

## 10.4 Neutral Stepping Stone Models

### 10.4.1 The two type stepping stone model

The neutral two type stepping stone model on a countable abelian group  $S$  with migration kernel  $p(\cdot)$  is given by the system

$$\begin{aligned} dX_t(x) &= \sum_{y \in S_1} p_{y-x} (X_t(y) - X_t(x)) dt \\ &\quad + \sqrt{2X_t(x)(1 - X_t(x))} dW_t(x) \\ x_0(x) &\in [0, 1], \quad x \in S \end{aligned}$$

This process can be embedded in the infinitely many types stepping stone model which we now consider.

### 10.4.2 The infinitely many types stepping stone model

Consider a collection (finite or countable) of subpopulations (demes), indexed by  $S$ . The subpopulation at  $\xi \in S$  at time  $t$  is described by a probability distribution  $X_\xi(t)$  over a space  $E = [0, 1]$  of possible types (alleles). In other words,  $X_\xi(t) \in \mathcal{P}(E)$ , the set of probability measures on  $E$  so that the state space is

$$(10.13) \quad (\mathcal{P}([0, 1]))^S.$$

Within each subpopulation there is mutation, selection and finite population sampling. Mutation is assumed produce a new type chosen by sampling from a fixed source distribution  $\theta \in \mathcal{P}(E)$ . Selection is prescribed by a fitness function  $V(x)$  in the haploid case or by  $V(x, y) = V(y, x)$  in the diploid case. Migration from site  $\xi$  to site  $\xi'$  is assumed to occur via a symmetric random walk with rates  $q_{\xi, \xi'} = p(\xi - \xi')$ . Finally Fleming-Viot continuous sampling is assumed to take place within each subpopulation. It is a basic property of this model that for any  $t > 0$ ,  $X_\xi(t)$  is a purely atomic random measure (with countably many atoms) and therefore can be represented in the form

$$X_\xi(t) = \sum_{k \in I} m_{\xi, k}(t) \delta_{y_k}$$

where  $m_{\xi, k}(t) \geq 0$  denotes the proportion of the population in subpopulation  $\xi$  of type  $y_k \in E$  at time  $t$ . Note that in this model two individuals are related if and only if they are of the same type.

We denote the vector  $\{\mu_\xi\}_{\xi \in S}$  by  $\bar{\mu}$ . The generator is then given by

(10.14)

$$\begin{aligned} GF(\bar{\mu}) &= c \cdot \sum_{\xi \in S} \int_{[0,1]} \frac{\partial F(\bar{\mu})}{\partial \mu_\xi(u)} (\theta(du) - \mu_\xi(du)) \\ &\quad + \sum_{\xi, \xi'} q_{\xi, \xi'} \int_{[0,1]} \frac{\partial F(\bar{\mu})}{\partial \mu_\xi(u)} (\mu_{\xi'}(du) - \mu_\xi(du)) \\ &\quad + \frac{\gamma}{2} \sum \int_{[0,1]} \int_{[0,1]} \frac{\partial^2 F(\bar{\mu})}{\partial \mu_\xi(u) \partial \mu_\xi(v)} Q_{\mu_\xi}(du, dv) \\ X_{0, \xi} &= \nu \forall \xi, \quad Q_\mu(du, dv) = \mu(du) \delta_u(dv) - \mu(du) \mu(dv). \end{aligned}$$

The first term corresponds to mutation with source distribution  $\theta$ , the second to spatial migration and the last to continuous resampling. The resampling rate coefficient  $\gamma$  is inversely proportional to the effective population size of a deme.

This existence and uniqueness of this system of interacting Fleming-Viot processes was established by Vaillancourt [586] and Handa [306].

The questions which we wish to investigate are

- the distribution in a given subpopulation, that is what is the joint distribution of the  $\{m_{\xi, k}\}$
- the spatial distribution of relatives
- how are these affected by the migration geometry.

### 10.4.3 The Dual Process Representation

Given  $n \in \mathbb{N}$  consider the collection

(10.15)

$$\begin{aligned} \Pi_n &= \{\bar{\eta} := (\eta, \pi)\} : \text{ where} \\ &\quad \pi \text{ is a partition of } \{1, \dots, n\}, \text{ that is,} \\ &\quad \pi : \{1, \dots, n\} \rightarrow \{1, \dots, |\pi|\} \text{ with } |\pi| \leq n, \\ &\quad \eta : \{1, \dots, |\pi|\} \rightarrow S. \end{aligned}$$

Now consider the family of functions in  $C((\mathcal{P}([0, 1]))^S \times \Pi)$  of the form

$$(10.16) \quad F_f(\bar{\mu}, \bar{\eta}) := \int_{[0,1]} \dots \int_{[0,1]} f(u_{\pi(1)}, \dots, u_{\pi(n)}) \mu_{\eta_1}(du_1) \dots \mu_{\eta_{|\pi|}}(du_{|\pi|})$$

with  $f \in C([0, 1]^n)$ .

We now consider a continuous time Markov chain,  $\bar{\eta}_t = (\eta_t, \pi_t)$ , with state space  $\Pi_n$  and jump rates:

- the partition elements perform continuous time symmetric random walks on  $S$  with rates  $q_{\xi, \xi'}$  and in addition a partition element can jump to  $\{\infty\}$  with rate  $c$  (once a partition element reaches  $\infty$  it remains there without change of further coalescence).
- each pair of partition elements during the period they reside at an element of  $S$  (but not  $\{\infty\}$ ) coalesce at rate  $\gamma$  to the partition element equal to the union of the two partition elements.

Let  $H$  denote the generator of  $\bar{\eta}$ . Then for a function of the form (10.16)

$$(10.17) \quad HF_f(\bar{\mu}, \bar{\eta}) = GF_f(\bar{\mu}, \bar{\eta}).$$

We then obtain the dual relationship

$$(10.18) \quad E(F_f(X_t, (\eta, \pi))) = E(F_f(X_0, (\eta_t, \pi_t)))$$

and this proves that the infinitely many types stepping stone martingale problem is well-posed.

**Remark 10.23** *Given the dual we can construct a spatially structured coalescent that describes the ancestral structure of a sample of a finite number of individuals located at the same or different sites.*

*Note that this is essentially equivalent to the coalescent geographically structured populations introduced by developed by Notohara (1990) [488] and Takahata (1991) [577].*

**Remark 10.24** *Note that as  $\gamma \rightarrow \infty$  the dual converges to the dual of the voter model and we can regard the voter model as the limit as  $\gamma \rightarrow \infty$  of the interacting Fisher-Wright diffusions.*

#### 10.4.4 Spatial homogeneity and the local-fixation coexistence dichotomy

In this subsection we consider the neutral stepping stone model without mutation.

**Theorem 10.25** *(Dawson-Greven-Vaillancourt (1995) [142], Theorem 0.1)*

*Let  $S$  be a countable abelian group and consider the infinitely many types stepping stone model with no mutation ( $c = 0$ ). Assume that the initial random field  $\{X_\xi(0)\}_{\xi \in S}$  is spatially stationary, ergodic, weakly mixing and has single site mean measure satisfying*

$$(10.19) \quad E\left(\int g(u)X_\xi(0, du)\right) = \int g(u)\theta(du), \quad \theta \in \mathcal{P}[0, 1].$$

*(a) If  $q_{\xi, \xi'}$  is a symmetric transient random walk on  $S$ , then the stepping stone process  $\{X_\xi(t)\}_{\xi \in S}$  converges in distribution to a nontrivial invariant  $\mathcal{P}([0, 1])$ -valued random field  $\{X_\xi(\infty)\}_{\xi \in S}$  which also has single site mean measure  $\theta$ .*

$\{X_\xi(\infty)\}_{\xi \in S}$  is spatially homogeneous (that is, the law is invariant under translations on  $S$ ), ergodic and weakly mixing, in particular

$$(10.20) \quad E(\langle x_\xi, f \rangle \langle x_\zeta, f \rangle) \rightarrow \langle \mu, f \rangle^2 \text{ as } d(\xi, \zeta) \rightarrow \infty, \quad \forall f \in L_\infty([0, 1]).$$

(b) In (a) the equilibrium state decomposes into countably many coexisting infinite families, namely,

$$(10.21) \quad X_\xi(\infty) = \sum_{k=1}^{\infty} a_{\xi,k} \delta_{y_k}$$

with  $\sum_x ia_{\xi,k} = \infty$  for each  $k$ .

(c) If  $p_\xi$  is recurrent, then the set of invariant measures is a convex set with extremal invariant measures are  $\delta_a$ ,  $a \in [0, 1]$ , that is, there is local fixation, and

$$(10.22) \quad \mathcal{L}(\{X_\xi(\infty)\}_{\xi \in S}) = \int (\delta_y)^S \theta(dy).$$

**Proof.** We sketch the main steps of the proof.

The proof uses the dual representation (10.18), (??). Note that  $|\pi_t|$  is monotone decreasing so that we can define

$$(10.23) \quad \pi_\infty = \lim_{t \rightarrow \infty} \pi_t, \quad \pi_\infty = \{\pi_\infty(1), \dots, \pi_\infty(n)\}.$$

Then we note that  $\hat{\eta}$  is prescribed by a *coalescing random walk with delay*. We let  $Z(t)$  be a random walk on  $S$  with transition kernel  $\{q_{\xi,\xi'}\}$ . Since we have assumed that the random walk is symmetric, then the difference process  $Z_1(t) - Z_2(t)$ , where  $Z_1, Z_2$  are independent copies of the random walk, is a random walk with jump rates  $2q_{\xi,\xi'}$ . We can assume that the system of coalescing random walks with delay is constructed on a probability space on which the sequence  $\{Z_i(t)\}_{i \in \mathbb{N}}$  of independent random walks and an independent collection of exponentially distributed random variables are defined.

**Lemma 10.26** *If the  $q$ -random walk is recurrent, then*

(a)

$$(10.24) \quad \mathcal{L}(\hat{\eta}_t) - \mathcal{L}((Z(t); \{1, \dots, n\})) \Rightarrow 0 \text{ as } t \rightarrow \infty$$

Given two initial sites  $0$  and  $\xi \neq 0$  and  $(\eta, (\{1\}, \{2\}))$ ,  $\eta_1 = 0, \eta_2 = \xi$ ,

$$(10.25) \quad P(\pi_t = \{1, 2\}) \leq \text{const} \cdot \int_0^t P(Z(s) = 0) ds \leq \frac{\text{const}}{|\xi|^{d-2}}$$

where  $Z(s)$  is a random walk starting at  $\xi$  and with jump rate 2.

(b) *If the  $q$ -random walk is transient, then*

$$(10.26) \quad \mathcal{L}(\eta_t | |\pi_\infty| = k) - \mathcal{L}(Z_1(t), \dots, Z_k(t)) \Rightarrow 0 \text{ as } t \rightarrow \infty$$

and  $P(|\pi_\infty| = 1) < 1$  provided that  $|\pi_0| \neq 1$ .

**Proof.** If the random walk is recurrent, then  $Z_1(t) - Z_2(t)$  visits 0 infinitely often and therefore they must coalesce with probability one.

If the random walk is transient, then there exists a random time  $\sigma < \infty$  a.s. such that  $\sigma$  is the last coalescence time in the system  $\widehat{\eta}_t$ . Denote by  $\xi^1(t), \dots, \xi^{|\pi_\infty|}(t)$  the position of the partition elements at time  $\sigma + t$ . The system  $\eta_u$  for times  $u = s + t + \sigma$  behaves like a system of  $|\pi_\infty|$  random walks in  $s$  starting at  $\xi^1(t) \dots \xi^{|\pi_\infty|}(t)$  and conditioned on never meeting. Since for every pair  $i \neq j$   $\xi^i(t) - \xi^j(t) \rightarrow \infty$  as  $t \rightarrow \infty$ , the event that  $\xi^i$  and  $\xi^j$  never meet after time  $t$  tends to one as  $t \rightarrow \infty$ . It remains to show that the distance between the distributions of the system of  $|\pi_\infty|$  independent random walks starting at  $(\xi^1(t) \dots \xi^{|\pi_\infty|}(t))$  and starting at  $(0, \dots, 0)$  tends to 0 as  $s \rightarrow \infty$ . This is verified using a coupling by randomized stopping times due to Greven (1987) [279] and a result of Choquet and Deny on transient random walks (see Spitzer [569], Ch 6. T1) - see ([142] for details).

■

We also note the following elementary result on random probability measures.

**Lemma 10.27** *Let  $X_1, X_2$  be a random probability measures on  $[0, 1]$ , having the same mean measures  $E(X_i) = \theta \in \mathcal{P}([0, 1])$ , that is, a measurable map from a probability space  $(\Omega, \mathcal{F}, P)$  to  $\mathcal{P}([0, 1])$ . Then (a)*

$$(10.27) \quad E\left[\left(\int g(y)X_i(dy)\right)^2\right] = E\left[\int g^2(y)X(dy)\right] \quad \forall g \in C([0, 1]),$$

then

$$(10.28) \quad X_i(\omega) = \delta_{y(\omega)} \quad \text{for a.e. } \omega \in \Omega \text{ and } \omega \rightarrow y \text{ is measurable.}$$

(b) *If in addition,*

$$(10.29) \quad E\left[\left(\int g(y)X_1(dy) \int g(y)X_2(dy)\right)\right] = E\left[\int g^2(y)X_1(dy)\right] \quad \forall g \in C([0, 1]),$$

then

$$(10.30) \quad X_1(\omega) = X_2(\omega) = \delta_{y(\omega)} \quad \text{for a.e. } \omega \in \Omega.$$

We return to the proof of the theorem.

(a) Recurrent Case.

Step 1. Let  $m = 2$  and take  $f(u_1, u_2) = g(u_1)g(u_2)$ ,  $\eta = (\xi, \xi)$ . Then by the dual representation and Lemma 10.26

$$\begin{aligned}
& E \left( \int_0^1 g(u) X_\xi(t, du) \right)^2 \\
&= E \left( \int g^2(u) X_{\eta_t^1}(0, du) 1(\pi_t = \{1, 2\}) \right. \\
(10.31) \quad & \left. + \int g(u) X_{\eta_t^1}(t, du) \cdot \int g(u) X_{\eta_t^2}(t, du) 1(\pi_t = \{\{1\}, \{2\}\}) \right) \\
&= E \left( \int g^2(u) X_{\eta_t^1}(0, du) \right) + o(t)
\end{aligned}$$

Therefore in the limit by Lemma 10.27(a) we have

$$(10.32) \quad X_\xi(\infty, du) = \delta_y, \text{ a.s.}$$

Since  $\mathcal{L}(X_\xi(t)) \in \mathcal{P}(\mathcal{P}([0, 1]))$ , the set  $\{\mathcal{L}(X_\xi(t))\}_{t \geq 0}$  is weakly relatively compact. By (10.38) a weak limit point must be concentrated on

$$(10.33) \quad M = \{\delta_u : u \in [0, 1]\}$$

that is,  $\mathcal{L}(X_\xi(\infty)) = \int_0^1 \delta_{\delta_u} H_\xi(du)$  with  $H_\xi \in \mathcal{P}([0, 1])$ . But we have

$$(10.34) \quad E \langle X_\xi(t), f \rangle = \langle \theta, f \rangle$$

so that for a limit point  $\mathcal{L}(\{X_\xi(\infty)\}_{\xi \in S})$

$$(10.35) \quad E \langle X_\xi(\infty), f \rangle = \langle \theta, f \rangle \quad \forall f \in C([0, 1]).$$

Therefore  $H_\xi = \theta$

$$(10.36) \quad \mathcal{L}(X_\xi(\infty)) = \int_0^1 \delta_{\delta_u} \theta(du).$$

Step 2. In order to show consensus of the components occurs for  $t \rightarrow \infty$  take  $m = 2$ ,  $f(u_1, u_2) = g(u_1)g(u_2)$  but use  $\eta = (\xi^1, \xi^2)$  with  $\xi^1 \neq \xi^2$ . Then again using Lemma 10.26

$$\begin{aligned}
& E \left( \int_0^1 g(u) X_{\xi^1}(t, du) \int_0^1 g(u) X_{\xi^2}(t, du) \right) \\
&= E \left( \int g^2(u) X_{\eta_t^1}(0, du) 1(\pi_t = \{1, 2\}) \right. \\
(10.37) \quad & \left. + \int g(u) X_{\eta_t^1}(0, du) \cdot \int g(u) X_{\eta_t^2}(0, du) 1(\pi_t = \{\{1\}, \{2\}\}) \right) \\
&= E \left( \int g^2(u) X_{\eta_t^1}(0, du) \right) + o(t)
\end{aligned}$$

The result then follows from Lemma 10.27(b), that is

$$(10.38) \quad (X_{\xi^1}(\infty), X_{\xi^2}(\infty)) = (\delta_y, \delta_y) \text{ for some random } y, \text{ a.s.}$$

where

$$(10.39) \quad P(y \in (a, b)) = \theta((a, b)).$$

Step 3. We can obtain the analogue of (10.38) for any finite  $\xi^1, \dots, \xi^k$ . Therefore we obtain

$$(10.40) \quad \mathcal{L}((x_\xi(t))_{\xi \in S}) \Rightarrow \int \delta_{(\delta_u)^S} \theta(du)$$

and the proof of (a) is complete.

(b) Transient case. To prove convergence of  $\mathcal{L}(t)$  as  $t \rightarrow \infty$  we first recall that

$$(10.41) \quad \pi_t \rightarrow \pi_\infty, \text{ (cf. (10.23)).}$$

Let  $n \in \mathbb{N}$  and  $f(x_1, \dots, x_n) = \prod_{i=1}^n f_i(x_i)$ . Then by the dual representation

$$\begin{aligned} E_{X(0)}(F(X(t), (\eta, \pi))) &= E_{(\eta, \pi)}(F(X(0), (\eta_t, \pi_t))) \\ &= \sum_{m=1}^n E_{(\eta, \pi)} \left( \langle X_{\eta_t^1}(0), \prod_{i \in \pi_t(1)} f_i \rangle, \dots, \langle X_{\eta_t^m}(0), \prod_{i \in \pi_t(m)} f_i \rangle 1(|\pi_t| = m) \right) \\ &\rightarrow E_{(\eta, \pi)} \left( \langle \theta, \prod_{i \in \pi_\infty(1)} f_i \rangle, \dots, \langle \theta, \prod_{i \in \pi_\infty(|\pi_\infty|)} f_i \rangle \right) \end{aligned}$$

where we have used the fact that  $|Z_i(t) - Z_j(t)| \rightarrow \infty$  in probability as  $t \rightarrow \infty$  and the weak mixing property of the initial random field so that for  $i \neq j$

$$\begin{aligned} &\lim_{t \rightarrow \infty} E \left( \int f_1(x) X_{Z_i(t)}(0, dx) \int f_2(y) X_{Z_j(t)}(0, dy) \right) \\ &= \lim_{t \rightarrow \infty} E \left( \int f_1(x) X_{Z_i(t)}(0, dx) \right) E \left( \int f_2(y) X_{Z_j(t)}(0, dy) \right) \\ &= \int f_1(x) \theta(dx) \int f_2(y) \theta(dy). \end{aligned}$$

This implies the convergence of the laws  $\mathcal{L}_t$ .

The proof of the weak mixing property is obtained by noting that if  $|\eta_1 - \eta_2| \rightarrow \infty$ , then

$$(10.42) \quad P(\pi_\infty = (\{1\}, \{2\})) \rightarrow 1 \text{ as } t \rightarrow \infty.$$

The proof that the limiting law  $\mathcal{L}_\infty$  is an invariant measure for the dynamics is standard. ■

**Remark 10.28** (*Population structure in 2 dimensions*)

The phenomenon of diffusive clustering in dimension  $d = 2$  was discovered by Cox and Griffeath (1986) [98].

More recently, coalescing random walks used to study the coalescence time and identity by descent between 2 randomly chosen individuals on a 2-d torus (Cox and Durrett (2002) [93], Cox, Durrett, Zähle (2005) [94])

**Homozygosity in large time scales**

Given a probability measure  $\mu$  on  $[0, 1]$  the *homozygosity* is defined by

$$(10.43) \quad \int_0^1 \int_0^1 1_{x=y} \mu(dx) \mu(dy) = \sum_{i=1}^{\infty} a_i^2$$

where  $\{a_i\}$  are the masses of the atoms (if any) in  $\mu$ , that is  $\mu = \sum a_i \delta_{y_i} + \mu_{diff}$  and  $\mu_{diff}$  is the non-atomic component of the measure.

It follows from Theorem 10.25 that in the recurrent case for any  $L \in \mathbb{N}$

$$(10.44) \quad \lim_{t \rightarrow \infty} E \left[ \frac{1}{N(L)} \sum_{|j| \leq L} \langle X_\xi(t) \otimes X_0(t), I_\Delta \rangle \right] = 1.$$

where  $I_\Delta = \{(x, y) : x = y\}$  and  $N(L)$  denotes the number of sites in a ball of radius  $L$  and for the transient case

$$(10.45) \quad \lim_{t \rightarrow \infty} E [\langle X_0(t) \otimes X_0(t), I_\Delta \rangle] < 1$$

**Theorem 10.29** Consider the stepping stone model on  $\mathbb{Z}^d$  and random walk kernel given by a nearest neighbour random walk. Let  $d \geq 3$  and  $X_0 = \nu$ , with  $\nu$  nonatomic. Then

(a)

$$(10.46) \quad \lim_{L \rightarrow \infty} \frac{1}{L^d} \sum_{|j| \leq L} \langle X_\xi(\infty) \otimes X_0(\infty), I_\Delta \rangle = 0,$$

(b) Each allelic type present at equilibrium has infinite total mass in  $\mathbb{Z}^d$  but has zero spatial density.

In addition, if  $X(0)$  is given the stationary measure, then

(c)

$$(10.47) \quad \int_0^\infty \langle X_0(t) \otimes X_0(0), I_\Delta \rangle dt < \infty$$

if and only if  $d \geq 5$ .

**Proof.** (a) We briefly sketch the argument. We note that if  $\pi = (\{1\}, \{2\})$ ,  $\eta_1 = 0, \eta_2 = \xi$  then

$$(10.48) \quad \lim_{t \rightarrow \infty} E[\langle X_\xi(t) \otimes X_0(t), I_\Delta \rangle] \leq P_{(\eta, \pi)}(\pi_t = \{1, 2\})$$

since if coalescence does not occur, the expected homozygosity is 0. But the probability that two random walks  $Z_0$  and  $Z_\xi$  starting at 0 and  $\xi$  coalesce by time  $t$  satisfies

$$(10.49) \quad \begin{aligned} & \lim_{t \rightarrow \infty} P(\text{coalesce by time } t) \\ &= \lim_{t \rightarrow \infty} E(1 - e^{-\gamma \int_0^t \mathbb{1}(Z_0(s)=Z_\xi(s)) ds}) \\ & \lim_{t \rightarrow \infty} \leq (1 - e^{-\gamma \int_0^t P(\mathbb{1}(Z_0(s)=Z_\xi(s))) ds}) \sim \frac{1}{|\xi|^{d-2}}. \end{aligned}$$

The result follows by summing and dividing by  $L^d$ .

(c) is the analogue of (10.12). ■

**Family decomposition and renormalization of the fluctuation field**

The decomposition of the infinitely many types stepping stone model and the related voter model provides a tool for the study of the renormalized fluctuation field. (Recall that the difference between the stepping stone model and the voter model is that coalescence of the random walks occurs with delay for the stepping stone model but is instantaneous for the voter model. Otherwise the structure of the infinite clusters is similar.) The following special case of a theorem of I. Zähle illustrates this.

**Theorem 10.30** [623] *Consider the equilibrium voter model  $\{X_\xi(t)\}_{\xi \in \mathbb{Z}^d} \in \{0, 1\}^{\mathbb{Z}^d}$  with nearest neighbour simple random walk kernel. For a bounded function  $\phi$  with bounded support let*

$$(10.50) \quad Z_r(\phi) := \frac{\sum_{\xi \in \mathbb{Z}^d} [X_\xi(\infty) - E(X_\xi(\infty))] \phi(\frac{\xi}{r})}{r^{\frac{d+2}{2}}}$$

*If  $d \geq 3$ , then as  $r \rightarrow \infty$ ,  $Z_r$  converges weakly to the Gaussian free field on  $\mathbb{R}^d$ , that is, the Gaussian field on  $\mathbb{R}^d$  with covariance kernel  $\frac{1}{r^{\frac{d-2}{2}}}$ .*

**Remark 10.31** *Recall that the dual of the voter model and the dual for the 2 type Wright-Fisher diffusion differ only in that for the voter model the coalescence is instantaneous and for the Wright-Fisher model coalescence occurs with delay. Using this observation the basic strategy of the proof of this theorem which involves the “infinite colour” decomposition can be applied to the case of the Wright-Fisher diffusion.*

## Chapter 10

# Spatial systems in large space and time scales

In this chapter we consider critical spatial branching systems and interacting neutral Fleming-Viot processes in large space and time scales. The behaviour of these systems is determined by potential theoretic properties of the migration process such as transience or recurrence. We begin with a brief review of some basic notions.

### 10.1 Migration processes on Abelian groups

In this section we give a brief review of the basic notions of random walks and Lévy processes on groups on abelian groups following [149].

Let  $S$  be a locally compact (additive) Abelian group with countable base and with Haar measure  $\rho$ . A discrete time random walk,  $\{W_n\}_{n \in \mathbb{Z}_+}$ , is prescribed by a transition function

$$P(x, dy) := P(W_{n+1} \in dy | W_n = x) = p(d(y - x))$$

where  $p$  is a probability measure on  $S$ . The corresponding  $k$ -step transition function is

$$P^k(x, dy) := P(W_{n+k} \in dy | W_n = x).$$

A continuous time random walk  $\{W_t : t \geq 0\}$  with jump rate 1 is then defined by the transition function

$$P_t(x, dy) := P_x(W_t \in dy), \quad t \geq 0,$$

$$P_t(x, dy) = \sum_{k=0}^{\infty} \frac{e^{-t} t^k}{k!} P^k(x, dy).$$

A natural generalization of continuous time random walks is the notion of Lévy process.

**Definition 10.1** A  $S$ -valued process  $\{X_t : t \geq 0\}$  is a Lévy process if it is stochastically continuous and has stationary and independent increments.

We associate to a Lévy process a semigroup  $\{T_t : t \geq 0\}$  on  $\mathcal{B}_c(S)$ , the space of bounded measurable functions on  $S$  with compact support, as follows:

$$T_t\varphi(x) = E_x(\varphi(X_t)),$$

The Green potential of  $X$  is the operator

$$G\varphi = \int_0^\infty T_t\varphi dt, \quad \varphi \in \mathcal{B}_c(S).$$

The fractional operator powers of  $G$  are given by

$$G^\zeta\varphi = \frac{1}{\Gamma(\zeta)} \int_0^\infty t^{\zeta-1} T_t\varphi dt, \quad \zeta > 0 \quad \varphi \in \mathcal{B}_c(S).$$

### 10.1.1 Transience-Recurrence Properties

In order to review the definitions of transience and recurrence, (following [150]) we consider the last exit time,  $L_A$ , of  $X$  from a non-empty set  $A$  defined by

$$L_A := \sup\{t > 0 : X_t \in A\} \quad (\text{if } \{t > 0 : X_t \in A\} \neq \emptyset)$$

**Definition 10.2** The Lévy process  $X_t$  on  $S$  is transient if for any compact set  $K$

$$P(L_K < \infty) = 1.$$

and recurrent if it is not transient.

The following result in the spirit of Sato and Watanabe [530], [529] is the basis for a finer classification of the transience properties of random walks in terms of the moments of last exit times.

**Proposition 10.3** Assume that  $X_t$  is transient, for any compact set  $K \subset S$

$$\sup_{x \in K} G1_K(x) < \infty$$

and for any compact set  $C$  contained in the interior of  $K$

$$\inf_{x \in C} G1_K(x) > 0.$$

Then there exist positive constants  $c_1$  and  $c_2$  such that for all  $\zeta > 0$  and  $x \in S$

$$c_1 G^{\zeta+1} 1_C(x) \leq E_x L_C^\zeta \leq c_2 G^{\zeta+1} 1_K(x).$$

**Proof.** See [150], Proposition 2.2.1. ■

**Definition 10.4** *The degree of transience,  $\gamma$ , of a transient Lévy process  $X$  is defined by*

$$\gamma := \sup\{\zeta > 0 : E_0 L_K^\zeta < \infty \text{ for all compact } K\},$$

or equivalently

$$\gamma := \sup\{\zeta > 0 : G^{\zeta+1} \varphi < \infty \text{ for } \varphi \in C_c^+(S)\}$$

where  $C_c^+(S)$  denotes the space of nonnegative continuous functions on  $S$  with compact support.

**Remark 10.5** *Sato and Watanabe introduced the set*

$$(10.1) \quad \mathcal{T} := \{\zeta > 0 : E_0 L_K^\zeta < \infty \text{ for all compact } K\}.$$

In [150] we consider the extended set

$$\mathcal{T} := \{\zeta > -1 : \int_1^\infty t^\zeta T_t \varphi dt < \infty \text{ for all } \varphi \in C_c^+(S)\},$$

and we call

$$\gamma := \sup\{\zeta > -1 : \zeta \in \mathcal{T}\}$$

the degree of the process. This coincides with the degree of transience if  $\gamma > 0$ , and if  $-1 < \gamma < 0$ , we call  $\gamma$  the degree of recurrence of the process.

Given  $k \in \mathbb{Z}_+$ , the process is said to be (cf. [148])

$$\begin{aligned} k - \text{strongly transient} & \quad \text{if } k \in \mathcal{T}, \quad \text{and} \\ k - \text{weakly-transient} & \quad \text{if } k - 1 \in \mathcal{T} \text{ and } k \notin \mathcal{T}. \end{aligned}$$

**Remark 10.6** *The degree of transience can be viewed as a generalization of the notion of “critical dimension”. Note that  $G^{\zeta+1} \varphi$  at  $\zeta = \gamma$  can be either finite or infinite - we will give examples of both possibilities below.*

### 10.1.2 Random walks and Lévy processes in $\mathbb{R}^d$ .

In this section we briefly review the classical results on random walks and Lévy processes in  $\mathbb{Z}^d$  and  $\mathbb{R}^d$ .

First recall that symmetric nearest neighbour random walks in  $\mathbb{Z}^d$  are recurrent in dimensions  $d = 1, 2$  and transient in dimensions  $d \geq 3$ . Moreover, since the rate of decay of the transition probabilities for simple symmetric  $d$ -dimensional random walk is  $p_t(0, 0) \sim \text{const.} t^{-d/2}$ , its degree is  $\gamma = d/2 - 1$ .

We next recall the classical characterization of Lévy processes in  $\mathbb{R}^d$ .

**Theorem 10.7** (*Lévy-Khintchine representation*) *A Lévy process in  $\mathbb{R}^d$  has the characteristic function (i.e. Fourier transform)*

$$E[e^{i(z, X_t)}] = \exp \left[ t \left( -\frac{1}{2}(z, Az) + \int_{\mathbb{R}^d} (e^{i(z, x)} - 1 - i(z, x)1_{\{|x| \leq 1\}}(x))\nu(dx) + i(m, z) \right) \right]$$

where  $A$  is a symmetric nonnegative definite  $d \times d$  matrix,  $\nu$  is a measure on  $\mathbb{R}^d \setminus \{0\}$  satisfying  $\nu(\{0\}) = 0$  and  $\int_{\mathbb{R}^d} (|x|^2 \wedge 1)\nu(dx) < \infty$ , and  $m \in \mathbb{R}^d$ .

For the proof see [528].

The case  $A = Id$ ,  $\nu = 0$ ,  $m = 0$  is the standard Brownian motion and the case  $A = 0$ ,  $m = 0$  and  $\nu(dx) = |x|^{-\alpha-d}dx$ , is the symmetric  $\alpha$ -stable process.

**Proposition 10.8** *For the  $\alpha$ -stable process on  $\mathbb{R}^d$  the degree is*

$$(10.2) \quad \gamma = \frac{d}{\alpha} - 1$$

and in this case

$$\int_0^t s^\gamma T_s \varphi ds \sim \text{const} \cdot \log t \rightarrow \infty$$

as  $t \rightarrow \infty$ .

The distribution of jumps of the  $\alpha$ -stable process has “long tails”.

## 10.2 The Persistence-Extinction Dichotomy for Critical Branching Systems

Consider the super-Brownian motion in  $\mathbb{R}^d$  with initial measure  $X_0 = m\lambda$ ,  $m > 0$  where  $\lambda$  is Lebesgue measure. If  $\sup |\phi(x)| \cdot (1 + |x|^2)^{\frac{\gamma}{2}} < \infty$ , then the solution,  $v_t(x) = V[\phi](t, x)$ , to

$$(10.3) \quad \frac{\partial v_t}{\partial t} = Av_t - \frac{\gamma}{2}v_t^2,$$

with  $A = \frac{\Delta}{2}$  is integrable and integrating both sides with respect to Lebesgue measure gives

$$\int v_t(x)dx = \frac{\gamma}{2} \int_0^t \int v_s^2(x)dx ds.$$

Therefore the large time limit of the Laplace functional

$$\begin{aligned} \lim_{t \rightarrow \infty} \mathbb{P}_{m\lambda}(\exp(-X_t(\phi))) &= \lim_{t \rightarrow \infty} \exp\left(-m \int v_t(x) dx\right) \\ &= \lim_{t \rightarrow \infty} \exp\left(-\frac{m\gamma}{2} \int_0^t \int v_s^2(x) dx ds\right) \end{aligned}$$

exists for every  $\phi \in \mathcal{B}_+$  since the right side is monotone in  $t$ . Therefore  $X_t$  converges in distribution as  $t \rightarrow \infty$  to a random measure on  $\mathbb{R}^d$  with probability law which we denote by  $\mathbb{P}_m^{eq}$ . Replacing  $\phi$  by  $\theta\phi$ ,  $\theta > 0$ , and evaluating the first and second derivatives with respect to  $\theta$  at  $\theta = 0$ , we can verify that the first and second moments are given by

$$\mathbb{P}_{m\lambda}(X_t(\phi)) = m \int \phi(x) dx$$

and

$$\begin{aligned} \mathbb{P}_{m\lambda}(X_t(\phi)^2) &= m^2 \left(\int \phi(x) dx\right)^2 + \gamma m \int_0^t \int \left(\int p_s(y-z)\phi(z) dz\right)^2 dy ds \\ &= m^2 \left(\int \phi(x) dx\right)^2 + \gamma m \int_0^t \left(\int p_{2s}(z_1-z_2)\phi(z_1)\phi(z_2) dz_1 dz_2\right) ds. \end{aligned}$$

Recalling that for the Brownian motion transition kernel  $\int_0^\infty p_s(z) ds$  diverges if  $d = 1, 2$  and is given by  $\frac{2c_d}{|z|^{d-2}}$  if  $d \geq 3$ , we obtain

$$\begin{aligned} \mathbb{P}_{m\lambda}(X_t(\phi)^2) &\uparrow \infty \text{ if } d = 1, 2 \\ &\uparrow m^2 \left(\int \phi(x) dx\right)^2 + \gamma m c_d \int \int \frac{\phi(z_1)\phi(z_2)}{|z_1-z_2|^{d-2}} dz_1 dz_2 \text{ if } d \geq 3. \end{aligned}$$

If  $d \geq 3$ , the above imply that  $\{X_t(\phi)\}_{t \geq 0}$  are uniformly integrable and  $\mathbb{P}_{m\lambda}(X_\infty(\phi)) = m\lambda(\phi)$ , that is, the limiting equilibrium random measure  $\mathbb{P}_m^{eq}$  has the same intensity,  $m$ , as the initial intensity - this behaviour is called *persistence*. Bramson, Cox and Greven (1997) [57] proved that  $\{\mathbb{P}_m^{eq} : m \in [0, \infty)\}$  is in fact the set of all extremal invariant measures.

**Theorem 10.9** [115] *Let  $X_\infty$  denote the equilibrium random measure for super-Brownian motion in  $\mathbb{R}^d$  with mean measure  $E(X_\infty(A)) = \lambda(A)$ . Let*

$$(10.4) \quad \langle X_\infty^K, \phi \rangle = \int \phi\left(\frac{x}{K}\right) X_\infty(dx),$$

and

$$(10.5) \quad V(\phi) := \gamma \left(\int \int |z_1 - z_2|^{d-2} \phi(z_1)\phi(z_2) dz_1 dz_2\right).$$

Then the rescaled fluctuations

$$(10.6) \quad \frac{\langle X_\infty^K, \phi \rangle - \langle \lambda, \phi \rangle}{K^{\frac{d+2}{2}} V(\phi)} \Rightarrow Z_\infty$$

where  $Z_\infty$  is the Gaussian free field, that is, the Gaussian random field with covariance kernel

$$(10.7) \quad \frac{1}{|x - y|^{d-2}}.$$

The divergence of the second moment in the low dimensional case suggests that the behaviour is qualitatively different in these dimensions. It was proved in Dawson (1977) [115] that in this case the spatially homogeneous super Brownian motion with  $X_0 = m\lambda$  suffers local extinction, that is,  $X_t(A) \rightarrow 0$  in probability as  $t \rightarrow \infty$  for any bounded set  $A$ . Iscoe (1986b) [331] has shown that  $X_t(A) \xrightarrow{a.s.} 0$  for any bounded set if  $d = 1$  and that this result is false if  $d = 2$ . In dimensions  $d = 1, 2$  Bramson, Cox and Greven ([56]) have established that  $\delta_0$  is the only measure which is invariant for the process  $X_t$  and that for any locally finite initial measure the system undergoes local extinction or explodes thus ruling out the possibility of an invariant measure with infinite mean.

### 10.2.1 Clumping in Low Dimensions

In order to describe the low dimensional behavior of  $X_t$  with  $X_0 = \lambda$  (Lebesgue) in more detail we introduce the space-time-mass rescaling

$$\begin{aligned} X_t^{K,\xi}(A) &:= K^{-\xi} X_{Kt}(K^{\frac{\xi}{d}} A) \\ X_0^{K,\xi}(A) &= |A|. \end{aligned}$$

Then

$$\begin{aligned} \mathbb{P}_\lambda(\exp(-X_t^{K,\xi}(\phi))) &= \exp(-\lambda(V_{Kt}\phi_K)) \quad \text{with} \\ \phi_K(x) &:= K^{-\xi}\phi(K^{-\frac{\xi}{d}}x). \end{aligned}$$

Note that

$$\tilde{v}(t, x) := K^\xi V_{Kt}\phi_K(K^{\frac{\xi}{d}}x)$$

satisfies

$$\begin{aligned} \frac{\partial \tilde{v}(t, x)}{\partial t} &= K^{1-\frac{2\xi}{d}} \Delta \tilde{v}(t, x) - \frac{\gamma}{2} K^{1-\xi} \tilde{v}(t, x)^2 \\ \tilde{v}(0, x) &= \phi(x) \end{aligned}$$

and therefore  $X^{K,\xi}$  is equivalent to a super Brownian motion with “diffusion coefficient”  $K^{1-\frac{2\xi}{d}}$  and “branching coefficient”  $\frac{\gamma}{2} K^{1-\xi}$ . The branching term dominates in the  $K \rightarrow \infty$  limit and the diffusion term dominates in the  $K \rightarrow 0$  limit if  $d < 2$  and the opposite occurs if  $d > 2$ .

**Theorem 10.10** (Dawson and Fleischmann 1988) [117] (a) Let  $d < 2$ . Then  $X^{K,\xi} \xrightarrow{K \rightarrow \infty} 0$  if  $\xi < 1$  and  $X^{K,\xi} \xrightarrow{K \rightarrow \infty} \lambda$  if  $\xi > 1$   
 (b) If  $d = 1$  and  $\xi = 1$ , then  $X_K$  converges in distribution as  $K \rightarrow \infty$  to the pure atomic process  $\{X_t^0\}_{t \geq 0}$  in which  $X_t^0$  is Poisson with intensity  $(\frac{\gamma}{2}t)X(0)$  and the mass of each atom evolves according to a Feller continuous state branching.  
 (c) If  $d = 2$ , then  $X^{K,1} \stackrel{D}{=} X$ , that is  $X$  is self-similar.

**Remark 10.11** (b) suggests that for  $d = 1$  at time  $K$  there are clumps of size  $K$  with interclump distance  $K$ .

In the case  $d = 2$ , the phenomenon of *diffusive clustering* arises. This is made precise in the following result of Klenke.

**Theorem 10.12** (Klenke (1997) [[386], Theorem 2]) Let  $d = 2$ , and  $I = (-\infty, 1]$ . For  $\alpha \in I$ , let

$$X_t^\alpha(B) := t^{-\alpha} X_t(t^{\alpha/2} B).$$

Then in the sense of finite dimensional distributions

$$\mathcal{L}^{\frac{(\log t)\lambda}{8\pi}}[\{X_t^\alpha(B)\}_{\alpha \in I}] \xrightarrow{t \rightarrow \infty} \mathcal{L}^1[\{Z_{1-\alpha}\}_{\alpha \in I} \cdot \lambda(B)]$$

where  $Z$  is a FB process with  $Z_0 = 1$ .

In the case  $d = 2$  Theorem 10.10 (c) provides a link between the small scale and large scale behaviours. In particular it implies that

$$X_{Kt}(B(0, 1)) \stackrel{D}{=} \frac{X_t(B(0, K^{-1/2}))}{K^{-1}}.$$

For  $t > 0$  the left side goes to zero in probability as  $K \rightarrow \infty$  because of the local extinction result which then shows that the local density at time  $t$  is 0 which implies that it does not have a non-trivial absolutely continuous component.

### 10.2.2 Ergodic Behaviour

The extinction-persistence result implies that if  $\phi$  has compact support, then  $X_t(\phi)$  converges to zero in probability if  $d \leq 2$  and converges in distribution to a non-degenerate limit if  $d > 2$ . This can be extended to an ergodic theorem in the latter case.

**Theorem 10.13** (Iscove (1986b) ([331]), Fleischmann and Gärtner (1986) ([252])).

- (a) For  $d > 2$  with probability one,  $\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t X_s ds = \lambda$  (in the vague topology).
- (b) For  $d = 2$ , as  $t \rightarrow \infty$   $\frac{1}{t} \int_0^t X_s ds$  converges a.s. in the vague topology to  $\eta\lambda$  where  $\eta$  is a non-degenerate infinitely divisible random variable with mean one.