flows of bridges constructions [BLG00], [Fou12]. However for complicated selection or recombination models this becomes intransparent.
4 Long time behavior

In this section we discuss first under which conditions $\U_1$ and more generally $\U^V$-valued processes have unique invariant distributions and are ergodic. In presence of migration we assume that the geographical space is finite.

Let us consider the case without marks first. To this end we briefly recall the Kingman coalescent measure tree. Consider Kingman’s $N$-coalescent tree defined as follows: Starting with $N$ lines coalesce each pair of lines which are present at rate $d$, which is the resampling rate of the forwards in time process, and continue until all lines have merged into one. Alternatively we can say that when $k \in \{2, \ldots, N\}$ lines are present the total coalescence rate is $d(k)$ and at a coalescence event a random pair is chosen to coalesce. Let $U_N = \{1, \ldots, N\}$ be the set of leaves and let the (random) metric $r_N$ given by the tree distance of a Kingman’s $N$-coalescent tree, that is $r_N(i,j)$ is twice the distance to the MRCA of the individuals $i$ and $j$, $1 \leq i, j \leq N$. Let $\mu_N$ be the uniform measure on $U_N$ and consider the metric measure space $U_N := ([U_N, r_N, \mu_N])$. By Theorem 4 in [GPW09] there is an $\U_1$-valued random variable $U_\infty$ so that

$$U_N \overset{N \to \infty}{\Rightarrow} U_\infty. \quad (4.1)$$

The limiting random variable was introduced in [Eva00] and is called the Kingman coalescent measure tree.

The following result is Theorem 3 in [GPW13] and shows in particular that the distribution of the Kingman coalescent measure tree is the unique invariant distribution of the neutral Fleming-Viot dynamics without marks.

**Theorem 4.1** (Long time behavior of the basic process). Let $\U = (\U_t)_{t \geq 0}$ be an $\U_1$-valued process with $\U_0 = \U \in \U_1$ and let $U_\infty \in \U_1$ be the Kingman coalescent measure tree. Then we have

$$\U_t \overset{t \to \infty}{\Rightarrow} U_\infty. \quad (4.2)$$

Now let us turn to the general case. Let $\pi_X$ be the projection from $X \times Y$ on $Y$. Given $\U_t = ([U_t, r_t, \mu_t])$, $t \geq 0$, we define the process $\zeta := (\zeta_t)_{t \geq 0}$ by projecting the sampling measures to the type space, i.e., we set

$$\zeta_t := (\pi_X)_t \mu_t, \quad t \geq 0. \quad (4.3)$$

Then $\zeta$ is the corresponding measure-valued Fleming-Viot process and conditions for its ergodicity are available in the literature. For example, under neutral evolution, i.e. $\alpha = 0$, ergodicity of $\zeta$ has been shown if the Markov pure jump mutation process on $\I$ with has a unique equilibrium distribution; see [Daw93]. In the case $\alpha > 0$ and $\chi = 0$, the process $\zeta$ is ergodic if mutation has a parent independent component. In the case with no parent-independent component in the mutation operator ergodicity of $\zeta$ has been shown in [EK98] using coupling techniques. In [DGT14] a set-valued dual allows to prove quite general ergodic theorems, even in the spatial context under some conditions on the mutation process.

Obviously, an $\U^V$-valued process cannot be ergodic if its projection on the type space, i.e., the corresponding measure-valued process, is not ergodic. Also it is easy to see that ergodicity of $\zeta$ is implied by the ergodicity of $\U$. The following result shows that also the converse implication holds.

**Theorem 4.2** (Long time behavior of the process with marks). Let $\U = (\U_t)_{t \geq 0}$ be an $\U^V$-valued process with $\U_0 = \U$ and let $\zeta$ be as above. Then, there exists a unique invariant distribution on $\U^V_{\text{comp}}$ and for a random variable $U_\infty$ with this distribution for all $\U \in \U^V$ we have

$$\U_t \overset{t \to \infty}{\Rightarrow} U_\infty \quad (4.4)$$

if and only if $\zeta$ has a unique equilibrium distribution.

Note that Theorem 4.2 tells us that ergodic distribution of types is given by the ergodic distribution of the corresponding measure-valued Fleming-Viot process, but does say little about
the “geometry” of the limiting genealogies. In the neutral case with mutation a combination of
Theorem 4.1 and Theorem 4.2 provides a more complete picture.

We next discuss processes on infinitive geographic space where new features occur. Indeed
spatial populations on infinite geographic spaces, for example countable Abelian groups like \( \mathbb{Z}^d \) or
continuum space models like \( \mathbb{R}^d \) show in their longtime behavior an interesting dichotomy between
low and high dimensions, or to be more precise, between transient and recurrent dichotomy
symmetrized migration arising from the difference of the positions of two tagged “individuals”. For example
the Fleming-Viot model in its neutral form and compact type space has for \( t \to \infty \) limiting states
which are monotype if the symmetrized migration is recurrent. This is the case for nearest neighbor
migration for \( d = 1, 2 \), whereas for the transient case, i.e., \( d \geq 3 \), we have equilibria with coexistence
or more precisely for every intensity measure \( \theta \) on \( \mathbb{I} \) we have a translation invariant shift ergodic
equilibrium with this intensity. What happens on the level of genealogies?

In the transient case a common ancestor may not exist locally as we obtain in the limit \( t \to \infty \)
infinite distances. We introduce therefore the transformation of the ultrametric (into another
ultrametric) given by:

\[
    r \mapsto r', \quad r'(x, x') = 1 - \exp(-r(x, x')) ,
\]

where the distance 1 corresponds exactly to infinite distance in the original metric \( r \). We denote
the transformed process by \( (\widetilde{U}^{FV}_t)_{t \geq 0} \).

Then we obtain the following. Consider initial distributions of the population on a countable
(infinite) Abelian group \( \mathbb{G} \) such that the projection on \( V = \mathbb{I} \times \mathbb{G} \) gives a translation invariant
shift ergodic law with \( E[\{ (\pi_{x'}, \nu)(\{ g \} \times \cdot) \} = \theta(\cdot) \in \mathcal{M}_1(\mathbb{I}) \). Note that this means that if \( \mathbb{G} \) is
infinite then the “sampling” measure is infinite as well.

**Theorem 4.3** (Longtime behavior of spatial \( \mathbb{U}^V \)-valued Fleming-Viot process \( \widetilde{U}^{FV}_t \)).

(a) If the kernel \( \tilde{a}(g, g') = \frac{1}{2} (a(g, g') + a(g', g)) \) is recurrent then

\[
    \mathcal{L}[\tilde{U}^{FV}_t] \xrightarrow{t \to \infty} \Gamma \in \mathcal{M}_1(\mathbb{U}^V),
\]

where \( \Gamma \) is concentrated on mono-ancestor and mono-type configurations, i.e., the states have
a.s. a finite essential diameter and \( \nu(U \times \cdot) = \int_U (\lambda \otimes \delta_t) \theta(du) \).

(b) For every \( \theta \in \mathcal{M}_1(\mathbb{I}) \) there exists an equilibrium measure \( \widetilde{\Gamma}_\theta \) which is translation-invariant
and shift-ergodic, satisfies \( E[\nu(U \times \cdot)] = \lambda \otimes \theta \), \( \lambda \) being the Haar measure on \( \mathbb{G} \) normed to
\( \lambda(\{0\}) = 1 \), such that

\[
    \mathcal{L}[\tilde{U}^{FV}_t] \xrightarrow{t \to \infty} \widetilde{\Gamma}_\theta .
\]

The essential diameter of the states attains 1 a.s.

This means that in the recurrent case we have mono-ancestor and mono-type populations
developing in any finite spatial window whereas in the transient case, locally we have coexistence
of descendants of different ancestors and, if \( \theta \) is not the point measure we also have coexistence of
different types. This is proved in [GKW18] for the more general case of \( \Lambda \)-Fleming-Viot models,
see [GSW16] for information on spatial tree-valued Fleming-Viot.

Similar questions can be addressed for spatial branching models where convergence to equilibria
can be established. Here a transformation of the metric as in (4.3) may be needed to obtain equilibria in spatial models where with positive probability no common ancestor of the population exists. See [DG18, GM18] for more information.

5 Two techniques of analysis for our processes

There are two major tools to investigate our processes for example to prove uniqueness or existence of
martingale problems, namely duality and Girsanov transformation. The former is also crucial
for analyzing the longtime behavior and the latter is useful for obtaining path properties of more
complicated processes from corresponding path properties of simpler processes. We explain the
techniques in the following in more detail.
5.1 Duality

We explain here the general concept of duality and give the results for genealogy-valued processes. Then we continue by discussing strong duality, a stronger concept allowing representations of the state. Finally we discuss the so called conditional duality.

5.1.1 The concept of duality

Let \((X_t)_{t \geq 0}\) be a Markov process with state space \((E, \mathcal{B})\), where \(E\) is a Polish space and \(\mathcal{B}\) the Borel \(\sigma\)-algebra. The process \(X\) is the solution of a martingale problem with operator \(L\) acting on the test functions \(\mathcal{F} \subseteq C_b(E, \mathbb{R})\), the \((L, \mathcal{F}, \delta_x)\)-martingale problem, with \(x \in E\).

Then we have a dual process \((Y_t)_{t \geq 0}\) with state space \((E', \mathcal{B}')\) contained in a Polish space, \(\mathcal{B}'\) being the Borel \(\sigma\)-algebra. This process is the solution of the \((L', \mathcal{F}', \delta_y)\)-martingale problem, \(\mathcal{F}' \subseteq C_b(E', \mathbb{R})\) such that for \(f' \in \mathcal{F}'\), \(L'f' \in C_b(E', \mathbb{R})\) and for the solution \(Y\) the random variables \(f'(Y_t)\) are integrable for all \(t\).

In order to define a Feynman-Kac duality we define a functional

\[
\beta_t = \int_0^t B(Y_s) \, ds \tag{5.1}
\]

where \(B\) is a bounded continuous function on \(E'\), the so called potential.

**Definition 5.1** (Duality relation, Feynman-Kac duality).

(a) We say that \(X\) and \(Y\) are in duality w.r.t. the duality function \(H : E \times E' \to \mathbb{R}\) if the following holds:

\[
\begin{align*}
(i) & \quad H(\cdot, y) \in C_b(E \times E', \mathbb{R}), \\
(ii) & \quad \{H(\cdot, y) : y \in E'\} \text{ is separating on } E, \\
(iii) & \quad \text{the following equality holds for all } t \geq 0:
\end{align*}
\]

\[
E_x[H(X_t, y)] = E_y[H(x, Y_t)], \quad \forall (x, y) \in E \times E'. \tag{5.2}
\]

(b) The process \(X\) and \(Y\) are in Feynman-Kac duality if for all \(t \geq 0\), (i) and (ii) above hold and (iii) is replaced by:

\[
E_x[H(X_t, y)] = E_y[H(x, Y_t) \exp(\beta_t)] \tag{5.3}
\]

and if additionally the r.h.s. is integrable for all \(t \geq 0\).

The duality relation can be established by showing the following relations:

\[
(LH(\cdot, y))(x) = (L'H(x, \cdot))(y) + B(y)H(x, y), \quad (x, y) \in E \times E', \tag{5.4}
\]

\[
LH(\cdot, y) \in \mathcal{F}, \quad L'H(x, \cdot) \in \mathcal{F}', \quad \forall (x, y) \in E \times E' \tag{5.5}
\]

and establishing the integrability condition at the end of the definition above.

**Remark 5.1** (General applications). The duality relations have some consequences for processes \(X\) and \(Y\) from the above definition:

- If a solution for the \((L', \mathcal{F}', \delta_y)\)-martingale problem exists, then a solution of the \((L, \mathcal{F}, \delta_x)\)-martingale problem is unique. Note that it is sometimes possible to drop the boundedness and/or continuity assumptions on the duality functions and potentials and still be able to use duality to establish uniqueness.

- If \(\mathcal{L}[(X_t)_{t \geq 0}]\) is tight and if \(\mathcal{L}[(Y_t)_{t \geq 0}] \Rightarrow \mathcal{L}[Y_\infty]\) as \(t \to \infty\) then \(\mathcal{L}[X_t] \Rightarrow \pi\) and \(\pi\) is an equilibrium distribution of the Markov process \(X\).  

Furthermore in many cases:
5 TWO TECHNIQUES OF ANALYSIS FOR OUR PROCESSES

- The existence of the process $Y$ as solution to its martingale problem and fulfillment of \((5.4)\) and \((5.5)\) allows to obtain the existence of a process $X$ solving the $(L,\mathcal{F},\delta_x)$-martingale problem.

- The duality might be helpful to deduce the Feller property of processes when their duals fulfill certain properties. Roughly speaking this is case when the dual process is a “finite” particle system. For one of the many examples see for instance Theorem 1(c) in [DGPI3] and its proof on p. 2602.

△

Of particular importance for us will be the case of moment duals, this means for population models that the function $H(\cdot, y)$ can be interpreted as testing a sample of size $n$ from the population. In the case of the Fisher-Wright diffusion or the Feller diffusion this gives with $H$ models that the function $\phi_{n}$ partition elements. The resulting process is denoted by $C_{t}$ distances between elements of the basic set grow at speed 2 as long as they belong to different $(\cdot)$. Then the state space of this process is $E_{n}$.

We define the potential $\mu_{n}$ and later want to view $(\phi_{n})$ will not change. To this end, we extend the state space $E_{n}$ by setting $E_{n}' = E_{n} \times \mathbb{D}_{n}$. Then the state space of this process is

\[
E_{n}' = \bigcup_{n=1}^{\infty} E_{n}' = \bigcup_{n=1}^{\infty} \mathbb{D}_{n}.
\]

(1) Consider the Kingman coalescent starting with $n$ individuals. The state of this process is an element of $S_{n}$ the set of all partitions of the basic set $\{1, \ldots, n\}$, i.e., a tuple $(p_{1}, \ldots, p_{|p|})$ with $p_{i} \subseteq \{1, \ldots, n\}, i \in 1, \ldots, |p|$, $\bigcup_{i=1}^{|p|} p_{i} = \{1, \ldots, n\}$ and $p_{i} \cap p_{j} = \emptyset$ for $i, j \in 1, \ldots, |p|$ with $i \neq j$.

We denote by $D_{n}$ the set of all $n \times n$ distance matrices, i.e., $D_{n} \subseteq \mathbb{R}^{n \times n}_{\geq 0}$ so that for $(\delta_{i,j})_{1 \leq i < j \leq n} \in \mathbb{D}_{n}$ we have $d_{i,j} \leq d_{i,k} + d_{j,k}$ and $d_{i,i} = 0$ for all $i, j, k = 1, \ldots, n$. We abbreviate $E_{n}' = S_{n} \times \mathbb{D}_{n}$. Then the state space of this process is

\[
E_{n}' = \bigcup_{n=1}^{\infty} E_{n}'.
\]

The dynamics is that every pair of partition elements independently coalesces at rate $d$, i.e., $(p_{1}, \ldots, p_{|p|}) \rightarrow (p_{1}, \ldots, \tilde{p}_{i}, \ldots, p_{1} \cup p_{i}, \ldots, p_{|p|})$ where $\tilde{p}_{i}$ denotes deletion at the $i$th position. The distances between elements of the basic set grow at speed 2 as long as they belong to different partition elements. The resulting process is denoted by $C$. For a given $n \in \mathbb{N}$, $\varphi \in C_{b}\left(\mathbb{R}_{+}^{\{2\}}, \mathbb{R}\right)$ we later want to view $(\varphi, n)$ as part of the state of the dual. In the neutral case the element $(\varphi, n)$ will not change. To this end, we extend the state space $E_{n}'$ by setting $E_{n}' = S_{n} \times \mathbb{D}_{n} \times C_{b}\left(\mathbb{R}_{+}^{\{2\}}, \mathbb{R}\right) \times \{n\}$.

(2) To define the duality function for a given $n \in \mathbb{N}$, $\varphi \in C_{b}\left(\mathbb{R}_{+}^{\{2\}}, \mathbb{R}\right)$ we consider the function

\[
H([U, r, \mu], (p, (\varphi, n))) = \int_{U} \cdots \int_{U} \varphi(x + x') \, d\mu \, \varphi(x + x'), \quad [U, r, \mu] \in U_{1}, (p, x') \in E_{n}'.
\]

We define the potential $B$

\[
B((p, x'), (\varphi, n)) = d \cdot \binom{|p|}{2}.
\]

Consider now the $U_{1}$-valued Fleming-Viot diffusion $\Omega^{FV}$ and the $U_{\text{fin}}$-valued Feller diffusion $\Omega^{Fel}$ with branching rate $b$, i.e., the resampling operator has coefficient $b$, then we have the following result.

**Theorem 5.1 (Duality-relation).**
(a) The processes $\mathcal{U}^{FV}$ and $\mathcal{C}$ are in duality w.r.t. $H$ from \eqref{5.7}.

(b) The process $\mathcal{U}^{Fel}$ and $\mathcal{C}$ are in Feynman-Kac duality w.r.t. to $H$ and potential $B$ from \eqref{5.4} and \eqref{5.8}, where $d = b$.

In the case of spatial models we consider the spatial coalescent where the state is enriched by a map

$$\Omega \to \Omega^{[p]}$$

(5.9)

which associates with every partition element a location, i.e. an element in $\mathbb{G}$. Accordingly the test function $\varphi$ will be replaced by $\varphi \cdot \psi$, where $\psi$ is a bounded function on $\mathbb{G}^n$, i.e. $\psi \in C_b(\mathbb{G}^n, \mathbb{R})$. In the case of infinite geographic spaces, i.e. on $\mathcal{U}^{\mathbb{G},\#}$, we restrict to $\psi$ with bounded support in $\mathbb{G}$. The dynamics is modified by adding a new mechanism. The partition elements perform independent random walks with rates $\alpha(\cdot, \cdot)$ until they coalesce and then the individuals in the new partition element now follow the same random walk. Coalescence occurs only for pairs of partition elements sharing the same geographical location.

Corollary 5.1. (Duality: spatial model)

For the $\mathcal{U}^{\mathbb{V}}$-valued interacting Fleming-Viot diffusion and the $\mathcal{U}^{\mathbb{G},\#}$-valued super random walk the duality theorem above holds with the modified ingredients.

Similarly we can consider multitype spatial populations with $\mathbb{V} = \mathbb{I} \times \mathbb{G}$ type frequency change by resampling respectively branching, but with the principle that types are inherited. If we have also types we extend $\psi$, i.e., $\psi \in C_b((\mathbb{I} \times \mathbb{G})^n, \mathbb{R})$. In this case we have to assign the $\mathbb{I}$-types to the partition element by choosing a type for a partition element for the duality relation at time $t$ by sampling the type from the sampling measure of the initial state of the forward process restricted to the position of the partition elements position at time $t$. Then partition elements will be assigned a type when we evaluate the duality function where the type is chosen according to the projection of $\mu$ on $\mathbb{I}$ at the location $g \in \mathbb{G}$ at the partition element at time $T$, i.e., $\mu_0(\mathbb{I} \times \{\cdot\} \times \{g\})$.

Somewhat more complicated are the multitype processes in particular if we include selection, mutation and recombination in the mechanism where already the measure-valued model requires a function-valued dual which is more subtle to explain already on that level, but in fact this constructions can be carried out on $\mathcal{U}^{\mathbb{V}}$ and even in the spatial setup.

The function-valued part is needed to have a dualy once we include selection and mutation or even recombination in the model. The dual process is built upon a spatial coalescent enriched with a distance matrix in addition to coalescence, migration and distance growth we have a birth mechanism which drives a function-valued process, i.e. at the “birth” transition a selection operation acts on the function. Furthermore there is action on the function via a mutation operation. Function-valued means here that we consider $\varphi$ and $\psi$ as part of the dual state where $\psi$ now follows a dynamic itself. See [DGL14] for an extensive treatment of the measure-valued case. We cannot give an account of this theory here. However we show in [DGP12] that one can extend this to the $\mathcal{U}^{\mathbb{I}}$-valued case. The key point is to take the same driving particle system as in the measure-valued case but to incorporate as well the function $\varphi$ of the distances into this picture.

5.1.3 Strong dual representation and conditional duality

Strong dual representation It turns out that we can extend the dual process in many of our models to an $\mathcal{U}^{\mathbb{I}}$-valued state by passing to the entrance law of the coalescence starting from countably many individuals. Then we introduce a metric $r'(\cdot, \cdot)$ on $\mathbb{N}$ by defining $T_{i,j}$ as the first time when $i, j$ are in the same partition element if the time is less than the finite time horizon $T$. Otherwise we set $T_{i,j}$ equal to $T$. Then we set

$$r'(i,j) = 2T_{i,j}; \quad i, j \in \mathbb{N}.$$  \hfill (5.10)

Furthermore we define on $\mathbb{N}^{[1,n]}$ the uniform distribution and extend this to all subsets which have a frequency. That way we obtain a sequence of ultrametric probability measure spaces $[(\mathcal{U}_n, r'_n, \mu_n)]$. These families of equivalence classes form a tight sequence under the law of the Kingman coalescent and we get a family of consistent laws. Therefore we have a state $[(\mathcal{U}', r', \mu')] \in \mathcal{U}_1$ on the completion of $(\mathbb{N}, r')$; see Section 4 in [OPW09]. We denote this random state as $\mathcal{C}_T$. 

We need next the operation of connecting two trees in a certain way which allows to use the fact that in the evolution of $\mathcal{U}_\text{fin}$-valued processes of the type $\hat{\mathfrak{U}}^\text{Fel}$, $\hat{\mathfrak{U}}^\text{FV}$ is special in the sense that the initial state only enters by the result of the evolution being glued onto it. This procedure connecting an ultrametric measure space $\hat{\mathfrak{U}}$ onto a given one $\hat{\mathfrak{U}}$, which corresponds to grafting $\hat{\mathfrak{U}}$ onto $\hat{\mathfrak{U}}$, we make precise next. Assume that $\hat{\mathfrak{U}}$ is the state of a process evolving for time $t$ of diameter $2t$ from $[(\mathcal{U},0,\mu)]$.

To build the glued object $[(\mathcal{U},r \perp \bar{r},\mu)] = [(\mathcal{U},r,\mu)] \perp [(\bar{U},\bar{r},\bar{\mu})]$ we proceed as follows. We represent the ultrametric measure space $\hat{\mathfrak{U}}$ by embedding it into a marked weighted $\mathbb{R}$-tree, such that the leaves represent $\text{supp}(\mu)$, compare [GPW13] with it the $\hat{\mathfrak{U}}$-state. Then we can define the ancestors of a leave $i$ at time $0$ denotes by $\text{anc}_t(i)$ as the point in the tree having distance $t$ to the leave. These ancestors we then associate with an element $\beta(i)$ in $U$ to obtain the new distance function. Then we want to extend the ancestral path of the $\mathbb{R}$-tree associated with $\hat{\mathfrak{U}}$ using the one of $\hat{\mathfrak{U}}$, to read off the distance $r \perp \bar{r}$ on $\hat{\mathfrak{U}}$. Let $(r \perp \bar{r})(x,x') = \bar{r}(x,x')$ if this value is less than $2t$ and define the distances $\geq 2t$ by $(r \perp \bar{r})(x,x') = r(\beta(\text{anc}_t(i)),\beta(\text{anc}_t(x')))$. How to define $\beta(\cdot)$?

We sample from $U$ according to $\mu$ points $x_1,x_2,\ldots$. Then we want to associate these elements with the $\bar{U}$ founding ancestors. How to match this with the at most countable set of all $\bar{U}$-ancestors? We can for any such ancestor execute for every element here a $\mu$-draw to match.

This works if the population has a dynamic where we can embed the $\mathbb{R}$-trees associated with the states in $\mathcal{U}$, all into each other. This is satisfied for the Fleming-Viot dynamics; see [Gri17].

**Theorem 5.2 (Strong duality).**

Let $(\mathfrak{U}_t^\text{FV})_{t \geq 0}$ be the $\mathbb{U}$-valued Fleming-Viot process. Then for every $T > 0$ we have

$$\mathcal{L}[\mathfrak{U}^\text{FV}_T] = \mathcal{L}[\mathfrak{U}_0 \perp \mathfrak{C}_{T}^\infty].$$

(5.11)

This representation allows to generate the complete state from the dual dynamic in form of the entrance law from a countably infinite population and the initial state. This is the proper generalization of the duality via graphical constructions into our context, which has played an important role for individual based models.

A similar result holds for the $\mathcal{U}_\text{fin}$-valued Feller diffusion. However here is an additional subtlety which we discuss next since this is only a conditional representation of the genealogy $\mathfrak{U}$ given the path of total masses.

**Conditioned dualities**

For many models the evolution of the total masses is again a Markov process evolving autonomously, since the evolution does not depend explicitly on the genealogy. In models with varying population sizes it is therefore often possible to condition on the complete path $(\mathfrak{U}_t)_{t\geq 0}$ and to then obtain for the conditioned law of the genealogy part $(\hat{\mathfrak{U}}_t)_{t\geq 0}$ a dual process, for every realization of the total mass process.

This is the case for the $\mathcal{U}_\text{fin}$-valued Feller diffusion (which solves uniquely the $(\Omega^\text{grow} + \Omega^\text{res},\Pi)$-martingale problem), where one obtains as a dual process the coalescent introduced above but where the coalescence rate $b$ is replaced by a time-dependent one, namely

$$b \cdot (\hat{\mathfrak{U}}_t)^{-1}, \text{ resp. } 0 \text{ if } \hat{\mathfrak{U}}_t = 0,$$

(5.12)

which also identifies the conditioned genealogy process as a time-inhomogeneous Fleming-Viot diffusion; see [GD12], [DG18]. In other words besides the Feynman-Kac duality we also have a conditioned duality. This means we can now get the following analogue of (5.11).

**Corollary 5.2.** (Conditioned strong duality: Feller)

Consider the $\mathcal{U}_\text{fin}$-valued Feller diffusion $\hat{\mathfrak{U}}^\text{Fel}$ and write $\hat{\mathfrak{U}}^\text{F} = (\hat{\mathfrak{U}}^\text{Fel},\hat{\mathfrak{U}}^\text{FV})$, then

$$\mathcal{L}\left[\hat{\mathfrak{U}}^\text{Fel}_T \mid (\mathfrak{U}^\text{FV}_t)_{t \geq 0} = \bar{u}\right] = \mathcal{L}\left[\hat{\mathfrak{U}}^\text{Fel}_0 \perp \mathfrak{C}_{T}^\infty(\bar{u})\right].$$

(5.13)

This says in particular that the process $\hat{\mathfrak{U}}$-conditioned on the process $\hat{\mathfrak{U}}$ is a time-inhomogeneous $\mathcal{U}$-valued Fleming-Viot process, so that we can obtain that the path properties of this process carry over to the Feller cases as for example that the states are non-atomic, or that we have a mark function if we consider multitype models, see Section 5.2 for these properties.
5.2 Girsanov transformation

The Girsanov transformation allows us to obtain certain evolutions of marked genealogies from some basic processes, Fleming-Viot models with selection, mutation and resampling from those with mutation and resampling alone being the most important example. In that case one can obtain the model with selection via Girsanov transform from the one with only resampling and mutation as we shall explain below.

If the geographic space in our population models is finite or if we even have a non-spatial model, certain of our evolutions have the property that an additional drift term in the generator as migration, selection, mutation or sub- and supercriticality terms in branching models have the property that they have a density w.r.t. the process without this terms on laws in path space over some finite time interval. In that case one can also often obtain this density explicitly with an appropriate Girsanov formula. This we explain next.

We note that on infinite geographic space this typically fails and one can obtain the path law only as limit of a sequence of approximate processes on suitable finite geographic spaces where the above reasoning then can be applied. Next we explain this for the $\mathbb{U}^1$-valued Fleming-Viot process.

We consider as basic process the $\mathbb{U}^1$-valued Fleming-Viot diffusion with mutation. Then we consider the case with selection with fitness function $\alpha \Psi$ where $\alpha \in \mathbb{R}^+$. We denote the respective processes by $U_{FV, mut,0}$ and $U_{FV, mut,\alpha \Psi}$.

For the Girsanov transform we need some ingredients. Based on the fitness function $\chi'$ consider

$$\Psi(U) = \frac{\alpha}{\gamma}(\mathcal{M}, \chi_{1,2})$$

where $\chi'_{k,\ell}(u, \nu) = \chi'_{k}(u_k, u_{\ell}, r_{k,\ell}, r_{\ell,k})$. (5.14)

Define $\mathcal{M} = (M_t)_{t \geq 0}$ where

$$M_t = \Psi(U_t) - \Psi(U_0) - \int_0^t \Omega_s \Psi(U_s) \, ds, \quad t \geq 0.$$ (5.15)

Denoting by $[\cdot]$ the quadratic variation of a semimartingale we have the following result. Its proof is a combination of Theorem 2 and equation (3.38) in [DGPI2].

**Theorem 5.3** (Absolute continuity and Girsanov transform).

(a) The law $\mathcal{L}[U_{t \in [0,T]}]$ and $\mathcal{L}[U_{t \in [0,T], \alpha \Psi}]$ are equivalent for $\alpha \geq 0$, for $T > 0$.

(b) The Radon-Nikodym derivative is given by

$$\frac{dQ^\alpha_T}{dP_T}(U) = e^{M_T - \frac{1}{2}[\mathcal{M}]_T},$$ (5.16)

where the quadratic variation of $\mathcal{M}$ is given by the formula:

$$[\mathcal{M}]_t = \frac{\alpha^2}{\gamma} \int_0^t \text{Var}_{\nu_s} [\chi'] \, ds,$$ (5.17)

where we write $\nu_s = \nu^U$ and $\text{Var}_{\nu_s} [\cdot]$ denotes variance w.r.t. measure $\nu_s$.

**Remark 5.2** (First and second order operators). The key point here is that the resampling operator is a second order operator whereas all other operators are first order operators; cf. Section 4 in [DGPI2]. This allows to use here some abstract theory on such operators due to Bakry and Émery; see [BE85].

The Girsanov representation has two mayor applications:

- reducing the well-posedness of the processes with selection to the one of the basic process,
- transferring path properties of the basic process to the one with selection.

For example the following path properties can be proven for the Fleming-Viot processes with selection by using the equivalence of laws with the neutral case, which is simpler to analyze (see [DGPI2], [DGPI3] for the results below):

\[ \]
• Continuity of paths.
• The asymptotics of the number of ancestors time $\varepsilon$ back from the present time $t$ is $2/\varepsilon$ as $\varepsilon \downarrow 0$.
• The non-atomicity of the states of the process for positive times, i.e., the fact that with probability one for $t > 0$ the sampling measure projected on $U$ has no atoms.
• The Fleming-Viot process with selection has a mark function for $t > 0$ if this holds for $t = 0$, i.e., the sampling measure on $U \times \mathbb{I}$ can be written as $\mu_t(dx, dv) = \mu_t^U(dx)\delta_{\kappa_t(x)}(dv)$ for a measurable $\kappa : U \to \mathbb{I}$, which is known for the neutral process; see [KL15].

This technique is also of use trying to handle models with recombination and selections, since it is possible to focus first on building recombination into the neutral model and then add selection, see [DCPT18].

6 Compactness and tightness of marked genealogies

We discuss here two points namely what are compact sets in the spaces $\mathbb{U}_1$, $\mathbb{U}_\text{fin}$ and their marked versions and how to formulate tightness criteria for probability measures on this spaces, respectively processes with values in these spaces.

(i) Most basic is the criterion for compactness of a set $K$ in $\mathbb{U}_1$ where one needs for $U = [(U, r, \mu)] \in K$:

• bounded distances,
• a no dust condition.

The first requires that pairwise distances in a set are bounded, i.e.

$$R(U) := \text{ess sup}_{\mu \otimes \mu} \{r(i, i')\} \leq M, \quad \forall i, i' \in U, \text{ for all } U \in K,$$ (6.1)

while the second guarantees that the number $N_\varepsilon(U)$ of $\varepsilon$-balls needed such that the sampling measure of the subset of $U$ covered by the union of the balls exceeds $(1 - \varepsilon)$ is bounded for all $U \in K$ and all $\varepsilon > 0$. Note that $N_\varepsilon(U)$ can be viewed as the number of ancestors of an $(1 - \varepsilon)$-fraction of the population.

In $\mathbb{U}_\text{fin}$ we need in addition to the above properties that the total masses are bounded, i.e. for some $M < \infty$:

$$M(U) = \bar{\mu} \leq M, \quad \forall U = [U, r, \mu] \in K,$$ (6.2)

If we want to extend this to $\mathbb{U}_\text{fin}^\text{V}$ the key point is that we need for a set $K \subseteq \mathbb{U}_\text{fin}^\text{V}$ to be compact that the projections on $\mathbb{U}_\text{fin}$ and on $M_\text{fin}(\text{V})$ are compact, the latter in the weak topology. (On $\mathbb{U}_\text{fin}^\text{V}$ one applies this to the localizations again to get the same picture.)

(ii) Next we pass to random variables with values in $\mathbb{U}_1$, $\mathbb{U}_\text{fin}$ and their marked versions, as well as the laws of the random variables. For tightness of a set of $\mathbb{R} \subseteq M_1(\mathbb{U})$ of laws we need that

$$\{L_\Gamma[(R(U), N_\varepsilon(U), M(U))], \Gamma \in \mathbb{R}\}$$ (6.3)

is for all $\varepsilon > 0$ tight in $M_1([0, \infty)^3)$.

(iii) The key task is now to pass to stochastic processes and to obtain the tightness of laws on sets of path of stochastic processes from the above facts. This requires to get “uniformly in time” by representing the process by graphical constructions, lookdown constructions or using special analytic information, on the operator of the martingale problem. Here one uses typically more about the ancestral structure and its evolution in time. Compare for example [GPW13, GSW16, Gri17, GKW18].
7 Perspectives

In this section we describe some current development in this area, in particular we describe some questions where the concepts introduced so far need to be further refined and generalized.

(1) The branching world

One issue is to study the branching world in more detail, from classical branching to logistic branching.

(i) The first point is to establish some important properties of the $U_{\text{fin}}$-valued processes of the branching type, as the $U_{\text{fin}}$-valued version of the branching property, a generalized version of the concept of infinite divisibility and a corresponding Lévy-Khintchine formula and to then use this to obtain more specifics of the longtime behavior and structure of populations. This point is pursued in [GGR17] and now in [GRG18], [DG18].

We introduce the subsets of $U_{\text{fin}}$ denoted

$$U_{\text{fin}}(h) \text{ and } U_{\text{fin}}(h)^{\downarrow}$$

as the elements with essential diameter $< 2h$ respectively $\leq 2h$ for $h > 0$.

The basic concept which is needed here is that of the $h$-tree tops of $U = [(U, r, \mu)]$, denoted $U(h)$ for $h > 0$. Namely consider for $(U, r)$ now $(U, r \wedge 2h)$ and restrict $\mu$ to the corresponding $\sigma$-algebra to obtain the $h$-tree top

$$U(h) \in U_{\text{fin}}(h)^{\downarrow}.$$  

We can then consider the $h$-concatenation as binary operation in $U_{\text{fin}}(h)^{\downarrow}$:

$$[(U_1, r_1, \mu_1)] \sqcup [(U_2, r_2, \mu_2)] = [(U_1 \sqcup U_2, r_1 \oplus r_2, \tilde{\mu}_1 + \tilde{\mu}_2)],$$

where

$$r_1 \oplus r_2(i_1, i_2) = \begin{cases} r_1(i_1, i_2) & \text{if } i_1, i_2 \in U_1, \\ r_2(i_1, i_2) & \text{if } i_1, i_2 \in U_2, \\ 2h & \text{if } i_1 \in U_1, i_2 \in U_2. \end{cases}$$

This operation defines for each $h > 0$ a

$$\text{topological semigroup } (U_{\text{fin}}(h)^{\downarrow}, \sqcup^h).$$

In particular we can associate with $U_{\text{fin}}$ the collection of semigroups $\{ (U_{\text{fin}}(h)^{\downarrow}, \sqcup^h), h > 0 \}$ and the collection $\{ T_h, h > 0 \}$ of truncation maps

$$T_h : U \to U_{\text{fin}}(h)^{\downarrow}, U \mapsto U(h).$$

One has acting on the semigroup in (7.5) the property that

$$T_{h'}(u \sqcup^h v) = T_{h'}(u) \sqcup^h T_{h'}(v) \text{ (consistency)},$$

for all $h' \in [0, h], h > 0, u, v \in U_{\text{fin}}(h)^{\downarrow}$.

Therefore we associate with $U_{\text{fin}}$ the pair of collections of topological semigroups and truncation maps:

$$\{ (U_{\text{fin}}(h)^{\downarrow}, \sqcup^h), h > 0 \}, \{ T_h; h > 0 \}.$$  

With these concepts one can generalize the branching property of an $U_{\text{fin}}$-valued process. We can define infinite divisibility for $U_{\text{fin}}$-valued random variables and prove a Lévy-Khintchine representation in terms of concatenations of Cox point processes on $U_{\text{fin}}(h)^{\downarrow}$ for all $h > 0$.

An $U_{\text{fin}}$-valued random variable $\mathcal{M}$ is $t$-infinitely divisible if for every $n \in \mathbb{N}$ and $h \in [0, t]$:

$$\mathcal{M}(h) \overset{(d)}{=} \mathcal{M}(h, 1) \sqcup^h \cdots \sqcup^h \mathcal{M}(h, n)$$

for i.i.d. $(U^{(h,i)})_{i=1,\ldots,n}$ with values in $U_{\text{fin}}(h)^{\downarrow}$. 
Then the Lévy-Khintchine formula on $\mathbb{U}_{fin}$ reads as follows. The formula represents the expectation of certain exponentials via the Lévy measure. We need the following ingredients.

We define the Laplace-transform of the random variable $\Upsilon$:

$$L_{\Upsilon}(\Phi^n,\phi) = \mathbb{E}\left[\exp\left(-\Phi^n,\phi(\Upsilon)\right)\right],$$

for a positive polynomial $\Phi^n,\phi$. We also need the $h$-truncated polynomial

$$\Phi^n_h,\phi = \Phi^n,\phi_h, \quad \phi_h(r) = \phi(r \wedge 2h).$$

Then the Lévy-Khintchine formula for an infinitely divisible random variable $\Upsilon$ says that there exists a unique Lévy measure $\lambda_\infty \in \mathcal{M}^\#(\mathbb{U}^\prime \setminus \{0\})$ with $\int (\bar{u} \wedge 1) \lambda_\infty(du) < \infty$ such that for all $h > 0 (h \in (0,t]$ for $t$-inf.div.):

$$- \log L_{\Upsilon}(\Phi_h) = \int_{\mathbb{U}^\prime \setminus \{0\}} (1 - e^{-\Phi_h(u)})\lambda_h(du),$$

where

$$\lambda_h(du) = \int_{\mathbb{U}^\prime \setminus \{0\}} \lambda_\infty(du)1(v(h) \in du) \in \mathcal{M}^\#(\mathbb{U}^\prime_{fin}(h)^{\prime \prime} \setminus \{0\}).$$

This allows to write the $h$-tops of $\Upsilon$ as follows:

$$\Upsilon(h) = \bigsqcup_{u \in N^{\lambda_h}} u,$$

where $N^{\lambda_h}$ is a Poisson point process on $\mathcal{M}^\#(\mathbb{U}^\prime \setminus \{0\})$ with intensity measure $\lambda_h$.

The marginals of the $\mathbb{U}^\prime_{fin}$-valued Feller diffusion are infinitely divisible if we start in an infinitely divisible initial law, see so that we can ask for the Lévy measure for $\Upsilon$ and its properties. This is carried out in [DG18].

Furthermore can we ask for the laws conditioned to survive forever or the size-biased law. These questions are studied in detail in [CGR17, GGR18] and [DG18].

(ii) Another direction here is to consider the analog of selection for branching type processes where a total mass dependent sub-/supercriticality in the branching rate occurs which reflects the carrying capacity $K$ of the environment where a population lives, introducing supercriticality for states where the total population size is below $K$ and subcriticality if it is above $K$. This is studied in [GMR18], where the $\mathbb{U}^\prime_{fin}$-valued spatial logistic Feller branching diffusion is constructed and where the longtime behavior is studied via the conditioned duality. The goal is to understand the changes in the genealogy induced by the competition for resources.

(2) Tree-valued processes with recombination From the point of view of classical population genetics a natural step in generalizing the tree-valued processes with mutation migration and selection is to also include recombination. The resulting process then would involve all the important evolutionary forces. To this end we need to extend the notion of (marked) ultra-metric measure spaces appropriately to incorporate multi-locus genealogies. This is work in progress, [DCPT18].

To better understand some of the difficulties that arise in the case with recombination, let us consider a processes without mutation, selection and migration and assume that the set of loci is given by a finite set $\mathbb{L}$. (All the forces that we exclude here for the sake of simplicity can be included and it is also possible to consider infinitely countable sets of loci.)

In presence of recombination with a finite set of loci $\mathbb{L}$ the genealogical distance of individuals along different loci might be different. The genealogies along all loci together can be encoded by a multi-ultra-metric space $(\mathbb{U}, (r_i)^{\mathbb{L} \times \mathbb{L}})$. In the single locus case the sampling measure $\mu$ was a measure on the Borel-$\sigma$-algebra on $\mathbb{U}$ induced by the corresponding metric. In the multi-locus case the set of individuals is still given by $\mathbb{U}$ but the sampling measure should be somehow connected to the whole set of metrics $(r_i)^{\mathbb{L}}$. As the domain for the sampling measures we choose the Borel-$\sigma$-algebra on $\mathbb{U}^{\mathbb{L}}$ generated by the product measure induced by $(r_i)^{\mathbb{L}}$ and we require that the sampling measures are concentrated on the diagonal of $\mathbb{U}^{\mathbb{L}}$. 


One can then introduce a concept of equivalence of such spaces and pass to the set of equivalence classes. Furthermore one can introduce a generalization of polynomials, distance matrix distributions and a generalized notion of Gromov-weak convergence. The corresponding topology can again be generated by a suitable Gromov-Prohorov metric generating a Polish state space for multi-loci-genealogies.

Finally, the tree-valued processes with recombination can be obtained as solutions to martingale problems.

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References

[Ald91a] David Aldous. The continuum random tree. I. *Ann. Probab.*, 19(1):1–28, 1991.

[Ald91b] David Aldous. The continuum random tree. II. An overview. In *Stochastic analysis (Durham, 1990)*, volume 167 of *London Math. Soc. Lecture Note Ser.*, pages 23–70. Cambridge Univ. Press, Cambridge, 1991.

[Ald93] David Aldous. The continuum random tree. III. *Ann. Probab.*, 21(1):248–289, 1993.

[ALW16] Siva Athreya, Wolfgang Löhr, and Anita Winter. The gap between Gromov-vague and Gromov-Hausdorff-vague topology. *Stochastic Process. Appl.*, 126(9):2527–2553, 2016.

[ALW17] Siva Athreya, Wolfgang Löhr, and Anita Winter. State spaces of (continuum) trees: R-trees versus algebraic trees, 2017. In preparation. Talk by W. Löhr at Workshop: Genealogies of Interacting Particle Systems, 07 Aug 2017, IMS Singapore.

[AN72] Krishna B. Athreya and Peter E. Ney. *Branching processes*. Springer-Verlag, New York-Heidelberg, 1972. Die Grundlehren der mathematischen Wissenschaften, Band 196.

[Arr81] Richard Alejandro Arratia. Coalescing Brownian motions and the voter model on Z. Unpublished partial manuscript, 1981.

[BÉ85] Dominique Bakry and Michel Émery. Diffusions hypercontractives. In *Séminaire de probabilités, XIX, 1983/84*, volume 1123 of *Lecture Notes in Math.*, pages 177–206. Springer, Berlin, 1985.

[BLG00] Jean Bertoin and Jean-François Le Gall. The Bolthausen-Sznitman coalescent and the genealogy of continuous-state branching processes. *Probab. Theory Related Fields*, 117(2):249–266, 2000.

[BLG03] Jean Bertoin and Jean-François Le Gall. Stochastic flows associated to coalescent processes. *Probab. Theory Related Fields*, 126(2):261–288, 2003.

[BLG05] Jean Bertoin and Jean-François Le Gall. Stochastic flows associated to coalescent processes. II. Stochastic differential equations. *Ann. Inst. H. Poincaré Probab. Statist.*, 41(3):307–333, 2005.

[CG86] J. Theodore Cox and David Griffeath. Diffusive clustering in the two-dimensional voter model. *Ann. Probab.*, 14(2):347–370, 1986.

[Daw93] Donald A. Dawson. Measure-valued Markov processes. In *École d’Été de Probabilités de Saint-Flour XXI—1991*, volume 1541 of *Lecture Notes in Math.*, pages 1–260. Springer, Berlin, 1993.
REFERENCES

[DG93] Donald A. Dawson and Andreas Greven. Hierarchical models of interacting diffusions: multiple time scale phenomena, phase transition and pattern of cluster-formation. *Probab. Theory Related Fields*, 96(4):435–473, 1993.

[DG14] Donald A. Dawson and Andreas Greven. *Spatial Fleming-Viot models with selection and mutation*, volume 2092 of *Lecture Notes in Mathematics*. Springer, Cham, 2014.

[DG18] Andrej Depperschmidt and Andreas Greven. Tree-valued Feller diffusion. in preparation, 2018.

[DGP11] Andrej Depperschmidt, Andreas Greven, and Peter Pfaffelhuber. Marked metric measure spaces. *Electron. Commun. Probab.*, 16:174–188, 2011.

[DGP12] Andrej Depperschmidt, Andreas Greven, and Peter Pfaffelhuber. Tree-valued Fleming-Viot dynamics with mutation and selection. *Ann. Appl. Probab.*, 22(6):2560–2615, 2012.

[DGP13] Andrej Depperschmidt, Andreas Greven, and Peter Pfaffelhuber. Path-properties of the tree-valued Fleming-Viot process. *Electron. J. Probab.*, 18(84):1–47, 2013.

[DGP18] Andrej Depperschmidt, Andreas Greven, and Peter Pfaffelhuber. Evolving genealogies of Fleming-Viot processes with recombination. in preparation, 2018.

[DGV95] Donald A. Dawson, Andreas Greven, and Jean Vaillancourt. Equilibria and quasi-equilibria for infinite collections of interacting Fleming-Viot processes. *Trans. Amer. Math. Soc.*, 347(7):2277–2360, 1995.

[DK99a] Peter Donnelly and Thomas G. Kurtz. Genealogical processes for Fleming-Viot models with selection and recombination. *Ann. Appl. Probab.*, 9(4):1091–1148, 1999.

[DK99b] Peter Donnelly and Thomas G. Kurtz. Particle representations for measure-valued population models. *Ann. Probab.*, 27(1):166–205, 1999.

[DL12] Donald A. Dawson and Zenghu Li. Stochastic equations, flows and measure-valued processes. *Ann. Probab.*, 40(2):813–857, 2012.

[DP91] Donald A. Dawson and Edwin A. Perkins. Historical processes. *Mem. Amer. Math. Soc.*, 93(454):iv+179, 1991.

[Dur88] Richard Durrett. *Lecture notes on particle systems and percolation*. The Wadsworth & Brooks/Cole Statistics/Probability Series. Wadsworth & Brooks/Cole Advanced Books & Software, Pacific Grove, CA, 1988.

[EK86] Stewart N. Ethier and Thomas G. Kurtz. *Markov processes: Characterization and convergence*. Wiley Series in Probability and Mathematical Statistics: Probability and Mathematical Statistics. John Wiley & Sons Inc., New York, 1986.

[EK98] Stewart N. Ethier and Thomas G. Kurtz. Coupling and ergodic theorems for Fleming-Viot processes. *Ann. Probab.*, 26(2):533–561, 1998.

[EM17] Steven N. Evans and Ilya Molchanov. The semigroup of metric measure spaces and its infinitely divisible probability measures. *Trans. Amer. Math. Soc.*, 369(3):1797–1834, 2017.

[Eva00] Steven N. Evans. Kingman’s coalescent as a random metric space. In *Stochastic models (Ottawa, ON, 1998)*, volume 26 of *CMS Conf. Proc.*, pages 105–114. Amer. Math. Soc., Providence, RI, 2000.

[FG94] Klaus Fleischmann and Andreas Greven. Diffusive clustering in an infinite system of hierarchically interacting diffusions. *Probab. Theory Related Fields*, 98(4):517–566, 1994.

[FINR04] Luiz Renato G. Fontes, Marco Isopi, Charles M. Newman, and Krishnamurthi Ravishankar. The Brownian web: characterization and convergence. *Ann. Probab.*, 32(4):2857–2883, 2004.
REFERENCES

[1] Clément Foucart. Generalized Fleming-Viot processes with immigration via stochastic flows of partitions. *ALEA Lat. Am. J. Probab. Math. Stat.*, 9(2):451–472, 2012.

[2] Andreas Greven, Patric K. Glöde, and Thomas Rippl. Branching trees I: Concatenation and infinite divisibility. *ArXiv 1612.01265*, submitted June 2017. [http://arxiv.org/abs/1612.01265](http://arxiv.org/abs/1612.01265)

[3] Andreas Greven, Anton Klimovsky, and Anita Winter. Evolving genealogies of spatial Λ-Cannings processes with mutation. In preparation, 2018.

[4] Patric K. Glöde. *Dynamics of genealogical trees for autocatalytic branching processes*. PhD thesis, Department Mathematik, Erlangen, Germany, 2012. [http://nbn-resolving.de/urn:nbn:de:bvb:29-opus-45453](http://nbn-resolving.de/urn:nbn:de:bvb:29-opus-45453)

[5] Andreas Greven, Vladica Limic, and Anita Winter. Representation theorems for interacting Moran models, interacting Fisher-Wright diffusions and applications. *Electron. J. Probab.*, 10:no. 39, 1286–1356, 2005.

[6] Andreas Greven and Chiranjib Mukherjee. Genealogies of spatial logistic branching models. In preparation, 2018.

[7] Andreas Greven, Peter Pfaffelhuber, and Anita Winter. Convergence in distribution of random metric measure spaces (Λ-coalescent measure trees). *Probab. Theory Related Fields*, 145(1-2):285–322, 2009.

[8] Andreas Greven, Peter Pfaffelhuber, and Anita Winter. Tree-valued resampling dynamics Martingale problems and applications. *Probab. Theory Related Fields*, 155(3-4):789–838, 2013.

[9] Andreas Greven, Thomas Rippl, and Patric K. Glöde. Branching processes — a general concept. In preparation, 2018.

[10] Max Grieshammer. *Measure Representations of Genealogical Processes and Applications to Fleming-Viot Models*. PhD thesis, Department Mathematik, Erlangen, Germany, 2017. [http://nbn-resolving.de/urn:nbn:de:bvb:29-opus4-85653](http://nbn-resolving.de/urn:nbn:de:bvb:29-opus4-85653)

[11] Andreas Greven, Rongfeng Sun, and Anita Winter. The evolving genealogy of fossils: Unique characterization by martingale problems and applications. In preparation 2018.

[12] Andreas Greven, Rongfeng Sun, and Anita Winter. Continuum space limit of the genealogies of interacting Fleming-Viot processes on Z. *Electron. J. Probab.*, 21:Paper No. 58, 64, 2016.

[13] Stephan Gufler. Pathwise construction of tree-valued Fleming-Viot processes. *Electron. J. Probab.*, 23:Paper No. 42, 58, 2018.

[14] Sandra Kliem and Wolfgang Löhr. Existence of mark functions in marked metric measure spaces. *Electron. J. Probab.*, 20:no. 73, 24, 2015.

[15] Achim Klenke. Different clustering regimes in systems of hierarchically interacting diffusions. *Ann. Probab.*, 24(2):660–697, 1996.

[16] Achim Klenke. Multiple scale analysis of clusters in spatial branching models. *Ann. Probab.*, 25(4):1670–1711, 1997.

[17] Sandra Kliem and Anita Winter. Evolving phylogenies of trait-dependent branching with mutation and competition, part I: Existence. *Stochastic Process. Appl.*, 2018.

[18] Cyril Labbé. From flows of Λ-Fleming-Viot processes to lookdown processes via flows of partitions. *Electron. J. Probab.*, 19:no. 55, 49, 2014.

[19] Jean-François Le Gall. Marches aléatoires, mouvement brownien et processus de branchement. In *Séminaire de Probabilités, XXIII*, volume 1372 of *Lecture Notes in Math.*, pages 258–274. Springer, Berlin, 1989.
[LG93] Jean-François Le Gall. The uniform random tree in a Brownian excursion. *Probab. Theory Related Fields*, 96(3):369–383, 1993.

[LG99] Jean-François Le Gall. *Spatial branching processes, random snakes and partial differential equations*. Lectures in Mathematics ETH Zürich. Birkhäuser Verlag, Basel, 1999.

[Lig85] Thomas M. Liggett. *Interacting particle systems*, volume 276 of *Grundlehren der Mathematischen Wissenschaften [Fundamental Principles of Mathematical Sciences]*. Springer-Verlag, New York, 1985.

[Löh13] Wolfgang Löhr. Equivalence of Gromov-Prohorov- and Gromov’s $\Box_\alpha$-metric on the space of metric measure spaces. *Electron. Commun. Probab.*, 18:no. 17, 10, 2013.

[LS81] Thomas M. Liggett and Frank Spitzer. Ergodic theorems for coupled random walks and other systems with locally interacting components. *Z. Wahrsch. Verw. Gebiete*, 56(4):443–468, 1981.

[LVW15] Wolfgang Löhr, Guillaume Voisin, and Anita Winter. Convergence of bi-measure $\mathbb{R}$-trees and the pruning process. *Ann. Inst. Henri Poincaré Probab. Stat.*, 51(4):1342–1368, 2015.

[NP89] Jacques Neveu and Jim Pitman. The branching process in a Brownian excursion. In *Séminaire de Probabilités, XXIII*, volume 1372 of *Lecture Notes in Math.*, pages 248–257. Springer, Berlin, 1989.

[NRS05] Charles M. Newman, Krishnamurthi Ravishankar, and Rongfeng Sun. Convergence of coalescing nonsimple random walks to the Brownian web. *Electron. J. Probab.*, 10:no. 2, 21–60, 2005.

[SSS17] Emmanuel Schertzer, Rongfeng Sun, and Jan M. Swart. The Brownian web, the Brownian net, and their universality. In *Advances in disordered systems, random processes and some applications*, pages 270–368. Cambridge Univ. Press, Cambridge, 2017.

[Win02] Anita Winter. Multiple scale analysis of spatial branching processes under the Palm distribution. *Electron. J. Probab.*, 7:No. 13, 72, 2002.