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  
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1. Background  
2. Two models  
3. Equilibrium  
4. Random environment  
5. Extensions  
6. Perspectives  
References  

1  
4  
5  
12  
17  
19  
20  
21
CHAPTER 1

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

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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 $G$ and the type space is $K$, then the state space of the process is

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

where $\mathcal{P}(K)$ denotes the set of probability measures on $K$. 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 $K = \{0, 1\}$, the process

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

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

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

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

$$X(0) = (x_i(0))_{i \in G} \in \{0, 1\}^G$$

is the initial state.

Suppose that

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

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

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

which are martingales whose volatility vanishes only at the boundary of $[0, 1]$ (where genetic diversity is lost). Consequently, for all $i \in G$, $x_i(t)$ converges in distribution as $t \to \infty$ 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,

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

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

$$(1.1.5) \quad x_i(0) = \theta \in [0, 1] \quad \forall i \in G.$$
1.2. TWO MODELS

$G$, 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

   \[
   \mathcal{L} \left[ X(t) \right] \xrightarrow{t \to \infty} \nu_\theta,
   \]

   where the limit law $\nu_\theta$ on $[0,1]^G$ is stationary and ergodic w.r.t. translations in $G$, with $E_{\nu_\theta}[x_i] = \theta \ \forall \ i \in G$. Furthermore, $\nu_\theta$ 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

   \[
   \mathcal{L} \left[ X(t) \right] \xrightarrow{t \to \infty} (1 - \theta) \delta_0 + \theta \delta_1.
   \]

   Furthermore, all invariant measures live on configurations exhibiting clustering of types, i.e., on the set $\{0^G, 1^G\}$, 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 \( G \) 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 \( F \subseteq C_b(\mathbb{P}(K), \mathbb{R}) \) be the algebra of
functions \( F \) of the form

\[
F(x) = \int_K x^{a_n} (du) \varphi(u), \quad x \in \mathbb{P}(K), \ n \in \mathbb{N}, \ \varphi \in C_b(\mathbb{K}^n, \mathbb{R}).
\]

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

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

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

\[
\Lambda(\{0\}) = 0, \quad \int_{[0,1]} \frac{\Lambda(dr)}{r} = \infty,
\]

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

\[
L^{c,d,\Lambda}_\theta = L^\theta_0 + L^d + L^\Lambda
\]

acting on \( F \in \mathcal{F} \) as

\[
(L^\theta_0 F)(x) = c \int_K (\theta - x)(da) \frac{\partial F(x)}{\partial x}[\delta_a],
\]

\[
(L^d F)(x) = d \int_K \int_K Q_x(du, dv) \frac{\partial^2 F(x)}{\partial x^2}[\delta_u, \delta_v],
\]

\[
(L^\Lambda F)(x) = \int_{[0,1]} \Lambda^*(dr) \int_K x(da) \left[ F((1-r)x + r \delta_a) - F(x) \right],
\]

where

\[
Q_x(du, dv) = x(du) \delta_u(dv) - x(du) x(dv)
\]
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 \( \theta \) of strength \( c \) (= immigration-emigration), a Fleming-Viot diffusion with volatility \( d \) (= Moran resampling), and a \( \Lambda \)-Cannings process with resampling measure \( \Lambda \) (= 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 \( \Omega_N = \bigoplus_{i \in \mathbb{N}} \mathbb{Z}^N \), where \( \mathbb{Z}^N \) is the cyclical group, i.e., the set \( \{0, 1, \ldots, N-1\} \) equipped with addition modulo \( N \). View \( \Omega_N \) 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

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

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

\[
(1.2.10) \quad \xi = (c_k)_{k \in \mathbb{N}_0}
\]

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

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

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 $\Lambda$-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

\[
dt \otimes \Lambda^*(dr).
\]

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 $M \to \infty$.

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 $\Lambda_k$-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 $\Lambda_k^*$, 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.,

\[
y_{i,k} = N^{-k} \sum_{j \in B_k(i)} x_j.
\]

Because the reshuffling is done first, the resampling always acts on a uniformly distributed state (‘panmictic resampling’). The continuum limit $M \to \infty$ 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

\[
L = L_{\text{mig}} + L_{\text{res}},
\]

where

\[
(L_{\text{mig}} F)(x) = \sum_{j \in \Omega_N} a(i, j) \int_{\mathbb{R}^2} (x_j - x_i)(da) \frac{dF}{dx_i}[\delta_a]
\]

with $\Omega_N = \{B_k(i) : i \in \Omega_N, k \in \mathbb{N}_0\}$. 

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

\[
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\]

where

\[
(L_{\text{mig}} F)(x) = \sum_{j \in \Omega_N} a(i, j) \int_{\mathbb{R}} (x_j - x_i)(da) \frac{dF}{dx_i}[\delta_a]
\]
1.2. TWO MODELS

(1.2.18) takes care of the migration and

\[
(L_{\text{res}}F)(x) = \sum_{i \in \Omega_N} \left( L_{i}^{d_0} F (x) + \int_{[0,1]} \Lambda_i^0 (dr) \int_{\mathbb{K}} x_i (da) \left[ F \left( \Phi_{r,a,B^*_i}(x) \right) - F(x) \right] + \sum_{k \in \mathbb{N}} N^{-2k} \int_{[0,1]} \Lambda_k^* (dr) \int_{\mathbb{K}} y_{i,k} (da) \left[ F \left( \Phi_{r,a,B_k(i)}(x) \right) - F(x) \right] \right),
\]

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

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

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 \( \Gamma \in \mathcal{P}^{\Omega_N} \), the \( (L,F,\Gamma) \)-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 \( \Lambda \)-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 \( \Lambda \), so that \( E' \) will be the set of marked partitions of a finite set, which we denote by \( \mathbb{S}^{\Omega_N} \).

We write \((\pi,g)\) for an element of \( \mathbb{S}^{\Omega_N} \), where \( g \in \Omega_N^{[\pi]} \), \( \pi \) is a partition of the set \( \{1,\ldots,n\} \), and the partition elements are labeled \( \pi_1,\ldots,\pi_k \) with \( k = |\pi| \). We specify a test function \( \varphi \in C_b(\mathbb{R}^{[\pi]} \times \mathbb{R}) \), 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 $c$, up to a coalescent event. In addition, the partition elements are subject to $\Lambda_k$-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 $\Lambda_k$-coalescence, we choose at rate $\Lambda_k(\text{dr})$ 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,

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

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

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 $K = \{0, 1\}$, 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:

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

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 $G = \mathbb{Z}^d$, 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:

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

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 \((X(t), Y(t))_{t⩾0}\) with
\[
X(t) = (x_i(t))_{i∈Z^d}, \quad Y(t) = ((y_{i,m}(t))_{m∈N_0})_{i∈Z^d},
\]
and the following system of coupled SDE’s:
\[
\begin{align*}
\frac{dx_i(t)}{dt} &= \sum_{j∈Z^d} a(i, j)[x_j(t) - x_i(t)]dt \\
&\quad + \sqrt{dx_i(t)(1-x_i(t))} \, dw_i(t) + \sum_{m∈N_0} K_m e_m [y_{i,m}(t) - x_i(t)]dt,
\end{align*}
\]
\[
\frac{dy_{i,m}(t)}{dt} = e_m [x_i(t) - y_{i,m}(t)]dt, \quad m ∈ N_0, \quad i ∈ Z^d.
\]
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
\[
\chi = \sum_{m∈N_0} K_m e_m < ∞
\]
and
\[
(1.2.30) \quad a(i, j) = a(j, i) \quad ∀ i, j ∈ Z^d.
\]
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
\[
L = \sum_{i∈G} \left( \sum_{j∈G} a(i, j)(x_j - x_i) \frac{∂}{∂x_i} + x_i(1 - x_i) \frac{∂^2}{∂x_i^2} \right) \\
+ \sum_{m∈N_0} \left[ K_m e_m (y_{i,m} - x_i) \frac{∂}{∂x_i} + e_m (x_i - y_{i,m}) \frac{∂}{∂y_{i,m}} \right],
\]
which acts on \(F\), 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 \(μ \in P([0, 1] × [0, 1]^{N_0})^{Z^d}\), the \((L, F, μ)\)-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:

\[ H((x_i)_{i \in \mathbb{Z}^d}, (y_{i,m})_{m \in \mathbb{N}_0})_{i \in \mathbb{Z}^d}, (n_i, ((m_{i,m})_{m \in \mathbb{N}_0})_{i \in \mathbb{Z}^d}) = x_i^{m_i}(y_{i,m})^{m_{i,m}}. \]

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

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

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 \( t \to \infty \) 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 \( \theta \),

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

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 \( q_\infty = \lim_{t \to \infty} q_t \) be the probability that the partition elements eventually coalesce. Then, using that the initial state is stationary and ergodic w.r.t. translations in \( \Omega_N \), we get

\[
 E[x_i^2(t)] = q_\infty \theta + (1 - q_\infty) \theta^2 = q_\infty \theta(1 - \theta) + \theta^2.
\]
1.3. EQUILIBRIUM

Hence

\[ E[x_i(t)(1 - x_i(t))] \xrightarrow{t \to \infty} (1 - q_\infty) \theta(1 - \theta), \]

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 \[12\]

\[ q_\infty = 1 \iff \sum_{k \in \mathbb{N}_0} \frac{1}{c_k} = \infty. \]

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

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

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

\[ c_k + N^{-1}\lambda_{k+1}, \quad k \in \mathbb{N}_0, \]

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

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

where \( B_k(0) \) is the \( k \)-block in \( \Omega_N \) around 0. Let

\[ \text{Var}_x(\psi) = Q_x(du, dv) \psi(u)\psi(v), \]

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

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

We proved the following in [26].

**Theorem 1.3.1** (Dichotomy for Cannings with block resampling).

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

\[ \lim_{t \to \infty} \inf_{i \in \Omega_N} \sup_{\psi \in C_b(\mathcal{K}, \mathbb{R})} \mathbb{E}_{x_i(t)}[\text{Var}(\psi)] > 0 \quad \forall i \in \Omega_N. \]
(b) [Clustering] If $H_N = \infty$, then
\[
\lim_{t \to \infty} \sup_{\psi \in C_b(K,\mathbb{R})} \mathbb{E}_{x_i(t)}[\text{Var}(\psi)] = 0 \quad \forall i \in \Omega_N.
\]
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 $\theta \in \mathcal{P}(K)$ and every $X(0)$ whose law is stationary and ergodic w.r.t. translations in $\Omega_N$ with single-site mean $\theta$,
\[
\mathcal{L} [X(t)] \xrightarrow{t \to \infty} \nu^\theta \in \mathcal{P}(\mathcal{P}(\mathbb{K})^{\Omega_N})
\]
for some unique law $\nu^\theta$ that is stationary and ergodic w.r.t. translations in $\Omega_N$ with single-site mean $\theta$.

(b) [Clustering] If $\bar{H}_N = \infty$, then for every $\theta \in \mathcal{P}(K)$,
\[
\mathcal{L} [X(t)] \xrightarrow{t \to \infty} \int_K \theta(du) \delta_{(\delta_u) \nu_N} \in \mathcal{P}(\mathcal{P}(\mathbb{K})^{\Omega_N}).
\]
We can now compare the classical process with the Cannings process. We focus on the volatility of the $k$-block averages
\[
Y^N_k(t) = \frac{1}{N^k} \sum_{j \in B_k(i)} x_i(tN^k), \quad i \in \Omega_N, \ t \geq 0,
\]
in the hierarchical mean-field limit $N \to \infty$. Let
\[
d^*_k = (d^*_k)_{k \in \mathbb{N}_0}
\]
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]
\[
d^*_1 = d_1 = \frac{c_0 \lambda_0}{c_0 + \mu_0}, \quad \frac{1}{d^*_k} = \frac{1}{c_k} + \frac{1}{d^*_k}, \quad k \in \mathbb{N},
\]
whose solution is
\[
d^*_k = \frac{1}{1 + \frac{1}{2} \lambda_0 \sigma_k}, \quad k \in \mathbb{N}, \quad \sigma_k = \sum_{l=0}^{k-1} \frac{1}{c_l}.
\]
Let
\[
d = (d_k)_{k \in \mathbb{N}_0}
\]
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 \( \mathbf{d} = (d_k)_{k \in \mathbb{N}_0} \):

(a) The maps \( \varepsilon \mapsto \mathbf{d} \) and \( \lambda \mapsto \mathbf{d} \) are component-wise non-decreasing.

(b) \( \mathbf{d} \geq \mathbf{d}^* \) component-wise.

(c) Clustering occurs if and only if \( \sum_{k \in \mathbb{N}_0} \frac{1}{c_k} \sum_{l=0}^k \lambda_l = \infty \).

(d) If \( \lim_{k \to \infty} \sigma_k = \infty \) and \( \sum_{k \in \mathbb{N}} \sigma_k \lambda_k < \infty \), then \( \lim_{k \to \infty} \sigma_k d_k = 1 \).

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

\[
\varrho = \sum_{m \in \mathbb{N}_0} K_m.
\]

The wake-up time of a typical individual, denoted by \( \tau \), has distribution

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

Suppose that

\[
K_m \sim A m^{-\alpha}, \quad e_m \sim B m^{-\beta}, \quad m \to \infty,
\]

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

\[
P(\tau \geq t) \sim C t^{-\gamma}, \quad t \to \infty,
\]

where

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

with \( \Gamma \) 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

\begin{equation}
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.
\end{equation}

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

\begin{equation}
\mathcal{L}[(X(t), Y(t))] \xrightarrow{t \to \infty} \nu^K_\theta \in \mathcal{P}(([0,1] \times [0,1])^{\mathbb{N}_0})^{\mathbb{Z}^d},
\end{equation}

where $\nu^K_\theta$ 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

\begin{equation}
\theta = \lim_{M \to \infty} \frac{x_0 + \sum_{m=0}^M K_m y_{0,m}}{1 + \sum_{m=0}^M K_m}.
\end{equation}

If $H_a = \infty$, then

\begin{equation}
\mathcal{L}[(X(t), Y(t))] \xrightarrow{t \to \infty} (1-\theta) \delta_{(0,0^{\mathbb{N}_0})^{\mathbb{Z}^d}} + \theta \delta_{(1,1^{\mathbb{N}_0})^{\mathbb{Z}^d}}.
\end{equation}

(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

\begin{equation}
H = \int_0^\infty dt \hat{a}_t(0,0) = \hat{G}(0,0),
\end{equation}

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.,

\[ \Omega^T_N = \bigcup_{k \in \mathbb{N}_0} \Omega^{(k)}_N, \quad \Omega^{(k)}_N = \Omega_N / B_k(0), \]

where \( \Omega_N / B_k(0) \) denotes the quotient group of \( \Omega_N \) modulo \( B_k(0) \) (recalling (1.2.9)). Note that the leaves of the tree form the set \( \Omega_N \). For \( \xi \in \Omega^T_N \), write

\[ |\xi| = \text{the height of } \xi \text{ (counting from the leaves)}, \]
i.e., \(|\xi| = k \) when \( \xi \in \Omega^{(k)}_N \) for \( k \in \mathbb{N}_0 \), and define

\[ B_{|\xi|}(\xi), \]
to be the set of sites in \( \Omega_N \) that lie below \( \xi \). We want to make the reshuffling-resampling spatially random. To that end, let

\[ \Lambda(\omega) = \{ \Lambda^\xi(\omega) : \xi \in \Omega^T_N \} \]
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 \( \omega \) to denote the random environment and the symbol \( P \) to denote the law of \( \omega \). We assume that \( \Lambda^\xi(\omega) \) is of the form

\[ \Lambda^\xi(\omega) = \lambda_{|\xi|} \chi^\xi(\omega), \]
where \( \Delta = (\lambda_k)_{k \in \mathbb{N}_0} \) is a deterministic sequence in \((0, \infty)\) and

\[ \{ \chi^\xi(\omega) : \xi \in \Omega^T_N \} \]
is a random field of \( \mathcal{M}_{\text{fin}}([0,1]) \)-valued resampling measures that is stationary under translations in \( \Omega^T_N \).

Abbreviate

\[ \rho^\xi(\omega) = \chi^\xi(\omega)((0, 1]), \]
which is the total mass of \( \chi^\xi(\omega) \). Clearly,

\[ \{ \rho^\xi(\omega) : \xi \in \Omega^T_N \} \]
is a random field of \((0, \infty)\)-valued total masses that is also stationary under translations in \( \Omega^T_N \). We assume that

\[ \mathbb{E}[\rho^\xi(\omega)] = 1, \quad \mathbb{E}[(\rho^\xi(\omega))^2] = C \in (0, \infty), \]
and that the sigma-algebra at infinity associated with (1.4.7), defined by
\( \mathcal{T} = \bigcap_{L \in \mathbb{N}_0} \mathcal{F}_L, \quad \mathcal{F}_L = \sigma(\rho^\xi(\cdot) \text{ with } \xi \in \Omega^T_N \text{ such that } d_{\Omega^T_N}(0, \xi) \geq L) \),
is trivial, where \( d_{\Omega^T_N} \) denote the hierarchical distance on \( \Omega^T_N \).

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 \( P \), the law of the initial state \( X(\omega; 0) \) is stationary and ergodic w.r.t. translations in \( \Omega_N \), with single-site mean
\[
\theta = \mathbb{E}[X_0(\omega; 0)] \in \mathcal{P}(K).
\]
Then, for \( P \)-a.e. \( \omega \), there exists an equilibrium measure \( \nu_\theta(\omega) \in \mathcal{P}(\mathcal{P}(K)^{\Omega_N}) \), arising as
\[
\lim_{t \to \infty} \mathcal{L}[X(\omega; t)] = \nu_\theta(\omega),
\]
satisfying
\[
\int_{\mathcal{P}(K)^{\Omega_N}} x_0 \nu_\theta(\omega)(dx) = \theta.
\]
Moreover, under the law \( P \), the random variable \( \nu_\theta(\omega) \) is stationary and ergodic w.r.t. translations in \( \Omega_N \).

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 \( \omega \)),
\[
\sup_{f \in C_b(K, \mathbb{R})} \int_{\mathcal{P}(K)^{\Omega_N}} \nu_\theta(\omega)(dx) \int_K [f(u) - \theta]^2 x_0(du) > 0,
\]
respectively, a *monotype equilibrium* (= clustering given \( \omega \)), i.e.,
\[
\nu_\theta(\omega) = \int_K \delta_{\delta_\theta \circ \mu_N}(du).
\]

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 \( C = \{\omega: \text{in } \omega \text{ coexistence occurs}\} \). Then \( P(C) \in \{0, 1\} \).*
(b) *\( P(C) = 1 \) if and only if
\[
\sum_{k \in \mathbb{N}_0} \frac{1}{c_k + N^{-1} \lambda_{k+1}} \sum_{l=0}^k \lambda_l < \infty.
\]
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 $c$ and $\lambda$ 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 $\Omega_N$ or $\mathbb{Z}^d$, namely, other countable abelian groups. Our results on the longtime behaviour on $\Omega_N$ (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 $g_{FW}(x) = x(1-x)$, $x \in [0,1]$, 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 $M \to \infty$ 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 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 $\geq -1$. 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 $\Omega_N$ 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 $N \to \infty$, 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**


