TREE-VALUED RESAMPLING DYNAMICS
(MARTINGALE PROBLEMS AND APPLICATIONS)

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The measure-valued Fleming-Viot process is a diffusion which models the evolution of allele frequencies in a multi-type population. In the neutral setting the Kingman coalescent is known to generate the genealogies of the “individuals” in the population at a fixed time. The goal of the present paper is to replace this static point of view on the genealogies by an analysis of the evolution of genealogies.

Ultra-metric spaces extend the class of discrete trees with edge length by allowing behavior such as infinitesimal short edges. We encode genealogies of the population at fixed times as elements in the space of (isometry classes of) ultra-metric measure spaces. The additional probability measure on the ultra-metric space allows to sample from the population. We equip this state space by the Gromov-weak topology and use well-posed martingale problems to construct tree-valued resampling dynamics for both the finite population (tree-valued Moran dynamics) and the infinite population (tree-valued Fleming-Viot dynamics).

As an application we study the evolution of the distribution of the lengths of the sub-trees spanned by sequentially sampled “individuals”. We show that ultra-metric measure spaces are uniquely determined by the distribution of the infinite vector of the subsequently evaluated lengths of sub-trees.

1. Introduction. In the present paper we construct and study the evolution of the genealogical structure of the neutral multi-type population model called the Fleming-Viot process ([FV78, FV79, Daw93, EK93, DGV95, Eth01]). This process arises as the large population limit of Moran models. The Moran model (MM) can be described as follows: consider a
population of fixed size with finitely many individuals which carry (genetic) types. Each pair resamples at constant rate. Resampling of a pair means that the pair dies and is replaced by two new individuals which are considered as the offspring of one of the randomly chosen individuals.

In stochastic population models genealogical trees are frequently used. This applies to both branching and resampling models. In branching models, genealogical trees arise, for example, as the Kallenberg tree and the Yule tree ([Kal77] [EO94]). More examples include continuum (mass) limits in branching models as the Brownian continuum random tree (CRT) or the Brownian snake ([Ald91] [LG99]). More general branching mechanisms lead to more general genealogies such as Levy trees ([DLG02]) which are the infinite variance offspring distribution counterpart of the Brownian CRTs or trees arising in catalytic branching systems ([GPW09b]), to name just a few. In resampling models, which are used for populations with a fixed size (or total mass), genealogical trees can be generated by coalescent processes. A moment duality leads to the connection of the Fleming-Viot process to the Kingman coalescent tree ([Kin82a] [Ald93] [Eva00] [GLW05]). More general Fleming-Viot processes which allow for an infinite offspring variance are studied in [BG03]. Their genealogical relationships are described by Λ-coalescents ([Pit99] [GPW09a]).

Notice that coalescent trees describe the genealogy of a population at a fixed time and give therefore a static picture only. The main goal of the present paper is to construct a dynamic picture. That is, we obtain the tree-valued Moran dynamics and the tree-valued Fleming-Viot dynamics modeling the evolution of genealogies (in forward time). We use techniques from the theory of martingale problems.

In the construction of the tree-valued resampling dynamics we stick to the simplest case of a neutral population model, i.e., neither mutation, nor selection and recombination are built into the model. Due to discreteness, the tree-valued Moran dynamics can be constructed by standard theory on piece-wise deterministic jump processes. However, the construction of the tree-valued Fleming-Viot dynamics requires more thought.

For coding genealogical trees and defining convergence, we will rely on the fact that genealogical distances between individuals define a metric. Note that genealogical distances between individuals which belong to the population at a fixed time satisfy the ultra-metricity property (see also [BK06] [MPV87] for the connection of ultra-metric spaces and tree-like structures in spin-glass theory). To take the individuals’ contribution to the population into account we further equip the resulting ultra-metric space with a probability measure. We then follow the theory of (ultra-)metric measure
spaces equipped with the Gromov-weak topology as developed in [GPW09a]. Convergence in the Gromov-weak topology means convergence of all finite sub-spaces sampled with respect to the corresponding probability measures. The space of ultra-metric measure trees complements the space of real trees (see [Dre84, DMT96, Ter97] and Remark 2.2) equipped with the Gromov-Hausdorff topology ([Gro99, BBI01]). Evolving genealogies in exchangeable population models - including the models under consideration - have been described by look-down processes ([DK96, DK99b, DK99a]). Look-down processes contain all information available in the model. In particular, they contain - though in an implicit way - all information about the trees. Since the crucial point in the construction of look-down processes is the use of labels as coordinates, they encode information which is often not needed. A first approach in the direction of a coordinate-free description has been already taken in spatial settings via historical processes in the context of branching ([DP91]) and resampling models ([GLW05]).

Markov dynamics with values in the space of “infinite” or continuum trees have been constructed only recently. These include excursion path valued Markov processes with continuous sample paths - which can therefore be thought of as tree-valued diffusions - as investigated in [Zam01, Zam02, Zam03], and dynamics working with real-trees, for example, the so-called root growth with re-grafting ([EPW06]), the so-called subtree prune and re-graft move ([EW06]) and the limit random mapping ([EL08]). While the RGRG have a projective property allowing for an explicit construction of the Feller semi-group as the limit semi-group of “finite” tree-valued dynamics arising in an algorithm for constructing uniform spanning trees, the SPR and the limit random mapping were constructed as candidates of the limit of “finite” tree-valued dynamics using Dirichlet forms. Unfortunately, Dirichlet forms are often inadequate for proving convergence theorems. Hence in order to be able to show that indeed the tree-valued Moran dynamics converge to the tree-valued Fleming-Viot dynamics, we use the characterization of the tree-valued dynamics as solutions of well-posed martingale problems. This is the first example in the literature where tree-valued Markov dynamics constructed as the solution of a well-posed martingale problem.

An important consequence of the construction of the tree-valued resampling dynamics as solutions of well-posed martingale problems is that it allows to study the evolution of continuous functionals of these processes and characterize which functionals form strong Markov processes. As an example we describe the evolution of the distribution of tree-lengths of subtrees spanned by subsequentially sampled “individuals”. With the depth of the tree another related interesting functional has been studied earlier in [PW06].
using the look-down construction of [DK99a]. Since the depth measures the
time to the most recent ancestor of all “individuals” of the population, it
is not continuous with respect to the Gromov-weak topology. It is shown in
[PW06] that the resulting process is not Markovian.

2. Main results (Theorems 1, 2 and 3). In this section we state our
main results. In Subsection 2.1 we recall concepts and terminology used to
define the state space which consists of (ultra-)metric measure spaces and
which we equip with the Gromov-weak topology. In Subsection 2.2 we state
the tree-valued Fleming-Viot martingale problem and its well-posedness,
and present the approximation by tree-valued particle dynamics in Subsec-
tion 2.3. In Subsection 2.4 we identify a unique equilibrium and state that
it will be approached as time tends to infinity. In Subsection 2.5 we discuss
possible extensions of the model.

2.1. State space: metric measure spaces. In [GPW09a] topological as-
pects of the space of metric measure spaces equipped with the Gromov-weak
topology are investigated. We will use this space as the state space for the
evolution of the genealogies of our models. In this subsection we recall basic
facts and notation.

As usual, given a topological space \((X, \mathcal{O})\) we denote by \(\mathcal{M}_1(X)\) \((\mathcal{M}_f(X))\)
the space of all probability (finite) measures, defined on the Borel-\(\sigma\)-algebra
of \(X\) and by \(\Rightarrow\) weak convergence in \(\mathcal{M}_1(X)\). Recall that the support of \(\mu\),
supp(\(\mu\)), is the smallest closed set \(X_0 \subseteq X\) such that \(\mu(X_0) = 1\). The push
forward of \(\mu\) under a measurable map \(\varphi\) from \(X\) into another metric space
\((Z, r_Z)\) is the probability measure \(\varphi_* \mu \in \mathcal{M}_1(Z)\) defined by
\[
\varphi_* \mu(A) := \mu(\varphi^{-1}(A)),
\]
for all Borel subsets \(A \subseteq X\). We denote by \(\mathcal{B}(X)\) and \(\mathcal{C}_b(X)\) the bounded real-valued functions on \(X\) which are measurable and continuous, respectively.

A metric measure space is a triple \((X, r, \mu)\) where \((X, r)\) is a metric space
such that \((\text{supp}(\mu), r)\) is complete and separable and \(\mu \in \mathcal{M}_1(X)\) is a proba-
bility measure on \((X, r)\). Two metric measure spaces \((X, r, \mu)\) and \((X', r', \mu')\)
are measure-preserving isometric or equivalent if there exists an isometry \(\varphi\)
between \(\text{supp}(\mu)\) and \(\text{supp}(\mu')\) such that \(\mu' = \varphi_* \mu\). It is clear that the prop-
erty of being measure-preserving isometric is an equivalence relation. We
write \((X, r, \mu)\) for the equivalence class of a metric measure space \((X, r, \mu)\).
Define the set of (equivalence classes of) metric measure spaces
\[
\mathbb{M} := \{ \chi = (X, r, \mu) : (X, r, \mu) \text{ metric measure space} \}.
\]
If \((X,r,\mu)\) is such that \(r\) is only a pseudo-metric on \(X\), (i.e. \(r(x,y) = 0\) is possible for \(x \neq y\)) we can still define its measure-preserving isometry class. Since this class contains also metric measure spaces, there is a bijection between the set of pseudo-metric measure spaces and the set of metric measure spaces and we will use both notions interchangeably.

We are typically only interested in functions of metric measure spaces that do not describe artifacts of the chosen representation, i.e., which are invariant under measure-preserving isometries. These are of a special form which we introduce next. For a metric space \((X,r)\) we define by

\[
R^{(X,r)} : \begin{cases} 
X^N 
\to \mathbb{R}_+^{(\mathbb{N})} 
\to (r(x_i,x_j))_{1 \leq i < j}
\end{cases}
\]

the map which sends a sequence of points in \(X\) to its (infinite) distance matrix, and denote, for a metric measure space \((X,r,\mu)\), the distance matrix distribution of \((X,r,\mu)\) by

\[
\nu^{(X,r,\mu)} := \left(R^{(X,r)} \right)_\ast \mu^\otimes N \in \mathcal{M}_1(\mathbb{R}_+^{(\mathbb{N})}).
\]

Obviously, \(\nu^{(X,r,\mu)}\) depends on \((X,r,\mu)\) only through its measure-preserving isometry class \(\chi = (X,r,\mu)\). We can therefore define:

**Definition 2.1 (Distance matrix distribution).** The distance matrix distribution \(\nu^\chi\) of \(\chi \in \mathbb{M}\) is the distance matrix distribution \(\nu^{(X,r,\mu)}\) of an arbitrary representative \((X,r,\mu) \in \chi\).

By Gromov’s reconstruction theorem metric measure spaces are uniquely determined by their distance matrix distribution (see Section 3.5 in [Gro99] and Proposition 2.6 in [GPW09a]). We therefore base our notion of convergence in \(\mathbb{M}\) on the convergence of distance matrix distributions. In [GPW09a] we introduced the Gromov-weak topology. In this topology a sequence \((\chi_n)_{n \in \mathbb{N}}\) in \(\mathbb{M}\) converges to \(\chi \in \mathbb{M}\) if and only if

\[
\nu^{\chi_n} \Rightarrow \nu^\chi \quad \text{as } n \to \infty
\]

in the weak topology on \(\mathcal{M}_1(\mathbb{R}_+^{(\mathbb{N})})\) (and, as usual, \(\mathbb{R}_+^{(\mathbb{N})}\) equipped with the product topology); compare Theorem 5 of [GPW09a]. Although \(\{\nu^\chi : \chi \in \mathbb{M}\} \subseteq \mathcal{M}_1(\mathbb{R}_+^{(\mathbb{N})})\) is not closed, we could show in Theorem 1 of [GPW09a] that \(\mathbb{M}\), equipped with the Gromov-weak topology, is Polish.
Several sub-spaces of $\mathcal{M}$ will be of special interest throughout the paper. Above all, these are the ultra-metric and compact metric measure spaces.

(The equivalence class of) a metric measure space $(X, r, \mu)$ is called ultra-metric iff

\begin{equation}
    r(u, w) \leq r(u, v) \vee r(v, w),
\end{equation}

for $\mu$-almost all $u, v, w \in X$. Define

\begin{equation}
    U := \{ u \in \mathcal{M} : u \text{ is ultra-metric} \}.
\end{equation}

\textbf{Remark 2.2 (Ultra-metric spaces are trees).} Notice that there is a close connection between ultra-metric spaces and $\mathbb{R}$-trees, i.e., complete path-connected metric spaces $(X, r_X)$ which satisfy the four-point condition

\begin{equation}
    r_X(x_1, x_2) + r_X(x_3, x_4) \\
    \leq \max \{ r_X(x_1, x_3) + r_X(x_2, x_4), r_X(x_1, x_4) + r_X(x_2, x_3) \},
\end{equation}

for all $x_1, x_2, x_3, x_4 \in X$ (see, for example, \cite{Dre84, DMT96, Ter97}). On the one hand, every complete ultra-metric space $(U, r_U)$ spans a path-connected complete metric space $(X, r_X)$ which satisfies the four point condition, such that $(U, r_U)$ is isometric to the set of leaves $X \setminus X^0$. On the other hand, given an $\mathbb{R}$-tree $(X, r_X)$ and a distinguished point $\rho \in X$ which is often referred to as the root of $(X, r_X)$, the level sets $X^t := \{ x \in X : r(\rho, x) = t \}$, for some $t \geq 0$, form ultra-metric sub-spaces of $(X, r_X)$.

Because of this connection between ultra-metric spaces and real trees, ultra-metric spaces are often (especially in phylogenetic analysis) referred to as \textit{ultra-metric trees}.

The next lemma implies that $U$ equipped with the Gromov-weak topology is again Polish.

\textbf{Lemma 2.3.} The sub-space $U \subset \mathcal{M}$ is closed.

\textbf{Proof.} Let $(u_n)_{n \in \mathbb{N}}$ be a sequence in $U$ and $\chi \in \mathcal{M}$ such that $u_n \to \chi$ in the Gromov-weak topology, as $n \to \infty$. Equivalently, by (2.5), $\nu^{u_n} \Rightarrow \nu^\chi$ in the weak topology on $\mathcal{M}_1(\mathbb{R}^+_0)$, as $n \to \infty$. Consider the open set

\begin{equation}
    A := \{(r_{i,j})_{1 \leq i < j} : r_{1,2} > r_{23} \vee r_{1,3} \text{ or } r_{2,3} > r_{1,2} \vee r_{1,3} \text{ or } r_{1,3} > r_{1,2} \vee r_{2,3} \}.
\end{equation}
By the Portmanteau Theorem, $\nu^x(A) \leq \liminf_{n \to \infty} \nu^{u_n}(A) = 0$. Thus, (2.6) holds for $\mu^\otimes 3$-all triples $(u,v,w) \in X^3$. In other words, $x$ is ultra-metric.

(The equivalence class of) a metric measure space $(X,r,\mu)$ is called compact if and only if the metric space $(\text{supp}(\mu),r)$ is compact. Define

$$M_c := \{x \in M : x \text{ is compact}\}.$$  

Moreover, we set

$$U_c := U \cap M_c.$$  

**Remark 2.4** $(M_c$ is not closed).  
(i) If $x = (X,r,\mu)$ is a finite metric measure space, i.e, $\#\text{supp}(\mu) < \infty$, then $x \in M_c$.  
(ii) Since elements of $M$ can be approximated by a sequence of finite metric measure spaces (see the proof of Proposition 5.3 in [GPW09a]), the sub-space $M_c$ is not closed. A similar argument shows that $U_c$ is not closed.  
(iii) In order to establish convergence within the space of compact metric measure spaces, we will provide a pre-compactness criterion in $M_c$ in Proposition 6.1.

2.2. **The martingale problem (Theorem 7).** In this subsection we define the tree-valued Fleming-Viot dynamics as the solution of a well-posed martingale problem. All proofs are given in Section 8. We start by recalling the terminology.

**Definition 2.5** (Martingale problem). Let $(E,\mathcal{O})$ be a metrizable space, $\mathbf{P}_0 \in \mathcal{M}_1(E)$, $\mathcal{F}$ a subspace of the space $\mathcal{B}(E)$ of bounded measurable functions on $E$ and $\Omega$ a linear operator on $\mathcal{B}(E)$ with domain $\mathcal{F}$.

The law $\mathbf{P}$ of an $E$-valued stochastic process $X = (X_t)_{t \geq 0}$ is called a solution of the $(\mathbf{P}_0,\Omega,\mathcal{F})$-martingale problem if $X_0$ has distribution $\mathbf{P}_0$, $X$ has paths in the space $\mathcal{D}_E([0,\infty))$ of $E$-valued cadlag functions from $[0,\infty)$ equipped with the Skorohod topology, almost surely, and for all $F \in \mathcal{F}$,

$$(2.12) \quad \left( F(X_t) - F(X_0) - \int_0^t ds \Omega F(X_s) \right)_{t \geq 0}$$  

is a $\mathbf{P}$-martingale with respect to the canonical filtration.

Moreover, the $(\mathbf{P}_0,\Omega,\mathcal{F})$-martingale problem is said to be well-posed if there is a unique solution $\mathbf{P}$. 

Recall that the classical measure-valued Fleming-Viot process \( \zeta = (\zeta_t)_{t \geq 0} \) is a probability measure-valued diffusion process, which describes the evolution of allelic frequencies. In particular, for a fixed time \( t \), the state \( \zeta_t \in \mathcal{M}_1(K) \) records the current distributions of allelic types on some (Polish) type space \( K \). This process is defined as the unique solution of the martingale problem corresponding to the following second order differential operator:

\[
\hat{\Omega}^1 F(\mu) = \frac{\gamma}{2} \int_K \int_K (\mu(du)\delta_u(dv) - \mu(dv)\mu(du)) \frac{\partial^2 F}{\partial \mu^2} [\delta_u, \delta_v],
\]

where for \( \mu' \in \mathcal{M}_f(K) \) and \( G : \mathcal{M}_f(K) \to \mathbb{R} \)

\[
\frac{\partial G(\mu)}{\partial \mu}[\mu'] := \lim_{\varepsilon \to 0} \frac{1}{\varepsilon} \left( G(\mu + \varepsilon \mu') - G(\mu) \right)
\]

and \( \frac{\partial^2 G(\mu)}{\partial \mu^2}[\mu', \mu''] := \frac{\partial}{\partial \mu} \left( \frac{\partial G(\mu)}{\partial \mu}[\mu'] \right)[\mu''], \) for \( \mu', \mu'' \in \mathcal{M}_f(K) \), whenever these limits exist (see, for example, [Daw93, p.13]).

For us more convenient is the following equivalent martingale problem (see [EK93]) which corresponds to the operator \( \hat{\Omega}^1 \) defined on functions \( \hat{\Phi} : \mathcal{M}_1(K) \to \mathbb{R} \) of the form

\[
\hat{\Phi}(\zeta) = \langle \zeta^N, \hat{\phi} \rangle := \int_{K^N} \zeta^N(du) \hat{\phi}(u)
\]

with \( u = (u_1, u_2, ...) \in K^N \) and \( \hat{\phi} \in \mathcal{C}_b(K^N) \) depending only on finitely many coordinates. On such functions (2.13) reads

\[
\hat{\Omega}^1 \hat{\Phi}(\zeta) = \frac{\gamma}{2} \sum_{k,l \geq 1} \left( \langle \zeta^N, \hat{\phi} \circ \hat{\theta}_{k,l} \rangle - \langle \zeta^N, \hat{\phi} \rangle \right),
\]

where the replacement operator \( \hat{\theta}_{k,l} \) is the map which replaces the \( l \)th component of an infinite sequence by the \( k \)th:

\[
\hat{\theta}_{k,l}(u_1, u_2, ..., u_{l-1}, u_l, u_{l+1}, ...) := (u_1, u_2, ..., u_{l-1}, u_k, u_{l+1}, ...).
\]

Here and in the following \( \gamma \in (0, \infty) \) is referred to as the resampling rate.

In order to state the martingale problem for the tree-valued Fleming-Viot process we need the notion of polynomials on \( \mathbb{M} \). 

**Definition 2.6 (Polynomials).** A function \( \Phi : \mathbb{M} \to \mathbb{R} \) is called a polynomial if there exists a bounded, measurable test function \( \phi : \mathbb{R}_+^{(N)} \to \mathbb{R} \), depending only on finitely many variables such that

\[
\Phi(\chi) = \langle \nu^\chi, \phi \rangle := \int_{\mathbb{R}_+^{(N)}} \nu^\chi(dr) \phi(r),
\]

\[ (2.18) \]

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where $r := (r_{i,j})_{1 \leq i < j}$.

**Remark 2.7** (Extension and degree of a polynomial). Let $\Phi$ and $\phi$ be as in Definition 2.6.

1. We extend the concept of polynomials to the case of positive, not necessarily bounded $\phi$. In this case, the right hand side of (2.18) can be infinite.
2. If $n \in \mathbb{N}$ is the minimal number such that there exists $\phi \in \mathcal{B}(\mathbb{R}_+^{(N)_2})$, depending only on $(r_{i,j})_{1 \leq i < j \leq n}$ such that (2.18) holds, $n$ is called the degree of $\Phi$ and $\phi$ is a minimal test function. In this case we write $\Phi^{n,\phi} := \Phi$.

**Remark 2.8** (Properties of polynomials). Let $\Phi = \Phi^{n,\phi}$ be as above, for some $n \in \mathbb{N}$ and $\phi : \mathbb{R}_+^{(N)_2} \rightarrow \mathbb{R}$.

(i) If $x = (X, r, \mu)$, then

$$
\Phi(x) = \int_{X^N} \mu^\otimes N(d(x_1, x_2, \ldots)) \phi\left((r_{i,j})_{1 \leq i < j}\right),
$$

where $\mu^\otimes N$ is the $N$-fold product measure of $\mu$.

(ii) Let $\Sigma_n$ be the set of all permutations of $\mathbb{N}$ which leave $n + 1, n + 2, \ldots$ fixed and $\Sigma_\infty = \bigcup_n \Sigma_n$. Given $\sigma \in \Sigma_\infty$, define

$$
\tilde{\sigma}((r_{i,j})_{1 \leq i < j}) := (r_{\sigma(i)\sigma(j)}, \sigma(i)\vee \sigma(j))_{1 \leq i < j}.
$$

The symmetrization of $\phi$ is given by

$$
\overline{\phi} = \frac{1}{n!} \sum_{\sigma \in \Sigma_n} \phi \circ \tilde{\sigma}.
$$

By symmetry of $\nu^\otimes$, $\langle \nu^\otimes, \phi \rangle = \langle \nu^\otimes, \overline{\phi} \rangle$, or equivalently, $\Phi^{n,\phi} = \Phi^{n,\overline{\phi}}$.

Recall from Subsection 2.1 the space $\mathcal{B}(\mathbb{R}_+^{(N)_2})$ of bounded measurable real-valued functions on $\mathbb{R}_+^{(N)_2}$. An element $\phi \in \mathcal{B}(\mathbb{R}_+^{(N)_2})$ is said to be differentiable
if for all $1 \leq i < j$ the partial derivatives $\frac{\partial \phi}{\partial r_{i,j}}$ exist and if $\sum_{1 \leq i < j} |\frac{\partial \phi}{\partial r_{i,j}}| < \infty$.

In this case we put

\begin{equation}
\text{div}(\phi) := \sum_{1 \leq i < j} \frac{\partial \phi}{\partial r_{i,j}} = 2 \sum_{1 \leq i < j} \frac{\partial \phi}{\partial r_{i,j}}.
\end{equation}

Denote by $C^1_b(\mathbb{R}_+^{(n)})$ the space of all bounded and continuously differentiable real-valued functions $\phi$ on $\mathbb{R}_+^{(n)}$ with bounded derivatives. The function spaces we will use in the sequel are the space

\begin{equation}
\Pi := \{ \Phi^{n,\phi} \in \Pi : n \in \mathbb{N}, \phi \in \mathcal{B}(\mathbb{R}_+^{(n)}) \},
\end{equation}

and its sub-spaces

\begin{equation}
\Pi^0 := \{ \Phi^{n,\phi} \in \Pi : n \in \mathbb{N}, \phi \in C_b(\mathbb{R}_+^{(n)}) \},
\end{equation}

and

\begin{equation}
\Pi^1 := \{ \Phi^{n,\phi} : n \in \mathbb{N}, \phi \in C^1_b(\mathbb{R}_+^{(n)}) \}.
\end{equation}

**Remark 2.9 (Polynomials form an algebra).** Observe that $\Pi, \Pi^0$ and $\Pi^1$ are algebras of functions. Specifically, given $\Phi^{n,\phi}, \Phi^{m,\psi} \in \Pi$,

\begin{equation}
\Phi^{n,\phi} \cdot \Phi^{m,\psi} = \Phi^{n+m,(\phi,\psi)_n} = \Phi^{n+m,(\psi,\phi)_m}
\end{equation}

where for $\phi, \psi \in \mathcal{B}(\mathbb{R}_+^{(n)})$ and $\ell \in \mathbb{N}$,

\begin{equation}
(\phi, \psi)_{\ell}(r) := \phi(r) \cdot \psi(\tau_\ell r),
\end{equation}

with $\tau_\ell((r_{i,j})_{1 \leq i < j}) = (r_{i+\ell, j+\ell})_{1 \leq i < j}$.

By Proposition 2.6 in [GPW09a], $\Pi$ and $\Pi^0$ separate points in $M$. Observing that $C^1_b(\mathbb{R}_+^{(n)})$ is dense in $C_b(\mathbb{R}_+^{(n)})$, we find that $\Pi^1$ separates points as well. \hfill \square

**Example 2.10.** Let $n := 2$ and $\phi(r) := \tilde{\phi}(r_{1,2})$ for $\tilde{\phi} \in C^1_b(\mathbb{R})$. Then

\begin{equation}
(\phi, \phi)_2(r) = \tilde{\phi}(r_{1,2}) \cdot \tilde{\phi}(r_{3,4}).
\end{equation}

\hfill \square
Remark 2.11 (Symmetric polynomials and the Gromov-weak topology).
Let \( x, x_1, x_2, \ldots \) in \( M \) and recall from Proposition 2.6 in [GPW09a] that \( \Phi \in \Pi^0 \) separates points in \( M \). Moreover, \( x_n \to x \) in the Gromov-weak topology iff \( \Phi(x_n) \to \Phi(x) \) for all \( \Phi \in \Pi^0 \), as \( n \to \infty \) (see Theorem 5 in [GPW09a]). Notice that the same is true if we restrict to \( \Phi \in \Pi^1 \) or to bounded and continuous test functions \( \phi \) which are invariant under finite permutations (compare Remark 2.8).

To lift the measure-valued Fleming-Viot process to the level of trees and thereby construct the tree-valued Fleming-Viot dynamics, we consider the martingale problem associated with the operator \( \Omega^{\uparrow} \) on \( \Pi \) with domain \( D(\Omega^{\uparrow}) = \Pi^1 \). To define \( \Omega^{\uparrow} \) we let for \( \Phi = \Phi_n, \phi \in \Pi^1 \),

\[
(2.29) \quad \Omega^{\uparrow} \Phi := \Omega^{\uparrow, \text{grow}} \Phi + \Omega^{\uparrow, \text{res}} \Phi.
\]

The growth operator \( \Omega^{\uparrow, \text{grow}} \) reflects the fact that the population gets older and therefore the genealogical distances grow at speed 2 as time goes on. We therefore put

\[
(2.30) \quad \Omega^{\uparrow, \text{grow}} \Phi(u) := \langle \nu^u, \text{div}(\phi) \rangle.
\]

For the resampling operator let

\[
(2.31) \quad \Omega^{\uparrow, \text{res}} \Phi(u) := \frac{\gamma}{2} \sum_{1 \leq k, l \leq n} \left( \langle \nu^u, \phi \circ \theta_{k,l} \rangle - \langle \nu^u, \phi \rangle \right),
\]

where we put \( r_{k,k} = 0 \) for all \( k \geq 1 \), and

\[
(2.32) \quad (\theta_{k,l((r_{i',j'}r_{i,j}')_{1 \leq i',j'} \leq n})))_{i,j} := \begin{cases} r_{i,j}, & \text{if } i, j \neq l \\ r_{i \land k, i \lor k}, & \text{if } j = l, \\ r_{j \land k, j \lor k}, & \text{if } i = l. \end{cases}
\]

Note that \( \Omega^{\uparrow} \Phi \in \Pi \) for all \( \Phi \in \Pi^1 \).

Example 2.12. If \( k := 1 \) and \( l := 3 \), then

\[
(2.33) \quad \theta_{1,3}(r) := \begin{pmatrix} r_{1,2} & 0 & r_{1,4} & r_{1,5} & r_{1,6} & \cdots \\ r_{1,2} & r_{2,4} & r_{2,5} & r_{2,6} & \cdots \\ r_{1,4} & r_{1,5} & r_{1,6} & \cdots \\ r_{4,5} & r_{4,6} & \cdots \\ r_{5,6} & \cdots \end{pmatrix}.
\]
Example 2.13. Let $n := 2$ and $\phi(r) = \tilde{\phi}(r_{1,2})$ be as in Example 2.10, $\rho_2 : r \mapsto r_{1,2}$ and $\nu^*_2 := (\rho_2)_* \nu^*$. Then

\begin{equation}
\Omega^1 \langle \nu^*, \phi \rangle(u) = 2 \langle \nu^*_2, \tilde{\phi}' \rangle + \gamma(\tilde{\phi}(0) - \langle \nu^*_2, \tilde{\phi} \rangle).
\end{equation}

Our first main result states that the martingale problem associated with $(\Omega^1, \Pi^1)$ is well-posed.

Theorem 1 (Well-posed martingale problem). Fix $P_0 \in M_1(U)$. The $(P_0, \Omega^1, \Pi^1)$-martingale problem has a unique solution.

This leads to the following definition.

Definition 2.14 (The tree-valued Fleming-Viot dynamics). Fix $P_0 \in M_1(U)$. The tree-valued Fleming-Viot dynamics with initial distribution $P_0$ is a stochastic process with distribution $P$, the unique solution of the $(P_0, \Omega^1, \Pi^1)$-martingale problem.

Proposition 2.15 (Sample path properties). The tree-valued Fleming-Viot dynamics $\mathcal{U}$ has the following properties.

(i) $\mathcal{U}$ has sample paths in $C_U([0, \infty))$, $P$-almost surely.
(ii) $\mathcal{U}_t \in U_\mathcal{E}$, for all $t > 0$, $P$-almost surely.
(iii) For all $t > 0$, $\nu^{\mathcal{U}_t}((0, \infty)^{(2)}) = 1$, $P$-almost surely. Moreover, the random set of exceptional times

\begin{equation}
\{ t \in [0, \infty) : \nu^{\mathcal{U}_t}((0, \infty)^{(2)}) < 1 \}
\end{equation}

is a Lebesgue null-set, $P$-almost surely. In particular, if $\mathcal{U}_t = (U_t, r_t, \mu_t)$, for all $t \geq 0$, then $\mu_t$ is non-atomic for Lebesgue almost all $t \in \mathbb{R}_+$.

Proposition 2.16 (Feller property). The tree-valued Fleming-Viot dynamics $\mathcal{U}$ is a strong Markov process. Moreover, it has the Feller property, i.e., $u \mapsto P[f(\mathcal{U}_t)|\mathcal{U}_0 = u]$ is continuous if $f \in C_b(\mathcal{U})$. 
Remark 2.17 (Extended Martingale problem). Notice that for all $\Phi \in \Pi^1$, $(\Phi(U_t))_{t \geq 0}$ is a $\mathbb{R}$-valued continuous semi-martingale. Hence by Itō’s formula for continuous semi-martingales (compare, for example, Theorem 32.8 in [RW00]) this implies that the operator $(\Omega^{\uparrow}, \Pi^1)$ extends to an operator on the algebra

\[(2.36) \quad \mathcal{F} = \{ f \circ \Phi : f \in B(\mathbb{R}), \Phi \in \Pi \}\]

with domain

\[(2.37) \quad \mathcal{F}^{2,1} = \{ f \circ \Phi : f \in C^2_b(\mathbb{R}), \Phi \in \Pi^1 \}\]

for $\Phi = (\nu, \phi)$ as follows:

\[(2.38) \quad \Omega^{\uparrow}(f \circ \Phi)(u) = f'(\langle \nu^u, \phi \rangle) \cdot \Omega^{\uparrow}\langle \nu^u, \phi \rangle(u) + \frac{1}{2} f''(\langle \nu^u, \phi \rangle) \cdot \left\{ \Omega^{\uparrow}\langle \nu^u, \phi \rangle^2(u) - 2\langle \nu^u, \phi \rangle \Omega^{\uparrow}\langle \nu^u, \phi \rangle(u) \right\}.

For $F = f \circ \Phi, \Phi = \Phi^{n,\phi} \in \Pi^1$, we therefore put

\[(2.39) \quad \Omega^{\uparrow,\text{grow}} F(u) := f'(\langle \nu^u, \phi \rangle) \cdot \langle \nu^u, \text{div}(\phi) \rangle
\]

and

\[(2.40) \quad \Omega^{\uparrow,\text{res}} F(u) := \frac{\gamma}{2} f'(\langle \nu^u, \phi \rangle) \cdot \sum_{k,l \geq 1} \langle \nu^u, \phi \circ \theta_{k,l} - \phi \rangle \cdot \sum_{k,l \geq 1} \langle \nu^u, \phi \circ \theta_{k,l} - \phi \rangle + \frac{\gamma}{2} n^2 f''(\langle \nu^u, \phi \rangle) \cdot \langle \nu^u, \text{sym}(\phi) \rangle \circ \theta_{1,n+1} - (\text{sym}(\phi))_n,
\]

where $\text{sym}(\phi)$ is the symmetrization of $\phi$ as defined in [221].

Corollary 2.18 (Quadratic variation). Let $U = (U_t)_{t \geq 0}$ be the tree-valued Fleming-Viot dynamics with initial distribution $P_0 \in \mathcal{M}_1(U)$ and $\Phi = \Phi^{n,\phi} \in \Pi^1$, Then $(\Phi(U_t))_{t \geq 0}$ is a continuous $P$-semi-martingale with quadratic variation

\[(2.41) \quad \langle \Phi(U) \rangle_t = \gamma n^2 \int_0^t ds \langle \nu^{U_s}, (\text{sym}(\phi))_n \circ \theta_{1,n+1} - (\text{sym}(\phi))_n \rangle.
\]
Remark 2.19 (Quadratic variation for a representative). Assume that for all \( t > 0 \), \( U_t = (U_t, r_t, \mu_t) \). Then the quadratic variation of \( (\Phi(U_t))_{t \geq 0} \) can be expressed as

\[
\langle \Phi(U) \rangle_t = \gamma n^2 \int_0^t ds \langle \mu_s, (\rho_s - \langle \mu_s, \rho_s \rangle)^2 \rangle,
\]

where \( \rho_s : U_s \to \mathbb{R} \) is defined as

\[
\rho_s(u_1) := \int \mu_s^\otimes N(d(u_2, u_3, \ldots)) \bar{\phi}((r_s(u_i, u_j))_{1 \leq i < j}).
\]

\[\square\]

Remark 2.20 (Another martingale problem formulation). We say that \( \Phi \in \Pi \) is minimal if \( \Phi \) is not of the form \( \Phi \neq \hat{\Phi} \cdot \tilde{\Phi} \) for some \( \hat{\Phi}, \tilde{\Phi} \in \Pi \) of degree > 0. Using (2.40) and Corollary 2.18 it is straightforward to give an alternative formulation for the martingale problem leading to the tree-valued Fleming-Viot dynamics:

Let \( P_0 \in \mathcal{M}_1(\mathbb{U}) \). A \( \mathbb{U} \)-valued process \( U = (U_t)_{t \geq 0} \) is the tree-valued Fleming-Viot dynamics with initial distribution \( P_0 \) iff

\[
(\Phi(U_t) - \Phi(U_0) - \int_0^t ds \Omega^1 \Phi(U_s))_{t \geq 0}
\]

is a martingale for all minimal \( \Phi \in \Pi^1 \) with quadratic variation given by (2.41).

\[\square\]

Remark 2.21 (Connection of measure- and tree-valued Fleming-Viot). Let us connect the tree- and measure-valued Fleming-Viot dynamics. On the one hand, consider the tree-valued Fleming-Viot dynamics. At time \( t > 0 \), decompose \( U_t = (U_t, r_t, \mu_t) \) in disjoint \( 2t \) balls with respect to \( r_t \). Then the collection of balls charged by \( \mu_t \) is a random finite set which can be ordered according to the weights of \( \mu_t \). On the other hand, consider the measure-valued Fleming-Viot process on \([0; 1]\), started in a measure which is absolutely continuous with respect to the Lebesgue measure. At time \( t \), this process has finitely many atoms. The size-ordered version of these atoms has the same distribution as the size-ordered weights of the \( 2t \)-balls of the tree-valued Fleming-Viot dynamics.

\[\square\]
Remark 2.22 (The process \(U\) as a diffusion). Since \(U\) has the strong Markov property with continuous paths, one would like to consider it as a diffusion, and hence express its generator via second order differential operators similar to (2.13). Due to the lack of a linear structure defining differential operators on \(M\) is not straightforward at all. We therefore explain here only how to proceed on the level of representatives.

Let \(F : U \rightarrow \mathbb{R}\). Then there exists a real valued function \(\tilde{F}\) acting on metric measure spaces (rather than their isometry classes) and such that for all \((\tilde{U}, r, \mu) \in U\) and \((U, r, \mu) \in (\tilde{U}, r, \mu)\),

\[
\tilde{F}((U, r, \mu)) = F((\tilde{U}, r, \mu)).
\]

We consider perturbations of the metric \(r\) and of the measure \(\mu\). That is, we define

\[
\frac{\partial \tilde{F}}{\partial r}(U, r, \mu) := \lim_{\varepsilon \rightarrow 0} \frac{1}{\varepsilon} (\tilde{F}(U, r + \varepsilon, \mu) - \tilde{F}(U, r, \mu)),
\]

with \((r + \varepsilon)(u, v) := r(u, v) + \varepsilon 1_{u \neq v}\), for all \(u, v \in U\), and for each \(\mu' \in \mathcal{M}_1((U, r))\),

\[
\frac{\partial \tilde{F}}{\partial \mu}(U, r, \mu)[\mu'] := \lim_{\varepsilon \rightarrow 0} \frac{1}{\varepsilon} (\tilde{F}(U, r, \mu + \varepsilon \mu') - \tilde{F}(U, r, \mu)),
\]

whenever the limits exist and \(\frac{\partial^2 \tilde{F}}{\partial \mu^2}(U, r, \mu)[\mu', \mu''] := \frac{\partial}{\partial \mu} \left( \frac{\partial \tilde{F}}{\partial \mu}(U, r, \mu)[\mu'] \right)[\mu'']\) as usual.

Then it is easy to check that \(U\) is a solution of the \((\Omega, \text{diff}, \mathcal{F}^{2,1})\)-martingale problem with the operator

\[
\Omega^{1, \text{diff}} F(u) := \frac{\partial \tilde{F}}{\partial r}(U, r, \mu) + \frac{\gamma}{2} \int_U \int_U (\mu(du) \delta_u(dv) - \mu(du) \mu(dv)) \frac{\partial^2 \tilde{F}}{\partial \mu^2}(\delta_u, \delta_v)
\]

provided that \((\tilde{U}, r, \mu) = u\) (recall \(\mathcal{F}^{2,1}\) from (2.37)).

Now the problem arises whether the generator of our Feller semigroup and the above differential operator on its domain do not only have a measure determining set in common but actually do agree. For that one would like to establish that the domain of the differential operator is dense in \(C_b(U)\) and \(\mathcal{F}^{1,2}\) is dense in the space of sufficiently smooth functions. Such questions are usually resolved with the help of the Stone-Weierstrass theorem which unfortunately does not apply here since our state space \(U\) is not locally compact. □
2.3. Particle approximation (Theorem 4). A classical result in population genetics gives the approximation of the measure-valued Fleming-Viot process by a finite size particle model - the so called Moran model - in the limit of large population size (see e.g. [Daw93, Eth01]). In this model ordered pairs of individuals are replaced by new pairs in a way that the “children” choose a parent - which then becomes their common ancestor - independently at random from the parent pair. In this subsection we state that also the tree-valued Fleming-Viot dynamics can be approximated by tree-valued resampling dynamics which correspond to the Moran model. To prepare the statement notice that the Moran model is most conveniently defined via its graphical representation (see Figure 1), which we formally describe in the sequel.

Fix a population size $N \in \mathbb{N}$, put $\mathcal{I} := \{1, 2, \ldots, N\}$ and choose a metric $r_0$ on $\mathcal{I}$.

Let then $\eta := \{\eta^{ij}; i, j \in \mathcal{I}\}$ be a realization of a family of rate $\gamma/2$ Poisson point processes. We say that for $i, i' \in \mathcal{I}$ and $0 \leq s \leq t < \infty$ there is a path of descent from $(i, s)$ to $(i', t)$ if there exist $n \in \mathbb{N}$, $s := u_0 \leq u_1 < u_2 < \ldots < u_n := t$ and $j_1 := i, j_n := i', j_1, \ldots, j_{n-1} \in \mathcal{I}$, such that for all $k \in \{1, \ldots, n\}$, $\eta^{j_{k-1}j_k}(u_{k-1}, u_k) = \eta^{j_{k-1}j_k}(u_k) = 1$ and $\eta^{m,j_{k-1}}(u_{k-1}, u_k) = 0$ for all $m \in \mathcal{I}$.

Notice that for all $(i, t) \in \mathcal{I} \times \mathbb{R}_+$ and $0 \leq s \leq t$ there exists almost surely, a unique

\begin{equation}
A_s(i, t) \in \mathcal{I}
\end{equation}
such that there is a path from \((A_s(i, t), s)\) to \((i, t)\). In the following we refer to the individual \(A_s(i, t)\) as the ancestor of \((i, t)\) back at time \(s\). For \(t \geq 0\), define the pseudo-metric \(r_t\) on \(I\) by
\[
(2.50) \\
r_t^\eta(i, j) := \begin{cases} 
2(t - \sup \{s \in [0, t] : A_s(i, t) = A_s(j, t)\}), & \text{if } A_0(i, t) = A_0(j, t), \\
2t + r_0(A_0(i, t), A_0(j, t)), & \text{if } A_0(i, t) \neq A_0(j, t),
\end{cases}
\]
for \(i, j \in I\). This induces as usual a metric space by passing to equivalence classes.

We then call \(U^N = (U^N_t)_{t \geq 0}\) the tree-valued Moran dynamics with population size \(N\), where for \(t \geq 0\), (recall (2.2))
\[
(2.51) \\
U^N_t := (I, r_t^\eta, 1/N \sum_{i \in I} \delta_i).
\]

The next result states that the convergence of Moran- to Fleming-Viot dynamics also holds on the level of trees.

**Theorem 2** (Convergence of tree-valued Moran to Fleming-Viot dynamics). For \(N \in \mathbb{N}\), let \(U^N\) be the tree-valued Moran dynamics with population size \(N\), and let \(U = (U_t)_{t \geq 0}\) be the tree-valued Fleming-Viot dynamics. If \(U^N_0 \Rightarrow U_0\), as \(N \to \infty\), weakly in the Gromov-weak topology, then
\[
(2.52) \\
U^N \Rightarrow U,
\]
weakly in the Skorohod topology on \(D_D([0, \infty))\).

**Remark 2.23.**

(i) In empirical population genetics, models for finite populations rather than infinite populations are of primary interest. Theorem 2 allows us to give an asymptotic analysis of functionals of the tree-valued Moran dynamics by studying the tree-valued Fleming-Viot dynamics which are simpler to handle analytically.

(ii) The measure-valued Fleming-Viot process is universal in the sense that it is the limit point of frequency paths of various exchangeable population models of constant size. (A precise condition, based on a result from [MS01], is given in (2.57).) We conjecture that the same universality holds on the level of trees, i.e., the tree-valued Fleming-Viot dynamics is the point of attraction of various exchangeable tree-valued dynamics. We will discuss universality as well as different potential limit points in more detail in Subsection 2.5. 

\[\square\]
2.4. Long-term behavior (Theorem 3). Genealogical relationships in neutral models are frequently studied since the introduction of the Kingman coalescent in [Kin82a]. This stochastic process describes the genealogy of a Moran population in equilibrium and its projective limit as the population size tends to infinity. In this section we formulate the related convergence result for the tree-valued resampling dynamics.

Recall that a partition of \( \mathbb{N} \) is a collection \( p = \{ \pi_1, \pi_2, \ldots \} \) of pairwise disjoint subsets of \( \mathbb{N} \), also called blocks, such that \( \mathbb{N} = \bigcup_i \pi_i \). The partition \( p \) defines an equivalence relation \( \sim_p \) on \( \mathbb{N} \) by \( i \sim_p j \) if and only if there exists a partition element \( \pi \in p \) with \( i, j \in \pi \). We denote by \( \mathcal{S} \) the set of partitions of \( \mathbb{N} \) and define the restrictions \( \rho_1, \rho_2, \ldots \) on \( \mathcal{S} \) by \( \rho_k \circ p := \{ \pi_i \cap \{1, \ldots, k\} : \pi_i \in p \} \). We say that a sequence \( p_1, p_2, \ldots \in \mathcal{S} \) converges to a partition \( p \) if the sequences \( \rho_k \circ p_n \) converge in the discrete topology to \( \rho_k \circ p \), for all \( k \in \mathbb{N} \).

Starting in \( p_0 = p \in \mathcal{S} \), the Kingman coalescent is the unique \( \mathcal{S} \)-valued strong Markov process \( K = (K_t)_{t \geq 0} \) such that any pair of blocks merges at rate \( \gamma \) (see, for example, [Kin82b, Pit99]).

Every realization \( k = (k_t)_{t \geq 0} \) of \( K \) gives a pseudo-metric \( r^k \) on \( \mathbb{N} \) defined by

\[
(2.53) \quad r^k(i, j) := 2 \cdot \inf \{ t \geq 0 : i \sim_{k_t} j \},
\]

i.e., \( r^k(i, j) \) is proportional to the time needed for \( i \) and \( j \) to coalesce. Note that \( (\mathbb{N}, r^k) \) is ultra-metric and that \( r^k(i, j) \) can be thought of as a genealogical distance. Denote then by \( (L^k, r^k) \) the completion of \( (\mathbb{N}, r^k) \). Clearly, \( (L^k, r^k) \) is also ultra-metric. Define \( H_N \) to be the map which takes a realization of the \( \mathcal{S} \)-valued coalescent and maps it to (an equivalence class of) a pseudo-metric measure space by

\[
(2.54) \quad H_N : \kappa \mapsto (L^k, r^k, \mu^k_N := \frac{1}{N} \sum_{i=1}^N \delta_i).
\]

Notice that for each \( N \), the map \( H_N \) is continuous.

By Theorem 4 in [GPW09a], there exists a \( \mathcal{U} \)-valued random variable \( U_{\infty} \) such that

\[
(2.55) \quad H_N(\kappa) \xrightarrow{\mathcal{U}_{\infty}} U_{\infty},
\]

weakly in the Gromov-weak topology. The limit object \( U_{\infty} \) is called the Kingman measure tree. Since the Kingman coalescent comes immediately down from \( \infty \), the Kingman measure tree is compact (see [Eva00]).

**THEOREM 3** (Convergence to the Kingman measure tree). Let \( \mathcal{U} = (\mathcal{U}_t)_{t \geq 0} \) be the tree-valued Fleming-Viot dynamics starting in \( \mathcal{U}_0 \) and \( \mathcal{U}_{\infty} \).
the Kingman coalescent measure tree. Then

\[ U_t \overset{t \to \infty}{\Rightarrow} U_\infty. \]

In particular, the distribution of \( U_\infty \) is the unique equilibrium distribution of the tree-valued Fleming-Viot dynamics.

**Remark 2.24 (Exchange of limits).** Recall from (2.51) the tree-valued Moran dynamics \( \{U^N = (U^N_t)_{t \geq 0}; N \in \mathbb{N}\} \). It is straightforward to check that for all \( N \in \mathbb{N} \) and for all possible initial states, \( U^N_t \overset{t \to \infty}{\Rightarrow} H_N(\chi) \), and therefore the limits \( N \to \infty \) (see Theorem 2) and \( t \to \infty \) (see Theorem 3) can be exchanged by (2.55).

### 2.5. Extensions

Several extensions of our construction of the tree-valued resampling dynamics are possible. In particular, we see three different directions.

- **A reintroduction of genetical types allows for type-dependent evolution.** In particular, this allows to construct tree-valued resampling dynamics under mutation and selection. Alternatively, if individuals are assigned a type describing the location in some geographical space, we can model spatial tree-valued resampling dynamics.
- By taking all individuals ever alive into account it is possible to construct a random genealogy including besides the current population all the fossils.
- Considering more general exchangeable resampling mechanisms than in the Moran model above leads to various different tree-valued limit dynamics.

The first two extensions require the introduction of extended state spaces and thereby a thorough investigation of their topological properties. However, the third extension does not and we next list the conjectures which are straightforward.

So far we have considered the tree-valued Moran resampling dynamics and their diffusion limit. A general framework for resampling dynamics is provided by the models of Cannings (see [Can74, Can75] and Section 3.3 in [Ewe04] for a survey). For a fixed population size \( N \in \mathbb{N} \), each Cannings model is characterized by a family of \( \mathbb{N} \)-valued exchangeable random variables \( \{V_1^N, ..., V_N^N\} \) with \( \sum_{i=1}^N V_i^N = N \) recording the numbers of offspring of the individuals currently alive. After random waiting times the population is replaced by a new population where the \( i \)th individual is replaced by
new individuals, \( i = 1, \ldots, N \). We can therefore extend our construction to more general exchangeable resampling dynamics. This includes, for example, resampling dynamics which allow for an infinite offspring variance in the forward and multiple mergers of ancestral lines in the backward picture. In the following we denote the tree-valued Cannings dynamics of size \( N \) by \( V^N = (V^N_t)_{t \geq 0} \).

Classifying coalescent processes for exchangeable models, \([MS01]\) have shown that genealogies of the measure-valued Cannings dynamics in discrete time, suitably rescaled, converge to the Kingman coalescent which is dual to the Fleming-Viot process provided

\[
\lim_{N \to \infty} \mathbb{E}[(V^N_1)^2] = 0 \quad \text{and} \quad \lim_{N \to \infty} \frac{1}{N} \mathbb{E}[(V^N_1)^3] = 0.
\]

We claim that the same results applies to the tree-valued dynamics.

**Conjecture 2.25 (”Light tail” Cannings converges to Fleming-Viot).** Assume that the offspring distributions satisfy (2.57). Under a suitable time rescaling, \((V^N_N)_{N \in \mathbb{N}}\) converges weakly to the tree-valued Fleming-Viot dynamics in the Skorohod topology on \( D_\mathbb{U}([0, \infty)) \), as \( N \to \infty \).

There are other regimes where the tree-valued Cannings dynamics converge but the limit is not a diffusion. In the sequel we focus on continuous-time Cannings models with \( V^N_i > 1 \) for at most one \( i \). These are most easily described using a measure \( \Lambda \in \mathcal{M}_f([0, 1]) \). The \( \Lambda \)-Cannings dynamics for population size \( N \in \mathbb{N} \) are given by the following two independent mechanisms:

- Each (unordered) pair resamples at constant rate \( \Lambda\{0\} \).
- For each \( x \in (0, 1] \), each individual kills at rate \( \frac{\Lambda(dx)}{N^2} \) a binomial number \( \text{Bin}(x, N) \) of individuals (including itself) and simultaneously replaces the gaps by the same number of copies of itself,

where \( \text{Bin}(x, N) \) denotes a random variable with binomial distribution with parameters \((x, N)\). In the following we denote by \( \mathcal{V}^{N, \Lambda} \) the corresponding tree-valued Cannings dynamics.

Next, consider the limit of infinite population size for the Cannings model. The long-term behavior of the genealogy of the Cannings model is given by \( \Lambda \)-coalescents, introduced in \([Pit99]\). It is known that \( \Lambda \)-coalescents can be associated with the \( \Lambda \)-coalescent measure tree, provided the dust-free property holds, i.e.,

\[
\int_0^1 \Lambda(dx) x^{-1} = \infty,
\]
Conjecture 2.26 (Λ-Cannings converge to Λ-resampling dynamics). Assume that the dust-free property (2.58) holds and that there exists a random element \( V_{N}^{\Lambda} \) with \( V_{0}^{N,\Lambda} \Rightarrow V_{0}^{\Lambda} \), as \( N \to \infty \).

(i) There exists a \( U \)-valued process \( V^{\Lambda} \in D_{U}(\mathbb{R}^{+}) \), with \( V_{N}^{N,\Lambda} \Rightarrow V^{\Lambda} \), as \( N \to \infty \).

(ii) The process \( V^{\Lambda} \) is Feller and strong Markov and has the \( \Lambda \)-coalescent measure tree as its unique equilibrium.

In the following we refer to the process \( V^{\Lambda} \) as the \textit{tree-valued Λ-resampling dynamics}.

Note first that \( \Lambda(0,1] > 0 \) implies that a substantial fraction of the population is replaced by one individual. Hence we expect continuous paths if and only if \( \Lambda = \gamma \delta_{0}, \) for some \( \gamma > 0 \).

Conjecture 2.27 (Continuous paths versus jumps). The following are equivalent.

(i) The process \( V^{\Lambda} \) has continuous path.

(ii) \( \Lambda = \gamma \delta_{0}, \) for some \( \gamma > 0 \).

(iii) The process \( V^{\Lambda} \) is the tree-valued Fleming-Viot dynamics.

When an individual replaces a fraction of the population, the measure has an atom. Nevertheless, tree growth destroys this atom immediately.

Conjecture 2.28 (\( V^{\Lambda} \) has no atoms). For Lebesgue almost all \( t \), the metric measure space \( V_{t}^{\Lambda} \) has no atoms.

Moreover, it is known that the \( \Lambda \)-coalescent comes down from infinity in infinitesimal small time if and only if

\[
\sum_{k=2}^{\infty} \gamma_{b}^{-1} < \infty
\]

with

\[
\gamma_{b} := \sum_{k=2}^{b} (k-1) \binom{b}{k} \int_{0}^{1} \Lambda(dx) x^{k-2} (1-x)^{b-k}.
\]

(see, Theorem 1 in [Sch00b]).
Since balls do either agree or are disjoint in ultra-metric spaces, the number of ancestral lines a time $\varepsilon > 0$ back equals the number of $2\varepsilon$-balls one needs to cover the ultra-metric space representing the coalescent tree. Hence we expect the following.

**Conjecture 2.29 (Compactness and “coming down from infinity”).** The following are equivalent.

(i) For each $t > 0$, $V_t^1 \in U_c$, almost surely.
(ii) The measure $\Lambda \in \mathcal{M}_f([0,1])$ satisfies Condition \ref{cond:compactness}.

We complete this subsection by pointing out that there are more general resampling dynamics in which $V_i^N > 1$ for more than one index $i \in \{1, ..., N\}$. In this case the genealogical trees are described by coalescent processes allowing for simultaneous multiple mergers (see, Sch00a).

**Outline.** The rest of the paper is organized as follows. As an application we study the evolution of subtree length distributions in Section 3. A duality relation of the tree-valued Fleming-Viot dynamics to the tree-valued Kingman coalescent is given in Section 4. In Section 5 we give a formal construction of tree-valued Moran dynamics using well-posed martingale problems. The Moran models build, as shown in Section 6, a tight sequence. Duality and tightness provide the tools necessary for the proof of Theorems 1 through 3, which are carried out in Section 8. In Section 9 we give the proofs of the applications of Section 3.

**3. Application: Subtree length distribution (Theorems 4 and 5).** In this section we investigate the distribution of the vector containing the lengths of the subtrees spanned by subsequently sampled points, which is referred to as the subtree length distribution. All proofs are given in Section 9.

The main result in Subsection 3.1 is that the subtree length distribution uniquely determines ultra-metric measure spaces. In Subsection 3.2 the corresponding martingale problem and its well-posedness is stated. In Subsection 3.3 we study with the mean sample Laplace transform a special functional of the subtree length distribution. This, in particular, allows for a description of the evolution of the number of segregating sites in a sample under a neutral infinite sites model.

**3.1. The subtree length distribution (Theorem 4).** Recall from Remark 2.2 that we can isometrically embed any ultra-metric space $(U, r_U)$ via a function $\varphi$ into a path-connected space $(X, r_X)$ which satisfies the four-point
condition (2.8) such that $X \setminus X^o$ is isometric to $(U, r_U)$. For a sequence $u_1, \ldots, u_n \in U$ with $n \in \mathbb{N}$, let
\begin{equation}
L_n^{(U, r_U)}(\{u_1, \ldots, u_n\}) := L_n^{(X, r_X)}(\{\varphi(u_1), \ldots, \varphi(u_n)\})
\end{equation}
where for an $\mathbb{R}$-tree $(X, r_X)$ with finitely many leaves the length of the tree is defined as the total mass of the one-dimensional Hausdorff measure on $(X, \mathcal{B}(X))$.

Note that the length of the tree spanned by a finite sample is a function of their mutual distances as we state next.

**Lemma 3.1 (Total length of a sub-tree spanned by a finite subset).** For a metric space $(X, r_X)$ satisfying the four point condition (2.8) and for all $x_1, \ldots, x_n \in X$,
\begin{equation}
L_n^{(X, r_X)}(\{x_1, \ldots, x_n\}) = \frac{1}{2} \inf \left\{ \sum_{i=1}^n r(x_i, x_{\sigma(i)}); \sigma \in \Sigma_1^n \right\},
\end{equation}
where $\Sigma_1^n := \{ \text{permutations of } \{1, \ldots, n\} \text{ with one cycle} \}$.

To specify the distribution of the length of the subtrees of subsequently sampled points we consider the map
\begin{equation}
\ell : \begin{cases} \mathbb{R}_+^{\binom{n}{2}} & \to \mathbb{R}_+^n, \\ \ell & \mapsto (0, \ell_2(\ell), \ell_3(\ell), \ldots), \end{cases}
\end{equation}
where for each $n \in \mathbb{N}$,
\begin{equation}
\ell_n(\ell) := \frac{1}{2} \inf \left\{ \sum_{i=1}^n r_i, \sigma(i); \sigma \in \Sigma_1^n \right\}.
\end{equation}
We then define the *subtree length distribution* of $u \in U$ by
\begin{equation}
\xi(u) := \ell_u \nu^u \in \mathcal{M}_1(\mathbb{R}_+^n).
\end{equation}

The first key result states that the subtree length distribution uniquely characterizes ultra-metric measure spaces.

**Theorem 4 (Uniqueness and continuity of tree lengths distribution).** The map $\xi : U \to \mathcal{M}_1(\mathbb{R}_+^n)$ from (3.5) is injective and continuous (where $\mathcal{M}_1(\mathbb{R}_+^n)$ is endowed with the weak topology and $\mathbb{R}_+^n$ with the product topology).
Remark 3.2 ($\xi(U)$ is complete and separable). We endow the space $\xi(U) \subseteq \mathcal{M}_1(\mathbb{R}^n_+)$ with a complete metric induced by $\xi$. For this purpose, take a complete metric $d^U(\cdot,\cdot)$ on $U$ and set for $\lambda_i \in \xi(U)$, $i = 1, 2$, using the injectivity of $\xi$

$$d^{\xi(U)}(\lambda_1, \lambda_2) := d_U(\xi^{-1}(\lambda_1), \xi^{-1}(\lambda_2))$$

(3.6)

It follows from completeness and separability of $U$ that $\xi(U)$ is also complete and separable, i.e., $\xi(U)$ is Polish.

Remark 3.3 (Conjecture about general tree spaces). Theorem 4 shows uniqueness of the tree-length distribution on the space of ultra-metric spaces. We are not aware of a counter-example, showing that injectivity fails to hold for metric measure spaces satisfying the four-point condition (2.8).

3.2. Martingale problem for the subtree length distribution (Theorem 5). We investigate the evolution of the subtree length distribution under the tree-valued Fleming-Viot dynamics. That is, given the tree-valued Fleming-Viot dynamics $U = (U_t)_{t \geq 0}$, we consider

$$\Xi = (\Xi_t)_{t \geq 0}, \quad \Xi_t := \xi(U_t).$$

(3.7)

To describe the process $\Xi$ via a martingale problem, we define the operator $\Omega^{\uparrow,\Xi}$ on the algebra $\Pi^{\Xi} := \{\Phi \circ \xi^{-1} : \Phi \in \Pi\}$ with domain $\Pi^{1,\Xi} := \{\Phi \circ \xi^{-1} : \Phi \in \Pi^1\}$ by

$$\Omega^{1,\Xi}(\Phi \circ \xi^{-1})(\lambda) := \Omega^1\Phi(\xi^{-1}(\lambda)),$$

(3.8)

for all $\lambda \in \xi(U)$.

In $\Pi^{1,\Xi}$ we find, in particular, functions $\Psi \in \Pi^{1,\Xi}$ which are of the form

$$\Psi^\psi(\lambda) = \int_{\mathbb{R}^n_+} \lambda(d\ell) \psi(\ell),$$

(3.9)

for a test function $\psi \in C^1_b(\mathbb{R}^n_+)$. The main result of the section is the following.

Theorem 5 (The subtree lengths distribution process). For $\mathbf{P}_0 \in \mathcal{M}_1(U)$, let $U$ be the tree-valued Fleming-Viot dynamics with initial distribution $\mathbf{P}_0$. 

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(i) The \((\xi, P_0, \Omega^{\uparrow}, \Pi^{\uparrow})\)-martingale problem is well-posed in \(\xi(U)\). Its unique solution is given by \(\Xi = (\Xi_t)_{t \geq 0}\) with \(\Xi_t = \xi(U_t)\), for \(t \geq 0\). The process \(\Xi\) has the Feller property. In addition, it has continuous sample paths, \(P\)-almost surely.

(ii) The action of \(\Omega^{\uparrow, \Xi}\) on a function \(\Psi\) of the form (3.9) is given by

\[
\Omega^{\uparrow, \Xi} \Psi(\lambda) := \sum_{n \geq 2} n \langle \lambda, \partial_{\ell_n} \psi \rangle + \gamma \sum_{n \geq 1} n \langle \lambda, \psi \circ \beta_n - \psi \rangle.
\]

where \(\beta_n : \mathbb{R}^N_+ \rightarrow \mathbb{R}^N_+\) is given by

\[
\beta_n : (\ell_1 = 0, \ell_2, \ell_3, \ldots) \mapsto (\ell_1 = 0, \ell_2, \ldots, \ell_{n-1}, \ell_n, \ell_{n+1}, \ldots).
\]

3.3. Explicit calculations. We consider in this section the \emph{mean sample Laplace transforms}, i.e., functions of the form (3.9) with test functions of the form

\[
\psi(\ell) = e^{-\sigma \ell_n}
\]

for some \(n \in \mathbb{N}\) and \(\sigma \in \mathbb{R}_+\) in (3.9) for each \(n \in \mathbb{N}\). Using (3.10) we obtain the following explicit expressions.

**Corollary 3.4 (Mean sample Laplace transforms).** Let \(\Xi = (\Xi_t)_{t \geq 0}\) be the solution of the \((\xi, P_0, \Omega^{\uparrow, \Xi}, \Pi^{\uparrow, \Xi})\) martingale problem. For all \(\sigma \in \mathbb{R}_+\) and \(n \geq 2\), set

\[
g_n(t, \sigma) := \mathbb{E} \left[ \int \Xi_t(d\ell) e^{-\sigma \ell_n} \right].
\]

Then,

\[
g_n(t, \sigma) = \frac{\Gamma(n) \Gamma(\frac{2}{\gamma} \sigma + 1)}{\Gamma(\frac{2}{\gamma} \sigma + n)} + n! \sum_{k=2}^{n} \frac{(n-1)!}{(k-1)!} (-1)^{k} \frac{\Gamma(\frac{2}{\gamma} \sigma + 2k - 1)}{\Gamma(\frac{2}{\gamma} \sigma + n + k)} \cdot e^{-k(\sigma+\frac{2}{\gamma}(k-1))t} \cdot \left\{ \left( \sum_{m=2}^{k} \frac{(k-1)!}{(m-1)!} (-1)^m \frac{\Gamma(\frac{2}{\gamma} \sigma + k + m - 1)}{m!} g_m(0; \sigma) \right) \right. \\
- \left. \frac{k-1}{k(\frac{2}{\gamma} \sigma + k - 1)} \Gamma(\frac{2}{\gamma} \sigma + k + 1) \right\}.
\]
In particular, if \( g^n(\sigma) = \lim_{t \to \infty} g^n(t; \sigma) \) then
\[
(3.15) \quad g^n(\sigma) = \mathbb{E}[e^{-\sigma \sum_{k=2}^{n} \mathcal{E}^k}],
\]
where \( \{\mathcal{E}^k; k = 2, \ldots, n\} \) are independent and \( \mathcal{E}^k \) is exponentially distributed with mean \( \frac{2}{(k-1)^2}, \ k = 2, \ldots, n \).

**Remark 3.5 (Length of \( n \)-Kingman coalescent).** Consider the Kingman coalescent started with \( n \) individuals, and let \( L_n \) denote the total length of the corresponding genealogical tree. Note that (3.15) implies the well-known fact (implicitly stated already in [Wat75]) that
\[
(3.16) \quad L_n \overset{d}{=} \sum_{k=2}^{n} \mathcal{E}^k
\]
The analog results for more general \( \Lambda \)-coalescents can be found in [DDSJ08, DIMR07].

**Example 3.6 (Tree length and number of segregated sites).** In empirical population genetics genealogical trees of samples are of great interest (e.g., [Ewe04]). Consider in addition to the Fleming-Viot dynamics state-independent neutral mutations at rate \( \frac{\theta}{2} > 0 \). Under the assumptions of the infinite sites model every mutation on the sampled tree can be seen in data taken from the sampled individuals and the total number of observed polymorphisms (segregating sites) equals the total number of mutations on the sample tree. Given the length \( L_{t(U,r)}(\{u_1, \ldots, u_n\}) \) of the sub-tree spanned by the sample \( \{u_1, \ldots, u_n\} \) the number of segregating sites, denoted by
\[
(3.17) \quad S_n(\{u_1, \ldots, u_n\}) := \#\{\text{mutations which fall on the sub-tree spanned by } \{u_1, \ldots, u_n\}\},
\]
is Poisson distributed with parameter \( \frac{\theta}{2} L_{t(U,r)}(\{u_1, \ldots, u_n\}) \). In particular, if \( \mathcal{U} = (\mathcal{U}_t)_{t \geq 0}, \mathcal{U}_t = (U_t, r_t, \mu_t) \) is the tree-valued Fleming-Viot dynamics,
\[
(3.18) \quad \mathbb{E}\left[ \int_0^\infty \mu_t^{\otimes n}(d(u_1, \ldots, u_n))e^{-\sigma S_n(\{u_1, \ldots, u_n\})} \right] = g^n(t; \frac{\theta}{2}(1-e^{-\sigma})).
\]
for \( \sigma \in \mathbb{R}_+ \), where \( g^n \) as defined in (3.13) and explicitly calculated in Corollary 3.4.
4. Duality. If applicable, duality is an extremely useful technique in
the study of Markov processes. It is well-known that the Kingman coales-
cent is dual to the neutral measure-valued Fleming-Viot process (see, for
e example,\[Daw93, Eth01\]). In this section this duality is lifted to the tree-
valued Fleming-Viot dynamics. We will apply the duality to show uniqueness
of the martingale problem for the tree-valued Fleming-Viot process and its
relaxation to the equilibrium Kingman measure tree in Section 8.

The dual process. Recall from Subsection 2.4 the Kingman coalescent
\( \mathcal{K} = (\mathcal{K}_t)_{t \geq 0} \) and its state space \( \mathcal{S} \) of partitions of \( \mathbb{N} \). Since we are constructing
a dual to the \( U \)-valued dynamics, we add a component which measures
genealogical distances. The state space of the dual tree-valued Kingman
coalescent therefore is

\[
\mathbb{K} := \mathcal{S} \times \mathbb{R}_+^{\binom{N}{2}},
\]
equipped with the product topology. In particular, since \( \mathcal{S} \) and \( \mathbb{R}_+^{\binom{N}{2}} \) are
Polish, \( \mathbb{K} \) is Polish as well.

In the following we call the \( \mathbb{K} \)-valued stochastic process \( \mathcal{K} = (\mathcal{K}_t)_{t \geq 0} \), with

\[
\mathcal{K}_t = (\mathcal{K}_t, r'_t)
\]
the tree-valued Kingman coalescent if it follows the dynamics:

**Coalescence.** \( \mathcal{K} = (\mathcal{K}_t)_{t \geq 0} \) is the \( \mathcal{S} \)-valued Kingman coalescent with
pair coalescence rate \( \gamma \).

**Distance growth.** At time \( t \), for all \( 1 \leq i < j \) with \( i \not\sim_{\mathcal{K}_t} j \), the
genealogical distance \( r'_t(i, j) \) grows with constant speed 2.

To state the duality relation it is necessary to associate a martingale
problem with the tree-valued Kingman coalescent. Consider for \( p \in \mathcal{S} \), the
coalescent operator \( \kappa_p : \mathcal{P}^2 \to \mathcal{S} \) such that for \( \pi, \pi' \in p \),

\[
\kappa_p(\pi, \pi') := (p \setminus \{\pi, \pi'\}) \cup \{\pi \cup \pi'\},
\]
i.e., \( \kappa_p \) sends two partition elements of the partition \( p \) to the new partition
obtained by coalescence of the two partition elements into one.

We consider the space

\[
\mathcal{G} := \{G \in \mathcal{B}(\mathbb{K}) : G(\cdot, r'_\cdot) \in \mathcal{C}(\mathcal{S}), \forall r'_\cdot \in \mathbb{R}_+^{\binom{N}{2}} \}
\]
and the domain

\[
\mathcal{G}^{1,0} := \{G \in \mathcal{G} : \text{div}_r' G \text{ exists}, \forall p \in \mathcal{S} \}.
\]
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with

\[ \text{div}_p' := \sum_{i \neq j} \frac{\partial}{\partial r_{i\wedge j,i\vee j}} = 2 \sum_{i \neq j, i < j} \frac{\partial}{\partial r_{i,j}}. \]

We then consider the martingale problem associated with the operator \( \Omega^\downarrow \) on \( G \) with domain \( G^{1,0} \), where \( \Omega^\downarrow := \Omega^\downarrow,\text{grow} + \Omega^\downarrow,\text{coal} \), with

\[ \Omega^\downarrow,\text{grow} G(p, x') := \text{div}_p'(G(p, x')) \]

and

\[ \Omega^\downarrow,\text{coal} G(p, x') := \gamma \sum_{\{\pi, \pi'\} \subseteq \pi, \pi \neq \pi'} (G(\kappa_p(\pi_1, \pi_2), x') - G(p, x')). \]

Fix \( P_0 \in \mathcal{M}_1(\mathbb{K}) \). By construction, the tree-valued Kingman coalescent solves the \((P_0, \Omega^\downarrow, G)\)-martingale problem.

The duality relation. We are ready to state a duality relation between the tree-valued Fleming-Viot dynamics and the tree-valued Kingman coalescent.

To introduce a class \( \mathcal{H} \) of duality functions, we identify every partition \( p \in \mathcal{S} \) with the map \( p \) which sends \( i \in \mathbb{N} \) to the block \( \pi \in p \) iff \( i \in \pi \), and put for \( p \in \mathcal{S} \),

\[ (\underline{x})^p := (r_{\min p(i), \min p(j)})_{1 \leq i < j}. \]

Let then for each \( n \in \mathbb{N} \) and \( \phi \in C^1_b(\mathbb{R}_+^{1\downarrow n}) \) depending on the coordinates \( (r_{i,j})_{1 \leq i < j \leq n} \) only, the function \( H^{n,\phi} : \mathbb{U} \times \mathbb{K} \to \mathbb{R} \) be defined as

\[ H^{n,\phi}(u, (p, x')) := \int u^n (\underline{x})^p \phi((\underline{x})^p + x'). \]

Notice that then the collection of functions

\[ \mathcal{H} = \{ H^{n,\phi}(\cdot, \kappa) : n \in \mathbb{N}, \kappa \in \mathbb{K}, \phi \in C^1_b(\mathbb{R}_+^{1\downarrow n}) \} \]

is equal to \( \Pi^1 \), and thus obviously separates points in \( \mathcal{M}_1(\mathbb{U}) \).

**Proposition 4.1 (Duality relation).** For \( P_0 \in \mathcal{M}_1(\mathbb{U}) \), \( \kappa \in \mathbb{K} \), let \( U = (U_t)_{t \geq 0} \) and \( K = (K_t)_{t \geq 0} \) be solutions of the \((P_0, \Omega^\downarrow, \Pi^1)\) and \((\delta_\kappa, \Omega^\downarrow, G)\)-martingale problem, respectively. Then

\[ \mathbb{E}[H(U_t, \kappa)] = \mathbb{E}[H(u, K_t)], \]

for all \( t \geq 0 \) and \( H \in \mathcal{H} \).
5 PROOF. We shall establish that for $H_{n,\phi} \in \mathcal{H}$,

\begin{equation}
\Omega^1 H_{n,\phi}(\cdot, \kappa) (u) = \Omega^1 H_{n,\phi}(u, \cdot) (\kappa)
\end{equation}

Using the fact that $H_{n,\phi}$ is bounded the assertion then follows from Theorem 4.4.11 (with $\alpha = \beta = 0$) in [EK86].

We will verify (4.13) for the two components of the dynamics separately. Observe first that by (2.30) and (4.7),

\begin{equation}
\Omega^1 \text{grow} H_{n,\phi}((\cdot), (p, r'))(u) = 2 \cdot \int \nu^u (dr) \sum_{1 \leq i < j} \frac{\partial}{\partial r_{i,j}} \phi((x)_i^p + r')
\end{equation}

where we have used in the second equality that $\frac{\partial}{\partial r_{i,j}} \phi((x)_i^p + r') = 0$, whenever $i \sim_p j$.

Similarly, using $\theta_{k,l}$ from (2.32),

\begin{equation}
\Omega^1 \text{res} H_{n,\phi}((\cdot), (p, r'))(u) = \gamma \int \nu^u (dr) \sum_{\{\pi, \pi'\} \subseteq (p, r')} (\phi(\theta_{k,l}(\pi^p, \pi')^p + r') - \phi(\pi^p + r'))
\end{equation}

Combining (4.14) with (4.15) yields (4.13) and thereby completes the proof.

5. Martingale problems for tree-valued Moran dynamics. Fix $N \in \mathbb{N}$, and recall from (2.51) in Subsection 2.3 the tree-valued Moran dynamics $U^N = (U^N_t)_{t \geq 0}$ of population size $N$. In this section we will characterize the tree-valued Moran dynamics as unique solutions of a martingale problem. We will then use an approximation argument to establish the existence of the solution to the Fleming-Viot martingale problem.

Notice that the states of the tree-valued Moran dynamics with population size $N$ are restricted to

\begin{equation}
\mathbb{U}_N := \{ u = (U, r, \mu) \in \mathbb{U} : N\mu \in \mathcal{N}(U) \} \subset \mathbb{U}_c,
\end{equation}
where $\mathcal{N}(U)$ is the set of integer-valued measures on $U$. Moreover, if $u \in \mathbb{N}_N$, then $u$ can be represented by the pseudo-metric measure space

\[(\{1, 2, ..., N\}, r', N^{-1} \sum_{i=1}^{N} \delta_i)\]

for some pseudo-metric $r'$ on $\{1, \ldots, N\}$. In the following we refer to the elements $i \in \{1, 2, \ldots, N\}$ as the individuals of the population of size $N$.

By construction, the tree-valued Moran dynamics are derived from the following particle dynamics on the representative (5.2):

**Resampling.** At rate $\frac{\gamma}{N} > 0$, a resampling event occurs between two individuals $k, l$ such that distances to $l$ are replaced by distances to $k$. This implies, in particular, that the genealogical distance between $k$ and $l$ is set to be zero. Equivalently, the measure changes from $\mu$ to $\mu + \frac{1}{N} \delta_k - \frac{1}{N} \delta_l$.

**Distance growth.** The distance between any two different individuals $i, j$ grows at speed 2.

**Example 5.1 (Distance growth for various $N$).** We illustrate the effects of the distance growth for $N = 2$, $N = 4$ and large $N$. Consider the ultra-metric space of all leaves in the tree from Figure 2(a). The numbers indicate weights of atoms in $\mu$. After some small time $\varepsilon$, this ultra-metric space evolves due to distance growth to different trees, depending on $N$. For $N = 2$, whenever we sample two different individuals, they must be taken from the two leaves. Therefore the distance between the two points in the ultra-metric space grows. For $N = 4$, we may sample two (but not more) individuals without replacement from the same point in the above tree. We therefore may sample two individuals from the same leaf which then splits into two branches whose lengths grow. For large $N$, we may sample a lot of individuals from one and the same point and therefore split into many branches whose lengths grow.

5.1. **The martingale problem for a fixed population size $N$.** In this subsection we characterize the resampling and distance growth dynamics by a martingale problem.

Fix $N \in \mathbb{N}$. Similarly as in (2.3), for a metric space $(U, r)$, define a map
which sends a sequence of $N$ points to the matrix of mutual distances

$$R^{N,(U,r)}: \left\{ \begin{array}{l}
U^N \rightarrow \mathbb{R}^{(N/2)} \\
(x_1, \ldots, x_N) \mapsto (r(x_i, x_j))_{1 \leq i < j \leq N}.
\end{array} \right.$$  \hspace{1cm} (5.3)

For a metric measure space $(U,r,\mu)$ with $N\mu \in \mathcal{N}(U)$, let

$$\mu^{\otimes_1 N}(d(u_1, \ldots, u_N))$$

$$:= \mu(du_1) \otimes \frac{\mu - \frac{1}{N}\delta_{u_1}(du_2) \otimes \cdots \otimes \mu - \frac{1}{N}\sum_{k=1}^{N-1} \delta_{u_k}(du_N)}{1 - \frac{(N-1)}{N}},$$

the sampling (without replacement) measure and define the $N$ distance matrix distribution (without replacement) $\nu^{N,(U,r,\mu)}$ of $u = (U,r,\mu) \in \mathbb{U}_N$ by

$$\nu^{N,u} := (R^{N,(U,r)})_{\mu^{\otimes_1 N}} \in \mathcal{M}_1(\mathbb{R}_+^{(N/2)}).$$

Observe that $u \in \mathbb{U}_N$ is uniquely characterized by its $N$ distance matrix distribution.

Once more, it is obvious that $\nu^{N,(U,r,\mu)}$ depends on $(U,r,\mu)$ only through its equivalence class $(U,r,\mu) \in \mathbb{U}_N$ leading to the following definition.

**Fig 2.** Tree growth in finite Moran models. (a) The starting tree has only two distinct points. (b) In a population of size 2 these two points grow in distance while two or more individuals can be sampled from the same point for larger $N$. 

Definition 5.2 (N-distance matrix distribution). For $N \in \mathbb{N}$, the N distance matrix distribution $\nu_{N,u}$ (without replacement) of $u \in U_N$ is defined as the N distance matrix distribution $\nu_{N,(U,r,\mu)}$ of an arbitrary representative $(U,r,\mu)$ of the equivalence class $u = (U,r,\mu)$.

For a measurable, bounded $\phi : \mathbb{R}^{(N)}_+ \to \mathbb{R}$, introduce the polynomial $\Phi = \Phi_N^\phi$ by

$$\Phi(u) = \langle \nu_{N,u}, \phi \rangle := \int_{\mathbb{R}^{(N)}_+} \nu_{N,u}(dr) \phi(r).$$

Notice that in contrast to the space of all polynomials the space of all polynomials of this special form does not form an algebra. Put therefore

$$\Pi_N := \text{algebra generated by } \{\Phi_N^\phi : \phi \in \mathcal{B}(\mathbb{R}^{(N)}_+)\},$$

and

$$\Pi_N^1 := \text{algebra generated by } \{\Phi_N^\phi : \phi \in \mathcal{C}^1_b(\mathbb{R}^{(N)}_+)\}.$$

We define an operator $\Omega_{\text{grow},N} := \Omega_{\text{grow},N}^1 + \Omega_{\text{res},N}^1$ on $\Pi_N$ whose action on $\Pi_N^1$ is given by independent superposition of resampling and distance growth.

We begin with the distance growth operator $\Omega_{\text{grow},N}^1$. Let $1 \in \mathbb{R}^{(N)}_+$ denote the matrix with all entries equal to 1, and define

$$\sigma_p(q) := p + q.$$  

In periods of length $\varepsilon > 0$ without resampling the $N$ distance matrix distribution changes due to tree growth from $\nu_{N,u}$ to $(\sigma_{2N})_* \nu_{N,u}$. Therefore,

$$\Omega_{\text{grow},N}^1 \Phi_N^\phi := \lim_{\varepsilon \downarrow 0} \frac{1}{\varepsilon} \left( \langle \nu_{N,u}, \phi \circ \sigma_{2N} \rangle - \langle \nu_{N,u}, \phi \rangle \right) = \langle \nu_{N,u}, \text{div}(\phi) \rangle,$$

with div from (2.22).

For the resampling operator $\Omega_{\text{res},N}^1$, consider first the action on a representative $(U,r,\mu)$ of the form (5.2). Any resampling event in which the individual $l$ is replaced by a copy of the individual $k$ changes the measure from $\mu$ to $\mu + \frac{1}{N} \delta_k - \frac{1}{N} \delta_l$. 


Therefore, since
\[ \sum_{1 \leq k, l \leq N} (R_{N,(U,r)})_* (\mu + \frac{1}{N} \delta_k - \frac{1}{N} \delta_l)^{\otimes 1_N} = \sum_{1 \leq k, l \leq N} (\theta_{k,l})_* \nu^{N,*} \]
we obtain for \( u = (U, r, \mu) \) that
\[ \Omega_{\uparrow, N}^{1, \text{res}} \Phi_N(u) = \frac{\gamma}{2} \sum_{1 \leq k, l \leq N} \left( \langle (R_{N,(U,r)})_* (\mu + \frac{1}{N} \delta_k - \frac{1}{N} \delta_l)^{\otimes 1_N}, \phi \rangle - \langle (R_{N,(U,r)})_* \mu^{\otimes 1_N}, \phi \rangle \right) \]
\[ = \frac{\gamma}{2} \sum_{1 \leq k, l \leq N} \left( \langle \nu^{N,*}, \phi \circ \theta_{k,l} \rangle - \langle \nu^{N,*}, \phi \rangle \right). \]
It is easy to see that for given \( N \in \mathbb{N} \), \( \Pi_1^N \) separates points in \( U_N \). We can therefore use the operator \( (\Omega_{\uparrow, N}^{1, \text{res}}, \Pi_1^N) \) to characterize the tree-valued Moran models analytically.

**Proposition 5.3 (Tree-valued Moran dynamics).** Fix \( N \in \mathbb{N} \) and let \( \Phi^0 \in \mathcal{M}_1(U_N) \). The \( (\Phi^0, \Omega_{\uparrow, N}^{1, \text{res}}, \Pi_1^N) \)-martingale problem is well-posed.

**Proof.** Let \( r_0 \) in (2.50) be such that the law of \( (\{1, 2, \ldots, N\}, r_0, \frac{1}{N} \sum_{i=1}^N \delta_i) \) equals \( \Phi^0_N \). Then the tree-valued Moran dynamics defined in (2.51) solve the \( (\Phi^0, \Omega_{\uparrow, N}^{1, \text{res}}, \Pi_1^N) \)-martingale problem, by construction. This proves existence.

For uniqueness – following the same line of argument as given in Section 4 – one can check that the \( (\Phi^0, \Omega_{\uparrow, N}^{1, \text{res}}, \Pi_1^N) \)-martingale problem is dual to the tree-valued Kingman coalescent where the duality functions \( \Phi \in \Pi_1^N \) are smooth polynomials that involve sampling without replacement (see, for example, Corollary 3.7 in [GLW05] where a similar duality is proved on the level of the measure-valued processes).

5.2. Convergence to the Fleming-Viot generator. The goal of this subsection is to show that the operator for the tree-valued Fleming-Viot martingale problem is the limit of the operator for the tree-valued Moran martingale problems. This is one ingredient for the proof of Theorem 2 given in Section 8.

**Proposition 5.4.** Let \( \Phi \in \Pi_1^N \). There exist \( \Phi_1 \in \Pi_1^N, \Phi_2 \in \Pi_1^N, \ldots \) such that
\[ \lim_{N \to \infty} \sup_{u \in U_N} |\Phi_N(u) - \Phi(u)| = 0, \]
and

\begin{equation}
\lim_{N \to \infty} \sup_{u \in U_N} |\Omega_{1, N} \Phi_N(u) - \Omega^1 \Phi(u)| = 0.
\end{equation}

**Proof.** First, define the extension operator

\begin{equation}
\iota_N : \begin{cases} 
\mathbb{R}^N \to \mathbb{R}^N \\
(r_{i,j})_{1 \leq i < j \leq N} \mapsto (r_{i=N+j=N}, r_{i=N+j=N})_{1 \leq i < j}
\end{cases}
\end{equation}

where \(i_{\sim N} := 1 + ((i - 1) \mod N)\). Fix \(\Phi = \Phi_{n, \phi} \in \Pi_1^N \subseteq \mathcal{C}_b(\mathbb{R}_+^N)\). For \(N \geq n\) set \(\Phi_N := \Phi_{n, \phi} \circ \iota_N \in \Pi_N^1\). By the definition of the \(N\)-
distance matrix distribution of a representative \((5.5)\), there is a \(C > 0\) such that

\begin{equation}
\sup_{u \in U_N} |\Phi_N(u) - \Phi(u)| = \sup_{u \in U_N} \left| \langle \nu^{N, u}, \phi \circ \iota_N \rangle - \langle \nu^\ast, \phi \rangle \right|
\end{equation}

\begin{equation}
\leq \frac{C}{N} ||\phi||
\end{equation}

for all \(N \geq n\). This shows \((5.13)\). For \((5.14)\) observe that \(\Omega_{1, N} \Phi(u) = \langle \nu^\ast, \psi \rangle\) and \(\Omega_{1, N} \Phi_N(u) = \langle \nu^{N, u}, \tilde{\psi} \rangle\) for continuous, bounded functions \(\psi\) and \(\tilde{\psi}\) satisfying \(\tilde{\psi} = \psi \circ \iota_N\). Hence, \((5.14)\) follows from \((5.16)\). ∎

### 5.3. Coupling tree-valued Moran dynamics.

In this section we show how to couple two tree-valued Moran dynamics. In particular, using a metric on ultra-metric measure spaces introduced in [GPW09a], we show that the coupled processes become closer as time evolves (Proposition 5.8). This will be an important ingredient in showing the Feller property of the tree-valued Fleming-Viot dynamics stated in Theorem 1.

We fix \(N \in \mathbb{N}\) and \(I := \{1, ..., N\}\). Informally, we couple two tree-valued Moran dynamics by using the same resampling events. For this, recall the Poisson processes \(\eta = \{\eta_{i,j} ; i, j \in I\}\) from Section 2.3 which determine resampling events. Recall from (2.49) the notion of ancestors \(A_s(i, t), i \in \mathbb{N}\) and \(0 \leq s \leq t\).

**Definition 5.5 (Coupled tree-valued Moran dynamics).** Let \(r_0^1\) and \(r_0^2\) be two pseudo-metrics on \(I\), \(U_0^{N,k} := u_k^N := (I, r_0^k, \sum_{i=1}^N \delta_i), k = 1, 2\) and
If we define for $t > 0$, $\mathcal{U}_t^{N,k}$, $k = 1, 2$ to be given through $r_t^{n,k}$, $k = 1, 2$, by (2.50) with $r_0$ replaced by $r_k^0$, $k = 1, 2$, respectively, then $(\mathcal{U}_t^{N,1}, \mathcal{U}_t^{N,2})_{t \geq 0}$ are referred to as the coupled tree-valued Moran dynamics started in $(u_1^N, u_2^N)$.

In order to compare $\mathcal{U}_t^{N,1}$ and $\mathcal{U}_t^{N,2}$ we use the following metric on $\mathcal{U}$ introduced in [GPW09a, Section 10].

**Definition 5.6 (Modified Eurandom metric).** The modified Eurandom distance between $u_1 = (U_1, r_1, \mu_1)$ and $u_2 = (U_1, r_1, \mu_1) \in \mathcal{U}$ is given by

$$d'_{\text{Eur}}(u_1, u_2) := \inf_{\tilde{\mu}} \int_{U_1} \int_{U_1} \tilde{\mu}(d(i_1, i_2)) \tilde{\mu}(d(j_1, j_2)) \left| r_1(i_1, j_1) - r_2(i_2, j_2) \right| \wedge 1$$

where the infimum is taken over all couplings of $\mu_1$ and $\mu_2$, i.e.,

$$\tilde{\mu} \in \{ \tilde{\mu}' \in M_1(U_1 \times U_2) : (\pi_k)_* \tilde{\mu}' = \mu_k, k = 1, 2 \},$$

with $\pi_k : U_1 \times U_2 \to U_k$ denoting the projection on the $k$th coordinate, $k = 1, 2$.

**Remark 5.7 (Connection to the Gromov-weak topology).** As noted in Proposition 10.5 in [GPW09a], the distance $d'_{\text{Eur}}$ is a metric and metrizes the Gromov-weak topology (but is not complete). In particular, for random objects $\mathcal{U}, \mathcal{U}_1, \mathcal{U}_2, \ldots$ in $\mathcal{U}$ which are all defined on the one probability space, we find that $\mathcal{U}_n \Rightarrow \mathcal{U}$ if $P[d'_{\text{Eur}}(\mathcal{U}_n, \mathcal{U})] \to 0$, as $n \to \infty$.

**Proposition 5.8 (Coupled tree-valued Moran dynamics get closer).** Let $(\mathcal{U}_t^{N,1}, \mathcal{U}_t^{N,2})_{t \geq 0}$ be the coupled tree-valued Moran dynamics started in $(u_1^N, u_2^N)$. Then for all $t > 0$,

$$d'_{\text{Eur}}(\mathcal{U}_t^{N,1}, \mathcal{U}_t^{N,2}) \leq d'_{\text{Eur}}(u_1^N, u_2^N),$$

almost surely.

**Proof.** We use the notation introduced in Definition 5.5. W.l.o.g. we write $u_k^N := (\mathcal{I}, r_0^k, \frac{1}{N} \sum_{i=1}^N \delta_i)$, $k = 1, 2$ and have

$$d'_{\text{Eur}}(u_1^N, u_2^N) := \frac{1}{N} \sum_{i,j} |r_0^1(i, j) - r_0^2(i, j)| \wedge 1$$
which can be arranged using isometries of $u_1^N$ or $u_2^N$. By the definition of the coupled tree-valued Moran dynamics (recall also (2.50))

\begin{equation}
|r_t^{n,1}(i,j) - r_t^{n,2}(i,j)| = |r_1(A_0(i,t), A_0(j,t)) - r_2(A_0(i,t), A_0(j,t))|.
\end{equation}

In particular, for all $t \geq 0$,

\begin{equation}
\inf_{\sigma \in \Sigma} \frac{1}{N} \sum_{i,j} \left| r_t^{n,1}(\sigma(i), \sigma(j)) - r_t^{n,2}(\sigma(i), \sigma(j)) \right| \wedge 1
\end{equation}

\begin{equation}
\leq \frac{1}{N} \sum_{i,j} \left| r_0(A_0(i,t), A_0(j,t)) - r_0(A_0(i,t), A_0(j,t)) \right| \wedge 1
\end{equation}

\begin{equation}
\leq \frac{1}{N} \sum \left| r_0(i,j) - r_0(i,j) \right| \wedge 1
\end{equation}

\begin{equation}
d'_{\text{Eur}}(u_1^N, u_2^N),
\end{equation}

as claimed.

6. Limit points are compact. Recall from (2.51) the definition of the tree-valued Moran dynamics $\mathcal{U}^N$ with population size $N \in \mathbb{N}$ (compare also Figure 1). In this section we show that potential limit points of the sequence \{U^N; N \in \mathbb{N}\} have cadlag sample paths in $\mathcal{U}$ and take values in the space of compact metric measure spaces for $t > 0$. In Subsection 6.1 we state a sufficient condition for relative compactness in $\mathcal{M}_c$. In Subsection 6.2 we apply this criterion to show that the sequence of Moran models $\mathcal{U}^N$ satisfies the compact containment condition.

6.1. Relative compactness in $\mathcal{M}_c$. We give a criterion for a set to be relatively compact in $\mathcal{M}_c$. In this subsection we are dealing with general (not necessarily ultra-) metric measure spaces. We define for $x \in \mathcal{M}$ the distance distribution $w_x \in \mathcal{M}_1(\mathbb{R}_+)$ by

\begin{equation}
w_x(A) := \nu^x \{ r \in (\mathbb{R}_+) : r_{1,2} \in A \},
\end{equation}

for all $A \in \mathcal{B}(\mathbb{R}_+)$.

The relative compactness criterion reads as follows:

**Proposition 6.1 (Relative compactness in $\mathcal{M}_c$).** A set $\Gamma \subseteq \mathcal{M}_c$ is relatively compact in the Gromov-weak topology on $\mathcal{M}_c$ if the following two conditions are satisfied.
6 LIMIT POINTS ARE COMPACT

(i) \{w_\epsilon : x \in \Gamma\} is tight in \mathcal{M}_1(\mathbb{R}_+).

(ii) For all \epsilon > 0 there exists \(N_\epsilon \in \mathbb{N}\) such that for all \(x \in \Gamma\) and \((X, r, \mu) \in x\), the metric space \((\text{supp} (\mu), r)\) can be covered by \(N_\epsilon\) open balls of radius \(\epsilon\).

Remark 6.2 (Relative compactness criterion is only sufficient). By Theorem 2 of [GPW09a], (i) is a necessary condition for relative compactness in \(M\). Note that (ii) is not necessary for relative compactness in \(M_c\): Consider, for example,

\[
\Gamma = \{x_n = (\{0, 1, \ldots, n\}, r_{\text{eucl}}, \text{Bin}(n, \frac{1}{n})) : n \in \mathbb{N}\} \subset M_c.
\]

Since \(x_n \to (\mathbb{N}, r_{\text{eucl}}, \delta_0)\), as \(n \to \infty\), the set \(\Gamma\) is relatively compact, but (ii) does not hold.

The proof of Proposition 6.1 is based on two Lemmata. Recall that for a metric space \((X, r)\) an \(\epsilon\)-separated set is a subset \(X' \subseteq X\) such that \(r(x', y') > \epsilon\), for all \(x', y' \in X'\) with \(x' \neq y'\).

Lemma 6.3 (Relation between \(\epsilon\)-balls and \(\epsilon\)-separated nets). Fix \(N \in \mathbb{N}\), a metric space \((X, r)\) with \(#X \geq N + 1\) and \(\epsilon > 0\). The following hold.

(i) If \((X, r)\) can be covered by \(N\) open balls of radius \(\epsilon\), then \((X, r)\) has no \(2\epsilon\)-separated sets of cardinality \(k \geq N + 1\).

(ii) If \((X, r)\) has no \(\epsilon\)-separated set of cardinality \(N + 1\), then \((X, r)\) can be covered by \(N\) closed balls of radius \(\epsilon\).

Proof. (i) Assume that \(x_1, \ldots, x_N \in X\) are such that \(X = \bigcup_{i=1}^{N} B_\epsilon(x_i)\), where we denote by \(B_\epsilon(x)\) the open ball around \(x \in X\) of radius \(\epsilon > 0\). Choose \((N + 1)\) distinct points \(y_1, \ldots, y_{N+1} \in X\). By the pigeonhole principle, two of the points must fall into the same ball \(B_\epsilon(x_i)\), for some \(i = 1, \ldots, N\), and are therefore in distance smaller than \(2\epsilon\). Hence \(\{y_1, \ldots, y_{N+1}\}\) is not \(2\epsilon\)-separated. Since \(y_1, \ldots, y_{N+1} \in X\) were chosen arbitrarily, the claim follows.

(ii) Again, we proceed by contradiction. Let \(K\) be the maximal possible cardinality of an \(\epsilon\)-separated set in \((X, r)\). By assumption, \(K \leq N\). Assume that \(S^K_\epsilon := \{x_1, \ldots, x_K\}\) is an \(\epsilon\)-separated set in \((X, r)\). We claim that \(X = \bigcup_{i=1}^{K} B_\epsilon(x_i)\), where \(B_\epsilon(x)\) denotes the closed ball around \(x \in X\) with radius \(\epsilon > 0\). Indeed, assume, to the contrary, that \(y \in X\) is such that \(r(y, x_i) > \epsilon\), for all \(i = 1, \ldots, K\), then \(S^K_\epsilon \cup \{y\}\) is an \(\epsilon\)-separated set of cardinality \(K + 1\), which gives the contradiction.
Lemma 6.4. Fix $\varepsilon > 0$ and $N \in \mathbb{N}$. Let $\chi = (X, r, \mu)$, $\chi_1 = (X_1, r_1, \mu_1)$, $\chi_2 = (X_2, r_2, \mu_2)$, ... be elements of $\mathbb{M}$ such that $\chi_n \to \chi$ in the Gromov-weak topology, as $n \to \infty$. If $(\text{supp}(\mu_1), r_1)$, $(\text{supp}(\mu_2), r_2)$, ... can be covered by $N$ open balls of radius $\varepsilon$ then $(\text{supp}(\mu), r)$ can be covered by $N$ closed balls of radius $2\varepsilon$.

Proof. Define the restriction operator $\rho_N((r_{i,j})_{1 \leq i < j}^N) := (r_{i,j})_{1 \leq i < j}^N$. By Lemma 6.3(i), there is no $n \in \mathbb{N}$ for which $(\text{supp}(\mu_n), r_n)$ has a $2\varepsilon$-separated set of cardinality $N + 1$. Set $B_{2\varepsilon} := (2\varepsilon, \infty)^{N+1}$. Notice that $\rho_{-1,N+1}B_{2\varepsilon}$ is open. Moreover, $(\text{supp}(\mu), r)$ has a $2\varepsilon$-separated set of cardinality $N + 1$ if and only if $(\rho_{N+1})_* \nu^r(B_{2\varepsilon}) > 0$. However,

\begin{equation}
0 \leq (\rho_{N+1})_* \nu^r(B_{2\varepsilon}) \leq \liminf_{n \to \infty} (\rho_{N+1})_* \nu^r_n(B_{2\varepsilon}) = 0
\end{equation}

by Theorem 5(b) in [GPW09a] together with the Portmanteau theorem, therefore $(\rho_{N+1})_* \nu^r(B_{2\varepsilon}) = 0$. By Lemma 6.3(ii), $(\text{supp}(\mu), r)$ can therefore be covered by $N$ closed balls of radius $2\varepsilon$.

Proof of Proposition 6.1. Assume (i) and (ii) hold for a set $\Gamma \subseteq \mathbb{M}_c$. First note that by Theorem 2 in [GPW09a] the set $\Gamma$ is relatively compact in $\mathbb{M}$. It remains to show that every limit point of $\Gamma$ is compact. To see this take $\chi \in \mathbb{M}$ and $\chi_1, \chi_2, \ldots \in \Gamma$ such that $\chi_n \to \chi$ in the Gromov-weak topology, as $n \to \infty$, and let $\varepsilon > 0$. By Assumption(ii) together with Lemma 6.4, $(\text{supp}(\mu), r)$ can be covered by $N_{\varepsilon/2}$ closed balls of radius $\varepsilon$. Therefore, $\chi$ is totally bounded which implies $\chi \in \mathbb{M}_c$, and we are done.

6.2. The compact containment condition for Moran models. The following result is an important step in the proof of tightness of the family of tree-valued Moran dynamics. Recall the distance distribution $w_0$ from (6.1). The next result states that the family $\{U^N; N \in \mathbb{N}\}$ satisfies the following compact containment conditions.

Proposition 6.5 (Compact containment). Let for each $N \in \mathbb{N}$, $U^N = (U^N_t)_{t \geq 0}$ be the tree-valued Moran dynamics with population size $N$.

(i) Assume that the family $\{w_0^N : N \in \mathbb{N}\}$ is tight in $\mathcal{M}_1(\mathbb{R}_+^+)$. Then, for all $T > 0$ and all $\varepsilon > 0$, there exists a compact set $\Gamma_{\varepsilon,T} \subseteq \mathbb{U}_c$ such that

\begin{equation}
\inf_{N \in \mathbb{N}} \mathbb{P}\{U^N_t \in \Gamma_{\varepsilon,T} \text{ for all } t \in [\varepsilon, T]\} > 1 - \varepsilon.
\end{equation}
(ii) Assume that the family $(U^N_0)_{N=1,2,...}$ is tight in $\mathcal{M}_1(\mathbb{U})$. Then, for all $T > 0$ and all $\varepsilon > 0$, there exists a compact set $\tilde{\Gamma}_{\varepsilon,T} \subseteq \mathbb{U}$ such that

$$\inf_{N \in \mathbb{N}} \mathbb{P}\{U^N_t \in \tilde{\Gamma}_{\varepsilon,T} \text{ for all } t \in [0,T]\} > 1 - \varepsilon.$$  

The proof relies on the graphical representation of the tree-valued Moran dynamics as illustrated in Figure 1. Recall from (2.49) the ancestor $A_{s}(i,t)$ back at time $s \leq t$ of the individual $i \in \{1,2,...,N\}$ living at time $t$. Denote by

$$S^N_\varepsilon(t) := \#\{A_{t-\varepsilon}(i,t) : i \in \{1,2,...,N\}\},$$

the number of ancestors a time $\varepsilon > 0$ back of the population of size $N$ at time $t$.

**Lemma 6.6 (Uniform bounds on the number of ancestors).**

(i) There exists a constant $C \in (0,\infty)$ such that for all $t > 0$ and $\varepsilon \in (0,\gamma^{3/16} \wedge t)$,

$$\sup_{N \in \mathbb{N}} \mathbb{P}\{S^N_\varepsilon(t) > \varepsilon^{-4/3}\} \leq C \varepsilon^2.$$  

(ii) For $T > 0$, there exists a constant $C = C(T) \in (0,\infty)$ such that for all $\varepsilon \in (0,\gamma^{3/16} \wedge T)$,

$$\sup_{N \in \mathbb{N}} \mathbb{P}\{\sup_{t \in [\varepsilon,T]} S^N_\varepsilon(t) > \varepsilon^{-4/3}\} \leq CT \varepsilon.$$  

**Proof.** (i) W.l.o.g. we assume that $N \geq \varepsilon^{-4/3}$. Consider the times

$$T^N_k(t) := t \wedge \inf \{\varepsilon > 0 : S^N_\varepsilon(t) \leq k\},$$

for $k = 1,2,...$. Since any pair of individuals coalesces at rate $\gamma$, $T^N_k$ is stochastically bounded by the sum of $(N-k)$ independent random variables $X_N,...,X_{k+1}$, where $X_i$ is exponentially distributed with parameter $\gamma(i^2)$, for $i = k+1,...,N$. Hence, for $k = 1,2,...,$

$$\mathbb{E}[T^N_k(t)] \leq \frac{1}{\gamma} \sum_{i=k+1}^{N} \binom{i}{2}^{-1} = \frac{2}{\gamma} \left(\frac{1}{k} - \frac{1}{N}\right) \leq \frac{2}{\gamma k},$$
and

\[(6.11) \quad \text{Var}[T_k^N(t)] \leq \frac{1}{\gamma^2} \sum_{i=k+1}^{N} \left( \frac{i}{2} \right)^{-2} \leq C' \gamma^2 k^3\]

for some $C' > 0$ which does not dependent of $t$. Here we have used that, for any real-valued random variable $X$ with second moments and all $t \in \mathbb{R}$,

\[(6.12) \quad \text{Var}[X \wedge t] = \text{Var}[(X - \mathbb{E}[X]) \wedge (t - \mathbb{E}[X])]\]

\[
\leq \mathbb{E}[((X - \mathbb{E}[X]) \wedge (t - \mathbb{E}[X]))^2] \\
\leq \mathbb{E}[(X - \mathbb{E}[X])^2] \\
= \text{Var}[X].
\]

Thus for all $\varepsilon \leq \frac{\gamma^2}{10} \wedge t$,

\[(6.13) \quad P\left\{ S^N_\varepsilon(t) > \varepsilon^{-4/3} \right\} = P\left\{ T^N_{\varepsilon - 4/3}(t) > \varepsilon \right\} \]

\[
\leq P\left\{ T^N_{\varepsilon - 4/3}(t) - \mathbb{E}[T^N_{\varepsilon - 4/3}(t)] \geq \varepsilon - \frac{2}{\gamma} \left\lceil \varepsilon^{-4/3} \right\rceil^{-1} \right\} \]

\[
\leq \frac{\text{Var}[T^N_{\varepsilon - 4/3}(t)]}{(\varepsilon - \frac{2}{\gamma} \left\lceil \varepsilon^{-4/3} \right\rceil^{-1})^2} \\
\leq C \varepsilon^2,
\]

for some $C > 0$.

(ii) Fix $N \in \mathbb{N}$, $T > 0$ and $\varepsilon \in (0, \frac{\gamma^2}{10} \wedge T)$, and let $t \in [\varepsilon, T]$. Observe that for all $s \in [0, t]$ and $\delta > 0$ such that $[s - \delta, s] \subseteq [t - \varepsilon, t]$,

\[(6.14) \quad S^N_\delta(s) \geq S^N_\varepsilon(t),\]

almost surely. Hence, for all $k > 0$,

\[(6.15) \quad \sup_{t \in [k\frac{T}{2} \cdot (k+1)\frac{T}{2}]} S^N_\varepsilon(t) \leq S^N_{\varepsilon/2}(k\frac{T}{2}).\]

Thus

\[(6.16) \quad P\left\{ \sup_{t \in [\varepsilon,T]} S^N_\varepsilon(t) > \varepsilon^{-4/3} \right\} \leq P\left\{ \sup_{k=1, \ldots, \lfloor 2T/\varepsilon \rfloor} S^N_{\varepsilon/2}(k\frac{T}{2}) > \varepsilon^{-4/3} \right\} \]

\[
\leq \sum_{k=1}^{\lfloor 2T/\varepsilon \rfloor} P\left\{ S^N_{\varepsilon/2}(k\frac{T}{2}) > \varepsilon^{-4/3} \right\} \\
\leq 2CT\varepsilon,
\]

and (6.8) follows.
PROOF OF PROPOSITION 6.5. In the whole proof we fix $T > 0$ and $\varepsilon > 0$. W.l.o.g. we take $\varepsilon < \frac{\gamma}{16} \wedge T$ and set $\varepsilon_k := \frac{\varepsilon}{2^{C(T)}} 2^{-k}$ with $C = C(T)$ from Lemma 6.6(ii).

(i) For $u = (U, r, \mu) \in \mathbb{U}$, denote by
\[(6.17) N_\varepsilon(u) := \min \{ N' \in \mathbb{N} : (\text{supp}(\mu), r) \text{ can be covered by } N' \text{ balls of radius } \varepsilon \}.
\]

By assumption, the family $\{w_{U_0^N} : N \in \mathbb{N}\}$ is tight, and we can therefore choose a constant $C_\varepsilon > 0$ such that
\[(6.18) w_{U_0^N}([C_\varepsilon; \infty)) < \varepsilon,
\]
for all $N \in \mathbb{N}$. Put
\[(6.19) \Gamma_{\varepsilon,T} := \Gamma_{1,\varepsilon,T} \cap \Gamma_{2,\varepsilon,T},
\]
where for $i = 1, 2$,
\[(6.20) \Gamma_{i,\varepsilon,T} := \bigcap_{k=1}^{\infty} \Gamma_{i,\varepsilon,T,k}
\]
with
\[(6.21) \Gamma_{1,\varepsilon,T,k} := \{ u \in \mathbb{U}_c : w_u([C_{\varepsilon_k} + 2T; \infty)) \leq \varepsilon_k \},
\]
and
\[(6.22) \Gamma_{2,\varepsilon,T,k} := \{ u \in \mathbb{U}_c : N_{2\varepsilon_k}(u) \leq \varepsilon_k^{-4/3} \}.
\]
Then $\Gamma_{\varepsilon,T}$ is relatively compact in $\mathbb{U}_c$ equipped with the Gromov-weak topology, by Proposition 6.1.

We next show that (6.4) holds. Notice first that (6.18) implies that
\[(6.23) \sup_{N \in \mathbb{N}, 0 \leq t \leq T} w_{U_t^N}([C_\varepsilon + 2T; \infty)) < \varepsilon,
\]
for all $\varepsilon > 0$, almost surely, since for any pair of two points the distance at any time $t \geq 0$ is not larger than $2t$ plus their initial distance. Hence,
\[(6.24) \mathbb{P}\{U_t^N \in \Gamma_{1,\varepsilon,T} \text{ for all } t \in [0, T]\} = 1.
\]
Moreover, we find that for all \( N \in \mathbb{N} \),
\[
\begin{align*}
P\{ \mathcal{U}_t^N \in \Gamma_{\varepsilon,T,k}^2 \text{ for all } t \in [\varepsilon_k, T] \} \\
= 1 - P\left( \bigcup_{t \in [\varepsilon_k, T]} \{ N_{2\varepsilon_k}(\mathcal{U}_t^N) > \varepsilon_k^{-4/3} \} \right) \\
= 1 - P\{ \sup_{t \in [\varepsilon_k, T]} S_{\varepsilon_k}^N(t) > \varepsilon_k^{-4/3} \}
\geq 1 - CT\varepsilon_k
\end{align*}
\]
(6.25)

by Lemma 6.6(ii). Hence
\[
\begin{align*}
P\{ \mathcal{U}_t^N \in \Gamma_{\varepsilon,T}^2 \text{ for all } t \in [\varepsilon, T] \} \\
\geq 1 - \sum_{k=1}^{\infty} P\{ \mathcal{U}_t^N \notin \Gamma_{\varepsilon,T,k}^2 \text{ for at least one } t \in [\varepsilon_k, T] \}
\geq 1 - \varepsilon
\end{align*}
\]
(6.26)

and we are done.

(ii) The family \( \{ \mathcal{U}_t^N = (U_0^N, r_0^N, \mu_0^N); N \in \mathbb{N} \} \) is tight by assumption. That is, for \( \varepsilon > 0 \) there is a compact set \( \tilde{\Gamma}_{\varepsilon} \subseteq \mathcal{U} \) such that \( \inf_{N \in \mathbb{N}} P\{ \mathcal{U}_t^N \in \tilde{\Gamma}_{\varepsilon} \} \geq 1 - \varepsilon \).

By the characterization of compactness given in Part(c) of Theorem 7.1 in [GPW09a] a subset \( \Gamma \subseteq \mathcal{U} \) is pre-compact if and only if for all \( \eta > 0 \) there exists a number \( N_\eta \in \mathbb{N} \) such that for all \( (U, r, \mu) \in \Gamma \) there is a subset \( U_\eta \subseteq U \) with
- \( \mu(U_\eta) \geq 1 - \eta \),
- \( U_\eta \) can be covered by at most \( N_\eta \) balls of radius \( \eta \), and
- \( U_\eta \) has diameter at most \( N_\eta \).

Hence, if \( \varepsilon, \eta > 0 \) are fixed, we can find a number \( N_{\varepsilon,\eta} \) such that for all \( N \in \mathbb{N} \) the following event occurs with probability at least \( 1 - \varepsilon \): if \( (U_0^N, r_0^N, \mu_0^N) \in \mathcal{U}_0^N \) there is \( V_{\varepsilon,\eta} = \{ u_1, \ldots, u_{N_{\varepsilon,\eta}} \} \subseteq U_0^N \) such that \( \mu_0^N(B_\eta(V_{\varepsilon,\eta})) > 1 - \eta \)

where
\[
B_\eta(V) := \bigcup_{x \in V} B_\eta(x)
\]
(6.27)

for \( V \subseteq U_0^N \). For \( k \in \mathbb{N} \) we set \( N_k := N_{\varepsilon_k, \varepsilon_k^2} \) and for \( N \in \mathbb{N} \) we take \( V_{N,k} \subseteq U_0^N \) with \#\( V_{N,k} = N_k \) such that
\[
P\{ \mu_0^N(B_{\varepsilon_k^2}(V_{N,k})) > 1 - \varepsilon_k^2 \} > 1 - \varepsilon_k
\]
(6.28)
We consider the set
\[(6.29) \hat{\Gamma}_\epsilon := \Gamma_{\epsilon,T}^1 \cap (\Gamma_{\epsilon,T}^2 \cup \Gamma_{\epsilon}^3)\]
with $\Gamma_{\epsilon,T}^1$ and $\Gamma_{\epsilon,T}^2$ from (6.19), and let
\[(6.30) \Gamma_{\epsilon}^3 := \bigcap_{k=1}^{\infty} \Gamma_{\epsilon,k},\]
and
\[(6.31) \Gamma_{\epsilon,k} := \{(U,r,\mu) \in U : \exists V \subseteq U, \#V = N_k, \mu(B_{2\epsilon_k}(V)) > 1 - \epsilon_k\}.\]

The set $\hat{\Gamma}_\epsilon$ is compact in $U$ as a finite union of compact sets. Furthermore, recalling the notion of an ancestor $A_0(t,u)$ of $u$ living at time $t$ back at time $0$ from (2.49),
\[(6.32) \liminf_{N \to \infty} \mathbb{P}\{\mathcal{U}_t^N \in \Gamma_{\epsilon,T,k}^3 \text{ for all } t \in [0;\epsilon_k]\}\]
\[\geq 1 - \limsup_{N \to \infty} \mathbb{P}\left\{ \inf_{t \in [0,\epsilon_k]} \sup_{V \subseteq U_t^N, |V| = N_k} \mu_t^N(B_{2\epsilon_k}(V)) \leq 1 - \epsilon_k \right\}\]
\[\geq 1 - \limsup_{N \to \infty} \mathbb{P}\left\{ \inf_{t \in [0,\epsilon_k]} \mu_t^N(B_{\epsilon_k}(\{u : A_0(u,t) \in B_{\epsilon_k}(V_{N,k})\}) \leq 1 - \epsilon_k \right\}\]
\[\geq 1 - \limsup_{N \to \infty} \mathbb{P}\left\{ \sup_{t \in [0,\epsilon_k]} \frac{1}{N} \#\{u \in U_t^N : A_0(u,t) \notin B_{\epsilon_k}(V_{N,k})\} > \epsilon_k \right\}\]
\[\geq 1 - \mathbb{P}\{ \sup_{t \in [0,\epsilon_k]} Z_{\epsilon_k}^t > \epsilon_k \}\]
\[\geq 1 - \epsilon_k^{-1} \mathbb{P}[Z_{\epsilon_k}^t = 1 - \epsilon_k]\]

with $Z^z$ denoting the Wright-Fisher diffusion starting in $z \in (0,1)$, i.e., the unique strong solution of $Z_t^z = z + \int_0^t \sqrt{\gamma Z_s^z(1 - Z_s^z)} dB_s$. In the above calculation we made use of the following: in the second inequality that at most $N_k$ balls of radius $2\epsilon_k$ in $U_t^N$, $0 \leq t \leq \epsilon_k$, cover the descendants of $B_{\epsilon_k}(V_{N,k})$; for the forth inequality the fraction of individuals at time $t$ whose ancestors back at time 0 don’t live in the $\epsilon_k^2$-neighborhood of $V_{N,k}$ evolves as the fraction of one of the two alleles of a two-allele Moran model which is known to converge weakly as a process towards the Wright-Fisher-diffusion which starts in $\epsilon_k^2$. In the fifth inequality we used Doob’s martingale inequality and the Chebychev inequality.

Combining (6.25) with (6.32) yields that
\[(6.33) \liminf_{N \to \infty} \mathbb{P}\{\mathcal{U}_t^N \in \Gamma_{\epsilon,T}^2 \cup \Gamma_{\epsilon,T}^3 \text{ for all } t \in [0;T]\} \geq 1 - \sum_{k=1}^{\infty} 2\epsilon_k \geq 1 - \frac{\epsilon}{CT}\]
which together with (6.24) gives the claim.

7. Limit points have continuous paths. It is well-known that the measure-valued Fleming-Viot process has continuous paths (e.g., [Daw93]). In this section we show that the same is true for the tree-valued Fleming-Viot dynamics by controlling the jump sizes in the approximating sequence of Moran models.

Recall from (2.51) in Subsection 2.3 the definition of a Moran model $U^N$ of population size $N \in \mathbb{N}$.

**Proposition 7.1** (Limit points have continuous paths). If $U^N \xrightarrow{N \to \infty} U$ for some process $U$ with sample paths in the Skorohod space, $\mathcal{D}_U([0, \infty))$, of c.c.l.g. functions from $[0, \infty)$ to $U$, then $U \in \mathcal{C}_U([0, \infty))$, almost surely.

**Remark 7.2** (The Gromov-Prohorov metric). In the proof we need a metric generating the Gromov-weak topology on $\mathcal{M}$. We use the Gromov-Prohorov metric $d_{\text{GPr}}$ defined as in [GPW09a]: For $x, y \in \mathcal{M}$ with $(X, r_X, \mu_X) \in x$ and $(Y, r_Y, \mu_Y) \in y$, put

$$(7.1) \quad d_{\text{GPr}}(x, y) := \inf_{(\varphi_X, \varphi_Y, Z)} d_{\text{Fr}}(\varphi_X \ast \mu_X, \varphi_Y \ast \mu_Y),$$

where the infimum is taken over isometric embeddings $\varphi_X$ and $\varphi_Y$ from $\text{supp}(\mu_X)$ and $\text{supp}(\mu_Y)$, respectively, into some common metric space $(Z, r_Z)$, and the Prohorov metric on $(Z, r_Z)$ is given by

$$(7.2) \quad d_{\text{Fr}}(\nu, \nu') = \inf \{ \varepsilon > 0 : \nu(A) \leq \nu'(B_\varepsilon(A)) + \varepsilon, \text{ for all closed } A \subseteq Z\},$$

where $B_\varepsilon(A)$ is defined as in (6.27). As shown in Theorem 5 of [GPW09a], the Gromov-Prohorov metric generates the Gromov-weak topology.

**Proof of Proposition 7.1.** Recall from Section 2.3 the construction of the tree-valued Moran dynamics $U^N$ based on Poisson point processes $\{\eta^{i,j}; 1 \leq i, j \leq N\}$ (compare also Figure 1). Note that the tree-valued Moran dynamics have paths in $\mathcal{D}_{U^c}(\mathbb{R}^+)$, almost surely.
If \( \eta^{ij}\{t\} = 0 \) for all \( 1 \leq i \neq j \leq N \), then \( U_t^N = U_t^N \). Otherwise, if \( \eta^{ij}\{t\} = 1 \), for some \( 1 \leq i \neq j \leq N \), then

\[
\begin{align*}
    d_{\text{GPTR}}(U_{t-}^N, U_t^N) &= d_{\text{GPTR}}(\{\{1, 2, \ldots, N\}, r_{t-}^N, \frac{1}{N} \sum_{k=1}^{N} \delta_k\}, \{\{1, 2, \ldots, N\}, r_{t}^N, \frac{1}{N} \sum_{k=1}^{N} \delta_k\}) \\
    &\leq d_{Pr}^{(\{1, 2, \ldots, N\}, r_{t-})} \left( \frac{1}{N} \sum_{k=1}^{N} \delta_k, \frac{1}{N} \delta_i - \frac{1}{N} \delta_j + \frac{1}{N} \sum_{k=1}^{N} \delta_k \right) \\
    &\leq \frac{2}{N},
\end{align*}
\]

and therefore

\[
\int_0^\infty dT e^{-T} \sup_{t \in [0, T]} d_{\text{GPTR}}(U_{t-}^N, U_t^N) \leq \frac{2}{N},
\]

for all \( T > 0 \) and almost all sample paths \( U^N \). Hence the assertion follows by Theorem 3.10.2 in [EK86].

8. Proofs of the main results (Theorems 1, 2, 3). In this section we give the proof of the main results stated in Section 2. Theorems 1 and 2 are proved simultaneously.

**Proof of Theorems 1 and 2.** Fix \( P_0 \in \mathcal{M}_1(U) \). Recall, for each \( N \in \mathbb{N} \), the state-space \( U_N \), and the \( U_N \)-valued Moran dynamics, \( U^N = (U_t^N)_{t \geq 0} \), from (5.1) and (2.51), respectively. Furthermore, let for each \( N \in \mathbb{N} \), \( P_0^N \in \mathcal{M}_1(U_N) \) be given such that \( P_0^N \Rightarrow P_0 \), as \( N \to \infty \).

By Proposition 5.3, the \( (P_0^N, \Omega^N, \Pi^N_U) \)-martingale problem is well-posed, and is solved by \( U^N \). Proposition 5.4 implies with a standard argument (see, for example, Lemma 4.5.1 in [EK86]) that if \( U^N \Rightarrow U \), for some \( U \in \mathcal{D}_U([0, \infty)) \), as \( N \to \infty \), then \( U \) solves the \( (P_0, \Omega^1, \Pi^1_U) \)-martingale problem. Hence for existence of solutions of the \( (P_0^N, \Omega^N, \Pi^N_U) \)-martingale problem is tight, or equivalently by Remark 2.9 combined with Remark 4.5.2 in [EK86] that the compact containment condition in \( U \) holds. However, the latter was proved in Proposition 6.5(ii).

By standard theory (see, for example, Theorem 4.4.2 in [EK86]), uniqueness of the \( (P_0, \Omega^1, \Pi^1_U) \)-martingale problem follows from uniqueness of the one-dimensional distributions of solutions of the \( (P_0^N, \Omega^N, \Pi^N_U) \)-martingale
problem. The latter can be verified using the duality of the tree-valued Fleming-Viot dynamics to the tree-valued Kingman coalescent, \( \mathcal{K} := (\mathcal{K}_t)_{t \geq 0} \), as defined in (1.2). That is, if \( \mathcal{U} = (\mathcal{U}_t)_{t \geq 0} \) is a solution of the \((\mathbb{P}_0, \Omega^1, \Pi^1)\)-martingale problem, then (1.12) holds for all \( \kappa \in \mathbb{K} \), \( t \geq 0 \) and \( H \in \mathcal{H} \). Since \( \mathcal{H} \) is separating in \( \mathcal{M}_1(\mathbb{U}) \) by Proposition 4.1(i), uniqueness of the one-dimensional distributions follows.

So far we have shown that the \((\mathbb{P}_0, \Omega^1, \Pi^1)\)-martingale problem is well-posed and its solution arises as the weak limit of the solutions of the \((\mathbb{P}_N^0, \Omega^1, \Pi^1_N)\)-martingale problems. In particular, the tree-valued Moran dynamics converge to the tree-valued Fleming-Viot dynamics. Hence we have shown Theorem 1 and Theorem 2.

**Proof of Proposition 2.15.** (i), (ii) The tree-valued Fleming-Viot dynamics is the weak limit of tree-valued Moran dynamics. Hence, Propositions 6.5(i) and 7.1 imply that the tree-valued Fleming-Viot dynamics have values in the space of compact ultra-metric measure spaces for each \( t > 0 \) and have continuous paths, respectively, almost surely.

(iii) Recall the functions \( g^n(t, \sigma) \) from (5.13). Note that for \( 1 \leq i < j \), by exchangeability,
\[
\mathbb{E}[\nu^t \{ r_{i,j} = 0 \}] = \lim_{\sigma \to \infty} \mathbb{E}[\int \nu^t (d\sigma) e^{-\sigma r_{i,j}}] = \lim_{\sigma \to \infty} g^2(t, \sigma) = 0,
\]
where we have used explicit calculations for the mean sample Laplace transform which we presented in more generality in Corollary 3.4. By dominated and monotone convergence,
\[
\mathbb{E}\left[ \int_0^\infty dt \nu^t (\mathbb{L}(0, \infty)^{(i,j)}) \right] \leq \sum_{1 \leq i < j} \lim_{T \to \infty} \int_0^T dt \mathbb{E}[\nu^t \{ r_{i,j} = 0 \}] = 0,
\]
almost surely, and hence, almost surely, \( \nu^t((0, \infty)^{(i,j)}) = 1 \) for Lebesgue almost all \( t \in \mathbb{R}_+ \).

**Proof of Proposition 2.16.** Note that the strong Markov property follows from the Feller property by general theory, [EK86, Theorem 4.4.2]. Let \( \mathcal{U}^u = (\mathcal{U}_t^u)_{t \geq 0} \) be the solution of the \((\delta_u, \Omega^1, \Pi^1)\)-martingale problem, i.e. the tree-valued Fleming-Viot dynamics, started in \( \mathcal{U}_0 = u \). For the Feller property, it suffices to show that \( u' \to u \) implies that \( \mathcal{U}_t^u' \Rightarrow \mathcal{U}_t^u \) for all
$u \in \mathbb{U}$ and $t > 0$. Recall the coupled tree-valued Moran dynamics from Section 5.3. For $u, u' \in \mathbb{U}$, take $u_N, u'_N \in \mathbb{U}_N$ with $u_N \to u$ and $u'_N \to u'$ in the Gromov-weak topology. Let $(\mathcal{U}_t^{N,1}, \mathcal{U}_t^{N,2})_{t \geq 0}$ be the coupled tree-valued Moran dynamics, started in $(u_N, u'_N)$. As in the proof of Theorems 1 and 2, the family of coupled tree-valued Moran dynamics \{$(\mathcal{U}_t^{N,1}, \mathcal{U}_t^{N,2})_{t \geq 0}; N \in \mathbb{N}$\} is tight. Let $(\mathcal{U}_t, \mathcal{U}_t')_{t \geq 0}$ be a weak limit point which must be a coupling of tree-valued Fleming-Viot dynamics by construction. Moreover, since the modified Eurandom metric (see Definition 5.6) is continuous in the Gromov-weak topology and bounded \(\mathbf{E}[d_{\text{Eur}}'(\mathcal{U}_t, \mathcal{U}_t')] = \lim_{N \to \infty} \mathbf{E}[d_{\text{Eur}}'(\mathcal{U}_t^{N,1}, \mathcal{U}_t^{N,2})] \leq \lim_{N \to \infty} d_{\text{Eur}}'(u_N, u'_N) = d_{\text{Eur}}'(u, u')\) by Proposition 5.8. In particular, $u'_n \to u$, as $n \to \infty$, implies that $\mathbf{E}[d_{\text{Eur}}'(\mathcal{U}_t, \mathcal{U}_t'^n)] \to 0$, as $n \to \infty$, which in turn implies $\mathcal{U}_t'^n \Longrightarrow \mathcal{U}_t$, as $n \to \infty$, by Remark 5.7.

**Proof of Corollary 2.18.** For $\Phi = \Phi^{n, \phi}$ as in the Corollary, observe that $\langle \nu^*, \phi \rangle^2 = \langle \nu^*, (\phi, \phi) \rangle_n$ with $(\phi, \phi)_n$ from (2.27). Therefore, given $\mathcal{U}_t = u$, we compute

\[d(\Phi(\mathcal{U}))_t = \Omega^1 \Phi^2(u) - 2\Phi(u) \Omega^1 \Phi(u) = \langle \nu^*, \text{div} \left((\phi, \phi)\right)_n \rangle \]

\[+ \frac{\gamma}{2} \sum_{k,l=1}^n \langle \nu^*, (\phi \circ \theta_{k,l}, \phi) \rangle_n + \langle \phi, \phi \circ \theta_{k,l} \rangle_n - 2\langle \phi, \phi \circ \theta_{k,l} \rangle_n \]

\[+ \gamma \sum_{k,l=1}^n \left( \langle \nu^*, (\phi, \phi) \circ \theta_{k,n+l} \rangle - \langle \nu^*, (\phi, \phi) \rangle_n \right) \]

and the result follows from the first two terms vanishing and

\[\sum_{k,l=1}^n \langle \nu^*, (\phi, \phi) \rangle_n \circ \theta_{k,n+l} = \sum_{k,l=1}^n \langle \nu^*, (\phi, \phi) \rangle_n \circ \theta_{k,n+l} = n^2 \langle \nu^*, (\phi, \phi) \rangle_n \circ \theta_{1,n+1} \]

with the symmetrization $\tilde{\phi}$ introduced in Remark 2.8(ii) and $\Phi^{n, \tilde{\phi}} = \Phi^{n, \phi}$. \qed
Proof of Theorem 3. In order to prove Theorem 3 we need two ingredients:

- The family \( \{ U_t; t > 1 \} \) is tight
- \( E^δ [ \Phi(U_t) ] \to E[\Phi(U_∞)] \), as \( t \to ∞ \), for all \( \Phi \in Π^1 \) and \( u \in U \).

Then, Theorem 3 follows from Lemma 3.4.3 of [EKS86].

We show tightness of \( \{ U_t; t > 1 \} \) in \( U \) using Theorem 3 and (3.3) of [GPW09a]. First, recalling (6.1) and when \( E[w_{U_t}] \) is the first moment measure of \( w_{U_t} \in M_1(M_1(\mathbb{R}_+)) \), for \( t \) and \( C > 0 \),

\[
E[w_{U_t}((C; ∞))] = \begin{cases} 
  e^{−γt} E[w_{U_0}((C−t; ∞))], & C ≥ t \\
  e^{−γC}, & C < t.
\end{cases}
\]

(8.6)

So, for given \( ε > 0 \), choose \( C > 0 \) large enough such that \( E[w_{U_0}((C); ∞)] < ε \) and \( e^{−γC} < ε \). Then, \( E[w_{U_t}((2C; ∞))] < ε \) for all \( t > 0 \) and so, \( \{ E[w_{U_t}], t > 1 \} \) is tight.

Secondly, for \( U_t = (U_t, r_t, µ_t) \), we have to show that for \( 0 < ε < 1 \) there is \( δ > 0 \) with

\[
\sup_{t > 1} E[µ_t\{u : µ(B_ε(u)) ≤ δ\}] < ε.
\]

(8.7)

Note that the probability on the left hand side does not depend on \( t \). Using that \( U_∞ \) is determined by \( Λ = γ · δ_0 \) in (4.7) of [GPW09a] we find

\[
\lim_{δ → 0} E[µ_t\{u : µ(B_ε(u)) ≤ δ\}] = \lim_{δ → 0} E[µ_∞\{u : µ(B_ε(u)) ≤ δ\}] = 0
\]

by (4.9) and (4.11) of [GPW09a]. So, tightness follows.

The assertion (ii) is an application of the duality relation from Proposition 4.1. Fix \( φ \in C^1_b(\mathbb{R}_+^{(2)}) \). We apply the duality relation (4.12) between the tree-valued Fleming-Viot dynamics and the tree-valued Kingman coalescent which starts in \( k_0 = (p_0, r'_0) \) with \( p_0 := \{n\}, n \in \mathbb{N} \) and \( r'_0 \equiv 0 \). Moreover we know from the construction of \( K \) that \( E^{δφ}_0 [ϕ(ε)] \to E[µ^∞, ϕ] \) and \( P_t \to \{N\} \), as \( t \to ∞ \) where \( U_∞ \) is the (rate \( γ \)) Kingman measure tree from (2.55). Hence, by (4.12),

\[
\lim_{t → ∞} E^{δφ}_t [ϕ^{t,h}, ϕ] = \lim_{t → ∞} E^{δφ}_t \left[ \int_{\mathbb{R}_+^{(2)}} ν^u(dx) φ((x)^{Pn} + u') \right]
\]

(8.9)

\[
= \lim_{t → ∞} E^{δφ}_t [ϕ(u')] = E[µ^∞, ϕ].
\]

Since \( φ \in C^1_b(\mathbb{R}_+^{(2)}) \) was chosen arbitrarily, (ii) follows and we are done. □
9. Proof of the applications (Proof of Theorems 4 and 5). In this section we prove the results stated in Section 3.

Proof of Lemma 3.1 Consider the traveling salesperson problem for a salesperson who must visit all leaves $x_1, ..., x_n$ of the tree and who starts at one leaf to which she comes back at the end of the trip. It is easy to see that such a path must pass all edges in both directions, so the length of the path is at least twice the tree length. It is also easy to see that taking an optimal path and leaving out leaf $x_i$ gives an optimal path for the remaining leaves $x_1, ..., x_{i-1}, x_{i+1}, ..., x_n$.

We claim that there is one path connecting the set of leaves such that each edge in the tree is passed exactly twice, which is equivalent to the assertion of the Lemma. Assume to the contrary that such an order does not exist. We take a path of minimal length. There must be one edge which is visited at least four times. W.l.o.g. we assume that this edge is internal, i.e. not adjacent to a leaf. So there are four points $x_i, x_j, x_k, x_l \in X$, visited in the order $x_i, x_j, x_k, x_l, x_i$, such that $[x_i; x_j] \cap [x_k \cap x_l]$ is visited at least four times, where $[x; y]$ is the path from $x$ to $y$ in $X$. Since leaving out leaves gives again an optimal path, leaving out all leaves except $x_i, x_j, x_k, x_l$ must lead to an optimal path connecting these four points. However, this optimal path must be $x_i, x_j, x_l, x_k, x_i$ (or its reverse), since this path passes all edges only twice. Hence, we have a contradiction and the assertion is proved. □

Proof of Theorem 4 We first show injectivity of $\xi$. Assume we are given a compact ultra-metric measure space $(U_0, r_0, \mu_0)$ and its equivalence class $u_0 = (U_0, r_0, \mu_0)$. We show that if

$$\lambda := \xi(u_0)$$

then

$$\xi^{-1}(\{\lambda\}) = \{u_0\}.$$  

We do this by explicitly reconstructing $u_0$ from $\lambda$.

We proceed in three steps. In the first two steps we consider the case where $\mu_0$ is supported by finitely many atoms. In Step 1 we follow an argument provided to us by Steve Evans which explains how to recover the isometry class of $(\text{supp}(\mu_0), r_0)$ from $\lambda$. In Step 2 we then recover the measure $\mu_0$. Finally, the case of a general element in $U$ is obtained by approximation via finite ultra-metric measure spaces in Step 3.
Step 1 (Evans’s reconstruction procedure for finite trees). Assume that 
\( u \in \xi^{-1}(\{\lambda\}) \) and that \( u = (U, r, \mu) \) with \#supp(\mu) < \infty. Put

\[
A_N := \{ (\ell_1 := 0, \ell_2, \ldots) : \ell_k > \ell_{k-1} \text{ for exactly } N - 1 \text{ different } k \}.
\]

First observe that \#supp(\mu) = N if and only if \( \lambda \) is supported on \( A_N \). That is, we can recover \#supp(\mu) from \( \lambda \). So, assume that \( \mu \) has \( N \) atoms and w.l.o.g. \( U := \{1, \ldots, N\} \). We will now recover \( r = (r_{i,j})_{1 \leq i < j \leq N} \) from \( \lambda \).

For that purpose, introduce on \( \mathbb{R}^N_+ \) the lexicographic ordering \( \prec \), i.e., \( \ell \prec \ell' \) iff for \( k^* := \min \{k : \ell_k \neq \ell'_k\} \) we have \( \ell_{k^*} < \ell'_{k^*} \). Let

\[
B := \{ \ell \in \text{supp}(\lambda) : \ell_1 < \ldots < \ell_N \}
\]

be the space of all vectors \( \ell \) which are accessible by sequentially sampling the \( N \) different points of \( U \) and evaluating subsequently the lengths of the sub-trees spanned by them. Moreover, let

\[
\ell^* := \min_{\prec} B,
\]

i.e., \( \ell^* := (\ell^*_k)_{k \in \mathbb{N}} \) is the minimal element in \( B \) with respect to the order relation \( \prec \).

W.l.o.g. we assume that the points in \( U \) are enumerated in such a way that for all \( n \in \{1, \ldots, N\} \),

\[
\ell^*_n := L_n^{(U,r)}(\{1, \ldots, n\}).
\]

Notice that if \( d^*_n \) denotes the depth of the sub-tree spanned by \( \{1, \ldots, n\} \), i.e., \( d^*_n := \frac{1}{2} \max \{r(i,j) : 1 \leq i, j \leq n\} \), for \( n \in \mathbb{N} \), then \( d^*_1 = 0 \) and the recursion

\[
d^*_n = \frac{1}{2} (d^*_{n-1} + (\ell^*_n - \ell^*_{n-1}) \lor d^*_{n-1}).
\]

holds for \( n \geq 2 \).

We claim that we can even recover \((r_{i,j})_{1 \leq i < j \leq N}\) from \((\ell^*_n)_{n=1,\ldots,N}\). In fact, for all \( n \in \mathbb{N} \),

\[
r_{n-1,n} = \min_{1 \leq k \leq n-1} r_{k,n},
\]

To see this, assume to the contrary that there is a minimal \( n \in \mathbb{N} \) for which we find a \( k < n - 1 \) such that \( r_{k,n} \) is minimal and \( r_{k,n} < r_{n-1,n} \). Choose the minimal \( l \) with \( k < l \leq n - 1 \) and \( r_{l,n} < r_{k,n} \). Then, sampling the \( l \) points \( 1, 2, \ldots, k, \ldots, l - 1, n \) (in that order) leads to the sequence of tree lengths \( \ell^*_1, \ell^*_2, \ldots, \ell^*_{l-1}, \ell^*_{l-1} + \frac{1}{2} r_{l,n} \). However, by the minimality of \( l \) we have
that \( r_{k,n} \geq r_{l-1,n} \) and by the ultra-metric property \( r_{k,n} < r_{l,n} \lor r_{l-1,n} = r_{l-1,l} \). Hence, the above tree lengths are smaller (with respect to \(<\)) than \( \ell_1^*, \ell_2^*, \ldots, \ell_{l-1}^*, \ell_l^* \) since \( \ell_i^* \geq \ell_i^* + \frac{1}{2} r_{l-1,l} \). So, assuming that (9.8) does not hold contradicts the assumption that \( \ell^* \) is minimal.

However, from (9.8) we conclude the following recursion: for all \( n \in \{2, \ldots, N\} \) and \( 1 \leq k \leq n - 1 \),

\[
(9.9) \quad r_{k,n} = r_{k,n-1} \lor 2(\ell_n^* - \ell_{n-1}^* - (d_n^* - d_{n-1}^*)).
\]

The latter together with the necessary requirements that \( r_{n,n} := 0 \) and \( r_{1,2} := \frac{1}{2} \ell_2^* \) determines the metric on \( U \) uniquely.

**Step 2 (Reconstruction of weights in finite trees).** In this step we will reconstruct weights \( (p_1, \ldots, p_N) \) on \( \{1, \ldots, N\} \) from the given \( \lambda \). Denote by \( \Gamma \subseteq \Sigma_N \) the set of permutations of \( \{1, \ldots, N\} \) for which the metric \( r \) given in Step 1 satisfies \( r_{i,j} = r_{\sigma(i),\sigma(j)} \) for all \( 1 \leq i, j \leq N \). Since we are interested in measure-preserving isometry classes only, we need to show that \( (p_1, \ldots, p_N) \) are uniquely determined up to permutations \( \sigma \in \Gamma \).

For all \( \underline{k} = (k_1, \ldots, k_{N-1}, k_N) \in \{0, 1, \ldots\}^{N-1} \times \{\infty\} \), define

\[
(9.10) \quad \ell^*_{\underline{k}} := (\ell_1^* = 0, \ell_1^*, \ell_1^*, \ell_2^*, \ell_2^*, \ell_2^*, \ell_3^*, \ell_3^*, \ell_3^*, \ldots)
\]

where \( \ell^* \) is the minimal subtree length vector in the support of \( \lambda \) from Step 1. Observe that sampling from the subtree length distribution first the point 1 a number of \( k_1 + 1 \) times, then the point 2, then one of the points in \( \{1, 2\} \) a number of \( k_2 \) times, and so on, results exactly in the vector \( \ell^*_{\underline{k}} \). Hence, taking all possible permutations \( \sigma \in \Gamma \) into account,

\[
\lambda(\ell^*_{\underline{k}}) = (\prod_{i=1}^{N} p_i) \cdot \sum_{\sigma \in \Gamma} \prod_{i=1}^{N-1} \left( \sum_{1 \leq j \leq i} p_{\sigma(j)} \right)^{k_i}
\]

\[
= \lambda(\ell^*) \cdot \prod_{\sigma \in \Gamma} \left( \sum_{1 \leq j \leq i} p_{\sigma(j)} \right)^{k_i}.
\]

We claim that (9.11) determines \( (p_1, \ldots, p_N) \) uniquely up to permutations \( \sigma \in \Gamma \).

To see this, observe that the algebra of functions on the \( N - 1 \)-dimensional simplex \( S_N \), generated by the functions

\[
(9.12) \quad \{ f((p_1, \ldots, p_N)) := \prod_{i=1}^{N-1} \left( \sum_{1 \leq j \leq i} p_j \right)^{k_i}; \ k_1, \ldots, k_{N-1} \in \mathbb{N}_0 \}
\]
separates points. Hence, $f \in C^b(S_N)$ can be approximated uniformly by functions in this algebra by the Stone-Weierstrass Theorem. Hence, by knowing $\lambda(\{\mathbb{L}_n^k\})/\lambda(\{\mathbb{L}^*\})$ for all $k$, using (9.11), we also know the values of

$$\sum_{\sigma \in \Gamma} f((p_{\sigma(1)}, \ldots, p_{\sigma(n)})$$

by an approximation argument.

In particular, we can find the set $A := \{(p_{\sigma(1)}, \ldots, p_{\sigma(N)}) : \sigma \in \Gamma\}$. By setting $\mu_i = p_i$ for an arbitrary $(p_1, \ldots, p_N) \in A$ we have recovered $\mu$ uniquely up to isometries such that $\xi^{-1}(\{\lambda\}) = \{u\}$ by construction.

**Step 3 (General ultra-metric measure spaces).** Let $u = (U, r, \mu) \in \xi^{-1}(\{u_0\})$ not necessarily finite anymore. We shall approximate $u$ by finite ultra-metric measure spaces which we then treat as described in the first two steps.

For that purpose, let for all $\varepsilon > 0$, the $\varepsilon$-shrunken pseudo-metric $r_\varepsilon$ on $U$ by putting

$$r_\varepsilon := 0 \vee (r - \varepsilon).$$

Notice that since $(\text{supp}(\mu), r)$ is ultra-pseudo-metric, $(\text{supp}(\mu), r_\varepsilon)$ is ultra-pseudo-metric as well, for all $\varepsilon$.

Moreover, for all $\varepsilon > 0$ there is a covering of $U$ of disjunct (closed) balls $B_1, B_2, \ldots \subseteq U$ of radius $\varepsilon$ with $\mu(B_1) \geq \mu(B_2) \geq \ldots$. Take $N_\varepsilon$ large enough such that for $B_\varepsilon = \bigcup_{i=1}^{N_\varepsilon} B_i$ we have $\mu(B_\varepsilon) > 1 - \varepsilon$ and $\mu(B_{N_\varepsilon}) > \mu(B_{N_\varepsilon + 1})$. Set $\mu_\varepsilon(\cdot) := \mu(\cdot|B_\varepsilon)$ and

$$u_\varepsilon := (U, r_\varepsilon, \mu_\varepsilon).$$

Then $u_\varepsilon$ is a finite metric measure space and $u_\varepsilon \to u$ in the Gromov-weak topology, as $\varepsilon \to 0$.

Given $u_1, u_2, \ldots \in U$, set $\ell_n := L_n^{(U, r)}(\{u_1, \ldots, u_n\})$ leading to the subtree length vector $(\ell_1, \ell_2, \ldots) \in \mathbb{R}_+^N$. We define the map $\mathbb{L}^\varepsilon : \mathbb{R}_+^N \to \mathbb{R}_+^N$ given by

$$\mathbb{L}^\varepsilon : (\ell_1, \ell_2, \ldots) \mapsto (\ell_1^\varepsilon, \ell_2^\varepsilon, \ldots)$$

with $\ell_1^\varepsilon = 0$ and $\ell_2^\varepsilon = 0 \vee (\ell_2 - \varepsilon)$ and for $n \geq 3$, recursively,

$$\ell_n^\varepsilon := \ell_{n-1}^\varepsilon + (\ell_n - \ell_{n-1} - \frac{1}{2}\varepsilon)^+. $$

Moreover, set

$$A_{\varepsilon, n} := \{ (\ell_1 = 0, \ell_2, \ldots) : \ell_i > \ell_{i-1} \text{ for exactly } N_\varepsilon - 1 \text{ different } i \in \{1, 2, \ldots, n\} \}. $$
and we observe that

\[ \xi(u^\varepsilon)(\cdot) = (\mathcal{L}_u \nu^\varepsilon) = \lim_{n \to \infty} \mathcal{L}_n^\varepsilon \lambda(\cdot | A_{\varepsilon,n}). \]

Now, take \( \tilde{u} \in \xi^{-1}(\{\lambda\}) \). Observe that \( \tilde{u}^\varepsilon \to \tilde{u} \) and \( u^\varepsilon \to u \) in the Gromov-weak topology, as \( \varepsilon > 0 \). Hence we are in a position to apply Steps 1 and 2 to find that \( \tilde{u}^\varepsilon \in \xi^{-1}(\lim_{n \to \infty} \mathcal{L}_n^\varepsilon \lambda(\cdot | A_{\varepsilon,n})) = \{u^\varepsilon\} \), for all \( \varepsilon > 0 \). This shows that \( u = \lim_{\varepsilon \to 0} u^\varepsilon = \lim_{\varepsilon \to 0} \tilde{u}^\varepsilon = \tilde{u} \).

As for continuity of \( \xi \), assume that \( (u_k)_{k \in \mathbb{N}} \) is a sequence in \( \mathcal{U} \) such that \( u_k \to u \), for some \( u \in \mathcal{U} \), in the Gromov-weak topology, as \( k \to \infty \). Then by definition, \( \Phi(u_k) \to \Phi(u) \), for all \( \Phi \in \Pi^0 \), as \( k \to \infty \). In particular, since the map \( x \mapsto \ell_n(x) \) is continuous as it is the minimum of finitely many continuous functions, for all \( n \in \mathbb{N}, (\xi(u_k), \psi) \to (\xi(u), \psi) \), for all \( \psi \in C_b(\mathbb{R}^N_+) \), or equivalently, \( \xi(u_k) \Rightarrow \xi(u) \) in the weak topology on \( \mathcal{M}_1(\mathbb{R}^N_+) \), as \( k \to \infty \).

Proof of Theorem 5

(i) Since \( \xi \) is bijective on \( \xi(\mathcal{U}) \), it is a consequence of Theorem 3.2 in \cite{Kur98} that the martingale problem for \( (\xi, \mathcal{P}(\mathcal{U}), \Omega^1, \Xi, \Pi^1) \) is well-posed. Moreover, by construction, \( (\xi(\mathcal{U}_t))_{t \geq 0} \) solves the martingale problem. In addition, since \( \mathcal{U} \) has the Feller property and \( \xi \) is continuous, \( \Xi \) is Feller, too. The last assertion follows from the continuity of the sample paths of the tree-valued Fleming-Viot dynamics and the continuity of \( \xi \).

(ii) With \( \ell \) from (3.4),

\[ \Omega^1(\Psi \circ \xi)(u) = \langle \nu^\star, \text{div}(\psi \circ \ell) + \gamma \sum_{1 \leq k < l} \langle \nu^u, \psi \circ \ell \circ \theta_{k,l} - \psi \circ \ell \rangle \]

\[ = \sum_{n \geq 2} n \langle \nu^u, \frac{\partial}{\partial \ell_n} (\psi \circ \ell) \rangle + \gamma \sum_{n \geq 2} (n-1) \langle \nu^\star, \psi \circ \beta_{n-1} \circ \ell - \psi \circ \ell \rangle \]

\[ = \sum_{n \geq 2} n \langle \xi(u), \frac{\partial}{\partial \ell_n} \psi \rangle + \gamma \sum_{n \geq 1} n \langle \xi(u), \psi \circ \beta_n - \psi \rangle \]

and we are done.

To prepare the proof of Corollary 3.4 we investigate for each time \( t \geq 0 \) the mean sample Laplace transform,

\[ g(t; \sigma) := \mathbb{E}[\Psi^\sigma(\Xi_t)], \]
of the subtree lengths distribution $\Xi_t$, where for $\sigma \in \mathbb{R}^N_+$,

$$
(9.22) \quad \Psi^\sigma(\Xi) := \int_{\mathbb{R}^N_+} \Xi(d\ell) \psi^\sigma(\ell)
$$

with the test function

$$
(9.23) \quad \psi^\sigma(\ell) := \exp(-\langle \sigma, \ell \rangle).
$$

As usual, $\langle \cdot, \cdot \rangle$ denotes the inner product.

**Lemma 9.1 (ODE system for the mean sample Laplace transforms).** For $\sigma \in \mathbb{R}^N_+$ having only finitely many non-zero entries, the functions $g(\cdot; \sigma)$ satisfy the following system of differential equations:

$$
(9.24) \quad \frac{d}{dt} g(t; \sigma) = \left( -\sum_{k=2}^\infty k\sigma_k g(t; \sigma) + \sum_{k=1}^\infty k \left( g(t; \tau_k \sigma) - g(t; \sigma) \right) \right)
$$

with the merging operator

$$
(9.25) \quad \tau_k : (\sigma_1, \ldots, \sigma_{k-1}, \sigma_k, \sigma_{k+1}, \sigma_{k+2}, \ldots) \mapsto (\sigma_1, \ldots, \sigma_{k-1}, \sigma_k + \sigma_{k+1}, \sigma_{k+2}, \ldots).
$$

**Proof.** By standard arguments, $\Psi^\sigma \in \Pi^\Xi$ and

$$
(9.26) \quad \frac{d}{dt} g(t; \sigma) = \mathbb{E}[\Omega^1.\Xi \Psi^\sigma(\Xi_t)].
$$

Hence, inserting $\Psi^\sigma$, and using $\psi^\sigma(\beta_k \ell) = \psi^{\tau_k \sigma}(\ell)$ for all $k = 1, 2, \ldots$, with $\beta_k$ from (9.20) and $\tau_k$ from (9.25), we find

$$
(9.27) \quad \frac{d}{dt} g(t, \sigma) = \mathbb{E} \left[ -\int \Xi_t(d\ell) \sum_{k=2}^\infty k\sigma_k \psi^\sigma(\ell) + \gamma \sum_{k=1}^\infty k \left( \psi^\sigma(\beta_k \ell) - \psi^\sigma(\ell) \right) \right]
= -\left( \sum_{k=2}^\infty k\sigma_k \right) g(t, \sigma) + \gamma \sum_{k=1}^\infty k \left( g(t, \tau_k \sigma) - g(t, \sigma) \right),
$$
after which

$$
\square
$$
Remark 9.2. Recall, for each \( n \in \mathbb{N} \), the function \( g^n \) from (3.13). For each \( n \geq 2 \) and \( \sigma \geq 0 \), applying (9.24) to \( \sigma = (\sigma k,n)_{k \geq 2} \) yields, setting \( g_1(t;\sigma) := 1 \),

\[
\frac{d}{dt}g^n(t;\sigma) = -n\sigma g^n(t;\sigma) + \frac{\gamma}{2} \left( g^{n-1}(t;\sigma) - g^n(t;\sigma) \right)
\]

(9.28)

\[
= \frac{\gamma}{2} n(n-1)g^{n-1}(t;\sigma) - \frac{\gamma}{2} n(\frac{2}{\gamma} \sigma + n - 1)g^n(t;\sigma),
\]

e.g.,

\[
\frac{d}{dt}(g^2(t;\sigma),g^3(t;\sigma),\ldots) = \frac{\gamma}{2} \left[ A(\frac{2}{\gamma} \sigma)(g^2(t;\sigma),g^3(t;\sigma),\ldots)^\top + b^\top \right],
\]

where

\[
b^\top := (2,0,\ldots)^\top
\]

and for \( \tilde{\sigma} \geq 0 \) the matrix \( A := A(\tilde{\sigma}) \) is defined by

\[
A_{k,l} := \begin{cases} 
  k(k-1), & \text{if } k = l + 1, \\
  -k(\tilde{\sigma} + k - 1), & \text{if } k = l, \\
  0, & \text{else},
\end{cases}
\]

(9.31)

for all \( k,l \geq 2 \).

The proof of Corollary 3.4 uses the following preparatory lemma.

Lemma 9.3. Fix \( \tilde{\sigma} \geq 0 \). Let \( B = (B_{k,l})_{k,l \geq 2} \) and \( B^{-1} = (B_{k,l}^{-1})_{k,l \geq 2} \) be matrices defined by

\[
B_{k,l} := \frac{k^l l^{(k-1)}}{l^{(l-1)}} \Gamma(\tilde{\sigma} + 2l) \Gamma(\tilde{\sigma} + k + l), \quad \text{and} \quad B_{k,l}^{-1} = \frac{(-1)^{k+l} l^{(k-1)}}{l^{(l-1)}} \Gamma(\tilde{\sigma} + k + l - 1) \Gamma(\tilde{\sigma} + 2k - 1).
\]

(i) The matrices \( B \) and \( B^{-1} \) are inverse to each other.

(ii) The matrix \( A = A(\tilde{\sigma}) = (A_{k,l})_{k,l \geq 2} \) has eigenvalues

\[
\lambda_k := -k(\tilde{\sigma} + k - 1), \quad k \geq 2.
\]

(iii) If \( D = (\lambda_k \delta_{k,l})_{k,l \geq 2} \) then

\[
f(A) = B f(D) B^{-1}
\]

(9.34)

for all analytical functions \( f : \mathbb{R}^{N^2} \to \mathbb{R}^{N^2} \). Specifically, \( A^{-1} = BD^{-1}B^{-1} \) and \( e^{At} = B e^{Dt} B^{-1} \) for all \( t \geq 0 \).
(iv) For $\tilde{\sigma} > 0$, let $A^{-1}(\tilde{\sigma}) = (A_{k,l}^{-1})_{k,l \geq 2}$ be given by $A_{k,l}^{-1} = 0$ for $k < l$ and

$$
A_{k,l}^{-1} := \frac{(k-1)!\Gamma(\tilde{\sigma} + l - 1)}{l!\Gamma(\tilde{\sigma} + k)}, \quad k \geq l.
$$

Then $A^{-1}$ and $A$ are inverse to each other.

**Proof.** First, we note that $A, A^{-1}, B, B^{-1}$ are lower triangular infinite matrices. This implies that the domain of the maps induced by these matrices is $\mathbb{R}^N$. In particular, we do not have to distinguish between left- and right inverse matrices of $A$ and $B$.

(i) We need to show that

$$(B \cdot B^{-1})_{k,l} = \delta_{k,l}$$

for $k \geq l \geq 2$. This is clear in the case where $k \leq l$. For $k > l \geq 2$, with constants $C$ changing from line to line, and using the abbreviations $\hat{k} := k - l$ and $\hat{\sigma} := \tilde{\sigma} + 2l - 1$,

$$(B \cdot B^{-1})_{k,l} = \sum_{m=l}^{k} B_{k,m} B_{m,l}^{-1}$$

for $k \geq l \geq 2$. This is clear in the case where $k \leq l$. For $k > l \geq 2$, with constants $C$ changing from line to line, and using the abbreviations $\hat{k} := k - l$ and $\hat{\sigma} := \tilde{\sigma} + 2l - 1$,

$$(B \cdot B^{-1})_{k,l} = \sum_{m=l}^{k} B_{k,m} B_{m,l}^{-1} = \sum_{m=l}^{k} \frac{\hat{k}!}{m!} \frac{(k-1)!}{m!} \frac{(k+l-1)!}{(k+m)!} \frac{(-1)^m \Gamma(\tilde{\sigma} + 2m)}{\Gamma(\tilde{\sigma} + k + m)} = C \sum_{m=l}^{k} (-1)^m \frac{(\hat{k} + m)!}{(k-m)!} \frac{\Gamma(\tilde{\sigma} + 2m)}{\Gamma(\tilde{\sigma} + k + m)} = C \sum_{m=0}^{\hat{k}} (-1)^m \frac{(\hat{k} + m)!}{\Gamma(\hat{k} + m + 1)!} \frac{\Gamma(\tilde{\sigma} + 2m)}{\Gamma(\tilde{\sigma} + \hat{k} + m + 1)} = 0,
$$

where we have used that

$$(9.38) \quad C \cdot \frac{(\hat{\sigma} + 2m)\Gamma(\hat{\sigma} + m)}{\Gamma(m+1)} = \frac{\Gamma(\hat{\sigma} + m + 1)}{\Gamma(m+1)\Gamma(\hat{\sigma} + 1)} + \frac{\Gamma(\hat{\sigma} + m)}{\Gamma(m)\Gamma(\hat{\sigma} + 1)}$$

and then applied Formula (5d) on page 10 in [Rio68].
(ii) Since $A$ is lower triangular, this is obvious.

(iii) Note that
\[(9.39) \quad (A \cdot B)_{2,l} - \lambda_l B_{2,l} = 0\]
and
\[(9.40) \quad \lambda_l - \lambda_k = \bar{\sigma}(k - l) + (k^2 - k - l^2 + l) = (k - l)(\bar{\sigma} + k + l - 1).\]

Thus for all $k \geq 3$ and $l \geq 2$,
\[(9.41) \quad B_{k,l} = \frac{k(k - 1)}{(k - l)(\bar{\sigma} + k + l - 1)} B_{k-1,l},\]
and since $A_{k,k} = \lambda_k$,
\[(9.42) \quad (A \cdot B)_{k,l} - \lambda_l B_{k,l} = A_{k,k-1} B_{k-1,l} + (\lambda_k - \lambda_l) B_{k,l}
= (k(k - 1) - k(k - 1)) B_{k-1,l}
= 0,\]
which proves that $B$ contains all eigenvectors of $A$. Hence the claim follows by standard linear algebra.

(iv) It is clear that $(A \cdot A^{-1})_{k,k} = 1,$ while for $k \neq l$,
\[(9.43) \quad (A \cdot A^{-1})_{k,l} = A_{k,k-1}A_{k-1,l}^{-1} + A_{k,k}A_{k,l}^{-1}
= k(k - 1) \frac{(k - 2)! \Gamma(\bar{\sigma} + l - 1)}{l! \Gamma(\bar{\sigma} + k - 1)} - k(\bar{\sigma} + k - 1) \frac{(k - 1)! \Gamma(\bar{\sigma} + l - 1)}{l! \Gamma(\bar{\sigma} + k)}
= 0.\]

\[\square\]

**Proof of Corollary 3.4.** Fix $n \in \mathbb{N}$ and $\sigma \geq 0$. Put
\[(9.44) \quad h^{\sigma,n}(t) := g^n(\frac{2t}{\tau}; \sigma).\]

By (9.28), the vector $h := (h^{\sigma,2}, h^{\sigma,3}, \ldots)^{\top}$ satisfies the linear system of ordinary differential equations
\[(9.45) \quad \frac{d}{dt} h = A h + b,\]
or equivalently,

\begin{equation}
    h(t) = e^{At}h(0) + e^{At}A^{-1}b - A^{-1}b,
\end{equation}

with $b = (2,0,0,...)^\top$ and $A = (A_{k,l})_{k,l \geq 2}$ as defined in (9.31). Consequently, if $B$, $B^{-1}$ and $D$ are as in Lemma 9.3 then

\begin{equation}
    h(t) = -A^{-1}b + Be^{Dt}(B^{-1}h(0) + D^{-1}B^{-1}b).
\end{equation}

Combining (9.44) with (9.47) yield the explicit expressions given in (3.14). Finally, by (9.47),

\begin{align}
    g^n(t;\sigma) & \rightarrow_{t \rightarrow \infty} -2\left(A\left(\frac{\sigma}{\gamma}\right)^{-1}\right)_{n,2} \\
    & = \frac{\Gamma(n)\Gamma(\tilde{\sigma} + 1)}{\Gamma(n + \tilde{\sigma})} \\
    & = \mathbb{E}\left[e^{-\sigma \sum_{k=2}^{n} e^k}\right].
\end{align}

Acknowledgement. We thank David Aldous, Steve Evans, Patric Glöde, Pleuni Pennings and Sven Piotrowiak for helpful discussions. We are particularly grateful to Steve Evans who provided the key argument in the proof of Theorem 4. We thank the referee for thorough reading of the paper and for useful comments and corrections which helped to improve the paper significantly.

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