Spatial populations with seed-bank

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PART II

SPATIAL POPULATIONS WITH SEED-BANK ON THE HIERARCHICAL GROUP

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CHAPTER 4

Models and main results

§4.1 Background, goals and outline

§4.1.1 Background

Single colony with seed-bank. In populations with a *seed-bank*, individuals can temporarily become dormant and refrain from reproduction, until they can become active again. In [10] and [12] the evolution of a population evolving according to the two-type Fisher-Wright model with seed-bank was studied. Individuals move in and out of the seed-bank at prescribed rates. Outside the seed-bank individuals are subject to *resampling*, while inside the seed-bank their resampling is *suspended*. Both the long-time behaviour and the genealogy of the population were analysed in detail.

Seed-banks are observed in many taxa, including plants, bacteria and other microorganisms. 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. [55]). After a varying and possibly large number of generations, a dormant individual can be resuscitated under more favourable conditions and reprise reproduction after having become active again. 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.

Multiple colonies with seed-bank. In [43] we considered a *spatial* version of the two-type Fisher-Wright model with seed-bank in which individuals can *migrate* between colonies, organised into a *geographic space*, each having a seed-bank consisting of *multiple layers*, each with their own rate of moving in (becoming dormant) and moving out (waking up). We found that the presence of the seed-bank *enhances genetic diversity* compared to the spatial model without seed-bank. Interestingly, we found that the seed-bank can affect the longtime behaviour of the system both qualitatively and quantitatively.

In [43] we settled existence and uniqueness of the spatial model when the geographic space is $\mathbb{Z}^d$, $d \in \mathbb{N}$. We proved convergence to equilibrium, showed that there is a dichotomy between *coexistence* (= locally multi-type equilibria) and *clustering* (= locally mono-type equilibria), and identified the parameter regime for both. We found a change of the dichotomy due to the presence of the seed-bank. Without seed-bank, for migration in the domain of attraction of Brownian motion, clustering occurs in $d = 1, 2$ and coexistence in $d \geq 3$, i.e., the *critical dimension* for the dichotomy is $d = 2$. With seed-bank, however, clustering becomes more difficult and occurs in $d = 2$ only when the wake-up time of a typical individual in the seed-bank has finite mean, and in $d = 1$ only when the wake-up time has a sufficiently thin tail. In other words, the seed-bank has a tendency to *lower* the critical dimension.

In fact, in [43] we found that our technique of proof works for geographic spaces that are *arbitrary* countable Abelian groups endowed with the discrete topology. The reason is that the dichotomy can be formulated in terms of how the *degree* of the random walk that underlies the migration balances with the exponent of the *tail* of the typical wake-up time. This raises the question how we can better understand the behaviour of spatial models with seed-bank close to criticality.

In [44] we established the so-called *finite-systems scheme*, i.e., we identified how a finite truncation of the system (both in the geographic space and in the seed-bank) behaves as both the time and the truncation level tend to infinity, properly tuned together. We found that if the wake-up time has finite mean, then the scaling time is proportional to the volume of the system and there is a *single universality class* for the scaling limit, namely, the system moves through a succession of equilibria of the infinite system with a density that evolves according to a Fisher-Wright diffusion. On the other hand, we found that if the wake-up time has infinite mean, then the scaling time grows faster than the volume of the system, and there are *two universality classes* depending on how fast the truncation level of the seed-bank grows compared to the truncation level of the geographic space.

§4.1.2 Goals

In the present paper we take as geographic space the *hierarchical group* Ω_N of order N. The reason for this choice is that Ω_N allows for more detailed computations. At the same time, migration on Ω_N can be used to *approximate* migration on $\mathbb{Z}^d$ in the *hierarchical mean-field limit* $N \to \infty$. In particular, by playing with the migration kernel we can approximate two-dimensional migration in the sense of potential theory. We consider migration kernels that in the limit as $N \to \infty$ are *critically recurrent*, i.e., the degree of the class of hierarchical migrations that we consider in the present paper converges to 0, either from above or from below.

The present paper has three goals:

(1) We apply the results obtained in [43] to Ω_N with $N < \infty$ fixed. We again find that part of the coexistence regime without seed-bank shifts into the clustering regime with seed-bank when the average wake-up time of a typical individual is infinite.

(2) We analyse a *space-time renormalised* system in the limit as $N \to \infty$. Namely, we show that the block averages on successive space-time scales each perform a diffusion with a *renormalised diffusion function*. In other words, we establish a *multi-scale version of the finite-systems scheme*. Also, we compare the behaviour of the space-time renormalised system with seed-bank to the one analysed in [21] and [20] without seed-bank.

(3) We exhibit *universal behaviour* in the clustering regime close to criticality. To do so, we analyse the attracting orbits of the renormalisation transformation,

acting on the space of diffusion functions, that connects successive hierarchical levels. We show that, in the *clustering regime* and after appropriate scaling, the renormalised diffusion function converges to the Fisher-Wright diffusion function as we move up in the hierarchy, irrespective of the diffusion function controlling the resampling. This convergence shows that the hierarchical system exhibits *universality* on large space-time scales in terms of the scaling limit. For several subclasses of parameters we identify the scaling of the renormalised diffusion function, which reveals a delicate interplay between the parameters controlling the migration and the seed-bank. This rate in turn determines the speed at which *mono-type clusters grow in space and time.*

In the *coexistence regime*, universality does *not* hold and the equilibrium depends on the diffusion function. Since the seed-bank enhances genetic diversity, it may be expected that equilibrium correlations between far away colonies decay faster with seed-bank than without seed-bank, an issue that will not be addressed.

Remark 4.1.1 (More general types). Throughout the paper we consider the *two-type* Fisher-Wright model with seed-bank, in the *continuum limit* where the number of individuals per colony tends to infinity. The extension to a general type space, called the Fleming-Viot model (see [25]), requires only standard adaptations and will not be considered here. In what follows, we *only* work with continuum models. However, we motivate these models by viewing them as the *large-colony-size limit* of individual-based models. For earlier work on hierarchically interacting Fisher-Wright diffusions without seed-bank we refer the reader to [20, 21, 25, 22] and [5, 6, 26]. ■

§4.1.3 Outline

The present paper consist of two parts:

- **Part I: Model and main results.** Sections 4.2–4.5 collect the main propositions and theorems. In Section 4.2 we define the hierarchical model and state some basic properties: the *well-posedness* of the associated martingale problem (Proposition 4.2.6), the *duality relation* (Proposition 4.2.7), and the *clustering criterion* via duality (Proposition 4.2.12). These properties were all derived in [43]. In Section 4.3 we state our main results for $N < \infty$. In particular, we compute the scaling of the wake-up time and the migration kernel (Theorem 4.3.2) and identify the *clustering regime* in terms of the coefficients controlling the migration and the seed-bank under the assumption that these are asymptotically polynomial or pure exponential (Theorem 4.3.3)). In Section 4.4 we state our main results for $N \to \infty$, the hierarchical mean-field limit. In particular, we introduce *block averages on successive hierarchical space-time scales*, analyse their limiting dynamics (Theorems 4.4.2 and 4.4.4), offer a heuristic explanation how this limiting dynamics arises, introduce a path topology called the Meyer-Zheng topology that is needed for a proper formulation, and introduce an object called the interaction chain, which describes how the diffent hierarchical levels interact with each other. In Section 4.5 we identify the *orbit of the renormalisation transformation* in the clustering regime (Theorem 4.5.1), identify the rate of scaling for the renormalised diffusion function (Theorem 4.5.3), and link this scaling to the rate of growth of mono-type clusters.

- **Part II: Preparations and proofs.** Chapters 5–10 provide the proofs of the theorems stated in Part I. These proofs consist of a long series of propositions and lemmas needed to build up the argument. In Chapter 5 we prove our main results for $N < \infty$. In Chapter 6 we focus on the *mean-field model* (consisting of a single hierarchy) and, respectively, state and prove a number of results that serve as preparation. In Chapters 7–8 we consider extensions of the mean-field model (consisting of finitely hierarchies), which serve as further preparation. In Chapter 9 we use the results in Sections 6–8 to deal with the full hierarchical model (consisting of infinitely many hierarchies), and prove our main results for $N \to \infty$. In Chapter 10 we analyse the orbit of the renormalisation transformation controlling the multi-scaling. Appendix B.1 contains a technical computation needed for the identification of the clustering regime. Appendix B.2 contains a basic introduction to convergence of paths in the Meyer-Zheng topology, which is needed for the main theorems.

Part I contains all the main results and their interpretations, and can be read without reference to Part II.

§4.2 Introduction of model and basic properties

Section 4.2.1 introduces the model ingredients, Section 4.2.2 gives the evolution equations, Section 4.2.3 states the well-posedness, Section 4.2.4 introduces the dual and states the duality relation, while Section 4.2.5 formulates the dichotomy between clustering versus coexistence in terms of the dual.

§4.2.1 Model: geographic space Ω_N, hierachical group of order N

Single colony. Our building block is the single-colony Fisher-Wright model with seed-bank defined in [12]. In that model, each individual in the population carries one of two types, $\heartsuit$ or $\diamondsuit$, and each individual can be either active or dormant. Active individuals *resample* until they become dormant. Dormant individuals suspend resampling until they become actieve again. The repository for the dormant individuals is called the *seed-bank.* When an active individual resamples, it randomly chooses another active individual and *adopts its type.* When an active individual becomes dormant, it randomly chooses a dormant individual and forces it to becomes active, i.e., the active and the dormant population *exchange* individuals (see Fig. 4.1). This exchange guarantees that the sizes of the active and the dormant population stay fixed over time. During the swap both the active and the dormant individual *retain their type.*

The types of the active population evolve through resampling and through exchange with the dormant population. The types of the the dormant population evolve only through exchange with the active population. It was shown in [12] that in the large-colony-size limit, i.e., as the number of individuals per colony tends to infinity and time is speeded up by the size of the colony, the two quantities

- $x(t)$ = the fraction of active individuals of type $\heartsuit$ at time t,

- $y(t)$ = the fraction of dormant individuals of type ♡ at time t,

satisfy the following system of coupled SDEs:

$$\begin{aligned} \mathrm{d}x(t) &= Ke\,[y(t)-x(t)]\,\mathrm{d}t + \sqrt{x(t)(1-x(t))}\,\mathrm{d}w(t),\\ \mathrm{d}y(t) &= e\,[x(t)-y(t)]\,\mathrm{d}t. \end{aligned} \tag{4.1}$$

Here, e denotes the rate at which an active individual *exchanges* with a dormant individual from the seed-bank, K denotes the relative size of the dormant population with respect to the active population, and $(w(t))_{t\geq 0}$ is a Brownian motion. The first term in the first equation describes the flow from the dormant population to the active population, the term in the second equation describes the flow from the active population to the dormant population, while the second term in the first equation describes the effect of resampling on the active population (see Fig. 4.1). Active individuals resample at rate 1. Since dormant individuals do not resample, we do not see such a term in the second equation. The formal derivation of the continuum equations can be found in [12] and in [43, Appendix A].

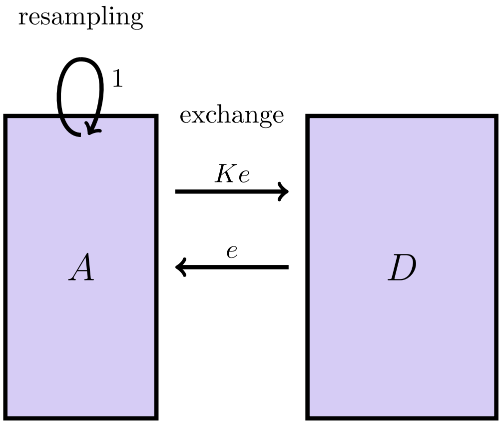

Figure 4.1: Active individuals resample at rate 1*. Active and dormant individuals exchange at rate* e*. The extra factor* K *arises from the fact that the dormant population is* K *times as large as the active population. Dormant individuals suspend resampling.*

Multi-colony. The present paper focuses on a *multi-colony* setting of the model described above, where the underlying geographic space is the hierarchical lattice of order N, given by ($\mathbb{N}_0 = \mathbb{N} \cup \{0\}$)

$$\Omega_N = \left\{ \xi = (\xi_k)_{k\in\mathbb{N}_0} \colon\ \xi_k \in \{0,1,\ldots,N-1\},\ \sum_{k\in\mathbb{N}_0} \xi_k < \infty \right\}, \tag{4.2}$$

which with addition modulo N becomes the hierarchical group of order N (see Fig. 4.2). The *hierarchical distance* on Ω_N is defined by

$$d_{\Omega_N}(\xi,\eta) = d_{\Omega_N}(0,\xi-\eta) = \min\{k\in\mathbb{N}_0 \colon\ \xi_l = \eta_l\ \forall\, l \geq k\}, \qquad \xi,\eta\in\Omega_N, \tag{4.3}$$

and is an ultra-metric, i.e.,

$$d_{\Omega_N}(\xi,\eta) \le \max\left\{d_{\Omega_N}(\xi,\zeta), d_{\Omega_N}(\eta,\zeta)\right\} \qquad \forall\, \xi,\eta,\zeta \in \Omega_N. \tag{4.4}$$

The choice of Ω_N as geographic space plays an important role for population models, and was first exploited in [65] in an attempt to formalise ideas coming from ecology. One interpretation is that the sequence $(\xi_k)_{k\in\mathbb{N}_0}$ encodes the 'address' of colony ξ: ξ_0 is the 'house', ξ_1 is the 'street', ξ_2 is the 'village', ξ_3 is the 'province', ξ_4 is the 'country', and so on. To describe the system on the hierarchical group we need three ingredients:

- Hierarchical migration.
- Layered seed-bank.
- Resampling rate.

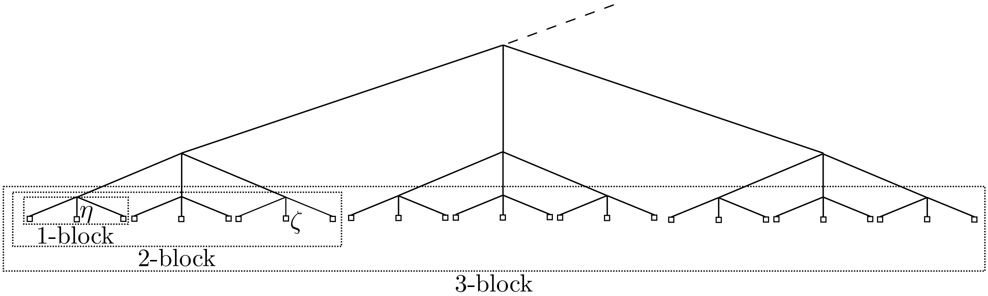

Figure 4.2: Close-ups of a 1-block, a 2-block and a 3-block in the hierarchical group of order $N = 3$. The elements of the group are the leaves of the tree (indicated by □'s). The hierarchical distance between two elements in the group is the graph distance to the most recent common ancestor in the tree: $d_{\Omega_3}(\eta,\zeta) = 2$ for η and ζ in the picture.

• Hierarchical migration

We construct a migration kernel $a^{\Omega_N}(\cdot,\cdot)$ on the hierarchical group Ω_N built from a sequence of migration rates

$$\underline{c} = (c_k)_{k\in\mathbb{N}_0} \in (0,\infty)^{\mathbb{N}_0} \tag{4.5}$$

that do not depend on N. Individuals migrate as follows:

- For all $k \in \mathbb{N}$, each individual chooses at rate c_{k-1}/N^{k-1} the block of radius k around its present location and selects a colony uniformly at random from that block. Subsequently it selects an individual in this colony uniformly at random and adopts its type.

Note that the block of radius k contains N^k colonies, and that the migration kernel is therefore given by

$$a^{\Omega_N}(\eta,\xi) = \sum_{k\ge d_{\Omega_N}(\eta,\xi)} \frac{c_{k-1}}{N^{k-1}}\frac{1}{N^k}, \quad \eta,\xi\in\Omega_N, \eta\neq\xi, \qquad a^{\Omega_N}(\eta,\eta) = 0, \quad \eta\in\Omega_N. \tag{4.6}$$

Throughout the paper, we assume that

$$\limsup_{k\to\infty} \frac{1}{k} \log c_k < \log N. \tag{4.7}$$

This guarantees that the total migration rate per individual is finite. Indeed, note that for every $\eta \in \Omega_N$,

$$\begin{aligned}\sum_{\xi\in\Omega_N} a^{\Omega_N}(\eta,\xi) &= \sum_{\xi\in\Omega_N} \sum_{k\geq d_{\Omega_N}(\eta,\xi)} \frac{c_{k-1}}{N^{2k-1}} \\ &= \sum_{k\in\mathbb{N}} \left[\sum_{\xi\in\Omega_N} \mathbf{1}_{\{d_{\Omega_N}(\eta,\xi)\leq k\}}\right] \frac{c_{k-1}}{N^{2k-1}} \\ &= \sum_{k\in\mathbb{N}} \frac{c_{k-1}}{N^{k-1}},\end{aligned} \tag{4.8}$$

which is finite because of (4.7).

Remark 4.2.1 (Degree of random walk). For a random walk on an Abelian group with time-t transition kernel $a_t^{\Omega_N}(\cdot,\cdot)$, the *degree* is defined as (see [19])

$$\delta = \sup\left\{\zeta \in (-1,\infty)\colon \int_0^\infty \mathrm{d}t\, t^\zeta a_t^{\Omega_N}(0,0) < \infty\right\}. \tag{4.9}$$

The degree is said to be δ^+, respectively, δ^- when the integral is finite, respectively, infinite *at* the degree. If $\delta > 0$, then δ is called the *degree of transience*. If $\delta \in (-1,0)$, then $-\delta$ is called the *degree of recurrence*. If the degree is 0^-, then the random walk is called *critically recurrent*. (It would be interesting to have a version of (4.9) that includes a slowly varying function in front of the power t^ζ. However, such an extension appears not to have been explored in the literature.) ■

By playing with $\underline{c}$ and letting $N \to \infty$, we can approximate migration for which the corresponding random walk is critically recurrent, i.e., $\delta^- = 0$. In that case both the potential theory and the Green function for the hierarchical random walk have the same asymptotics as the potential theory and the Green function for a critically recurrent random walk on $\mathbb{Z}^2$ in the domain of attraction of Brownian motion. Therefore, by tuning $\underline{c}$ properly, we can mimic migration on the geographic space $\mathbb{Z}^2$ (for which $\delta^- = 0$), an idea that was exploited in [25], [22], [23], [41], [42].

- **Layered seed-bank**

To create a layered seed-bank, dormant individuals are labeled with a colour $m \in \mathbb{N}_0$. An active individual that becomes dormant is assigned a colour $m \in \mathbb{N}_0$. When an active individual becomes dormant with colour m, it exchanges with a dormant individual of colour m. This dormant individual becomes active, *loses* its colour, but *retains* its type. To describe the layered seed-bank we need two sequences

$$\begin{aligned}\underline{K} &= (K_m)_{m\in\mathbb{N}_0} \in (0,\infty)^{\mathbb{N}_0},\\ \underline{e} &= (e_m)_{m\in\mathbb{N}_0} \in (0,\infty)^{\mathbb{N}_0},\end{aligned} \tag{4.10}$$

both not depending on N, which we interpret as follows:

- K_m is the relative size of the dormant population of colour m with respect to the active population, i.e.,

$$K_m = \frac{\text{size } m\text{-dormant population}}{\text{size active population}}. \tag{4.11}$$

- At rate $K_m \frac{e_m}{N^m}$ an active individual becomes dormant, is assigned colour m, and retains its type. At the same time a dormant individual with colour m becomes active, loses its colour, and retains its type. By defining the rates in this way, the layered structure of the seed-bank is tuned to the hierarchical structure of the geographic space.

By giving the seed-bank a layered structure, we are able to tune the distribution of the wake-up time, i.e., the time an individual spends in the seed-bank before waking up. In particular, we will see that a layered seed-bank enables us to model wake up times with a *fat tail*, while at the same time preserving the Markov property of the evolution.

Since active and dormant individuals *exchange*, K_m remains constant over time for all $m \in \mathbb{N}_0$. Throughout the paper we assume that

$$\limsup_{m\to\infty} \frac{1}{m} \log(K_m e_m) < \log N. \tag{4.12}$$

This guarantees that the total rate of exchange per individual, given by

$$\chi = \sum_{m\in\mathbb{N}_0} K_m \frac{e_m}{N^m}, \tag{4.13}$$

is finite. On the other hand, the relative size of the dormant population with respect to the active population

$$\rho = \sum_{m\in\mathbb{N}_0} K_m \tag{4.14}$$

can be either finite or infinite. We will see that $\rho < \infty$ and $\rho = \infty$ represent two *different regimes.*

- **Resampling rate**

To describe the resampling we use a diffusion function g that is taken from the set

$$\mathcal{G} = \Big\{ g(x)\colon\ [0,1] \to [0,\infty)\colon\ g(0) = g(1) = 0,\ g(x) > 0\ \forall\, x \in (0,1),\ g \text{ Lipschitz} \Big\}, \tag{4.15}$$

and think of $h(x) = g(x)/x(1-x)$ as the rate of resampling at type frequency x. The choice $g = dg_{\mathrm{FW}}$, $d \in (0,\infty)$, with $g_{\mathrm{FW}}(x) = x(1-x)$, $x \in [0,1]$, corresponds to Fisher-Wright resampling at rate d. We use a collection of independent Brownian motions

$$W = \big((w_\xi(t))_{t\geq 0}\big)_{\xi\in\Omega_N} \tag{4.16}$$

to describe the fluctuations of the type frequencies caused by the resampling in each colony.

§4.2.2 Evolution equations

- **Evolution of single colonies**

With the above three ingredients, we can now describe the evolution of the system. For $\xi \in \Omega_N$, define

$$\begin{aligned} x_\xi(t) = & \text{ the fraction of active individuals of type } \heartsuit \text{ at colony } \xi \text{ at time } t, \\ y_{\xi,m}(t) = & \text{ the fraction of } m\text{-dormant individuals of type } \heartsuit \text{ at colony } \xi \text{ and time } t. \end{aligned} \tag{4.17}$$

Note that $x_\xi(t) \in [0,1]$ and $y_{\xi,m}(t) \in [0,1]$ for all $\xi \in \Omega_N$, $m \in \mathbb{N}_0$, $t \geq 0$. Therefore the state space of a single colony is $\mathfrak{s} = [0,1] \times [0,1]^{\mathbb{N}_0}$, and the state space of the system is

$$S = \mathfrak{s}^{\Omega_N}. \tag{4.18}$$

Our object of interest is the random process taking values in S, written

$$(X^{\Omega_N}(t), Y^{\Omega_N}(t))_{t\geq 0}, \qquad (X^{\Omega_N}(t), Y^{\Omega_N}(t)) = \big(x_\xi(t), (y_{\xi,m}(t))_{m\in\mathbb{N}_0}\big)_{\xi\in\Omega_N}, \tag{4.19}$$

whose components evolve according to the following SSDE (= system of stochastic differential equations):

$$\begin{aligned} \mathrm{d}x_\xi(t) = & \sum_{\eta\in\Omega_N} a^{\Omega_N}(\xi,\eta)[x_\eta(t) - x_\xi(t)]\,\mathrm{d}t + \sqrt{g(x_\xi(t))}\,\mathrm{d}w_\xi(t) \\ & + \sum_{m\in\mathbb{N}_0} \frac{K_m e_m}{N^m}\,[y_{\xi,m}(t) - x_\xi(t)]\,\mathrm{d}t, \qquad (4.20) \\ \mathrm{d}y_{\xi,m}(t) = & \frac{e_m}{N^m}\,[x_\xi(t) - y_{\xi,m}(t)]\,\mathrm{d}t, \quad m \in \mathbb{N}_0, \qquad \xi \in \Omega_N. \end{aligned}$$

The first term in the first equation describes the evolution of the active population at colony ξ due to migration, the second term due to the resampling. The third term in the first equation and the term in the second equation describe the exchange between the active and the dormant population at colony ξ (see Fig. 4.3). Since dormant individuals are not subject to resampling or migration, the dynamics of the dormant population is completely determined by the exchange with the active population. For the *initial state* we assume that

$$\begin{aligned} & \mathcal{L}(X^{\Omega_N}(0), Y^{\Omega_N}(0)) = \mu^{\otimes\Omega_N} \\ & \text{with } \mathbb{E}^\mu[x_\xi(0)] = \theta_x,\ \mathbb{E}^\mu[y_{\xi,m}(0)] = \theta_{y_m} \text{ with } \lim_{m\to\infty} \theta_{y_m} = \theta \text{ for some } \theta \in [0,1]. \end{aligned} \tag{4.21}$$

The last assumption in (4.21), which in [43] was referred to as μ being *colour regular*, guarantees that for finite N the system in (4.20) converges to an ergodic equilibrium.

Remark 4.2.2. *[Notation]* Throughout the sequel we use lower case letters for *single components* and upper case letters for *systems of single components*. We exhibit the geographic space for the system, but suppress it from the components. ■

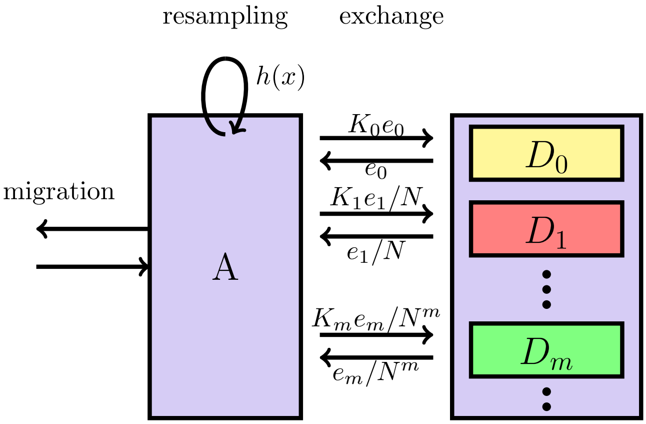

Figure 4.3: Active individuals (A) are subject to migration, resampling and exchange with dormant individuals (D). When active individuals become dormant they are assigned a colour (D_m, $m \in \mathbb{N}_0$), which they lose when they become active again. The resampling rate in the active state at type-♡ frequency x equals $h(x) = g(x)/x(1-x)$ with $g \in \mathcal{G}$ (e.g. for the standard Fisher-Wright diffusion the resampling rate is 1).

- **Evolution of block averages**

The choice of the migration kernel in (4.6) implies that, for every $k \in \mathbb{N}$, at rate $\asymp \frac{1}{N^k}$ individuals choose a space horizon of distance $k+1$ and subsequently choose a random colony from that space horizon. Therefore, in order to see interactions over a distance $k+1$, we need to speed up time by a factor N^k. A similar observation applies to the interaction with the seed-bank. Dormant individuals with colour k become active at rate $\asymp \frac{1}{N^k}$. Therefore, in order to see interactions with the k-dormant population, we need to speed up time by a factor N^k. To analyse the effective interaction on time scale N^k, we introduce *successive block averages* labelled by $k \in \mathbb{N}_0$.

Definition 4.2.3 (Block averages). For $k \in \mathbb{N}_0$, let $B_k(0) = \{\eta \in \Omega_N \colon d_{\Omega_N}(0, \eta \leq k\}$ denote the k-block around 0. Define the k-block average around 0 at time $N^k t$ by

$$\begin{aligned} x_k^{\Omega_N}(t) &= \frac{1}{N^k} \sum_{\eta \in B_k(0)} x_\eta(N^k t), \\ y_{m,k}^{\Omega_N}(t) &= \frac{1}{N^k} \sum_{\eta \in B_k(0)} y_{\eta,m}(N^k t), \qquad m \in \mathbb{N}_0. \end{aligned} \tag{4.22}$$

The k-block average represents the dynamics of the system on space-time scale k. ■

By translation invariance of the SSDE in (4.20), each $\xi \in \Omega_N$ can serve as the origin. In the remainder of the paper we consider without loss of generality the k-block average around $\xi = 0$, and suppress the center 0 from the notation.

Remark 4.2.4 (Notation). We use lower case letters for the block averages because they live in the space of components $\mathfrak{s} = [0,1] \times [0,1]^{\mathbb{N}_0}$. At the same time we exhibit the geographic space Ω_N for the block averages because they are functionals of the system of components (recall Remark 4.2.2). ■

Using Definition 4.2.3 and inserting the specific choice of the migration kernel defined in (4.6), we can rewrite (4.20) for $\xi = 0$ as follows (0-blocks are single components):

$$\begin{aligned}
\mathrm{d}x_0^{\Omega_N}(t) &= \sum_{l\in\mathbb{N}} \frac{c_{l-1}}{N^{l-1}} \left[x_l^{\Omega_N}(N^{-l}t) - x_0^{\Omega_N}(t)\right] \mathrm{d}t + \sqrt{g\big(x_0^{\Omega_N}(t)\big)}\, \mathrm{d}w(t) \\
&\qquad + \sum_{m\in\mathbb{N}_0} \frac{K_m e_m}{N^m} \left[y_{m,0}^{\Omega_N}(t) - x_0^{\Omega_N}(t)\right] \mathrm{d}t, \\
\mathrm{d}y_{m,0}^{\Omega_N}(t) &= \frac{e_m}{N^m} \left[x_0^{\Omega_N}(t) - y_{m,0}^{\Omega_N}(t)\right] \mathrm{d}t, \qquad m \in \mathbb{N}_0.
\end{aligned} \tag{4.23}$$

From (4.23) we see that migration between colonies can be expressed as a drift towards block averages at a higher hierarchical level.

The SSDE for the k-block average on time scale N^k reads as follows (recall (4.22)):

$$\begin{aligned}
\mathrm{d}x_k^{\Omega_N}(t) &= \sum_{l\in\mathbb{N}} \frac{c_{k+l-1}}{N^{l-1}} \left[x_{k+l}^{\Omega_N}(N^{-l}t) - x_k^{\Omega_N}(t)\right] \mathrm{d}t + \sqrt{\frac{1}{N^k} \sum_{i\in B_k(0)} g\big(x_i(N^k t)\big)}\, \mathrm{d}w_k(t) \\
&\qquad + \sum_{m\in\mathbb{N}_0} N^k \frac{K_m e_m}{N^m} \left[y_{m,k}^{\Omega_N}(t) - x_k^{\Omega_N}(t)\right] \mathrm{d}t, \\
\mathrm{d}y_{m,k}^{\Omega_N}(t) &= N^k \frac{e_m}{N^m} \left[x_k^{\Omega_N}(t) - y_{m,k}^{\Omega_N}(t)\right] \mathrm{d}t, \qquad m \in \mathbb{N}_0.
\end{aligned} \tag{4.24}$$

To deduce these equations from (4.20), we sum over $\xi \in B_k$, speed up time by a factor N^k, insert the specific choice of the migration kernel in (4.6), and use the standard scaling properties of Brownian motion: $w(ct) =^d \sqrt{c}\, w(t)$ and $\sqrt{a} w(t) + \sqrt{b} w'(t) =^d \sqrt{a+b}\, w''(t)$, with $w(t)$ and $w'(t)$ independent Brownian motions, and with $=^d$ denoting equality in distribution. This computation is spelled out in Section 9.

Remark 4.2.5 (Separation space-time scales). The *block averages* and their evolution equations in (4.24) will be key objects in the analysis of the hierarchical mean-field limit $N \to \infty$. We will see that the limit $N \to \infty$ brings about considerable simplifications. In Section 4.4 we discuss these simplifications in detail. In particular, a *complete separation of space-time scales* takes places, in which each block average lives on its own time scale, effectively interacts with only one seed-bank, and effectively feels a drift towards the block average one hierarchical level up. ■

§4.2.3 Well-posedness

The generator of the system in (4.20) is given by

$$\begin{aligned} G \;=\; & \sum_{\xi\in\Omega_N}\Bigg(\sum_{\eta\in\Omega_N} a^{\Omega_N}(\xi,\eta)[x_\eta(t)-x_\xi(t)]\frac{\partial}{\partial x_\xi}+\frac{1}{2}g(x_\xi(t))\frac{\partial^2}{\partial x_\xi^2} \qquad (4.25)\\ & +\sum_{m\in\mathbb{N}_0}\left[\frac{K_m e_m}{N^m}[y_{\xi,m}(t)-x_\xi(t)]\frac{\partial}{\partial x_\xi}+\frac{e_m}{N^m}[x_\xi(t)-y_{\xi,m}(t)]\frac{\partial}{\partial y_{\xi,m}}\right]\Bigg). \end{aligned}$$

Let

$$\begin{aligned} \mathcal{F}=\Big\{f\in C_b([0,\infty),S)\colon\ & f \text{ depends on finitely many components}\\ & \text{and is twice continuously differentiable in each component}\Big\}. \end{aligned} \tag{4.26}$$

Proposition 4.2.6 (Well-posedness). (a) *The SSDE in* (4.20) *has a unique strong solution in* $C([0,\infty),S)$*, whose law is the unique solution of the* $(G,\mathcal{F},\delta_u)$*-martingale problem for all* $u\in S$*.*

(b) *The process starting from* $u\in S$ *is Feller and strong Markov. Consequently, the SSDE in* (4.20) *defines a unique Borel Markov process starting from any initial law on* S*.*

Proof. Comparing with what is called model 2 in [43], we see that the Abelian group is chosen as in (4.2), the transition kernel is chosen as in (4.6), and the rates in and out of the seed-bank are $\frac{e_m}{N^m}$ and $\frac{K_m e_m}{N^m}$ for colour m. Hence the claim follows from [67], in the same way as shown in the proof of [43, Theorem 2.1]. □

Henceforth we write $\mathbb{P}$ and $\mathbb{E}$ to denote probability and expectation with respect to the random process in (4.19).

§4.2.4 Duality

If $g=dg_{\mathrm{FW}}$, then our model has a tractable dual, which turns out to play a crucial role in the analysis of the long-time behaviour. In this section we introduce the dual process following the same line of argument as in [43, Section 2.4]. There it was shown that the spatial Fisher-Wright diffusion with seed-bank is dual to a so-called *block-counting process* of a seed-bank coalescent. The latter describes the ancestral lines of $n\in\mathbb{N}$ individuals sampled from the current population backwards in time in terms of partition elements. At time zero the ancestral line of each individual is represented by a partition element. Traveling backwards in time, two partition elements merge as soon as their ancestral lines coalesce, i.e., two individuals have the same ancestor from that time onwards. Hence the seed-bank coalescent divides the ancestral lines of the $n\in\mathbb{N}$ individuals into subgroups of individuals with the same ancestor (i.e., individuals that are identical by descent). Therefore the seed-bank coalescent generates the ancestral lineages of the individuals evolving according to a Fisher-Wright diffusion with seed-bank, i.e., generates their full genealogy. The

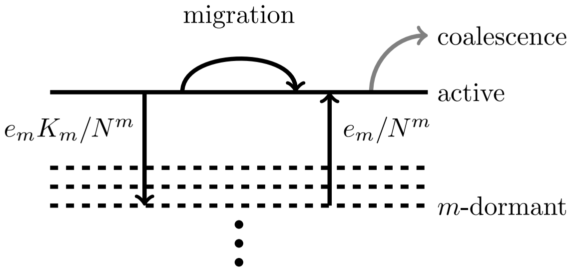

Figure 4.4: Transition scheme for an ancestral lineage in the dual, which moves according to the transition kernel $b(\cdot,\cdot)$ *defined in* (4.31)*. Two active ancestral lineages that are at the same colony coalesce at rate* d*.*

corresponding block-counting process counts the number of partition elements that are left when we travel backwards in time.

Formally, the spatial seed-bank coalescent is described as follows. Let

$$\mathbb{S} = \Omega_N \times \{A, (D_m)_{m\in\mathbb{N}_0}\} \tag{4.27}$$

be 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 $\{1,\dots,n\}$, where the partition elements are marked with a position vector giving their locations. A state is written as π, where

$$\begin{aligned}&\pi = ((\pi_1,\eta_1),\dots,(\pi_{\bar n},\eta_{\bar n})), \quad \bar n = |\pi|,\\ &\pi_\ell \subset \{1,\dots,n\}, \quad \{\pi_1,\cdots\pi_{\bar n}\} \text{ is a partition of } \{1,\dots,n\},\\ &\eta_\ell \in \mathbb{S}, \quad \ell\in\{1,\dots,\bar n\}, \quad 1\le \bar n \le n.\end{aligned} \tag{4.28}$$

A marked partition element (π_ℓ,η_ℓ) is called active if $\eta_\ell = (\xi, A)$ and m-dormant if $\eta_\ell = (\xi, D_m)$ for some $\xi\in\Omega_N$. The n-spatial seed-bank coalescent is denoted by

$$(\mathcal{C}^{(n)}(t))_{t\geqslant 0}, \tag{4.29}$$

and starts from

$$\mathcal{C}^{(n)}(0) = \pi(0), \qquad \pi(0) = \{(\{1\},\eta_{\ell_1}),\dots,(\{n\},\eta_{\ell_n})\}, \qquad \eta_{\ell_1},\dots,\eta_{\ell_n}\in\mathbb{S}. \tag{4.30}$$

The n-spatial seed-bank coalescent is the Markov process that evolves according to the following two rules (see Figs. 4.4–4.5).

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

$$b^{\Omega_N}((\xi,R_\xi),(\eta,R_\eta)) = \begin{cases} a^{\Omega_N}(\xi,\eta), & \text{if } R_\xi = R_\eta = A,\\ K_m\frac{e_m}{N^m}, & \text{if } \xi=\eta,\ R_\xi = A,\ R_\eta = D_m,\ \text{for } m\in\mathbb{N}_0,\\ \frac{e_m}{N^m}, & \text{if } \xi=\eta,\ R_\xi = D_m,\ R_\eta = A,\ \text{for } m\in\mathbb{N}_0,\\ 0, & \text{otherwise,}\end{cases} \tag{4.31}$$

where $a^{\Omega_N}(\cdot,\cdot)$ is the migration kernel defined in (4.6), K_m, $m\in\mathbb{N}_0$ are the relative sizes of the m-dormant population and the active population defined in

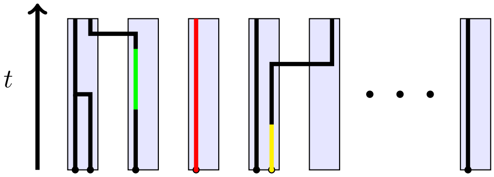

Figure 4.5: Picture of the evolution of lineages in the spatial coalescent. The purple blocks depict the colonies, the black lines the active lineages, and the coloured lines the dormant lineages. Blue lineages can migrate. Two black lineages can coalesce when they are at the same colony. Red dormant lineages first have to become black and active before they can migrate or coalesce with other black and active lineages. Note that the dual runs backwards in time.

(4.11), and e_m, $m \in \mathbb{N}_0$ are the coefficients controlling the exchange between the active and the dormant population defined in (4.10). Thus, an active partition element migrates according to the transition kernel $a^{\Omega_N}(\cdot,\cdot)$ and becomes m-dormant at rate $K_m \frac{e_m}{N^m}$, while an m-dormant partition element can only become active and does so at rate $\frac{e_m}{N^m}$.

(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.

Fig. 4.4 gives a schematic overview of the possible transitions of a single lineage, while Fig. 4.5 gives an example of the evolution in the dual. 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 $(\xi, R_\xi) \in \Omega_N \times \{A, (D_m)_{m\in\mathbb{N}_0}\}$ the number of partition elements of $\mathcal{C}^{(n)}(t)$, i.e.,

$$\begin{aligned} &L(t) = \big(L_{(\xi,A)}(t), \big(L_{(\xi,D_m)}(t)\big)_{m\in\mathbb{N}_0}\big)_{\xi\in\Omega_N},\\ &L_{(\xi,A)}(t) = L_{(\xi,A)}(\mathcal{C}^{(n)}(t)) = \sum_{\ell=1}^{\bar{n}} 1_{\{\eta_\ell(t)=(\xi,A)\}},\\ &L_{(\xi,D_m)}(t) = L_{(\xi,D_m)}(\mathcal{C}^{(n)}(t)) = \sum_{\ell=1}^{\bar{n}} 1_{\{\eta_\ell(t)=(\xi,D_m)\}}, \qquad m \in \mathbb{N}_0. \end{aligned} \tag{4.32}$$

The state space of $(L(t))_{t\geq 0}$ is $S' = (\mathbb{N}_0 \times \mathbb{N}_0^{\mathbb{N}_0})^{\Omega_N}$. We denote the elements of S' by sequences $(m_\xi, (n_{\xi,D_m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N}$, and define $\delta_{(\eta,R_\eta)} \in S'$ to be the element of S' that is 0 at all sites $(\xi, R_\xi) \in \Omega_N \times \{A, (D_m)_{m\in\mathbb{N}_0}\}\backslash(\eta, R_\eta)$, and 1 at the site (η, R_η). From the evolution of $\mathcal{C}^{(n)}(t)$ described below (4.29) we see that the block-counting process has the following transition kernel:

$$
\begin{aligned}
&(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N} \to \\
&\quad\begin{cases}
(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N} - \delta_{(\eta,A)} + \delta_{(\zeta,A)}, & \text{at rate } m_\eta a(\eta,\zeta) \text{ for } \eta,\zeta\in\Omega_N,\\
(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N} - \delta_{(\eta,A)}, & \text{at rate } d\binom{m_\eta}{2} \text{ for } \eta\in\Omega_N,\\
(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N} - \delta_{(\eta,A)} + \delta_{(\eta,D_m)}, & \text{at rate } m_\eta K_m \frac{e_m}{N^m} \text{ for } \eta\in\Omega_N,\\
(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N} + \delta_{(\eta,A)} - \delta_{(\eta,D_m)}, & \text{at rate } n_{\eta,m} \frac{e_m}{N^m} \text{ for } \eta\in\Omega_N.
\end{cases}
\end{aligned}
\tag{4.33}
$$

The process $(Z(t))_{t\geq 0}$ defined in (4.20) is dual to the block-counting process $(L(t))_{t\geq 0}$ with *duality function* $H\colon\ S\times S'\to\mathbb{R}$ defined by

$$
H\Big(\big(x_\xi,(y_{\xi,m})_{m\in\mathbb{N}_0}\big)_{\xi\in\Omega_N},\big(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0}\big)_{\xi\in\Omega_N}\Big) = \prod_{\xi\in\Omega_N} x_\xi^{m_\xi} \prod_{m\in\mathbb{N}_0} y_{\xi,m}^{n_{\xi,D_m}}. \tag{4.34}
$$

Proposition 4.2.7 (Duality relation). *Let* H *be as in* (4.34)*. Then, for all* $(x_\xi,(y_{\xi,m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N}\in S$ *and* $(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0})_{\xi\in\Omega_N}\in S'$*,*

$$
\begin{aligned}
&\mathbb{E}_{\left(x_\xi,(y_{\xi,m})_{m\in\mathbb{N}_0}\right)_{\xi\in\Omega_N}}\Big[H\Big(\big(x_\xi(t),(y_{\xi,m}(t))_{m\in\mathbb{N}_0}\big)_{\xi\in\Omega_N},(m_\xi,n_\xi)_{\xi\in\Omega_N}\Big)\Big]\\
&= \mathbb{E}_{\left(m_\xi,(n_{\xi,D_m})_{m\in\mathbb{N}_0}\right)_{\xi\in\Omega_N}}\Big[H\Big(\big(x_\xi,(y_{\xi,m})_{m\in\mathbb{N}_0}\big)_{\xi\in\Omega_N},\big(L_{(\xi,A)}(t),(L_{(\xi,D_m)}(t))_{m\in\mathbb{N}_0}\big)_{\xi\in\Omega_N}\Big)\Big]
\end{aligned}
\tag{4.35}
$$

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

Proposition 4.2.7 was proved in [43, Section 2.4]. Since the duality function H captures all the mixed moments of $(Z(t))_{t\geq 0}$, the duality relation is that of a *moment dual.*

Remark 4.2.8 (Duality relation in terms of the effective geographic space). Interpreting $(Z(t))_{t\geq 0}$ as a process on the effective geographic space $\mathbb{S}=\Omega_N\times\{A,(D_m)_{m\in\mathbb{N}_0}\}$, we can rewrite (4.20) as

$$
\begin{aligned}
\mathrm{d}z_{(\xi,R_\xi)}(t) = &\sum_{(\xi,R_\xi)\in\mathbb{S}} b^{\Omega_N}((\xi,R_\xi),(\eta,R_\eta))[z_{(\eta,R_\eta)}(t)-z_{(\xi,R_\xi)}(t)]\,\mathrm{d}t\\
&+ 1_{\{R_\xi=A\}}\sqrt{g(z_{(\xi,R_\xi)}(t))}\,\mathrm{d}w_\xi(t), \qquad (\xi,R_\xi)\in\mathbb{S},
\end{aligned}
\tag{4.36}
$$

where $b^{\Omega_N}(\cdot,\cdot)$ is the transition kernel defined in (4.31). If $g=dg_{\mathrm{FW}}$, then we can write its dual process as follows. Let $(L(t))_{t\geq 0}=(L(\mathcal{C}(t))_{t\geq 0}$ be the block-counting process that at each site $(\xi,\mathbb{R}_\xi)\in\mathbb{S}$ counts the number of partition elements of $\mathcal{C}(t)$, i.e.,

$$
\begin{aligned}
L(t) &= (L_{(\xi,R_\xi)}(t))_{(\xi,R_\xi)\in\mathbb{S}},\\
L_{(\xi,R_\xi)}(t) &= L_{(\xi,R_\xi)}(\mathcal{C}(t)) = \sum_{\ell=1}^{\bar{n}} 1_{\{\eta_\ell(t)=(\xi,R_\xi)\}}.
\end{aligned}
\tag{4.37}
$$

Rewrite the duality function H in (4.34) as

$$
H\Big(\big(z_{(\xi,R_\xi)},l_{(\xi,R_\xi)}\big)_{(\xi,R_\xi)\in\mathbb{S}}\Big) = \prod_{(\xi,R_\xi)\in\mathbb{S}} z_{(\xi,R_\xi)}^{l_{(\xi,R_\xi)}}. \tag{4.38}
$$

Then, for $z \in S$ and $l \in S'$, the duality relation in (4.35) reads

$$\mathbb{E}_{z(\xi,R_\xi)}\big[H(z_{(\xi,R_\xi)}(t), l_{(\xi,R_\xi)})\big] = \mathbb{E}_{l(\xi,R_\xi)}\big[H(z_{(\xi,R_\xi)}, L_{(\xi,R_\xi)}(t))\big]. \tag{4.39}$$

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 process moving according to the transition kernel $b(\cdot,\cdot)$ defined in (4.31). Interpreting the duality relation in terms of the geographic space Ω_N, we see that an ancestral lineage is a random walk on Ω_N, with internal states A and $(D_m)_{m\in\mathbb{N}_0}$. Both interpretations turn out to be useful when we analyse the long-time behaviour of the system. ■

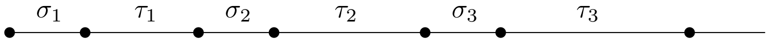

Figure 4.6: Renewal process induced by a lineage in the dual moving according to the transition kernel $b(\cdot,\cdot)$. For $k \in \mathbb{N}$, σ_k denotes the kth active period and τ_k the kth dormant period.

Remark 4.2.9 (The renewal process induced by the dual process). The partition elements describing the dual process give rise to a renewal process on the active state A and the dormant state $D = \bigcup_{m\in\mathbb{N}_0} D_m$. Since the only transition a dormant lineage can make is to become active, irrespectively of its colour, each dual lineage induces a sequence of active and dormant time lapses. Let $(\sigma_k)_{k\in\mathbb{N}}$ denote the successive active time periods and $(\tau_k)_{k\in\mathbb{N}}$ the successive dormant time periods (see Fig. 4.6). Then $(\sigma_k)_{k\in\mathbb{N}}$ and $(\tau_k)_{k\in\mathbb{N}}$ are sequences of i.i.d. random variables with marginal laws (recall (4.13))

$$\mathbb{P}(\sigma_1 > t) = \mathrm{e}^{-\chi t}, \quad \mathbb{P}(\tau_1 > t) = \sum_{m\in\mathbb{N}_0} \frac{K_m \frac{e_m}{N^m}}{\chi}\, \mathrm{e}^{-\frac{e_m}{N^m} t}, \qquad t \geq 0. \tag{4.40}$$

Remark 4.2.10 (Wake up times). The renewal process in Fig. 4.6 is key to understanding the long-time behaviour of the model (as we will see in Section 4.3). Note that

$$\tau = \tau_1 \tag{4.41}$$

represents *the typical wake-up time of a lineage in the dual.* By choosing specific sequences $(K_m)_{m\in\mathbb{N}_0}$ and $(e_m)_{m\in\mathbb{N}_0}$ we can mimic different wake-up time distributions. In particular, if we allow $\rho = \sum_{m\in\mathbb{N}_0} K_m = \infty$ (recall (4.14)), then τ may have a fat-tail (examples are given in Section 4.3). In other words, *the internal structure of the seed-bank allows us to model fat-tailed wake-up times without loosing the Markov property of the evolution.* ■

Note that even when there is no dual, i.e., $g \in \mathcal{G}$ with $g \neq dg_{\mathrm{FW}}$, we can still define τ by (4.41), since τ_1 in (4.40) is a random variable that depends only on the sequences $(K_m)_{m\in\mathbb{N}_0}$ and $(e_m)_{m\in\mathbb{N}_0}$, and we can still interpret τ as the typical wake-up time of an individual in the population. ■

§4.2.5 Clustering criterion

- **Clustering criterion for Fisher-Wright diffusion function**

In [43] we showed that the system exhibits a dichotomy between *coexistence* (= locally multi-type equilibria) and *clustering* (= locally mono-type equilibria). The clustering criterion is based on the dual and requires the notion of colour regularity. We call a law translation invariant when it is *invariant under the group action.*

Definition 4.2.11 (Colour regular initial measures). We say that a translation invariant initial measure $\mu(0)$ is *colour regular* when

$$\lim_{m\to\infty} \mathbb{E}_{\mu(0)}[y_{0,m}] \quad \text{exists.} \tag{4.42}$$

This condition is needed because, as time progresses, lineages starting from slower and slower seed-banks become active and bring new types into the active population. Without control on the initial states of the slow seed-banks, there may be no convergence to equilibrium. ■

The key clustering criterion is the following.

Proposition 4.2.12 (Clustering criterion). *Suppose that $\mu(0)$ is translation invariant. If $\rho = \infty$ (recall (4.14)), then additionally suppose that $\mu(0)$ is colour regular. 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 4.2.12 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 was given in [43, Section 4.3]. The proof is valid for any geographic space given by a countable Abelian group endowed with the discrete topology, of which Ω_N is an example.

- **Clustering criterion for general diffusion function**

For $g \in \mathcal{G}$ with $g \neq dg_{\mathrm{FW}}$ no dual is available and hence we cannot use the clustering criterion in Proposition 4.2.12. However, as shown in [43], we can argue by duality comparison arguments (see [43, Lemma 5.5 and Lemma 6.3]) that the system evolving according to (4.20) with $g \in \mathcal{G}$ clusters if and only if the system with $g = dg_{\mathrm{FW}}$ for some $d \in (0,\infty)$ clusters. In particular, for $g = dg_{\mathrm{FW}}$, $d \in (0,\infty)$, whether or not the system clusters does not depend on the resampling rate d.

§4.3 Main results: $N < \infty$, identification of clustering regime

In this section we identify the *clustering regime*, i.e., the range of *parameters* for which the clustering criterion in Proposition 4.2.12 is met. In [43, Section 3.2, Theorem

3.3] we derived a necessary and sufficient condition for when clustering prevails, for any geometric space given by a countable Abelian group endowed with the discrete topology. Recall χ in (4.13), ρ in (4.14) and τ in (4.41),. From (4.40) it follows that

$$\mathbb{E}[\tau] = \sum_{m\in\mathbb{N}_0} \frac{K_m}{\chi} = \frac{\rho}{\chi}, \tag{4.43}$$

and hence the mean wake-up time is finite if $\rho < \infty$ and infinite if $\rho = \infty$. In Section 4.3.1 we look at $\rho < \infty$ and in Section 4.3.2 at $\rho = \infty$. In Section 4.3.3 we summarise our findings and identify the clustering regime.

§4.3.1 Finite mean wake-up time

Suppose that the system evolving according to (4.20) has a translation invariant initial measure $\mu(0)$ with density $\theta \in (0,1)$. Then [43, Theorem 3.3] says that for $\rho < \infty$ clustering occurs if and only if

$$\int_1^\infty \mathrm{d}t\, a_t^{\Omega_N}(0,0) = \infty. \tag{4.44}$$

It is known that (4.44) holds for the hierarchical migration defined in (4.6) if and only if [19, Section 3]

$$\sum_{k\in\mathbb{N}_0} \frac{1}{c_k} = \infty. \tag{4.45}$$

Hence, for $\rho < \infty$, the clustering criterion depends on the migration kernel *only* and the seed-bank has no effect.

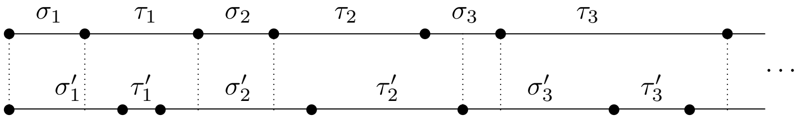

Figure 4.7: Successive periods during which the two random walks are active and dormant (recall (4.40) *and Fig. 4.6). The time lapses between successive pairs of dotted lines represent periods of* joint activity.

In view of Proposition 4.2.12, if $g = dg_{\mathrm{FW}}$, then clustering prevails if and only if two lineages in the dual coalesce with probability 1. Recall that two lineages in the dual can only coalesce when they are at the same site and are both active. Since the rate of coalescence is $d \in (0,\infty)$, each time this happens the two lineages have a positive probability to coalesce before moving or becoming dormant. Therefore, clustering prevails if and only if two lineages meet infinitely often while being active. This happens exactly when (4.44) holds. The fact that the seed-bank plays no role can be seen from the dual. Each lineage in the dual moves according to the transition kernel $b(\cdot,\cdot)$ (recall (4.31)). Looking at the renewal process induced by the dual process (recall Remark 4.2.9 and Fig. 4.7), we see that for $\rho < \infty$ the probability that a lineage in the dual is active at time t is approximately $\frac{1}{1+\rho}$ for large t. The total activity time of a lineage up to time t is therefore approximately $\frac{1}{1+\rho}t$ for large t. Hence the total time the two lineages in the dual are at the same site and are both active is approximately

$$\int_1^\infty \mathrm{d}t \left(\frac{1}{1+\rho}\right)^2 a_{2\frac{1}{1+\rho}t}(0,0), \tag{4.46}$$

By Polya's argument, if the integral in (4.46) is infinite, then two lineages in the dual meet infinitely often while being active. After a variable transformation, (4.46) becomes the integral in (4.44) up to a constant. (For a formal proof of the criterion in (4.44), we refer to [43].) By the above argument, we can think of the integral in (4.44) as the *total hazard of coalescence* of two dual lineages. To get the result for general $g \in \mathcal{G}$ we must invoke the duality comparison arguments mentioned in Section 4.2.5.

In terms of the degree of the random walk (recall Remark 4.2.1), (4.44) corresponds to hierarchical migration with degree 0^-. The same criterion as in (4.44) was found in [36] for interacting Fisher-Wright diffusions on the hierarchical lattice without seed-bank ($\rho = 0$). Hence we conclude that for $\rho < \infty$ the seed-bank does not affect the dichotomy.

§4.3.2 Infinite mean wake-up time

If $\rho = \infty$, then the seed-bank does affect the dichotomy. To apply the criterion in [43, Theorem 3.3], we assume that the system evolving according to (4.20) has a translation-invariant initial measure $\mu(0)$ with density $\theta \in (0,1)$ that is colour regular.

The criterion for clustering that was derived in [43] for $\rho = \infty$ applies to wake-up times τ (recall (4.41)) of the form

$$\frac{\mathbb{P}(\tau \in \mathrm{d}t)}{\mathrm{d}t} \sim \varphi(t)\, t^{-(1+\gamma)}, \quad t \to \infty, \quad \gamma \in (0,1], \tag{4.47}$$

with φ *slowly varying at infinity.* Define

$$\hat{\varphi}(t) = \begin{cases} \varphi(t), & \gamma \in (0,1), \\ \mathbb{E}\left[\tau \wedge t\right] & \gamma = 1. \end{cases} \tag{4.48}$$

As shown in [8, Section 1.3], every slowly varying function φ may be assumed to be infinitely differentiable and to be represented by the integral

$$\varphi(t) = \exp\left[\int_{(\cdot)}^t \frac{\mathrm{d}u}{u}\,\psi(u)\right] \tag{4.49}$$

for some $\psi\colon [0,\infty) \to \mathbb{R}$ such that $\lim_{u\to\infty} |\psi(u)| = 0$. From (4.47) we see that $\hat{\varphi}(t)$ is also slowly varying. If we assume that $|\psi(u)| \leq C/\log u$ for some $C < \infty$, then the system clusters if and only if (see [43, Section 3.2])

$$\int_{(\cdot)}^\infty \mathrm{d}t\, \hat{\varphi}(t)^{-1/\gamma}\, t^{-(1-\gamma)/\gamma}\, \hat{a}_t(0,0) = \infty. \tag{4.50}$$

Note that γ in (4.47) is the *tail exponent* of the typical wake-up time τ (recall Remark 4.2.9) and depends on the sequences $\underline{e}, \underline{K}$ in (4.10) governing the exchange with the seed-bank. If $g = dg_{\mathrm{FW}}$, then in view of Theorem 4.2.12 the criterion in (4.50) determines whether two lineages in the dual coalesce with probability 1.

In Section 5 we will use the renewal process induced by the dual (recall Remark 4.2.9) to show that (4.50) indeed gives the *total hazard of coalescence* of two dual lineages. Therefore the integral in (4.50) is the counterpart of (4.44). The rate of coalescence again does not affect the dichotomy: in [43] a duality comparison argument was used to show that (4.50) gives the clustering criterion also for $g \in \mathcal{G}$ with $g \neq dg_{\mathrm{FW}}$. The effect of the seed-bank on the dichotomy is embodied by the term $\hat{\varphi}(t)^{-1/\gamma}\, t^{-(1-\gamma)/\gamma}$ in (4.50). The criterion in (4.50) shows that there is a competition between migration and exchange with the seed-bank.

For the special case where $\hat{\varphi}(t) \asymp 1$, the criterion in (4.50) says that (recall Remark 4.2.1)

$$\text{clustering} \quad \Longleftrightarrow \quad \text{either } \delta^- \leq -\frac{1-\gamma}{\gamma} \text{ or } \delta^+ < -\frac{1-\gamma}{\gamma}. \tag{4.51}$$

Condition (4.50) implies that for $\gamma \in (0, \frac{1}{2})$ no clustering is possible: the typical wake-up time has such a heavy tail that with a positive probability two dual lineages do not meet, irrespective of the migration.

Definition 4.3.1. In what follows we will focus on the following two specific parameter regimes:

- *Asymptotically polynomial*, i.e.,

$$\begin{aligned} &K_k \sim Ak^{-\alpha}, \quad e_k \sim Bk^{-\beta}, \quad c_k \sim Fk^{-\phi}, \quad k \to \infty,\\ &A, B, F \in (0,\infty),\ \alpha, \beta, \phi \in \mathbb{R}. \end{aligned} \tag{4.52}$$

- *Pure exponential*, i.e.,

$$K_k = K^k, \quad e_k = e^k, \quad c_k = c^k, \quad k \in \mathbb{N}_0,\ K, e, c \in (0,\infty). \tag{4.53}$$

Note that both (4.7) and (4.12) are satisfied for $N \to \infty$. Also note that an infinite seed-bank corresponds to $\alpha \in (-\infty, 1]$, respectively, $K \in [1,\infty)$. □

The scaling of the wake-up time and the migration kernel in these parameter regimes are as follows.

Theorem 4.3.2 (Scaling of wake-up time and migration kernel). *Suppose that $\rho = \infty$. Then*

(a) Subject to (4.52)*,*

$$\gamma = 1, \quad \varphi(t) \asymp (\log t)^{-\alpha}, \quad \hat{\varphi}(t) \asymp \begin{cases} (\log t)^{1-\alpha}, & \alpha \in (-\infty, 1),\\ \log\log t, & \alpha = 1, \end{cases} \tag{4.54}$$

$$a_t^{\Omega_N}(0,0) \asymp t^{-1} \log^{\phi} t.$$

(b) Subject to (4.53)*,*

$$\gamma = \gamma_{N,K,e} = \frac{\log(N/Ke)}{\log(N/e)}, \quad \varphi(t) \asymp 1, \quad \hat{\varphi}(t) \asymp \begin{cases} 1, & K \in (1,\infty),\\ \log t, & K = 1, \end{cases} \tag{4.55}$$

$$a_t^{\Omega_N}(0,0) \asymp t^{-1-\delta_{N,c}},$$

where

$$\delta_{N,c} = \frac{\log c}{\log(N/c)}. \tag{4.56}$$

Theorem 4.3.2 will be proved in Section 5.

Note that, by (4.55), $\gamma_{N,K,e} = 1$ for all N when $K = 1$, while $\gamma_{N,K,e} < 1$ for all N when $K > 1$, but with $\gamma_{N,K,e} \uparrow 1$ as $N \to \infty$. Also note that, subject to (4.52), (4.54) says that the degree of the random walk is 0^- for $\phi \geq -1$ and 0^+ for $\phi < -1$, while subject to (4.53), by (4.55), the degree of the random walk is $\delta^-_{N,c}$, which is 0 for all N when $c = 1$, and tends to 0 as $N \to \infty$ from above when $c > 1$ and from below as $c < 1$. Thus, both (4.52) and (4.53) with $N \to \infty$ correspond to a *critically recurrent migration* and a *critically infinite seed-bank*.

§4.3.3 Clustering regime

Summarising the above discussion, we can now identify the clustering regime for both finite and infinite seed-banks.

Theorem 4.3.3 (Clustering regime). (1) *If $\rho < \infty$, then clustering prevails if and only if*

$$\sum_{k \in \mathbb{N}_0} \frac{1}{c_k} = \infty. \tag{4.57}$$

(2) *If $\rho = \infty$, then clustering prevails for N large enough*

(a) Subject to (4.52) *if and only if*

$$-\phi \leq \alpha \leq 1. \tag{4.58}$$

(b) Subject to (4.53) *if and only if*

$$Kc \leq 1 \leq K. \tag{4.59}$$

Also Theorem 4.3.3 will be proved in Section 5.

Note that for $\rho < \infty$ the clustering regime follows by combining (4.44) and (4.45), while for $\rho = \infty$ the clustering regime follows by substituting into (4.50) the scaling of the wake-up times and the migration kernel stated in Theorem 4.3.2.

Remark 4.3.4. Note that subject to (4.52), respectively, (4.53), $\rho < \infty$ implies that $\alpha > 1$, respectively, $K < 1$, and so the clustering regime is $-\phi \leq 1$, respectively, $c \leq 1$ (recall (4.57)), which are less stringent than (4.58), respectively, (4.59). ■

§4.4 Main results: $N \to \infty$, renormalisation and multi-scale limit

This section contains our multi-scale hierarchical limit theorems. The multi-scale hierarchical limit theorems analyse the evolution of the block averages defined in Definition 4.2.3. In Section 4.4.1 we recall a path topology referred to as the *Meyer-Zheng* *topology*, which we will need in part of our multi-scale hierarchical limit theorems. In Section 4.4.2 we present the conceptual ingredients needed for our theorems. In Section 4.4.3 we state two versions of the hierarchical multi-scale limit (Theorems 4.4.2 and 4.4.4), and comment on how they are related to each other. In Section 4.4.4 we explain how they arise from a heuristic analysis of the SSDE in (4.20).

§4.4.1 Intermezzo: Meyer-Zheng topology

Recall the block averages defined in (4.2.3) and their evolution equations in (4.24). In the limit as $N \to \infty$, some of the pre-factors in (4.24) diverge as a result of the speeding up of time. This makes the processes increasingly more volatile: paths becomes rougher and rougher during rarer and rarer times. Therefore we cannot work with weak convergence on path space $C([0,\infty),E)$ w.r.t. the topology generated by the *sup-norm* on compacts, or on path space $D([0,\infty),E)$ w.r.t. the Skorohod metric on compacts. Rather we must follow the methodology used in [23, pp. 792–794] and employ the so-called *Meyer-Zheng topology* on *pseudopaths*, (see [59]), which is based on the following idea. Consider functions $f\colon\ [0,\infty) \to E$, with (E,d) a Polish space, and sequences of functions $(f_n)_{n\in\mathbb{N}}$ that are càdlàg paths, i.e., functions in the Skorohod space $D([0,\infty),E)$. Then $(f_n)_{n\in\mathbb{N}}$ converges to f in the Meyer-Zheng topology if and only if

$$\lim_{n\to\infty} \int_a^b \mathrm{d}t \left[1 \wedge d(f(t), f_n(t))\right] = 0 \qquad \forall\ 0 \leq a < b < \infty. \tag{4.60}$$

However, the topology induced by the metric in (4.60) does not turn $D([0,\infty),E)$ into a *closed* space (while in order to apply the classical theory of weak convergence of probability laws on path space we need the path space to be Polish).

To turn the idea from (4.60) into a manageable topology, we proceed by defining a *space of pseudopaths* equipped with the *Meyer-Zheng topology.* If (E,d) is a Polish space and $s \mapsto v(s)$ is a measurable map from $[0,\infty)$ to E, then the pseudopath ψ_v is the *probability measure* ρ on $[0,\infty) \times E$, defined by

$$\rho((a,b)\times B) = \int_a^b \mathrm{d}s\, \mathrm{e}^{-s}\, 1_B(v(s)), \qquad B \in \mathcal{B}(E), \tag{4.61}$$

Hence ψ_v is the image measure of $\mathrm{e}^{-t}\mathrm{d}t$ under the mapping $t \to (t, v(t))$. In other words, we consider the *weighted occupation measure* of the path in E in order to describe paths that are *regular representatives* in the space of functions once we take into account (4.60). Note that a piece-wise constant càdlàg path is uniquely determined by its occupation measure. So is a continuous path with continuous local times. The space of all pseudopaths is denoted by Ψ.

Since pseudopaths are measures on $[0,\infty]\times E$, convergence of pseudopaths is defined as *weak convergence* of *probability measures on* $[0,\infty]\times E$. A sequence $(v_n)_{n\in\mathbb{N}}$ of measurable maps from $[0,\infty)\times E$ is said to converge in the Meyer-Zheng topology to a measurable map v if $\lim_{n\to\infty}\psi_{v_n} = \psi_v$, i.e., $\lim_{n\to\infty}\psi_{v_n} f = \psi_v f$ for all continuous bounded functions f on $[0,\infty]\times E$.

Remark 4.4.1 (Pseudopaths). The space Ψ of pseudopaths endowed with the Meyer-Zheng topology is Polish, but the space $D([0,\infty),E)$ endowed with the Meyer-Zheng topology is not Polish (see [59, p. 372]). ■

In what follows, each time convergence holds in the Meyer-Zheng topology we will say so explicitly. If no topology is mentioned, then we mean convergence in $\mathcal{C}_b([0,\infty),[0,1])$. In Appendix B.2 we collect some basic facts about the Meyer-Zheng topology taken from [59] and [53].

§4.4.2 Main ingredients for the hierarchical multi-scale limit

Recall the definition of θ_x and θ_{y_m} in (4.21). Define

$$\vartheta_k = \frac{\theta_x + \sum_{m=0}^k K_m \theta_{y_m}}{1+\sum_{m=0}^k K_m}, \qquad k \in \mathbb{N}_0. \tag{4.62}$$

For $\rho < \infty$, and for $\rho = \infty$ under the additional assumption of colour regularity (recall Proposition 4.2.12), we have

$$\lim_{k\to\infty} \vartheta_k = \theta \quad \text{ for some } \theta \in [0,1]. \tag{4.63}$$

Define the *slowing-down constants* ($E_0 = 1$)

$$E_k = \frac{1}{1+\sum_{m=0}^{k-1} K_m}, \qquad k \in \mathbb{N}_0. \tag{4.64}$$

For $l \in \mathbb{N}_0$, let

$$\big(\theta, (y_{m,l})_{m\in\mathbb{N}_0}\big) \tag{4.65}$$

be a sequence of random variables taking values in $[0,1]$, and let

$$\Big(z_{l,(\theta,(y_{m,l})_{m\in\mathbb{N}_0})}(t)\Big)_{t\geq 0} = \Big(x_l(t), (y_{m,l}(t))_{m\in\mathbb{N}_0}\Big)_{t\geq 0} \tag{4.66}$$

be the *full process* evolving according to

$$\begin{aligned} \mathrm{d}x_l(t) = E_l \Bigg[c_l[\theta - x_l(t)]\,\mathrm{d}t + \sqrt{(\mathcal{F}^{(l)}g)(x_l(t))}\,\mathrm{d}w(t) + K_l e_l\,[y_{l,l}(t) - x_l(t)]\,\mathrm{d}t\Bigg],\\ \begin{array}{ll} y_{m,l}(t) = x_l(t), & 0 \leq m < l,\\ \mathrm{d}y_{l,l}(t) = e_l\,[x_l(t) - y_{l,l}(t)]\,\mathrm{d}t, & m = l,\\ y_{m,l}(t) = y_{m,l}, & m > l. \end{array}\end{aligned} \tag{4.67}$$

where $\mathcal{F}^{(l)}g$ is an element of $\mathcal{G}$, (recall (4.15)), that will be defined in (4.76) below. By [72] the above SSDE has a unique solution for every initial measure. For $l \in \mathbb{N}_0$, let

$$(z^{\mathrm{eff}}_{l,\theta}(t))_{t\geq 0} = \big(x^{\mathrm{eff}}_l(t), y^{\mathrm{eff}}_{l,l}(t)\big)_{t\geq 0} \tag{4.68}$$

be the *effective process* evolving according to

$$\begin{aligned} \mathrm{d}x_l^{\mathrm{eff}}(t) &= E_l\left[c_l\,[\theta - x_l^{\mathrm{eff}}(t)]\,\mathrm{d}t + \sqrt{(\mathcal{F}^{(l)}g)(x_l^{\mathrm{eff}}(t))}\,\mathrm{d}w(t) + K_l e_l\,[y_{l,l}^{\mathrm{eff}}(t) - x_l^{\mathrm{eff}}(t)]\,\mathrm{d}t\right],\\ \mathrm{d}y_{l,l}^{\mathrm{eff}}(t) &= e_l\,[x_l^{\mathrm{eff}}(t) - y_{l,l}^{\mathrm{eff}}(t)]\,\mathrm{d}t. \end{aligned} \tag{4.69}$$

Comparing (4.67) with (4.69), we see that the effective process looks at the non-trivial components of the full process.

Apart from (4.66) and (4.68), we need the following list of *ingredients* to formally state the multi-scale limit:

(a) For $l \in \mathbb{N}_0$ and $t > 0$, define the *estimators* for the finite system by

$$\begin{aligned} \bar{\Theta}^{(l),\Omega_N}(t) &= \frac{1}{N^l}\sum_{\xi\in B_l}\frac{x_\xi^{\Omega_N}(t) + \sum_{m=0}^{l-1}K_m y_{\xi,m}^{\Omega_N}(t)}{1+\sum_{m=0}^{l-1}K_m},\\ \Theta_x^{(l),\Omega_N}(t) &= \frac{1}{N^l}\sum_{\xi\in B_l} x_\xi^{\Omega_N}(t),\\ \Theta_{y_m}^{(l),\Omega_N}(t) &= \frac{1}{N^l}\sum_{\xi\in B_l} y_{\xi,m}^{\Omega_N}(t), \qquad m\in\mathbb{N}_0, \end{aligned} \tag{4.70}$$

and put

$$\begin{aligned} \mathbf{\Theta}^{(l),\Omega_N}(t) &= \big(\Theta_x^{(l),\Omega_N}(t), \big(\Theta_{y_m}^{(l),\Omega_N}(t)\big)_{m\in\mathbb{N}_0}\big),\\ \mathbf{\Theta}^{\mathrm{eff},(l),\Omega_N}(t) &= \big(\bar{\Theta}^{(l),\Omega_N}(t), \Theta_{y_l}^{(l),\Omega_N}(t)\big). \end{aligned} \tag{4.71}$$

We call $(\mathbf{\Theta}^{(l),\Omega_N}(t))_{t\geq 0}$ the *full estimator process* and $(\mathbf{\Theta}^{\mathrm{eff},(l),\Omega_N}(t))_{t\geq 0}$ the *effective process*. Note that $\Theta_x^{(l),\Omega_N}(t)$ is the empirical average of the active components in the l-block, while $\Theta_{y_m}^{(l),\Omega_N}(t)$, is the empirical average of the m-dormant components in the l-block, both without scaling of time. Note that $\Theta_x^{(l),\Omega_N}(N^l t) = x_l^{\Omega_N}(t)$. The *level-$l$ estimator* $\bar{\Theta}^{(l),\Omega_N}(t)$ will play an important role in our analysis. Using (4.24), we can derive the evolution equations of $\bar{\Theta}^{(l),\Omega_N}(N^l t)$. We see that in the evolution of $\bar{\Theta}^{(l),\Omega_N}(N^l t)$ no rates appear that tend to infinity as $N\to\infty$. However, in the evolution of $\Theta_x^{(l),\Omega_N}(N^l t)$ and $\Theta_{y_m}^{(l),\Omega_N}(N^l t)$ for $m < l$ the rates describing the interaction between the active and the dormant population tend to infinity as $N\to\infty$.

(b) For $l\in\mathbb{N}_0$, consider *time scales* $N^l t_l$ such that

$$\mathcal{L}\big[\bar{\Theta}^{(l),\Omega_N}(N^l t_l - L(N)N^{l-1}) - \bar{\Theta}^{(l),\Omega_N}(N^l t_l)\big] = \delta_0 \tag{4.72}$$

for all $L(N)$ satisfying $\lim_{N\to\infty} L(N) = \infty$ and $\lim_{N\to\infty} L(N)/N = 0$, but not for $L(N) = N$. In words, $N^l t_l$ is the time scale on which $(\bar{\Theta}^{(l),\Omega_N}(N^l t_l))_{t_l>0}$ is no longer a fixed process.

(c) For $l\in\mathbb{N}_0$ the *invariant measure* for the limiting evolution of the l-block averages in (4.67) is denoted by

$$\Gamma_{(\theta,y_l)}^{(l)}, \qquad y_l = (y_{m,l})_{m\in\mathbb{N}_0}. \tag{4.73}$$

(The existence of and convergence to this equilibrium will be proved in Section 9.2.) Note that $\Gamma^{(l)}_{(\theta,y_l)}$ depends on choice of the rates E_l, c_l, K_l, e_l in (4.67). The *invariant measure* of the limiting evolution for the effective l-block process in (4.69) is denoted by

$$\Gamma^{\mathrm{eff},(l)}_{\theta}. \tag{4.74}$$

Also $\Gamma^{\mathrm{eff},(l)}_{\theta}$ depends on the choice of the rates E_l, c_l, K_l, e_l.

(d) For $l \in \mathbb{N}_0$, let $\mathcal{F}^{E_l,c_l,K_l,e_l}$ denote the *renormalisation transformation* acting on $\mathcal{G}$ defined by

$$(\mathcal{F}^{E_l,c_l,K_l,e_l} g)(\theta) = \int_{[0,1]^2} g(x)\, \Gamma^{\mathrm{eff},(l)}_{\theta}(\mathrm{d}x), \qquad \theta \in [0,1]. \tag{4.75}$$

(In Section 6.3 we show that $\mathcal{F}g \in \mathcal{G}$.) For $k \in \mathbb{N}_0$, define the *iterate* of the renormalisation transformation as the composition

$$\mathcal{F}^{(k)} = \mathcal{F}^{E_{k-1},c_{k-1},K_{k-1},e_{k-1}} \circ \cdots \circ \mathcal{F}^{E_0,c_0,K_0,e_0}. \tag{4.76}$$

(e) For $k \in \mathbb{N}_0$, define the *interaction chain* [25]

$$(M^k_{-l})_{-l=-(k+1),-k,\dots,0} \tag{4.77}$$

as the *time-inhomogeneous* Markov chain on $[0,1] \times [0,1]^{\mathbb{N}_0}$ with initial state

$$M^k_{-(k+1)} = (\vartheta_k, \overbrace{\vartheta_k, \cdots, \vartheta_k}^{k+1 \text{ times}}, \theta_{y_{k+1}}, \theta_{y_{k+2}}, \cdots) \tag{4.78}$$

that evolves from time $-(l+1)$ to time $-l$ according to the transition kernel $Q^{[l]}$ on $[0,1] \times [0,1]^{\mathbb{N}_0}$ given by

$$Q^{[l]}(u, \mathrm{d}v) = \Gamma^{(l)}_{u}(\mathrm{d}v). \tag{4.79}$$

(See Fig. 4.9.) For $k \in \mathbb{N}_0$, define the *effective interaction chain*

$$(M^{\mathrm{eff},k}_{-l})_{-l=-(k+1),-k,\dots,0} \tag{4.80}$$

as the *time-inhomogeneous* Markov chain on $[0,1] \times [0,1]$ with initial state

$$M^{\mathrm{eff},k}_{-(k+1)} = (\vartheta_k, \theta_{y_{k+1}}) \tag{4.81}$$

that evolves from time $-(l+1)$ to time $-l$ according to the transition kernel $Q^{[l]}$ on $[0,1] \times [0,1]$ given by

$$Q^{\mathrm{eff},[l]}(u, \mathrm{d}v) = \Gamma^{\mathrm{eff},(l)}_{u_x}(\mathrm{d}v), \tag{4.82}$$

where u_x denotes the first component of $u = (u_x, u_y)$.(See Fig. 4.8.) We denote the components of $\left(M^{\mathrm{eff},k}_{-l}\right)$ by

$$M^{\mathrm{eff},k}_{-l} = \big(M^{\mathrm{eff},k}_{-l,x}, M^{\mathrm{eff},k}_{-l,y}\big). \tag{4.83}$$

$$\begin{tikzcd}
M^{k,\mathrm{eff}}_{-(k+1)} = (\vartheta_k, \theta_{k+1}) \arrow[d, "Q^{[k]}\left(M^{k,\mathrm{eff}}_{-(k+1)}, (du,dv)\right) = \Gamma^{\mathrm{eff}}_{\vartheta_k}(du,dv)"] \\
M^{k,\mathrm{eff}}_{-k} = (x_k(t_k), y_{k,k}(t_k)) \arrow[d, "Q^{[k-1]}\left(M^{k,\mathrm{eff}}_{-k}, (du,dv)\right) = \Gamma^{\mathrm{eff}}_{x_k(t_k)}(du,dv)"] \\
M^{k,\mathrm{eff}}_{-(k-1)} = (x_{k-1}(t_{k-1}), y_{k-1,k-1}(t_{k-1})) \arrow[d, "Q^{[k-2]}\left(M^{k,\mathrm{eff}}_{-(k-1)}, (du,dv)\right) = \Gamma^{\mathrm{eff}}_{x_{k-1}(t_{k-1})}(du,dv)"] \\
\vdots \arrow[d] \\
M^{k,\mathrm{eff}}_{-1} = (x_1(t_1), y_{1,1}(t_1)) \arrow[d, "Q^{[0]}\left(M^{k,\mathrm{eff}}_{-1}, (du,dv)\right) = \Gamma^{\mathrm{eff}}_{x_1(t_1)}(du,dv)"] \\
M^{k,\mathrm{eff}}_{0} = (x_0(t_0), y_{0,0}(t_0))
\end{tikzcd}$$

Figure 4.8: Effective interaction chain.

§4.4.3 Hierarchical multi-scale limit theorems

First we present and discuss the scaling of the effective process. Afterwards we do the same for the full process.

- **Effective process**

We present one of our main theorems, the hierarchical mean-field limit for the effective process. We will use the process and notation introduced in Section 4.4.2.

Theorem 4.4.2 (Hierarchical mean-field: the effective process). *Suppose that the initial state of the hierarchical system is given by* (4.21)*. Let* $L(N)$ *be such that* $\lim_{N\to\infty} L(N) = \infty$ *and* $\lim_{N\to\infty} L(N)/N = 0$*. For* $k \in \mathbb{N}$ *and* $t_k, \dots, t_0 \in (0,\infty)$*, set* $\bar{t} = N^k L(N) + \sum_{n=0}^{k} N^n t_n$*.*

(a) For $k \in \mathbb{N}$*,*

$$\lim_{N\to\infty} \mathcal{L}\left[\left(\mathbf{\Theta}^{\mathrm{eff},(l),\Omega_N}(\bar{t}\,)\right)_{l=k+1,k,\dots,0}\right] = \mathcal{L}\left[(M^{\mathrm{eff},k}_{-l})_{-l=-(k+1),-k,\dots,0}\right]. \qquad (4.84)$$

(b) For $k \in \mathbb{N}$,

$$\begin{aligned}
l > k\colon\ & \lim_{N\to\infty} \mathcal{L}\left[\left(\boldsymbol{\Theta}^{\mathrm{eff},(l),\Omega_N}(\bar{t}+N^k t)\right)_{t>0}\right] = \delta_{(\vartheta_l,\theta_{y_l})},\\
l = k\colon\ & \lim_{N\to\infty} \mathcal{L}\left[\left(\boldsymbol{\Theta}^{\mathrm{eff},(l),\Omega_N}(\bar{t}+N^l t)\right)_{t>0}\right] = \mathcal{L}\left[\left(z^{\mathrm{eff}}_{k,M^{\mathrm{eff},k}_{-(k+1),x}}(t)\right)_{t>0}\right],\\
l < k\colon\ & \lim_{N\to\infty} \mathcal{L}\left[\left(\boldsymbol{\Theta}^{\mathrm{eff},(l),\Omega_N}(\bar{t}+N^l t)\right)_{t>0}\right] = \mathcal{L}\left[\left(z^{\mathrm{eff}}_{l,M^{\mathrm{eff},k}_{-(l+1),x}}(t)\right)_{t>0}\right],
\end{aligned} \tag{4.85}$$

where the initial laws of the limiting processes are given by (see Fig. 4.8)

$$\begin{aligned}
&\mathcal{L}\left[z^{\mathrm{eff}}_{k,M^k_{-(k+1),x}}(0)\right] = \Gamma^{\mathrm{eff},(k)}_{M^k_{-(k+1),x}},\\
&\mathcal{L}\left[z^{\mathrm{eff}}_{k,M^k_{-(k+1),x}}(0)\right] = \Gamma^{\mathrm{eff},(k)}_{M^k_{-(l+1),x}},\\
&\Gamma^{\mathrm{eff},(l)}_{M^k_{-(l+1)}} = \int_{[0,1]^2}\cdots\int_{[0,1]^2}\Gamma^{\mathrm{eff},(k)}_{M^k_{-(k+1)}}(\mathrm{d}u_k)\cdots\Gamma^{\mathrm{eff},(l+1)}_{u_{l+2}}(\mathrm{d}u_{l+1})\Gamma^{\mathrm{eff},(l)}_{u_{l+1}}
\end{aligned} \tag{4.86}$$

Theorem 4.4.2 can be interpreted as follows. The statement in (a) shows that if we look at the effective process on multiple space-time scales simultaneously, then the joint distribution of the different block averages is the law of the two-dimensional interaction chain defined in (4.80) and depicted in Fig. 4.8. Note that the process $(\boldsymbol{\Theta}^{\mathrm{eff},(l),\Omega_N}(\bar{t}+N^l t))_{t>0}$ has at each level a different colour seed-bank average as second component, which is called *the effective seed-bank*. The statement in (b) describes the law of the path on different time scales.

- On time scale $\bar{t}+N^k t$ the l-block averages with $l > k$ are not moving, i.e., $(\boldsymbol{\Theta}^{\mathrm{eff},(l),\Omega_N}(\bar{t}+N^k t))_{t>0}$ converges to the constant process taking the value $(\vartheta_l,\theta_{y_l}) = \boldsymbol{\Theta}^{\mathrm{eff},(l),\Omega_N}(0)$.
- On time scale $\bar{t}+N^k t$ the k-block averages have reached equilibrium. The full k-block average feels a drift towards the full $(k+1)$-block average, which is still in its initial state ϑ_k. Therefore migration between the k-blocks in the hierarchical mean-field limit is replaced by a drift towards ϑ_k, and the k-blocks become independent. This phenomenon is called *decoupling* (or 'propagation of chaos'). The resampling function for the full estimator converges to $\mathcal{F}^{(k)}g$ (see (4.75)), the average diffusion function of the k-blocks. Finally, the full k-block exchanges individuals with the k-dormant population. Hence the k-dormant population is the effective seed-bank on space-timescale k Both the migration and the renormalisation are qualitatively similar to that of the hierarchical system without seed-bank [21]. However, the seed-bank still quantitatively affects the migration and the resampling through the slowing-down factor E_k. (In Section 4.4.4 we will see how the latter arises.)
- On time scale $\bar{t}+N^l t$ the l-block averages with $l < k$ are in a *quasi-equilibrium*. The full l-block averages feel a drift towards the instantaneous value of the $(l+1)$-block average at time $\bar{t}$. Therefore also the l-block averages decouple.

> The $(l+1)$-block average is not moving on time scale $\bar{t}+N^l t$, and so for $t = L(N)$ we see that the l-block averages equilibrate faster than the $(l+1)$-block averages moves. The resampling function is given by $\mathcal{F}^{(l)}g$, which is to be interpreted as the average diffusion function of the l-blocks. The full average interacts with the l-blocks of the l-dormant population, which is the effective seed-bank on level l. Again the full l-block average feels a slowing-down factor E_l.

Note that Theorem 4.4.2 only describes the limiting process of the combined block average $\bar{\Theta}^{(l),\Omega_N}$ and the effective seed-bank $\Theta^{(l),\Omega_N}_{y_l}$. It does not provide a full description of the system, which is in Theorem 4.4.4 below. We will see later that Theorem 4.4.2 does describe all the *non-trivial* components of the system.

Remark 4.4.3 (Quasi equilibria). Note that Theorem 4.4.2 does not depend on the choice of $t_k, \dots, t_0 \in (0,\infty)$. Since at each level $0 \leq l \leq k$ we start from time $\bar{t}$, the l-block averages have already reached a quasi-equilibrium. ■

$$\begin{tikzcd}
M^k_{-(k+1)} = \big(\vartheta_k, \overbrace{\vartheta_k, \cdots, \vartheta_k}^{k+1 \text{ times}}, \theta_{y_{k+1}}, \theta_{y_{k+2}}, \cdots\big) \arrow[d, "Q^{[k]}\left(M^k_{-(k+1)}, \mathrm{d}u\right) = \Gamma_{M^k_{-(k+1)}}(\mathrm{d}u)"] \\
M^k_{-k} = \big(x_k(t_k), \overbrace{x_k(t_k), \cdots, x_k(t_k)}^{k \text{ times}}, y_{k,k}(t_k), \theta_{y_{k+1}}, \theta_{y_{k+2}}, \cdots\big) \arrow[d, "Q^{[k-1]}\left(M^k_{-k}, \mathrm{d}u\right) = \Gamma_{M^k_{-k}}(\mathrm{d}u)"] \\
M^k_{-(k-1)} = \big(x_{k-1}(t_{k-1}), \overbrace{x_{k-1}(t_{k-1}), \cdots, x_{k-1}(t_{k-1})}^{k-1 \text{ times}}, y_{k-1,k-1}(t_{k-1}), y_{k,k}(t_k), \theta_{y_{k+1}}, \theta_{y_{k+2}}, \cdots\big) \arrow[d, "Q^{[k-2]}\left(M^k_{-(k-1)}, \mathrm{d}u\right) = \Gamma_{M^k_{-(k-1)}}(\mathrm{d}u)"] \\
\vdots \arrow[d] \\
M^k_{-1} = \big(x_1(t_1), x_1(t_1), y_{1,1}(t_1), y_{2,2}(t_2), \cdots, y_{k-1,k-1}(t_{k-1}), y_{k,k}(t_k), \theta_{y_{k+1}}, \theta_{y_{k+2}}, \cdots\big) \arrow[d, "Q^{[0]}\left(M^k_{-1}, \mathrm{d}u\right) = \Gamma_{M^k_{-1}}(\mathrm{d}u)"] \\
M^k_0 = \big(x_0(t_0), y_{0,0}(t_0), y_{1,1}(t_1), y_{2,2}(t_2), \cdots, y_{k-1,k-1}(t_{k-1}), y_{k,k}(t_k), \theta_{y_{k+1}}, \theta_{y_{k+2}}, \cdots\big)
\end{tikzcd}$$

Figure 4.9: Full interaction chain.

- **Full process**

To state our second main theorem, we will again use the process and the notation as defined in Section 4.4.2.

Theorem 4.4.4 (Hierarchical mean-field: full process). *Suppose that the initial state is given by* (4.21). *Let* $L(N)$ *be such that* $\lim_{N\to\infty} L(N) = \infty$ *and* $\lim_{N\to\infty} L(N)/N = 0$. *For* $k \in \mathbb{N}$ *and* $t_k, \dots, t_0 \in (0,\infty)$, *set* $\bar{t} = N^k L(N) + \sum_{n=0}^{k} N^n t_n$.

(a) For $k \in \mathbb{N}$,

$$\lim_{N\to\infty} \mathcal{L}\left[\left(\boldsymbol{\Theta}^{(l),\Omega_N}(\bar{t})\right)_{l=k+1,k,\dots,0}\right] = \mathcal{L}\left[(M^k_{-l})_{-l=-(k+1),-k,\dots,0}\right]. \tag{4.87}$$

(b) For $k \in \mathbb{N}$,

$$\begin{aligned}
l > k\colon\ & \lim_{N\to\infty} \mathcal{L}\left[\left(\boldsymbol{\Theta}^{(l),\Omega_N}(\bar{t}+N^k t)\right)_{t>0}\right] = \delta_{(M^k_{-(k+1)})},\\
l = k\colon\ & \lim_{N\to\infty} \mathcal{L}\left[\left(\boldsymbol{\Theta}^{(l),\Omega_N}(\bar{t}+N^l t)\right)_{t>0}\right] = \mathcal{L}\left[\left(z_{k,M^k_{-(k+1)}}(t)\right)_{t>0}\right],\\
l < k\colon\ & \lim_{N\to\infty} \mathcal{L}\left[\left(\boldsymbol{\Theta}^{(l),\Omega_N}(\bar{t}+N^l t)\right)_{t>0}\right] = \mathcal{L}\left[\left(z_{l,M^k_{-(l+1)}}(t)\right)_{t>0}\right],
\end{aligned} \tag{4.88}$$

in the Meyer-Zheng topology,

where the initial laws of the limiting processes are given by (see Fig. 4.9)

$$\begin{aligned}
&\mathcal{L}\left[z_{k,M^k_{-(k+1),x}}(0)\right] = \Gamma^{(k)}_{M^k_{-(k+1)}},\\
&\mathcal{L}\left[z_{k,M^k_{(k+1),x}}(0)\right] = \Gamma^{(l)}_{M^k_{-(l+1)}},\\
&\Gamma^{(l)}_{M^k_{-(l+1)}} = \int_{\mathfrak{s}} \cdots \int_{\mathfrak{s}} \int_{\mathfrak{s}} \Gamma^{(k)}_{M^k_{-(k+1)}}(\mathrm{d}u_k)\Gamma^{(k-1)}_{u_k}(\mathrm{d}u_{k-1}) \cdots \Gamma^{(l+1)}_{l+2}(\mathrm{d}u_1)\Gamma^{(l)}_{u_{l+1}}
\end{aligned} \tag{4.89}$$

Remark 4.4.5 (Convergence in the Meyer-Zheng topology). Note that Theorem 4.4.4(b) is stated in the Meyer-Zheng topology. This topology is needed because at time-scales $N^l t$ rates occur in(4.24) that tend to infinity as $N \to \infty$. In Section 4.4.4 we define the Meyer-Zheng topology and explain why it is neeeded. ■

The statement in (a) shows that if we look at multiple space-time scales simultaneously, then the joint distribution of the different block averages behaves like the infinite-dimensional interaction chain defined in (4.77). The statement in (b) describes the law of the path on different times scales.

- On time scale $N^k t$, the l-block averages with $l > k$ are not moving, i.e., $(\boldsymbol{\Theta}^{(l),\Omega_N}(\bar{t}+N^k t))_{t>0}$ is a constant process. However, there is a difference between seed-banks with colour $m > k$ and seed-banks with colour $0 \leq m \leq k$ in the way they interact with the active population. For $m > k$, even the m-dormant single colonies have not yet moved at time $\bar{t}+N^k t$, and hence are still in their initial states, with expectations $(\theta_{y_m})_{m=l+1}^{\infty}$. Therefore, also the l-block averages of m-dormant populations are still in their initial states, with expectations $(\theta_{y_m})_{m=l+1}^{\infty}$. For $l \leq k$ the m-dormant single colonies with $m \leq k$ at time $\bar{t}+N^k t$ have already interacted with the active population. Due to this interaction, for $l > k$ the l-block averages of m-dormant populations with $m \leq k$ are in state ϑ_k instead of their initial state θ_{y_m}. However, on time scale $\bar{t}+N^k t$

l-block averages of m-dormant populations are not moving. (In Section 4.4.4 we explain how the shift from θ_{y_m} to ϑ_k occurs.) Also the l-block averages of the active population are in state ϑ_k.

- On time scale $\bar{t} + N^k t$, the k-block averages have reached equilibrium. We see that the active k-block average and the k-dormant k-block average evolve together like the effective k-block process in Theorem 4.4.2. Therefore the evolution of the active k-block average is slowed down by a factor E_k, the active k-block feels a drift towards ϑ_k (the value of the active $(k+1)$-block average at time $\bar{t}$), resamples with diffusion function $\mathcal{F}^{(k)}g$, and exchanges individuals with the k-dormant k-block. The k-dormant k-block average evolves only via interaction with the active k-block. The m-dormant k-block averages with colour $0 \leq m < k$ equal the active k-block average and hence follow their evolution. The m-dormant k-blocks with colour $m > k$ are still in their initial states, since on time scale $\bar{t} + N^k t$ even single colony seed-banks with colour $m > k$ have not yet started to interact with the active population.

- On time scale $\bar{t} + N^l t$, for $0 \leq l < k$, the l-block averages are in a quasi-equilibrium. Again, the active l-block and the l-dormant l-block average, which is the effective seed-bank, behave as the effective process in 4.4.2. Hence, the active l-block average feels a drift towards the instantaneous value of the active $(l+1)$-block average, which is given by the first component of the interaction chain $M^k_{-(l+1)}$, resamples according to the renormalised diffusion function $\mathcal{F}^{(l)}g$, and exchanges with the l-block of the l-dormant population. The evolution of the active l-block average is slowed down by a factor E_l. The l-block of the l-dormant population exchanges individuals with the active population. The l-blocks of the m-dormant population with colours $0 \leq m < l$ follow the active population. The states of the m-dormant population with colour $m > l$ are given by the corresponding components in the interaction chain $M^k_{-(l+1)}$. Hence the l-block averages with colours $m > k$ are still in their initial states θ_{y_m}, because on time scale $\bar{t} + N^l t$ even the single dormant colonies with colour $m > k$ have not yet interacted with the active population. However, something interesting is happening with the colours $l < m \leq k$: they are in a state obtained on the time scale in which they where effective, i.e., for $l < m \leq k$ the m-dormant l-block average is in state $y_{m,m}(\bar{t})$. This happens because at time $\bar{t}$ the single colonies have already interacted with the active population, but on time scale $N^l t$ they do not interact anymore with the active population. (Also this effect will be further explained in Section 4.4.4.)

Remark 4.4.6 (Comparison to system without seed-bank). Comparing Theorem 4.4.4 with the multi-scale limit theorems derived for the hierarchical system without seed-bank [21], [20], [25], we see that the seed-bank affects the system both quantitatively and qualitatively. First, the active population is *slowed down* by the total size of the seed-banks it has interacted with, represented by the slowing-down factors $(E_l)_{l \in \mathbb{N}_0}$. Second, the interaction with the *effective seed-bank* on each space-time scale is special to the system with seed-bank. Still, the *decoupling* of the active component and the *renormalisation transformation* for the diffusion function are similar as in the system without seed-bank.

Remark 4.4.7 ($k \to \infty$ limit of the interaction chain). The result in (4.85) raises the question how the hierarchical multi-scale limit behaves for large k. We find the following dichotomy:

$$\lim_{k\to\infty} \mathcal{L}\left[(M^k_{-(k+1),-k,\cdots,0})\right] = \mathcal{L}\left[(M^\infty_k)_{k\in\mathbb{Z}^-}\right], \tag{4.90}$$

where in the *clustering regime*

$$\mathcal{L}\left[(M^\infty_k)_{k\in\mathbb{Z}^-}\right] = \theta\delta_{(1,1^{\mathbb{N}_0})^{\mathbb{Z}^-}} + (1-\theta)\delta_{(0,0^{\mathbb{N}_0})^{\mathbb{Z}^-}} \tag{4.91}$$

and in the *coexistence regime* $M^\infty = (M^\infty_k)_{k\in\mathbb{Z}^-}$ is a realisation of the unique entrance law of the interaction chain at time $-\infty$ with

$$\lim_{l\to\infty} M^\infty_{-l} = (\theta,\theta). \tag{4.92}$$

In the latter case, M^∞ corresponds to the equilibrium vector of block averages around site 0, whose law agrees with that of the equilibrium block averages for the mean-field model after we take the limit $N \to \infty$ (see [25, Proposition 6.2 and 6.3]). ■

Remark 4.4.8 (Interaction field). Theorem 4.4.4 looks at the tower of block averages over a fixed site, namely, 0. In order to study the cluster formation in the clustering regime or the equilibria in the coexistence regime, we must analyse the dependence structure between the towers of block averages over *different* sites. We can show that, in the limit as $N \to \infty$, an interacting random field emerges, indexed by a tree with countably many edges coming out of every site at every level. This random field has the property that the averages over any two points η, η' with $d(\eta,\eta') = l$, follow a single interaction chain in equilibrium from $k+1$ until l (or from $-\infty$ until l in the entrance law) and, conditional on the state in l, evolve independently as the interaction chain beyond l. This corresponds to what is called *propagation of chaos* of the $(l-1)$-block averages given the l-block average. For the model without seed-bank such results are described in [25, Section 0(e)]. Using our results for the model with seed-bank above, we can in principle follow an analogous line of argument. We refrain from spelling out the details. ■

§4.4.4 Heuristics behind the multi-scale limit

The proofs of Theorems 4.4.2 and 4.4.4 written out in Sections 6.1–9, are long and technical. In order to help the reader appreciate these proofs, we provide the heuristics in this section.

- **Evolution of the block-averages**

Recall the block averages introduced in Definition 4.2.3 and their evolution defined in (4.24). In the limit as $N \to \infty$, we heuristically obtain from the SSDE in (4.24) the following results for the k-block process

$$(x^{\Omega_N}_k(t), (y^{\Omega_N}_{m,k}(t))_{m\in\mathbb{N}_0})_{t\geq 0}. \tag{4.93}$$

- **Migration.** Recall that the migration is captured by the first term of the first equation in (4.24), i.e., the first term of the evolution of the active part of the population. Letting $N \to \infty$, we see that in the sum over l only the term $l = 1$ contributes. Hence we expect that the effective migration felt by the active k-block average is towards $x^{\Omega_N}_{k+1}(0)$, the initial state of the active $(k+1)$-block average. Note that the migration term in (4.24) can be written as

$$\sum_{l\in\mathbb{N}} \frac{c_{k+l-1}}{N^{l-1}} \left[x^{\Omega_N}_{k+l}(N^{-l}t) - x^{\Omega_N}_{k}(t)\right] = \sum_{l\in\mathbb{N}} \frac{c_{k+l-1}}{N^{l-1}} \left[\frac{1}{N^l}\sum_{k=0}^{N^l-1} x^{\Omega_N}_{k}(t) - x^{\Omega_N}_{k}(t)\right]. \tag{4.94}$$

  The drift towards the $(k+1)$-block average is therefore also a drift towards the current average of the k-blocks in the $(k+1)$-block. In the limit as $N \to \infty$, the latter can be approximated by $\mathbb{E}[x_k(t)]$. Effectively, as $N \to \infty$, the k-blocks become independent given the the value of $x^{\Omega_N}_{k+1}(0)$, i.e., there is *decoupling.*

- **Resampling.** Recall that the diffusion term in the evolution equation of the active population represents the resampling. Therefore we see that the active k-block resamples at a rate that is the average resampling rate over the k-block. For $k = 1$, the resampling rate of the 1-block is the average of the resampling ratse of the single colonies. Therefore, in the limit $N \to \infty$, due to the decoupling described above, we expect that the resampling rate for the 1 block is given by $\mathbb{E}[g]$, where the expectation is w.r.t. the quasi-equilibrium of the single colonies. This expectation is exaclty the renormalised diffusion function $\mathcal{F}g$ (see (4.75)). For the k-block, we may interpret the diffusion function to be the average of the diffusion function for the $(k-1)$-blocks. By "induction" we assume that the $(k-1)$ blocks resample at rate $\mathcal{F}^{(k-1)}g$. Hence, due to the decoupling of the $(k-1)$-blocks as $N \to \infty$, we expect the resampling rate for the k blocks to equal $\mathbb{E}[\mathcal{F}^{(k-1)}g]$, where the expectation is w.r.t. the quasi-equlibrium of the $(k-1)$-blocks. This yields another iteration of the renormalisation transformation (see (4.76)). Hence, we expect the diffusion function for the k-blocks to converge to $\mathcal{F}^{(k)}g$.

- **Exchange with the seed-bank.** Recall that the last term of the first equation in (4.24) and the second equation in (4.24) together describe the exchange of the active k-block with the m-dormant k-block. To describe the limiting behaviour as $N \to \infty$, we distinguish three cases: $0 \leq m < k$, $m = k$, $m > k$.

  - If $0 \leq m < k$, then we see that the rate of exchange between the active k-block and the m-dormant k-block tends to infinity as $N \to \infty$. We therefore expect them to equalise, i.e.,

$$\lim_{N\to\infty} \mathcal{L}\left[\left(x^{\Omega_N}_{k}(t) - y^{\Omega_N}_{m,k}(t)\right)_{t>0}\right] = \delta_0, \tag{4.95}$$

    where 0 should be interpreted as the process equal to 0, $(0)_{t>0}$. Hence we see that m-dormant k-block follows the active k-block immediately. (To formalise this fact, we need the *Meyer-Zheng topology* [59].)
  - If $m = k$, then there is a non-trivial exchange between the active k-block and the k-dormant k-block.

  - If $m > k$, then the exchange rate between the active k-block and the m-dormant k-block tends to zero as $N \to \infty$.

Thus, only the k-dormant k-block has a non-trivial interaction with the active k-block. We express this by saying that on space-time scale k the k-dormant population plays the role of the *effective seed-bank*.

• Limiting evolution of the block-averages

To determine the limiting evolution of the full block-averages process, we first have a look at the limiting evolution of the effective process.

The effective process. To determine the limit as $N \to \infty$ of (4.24), we need to get rid of the diverging rates. Instead of only looking at the k-block process $(x_k^{\Omega_N}(t), (y_{m,k}^{\Omega_N}(t))_{m\in\mathbb{N}_0})_{t\geq 0}$, which evolves according to (4.24), we look at the *effective k-block process* defined as

$$\left(\bar{x}_k^{\Omega_N}(t), y_{k,k}^{\Omega_N}(t)\right)_{t\geq 0}, \tag{4.96}$$

where we abbreviate

$$\bar{x}_k^{\Omega_N}(t) = \frac{x_k^{\Omega_N}(t) + \sum_{m=0}^{k-1} K_m y_{m,k}^{\Omega_N}(t)}{1 + \sum_{m=0}^{k-1} K_m}. \tag{4.97}$$

By (4.95) and the heuristic discussion given above, the process in (4.96) equals $(x_k^{\Omega_N}(t), y_{k,k}^{\Omega_N}(t))_{t\geq 0}$ in the limit as $N \to \infty$, i.e., it describes the joint distribution of the active k-block and the effective dormant k-block, which is the k-dormant k-block. Using (4.24), we see that the process in (4.96) evolves according to the SSDE

$$\begin{aligned}
\mathrm{d}\bar{x}_k^{\Omega_N}(t) &= E_k \sum_{l\in\mathbb{N}} \frac{c_{k+l-1}}{N^{l-1}} \left[x_{k+l}^{\Omega_N}(N^{-l}t) - x_k^{\Omega_N}(t)\right] \mathrm{d}t \\
&\quad + E_k \sqrt{\frac{1}{N^k} \sum_{\xi\in B_k(0)} g(x_\xi(N^k t))}\, \mathrm{d}w_k(t) \\
&\quad + E_k \sum_{m=k}^{\infty} N^k \frac{K_m e_m}{N^m} \left[y_{m,k}^{\Omega_N}(t) - x_k^{\Omega_N}(t)\right] \mathrm{d}t, \\
\mathrm{d}y_{k,k}^{\Omega_N}(t) &= e_k \left[x_k^{\Omega_N}(t) - y_{k,k}^{\Omega_N}(t)\right] \mathrm{d}t.
\end{aligned} \tag{4.98}$$

In (4.98) no infinite rates appear anymore. In the limit as $N \to \infty$, by (4.95) we can approximate

$$x_k^{\Omega_N}(t) \approx y_{m,k}^{\Omega_N}(t), \qquad 0 \leq m < k, \tag{4.99}$$

such that

$$x_k^{\Omega_N}(t) \approx \bar{x}_k^{\Omega_N}(t). \tag{4.100}$$

We can therefore approximate (4.98) by

$$
\begin{aligned}
\mathrm{d}\bar{x}_k^{\Omega_N}(t) &= E_k \sum_{l\in\mathbb{N}} \frac{c_{k+l-1}}{N^{l-1}} \big[\bar{x}_{k+l}^{\Omega_N}(N^{-l}t) - \bar{x}_k^{\Omega_N}(t)\big]\,\mathrm{d}t \\
&\quad + E_k \sqrt{\frac{1}{N^k} \sum_{\xi\in B_k(0)} g\big(\bar{x}_\xi(N^k t)\big)}\,\mathrm{d}w_k(t) \\
&\quad + E_k \sum_{m=k}^{\infty} N^k \frac{K_m e_m}{N^m} \big[y_{m,k}^{\Omega_N}(t) - \bar{x}_k^{\Omega_N}(t)\big]\,\mathrm{d}t, \\
\mathrm{d}y_{k,k}^{\Omega_N}(t) &= e_k \big[\bar{x}_k^{\Omega_N}(t) - y_{k,k}^{\Omega_N}(t)\big]\,\mathrm{d}t.
\end{aligned}
\tag{4.101}
$$

Hence, in the limit as $N \to \infty$, the process in (4.96) becomes autonomous. Moreover, assuming that $\lim_{N\to\infty} \bar{x}_{l+1}^{\Omega_N}(0) = \vartheta_l$, we see that (4.101) approaches the effective process defined in (4.69), with

$$
\theta = \vartheta_l, \quad E = E_k, \quad c = c_k, \quad e = e_k, \quad K = K_k, \quad g = \mathcal{F}^{(k)} g. \tag{4.102}
$$

In particular, we see that the *slowing-down constant* E_k arises because the active population is the only part of the first component of (4.96). Note that therefore only a part, the active part, from the first component migrates, resamples and exchanges with the seed-bank. Due to the infinite rates, the active population "drags along all the fast seed-banks with total size $\sum_{m=0}^{k-1} K_m$". This causes the slowing down factors E_k.

Since there are no infinite rates in the evolution of the effective process, we can use the classical path space topology. This allows us in the proof in Sections 6.1–9 to build on techniques developed for the hierarchical mean-field model without seed-bank in [20], [25]. It turns out that the *effective process* is very useful in our analysis.

From the effective process to the full process. For large N, by (4.99) and (4.100), the evolution of our original process $(x_k^{\Omega_N}(t), (y_{m,k}^{\Omega_N}(t))_{m\in\mathbb{N}_0})_{t\geq 0}$ can be approximated by

$$
\begin{aligned}
\mathrm{d}\bar{x}_k^{\Omega_N}(t) &\approx E_k \sum_{l\in\mathbb{N}} \frac{c_{k+l-1}}{N^{l-1}} \big[\bar{x}_{k+l}^{\Omega_N}(N^{-l}t) - \bar{x}_k^{\Omega_N}(t)\big]\,\mathrm{d}t \\
&\quad + E_k \sqrt{\frac{1}{N^k} \sum_{\xi\in B_k(0)} g(\bar{x}_\xi(N^k t))}\,\mathrm{d}w_k(t) \\
&\quad + E_k \sum_{m=k}^{\infty} N^k \frac{K_m e_m}{N^m} \big[y_{m,k}^{\Omega_N}(t) - \bar{x}_k^{\Omega_N}(t)\big]\,\mathrm{d}t, \\
y_{k,k}^{\Omega_N}(t) &= \bar{x}_k^{\Omega_N}(t), \\
\mathrm{d}y_{k,k}^{\Omega_N}(t) &= e_k \big[\bar{x}_k^{\Omega_N}(t) - y_{k,k}^{\Omega_N}(t)\big]\,\mathrm{d}t, \\
y_{k,k}^{\Omega_N}(t) &= y_{m,k}^{\Omega_N}(0).
\end{aligned}
\tag{4.103}
$$

By the ergodic theorem for exchangeable measures, we can assume that

$$\lim_{N\to\infty} \bar{x}^{\Omega_N}_{k+1}(0) = \vartheta_k \; a.s. \tag{4.104}$$

We expect that (4.103) approaches (4.67) with

$$\theta = \vartheta_k, \quad E = E_k, \quad c = c_k, \quad e = e_k, \quad K = K_k, \quad g = \mathcal{F}^{(k)}g. \tag{4.105}$$

To prove that

$$\lim_{N\to\infty} \mathcal{L}[y^{\Omega_N}_{m,k}(t)] = \lim_{N\to\infty} \mathcal{L}[\bar{x}^{\Omega_N}_k(t)], \qquad 0 \le m < k-1, \tag{4.106}$$

we need *the Meyer-Zheng topology* explained in Section 4.4.1. In the proof in Sections 6.2–9 we show how the above approximations can be made rigorous.

Conserved quantities. Note that, by (4.24) and (4.94), for each $k \in \mathbb{N}_0$

$$\mathbb{E}\left[\frac{x^{\Omega_N}_k(t) + \sum_{m\in\mathbb{N}_0} K_m y^{\Omega_N}_k(t)}{1 + \sum_{m\in\mathbb{N}_0} K_m}\right] = \theta, \qquad t \ge 0, \tag{4.107}$$

is a conserved quantity. For each $k \in \mathbb{N}$ we obtain that for $l \ge k$

$$\lim_{N\to\infty} \mathbb{E}\left[\frac{x^{\Omega_N}_k(t) + \sum_{m=0}^{l} K_m y^{\Omega_N}_k(t)}{1 + \sum_{m=0}^{l} K_m}\right] = \vartheta_l, \tag{4.108}$$

is a conserved quantity. For the effective process, (4.101) implies that

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}[\bar{x}^{\Omega_N}_k(t)] &= E_k K_k e_k \Big(\mathbb{E}[y^{\Omega_N}_{k,k}(t)] - \mathbb{E}[\bar{x}^{\Omega_N}_k(t)]\Big), \\ \frac{\mathrm{d}}{\mathrm{d}t}\mathbb{E}[y^{\Omega_N}_{k,k}(t)] &= e_k \Big(\mathbb{E}[\bar{x}^{\Omega_N}_k(t)] - \mathbb{E}[y^{\Omega_N}_{k,k}(t)]\Big). \end{aligned} \tag{4.109}$$

Recall that

$$\mathbb{E}[\bar{x}^{\Omega_N}_k(0)] = \mathbb{E}\left[\frac{x^{\Omega_N}_k(0) + \sum_{m=0}^{k-1} K_m y^{\Omega_N}_{m,k}(0)}{1 + \sum_{m=0}^{k-1} K_m}\right] = \vartheta_{k-1}, \quad \mathbb{E}[y^{\Omega_N}_{k,k}(0)] = \theta_{y_k}. \tag{4.110}$$

Therefore we can solve (4.109) explicitly as

$$\begin{aligned} \mathbb{E}[\bar{x}^{\Omega_N}_k(t)] &= \vartheta_k + \frac{E_k K_k}{1 + E_k K_k}(\vartheta_{k-1} - \theta_{y_k})\,\mathrm{e}^{-(E_k K_k + 1)e_k t}, \\ \mathbb{E}[y^{\Omega_N}_{k,k}(t)] &= \vartheta_k - \frac{1}{1 + E_k K_k}(\vartheta_{k-1} - \theta_{y_k})\,\mathrm{e}^{-(E_k K_k + 1)e_k t}. \end{aligned} \tag{4.111}$$

The above computation shows what happens to $\mathbb{E}[\bar{x}^{\Omega_N}_k(t)]$ if we move one space-time scale up in the hierarchy, namely, a new seed-bank starts interacting with the active population. This causes that ϑ_{k-1} is pulled a bit towards θ_{y_k}, so that also $\mathbb{E}[\bar{x}^{\Omega_N}_k(t)]$ changes a bit. Each new seed-bank that opens up changes the expectation of the active population, which results in the sequence $(\theta_x, \vartheta_0, \vartheta_1, \vartheta_2, \ldots)$ for the expectation of the active population on space-time scales $\{0,1,2,3,\cdots\}$. From (4.94) we see that the drift of $\bar{x}_k^{\Omega_N}(t)$ is towards

$$\bar{x}_{k+1}^{\Omega_N}(N^{-1}t) = \frac{1}{N^k}\sum_{k=0}^{N^k-1} x_k^{\Omega_N}(t) \approx \mathbb{E}[\bar{x}_k^{\Omega_N}(t)], \tag{4.112}$$

where the last approximation can be made because the k-blocks decouple. Hence, in the limit as $N\to\infty$, once the k-blocks are in a quasi-equilibrium we can replace the drift towards $\bar{x}_{k+1}^{\Omega_N}(N^{-1}t)$ by a drift towards $\mathbb{E}[\bar{x}_k^{\Omega_N}(t)] = \vartheta_k$.

Shifting averages. Recall the full estimator process $(\mathbf{\Theta}^{(l),\Omega_N}(t))_{t>0}$ defined in (4.71). Equation 4.23 implies that the evolution of the estimator process is given by

$$\begin{aligned} \mathrm{d}\Theta_x^{(l),\Omega_N}(t) &= \sum_{n=l+1}^{\infty} \frac{c_{n-1}}{N^{n-1}}[\Theta_x^{(n),\Omega_N}(t) - \Theta_x^{(l)}(t)]\,\mathrm{d}t \\ &\quad + \sqrt{\frac{1}{N^{2l}}\sum_{\xi\in B_l} g\big(x_\xi(t)\big)}\,\mathrm{d}w(t) \\ &\quad + \sum_{m\in\mathbb{N}_0}\frac{K_m e_m}{N^m}[\Theta_{y_m}^{(l),\Omega_N}(t) - \Theta_x^{(1),\Omega_N}(t)]\,\mathrm{d}t, \\ \mathrm{d}\Theta_{y_m}^{(l),\Omega_N}(t) &= \frac{e_m}{N^m}[\Theta_x^{(l),\Omega_N}(t) - \Theta_{y_m}^{(l),\Omega_N}(t)]\,\mathrm{d}t,\ m\in\mathbb{N}_0. \end{aligned} \tag{4.113}$$

Looking at the estimator process $(\mathbf{\Theta}^{(l),\Omega_N}(t))_{t>0}$ on time scale $N^k t$, we see that

$$\begin{aligned} \mathrm{d}\Theta_x^{(l),\Omega_N}(N^k t) &= \sum_{n=l+1}^{\infty} \frac{c_{n-1}}{N^{n-1-k}}\left[\Theta_x^{(n),\Omega_N}(N^k t) - \Theta_x^{(l),\Omega_N}(N^k t)\right]\,\mathrm{d}t \\ &\quad + \sqrt{\frac{N^k}{N^{2l}}\sum_{\xi\in B_l} g\big(x_\xi(N^k t)\big)}\,\mathrm{d}w(t) \\ &\quad + \sum_{m\in\mathbb{N}_0}\frac{K_m e_m}{N^{m-k}}\left[\Theta_{y_m}^{(l),\Omega_N}(N^k t) - \Theta_x^{(l),\Omega_N}(N^k t)\right]\,\mathrm{d}t, \\ \mathrm{d}\Theta_{y_m}^{(l),\Omega_N}(N^k t) &= \frac{e_m}{N^{m-k}}\left[\Theta_x^{(l),\Omega_N}(N^k t) - \Theta_{y_m}^{(l),\Omega_N}(N^k t)\right]\,\mathrm{d}t, \qquad m\in\mathbb{N}_0. \end{aligned} \tag{4.114}$$

From (4.114) we get that, on time scale $N^k t$, for all $l\geq k+1$,

$$\Theta^{(l),\Omega_N}(N^k t) = \frac{\Theta_x^{(l),\Omega_N}(N^k t) + \sum_{m=0}^{l-1} K_m \Theta_{y_m}^{(l),\Omega_N}(N^k t)}{1+\sum_{m=0}^{l-1}K_m}, \qquad t\geq 0, \tag{4.115}$$

is a conserved quantity in the limit as $N\to\infty$, and for $t\geq 0$,

$$\lim_{N\to\infty}\Theta^{(l),\Omega_N}(N^k t) = \frac{\theta_x + \sum_{m=0}^{l-1}K_m\theta_{y_m}}{1+\sum_{m=0}^{l-1}K_m} = \vartheta_l,\ \text{in probability.} \tag{4.116}$$

For $m > k$, also $\Theta_{y_m}^{(l),\Omega_N}(N^k t)$ is a conserved quantity, and

$$\lim_{N\to\infty} \Theta_{y_m}^{(l),\Omega_N}(N^k t) = \theta_{y_m}, \qquad t \geq 0. \tag{4.117}$$

However, for $l \geq k+1$, $\Theta_x^{(l),\Omega_N}(N^k t)$ and $(\Theta_{y_m}^{(l),\Omega_N}(N^k t))_{m=0}^{k}$ are not conserved quantities in the limit as $N \to \infty$. Note that from 4.24 we heuristically see that the full l-block estimator process $(\boldsymbol{\Theta}^{(l),\Omega_N}(N^k t))_{t\geq 0}$ with $l > k$ converges to the process

$$\left(\Theta_x^{(l)}(t), \left(\Theta_{y_m}^{(l)}(t)\right)_{m\in\mathbb{N}_0}\right)_{t>0}, \tag{4.118}$$

which evolves according to

$$\begin{aligned}
&\mathrm{d}\Theta_x^{(l)}(t) = E_{k-1}K_k e_k[\Theta_{y_k}^{(l)}(t) - \Theta_x^{(l),\Omega_N}(t)]\,\mathrm{d}t,\\
&\begin{array}{rclr}
\Theta_{y_m}^{(l)}(t) & = & \Theta_x^{(l)}(t), & m < k,\\
\mathrm{d}\Theta_{y_k}^{(l)}(t) & = & e_k[\Theta_x^{(l)}(t) - \Theta_{y_k}^{(l)}(t)]\,\mathrm{d}t, & m = k,\\
\Theta_{y_m}^{(l)}(t) & = & \theta_{y_m}, & m > k.
\end{array}
\end{aligned} \tag{4.119}$$

This system can be explicitly solved as

$$\begin{aligned}
\Theta_x^{(l)}(t) = {} & \frac{\Theta_x^{(l)}(0) + E_{k-1}K_k\Theta_{y_k}^{(l)}(0)}{1+E_{k-1}K_k}\\
& + \frac{E_{k-1}K_k}{1+E_{k-1}K_k}[\Theta_x^{(l),\Omega_N}(0) - \Theta_{y_k}^{(l)}(0)]\,\mathrm{e}^{-(E_{k-1}K_k e_k + e_k)t},\\
\Theta_{y_m}^{(l)}(t) = {} & \Theta_x^{(l)}(t), \qquad\qquad m < k,\\
\Theta_{y_k}^{(l)}(t) = {} & \tfrac{\Theta_x^{(l)}(0)+E_{k-1}K_k\Theta_{y_k}^{(l)}(0)}{1+E_{k-1}K_k}\\
& -\tfrac{1}{1+E_{k-1}K_k}[\Theta_x^{(l),\Omega_N}(0) - \Theta_{y_k}^{(l)}(0)]\,\mathrm{e}^{-(E_{k-1}K_k e_k + e_k)t}, \qquad m = k,\\
\Theta_{y_m}^{(l)}(t) = {} & \theta_{y_m}, \qquad\qquad m > k.
\end{aligned} \tag{4.120}$$

The latter shows that, each time we enter a new space-time scale, all the large active blocks interact with the large effective dormant blocks until they equalise. Thus, on each space-time scale, all the active l-blocks and the dormant l-blocks of colour $m \leq l$ move for a short period of time. As a consequence, the value of $\Theta_x^{(l)}(0)$ depends on the scaling we choose. To illustrate this, we note that

$$\begin{aligned}
\lim_{N\to\infty} \Theta_x^{(l),\Omega_N}(0) &= \theta_x,\\
\lim_{N\to\infty} \Theta_x^{(l),\Omega_N}(L(N)+t) &= \vartheta_0,\\
\lim_{N\to\infty} \Theta_x^{(l),\Omega_N}((L(N)N^n + N^n t)) &= \vartheta_n, \quad 0 \leq n \leq k.
\end{aligned} \tag{4.121}$$

Hence under the scaling $N^k t$ the $\lim_{N\to\infty} \frac{L(N)N^n+N^n t}{N^k} = 0$ and therefore for consistentcy one would like to have

$$\begin{aligned}
\lim_{N\to\infty} \Theta_x^{(l),\Omega_N}(0) &= \lim_{N\to\infty} \Theta_x^{(l),\Omega_N}\left(N^k \frac{L(N)+t}{N^k}\right)\\
&= \lim_{N\to\infty} \Theta_x^{(l),\Omega_N}\left(N^k \frac{L(N)N^n+N^n t}{N^k}\right) \quad 0 \leq n \leq k,
\end{aligned} \tag{4.122}$$

but this contradicts with (4.121). Hence, if $(t(N))_{N\in\mathbb{N}}$ is a sequence such that $\lim_{N\to\infty} N^k t(N) = 0$, then the value of the limit

$$\lim_{N\to\infty} \Theta_x^{(l),\Omega_N}(N^k t(N)) \tag{4.123}$$

depends on $(t(N))_{N\in\mathbb{N}}$. Moreover, to obtain a limiting process for $(\boldsymbol{\Theta}^{(l),\Omega_N}(N^k t))_{t\geq 0}$ we need convergence also at time 0, while it is not clear what $N^k t \downarrow 0$ means. To circumvent these subtleties, we look at the process at times $t > 0$ and use as starting time $\bar{t}$ defined in Theorem 4.4.2.

From (4.120) it follows that, for $l \geq k$,

$$\begin{aligned}
&\lim_{N\to\infty} \Theta_x^{(l),\Omega_N}(\bar{t}\,) = \vartheta_k, \text{ in probability,}\\
&\lim_{N\to\infty} \Theta_{y_m}^{(l),\Omega_N}(\bar{t}\,) = \vartheta_k, \quad m \leq k, \text{ in probability,}\\
&\lim_{N\to\infty} \Theta_{y_m}^{(l),\Omega_N}(\bar{t}\,) = \theta_{y_m}, \quad m > k \text{ in probability.}
\end{aligned} \tag{4.124}$$

Note that the shifting of averages mentioned earlier is closely related to the conserved quantities discussed in Section 4.4.4 because, for large N,

$$\lim_{N\to\infty} \Theta_x^{(l),\Omega_N}(\bar{t}\,) \approx \mathbb{E}[x_k^{\Omega_N}], \tag{4.125}$$

where the expectation is taken in the quasi-equilibrium the k-blocks have attained after scaling with time $\bar{t}$.

- **Formation of the interaction chain**

In Section 4.4.4 we saw how subsequent space-time scales are connected via the migration term. In this section we show how the interaction chain arises from this connection. We first show how the effective interaction chain arises for the effective process. Then we show how the full interaction chain is formed, by studying the slow seed-banks.

Connections between different space-time scales Let $\bar{t}$ be as in Theorem 4.4.2. From (4.113) it follows that the process $(\boldsymbol{\Theta}^{(l),\Omega_N}(\bar{t}+N^l t))_{t>0}$ evolves according to

$$\begin{aligned}
\mathrm{d}\Theta_x^{(l),\Omega_N}(\bar{t}+N^l t) = &\sum_{n=l+1}^{\infty} \frac{c_{n-1}}{N^{n-1-l}}[\Theta_x^{(n),\Omega_N}(\bar{t}+N^l t) - \Theta_x^{(l)}(\bar{t}+N^l t)]\,\mathrm{d}t\\
&+ \sqrt{\frac{1}{N^l}\sum_{\xi\in B_l} g\big(x_\xi(\bar{t}+N^l t)\big)}\,\mathrm{d}w(t)\\
&+ \sum_{m\in\mathbb{N}_0} \frac{K_m e_m}{N^{m-l}}[\Theta_{y_m}^{(l),\Omega_N}(\bar{t}+N^l t) - \Theta_x^{(1),\Omega_N}(\bar{t}+N^l t)]\,\mathrm{d}t,\\
\mathrm{d}\Theta_{y_m}^{(l),\Omega_N}(\bar{t}+N^l t) = &\frac{e_m}{N^{m-l}}[\Theta_x^{(l),\Omega_N}(\bar{t}+N^l t) - \Theta_{y_m}^{(l),\Omega_N}(\bar{t}+N^l t)]\,\mathrm{d}t, \qquad m\in\mathbb{N}_0.
\end{aligned} \tag{4.126}$$

Therefore, in the limit as $N \to \infty$, the active population $\Theta_x^{(l),\Omega_N}(\bar{t} + N^l t)$ feels a drift towards the $(l+1)$-block average $\Theta_x^{(l+1),\Omega_N}(\bar{t} + N^{l+1}t)$. If $l = k$, then

$$\lim_{N\to\infty} \mathcal{L}[\boldsymbol{\Theta}^{(k+1),\Omega_N}(\bar{t} + N^k t)] = \lim_{N\to\infty} \mathcal{L}[\boldsymbol{\Theta}^{(k+1),\Omega_N}(\bar{t})], \tag{4.127}$$

since the $(k+1)$-block has not yet started to move at time $\bar{t} + N^k t$. From (4.124) it follows that

$$\lim_{N\to\infty} \Theta_x^{(k+1),\Omega_N}(\bar{t} + N^k t) = \vartheta_k \, \textit{in probability}. \tag{4.128}$$

Therefore the drift of the active population $\Theta_x^{(l),\Omega_N}(\bar{t} + N^l t)$ is towards ϑ_k. Since $\bar{t} > L(N)N^k$, the process $\boldsymbol{\Theta}^{(k),\Omega_N}(\bar{t} + N^k t)$ has, in the limit $N \to \infty$, already reached its equilibrium, which is denoted by $\Gamma_{\bar{\vartheta}_k}$, where

$$\bar{\vartheta}_k = (\vartheta_k, \overbrace{\vartheta_k, \cdots, \vartheta_k}^{k+1 \text{ times}}, \theta_{y_{k+1}}, \theta_{y_{k+2}}, \cdots), \tag{4.129}$$

so that we recognise $(\bar{\vartheta}_k) = M^k_{-(k+1)}$. From (4.124) with $l = k+1$ we see that $(\bar{\vartheta}_k) = M^k_{-(k+1)}$ represents the state of $\boldsymbol{\Theta}^{(k+1),\Omega_N}(\bar{t})$.

If we look on time scale $\bar{t} + N^{k-1}t$, then we see that the active $(k-1)$-block averages feels a drift towards the active k-block average. The active k-block does not move on time scale N^{k-1}, but it has already moved at time $\bar{t}$. At time $\bar{t}$ the active k-block has even reached its quasi-equilibrium, given by $\Gamma^{(k)}_{\vartheta_k}$. Thus, the drift of the active $(k-1)$-block average is towards the instantaneous state of the active k-block average, which has distribution $\Gamma^{(k)}_{\bar{\vartheta}_k}$. This explains the first step in the interaction chain.

For $0 \leq l < k$, the active l-block average feels a drift towards the $(l+1)$-block average. The latter does not evolve on time scale $N^l t$, but it has already moved at time $\bar{t}$. Therefore it is no longer in its initial state, but in a quasi-equilibrium $\Gamma_u^{(l+2)}$, where u is the value of the active $(l+1)$-block averages determined via the interaction chain, recall Figure 4.9. This explains how the different space-time scales are connected via the active block averages. The states of the different seed-bank averages is a little bit more complicated. Below we give a very short heuristic explanation of the different seed-banks in the interaction chain.

For the effective process $(\boldsymbol{\Theta}^{\mathrm{eff},(l),\Omega_N}(t))_{t>0}$ instead of the full process $(\boldsymbol{\Theta}^{(l),\Omega_N}(t))_{t>0}$, we can consider in (4.113) only the active block average and the effective seed-bank average with $m = l$ (recall that the full block average equals the active block average). According to the above explanation, we have to replace $\Gamma^{(k)}_{\bar{\vartheta}_k}$ by $\Gamma^{\mathrm{eff},(k)}_{\vartheta_k}$ and $\Gamma^{(l)}_u$ by $\Gamma^{\mathrm{eff},(l)}_u$. Hence we find the effective interaction chain defined in (4.80) and depicted in Figure 4.8.

Slow seed-banks. From (4.124) we see that if $l \geq k$ and we use the scaling $\bar{t}$, then all l-blocks of seed-banks with colour $0 \leq m \leq k$ equal ϑ_k, and all l-blocks of seed-banks with colour $m > k$ equal their initial values θ_{y_m}. Something interesting happens when we choose $0 \leq l < k$ and use the scaling $\bar{t} + N^l t$. The single colonies of seed-banks with colour $0 \leq m < l$ on time scale $\bar{t} + N^l t$ follow the active population, and hence their l-block averages equal the l-block average of the active population.

The l-block average of the seed-bank with colour l has a non-trivial interaction with the active l-block. The l-blocks of seed-banks with colour $m > k$ have not yet moved and hence are still in their initial states $(\theta_{y_m})_{m=k+1}^{\infty}$. However, (4.126) implies that the single colonies of the seed-banks with colour $k \geq m > l$ are not moving on time scale $\bar{t} + N^l t$, even though they had already moved at time $\bar{t}$. Therefore the l-blocks averages of seed-banks with colour $l < m \leq k$ are no longer in their initial state at time $\bar{t}$. Note that they are also not in the state ϑ_k, since this is the state of their k-block averages and not of their l-block averages. The single colony seed-banks with colour $l < m \leq k$ are in the state given by

$$y_{m,0}(\bar{t}\,) = \int_0^{\bar{t}} \mathrm{d}s\, \frac{e_m}{N^m}[x_0(s) - y_{m,0}(s)]. \tag{4.130}$$

Hence, for large N,

$$y_{m,0}(\bar{t}) \approx \int_0^{L(N)N^k + N^k t_k + \cdots + N^m t_m} \mathrm{d}s\, \frac{e_m}{N^m}[x_0(s) - y_{m,0}(s)]. \tag{4.131}$$

Similarly, for the l-block average with colour m we have

$$\begin{aligned}
\Theta_{y_m}^{(l),\Omega_N}(\bar{t}\,) &= \int_0^{\bar{t}} \mathrm{d}s\, \frac{e_m}{N^m}[\Theta_x^{(l),\Omega_N}(s) - \Theta_{y_m}^{(l),\Omega_N}(s)] \\
&\approx \int_0^{L(N)N^k + N^k t_k + \cdots + N^m t_m} \mathrm{d}s\, \frac{e_m}{N^m}[\Theta_x^{(l),\Omega_N}(s) - \Theta_{y_m}^{(l),\Omega_N}(s)].
\end{aligned} \tag{4.132}$$

Thus, we see that the state of $\Theta_{y_m}^{(l),\Omega_N}(\bar{t})$ is completely determined at time $L(N)N^k + N^k t_k + \cdots + N^m t_m$, i.e., the last time before $\bar{t} + N^l t$ that the single colony seed-banks of colour m had an opportunity to move. Up to time $L(N)N^k + N^k t_k + \cdots + N^m t_m$, the single colony seed-banks with colour m interact at a very slow rate with the active single colonies, and similarly for the l-blocks. Therefore effectively the colour-m seed-bank interacts with a "time-average on scale $N^m t_m$" of the active population. On time scale $N^m t_m$, a single active colony migrates very fast in its $(m-1)$-block. As a consequence at time $\bar{t} + N^m t_m$ individuals that start from a particular colony, e.g. site 0, are spread uniformly over the m-block containing this site. Hence the interaction of a single m-dormant colony with the active population can be intuitively interpreted as an interaction with the active m-block, and similarly for an m-dormant l-block. Once we move to lower time scales, the m-dormant single colonies do not interact with the active colony anymore. In the detailed proofs we show that one consequence of this is that, for $l < m$,

$$\begin{aligned}
\Theta_{y_m}^{(l),\Omega_N}(\bar{t} + N^l t) &\approx \Theta_{y_m}^{(l),\Omega_N}(L(N)N^k + N^k t_k + \cdots + N^m t_m) \\
&\approx \Theta_{y_m}^{(m),\Omega_N}(L(N)N^k + N^k t_k + \cdots + N^m t_m).
\end{aligned} \tag{4.133}$$

Thus, the l-block averages of colours $l \leq m \leq k$ equal the state of the corresponding m-block. This is the $(m+2)$-th component of the interaction chain at level l.

Conclusion. Combining the intuitive descriptions in Sections 4.4.4-4.4.4, we see how Theorems 4.4.2 and Theorems 4.4.4 come about. Their proofs will rely on coupling techniques and a detailed analysis of the SSDEs. This analysis will be done in several steps. In Sections 6.1–6.3 we first deal with a simplified system, the mean-field model, for which we derive the McKean-Vlasov limit and the mean-field finite-systems scheme. In Sections 7–9 we extend our analysis to finitely many hierarchical levels. In particular, we go through the following list of systems of increasing complexity, each being a simplified version of the system defined by (4.19) and each capturing a key feature:

(a) Two-colour mean-field finite-systems scheme (Section 7.1).

(b) Two-level hierarchical mean-field system (Section 8.1).

(c) Finite-level mean-field system (Section 9.1).

In Section 9 we put the pieces together to prove the multi-scaling for the infinite-level system given in Theorems 4.4.2 and 4.4.4.

§4.5 Main results $N \to \infty$: Orbit and cluster formation

In the hierarchical mean-field limit we say that the system clusters when the colonies gradually form larger and larger mono-type blocks. In Section 4.5.1 we determine whether, in the hierarchical mean-field limit, the system clusters along successive space-time scales. How this happens is captured by the interaction chain. We introduce a sequence of scaling factors $(A_k)_{k\in\mathbb{N}_0}$, where A_k is defined in terms of the rates $(c_k)_{k\in\mathbb{N}_0}$, $(e_k)_{k\in\mathbb{N}_0}$, $(K_k)_{k\in\mathbb{N}_0}$ and the factors $(E_k)_{k\in\mathbb{N}_0}$. Using these scaling factors, we analyse the orbit of the renormalisation transformation and establish *universality*: $A_k\mathcal{F}^{(k)}g$ converges as $k \to \infty$ to the Fisher-Wright diffusion function, irrespective of the choice of g. In Section 4.5.2 we show how the scaling factors A_k are connected to the *growth of mono-type clusters*. In Section 4.5.3 we identify the asymptotics of A_k as $k \to \infty$ in terms of the model parameters.

§4.5.1 Orbit of renormalisation transformations

To determine whether clustering occurs, we start from larger and larger time scales and use the interaction chain to see whether mono-type clusters are formed in the single colonies. Recall the kernels introduced in (4.79) that describe the connection between subsequent hierarchical levels in the interaction chain. Define the following composition of kernels (see Fig. 4.10):

$$Q^{(n)} = Q^{[n]} \circ \cdots \circ Q^{[0]}, \qquad n \in \mathbb{N}. \tag{4.134}$$

In words, $Q^{(n)}(z_n, \mathrm{d}z_0)$ is the probability density to see the population of a single colony in state z_0 given that the $(n+1)$-block average equals z_n.

In Section 4.3 we identified the clustering regime for fixed $N < \infty$. In this section we identify the clustering regime in the hierarchical mean-field limit. In the clustering regime, in the hierarchical mean-field limit, an interesting question is to determine how $\mathcal{F}^{(n)}g$ (recall (4.76)) scales with n. We identify the scaling and show that it does *not* depend on g (see Fig. 4.11).

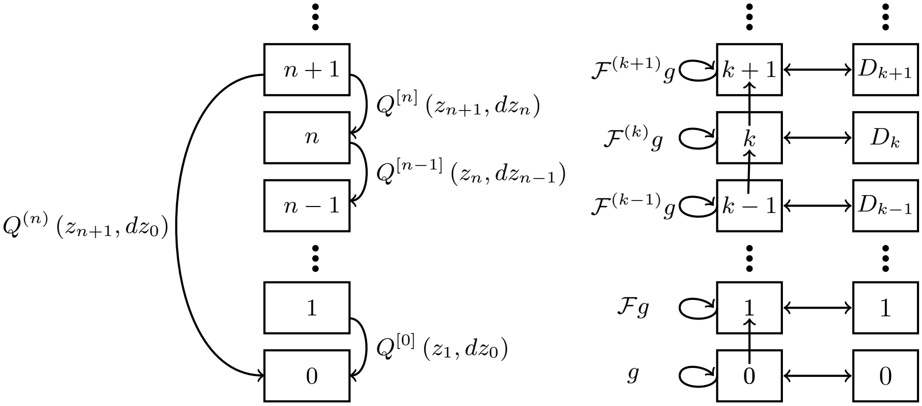

Figure 4.10: Left: *The interaction chain that connects successive hierarchical levels downwards. The arrows on the right correspond to* (4.79)*, the arrow on the left corresponds to* (4.134)*.* Right: *The renormalisation transformation that connects successive hierarchical levels upwards. The vertical arrows correspond to* (4.76)*. The horizontal arrows represent the interaction with the effective seed-bank. The arrows on the left represent the resampling driven by the renormalised diffusion function.*

To state the clustering result, abbreviate

$$\bar{\vartheta}^{(n)} = (\vartheta_n, \overbrace{\vartheta_n, \cdots, \vartheta_n}^{n+1 \text{ times}}, \theta_{y_{n+1}}, \theta_{y_{n+2}}, \cdots). \tag{4.135}$$

Theorem 4.5.1 (Renormalised scaling). *Let c_k be as in* (4.5)*, e_k and K_k as in* (4.10) *and E_k as in* (4.64)*. Define*

$$A_n = \frac{1}{2} \sum_{k=0}^{n-1} \frac{E_k}{c_k} \frac{(E_k c_k + e_k)}{(E_k c_k + e_k) + E_k K_k e_k}, \qquad n \in \mathbb{N}. \tag{4.136}$$

Then

$$\lim_{n\to\infty} Q^{(n)}\big(\bar{\vartheta}^{(n)}, \cdot\big) = (1-\theta)\, \delta_{(0,0^{\mathbb{N}_0})} + \theta\, \delta_{(1,1^{\mathbb{N}_0})} \tag{4.137}$$

if and only if

$$\lim_{n\to\infty} A_n = \infty. \tag{4.138}$$

Moreover, if (4.138) *holds, then for all $g \in \mathcal{G}$,*

$$\lim_{n\to\infty} A_n \mathcal{F}^{(n)} g = g_{\mathrm{FW}} \quad \textit{pointwise}, \tag{4.139}$$

with $g_{\mathrm{FW}}(x) = x(1-x)$, $x \in [0,1]$.

The proof of Theorem 4.5.1 is given in Section 10. The scaling factors A_n can be interpreted as clustering coefficients: in Section 4.5.2 we will show that the faster the A_n grow to infinity, the faster we expect to see clusters grow. The property in (4.137) corresponds to the *clustering regime*. According to (4.139), even though A_n depends on the choice of the sequences $\underline{K}, \underline{e}, \underline{c}$ in (4.5) and (4.10), the limit $A_n\mathcal{F}^{(n)}g$ as $n \to \infty$ is *universal*: irrespective of the choice of $g \in \mathcal{G}$, the limit is the standard Fisher-Wright diffusion function g_{FW}. Thus, g_{FW} is the *global attractor of the renormalisation transformation* (see Fig. 4.11).

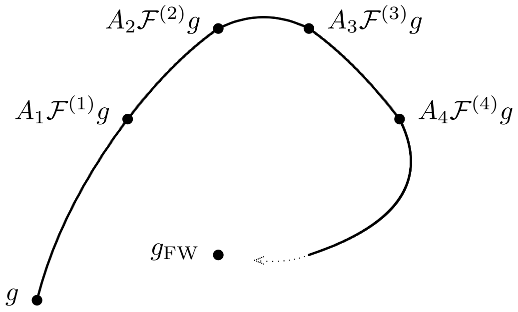

Figure 4.11: Flow of the iterates $\mathcal{F}^{(n)}g$, $n \in \mathbb{N}_0$, of the renormalisation transformation acting on the class $\mathcal{G}$. After multiplication by A_n, the flow is globally attracted by g_{FW}.

§4.5.2 Growth of mono-type clusters

In the *clustering regime* we are interested in how fast mono-type clusters grow in space over time. For the system on $\mathbb{Z}^d$ and Ω_N without seed-bank the growth rate has been studied in detail. Different growth rates were found for *strongly recurrent* and *critically recurrent* migration. Typical examples on Ω_N are migrations with coefficients $c_k = c^k$ with $c \in (0,1)$, respectively, $c_k = C$ with $C \in (0,\infty)$. Typical examples on $\mathbb{Z}$, respectively, $\mathbb{Z}^2$ are migrations with zero mean and finite variance. For these models the following behaviour occurs.

- In the strongly recurrent case, mono-type clusters grow fast and cover a volume that increases at time t at a rate that is given by the Green function up to time t of the underlying random walk, times a certain random constant that can be determined explicitly and that is independent of the diffusion function $g \in \mathcal{G}$ [33], [51]. The cluster growth is monitored by considering families of balls growing in time at such a speed that, starting from a translation invariant and ergodic initial state, the mean of the configuration in the ball is still close to the starting mean but begins to move. *Fast clustering* means that the cluster covers multiples of a scale that eventually lies in every finite family of balls with the above property.

- In the critically recurrent case, the volume grows only moderately fast, like $N^{(1-U)t}$ as $t \to \infty$, with $U \in [0,1]$ a random variable. In other words, the cluster sizes have random orders of magnitude, an effect known as *diffusive clustering.* For $c_k = C \in (0,\infty)$, $k \in \mathbb{N}_0$, the distribution of U can be identified by studying the fraction of active individuals of type 1 in a ball of size $N^{(1-u)t}$, which can be shown to converge to $V(\log \frac{1}{1-u})$ as $t \to \infty$ with $(V(s))_{s \geq 0}$ the standard Fisher-Wright diffusion, irrespective of the choice of $g \in \mathcal{G}$ [35], [36].

- For more general migration it is possible that mono-type clusters grow slower than any positive power of t as $t \to \infty$. This occurs for recurrent migration in which the Green function up to time t grows like $o(\log t)$. For this regime only few results are available [25].

From the perspective of explaining *universality* in $g \in \mathcal{G}$ in the hierarchical mean-field limit $N \to \infty$, the above type of behaviour has been studied in detail in [25] and [41] for the Fleming-Viot model, respectively, the Cannings model without seed-bank. The renormalisation analysis for the model with seed-bank allows us to study how the seed-bank affects the cluster growth. In what follows we give a sketch of *three regimes of cluster growth.*

Types of clustering. If a ball in Ω_N lies in a mono-type cluster, then the block average of the active and the dormant components in this ball are all close to either 0 or 1. We can therefore analyse the growth rate of mono-type clusters by analysing at which hierarchical level block averages hit 0 or 1 in the limit as $N \to \infty$. To that end, we look at the interaction chain $M^k_{-l(k)}$ for $k \to \infty$, where the *level scaling function* $l\colon \mathbb{N}_0 \to \mathbb{N}_0$ is non-decreasing with $\lim_{k\to\infty} l(k) = \infty$ and is suitably chosen such that we obtain a *non-trivial clustering limiting law*, i.e.,

$$\lim_{k\to\infty} \mathcal{L}\big[M^k_{-l(k)}\big] = \mathcal{L}\big[\hat{\theta}\,\big], \tag{4.140}$$

where the limiting sequence of random frequencies $\hat{\theta}$ satisfies

$$0 < \mathbb{P}\big(\hat{\theta} \in \{0^{\mathbb{N}_0}, 1^{\mathbb{N}_0}\}\big) < 1. \tag{4.141}$$

In line with [25] and [22], in order to analyse the growth of mono-type clusters on multiple space-time scales in the hierarchical mean-field limit, it is natural to consider a family of non-decreasing functions $l_\chi\colon \mathbb{N}_0 \to \mathbb{N}_0$, $\chi \in I \subseteq [0,\infty)$, called the *cluster scales*, satisfying (4.140)–(4.141):

(1) **F**ast clustering: $\lim_{k\to\infty} l_\chi(k)/k = 1$ for all $\chi \in I$.

(2) **Di**ffusive clustering: $\lim_{k\to\infty} l_\chi(k)/k = \kappa(\chi)$ for all $\chi \in [0,1]$, where $\chi \mapsto \kappa(\chi)$ is continuous and non-increasing with $\kappa(0) = 1$ and $\kappa(1) = 0$.

(3) **S**low clustering: $\lim_{k\to\infty} l_\chi(k)/k = 0$ for all $\chi \in I$. (This regime borders with the regime of coexistence.)

We write $(M^\infty_\chi)_{\chi\in I}$ with $M^\infty_\chi = \lim_{k\to\infty} M^k_{-l_\chi(k)}$ to denote the *cluster process.*

Remark 4.5.2. Examples are:

(1) $I = \mathbb{N}_0$, $l_\chi(k) = k - \chi$.

(2) $I = [0,1]$, $l_\chi(k) = \lfloor (1-\chi)k \rfloor$.

(3) $I = [0,1]$, $l_\chi(k) = \lfloor L(k^{1-\chi}) \rfloor$ with $L(0) = 0$, L non-decreasing and sublinear.

In words, the clusters cover blocks of level: (1) $k-\chi$; (2) $\lfloor(1-\chi)k\rfloor$; (3) $L(k^{1-\chi})$. For the model without seed-bank and with migration coefficients $c_k = c^k$ with $c \in (0,1)$, case (1) is realised with a Markov chain $(M_l^{\infty})_{l\in\mathbb{N}_0}$ as scaling limit, while for $c_k = C$, case (2) is realised with a time-transformed Fisher-Wright diffusion in χ as scaling limit. (For finite N, this corresponds to the first and the second example given in the first paragraph of this section.) For the model without seed-bank, these scales have been shown to satisfy the required conditions. Case (3) also appears for the model without seed-bank, but detailed information on scales and scaling limits is lacking. As we will see below, seed-banks can slow down cluster growth, so case (3) is worthwhile to be studied in more detail. ■

Recall (4.136). Fast clustering corresponds to $A_k \gg k$, diffusive clustering to $A_k \asymp k$, and slow clustering to $A_k \ll k$ for large k. Theorem 4.5.3 below shows that, subject to (4.52) and (4.53), all three regimes are possible for the model with seed-bank. The regimes are the same as for the model without seed-bank when $\rho < \infty$, but different when $\rho = \infty$.

For systems without seed-bank, examples of the three types of clustering can be found in the literature: diffusive clustering in [2], [16] (voter model on $\mathbb{Z}$, respectively, $\mathbb{Z}^2$) and in [20], [35], [25], [51] (interacting Fleming-Viot processes on Ω_N with $N < \infty$, respectively, $N \to \infty$), all types of clustering in [22], [52] , [71] (interacting Feller diffusions on Ω_N with $N \to \infty$) and in [41], [42] (interacting Cannings processes on Ω_N in non-random and random environment with $N \to \infty$).

For the model with seed-bank we have to use the asymptotics of $(A_k)_{k\in\mathbb{N}}$ to identify the set I and the family $(l_\chi(\cdot))_{\chi\in I}$, and show that $(M^k_{-l_\chi(k)})_{\chi\in I}$ converges as $k\to\infty$ to a Markov process, which we want to identify.

Computations. In the following we demonstrate how we can carry out the above task. The key idea is to study first and second moments of the interaction chain, as well as sums of variances in order to get a handle on the quadratic variation process. To that end we calculate

$$V^k_{-l} = \text{ the conditional variance of the active part of } M^k_{-l} \text{ given } M^k_{-(l+1)} \tag{4.142}$$

and consider the sum of random variables $A_{k,n} = \sum_{-(k+1)\le -l\le -n} V^k_{-l}$, $n \in \mathbb{N}_0$. In order for the system to cluster, we must have $\lim_{k\to\infty} A_{k,n} = 0$ for every $n \in \mathbb{N}_0$. The *volatility profile* is given by

$$(p_\chi(k))_{\chi\in[0,1]}, \qquad p_\chi(k) = A_{k,l_\chi(k)}/A_{k,0}. \tag{4.143}$$

This profile is a *random variable* that depends on the interaction chain up to $M^k_{-l_\chi(k)}$. Since $A_{k,l_\chi(k)} = A_{k,0} - A_{l_\chi(k)-1,0}$, we have $p_\chi(k) = (A_{k,0} - A_{l_\chi(k)-1,0})/A_{k,0}$. For diffusive clustering, for instance, we want to show that

$$\lim_{k\to\infty} p_\chi(k) = 1 - \kappa(\chi), \qquad \chi \in [0,1], \tag{4.144}$$

while for fast clustering the limit is 0 and for slow clustering the limit is 1. From (4.139) we know that the scaled renormalised diffusion function $A_n\mathcal{F}^{(n)}(g)$ tends to the standard Fisher-Wright diffusion function as $n \to \infty$. Since the latter hits the boundary $\{0,1\}$ after some finite time, the coefficients A_n describe the speed at which the interaction chain hits this boundary. We next make this idea precise and show how it can be used to obtain information about the growth of mono-type clusters.

The kernels defined in Section 4.5.1 allow us to compute the first and second moments of all the block averages, which will be done in Section 10.1 (Propositions 10.1.1–10.2.2). In particular, using the interaction chain starting between at $-n$ and running until $-m$ with $-n < -m \leq 0$, and considering the m-block averages on time scale $N^m t$ in the limit $N \to \infty$, we find that the variance of the active component x_m^n of M_{-m}^n equals

$$\mathbb{V}\mathrm{ar}(x_m^n) = \mathbb{E}\left[(x_m^n - \vartheta_n)^2\right] = A_m^n (\mathcal{F}^{(n+1)} g)(\vartheta_n), \tag{4.145}$$

where

$$A_m^n = \frac{1}{2} \sum_{k=m}^{n} \frac{E_k}{c_k} \frac{(E_k c_k + e_k)}{(E_k c_k + e_k) + E_k K_k e_k}. \tag{4.146}$$

(Note that $A_n = A_0^{n-1}$.) On the other hand, since $x_m^n \in (0,1)$ we have $\mathbb{V}\mathrm{ar}(x_m^n) \in (0,1)$ and $A_m^n(\mathcal{F}^{(n+1)})(\vartheta_n) \in (0,1)$. Taking $m=0$, we get $(\mathcal{F}^{(n+1)} g)(\vartheta_n) \in (0, \frac{1}{A_0^n})$. This implies that

$$(\mathcal{F}^{(n+1)} g)(\vartheta_n) = \int_{[0,1]^2} (\mathcal{F}^m g)(x_m)\, Q_m^{(n)}((\vartheta_n, \theta_{y,n}), \mathrm{d}z_m) \in \left(0, \tfrac{1}{A_0^n}\right). \tag{4.147}$$

Since $\lim_{n\to\infty} A_n(\mathcal{F}^{(n+1)} g) = g_{\mathrm{FW}}$, for large enough m,n we can approximate $\mathcal{F}^{(m)} g \approx g_{\mathrm{FW}}/A_0^m$. Therefore

$$\int \frac{g_{\mathrm{FW}}}{A_0^m}(x_m)\, Q_m^{(n)}((\vartheta_n, \theta_{y,n}), \mathrm{d}z_m) \in \left(0, \tfrac{1}{A_0^n}\right), \tag{4.148}$$

or, equivalently,

$$\int_{[0,1]^2} x_m(1-x_m)\, Q_m^{(n)}((\vartheta_n, \theta_{y,n}), \mathrm{d}z_m) \in \left(0, \tfrac{A_0^m}{A_0^n}\right). \tag{4.149}$$

Hence, if $A_0^m / A_0^n < \epsilon$ with $\epsilon > 0$ small, then we know that with high probability the system on time scale n has clusters with a radius of size m. (Note that for the interaction chain this means that the variance is almost entirely centred between n and m.) Therefore the speed at which A_0^m/A_0^n converges to zero as $m,n \to \infty$ says something about the speed at which monotype clusters form.

To capture the cluster growth, we must decide how we let $m,n \to \infty$. For this we look for clusters of radius $l_\chi(n)$ with $\chi \in I$. Put

$$f^n(l_\chi(n)) = \frac{A_0^{l_\chi(n)}}{A_0^n}, \tag{4.150}$$

and define, for $\epsilon > 0$,

$$\mathcal{X}_\epsilon^n = \inf\{\chi \in I \colon\ f^n(l_\chi(n)) < \epsilon\}. \tag{4.151}$$

Then the three types of clustering correspond to:

(1) **F**ast clustering: $\lim_{n\to\infty} l_{\mathcal{X}_\epsilon^n}(n)/n = 1$.

(2) **D**iffusive clustering: $\lim_{n\to\infty} l_{\mathcal{X}_\epsilon^n}(n)/n = R$ for some random variable R taking values in $(0,1)$.

(3) **S**low clustering: $\lim_{n\to\infty} l_{\mathcal{X}_\epsilon^n}(n)/n = 0$.

In terms of the interaction chain starting from $-k$ with $k \to \infty$, in view of (4.145) this corresponds to the variance in the interaction chain being concentrated near the beginning, being spread out or being concentrated near the end.

§4.5.3 Rates of scaling for renormalised diffusion function

For the system without seed-bank, we have $K_k = e_k = 0$ and $E_k = 1$ for all $k \in \mathbb{N}_0$. Hence

$$A_n = \frac{1}{2}\sum_{k=0}^{n-1}\frac{1}{c_k} \tag{4.152}$$

and (4.137) holds if and only if

$$\sum_{k\in\mathbb{N}_0}\frac{1}{c_k} = \infty. \tag{4.153}$$

Various subcases were analysed in [5]. For the system with seed-bank because $E_0 = 1$ and $E_k < 1$ (see (4.64)), it follows from (4.136) that

$$A_n < \frac{1}{2}\sum_{k=0}^{n-1}\frac{1}{c_k}. \tag{4.154}$$

Thus we see that the seed-bank *weakens clustering*, i.e., enhances genetic diversity, even in the hierarchical mean-field limit.

We identify the clustering regime in the setting where the coefficients are *asymptotically polynomial*, as in (4.52), or are *pure exponential*, as in (4.53). It turns out that there is a delicate interplay between the migration and the seed-bank, resulting in 4 different scalings for asymptotically polynomial coefficients and 8 different scalings for pure exponential coefficients.

Theorem 4.5.3 (Rates of scaling for diffusion function). *Let ρ be as defined in* (4.14).

(I) *If $\rho < \infty$, then* (4.138) *holds if and only* (4.153) *hold, and*

$$A_n \sim \frac{1}{2(1+\rho)}\sum_{m=0}^{k-1}\frac{1}{c_k}. \tag{4.155}$$

(II) *If $\rho = \infty$, then* (4.138) *holds in the following cases:*

- *Subject to* (4.52) *if and only if* $-\phi \le \alpha \le 1$*, with*

$$\begin{aligned} -\phi < \alpha < 1\colon &\quad A_n \sim C_1\, n^{\alpha+\phi},\\ -\phi = \alpha < 1\colon &\quad A_n \sim C_2\, \log n,\\ -\phi < \alpha = 1\colon &\quad A_n \sim C_3\, \frac{n^{1+\phi}}{\log n},\\ -\phi = \alpha = 1\colon &\quad A_n \sim C_4\, \log\log n, \end{aligned} \tag{4.156}$$

where

$$C_1 = \tfrac{1}{2AF}\tfrac{1-\alpha}{\alpha+\phi}, \quad C_2 = \tfrac{1}{2AF}(1-\alpha), \quad C_3 = \tfrac{1}{2AF}\tfrac{1}{1+\phi}, \quad C_4 = \tfrac{1}{2AF}. \tag{4.157}$$

The values of B, β *play no role for the clustering, nor for the asymptotics.*

- *Subject to* (4.53) *if and only if* $Kc \le 1 \le K$*, with*

$$\begin{aligned} c < Ke,\ Kc < 1\colon &\quad A_n \sim \hat{C}_1\,(Kc)^{-(n-1)},\\ c < Ke,\ Kc = 1\colon &\quad A_n \sim \bar{C}_1\, n,\\ c = Ke,\ Kc < 1\colon &\quad A_n \sim \hat{C}_2\,(Kc)^{-(n-1)},\\ c = Ke,\ Kc = 1\colon &\quad A_n \sim \bar{C}_2\, n,\\ c > Ke,\ Kc < 1\colon &\quad A_n \sim \hat{C}_3\,(Kc)^{-(n-1)},\\ c > Ke,\ Kc = 1\colon &\quad A_n \sim \bar{C}_3\, n,\\ c < 1 = K\colon &\quad A_n \sim \tilde{C}_1\, n^{-1}\, c^{-(n-1)},\\ c = 1 = K\colon &\quad A_n \sim \tilde{C}_2 \log n, \end{aligned} \tag{4.158}$$

where

$$\begin{aligned} &\hat{C}_1 = \tfrac{K-1}{2K(1-Kc)}, && \hat{C}_2 = \tfrac{(K-1)^2}{2(2K-1)(1-Kc)}, && \hat{C}_3 = \tfrac{K-1}{2(1-Kc)},\\ &\bar{C}_1 = \tfrac{K-1}{2K}, && \bar{C}_2 = \tfrac{(K-1)^2}{2(2K-1)}, && \bar{C}_3 = \tfrac{K-1}{2},\\ &\tilde{C}_1 = \tfrac{1}{2(1-c)}, && \tilde{C}_2 = \tfrac{1}{2}. \end{aligned} \tag{4.159}$$

The value of e plays no role for the clustering, but does for the asymptotics.

The proof of Theorem 4.5.3 is given in Section 10. Part (I) shows that for $\rho < \infty$ the clustering regime is the same as for the system without seed-bank. The scaling of A_n is controlled by the migration and is reduced by a factor $1/(1+\rho)$ with respect to the seed-bank. Part (II) shows that for $\rho = \infty$ the clustering regime is different from that for the system without seed-bank. Clustering is harder to achieve: since $\lim_{k\to\infty} E_k = 0$ the growth rate of A_n is *strictly smaller* than without seed-bank.

Furthermore, subject to (4.52), if $-\phi < \alpha < 1$, then the growth rate of A_n drops down from $\asymp n^{1+\phi}$ without seed-bank to $\asymp n^{\alpha+\phi}$ with seed-bank, while if $-\phi = \alpha = 1$, then it drops down from $\asymp \log n$ to $\asymp \log\log n$. Similarly, subject to (4.53), if $Kc < 1 < K$, then the growth rate of A_n drops down from $\asymp c^{-n}$ to $\asymp (Kc)^{-n}$, while if $c = K = 1$, then it drops down from $\asymp n$ to $\asymp \log n$.

Returning to the observations made in Section 4.5.2, we see that the three clustering regimes also appear in the model with seed-bank, both for $\rho < \infty$ and $\rho = \infty$, and in the latter case are accompanied by different migration coefficients. The scaling results mentioned in Section 4.5.2 can in principle be deduced from the asymptotics of A_n as $n \to \infty$ in Theorem 4.5.3. It would be interesting to work out the details and to identify the limiting processes that control the cluster growth.