Spatial populations with seed-bank

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PART I

SPATIAL POPULATIONS WITH SEED-BANK: WELL-POSEDNESS, DUALITY AND EQUILIBRIUM

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CHAPTER 2

Spatial populations with seed-bank, models and results

§2.1 Background and outline

§2.1.1 Background and goals

In populations with a seed-bank, individuals can become dormant and stop reproducing themselves, until they can become active and start reproducing themselves again. In [10] and [12], the evolution of a population evolving according to the Fisher-Wright model with a *seed-bank* was studied. In this model individuals are subject to *resampling* and can move in and out of a seed-bank. While in the seed-bank they suspend resampling, i.e., the seed-bank acts as a repository for the genetic information of the population. Individuals that do not reside in the seed-bank are called *active*, those that do are called *dormant*. In the present paper we extend the single-colony Fisher-Wright model with seed-bank introduced in [12] to a multi-colony setting in which individuals live in different colonies and move between colonies. In other words, we introduce *spatialness*.

Seed-banks are observed in many taxa, including plants, bacteria and other micro-organisms. Typically, they arise as a response to unfavourable environmental conditions. The dormant state of an individual is characterised by low metabolic activity and interruption of phenotypic development (see e.g. Lennon and Jones [55]). After a varying and possibly large number of generations, dormant individuals can be resuscitated under more favourable conditions and reprise reproduction after having become active. This strategy is known to have important implications for population persistence, maintenance of genetic variability and stability of ecosystems. It acts as a *buffer* against evolutionary forces such as genetic drift, selection and environmental variability. The importance of this evolutionary trait has led to several attempts to model seed-banks from a mathematical perspective, see e.g. [50], [11], [40], [9]. In [12] it was shown that the continuum model obtained by taking the large-colony-size limit of the individual-based model with seed-bank is the Fisher-Wright diffusion with seed-bank. Also the long-time behaviour and the genealogy of the continuum model with seed-bank were analysed in [12].

In the present paper we consider a *spatial* version of the continuum model with seed-bank, in which individuals live in colonies, each with their own seed-bank, and are allowed to *migrate* between colonies. Our goal is to understand the change in behaviour compared to the spatial model without seed-bank. The latter has been the object of intense study. A sample of relevant papers and overviews is [66], [17], [20], [25], [22], [33], [29], [27], [24], [41]. We expect the presence of the seed-bank to affect the long-time behaviour of the system not only quantitatively but also qualitatively. To understand how this comes about, we must find ways to deal with the *richer behaviour* of the population caused by the motion in and out of the seed-bank. Earlier work on a spatial model with seed-bank, migration and mutation was carried out in [28], where the probability to be identical by decent for two individuals drawn randomly from two colonies was computed as a function of the distance between the colonies.

It has been recognised that qualitatively different behaviour may occur when the wake-up time in the seed-bank changes from having a thin tail to having a fat tail [55]. One challenge in modelling seed-banks has been that fat tails destroy the Markov property for the evolution of the system. A key idea of the present paper is that we can *enrich the seed-bank with internal states* – which we call colours – to allow for fat tails and still preserve the Markov property for the evolution. We will see that fat tails induce *new universality classes.*

The main goals of the present paper are the following:

(1) Identify the typical features of the long-time behaviour of populations with a seed-bank. In particular, prove convergence to equilibrium, and identify the parameter regimes for *clustering* (= convergence towards locally mono-type equilibria) and *coexistence* (= convergence towards locally multi-type equilibria).

(2) Identify the role of finite versus infinite mean wake-up time. Identify the *critical dimension* in case the geographic space is $\mathbb{Z}^d$, $d \geq 1$, i.e., the dimension at which the crossover between clustering and coexistence occurs for migration with finite variance.

  (2a) Show that if the wake-up time has *finite mean*, then the dichotomy between coexistence and clustering is controlled by the migration only and the seed-bank has no effect. In particular, clustering prevails when the symmetrised migration kernel is recurrent while coexistence prevails when it is transient. This is the classical dichotomy for populations without seed-bank [14]. The critical dimension is $d = 2$.

  (2b) Show that if the wake-up time has *infinite mean* with *moderately fat tails*, then the dichotomy is controlled by both the migration and the seed-bank. In particular, the parameter regimes for clustering and coexistence reveal an interesting interplay between rates for migration and rates for exchange with the seed-bank. The critical dimension is $1 < d < 2$.

  (2c) Show that if the wake-up time has *infinite mean* with *very fat tails*, then the dichotomy is controlled by the seed-bank only and the migration has no effect. The critical dimension is $d = 1$.

We focus on the situation where the individuals can be of two types. The extension to infinitely many types, called the Fleming-Viot measure-valued diffusion, only requires standard adaptations and will not be considered here (see [25]). Also, instead of Fisher-Wright resampling we will allow for state-dependent resampling, i.e., the rate of resampling in a colony depends on the fractions of the two types in that colony. In what follows we only work with *continuum* models, in which the components represent *type frequencies* in the colonies labelled by a discrete geographic space.

The techniques of proof that we use include duality, moment relations, semigroup comparisons and coupling. These techniques are standard, but have to be adapted to the fact that individuals move into and out of seed-banks. Since there is no resampling and no migration in the seed-bank, the motion of ancestral lineages in the dual process looses part of the random-walk structure that is crucial in models without seed-bank. Moreover, for seed-banks with infinite mean wake-up times, we encounter *fat-tailed* wake-up time distributions in the dual process, and we need to deal with lineages that are dormant most of the time and therefore are much slower to coalesce. The coupling arguments also change. Already in a single colony, if the seed-bank has infinitely many internal states, then we are dealing with an infinite system in which the manipulation of Lyapunov functions and the construction of successful couplings from general classes of initial states is hard. In the multi-colony setting this becomes even harder, and conceptually challenging issues arise.

§2.1.2 Outline

In Section 2.2 we introduce three models of increasing generality, establish their well-posedness via a martingale problem, and introduce their dual processes, which play a crucial role in the analysis. In Section 2.3 we state our main results. We focus on the long-time behaviour, prove convergence to equilibrium, and establish a *dichotomy* between clustering and coexistence. We show that this dichotomy is *affected by the presence of the seed-bank*, namely, the dichotomy depends not only on the migration rates, but can also depend on the relative sizes of the active and the dormant population and their rates of exchange. In particular, if the dormant population is much larger than the active population, then the residence time in the seed-bank has a fat tail that *enhances genetic diversity significantly*.

Sections 3.1–3.4 are devoted to the proofs of the theorems stated in Sections 2.2–2.3. In Appendix A.1 we give the derivation of the single-colony continuum model from the single-colony individual-based Fisher-Wright model in the large-colony-size limit. In the individual-based model active individuals *exchange* with dormant individuals, i.e., for each active individual that becomes dormant a dormant individual becomes active. In Appendix A.2 we look at the continuum limit of the single-colony individual-based Moran model in which active and dormant individuals no longer exchange state but rather change state independently. We show that change instead of exchange does not affect the long-time behaviour. Appendices A.3 and A.4 contain the proof of technical lemmas that are needed in the proof of the convergence to equilibrium.

In three companion papers we deal with three further aspects:

(I) In [44] we establish the *finite-systems scheme*, i.e., we identify in the coexistence regime how a finite truncation of the system behaves as both the time and the truncation level tend to infinity, properly tuned together. This underlines the relevance of systems with an infinite geographic space and a seed-bank with infinitely many colours for the description of systems with a large finite geographic space and a seed-bank with a large finite number of colours. We show that there is a *single universality class* for the scaling limit, represented by a Fisher-Wright diffusion whose volatility constant is *reduced* by the seed-bank. We show that if the wake-up time has finite mean, then the scaling time is *proportional* to the geographical volume of the system, while if the wake-up time has infinite mean, then the scaling time grows *faster* than the geographical volume of the system. We also investigate what happens for systems with a large finite geographic space and a seed-bank with infinitely many colours, where the behaviour turns out to be different.

(II) In [45] we consider the special case where the colonies are organised in a *hierarchical fashion*, i.e., the geographic space is the hierarchical group Ω_N of order N. We identify the parameter regime for clustering for all $N < \infty$, and analyse the *multi-scale behaviour* of the system in the hierarchical mean-field limit $N \to \infty$ by looking at block averages on successive hierarchical space-time scales. Playing with the migration kernel, we can choose the migration to be close to critically recurrent in the sense of potential theory. By letting $N \to \infty$ we can approach the *critical dimension*, so that the migration becomes similar to migration on the two-dimensional Euclidean geographic space. With the help of *renormalisation arguments* we show that, close to the critical dimension, the scaling behaviour on large space-time scales is *universal.*

(III) Our goal for the fourth paper is to identify the *pattern of cluster formation* in the clustering regime (= how fast mono-type clusters grow in time) and describe the *genealogy* of the population. The latter provides further insight into how the seed-bank enhances genetic diversity.

In these papers too we will see that the seed-bank can cause not only quantitative but also qualitative changes in the scaling behaviour of the system.

§2.2 Introduction of the three models and their basic properties

In Section 2.2.1 we give a formal definition of the three models of increasing generality. In Section 2.2.2 we comment on their biological significance. In Section 2.2.3 we establish their well-posedness via a martingale problem (Theorem 2.2.4). In Section 2.2.4 we introduce the associated dual processes and state the relevant duality relations (Theorems 2.2.5, 2.2.8 and 2.2.10). In Section 2.2.5 we use these duality relations to formulate a criterion for clustering versus coexistence (Theorems 2.2.11 and 2.2.13).

§2.2.1 Migration, resampling and seed-bank: three models

In this section we extend the model for a population with seed-bank from [12] to three models of increasing generality for spatial populations with seed-bank. In each of the three models, we consider populations of individuals of two types – either $\heartsuit$ or $\diamondsuit$ – located in a *geographic space* $\mathbb{G}$ that is a countable Abelian group endowed with the discrete topology. In each of the three models, the population in a colony consist of an *active* part and a *dormant* part. The *repository* of the dormant population at colony $i \in \mathbb{G}$ is called the seed-bank at $i \in \mathbb{G}$. Individuals in the active part of a colony $i \in \mathbb{G}$ can resample, migrate and exchange with a dormant population. Individuals in the dormant part of a colony $i \in \mathbb{G}$ only exchange with the active population. An active individual that resamples chooses uniformly at random another individual from its colony and adopts its type. (Alternatively, resampling may be viewed as the active individual being replaced by a copy of the active individual chosen. Because individuals carry a type and not a label, this gives the same model.) When an active individual at colony $i \in \mathbb{G}$ migrates, it chooses a parent from another colony $j \in \mathbb{G}$ and adopts its type. In each of the three models the migration is described by a *migration kernel* $a(\cdot,\cdot)$, which is an irreducible $\mathbb{G} \times \mathbb{G}$ matrix of transition rates satisfying

$$a(i,j) = a(0,j-i) \quad \forall\, i,j \in \mathbb{G}, \qquad \sum_{i\in\mathbb{G}} a(0,i) < \infty. \tag{2.1}$$

Here, $a(i,j)$ is to be interpreted as the rate at which an active individual at colony $i \in \mathbb{G}$ chooses a parent in the active part of colony $j \in \mathbb{G}$ and adopts its type. An active individual that becomes dormant *exchanges* with a randomly chosen dormant individual that becomes active. The three models we discuss in the present paper differ in the way the active population exchanges with the dormant population. However, in each of the three models the exchange mechanism guarantees that the sizes of the active and the dormant population stay fixed over time. The dormant part of the population only evolves due to exchange of individuals with the active part of the population.

Since we look at continuum models obtained from individual-based models, we are interested in the frequencies of type $\heartsuit$ in the different colonies. In Appendix A.1 we discuss the individual-based models underlying the continuum models described below.

Remark 2.2.1 (Notation). Throughout the paper we use lower case letters for *components* and upper case letters for *systems of components.* ■

Model 1: single-layer seed-bank. Each colony $i \in \mathbb{G}$ has an active part A and a dormant part D. Therefore we say that *the effective geographic space* is given by $\mathbb{G} \times \{A, D\}$. For $i \in \mathbb{G}$ and $t \geq 0$, let $x_i(t)$ denote the fraction of individuals in colony i of type $\heartsuit$ that are active at time t, and $y_i(t)$ the fraction of individuals in colony i of type $\heartsuit$ that are dormant at time t. Then the system is described by the process

$$(Z(t))_{t\geq 0}, \qquad Z(t) = \big(z_i(t)\big)_{i\in\mathbb{G}}, \qquad z_i(t) = (x_i(t), y_i(t)), \tag{2.2}$$

on the state space

$$E = ([0,1] \times [0,1])^{\mathbb{G}}, \tag{2.3}$$

and $(Z(t))_{t\geq 0}$ evolves according to the following SSDE:

$$\begin{aligned} \mathrm{d}x_i(t) &= \sum_{j\in\mathbb{G}} a(i,j)\,[x_j(t)-x_i(t)]\,\mathrm{d}t + \sqrt{dx_i(t)[1-x_i(t)]}\,\mathrm{d}w_i(t) \qquad (2.4)\\ &\quad + Ke\,[y_i(t)-x_i(t)]\,\mathrm{d}t,\\ \mathrm{d}y_i(t) &= e\,[x_i(t)-y_i(t)]\,\mathrm{d}t, \qquad i\in\mathbb{G}, \qquad (2.5)\end{aligned}$$

where $(w_i(t))_{t\geq 0}$, $i\in\mathbb{G}$, are independent standard Brownian motions. As initial state $Z(0)=z$ we may pick any $z\in E$. The first term in (2.4) describes the *migration* of active individuals at rate $a(i,j)$. The second term in (2.4) describes the *resampling* of individuals at rate $d\in(0,\infty)$. The third term in (2.4) together with the term in (2.5) describe the *exchange* of active and dormant individuals at rate $e\in(0,\infty)$.

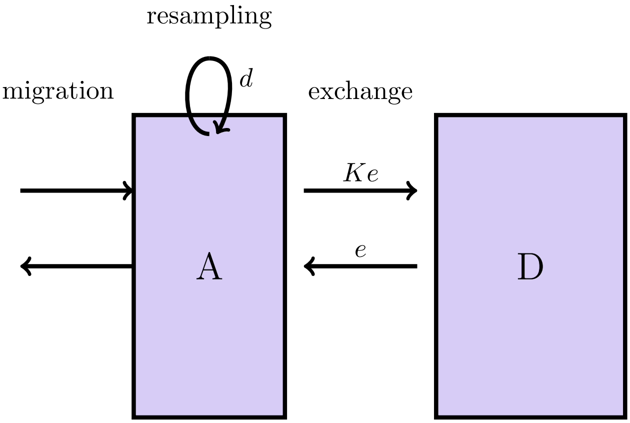

Figure 2.1: The evolution in model 1. Individuals are subject to migration, resampling and exchange with the seed-bank.

The factor $K\in(0,\infty)$ is defined by

$$K = \frac{\text{size dormant population}}{\text{size active population}}, \tag{2.6}$$

and is the same for all colonies $i\in\mathbb{G}$. The factor K turns up in the scaling limit of the individual-based model when there is an *asymmetry* between the sizes of the active and the dormant population (see Appendix A.1). In Fig. 2.1 we give a schematic illustration of the process (2.4)–(2.5). A detailed description of the underlying individual-based model, as well as a derivation of the continuum limit (2.4)–(2.5) from the individual-based model following [12], can be found in Appendix A.1. The continuum limit is also referred to as the frequency limit or the diffusion limit.

Remark 2.2.2 (Interpretation of the state space.). Note that the *state space* of the system can also be written as

$$E = [0,1]^{\mathbb{S}}, \qquad \mathbb{S} = \mathbb{G} \times \{A, D\}, \tag{2.7}$$

where A denotes the reservoir of the active population and D the repository of the dormant population. With that interpretation, the process is denoted by

$$(Z(t))_{t\geq 0}, \qquad Z(t) = \big(z_u(t)\big)_{u\in\mathbb{S}} \tag{2.8}$$

with $z_u(t) = x_i(t)$ if $u = (i, A)$ and $z_u(t) = y_i(t)$ if $u = (i, D)$. To analyse the system we need both interpretations of the state space. ■

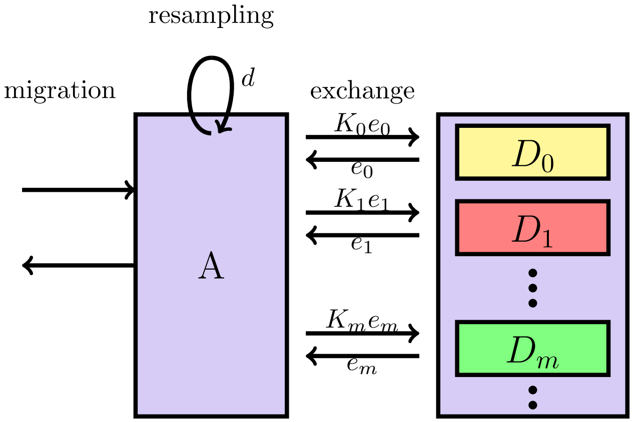

Figure 2.2: The evolution in model 2. Individuals are subject to migration, resampling and exchange with the seed-bank, as in model 1. Additionally, when individuals become dormant they get a colour and when they become active they loose their colour.

Model 2: multi-layer seed-bank. In this model we give the seed-bank an internal structure by colouring the dormant individuals with countably many colours $m \in \mathbb{N}_0$. Active individuals that become dormant are assigned a colour m that is drawn randomly from an infinite sequence of colours labeled by $\mathbb{N}_0$ (see Fig. 2.2 for an illustration). As will be explained in Section 2.2.2, this captures the *different ways in which individuals can enter into the seed-bank.* In Section 2.2.4 we will show how this internal structure allows for fat tails in the wake-up times of individuals while preserving the Markov property.

For each $i \in \mathbb{G}$ a colony now consists of an active part A and a whole sequence $(D_m)_{m\in\mathbb{N}_0}$ of dormant parts, labeled by their colour $m \in \mathbb{N}_0$. Therefore in this model the *effective geographic space* is given by $\mathbb{G} \times \{A, (D_m)_{m\in\mathbb{N}_0}\}$.

As before, for $i \in \mathbb{G}$, let $x_i(t)$ denote the fraction of individuals in colony i of type $\heartsuit$ that are active at time t, but now let $y_{i,m}(t)$ denote the fraction of individuals in colony i of type ♡ that are dormant with colour m at time t. Then the system is described by the process

$$(Z(t))_{t\geq 0}, \qquad Z(t) = \big(z_i(t)\big)_{i\in\mathbb{G}}, \qquad z_i(t) = (x_i(t), (y_{i,m}(t))_{m\in\mathbb{N}_0}), \tag{2.9}$$

on the state space

$$E = ([0,1]\times[0,1]^{\mathbb{N}_0})^{\mathbb{G}}. \tag{2.10}$$

Suppose that active individuals exchange with dormant individuals with colour m at rate $e_m \in (0,\infty)$, and let the factor $K_m \in (0,\infty)$ capture the asymmetry between the size of the active population and the m-dormant population, i.e., similarly as in (2.6),

$$K_m = \frac{\text{size } m\text{-dormant population}}{\text{size active population}}, \qquad m\in\mathbb{N}_0, \tag{2.11}$$

where $K_m \in (0,\infty)$ is the same for all colonies. Then the process $(Z(t))_{t\geq 0}$ evolves according to the SSDE

$$\begin{aligned} \mathrm{d}x_i(t) &= \sum_{j\in\mathbb{G}} a(i,j)\,[x_j(t)-x_i(t)]\,\mathrm{d}t + \sqrt{dx_i(t)[1-x_i(t)]}\,\mathrm{d}w_i(t) \qquad (2.12)\\ &\quad + \sum_{m\in\mathbb{N}_0} K_m e_m\,[y_{i,m}(t)-x_i(t)]\,\mathrm{d}t,\\ \mathrm{d}y_{i,m}(t) &= e_m\,[x_i(t)-y_{i,m}(t)]\,\mathrm{d}t, \qquad m\in\mathbb{N}_0,\ i\in\mathbb{G}, \qquad (2.13) \end{aligned}$$

where we have to assume that

$$\sum_{m\in\mathbb{N}_0} K_m e_m < \infty, \tag{2.14}$$

since otherwise active individuals become dormant instantly. Comparing (2.12)–(2.13) with the SSDE of model 1 in (2.4)–(2.5), we see that active individuals migrate (the first term in (2.12)), resample (the second term in (2.12)), but now interact with a whole sequence of dormant populations (the third term in (2.12) and the term in (2.13)). As initial state $Z(0) = z$ we may again take any $z \in E$.

Remark 2.2.3 (Interpretation of the state space.). Note that, like in Remark 2.2.2, the *state space* of the system can also be written as

$$E = [0,1]^{\mathbb{S}}, \qquad \mathbb{S} = \mathbb{G}\times\{A, (D_m)_{m\in\mathbb{N}_0}\}. \tag{2.15}$$

With this interpretation, the process is denoted by

$$(Z(t))_{t\geq 0}, \qquad Z(t) = \big(z_u(t)\big)_{u\in\mathbb{S}}, \tag{2.16}$$

with $z_u(t) = x_i(t)$ if $u = (i,A)$ and $z_u(t) = y_{i,m}(t)$ if $u = (i,D_m)$ for $m\in\mathbb{N}_0$. ■

Model 3: multi-layer seed-bank with displaced seeds. We can extend the mechanism of model 2 by allowing active individuals that become dormant to do so in a randomly chosen colony. This amounts to introducing a sequence of irreducible *displacement kernels* $a_m(\cdot,\cdot)$, $m \in \mathbb{N}_0$, satisfying

$$a_m(i,j) = a_m(0,j-i) \quad \forall\, i,j \in \mathbb{G}, \qquad \sum_{i\in\mathbb{G}} a_m(0,i) = 1 \quad \forall\, m \in \mathbb{N}_0, \tag{2.17}$$

and replacing (2.12)–(2.13) by

$$\begin{aligned} \mathrm{d}x_i(t) &= \sum_{j\in\mathbb{G}} a(i,j)\,[x_j(t)-x_i(t)]\,\mathrm{d}t + \sqrt{dx_i(t)[1-x_i(t)]}\,\mathrm{d}w_i(t) \qquad (2.18)\\ &\quad + \sum_{j\in\mathbb{G}}\sum_{m\in\mathbb{N}_0} K_m e_m\, a_m(j,i)\,[y_{j,m}(t)-x_i(t)]\,\mathrm{d}t,\\ \mathrm{d}y_{i,m}(t) &= \sum_{j\in\mathbb{G}} e_m\, a_m(i,j)\,[x_j(t)-y_{i,m}(t)]\,\mathrm{d}t, \qquad m\in\mathbb{N}_0,\ i\in\mathbb{G}. \qquad (2.19) \end{aligned}$$

Here, the third term in (2.18) together with the term in (2.19) describe the *switch of colony* when individuals exchange between active and dormant. Namely, with probability $a_m(i,j)$ simultaneously an active individual in colony i becomes dormant with colour m in colony j and a randomly chosen dormant individual with colour m in colony j becomes active in colony i. The state space E is the same as in (2.10). Also (2.9), (2.11), (2.14) and (2.16) remain the same.

Two key quantities. In models 2 and 3 we must assume that

$$\chi = \sum_{m\in\mathbb{N}_0} K_m e_m < \infty \tag{2.20}$$

in order to make sure that active individuals do not become dormant instantly. Define

$$\rho = \sum_{m\in\mathbb{N}_0} K_m = \frac{\text{size dormant population}}{\text{size active population}}. \tag{2.21}$$

It turns out that ρ and χ are two key quantities of our system. In particular, we will see that the long-time behaviour of model 2 and model 3 is different for $\rho < \infty$ and $\rho = \infty$.

§2.2.2 Comments

(1) Models 1–3 are increasingly more general. Model 2 is the special case of model 3 when $a_m(0,0) = 1$ for all $m \in \mathbb{N}_0$, while model 1 is the special case of model 2 when $e_0 = e$, $K_0 = K$ and $e_m = K_m = 0$ for all $m \in \mathbb{N}$. Nonetheless, in what follows we prefer to state our main theorems for each model separately, in order to exhibit the increasing level of complexity. In Appendix A.1 we explain how (2.4)–(2.5), (2.12)–(2.13) and (2.18)–(2.19) arise as the large-colony-size limit of individual-based Fisher-Wright models.

(2) As geographic space $\mathbb{G}$ we allow *any* countable Abelian group endowed with the discrete topology. Key examples are the Euclidean lattice $\mathbb{G} = \mathbb{Z}^d$, $d \in \mathbb{N}$, and the hierarchical lattice $\mathbb{G} = \Omega_N$, $N \in \mathbb{N}$. In this paper we will focus $\mathbb{G} = \mathbb{Z}^d$. The case $\mathbb{G} = \Omega_N$ will be considered in more detail in [45].

(3) In model 1, each colony has a seed-bank that serves as a *repository* for the genetic information (type $\heartsuit$ or $\diamondsuit$) carried by the individuals. Because the active and the dormant population exchange individuals, the genetic information can be temporarily stored in the seed-bank and thereby be withdrawn from the resampling. We may think of dormant individuals as seeds that drop into the soil and preserve their type until they come to the surface again and grow into a plant.

In model 2, the seed-bank is a repository for seeds with one of infinitely many colours. *The colours provide us with a tool to model different distributions for the time an individual stays dormant without loosing the Markov property for the evolution of the system.* Tuning the parameters K_m and e_m properly and subsequently forgetting about the colours, we can mimic different distributions for the time an individual stays dormant. This is of biological significance, especially in colonies of bacteria, where individuals stay dormant for random times whose distribution is fat-tailed (see [55]).

In model 3, the seed may even be blown elsewhere. Individuals that displace before becoming dormant are observed in plant-species as well as in bacteria populations (see [55]).

(4) In Appendix A.2 we comment on what happens when the rates to become active or dormant are decoupled, i.e., individuals are no longer subject to exchange but move in and out of the seed-bank independently. This leads to a Moran model where the sizes of the active and the dormant population can fluctuate. We will show that, modulo a change of variables and a short transient period in which the sizes of the active and the dormant population establish equilibrium, this model has the same behaviour as the model with exchange.

(5) In (2.4), (2.12) and (2.18) we may replace the diffusion functions dg_{FW}, $d \in (0,\infty)$, where

$$g_{\mathrm{FW}}(x) = x(1-x), \qquad x \in [0,1], \tag{2.22}$$

is the Fisher-Wright diffusion function, by a *general diffusion function* in the class $\mathcal{G}$ defined by

$$\mathcal{G} = \Big\{ g\colon\ [0,1] \to [0,\infty)\colon\ g(0) = g(1) = 0,\ g(x) > 0\ \forall\, x \in (0,1),\ g \text{ Lipschitz} \Big\}. \tag{2.23}$$

This class is appropriate because a diffusion with a diffusion function $g \in \mathcal{G}$ stays confined to $[0,1]$, yet can go everywhere in [0,1] (Breiman [13, Chapter 16, Section 7]). Picking $g \neq g_{\mathrm{FW}}$ amounts to allowing the resampling rate to be *state-dependent*, i.e., the resampling rate in state x equals $g(x)/x(1-x)$, $x \in (0,1)$. An example is the Kimura-Ohta diffusion function $g(x) = [x(1-x)]^2$,

$x \in [0,1]$, for which the resampling rate is equal to the genetic diversity of the colony. *In the sequel we allow for general diffusion functions $g \in \mathcal{G}$ in all three models, unless stated otherwise.*

§2.2.3 Well-posedness

For every law on E, with E depending on the choice of model, we want the SSDE for models 1, 2 and 3 to define a Borel Markov process, i.e., the law of the path is a Borel measurable function of the initial state for every starting point in the state space [17, p.62]. We use a martingale problem, in the sense of [32, p.173], to characterize the SSDE. Let

$$\begin{aligned}\mathcal{F} = \Big\{ f \in C_b(E,\mathbb{R})\colon\ & f \text{ depends on finitely many components} \\ & \text{and is twice continuously differentiable in each component}\Big\}.\end{aligned} \tag{2.24}$$

The generator G of the process acting on $\mathcal{F}$ reads for model 1 ((2.4)–(2.5)),

$$\begin{aligned} G = \sum_{i\in\mathbb{G}} \Bigg(\Bigg[\sum_{j\in\mathbb{G}} a(i,j)(x_j - x_i) \Bigg] \frac{\partial}{\partial x_i} + \frac{1}{2} g(x_i) \frac{\partial^2}{\partial x_i^2} \\ + Ke\,(y_i - x_i)\frac{\partial}{\partial x_i} + e\,(x_i - y_i)\frac{\partial}{\partial y_i} \Bigg), \end{aligned} \tag{2.25}$$

for model 2 ((2.12)–(2.13)),

$$\begin{aligned} G = \sum_{i\in\mathbb{G}} \Bigg(\Bigg[\sum_{j\in\mathbb{G}} a(i,j)(x_j - x_i) \Bigg] \frac{\partial}{\partial x_i} + \frac{1}{2} g(x_i) \frac{\partial^2}{\partial x_i^2} \\ + \sum_{m\in\mathbb{N}_0} \Bigg[K_m e_m\,(y_{i,m} - x_i)\frac{\partial}{\partial x_i} + e_m\,(x_i - y_{i,m})\frac{\partial}{\partial y_{i,m}} \Bigg] \Bigg), \end{aligned} \tag{2.26}$$

while for model 3 ((2.18)–(2.19)) the last term in the right-hand side of (2.26) is to be replaced by

$$\sum_{i,j\in\mathbb{G}} \sum_{m\in\mathbb{N}_0} \Bigg[K_m e_m\, a_m(j,i)\,(y_{j,m} - x_i)\frac{\partial}{\partial x_i} + e_m\, a_m(i,j)\,(x_j - y_{i,m})\frac{\partial}{\partial y_{i,m}} \Bigg]. \tag{2.27}$$

Theorem 2.2.4 (Well-posedness: models 1–3). *For each of the three models the following holds:*
(a) The SSDE has a unique strong solution in $C([0,\infty),E)$. Its law is the unique solution of the $(G,\mathcal{F},\delta_u)$-martingale problem for all $u \in E$.
(b) The process starting in $u \in E$ is Feller and strong Markov. Consequently, the SSDE defines a unique Borel Markov process starting from any initial law on E.

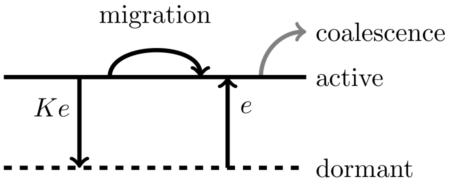

Figure 2.3: Transition scheme for an ancestral lineage in the dual, which moves according to the transition kernel $b(\cdot,\cdot)$ *in* (2.31)*. Two active ancestral lineages that are at the same colony coalesce at rate* d*.*

§2.2.4 Duality

For $g = dg_{\mathrm{FW}}$ the three models have a tractable dual, which will be seen to play a crucial role in the analysis of their long-time behaviour. For $g \neq dg_{\mathrm{FW}}$ the three models do not have a tractable dual. However, we compare them with models that do and determine their long-time behaviour. In [12, Sections 2.2 and 3] it was shown that the non-spatial Fisher-Wright diffusion with seed-bank is dual to the so-called *block-counting process* of a seed-bank coalescent. The latter describes the evolution of the number of partition elements in a partition of $n \in \mathbb{N}$ individuals, sampled from the current population, into subgroups of individuals with the same ancestor (i.e., individuals that are identical by descent). The enriched dual generates the ancestral lineages of the individuals evolving according to a Fisher-Wright diffusion with seed-bank, i.e., generates their full genealogy. The corresponding block-counting process counts the number of ancestral lineages left when traveling backwards in time. In this section we will extend the duality results in [12] to the spatial setting.

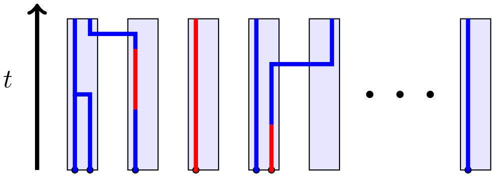

Figure 2.4: Picture of the evolution of lineages in the spatial coalescent. The purple blocks depict the colonies, the blue lines the active lineages, and the red lines the dormant lineages. Blue lineages can migrate and become dormant, (i.e., become red lineages). Two blue lineages can coalesce when they are at the same colony. Red dormant lineages first have to become active (blue) before they can coalesce with other blue and active lineages or migrate. Note that the dual runs backwards in time*. The collection of all lineages determines the genealogy of the system.*

Model 1. Recall that for model 1, $\mathbb{S} = \mathbb{G} \times \{A, D\}$ is the effective geographic space. For $n \in \mathbb{N}$ the state space of the n-spatial seed-bank coalescent is the set of partitions of $\{1, \ldots, n\}$, where the partition elements are marked with a position vector giving their location. A state is written as π, where

$$\begin{aligned}&\pi=((\pi_1,\eta_1),\dots,(\pi_{\bar n},\eta_{\bar n})),\quad \bar n=|\pi|,\\ &\pi_\ell\subset\{1,\dots,n\},\ \{\pi_1,\cdots\pi_{\bar n}\}\ \text{ is a partition of } \{1,\dots,n\},\\ &\eta_\ell\in\mathbb{S},\quad \ell\in\{1,\dots,\bar n\},\quad 1\le\bar n\le n.\end{aligned}\tag{2.28}$$

A marked partition element (π_ℓ,η_ℓ) is called active if $\eta_\ell=(j,A)$ and called dormant if $\eta_\ell=(j,D)$ for some $j\in\mathbb{G}$. The n-spatial seed-bank coalescent is denoted by

$$(\mathcal{C}^{(n)}(t))_{t\geqslant 0},\tag{2.29}$$

and starts from

$$\mathcal{C}^{(n)}(0)=\pi(0),\qquad \pi(0)=\{(\{1\},\eta_{\ell_1}),\dots,(\{n\},\eta_{\ell_n})\},\qquad \eta_{\ell_1},\dots,\eta_{\ell_n}\in\mathbb{S}.\tag{2.30}$$

The n-spatial seed-bank coalescent is a Markov process that evolves according to the following two rules.

(a) Each partition element moves independently of all other partition elements according the kernel

$$b^{(1)}((i,R_i),(j,R_j))=\begin{cases}a(i,j), & \text{if } R_i=R_j=A,\\ Ke, & \text{if } i=j,\ R_i=A,\ R_j=D,\\ e, & \text{if } i=j,\ R_i=D,\ R_j=A,\\ 0, & \text{otherwise},\end{cases}\tag{2.31}$$

where $a(\cdot,\cdot)$ is the migration kernel defined in (2.1), K is the relative size of the dormant population defined in (2.6), and e is the rate of exchange between the active and the dormant population shown in (2.4)–(2.5). Therefore an active partition element migrates according to the transition kernel $a(\cdot,\cdot)$ and becomes dormant at rate Ke, while a dormant partition element can only become active and does so at rate e. In (2.31), the notation $b^{(1)}$ marks that the kernel refers to model 1. Later we will use the notation $b^{(2)}$ for model 2 and $b^{(3)}$ for model 3.

(b) Independently of all other partition elements, two partition elements that are at the same colony and are both active coalesce with rate d, i.e., the two partition elements merge into one partition element.

The spatial seed-bank coalescent $(\mathcal{C}(t))_{t\geq 0}$ is defined as the projective limit of the n-spatial seed-bank coalescents $(\mathcal{C}^{(n)}(t))_{t\geq 0}$ as $n\to\infty$. This object is well-defined by Kolmogorov's extension theorem (see [12, Section 3]).

For $n\in\mathbb{N}$ we define the block-counting process $(L(t))_{t\geq 0}$ corresponding to the n-spatial seed-bank coalescent as the process that counts at each site $(i,R_i)\in\mathbb{G}\times\{A,D\}$ the number of partition elements of $\mathcal{C}^{(n)}(t)$, i.e.,

$$\begin{aligned}&L(t)=\big(L_{(i,A)}(t),L_{(i,D)}(t)\big)_{i\in\mathbb{G}},\\ &L_{(i,A)}(t)=L_{(i,A)}(\mathcal{C}^{(n)}(t))=\sum_{\ell=1}^{\bar n}1_{\{\eta_\ell(t)=(i,A)\}},\\ &L_{(i,D)}(t)=L_{(i,D)}(\mathcal{C}^{(n)}(t))=\sum_{\ell=1}^{\bar n}1_{\{\eta_\ell(t)=(i,D)\}}.\end{aligned}\tag{2.32}$$

Therefore $(L(t))_{t\geq 0}$ has state space $E' = (\mathbb{N}_0 \times \mathbb{N}_0)^{\mathbb{G}}$. We denote the elements of E' by sequences $(m_i,n_i)_{i\in\mathbb{G}}$, and define $\delta_{(j,R_j)} \in E'$ to be the element of E' that is 0 at all sites $(i,R_i) \in \mathbb{G}\times\{A,D\}\backslash(j,R_j)$, but 1 at the site (j,R_j). From the evolution of $\mathcal{C}^{(n)}(t)$ described below (2.29) we see that the block-counting process has the following transition kernel:

$$(m_i,n_i)_{i\in\mathbb{G}} \to \begin{cases} (m_i,n_i)_{i\in\mathbb{G}} - \delta_{(j,A)} + \delta_{(k,A)}, & \text{at rate } m_j a(j,k) \text{ for } j,k \in \mathbb{G},\\ (m_i,n_i)_{i\in\mathbb{G}} - \delta_{(j,A)}, & \text{at rate } d\binom{m_j}{2} \text{ for } j \in \mathbb{G},\\ (m_i,n_i)_{i\in\mathbb{G}} - \delta_{(j,A)} + \delta_{(j,D)}, & \text{at rate } m_j Ke \text{ for } j \in \mathbb{G},\\ (m_i,n_i)_{i\in\mathbb{G}} + \delta_{(j,A)} - \delta_{(j,D)}, & \text{at rate } n_j e \text{ for } j \in \mathbb{G}. \end{cases} \tag{2.33}$$

The process $(Z(t))_{t\geq 0}$ defined in (2.4)–(2.5) is dual to the block-counting process $(L(t))_{t\geq 0}$. The duality function $H\colon\ E\times E' \to \mathbb{R}$ is defined by

$$H\Big((x_i,y_i)_{i\in\mathbb{G}},(m_i,n_i)_{i\in\mathbb{G}}\Big) = \prod_{i\in\mathbb{G}} x_i^{m_i} y_i^{n_i}. \tag{2.34}$$

The *duality relation* reads as follows.

Theorem 2.2.5 (Duality relation: model 1). *Let H be defined as in* (2.34). *Then for all* $(x_i,y_i)_{i\in\mathbb{G}} \in E$ *and* $(m_i,n_i)_{i\in\mathbb{G}} \in E'$,

$$\begin{aligned} &\mathbb{E}_{(x_i,y_i)_{i\in\mathbb{G}}}\Big[H\Big((x_i(t),y_i(t))_{i\in\mathbb{G}},(m_i,n_i)_{i\in\mathbb{G}}\Big)\Big]\\ &\qquad = \mathbb{E}_{(m_i,n_i)_{i\in\mathbb{G}}}\Big[H\Big((x_i,y_i)_{i\in\mathbb{G}},(L_{(i,A)}(t),L_{(i,D)}(t))_{i\in\mathbb{G}}\Big)\Big] \end{aligned} \tag{2.35}$$

with $\mathbb{E}$ *the generic symbol for expectation (on the left over the original process, on the right over the dual process).*

Since the duality function H gives all the mixed moments of $(Z(t))_{t\geq 0}$, the duality relation in Theorem 2.2.5 is called a *moment dual.*

Remark 2.2.6 (Effective geographic space). Interpreting $(Z(t))_{t\geq 0}$ as a process on the effective geographic space $\mathbb{S}$, recall Remark 2.2.2, we can rewrite the duality relation. Let the block-counting process $(L(t))_{t\geq 0} = (L(\mathcal{C}(t))_{t\geq 0}$ count at each site $u \in \mathbb{S}$ the number of partition elements of $\mathcal{C}(t)$, i.e.,

$$\begin{aligned} L(t) &= (L_u(t))_{u\in\mathbb{S}},\\ L_u(t) &= L_u(\mathcal{C}(t)) = \sum_{\ell=1}^{\bar{n}} 1_{\{\eta_\ell(t)=u\}}, \end{aligned} \tag{2.36}$$

and rewrite the duality function H in (2.34) as

$$H((z_u,l_u)_{u\in\mathbb{S}}) = \prod_{u\in\mathbb{S}} z_u^{l_u}. \tag{2.37}$$

Then, for $z \in \mathbb{E}$ and $l \in \mathbb{E}'$, the *duality relation* reads

$$\mathbb{E}\big[H(z_u(t),l_u)\big] = \mathbb{E}\big[H(z_u,L_u(t))\big]. \tag{2.38}$$

Interpreting the duality relation in terms of the effective geographic space $\mathbb{S}$, we see that each ancestral lineage in the dual is a Markov chain that moves according to the transition kernel $b^{(1)}(\cdot,\cdot)$. Interpreting the duality relation in terms of the geographic space $\mathbb{G}$, we see that an ancestral lineage is a random walk moving on $\mathbb{G}$, with internal states A and D. Both interpretations turn out to be useful in analysing the long-time behaviour of the system. ■

Remark 2.2.7 (Wake-up times). Define (see Fig. 2.3)

$$\begin{aligned}\sigma &= \text{typical time spent by an ancestral lineage in state } A\\ &\quad\ \text{before switching to state } D,\\ \tau &= \text{typical time spent by an ancestral lineage in state } D\\ &\quad\ \text{before switching to state } A.\end{aligned} \tag{2.39}$$

(Here, the word typical refers to what happens to an ancestral lineage each time it switches state at some geographic location. For a more precise definition we refer to Section 3.2.2 and Fig. 3.1.) It follows from (2.31) that

$$\begin{aligned}\mathbb{P}(\sigma > t) &= \mathrm{e}^{-Ket},\\ \mathbb{P}(\tau > t) &= \mathrm{e}^{-et}.\end{aligned} \tag{2.40}$$

An ancestral lineage in the dual of the spatial seed-bank process behaves as an ancestral lineage in the dual of a spatial Fisher-Wright diffusion without seed-bank (see e.g. [36]), but becomes dormant every once in a while. On the long run we expect an ancestral lineage to be active only a fraction $\frac{1}{1+K}$ of the time. We will see in Section 3.2 that the effect of the seed-bank on the long-time behaviour of the ancestral lineages in the dual is a slow down by a factor $\frac{1}{1+K}$ compared to the long-time behaviour of the ancestral lineages in the dual of interacting Fisher-Wright diffusions without seed-bank. ■

Model 2. The dual for model 2 arises naturally from the dual for model 1 by adding internal states to the seed-bank and adapting the rates of becoming active and dormant accordingly. Recall that for model 2 the effective geographic space is $\mathbb{S} = \mathbb{G} \times \{A, (D_m)_{m\in\mathbb{N}_0}\}$. Migration and coalescence are as before, but at every colony switches between an active copy A and a dormant copy D_m now occur at rates e_m, respectively, $K_m\, e_m$. The spatial coalescent $(\mathcal{C}(t))_{t\geq 0}$ in (2.29) starts from an initial configuration like (2.30) and evolves according to the same two rules, but the transition kernel $b(\cdot,\cdot)$ must be replaced by

$$b^{(2)}((i,R_i),(j,R_j)) = \begin{cases} a(i,j), & R_i = R_j = A,\\ K_m e_m, & i = j,\ R_i = A,\ R_j = D_m, m \in \mathbb{N}_0,\\ e_m, & i = j,\ R_i = D_m,\ m \in \mathbb{N}_0,\ R_j = A,\\ 0, & \text{otherwise.}\end{cases} \tag{2.41}$$

The corresponding block-counting process becomes

$$\begin{aligned} L(t) &= \Big(L_{(i,A)}(t), \big(L_{(i,D_m)}(t)\big)_{m\in\mathbb{N}_0}\Big)_{i\in\mathbb{G}}, \\ L_{(i,A)}(t) &= L_{(i,A)}(\mathcal{C}(t)) = \sum_{\ell=1}^{\bar{n}} 1_{\{\eta_\ell(t)=(i,A)\}}, \\ L_{(i,D_m)}(t) &= L_{(i,D_m)}(\mathcal{C}(t)) = \sum_{\ell=1}^{\bar{n}} 1_{\{\eta_\ell(t)=(i,D_m)\}},\ m\in\mathbb{N}_0. \end{aligned} \tag{2.42}$$

The state space is now given by $E' = \Big(\mathbb{N}_0\times\mathbb{N}_0^{\mathbb{N}_0}\Big)^{\mathbb{G}}$, and the transition kernel becomes

$$\begin{aligned} &(m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}} \\ &\quad\to \begin{cases} (m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}} - \delta_{(j,A)} + \delta_{(k,A)}, & \text{at rate } m_j a(j,k) \text{ for } j,k\in\mathbb{G}, \\ (m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}} - \delta_{(j,A)}, & \text{at rate } d\binom{m_j}{2} \text{ for } j\in\mathbb{G}, \\ (m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}} - \delta_{(j,A)} + \delta_{(j,D_m)}, & \text{at rate } m_j K_m e_m \text{ for } j\in\mathbb{G}, \\ (m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}} + \delta_{(j,A)} - \delta_{(j,D_m)}, & \text{at rate } n_{j,m} e_m \text{ for } j\in\mathbb{G}. \end{cases} \end{aligned} \tag{2.43}$$

The duality function $H\colon\ E\times E'\to\mathbb{R}$ is defined by

$$H\Big((x_i,y_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0},(m_i,n_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0}\Big) = \prod_{i\in\mathbb{G}}\prod_{m\in\mathbb{N}_0} x_i^{m_i} y_{i,m}^{n_{i,m}}. \tag{2.44}$$

Theorem 2.2.8 (Duality relation: model 2). *For* $(x_i,y_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0}\in E$ *and* $(m_i,n_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0}\in E'$,

$$\begin{aligned} &\mathbb{E}_{(x_i,y_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0}}\Big[H\Big((x_i(t),y_{i,m}(t))_{i\in\mathbb{G},m\in\mathbb{N}_0},(m_i,n_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0}\Big)\Big] \\ &\quad= \mathbb{E}_{(m_i,n_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0}}\Big[H\Big((x_i,y_{i,m})_{i\in\mathbb{G},m\in\mathbb{N}_0},(L_{(i,A)}(t),L_{(i,D_m)}(t))_{i\in\mathbb{G},m\in\mathbb{N}_0}\Big)\Big]. \end{aligned} \tag{2.45}$$

By rewriting the block-counting process as in Remark 2.2.6, the duality function can be rewritten as

$$H((z_u,l_u)_{u\in\mathbb{S}}) = \prod_{u\in\mathbb{S}} z_u^{l_u} \tag{2.46}$$

and the *duality relation* reads

$$\mathbb{E}\Big[H\Big((z_u(t))_{u\in\mathbb{S}},(l_u)_{u\in\mathbb{S}}\Big)\Big] = \mathbb{E}\Big[H\Big((z_u)_{u\in\mathbb{S}},(L_u(t))_{u\in\mathbb{S}}\Big)\Big]. \tag{2.47}$$

Remark 2.2.9 (Fat-tailed wake-up times.). Recall the definition of χ in (2.20) and the definition of ρ in (2.21). Define

$$\begin{aligned} \sigma = {}& \text{typical time spent by an ancestral lineage in the active state } A \\ &\quad \text{before switching to a dormant state } \cup_{m\in\mathbb{N}_0} D_m, \\ \tau = {}& \text{typical time spent by an ancestral lineage in the dormant state } \cup_{m\in\mathbb{N}_0} D_m \\ &\quad \text{before switching to the active state } A. \end{aligned} \tag{2.48}$$

Note that τ does not look at the colour of the dormant state. It follows from (2.41) that

$$\begin{aligned}\mathbb{P}(\sigma > t) &= \mathrm{e}^{-\chi t},\\ \mathbb{P}(\tau > t) &= \sum_{m\in\mathbb{N}_0} \frac{K_m e_m}{\chi} \mathrm{e}^{-e_m t},\end{aligned} \tag{2.49}$$

independently of the colony $i \in \mathbb{G}$. Hence

$$\mathbb{E}[\tau] = \frac{\rho}{\chi}. \tag{2.50}$$

If $\rho < \infty$, then we invoke the seed-bank colours and use the balance equations for recurrent Markov chains to see that each ancestral lineage in the dual in the long run spends a fraction $\frac{\rho}{1+\rho}$ of the time in the dormant state. Like in model 1, an ancestral lineage in the dual behaves like an ancestral lineage in the dual of interacting Fisher-Wright diffusions, but is slowed down by a factor $\frac{\rho}{1+\rho}$. However, if $\rho = \infty$, then (2.41) together with (2.50) imply that each ancestral lineage in the dual behaves like a null-recurrent Markov chain on $\{A, (D_m)_{m\in\mathbb{N}_0}\}$, and consequently the probability to be active tends to 0 as $t \to \infty$. Therefore we may expect that the long-time behaviour of the system is affected by the seed-bank. In particular, choosing

$$\begin{aligned}&K_m \sim A\, m^{-\alpha}, \quad e_m \sim B\, m^{-\beta}, \quad m \to \infty,\\ &A, B \in (0,\infty), \quad \alpha, \beta \in \mathbb{R}\colon\ \alpha \leq 1 < \alpha + \beta,\end{aligned} \tag{2.51}$$

we see that (2.49) implies

$$\mathbb{P}(\tau > t) \sim C t^{-\gamma}, \qquad t \to \infty, \tag{2.52}$$

with $\gamma = \frac{\alpha+\beta-1}{\beta}$ and $C = \frac{A}{\chi\beta} B^{1-\gamma}\,\Gamma(\gamma)$, where Γ is the Gamma-function. The conditions on α, β guarantee that $\rho = \infty$, $\chi < \infty$ (recall (2.20) and (2.21)). Examples are: $\alpha = 0$, $\beta > 1$ and $\alpha \in (0,1)$, $\beta > 1-\alpha$. Thus, for $\rho = \infty$ we can model individuals with a fat-tailed wake-up time simply by not taking their colours into account. *The internal structure of the seed-bank captured by the colours allows us to model fat-tailed wake-up times without loosing the Markov property for the evolution.* ■

Model 3. The effective geographic space is again $\mathbb{S} = \mathbb{G}\times\{A, (D_m)_{m\in\mathbb{N}_0}\}$. On top of migration and coalescence, each switch from A to D_m and vice versa is accompanied by a displacement according to the displacement kernel $a_m(\cdot,\cdot)$ defined in (2.17). Therefore each lineage in the dual evolves according to

$$b^{(3)}((i,R_i),(j,R_j)) = \begin{cases} a(i,j), & R_i = R_j = A,\\ K_m e_m a_m(j,i), & R_i = A,\ R_j = D_m, m \in \mathbb{N}_0,\\ e_m a_m(i,j), & R_i = D_m,\ m \in \mathbb{N}_0\, R_j = A.\end{cases} \tag{2.53}$$

Again, when two ancestral lineages are active at the same site they coalesce at rate 1 and the corresponding block-counting process evolves according to the transition kernel

$$
\begin{aligned}
&(m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}}\\
&\quad\to\begin{cases}
(m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}}-\delta_{(j,A)}+\delta_{(k,A)}, & \text{at rate } m_j a(j,k) \text{ for } j,k\in\mathbb{G},\\
(m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}}-\delta_{(j,A)}, & \text{at rate } d\binom{m_j}{2} \text{ for } j\in\mathbb{G},\\
(m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}}-\delta_{(j,A)}+\delta_{(k,D_m)}, & \text{at rate } m_j K_m e_m a_m(k,j) \text{ for } j\in\mathbb{G},\\
(m_i,(n_{i,m})_{m\in\mathbb{N}_0})_{i\in\mathbb{G}}+\delta_{(k,A)}-\delta_{(j,D_m)}, & \text{at rate } n_{j,m} e_m a_m(j,k) \text{ for } j\in\mathbb{G}.
\end{cases}
\end{aligned}
\tag{2.54}
$$

Theorem 2.2.10 (Duality relation: model 3). *The same duality relation holds as in* (2.45)*, where now the dual dynamics includes not only the exchange between active and dormant but also the accompanying displacement in space.*

§2.2.5 Dichotomy criterion

For $g = dg_{\mathrm{FW}}$ the duality relations in Theorems 2.2.5, 2.2.8 and 2.2.10 provide us with the following criterion to characterise the long-term behaviour. If, in the limit as $t \to \infty$, locally only one type survives in the population, then we say that the system exhibits *clustering*. If, in the limit as $t \to \infty$, locally both types survive in the population, then we say that the system exhibits *coexistence*. For model 1 the criterion reads as follows.

Theorem 2.2.11 (Dichotomy criterion: model 1). *Suppose that $\mu(0)$ is invariant and ergodic under translations. Let $d \in (0,\infty)$. Then the system with $g = dg_{\mathrm{FW}}$ clusters if and only if in the dual two partition elements coalesce with probability* 1.

The idea behind Theorem 2.2.11 is as follows. If in the dual two partition elements coalesce with probability 1, then a random sample of n individuals drawn from the current population has a common ancestor some finite time backwards in time. Since individuals inherit their type from their parent individuals, this means that all n individuals have the same type. A formal proof will be given in Section 3.1.3.

For model 2–3 we need an extra assumption on $\mu(0)$ when $\rho = \infty$.

Definition 2.2.12 (Colour regular initial measures). We say that $\mu(0)$ is *colour regular* when

$$
\lim_{N\to\infty} \mathbb{E}_{\mu(0)}[y_{0,N}] \quad \text{exists}, \tag{2.55}
$$

i.e., $\mu(0)$ has asymptotically converging colour means. □

Thus, colour regularity is a condition on the deep seed-banks (where deep means $m \to \infty$). This condition is needed because as time proceeds lineages starting from deeper and deeper seed-banks become active for the first time, and bring new types into the active population. Without control on the initial states of the deep seed-banks, there may be no convergence to equilibrium.

Theorem 2.2.13 (Dichotomy criterion: models 2–3). *The same as in Theorem 2.2.11 is true for $\rho < \infty$, but for $\rho = \infty$ additionally requires that $\mu(0)$ is colour regular.*

Remark 2.2.14 (Clustering criterion general $g \in \mathcal{G}$). In Section 2.3 we will see that the dichotomy criterion in Theorems 2.2.11 and 2.2.13 for $g = dg_{\mathrm{FW}}$ does not depend on d, the rate of resampling. We will use *duality comparison arguments* to carry over the dichotomy criterion in Theorems 2.2.11 and 2.2.13 to $g \in \mathcal{G}$. We will see later that for all three models the system with g exhibits clustering if and only if the system with g_{FW} exhibits clustering. ■

Remark 2.2.15 (Liggett conditions). We will see in Section 3.3.3 that, for model 2 with $\rho = \infty$, if an initial measure μ is invariant and ergodic under translations and is colour regular, then the Markov chain evolving according to $b^{(2)}(\cdot,\cdot)$ satisfies the following two conditions:

(1)

$$\lim_{t\to\infty} \sum_{(k,R_k)\in\mathbb{G}\times\{A,(D_m)_{m\in\mathbb{N}_0}\}} b_t^{(2)}\big((i,R_i),(k,R_k)\big)\,\mathbb{E}_\mu[z_{(k,R_k)}] = \theta, \tag{2.56}$$

(2)

$$\begin{aligned}\lim_{t\to\infty} \sum_{(k,R_k),(l,R_l)\in\mathbb{G}\times\{A,(D_m)_{m\in\mathbb{N}_0}\}} & b_t^{(2)}\big((i,R_i),(k,R_k)\big)\, b_t^{(2)}\big((j,R_j),(l,R_l)\big)\\ & \times \mathbb{E}_\mu[z_{(k,R_k)} z_{(l,R_l)}] = \theta^2.\end{aligned} \tag{2.57}$$

These are precisely the conditions in [56, Chapter V.1] necessary to determine the dichotomy in the long-time behaviour of the voter model. We show that (1) and (2) imply convergence to a unique equilibrium that is invariant and ergodic under translations. It is difficult to identify exactly which initial measures μ satisfy (1) and (2). This is the reason why we work with sufficient conditions and need the notion of colour regularity.

For model 2 with $\rho < \infty$, conditions (1) and (2) are satisfied when $\mu(0)$ is invariant and ergodic under translations, and colour regularity is not needed. The same holds for model 1, once the state space is replaced by $\mathbb{G} \times \{A, D\}$ and $b^{(2)}(\cdot,\cdot)$ is replaced by $b^{(1)}(\cdot,\cdot)$. Also for model 3 conditions (1) and (2) hold after replacing $b^{(2)}(\cdot,\cdot)$ by $b^{(3)}(\cdot,\cdot)$. If $\rho = \infty$ in model 3 we need to assume colour regularity, if $\rho < \infty$, this is not needed. ■

§2.3 Long-time behaviour

In this section we study the long-time behaviour of models 1–3. In Sections 2.3.1–2.3.3 we prove convergence to a unique equilibrium measure, establish the dichotomy between clustering and coexistence, and identify which of the two occurs in terms of the migration kernel and the rates governing the exchange with the seed-bank (Theorems 2.3.1–2.3.6).

Throughout the sequel, g is a general diffusion function from the class $\mathcal{G}$ defined in (2.23). Special cases are the multiples of the standard Fisher-Wright diffusion function: $g = dg_{\mathrm{FW}}$, $d \in (0,\infty)$, with $g_{\mathrm{FW}}(x) = x(1-x)$, $x \in [0,1]$. We use the following notation (with $\mathcal{P}(E)$ denotes the set of probability measures on E):

$$\begin{aligned} \mathcal{T} &= \big\{\mu \in \mathcal{P}(E)\colon\ \mu \text{ is invariant under translations in } \mathbb{G}\big\}, \\ \mathcal{T}^{\mathrm{erg}} &= \big\{\mu \in \mathcal{T}\colon\ \mu \text{ is ergodic under translations in } \mathbb{G}\big\}, \\ \mathcal{I} &= \big\{\mu \in \mathcal{T}\colon\ \mu \text{ is invariant under the evolution}\big\}. \end{aligned} \tag{2.58}$$

§2.3.1 Long-time behaviour of Model 1

Let $a(\cdot,\cdot)$ be as in (2.1). Define the *symmetrized* migration kernel

$$\hat{a}(i,j) = \tfrac{1}{2}[a(i,j) + a(j,i)], \qquad i,j \in \mathbb{G}, \tag{2.59}$$

which describes the difference of two independent copies of the migration each driven by $a(\cdot,\cdot)$. Let $\hat{a}_t(0,0)$ denote the time-t transition kernel of the random walk with migration kernel $\hat{a}(\cdot,\cdot)$, and suppose that

$$t \mapsto \hat{a}_t(0,0) \text{ is regularly varying at infinity.} \tag{2.60}$$

(Examples can be found in [47, Chapter 3].) Define

$$I_{\hat{a}} = \int_1^\infty \mathrm{d}t\, \hat{a}_t(0,0). \tag{2.61}$$

Note that $I_{\hat{a}} = \infty$ if and only if $\hat{a}(\cdot,\cdot)$ is recurrent (see e.g. [69, Chapter 1]). Define

$$\theta = \mathbb{E}_{\mu(0)}\left[\frac{x_0 + Ky_0}{1+K}\right]. \tag{2.62}$$

If $\mu(0)$ is invariant and ergodic under translations, then θ is the initial density of ♡ in the population.

From the SSDE in (2.4)–(2.5) we see that

$$\left(\frac{x_0(t) + Ky_0(t)}{1+K}\right)_{t\geq 0} \tag{2.63}$$

is a martingale. In particular,

$$\theta = \mathbb{E}_{\mu(t)}\left[\frac{x_0 + Ky_0}{1+K}\right] \qquad \forall\, t \geq 0. \tag{2.64}$$

For $\theta \in [0,1]$, we define

$$\mathcal{T}_\theta^{\mathrm{erg}} = \left\{\mu \in \mathcal{T}^{\mathrm{erg}}\colon\ \mathbb{E}_{\mu(0)}\left[\frac{x_0 + Ky_0}{1+K}\right] = \theta\right\}. \tag{2.65}$$

Write $\mu(t)$ to denote the law of $(Z(t))_{t\geq 0}$, defined in (2.2). Recall that associated means that increasing functions of the configuration are positively correlated, i.e., if $f\colon E \to \mathbb{R}$ and $g\colon E \to \mathbb{R}$ depend on only finitely many coordinates and are coordinate-wise increasing, then

$$\mathbb{E}_{\nu_\theta}[f(x)g(x)] \geq \mathbb{E}_{\nu_\theta}[f(x)]\, \mathbb{E}_{\nu_\theta}[g(x)]. \tag{2.66}$$

Theorem 2.3.1 (Long-time behaviour: model 1). *Suppose that* $\mu(0) \in \mathcal{T}_\theta^{\mathrm{erg}}$.

(a) *(Coexistence regime) If* $\hat{a}(\cdot,\cdot)$ *is transient, i.e.,* $I_{\hat{a}} < \infty$, *then*

$$\lim_{t\to\infty} \mu(t) = \nu_\theta, \tag{2.67}$$

where

$$\begin{aligned}
&\nu_\theta \text{ is an equilibrium measure for the process on } E, && (2.68)\\
&\nu_\theta \text{ is invariant, ergodic and mixing under translations,} && (2.69)\\
&\nu_\theta \text{ is associated,} && (2.70)\\
&\mathbb{E}_{\nu_\theta}[x_0] = \mathbb{E}_{\nu_\theta}[y_0] = \theta, && (2.71)
\end{aligned}$$

with $\mathbb{E}_{\nu_\theta}$ *denoting expectation over* ν_θ.

(b) *(Clustering regime) If* $\hat{a}(\cdot,\cdot)$ *is recurrent, i.e.,* $I_{\hat{a}} = \infty$, *then*

$$\lim_{t\to\infty} \mu(t) = \theta\,[\delta_{(1,1)}]^{\otimes\mathbb{G}} + (1-\theta)\,[\delta_{(0,0)}]^{\otimes\mathbb{G}}. \tag{2.72}$$

The results in (2.67)–(2.72) say that the system converges to an equilibrium whose density of type ♡ equals θ in (2.62), a parameter that is controlled by the initial state $\mu(0)$ and the asymmetry parameter K. The equilibrium can be either locally mono-type or locally multi-type, depending on whether the symmetrised migration kernel is recurrent or transient. If the equilibrium is mono-type, then the system grows large mono-type clusters (= clustering). If the equilibrium is multi-type, then the system allows ♡ and ♢ to mix (= coexistence). In the case of coexistence, the equilibrium measure ν_θ also depends on the migration kernel $a(\cdot,\cdot)$, the values of the parameters e, K, and the diffusion function $g \in \mathcal{G}$ (recall (2.23)). The dichotomy itself, however, is *controlled by* $I_{\hat{a}}$ *only*. In particular, $g \in \mathcal{G}$ plays no role, a fact that will be shown with the help of a *duality comparison* argument. In view of Theorem 2.2.11, if $g = dg_{\mathrm{FW}}$, then $I_{\hat{a}} = \infty$ implies that with probability 1 two ancestral lineages in the dual coalesce. Therefore $I_{\hat{a}} = \infty$ is said to be *the total hazard of coalescence*. Remarkably, this dichotomy is the same as the dichotomy observed for systems without seed-bank (see [14]): clustering prevails for recurrent migration; coexistence prevails for transient migration; for $\mathbb{G} = \mathbb{Z}^d$ the critical dimension is $d = 2$. From the proof in Section 3.2.2 it will become clear that in the dual the ancestral lineages in the long run behave like the ancestral lineages without seed-bank, but are slowed down by a factor $\frac{1}{1+K}$. Consequently, the dormant periods of the ancestral lineages do not affect the dichotomy of the system. In particular, it does not affect the critical dimension separating clustering from coexistence.

Remark 2.3.2 (Ergodic decomposition). Because $\mathcal{T}$ is a Choquet simplex, Theorem 2.3.1 carries over from $\mu(0) \in \mathcal{T}^{\mathrm{erg}}$ to $\mu(0) \in \mathcal{T}$, after decomposition into ergodic components. ■

§2.3.2 Long-time behaviour of Model 2

For model 2 we need the extra condition that $a(\cdot,\cdot)$ is *symmetric*, i.e.,

$$a(i,j) = a(j,i) \qquad \forall\, i,j \in \mathbb{G}. \tag{2.73}$$

Note that $\hat{a}_t(0,0) = a_t(0,0)$ because of (2.73). Below we comment on what happens when we drop this assumption. Recall (2.20)–(2.21). It turns out that the long-time behaviour of model 2 is different for $\rho < \infty$ and $\rho = \infty$.

Case $\rho < \infty$. For a finite seed-bank, we define the initial density as

$$\theta = \mathbb{E}_{\mu(0)}\left[\frac{x_0 + \sum_{m\in\mathbb{N}_0} K_m\, y_{0,m}}{1+\rho}\right], \tag{2.74}$$

which is the counter part of (2.62) in model 1. Like in model 1, it follows from the SSDE in (2.12)–(2.13) that

$$\left(\frac{x_0(t) + \sum_{m\in\mathbb{N}_0} K_m\, y_{0,m}(t)}{1+\rho}\right)_{t\geq 0} \tag{2.75}$$

is a martingale. Hence also here the density is a preserved quantity under the evolution of the system. The dichotomy is controlled by the same integral $I_{\hat{a}}$ as defined in (2.61) for model 1.

Case $\rho = \infty$. For an infinite seed-bank, we assume that (recall Remark 2.2.9)

$$\begin{aligned} &K_m \sim A\, m^{-\alpha}, \quad e_m \sim B\, m^{-\beta}, \quad m \to \infty,\\ &A, B \in (0,\infty), \quad \alpha,\beta \in \mathbb{R}\colon\ \alpha \leq 1 < \alpha+\beta, \end{aligned} \tag{2.76}$$

for which

$$P(\tau > t) \sim C\, t^{-\gamma}, \quad t \to \infty, \tag{2.77}$$

with $\gamma = \frac{\alpha+\beta-1}{\beta} \in (0,1)$ and $C = \frac{A}{\beta}\, B^{1-\gamma}\, \gamma\Gamma(\gamma) \in (0,\infty)$, where Γ is the Gamma-function. In addition, we assume that the initial measure $\mu(0)$ is colour regular (recall Definition 2.2.12), and define

$$\theta = \lim_{m\to\infty} \mathbb{E}[y_{0,m}]. \tag{2.78}$$

This ensures the existence of the initial density

$$\theta = \lim_{M\to\infty} \mathbb{E}_{\mu(0)}\left[\frac{x_0 + \sum_{m=0}^{M} K_m\, y_{0,m}}{1 + \sum_{m=0}^{M} K_m}\right]. \tag{2.79}$$

It turns out that the dichotomy is controlled by the integral

$$I_{\hat{a},\gamma} = \int_1^\infty \mathrm{d}t\; t^{-(1-\gamma)/\gamma}\, \hat{a}_t(0,0) \tag{2.80}$$

instead of the integral $I_{\hat{a}}$ for $\rho < \infty$.

For $\theta \in (0,1)$, define (both for $\rho < \infty$ and $\rho = \infty$)

$$\mathcal{T}^{\mathrm{erg}}_\theta = \left\{\mu \in \mathcal{T}^{\mathrm{erg}} \colon \lim_{M\to\infty} \mathbb{E}_{\mu(0)}\left[\frac{x_0 + \sum_{m=0}^M K_m y_{0,m}}{1+\sum_{m=0}^M K_m}\right] = \theta\right\}. \tag{2.81}$$

Theorem 2.3.3 (Long-time behaviour: model 2). (I) *Let $\rho < \infty$. Assume* (2.60) *and* (2.73). *Suppose that $\mu(0) \in \mathcal{T}^{\mathrm{erg}}_\theta$.*

(a) *(Coexistence regime) If $I_{\hat{a}} < \infty$, then*

$$\lim_{t\to\infty} \mu(t) = \nu_\theta, \tag{2.82}$$

where

$$\nu_\theta \text{ is an equilibrium measure for the process on } E, \tag{2.83}$$

$$\nu_\theta \text{ is invariant, ergodic and mixing under translations}, \tag{2.84}$$

$$\nu_\theta \text{ is associated}, \tag{2.85}$$

$$\mathbb{E}_{\nu_\theta}[x_0] = \mathbb{E}_{\nu_\theta}[y_{0,m}] = \theta \;\forall\, m \in \mathbb{N}_0, \tag{2.86}$$

with $\mathbb{E}_{\nu_\theta}$ denoting expectation over ν_θ. Moreover,

$$\begin{aligned} \liminf_{m\to\infty} e_m > 0 &\colon \liminf_{m\to\infty} \mathrm{Var}_{\nu_\theta}(y_{0,m}) > 0,\\ \limsup_{m\to\infty} e_m = 0 &\colon \limsup_{m\to\infty} \mathrm{Var}_{\nu_\theta}(y_{0,m}) = 0. \end{aligned} \tag{2.87}$$

(b) *(Clustering regime) If $I_{\hat{a}} = \infty$, then*

$$\lim_{t\to\infty} \mu(t) = \theta\,[\delta_{(1,1^{\mathbb{N}_0})}]^{\otimes\mathbb{G}} + (1-\theta)\,[\delta_{(0,0^{\mathbb{N}_0})}]^{\otimes\mathbb{G}}. \tag{2.88}$$

(II) *Let $\rho = \infty$. Assume* (2.60), (2.73) *and* (2.76). *Suppose that $\mu(0) \in \mathcal{T}^{\mathrm{erg}}$ and, in addition, is colour regular with initial density θ given by* (2.79). *Then the same results as in* (I) *hold after $I_{\hat{a}}$ in* (2.61) *is replaced by $I_{\hat{a},\gamma}$ in* (2.80). *Moreover,*

$$\lim_{M\to\infty} \mathbb{E}_{\nu_\theta}\left[\frac{x_0 + \sum_{m=0}^M K_m\, y_{0,m}}{1+\sum_{m=0}^M K_m}\right] = \theta, \tag{2.89}$$

and ν_θ is colour regular.

The result in part (I) shows that for $\rho < \infty$ the long-time behaviour is similar to that of model 1. Like in model 1, the results in (2.82)–(2.88) say that the system converges to an equilibrium whose density of type ♡ equals θ in (2.62), the density of ♡ under the initial measure $\mu(0)$. Again, the equilibrium can be either mono-type or multi-type, depending on whether the symmetrised migration kernel is recurrent or transient. Like in model 1, in both cases the equilibrium measure depends on θ. In the case of coexistence, the equilibrium measure ν_θ also depends on the migration kernel $a(\cdot,\cdot)$, the sequences of parameters $(e_m)_{m\in\mathbb{N}_0}$ and $(K_m)_{m\in\mathbb{N}_0}$, and the diffusion function $g \in \mathcal{G}$ (recall (2.23)). Again, the dichotomy itself is *controlled by* $I_{\hat{a}}$ *only*, and the resampling rate given by $g \in \mathcal{G}$ plays no role. Therefore if $g = dg_{FW}$, in view of Theorem 2.2.11, whether or not two ancestral lineages in the dual coalesce with probability 1 is still only determined by the migration kernel $a(\cdot,\cdot)$. The same dichotomy holds as for systems without seed-bank (see [14]). Therefore part (I) of Theorem 2.3.3 indicates that, as long as the dormant periods of the ancestral lineages in the dual have a finite mean ($\frac{\rho}{1+\rho}$; recall Remark 2.2.9), the seed-bank does not affect the dichotomy of the system.

Even so, (2.87) indicates that there is interesting behaviour in the deep seed-banks. Indeed, when the exchange rate e_m between the m-dormant and the active population is bounded away from zero as $m \to \infty$ the deep seed-banks are asymptotically *random*, while when e_m tend to zero as $m \to \infty$ the deep seed-banks are asymptotically *deterministic*. The latter means that the deep seed-banks serve as a reservoir, containing a fixed mixture of types. For $\rho < \infty$ this reservoir is too small to influence the dichotomy of the system, but not for $\rho = \infty$.

For $\rho = \infty$ the system again converges to an equilibrium whose density of type $\heartsuit$ equals θ in (2.79), the density of $\heartsuit$ under the initial measure $\mu(0)$. The equilibrium can be mono-type or multi-type, but *the dichotomy criterion has changed.* Instead of $I_{\hat{a}}$, the dichotomy is now controlled by the integral $I_{\hat{a},\gamma}$ (recall (2.80)), where γ is the parameter determined by relative sizes K_m of the colour m-dormant populations with respect to the active population and the exchanges rates $(e_m)_{m\in\mathbb{N}_0}$ with the seed-bank, recall (2.76)–(2.77). If $g = dg_{FW}$, γ is the parameter of the tail of the wake-up time of an ancestral lineages in the dual (recall (2.2.9)). Therefore if $g = dg_{Fw}$, in view of Theorem 2.2.13, we see that the dormant periods of the ancestral lineages in the dual do affect whether or not two ancestral lineages in the dual coalesce with probability 1. For general $g \in \mathcal{G}$, the integral $I_{\hat{a},\gamma}$ in (2.80) shows a *competition* between migration and exchange. The smaller γ is, the longer the individuals remain dormant in the seed-bank, the smaller $I_{\hat{a},\gamma}$ is, and the more coexistence becomes likely. As a consequence clustering requires more stringent conditions than recurrent migration; for $\mathbb{G} = \mathbb{Z}^d$ the critical dimension is $1 < d < 2$ for $\gamma \in [\frac{1}{2}, 1]$ and $d = 1$ for $\gamma \in (0, \frac{1}{2})$. The *seed-bank enhances genetic diversity.* Note that $\gamma \uparrow 1$ links up with the case $\rho < \infty$, where coexistence occurs if and only if the migration is transient. Also note that for $\gamma \in (0, \frac{1}{2})$ there is always coexistence *irrespective of the migration.*

In the case of clustering the equilibrium measure only depends on θ, while in the case of coexistence, like for $\rho < \infty$, ν_θ depends on the migration kernel $a(\cdot,\cdot)$, the sequences of parameters $(e_m)_{m\in\mathbb{N}_0}$, $(K_m)_{m\in\mathbb{N}_0}$, and the diffusion function $g \in \mathcal{G}$. Since we assumed (2.76), we have $\limsup_{m\to\infty} e_m = 0$, and so we are automatically in the second case of (2.87). Hence the deep seed-banks are asymptotically deterministic, i.e., the m-dormant population converges in law to a deterministic state θ as $m \to \infty$. Roughly speaking, in case $g = dg_{FW}$, in equilibrium the volatility of a colour is inversely proportional to its average wake-up time in the dual. Since $\rho = \infty$, for each $M \in \mathbb{N}_0$ we have $\sum_{m=M}^{\infty} K_m = \infty$, and in the coexistence regime the effect of the seed-bank can be interpreted as a migration towards an infinite reservoir with deterministic density θ.

Like for model 1, also here $\mathcal{T}$ is a Choquet simplex, and Theorem 2.3.3 carries over from $\mathcal{T}^{\mathrm{erg}}$ to $\mathcal{T}$, after decomposition into ergodic components.

Example of effect of infinite seed-bank. For a symmetric migration kernel with finite second moment the following holds:

- For $\mathbb{G} = \mathbb{Z}^2$, $\hat{a}_t(0,0) \asymp t^{-1}$, $t \to \infty$, and so coexistence occurs for all $\gamma \in (0,1)$.
- For $\mathbb{G} = \mathbb{Z}$, $\hat{a}_t(0,0) \asymp t^{-1/2}$, $t \to \infty$, and so coexistence occurs if and only if $\gamma \in (0, \frac{2}{3})$.

In both cases the migration is recurrent, so that clustering prevails in model 1.

Corollary 2.3.4 (Three regimes). *Under the conditions of Theorem 2.3.3, the system in* (2.12)–(2.13) *has three different parameter regimes:*

(1) $\gamma \in (1,\infty)$*: migration determines the dichotomy.*

(2) $\gamma \in [\frac{1}{2}, 1]$*: interplay between migration and seed-bank determines the dichotomy.*

(3) $\gamma \in (0, \frac{1}{2})$*: seed-bank determines the dichotomy.*

Role of symmetry in migration. Unlike in model 1, it is *not* possible to remove the symmetry assumption in (2.73), as the following counterexample shows. We consider model 2 with $\rho < \infty$ under assumption (2.60), but we do not assume (2.73).

- **Counterexample:** Let $\mathbb{G} = \mathbb{Z}^2$, and for $\eta \in (0,1)$ pick

$$a(i,j) = \begin{cases} \frac{1}{4}(1+\eta), & j = i + (1,0) \text{ or } i + (0,1), \\ \frac{1}{4}(1-\eta), & j = i - (1,0) \text{ or } i - (0,1), \end{cases} \tag{2.90}$$

i.e., two-dimensional nearest-neighbour random walk with drift upward and rightward. Suppose that τ in (2.77) has a *one-sided stable distribution* with parameter $\gamma \in (1,2)$ (obtained from (2.76) but with $\alpha, \beta \in \mathbb{R}$: $1 < \alpha < 1 + \beta$). Then coexistence occurs while $I_{\hat{a}} = \infty$.

Recall that for the two-dimensional nearest-neighbour random walk without drift we get clustering according to Theorem 2.3.3, independently of the distribution of τ. The key feature of the counterexample is that it corresponds to $\mathbb{E}(\tau) < \infty$ and $\mathbb{E}(\tau^2) = \infty$. Hence the central limit theorem fails for τ. We will see in Section 3.3.5 that the failure of the central limit theorem for τ is responsible for turning clustering into coexistence.

The above raises the question to what extent the equilibrium behaviour depends on the nature of the geographic space. To answer this question, we need a key concept for random walks on countable Abelian groups, which we describe next.

Remark 2.3.5 (Dichotomy criterion and degrees of random walk). We can read the condition $I_{\hat{a},\gamma} < \infty$ for coexistence versus $I_{a,\gamma} = \infty$ for clustering in terms of the *degree* of the random walk. Namely, let $\hat{a}(\cdot,\cdot)$ be the transition kernel of an irreducible random walk on a countable Abelian group. Then the degree δ of $\hat{a}(\cdot,\cdot)$ is defined as

$$\delta = \sup\left\{\zeta > -1\colon \int_1^\infty \mathrm{d}t\, t^\zeta\, \hat{a}_t(0,0) < \infty\right\}. \tag{2.91}$$

The degree is defined to be δ^+ when the integral is finite *at* the degree and δ^- when the integral is infinite *at* the degree. Hence we can rephrase the dichotomy criterion in Theorem 2.3.3 as

$$\text{clustering} \quad \Longleftrightarrow \quad \text{either } -\frac{1-\gamma}{\gamma} \geq \delta^- \text{ or } -\frac{1-\gamma}{\gamma} > \delta^+. \tag{2.92}$$

For further details we refer to [18], [19], which relate the degree of the random walk to the tail of its return time to the origin. ■

Modulation of wake-up time with slowly varying function. Under weak conditions it is possible to modulate (2.77) by a slowly varying function. Assume that

$$\frac{\mathbb{P}(\tau \in \mathrm{d}t)}{\mathrm{d}t} \sim \varphi(t)\, t^{-(1+\gamma)}, \quad t \to \infty, \tag{2.93}$$

with φ *slowly varying at infinity.* Define

$$\hat{\varphi}(t) = \begin{cases} \varphi(t), & \gamma \in (0,1), \\ \int_1^t \mathrm{d}s\, \varphi(s) s^{-1}, & \gamma = 1. \end{cases} \tag{2.94}$$

As shown in [8, Section 1.3], without loss of generality we may take $\hat{\varphi}$ to be infinitely differentiable and to be represented by the integral

$$\hat{\varphi}(t) = \exp\left[\int_{(\cdot)}^t \frac{\mathrm{d}u}{u}\, \psi(u)\right] \tag{2.95}$$

for some $\psi\colon [0,\infty) \to \mathbb{R}$ such that $\lim_{u\to\infty} |\psi(u)| = 0$. If we assume that ψ eventually has a sign and satisfies $|\psi(u)| \leq C/\log u$ for some $C < \infty$, then (2.80) needs to be replaced by

$$I_{\hat{a},\gamma,\varphi} = \int_1^\infty \mathrm{d}t\, \hat{\varphi}(t)^{-1/\gamma}\, t^{-(1-\gamma)/\gamma}\, \hat{a}_t(0,0). \tag{2.96}$$

A proof is given in Section 3.3.6. The modulation of the wake-up time by a slowly varying function appears naturally for the model on the hierarchical group, analysed in [45]. There the integral criterion for the dichotomy in (2.96) is needed to apply Theorem 2.3.3.

§2.3.3 Long-time behaviour of Model 3

It remains to see how the switch of colony during the exchange affects the dichotomy. We will focus on the special case where the displacement kernels do not depend on m, i.e.,

$$a_m(\cdot,\cdot) = a^\dagger(\cdot,\cdot) \qquad \forall\, m \in \mathbb{N}_0, \tag{2.97}$$

with $a^\dagger(\cdot,\cdot)$ an irreducible *symmetric* random walk kernel on $\mathbb{G}\times\mathbb{G}$. Let $\hat{a}^\dagger_t(\cdot,\cdot)$ denote the time-t transition kernel of the random walk with symmetrised displacement kernel $\hat{a}^\dagger(\cdot,\cdot)$ $(= a^\dagger(\cdot,\cdot))$ and jump rate 1. Assume that (compare with (2.60))

$$\begin{aligned} &t \mapsto (\hat{a}_t * \hat{a}^\dagger_t)(0,0) \text{ is regularly varying at infinity,}\\ &(\hat{a}_{Ct} * \hat{a}^\dagger_t)(0,0) \asymp (\hat{a}_t * \hat{a}^\dagger_t)(0,0) \text{ as } t\to\infty \text{ for every } C\in(0,\infty), \end{aligned} \tag{2.98}$$

where $*$ stands for convolution. Let

$$I_{\hat{a}*\hat{a}^\dagger} = \int_1^\infty \mathrm{d}t\ (\hat{a}_t * \hat{a}^\dagger_t)(0,0) \tag{2.99}$$

and

$$I_{\hat{a}*\hat{a}^\dagger,\gamma} = \int_1^\infty \mathrm{d}t\ t^{-(1-\gamma)/\gamma}\,(\hat{a}_t * \hat{a}^\dagger_t)(0,0). \tag{2.100}$$

Theorem 2.3.6 (Long-time behaviour: model 3). *Suppose that, in addition to the assumptions of Theorem 2.3.3, both* (2.97) *and* (2.98) *hold. Then the same results as for model* 2 *hold: (I) for $\rho<\infty$ after $I_{\hat{a}}$ in* (2.61) *is replaced by $I_{\hat{a}*\hat{a}^\dagger}$ in* (2.99)*; (II) for $\rho=\infty$ after $I_{\hat{a},\gamma}$ in* (2.80) *is replaced by $I_{\hat{a}*\hat{a}^\dagger,\gamma}$ in* (2.100)*.*

In the case of coexistence the equilibrium measure ν_θ depends on $a(\cdot,\cdot)$, $a^\dagger(\cdot,\cdot)$, $(e_m)_{m\in\mathbb{N}_0}$, $(K_m)_{m\in\mathbb{N}_0}$ and $g\in\mathcal{G}$. The dichotomy itself, however, is controlled by $I_{\hat{a}*\hat{a}^\dagger}$, respectively, $I_{\hat{a}*\hat{a}^\dagger,\gamma}$ alone.

An interesting observation is the following. Since $\hat{a}_t(\cdot,\cdot)$ and $\hat{a}^\dagger_t(\cdot,\cdot)$ are symmetric, we have (by a standard Fourier argument)

$$\hat{a}_t(i,j) \le \hat{a}_t(0,0), \qquad \hat{a}^\dagger_t(i,j) \le \hat{a}^\dagger_t(0,0) \qquad \forall\, i,j\in\mathbb{G}\ \forall\, t\ge 0. \tag{2.101}$$

Hence, $I_{\hat{a}*\hat{a}^\dagger,\gamma} \le I_{\hat{a},\gamma} \wedge I_{\hat{a}^\dagger,\gamma}$. Consequently, the extra displacement in model 3 can only make coexistence more likely compared to model 2, which is intuitively plausible.

If $a(\cdot,\cdot)=a^\dagger(\cdot,\cdot)$, then $(a_t * a^\dagger_t)(0,0)=a_{2t}(0,0)$ and therefore the dichotomy is the same as for model 2. Hence the extra displacement has in this case no effect on the dichotomy. However, if the displacement is transient while the migration is recurrent, then there is a difference. For instance, if $\rho<\infty$, the migration is a simple random walk on $\mathbb{Z}$, and the displacement is a symmetric random walk on $\mathbb{Z}$ with infinite mean, e.g. $a^\dagger(0,x)=a^\dagger(0,-x)\sim D|x|^{-\delta}$, $D\in(0,\infty)$, $\delta\in(1,2)$, then $I_{\hat{a}}=\infty$, $I_{\hat{a}^\dagger}<\infty$ and $I_{\hat{a}*\hat{a}^\dagger}<\infty$ [69, Section 8]. Therefore there is clustering in model 2, but coexistence in model 3.