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Probabilistic Structures in Evolution

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Contents

Chapter 1. From high to low volatility: spatial Cannings with block resampling and spatial Fleming-Viot with seed-bank ANDREAS GREVEN AND FRANK DEN HOLLANDER	1
1.1. Background	4
1.2. Two models	5
1.3. Equilibrium	12
1.4. Random environment	17
1.5. Extensions	19
1.6. Perspectives	20
References	21

From high to low volatility: spatial Cannings with block resampling and spatial Fleming-Viot with seed-bank

ANDREAS GREVEN AND FRANK DEN HOLLANDER

In neutrally evolving populations subject to resampling and migration on geographic spaces, the longtime behaviour exhibits a classical dichotomy between clustering of types versus coexistence of types (= between convergence to locally monotype equilibria versus locally multitype equilibria). Which of the two scenarios prevails depends on whether the difference between the lineages of two typical individuals is a recurrent random walk or a transient random walk. In the present contribution, for two classes of models we present results on how this dichotomy is affected when the resampling has either high volatility or low volatility:

- (I) The spatial Cannings model with block resampling, where a positive fraction of the individuals in the next generation may inherit the type of a single individual in the previous generation.
- (II) The spatial Fleming-Viot model with seed-bank, where individuals may become dormant for awhile, suspending resampling and migration, until they become active again.

We will see that the dichotomy is shifted towards more clustering in class (I) and towards more coexistence in class (II). In particular, in class (II) we will see that for recurrent random walks (which are typical for two-dimensional geographic spaces) an infinite seed-bank turns clustering into coexistence. We will also explore the impact of allowing resampling that is controlled by a random environment. Along the way we discuss robustness, universality and critical dimension.

Contents

1.1. Background

A classical model for a spatial population evolving through neutral resampling and migration is a system of interacting Fleming-Viot diffusions. If the *geographic space* is \mathbb{G} and the *type space* is \mathbb{K} , then the state space of the process is

$$(1.1.1) \quad \mathcal{P}(\mathbb{K})^{\mathbb{G}},$$

where $\mathcal{P}(\mathbb{K})$ denotes the set of probability measures on \mathbb{K} . The process is defined via a *well-posed martingale problem*, which arises as the diffusion limit of an individual-based model, called the Moran model. In case $\mathbb{K} = \{0, 1\}$, the process

$$(1.1.2) \quad X = (X(t))_{t \geq 0}, \quad X(t) = (x_i(t))_{i \in \mathbb{G}} \in [0, 1]^{\mathbb{G}},$$

where $x_i(t)$ denotes the fraction of individuals of type 1 in colony i at time t , takes the form of a system of coupled SDE's

$$(1.1.3) \quad dx_i(t) = \sum_{j \in \mathbb{G}} a(i, j) [x_j(t) - x_i(t)] dt + \sqrt{dx_i(t)(1 - x_i(t))} dw_i(t), \quad i \in \mathbb{G},$$

where $(w_i(t))_{t \geq 0}$, $i \in \mathbb{G}$, are independent standard Brownian motions, $a(\cdot, \cdot)$ is the *migration kernel* on $\mathbb{G} \times \mathbb{G}$, d is the *volatility constant*, and

$$(1.1.4) \quad X(0) = (x_i(0))_{i \in \mathbb{G}} \in [0, 1]^{\mathbb{G}}$$

is the *initial state*.

Suppose that

$$(1.1.5) \quad x_i(0) = \theta \in [0, 1] \quad \forall i \in \mathbb{G}.$$

Without migration, the system in (1.1.3) reduces to a system of independent Fisher-Wright diffusions,

$$(1.1.6) \quad dx_i(t) = \sqrt{dx_i(t)(1 - x_i(t))} dw_i(t), \quad i \in \mathbb{G},$$

which are martingales whose volatility vanishes only at the boundary of $[0, 1]$ (where genetic diversity is lost). Consequently, for all $i \in \mathbb{G}$, $x_i(t)$ converges in distribution as $t \rightarrow \infty$ to the probability measure $(1 - \theta)\delta_0 + \theta\delta_1$. Without resampling, however, the system in (1.1.3) reduces to a deterministic flow,

$$(1.1.7) \quad dx_i(t) = \sum_{j \in \mathbb{G}} a(i, j) [x_j(t) - x_i(t)] dt, \quad i \in \mathbb{G},$$

and $x_i(t) = \theta$ for all $i \in \mathbb{G}$ and all $t \geq 0$. Thus, in (1.1.3) we have two *competing* mechanisms and the outcome for the longtime behaviour depends on the properties $a(\cdot, \cdot)$, irrespective of the value of d (see [11, 15, 41, 42]).

Indeed, let \mathbb{G} be an Abelian group and let us start the process in a translation invariant and spatially ergodic random initial state $X(0)$ with $E[x_i(0)] = \theta \in [0, 1]$, $i \in \mathbb{G}$. Define the symmetrized migration kernel $\hat{a}(i, j) = \frac{1}{2} [a(i, j) + a(j, i)]$, $i, j \in \mathbb{G}$

\mathbb{G} , which is the transition kernel for the difference of the lineages of two typical individuals. Then the following *dichotomy* holds (\mathcal{L} denotes law):

(1) If \hat{a} is *transient*, then

$$(1.1.8) \quad \mathcal{L}[X(t)] \xrightarrow[t \rightarrow \infty]{} \nu_\theta,$$

where the limit law ν_θ on $[0, 1]^\mathbb{G}$ is stationary and ergodic w.r.t. translations in \mathbb{G} , with $E_{\nu_\theta}[x_i] = \theta \forall i \in \mathbb{G}$. Furthermore, ν_θ is an extremal *invariant measure* that lives on configurations exhibiting coexistence of types for every $\theta \in (0, 1)$.

(2) If \hat{a} is *recurrent*, then

$$(1.1.9) \quad \mathcal{L}[X(t)] \xrightarrow[t \rightarrow \infty]{} (1 - \theta) \delta_{0^\mathbb{G}} + \theta \delta_{1^\mathbb{G}}.$$

Furthermore, all invariant measures live on configurations exhibiting clustering of types, i.e., on the set $\{0^\mathbb{G}, 1^\mathbb{G}\}$, for every $\theta \in [0, 1]$.

Thus, if the difference random walk is transient, then in equilibrium *coexistence* of types prevails, while if the difference random walk is recurrent, then in equilibrium *clustering* of types prevails.

In population genetics deviations from this classical dichotomy are observed in many instances. The reason is that the change of generation referred to as resampling may be *more volatile* or *less volatile* than in the standard model described above. Consequently, even for a fixed migration kernel, a shift from coexistence to clustering or vice versa may occur due to a change of volatility. In the present contribution we describe two model classes exhibiting such a shift (Section 1.2) and describe their equilibrium behaviour (Section 1.3). A question that naturally arises in this context is: What is the effect of including *spatially inhomogeneous* evolution mechanisms? We will see that the observed shift in the dichotomy is *robust* against such an extension, but that other properties are not (Section 1.4). We close by discussing extensions (Section 1.5) and future perspectives (Section 1.6).

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1.2. Two models

Models that exhibit a *high* volatile change of generation are the Cannings model [9, 10, 37, 38, 39, 40] and its spatial variant treated in [1, 6, 7, 8, 26, 27]. Below we will focus on a model class that uses the discrete *hierarchical group* as geographic space [12, 13, 15]. Models that exhibit a *low* volatile change of generation are the Fleming-Viot model with seed-bank [3, 4, 24] and its spatial

variant treated in [28, 29]. Below we will focus on a model class that uses the discrete *Euclidean group* as geographic space.

1.2.1. (I) THE SPATIAL CANNINGS PROCESS WITH BLOCK RESAMPLING

Cannings [9, 10] introduced a class of individual-based models in which a positive fraction of the individuals in the next generation may inherit their type from a single individual in the present generation, even in the large-population-size limit. More recently this idea was extended to spatial models [1, 6]. We will choose as geographic space the *hierarchical group*, allow for Cannings resampling at all hierarchical levels *simultaneously*, and let migration be driven by a random walk that is well-adapted to the hierarchical structure.

1.2.1.1. *Single colony.* Consider first the simple case where \mathbb{G} consists of only one site, with a cemetery and a source, emigration to the cemetery at rate c and immigration from the source at rate c . Let $\mathcal{F} \subseteq C_b(\mathcal{P}(\mathbb{K}), \mathbb{R})$ be the algebra of functions F of the form

$$(1.2.1) \quad F(x) = \int_{\mathbb{K}} x^{\otimes n}(\mathrm{d}u) \varphi(u), \quad x \in \mathcal{P}(\mathbb{K}), n \in \mathbb{N}, \varphi \in C_b(\mathbb{K}^n, \mathbb{R}).$$

Define the second Gâteaux-derivative of F with respect to x as

$$(1.2.2) \quad \frac{\partial^2 F(x)}{\partial x^2}[\delta_u, \delta_v] = \frac{\partial}{\partial x} \left(\frac{\partial F(x)}{\partial x}[\delta_u] \right) [\delta_v], \quad u, v \in \mathbb{K}.$$

For $\theta \in \mathcal{P}(\mathbb{K})$, $c, d \in [0, \infty)$, $\Lambda \in \mathcal{M}_{\text{fin}}([0, 1])$ (= the set of non-negative finite measures on $[0, 1]$) such that

$$(1.2.3) \quad \Lambda(\{0\}) = 0, \quad \int_{(0,1]} \frac{\Lambda(\mathrm{d}r)}{r} = \infty,$$

let $L_\theta^{c,d,\Lambda}: \mathcal{F} \rightarrow C_b(\mathcal{P}(\mathbb{K}), \mathbb{R})$ be the linear operator

$$(1.2.4) \quad L_\theta^{c,d,\Lambda} = L_\theta^c + L^d + L^\Lambda$$

acting on $F \in \mathcal{F}$ as

$$(1.2.5) \quad \begin{aligned} (L_\theta^c F)(x) &= c \int_{\mathbb{K}} (\theta - x)(\mathrm{d}a) \frac{\partial F(x)}{\partial x}[\delta_a], \\ (L^d F)(x) &= d \int_{\mathbb{K}} \int_{\mathbb{K}} Q_x(\mathrm{d}u, \mathrm{d}v) \frac{\partial^2 F(x)}{\partial x^2}[\delta_u, \delta_v], \\ (L^\Lambda F)(x) &= \int_{(0,1]} \Lambda^*(\mathrm{d}r) \int_{\mathbb{K}} x(\mathrm{d}a) [F((1-r)x + r\delta_a) - F(x)], \end{aligned}$$

where

$$(1.2.6) \quad Q_x(\mathrm{d}u, \mathrm{d}v) = x(\mathrm{d}u) \delta_u(\mathrm{d}v) - x(\mathrm{d}u) x(\mathrm{d}v)$$

is the Fleming-Viot diffusion coefficient, and $\Lambda^* \in \mathcal{M}([0, 1])$ (= the set of non-negative sigma-finite measures on $[0, 1]$) is defined by

$$(1.2.7) \quad \Lambda^*({0}) = 0, \quad \Lambda^*(dr) = \frac{\Lambda(dr)}{r^2}, \quad r \in (0, 1].$$

The three parts of $L_\theta^{c,d,\Lambda}$ correspond to: a *drift* towards θ of strength c (= immigration-emigration), a *Fleming-Viot diffusion* with *volatility* d (= Moran resampling), and a Λ -Cannings process with resampling measure Λ (= Cannings resampling).

We need to generalise the above set-up to the hierarchical group, with resampling and migration taking place at all hierarchical levels simultaneously.

1.2.1.2. *Hierarchical group.* Define [14, 40]

$$(1.2.8) \quad \Omega_N = \bigoplus_{i \in \mathbb{N}} Z_N,$$

where Z_N is the cyclical group, i.e., the set $\{0, 1, \dots, N-1\}$ equipped with addition modulo N . View Ω_N as set of addresses, each of which specifies one of N houses, in one of N neighbourhoods, in one of N villages, etc. In particular, (1.2.8) says that $i \in \Omega_N$ has the form $(i_k)_{k \in \mathbb{N}_0}$ with $\sum_{k \in \mathbb{N}_0} i_k < \infty$. We define the hierarchical distance

$$(1.2.9) \quad d_{\Omega_N}(i, j) = \min\{l \in \mathbb{N}_0 : i_l = j_l \ \forall l \geq l\}, \quad i, j \in \Omega_N,$$

and denote the k -ball around i by $B_k(i)$.

1.2.1.3. *Forward evolution.* First we introduce the migration mechanism. As parameters we have a sequence of numbers

$$(1.2.10) \quad \underline{c} = (c_k)_{k \in \mathbb{N}_0}$$

with $c_k \in (0, \infty)$. At rate c_k/N^k the random walk chooses the ball with radius k around its current position, and draws its next position according to the uniform distribution on that ball. To ensure that only finitely many jumps occur in finite time, we need to assume that

$$(1.2.11) \quad \sum_{k \in \mathbb{N}_0} \frac{c_k}{N^k} < \infty.$$

Next, we introduce the resampling mechanism. As parameters we have a sequence of resampling measures

$$(1.2.12) \quad \underline{\Lambda} = (\Lambda_k)_{k \in \mathbb{N}_0},$$

with $\Lambda_k \in \mathcal{M}_{\text{fin}}([0, 1])$ playing the role of the resampling measure on hierarchical level k . We assume that $\Lambda_k({0}) = 0$, $k \in \mathbb{N}_0$, and

$$(1.2.13) \quad \int_{(0,1]} \frac{\Lambda_0(dr)}{r} = \infty, \quad \int_{(0,1]} \frac{\Lambda_k(dr)}{r^2} < \infty, \quad k \in \mathbb{N}.$$

In the *non-spatial setting*, the Λ -Cannings model with $\Lambda \in \mathcal{M}_{\text{fin}}([0, 1])$ is defined as follows (see [22, 38, 39]). Consider an inhomogeneous Poisson point process on $[0, \infty) \times [0, 1]$ with intensity measure

$$(1.2.14) \quad dt \otimes \Lambda^*(dr).$$

For each point (t, r) in this point process, we carry out the following transition at time t . *Mark* each of $M \in \mathbb{N}$ individuals independently with a 0 or a 1 with probability $1 - r$, respectively, r . *All* individuals marked by a 1 are killed and are replaced by copies of a *single* individual (‘the parent’) that is drawn uniformly from all the individuals marked by a 1. The continuum frequency limit is obtained by letting $M \rightarrow \infty$.

In the *spatial setting* we apply Cannings resampling *at all hierarchical levels simultaneously*, in combination with a *reshuffling*: for each $k \in \mathbb{N}_0$, we first reassign to every individual in the k -ball a new position according to the uniform distribution on that ball, and afterwards apply the Λ_k -Cannings resampling mechanism. More precisely:

- For every $i \in \Omega_N$ and $k \in \mathbb{N}_0$, choose the block $B_k(i)$ at rate $1/N^{2k}$.
- Each individual in $B_k(i)$ is first moved to a uniformly chosen random location in $B_k(i)$, i.e., a reshuffling takes place. After that, r is drawn according to the intensity measure Λ_k^* , and with probability r each of the individuals in $B_k(i)$ is replaced by an individual of type a , with a drawn according to the empirical type distribution in $B_k(i)$, i.e.,

$$(1.2.15) \quad y_{i,k} = N^{-k} \sum_{j \in B_k(i)} x_j.$$

Because the reshuffling is done first, the resampling always acts on a uniformly distributed state (‘panmictic resampling’). The continuum limit $M \rightarrow \infty$ is the process that we want to study. To show that this process is characterised by a *well-posed martingale problem*, we need to specify its generator.

The generator L for the spatial Canning process with block resampling is

$$(1.2.16) \quad L = L_{\text{mig}} + L_{\text{res}},$$

where

$$(1.2.17) \quad (L_{\text{mig}}F)(x) = \sum_{j \in \Omega_N} a(i, j) \int_{\mathbb{K}} (x_j - x_i)(da) \frac{dF}{dx_i}[\delta_a]$$

takes care of the *migration* and

$$(1.2.18) \quad \begin{aligned} & (L_{\text{res}}F)(x) \\ &= \sum_{i \in \Omega_N} \left((L_i^{d_0}F)(x) + \int_{(0,1]} \Lambda_0^*(dr) \int_{\mathbb{K}} x_i(da) [F(\Phi_{r,a,\{i\}}(x)) - F(x)] \right. \\ & \quad \left. + \sum_{k \in \mathbb{N}} N^{-2k} \int_{(0,1]} \Lambda_k^*(dr) \int_{\mathbb{K}} y_{i,k}(da) [F(\Phi_{r,a,B_k(i)}(x)) - F(x)] \right), \end{aligned}$$

takes care of the *reshuffling-resampling*. Here, $\Phi_{r,a,B_k(i)}: \mathcal{P}(\mathbb{K})^{\Omega_N} \rightarrow \mathcal{P}(\mathbb{K})^{\Omega_N}$ is the *reshuffling-resampling map* acting as

$$(1.2.19) \quad \left[(\Phi_{r,a,B_k(i)}(x)) \right]_j = \begin{cases} (1-r)y_{i,k} + r\delta_a, & j \in B_k(i), \\ x_i, & j \notin B_k(i), \end{cases}$$

where $r \in [0,1]$, $a \in \mathbb{K}$, $k \in \mathbb{N}_0$, $i \in \Omega_N$, and $L_i^{d_0}$ is the Fleming-Viot diffusion operator with volatility d_0 acting on the colony x_i .

We proved the following in [26].

Theorem 1.2.1 (The spatial Cannings process with block resampling is well defined). *For every initial law $\Gamma \in \mathcal{P}(\mathbb{K})^{\Omega_N}$, the (L, \mathcal{F}, Γ) -martingale problem is well-posed and defines a strong Markov and Feller process.*

1.2.1.4. *Looking backward: Duality.* An important tool in the analysis of the Cannings process with block resampling is *duality* with what is called the spatial $\underline{\Lambda}$ -coalescent, with the duality function given by mixed spatial monomials. For the proper set-up of duality we refer to [23]. In a duality relation we have a process X with state space E , a dual process Y with state space E' , and a function

$$(1.2.20) \quad H: E \times E' \rightarrow \mathbb{R}, \quad H \in C_b(E \times E', \mathbb{R}),$$

such that

$$(1.2.21) \quad E_x [H(X_t, Y)] = E_y [H(X_0, Y_t)], \quad (x, y) \in E \times E', t \geq 0.$$

In our setting the process Y will be a spatial coalescent driven by $\underline{\Lambda}$, so that E' will be the set of *marked partitions of a finite set*, which we denote by

$$(1.2.22) \quad \mathbb{S}^{\Omega_N}.$$

We write (π, g) for an element of \mathbb{S}^{Ω_N} , where $g \in \Omega_N^{|\pi|}$, π is a partition of the set $\{1, \dots, n\}$, and the partition elements are labeled π_1, \dots, π_k with $k = |\pi|$. We specify a test function $\varphi \in C_b(\mathbb{K}^{|\pi|}, \mathbb{R})$, which we add to the dual configuration and which remains fixed during the evolution. This allows us to bring the duality relation into a standard form for a single function H , with the property that $\{H(\cdot, y), y \in E'\}$ *separates measures* on the state space E and is *convergence determining* (see [23]).

The partition elements perform random walks driven by \underline{c} , up to a coalescent event. In addition, the partition elements are subject to Λ_k -*coalescence with reshuffling* in k -blocks for every $k \in \mathbb{N}_0$. For the reshuffling, all partition elements in the k -block are independently assigned new positions drawn uniformly from the block. For the Λ_k -coalescence, we choose at rate $\Lambda_k(dr)$ a number $r \in (0, 1]$ and mark every partition element with probability r . All marked partition elements coalesce into a single partition element. The function H is given by a *polynomial*,

$$(1.2.23) \quad H(x; [(\pi, g), \varphi]) = \int_{\mathbb{K}^{|\pi|}} \varphi(\underline{u}) x_{g_1}(du_1) \times \cdots \times x_{g_{|\pi|}}(u_{|\pi|}),$$

where $\underline{u} = (u_1, \dots, u_{|\pi|})$.

1.2.2. (II) THE SPATIAL FLEMING-VIOT PROCESS WITH SEED-BANK

1.2.2.1. *Forward evolution.* In various situations in population genetics, coexistence of types is observed even when the classical Fleming-Viot model predicts clustering. The reason is that individuals may become *dormant* (i.e., suspend resampling, migration, mutation, etc.) until they become active again. This is modelled by adding seed-banks. For example, in case $\mathbb{K} = \{0, 1\}$, letting $X(t)$ and $Y(t)$ denote the frequencies of type 1 at time t in the active population, respectively, the dormant population, we get the following system of coupled SDE's:

$$(1.2.24) \quad \begin{aligned} dX(t) &= \sqrt{dX(t)(1-X(t))} dw(t) + Ke[Y(t) - X(t)] dt, \\ dY(t) &= e[X(t) - Y(t)] dt. \end{aligned}$$

Here, e is the rate of *exchange* between active and dormant individuals, and K is the *ratio* of the sizes of the dormant population and the active population. This system was introduced and analysed in [3, 4, 20, 21].

Including migration into the picture, focussing on the choice $\mathbb{G} = \mathbb{Z}^d$, we consider $(X(t), Y(t))_{t \geq 0}$ with

$$(1.2.25) \quad X(t) = (x_i(t))_{i \in \mathbb{Z}^d}, \quad Y(t) = (y_i(t))_{i \in \mathbb{Z}^d},$$

and obtain the following system of coupled SDE's:

$$(1.2.26) \quad \begin{aligned} dx_i(t) &= \sum_{j \in \mathbb{Z}^d} a(i, j)[x_j(t) - x_i(t)] dt \\ &\quad + \sqrt{dx_i(t)(1-x_i(t))} dw_i(t) + Ke[y_i(t) - x_i(t)] dt, \\ dy_i(t) &= e[x_i(t) - y_i(t)] dt, \quad i \in \mathbb{Z}^d. \end{aligned}$$

It turns out that this system exhibits a quantitative change in its longtime behaviour, but not a qualitative change. In particular, the dichotomy of clustering versus coexistence holds under the same condition of recurrent versus transient migration.

To remedy the above situation, already in the non-spatial model it has been proposed to introduce wake-up times (from dormant to active) with fat tails (see [3, 4, 22]). However, this necessarily leads to *non-Markovian* models, which are difficult to analyse. We therefore introduce what we call a sequence of *coloured seed-banks in every colony*, with wake-up rates that allow for the wake-up time of a *typical* individual to have a *fat tail*, so that with the colours included in the state space the process is still *Markov*. In other words, we consider $(X(t), Y(t))_{t \geq 0}$ with

$$(1.2.27) \quad X(t) = (x_i(t))_{i \in \mathbb{Z}^d}, \quad Y(t) = ((y_{i,m}(t))_{m \in \mathbb{N}_0})_{i \in \mathbb{Z}^d},$$

and the following system of coupled SDE's:

$$(1.2.28) \quad \begin{aligned} dx_i(t) &= \sum_{j \in \mathbb{Z}^d} a(i, j) [x_j(t) - x_i(t)] dt \\ &\quad + \sqrt{dx_i(t)(1 - x_i(t))} dw_i(t) + \sum_{m \in \mathbb{N}_0} K_m e_m [y_{i,m}(t) - x_i(t)] dt, \\ dy_{i,m}(t) &= e_m [x_i(t) - y_{i,m}(t)] dt, \quad m \in \mathbb{N}_0, \quad i \in \mathbb{Z}^d. \end{aligned}$$

Here, e_m is the rate of exchange between active and m -dormant individuals, and K_m the ratio of the sizes of the m -dormant population and the active population.

We require that

$$(1.2.29) \quad \chi = \sum_{m \in \mathbb{N}_0} K_m e_m < \infty$$

and

$$(1.2.30) \quad a(i, j) = a(j, i) \quad \forall i, j \in \mathbb{Z}^d.$$

Assumption (1.2.29) guarantees that the total flow from the active to the dormant population is finite in finite time, while assumption (1.2.30) is *necessary* for our claims on the longtime behaviour stated below.

The system of SDE's in (1.2.28) determines the generator

$$(1.2.31) \quad \begin{aligned} L = \sum_{i \in \mathbb{G}} \left(\left[\sum_{j \in \mathbb{G}} a(i, j) (x_j - x_i) \right] \frac{\partial}{\partial x_i} + x_i (1 - x_i) \frac{\partial^2}{\partial x_i^2} \right. \\ \left. + \sum_{m \in \mathbb{N}_0} \left[K_m e_m (y_{i,m} - x_i) \frac{\partial}{\partial x_i} + e_m (x_i - y_{i,m}) \frac{\partial}{\partial y_{i,m}} \right] \right), \end{aligned}$$

which acts on \mathcal{F} , the algebra of twice continuously differentiable functions depending on finitely many components. We proved the following in [28].

Theorem 1.2.2 (The spatial Fleming-Viot process with seed-bank is well defined). *For every initial law $\mu \in \mathcal{P}([0, 1] \times [0, 1]^{\mathbb{N}_0})^{\mathbb{Z}^d}$, the (L, \mathcal{F}, μ) -martingale problem is well-posed and defines a strong Markov and Feller process.*

1.2.2.2. *Looking backward: Duality.* The dual process is again a spatial coalescent. However, now the coalescence and the migration occur in the active state only. The migration is *no longer a random walk*. In particular, for two partition elements to be able to coalesce they need to be at the same site and both be active. This already indicates that coalescence is less likely to happen.

The duality function is again given by mixed spatial moments:

$$(1.2.32) \quad H\left((x_i)_{i \in \mathbb{Z}^d}, ((y_{i,m})_{m \in \mathbb{N}_0})_{i \in \mathbb{Z}^d}, (n_i, ((m_{i,m})_{m \in \mathbb{N}_0})_{i \in \mathbb{Z}^d}\right) = x_i^{n_i} (y_{i,m})^{m_{i,m}}.$$

Here, n_i is the number of active partition elements at colony i and $m_{i,m}$ is the number of dormant partition elements of colour m at colony i . The partition elements independently follow a Markov chain on $\mathbb{Z}^d \times \mathbb{N}_0$, until they meet on \mathbb{Z}^d and coalesce at rate d . In other words, coalescence works as before, but only in the active state, while in the dormant state nothing happens. The Markov chain has transition rates $b(\cdot, \cdot)$ given by

$$(1.2.33) \quad b(i, j) = \begin{cases} a(i, j), & i, j \in \mathbb{Z}^d, \\ 0, & i, j \in \mathbb{N}_0, \\ K_m e_m, & i \in \mathbb{N}_0, j \in \mathbb{Z}^d, \\ e_m, & i \in \mathbb{Z}^d, j \in \mathbb{N}_0. \end{cases}$$

1.3. Equilibrium

We next present our results for the two model classes introduced in Section 1.2. We start by recalling the classical model of interacting Fisher-Wright diffusions labelled by the hierarchical group.

The longterm behaviour in the classical model is best understood by using the duality of interacting Fisher-Wright diffusions with a spatial coalescent. First note that the function $E[x_i(t)(1 - x_i(t))]$ converges to 0 as $t \rightarrow \infty$ if $x_i(t)$ concentrates on the boundary of $[0, 1]$, and remains strictly positive otherwise. With the help of duality we calculate, for any initial state that is translation invariant and ergodic with mean component θ ,

$$(1.3.1) \quad E[x_i(t)] = \theta, \\ E[(x_i(t))^2] = q_t \theta + (1 - q_t) \sum_{j, k \in \Omega_N} E[x_j(0), x_k(0)] p_t((i, j), (i, k)),$$

where q_t is the probability for two partition elements to coalesce by time t , and $p_t((i, j), (i, k))$ is the probability conditional on non-coalescence for two partition elements, both starting from i , to be at j and k at time t . Let $q_\infty = \lim_{t \rightarrow \infty} q_t$ be the probability that the partition elements eventually coalesce. Then, using that the initial state is stationary and ergodic w.r.t. translations in Ω_N , we get

$$(1.3.2) \quad E[x_i^2(t)] \xrightarrow{t \rightarrow \infty} q_\infty \theta + (1 - q_\infty) \theta^2 = q_\infty \theta (1 - \theta) + \theta^2.$$

Hence

$$(1.3.3) \quad E[x_i(t)(1 - x_i(t))] \xrightarrow[t \rightarrow \infty]{} (1 - q_\infty)\theta(1 - \theta),$$

which is zero when $q_\infty = 1$ or $\theta \in \{0, 1\}$, and strictly positive when $q_\infty < 1$ and $\theta \notin \{0, 1\}$. It is known that [12]

$$(1.3.4) \quad q_\infty = 1 \iff \sum_{k \in \mathbb{N}_0} \frac{1}{c_k} = \infty.$$

1.3.1. (I) SPATIAL CANNINGS WITH BLOCK RESAMPLING

In the case of the *Cannings process with block resampling*, for the coalescent starting from two partition elements there is a strictly positive probability to coalesce *from any distance*. This makes it possible for them to coalesce with probability 1 even when $q_\infty < 1$. In other words, coexistence may change to clustering due to block resampling.

Indeed, set

$$(1.3.5) \quad \lambda_k = \Lambda_k([0, 1]), \quad k \in \mathbb{N}_0,$$

and let $P_t(\cdot, \cdot)$ denote the time- t transition kernel of the random walk on Ω_N with migration coefficients

$$(1.3.6) \quad c_k + N^{-1}\lambda_{k+1}, \quad k \in \mathbb{N}_0,$$

starting at 0. Here, the extra term $N^{-1}\lambda_{k+1}$ comes from the reshuffling that takes place before the resampling, which induces additional migration. Define the *hazard*

$$(1.3.7) \quad H_N = \sum_{k \in \mathbb{N}_0} \lambda_k N^k \int_0^\infty ds P_{2s}(0, B_k(0)),$$

where $B_k(0)$ is the k -block in Ω_N around 0. Let

$$(1.3.8) \quad \text{Var}_x(\psi) = Q_x(du, dv) \psi(u)\psi(v),$$

with $Q_x(du, dv)$ defined in (1.2.6), and

$$(1.3.9) \quad E_{\nu_\theta}[\text{Var}_{(\cdot)}(\psi)] = \int_{\mathcal{P}(\mathbb{K})} \nu_\theta(dx) \text{Var}_x(\psi).$$

We proved the following in [26].

Theorem 1.3.1 (Dichotomy for Cannings with block resampling).

(a) **[Coexistence]** If $H_N < \infty$, then

$$(1.3.10) \quad \liminf_{t \rightarrow \infty} \sup_{\psi \in C_b(\mathbb{K}, \mathbb{R})} \mathbb{E}_{x_i(t)}[\text{Var}(\psi)] > 0 \quad \forall i \in \Omega_N.$$

(b) **[Clustering]** If $H_N = \infty$, then

$$(1.3.11) \quad \lim_{t \rightarrow \infty} \sup_{\psi \in C_b(\mathbb{K}, \mathbb{R})} \mathbb{E}_{x_i(t)}[\text{Var}(\psi)] = 0 \quad \forall i \in \Omega_N.$$

This in turn leads to the following picture:

Theorem 1.3.2 (Ergodic behaviour for finite N). *The following dichotomy holds:*

(a) **[Coexistence]** If $\bar{H}_N < \infty$, then for every $\theta \in \mathcal{P}(\mathbb{K})$ and every $X(0)$ whose law is stationary and ergodic w.r.t. translations in Ω_N with single-site mean θ ,

$$(1.3.12) \quad \mathcal{L}[X(t)] \xrightarrow[t \rightarrow \infty]{} \nu_\theta^{c, \lambda} \in \mathcal{P}(\mathcal{P}(\mathbb{K})^{\Omega_N})$$

for some unique law $\nu_\theta^{c, \lambda}$ that is stationary and ergodic w.r.t. translations in Ω_N with single-site mean θ .

(b) **[Clustering]** If $\bar{H}_N = \infty$, then for every $\theta \in \mathcal{P}(\mathbb{K})$,

$$(1.3.13) \quad \mathcal{L}[X(t)] \xrightarrow[t \rightarrow \infty]{} \int_{\mathbb{K}} \theta(du) \delta_{(\delta_u)\Omega_N} \in \mathcal{P}(\mathcal{P}(\mathbb{K})^{\Omega_N}).$$

We can now compare the classical process with the Cannings process. We focus on the *volatility of the k -block averages*

$$(1.3.14) \quad Y_k^{(N)}(t) = \frac{1}{N^k} \sum_{j \in B_k(i)} x_j(tN^k), \quad i \in \Omega_N, t \geq 0,$$

in the *hierarchical mean-field limit* $N \rightarrow \infty$. Let

$$(1.3.15) \quad \underline{d}^* = (d_k^*)_{k \in \mathbb{N}_0}$$

be the sequence of volatilities of the k -block averages when $\mu_0 > 0$ and $\mu_k = 0$ for all $k \in \mathbb{N}$, i.e., when there is resampling in single colonies but not in blocks of colonies. This sequence has initial value $d_0^* = 0$ and satisfies the recursion relation [26]

$$(1.3.16) \quad d_1^* = d_1 = \frac{c_0 \mu_0}{c_0 + \mu_0}, \quad \frac{1}{d_{k+1}^*} = \frac{1}{c_k} + \frac{1}{d_k^*}, \quad k \in \mathbb{N},$$

whose solution is

$$(1.3.17) \quad d_k^* = \frac{\frac{1}{2} \lambda_0}{1 + \frac{1}{2} \lambda_0 \sigma_k}, \quad k \in \mathbb{N}, \quad \sigma_k = \sum_{l=0}^{k-1} \frac{1}{c_l}.$$

Let

$$(1.3.18) \quad \underline{d} = (d_k)_{k \in \mathbb{N}_0}$$

be the sequence of volatilities of k -block averages in the spatial Cannings process with block resampling. We proved the following in [26].

Theorem 1.3.3 (Comparison of hierarchical Fleming-Viot and hierarchical Cannings). *The following hold for $\underline{d} = (d_k)_{k \in \mathbb{N}_0}$:*

- (a) *The maps $\underline{c} \mapsto \underline{d}$ and $\underline{\lambda} \mapsto \underline{d}$ are component-wise non-decreasing.*
- (b) *$\underline{d} \geq \underline{d}^*$ component-wise.*
- (c) *Clustering occurs if and only if $\sum_{k \in \mathbb{N}_0} (1/c_k) \sum_{l=0}^k \lambda_l = \infty$.*
- (d) *If $\lim_{k \rightarrow \infty} \sigma_k = \infty$ and $\sum_{k \in \mathbb{N}} \sigma_k \lambda_k < \infty$, then $\lim_{k \rightarrow \infty} \sigma_k d_k = 1$.*

In particular, (a),(b) say that both migration and reshuffling-resampling increase the volatility, (c) says that the dichotomy due to migration is affected by the reshuffling-resampling only when the latter is *strong enough*, i.e., when $\sum_{k \in \mathbb{N}_0} \lambda_k = \infty$, while (d) says that the scaling behaviour of d_k in the clustering regime is unaffected by the reshuffling-resampling when the latter is *weak enough*, i.e., when $\sum_{k \in \mathbb{N}} \sigma_k \lambda_k < \infty$.

1.3.2. (II) SPATIAL FLEMING-VIOT WITH SEED-BANK

For the system with seed-bank we obtain the following dichotomy for the longtime behaviour. Define

$$(1.3.19) \quad \varrho = \sum_{m \in \mathbb{N}_0} K_m.$$

The wake-up time of a typical individual, denoted by τ , has distribution

$$(1.3.20) \quad P(\tau \geq t) = \sum_{m \in \mathbb{N}_0} \frac{K_m e_m}{\chi} e^{-e_m t}.$$

Suppose that

$$(1.3.21) \quad K_m \sim A m^{-\alpha}, \quad e_m \sim B m^{-\beta}, \quad m \rightarrow \infty,$$

where $A, B \in (0, \infty)$ and $\alpha, \beta \in \mathbb{R}$ with $\alpha < 1 < \alpha + \beta$. Subject to (1.3.21), we have

$$(1.3.22) \quad P(\tau \geq t) \sim C t^{-\gamma}, \quad t \rightarrow \infty,$$

where

$$(1.3.23) \quad \gamma = \frac{\alpha + \beta - 1}{\beta} \in (0, 1), \quad C = \frac{A}{\beta} B^{1-\gamma} \gamma \Gamma(\gamma) \in (0, \infty),$$

with Γ the Gamma-function.

There is a principal difference between the cases $\varrho < \infty$ and $\varrho = \infty$. We proved the following in [28].

Theorem 1.3.4 (Dichotomy and longtime behaviour). *Suppose that the law of $(X(0), Y(0))$ is stationary and ergodic w.r.t. translations in \mathbb{Z}^d with single-site*

mean $\theta \in [0, 1]$. Define the hazards

$$(1.3.24) \quad H_a = \int_0^\infty a_t(0, 0) dt, \quad H_{a, \gamma} = \int_0^\infty a_t(0, 0) t^{-(1-\gamma)/\gamma} dt.$$

(a) Suppose that $\varrho < \infty$. If $H_a < \infty$, then

$$(1.3.25) \quad \mathcal{L}[(X(t), Y(t))] \xrightarrow[t \rightarrow \infty]{} \nu_\theta^{K, \varepsilon} \in \mathcal{P}([0, 1] \times [0, 1]^{\mathbb{N}_0} \mathbb{Z}^d),$$

where $\nu_\theta^{K, \varepsilon}$ is an equilibrium measure that is stationary and ergodic w.r.t. translations in \mathbb{Z}^d , and satisfies $E_{\nu_\theta}[(x_i, y_i)] = (\theta, \theta)$, where

$$(1.3.26) \quad \theta = \lim_{M \rightarrow \infty} \left[\frac{x_0 + \sum_{m=0}^M K_m y_{0,m}}{1 + \sum_{m=0}^M K_m} \right].$$

If $H_a = \infty$, then

$$(1.3.27) \quad \mathcal{L}[(X(t), Y(t))] \xrightarrow[t \rightarrow \infty]{} (1 - \theta) \delta_{(0, 0^{\mathbb{N}_0}) \mathbb{Z}^d} + \theta \delta_{(1, 1^{\mathbb{N}_0}) \mathbb{Z}^d}.$$

(b) Suppose that $\varrho = \infty$. Then the above dichotomy holds with H_a replaced by $H_{a, \gamma}$.

We see that if $\varrho = \infty$, then the dichotomy is shifted and *recurrent migration* can still lead to *coexistence*. For $\gamma \in (\frac{1}{2}, 1)$ there is an interesting competition between the migration and the seed-bank, while for $\gamma \in (0, \frac{1}{2})$ the seed-bank completely dominates and coexistence occurs no matter what is the migration. In particular, in $d = 2$ for symmetric migration with finite second moments, there is *clustering without seed-bank but coexistence with seed-bank* (for all $\gamma \in (0, 1)$). For biology this is an important observation.

1.3.3. THE THREE MODEL CLASSES IN COMPARISON

We can now compare the longtime behaviour in the different models described above. The key quantity is the *hazard of two dual partition elements to coalesce*. In the classical model the hazard is

$$(1.3.28) \quad H = \int_0^\infty dt \hat{a}_t(0, 0) = \hat{G}(0, 0),$$

where $\hat{G}(\cdot, \cdot)$ is the Green function of the difference random walk. We saw that in the other two models the hazard is different. Nevertheless, in the formula for the hazard the transition kernel $a_t(\cdot, \cdot)$ still appears (with $\hat{a}_t(\cdot, \cdot) = a_t(\cdot, \cdot)$ because in (1.2.30) we assumed $a(\cdot, \cdot)$ to be symmetric). The Cannings model with block resampling gives a *decrease of the effective dimension*, while the Fleming-Viot model with seed-bank gives an *increase of the effective dimension*, both resulting in a change of the critical dimension. This can be made quantitative with the help of the so-called degree of the random walk, for which we refer the reader to [12, 13].

1.4. Random environment

Often it is more realistic to assume that the mechanism of evolution is *spatially inhomogeneous*. The important question is whether this change affects the long-time behaviour qualitatively or not. We will explore this issue for the Cannings process with block resampling. In particular, we will look at the situation where the *resampling rates* are spatially inhomogeneous.

To define the modification of the model introduced in Section 1.2.1.3, we need to consider the *full tree*, i.e.,

$$(1.4.1) \quad \Omega_N^{\mathbb{T}} = \bigcup_{k \in \mathbb{N}_0} \Omega_N^{(k)}, \quad \Omega_N^{(k)} = \Omega_N / B_k(0),$$

where $\Omega_N / B_k(0)$ denotes the quotient group of Ω_N modulo $B_k(0)$ (recall (1.2.9)). Note that the leaves of the tree form the set Ω_N . For $\xi \in \Omega_N^{\mathbb{T}}$, write

$$(1.4.2) \quad |\xi| = \text{the height of } \xi \text{ (counting from the leaves),}$$

i.e., $|\xi| = k$ when $\xi \in \Omega_N^{(k)}$ for $k \in \mathbb{N}_0$, and define

$$(1.4.3) \quad B_{|\xi|}(\xi),$$

to be the set of sites in Ω_N that lie below ξ . We want to make the reshuffling-resampling *spatially random*. To that end, let

$$(1.4.4) \quad \underline{\Lambda}(\omega) = \{\Lambda^\xi(\omega) : \xi \in \Omega_N^{\mathbb{T}}\}$$

be a random field of $\mathcal{M}_{\text{fin}}([0, 1])$ -valued resampling measures indexed by the tree. Throughout the paper, we use the symbol ω to denote the *random environment* and the symbol \mathbb{P} to denote the *law* of ω . We assume that $\Lambda^\xi(\omega)$ is of the form

$$(1.4.5) \quad \Lambda^\xi(\omega) = \lambda_{|\xi|} \chi^\xi(\omega),$$

where $\underline{\lambda} = (\lambda_k)_{k \in \mathbb{N}_0}$ is a deterministic sequence in $(0, \infty)$ and

$$(1.4.6) \quad \{\chi^\xi(\omega) : \xi \in \Omega_N^{\mathbb{T}}\}$$

is a random field of $\mathcal{M}_{\text{fin}}([0, 1])$ -valued resampling measures that is *stationary under translations* in $\Omega_N^{\mathbb{T}}$.

Abbreviate

$$(1.4.7) \quad \rho^\xi(\omega) = \chi^\xi(\omega)((0, 1]),$$

which is the total mass of $\chi^\xi(\omega)$. Clearly,

$$(1.4.8) \quad \{\rho^\xi(\omega) : \xi \in \Omega_N^{\mathbb{T}}\}$$

is a random field of $(0, \infty)$ -valued total masses that is also stationary under translations in $\Omega_N^{\mathbb{T}}$. We assume that

$$(1.4.9) \quad \mathbb{E}[\rho^\xi(\omega)] = 1, \quad \mathbb{E}[(\rho^\xi(\omega))^2] = C \in (0, \infty),$$

and that the sigma-algebra at infinity associated with (1.4.7), defined by

$$(1.4.10) \quad \mathcal{T} = \bigcap_{L \in \mathbb{N}_0} \mathcal{F}_L, \quad \mathcal{F}_L = \sigma\left(\rho^\xi(\cdot) \text{ with } \xi \in \Omega_N^\mathbb{T} \text{ such that } d_{\Omega_N^\mathbb{T}}(0, \xi) \geq L\right),$$

is trivial, where $d_{\Omega_N^\mathbb{T}}$ denote the hierarchical distance on $\Omega_N^\mathbb{T}$.

We proved the following in [27].

Theorem 1.4.1 (Longtime behaviour for Cannings in random environment). *Fix $N \in \mathbb{N} \setminus \{1\}$. Suppose that, under the law \mathbb{P} , the law of the initial state $X(\omega; 0)$ is stationary and ergodic w.r.t. translations in Ω_N , with single-site mean*

$$(1.4.11) \quad \theta = \mathbb{E}[X_0(\omega; 0)] \in \mathcal{P}(\mathbb{K}).$$

Then, for \mathbb{P} -a.e. ω , there exists an equilibrium measure $\nu_\theta(\omega) \in \mathcal{P}(\mathcal{P}(\mathbb{K})^{\Omega_N})$, arising as

$$(1.4.12) \quad \lim_{t \rightarrow \infty} \mathcal{L}[X(\omega; t)] = \nu_\theta(\omega),$$

satisfying

$$(1.4.13) \quad \int_{\mathcal{P}(\mathbb{K})^{\Omega_N}} x_0 \nu_\theta(\omega)(dx) = \theta.$$

Moreover, under the law \mathbb{P} , the random variable $\nu_\theta(\omega)$ is stationary and ergodic w.r.t. translations in Ω_N .

The proof of Theorem 1.4.1 is based on a computation with the dual process, which allows us to control second moments. In random environment this computation involves two random walks in the same environment, and the *difference* of the two random walks is *not* a random walk itself. We identify the parameter regime for which $\nu_\theta(\omega)$ is a *multitype equilibrium* (= coexistence given ω),

$$(1.4.14) \quad \sup_{f \in C_b(\mathbb{K}, \mathbb{R})} \int_{\mathcal{P}(\mathbb{K})^{\Omega_N}} \nu_\theta(\omega)(dx) \int_{\mathbb{K}} [f(u) - \theta]^2 x_0(du) > 0,$$

respectively, a *monotype equilibrium* (= clustering given ω), i.e.,

$$(1.4.15) \quad \nu_\theta(\omega) = \int_{\mathbb{K}} \delta_{(\delta_u)^{\Omega_N}} \theta(du).$$

We proved the following in [27].

Theorem 1.4.2 (Dichotomy for Cannings in random environment). *Fix $N \in \mathbb{N} \setminus \{1\}$ and assume (1.4.5)–(1.4.10).*

- (a) *Let $\mathcal{C} = \{\omega : \text{in } \omega \text{ coexistence occurs}\}$. Then $\mathbb{P}(\mathcal{C}) \in \{0, 1\}$.*
- (b) *$\mathbb{P}(\mathcal{C}) = 1$ if and only if*

$$(1.4.16) \quad \sum_{k \in \mathbb{N}_0} \frac{1}{c_k + N^{-1} \lambda_{k+1}} \sum_{l=0}^k \lambda_l < \infty.$$

Thus, we see that the dichotomy between coexistence and clustering is preserved: the effect of the random environment is not qualitative: only quantitative changes occur. For example, the random environment *lowers the volatility* d_k on every hierarchical scale k compared to the average environment. The intuition behind this is that the random environment causes fluctuations in the resampling, which in turn reduce the clustering. For some choices of \underline{c} and $\underline{\lambda}$ the random environment *slows down the growth of the monotype clusters*, i.e., enhances the diversity of types.

1.5. Extensions

Having completed our brief description of the two model classes (I) and (II), we discuss some interesting questions that are treated in our papers but that we cannot discuss in detail here.

1.5.1. ON SOME GENERALISATIONS OF THE MODEL CLASSES

Our models allow for more general geographic spaces replacing Ω_N or \mathbb{Z}^d , namely, other countable abelian groups. Our results on the longtime behaviour on Ω_N (for Cannings with block resampling) and on \mathbb{Z}^d (for Fleming-Viot with seed-bank) in fact hold more generally on countable, abelian and irreducible groups. Furthermore, concerning resampling, for example, in case $\mathbb{K} = \{0, 1\}$ we can replace the volatility function $g_{\text{FW}}(x) = x(1-x)$, $x \in [0, 1]$, in the classical Fisher-Wright diffusion by volatility functions $g(x)$ with $g(0) = g(1) = 0$, $g(x) > 0$ for $x \in (0, 1)$, and g locally Lipschitz on $[0, 1]$. This requires some new methods of proof, including coupling, since duality cannot be used anymore. However, the same phenomena prevail.

In the case of *more than two types*, i.e., when we pass from the Fisher-Wright model to the Fleming-Viot model, the basic questions about *uniqueness* of the martingale problem remain *open* for state-dependent volatility, and only small sets of possible volatility functions can be handled (see [16]). Still, the same phenomena persist once we assume well-posedness. Our methods should in principle also carry over to the multitype case in the presence of seed-banks, but this has to be worked out in more detail.

1.5.2. JUSTIFICATION OF THE MODEL: LIMITS OF INDIVIDUAL-BASED MODELS

Our models arise from individual-based models with M individuals (respectively, M individuals per site) in the limit as $M \rightarrow \infty$ when the individuals carry mass $1/M$. This justifies the form of the generators as they appeared above. We can show tightness in path space and obtain convergence to the solution of the martingale problem. We can show that many individual-based models converge to the same diffusion model. For example, we can relax the assumption that active

and dormant states follow a strict exchange, as used above, and allow for active individuals to become dormant at a prescribed rate and dormant individuals to become active at a another prescribed rate, independently.

1.5.3. ANALYSIS CLOSE TO THE CRITICAL DIMENSION

On \mathbb{Z}^d the *critical dimension* is $d = 2$, which separates recurrence from transience and which itself is recurrent. Thus, for $d \leq 2$ we have clustering and for $d \geq 3$ we have coexistence. For the behaviour of spatial populations in general we should find that it is the *interplay* of the dimension and the structure of the migration kernel that determines clustering or coexistence. Dawson, Gorostiza and Wakolbinger [12, 13] showed that the proper concept is the *degree* of the underlying random walk, which is a real number ≥ -1 . Here, -1 corresponds to positive recurrence (in the classical sense of finite mean return time), the interval $(-1, 0)$ corresponds to strong recurrence (for instance, simple random walk on \mathbb{Z}), 0 to critical recurrence, $(0, 1]$ to transience, and $(1, \infty)$ to strong transience.

The random walk on Ω_N with $c_k = c^k$, $k \in \mathbb{N}_0$, and $c \in (0, N)$ has degree $\log c / (\log N - \log c)$. Hence the degree is 0 for $c = 1$ (the critical case), but converges to 0 as $N \rightarrow \infty$, either from above or from below depending on whether $c > 1$ or $c < 1$. This means that we may approach criticality and may examine the issue of finding all universality classes for the large scale behaviour. In [24, 25, 29] we gave concrete answers in terms of a so-called *renormalisation analysis*.

1.6. Perspectives

We close with a brief look at the future. The model classes we have discussed in the present contribution pose many challenges and should be investigated further from at least two perspectives:

- Define and analyse the process of *evolving genealogies* of populations, using the approach by Depperschmidt, Greven, Pfaffelhuber and Winter outlined in [17]. Exploit this process to investigate the effect on the genealogy of an increase or a decrease of the resampling volatility.
- Identify the *universality classes* for the large space-time scaling. This can be done by taking the *spatial continuum limit*, in which case the possible limit dynamics represent the possible universality classes.

The genealogies are described by equivalence classes of ultrametric measure spaces, as developed in [18, 30], and the evolution of the process is given via martingale problem, an approach developed for non-spatial models in [19, 31] and for spatial models in [32, 33]. For models with seed-bank, because of the presence of long inactive ancestral lines this approach requires a technique developed by Gufler [34, 35], which codes the length of the pieces of ancestral path in order to treat singular settings.

The continuum space limit for genealogies must be based on ideas going back to [33], where the Fleming-Viot model on the geographic space \mathbb{R} was treated. We need to extend this analysis to the *continuum* hierarchical group, and we need to cope with the Cannings mechanism. This involves replacing the Brownian motion and the Brownian web by Lévy-processes and Lévy-webs.

References

- [1] N.H. Barton, A.M. Etheridge and A. Véber. A new model for evolution in a spatial continuum. *Electron. J. Probab.*, 15 (paper no. 7):162–216, 2010.
- [2] J. Blath, A.M. Etheridge and M. Meredith. Coexistence in locally regulated competing populations and survival of branching annihilating random walk. *Ann. Appl. Probab.*, 17:1474–1507, 2007.
- [3] J. Blath, A. Gonzales Casanova, N. Kurt and D. Spano. The ancestral process of long-range seed bank models. *J. Appl. Prob.*, 50:741–759, 2013.
- [4] J. Blath, A. Gonzales Casanova, N. Kurt and M. Wilke-Berenguer. A new coalescent for seed-bank models. *Ann. Appl. Probab.*, 26:857–891, 2016.
- [5] N. Berestycki. Recent progress in coalescent theory. *Ensaïos Matemáticos*, 16:1–193, 2009.
- [6] N. Berestycki, A.M. Etheridge and A. Véber. Large scale behaviour of the spatial Λ -Fleming-Viot process. *Ann. Inst. Henri Poincaré Probab. Stat.*, 49:374–401, 2013.
- [7] M. Birkner and J. Blath. Computing likelihoods for coalescents with multiple collisions in the infinitely many sites model. *J. Math. Biol.*, 57:435–465, 2008.
- [8] M. Birkner and J. Blath. Measure-valued diffusions, general coalescents and population genetic inference. Trends in Stochastic Analysis, *London Math. Soc. Lecture Note Ser. 353*, Cambridge University Press, Cambridge, 2009, pp. 329–363.
- [9] C. Cannings. The latent roots of certain Markov chains arising in genetics: a new approach. I. Haploid models, *Adv. Appl. Probab.* 6:260–290, 1974.
- [10] C. Cannings. The latent roots of certain Markov chains arising in genetics: a new approach. II. Further haploid models, *Adv. Appl. Probab.* 7:264–282, 1975.
- [11] J.T. Cox and A. Greven. Ergodic theorems for infinite systems of locally interacting diffusions. *Ann. Probab.*, 22:833–853, 1994.
- [12] D.A. Dawson, L.G. Gorostiza and A. Wakolbinger. Hierarchical random walks. In *Asymptotic Methods in Stochastics, Fields Institute Communications 44*, Amer. Math. Soc., Providence, RI, 2004, pp. 173–193.
- [13] D.A. Dawson, L.G. Gorostiza and A. Wakolbinger. Degrees of transience and recurrence and hierarchical random walks. *Potential Anal.*, 22:305–350, 2005.
- [14] D.A. Dawson and A. Greven. *Spatial Fleming-Viot models with selection and mutation*, volume 2092 of *Springer Lecture Notes in Math*. Springer Verlag, 2014.
- [15] D.A. Dawson, A. Greven and J. Vaillancourt. Equilibria and quasi-equilibria for infinite systems of Fleming-Viot processes. *Trans. Amer. Math. Soc.*, 347:2277–2360, 1995.
- [16] D.A. Dawson and P. March. Resolvent estimates for Fleming-Viot operators and uniqueness of solutions to related martingale problems. *J. Funct. Anal.*, 132:417–472, 1995.
- [17] A. Depperschmidt and A. Greven. Tree-Valued Feller Diffusion. <http://arxiv.org/abs/1904.02044>, 2019.

- [18] A. Depperschmidt, A. Greven and P. Pfaffelhuber. Marked metric measure spaces. *Electron. Comm. Probab.*, 16:174–188, 2011.
- [19] A. Depperschmidt, A. Greven and P. Pfaffelhuber. Path-properties of the tree-valued Fleming-Viot dynamics. *Electron. J. Probab.*, 18:1-47, 2013.
- [20] R. Der, C.L. Epstein and J.B. Plotkin. Generalized population models and the nature of genetic drift. *Theoretical Population Biology*, 80:80–99, 2011.
- [21] B. Eldon and J. Wakeley. Coalescent processes when the distribution of offspring number among individuals is highly skewed. *Genetics* 172:2621–2633, 2006.
- [22] A.M. Etheridge. Some Mathematical Models from Population Genetics. École d’Été de Probabilités de Saint-Flour XXXIX-2009, *Lecture Notes in Mathematics* 2012, Springer, Berlin, 2011.
- [23] S.N. Ethier and T.G. Kurtz. Markov Processes. Characterization and Convergence. *John Wiley & Sons*, 1986.
- [24] N. Freeman. The segregated Λ -coalescent. *Ann. Probab.*, 43:435-467, 2015.
- [25] A. Gonzales Casanova, E. Aguirre-von Wobeser, G. Espin, L. Servin-Gonzalez, N. Kurt, D. Spano, J. Blath, and G. Soberon-Chavez. Strong seed-bank effects in bacterial evolution. *J. Theor. Biol.*, 356:62–70, 2014.
- [26] A. Greven, F. den Hollander, S. Kliem and A. Klimovsky. Renormalisation of hierarchically interacting Cannings processes. *ALEA Lat. Am. J. Probab. Math. Stat.*, 11:43–140, 2014.
- [27] A. Greven, F. den Hollander and A. Klimovsky. The hierarchical Cannings process in random environment. *ALEA Lat. Am. J. Probab. Math. Stat.*, 15:295-351, 2018.
- [28] A. Greven, F. den Hollander and M. Oomen. Spatial populations with seed-bank: well-posedness, equilibrium and finite-systems scheme. *Preprint*, 2019.
- [29] A. Greven, F. den Hollander and M. Oomen. Spatial populations with seed-bank: renormalisation on the hierarchical group. *Preprint*, 2019.
- [30] A. Greven, P. Pfaffelhuber and A. Winter. Convergence in distribution of random metric measure spaces (Λ -coalescent measure trees). *Probab. Theory Relat. Fields*, 145:285–322, 2009.
- [31] A. Greven, P. Pfaffelhuber and A. Winter. Tree-valued resampling dynamics martingale problems and applications. *Probab. Theory Relat. Fields*, 155:789–838, 2013.
- [32] A. Greven, T. Rippl and P. Glöde. Branching processes: a general concept. <http://arxiv.org/abs/1807.01921>, 2018.
- [33] A. Greven, R. Sun and A. Winter. Continuum space limit of the genealogies of interacting Fleming-Viot processes on \mathbb{Z}^1 . *Electron. J. Probab.* 21 (paper no. 58):1–64, 2016.
- [34] S. Gufler. Pathwise construction of tree-valued Fleming-Viot processes. *Electron. J. Probab.*, 23 (paper no. 42):1–58, 2018.
- [35] S. Gufler. A representation for exchangeable coalescent trees and generalized tree-valued Fleming-Viot processes. *Electron. J. Probab.*, 23 (paper no. 41):1–42, 2018.
- [36] F. den Hollander and G. Pederzani. Multi-colony Wright-Fisher with seed-bank. *Indag. Math.*, 28:637–669, 2017.
- [37] I. Kaj, S.M. Krone and M. Lascoux. Coalescent theory for seed bank models. *J. Appl. Prob.*, 38:285–300, 2001.
- [38] V. Limic and A. Sturm. The spatial Λ -coalescent. *Electron. J. Probab.*, 11 (paper no. 15): 363–393, 2006.

- [39] J. Pitman. Coalescents with multiple collisions. *Ann. Probab.* 27:870–1902, 1999.
- [40] J. Pitman. Combinatorial Stochastic Processes. École d'Été de Probabilités de Saint-Flour XXXII-2002, Lecture Notes in Mathematics 1875, Springer, Berlin, 2006.
- [41] S. Sawyer and J. Felsenstein. Isolation by distance in a hierarchically clustered population. *J. Appl. Probab.*, 20:1–10, 1983.
- [42] T. Shiga. An interacting system in population genetics. *J. Math. Kyoto Univ.*, 20:213–242, 1980.
- [43] T. Shiga and A. Shimizu. Infinite-dimensional stochastic differential equations and their applications. *J. Math. Kyoto Univ.*, 20:395–416, 1980.

