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## **Dormancy in stochastic interacting systems**

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# Dormancy in Stochastic Interacting Systems

Shubhamoy Nandan

Cover pages, part, and chapter openers: images obtained by taking screenshots of a simulation (available at <https://chainserver.pythonanywhere.com/hiv-dormancy>) made by the author of this thesis. The 3D model used in the simulation is of an HIV-cell which is known to exhibit dormancy (or *latency*) lasting up to 10 or 15 years.

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# Dormancy in Stochastic Interacting Systems

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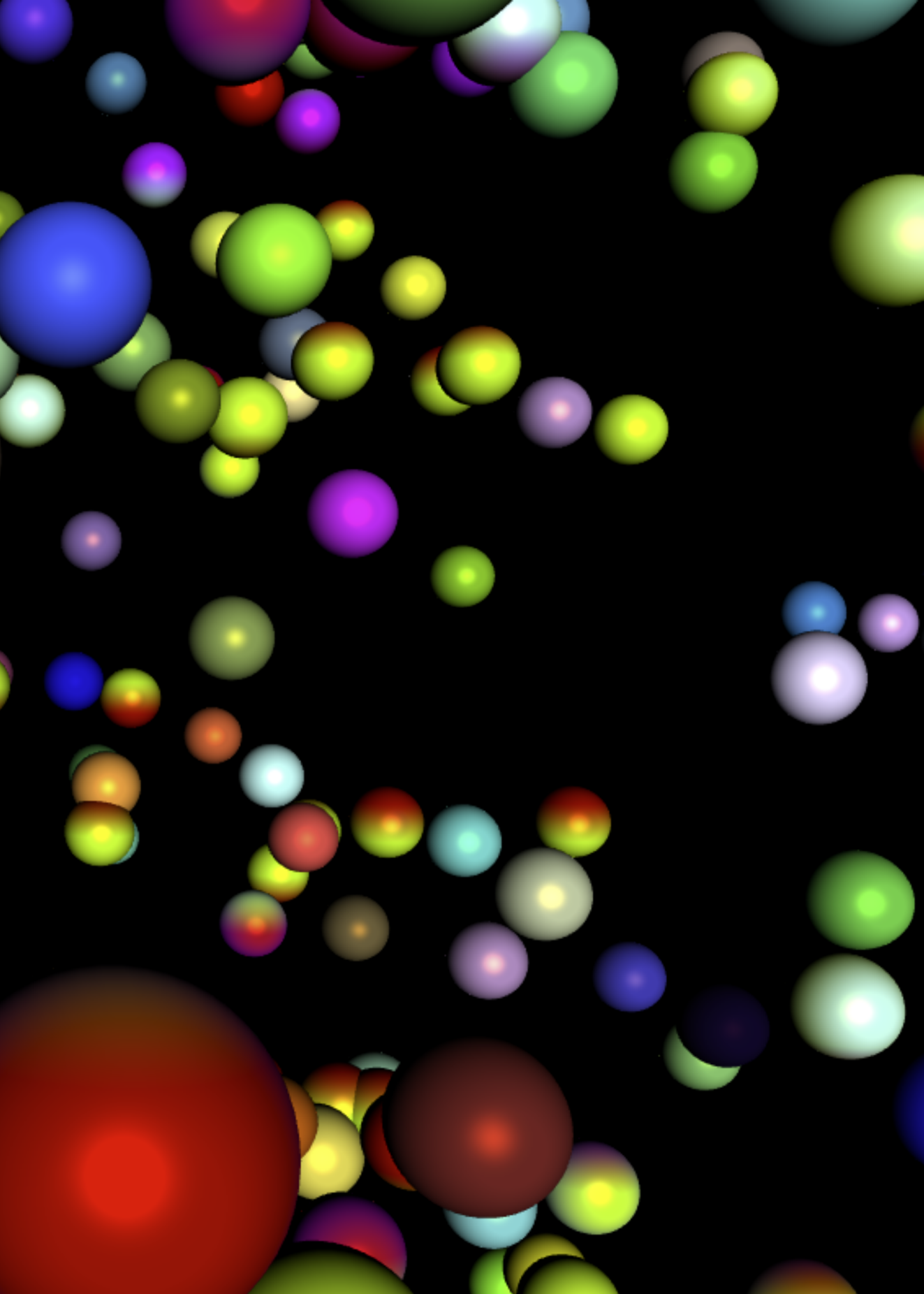
# Contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
§1.1	Introduction to Part I . . . . .	2
§1.1.1	Bits and pieces of genetics . . . . .	2
§1.1.2	Mathematics of evolution . . . . .	3
§1.1.3	The Moran model with seed-bank . . . . .	11
§1.1.4	Spatially inhomogeneous Moran model with seed-banks . . . . .	15
§1.1.5	Summary of Part I . . . . .	19
§1.2	Introduction to Part II . . . . .	24
§1.2.1	Hydrodynamic scaling limit . . . . .	25
§1.2.2	Non-equilibrium steady state . . . . .	29
§1.2.3	Summary of Part II . . . . .	32
§1.3	Further research . . . . .	37
§1.4	Outline of the thesis . . . . .	39
<b>I</b>	<b>Spatially inhomogeneous populations with seed-bank</b>	<b>43</b>
<hr/>		
<b>2</b>	<b>Spatially inhomogeneous populations with seed-bank: duality, existence, equilibrium</b>	<b>45</b>
§2.1	Background, motivation and outline . . . . .	46
§2.2	Main theorems . . . . .	47
§2.2.1	Quick definition of the multi-colony system . . . . .	48
§2.2.2	Well-posedness and duality . . . . .	49
§2.2.3	Equilibrium: coexistence versus clustering . . . . .	50
§2.3	Single-colony model and basic theorems . . . . .	51
§2.3.1	Definition: resampling and exchange . . . . .	51
§2.3.2	Duality and equilibrium . . . . .	52
§2.3.3	Interacting seed-bank coalescent . . . . .	54
§2.4	Multi-colony model and basic theorems . . . . .	56
§2.4.1	Definition: resampling, exchange and migration . . . . .	57
§2.4.2	Spatially interacting seed-bank coalescent . . . . .	59
§2.4.3	Well-posedness and equilibrium . . . . .	62
§2.4.4	Clustering criterion . . . . .	63
§2.5	Proofs: duality and equilibrium for the single-colony model . . . . .	64

§2.5.1	Duality and change of representation . . . . .	64
§2.5.2	Equilibrium . . . . .	67
§2.6	Proofs: duality and well-posedness for the multi-colony model . . . . .	69
§2.6.1	Uniqueness of dual . . . . .	69
§2.6.2	Duality relation . . . . .	71
§2.6.3	Well-posedness . . . . .	77
§2.7	Proofs: equilibrium and clustering criterion for the multi-colony model	80
§2.7.1	Convergence to equilibrium . . . . .	80
§2.7.2	Genetic variability (heterozygosity) . . . . .	81
§2.7.3	Dual: single particle . . . . .	82
§2.7.4	Dual: two particles . . . . .	84
§2.7.5	Proof of clustering criterion . . . . .	86
<b>3</b>	<b>Spatially inhomogeneous populations with seed-bank: clustering regime</b>	<b>91</b>
§3.1	Introduction . . . . .	92
§3.2	Main theorems . . . . .	92
§3.2.1	Preliminaries: assumption and notations . . . . .	93
§3.2.2	Clustering versus coexistence . . . . .	93
§3.3	Dual processes: comparison between different systems . . . . .	96
§3.3.1	Two-particle dual and auxiliary duals . . . . .	96
§3.3.2	Comparison between interacting duals . . . . .	100
§3.3.3	Comparison with non-interacting dual . . . . .	104
§3.3.4	Conclusion . . . . .	106
§3.4	Proofs: clustering criterion and clustering regime . . . . .	110
§3.4.1	Proof of clustering criterion . . . . .	110
§3.4.2	Independent particle system and clustering regime. . . . .	110
§3.5	Discussion . . . . .	116
<b>4</b>	<b>Spatial populations with seed-banks in random environment</b>	<b>119</b>
§4.1	Introduction . . . . .	120
§4.2	Main theorems . . . . .	121
§4.2.1	Recollection of previous results and basic notations . . . . .	121
§4.2.2	Clustering in a fixed environment . . . . .	122
§4.2.3	Clustering in random environment . . . . .	125
§4.2.4	Discussion . . . . .	127
§4.3	Single-particle dual in random environment . . . . .	129
§4.3.1	Subordinate Markov chain and auxiliary environment process . . . . .	130
§4.3.2	Stationary environment process and weak convergence . . . . .	133
§4.3.3	Transference of convergence: discrete to continuous . . . . .	138
§4.4	Proof of main theorems . . . . .	140
§4.4.1	Preliminaries: consistency of dual process . . . . .	140
§4.4.2	Proofs: clustering in fixed and random environment . . . . .	142
<b>A</b>	<b>Appendix: Chapter 3</b>	<b>147</b>

§A.1 Two-particle dual and alternative representation . . . . .	147
§A.2 Completion of the proof of a theorem on the clustering regime . . . . .	149
<b>B Appendix: Chapter 4</b>	<b>155</b>
§B.1 Proof of stationarity of environment process and law of large numbers	155
§B.1.1 Stationary distribution of environment process . . . . .	155
§B.1.2 An application: strong law of large numbers . . . . .	158
§B.2 Fundamental theorem of Markov chains . . . . .	160
<b>II Dormancy in switching interacting particle system</b>	<b>165</b>
<hr/>	
<b>5 Switching interacting particle systems</b>	<b>167</b>
§5.1 Introduction . . . . .	168
§5.1.1 Background and motivation . . . . .	168
§5.1.2 Three models . . . . .	170
§5.1.3 Duality and stationary measures . . . . .	171
§5.1.4 Outline . . . . .	173
§5.2 The hydrodynamic limit . . . . .	174
§5.2.1 From microscopic to macroscopic . . . . .	174
§5.2.2 Existence, uniqueness and representation of the solution . . . . .	180
§5.3 The system with boundary reservoirs . . . . .	183
§5.3.1 Model . . . . .	184
§5.3.2 Duality . . . . .	186
§5.3.3 Non-equilibrium stationary profile . . . . .	188
§5.3.4 The stationary current . . . . .	199
§5.3.5 Discussion: Fick's law and uphill diffusion . . . . .	203
§5.3.6 The width of the boundary layer . . . . .	208
<b>C Appendix: Chapter 5</b>	<b>213</b>
<b>Bibliography</b>	<b>215</b>
<b>Samenvatting</b>	<b>227</b>
<b>Summary</b>	<b>230</b>
<b>Acknowledgements</b>	<b>233</b>
<b>Curriculum Vitae</b>	<b>235</b>
<b>Publications</b>	<b>236</b>





# CHAPTER 1

## Introduction

The present thesis consists of two parts. Part I focusses on the study of a particular class of *interacting particle systems* that describe genetic evolution of spatially structured populations with *seed-banks*. Part II focusses on the study of the *hydrodynamic scaling limit* of three interacting particle systems that incorporate *dormancy* and on the analysis of their non-equilibrium behaviour in the presence of boundary reservoirs.

## §1.1 Introduction to Part I

Probability theory is the area of mathematics that aims at understanding the intrinsic stochastic nature of real-world phenomena by means of the abstract language of mathematics. Within this area, population genetics takes a special place because it brings together mathematics and biology. The primary goal of mathematical population genetics is to understand via tailored mathematical models how evolutionary forces, demographic factors, etc., affect the genealogy and frequency distribution of genotypes in biological populations.

We give a brief overview of the basic concepts that are central to understanding of the genetic evolution of a population in Section 1.1.1. We borrow from [82, 45].

### §1.1.1 Bits and pieces of genetics

Among the numerous factors that contribute to the evolution of a population *resampling*, *mutation*, *natural selection*, *recombination* and *migration* play a central role.

Resampling (or reproduction, in which individuals transfer their gene type to future generations) is the most basic biological activity of almost any living organism. A biologist would prefer to use the word “random genetic drift” to describe the evolutionary effect of resampling in a *panmictic* population, where every individual is equally likely to be the parent of an offspring. Many populations, such as humans, birds, etc., do not seem to exhibit panmixia when mating is categorised on the basis of certain phenotypical characteristics only, but they often appear to do so when the traits under investigations are genotypes [82]. Therefore the assumption of a population being panmictic (or homogeneously mixing), which we adopt throughout this thesis, is reasonable in many circumstances. Resampling (or random mating) in a population is a source of stochasticity that pervades the gene pool of subsequent generations. It induces random fluctuations of various genotype frequencies in a natural way and drives the population towards forming a *homozygous gene pool*, i.e., a gene pool containing only a single genotype.

Mutation introduces novel gene types into a population. It is the molecular equivalent of errors that typically occur when humans carry out complex activities. In the process of replication of genetic material during resampling, spontaneous local changes may occur in the allelic composition of genes. These errors in the reproduction of genetic material give rise to different genotypes. Mutations can also occur during the reparation of damaged cells. Both beneficial and deleterious mutations are rare, but usually have significant evolutionary effects on the population.

The concept of natural selection in evolutionary theory was introduced by Charles Darwin in the mid 19th century. Selection is a force of nature that acts as a further propellant in creating a homozygous gene pool, containing only the *advantageous* genotypes of a population. Under the influence of selection, fitter types in a population have certain advantages while competing for inheritance, and cause the population to adapt more efficiently to environmental changes over time.

Recombination is a phenomena observed in populations consisting of *diploid* individuals. Diploid individuals carry two copies of genetic material in their cells instead

of one (the latter occurs in populations consisting of *haploid* individuals). Offspring of diploid populations, such as humans, have two parents. During reproduction, instead of inheriting a single identical copy of the genetic material from each parent, they inherit a recombined version in which the two copies of the parental genes undergo molecular changes via exchange of material between them. Therefore, even though a recombination event affects the genotype frequencies in an offspring, it does not alter the overall frequency of the alleles that constitute a specific genotype. In this thesis, we will only be concerned with the evolutionary behaviour of haploid populations where recombination is of no relevance.

The demography of populations is in general structured, in the sense that they admit a *carrying capacity* imposed by the surrounding habitat. Even biological cells always arrange themselves in a certain spatial order and this affects the transfer of genetic material. In population genetics the term migration, or more precisely, *migration of genetic material* is therefore construed in the broadest possible sense. A major goal of population genetics is to gain a better understanding of the effect of population structure on evolutionary quantities, such as the heterozygosity in a population, the fixation probability, (i.e., the likelihood of a specific genotype overtaking an entire population) etc. In this thesis, we analyse the role of migration in structured populations with varying capacities. For this purpose, we only consider a *conservative* migration that preserves the local population sizes. This particular choice of migration may not seem the most sensible from a pragmatic point of view. However, as we will see later, the assumption of conservative migration allows for a considerable simplification of the underlying mathematics.

In recent years, researchers in population genetics have started to analyse populations with a *seed-bank* in which individuals temporarily become dormant. Dormancy refers to the ability of an organism to enter into a reversible state of reduced metabolic activity in response to adverse environmental conditions. In the dormant state, organisms refrain from reproduction, and other phenotypic development, until they become active again. While dormancy is a trait found mostly in microbial populations, the natural analogue of dormancy in plant populations is the suspension of seed germination in difficult ecological circumstances. Several experiments suggest that populations exhibiting dormancy have better heterogeneity, survival fitness and resilience [149, 157]. Dormancy appears to be ubiquitous to many forms of life, and to be an important evolutionary trait [109, 142]. The direct effect of this trait is not easily detected when viewed on the evolutionary time scale. Various attempts have been made to better understand dormancy from a mathematical perspective (see e.g. [108, 18] for a broad overview).

## §1.1.2 Mathematics of evolution

Now that the reader knows what basic evolutionary biology is all about and what it consists of, we shift our focus towards the mathematical aspects. In this thesis, we only deal with stochastic models of genetic evolution that incorporate resampling, migration and dormancy in spatially structured populations. For models that include other evolutionary forces, such as mutation, selection, recombination, etc., we refer

the reader to [153, 124, 87, 57, 5].

**Fisher-Wright model.** The mathematics of population genetics starts with the pioneering works of Fisher [61], Wright [153, 154] and Moran [123, 124]. Fisher and Wright introduced a classical model – later called the Fisher-Wright model – that describes the evolution of a panmictic population of constant and finite size under the sole influence of resampling. In this model, the offspring of the population follows a multinomial sampling distribution, reflecting the panmictic nature of the population, and the offspring replaces the entire parent generation at discrete instants of time. Under the model dynamics, each offspring inherits the genetic type of an arbitrarily chosen parent and the total number of offspring produced in each generation is the same as the total size of the parent population. Therefore, in this model the initial population size is conserved over time. This type of modelling is suitable for seasonally breeding small populations, such as plants, animals, etc., with a fixed average life span, in which the successive generations are non-overlapping. The Fisher-Wright model is computationally intensive, but it encompasses evolutionary behaviour of haploid populations as well as diploid populations. The application of the model to diploid populations is valid only if the population is panmictic and monoecious (such as plant populations where self-fertilisation can occur) with size  $2N$ , where  $N \in \mathbb{N}$  is interpreted as the true size of the population.

**Moran model.** In many biological populations, such as microbes, humans, etc., the assumption of non-overlapping generations breaks down and evolution takes place in continuous time. In such scenarios, discrete-time mathematical models do not approximate the evolutionary behaviour of the population well enough and a need for continuous-time models arises. In 1958 Moran introduced a mathematical model [123] – later called the *Moran model* – that is a continuous-time birth and death process with finite state space, and describes the genetic evolution of a panmictic haploid population with finite size. This model, although less popular among biologists, retains all the basic qualitative features of the Fisher-Wright model. Moreover, one advantage in working with this model is that it is analytically more tractable. In this thesis, the Moran model will serve as the primary building block for the modelling of resampling, migration and dormancy in spatially structured populations. Therefore it is useful to take a closer look at its ingredients.

In the Moran model, one considers a finite population of  $N \in \mathbb{N}$  reproductively (via resampling) active haploid individuals. Each individual initially carries a genotype that comes from the gene pool or type space (the collection of all potential genotypes) of the population. For simplicity, we assume that the type space contains only two genotypes, say ♡ and ♠. Models that deal with populations having infinitely many genotypes are known as Fleming-Viot processes (see e.g. [42]) and will not be considered here. According to the Moran dynamics, the population evolves over time via resampling as follows (see Fig. 1.1):

- Each individual in the population carries a *resampling clock* that rings after a random time with exponential distribution of mean 2. When the clock rings, the

individual chooses a parent from the  $N$  individuals (possibly itself) uniformly at random and *adopts* its type.

An equivalent and perhaps more natural description is:

- Each (unordered) *pair* of individuals in the population carries a clock that rings after a random time with exponential distribution of mean 2. When a clock rings, one of the two individuals gives birth to an offspring and the other individual dies.

We will stick to the former description of the model because it is mathematically more convenient. Note that the individuals are assumed to have an equal birth and death rate, which, similarly as in the Fisher-Wright model, forces the total population size to remain constant over time. Also observe that the rate of resampling is chosen to be  $\frac{1}{2}$ . This choice is made only to make the Moran model run at the same time scale as the Fisher-Wright model and has no other reasoning behind it. In population genetics, one is usually interested in the collective behaviour of an evolving population in which the genotypic information on a specific individual hardly matters. Because of this, we may choose not to label each individual of the population and instead to focus on the genetic configuration of the population as a whole. Since the individuals carry one

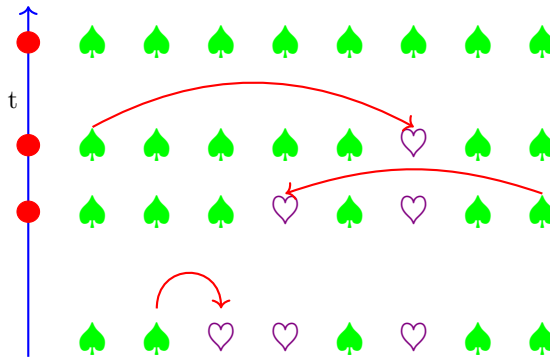


Figure 1.1: A schematic representation of a haploid population evolving under Moran dynamics. Individuals carry one of two types: ♡ and ♠. Red dots in the continuous time line stand for a resampling event. The arrows indicate simultaneous birth and death event involved in a pair of individuals.

of two genotypes and the population size is a conserved quantity, we need only one variable in order to fully specify the overall genetic evolution of the finite population, namely, the *number* of individuals having a particular type. Let us denote by  $X(t)$  the number of type-♡ individuals in the population at time  $t$ . Since the time lapses between successive resampling events are assumed to be exponentially distributed and the population is panmictic, we see that

$$z := (X(t))_{t \geq 0} \quad (1.1)$$

becomes a continuous-time Markov process with state space  $[N] := \{0, 1, \dots, N\}$ . As is the case with any Markov process, the time evolution of  $z$  is characterised by

its behaviour in an infinitesimal time interval. Mathematically, this information is contained in the so-called *infinitesimal generator* of the process  $z$ . As the concept of the generator of a Markov process will be frequently exploited in various parts of this thesis, we briefly elaborate on the connection between an infinitesimal generator and a Markov process. In order to avoid technicalities, we will skip the subtleties behind the estimation.

**Markov generator.** The generator of a time-homogeneous Feller Markov process  $Z := (Z_t)_{t \geq 0}$  is a linear operator  $G$  defined on a suitable dense subspace  $\text{dom}(G)$  (referred to as the domain of  $G$ ) of a Banach space  $V$  (a normed and complete linear space) containing functions (often assumed to be continuous and bounded) on the state space  $\mathcal{X}$  of the process  $Z$ , which often is an uncountable set. Due to the Markovian nature of  $Z$ , the canonical law of  $Z$  is determined by the family of one-dimensional distributions  $(\mu_t)_{t \geq 0}$ , where  $\mu_t$  is the distribution of  $Z_t$ . These one-dimensional distributions, in turn, can be fully characterised by a one-parameter family of linear contraction operators – the so-called *semigroup*  $(S_t)_{t \geq 0}$  associated with  $Z$  – that are defined on  $V$ . The relation between the contractions  $(S_t)_{t \geq 0}$  and the distributions  $(\mu_t)_{t \geq 0}$  comes from a *topological duality* (cf. [112, Theorem 1.5, Chapter I]) and is given by

$$\int_{\mathcal{X}} S_t f \, d\mu_0 = \int_{\mathcal{X}} f \, d\mu_t, \quad f \in V, t \geq 0. \quad (1.2)$$

In particular, taking  $\mu_0$  to be the Dirac distribution concentrated at  $z \in \mathcal{X}$ , we see that

$$(S_t f)(z) = \mathbb{E}_z[f(Z_t)], \quad f \in V, t \geq 0, \quad (1.3)$$

where  $\mathbb{E}_z$  denotes the expectation taken w.r.t. the law of  $Z$  started at  $z$ . Therefore, constructing the canonical law of  $Z$  is equivalent to specifying the semigroup  $(S_t)_{t \geq 0}$ . This is where the densely defined linear operator  $G$  becomes relevant.

In order to construct the semigroup  $(S_t)_{t \geq 0}$  of the Markov process  $Z$ , one can appeal to the Hille-Yosida theorem (cf. [58, Theorem 2.6]), which provides a necessary and sufficient criterion on  $G$  to *generate* the semigroup. Alternatively, one can obtain the associated semigroup by formulating a *well-posed Martingale Problem* for the generator  $G$  (cf. [112, Section 5, Chapter I]). In this thesis we will adopt the latter approach in order to extend the Moran model to the context of spatially structured populations. The generator and the semigroup are related by

$$Gf = \lim_{t \downarrow 0} \frac{S_t f - f}{t}, \quad f \in \text{dom}(G) \subseteq V, \quad (1.4)$$

where the above convergence is in the chosen Banach space  $V$ . In general, it is not easy to specify the full domain  $\text{dom}(G)$  of the generator  $G$  explicitly. However, if the state space  $\mathcal{X}$  of the process  $Z$  is a countable set equipped with the discrete topology, then in most situations both  $\text{dom}(G)$  and  $V$  can be taken as  $\mathcal{F}_b(\mathcal{X})$ , the space of all bounded functions on  $\mathcal{X}$  endowed with the sup norm  $\|\cdot\|_\infty$ , which is defined as

$$\|f\|_\infty := \sup_{z \in \mathcal{X}} |f(z)|, \quad f \in \mathcal{F}_b(\mathcal{X}). \quad (1.5)$$

In case of the Moran model, the generator  $G_{\text{Mor}}$  of the Markov process  $z$  defined in (1.1) is given by

$$G_{\text{Mor}}f(x) = \frac{(N-x)x}{2N}[f(x+1) - f(x)] + \frac{x(N-x)}{2N}[f(x-1) - f(x)], \quad (1.6)$$

where  $x \in [N]$  and  $f \in \mathcal{F}_b([N])$ . To see how this expression comes about, we can use (1.3)–(1.4) to write

$$G_{\text{Mor}}f(x) = \lim_{t \rightarrow 0} \frac{\mathbb{E}_x[f(X_t)] - f(x)}{t} = \lim_{t \rightarrow 0} \mathbb{E}_x \left[ \frac{f(X_t) - f(X_0)}{t} \right]. \quad (1.7)$$

In other words,  $G_{\text{Mor}}f(x)$  is the average infinitesimal rate of change of the observable  $f$  when the population evolving via the Moran dynamics initially contains  $x$  individuals of type  $\heartsuit$ . In an infinitesimal time interval, the number  $x$  of type- $\heartsuit$  individuals increases by 1 if a type- $\spadesuit$  individual in the population chooses a type- $\heartsuit$  individual as its parent, and decreases by 1 if a type- $\heartsuit$  individual chooses a type- $\spadesuit$  individual as its parent. The former event reflects the change  $[f(x+1) - f(x)]$  of the observable  $f$  and happens at a cumulative average rate  $\frac{(N-x)x}{2N}$ , the latter event reflects the change  $[f(x-1) - f(x)]$  of the observable  $f$  and happens at the same rate  $\frac{x(N-x)}{2N}$ . The reason for the rates being equal can be explained as follows. Each individual in the population resamples at rate  $\frac{1}{2}$ . For the former event to occur, an individual of type  $\spadesuit$  must resample, which happens at total rate given by  $\frac{(N-x)}{2}$ , the number of type- $\spadesuit$  individuals during resampling multiplied by the resampling rate, and while resampling this individual must pick uniformly at random a type- $\heartsuit$  individual, which has probability  $\frac{x}{N}$ . Therefore, the cumulative rate of occurrence of the former event is  $\frac{x(N-x)}{2N}$ . A similar argument applies to the latter event.

**Genealogy in the Moran model.** The Moran model is particularly popular in population genetics because it is equivalent to a *birth* and *death* process, which is well understood in the Markov process literature. Many quantities of biological interests, such as the probability of two randomly chosen individuals being identical by descent, the amount of heterozygosity in the population, etc., can be explicitly computed.

Another advantage in the Moran model is that the *genealogy* (i.e., the process that tracks the ancestral lineages of individuals backwards in time) of finitely many individuals sampled from the panmictic Moran population is *exactly* governed by the so-called *Kingman coalescent process* (cf. [96]). This is in contrast to the Fisher-Wright model, where the individual ancestral lines inherit the Kingman coalescent structure only in the *large-population-size* limit, and when viewed on a time scale proportional to the size of the population. The method of analysing the evolution of a population by tracing individual genealogies all the way back to their ancestors was initiated by Kingman [96], who introduced the aforementioned coalescent process. The genealogical approach to studying evolutionary stochastic processes is now a widespread technique in population genetics. The pioneering work in [96] has in fact inspired the current development of coalescent theory that encompasses not only the Kingman coalescent, but also other coalescent processes [137, 7], such as the  $\beta$ -coalescent, the  $\Lambda$ -coalescent, etc.



The Kingman coalescent process

$$\mathcal{C} := (\mathcal{C}_t)_{t \geq 0} \quad (1.8)$$

is a continuous-time Markov process and takes values in the set of all partitions of the natural numbers. A state of the partition-valued process is a mathematical representation of the genealogical relation between individuals of a population that reproduce by resampling. In particular, a block in the time- $t$  state  $\mathcal{C}_t$  stands for an ancestor of the individuals that are alive in the evolved Moran population at time  $t$ . The individuals that descend from the ancestor specified by a block are marked by the natural numbers within the block. The coalescent process  $\mathcal{C}$  evolves *backwards* in time, while the population in the Moran process evolves *forwards* in time. In the time evolution of the process, each pair of blocks in a partition coalesces at rate 1 to form a new partition containing one block less than before. This process appropriately describes the genealogy of individuals as long as we assume that the individuals reproduce independently at rate  $\frac{1}{2}$  and measure time in units of length  $N$ , where  $N$  is the size of the constituent population.

In [55] (see also [138, 77]) the connection between the genealogy in a Moran population and the Kingman coalescent was established in a mathematical framework, where a “particle model” representation of an *infinite* population model is obtained via the so-called “look-down” construction. The look-down construction demonstrates that a population of any finite size evolving according to the Moran dynamics can be consistently embedded into the infinite population model (cf. [55, Lemma 2.1]). In this formulation of the Moran model, one obtains a strong (pathwise) form of *stochastic duality* between the Moran process and the Kingman coalescent process. The strong duality, in turn, implies what is known as a *weak* stochastic duality between the Moran process  $z$  and the *block-counting process*

$$\bar{\mathcal{C}} := (|\mathcal{C}_t|)_{t \geq 0} \quad (1.9)$$

associated to the Kingman coalescent process. Here, for a partition  $\mathcal{R}$  of natural numbers,  $|\mathcal{R}|$  denotes the number of blocks in  $\mathcal{R}$ . Let us elaborate a bit on the notion of weak stochastic duality and on the process  $\bar{\mathcal{C}}$ , as these will be central to the theme of this thesis.

**Stochastic duality.** The concept of weak stochastic duality relates two Markov processes in an *intertwined state*. More precisely, we say that two Markov processes  $(K_t)_{t \geq 0}$  and  $(L_t)_{t \geq 0}$ , taking values in their respective state spaces, say  $\Omega$  and  $\hat{\Omega}$ , are dual to each other w.r.t. a (bounded and measurable) duality function  $D(\cdot, \cdot) : \Omega \times \hat{\Omega} \rightarrow \mathbb{R}$  if the following intertwining relation is satisfied:

$$\mathbb{E}_k[D(K_t, l)] = \mathbb{E}^l[D(k, L_t)], \quad \forall t \geq 0, (k, l) \in \Omega \times \hat{\Omega}, \quad (1.10)$$

where the expectation in the left-hand (resp. right-hand) side is taken w.r.t. the law of the process  $(K_t)_{t \geq 0}$  (resp.  $(L_t)_{t \geq 0}$ ) started at  $k \in \Omega$  (resp.  $l \in \hat{\Omega}$ ). When the duality function is nice enough, the above relation can be characterised in terms of the infinitesimal generators of the two processes. In particular, one can see from [91,

Proposition 1.2] that if, for all  $(k, l) \in \Omega \times \hat{\Omega}$ , the two functions  $D(\cdot, l) : \Omega \rightarrow \mathbb{R}$  and  $D(k, \cdot) : \hat{\Omega} \rightarrow \mathbb{R}$  are in the domain of the infinitesimal generators  $\hat{K}$  and  $\hat{L}$  of the two respective Markov processes, then the relation in (1.10) holds if and only if

$$(\hat{K}D(\cdot, l))(k) = (\hat{L}D(k, \cdot))(l), \quad \forall (k, l) \in \Omega \times \hat{\Omega}. \quad (1.11)$$

In the case where the generators  $\hat{K}$  and  $\hat{L}$  are equal and belong to the same Markov process, the latter is said to be *self-dual* w.r.t. the duality function  $D(\cdot, \cdot)$ .

The notion of weak stochastic duality discussed above is very general and has developed into a powerful technique for analysing Markov processes. A sample of references for an overview on this topic is [71, 25, 24, 91]. In population genetics, weak stochastic duality between two Markov processes often originates from a strong pathwise duality, where the dual process is *graphically* constructed by looking at the original process backwards in time. This is because, in certain special situations, the original Markov process models the evolution of a biological population in such a way that the underlying genealogical process also is Markovian. These dualities are referred to as *sampling duality* relations in the literature on population genetics, because the associated duality function can be seen as a *formula* for sampling individuals from the population. The Moran model is no exception in this respect. Indeed, the process  $z$  in (1.1) is in a sampling duality relation with the block-counting process  $\bar{C}$  in (1.9). The duality relation, as is demonstrated in [55], comes from a strong pathwise duality between the Moran process and the Kingman coalescent process. In practice, stochastic duality is relevant in the context of Markov processes only. Let us therefore point out that  $\bar{C}$  is in fact a pure death Markov process with values in the set  $\mathbb{N}$  of all natural numbers. The process  $\bar{C}$  has transition rates

$$n \mapsto n - 1 \quad \text{at rate} \quad \binom{n}{2} \mathbb{1}_{\{n \geq 2\}}, \quad n \in \mathbb{N}. \quad (1.12)$$

The sampling duality relation between the process  $z$  started at a state  $x \in [N]$ ,  $N \in \mathbb{N}$ , and the block-counting process  $\bar{C}$  started at  $n \in \mathbb{N}$  is given by

$$\mathbb{E}_x \left[ \frac{\binom{X_t}{n}}{\binom{N}{n}} \mathbb{1}_{\{n \leq X_t\}} \right] = \mathbb{E}^n \left[ \frac{\binom{x}{|\mathcal{C}_t|}}{\binom{N}{|\mathcal{C}_t|}} \mathbb{1}_{\{|\mathcal{C}_t| \leq x\}} \right], \quad t \geq 0, \quad (1.13)$$

where the expectation on the left-hand side is taken w.r.t. the law of the Moran process  $z$  and the expectation on the right-hand side is taken w.r.t. the law of the block-counting process  $\bar{C}$ . In words, the above relation says: the probability that  $n$  individuals sampled from the time- $t$  Moran population of size  $N$  have type  $\heartsuit$  is the same as the probability that all ancestors identified by tracing the  $n$  sampled lineages backwards in time from time  $t$  to time 0 have type  $\heartsuit$ .

The weak form of the above duality conceals the embedded coalescent structure in the backwards time evolution of the lineages. Therefore it gives little insight into the dual process. However, this form of duality is more pronounced in the literature, because it allows for the possibility of *constructing* multiple duality functions and dual processes for a single Markov process. This is usually achieved by studying the so-called *Lie-algebraic* structure of the associated infinitesimal generator (see e.g.,

[71]). The general principle in the algebraic framework of duality is to express the Markov generator of the original process in terms of elementary algebraic operators that constitute some well-known Lie algebra, and perform an Ansatz via a well-chosen duality function for the construction of a dual Markov generator.

The duality relation in (1.13) is extremely useful for obtaining analytic expressions of many quantities related to the Moran process. To demonstrate just how useful the relation in (1.13) is, let us consider the problem of computing the probability that a two-type ( $\heartsuit$  and  $\spadesuit$ ) panmictic population of size  $N \in \mathbb{N}$  evolving via the Moran dynamics eventually ends up with a homozygous gene pool containing only the gene type  $\heartsuit$ . First observe that, with probability 1, the Moran population eventually fixates to a single gene type. The reason is that the reproduction via resampling is a dissipative mechanism that causes loss of individual genetic information in the Moran population. As the total population is of finite size, only one of the two gene types survives in the long term and the entire population fixates to a single gene type. To compute the fixation probability, we first observe that the process  $z = (X_t)_{t \geq 0}$  in (1.1) is a bounded Martingale that converges a.s. to one of the two absorbing states  $N$  and  $0$ . Here, we recall that  $X_t$  is the number of type- $\heartsuit$  individuals in the population of fixed size  $N$  at time  $t$ . In particular, from (1.13) we see that the fixation probability (in law) to the type  $\heartsuit$  is given by

$$\lim_{t \rightarrow \infty} \mathbb{E}_x \left[ \frac{\binom{X_t}{n}}{\binom{N}{n}} \mathbb{1}_{\{n \leq X_t\}} \right],$$

which by the duality relation in (1.13) is equal to

$$\lim_{t \rightarrow \infty} \mathbb{E}^n \left[ \frac{\binom{x}{|\mathcal{C}_t|}}{\binom{N}{|\mathcal{C}_t|}} \mathbb{1}_{\{|\mathcal{C}_t| \leq x\}} \right],$$

with the expectation taken w.r.t. the block-counting process  $(|\mathcal{C}_t|)_{t \geq 0}$  corresponding to the Kingman coalescent with initial state  $n$ . Since the block-counting process starting from any natural number  $n$  eventually fixates at the value 1 in the limit  $t \rightarrow \infty$ , the above expression equals  $\frac{x}{N}$  which gives the desired fixation probability.

In [25] the Lie-algebraic method of duality is applied to the context of mathematical models in population genetics. In particular, the duality in (1.13) is retrieved from an algebraic representation of the infinitesimal generator associated to the Moran process given in (1.6) (see e.g., [25, Section 4]). In this thesis, instead of following the standard route of genealogy-tracing, we exploit the Lie-algebraic framework of duality in order to obtain two dual processes corresponding to, respectively, the single and the multi-colony Moran process with seed-banks. In the next section we extend the standard Moran model to include a *seed-bank* component that models the presence of dormancy in the population. The single-colony Moran model with seed-bank serves as the building block for the construction of the multi-colony (spatial) Moran model with seed-banks.

### §1.1.3 The Moran model with seed-bank

In a stochastic individual-based model, dormancy is mathematically incorporated by turning off *resampling* for a random and possibly extended period of time. This way of modelling dormancy introduces memory, and thereby gives rise to a rich behaviour of the underlying stochastic system. The first mathematical model dealing with the effect of dormancy goes back to [34]. Since then several other ways to model seed-banks have emerged [92, 16, 14]. For example, in the model proposed in [92], the Fisher-Wright model [153] was extended to include a *weak* seed-bank, where individuals reproduce offspring several generations ahead in time, with the skipped generations being interpreted as a dormant period for the offspring. In this model the resulting genealogy of the population becomes stretched over time and retains the same coalescent structure described by the Kingman coalescent process  $\mathcal{C} = (\mathcal{C}_t)_{t \geq 0}$ . In [13, 12], a different qualitative behaviour was observed by including a *strong* seed-bank component, which enables the dormant individuals to have wake-up times with fat tails. A trade-off in these models was the loss of the Markov property in the time evolution of the system. This issue was partially tackled in [14], which introduced the *seed-bank coalescent*, a new class of coalescent structures that, broadly speaking, describe the genealogy of a population exhibiting extreme dormancy.

While the works mentioned above deal with seed-bank models only in the *diffusive regime*, obtained after taking the *large-colony-size-limit* of individual-based models, it is biologically more reasonable to consider seed-bank models with populations that have *finite* sizes. A natural candidate for models dealing with finite populations is the Moran model introduced earlier. In this section we extend the Moran model to include a seed-bank component that captures the effect of dormancy in the Moran population.

**Single-colony Moran model with seed-bank.** The seed-bank modelling in the Moran process is achieved by subdividing the constituent population of total size, say  $(N + M) \in \mathbb{N}$ , into two subpopulations, namely, an *active* population of size  $N \in \mathbb{N}$  and a *dormant* population of size  $M \in \mathbb{N}$ , and turning reproduction via resampling off in the dormant population. In order to preserve the flow of gene information between the two subpopulations, we further introduce an *exchange* mechanism. More precisely, during the exchange events individuals of the active population swap places with the individuals in the dormant population. While doing so both the dormant and the active individuals keep their gene type. In this way, individuals can be either in an active state or a dormant state depending on the subpopulation they reside in. However, as the dormant individuals do not resample (i.e., do not reproduce), they cause an overall slow-down of the random genetic drift that arises from random resampling. Because of this, we refer to the dormant population as the seed-bank of the active population. A schematic description of the single-colony Moran process with seed-bank is given in Fig. 1.2. Likewise, in the Moran process without seed-bank the total sizes of the two subpopulations remain constant in time. Therefore, as long as the quantities of interest are the gene frequencies, we may describe the biological system with just two variables, namely, the number  $X(t)$  of type- $\heartsuit$  active individuals and the number  $Y(t)$  of type- $\heartsuit$  dormant individuals at time  $t \geq 0$ . In terms of mathematics, the individuals

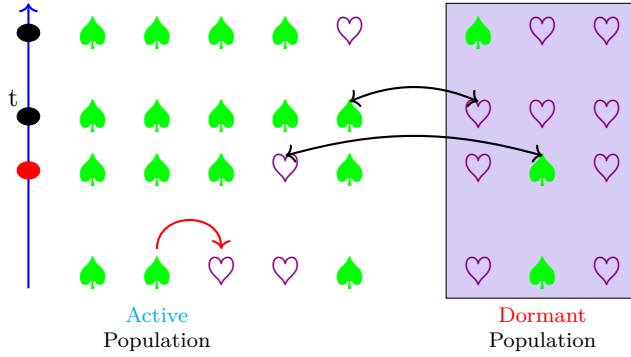


Figure 1.2: A schematic representation of a haploid population with seed-bank evolving under Moran dynamics. The active population has size  $N = 5$  and the seed-bank is of size  $M = 3$ . Individuals carry one of two types:  $\heartsuit$  and  $\spadesuit$ . Red (black) dots in the continuous timeline stand for resampling (exchange) event. The red (black) arrows indicate simultaneous birth-death (exchange) event involved in a pair of individuals.

update their gene types according to the following rules:

- (1) At rate  $\frac{1}{2}$  each individual in the active population resamples type.
- (2) At rate  $\lambda > 0$  each individual in the active population exchanges *type* with an individual chosen uniformly at random from the seed-bank.

As the reproduction and the exchange events happen at uniform rates, the process

$$z = (z(t))_{t \geq 0}, \quad z(t) = (X(t), Y(t)), \quad (1.14)$$

forms a bivariate Markov process in continuous time. The process  $z$  lives in the state space  $[N] \times [M]$  and makes the transitions

$$(x, y) \mapsto \begin{cases} (x - 1, y) & \text{at rate } \frac{x(N-x)}{2N}, \\ (x + 1, y) & \text{at rate } \frac{x(N-x)}{2N}, \\ (x - 1, y + 1) & \text{at rate } \lambda x \frac{M-y}{M}, \\ (x + 1, y - 1) & \text{at rate } \lambda K \frac{N-n}{N}, \end{cases} \quad (1.15)$$

where  $x \in [N]$ ,  $y \in [M]$ , and  $K^{-1} := \frac{M}{N}$  is the relative strength of the seed-bank. This model is in fact a continuous-time version of the two-island model introduced in [126] and allows for different sizes of the two subpopulations. While the model in [126] was analysed in the large population size limit, we keep the population size finite. By using the algebraic framework of stochastic duality we characterise the equilibrium behaviour of the model in Chapter 2. We also do the same for the multi-colony model with seed-banks, which we introduce in the next section.

**Genealogy in the single-colony Moran model with seed-bank.** In the single-colony Moran model with seed-bank, the *genealogy* of finitely many individuals sampled

from the two subpopulations of size  $N$  and  $M$  can be explained in terms of a partition-valued coalescent process similarly as in case of the Moran process. However, because of the addition of a seed-bank component, blocks of a partition can be in one of two states:  $A$  (active state) and  $D$  (dormant state). Recall that the genealogy in the Moran model is described by the Kingman coalescent process, where a pair of blocks of a partition coalesce at rate 1 independently of each other. This is in contrast to the genealogy in our Moran model with seed-bank. Because of the restriction to *finite size* of the active and the dormant population, and also due to the exchange mechanism involved in the two subpopulations, the independence formerly present in the coalescent structure of the genealogy is partially lost. In particular, active and dormant blocks of a partition *interact* with each other. The interaction between the blocks, or more precisely “the ancestors”, appears because of the subdivision of the Moran population into two subpopulations of finite sizes, which in some way destroys the exchangeable labelling proposed in [55] of the individuals in the population. For this reason, we name the associated partition valued genealogical process an *interacting seed-bank coalescent*. To remain consistent with the previous terminologies, we will use the word lineage to refer to a block in a partition.

Let  $\mathcal{P}_k$  be the set of partitions of  $\{1, 2, \dots, k\}$ . For  $\xi \in \mathcal{P}_k$ , denote the number of lineages in  $\xi$  by  $|\xi|$ . Furthermore, for  $j, k, l \in \mathbb{N}$ , define

$$\mathcal{M}_{j,k,l} = \left\{ \vec{u} \in \{A, D\}^j : \begin{array}{l} \text{the numbers of } A \text{ and } D \text{ in } \vec{u} \\ \text{are at most } k \text{ and } l, \text{ respectively} \end{array} \right\}. \quad (1.16)$$

The state space of the genealogical process is  $\mathcal{P}_{N,M} = \{(\xi, \vec{u}) : \xi \in \mathcal{P}_{N+M}, \vec{u} \in \mathcal{M}_{|\xi|,N,M}\}$ . Note that  $\mathcal{P}_{N,M}$  contains only those marked partitions of  $\{1, 2, \dots, N+M\}$  that have at most  $N$  active lineages and  $M$  dormant lineages. This is because we can only sample at most  $N$  active and  $M$  dormant individuals from the population.

Before we give the formal definition, let us introduce some basic notations. For  $\pi, \pi' \in \mathcal{P}_{N,M}$ , we say that  $\pi \succ \pi'$  if  $\pi'$  can be obtained from  $\pi$  by merging two active lineages. Similarly, we say that  $\pi \bowtie \pi'$  if  $\pi'$  can be obtained from  $\pi$  by altering the state of a single lineage ( $A \rightarrow D$  or  $D \rightarrow A$ ). We write  $|\pi|_A$  and  $|\pi|_D$  to denote the number of active and dormant lineages present in  $\pi$ , respectively.

**Definition 1.1.1 (Interacting seed-bank coalescent).** The *interacting seed-bank coalescent* is the continuous-time Markov chain with state space  $\mathcal{P}_{M,N}$  characterised by the following transition rates:

$$\pi \mapsto \pi' \text{ at rate } \begin{cases} \frac{1}{N} & \text{if } \pi \succ \pi', \\ \lambda \left(1 - \frac{|\pi|_D}{M}\right) & \text{if } \pi \bowtie \pi' \text{ by a change of state of} \\ & \text{one lineage in } \pi \text{ from } A \text{ to } D, \\ \lambda K \left(1 - \frac{|\pi|_A}{N}\right) & \text{if } \pi \bowtie \pi' \text{ by a change of state of} \\ & \text{one lineage in } \pi \text{ from } D \text{ to } A, \end{cases} \quad (1.17)$$

■

where  $\pi, \pi' \in \mathcal{P}_{N,M}$  and  $K = \frac{N}{M}$ . The factor  $1 - \frac{|\pi|_D}{M}$  in the transition rate of a single active lineage when  $\pi$  becomes dormant reflects the fact that, as the seed-bank gets

full, it becomes more difficult for an active lineage to enter the seed-bank. Similarly, as the number of active lineages decreases due to the coalescence, it becomes easier for a dormant lineage to leave the seed-bank and become active. This also tells us that there is a *repulsive interaction* between the lineages of the same state ( $A$  or  $D$ ). As the sizes  $N$  and  $M$  of the two subpopulations get large, the interaction becomes weak. In particular, as  $N, M \rightarrow \infty$ , after proper space-time scaling, the interacting seed-bank coalescent converges weakly to a limiting coalescent process known as the *seed-bank coalescent* [14], where interaction between the lineages is no longer present.

**Single-colony block-counting process and duality.** In order to obtain a sampling duality relation between the Moran model with seed-bank and the interacting seed-bank coalescent, we consider the block-counting process associated with the coalescent. If

$$\mathcal{C}_{\text{in}} := (\mathcal{C}_{\text{in}}(t))_{t \geq 0} \tag{1.18}$$

denotes the interacting seed-bank coalescent process in Definition 1.1.1, then we define by  $n_t$  (resp.  $m_t$ ) the number of *active* (resp. *dormant*) lineages in the time- $t$  state  $\mathcal{C}_{\text{in}}(t)$  of the partition-valued process. We see from the definition of  $\mathcal{C}_{\text{in}}$  that the process

$$z_* = (z_*(t))_{t \geq 0}, \quad z_*(t) = (n_t, m_t), \tag{1.19}$$

also forms a continuous-time Markov process with values in  $[N] \times [M] \setminus \{(0, 0)\}$ . The transition rates of the block-counting process are given by

$$(n, m) \mapsto \begin{cases} (n-1, m) & \text{at rate } \frac{1}{N} \binom{n}{2} \mathbb{1}_{\{n \geq 2\}}, \\ (n-1, m+1) & \text{at rate } \lambda n \frac{M-m}{m}, \\ (n+1, m-1) & \text{at rate } \lambda K m \frac{N-n}{N}, \end{cases} \tag{1.20}$$

where  $(n, m) \in [N] \times [M]$  is such that  $(n, m) \neq (0, 0)$  and  $K = \frac{N}{M}$ . The first transition in (1.20) corresponds to the coalescence of two active lineages in the coalescent process  $\mathcal{C}_{\text{in}}$ , while the last two transitions reflect the transition of a lineage from an active (resp. dormant) state to a dormant (resp. active) state. In the sense of the earlier discussed weak stochastic duality, the block-counting process  $z_*$  is dual to the Moran process  $z$  with seed-bank given in (1.14). In particular, they satisfy the sampling duality relation given by

$$\mathbb{E}_{(x,y)} \left[ \frac{\binom{X(t)}{n} \binom{Y(t)}{m}}{\binom{N}{n} \binom{M}{m}} \mathbb{1}_{\{n \leq X(t), m \leq Y(t)\}} \right] = \mathbb{E}^{(n,m)} \left[ \frac{\binom{x}{n_t} \binom{y}{m_t}}{\binom{N}{n_t} \binom{M}{m_t}} \mathbb{1}_{\{n_t \leq x, m_t \leq y\}} \right], \quad t \geq 0, \tag{1.21}$$

where the expectation on the left-hand side is taken w.r.t. the law of the process  $z$  started at  $(x, y) \in [N] \times [M]$  and the expectation on the right-hand side is taken w.r.t. the law of the process  $z_*$  started at  $(n, m) \in [N] \times [M]$ . The duality relation in (1.21) contains all the essential information on the process  $z$  that is needed in order to carry out an analysis of its long-time behaviour. Indeed, with the help of this relation we easily obtain the following characterisation:

**Theorem 1.1.2 (Equilibrium, [Corollary 2.3.4, Chapter 2]).** *Suppose that  $z$  starts from initial state  $(X, Y) \in [N] \times [M]$ . Then  $(X(t), Y(t))$  converges in law as  $t \rightarrow \infty$  to a random vector  $(X_\infty, Y_\infty)$  with distribution*

$$\mathcal{L}_{(X,Y)}(X_\infty, Y_\infty) = \frac{X+Y}{N+M} \delta_{(N,M)} + \left(1 - \frac{X+Y}{N+M}\right) \delta_{(0,0)}, \quad (1.22)$$

where, for  $v \in [N] \times [M]$ ,  $\delta_v$  denotes the Dirac distribution concentrated at  $v$ .

The mathematical details of the above result can be found in Section 2.3 of Chapter 2. In words, this result says that as time progresses the heterozygosity in the Moran population with seed-bank is lost and the entire gene pool fixates (in law) to one of the two types:  $\heartsuit$  and  $\spadesuit$ . The probability of fixation to the all type- $\heartsuit$  configuration in the long run is given by  $\frac{X+Y}{N+M}$ , which is the initial frequency of type  $\heartsuit$  in the *entire* population. Thus, the addition of a seed-bank component has no significant effect on the overall qualitative behaviour of the model. However, we will see later that for the spatial model with seed-banks this is no longer the case, and seed-banks can potentially change the quantitative as well the qualitative behaviour of the model.

## §1.1.4 Spatially inhomogeneous Moran model with seed-banks

All models discussed so far study the effect of dormancy in a single-colony population and are mainly concerned with the underlying genealogy in the diffusive regime. Seed-bank models dealing with *geographically structured* populations are rare, and mathematically rigorous results are still under development. Only recently, in [76] (see also [48]), single-colony seed-bank models were extended to the *spatial* setting by incorporating *migration* of individuals between different colonies. These works are concerned with structured populations having *large* sizes, where the evolution of the demographics, such as gene frequencies, etc., is primarily governed by a system of coupled stochastic differential equations. In these works, the challenge of modelling seed-banks with fat-tailed exit times is overcome by adding internal layers to the seed-banks, where *active* individuals before entering into a layer of the seed-bank acquire a *colour* that determines the wake-up time. Three different seed-bank models of increasing generality were introduced. A full description of the different regimes in the long-time behaviour of these models was obtained in [76] for the geographic space  $\mathbb{Z}^d$ ,  $d \geq 1$ , whereas a multi-scale *renormalisation* analysis on the hierarchical group was carried out in [75]. Moreover, the finite-systems scheme was established [130, 74] as well (i.e., how a truncated version of the system behaves on a properly tuned time scale as the truncation level tends to infinity).

**Spatially inhomogeneous Moran model with seed-banks.** The novelty in the spatial model introduced in Section 2.4 is that it addresses geographically structured populations with seed-banks having preassigned *finite* sizes. Mathematically, the model is described in terms of an *interacting particle system* (see [112] for an overview) evolving in an *inhomogeneous* state space. The spatial model is the main object of our



study in Chapters 2–4 and captures the interplay of three fundamental evolutionary forces, namely, resampling, dormancy and migration, in structured populations.

Informally, we may describe the model as follows. A schematic description of the model is given in Fig. 1.3. We consider multiple colonies consisting of two subpopulations, namely, an active population and a dormant population. The colonies are labelled by the  $d$ -dimensional integer lattice  $\mathbb{Z}^d$ , which plays the role of a geographic space. The dormant population at colony  $i \in \mathbb{Z}^d$  is called the seed-bank of the corresponding active population. As in the single-colony model, each individual in the population carries one of the two gene types:  $\heartsuit$  and  $\spadesuit$ . The active and the dormant population at colony  $i \in \mathbb{Z}^d$  have finite sizes given by, respectively,  $N_i \in \mathbb{N}$  and  $M_i \in \mathbb{N}$ . With each colony  $i \in \mathbb{Z}^d$  we associate the variables  $(X_i(t), Y_i(t))$ , with  $X_i(t)$  and  $Y_i(t)$ , respectively, the number of type- $\heartsuit$  active and dormant individuals at colony  $i$  at time  $t \geq 0$ . The gene types of the individuals in each colony evolve over time according to the resampling and exchange dynamics described earlier in the context of the single-colony Moran model with seed-bank. To simplify our analysis in the spatial model and to be consistent with the single-colony model, we fix the *intra-colony* resampling and exchange rates at  $\frac{1}{2}$  and  $\lambda > 0$ , respectively. In order to also introduce *interaction* between the subpopulations at different colonies, we incorporate *conservative migration of active* individuals. The latter is achieved by letting individuals in the active populations resample gene types not only from the active population in their own colony, but also from active populations in other colonies. In this way, the genetic information can still flow between the subpopulations at different colonies. However, the individuals themselves stay put, which results in conservation over time of the initial local population sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$ .

We specify the *inter-colony* resampling rates for the active individuals by a *migration kernel* denoted by  $a(\cdot, \cdot)$ . The kernel  $a(\cdot, \cdot)$  is an irreducible matrix of transition

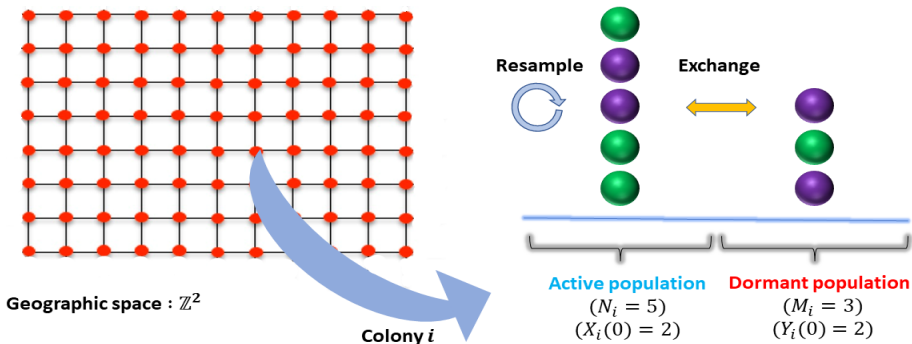


Figure 1.3: A schematic representation of the spatial populations on geographic space  $\mathbb{Z}^2$  for the choice of population sizes  $\epsilon := (N_k, M_k)_{k \in \mathbb{Z}^2}$ . Purple individuals are of type  $\heartsuit$  and green individuals are of type  $\spadesuit$ . The active (resp. dormant) population at colony  $i$  has size  $N_i = 5$  (resp.  $M_i = 3$ ). The system evolves in time under the influence of resampling and exchange.

rates whose entries are labelled by the elements in  $\mathbb{Z}^d \times \mathbb{Z}^d$  and satisfies

$$a(i, j) = a(0, j - i) \quad \forall i, j \in \mathbb{Z}^d, \quad \sum_{i \in \mathbb{Z}^d} a(0, i) < \infty. \quad (1.23)$$

Here,  $a(i, j)$  is the rate at which active individuals of colony  $i \in \mathbb{Z}^d$  resample from the active population at colony  $j \in \mathbb{Z}^d$ . Note that our previous assumption on the intra-colony resampling rates requires us to put  $a(0, 0) = \frac{1}{2}$ . As indicated before, the process defined by

$$Z := (Z(t))_{t \geq 0}, \quad Z(t) := (X_i(t), Y_i(t))_{i \in \mathbb{Z}^d}, \quad (1.24)$$

forms an interacting particle system taking values in the inhomogeneous configuration space

$$\mathcal{X} := \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i]. \quad (1.25)$$

The configuration  $Z(t)$  specifies the gene types of the individuals in *all* the subpopulations at time  $t$ . As is typically the case for interacting particle systems, the time evolution of a single component in the configuration  $Z(t)$  is not Markovian in nature. However, the configuration  $Z(t)$  itself as a whole evolves in a Markovian manner. The different components of the process  $Z$  interact with each other due to the presence of the three evolutionary forces: resampling, dormancy and migration. The population sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$  and the migration kernel  $a(\cdot, \cdot)$  are key parameters that dictate the long-run behaviour of  $Z(t)$ . Whereas, the intra-colony exchange rate  $\lambda$  only affects the time scale on which different components of the configuration  $Z(t)$  evolve. Because the rate  $\lambda$  does not vary across colonies, it does not have a significant role in the analysis of the process  $Z$ .

**Spatially interacting seed-bank coalescent.** As we observed before, stochastic duality plays an important role in the analysis of models in population genetics. Duality is a formidable tool that allows one to perform exact computations in many stochastic interacting systems. Because the local population sizes in our spatial model are conserved quantities, the model has the advantage that it admits a dual process like in the single-colony Moran process with seed-bank. The underlying genealogy of the spatial model is described by a *spatially interacting structured seed-bank coalescent*. In the spatial seed-bank coalescent, lineages switch between an active and a dormant state, and perform interacting coalescing random walks on the geographic space  $\mathbb{Z}^d$ . To avoid technicalities, we refrain from providing a formal description of the genealogical process via partition-valued Markov chain. Our principle aim in this thesis is to characterise equilibrium behaviour of the spatial Moran process  $Z$  with the help of the dual process. For this purpose, an analysis of the block-counting process  $Z_*$  associated with the spatial seed-bank coalescent process is sufficient. We will introduce the block-counting process  $Z_*$  in the next paragraph. For the sake of completeness, we briefly describe the spatial seed-bank coalescent process via an interacting particle system (see Fig. 1.4). At each site  $i \in \mathbb{Z}^d$  there are two reservoirs, an *active* reservoir and a *dormant* reservoir, with, respectively,  $N_i$  and  $M_i$  labelled locations. Each location can accommodate at most one particle. We refer to the particles in an active

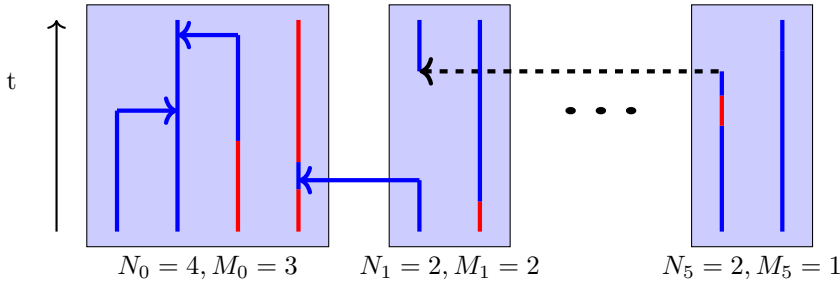


Figure 1.4: Schematic transitions of the particles in the spatially interacting structured seed-bank coalescent in dimension  $d = 1$ . Each block depicts the reservoirs located at sites of  $\mathbb{Z}$ . The blue lines represent the evolution of active particles, whereas the red lines represent the evolution of dormant particles.

and a dormant reservoir as *active* particles and *dormant* particles, respectively. The system evolves according to the following rules:

- (a) An active particle at site  $i \in \mathbb{Z}^d$  becomes dormant at rate  $\lambda$  by moving into a random labelled location (out of  $M_i$  many) in the dormant reservoir at site  $i$  when the chosen labelled location is empty, otherwise it remains in the active reservoir.
- (b) A dormant particle at site  $i \in \mathbb{Z}^d$  becomes active at rate  $\lambda K_i$  with  $K_i = \frac{N_i}{M_i}$  by moving into a random labelled location (out of  $N_i$  many) in the active reservoir at site  $i$  when the chosen labelled location is empty, otherwise it remains in the dormant reservoir.
- (c) An active particle at site  $i$  chooses a random labelled location (out of  $N_j$  many) from the active reservoir at site  $j$  at rate  $a(i, j)$  and does the following:
  - If the chosen location in the active reservoir at site  $j$  is empty, then the particle moves to site  $j$  and thereby migrates from the active reservoir at site  $i$  to the active reservoir at site  $j$ .
  - If the chosen location in the active reservoir at site  $j$  is occupied by a particle, then it coalesces with that particle.

Observe that an active particle can migrate between different sites in  $\mathbb{Z}^d$  and two active particles can coalesce even when residing in different colonies.

**Spatial block-counting process and stochastic duality.** We obtain the block-counting *dual process*

$$Z_* := (Z_*(t))_{t \geq 0}, \quad Z_*(t) := (n_i(t), m_i(t))_{i \in \mathbb{Z}^d}, \quad (1.26)$$

from the spatial coalescent by counting the number of particles at each site  $i \in \mathbb{Z}^d$ . More precisely, we define by  $n_i(t)$  (resp.  $m_i(t)$ ) the number of active (resp. dormant) particles that are present at site  $i \in \mathbb{Z}^d$  at time  $t \geq 0$ . Like the spatial Moran process

$Z$ , the block-counting dual process  $Z_*$  is also an interacting particle system and takes values on the same state space  $\mathcal{X}$ . Under mild conditions on the *active* population sizes  $(N_i)_{i \in \mathbb{Z}^d}$  and the migration kernel  $a(\cdot, \cdot)$ , a sampling duality relation can be established between the two processes  $Z$  and  $Z_*$ . In particular, if  $D(\cdot, \cdot) : \mathcal{X} \times \mathcal{X} \rightarrow [0, 1]$  is defined as

$$D((X_i, Y_i)_{i \in \mathbb{Z}^d}, (n_i, m_i)_{i \in \mathbb{Z}^d}) := \prod_{i \in \mathbb{Z}^d} \frac{\binom{X_i}{n_i} \binom{Y_i}{m_i}}{\binom{N_i}{n_i} \binom{M_i}{m_i}} \mathbb{1}_{\{n_i \leq X_i, m_i \leq Y_i\}} \quad (1.27)$$

with  $(X_i, Y_i)_{i \in \mathbb{Z}^d}, (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$ , then one has

$$\mathbb{E}_\eta[D(Z(t), \xi)] = \mathbb{E}^\xi[D(\eta, Z_*(t))] \quad \forall t \geq 0, \quad (1.28)$$

where the expectation on the left-hand side is taken w.r.t. the law of the process  $Z$  started at  $\eta \in \mathcal{X}$  and the expectation on the right-hand side is taken w.r.t. the law of the process  $Z_*$  started at  $\xi \in \mathcal{X}$ . The duality relation in (1.28) is very useful for analysing the spatial Moran process  $Z$ . In fact, the relation fully characterises all the mixed moments of the process  $Z$  in terms of the dual process  $Z_*$ . Even though the dual process is tricky to analyse because of the interaction in the dual particles, it is much simpler than the spatial Moran process  $Z$ .

### §1.1.5 Summary of Part I

Having introduced the basic ingredients of Part I in Sections 1.1.3–1.1.4, we can now summarise the primary goals:

- (1) Introduce a stochastic model that addresses genetic evolution in spatially structured populations with seed-banks whose sizes are *finite* and depend on the geographic location of the populations. Prove *existence* and *uniqueness* of the process  $Z = (Z(t))_{t \geq 0}$  via well-posedness of an associated martingale problem and duality with a system of interacting coalescing random walks.
- (2) The constructed process  $Z$  modelling the genetic evolution falls in the class of interacting particle systems that are Markov processes with large number of interacting components. An interesting phenomenon often observed in the long-time behaviour of such systems is the occurrence of a *phase transition*. Loosely speaking, a phase transition corresponds to an abrupt change in equilibrium behaviour as underlying model parameters cross certain critical values. In our model, the parameter controlling the phase transition turns out to be the dimension of the geographic space. In low dimensions, the invariant distributions of the model are *degenerate*, in the sense that they are concentrated on the absorbing configurations of the process. These are nothing but the two extremes of the possible gene type configurations, where either all individuals carry type  $\heartsuit$  or all carry type  $\spadesuit$ . Convergence phenomena such as these are called *clustering* because locally mono-type clusters grow in the geographic space as the system approaches equilibrium. In higher dimensions, however, the model admits a *one-parameter family* of invariant distributions labelled by a continuous parameter, namely, the *average density* of a specific gene type in the population. In this

case, the system at equilibrium exhibits *coexistence*, i.e., individuals of different gene types coexist with each other. One goal in Part I is to identify a necessary and sufficient criterion for the occurrence of such a dichotomy in the equilibrium behaviour of our model.

- (3) As we indicated before, the population sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$  and the migration kernel  $a(\cdot, \cdot)$  are the primary parameters that determine the dichotomy of coexistence versus clustering in the spatial Moran process. Another goal in Part I is to identify the range of these parameter values under which the criterion for clustering versus coexistence is met.
- (4) Identify the *domain of attraction* of each equilibrium in the clustering and in the coexistence regime. Here, for an equilibrium state  $\nu$  of the process  $Z$ , the domain of attraction of  $\nu$  is the set of all probability distributions  $\mu$  such that the process  $Z$  starting from initial distribution  $\mu$  converges to the equilibrium state  $\nu$  as time evolves.
- (5) In the clustering regime, the equilibrium states of the spatial process concentrate on homozygous gene configurations. A quantity of particular interest in this regime is the *fixation probability*, which quantifies the probability of a specific gene type, say type  $\heartsuit$ , taking over the entire population. If model parameters such as the population sizes are arbitrary, then standard techniques fail to provide closed-form expressions for this probability. However, as the theory of stochastic homogenisation suggests, macroscopic quantities such as the fixation probability do not feel the irregularities in the microscopic parameters when they are modelled by a *random environment*. A random environment in a stochastic model adds a second source of randomness and is typically used to capture stochastic effects in the irregularities. In most scenarios, a law of large numbers sets in and many macroscopic quantities behave similarly as those evolving in a suitably *homogenised* environment. Another goal in Part I is to see whether homogenisation occurs. The spatial model can be naturally extended to the setting of a random environment by sampling the population sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$  beforehand at random from a preassigned probability distribution. In this context, the aim is to carry out a clustering analysis for the spatial process and show that the fixation probability homogenises as the result of an appropriate ‘averaging effect’.

We address the above 5 goals in the three chapters of Part I, which are based on the material of three papers on the spatial Moran process  $Z$  defined in (1.24).

**Chapter 2.** In this chapter we address the goals outlined in (1) and (2). To this end, we first lay out the mathematical foundations for modelling genetic evolution of *structured* and *finite* populations with *seed-banks* in stochastic settings. In particular, the main objective is to construct the spatial Moran process  $Z$ , which is a novel interacting particle system (see [112] for an overview) modelling stochastic evolution of gene types in spatially structured finite populations with seed-banks. Modelling genetic evolutions of finite populations via interacting particle systems is rare in mathematical population genetics. Most research in this area concerns only large populations,

and deal with stochastic differential equations arising from the so-called diffusive limit of individual-based models. Inclusion of seed-banks in such models is relatively new as well.

In [16, 14, 15], the continuum version of the celebrated Fisher-Wright model is modified to include a seed-bank component, and in [76, 75] this model is further extended to incorporate spatialness. However, the results in these works apply to *large* populations only. The starting point of this chapter is therefore the Moran model describing a single population of finite size.

We modify the single-colony Moran model to accommodate a suitable seed-bank component. A brief introduction of this model is given in Section 1.1.3. In order to characterise the equilibrium behaviour of this model, we utilise the recently developed theory of stochastic duality [71, 25, 24]. In particular, we identify the associated dual process by following the Lie-algebraic approach to stochastic duality described in [148]. We derive a finite-dimensional representation for the infinitesimal Markov generator of the process by viewing it as an abstract element of the  $\mathfrak{su}(2)$  Lie algebra. Furthermore, by making an Ansatz with respect to a well-chosen intertwiner (i.e., the duality function), we identify the dual representation of the Markov generator, which indeed turns out to be the infinitesimal generator of a dual Markov process. This finding aligns with the general prognosis of the Lie-algebraic approach, namely, that identifying Markov generators in terms of elementary operators from a carefully chosen Lie algebra may lead to constructing new dual processes. We exploit the duality to fully characterise the equilibrium behaviour of the single-colony Moran model with seed-bank. It turns out that, despite the presence of a seed-bank component, the model qualitatively behaves as a single Moran population of finite size without a seed-bank. This is so because both the seed-bank and the reproductively active population have finite capacity.

Subsequently, we extend the single-colony model to the multi-colony Moran process  $Z = (Z(t))_{t \geq 0}$  introduced in Section 1.1.4 which describes spatially structured populations of finite sizes each equipped with their own seed-bank. Using the same representations of the  $\mathfrak{su}(2)$  Lie algebra, we identify the process  $Z_* = (Z_*(t))_{t \geq 0}$  in (1.26) as a dual of  $Z$ . We construct the process  $Z$  by establishing well-posedness of an appropriate martingale problem, where the uniqueness of the process follows from the duality relation in (1.28). We also characterise the structural properties of the set of all invariant distributions for  $Z$ , by establishing a dichotomy between *clustering* and *coexistence*. This kind of dichotomy in the equilibrium behaviour mainly surfaces in spatial models that possess more than one *absorbing* configuration. Examples of such models include the voter model [111], the stepping stone model [140], and the model introduced in [39] addressing populations with spatial structure but no seed-banks. The same dichotomy is found in the more recent models introduced in [76, 75], which include both spatialness and seed-bank effects. Our main result in this chapter confirms that a similar dichotomy holds even when the constituent population sizes are finite and spatially varying. The dichotomy is determined by a necessary and sufficient criterion formulated in terms of the time evolution of the dual process  $Z_*$  started from two lineages (particles). In particular, the criterion says that the process  $Z$  remains in the clustering regime if and only if two dual lineages in the process  $Z_*$

eventually coalesce with probability 1. The duality relation between  $Z$  and  $Z_*$  allows us to express the average heterogeneity in the subpopulations at time  $t$  in terms of the time- $t$  state of two dual particles. We use this to show that the heterogeneity vanishes everywhere if and only if the two particles coalesce eventually with probability 1.

**Chapter 3.** In this chapter we address the goal outlined in (3). We focus on the parameter regime for which the spatial process  $Z$  exhibits clustering. From the clustering criterion given in Chapter 2, it is clear that this regime is uniquely characterised by the long-time behaviour of the dual process  $Z_*$ . In particular, eventual coalescence of two dual lineages is equivalent to the existence of a common ancestor for the spatial populations, and therefore the almost sure occurrence of this event necessarily eliminates the possibility of  $Z$  attaining a multi-type equilibrium, where individuals of different gene types can coexist.

The above scenario is common in spatial models (see e.g., [39]) where the stochastic evolution of demographics such as allele frequencies in subdivided populations are diffusively approximated. The recent results in [76] establish similar dichotomies between clustering and coexistence for three diffusively rescaled models describing spatial populations with seed-banks. It is shown that when the sizes of the seed-banks are a constant multiple of the sizes of the active populations, the dichotomy of clustering versus coexistence is solely determined by the underlying migration kernel and, apart from causing a quantitative delay in the loss of heterozygosity of the populations, seed-banks have no significant qualitative effect.

The main result in this chapter asserts that the picture remains the same for spatially structured finite populations with seed-banks of varying capacities, as long as the variations in the relative sizes of the seed-banks are of the same order. In particular, we show that if the relative sizes of the seed-banks, defined as the ratio of the dormant and the active population sizes, are uniformly bounded over the geographic space  $\mathbb{Z}^d$ , then the process  $Z$  clusters if and only if the symmetrised migration kernel defined by

$$\hat{a}(i, j) := \frac{1}{2}[a(i, j) + a(j, i)], \quad i, j \in \mathbb{Z}^d, \quad (1.29)$$

is recurrent. The last result is proven under a non-clumping criterion on the active population sizes  $(N_i)_{i \in \mathbb{Z}^d}$ , and the converse is proven under the stronger assumption of symmetry of the migration kernel  $a(\cdot, \cdot)$ . The non-clumping criterion imposed on the sizes  $(N_i)_{i \in \mathbb{Z}^d}$  of the active populations requires that

$$\inf_{i \in \mathbb{Z}^d} \sum_{j: \|j-i\| \leq R} \frac{1}{N_j} > 0 \quad (1.30)$$

for some  $R < \infty$ . This essentially says that there exists a threshold  $N < \infty$  and a range  $R < \infty$  such that within any finite region of the geographic space of radius  $R$ , there is at least one active population of size at most  $N$ . This criterion ensures that the time scale at which pairs of lineages in different parts of the geographic space coalesce are of the same order. We expect a close connection between the above criterion and the existence of a common ancestor of the spatial populations. We derive an alternative clustering criterion for the clustering versus coexistence dichotomy. This alternative criterion is defined in terms of almost sure absorption of an auxiliary Markov process and turns out to be easier to analyse than the original criterion.

**Chapter 4.** In this chapter we address the goals outlined in (4) and (5). We study the spatial process  $Z$  in the parameter regime where clustering occurs. In particular, we provide a full description of the set of all initial distributions for which the spatial process  $Z$  converges to an equilibrium.

A well-established method in the literature for studying stationary states of a Markov process having duality properties is to characterise all functions that are harmonic for an associated dual process. Depending on the complexity of the dual process and the duality function, often a full characterisation is possible. For instance, a generous use of this method is found in [111, 105], where ergodic properties of many well-known interacting particle systems are derived. Relevant examples in the context of diffusion processes arising in population genetics include [140, 39, 76, 75]. The standard technique used in this method involves constructing a successful coupling between two copies of the dual process started from two different initial states, which necessarily forces all bounded harmonic functions of the process to be constant. By leveraging the duality relation, this result is transferred to the original process, and a criterion is established that intertwines the domain attraction of each equilibrium with the set of constant harmonic functions of the dual.

In our context, it turns out that a successful coupling between two copies of the dual started from different initial configuration indeed exists when the original process  $Z$  exhibits clustering. This enables us to derive a necessary and sufficient criterion for determining the initial distributions that converge weakly to a mono-type equilibrium under the time evolution of the spatial process. This criterion is formulated in terms of the transition kernel of a single dual particle, and is valid only in the clustering regime of the original process. The criterion also characterises the fixation probability. The fixation probability quantifies the probability of a specific gene type, say type  $\heartsuit$ , spreading over every subpopulation at the attained equilibrium. This probability depends on how the type- $\heartsuit$  individuals are initially distributed over different subpopulations. As pointed out in goal (5), an explicit characterisation of this probability is not feasible when the model parameters are arbitrary. However, by sampling the population sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$  from a random field that is stationary and ergodic under translation, we are able to derive an expression for this probability. The formula is given in terms of an annealed average of the type- $\heartsuit$  densities in the active and the dormant population, biased by the ratio of the two population sizes at the target colony. We obtain this result under the assumption that the migration kernel  $a(\cdot, \cdot)$  is symmetric and recurrent, and the initial frequency distribution of the type- $\heartsuit$  individuals in each colony is consistent with a global profile of the population sizes. Our results in this chapter hold only when the geographic space  $\mathbb{Z}^d$  has dimension  $d \leq 2$ .

For the proof of the results, we make heavy use of the associated single-particle dual process. To be precise, we show that under the symmetry and recurrence assumptions on the migration kernel, the environment seen by a single dual particle in a typical random environment converges in law to an invariant distribution. Finally, by exploiting the intertwining relation between the domain of attraction of the mono-type equilibrium of  $Z$  and the transition probability kernel of a single dual particle, we lift this convergence to the spatial process  $Z$ .



## §1.2 Introduction to Part II

The main motivation for studying systems of interacting particles originally comes from statistical physics. Time evolution of state variables in physical systems, such as gaseous material in a closed container, or flow of water through a pipe, etc., are complex processes governed by many parameters. An obvious attribute that is common to all such systems is the presence of small particles in large numbers. The motion of each individual particle is often subject to a local interaction rule and typically correlates to the characteristics of all nearby particles. As an outcome, the evolution equation for a single particle is no longer closed. Only a large number of coupled equations can describe the particle motion in a satisfactory manner. The disadvantage is that we lose tractability – or so it would seem in hindsight.

In a series of pioneering works [144]-[146] in the late 1960s, Spitzer initiated the study of Markov processes with locally interacting components. In subsequent years, Liggett, along with many other authors, provided a complete description of all the possible invariant measures for several such processes. These works, most of which are summarised in Liggett’s monograph [112], gave birth to the novel mathematical framework of interacting particle systems, and have since developed into a prominent field of study. Within this framework, it becomes possible to rigorously describe the spatio-temporal evolution of a microscopic system that, in principle, can consist of infinitely many particles.

As explained earlier, Part I of this thesis uses the tools and methods of the interacting particle system framework. While this formulation is predominant in the context of physical systems, in Part I we draw motivations from mathematical biology instead, and utilise the framework to describe evolutionary consequences of dormancy in spatially structured populations. It is, however, not necessary to view dormancy as a trait inherent to biological systems alone. Indeed, in a physical system, dormancy may be considered as an internal state of the particles that causes hindrance to their microscopic dynamics, such as motion under the influence of a driving force. Even in chemical reactions, variation in activity levels of a reactant may be interpreted as a form of dormancy. In Part II, our principle aim is to investigate the effect of dormancy in the broader framework of interacting particle systems.

In this thesis, three such interacting particle systems are considered: the independent particle system, the exclusion process and the inclusion process. The first two systems were originally introduced by Spitzer [145], and have been treated extensively in the literature. The ergodic behaviour of these two systems is well-understood and their scaling limits are also well-known. The inclusion process, on the other hand, was introduced in [70], and its invariant distributions were fully characterised only recently [105]. Given the rich equilibrium behaviour of many mathematical population genetics models with dormancy, it is appealing to endow these three particle systems with dormant characteristics and see how they behave in the long run. Unfortunately, many of the standard techniques, such as stochastic duality, break down after the inclusion of a dormant state. Consequently, we must be careful in choosing how to incorporate dormancy. In Part II we deal with suitably crafted *multi-layer* versions of the particle systems that capture interesting phenomena under dormancy while pre-

serving the original duality properties in a natural way. Before we set the stage, in the next two sections we briefly shed light on two important aspects of interacting particle systems – hydrodynamic scaling limits (see [120] for an extensive overview) and non-equilibrium steady state behaviour – both of which are central to the analysis presented in Part II.

### §1.2.1 Hydrodynamic scaling limit

The primary reason for studying interacting particle systems is to arrive at a mathematically rigorous microscopic description of the evolution of physical systems. But the usefulness lies not only in explaining microscopic properties, but also in predicting the behaviour of macroscopic observables associated with the physical system. In particular, the stochastic nature of interacting particle systems puts sophisticated probabilistic tools, such as the law of large numbers and the central limit theorem, at our disposal to elucidate emergent phenomena of physical systems in a rigorous mathematical framework. Here, physically emergent phenomena include, but are not limited to, universal laws of physics, such as Fourier’s law of heat conduction or Fick’s law of diffusion. The general idea behind the so-called “hydrodynamic scaling” formalism is to give a mathematically precise meaning to these emergent phenomena by exploiting various probabilistic limiting techniques and space-time scaling arguments. One may view such formalism as the transition from the microscopic world of particles to the macroscopic world of measurable observables.

In many cases, the precise choice of the type of interaction between the physical particles turns out to be irrelevant, because the emergent phenomena are often insensitive to the fine details of the microscopic laws of interaction. For example, it is possible to derive the evolution equation of heat conduction as the hydrodynamic scaling limit of both the independent particle system and the simple symmetric exclusion process. To explain the last statement, let us recall the definitions of the three particle systems, and briefly elaborate on how a suitable space-time scaling of these systems can give rise to the heat equation in the macroscopic limit.

**Independent particle system.** The independent particle system is a mathematical description of the time evolution of a *collection* of *indistinguishable* particles that do not influence each other in any way and move on a countable phase space  $\mathcal{S}$  in a Markovian manner. For simplicity, let us fix the phase space  $\mathcal{S}$  to be the integer lattice  $\mathbb{Z}$ . We assume that each particle performs a continuous-time simple symmetric random walk on  $\mathbb{Z}$  at rate 2. Following the terminologies of the interacting particle system framework, we can specify the time- $t$  state of such a system by a configuration

$$\eta_{\text{in}}(t) \in \mathbb{N}_0^{\mathbb{Z}}, \quad \eta_{\text{in}}(t) := (\eta_{\text{in}}(i, t))_{i \in \mathbb{Z}},$$

with  $\eta(i, t)$  being interpreted as the number of particles at site  $i \in \mathbb{Z}$  at time  $t \geq 0$ . The process  $\eta_{\text{in}}$  defined by

$$\eta_{\text{in}} := (\eta_{\text{in}}(t))_{t \geq 0}, \quad \eta_{\text{in}}(t) = (\eta_{\text{in}}(i, t))_{i \in \mathbb{Z}}, \quad t \geq 0, \quad (1.31)$$

is the simplest example of an interacting particle system, with a Markov generator

$$(L_{\text{in}}f)(\eta) := \sum_{x \in \mathbb{Z}} \eta_x \sum_{|x-y|=1} [f(\eta^{x,y}) - f(\eta)] \quad (1.32)$$

acting on a suitable test function  $f$  and evaluated at a configuration  $\eta = (\eta_x)_{x \in \mathbb{Z}}$ . Here, for  $x, y \in \mathbb{Z}$  and a configuration  $\eta = (\eta_i)_{i \in \mathbb{Z}}$ ,  $\eta^{x,y}$  denotes the configuration obtained from  $\eta$  by removing a particle from an occupied site  $x$  and putting it at site  $y$ . In other words,

$$\eta^{x,y} := (\eta_i - \mathbb{1}_{\{i=x, \eta_x \geq 1\}} + \mathbb{1}_{\{i=y, \eta_x \geq 1\}})_{i \in \mathbb{Z}}. \quad (1.33)$$

Note that, in order for the generator  $L_{\text{in}}$  to uniquely specify a Markov process, some regularity restrictions must be imposed on the initial configuration of the process. We refrain from addressing these technical subtleties here.

**Simple symmetric exclusion process.** While the independent particle system is a natural example, it does a poor job in modelling physical systems in which particles are interacting. Studies of even the simplest form of particle interaction can provide useful insights. The aforementioned simple symmetric exclusion process (SSEP) was introduced by Spitzer [145] as a toy model for lattice gases at infinite temperature, and has been studied extensively in the literature since. This process is obtained from the independent particle system by imposing a local interaction called *exclusion rule*: two particles are not allowed to occupy the same location. Consequently, all jumps of the independent particles leading to a violation of the exclusion rule are suppressed. For the exclusion rule to make sense, one must of course start the system at a configuration where all particles are initially at distinct locations. The resulting Markov process

$$\bar{\eta}_{\text{ex}} := (\bar{\eta}_{\text{ex}}(t))_{t \geq 0}, \quad \bar{\eta}_{\text{ex}}(t) := (\bar{\eta}_{\text{ex}}(i, t))_{i \in \mathbb{Z}}, \quad t \geq 0, \quad (1.34)$$

evolves on the state space  $\{0, 1\}^{\mathbb{Z}}$  and has the formal generator

$$(L_{\text{ex}}f)(\eta) = \sum_{\substack{x, y \in \mathbb{Z}, \\ |x-y|=1}} \eta_x (1 - \eta_y) [f(\eta^{x,y}) - f(\eta)], \quad (1.35)$$

where  $f : \{0, 1\}^{\mathbb{Z}} \rightarrow \mathbb{R}$  is a cylinder function and  $\eta \in \{0, 1\}^{\mathbb{Z}}$ .

**Simple symmetric inclusion process.** The simple symmetric inclusion process (SIP) introduced in [70] is the opposite analogue of the exclusion process. In this process the underlying particles interact by “inviting” the neighbouring particles to their own locations rather than driving them away. The additional interaction is superimposed onto the independent motions of the microscopic particles and the interaction strength is assumed to be linearly increasing with the number of particles at a destination site. The resulting process

$$\eta_{\text{inc}} := (\eta_{\text{inc}}(t))_{t \geq 0}, \quad \eta_{\text{inc}}(t) := (\eta_{\text{inc}}(x, t))_{x \in \mathbb{Z}}, \quad t \geq 0, \quad (1.36)$$

obtained from counting the number of particles at each site in  $\mathbb{Z}$  evolving over time, therefore lives on the state space  $\mathbb{N}^{\mathbb{Z}}$ . The process  $\eta_{\text{inc}}$  is Markovian and has the formal generator

$$(L_{\text{inc}}f)(\eta) := \sum_{x \in \mathbb{Z}} \eta_x \sum_{|x-y|=1} (1 + \eta_y)[f(\eta^{x,y}) - f(\eta)], \quad (1.37)$$

where  $f$  is a suitable test function and  $\eta = (\eta_x)_{x \in \mathbb{Z}}$  is a configuration.

**Hydrodynamics: the heat equation.** With the above mathematical definitions at hand, we can now concentrate on hydrodynamic scaling. As we have already explained, hydrodynamic behaviour of a microscopic system refers to a description of how the constituent quantities evolve when viewed from a macroscopic frame of reference. In the macroscopic world, most wildly fluctuating microscopic quantities scale down to trivial states, and only a few of the many degrees of freedom survive in the form of certain conserved thermodynamic quantities such as *energy*, *temperature*, *particle density*, etc. These macroscopic quantities behave in a much smoother way than their microscopic counterparts. Depending on how one models the underlying microscopic randomness, these quantities can often be shown to satisfy a *deterministic* partial differential equation. As we will note shortly, in case of the independent particle system and the exclusion process, the partial differential equation associated with the hydrodynamic limit is nothing but the heat equation.

In order to carry out the hydrodynamic scaling, one must first renormalise space and time by suitable scaling parameters that quantify the relationship between the microscopic and the macroscopic world. In this regard, it is standard to assume that spatial distance scales linearly as one zooms out from the microscopic view to the macroscopic view. However, as time is typically measured relative to the external observer, one should also take the average spatial spread of the microscopic particles into consideration while rescaling the time parameter. In the case of particles that evolve according to the two random processes  $\eta_{\text{in}}$  and  $\bar{\eta}_{\text{ex}}$  defined above, the average spread in time  $t$  is of order  $\sqrt{t}$ . This is well-known in the context of independent particle systems, but is not obvious for the exclusion process. We refer the interested reader to [119], where it is shown that the typical distance covered by a free particle and a particle subject to the exclusion rule are asymptotically of the same order. Thus, in order to visualise a non-trivial motion of the particles from the macroscopic point of view, temporal scaling should be taken quadratically proportional to the spatial scaling.

Having justified the choice for the space-time scaling parameters, we can now consider the following two measure-valued random quantities associated with the processes in (1.31) and (1.34):

$$X_{\text{in}}^N(t)(\cdot) := \frac{1}{N} \sum_{x \in \mathbb{Z}} \eta_{\text{in}}(x, N^2t) \delta_{x/N}(\cdot), \quad X_{\text{ex}}^N(t)(\cdot) := \frac{1}{N} \sum_{x \in \mathbb{Z}} \bar{\eta}_{\text{ex}}(x, N^2t) \delta_{x/N}(\cdot). \quad (1.38)$$

Here,  $N \in \mathbb{N}$  is the parameter quantifying the amount of dilation performed while zooming out from the microscopic world to the macroscopic world, and will eventually be set to diverge to infinity. Mathematically,  $X_{\text{in}}^N$  and  $X_{\text{ex}}^N$  describe what the empirical

distribution of the particle densities in the two microscopic processes  $\eta_{\text{in}}$  and  $\bar{\eta}_{\text{ex}}$  look like from the macroscopic perspective. Observe that the two processes  $t \mapsto X_{\text{in}}^N(t)$  and  $t \mapsto X_{\text{ex}}^N(t)$  indeed take values in the space of non-negative Radon measures. In particular, it is easily seen that for any compact  $A \subseteq \mathbb{R}$ ,

$$X_{\text{in}}^N(t)(A) = \frac{1}{N} \sum_{x \in \mathbb{Z}} \eta_{\text{in}}(x, N^2 t) \mathbb{1}_A\left(\frac{x}{N}\right) < \infty. \quad (1.39)$$

The hydrodynamic scaling procedure tells that the two processes  $\{X_{\text{in}}^N(t) : t \geq 0\}$  and  $\{X_{\text{ex}}^N(t) : t \geq 0\}$  converge to a non-trivial *deterministic* limiting process, in a probabilistic sense, as we pass from the microscopic viewpoint to the macroscopic viewpoint by letting  $N \rightarrow \infty$ . More precisely, the following holds:

**Theorem 1.2.1 (Hydrodynamic scaling, [120, Theorem 2.8.1] and [69]).**

Let  $\bar{\rho} \in C_b(\mathbb{R})$  be a bounded and continuous macroscopic profile, and let  $(\mu_N)_{N \in \mathbb{N}}$  (resp.,  $(\bar{\mu}_N)_{N \in \mathbb{N}}$ ) be a sequence of probability measures on  $\mathbb{N}^{\mathbb{Z}}$  (resp.,  $\{0, 1\}^{\mathbb{Z}}$ ) such that, for any  $\delta > 0$ ,  $g \in C_c^\infty(\mathbb{R})$ ,

$$\begin{aligned} \lim_{N \rightarrow \infty} \mu_N \left( \eta \in \mathbb{N}^{\mathbb{Z}} : \left| \frac{1}{N} \sum_{x \in \mathbb{Z}} g\left(\frac{x}{N}\right) \eta(x) - \int_{\mathbb{R}} g(x) \bar{\rho}(x) dx \right| > \delta \right) &= 0, \\ \lim_{N \rightarrow \infty} \bar{\mu}_N \left( \bar{\eta} \in \{0, 1\}^{\mathbb{Z}} : \left| \frac{1}{N} \sum_{x \in \mathbb{Z}} g\left(\frac{x}{N}\right) \bar{\eta}(x) - \int_{\mathbb{R}} g(x) \bar{\rho}(x) dx \right| > \delta \right) &= 0. \end{aligned} \quad (1.40)$$

Let  $\mathbb{P}_{\mu_N}$  (resp.,  $\bar{\mathbb{P}}_{\bar{\mu}_N}$ ) be the law of the measure-valued process  $t \mapsto X_{\text{in}}^N(t)$  (resp.,  $t \mapsto X_{\text{ex}}^N(t)$ ) in (1.38) induced by the initial distribution  $\mu_N$  (resp.,  $\bar{\mu}_N$ ). Then, for any  $T > 0$ ,  $\delta > 0$  and  $g \in C_c^\infty(\mathbb{R})$ ,

$$\begin{aligned} \lim_{N \rightarrow \infty} \mathbb{P}_{\mu_N} \left( \sup_{t \in [0, T]} \left| \int_{\mathbb{R}} g(x) dX_{\text{in}}^N(t)\{x\} - \int_{\mathbb{R}} g(x) \rho(x, t) dx \right| > \delta \right) &= 0, \\ \lim_{N \rightarrow \infty} \bar{\mathbb{P}}_{\bar{\mu}_N} \left( \sup_{t \in [0, T]} \left| \int_{\mathbb{R}} g(x) dX_{\text{ex}}^N(t)\{x\} - \int_{\mathbb{R}} g(x) \rho(x, t) dx \right| > \delta \right) &= 0, \end{aligned} \quad (1.41)$$

where  $\rho(\cdot, \cdot)$  is the unique strong solution of the heat equation

$$\begin{cases} \partial_t \rho = \Delta \rho_0, \\ \rho(x, 0) = \bar{\rho}(x). \end{cases} \quad (1.42)$$

The above theorem asserts that both measure-valued processes  $t \mapsto X_{\text{in}}^N(t)$  and  $t \mapsto X_{\text{ex}}^N(t)$  converge weakly, in probability, to a limiting measure-valued process  $t \mapsto X_t$ , where  $X_t$  is a deterministic measure on  $\mathbb{R}$  for each  $t \geq 0$ . Furthermore,  $X_t$  is absolutely continuous w.r.t. the Lebesgue measure on  $\mathbb{R}$  with density  $\rho(\cdot, t)$ , i.e.,

$$dX_t\{x\} = \rho(x, t) dx, \quad t \geq 0, x \in \mathbb{R}, \quad (1.43)$$

and  $(\rho(\cdot, t))_{t \geq 0}$  is the unique strong solution of the heat equation in (1.42). To keep matters simple, we skip the technical details of the proof, which essentially exploits

stochastic self-duality properties of the two microscopic systems, along with Donsker's invariance principle for a simple symmetric random walk.

Now that we have seen how one retrieves the well-known heat equation from two seemingly complex microscopic particle systems, it is natural to wonder about the macroscopic effect of introducing dormant characteristics at the microscopic level. The first half of Part II is devoted to studying such effects. In particular, we discuss the hydrodynamic scaling behaviour of the three microscopic systems introduced above, supplemented with “dormancy”. Our results will be summarised in Section 1.2.3.

## §1.2.2 Non-equilibrium steady state

In Section 1.2.1 we motivated the study of interacting particle systems as a mathematical way of modelling physical systems consisting of a large number of microscopic components. Interacting particle systems are Markov processes on an uncountable state space that typically deal with the evolution of infinitely many variables, such as the location of infinitely many particles, the infection status or gene type of individuals in an infinite population, etc. In reality, however, physical or biological systems consist of a large yet finite number of components. This presents an undesirable discrepancy between theoretical models and real physical systems. The standard way to overcome this discrepancy is by restricting the proposed model to a finite region of interest.

To illustrate the idea, consider the process of heat conduction on a one-dimensional metal rod (see Fig. 1.5). We can assume that the microscopic structure of the rod is discrete and can be represented by the integer lattice  $\mathbb{Z}$ . As observed in Section 1.2.1, the spatio-temporal macroscopic heat profile in the rod, which is given by the solution of the heat equation in (1.42), can be thought of as a by-product of the process  $t \mapsto (\eta_{\text{in}}(i, t))_{i \in \mathbb{Z}}$  in (1.31) where particles perform independent random walks on the microscopic lattice structure of the metal rod. If initially the metal rod has not yet reached a global thermal equilibrium in terms of the macroscopic heat conduction, and we focus on the heat profile of a segment of the rod, called the *bulk*, with a length that is negligible compared to the total length of the rod, then we will observe that the heat profile in the bulk first attains a *local equilibrium*. This local equilibrium typically depends on the initial cumulative amount of heat contained in the complement of the bulk, called *external reservoirs*, at both ends of the rod. If the sizes of the reservoirs are large enough, then the average amount of heat contained within them endure negligible effects from the heat profile of the bulk, and therefore remain almost constant throughout the macroscopic evolution of the bulk profile. From the microscopic perspective, the spatial extent of the bulk is so small compared to the external reservoirs that the interactions between particles in the reservoirs only have an average effect on the random motions of the particles in the bulk.

**Independent particle system with reservoirs.** In view of the above, a mathematically more accurate understanding for the local equilibrium can be achieved by modelling the collective effects of the two external reservoirs on the bulk variables with two individual *boundary reservoirs*. The modified dynamics is such that microscopic particles can escape from the bulk to enter the boundary reservoirs independently of

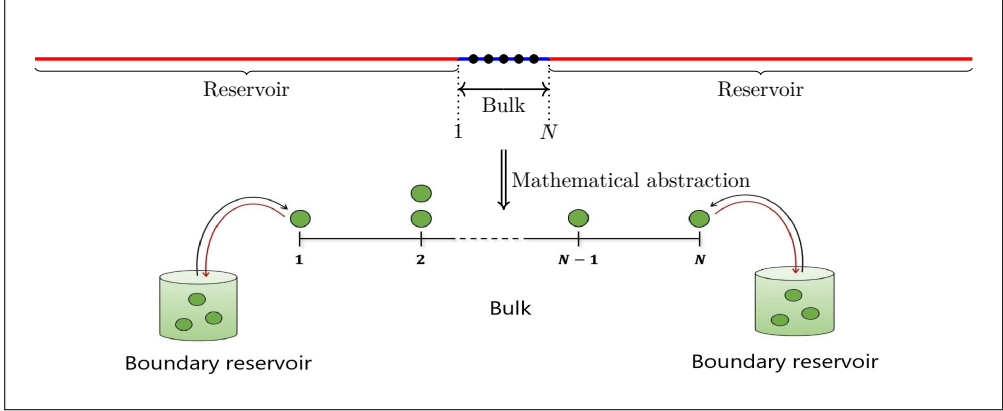


Figure 1.5: A schematic representation of bulk and reservoirs in a one-dimensional metal rod. The length of the bulk is  $N \in \mathbb{N}$  in microscopic units, and is small compared to the lengths of the reservoirs.

each other, while each reservoir can put particles at the boundary sites at a *constant rate* determined by the cumulative amount of “heat” contained within them. As an outcome, we obtain a new microscopic process  $\hat{\eta}_{\text{in}}$  defined as

$$\hat{\eta}_{\text{in}} := (\hat{\eta}_t)_{t \geq 0}, \quad \hat{\eta}_t := (\hat{\eta}(i, t))_{i \in [N]_*}, \quad t \geq 0, \quad (1.44)$$

where  $[N]_* := \{1, \dots, N\}$  and  $\hat{\eta}(i, t)$  represents the number of particles at site  $i \in [N]_*$  in the bulk at time  $t \geq 0$ . The process  $\hat{\eta}_{\text{in}}$  is a continuous-time Markov chain with generator

$$\hat{L}_{\text{in}} := \hat{L}^{\text{bulk}} + \hat{L}^{\text{res}}. \quad (1.45)$$

The action of  $\hat{L}^{\text{bulk}}$  and  $\hat{L}^{\text{res}}$  on a test function  $f : \mathbb{N}_0^{[N]_*} \rightarrow \mathbb{R}$  is as follows:

$$(\hat{L}^{\text{bulk}} f)(\eta) := \sum_{x \in [N]_*} \eta_x \sum_{\substack{y \in [N]_* \\ |x-y|=1}} [f(\eta^{x,y}) - f(\eta)], \quad (1.46)$$

and

$$\begin{aligned} (\hat{L}^{\text{res}} f)(\eta) := & \eta_1 [f(\eta^{1,-}) - f(\eta)] + \eta_N [f(\eta^{N,-}) - f(\eta)] \\ & + \rho_L [f(\eta^{1,+}) - f(\eta)] + \rho_R [f(\eta^{N,+}) - f(\eta)], \end{aligned} \quad (1.47)$$

where  $\eta := (\eta_x)_{x \in [N]_*} \in \mathbb{N}_0^{[N]_*}$  is a configuration representing the number of particles at each site in the bulk,  $\rho_L > 0$  (resp.,  $\rho_R > 0$ ) is the rate at which the left (resp., right) reservoir injects new particles at site 1 (resp.,  $N$ ), the configurations  $\{\eta^{x,y} : x, y \in [N]_*\}$  are obtained from  $\eta$  by using (1.33), and

$$\eta^{x,-} := (\eta_i - \mathbb{1}_{\{i=x, \eta_i \geq 1\}})_{i \in [N]_*}, \quad \eta^{x,+} := (\eta_i + \mathbb{1}_{\{i=x\}})_{i \in [N]_*}, \quad x \in [N]_*. \quad (1.48)$$

Observe from (1.46)–(1.47) that  $\hat{L}^{\text{bulk}}$  is responsible for the independent motions of the particles in the bulk, while  $\hat{L}^{\text{res}}$  dictates the interactions between the particles and the reservoirs at the two boundary sites 1 and  $N$ .

**Non-equilibrium steady state.** The process  $\widehat{\eta}_{\text{in}}$  is well-known in the literature (see e.g., [110, 24]) and admits a unique equilibrium distribution  $\nu_{\rho_L, \rho_R}$  due to the presence of the reservoirs. It exhibits interesting behaviour in the equilibrium  $\nu_{\rho_L, \rho_R}$ , whose explicit form is known as well (see [24, Proposition 4.5]). To be specific, when the two boundary reservoirs operate at identical environmental conditions, i.e., when they are in thermal equilibrium w.r.t. each other because  $\rho_L = \rho_R = \rho$ , the variables  $\{\widehat{\eta}_x : x \in [N]_*\}$  denoting the number of particles at different sites in the bulk behave independently of each other with a Poisson distribution of mean  $\rho$ . In contrast, if the reservoirs are not at thermal equilibrium (i.e.,  $\rho_L \neq \rho_R$ ), then the variables  $\{\widehat{\eta}_x : x \in [N]_*\}$  remain independent, but no longer follow an identical marginal distribution under the law  $\nu_{\rho_L, \rho_R}$ . In this scenario  $\nu_{\rho_L, \rho_R}$  is referred to as a *non-equilibrium steady state* of the bulk (or, equivalently, of the process  $\widehat{\eta}_{\text{in}}$ ), because it describes the physical phenomenon that, even though the metal rod is not in a global equilibrium (as  $\rho_L \neq \rho_R$ ), it is nonetheless in a microscopic local equilibrium  $\nu_{\rho_L, \rho_R}$  when viewed only in the bulk.

**Fick's law of mass transport.** In the presence of the reservoirs, the macroscopic properties of the bulk variables in the metal rod undergo only minor changes. By means of hydrodynamic scaling of the process  $\widehat{\eta}_{\text{in}}$  in (1.44), we can easily extract properties of the corresponding *macroscopic local equilibrium*. In fact, the macroscopic heat profile in the bulk still follows the same heat equation (interpreted in the sense of hydrodynamics)

$$\begin{cases} \partial_t \rho = \Delta \rho, \\ \rho(x, 0) = \bar{\rho}(x), \end{cases} \quad x \in [0, 1], \quad (1.49)$$

but with additional boundary conditions

$$\begin{cases} \rho(0, t) = \bar{\rho}(0) = \rho_L, \\ \rho(1, t) = \bar{\rho}(1) = \rho_R, \end{cases} \quad t \geq 0, \quad (1.50)$$

that arise precisely due to the coupling with the two boundary reservoirs.

Heat conduction in a metal rod is but one example where the macroscopic equation in (1.49)–(1.50) is used to model the underlying physical process. Many physical experiments suggest that the transport of a solute between two compartments (or ‘reservoirs’) separated by a thin layer of membrane (or ‘bulk’) is governed by the same equation. More generally, the continuity equation for mass transport, which basically is a consequence of the conservation of total mass, states that

$$\frac{\partial \rho}{\partial t} = -\nabla \cdot J, \quad (1.51)$$

where  $\rho(x, t)$  is the density of the solute at a macroscopic position  $x \in [0, 1]$  at time  $t \geq 0$ , and  $J : [0, 1] \times \mathbb{R}^+ \rightarrow \mathbb{R}$  is the instantaneous diffusion flux measuring the amount of solute passing through a unit area per unit time. Experimental results based on analysis of single-component diffusions in homogeneous media align with the prediction of the so-called *Fick's law*, which postulates that the diffusion flux  $J$  is



in a direction opposite to the gradient of the concentration, i.e., for some diffusivity constant  $\sigma > 0$ ,

$$J = -\sigma \nabla \rho. \quad (1.52)$$

Combining (1.51)–(1.52), one recovers the familiar diffusion (or heat) equation given in (1.49).

**Uphill diffusion.** In situations where Fick’s law does not hold, *uphill* diffusion becomes possible. Uphill diffusion is characterised by the flow of a solute from an area with a lower concentration to an area with a higher concentration. In homogeneous media, diffusion of a single component obeys Fick’s law and therefore the flow is always downhill. However, in a multi-component mixture, interaction between different components can change their diffusive characteristics in such a way that the overall effect results in uphill diffusion of the total density [102]. In particular, if a single component exhibits ‘dormant characteristics’ and therefore represents a solute with a mixture of both states (active and dormant), then it is reasonable to expect interesting behaviour at equilibrium, such as the violation of Fick’s law, uphill diffusion, etc.

An aim in the second half of Part II is to incorporate boundary reservoirs into the three multi-layer systems with dormancy, which will be briefly introduced in the next section, and study properties of their corresponding microscopic non-equilibrium steady states. Furthermore, in the context of mass transport, by studying the associated macroscopic properties of the systems, we investigate how the interplay between active and dormant states of a single component can give rise to uphill diffusion.

### §1.2.3 Summary of Part II

We start by describing how the three earlier defined interacting particle systems are adapted in order to include dormant characteristics.

**Three switching interacting particle systems.** We modify the three particle systems introduced in Section 1.2.1 by allowing the underlying particles to switch into a “mild” or a “pure” dormant state independently of each other. The mild dormant state of a particle causes a slowdown in its random motion. In particular, the particles move at a slower (or zero) rate in their mild (or pure) dormant state. Formally, for  $\sigma \in \{-1, 0, 1\}$  we introduce the modified interacting particle systems on  $\mathbb{Z}$  where the particles randomly switch their jump rate between two possible values, 1 and  $\epsilon \in [0, 1]$ , depending on whether they are in an active or a dormant state. For  $\sigma = -1$  the particles evolve as in the simple symmetric exclusion process, for  $\sigma = 0$  the particles perform independent random walks, while for  $\sigma = 1$  the particles evolve as in the simple symmetric inclusion process. Furthermore, the type of a particle can change at rate  $\gamma > 0$  and the total rate of these changes is tuned to the underlying interaction rule. Observe that the dormant particles are still allowed to jump, but at a slower rate  $\epsilon$  than the active particles. Let

$$\begin{aligned} \eta_0(x, t) &:= \text{number of active particles at site } x \text{ at time } t \geq 0, \\ \eta_1(x, t) &:= \text{number of dormant particles at site } x \text{ at time } t \geq 0. \end{aligned}$$

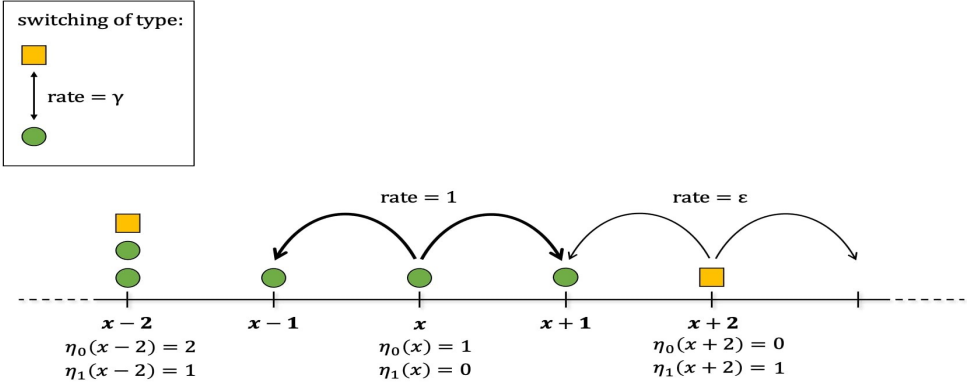


Figure 1.6: Representation of the switching random walks via slow (dormant) and fast (active) particles.

The process

$$(\eta_0(t), \eta_1(t))_{t \geq 0}, \quad (\eta_0(t), \eta_1(t)) := (\eta_0(x, t), \eta_1(x, t))_{x \in \mathbb{Z}}, \quad (1.53)$$

lives on the state space  $\mathcal{X} := \bar{\mathcal{X}} \times \bar{\mathcal{X}}$ , where

$$\bar{\mathcal{X}} := \begin{cases} \{0, 1\}^{\mathbb{Z}}, & \text{if } \sigma = -1, \\ \mathbb{N}_0^{\mathbb{Z}}, & \text{if } \sigma \in \{0, 1\}, \end{cases} \quad (1.54)$$

and forms a Markov process that we refer to as *switching exclusion process* for  $\sigma = -1$ , *switching random walks* for  $\sigma = 0$  (see Fig. 1.6), and *switching inclusion process* for  $\sigma = 1$ . Before giving the explicit form of the generator, it is convenient to define, for  $\sigma \in \{-1, 0, 1\}$ ,

$$L_\sigma := \begin{cases} L_{\text{ex}}, & \text{if } \sigma = -1, \\ L_{\text{in}}, & \text{if } \sigma = 0, \\ L_{\text{inc}}, & \text{if } \sigma = 1, \end{cases} \quad (1.55)$$

where the three generators  $L_{\text{in}}, L_{\text{ex}}$  and  $L_{\text{inc}}$  are as in (1.32), (1.35) and (1.37), respectively. The generator  $L_\sigma$  encodes the three processes, namely, the independent particle system, the exclusion process and the inclusion process, in a single generator and can be used to describe the generator for the switching process in a simplified form. Indeed, the generator  $L_{\epsilon, \gamma}$  of the switching process acts on a suitable test function  $f : \mathcal{X} \rightarrow \mathbb{R}$  as

$$(L_{\epsilon, \gamma} f)(\eta_0, \eta_1) := (L_\sigma f(\cdot, \eta_1))(\eta_0) + \epsilon(L_\sigma f(\eta_0, \cdot))(\eta_1) + \gamma(L_{0 \uparrow 1} f)(\eta_0, \eta_1), \quad (1.56)$$

where  $(\eta_0, \eta_1) := (\eta_0(x), \eta_1(x))_{x \in \mathbb{Z}} \in \mathcal{X}$  and  $L_{0 \uparrow 1}$  acts on  $f$  as

$$(L_{0 \uparrow 1} f)(\eta_0, \eta_1) := \sum_{x \in \mathbb{Z}} \left\{ \eta_0(x)(1 + \sigma \eta_1(x)) [f(\eta_0^{x, -}, \eta_1^{x, +}) - f(\eta)] \right. \\ \left. + \eta_1(x)(1 + \sigma \eta_0(x)) [f(\eta_0^{x, +}, \eta_1^{x, -}) - f(\eta)] \right\} \quad (1.57)$$

and is part of the generator  $L_{\epsilon,\gamma}$  that describes the switching between the two states (active or dormant) of a particle. Here, for a configuration  $\eta \in \bar{\mathcal{X}}$  and a site  $x \in \mathbb{Z}$  the configurations  $\eta^{x,+}, \eta^{x,-}$  are defined as in (1.48).

Observe in (1.56) that the first (resp., the second) term on the right-hand side describes the motions of the active (resp., the dormant) particles according to the interaction rule of the particle system. Also observe that in (1.57) the total rate at which a particle changes its state from active to dormant or vice versa depends on the particular interaction between the particles. Indeed, the switching between the particle types happens independently when  $\sigma = 0$ . In case  $\sigma = -1$ , an active particle at a site prohibits another dormant particle at the same site to become active and vice versa. In case  $\sigma = 1$ , an active particles encourages another dormant particle to become active at the same site and vice versa. We emphasise that the type of interaction between particles of opposite states is intentionally chosen to be the same as the interaction between particles of the same state. This choice is in fact crucial for preserving the self-duality properties of the particle systems without dormancy.

**Hydrodynamics: reaction-diffusion equation.** In order to study the hydrodynamic scaling limit of the switching process  $t \mapsto (\eta_0(t), \eta_1(t))$  introduced in (1.53) we consider the following scaling of space and time. We introduce a coarse-graining parameter  $N \in \mathbb{N}$  and scale space by  $1/N$ , time by  $N^2$ , the switching rate  $\gamma_N$  by  $1/N^2$ , and let  $N \rightarrow \infty$  to obtain a system of macroscopic equations associated with the switching interacting particle system. Note that while coarse graining, i.e., zooming out of the microscopic world to the macroscopic world, we keep the rates at which particles move constant. This is because we scale time by  $N^2$ , which automatically takes care of scaling the rate of the spatial movement of the particles. Similarly as in the three original particle systems, we consider the following (Radon) measure-valued quantities associated with the switching process in order to study hydrodynamic behaviour:

$$\mathsf{X}_0^N(t) := \frac{1}{N} \sum_{x \in \mathbb{Z}} \eta_0(x, tN^2) \delta_{x/N}, \quad \mathsf{X}_1^N(t) := \frac{1}{N} \sum_{x \in \mathbb{Z}} \eta_1(x, tN^2) \delta_{x/N}. \quad (1.58)$$

Here,  $\delta_y$  stands for the Dirac measure at  $y \in \mathbb{R}$ . The variables  $\mathsf{X}_0^N(t)$  and  $\mathsf{X}_1^N(t)$  in (1.58) are the empirical densities of, respectively, the active and the dormant particles at time  $t \geq 0$ . Note that, because the switching process  $t \mapsto (\eta_0(t), \eta_1(t))$  has a càdlàg path, the corresponding path associated with the process  $t \mapsto (\mathsf{X}_0^N(t), \mathsf{X}_1^N(t))$  is càdlàg as well. By exploiting the self-duality property along with some mild regularity conditions on the initial distributions of the rescaled switching process, we can show that the weak limit as  $N \rightarrow \infty$  of  $t \mapsto (\mathsf{X}_0^N(t), \mathsf{X}_1^N(t))$  in the Skorokhod topology is the deterministic continuous measure-valued path  $t \mapsto (\mathsf{X}_0(t), \mathsf{X}_1(t))$  with

$$d\mathsf{X}_i(t)\{x\} = \rho_i(x, t) dx, \quad t \geq 0, x \in \mathbb{R}, i \in \{0, 1\}, \quad (1.59)$$

where  $\rho_0(\cdot, \cdot)$  and  $\rho_1(\cdot, \cdot)$  are the unique bounded strong solutions of the reaction-diffusion equation

$$\begin{cases} \partial_t \rho_0 = \Delta \rho_0 + \Upsilon(\rho_1 - \rho_0), \\ \partial_t \rho_1 = \epsilon \Delta \rho_1 + \Upsilon(\rho_0 - \rho_1), \end{cases} \quad (1.60)$$

with initial conditions

$$\begin{cases} \rho_0(\cdot, 0) = \bar{\rho}_0(\cdot), \\ \rho_1(\cdot, 0) = \bar{\rho}_1(\cdot). \end{cases} \quad (1.61)$$

In (1.60) the parameter  $\Upsilon$  is the limiting value of the rescaled switching rates  $(\gamma_N)_{N \in \mathbb{N}}$  associated with the switching process, i.e.,  $\lim_{N \rightarrow \infty} N^2 \gamma_N = \Upsilon$ , and intuitively corresponds to the rate of switching (between active and dormant particles) events on the macroscopic scale. In (1.61) the initial macroscopic profiles  $\bar{\rho}_0$  and  $\bar{\rho}_1$  are assumed to be bounded continuous functions. These regularity conditions on the initial profiles are needed in order to ensure the existence and uniqueness of strong solutions of (1.60) (see e.g., [68, Chapter 5, Section 4, Theorem 4.1]).

The partial differential equations of type (1.60) fall in the class of reaction-diffusion equations, which are used to model time-dependent evolution of concentrations of certain substances in a solution due to diffusion and chemical reaction. Our finding that the hydrodynamic equation of a microscopic process with dormancy is a reaction-diffusion equation suggests that dormancy at a microscopic level can induce non-trivial effects on a macroscopic level and has the potential to change the qualitative behaviour of physical or chemical systems. Indeed, if  $\rho_0, \rho_1$  are smooth enough and satisfy (1.60), then by taking extra derivatives we see that the total density  $\rho := \rho_0 + \rho_1$  satisfies the *thermal telegrapher equation*

$$\partial_t (\partial_t \rho + 2\Upsilon \rho) = -\epsilon \Delta (\Delta \rho) + (1 + \epsilon) \Delta (\partial_t \rho + \Upsilon \rho), \quad (1.62)$$

which is second order in  $\partial_t$  and fourth order in  $\partial_x$  (see [2, 86] for a derivation). Note from (1.62) that the total density does not satisfy the usual diffusion equation of type (1.49). This fact is investigated in detail in the second half of Part II where we analyse the non-Fick property of  $\rho$ .

**Non-equilibrium behaviour: uphill diffusion.** In the second half of Part II, we look at the non-equilibrium steady state behaviour of the switching process by introducing boundary reservoirs similar to the ones included in the process  $\hat{\eta}_{\text{in}}$  in (1.44). In particular, we restrict the switching process to a finite region  $[N]_* := \{1, \dots, N\}$  of  $\mathbb{Z}$  where  $N \geq 2$ , and add two boundary reservoirs at each site 1 and  $N$  (see Fig. 1.7). The two reservoirs at a boundary site control the injection and absorption of, respectively, active and dormant particles. The rates at which particles are injected or absorbed by the reservoirs are chosen according to the type of interaction rule in the switching process. This is because when the rates associated with the reservoir dynamics are compatible with the dynamics of the particles in the bulk, the switching process admits a dual process. We already mentioned earlier that the switching process without the reservoirs is self-dual, a property it inherits from the three underlying particle systems, namely, the independent particle system, the exclusion process and the inclusion process. In the presence of the reservoirs, the bulk dynamics in the switching process preserves the self-duality property as well, but the reservoirs in the dual process become absorbing. Therefore the corresponding dual also consists of a system of active and dormant particles, where particles perform the same dynamics as before in the bulk, but are eventually absorbed at the boundary sites by the two

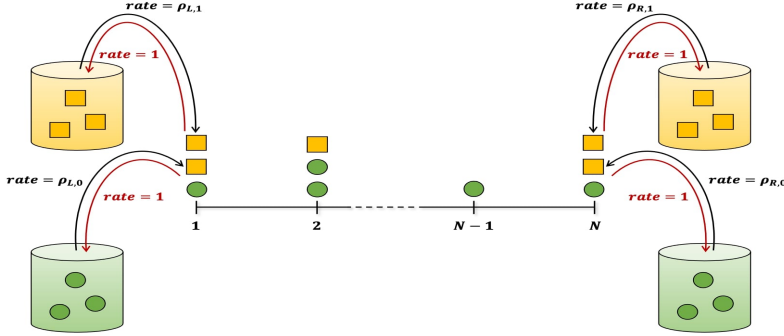


Figure 1.7: Representation of the switching process with boundary reservoirs when  $\sigma = 0$ . Green particles are active and yellow particles are dormant. Here,  $\rho_{L,0}, \rho_{R,0}, \rho_{L,1}, \rho_{R,1}$  are positive parameters controlling the rates at which reservoirs put or remove particles at the boundary sites.

reservoirs at certain rates. To avoid technicalities we refrain from giving the precise mathematical definition of the dual here (see Section 5.3.2). The absorbing nature of the dual immensely simplify the analysis of the switching process with reservoirs and allows for a partial characterisation of the unique non-equilibrium steady state  $\mu_{\text{stat}}$  of the process. In particular, we obtain explicit expressions for the stationary microscopic profile  $(\theta_0^{(N)}(x), \theta_1^{(N)}(x))_{x \in [N]^*}$  defined by

$$\theta_i^{(N)}(x) := \mathbb{E}_{\mu_{\text{stat}}}[\eta_i(x, t)], \quad x \in \{1, \dots, N\}, t \geq 0, i \in \{0, 1\}, \quad (1.63)$$

where  $t \mapsto (\eta_0(x, t), \eta_1(x, t))_{x \in [N]^*}$  is the switching process with reservoirs.

By computing the average flux of the particles in the stationary switching process with the help of the dual process, we are able to characterise the stationary microscopic current through each horizontal edge of the graph  $\{1, \dots, N\}$ . It turns out that in stationarity the total average current through each horizontal edge is the same and is of the order  $\frac{1}{N}$ . Therefore, an unambiguous notion of *uphill current* is obtained by imposing that the sign of the stationary current through each edge is the same as the sign of the total density gradient of the particles at the two boundary sites.

We also study the macroscopic behaviour of the stationary switching process with reservoirs under the same scaling of the microscopic parameters as was done in the context of hydrodynamic scaling. We derive the stationary macroscopic profiles of the system by taking the pointwise limit of the microscopic stationary profiles. To be more precise, we obtain the stationary macroscopic profile  $(\rho_0^{\text{stat}, \epsilon}(y), \rho_1^{\text{stat}, \epsilon}(y))_{y \in [0, 1]}$  by setting

$$\rho_i^{\text{stat}, \epsilon}(y) := \lim_{N \rightarrow \infty} \theta_i^{(N)}(\lceil yN \rceil), \quad y \in [0, 1], i \in \{0, 1\}. \quad (1.64)$$

When  $\epsilon > 0$ , i.e., microscopic particles only admit a mild dormant state, it turns out that the stationary macroscopic profiles  $\rho_0^{\text{stat}, \epsilon}(\cdot), \rho_1^{\text{stat}, \epsilon}(\cdot)$  constitute the unique

smooth strong solution of the boundary value problem

$$\begin{cases} 0 = \Delta u_0 + \Upsilon(u_1 - u_0), \\ 0 = \epsilon \Delta u_1 + \Upsilon(u_0 - u_1), \end{cases} \quad (1.65)$$

with boundary conditions

$$\begin{cases} u_0(0) = \rho_{L,0}, & u_0(1) = \rho_{R,0}, \\ u_1(0) = \rho_{L,1}, & u_1(1) = \rho_{R,1}, \end{cases} \quad (1.66)$$

However, when  $\epsilon = 0$ , i.e., microscopic particles only admit a pure dormant state, in the non-equilibrium situation (i.e., the two reservoirs at a boundary site are not in thermal equilibrium) the stationary macroscopic profile  $\rho_1^{\text{stat},0}$  for the dormant particles has a discontinuity near the boundary sites. By taking  $\epsilon \downarrow 0$  and analysing the limiting behaviour of the stationary macroscopic profile  $\rho_1^{\text{stat},\epsilon}$ , we find that the discontinuity of  $\rho_1^{\text{stat},0}$  appears as a sudden bump in the smooth stationary profile  $\rho_1^{\text{stat},\epsilon}$  at a distance of order  $\sqrt{\epsilon} \log(1/\epsilon)$  from the boundary sites (see Proposition 5.3.20 for a precise statement).

The precise microscopic parameter regime for an uphill current is difficult to describe. However, in the macroscopic setting, the uphill regime becomes simpler and can be described by a continuous manifold determined by the parameters  $a_0 := \rho_{R,0} - \rho_{L,0}$ ,  $a_1 := \rho_{R,1} - \rho_{L,1}$  and  $\epsilon$ . In particular, we show that a macroscopic uphill current takes place in the non-equilibrium situation if and only if

$$a_0^2 + (1 + \epsilon) a_0 a_1 + \epsilon a_1^2 < 0. \quad (1.67)$$

## §1.3 Further research

**Finite-systems scheme.** In Part I of this thesis, we study an interacting particle system  $t \mapsto Z(t)$  that approximates the behaviour of genetic evolution in structured populations with seed-banks. In our model, the populations are assumed to be located on the  $d$ -dimensional integer lattice  $\mathbb{Z}^d$ . Although in general such infinite systems reasonably well approximate real-world populations distributed over a large geographic space, real-world geographic regions are never infinite. Therefore, from the applied point of view, one is usually interested in the behaviour of the process  $t \mapsto Z_\Lambda(t)$  evolving on a finite geographic space  $\Lambda \subset \mathbb{Z}^d$ . The corresponding process  $Z_\Lambda$  restricted to  $\Lambda$  clusters almost surely in a finite random time  $\tau_\Lambda$  regardless of the starting configuration. Understanding the asymptotic behaviour of the time  $\tau_\Lambda$  and the process  $Z_\Lambda$  as the size  $|\Lambda|$  tends to infinity is crucial for any practical use of the model. In the so-called finite-systems scheme studied in e.g., [38, 40, 74], the aim is to provide mathematically precise statements on the comparison between  $Z_\Lambda$  and  $Z$  as  $\Lambda \uparrow \mathbb{Z}^d$ .

In the coexistence regime of the infinite-volume process  $Z$ , there is a one-parameter family of non-trivial equilibria  $\{\nu_\theta : \theta \in [0, 1]\}$  parametrised by the density  $\theta$  of a fixed gene type. If the infinite-volume process  $Z$  is in the coexistence regime, then we expect that, as  $\Lambda \uparrow \mathbb{Z}^d$ , the law of the finite-volume process  $Z_\Lambda$  on a deterministic time scale  $t_\Lambda$  close to  $\tau_\Lambda$  locally approximates the law  $\nu_\theta$ , where the density parameter

$\theta$  is a random macroscopic quantity  $Y_t \in [0, 1]$  for any  $t > 0$  such that  $\frac{t_\Lambda}{|\Lambda|} \xrightarrow{|\Lambda| \uparrow \infty} t$ . Depending on whether the average relative strengths of the seed-banks are finite or infinite, the behaviour of  $t \mapsto Y_t$  is expected to fall in different *universality classes*. For instance, in the case when seed-banks have finite relative strength on average, we expect the evolution of  $t \mapsto Y_t$  to be governed by the Wright-Fisher diffusion, with a diffusion constant that is slowed down by an extra factor capturing the finite average relative seed-bank strength. However, if the average relative strength of the seed-banks is infinite, then different universality classes may appear depending on how fast the seed-bank strengths grow as  $\Lambda \uparrow \mathbb{Z}^d$  compared to the time scale  $t_\Lambda$ . It may happen that the evolution of  $t \mapsto Y_t$  is no longer a diffusion, but rather a jump process.

**Interplay of dormancy, selection and mutation.** In Part I, we considered a stochastic model for the genetic evolution of spatially structured populations under the influence of migration, resampling and dormancy. As mentioned earlier in Section 1.1.1, two other important evolutionary forces are selection and mutation. It would be interesting to incorporate these into our model and see how dormancy competes with them. In [57] the authors introduced a Moran model with selection and mutation where the process admits a dual with a similar hypergeometric duality function as in our model. Although their model is concerned with a single finite population, it can be seamlessly extended to the spatial setting with seed-banks similarly like in our context without loss of the duality property. The corresponding dual process is expected to be a branching coalescing interacting particle system, where particles can be active or dormant. Active particles can migrate (due to migration), coalesce with another active particle to form a single active particle (due to resampling), branch into two active particles (due to selection), die (due to mutation), and fall asleep (due to dormancy). In the presence of mutation, we obtain a Feynman-Kac type duality relation between the original process and the dual process.

A typical trend in population genetic models that incorporate mutation but no dormancy is *ergodicity*, i.e., the process converges to a unique equilibrium starting from any initial state (see e.g., [140, Theorem 1.1]). However, in the modified spatial model with mutation and dormancy, seed-banks with an infinite average relative strength may prevent ergodicity altogether and cause a *phase transition* depending on the mutation rate and the relative seed-bank strength in different colonies. The reason behind such speculation is that ergodicity of the original process arises from the annihilating nature of the particles in the dual. If the relative seed-bank strengths are infinite on average, then the dual particles spend most of their time in the dormant state and therefore annihilation events, which happen only when the particles are active, become rare. It will be interesting to turn these heuristics into precise mathematical statements and see how seed-banks give rise to qualitatively different equilibrium behaviour.

**Dormancy in fluctuating random environment.** In Chapter 4 we study the spatial Moran process with seed-banks in a *static* random environment. The random environment is obtained by sampling the constituent population sizes from a translation-invariant ergodic random field and remains static throughout the evolution of the process. However, in real-world scenario the population sizes are more likely

to change over time. This calls for a model with seed-banks evolving in a *dynamic* random environment. In this setting, the corresponding process becomes a time-inhomogeneous Markov process that is relatively difficult to analyse. Furthermore, we typically lose the stochastic duality property that is crucial for the analysis of the process. These difficulties make the model in the dynamic random environment more interesting from a mathematical point of view because it requires the development of novel techniques.

**Systems with multi-layer seed-banks.** In the stochastic systems considered in Part I and Part II the constituent seed-banks consist of only one layer.

In the spatial Moran process introduced in Part I the seed-bank in each colony has a finite size that depends on the location of the colony. Because of the location-dependent population sizes, the state space of the process is not translation invariant. On the one hand, the lack of translation invariance makes the analysis of ergodic properties of the process more complicated. On the other hand, if we recover the translation invariance by considering equal population sizes in each colony, then we no longer see the effect of seed-banks on the equilibrium behaviour of the process. To be more precise, the process in the homogeneous state space behaves exactly like the process without seed-banks, where dichotomy of coexistence vs clustering is solely determined by the migration kernel. A solution to this problem can be obtained by extending our model to a multi-layer setting. In particular, following the second model introduced in [76], we can preserve both the translation invariance and the effect of seed-banks by incorporating seed-banks with infinitely many layers at each colony. More precisely, we keep the sizes of the active populations constant and put infinitely many seed-banks of equal size at each colony. Active individuals adopt a colour before entering into a seed-bank, which determines the average of their wake-up time from the dormant state. The advantage of this extension is that we do not destroy the duality property and keep the translation-invariance of the state-space of the underlying process. We expect a similar dichotomy between clustering vs coexistence, but the criterion determining which of the two occurs will heavily rely on the strength of the deep seed-banks and the migration mechanism.

A similar extension for the switching process in Part II to the multi-layer setting is available, where we preserve the self-duality property of the original process. It will be interesting to see if uphill diffusion indeed can appear in such a setting and, if so, in what manner it changes the qualitative behaviour of the system.

## §1.4 Outline of the thesis

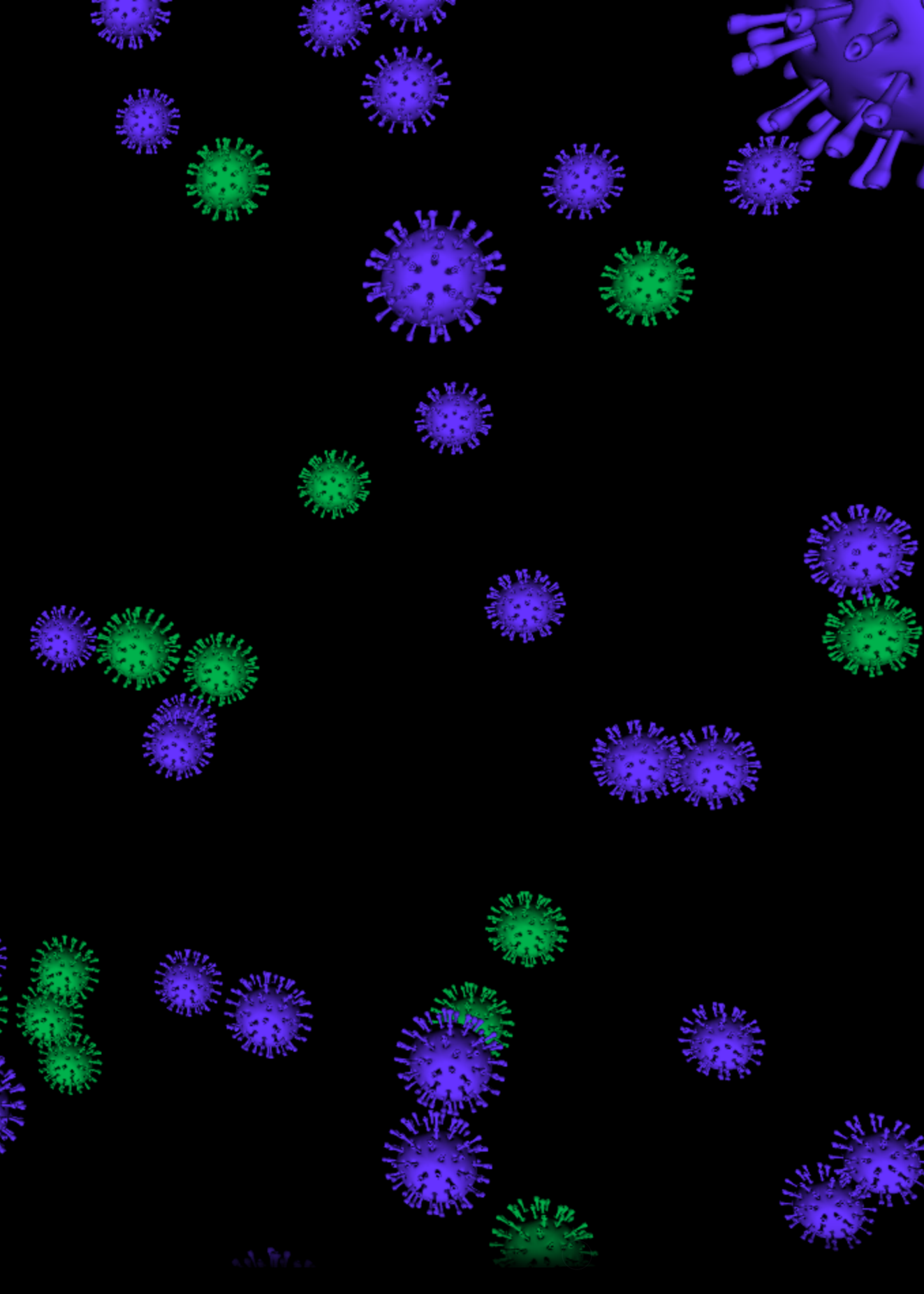
Part I of this thesis is based on [46, 47, 125] and consists of Chapters 2–4. In Chapter 2 we introduce the interacting particle system describing genetic evolution of spatially structured populations with seed-banks and state our main results on the well-posedness of the model, sampling duality relation with a dual interacting particle system, and the dichotomy between mono-type equilibria (clustering regime) and multi-type equilibria (coexistence regime). In Chapter 3 we refine the criterion



for the clustering regime given in Chapter 2 and identify the precise parameter regime for clustering, which is determined by the relative seed-bank strengths and the migration kernel. In Chapter 4 we extend the model in Chapter 2 to a static random environment setting. Under mild assumptions on the law of the environment and the migration kernel, we state and prove homogenisation results on the equilibrium behaviour of the process in the clustering regime.

Part II of this thesis is based on [62] and consists of Chapter 5. In Chapter 5 we introduce a switching interacting particle system, where particles can be in an active state or a (mild/pure) dormant state. We state and prove results on the hydrodynamic scaling limit, the stochastic duality property of the process etc. Furthermore, we study the non-equilibrium behaviour of the process in the presence of boundary reservoirs and state results on uphill diffusion of the particles, a phenomenon that manifests itself as an outcome of the reaction-diffusion type interactions between active and (mild or pure) dormant particles.





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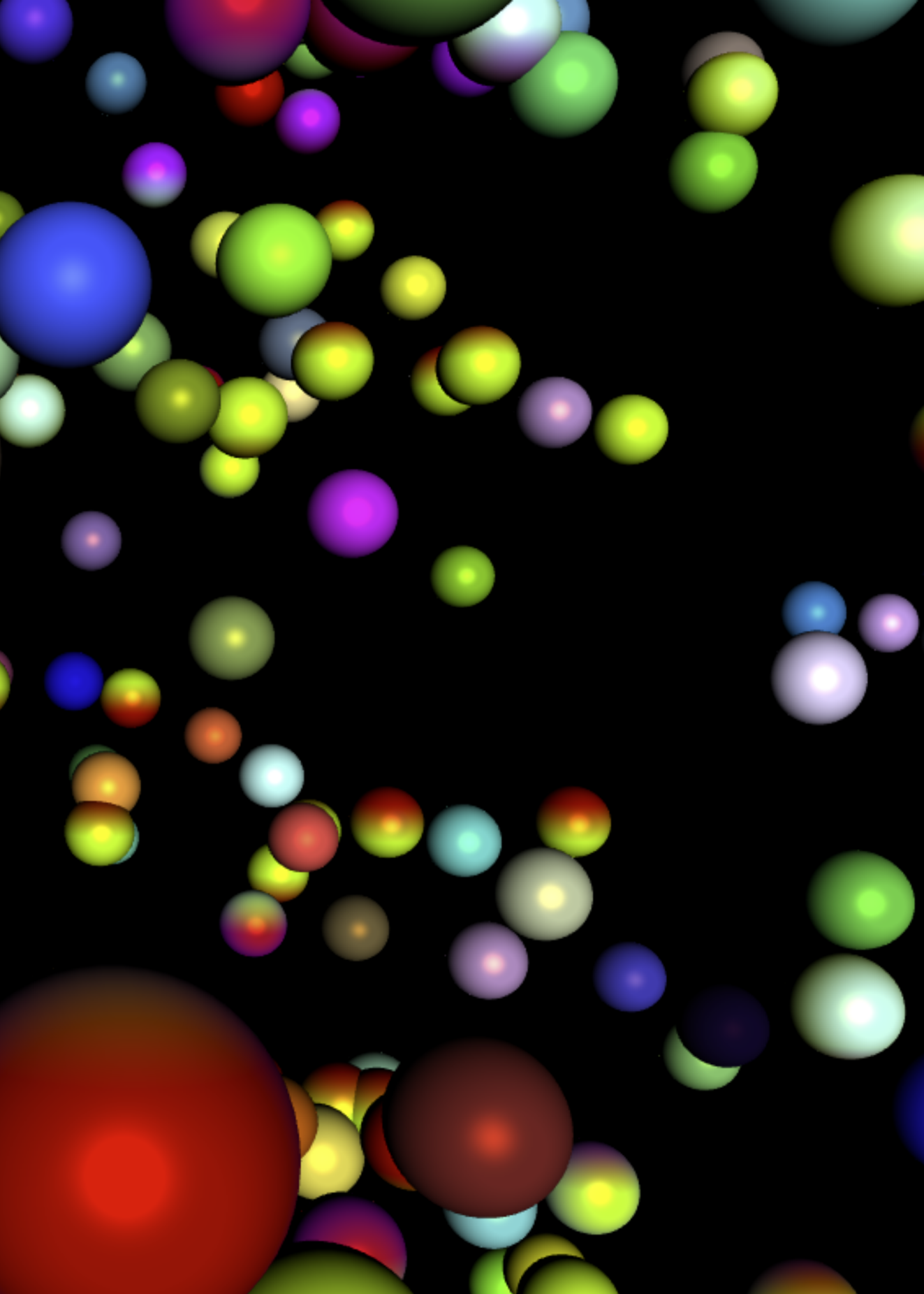
**PART I**

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**SPATIALLY INHOMOGENEOUS  
POPULATIONS WITH  
SEED-BANK**

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# Spatially inhomogeneous populations with seed-bank: duality, existence, equilibrium

This chapter is based on the following paper:

F. den Hollander and S. Nandan. Spatially inhomogeneous populations with seed-banks: I. Duality, existence and clustering. *J. Theor. Probab.*, 35(3):1795–1841, 2021.

## Abstract

We consider a system of interacting Moran models with seed-banks. Individuals live in colonies and are subject to resampling and migration as long as they are *active*. Each colony has a seed-bank into which individuals can retreat to become *dormant*, suspending their resampling and migration until they become active again. The colonies are labelled by  $\mathbb{Z}^d$ ,  $d \geq 1$ , playing the role of a *geographic space*. The sizes of the active and the dormant population are *finite* and depend on the *location* of the colony. Migration is driven by a random walk transition kernel. Our goal is to study the equilibrium behaviour of the system as a function of the underlying model parameters.

In the present paper we show that, under mild condition on the sizes of the active population, the system is well-defined and has a dual. The dual consists of a system of *interacting* coalescing random walks in an *inhomogeneous* environment that switch between an active state and a dormant state. We analyse the dichotomy of *coexistence* (= multi-type equilibria) versus *clustering* (= mono-type equilibria), and show that clustering occurs if and only if two random walks in the dual starting from arbitrary states eventually coalesce with probability one. The presence of the seed-bank *enhances genetic diversity*. In the dual this is reflected by the presence of time lapses during which the random walks are dormant and do not move.

## §2.1 Background, motivation and outline

Dormancy is an evolutionary trait observed in plants, bacteria and other microbial populations, where an organism enters a reversible state of low metabolic activity as a response to adverse environmental conditions. The dormant state of an organism in a population is characterised by interruption of basic reproduction and phenotypic development during periods of environmental stress [109, 142]. The dormant organisms reside in what is called a *seed-bank* of the population. After a varying and possibly large number of generations, dormant organisms can be resuscitated under more favourable conditions and reprise reproduction after becoming *active* by leaving the seed-bank. This strategy is known to have important implications for the genetic diversity and overall fitness of the underlying population [109, 108], since the seed-bank of a population often acts as a *buffer* against evolutionary forces such as genetic drift, selection and environmental variability. The importance of dormancy has led to several attempts to model seed-banks from a mathematical perspective ([16, 14]; see also [18] for a broad overview).

In [16] and [14], the Fisher-Wright model with *seed-bank* was introduced and analysed. In the Fisher-Wright model with seed-bank, individuals live in a colony, are subject to *resampling* where they adopt each other's type, and move in and out of the seed-bank where they suspend resampling. The seed-bank acts as a repository for the genetic information of the population. Individuals that reside inside the seed-bank are called *dormant*, those that reside outside are called *active*. Both the long-time behaviour and the genealogy of the population were analysed for the continuum model obtained by letting the size of the colony tend to infinity, called the Fisher-Wright diffusion with seed-bank.

In [76, 75, 74], the continuum model was extended to a *spatial* setting in which individuals live in multiple colonies, labelled by a countable Abelian group playing the role of a *geographic space*. In the spatial model with seed-banks, each colony is endowed with its own seed-bank and individuals are allowed to *migrate* between colonies. The goal was to understand the change in behaviour compared to the spatial model without seed-bank.

To date, most of the results in the literature on seed-bank models are derived only in the setting of *large-colony-size* limit, where the evolution in the model is described by a system of coupled SDE's. In [48], a multi-colony Fisher-Wright model with seed-banks was introduced where the colony sizes are finite. However, this model is restricted to *homogeneous* population sizes and a finite geographic space. In this chapter we introduce an individual-based spatial model with seed-banks in continuous time where the sizes of the underlying populations are *finite* and *vary* across colonies. The latter make the model more interesting from a biological perspective, but raise extra technical challenges. The key tool that we use to tackle these challenges is *stochastic duality*[71, 25]. The spatial model introduced in this chapter fits in the realm of interacting particle systems, which often exhibit additional structures such as duality[112, 134]. In particular, our spatial model can be viewed as a *hybrid* of the well-known Voter Model and the *generalized Symmetric Exclusion Process*,  $2j$ -SEP,  $j \in \mathbb{N}/2$  [26, 71, 111]. Both the Voter Model and the  $2j$ -SEP enjoy the stochastic

duality property, and our system inherits this as well: it is dual to a system consisting of *coalescing* random walks with *repulsive* interactions. The resulting dual process shares striking resemblances with the dual processes of the Voter Model and  $2j$ -SEP, because the original process is a modified hybrid of them. It has been recognised in the literature [150, 108, 109, 16, 14] that qualitatively different behaviour may occur when the exit time of a typical individual from the seed-bank can become large. Our model can address this phenomenon as well, due to the *inhomogeneity* in the seed-bank sizes. Our main goals are the following:

- (1) Introduce a model with seed-banks whose size is *finite* and depends on the geographic location of the colony. Prove *existence* and *uniqueness* of the process via well-posedness of an associated martingale problem and duality with a system of interacting coalescing random walks.
- (2) Identify a criterion for *coexistence* (= convergence towards multi-type equilibria) and *clustering* (= convergence towards mono-type equilibria). Show that there is a one-parameter family of equilibria controlled by the density of types.
- (3) Identify the *domain of attraction* of the equilibria.
- (4) Identify the *parameter regime* under which the criterion for clustering is met. In case of clustering, find out how fast the mono-type clusters grow in space-time. In case of coexistence, establish mixing properties of the equilibria.

In this chapter we settle (1) and (2). In Chapter 3 we will deal with (4) and we will partially address (3) in Chapter 4. We focus on the situation where the individuals can be of *two types*. The extension to infinitely many types, called the Fleming-Viot measure-valued diffusion, only requires standard adaptations and will not be considered here.

The chapter is organised as follows. In Section 2.2 we give a quick definition of the spatial model and state our main theorems about the well-posedness, the duality and the clustering criterion. In Section 2.3 we define and analyse a single-colony model. In Section 2.4 we extend the single-colony model to the spatial model, prove that the martingale problem associated with its generator is well-posed, establish duality with an spatially interacting seed-bank coalescent, demonstrate that the system exhibits a dichotomy between clustering and coexistence, and formulate a necessary and sufficient condition for clustering to prevail in terms of the dual, called the *clustering criterion*. Sections 2.5–2.7 are devoted to the proof of our main theorems.

## §2.2 Main theorems

In Section 2.2.1 we give a quick definition of the spatial system of populations with seed-banks. In Section 2.2.2 we argue that, under mild conditions on the sizes of the *active* population, the system is well-defined and has a *dual* that consists of finitely many interacting coalescing random walks. In Section 2.5.1



## §2.2.1 Quick definition of the multi-colony system

We consider the integer lattice  $\mathbb{Z}^d, d \geq 1$ , as a *geographic space*, where each  $i \in \mathbb{Z}^d$  represents a colony consisting of an *active* population and a *dormant* population. For  $i \in \mathbb{Z}^d$ , we write  $(N_i, M_i) \in \mathbb{N}^2$  to denote the *size* of the active, respectively, the dormant population at colony  $i$ . The sizes of the populations are preassigned and can vary across different colonies. Further, every individual of a population carries one of two *genetic types*:  $\heartsuit$  and  $\spadesuit$ . Individuals in the active (resp. dormant) populations are called active (resp. dormant), and are subject to *resampling* and *exchange*:

- (1) Active individuals in any colony resample with active individuals in *any* colony.
- (2) Active individuals in any colony exchange with dormant individuals in the *same* colony.

For (1) we assume that each active individual at colony  $i$  at rate  $a(i, j)$  uniformly draws an active individual at colony  $j$  and *adopts its type*. For (2) we assume that each active individual at colony  $i$  at rate  $\lambda$  uniformly draws a dormant individual at colony  $i$  and the two individuals *trade places while keeping their type* (i.e., the active individual becomes dormant and the dormant individual becomes active). Dormant individuals do *not* resample and thereby cause an overall slow-down of the random genetic drift that arises from (1). Because of this, we refer to the dormant populations as the *seed-banks* of the spatial system. Although the exchange rate  $\lambda$  could be made to vary across colonies, for the sake of simplicity we choose it to be constant.

We put

$$K_i := \frac{N_i}{M_i}, \quad i \in \mathbb{Z}^d, \quad (2.1)$$

for the *ratios* of the sizes of the active and the dormant population in each colony. Observe that  $K_i^{-1} = \frac{M_i}{N_i}$  quantifies the *relative strength* of the seed-bank at colony  $i \in \mathbb{Z}^d$ . We impose the following conditions on the *migration kernel*  $a(\cdot, \cdot)$ :

**Assumption 2.A (Homogeneous migration).** The migration kernel  $a(\cdot, \cdot)$  satisfies:

- (1)  $a(\cdot, \cdot)$  is irreducible in  $\mathbb{Z}^d$ .
- (2)  $a(i, j) = a(0, j - i)$  for all  $i, j \in \mathbb{Z}^d$ .
- (3)  $c := \sum_{i \in \mathbb{Z}^d \setminus \{0\}} a(0, i) < \infty$  and  $a(0, 0) > 0$ .

Part (2) ensures that the way genetic information moves between colonies is homogeneous in the geographic space. Part (3) ensures that the total rate of resampling of a single individual is finite and that resampling is possible also at the same colony. ■

Since it is crucial for our analysis that the population sizes remain constant, we view migration as a change of types without the individuals actually moving themselves. In this way, genetic information moves between colonies while the individuals themselves stay put.

**Remark 2.2.1.** In what follows, the geographic space can be any countable Abelian group. The choice of  $a(0, 0) = \frac{1}{2}$  in Assumption 2.A has been made only to make our model fit with the classical single-colony Moran model. The value of  $a(0, 0)$  represents the rate at which individuals resample from their own colony and in principle can be set to any positive real number.

At each colony  $i$  we register the pair  $(X_i(t), Y_i(t))$ , representing the number of active, respectively, dormant individuals of type  $\heartsuit$  at time  $t$  at colony  $i$ . We write  $(N_i, M_i)$  to denote the *size* of the active, respectively, dormant population at colony  $i$ . The resulting Markov process is an *interacting particle system* denoted by

$$(Z(t))_{t \geq 0}, \quad Z(t) = (X_i(t), Y_i(t))_{i \in \mathbb{Z}^d}, \quad (2.2)$$

and lives on the *inhomogeneous* state space

$$\mathcal{X} := \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i], \quad (2.3)$$

where  $[n] = \{0, 1, \dots, n\}$ ,  $n \in \mathbb{N}$ . It is implicitly assumed that the state space  $\mathcal{X}$  is equipped with the natural product topology, under which it becomes compact by virtue of Tychonoff's theorem. The space  $D([0, \infty), \mathcal{X})$  containing all càdlàg functions on  $\mathcal{X}$  is endowed with the Skorokhod topology and plays the role of the ambient probability space for the process  $Z$ . In Section 2.4.1 we carry out the formal mathematical construction of the process  $Z$ . In Section 2.4.2–2.4.3 we will show that, under mild assumptions on the model parameters, the Markov process in (2.2) is well-defined and has a *dual*  $(Z_*(t))_{t \geq 0}$ .

## §2.2.2 Well-posedness and duality

**Theorem 2.2.2 (Well-posedness and duality).** *Suppose that Assumption 2.A is in force. Then the Markov process  $(Z(t))_{t \geq 0}$  in (2.2) has a factorial moment dual  $(Z_*(t))_{t \geq 0}$  living in the state space  $\mathcal{X}_* \subset \mathcal{X}$  consisting of all configurations with finite mass, and the martingale problem associated with (2.2) is well-posed under either of the two following conditions:*

- (a)  $\lim_{\|i\| \rightarrow \infty} \|i\|^{-1} \log N_i = 0$  and  $\sum_{i \in \mathbb{Z}^d} e^{\delta \|i\|} a(0, i) < \infty$  for some  $\delta > 0$ ,
- (b)  $\sup_{i \in \mathbb{Z}^d \setminus \{0\}} \|i\|^{-\gamma} N_i < \infty$  and  $\sum_{i \in \mathbb{Z}^d} \|i\|^{d+\gamma+\delta} a(0, i) < \infty$  for some  $\gamma > 0$  and some  $\delta > 0$ .

**Remark 2.2.3 (Higher moments).** Unfortunately, because of conditions (a) and (b) in Theorem 2.2.2, the migration kernel  $a(\cdot, \cdot)$  is required to have at least  $d + \delta$  finite moment for some  $\delta > 0$ . We believe that this can be relaxed to a weaker moment condition.

Theorem 2.2.2 provides us with two sufficient conditions under which the system is well-defined and has a tractable dual. It shows a *trade-off*: the more we restrict the tails of the migration kernel, the less we need to restrict the sizes of the active population. The sizes of the dormant population play no role because all the events

(resampling, migration and exchange) in our model are initiated by active individuals and dormant individuals do not feel the spatial extent of the geographic space. The dual process

$$Z_* := (Z_*(t))_{t \geq 0}, \quad Z_*(t) := (n_i(t), m_i(t))_{i \in \mathbb{Z}^d}, \quad (2.4)$$

is an interacting particle system on the state space

$$\mathcal{X}_* := \left\{ (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X} : \sum_{i \in \mathbb{Z}^d} (n_i + m_i) < \infty \right\}, \quad (2.5)$$

and consists of finite collections of particles that switch between an *active* state and a *dormant* state. The variable  $n_i(t)$  (resp.  $m_i(t)$ ) in (2.4) counts the number of active (resp. dormant) dual particles present at location  $i \in \mathbb{Z}^d$  at time  $t \geq 0$ . The dual particles perform *interacting coalescing* random walks on  $\mathbb{Z}^d$  as long as they are in the active state, with rates that are determined by the population sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$ , the migration kernel  $a(\cdot, \cdot)$  and the exchange rate  $\lambda$ . Theorem 2.4.5, Corollary 2.4.6 and Theorem 2.4.8 in Section 2.4 contain the fine details.

### §2.2.3 Equilibrium: coexistence versus clustering

A natural question that arises in the discussion of any model is whether an equilibrium exists. To answer this, let us denote by  $\mathcal{P}(\mathcal{X})$  the set of all probability distributions on  $\mathcal{X}$ , and let  $\delta_\heartsuit \in \mathcal{P}(\mathcal{X})$  (resp.,  $\delta_\spadesuit$ ) be the Dirac distribution concentrated at the configuration  $(N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$  (resp.,  $(0, 0)_{i \in \mathbb{Z}^d}$ ). Observe that the process  $Z$  is absorbed at the configuration  $(N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$  (resp.,  $(0, 0)_{i \in \mathbb{Z}^d}$ ) when all individuals in the spatial system are of type- $\heartsuit$  (resp., type- $\spadesuit$ ), and therefore,  $\delta_\heartsuit, \delta_\spadesuit$  are two trivial extremal equilibria for the process  $Z$ . Indeed, when all individuals in the spatial system have the same genetic type, neither resampling nor exchange can reintroduce the missing type, and thereby push the system to an out-of-equilibrium state. This immediately raises the question of existence of any other equilibrium apart from these two trivial ones, and is the reason for introducing the following definition:

**Definition 2.2.4 (Clustering and Coexistence).** We say that the process  $Z$  is in the *clustering* regime if  $\delta_\heartsuit$  and  $\delta_\spadesuit$  are the only two extremal equilibrium. Otherwise, we say that the process is in the *coexistence* regime. ■

**Remark 2.2.5.** In the clustering regime any equilibrium  $\nu \in \mathcal{P}(\mathcal{X})$  of the process  $Z$  is a mixture of  $\delta_\heartsuit$  and  $\delta_\spadesuit$ . Thus, in the clustering regime the process  $Z$  admits only mono-type equilibrium. In other words, if the process  $Z$  exhibits clustering and is in equilibrium, all individuals in the spatial system are of type  $\heartsuit$  or of type  $\spadesuit$ .

In Section 2.4 we will show that clustering is equivalent to *coalescence* occurring eventually with probability 1 in the dual consisting of *two* particles. This will be the main route to the dichotomy.

**Theorem 2.2.6 (Equilibrium).** *If the initial distribution of the system is such that each active and each dormant individual adopts a type with the same probability independently of other individuals, then the system admits a one-parameter family of equilibria.*

- (a) *The family of equilibria is parameterised by the probability to have one of the two types.*
- (b) *The system converges to a mono-type equilibrium if and only if two random walks in the dual starting from arbitrary states eventually coalesce with probability one.*

Theorem 2.2.6 tells us that the system converges to an equilibrium when it is started from a specific class of initial distributions, namely, products of binomials. It also provides a *criterion* in terms of the dual that determines whether the equilibrium is mono-type or multi-type. Theorem 2.4.9, Corollary 2.4.10 and Theorem 2.4.12 in Section 2.4 contain the fine details.

## §2.3 Single-colony model and basic theorems

In Section 2.3.1 we define the single-colony model which serves as the base ingredient for the construction of the multi-colony model that we will introduce in the next section. In Section 2.3.2 we identify the dual of the single-colony model and analyse its equilibrium behaviour. In Section 2.3.3 we discuss the genealogy of the population in the single-colony model in terms of an interacting seed-bank coalescent.

### §2.3.1 Definition: resampling and exchange

Consider two populations, called *active* and *dormant*, consisting of  $N$  and  $M$  haploid individuals, respectively. Individuals in the population carry one of two genetic types:  $\heartsuit$  and  $\spadesuit$ . Dormant individuals reside inside the *seed-bank*, active individuals reside outside. The dynamics of the single-colony Moran model with seed-bank is as follows:

- Each individual in the active population carries a *resampling clock* that rings at rate 1. When the clock rings, the individual randomly chooses an active individual and *adopts* its type.
- Each individual in the active population also carries an *exchange clock* that rings at rate  $\lambda$ . When the clock rings, the individual randomly chooses a dormant individual and exchanges state, i.e., becomes dormant and forces the chosen dormant individual to become active. During the exchange the two individuals *retain* their type.

Since the sizes of the two populations remain constant, we only need two variables to describe the dynamics of the population, namely, the number of a type- $\heartsuit$  individuals in both populations (see Table 2.1).

Let  $x$  and  $y$  denote the number of individuals of type  $\heartsuit$  in the active and the dormant population, respectively. After a resampling event,  $(x, y)$  can change to  $(x - 1, y)$  or  $(x + 1, y)$ , while after an exchange event  $(x, y)$  can change to  $(x - 1, y + 1)$  or  $(x + 1, y - 1)$ . Both changes in the resampling event occur at rate  $x \frac{N-x}{N}$ . In the exchange event, however, to see  $(x, y)$  change to  $(x - 1, y + 1)$ , an exchange clock of a type- $\heartsuit$  individual in the active population has to ring (which happens at rate  $\lambda x$ ), and that individual has to choose a type- $\spadesuit$  individual in the dormant population

Initial state	Event	Final state	Transition rate
$(x, y)$	Resampling	$(x - 1, y)$	$x(N-x)/N$
		$(x + 1, y)$	$x(N-x)/N$
	Exchange	$(x - 1, y + 1)$	$\lambda x(M-y)/M$
		$(x + 1, y - 1)$	$\lambda(N-x)y/M$

Table 2.1: Scheme of transitions in the single-colony model.

(which happens with probability  $\frac{M-y}{M}$ ). Hence the total rate at which  $(x, y)$  changes to  $(x - 1, y + 1)$  is  $\lambda x \frac{M-y}{M}$ . By the same argument, the total rate at which  $(x, y)$  changes to  $(x + 1, y - 1)$  is  $\lambda(N - x) \frac{y}{M}$ .

For convenience we multiply the rate of resampling by a factor  $\frac{1}{2}$ , in order to make it compatible with the Fisher-Wright model. Thus, the generator  $G$  of the process is given by

$$G = G_{\text{Mor}} + G_{\text{Exc}}, \quad (2.6)$$

where

$$(G_{\text{Mor}}f)(x, y) = \frac{x(N-x)}{2N} [f(x-1, y) + f(x+1, y) - 2f(x, y)] \quad (2.7)$$

describes the Moran resampling of active individuals at rate  $\frac{1}{2}$  and

$$\begin{aligned} (G_{\text{Exc}}f)(x, y) &= \frac{\lambda}{M} x(M-y) [f(x-1, y+1) - f(x, y)] \\ &\quad + \frac{\lambda}{M} y(N-x) [f(x+1, y-1) - f(x, y)] \end{aligned} \quad (2.8)$$

describes the exchange between active and dormant individuals at rate  $\lambda$ . From here onwards, we denote the Markov process associated with the generator  $G$  by

$$z = (z(t))_{t \geq 0}, \quad z(t) = (X(t), Y(t)), \quad (2.9)$$

where  $X(t)$  and  $Y(t)$  are the number of type- $\heartsuit$  active and dormant individuals at time  $t$ , respectively. The process  $z$  has state space  $[N] \times [M]$ , where  $[N] = \{0, 1, \dots, N\}$  and  $[M] = \{0, 1, \dots, M\}$ . Note that the process  $z$  is well-defined because it is a continuous-time Markov chain with finitely many states.

## §2.3.2 Duality and equilibrium

The classical Moran model [123] is known to be dual to the block-counting process of the Kingman coalescent. In this section we show that the single-colony Moran model with seed-bank also has a coalescent dual.

**Definition 2.3.1 (Single-colony block-counting process).** The *block-counting process* of the interacting seed-bank coalescent (defined later in Definition 2.3.5) is the continuous-time Markov chain

$$z_* = (z_*(t))_{t \geq 0}, \quad z_*(t) = (n_t, m_t), \quad (2.10)$$

taking values in the state space  $[N] \times [M]$  with transition rates

$$(n, m) \mapsto \begin{cases} (n-1, m+1) & \text{at rate } \lambda n \left(1 - \frac{m}{M}\right), \\ (n+1, m-1) & \text{at rate } \lambda K m \left(1 - \frac{n}{N}\right), \\ (n-1, m) & \text{at rate } \frac{1}{N} \binom{n}{2} \mathbb{1}_{\{n \geq 2\}}, \end{cases} \quad (2.11)$$

where  $K = \frac{N}{M}$  is the *ratio* of the sizes of the active and the dormant population. ■

The first two transitions in (2.11) correspond to exchange, the third transition to resampling. Later in this section we describe the associated *interacting seed-bank coalescent* process, which gives the genealogy of  $z$ .

The following result gives the duality between  $z$  and  $z_*$ .

**Theorem 2.3.2 (Single-colony duality).** *The process  $z$  is dual to the process  $z_*$  via the duality relation*

$$\mathbb{E}_{(X,Y)} \left[ \binom{X(t)}{n} \binom{Y(t)}{m} \mathbb{1}_{\{n \leq X(t), m \leq Y(t)\}} \right] = \mathbb{E}^{(n,m)} \left[ \binom{X}{n(t)} \binom{Y}{m(t)} \mathbb{1}_{\{n(t) \leq X, m(t) \leq Y\}} \right], \quad t \geq 0, \quad (2.12)$$

where  $\mathbb{E}$  stands for generic expectation. On the left the expectation is taken over  $z$  with initial state  $z(0) = (X, Y) \in [N] \times [M]$ , on the right the expectation is taken over  $z_*$  with initial state  $z_*(0) = (n, m) \in [N] \times [M]$ .

Note that the duality relation fixes the factorial moments and thereby the mixed moments of the random vector  $(X(t), Y(t))$ . This enables us to determine the equilibrium distribution of  $z$ .

Although the above duality is new in the literature on seed-banks, the notion of factorial duality is not uncommon in mathematical models involving finite and fixed population sizes [57, 73]. Similar types of dualities are often found for other models too (e.g. self-duality of independent random walks, exclusion and inclusion processes, etc. [71]). Remarkably, in the special case where  $N = M = 2j$  for some  $j \in \mathbb{N}/2$ , Giardinà et al. (2009) [71, Section 3.2] identified the same duality relation as in (2.12) as a self-duality for the generalized  $2j$ -SEP on two-sites. This is not surprising given the fact that the exchange rates between active and dormant individuals defined in Table 2.1 are precisely the rates (up to rescaling) for the  $2j$ -SEP on two sites. We refer the reader to Section 2.5.1 to gain further insights into this.

**Proposition 2.3.3 (Convergence of moments).** *For any  $(X, Y), (n, m) \in [N] \times [M]$  with  $(n, m) \neq (0, 0)$ ,*

$$\lim_{t \rightarrow \infty} \mathbb{E}_{(X,Y)} [X(t)^n Y(t)^m] = N^n M^m \frac{X+Y}{N+M}. \quad (2.13)$$

Since the vector  $(X(t), Y(t))$  takes values in  $[N] \times [M]$ , which has  $(N+1)(M+1)$  points, the above proposition determines the limiting distribution of  $(X(t), Y(t))$ .

**Corollary 2.3.4 (Equilibrium).** *Suppose that  $z$  starts from initial state  $(X, Y) \in [N] \times [M]$ . Then  $(X(t), Y(t))$  converges in law as  $t \rightarrow \infty$  to a random vector  $(X_\infty, Y_\infty)$*

whose distribution is given by

$$\mathcal{L}_{(X,Y)}(X_\infty, Y_\infty) = \frac{X+Y}{N+M} \delta_{(N,M)} + \left(1 - \frac{X+Y}{N+M}\right) \delta_{(0,0)}. \quad (2.14)$$

Note that the equilibrium behaviour of  $z$  is the same as for the classical Moran model without seed-bank. The fixation probability of type  $\heartsuit$  is  $\frac{X+Y}{N+M}$ , which is nothing but the initial frequency of type- $\heartsuit$  individuals in the *entire population*. Even though the presence of the seed-bank delays the time of fixation, because of its finite size it has no significant effect on the overall qualitative behaviour of the process. We will see in Section 2.4.1 that the situation is different in the multi-colony model.

### §2.3.3 Interacting seed-bank coalescent

In our model, the *genealogy* of a sample taken from the finite population of  $N + M$  individuals is governed by a partition-valued coalescent process similarly as for the genealogy of the classical Moran model. However, due the presence of the seed-bank, blocks of a partition are marked as  $A$  (active) and  $D$  (dormant). Unlike in the genealogy of the classical Moran model, the blocks *interact* with each other. This interaction is present because of the restriction to *finite size* of the active and the dormant population. For this reason, we name the block process an *interacting seed-bank coalescent*. For convenience, we will use the word lineage to refer to a block in a partition.

Let  $\mathcal{P}_k$  be the set of partitions of  $\{1, 2, \dots, k\}$ . For  $\xi \in \mathcal{P}_k$ , denote the number of lineages in  $\xi$  by  $|\xi|$ . Furthermore, for  $j, k, l \in \mathbb{N}$ , define

$$\mathcal{M}_{j,k,l} = \left\{ \vec{u} \in \{A, D\}^j : \begin{array}{l} \text{the numbers of } A \text{ and } D \text{ in } \vec{u} \\ \text{are at most } k \text{ and } l, \text{ respectively} \end{array} \right\}. \quad (2.15)$$

The state space of the process is  $\mathcal{P}_{N,M} = \{(\xi, \vec{u}) : \xi \in \mathcal{P}_{N+M}, \vec{u} \in \mathcal{M}_{|\xi|, N, M}\}$ . Note that  $\mathcal{P}_{N,M}$  contains only those marked partitions of  $\{1, 2, \dots, N + M\}$  that have at most  $N$  active lineages and  $M$  dormant lineages. This is because we can only sample at most  $N$  active and  $M$  dormant individuals from the population.

Before we give the formal definition, let us introduce some basic notations. For  $\pi, \pi' \in \mathcal{P}_{N,M}$ , we say that  $\pi \succ \pi'$  if  $\pi'$  can be obtained from  $\pi$  by merging two active lineages. Similarly, we say that  $\pi \bowtie \pi'$  if  $\pi'$  can be obtained from  $\pi$  by altering the state of a single lineage ( $A \rightarrow D$  or  $D \rightarrow A$ ). We write  $|\pi|_A$  and  $|\pi|_D$  to denote the number of active and dormant lineages present in  $\pi$ , respectively.

**Definition 2.3.5 (Interacting seed-bank coalescent).** The *interacting seed-bank coalescent* is the continuous-time Markov chain with state space  $\mathcal{P}_{M,N}$  characterised by the following transition rates:

$$\pi \mapsto \pi' \text{ at rate } \begin{cases} \frac{1}{N} & \text{if } \pi \succ \pi', \\ \lambda \left(1 - \frac{|\pi|_D}{M}\right) & \text{if } \pi \bowtie \pi' \text{ by change of state of} \\ & \text{one lineage in } \pi \text{ from } A \text{ to } D, \\ \lambda K \left(1 - \frac{|\pi|_A}{N}\right) & \text{if } \pi \bowtie \pi' \text{ by change of state of} \\ & \text{one lineage in } \pi \text{ from } D \text{ to } A. \end{cases} \quad (2.16)$$

The factor  $1 - \frac{|\pi|_D}{M}$  in the transition rate of a single active lineage when  $\pi$  becomes dormant reflects the fact that, as the seed-bank gets full, it becomes more difficult for an active lineage to enter the seed-bank. Similarly, as the number of active lineages decreases due to the coalescence, it becomes easier for a dormant lineage to leave the seed-bank and become active. This also tells us that there is a *repulsive interaction* between the lineages of the same state ( $A$  or  $D$ ). Due to this interaction, it is tricky to study the coalescent. As  $N, M$  get large, the interaction becomes weak. As  $N, M \rightarrow \infty$ , after proper space-time scaling, the coalescent converges weakly to a limit coalescent where the interaction is no longer present. In fact, it can be shown that when both the time and the parameters are scaled properly, the coalescent converges weakly as  $N, M \rightarrow \infty$  to the *seed-bank coalescent* described in [14].

We can also describe the coalescent in terms of an interacting particle system with the help of a graphical representation (see Figure 2.1). The interacting particle system consists of two reservoirs, called *active* reservoir and *dormant* reservoir, having  $N$  and  $M$  labeled sites, respectively, each of which can be occupied by at most one particle. The particles in the active and dormant reservoir are called *active* and *dormant* particles, respectively. The active particles can coalesce with each other, in the sense that if an active particle occupies a labeled site where an active particle is present already, then the two particles are glued together to form a single particle at that site. Active particles can become dormant by moving to an empty site in the dormant reservoir, while dormant particles can become active by moving to an empty site in the active reservoir. The transition rates are as follows:

- An active particle tries to coalesce with another active particle at rate  $\frac{1}{2}$  by choosing uniformly at random a labeled site in the active reservoir. If the chosen site is empty, then it ignores the transition, otherwise it coalesces with the active particle present at the new site.
- An active particle becomes dormant at rate  $\lambda$  by moving to a random labeled site in the dormant reservoir when the chosen site is empty, otherwise it remains in the active reservoir.
- A dormant particle becomes active at rate  $\lambda K$  by moving to a random labeled site in the active reservoir when the chosen site is empty, otherwise it remains in the dormant reservoir.

Clearly, the particles *interact with each other* due to the finite capacity of the two reservoirs. If  $N, M \rightarrow \infty$ , then the probability to choose an empty site in a reservoir tends to 1, and so the system converges (after proper scaling) to an interacting particle system where the particles move independently between the two reservoirs.

Note that if we define  $n_t =$  number of active particles at time  $t$  and  $m_t =$  number of dormant particles at time  $t$ , then  $z_* = (n_t, m_t)_{t \geq 0}$  is the block-counting process defined in Definition 2.3.1. Also, if we remove the labels of the sites in the two reservoirs and represents the particle configuration by an element of  $\mathcal{P}_{N,M}$ , then we obtain the



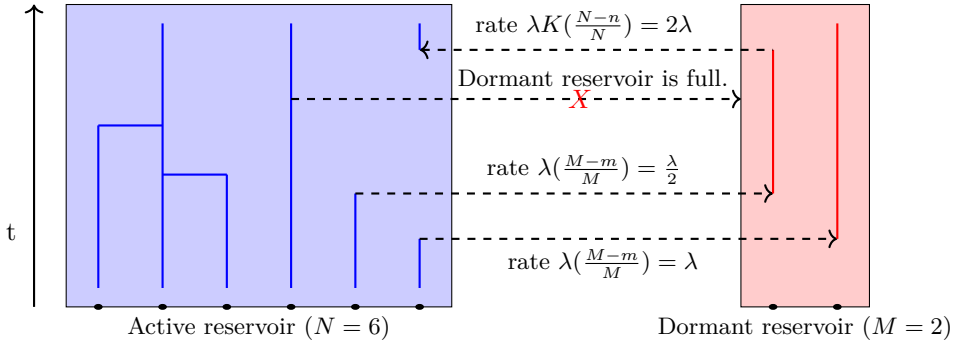


Figure 2.1: Scheme of transitions for an interacting particle system with an active reservoir of size  $N = 6$  and a dormant reservoir of size  $M = 2$ , so that  $K = \frac{N}{M} = \frac{6}{2} = 3$ . The effective rate for each of  $n$  active particles to become dormant is  $\lambda \frac{M-m}{M}$  when the dormant reservoir has  $m$  particles. Similarly, the effective rate for each of  $m$  dormant particles to become active is  $\lambda K \frac{N-n}{N}$  when the active reservoir has  $n$  particles.

interacting seed-bank coalescent described in Definition 2.3.5. Even though it is natural to describe the genealogical process via a partition-valued stochastic process, we will stick with the interacting particle system description of the dual, since this will be more convenient for the multi-colony model.

## §2.4 Multi-colony model and basic theorems

In this section we consider multiple colonies, each with their own seed-bank. Each colony has an *active* population and a *dormant* population. We take  $\mathbb{Z}^d$  as the underlying *geographic space* where the colonies are located (any countable Abelian group will do). With each colony  $i \in \mathbb{Z}^d$  we associate a variable  $(X_i, Y_i)$ , with  $X_i$  and  $Y_i$  the number of type- $\heartsuit$  active and dormant individuals, respectively, at colony  $i$ . Let  $(N_i, M_i)$  denote the size of the active and the dormant population at colony  $i$ . In each colony active individuals are subject to resampling and migration, and to exchange with dormant individuals that are in the same colony. Dormant individuals are not subject to resampling and migration.

Since it is crucial for our duality to keep the population sizes constant, we consider migration of types without the individuals actually moving themselves. To be precise, by a migration from colony  $j$  to colony  $i$  we mean that an active individual from colony  $i$  randomly chooses an active individual from colony  $j$  and adopts its type. In this way, the *genetic information* moves from colony  $j$  to colony  $i$ , while the individuals themselves stay put.

In Section 2.4.1 we introduce the multi-colony model. Our focus is on well-posedness, duality and convergence to equilibrium. In Section 2.4.2 we analyse the associated dual process. In Section 2.4.3 we deal with the well-posedness and equilibrium behaviour of the spatial process. Finally, in Section 2.4.4 we provide a necessary and sufficient criterion for clustering.

## §2.4.1 Definition: resampling, exchange and migration

We assume that each active individual at colony  $i$  resamples from colony  $j$  at rate  $a(i, j)$ , adopting the type of a uniformly chosen active individual at colony  $j$ . Here, the *migration kernel*  $a(\cdot, \cdot)$  is assumed to satisfy Assumption 2.A. After a migration to colony  $i$ , the only variable that is affected is  $X_i$ , the number of type-♥ active individuals at colony  $i$ . The final state can be either  $X_i - 1$  or  $X_i + 1$  depending on whether a type-♥ active individual from colony  $i$  chooses a type-♠ active individual from another colony or a type-♠ active individual from colony  $i$  chooses a type-♥ active individual from another colony. The rate at which  $X_i$  changes to  $X_i - 1$  due to a migration from colony  $j$  is

$$a(i, j)X_i \frac{N_j - X_j}{N_j},$$

while the rate at which  $X_i$  changes to  $X_i + 1$  due to a migration from colony  $j$  is

$$a(i, j)(N_i - X_i) \frac{X_j}{N_j}.$$

Note that for  $i = j$  the migration rate is

$$a(i, i)X_i \frac{N_i - X_i}{N_i} = \frac{X_i(N_i - X_i)}{2N_i}, \quad (2.17)$$

which is the same as the effective birth and death rate in the single-colony Moran model. Thus, the resampling within each colony is already taken care of via the migration.

It remains to define the associated exchange mechanism between the active and the dormant individuals in a colony. The exchange mechanism is the same as in the single-colony model, i.e., in each colony each active individual at rate  $\lambda$  performs an exchange with a dormant individual chosen uniformly from the seed-bank of that colony. For simplicity, we take the exchange rate  $\lambda$  to be the same in each colony.

The state space  $\mathcal{X}$  of the process is

$$\mathcal{X} := \prod_{i \in \mathbb{Z}^d} \{0, 1, \dots, N_i\} \times \{0, 1, \dots, M_i\} = \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i]. \quad (2.18)$$

A configuration  $\eta \in \mathcal{X}$  is denoted by  $\eta = (X_i, Y_i)_{i \in \mathbb{Z}^d}$ , with  $X_i \in [N_i]$  and  $Y_i \in [M_i]$ .

Initial state	Event	Final state	Transition rate
$(X_i, Y_i)_{i \in \mathbb{Z}^d}$	Migration from colony $j$ to $i$	$(\dots, (X_i - 1, Y_i), \dots)$	$a(i, j)X_i(N_j - X_j)/N_j$
		$(\dots, (X_i + 1, Y_i), \dots)$	$a(i, j)(N_i - X_i)X_j/N_j$
	Exchange at colony $i$	$(\dots, (X_i - 1, Y_i + 1), \dots)$	$\lambda X_i(M_i - Y_i)/M_i$
		$(\dots, (X_i + 1, Y_i - 1), \dots)$	$\lambda(N_i - X_i)Y_i/M_i$

Table 2.2: Scheme of transitions in the multi-colony model.

For each  $i \in \mathbb{Z}^d$ , let  $\vec{\delta}_{i,A}$  and  $\vec{\delta}_{i,D}$  be the configurations defined as

$$\vec{\delta}_{i,A} := (\mathbb{1}_{\{n=i\}}, 0)_{n \in \mathbb{Z}^d}, \quad \vec{\delta}_{i,D} := (0, \mathbb{1}_{\{n=i\}})_{n \in \mathbb{Z}^d}, \quad (2.19)$$

and for two configurations  $\eta_1 = (\bar{X}_i, \bar{Y}_i)_{i \in \mathbb{Z}^d}$  and  $\eta_2 = (\hat{X}_i, \hat{Y}_i)_{i \in \mathbb{Z}^d}$ ,  $\eta_1 \pm \eta_2 := (X_i, Y_i)_{i \in \mathbb{Z}^d}$  is defined component-wise by

$$X_i = \bar{X}_i \pm \hat{X}_i, \quad Y_i = \bar{Y}_i \pm \hat{Y}_i. \quad (2.20)$$

Throughout the remainder of this chapter, we adopt the convention given in (2.20) for addition and subtraction of configurations in  $\mathcal{X}$ .

The generator  $L$  for the process, acting on functions in

$$\mathcal{D} = \{f \in C(\mathcal{X}) : f \text{ depends on finitely many coordinates}\}, \quad (2.21)$$

is given by

$$L = L_{\text{Mig}} + L_{\text{Res}} + L_{\text{Exc}}, \quad (2.22)$$

where

$$(L_{\text{Mig}}f)(\eta) = \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d, \\ j \neq i}} \frac{a(i,j)}{N_j} \left\{ X_i(N_j - X_j) [f(\eta - \vec{\delta}_{i,A}) - f(\eta)] \right. \\ \left. + X_j(N_i - X_i) [f(\eta + \vec{\delta}_{i,A}) - f(\eta)] \right\} \quad (2.23)$$

describes the resampling of active individuals in *different* colonies (= migration),

$$(L_{\text{Res}}f)(\eta) = \sum_{i \in \mathbb{Z}^d} \frac{X_i(N_i - X_i)}{2N_i} [f(\eta - \vec{\delta}_{i,A}) + f(\eta + \vec{\delta}_{i,A}) - 2f(\eta)] \quad (2.24)$$

describes the resampling of active individuals in the *same* colony, and

$$(L_{\text{Exc}}f)(\eta) = \sum_{i \in \mathbb{Z}^d} \frac{\lambda}{M_i} \left\{ X_i(M_i - Y_i) [f(\eta - \vec{\delta}_{i,A} + \vec{\delta}_{i,D}) - f(\eta)] \right. \\ \left. + Y_i(N_i - X_i) [f(\eta + \vec{\delta}_{i,A} - \vec{\delta}_{i,D}) - f(\eta)] \right\} \quad (2.25)$$

describes the exchange of active and dormant individuals in the *same* colony.

From now on, we denote the process associated with the generator  $L$  by

$$Z = (Z(t))_{t \geq 0}, \quad Z(t) = (X_i(t), Y_i(t))_{i \in \mathbb{Z}^d}, \quad (2.26)$$

with  $X_i(t)$  and  $Y_i(t)$  representing the number of type- $\heartsuit$  active and dormant individuals at colony  $i$  at time  $t$ , respectively. Since  $Z$  is an interacting particle system, in order to show existence and uniqueness of the process, we can in principle follow the method described by Liggett in [112, Chapter I, Section 3]. However, for Liggett's method to work, a uniform bound on the sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$  is needed that we want to avoid. Fortunately, if  $L$  is a Markov pregenerator (see [112, Definition 2.1]), then we can construct the process by providing a unique solution to the martingale problem for  $L$ . The following proposition tells us that  $L$  is indeed a Markov pregenerator and thus prepares the ground for proving the well-posedness of the martingale problem for  $L$ .

**Proposition 2.4.1 (Pregenerator).** *The generator  $L$  defined in (2.22), acting on functions in  $\mathcal{D}$  defined in (2.21), is a Markov pregenerator.*

The existence of solutions to the martingale problem will be shown by using the techniques described in [112]. In order to establish uniqueness of the solution, we will need to exploit the dual process.

## §2.4.2 Spatially interacting seed-bank coalescent

The dual process is a block-counting process associated to a spatial version of the interacting seed-bank coalescent described in Section 2.3.3. We briefly describe the spatial coalescent process in terms of an interacting particle system.

At each site  $i \in \mathbb{Z}^d$  there are two reservoirs, an *active* reservoir and a *dormant* reservoir, with  $N_i \in \mathbb{N}$  and  $M_i \in \mathbb{N}$  labeled locations, respectively. Each location in a reservoir can accommodate at most one particle. As before, we refer to the particles in an active and dormant reservoir as *active* particles and *dormant* particles, respectively. The dynamics of the interacting particle system is as follows (see Figure 2.2).

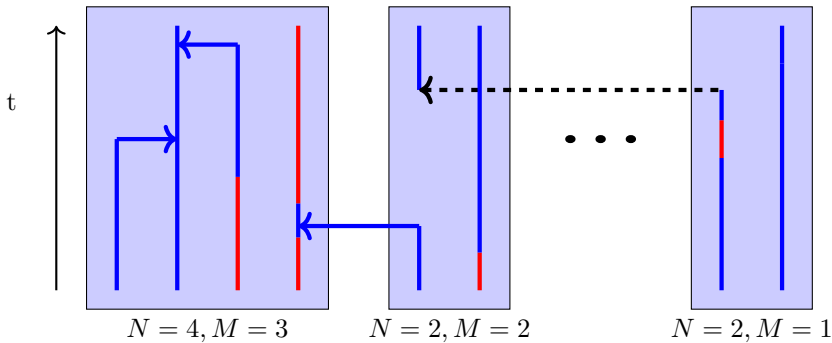


Figure 2.2: Scheme of transitions in the interacting particle system. Each block depicts the reservoirs located at sites of  $\mathbb{Z}^d$ . The blue lines represent the evolution of active particles, the red lines represent the evolution of dormant particles.

- An active particle at site  $i \in \mathbb{Z}^d$  becomes dormant at rate  $\lambda$  by moving to a random labeled location (out of  $M_i$  many) in the dormant reservoir at site  $i$  when the chosen labeled location is empty, otherwise it remains in the active reservoir.
- A dormant particle at site  $i \in \mathbb{Z}^d$  becomes active at rate  $\lambda K_i$  with  $K_i = \frac{N_i}{M_i}$  by moving to a random labeled location (out of  $N_i$  many) in the active reservoir at site  $i$  when the chosen labeled location is empty, otherwise it remains in the dormant reservoir.
- An active particle at site  $i$  chooses a random labeled location (out of  $N_j$  many) from the active reservoir at site  $j$  at rate  $a(i, j)$  and does the following:
  - If the chosen location in the active reservoir at site  $j$  is empty, then the particle moves to site  $j$  and thereby migrates from the active reservoir at site  $i$  to the active reservoir at site  $j$ .
  - If the chosen location in the active reservoir at site  $j$  is occupied by a particle, then it coalesces with that particle.

Note that an active particle can migrate between different sites in  $\mathbb{Z}^d$  and can coalesce with another active particle even when they are at different sites in  $\mathbb{Z}^d$ . For simplicity, we will impose the same assumptions on the migration kernel  $a(\cdot, \cdot)$  as stated in Assumption 2.A. A configuration  $(\eta_i)_{i \in \mathbb{Z}^d}$  of the particle system is an element of  $\prod_{i \in \mathbb{Z}^d} \{0, 1\}^{N_i} \times \{0, 1\}^{M_i}$ . For  $i \in \mathbb{Z}^d$ ,  $\eta_i$  represents the state of the labeled locations in the active and the dormant reservoir at site  $i$  (1 means occupied by a particle, 0 means empty).

Below we give the definition of the block-counting process associated to the spatial coalescent process described above. Although it is an interesting problem to construct the block-counting process starting from a configuration with infinitely many particles, we will restrict ourselves to configurations with *finitely many particles* only, because this makes the state space countable. Thus, the block-counting process is a continuous-time Markov chain on a countable state space and hence, in the definition below, it suffices to specify the possible transitions and their respective rates only.

**Definition 2.4.2 (Dual).** The dual process

$$Z_* = (Z_*(t))_{t \geq 0}, \quad Z_*(t) = (n_i(t), m_i(t))_{i \in \mathbb{Z}^d}, \quad (2.27)$$

is a continuous-time Markov chain with state space

$$\mathcal{X}_* := \left\{ (n_i, m_i)_{i \in \mathbb{Z}^d} \in \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i] : \sum_{i \in \mathbb{Z}^d} (n_i + m_i) < \infty \right\} \quad (2.28)$$

and with transition rates

$$(n_k, m_k)_{k \in \mathbb{Z}^d} \rightarrow \begin{cases} (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} & \text{at rate } \frac{2a(i,i)}{N_i} \binom{n_i}{2} \mathbb{1}_{\{n_i \geq 2\}} \\ & + \sum_{j \in \mathbb{Z}^d \setminus \{i\}} \frac{n_i a(i,j) n_j}{N_j} \quad \text{for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} + \vec{\delta}_{i,D} & \text{at rate } \frac{\lambda n_i (M_i - m_i)}{M_i} \quad \text{for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} + \vec{\delta}_{i,A} - \vec{\delta}_{i,D} & \text{at rate } \frac{\lambda (N_i - n_i) m_i}{M_i} \quad \text{for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} + \vec{\delta}_{j,A} & \text{at rate } \frac{n_i a(i,j) (N_j - n_j)}{N_j} \quad \text{for } i \neq j \in \mathbb{Z}^d, \end{cases} \quad (2.29)$$

where the configurations  $\vec{\delta}_{i,A}, \vec{\delta}_{i,D} \in \mathcal{X}_* \subset \mathcal{X}$  are as in (2.19), and additions and subtractions of configurations are performed in accordance with (2.20).  $\blacksquare$

In (2.27) the coordinates  $n_i(t)$  and  $m_i(t)$  denote the number of active and dormant dual particles at site  $i \in \mathbb{Z}^d$  at time  $t$ . The first transition describes the coalescence of an active particle at site  $i$  with other active particles elsewhere. The second and third transition describe the movement of particles between the active and the dormant reservoir at site  $i$ . The fourth transition describes the migration of an active particle from site  $i$  to site  $j$ . The following lemma tells us that the dual process  $Z_*$  is a well-defined and non-explosive (equivalent to uniqueness) Feller process on the countable state space  $\mathcal{X}_*$ .

**Lemma 2.4.3 (Uniqueness of dual).** *There exists a unique minimal Feller process  $(Z_*(t))_{t \geq 0}$  on  $\mathcal{X}_*$  with transition rates given in (2.29).*

Before we proceed we recall the definition of the martingale problem.

**Definition 2.4.4 (Martingale problem).** Suppose that  $(L, \mathcal{D})$  is a Markov pregenerator, and let  $\eta \in \mathcal{X}$ . A probability measure  $\mathbb{P}_\eta$  (or, equivalently, a process with law  $\mathbb{P}_\eta$ ) on  $D([0, \infty), \mathcal{X})$  is said to solve the martingale problem for  $L$  with initial point  $\eta$  if

- (a)  $\mathbb{P}_\eta[\xi_{(\cdot)} \in D([0, \infty), \mathcal{X}) : \xi_0 = \eta] = 1$ .
- (b)  $(f(\eta_t) - \int_0^t (Lf)(\eta_s) ds)_{s \geq 0}$  is a martingale relative to  $(\mathbb{P}_\eta, (\mathcal{F}_t)_{t \geq 0})$  for all  $f \in \mathcal{D}$ , where  $(\eta_t)_{t \geq 0}$  is the coordinate process on  $D([0, \infty), \mathcal{X})$  and  $(\mathcal{F}_t)_{t \geq 0}$  is the filtration given by  $\mathcal{F}_t := \sigma(\eta_s \mid s \leq t)$  for  $t \geq 0$ .

■

The following theorem gives the duality relation between the dual process  $Z_*$  and any solution to the martingale problem for  $(L, \mathcal{D})$ . This type of duality is sometimes referred to as martingale duality.

**Theorem 2.4.5 (Duality relation).** *Let the process  $Z$  with law  $\mathbb{P}_\eta$  be a solution to the martingale problem for  $(L, \mathcal{D})$  starting from initial state  $\eta = (X_i, Y_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$ . Let  $Z_*$  be the dual process with law  $\mathbb{P}^\xi$  starting from initial state  $\xi = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$ . For  $t \geq 0$ , let  $\Gamma(t)$  be the random variable defined by*

$$\Gamma(t) := \max \left\{ \|i\| : i \in \mathbb{Z}^d, n_i(s) + m_i(s) > 0 \text{ for some } 0 \leq s \leq t \right\}. \quad (2.30)$$

Suppose that the sizes  $(N_i)_{i \in \mathbb{Z}^d}$  of the active populations are such that, for any  $T > 0$ ,

$$\sum_{i \in \mathbb{Z}^d} N_i \mathbb{P}^\xi(\Gamma(T) \geq \|i\|) < \infty. \quad (2.31)$$

Then, for any  $t \geq 0$ ,

$$\mathbb{E}_\eta \left[ \prod_{i \in \mathbb{Z}^d} \frac{\binom{X_i(t)}{n_i} \binom{Y_i(t)}{m_i}}{\binom{N_i}{n_i} \binom{M_i}{m_i}} \mathbb{1}_{\{n_i \leq X_i(t), m_i \leq Y_i(t)\}} \right] = \mathbb{E}^\xi \left[ \prod_{i \in \mathbb{Z}^d} \frac{\binom{X_i}{n_i(t)} \binom{Y_i}{m_i(t)}}{\binom{N_i}{n_i(t)} \binom{M_i}{m_i(t)}} \mathbb{1}_{\{n_i(t) \leq X_i, m_i(t) \leq Y_i\}} \right], \quad (2.32)$$

where the expectations are taken with respect to  $\mathbb{P}_\eta$  and  $\mathbb{P}^\xi$ , respectively.

Note that the duality function is a product over all colonies of the duality function that appeared in the single-colony model. The infinite products are well-defined: all but finitely many factors are 1, because of our assumption that there are only *finitely many particles* in the dual process. Also note that there is no restriction on  $(M_i)_{i \in \mathbb{Z}^d}$ , the sizes of the dormant populations. This is because dormant individuals do not migrate and therefore do not feel the spatial extent of the system.

At first glance it may seem that (2.31) imposes a severe restriction on  $(N_i)_{i \in \mathbb{Z}^d}$ , the sizes of the active populations. However, this is not the case. The following corollary provides us with a large class of active population sizes for which Theorem 2.4.5 is true under mild assumptions on the migration kernel  $a(\cdot, \cdot)$ .

**Corollary 2.4.6 (Duality criterion).** *Suppose that Assumption 2.A is in force. Then (2.31), and consequently the duality relation in (2.32), hold for every  $(N_i)_{i \in \mathbb{Z}^d} \in \mathcal{N}$ , where*

(a) *either*

$$\mathcal{N} := \left\{ (N_i)_{i \in \mathbb{Z}^d} \in \mathbb{N}^{\mathbb{Z}^d} : \lim_{\|i\| \rightarrow \infty} \frac{1}{\|i\|} \log N_i = 0 \right\} \quad (2.33)$$

*when  $\sum_{i \in \mathbb{Z}^d} e^{\delta \|i\|} a(0, i) < \infty$  for some  $\delta > 0$ ,*

(b) *or*

$$\mathcal{N} := \left\{ (N_i)_{i \in \mathbb{Z}^d} \in \mathbb{N}^{\mathbb{Z}^d} : \sup_{i \in \mathbb{Z}^d \setminus \{0\}} \frac{N_i}{\|i\|^\delta} < \infty \right\} \quad (2.34)$$

*when  $\sum_{i \in \mathbb{Z}^d} \|i\|^\gamma a(0, i) < \infty$  for some  $\delta > 0$  and some  $\gamma > d + \delta$ .*

Corollary 2.4.6 shows a *trade-off*: the more we restrict the tails of the migration kernel, the less we need to restrict the sizes of the active populations.

### §2.4.3 Well-posedness and equilibrium

**Well-posedness.** We use a martingale problem for the generator  $L$  defined in (2.22), in the sense of [58, p.173], to construct  $Z$ . The following proposition gives existence of solutions for any choice of the reservoir sizes. As for the uniqueness of solutions, we will see that a restriction on the sizes of the active populations is required.

**Proposition 2.4.7 (Existence).** *Let  $L$  be the generator defined in (2.22) acting on the set of local functions  $\mathcal{D}$  defined in (2.21). Then for all  $\eta \in \mathcal{X}$  there exists a solution  $\mathbb{P}_\eta$  (a probability measure on  $D([0, \infty), \mathcal{X})$ ) to the martingale problem of  $(L, \mathcal{D})$  with initial state  $\eta$ .*

The following theorem gives the well-posedness of the martingale problem for  $(L, \mathcal{D})$  under a restricted class of sizes of the active populations and thus proves the existence of a unique Feller Markov process describing our multi-colony model.

**Theorem 2.4.8 (Well-posedness).** *Let  $(N_i)_{i \in \mathbb{Z}^d} \in \mathcal{N}$  and  $(M_i)_{i \in \mathbb{Z}^d} \in \mathbb{N}^{\mathbb{Z}^d}$ , and let  $L$  be the generator defined in (2.22) acting on the set of local functions  $\mathcal{D}$  defined in (2.21). Then the following hold:*

- (a) *For all  $\eta \in \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i]$  there exists a unique solution  $Z$  in  $D([0, \infty), \mathcal{X})$  of the martingale problem for  $(L, \mathcal{D})$  with initial state  $\eta$ .*
- (b)  *$Z$  is Feller and strong Markov, and its generator is an extension of  $(L, \mathcal{D})$ .*

In view of the above result, from here onwards, we implicitly assume that the restriction on  $(N_i)_{i \in \mathbb{Z}^d}$  to  $\mathcal{N}$  is always in force.

**Equilibrium.** Let us set  $Z_i(t) := (X_i(t), Y_i(t))$  for  $i \in \mathbb{Z}^d$  and denote by  $\mu(t)$  the distribution of  $Z(t)$ . Further, for each  $\theta \in [0, 1]$  and  $i \in \mathbb{Z}^d$ , let  $\nu_\theta^i$  be the probability measure on  $[N_i] \times [M_i]$  defined as

$$\nu_\theta^i := \text{Binomial}(N_i, \theta) \otimes \text{Binomial}(M_i, \theta). \quad (2.35)$$

For  $\theta \in [0, 1]$ , let  $\nu_\theta$  be the distribution on  $\mathcal{X}$  defined by  $\nu_\theta := \bigotimes_{i \in \mathbb{Z}^d} \nu_\theta^i$  and set

$$\mathcal{J} := \left\{ \nu_\theta \mid \theta \in [0, 1] \right\}. \quad (2.36)$$

Let  $D : \mathcal{X} \times \mathcal{X}_* \rightarrow [0, 1]$  be the function defined by

$$D((X_k, Y_k)_{k \in \mathbb{Z}^d}; (n_k, m_k)_{k \in \mathbb{Z}^d}) := \prod_{i \in \mathbb{Z}^d} \frac{\binom{X_i}{n_i} \binom{Y_i}{m_i}}{\binom{N_i}{n_i} \binom{M_i}{m_i}} \mathbb{1}_{\{n_i \leq X_i, m_i \leq Y_i\}}. \quad (2.37)$$

**Theorem 2.4.9 (Convergence to equilibrium).** *Suppose that  $\mu(0) = \nu_\theta \in \mathcal{J}$  for some  $\theta \in [0, 1]$ . Then there exists a probability measure  $\nu$  determined by the parameter  $\theta$  such that*

- (a)  $\lim_{t \rightarrow \infty} \mu(t) = \nu$ .
- (b)  $\nu$  is an equilibrium for the process  $Z$ .
- (c)  $\mathbb{E}_\nu[D(Z(0); \eta)] = \lim_{t \rightarrow \infty} \mathbb{E}^\eta[\theta^{|Z_*(t)}|]$ , where  $D(\cdot, \cdot)$  is defined in (2.37), the right expectation is taken w.r.t. the dual process  $Z_*$  started at configuration  $\eta = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$  and  $|Z_*(t)| := \sum_{i \in \mathbb{Z}^d} [n_i(t) + m_i(t)]$  is the total number of dual particles present at time  $t$ .

**Corollary 2.4.10.** *Let  $\nu$  be the equilibrium measure of  $Z$  in Theorem 2.4.9 corresponding to  $\theta \in [0, 1]$ . Then*

$$\mathbb{E}_\nu \left[ \frac{X_i(0)}{N_i} \right] = \mathbb{E}_\nu \left[ \frac{Y_i(0)}{M_i} \right] = \theta. \quad (2.38)$$

### §2.4.4 Clustering criterion

We next analyse the long-time behaviour of the multi-colony model. Our interest is to capture the nature of the equilibrium. To be precise, we investigate whether coexistence of different types is possible in equilibrium. The measures  $\bigotimes_{i \in \mathbb{Z}^d} \delta_{(0,0)}$  and  $\bigotimes_{i \in \mathbb{Z}^d} \delta_{(N_i, M_i)}$  are the trivial equilibria where the system concentrates on only one of the two types. When the system converges to an equilibrium that is not a mixture of these two trivial equilibria, we say that *coexistence* happens. For  $i \in \mathbb{Z}^d$ , let us denote the frequency of type- $\heartsuit$  active and dormant individuals at colony  $i$  at time  $t$  by  $x_i(t) := \frac{X_i(t)}{N_i}$  and  $y_i(t) := \frac{Y_i(t)}{M_i}$  respectively.

**Definition 2.4.11 (Clustering and Coexistence).** The system is said to exhibit *clustering* if the following hold:



- (a)  $\lim_{t \rightarrow \infty} \mathbb{P}_\mu(x_i(t) \in \{0, 1\}) = 1, \quad \lim_{t \rightarrow \infty} \mathbb{P}_\mu(y_i(t) \in \{0, 1\}) = 1,$
- (b)  $\lim_{t \rightarrow \infty} \mathbb{P}_\mu(x_i(t) \neq x_j(t)) = 0, \quad \lim_{t \rightarrow \infty} \mathbb{P}_\mu(y_i(t) \neq y_j(t)) = 0,$
- (c)  $\lim_{t \rightarrow \infty} \mathbb{P}_\mu(x_i(t) \neq y_j(t)) = 0,$

for all  $i, j \in \mathbb{Z}^d$  and any initial distribution  $\mu \in \mathcal{P}(\mathcal{X})$  such that the process  $Z$  in (2.2) with initial distribution  $\mu$  converges to an equilibrium as  $t \rightarrow \infty$ . Otherwise, the system is said to exhibit *coexistence*. ■

Observe that the above definition and Definition 2.2.4 are equivalent. Indeed, the above conditions make sure that if an equilibrium exists, then it is a mixture of the two trivial equilibria.

The following criterion, which follows from Corollary 2.4.6, gives an equivalent condition for clustering.

**Theorem 2.4.12 (Clustering criterion).** *The system clusters if and only if in the dual process defined in Definition 2.4.2 two particles, starting from any locations in  $\mathbb{Z}^d$  and any states (active or dormant), coalesce with probability 1.*

Note that the system clusters if and only if the genetic variability at time  $t$  between any two colonies converges to 0 as  $t \rightarrow \infty$ . From the duality relation in Theorem 2.4.5 it follows that this quantity is determined by the state of the dual process starting from two particles.

## §2.5 Proofs: duality and equilibrium for the single-colony model

Section 2.5.1 contains the proof of Theorem 2.3.2, which follows the algebraic approach to duality described in [25, 148]. Section 2.5.2 contains the proof of Proposition 2.3.3 and Corollary 2.3.4, which uses the duality in the single-colony model.

### §2.5.1 Duality and change of representation

Before we proceed with the proof of Theorem 2.3.2, and other results related to *stochastic duality*, it is worth stressing the importance of duality theory. Though originally introduced in the context of interacting particle systems, over the last decade duality theory has gained popularity in various fields, ranging from statistical physics and stochastic analysis to population genetics. One reason behind this wide interests is the simplification that duality provides: it often allows one to extract information about a complex stochastic process through a simpler process. To date, in the literature there exist two systematic approaches towards duality, namely, pathwise construction and Lie-algebraic framework. The former of the two approaches is more practical and widespread in the context of mathematical population genetics [77, 55, 88, 90], while the latter has been developed more recently and reveals deeper mathematical structures behind duality, and often also provides a larger class of duality functions (see e.g., [25], [67], [80], [148] for a general overview and further references). In what

follows, we adopt the Lie-algebraic framework suggested by Carinci et al. (2015)[25] and prepare the ground for this setting. The downside is that this approach does not capture the underlying genealogy of the original process. However, it does offer the opportunity to obtain a larger class of duality functions by applying symmetries from the Lie algebra to an already existing duality function [71]. In this exposition we refrain from exploring the latter aspect of the Lie-algebraic framework.

We start with briefly recalling that a (real) Lie algebra  $\mathfrak{g}$  is a linear space over  $\mathbb{R}$  endowed with a so-called *Lie bracket*  $[\cdot, \cdot]: \mathfrak{g} \times \mathfrak{g} \rightarrow \mathfrak{g}$  that is bilinear, skew-symmetric and satisfies the *Jacobi identity* [148]. The requirement of the bilinearity and skew-symmetry uniquely characterizes a Lie bracket by its action on a basis of  $\mathfrak{g}$ . An example of a (real) Lie algebra is the well-known  $\mathfrak{su}(2)$ -algebra, which is the 3-dimensional vector space over  $\mathbb{R}$  defined by the action of a Lie bracket on its basis elements  $\{J^+, J^-, J^0\}$  as

$$[J^0, J^+] = J^+, \quad [J^0, J^-] = -J^-, \quad [J^-, J^+] = -2J^0. \quad (2.39)$$

For  $\alpha \in \mathbb{N}$ , let  $V_\alpha$  be the linear space of all functions  $f: [\alpha] \rightarrow \mathbb{R}$ , and let  $\mathfrak{gl}(V_\alpha)$  denote the space of all linear operators on  $V_\alpha$ . Note that  $\mathfrak{gl}(V_\alpha)$  is a  $(1 + \alpha)^2$ -dimensional Lie algebra with the natural choice of Lie bracket given by  $[A, B] := AB - BA$  for  $A, B \in \mathfrak{gl}(V_\alpha)$ . Let us define the operators  $J^{\alpha, \pm}, J^{\alpha, 0}, A^{\alpha, \pm}, A^{\alpha, 0} \in \mathfrak{gl}(V_\alpha)$  acting on  $f: [\alpha] \rightarrow \mathbb{R}$  as

$$\begin{aligned} J^{\alpha, +} f(n) &= (\alpha - n)f(n + 1), & J^{\alpha, -} f(n) &= nf(n - 1), & J^{\alpha, 0} f(n) &= (n - \frac{\alpha}{2})f(n), \\ A^{\alpha, +} &= J^{\alpha, -} - J^{\alpha, +} - 2J^{\alpha, 0}, & A^{\alpha, -} &= J^{\alpha, +}, & A^{\alpha, 0} &= J^{\alpha, +} + J^{\alpha, 0}. \end{aligned} \quad (2.40)$$

It is straightforward to see that

$$[A^{\alpha, 0}, A^{\alpha, \pm}] = \pm A^{\alpha, \pm}, \quad [A^{\alpha, -}, A^{\alpha, +}] = -2A^{\alpha, 0}, \quad (2.41)$$

which are the same commutation relations as in (2.39). Thus, for each  $\alpha \in \mathbb{N}$ , the Lie homomorphism  $\phi_\alpha: \mathfrak{su}(2) \rightarrow \mathfrak{gl}(V_\alpha)$  defined by its action on the generators  $\{J^+, J^-, J^0\}$  given by

$$J^+ \mapsto A^{\alpha, +}, \quad J^- \mapsto A^{\alpha, -}, \quad J^0 \mapsto A^{\alpha, 0}, \quad (2.42)$$

is a finite-dimensional representation of  $\mathfrak{su}(2)$ . Similarly, we can verify that, for each  $\alpha \in \mathbb{N}$ ,

$$\{J^{\alpha, +}, J^{\alpha, -}, J^{\alpha, 0}\}$$

form a representation of the *dual*  $\mathfrak{su}(2)$ -algebra (defined by the commutation relations in (2.39), but with opposite signs).

Below we introduce the notion of duality between two operators and prove a lemma that will be crucial in the proof of duality of both the single-colony and the multi-colony model. The relevance to our context of the above discussion on  $\mathfrak{su}(2)$  and its dual algebra will become clear as we go along.

**Definition 2.5.1 (Operator duality).** Let  $A$  and  $B$  be two operators acting on functions  $f: \Omega \rightarrow \mathbb{R}$  and  $g: \hat{\Omega} \rightarrow \mathbb{R}$  respectively. We say that  $A$  is dual to  $B$  with respect to the duality function  $D: \Omega \times \hat{\Omega} \rightarrow \mathbb{R}$ , denoted by  $A \xrightarrow{D} B$ , if  $(AD(\cdot, y))(x) = (BD(x, \cdot))(y)$  for all  $(x, y) \in \Omega \times \hat{\Omega}$ . ■

The following lemma intertwines the  $\mathfrak{su}(2)$  and its dual algebra with a duality function.

**Lemma 2.5.2 (Single-colony intertwiner).** For  $\alpha \in \mathbb{N}$ , let  $d_\alpha: [\alpha] \times [\alpha] \rightarrow [0, 1]$  be the function defined by

$$d_\alpha(x, n) = \frac{\binom{x}{n}}{\binom{\alpha}{n}} \mathbb{1}_{\{n \leq x\}}. \quad (2.43)$$

Then the following duality relations hold:

$$J^{\alpha,+} \xrightarrow{d_\alpha} A^{\alpha,+}, \quad J^{\alpha,-} \xrightarrow{d_\alpha} A^{\alpha,-}, \quad J^{\alpha,0} \xrightarrow{d_\alpha} A^{\alpha,0}. \quad (2.44)$$

*Proof.* By straightforward calculations, it can be shown that  $d_\alpha(x, n)$  satisfies the relations

$$\begin{aligned} (\alpha - x) d_\alpha(x + 1, n) &= n [d_\alpha(x, n - 1) - d_\alpha(x, n)] + (\alpha - n) [d_\alpha(x, n) - d_\alpha(x, n + 1)], \\ x d_\alpha(x - 1, n) &= (\alpha - n) d_\alpha(x, n + 1), \\ x d_\alpha(x, n) &= (\alpha - n) d_\alpha(x, n + 1) + n d_\alpha(x, n), \end{aligned} \quad (2.45)$$

from which the above dualities in (2.44) follow immediately.  $\square$

**Remark 2.5.3 (Seed-bank and  $\mathfrak{su}(2)$ -algebra).** The basic idea behind the algebraic approach to duality is to write the generator of a given process in terms of simple operators that form a representation of some known Lie algebra and to make an Ansatz to obtain an intertwiner of the chosen representation. The intertwiner  $d_\alpha$  in the above lemma was first identified in [73, Lemma 1] as a duality function in disguise for the classical duality between the Moran model and the block-counting process of Kingman's coalescent. Recently, in [25] this duality was put in the algebraic framework by deriving it from an intertwining via  $d_\alpha$  of two representations of the *Heisenberg algebra*  $\mathcal{H}(1)$ . The connection of  $d_\alpha$  to the  $\mathfrak{su}(2)$ -algebra was also made in [71, Section 3.2], where the authors obtained a self-duality function of  $2j$ -SEP factorized in terms of  $d_\alpha$  by considering symmetries related to the  $\mathfrak{su}(2)$ -algebra. The relation of our seed-bank model to the  $\mathfrak{su}(2)$ -algebra becomes clear once we realize that the seed-bank component in our single-colony model is an *inhomogeneous* version of the  $2j$ -SEP on two-sites. Thus, it is natural to expect that the classical duality of Moran model can be retrieved from representations of  $\mathfrak{su}(2)$ -algebra as well. The above lemma indeed provides the ingredients to establish the duality of our single-colony model from representations of the  $\mathfrak{su}(2)$ -algebra. Although it is possible to guess the dual process of the single-colony model without going into the Lie-algebraic framework, the true usefulness of this approach lies in identifying the dual of the spatial model, where such speculation is no longer feasible.

*Proof of Theorem 2.3.2.* Recall that both  $Z = (X(t), Y(t))_{t \geq 0}$  and  $Z_* = (n_t, m_t)_{t \geq 0}$  live on the state space  $\Omega = [N] \times [M]$ . Let  $D: \Omega \times \Omega \rightarrow [0, 1]$  be the function defined by

$$D((X, Y); (n, m)) = \frac{\binom{X}{n}}{\binom{N}{n}} \frac{\binom{Y}{m}}{\binom{M}{m}} \mathbb{1}_{\{n \leq X, m \leq Y\}} = d_N(X, n) d_M(Y, m), \quad (X, Y), (n, m) \in \Omega. \quad (2.46)$$

Let  $G = G_{\text{Mor}} + G_{\text{Exc}}$  be the generator of the process  $Z$ , where  $G_{\text{Mor}}, G_{\text{Exc}}$  are as in (2.7)–(2.8). Also note from Definition 2.4.2 that the generator  $\widehat{G}$  of the dual process is given by  $\widehat{G} = G_{\text{King}} + G_{\text{Exc}}$  where  $G_{\text{King}}: C(\Omega) \rightarrow C(\Omega)$  is defined as

$$(G_{\text{King}}f)(n, m) = \frac{n(n-1)}{2N} [f(n-1, m) - f(n, m)], \quad (n, m) \in \Omega. \quad (2.47)$$

Since  $\Omega$  is countable, it is enough to show the generator criterion for duality, i.e.,

$$(GD(\cdot; (n, m)))(X, Y) = (\widehat{G}D((X, Y); \cdot))(n, m), \quad (X, Y), (n, m) \in \Omega. \quad (2.48)$$

In our notation, (2.48) translates into  $G \xrightarrow{D} \widehat{G}$ . It is somewhat tedious to verify (2.48) by direct computation. Rather, we will write down a proof with the help of the elementary operators defined in (2.40). This approach will also reveal the underlying change of representation of the two operators  $G, \widehat{G}$  that is embedded in the duality.

Note that

$$\begin{aligned} G_{\text{King}} &= \frac{1}{2N} \left[ (A_1^{N,+} - A_1^{N,-} + 2A_1^{N,0})A_1^{N,0} + \frac{N}{2}(A_1^{N,+} + A_1^{N,-} - N) \right], \\ G_{\text{Mor}} &= \frac{1}{2N} \left[ J_1^{N,0}(J_1^{N,+} - J_1^{N,-} + 2J_1^{N,0}) + \frac{N}{2}(J_1^{N,+} + J_1^{N,-} - N) \right], \\ G_{\text{Exc}} &= \frac{\lambda}{M} \left[ J_1^{N,+}J_2^{M,-} + J_1^{N,-}J_2^{M,+} + 2J_1^{N,0}J_2^{M,0} - \frac{NM}{2} \right] \\ &= \frac{\lambda}{M} \left[ A_1^{N,+}A_2^{M,-} + A_1^{N,-}A_2^{M,+} + 2A_1^{N,0}A_2^{M,0} - \frac{NM}{2} \right], \end{aligned} \quad (2.49)$$

where the subscripts indicate which variable of the associated function the operators act on. For example,  $J_1^{N,+}$  and  $J_2^{M,+}$  act on the first and second variable, respectively. So, for a function  $f: [N] \times [M] \rightarrow \mathbb{R}$ , we have  $(J_1^{N,+}f)(n, m) = (J^{N,+}f(\cdot; m))(n)$  and  $(J_2^{M,+}f)(n, m) = (J^{M,+}f(n; \cdot))(m)$ . The equivalent version of Lemma 2.5.2 holds for these operators with subscript as well, except that the duality function is  $D$ . In other words,  $J_1^{N,+} \xrightarrow{D} A_1^{N,+}$ ,  $J_2^{M,+} \xrightarrow{D} A_2^{M,+}$ , and so on. Using these duality relations and the representations in (2.49), we have  $G_{\text{Mor}} \xrightarrow{D} G_{\text{King}}$  and  $G_{\text{Exc}} \xrightarrow{D} G_{\text{Exc}}$ , where we use:

- Two operators acting on different sites commute with each other.
- For some duality function  $d$  and operators  $A, B, \hat{A}, \hat{B}$ , if  $A \xrightarrow{d} \hat{A}, B \xrightarrow{d} \hat{B}$ , then, for any constants  $c_1, c_2$ ,  $AB \xrightarrow{d} \hat{B}\hat{A}$  and  $c_1A + c_2B \xrightarrow{d} c_1\hat{A} + c_2\hat{B}$ .

Since  $G = G_{\text{Mor}} + G_{\text{Exc}}$  and  $\widehat{G} = G_{\text{King}} + G_{\text{Exc}}$ , we have  $G \xrightarrow{D} \widehat{G}$ , which proves the claim.  $\square$

## §2.5.2 Equilibrium

*Proof of Proposition 2.3.3.* For  $x \in \mathbb{R}$  and  $r \in \mathbb{N}$ , let  $(x)_r$  be the *falling factorial* defined as

$$(x)_r = x(x-1) \times \cdots \times (x-r+1), \quad (2.50)$$

where we put  $(x)_r = 1$  when  $r = 0$ . For any  $n \in \mathbb{N}_0$ , we can write  $x^n$  as

$$x^n = \sum_{j=0}^n c_{n,j}(x)_j, \quad (2.51)$$

where the constants  $c_{n,j}$  (known as the Stirling numbers of the second kind) are unique and depend only on  $n$  and  $j \in [n]$ . Let  $(n, m) \in \Omega = [N] \times [M]$  be such that  $(n, m) \neq (0, 0)$ , and let  $(n_t, m_t)_{t \geq 0}$  be the dual process in Definition 2.4.2. It follows from (2.51) and Theorem 2.3.2 that

$$\begin{aligned} & \lim_{t \rightarrow \infty} \mathbb{E}_{(X,Y)}[X(t)^n Y(t)^m] \\ &= \sum_{i=0}^n \sum_{j=0}^m c_{n,i} c_{m,j} \lim_{t \rightarrow \infty} \mathbb{E}_{(X,Y)}[(X(t))_i (Y(t))_j] \\ &= \sum_{i=0}^n \sum_{j=0}^m c_{n,i} c_{m,j} (N)_i (M)_j \lim_{t \rightarrow \infty} \mathbb{E}_{(X,Y)}[D((X(t), Y(t)); (i, j))] \\ &= \sum_{i=0}^n \sum_{j=0}^m c_{n,i} c_{m,j} (N)_i (M)_j \lim_{t \rightarrow \infty} \mathbb{E}^{(i,j)}[D((X, Y); (n_t, m_t))], \end{aligned} \quad (2.52)$$

where  $D: \Omega \times \Omega \rightarrow [0, 1]$  is the duality function in Theorem 2.3.2, defined by

$$D((X, Y); (n, m)) = \frac{\binom{X}{n} \binom{Y}{m}}{\binom{N}{n} \binom{M}{m}} \mathbb{1}_{\{n \leq X, m \leq Y\}} \equiv \frac{(X)_n (Y)_m}{(N)_n (M)_m}, \quad (2.53)$$

and the expectation in the last line of (2.52) is with respect to the dual process. Let  $T$  be the first time at which there is only one particle left in the dual, i.e.,  $T = \inf\{t > 0: n_t + m_t = 1\}$ . Note that, for any initial state  $(i, j) \in \Omega \setminus \{(0, 0)\}$ ,  $T < \infty$  with probability 1, and the distribution of  $(n_t, m_t)$  converges as  $t \rightarrow \infty$  to the invariant distribution  $\frac{N}{N+M} \delta_{(1,0)} + \frac{M}{N+M} \delta_{(0,1)}$ . So, for any  $(i, j) \in \Omega \setminus \{(0, 0)\}$ ,

$$\begin{aligned} & \lim_{t \rightarrow \infty} \mathbb{E}^{(i,j)}[D((X, Y); (n_t, m_t))] \\ &= \lim_{t \rightarrow \infty} \mathbb{E}^{(i,j)}[D((X, Y); (n_t, m_t)) \mid T \leq t] \mathbb{P}^{(i,j)}(T \leq t) \\ & \quad + \lim_{t \rightarrow \infty} \underbrace{\mathbb{E}^{(i,j)}[D((X, Y); (n_t, m_t)) \mid T > t]}_{\leq 1} \mathbb{P}^{(i,j)}(T > t) \\ &= \lim_{t \rightarrow \infty} \left[ \frac{X}{N} \mathbb{P}^{(i,j)}(n_t = 1, m_t = 0) + \frac{Y}{M} \mathbb{P}^{(i,j)}(n_t = 0, m_t = 1) \right] \\ &= \frac{X}{N} \frac{N}{N+M} + \frac{Y}{M} \frac{M}{N+M} = \frac{X+Y}{N+M}, \end{aligned} \quad (2.54)$$

where we use that the second term after the first equality converges to 0 because  $T < \infty$  with probability 1. Combining (2.54) with (2.52), we get

$$\begin{aligned}
 & \lim_{t \rightarrow \infty} \mathbb{E}_{(X,Y)}[X(t)^n Y(t)^m] \\
 &= \sum_{i=0}^n \sum_{j=0}^m c_{n,i} c_{m,j} (N)_i (M)_j \lim_{t \rightarrow \infty} \mathbb{E}^{(i,j)}[D((X,Y); (n_t, m_t))] \\
 &= \frac{X+Y}{N+M} \left( \sum_{i=0}^n c_{n,i} (N)_i \right) \left( \sum_{j=0}^m c_{m,j} (M)_j \right) + \left( 1 - \frac{X+Y}{N+M} \right) c_{n,0} c_{m,0} \\
 &= N^n M^m \frac{X+Y}{N+M},
 \end{aligned} \tag{2.55}$$

where the last equality follows from (2.51) and the fact that  $c_{n,0} c_{m,0} = 0$  when  $(n, m) \neq (0, 0)$ . □

*Proof of Corollary 2.3.4.* Note that the distribution of a two-dimensional random vector  $(Z_1, Z_2)$  taking values in  $[N] \times [M]$  is determined by the mixed moments  $\mathbb{E}[Z_1^i Z_2^j]$ ,  $i, j \in [N] \times [M]$ . For  $i \in I = [NM]$ , let  $p_i = \mathbb{P}((Z_1, Z_2) = f^{-1}(i))$ , where  $f: [N] \times [M] \rightarrow I$  is a bijection. For  $i \in I$ , let  $c_i = \mathbb{E}[Z_1^x Z_2^y]$ , where  $(x, y) = f^{-1}(i)$ . We can write  $\vec{c} = A\vec{p}$ , where  $\vec{p} = (p_i)_{i \in I}$ ,  $\vec{c} = (c_i)_{i \in I}$  and  $A$  is an invertible  $(N+1)(M+1) \times (N+1)(M+1)$  matrix. Hence,  $\vec{p} = A^{-1}\vec{c}$  is uniquely determined by the mixed moments, and convergence of the mixed moments of  $(X(t), Y(t))$  as shown in Proposition 2.3.3 is enough to conclude that  $(X(t), Y(t))$  converges in distribution as  $t \rightarrow \infty$  to a random vector  $(X_\infty, Y_\infty)$  taking values in  $[N] \times [M]$ . The distribution of  $(X_\infty, Y_\infty)$  is also uniquely determined, and is given by  $\frac{X+Y}{N+M} \delta_{(N,M)} + (1 - \frac{X+Y}{N+M}) \delta_{(0,0)}$ . □

## §2.6 Proofs: duality and well-posedness for the multi-colony model

In Section 2.6.1, we give the proof of Lemma 2.4.3 on the existence and uniqueness of the dual process. In Section 2.6.2, we introduce equivalent versions for the multi-colony setting of the operators defined in (2.40) for the single-colony setting, and use these to prove Theorem 2.4.5 and Corollary 2.4.6. In Section 2.6.3 we prove Proposition 2.4.1, Proposition 2.4.7 and Theorem 2.4.8.

### §2.6.1 Uniqueness of dual

*Proof of Lemma 2.4.3.* Note that the rate-matrix is nothing but the dual generator  $L_{\text{dual}}$  obtained from the rates specified in (2.29). The action of  $L_{\text{dual}}$  on a function

$f: \mathcal{X}_* \rightarrow \mathbb{R}$  is given by

$$\begin{aligned}
 (L_{\text{dual}}f)(\xi) &= \sum_{i \in \mathbb{Z}^d} \left[ \frac{n_i(n_i-1)}{2N_i} + n_i \sum_{\substack{j \in \mathbb{Z}^d, \\ j \neq i}} a(i, j) \frac{n_j}{N_j} \right] [f(\xi - \vec{\delta}_{i,A}) - f(\xi)] \\
 &+ \sum_{i \in \mathbb{Z}^d} \lambda n_i \frac{(M_i - m_i)}{M_i} [f(\xi - \vec{\delta}_{i,A} + \vec{\delta}_{i,D}) - f(\xi)] \\
 &+ \sum_{i \in \mathbb{Z}^d} \lambda (N_i - n_i) \frac{m_i}{M_i} [f(\xi + \vec{\delta}_{i,A} - \vec{\delta}_{i,D}) - f(\xi)] \\
 &+ \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} a(i, j) n_i \frac{N_j - n_j}{N_j} [f(\xi - \vec{\delta}_{i,A} + \vec{\delta}_{j,A}) - f(\xi)],
 \end{aligned} \tag{2.56}$$

where  $\xi = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$  and the configurations  $\vec{\delta}_{i,A}, \vec{\delta}_{i,D} \in \mathcal{X}_* \subset \mathcal{X}$  are as in (2.19). It is enough to show that  $L_{\text{dual}}$  satisfies the well-known Foster-Lyapunov criterion for stability (see for e.g. [122, Theorem 2.1] or [31, Theorem (1.11)] for Markov processes on countable state spaces), i.e.,

$$(L_{\text{dual}}V)(\xi) \leq pV(\xi) \quad \forall \xi \in \mathcal{X}_*, \tag{2.57}$$

for some  $p > 0$  with  $V: \mathcal{X}_* \rightarrow (0, \infty)$  a function such that there exist  $(E_k)_{k \in \mathbb{N}}$  with  $E_k \uparrow \mathcal{X}_*$  and  $\inf_{x \notin E_k} V(x) \rightarrow \infty$  as  $k \rightarrow \infty$ .

Let us define the function  $V: \mathcal{X}_* \rightarrow (0, \infty)$  as

$$V((n_i, m_i)_{i \in \mathbb{Z}^d}) := 1 + \sum_{i \in \mathbb{Z}^d} (n_i + m_i), \quad (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*, \tag{2.58}$$

and, for  $k \in \mathbb{N}$ , set

$$E_k := \left\{ (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_* : \sum_{i \in \mathbb{Z}^d} n_i + m_i \leq k \right\}. \tag{2.59}$$

Since  $\mathcal{X}_*$  contains configurations with finitely many particles,  $V$  is well-defined. It is straightforward to see that

$$E_k \uparrow \mathcal{X}_*, \quad \lim_{k \rightarrow \infty} \inf_{x \notin E_k} V(x) = \infty. \tag{2.60}$$

Let  $\xi = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$  be arbitrary. Note that, for any  $i, j \in \mathbb{Z}^d$  with  $i \neq j$ ,

$$\begin{aligned}
 [V(\xi - \vec{\delta}_{i,A}) - V(\xi)] &= -\mathbb{1}_{\{n_i \geq 1\}}, \\
 [V(\xi + \vec{\delta}_{i,A} - \vec{\delta}_{i,D}) - V(\xi)](N_i - n_i)m_i &= 0, \\
 [V(\xi - \vec{\delta}_{i,A} + \vec{\delta}_{i,D}) - V(\xi)]n_i(M_i - m_i) &= 0, \\
 [V(\xi - \vec{\delta}_{i,A} + \vec{\delta}_{j,A}) - V(\xi)]n_i(N_j - n_j) &= 0
 \end{aligned} \tag{2.61}$$

and so by using (2.56) we obtain

$$\begin{aligned}
 |(L_{\text{dual}}V)(\xi)| &\leq \sum_{i \in \mathbb{Z}^d} \left[ \frac{n_i(n_i-1)}{2N_i} + n_i \sum_{\substack{j \in \mathbb{Z}^d, \\ j \neq i}} a(i, j) \frac{n_j}{N_j} \right] |V(\xi - \vec{\delta}_{i,A}) - V(\xi)| \\
 &\leq \sum_{i \in \mathbb{Z}^d} \left[ \frac{n_i}{2} + n_i \sum_{j \in \mathbb{Z}^d} a(i, j) \right] \leq \max\{1, c\} \sum_{i \in \mathbb{Z}^d} n_i \leq \max\{1, c\} V(\xi),
 \end{aligned} \tag{2.62}$$

where  $c = \sum_{i \in \mathbb{Z}^d} a(0, i) < \infty$ . Hence, setting  $p := \max\{1, c\} > 0$ , we have that

$$(L_{\text{dual}}V)(\xi) \leq |(L_{\text{dual}}V)(\xi)| \leq p V(\xi), \tag{2.63}$$

which proves the claim.  $\square$

## §2.6.2 Duality relation

**Generators and intertwiners.** Let  $f \in C(\mathcal{X})$  and  $\eta = (X_i, Y_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$ , and let  $\vec{\delta}_{i,A}, \vec{\delta}_{i,D}$  be as in (2.19). Define the action of the multi-colony operators as in Table 2.3.

Operators acting on variable $X_i, i \in \mathbb{Z}^d$	Operators acting on variable $Y_i, i \in \mathbb{Z}^d$
$J_{i,A}^{N_i,+} f(\eta) = (N_i - X_i) f(\eta + \vec{\delta}_{i,A})$	$J_{i,D}^{M_i,+} f(\eta) = (M_i - Y_i) f(\eta + \vec{\delta}_{i,D})$
$J_{i,A}^{N_i,-} f(\eta) = X_i f(\eta - \vec{\delta}_{i,A})$	$J_{i,D}^{M_i,-} f(\eta) = Y_i f(\eta - \vec{\delta}_{i,D})$
$J_{i,A}^{N_i,0} f(\eta) = (X_i - \frac{N_i}{2}) f(\eta)$	$J_{i,D}^{M_i,0} f(\eta) = (Y_i - \frac{M_i}{2}) f(\eta)$
$A_{i,A}^{N_i,+} = J_{i,A}^{N_i,-} - J_{i,A}^{N_i,+} - 2J_{i,A}^{N_i,0}$	$A_{i,D}^{M_i,+} = J_{i,D}^{M_i,-} - J_{i,D}^{M_i,+} - 2J_{i,D}^{M_i,0}$
$A_{i,A}^{N_i,-} = J_{i,A}^{N_i,+}$	$A_{i,D}^{M_i,-} = J_{i,D}^{M_i,+}$
$A_{i,A}^{N_i,0} = J_{i,A}^{N_i,+} + J_{i,A}^{N_i,0}$	$A_{i,D}^{M_i,0} = J_{i,D}^{M_i,+} + J_{i,D}^{M_i,0}$

Table 2.3: Action of operators on  $f \in C(\mathcal{X})$ .

The same duality relations as in Lemma 2.5.2 hold for these operators as well. The only difference is that the duality function becomes the site-wise product of the duality functions appearing in the single-colony model.

**Lemma 2.6.1 (Multi-colony intertwiner).** Let  $D: \mathcal{X} \times \mathcal{X}_* \rightarrow [0, 1]$  be the function defined by

$$D((X_k, Y_k)_{k \in \mathbb{Z}^d}; (n_k, m_k)_{k \in \mathbb{Z}^d}) = \prod_{i \in \mathbb{Z}^d} \frac{\binom{X_i}{n_i}}{\binom{N_i}{n_i}} \frac{\binom{Y_i}{m_i}}{\binom{M_i}{m_i}} \mathbb{1}_{\{n_i \leq X_i, m_i \leq Y_i\}}, \tag{2.64}$$

where  $(X_k, Y_k)_{k \in \mathbb{Z}^d} \in \mathcal{X}$  and  $(n_k, m_k)_{k \in \mathbb{Z}^d} \in \mathcal{X}_*$ . Then, for every  $i \in \mathbb{Z}^d$  and  $s \in \{0, +, -\}$ ,

$$J_{i,A}^{N_i,s} \xrightarrow{D} A_{i,A}^{N_i,s}, \quad J_{i,D}^{M_i,s} \xrightarrow{D} A_{i,D}^{M_i,s}. \tag{2.65}$$



*Proof.* The proof is exactly the same as the proof of Lemma 2.5.2.  $\square$

**Proposition 2.6.2 (Generator criterion).** *Let  $L$  be the generator defined in (2.22), and  $\hat{L}$  the generator of the dual process defined in Definition 2.4.2. Furthermore, let  $D: \mathcal{X} \times \mathcal{X}_* \rightarrow [0, 1]$  be the function defined in Lemma 2.6.1. Then  $L \xrightarrow{D} \hat{L}$ .*

*Proof.* Recall that  $L = L_{\text{Mig}} + L_{\text{Res}} + L_{\text{Exc}}$ , where  $L_{\text{Mig}}, L_{\text{Res}}, L_{\text{Exc}}$  are defined in (2.23)–(2.25). In terms of the operators defined earlier, these have the following representations:

$$\begin{aligned} L_{\text{Mig}} &= \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} \frac{a(i,j)}{N_j} \left[ \left( J_{i,A}^{N_i,+} - J_{i,A}^{N_i,-} + 2J_{i,A}^{N_i,0} \right) J_{j,A}^{N_j,0} + \frac{N_j}{2} \left( J_{i,A}^{N_i,+} + J_{i,A}^{N_i,-} - N_i \right) \right], \\ L_{\text{Res}} &= \sum_{i \in \mathbb{Z}^d} \frac{1}{2N_i} \left[ J_{i,A}^{N_i,0} \left( J_{i,A}^{N_i,+} - J_{i,A}^{N_i,-} + 2J_{i,A}^{N_i,0} \right) + \frac{N_i}{2} \left( J_{i,A}^{N_i,+} + J_{i,A}^{N_i,-} - N_i \right) \right], \\ L_{\text{Exc}} &= \sum_{i \in \mathbb{Z}^d} \frac{\lambda}{M_i} \left[ J_{i,A}^{N_i,+} J_{i,D}^{M_i,-} + J_{i,A}^{N_i,-} J_{i,D}^{M_i,+} + 2J_{i,A}^{N_i,0} J_{i,D}^{M_i,0} - \frac{N_i M_i}{2} \right] \\ &= \sum_{i \in \mathbb{Z}^d} \frac{\lambda}{M_i} \left[ A_{i,A}^{N_i,+} A_{i,D}^{M_i,-} + A_{i,A}^{N_i,-} A_{i,D}^{M_i,+} + 2A_{i,A}^{N_i,0} A_{i,D}^{M_i,0} - \frac{N_i M_i}{2} \right]. \end{aligned} \tag{2.66}$$

Similarly, the generator  $\hat{L}$  of the dual process defined in Definition 2.4.2 acting on  $f \in C(\mathcal{X}_*)$  is given by  $\hat{L} = \hat{L}_{\text{Mig}} + L_{\text{Exc}} + L_{\text{King}}$ , where

$$\begin{aligned} \hat{L}_{\text{Mig}} f(\xi) &= \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} \frac{a(i,j)}{N_j} \left\{ n_i (N_j - n_j) [f(\xi - \vec{\delta}_{i,A} + \vec{\delta}_{j,A}) - f(\xi)] \right. \\ &\quad \left. + n_i n_j [f(\xi - \vec{\delta}_{i,A}) - f(\xi)] \right\}, \end{aligned} \tag{2.67}$$

$$L_{\text{King}} f(\xi) = \sum_{i \in \mathbb{Z}^d} \frac{n_i(n_i-1)}{2N_i} [f(\xi - \vec{\delta}_{i,A}) + f(\xi + \vec{\delta}_{i,A}) - 2f(\xi)],$$

for  $\xi = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$ . The representations of these operators are

$$\begin{aligned} \hat{L}_{\text{Mig}} &= \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} \frac{a(i,j)}{N_j} \left[ A_{j,A}^{N_j,0} \left( A_{i,A}^{N_i,+} - A_{i,A}^{N_i,-} + 2A_{i,A}^{N_i,0} \right) \right. \\ &\quad \left. + \frac{N_j}{2} \left( A_{i,A}^{N_i,+} + A_{i,A}^{N_i,-} - N_i \right) \right], \\ L_{\text{King}} &= \sum_{i \in \mathbb{Z}^d} \frac{1}{2N_i} \left[ \left( A_{i,A}^{N_i,+} - A_{i,A}^{N_i,-} + 2A_{i,A}^{N_i,0} \right) A_{i,A}^{N_i,0} + \frac{N_i}{2} \left( A_{i,A}^{N_i,+} + A_{i,A}^{N_i,-} - N_i \right) \right]. \end{aligned} \tag{2.68}$$

From Lemma 2.6.1 and the representations in (2.66)–(2.68), we see that  $L_{\text{Mig}} \xrightarrow{D} \hat{L}_{\text{Mig}}$ ,  $L_{\text{Res}} \xrightarrow{D} L_{\text{King}}$  and  $L_{\text{Exc}} \xrightarrow{D} L_{\text{Exc}}$ , which yields  $L \xrightarrow{D} \hat{L}$ .  $\square$

As shown in [91, Proposition 1.2], the generator criterion is enough to get the required duality relation of Theorem 2.4.5 when both  $L$  and  $\hat{L}$  are Markov generators

of Feller processes. Since it is not a priori clear whether  $L$  (or its extension) is a Markov generator, we need to use [58, Theorem 4.11, Corollary 4.13].

**Proof of duality relation.**

*Proof of Theorem 2.4.5.* We combine [58, Theorem 4.11 and Corollary 4.13] and reinterpret these in our context:

- Let  $(\eta_t)_{t \geq 0}$  and  $(\xi_t)_{t \geq 0}$  be two independent processes on  $E_1$  and  $E_2$  that are solutions to the martingale problem for  $(L_1, \mathcal{D}_1)$  and  $(L_2, \mathcal{D}_2)$  with initial states  $x \in E_1$  and  $y \in E_2$ . Assume that  $D: E_1 \times E_2 \rightarrow \mathbb{R}$  is such that  $D(\cdot; \xi) \in \mathcal{D}_1$  for any  $\xi \in E_2$  and  $D(\eta; \cdot) \in \mathcal{D}_2$  for any  $\eta \in E_1$ . Also assume that for each  $T > 0$  there exists an integrable random variable  $U_T$  such that

$$\begin{aligned} \sup_{0 \leq s, t \leq T} |D(\eta_t; \xi_s)| &\leq U_T, & \sup_{0 \leq s, t \leq T} |(L_1 D(\cdot; \xi_s))(\eta_t)| &\leq U_T, \\ \sup_{0 \leq s, t \leq T} |(L_2 D(\eta_t; \cdot))(\xi_s)| &\leq U_T. \end{aligned} \tag{2.69}$$

If  $(L_1 D(\cdot; y))(x) = (L_2 D(x; \cdot))(y)$ , then  $\mathbb{E}_x[D(\eta_t; y)] = \mathbb{E}^y[D(x, \xi_t)]$  for all  $t \geq 0$ .

To apply the above, pick  $E_1 = \mathcal{X}$ ,  $E_2 = \mathcal{X}_*$ ,  $L_1 = L$ ,  $L_2 = L_{\text{dual}}$ ,  $\mathcal{D}_1 = \mathcal{D}$ ,  $\mathcal{D}_2 = C(\mathcal{X}_*)$ , where  $L_{\text{dual}}$  is the generator of the dual process  $Z_*$  and set  $D$  to be the function defined in Lemma 2.6.1. Note that, since  $\mathcal{D}$  contains local functions only,  $D(\cdot; \xi) \in \mathcal{D}$  for any  $\xi \in \mathcal{X}_*$  and, since  $\mathcal{X}_*$  is countable,  $D(\eta; \cdot) \in C(\mathcal{X}_*)$  for any  $\eta \in \mathcal{X}$ . Fix  $x = (X_i, Y_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$  and  $y = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$ . Note that, by Proposition 2.6.2,  $(L_1 D(\cdot; y))(x) = (L_2 D(x; \cdot))(y)$ . Pick  $(\xi_t)_{t \geq 0}$  to be the process  $Z_*$  with initial state  $y$ . Note that  $(\xi_t)_{t \geq 0}$  is the unique solution to the martingale problem for  $(L_{\text{dual}}, C(\mathcal{X}_*))$  with initial state  $y$ . Let  $(\eta_t)_{t \geq 0}$  denote any solution  $Z$  to the martingale problem for  $(L, \mathcal{D})$  with initial state  $x$ . Fix  $T > 0$  and note that, for  $0 \leq s, t < T$ ,

$$\begin{aligned} (L_1 D(\cdot; \xi_s))(\eta_t) &= \sum_{i \in \mathbb{Z}^d} X_i(t) \left[ \sum_{j \in \mathbb{Z}^d} a(i, j) \frac{N_j - X_j(t)}{N_j} \right] [D(\eta_t - \vec{\delta}_{i,A}; \xi_s) - D(\eta_t; \xi_s)] \\ &\quad + \sum_{i \in \mathbb{Z}^d} (N_i - X_i(t)) \left[ \sum_{j \in \mathbb{Z}^d} a(i, j) \frac{X_j(t)}{N_j} \right] [D(\eta_t + \vec{\delta}_{i,A}; \xi_s) - D(\eta_t; \xi_s)] \\ &\quad + \sum_{i \in \mathbb{Z}^d} \lambda X_i(t) \frac{M_i - Y_i(t)}{M_i} [D(\eta_t - \vec{\delta}_{i,A} + \vec{\delta}_{i,D}; \xi_s) - D(\eta_t; \xi_s)] \\ &\quad + \sum_{i \in \mathbb{Z}^d} \lambda (N_i - X_i(t)) \frac{Y_i(t)}{M_i} [D(\eta_t + \vec{\delta}_{i,A} - \vec{\delta}_{i,D}; \xi_s) - D(\eta_t; \xi_s)] \end{aligned} \tag{2.70}$$

and

$$\begin{aligned}
 (L_2 D(\eta_t; \cdot))(\xi_s) &= \sum_{i \in \mathbb{Z}^d} n_i(s) \left[ \frac{n_i(s)-1}{2N_i} + \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} \frac{a(i,j)n_j(s)}{N_j} \right] [D(\eta_t; \xi_s - \vec{\delta}_{i,A}) - D(\eta_t; \xi_s)] \\
 &+ \sum_{i \in \mathbb{Z}^d} \lambda n_i(s) \frac{M_i - m_i(s)}{M_i} [D(\eta_t; \xi_s - \vec{\delta}_{i,A} + \vec{\delta}_{i,D}) - D(\eta_t; \xi_s)] \\
 &+ \sum_{i \in \mathbb{Z}^d} \lambda (N_i - n_i(s)) \frac{m_i(s)}{M_i} [D(\eta_t; \xi_s + \vec{\delta}_{i,A} - \vec{\delta}_{i,D}) - D(\eta_t; \xi_s)] \\
 &+ \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} a(i,j) n_i(s) \frac{N_j - n_j(s)}{N_j} [D(\eta_t; \xi_s - \vec{\delta}_{i,A} + \vec{\delta}_{j,A}) - D(\eta_t; \xi_s)].
 \end{aligned} \tag{2.71}$$

The random variable  $\Gamma(t)$  defined in Theorem 2.4.5 is stochastically increasing in time  $t$ , and if we change the configuration  $\eta_t$  outside the box  $[0, \Gamma(s)]^d \cap \mathbb{Z}^d$ , then the value of  $D(\eta_t; \xi_s)$  does not change. Consequently, all the summands in (2.70) for  $\|i\| > \Gamma(s)$ ,  $i \in \mathbb{Z}^d$ , are 0, and since  $\Gamma(s) \leq \Gamma(T)$  we have the estimate

$$|(L_1 D(\cdot; \xi_s))(\eta_t)| \leq 2(c + \lambda) \sum_{\substack{i \in \mathbb{Z}^d \\ \|i\| \leq \Gamma(s)}} N_i \leq 2(c + \lambda) \sum_{\substack{i \in \mathbb{Z}^d \\ \|i\| \leq \Gamma(T)}} N_i, \tag{2.72}$$

where  $c = \sum_{i \in \mathbb{Z}^d} a(0, i)$ . Now, by Definition 2.4.2, the process  $(\xi_t)_{t \geq 0}$  is the interacting particle system with coalescence in which the total number of particles can only decrease in time, and so  $\sum_{i \in \mathbb{Z}^d} (n_i(s) + m_i(s)) \leq N$ , where  $N = \sum_{i \in \mathbb{Z}^d} (n_i + m_i)$ . Also, since  $s \leq T$ , for  $i \in \mathbb{Z}^d$  with  $\|i\| > \Gamma(T)$  we have  $n_i(s) = m_i(s) = 0$ . Hence, from (2.71) we get

$$|(L_2 D(\eta_t; \cdot))(\xi_s)| \leq 2(c + \lambda)N + 2\lambda \sum_{\substack{i \in \mathbb{Z}^d \\ \|i\| \leq \Gamma(T)}} N_i. \tag{2.73}$$

Define the random variable  $U_T$  by

$$U_T = 1 + 2(c + \lambda)N + 2(c + \lambda) \sum_{\substack{i \in \mathbb{Z}^d \\ \|i\| \leq \Gamma(T)}} N_i. \tag{2.74}$$

Then, combining (2.72)–(2.73) with the fact that the function  $D$  takes values in  $[0, 1]$ , we see that  $U_T$  satisfies all the conditions stated in (2.69), while the assumption in (2.31) of Theorem 2.4.5 ensures the integrability of  $U_T$ .  $\square$

### Proof of duality criterion.

*Proof of Corollary 2.4.6.* Let  $\xi = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$  and  $T > 0$  be fixed. By Theorem 2.4.5, it suffices to show that, for any  $(N_i)_{i \in \mathbb{Z}^d} \in \mathcal{N}$ ,

$$\sum_{i \in \mathbb{Z}^d} N_i \mathbb{P}^\xi(\Gamma(T) \geq \|i\|) < \infty, \tag{2.75}$$

where  $\mathbb{P}^\xi$  is the law of the dual process  $Z_*$  started from initial state  $\xi$ . Let  $n = \sum_{i \in \mathbb{Z}^d} (n_i + m_i)$  be the initial number of particles, and let  $N(t)$  be the total number of migration events within the time interval  $[0, t]$ . We will construct a Poisson process  $N^*$  via coupling such that  $N(t) \leq N^*(t)$  for all  $t \geq 0$  with probability 1. For this purpose, let us consider  $n$  independent particles performing a random walk on  $\mathbb{Z}^d$  according to the migration kernel  $a(\cdot, \cdot)$ . For each  $k = 1, \dots, n$ , let  $\xi_k(t)$  and  $\xi_k^*(t)$  denote the position of the  $k$ -th dependent and independent particle at time  $t$ , respectively. We take  $\xi_k(0) = \xi_k^*(0)$  and couple each  $k$ -th interacting particle with the  $k$ -th independent particle as below:

- If the independent particle makes a jump from site  $\xi_k^*(t)$  to  $j^* \in \mathbb{Z}^d$ , then the dependent particle jumps from  $\xi_k(t)$  to  $j = \xi_k(t) + (j^* - \xi_k^*(t))$  with probability  $p_k(t)$  given by

$$p_k(t) = \begin{cases} 1 - \frac{n_j(t)}{N_j} & \text{if the dependent particle is in an} \\ & \text{active and non-coalesced state,} \\ 0 & \text{otherwise,} \end{cases} \quad (2.76)$$

where  $n_j(t)$  is the number of active particles at site  $j$ .

- The dependent particle does the other transitions (waking up, becoming dormant and coalescence) independently of the previous migration events, with the prescribed rates defined in Definition 2.4.2.

Note that, since the migration kernel is translation invariant, under the above coupling the effective rate at which a dependent particle migrates from site  $i$  to  $j$  is  $n_i a(i, j) (1 - \frac{n_j}{N_j})$  when there are  $n_i$  and  $n_j$  active particles at site  $i$  and  $j$ , respectively. Also, if  $N_k(t)$  and  $N_k^*(t)$  are the number of migration steps made within the time interval  $[0, t]$  by the  $k$ -th dependent and independent particle, respectively, then under this coupling  $N_k(t) \leq N_k^*(t)$  with probability 1. Set  $N^*(\cdot) = \sum_{k=1}^n N_k^*(\cdot)$ . Then, clearly,

$$N(\cdot) \leq \sum_{k=1}^n N_k(\cdot) \leq N^*(\cdot) \text{ with probability 1.} \quad (2.77)$$

Also,  $N^*$  is a Poisson process with intensity  $cn$ , since each independent particle migrates at a total rate  $c$ .

Let  $Y_l, X_l \in \mathbb{Z}^d$  denote the step at the  $l$ -th migration event in the dependent and independent particle systems, respectively. Note that  $(X_l)_{l \in \mathbb{N}}$  are i.i.d. with distribution  $(a(0, i))_{i \in \mathbb{Z}^d}$ . Since, under the above coupling, a dependent particle copies the step of an independent particle with a certain probability (possibly 0), and  $\Gamma(0)$  is the minimum length of the box within which all  $n$  dependent particles at time 0 are located, we have, for any  $t \geq 0$ ,

$$\Gamma(t) \leq \Gamma(0) + \sum_{l=1}^{N(t)} |Y_l| \leq \Gamma(0) + \sum_{l=1}^{N^*(t)} |X_l|. \quad (2.78)$$

Therefore

$$\mathbb{P}^\xi(\Gamma(T) \geq k) \leq \mathbb{P}(S_{N^*(T)} \geq k - \Gamma(0)) \quad \forall k \geq 0, \quad (2.79)$$

where  $S_{N^*(T)} = \sum_{l=1}^{N^*(T)} |X_l|$ .

To prove part (a), note that  $\mathbb{E}[e^{\delta S_{N^*(T)}}] < \infty$  and so, by Chebyshev's inequality,

$$\mathbb{P}(S_{N^*(T)} \geq x) = \mathbb{P}(e^{\delta S_{N^*(T)}} \geq e^{\delta x}) \leq \mathbb{E}[e^{\delta S_{N^*(T)}}] e^{-\delta x}. \quad (2.80)$$

Thus, the inequality in (2.79) reduces to

$$\mathbb{P}^\xi(\Gamma(T) \geq k) \leq V e^{-\delta k} \quad \forall k \geq 0, \quad (2.81)$$

where

$$V = \mathbb{E}[\exp\{\delta\Gamma(0) + \delta S_{N^*(T)}\}] < \infty. \quad (2.82)$$

For  $k \in \mathbb{N}$ , let  $\alpha_k = \#\{i \in \mathbb{Z}^d: \|i\|_\infty = k\}$ . Then,

$$\alpha_k = (2k+1)^d - (2k-1)^d \leq 4^d k^{d-1}. \quad (2.83)$$

Hence

$$\begin{aligned} \sum_{i \in \mathbb{Z}^d \setminus \{0\}} N_i \mathbb{P}^\xi(\Gamma(T) \geq \|i\|) &\leq \sum_{k \in \mathbb{N}} c_k \alpha_k \mathbb{P}^\xi(\Gamma(T) \geq k) \\ &\leq \sum_{k \in \mathbb{N}} c_k 4^d k^{d-1} \mathbb{P}^\xi(\Gamma(T) \geq k), \end{aligned} \quad (2.84)$$

where  $c_k = \sup\{N_i: \|i\|_\infty = k, i \in \mathbb{Z}^d\}$ . Since, under the assumption of part (a),  $\lim_{k \rightarrow \infty} \frac{1}{k} \log c_k = 0$ , there exists a  $K \in \mathbb{N}$  such that  $c_k \leq e^{\delta k/2}$  for all  $k \geq K$ . Hence, using (2.81), we find that

$$\sum_{i \in \mathbb{Z}^d} N_i \mathbb{P}^\xi(\Gamma(T) \geq \|i\|) \leq N_0 + \sum_{k=1}^{K-1} c_k \alpha_k + 4^d V \sum_{k=K}^{\infty} k^{d-1} e^{-\delta k/2} < \infty, \quad (2.85)$$

which settles part (a).

To prove part (b), note that, under the assumption  $\sum_{i \in \mathbb{Z}^d} \|i\|^\gamma a(0, i) < \infty$  for some  $\gamma > d + \delta$ , we have  $\mathbb{E}[S_{N^*(T)}^\gamma] < \infty$ , and since  $S_{N^*(T)}$  is a positive random variable, we get

$$\mathbb{P}(S_{N^*(T)} \geq x) \leq \mathbb{E}[S_{N^*(T)}^\gamma] x^{-\gamma}. \quad (2.86)$$

From (2.79) we get

$$\mathbb{P}^\xi(\Gamma(T) \geq k) \leq \frac{V}{(k - \Gamma(0))^\gamma} \quad \forall k > \Gamma(0), \quad (2.87)$$

where  $V = \mathbb{E}[S_{N^*(T)}^\gamma]$ . By the assumption of part (b), there exists a  $C > 0$  such that

$$c_k = \sup\{N_i: \|i\|_\infty = k, i \in \mathbb{Z}^d\} \leq C k^\delta \quad (2.88)$$

and so using (2.84), we obtain

$$\sum_{i \in \mathbb{Z}^d} N_i \mathbb{P}^\xi(\Gamma(T) \geq \|i\|) \leq N_0 + \sum_{k \leq \Gamma(0)} c_k \alpha_k + 4^d C V \sum_{k > \Gamma(0)} \frac{k^{d+\delta-1}}{(k - \Gamma(0))^\gamma} < \infty, \quad (2.89)$$

which settles part (b). □

### §2.6.3 Well-posedness

In this section we prove Proposition 2.4.1, Proposition 2.4.7 and Theorem 2.4.8.

**Existence.** Since the state space  $\mathcal{X}$  is compact, the theory described in [112, Chapter I, Section 3] is applicable in our setting without any significant changes. The interacting particle systems in [112] have state space  $W^S$ , where  $W$  is a compact phase space and  $S$  is a countable site space. In our setting, the site space is  $S = \mathbb{Z}^d$ , but the phase space differs at each site, i.e.,  $[N_i] \times [M_i]$  at site  $i \in \mathbb{Z}^d$ . The general form of the generator of an interacting particle system in [112] is

$$(\Omega f)(\eta) = \sum_T \int_{W_T} c_T(\eta, d\xi) [f(\eta^\xi) - f(\eta)], \quad \eta \in \mathcal{X}, \quad (2.90)$$

where the sum is taken over all finite subsets  $T$  of  $S$ , and  $\eta^\xi$  is the configuration

$$\eta_i^\xi = \begin{cases} \xi_i & \text{if } i \in T, \\ \eta_i & \text{else.} \end{cases} \quad (2.91)$$

For finite  $T \subseteq \mathcal{X}$ ,  $c_T(\eta, d\xi)$  is a finite positive measure on  $W_T = W^T$ . To make the latter compatible with our setting, we define  $W_T = \prod_{i \in T} [N_i] \times [M_i]$ . The interpretation is that  $\eta$  is the current configuration of the system,  $c_T(\eta, W_T)$  is the total rate at which a transition occurs involving *all* the coordinates in  $T$ , and  $c_T(\eta, d\xi)/c_T(\eta, W_T)$  is the distribution of the restriction to  $T$  of the new configuration after that transition has taken place. Fix  $\eta = (X_i, Y_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$ . Comparing (2.90) with the formal generator  $L$  defined in (2.22), we see that the form of  $c_T(\cdot, \cdot)$  is as follows:

- (a)  $c_T(\eta, d\xi) = 0$  if  $|T| \geq 2$ .
- (b) For  $|T| = 1$ , let  $T = \{i\}$  for some  $i \in \mathbb{Z}^d$ . Then  $c_T(\eta, \cdot)$  is the measure on  $[N_i] \times [M_i]$  given by

$$\begin{aligned} c_T(\eta, \cdot) &= X_i \left[ \sum_{j \in \mathbb{Z}^d} a(i, j) \frac{N_j - X_j}{N_j} \right] \delta_{(X_{i-1}, Y_i)}(\cdot) \\ &\quad + (N_i - X_i) \left[ \sum_{j \in \mathbb{Z}^d} a(i, j) \frac{X_j}{N_j} \right] \delta_{(X_{i+1}, Y_i)}(\cdot) \\ &\quad + \lambda X_i \frac{M_i - Y_i}{M_i} \delta_{(X_{i-1}, Y_{i+1})}(\cdot) + \lambda (N_i - X_i) \frac{Y_i}{M_i} \delta_{(X_{i+1}, Y_{i-1})}(\cdot). \end{aligned} \quad (2.92)$$

Note that the total mass is

$$\begin{aligned} c_T(\eta, W_T) &= X_i \left[ \sum_{j \in \mathbb{Z}^d} a(i, j) \frac{N_j - X_j}{N_j} \right] + (N_i - X_i) \left[ \sum_{j \in \mathbb{Z}^d} a(i, j) \frac{X_j}{N_j} \right] \\ &\quad + \lambda X_i \frac{M_i - Y_i}{M_i} + \lambda (N_i - X_i) \frac{Y_i}{M_i}. \end{aligned} \quad (2.93)$$

**Lemma 2.6.3 (Bound on rates).** *Let  $c = \sum_{i \in \mathbb{Z}^d} a(0, i) < \infty$ . For a finite set  $T \subseteq \mathbb{Z}^d$ , let  $c_T = \sup_{\eta \in \mathcal{X}} c_T(\eta, W_T)$ . Then  $c_T \leq (c + \lambda) \mathbb{1}_{\{|T|=1\}} \sup_{i \in T} N_i$  with  $c = \sum_{i \in \mathbb{Z}^d} a(0, i)$ .*

*Proof.* Clearly,  $c_T = 0$  if  $|T| \geq 2$ . So let  $T = \{i\}$  for some  $i \in \mathbb{Z}^d$ . We see that, for  $\eta = (X_k, Y_k)_{k \in \mathbb{Z}^d}$ ,  $c_T(\eta, W_T) \leq cX_i + c(N_i - X_i) + \lambda X_i + \lambda(N_i - X_i) = (c + \lambda)N_i = (c + \lambda) \sup_{i \in T} N_i$ . □

*Proof of Proposition 2.4.1.* By [112, Proposition 6.1 of Chapter I], it suffices to show that

$$\sum_{T \ni i} c_T < \infty \quad \forall i \in S, \quad (2.94)$$

where the sum is taken over all finite subsets  $T \subseteq S$  containing  $i \in S$ . Since in our case  $S = \mathbb{Z}^d$ , we let  $i \in \mathbb{Z}^d$  be fixed. By Lemma 2.6.3, the sum reduces to  $c_{\{i\}}$ , and clearly  $c_{\{i\}} \leq (c + \lambda)N_i < \infty$ . □

*Proof of Proposition 2.4.7.* By [112, Proposition 6.1 and Theorem 6.7 of Chapter I], to show existence of solutions to the martingale problem for  $(L, \mathcal{D})$ , it is enough to prove that (2.94) is satisfied. But we already showed this in the proof of Proposition 2.4.1. □

**Uniqueness.** Before we turn to the proof of Theorem 2.4.8, we state and prove the following proposition, which, along with the duality established in Corollary 2.4.6, will play a key role in the proof of the uniqueness of solutions to the martingale problem.

**Proposition 2.6.4 (Separation).** *Let  $D: \mathcal{X} \times \mathcal{X}_* \rightarrow [0, 1]$  be the duality function defined in Lemma 2.6.1. Define the set of functions  $\mathcal{M} = \{D(\cdot; \xi) : \xi \in \mathcal{X}_*\}$ . Then  $\mathcal{M}$  is separating on the set of probability measures on  $\mathcal{X}$ .*

*Proof.* Let  $\mathbb{P}$  be a probability measure on  $\mathcal{X} = \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i]$ . It suffices to show that the finite-dimensional distributions of  $\mathbb{P}$  are determined by  $\{\int_{\mathcal{X}} f d\mathbb{P} : f \in \mathcal{M}\}$ . Note that it is enough to show the following:

- Let  $X = (X_1, X_2, \dots, X_n) \in \prod_{i=1}^n [N_i]$  be an  $n$ -dimensional random vector with some distribution  $\mathbb{P}_X$  on  $\prod_{i=1}^n [N_i]$ . Then  $\mathbb{P}_X$  is determined by the family

$$\mathcal{F} = \left\{ \mathbb{E} \left[ \prod_{i=1}^n \frac{\binom{X_i}{\alpha_i}}{\binom{N_i}{\alpha_i}} \right] : (\alpha_i)_{1 \leq i \leq n} \in \prod_{i=1}^n [N_i] \right\}. \quad (2.95)$$

By (2.51), the family  $\mathcal{F}$  is equivalent to the family

$$\mathcal{F}^* = \left\{ \mathbb{E} \left[ \prod_{i=1}^n X_i^{\alpha_i} \right] : (\alpha_i)_{1 \leq i \leq n} \in \prod_{i=1}^n [N_i] \right\} \quad (2.96)$$

containing the mixed moments of  $(X_1, \dots, X_n)$ . Since  $X$  takes a total of  $N = \prod_{i=1}^n (N_i + 1)$  many values, we can write the distribution  $\mathbb{P}_X$  as the  $N$ -dimensional

vector  $\vec{p} = (p_1, \dots, p_N)$ , where  $p_i = \mathbb{P}_X(X = f^{-1}(i))$  and  $f: \prod_{i=1}^n [N_i] \rightarrow \{1, \dots, N\}$  is the bijection defined by

$$f(x_1, x_2, \dots, x_n) = \sum_{i=1}^{n-1} \left( \prod_{j=i+1}^n (N_j + 1) \right) x_i + x_n + 1, \quad (x_1, \dots, x_n) \in \prod_{i=1}^n [N_i]. \quad (2.97)$$

Note that  $\mathcal{F}^*$  also contains  $N$  elements, and so we can write  $\mathcal{F}^*$  as the  $N$ -dimensional vector  $\vec{e} = (e_1, \dots, e_N)$ , where  $e_i = \mathbb{E}[\prod_{k=1}^n X_k^{\alpha_k}]$ ,  $(\alpha_1, \dots, \alpha_n) = f^{-1}(i)$ . We show that there exists an invertible linear operator that maps  $\vec{p}$  to  $\vec{e}$ . Indeed, for  $i = 1, \dots, n$ , define the  $(N_i + 1) \times (N_i + 1)$  Vandermonde matrix  $A_i$ ,

$$A_i = \begin{bmatrix} 1 & 1 & 1 & \dots & 1 \\ \alpha_1 & \alpha_2 & \alpha_3 & \dots & \alpha_{N_i+1} \\ \alpha_1^2 & \alpha_2^2 & \alpha_3^2 & \dots & \alpha_{N_i+1}^2 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_1^{N_i} & \alpha_2^{N_i} & \alpha_3^{N_i} & \dots & \alpha_{N_i+1}^{N_i} \end{bmatrix}, \quad (\alpha_1, \alpha_2, \dots, \alpha_{N_i+1}) = (0, 1, \dots, N_i). \quad (2.98)$$

Being Vandermonde matrices, all  $A_i$  are invertible. Finally, define the  $N \times N$  matrix  $A$  by  $A = A_1 \otimes A_2 \otimes \dots \otimes A_n$ , where  $\otimes$  denotes the Kronecker product for matrices. Then  $A$  is invertible because all  $A_i$  are. Also, we can check that  $A\vec{p} = \vec{e}$ , and hence the distribution of  $X$  given by  $\vec{p} = A^{-1}\vec{e}$  is uniquely determined by  $\vec{e}$ , i.e., the family  $\mathcal{F}^*$ . □

*Proof of Theorem 2.4.8.* We use [58, Proposition 4.7], which states the following (re-interpreted in our setting):

- Let  $\mathcal{S}_1$  be compact and  $\mathcal{S}_2$  be separable. Let  $x \in \mathcal{S}_1, y \in \mathcal{S}_2$  be arbitrary and  $D: \mathcal{S}_1 \times \mathcal{S}_2 \rightarrow \mathbb{R}$  be such that the set  $\{D(\cdot; z): z \in \mathcal{S}_2\}$  is separating on the set of probability measures on  $\mathcal{S}_1$ . Assume that, for any two solutions  $(\eta_t)_{t \geq 0}$  and  $(\xi_t)_{t \geq 0}$  of the martingale problem for  $(L_1, \mathcal{D}_1)$  and  $(L_2, \mathcal{D}_2)$  with initial states  $x$  and  $y$ , the duality relation holds:  $\mathbb{E}_x[D(\eta_t, y)] = \mathbb{E}^y[D(x, \xi_t)]$  for all  $t \geq 0$ . If for every  $z \in \mathcal{S}_2$  there exists a solution to the martingale problem for  $(L_2, \mathcal{D}_2)$  with initial state  $z$ , then for every  $\eta \in \mathcal{S}_1$  uniqueness holds for the martingale problem for  $(L_1, \mathcal{D}_1)$  with initial state  $\eta$ .

Pick  $\mathcal{S}_1 = \mathcal{X}$ ,  $\mathcal{S}_2 = \mathcal{X}_*$ ,  $(L_1, \mathcal{D}_1) = (L, \mathcal{D})$  and  $(L_2, \mathcal{D}_2) = (L_{\text{dual}}, C(\mathcal{X}_*))$ , where  $L_{\text{dual}}$  is the generator of the dual process  $Z_*$ . Note that in our setting the martingale problem for  $(L_{\text{dual}}, C(\mathcal{X}_*))$  is already well-posed (the unique solution is the dual process  $Z_*$  in Lemma 2.4.3). Hence, combining the above observations with Proposition 2.6.4 and Corollary 2.4.6, we get uniqueness of the solutions to the martingale problem for  $(L, \mathcal{D})$  for every initial state  $\eta \in \mathcal{X}$ .

The second claim follows from [112, Theorem 6.8 of Chapter I]. □



## §2.7 Proofs: equilibrium and clustering criterion for the multi-colony model

In Section 2.7.1 we prove Theorem 2.4.9 and Corollary 2.4.10. In Section 2.7.2 we derive expressions for the single-site genetic variability in terms of the dual process. In Section 2.7.3 we use one dual particle to write down expressions for first moments. In Section 2.7.4 we use two dual particles to write down expressions for second moments. In Section 2.7.5 we use these expressions to prove Theorem 2.4.12.

### §2.7.1 Convergence to equilibrium

*Proof of Theorem 2.4.9.* Since the state space  $\mathcal{X}$  is compact and thus the set of all probability measures on  $\mathcal{X}$  is compact as well, by Prokhorov's theorem. It therefore suffices to prove convergence of the finite-dimensional distributions of  $Z(t) = (X_i(t), Y_i(t))_{i \in \mathbb{Z}^d}$ . Now recall from the proof of Proposition 2.6.4 that the distribution of an  $n$ -dimensional random vector  $X(t) := (X_1(t), \dots, X_n(t))$  taking values in  $\prod_{l=1}^n [N_l]$  is determined by

$$\mathcal{F}_t = \left\{ \mathbb{E} \left[ \prod_{l=1}^n \frac{\binom{X_l(t)}{\alpha_l}}{\binom{N_l}{\alpha_l}} \right] : (\alpha_l)_{1 \leq l \leq n} \in \prod_{l=1}^n [N_l] \right\}. \quad (2.99)$$

In fact, the distribution of  $X(t)$  converges if and only if

$$\lim_{t \rightarrow \infty} \mathbb{E} \left[ \prod_{l=1}^n \frac{\binom{X_l(t)}{\alpha_l}}{\binom{N_l}{\alpha_l}} \right] \text{ exists} \quad \forall (\alpha_l)_{1 \leq l \leq n} \in \prod_{l=1}^n [N_l]. \quad (2.100)$$

Since our duality function is given by

$$D((X_k, Y_k)_{k \in \mathbb{Z}^d}; (n_k, m_k)_{k \in \mathbb{Z}^d}) = \prod_{i \in \mathbb{Z}^d} \frac{\binom{X_i}{n_i}}{\binom{N_i}{n_i}} \frac{\binom{Y_i}{m_i}}{\binom{M_i}{m_i}} \mathbb{1}_{\{n_i \leq X_i, m_i \leq Y_i\}}, \quad (2.101)$$

it suffices to show that  $\lim_{t \rightarrow \infty} \mathbb{E}_{\nu_\theta} [D(Z(t); \eta)]$  exists for all  $\eta \in \mathcal{X}_*$ . Let  $\eta \in \mathcal{X}_*$  be fixed. By duality, we have

$$\begin{aligned} \mathbb{E}_{\nu_\theta} [D(Z(t); \eta)] &= \int_{\mathcal{X}} \mathbb{E}_\xi [D(Z(t); \eta)] d\nu_\theta(\xi) \\ &= \int_{\mathcal{X}} \mathbb{E}^\eta [D(\xi; Z_*(t))] d\nu_\theta(\xi) = \mathbb{E}^\eta \left[ \int_{\mathcal{X}} D(\xi; Z_*(t)) d\nu_\theta(\xi) \right], \end{aligned} \quad (2.102)$$

where  $\mathbb{E}_\xi$  denotes expectation w.r.t. the law of  $Z(t)$  started at configuration  $\xi \in \mathcal{X}$ ,  $Z_*(t) = (n_i(t), m_i(t))_{i \in \mathbb{Z}^d}$  is the dual process started at configuration  $\eta$ , and  $\mathbb{E}^\eta$  denotes expectation w.r.t. the law of the dual process. A straightforward computation shows that if  $V$  is a random variable with distribution Binomial( $N, p$ ), then  $\mathbb{E} \left[ \frac{\binom{V}{n}}{\binom{N}{n}} \right] = p^n$  for  $0 \leq n \leq N$ . Since  $(X_i(0), Y_i(0))_{i \in \mathbb{Z}^d}$  are all independent under  $\nu_\theta$  with Binomials as marginal distributions, we have

$$\mathbb{E}_{\nu_\theta} [D(Z(t); \eta)] = \mathbb{E}^\eta \left[ \prod_{i \in \mathbb{Z}^d} \theta^{n_i(t)} \theta^{m_i(t)} \right] = \mathbb{E}^\eta [\theta^{|Z_*(t)|}], \quad (2.103)$$

where  $|Z_*(t)| := \sum_{i \in \mathbb{Z}^d} n_i(t) + m_i(t)$  is total number of particles in the dual process at time  $t$ . Now, since the dual process is coalescing,  $|Z_*(t)|$  is decreasing in  $t$ . Since  $\theta \in [0, 1]$ , we see that  $\mathbb{E}_{\nu_\theta}[D(Z(t); \eta)]$  is increasing in  $t$ . Thus,  $\lim_{t \rightarrow \infty} \mathbb{E}_{\nu_\theta}[D(Z(t); \eta)]$  exists, which proves the existence of an equilibrium measure  $\nu$  such that the distribution of  $Z(t)$  weakly converges to  $\nu$ . Also, by definition,

$$\mathbb{E}_\nu[D(Z(0); \eta)] = \lim_{t \rightarrow \infty} \mathbb{E}_{\nu_\theta}[D(Z(t); \eta)] = \lim_{t \rightarrow \infty} \mathbb{E}^\eta[\theta^{|Z_*(t)|}]. \quad (2.104)$$

□

*Proof of Corollary 2.4.10.* This follows by choosing  $\eta = \vec{\delta}_{i,A}$  and  $\eta = \vec{\delta}_{i,D}$  in the last part of Theorem 2.4.9 and noting that  $\mathbb{E}^\eta[\theta^{|Z_*(t)|}] = \theta$  when  $|\eta| = 1$ .

□

## §2.7.2 Genetic variability (heterozygosity)

For  $i, j \in \mathbb{Z}^d$  and  $t \geq 0$ , define

$$\Delta_{i,j}(t) = \Delta_{(i,A),(j,A)}(t) + \Delta_{(i,A),(j,D)}(t), \quad (2.105)$$

where

$$\Delta_{(i,A),(j,A)}(t) = \begin{cases} \frac{X_i(t)(N_j - X_j(t))}{N_i N_j} + \frac{X_j(t)(N_i - X_i(t))}{N_j N_i} & \text{if } i \neq j, \\ \frac{2X_i(t)(N_i - X_i(t))}{N_i(N_i - 1)} & \text{if } i = j \text{ and } N_i \neq 1, \\ 0 & \text{otherwise,} \end{cases} \quad (2.106)$$

is the genetic variability (mostly referred to as ‘sample heterozygosity’ in population genetics) at time  $t$  between the active populations of colony  $i$  and  $j$ , i.e., the probability that two individuals drawn randomly from the two populations at time  $t$  are of different type, and

$$\Delta_{(i,A),(j,D)}(t) = \frac{X_i(t)(M_j - Y_j(t))}{N_i M_j} + \frac{(N_i - X_i(t))Y_j(t)}{N_i M_j} \quad (2.107)$$

is the genetic variability at time  $t$  between the active population of colony  $i$  and the dormant population of colony  $j$ . Note that the conditions in Definition 2.4.11 are equivalent to

$$\lim_{t \rightarrow \infty} \mathbb{E}_\mu[\Delta_{i,j}(t)] = 0 \quad \forall i, j \in \mathbb{Z}^d, \quad (2.108)$$

where the expectation is taken conditional on an arbitrary initial distribution  $\mu$  for which the system admits convergence to an equilibrium. To simplify notations, we suppress the subscript  $\mu$  while taking expectations w.r.t. the law of the process  $Z$  with initial distribution  $\mu$ . We use the dual process to compute  $\mathbb{E}(\Delta_{(i,A),(j,A)}(t))$  and  $\mathbb{E}(\Delta_{(i,A),(j,D)}(t))$ , namely,

$$\mathbb{E}(\Delta_{(i,A),(j,A)}(t)) = \begin{cases} \mathbb{E} \left[ \frac{X_i(t)}{N_i} \right] + \mathbb{E} \left[ \frac{X_j(t)}{N_j} \right] - 2 \mathbb{E} \left[ \frac{X_i(t)X_j(t)}{N_i N_j} \right] & \text{if } i \neq j, \\ 2 \left( \mathbb{E} \left[ \frac{X_i(t)}{N_i} \right] - \mathbb{E} \left[ \frac{X_i(t)(X_i(t)-1)}{N_i(N_i-1)} \right] \right) & \text{otherwise,} \end{cases} \quad (2.109)$$

and

$$\mathbb{E}[\Delta_{(i,A),(j,D)}(t)] = \mathbb{E}\left[\frac{X_i(t)}{N_i}\right] + \mathbb{E}\left[\frac{Y_j(t)}{M_j}\right] - 2\mathbb{E}\left[\frac{X_i(t)Y_j(t)}{N_i M_j}\right]. \quad (2.110)$$

Thus, in terms of the duality function  $D$  defined in Lemma 2.6.1,

$$\begin{aligned} \mathbb{E}[\Delta_{(i,A),(j,A)}(t)] &= \mathbb{E}\left[D(Z(t); \vec{\delta}_{i,A})\right] + \mathbb{E}\left[D(Z(t); \vec{\delta}_{j,A})\right] \\ &\quad - 2\mathbb{E}\left[D(Z(t); \vec{\delta}_{i,A} + \vec{\delta}_{j,A})\right], \end{aligned} \quad (2.111)$$

where  $\vec{\delta}_{i,A}, \vec{\delta}_{j,A}$  are defined in (2.19). Similarly,

$$\begin{aligned} \mathbb{E}[\Delta_{(i,A),(j,D)}(t)] &= \mathbb{E}\left[D(Z(t); \vec{\delta}_{i,A})\right] + \mathbb{E}\left[D(Z(t); \vec{\delta}_{j,D})\right] \\ &\quad - 2\mathbb{E}\left[D(Z(t); \vec{\delta}_{i,A} + \vec{\delta}_{j,D})\right]. \end{aligned} \quad (2.112)$$

Since, by the duality relation in (2.32),

$$\mathbb{E}\left[D(Z(t); Z_*(0))\right] = \mathbb{E}\left[D(Z(0); Z_*(t))\right], \quad (2.113)$$

we have

$$\begin{aligned} \mathbb{E}^{\vec{\delta}_{i,A}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] &= \mathbb{E}\left[\frac{X_i(t)}{N_i}\right], \quad \mathbb{E}^{\vec{\delta}_{i,D}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] = \mathbb{E}\left[\frac{Y_i(t)}{M_i}\right], \\ \mathbb{E}^{\vec{\delta}_{i,A} + \vec{\delta}_{j,A}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] &= \begin{cases} \mathbb{E}\left[\frac{X_i(t)(X_i(t)-1)}{N_i(N_i-1)}\right] & \text{if } i = j, \\ \mathbb{E}\left[\frac{X_i(t)X_j(t)}{N_i N_j}\right] & \text{otherwise,} \end{cases} \\ \mathbb{E}^{\vec{\delta}_{i,A} + \vec{\delta}_{j,D}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] &= \mathbb{E}\left[\frac{X_i(t)Y_j(t)}{N_i M_j}\right], \end{aligned} \quad (2.114)$$

where the expectation in the left-hand side is taken with respect to the dual process  $(Z_*(t))_{t \geq 0} = Z_*$  defined in Definition 2.4.2. Combining the above with (2.111)–(2.112), we get

$$\begin{aligned} \mathbb{E}[\Delta_{(i,A),(j,A)}(t)] &= \left(\mathbb{E}^{\vec{\delta}_{i,A}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] - \mathbb{E}^{\vec{\delta}_{i,A} + \vec{\delta}_{j,A}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right]\right) \\ &\quad + \left(\mathbb{E}^{\vec{\delta}_{j,A}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] - \mathbb{E}^{\vec{\delta}_{i,A} + \vec{\delta}_{j,A}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right]\right) \end{aligned} \quad (2.115)$$

and

$$\begin{aligned} \mathbb{E}[\Delta_{(i,A),(j,D)}(t)] &= \left(\mathbb{E}^{\vec{\delta}_{i,A}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] - \mathbb{E}^{\vec{\delta}_{i,A} + \vec{\delta}_{j,D}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right]\right) \\ &\quad + \left(\mathbb{E}^{\vec{\delta}_{j,D}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right] - \mathbb{E}^{\vec{\delta}_{i,A} + \vec{\delta}_{j,D}}\left[\mathbb{E}\left[D(Z(0); Z_*(t))\right]\right]\right). \end{aligned} \quad (2.116)$$

In Sections 2.7.3–2.7.4 we derive expressions for the terms appearing in (2.115)–(2.116).

### §2.7.3 Dual: single particle

We saw earlier that, in order to compute the first moment of  $X_i(t)$  and  $Y_i(t)$ , we need to put a single particle at site  $i$  in the active and the dormant state as initial

configurations, respectively. This motivates us to analyse the dual process when it starts with a single particle. The generator  $L_{\text{dual}}$  of the dual process can be written as

$$L_{\text{dual}} = L_{\text{Coal}} + L_{AD} + L_{DA} + L_{\text{Mig}}, \quad (2.117)$$

where

$$(L_{\text{Coal}}f)(\xi) = \sum_{i \in \mathbb{Z}^d} \frac{n_i(n_i-1)}{2N_i} [f(\xi - \vec{\delta}_{i,A}) - f(\xi)] \quad (2.118)$$

$$+ \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} \frac{a(i,j)}{N_j} n_i n_j [f(\xi - \vec{\delta}_{i,A}) - f(\xi)], \quad (2.119)$$

$$(L_{AD}f)(\xi) = \sum_{i \in \mathbb{Z}^d} \frac{\lambda n_i (M_i - m_i)}{M_i} [f(\xi - \vec{\delta}_{i,A} + \vec{\delta}_{i,D}) - f(\xi)], \quad (2.120)$$

$$(L_{DA}f)(\xi) = \sum_{i \in \mathbb{Z}^d} \frac{\lambda m_i (N_i - n_i)}{M_i} [f(\xi + \vec{\delta}_{i,A} - \vec{\delta}_{i,D}) - f(\xi)], \quad (2.121)$$

$$(L_{\text{Mig}}f)(\xi) = \sum_{i \in \mathbb{Z}^d} \sum_{\substack{j \in \mathbb{Z}^d \\ j \neq i}} \frac{a(i,j)}{N_j} n_i (N_j - n_j) [f(\xi - \vec{\delta}_{i,A} + \vec{\delta}_{j,A}) - f(\xi)], \quad (2.122)$$

for  $f \in C(\mathcal{X}_*)$  and  $\xi = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*$ .

When there is a single particle in the system at time 0, and consequently at any later time, the only parts of the generator that are non-zero are  $L_{AD}$ ,  $L_{DA}$  and  $L_{\text{Mig}}$ . Here,  $L_{AD}$  turns an active particle at site  $i$  into a dormant particle at site  $i$  at rate  $\lambda$ ,  $L_{DA}$  turns a dormant particle at site  $i$  into an active particle at site  $i$  at rate  $\lambda K_i$ , with  $K_i = \frac{N_i}{M_i}$ , while  $L_{\text{Mig}}$  moves an active particle at site  $i$  to site  $j \neq i$  at rate  $a(i, j)$ . Let us denote the state of the particle at time  $t$  by  $\Theta(t) \in \mathbb{Z}^d \times \{A, D\}$ , where the first coordinate of  $\Theta(t)$  is the location of the particle and the second coordinate indicates whether the particle is active ( $A$ ) or dormant ( $D$ ). Let  $\mathbb{P}^\xi$  be the law of the process  $(\Theta(t))_{t \geq 0}$  with initial state  $\xi$ .

**Lemma 2.7.1 (First moments).**

$$\begin{aligned} \mathbb{E} \left[ \frac{X_i(t)}{N_i} \right] &= \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{X_k(0)}{N_k} \right] \mathbb{P}^{(i,A)}(\xi(t) = (k, A)) + \mathbb{E} \left[ \frac{Y_k(0)}{M_k} \right] \mathbb{P}^{(i,A)}(\xi(t) = (k, D)), \\ \mathbb{E} \left[ \frac{Y_i(t)}{M_i} \right] &= \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{X_k(0)}{N_k} \right] \mathbb{P}^{(i,D)}(\xi(t) = (k, A)) + \mathbb{E} \left[ \frac{Y_k(0)}{M_k} \right] \mathbb{P}^{(i,D)}(\xi(t) = (k, D)). \end{aligned} \quad (2.123)$$

*Proof.* Recall that, via the duality relation,

$$\mathbb{E} \left[ \frac{X_i(t)}{N_i} \right] = \mathbb{E}^{\vec{\delta}_{i,A}} \left[ \mathbb{E} \left[ \prod_{k \in \mathbb{Z}^d} \frac{\binom{X_k(0)}{n_k(t)} \binom{Y_k(0)}{m_k(t)}}{\binom{N_k}{n_k(t)} \binom{M_k}{m_k(t)}} \mathbb{1}_{\{n_k(t) \leq X_k(0), m_k(t) \leq Y_k(0)\}} \right] \right], \quad (2.124)$$

where the expectation in the right-hand side is taken with respect to the dual process with initial state  $\vec{\delta}_{i,A}$  (a single active particle at site  $i$ ), which has law  $\mathbb{P}^{(i,A)}$ . Since the term inside the expectation is equal to  $\frac{X_k(0)}{N_k}$  or  $\frac{Y_k(0)}{M_k}$ , depending on whether

$\xi(t) = (k, A)$  or  $\xi(t) = (k, D)$ , the claim follows immediately. The same argument holds for  $\mathbb{E}[\frac{Y_i(t)}{M_i}]$  with initial condition  $(i, D)$  in the dual process.  $\square$

## §2.7.4 Dual: two particles

We need to find expressions for the second moments appearing in (2.109)–(2.110) in order to fully specify  $\mathbb{E}(\Delta_{(i,A),(j,A)}(t))$  and  $\mathbb{E}(\Delta_{(i,A),(j,D)}(t))$ . This requires us to analyse the dual process starting from two particles. Unlike for the single-particle system, now all parts of the generator  $L_{\text{dual}}$  (see (2.117)) are non-zero, until the two particles coalesce into a single particle. The two particles repel each other: one particle discourages the other particle to come to the same location. The rates in the two-particle system are:

- **(Migration)** An active particle at site  $i$  migrates to site  $j$  at rate  $a(i, j)$  if there is no active particle at site  $j$ , otherwise at rate  $a(i, j)(1 - \frac{1}{N_j})$ .
- **(Active to Dormant)** An active particle at site  $i$  becomes dormant at site  $i$  at rate  $\lambda$  if there is no dormant particle at site  $i$ , otherwise at rate  $\lambda(1 - \frac{1}{M_i})$ .
- **(Dormant to Active)** A dormant particle at site  $i$  becomes active at site  $i$  at rate  $\lambda K_i$  if there is no active particle at site  $i$ , otherwise at rate  $\lambda(K_i - \frac{1}{M_i})$ .
- **(Coalescence)** An active particle at site  $i$  coalesces with another active particle at site  $j$  at rate  $\frac{a(i,j)}{N_j}$ .

Note that after coalescence has taken place, there is only one particle left in the system, which evolves as the single-particle system.

Let  $(\xi_1(t), \xi_2(t), c(t)) \in \mathcal{S}^* \times \mathcal{S}^* \times \{0, 1\}$  be the configuration of the two-particle system at time  $t$ , where  $\mathcal{S}^* = \mathbb{Z}^d \times \{A, D\}$ . Here  $\xi_1(t)$  and  $\xi_2(t)$  represent the location and state of the two particles. The variable  $c(t)$  takes value 1 if the two particles have coalesced into a single particle by time  $t$ , and 0 otherwise. It is necessary to add the extra variable  $c(t)$  to the configuration in order to make the process Markovian (the rates depend on whether there are one or two particles in the system). To avoid triviality we assume that  $c(0) = 0$  with probability 1, i.e., two particles at time 0 are always in a non-coalesced state. We denote the law of the process  $(\xi_1(t), \xi_2(t), c(t))_{t \geq 0}$  by  $\mathbb{P}^\xi$ , where the initial condition is  $\xi \in \mathcal{S}^* \times \mathcal{S}^*$ . It is to be noted that, since the number of active and dormant particles at a site  $i$  at any time are limited by  $N_i$  and  $M_i$ , respectively, the two-particle system is not defined whenever it is started from an initial configuration violating the maximal occupancy of the associated sites. Let  $\tau$  be the first time at which the coalescence event has occurred, i.e.,

$$\tau = \inf\{t \geq 0: c(t) = 1\}. \tag{2.125}$$

Note that, conditional on  $\tau < t$ ,  $\xi_1(s) = \xi_2(s)$  for all  $s \geq t$  with probability 1. Define,

$$M_{(i,\alpha),(j,\beta)}(t) = \begin{cases} \frac{X_i(t)(X_i(t)-1)}{N_i(N_i-1)} & \text{if } i = j \text{ and } \alpha = \beta = A, \\ \frac{X_i(t)X_j(t)}{N_iN_j} & \text{if } i \neq j \text{ and } \alpha = \beta = A, \\ \frac{Y_i(t)(Y_i(t)-1)}{M_i(M_i-1)} & \text{if } i = j \text{ and } \alpha = \beta = D, \\ \frac{Y_i(t)Y_j(t)}{M_iM_j} & \text{if } i \neq j \text{ and } \alpha = \beta = D, \\ \frac{X_i(t)Y_j(t)}{N_iM_j} & \text{if } \alpha = A \text{ and } \beta = D, \\ \frac{Y_i(t)X_j(t)}{M_iN_j} & \text{otherwise,} \end{cases} \quad (2.126)$$

where  $i, j \in \mathbb{Z}^d$  and  $\alpha, \beta \in \{A, D\}$ . To avoid ambiguity, we set  $M_{(i,\alpha),(j,\beta)}(\cdot) = 0$  when  $((i, \alpha), (j, \beta))$  is not a valid initial condition for the two-particle system.

**Lemma 2.7.2 (Second moments).** *For every valid initial condition  $((i, \alpha), (j, \beta)) \in (\mathbb{Z}^d \times \{A, D\})^2$  of the two-particle system,*

$$\begin{aligned} \mathbb{E} [M_{(i,\alpha),(j,\beta)}(t)] &= Q((i, \alpha), (j, \beta), t) + \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{X_k(0)}{N_k} \right] \mathbb{P}^{((i,\alpha),(j,\beta))} (\xi_1(t) = (k, A), \tau < t) \\ &\quad + \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{Y_k(0)}{M_k} \right] \mathbb{P}^{((i,\alpha),(j,\beta))} (\xi_1(t) = (k, D), \tau < t), \end{aligned} \quad (2.127)$$

where

$$\begin{aligned} &Q((i, \alpha), (j, \beta), t) \\ &= \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{X_k(0)(X_k(0)-1)}{N_k(N_k-1)} \right] \mathbb{P}^{((i,\alpha),(j,\beta))} (\xi_1(t) = \xi_2(t) = (k, A), \tau \geq t) \\ &\quad + \sum_{\substack{k, l \in \mathbb{Z}^d \\ k \neq l}} \mathbb{E} \left[ \frac{X_k(0)X_l(0)}{N_kN_l} \right] \mathbb{P}^{((i,\alpha),(j,\beta))} (\xi_1(t) = (k, A), \xi_2(t) = (l, A), \tau \geq t) \\ &\quad + \sum_{k, l \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{X_k(0)Y_l(0)}{N_kM_l} \right] \mathbb{P}^{((i,\alpha),(j,\beta))} (\xi_1(t) = (k, A), \xi_2(t) = (l, D), \tau \geq t) \\ &\quad + \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{Y_k(0)(Y_k(0)-1)}{M_k(M_k-1)} \right] \mathbb{P}^{((i,\alpha),(j,\beta))} (\xi_1(t) = \xi_2(t) = (k, D), \tau \geq t) \\ &\quad + \sum_{\substack{k, l \in \mathbb{Z}^d \\ k \neq l}} \mathbb{E} \left[ \frac{Y_k(0)Y_l(0)}{M_kM_l} \right] \mathbb{P}^{((i,\alpha),(j,\beta))} (\xi_1(t) = (k, D), \xi_2(t) = (l, D), \tau \geq t). \end{aligned} \quad (2.128)$$

*Proof.* Note that  $M_{(i,\alpha),(j,\beta)}(t) = D(Z(t); \vec{\delta}_{i,\alpha} + \vec{\delta}_{j,\beta})$ , where  $D$  is the duality function. So, via the duality relation, we have

$$\mathbb{E} [M_{(i,\alpha),(j,\beta)}(t)] = \mathbb{E}^{\vec{\delta}_{i,\alpha} + \vec{\delta}_{j,\beta}} \left[ \mathbb{E} \left[ \prod_{k \in \mathbb{Z}^d} \frac{\binom{X_k(0)}{n_k(t)} \binom{Y_k(0)}{m_k(t)}}{\binom{N_k}{n_k(t)} \binom{M_k}{m_k(t)}} \mathbb{1}_{\{n_k(t) \leq X_k(0), m_k(t) \leq Y_k(0)\}} \right], \quad (2.129)$$

where the expectation in the right-hand side is taken with respect to the dual process when the initial condition has one particle at site  $i$  with state  $\alpha$  and one particle at site  $j$  with state  $\beta$ , which has law  $\mathbb{P}^{((i,\alpha),(j,\beta))}$ . Depending on the configuration of the process at time  $t$ , the right-hand side of (2.129) equals the desired expression.  $\square$

The following lemma provides a nice comparison between the one-particle and two-particle system.

**Lemma 2.7.3 (Correlation inequality).** *Let  $(\xi(t))_{t \geq 0}$  and  $(\xi_1(t), \xi_2(t), c(t))_{t \geq 0}$  be the processes defined in Section 2.7.3 and 2.7.4, respectively, and  $\tau$  the first time of coalescence defined in (2.125). Then, for any valid initial condition  $((i, \alpha), (j, \beta)) \in (\mathbb{Z}^d \times \{A, D\})^2$  of the two-particle system and any  $(k, \gamma) \in \mathbb{Z}^d \times \{A, D\}$ ,*

$$\mathbb{P}^{(i,\alpha)}(\xi(t) = (k, \gamma)) \geq \mathbb{P}^{((i,\alpha),(j,\beta))}(\xi_1(t) = (k, \gamma), \tau < t). \quad (2.130)$$

*Proof.* Let  $\alpha = A$  and  $i, j, k \in \mathbb{Z}^d$  be fixed. Let  $\eta = Z(0)$  be the initial configuration defined as,

$$(X_n(0), Y_n(0)) = \begin{cases} (N_k, 0) & \text{if } n = k \text{ and } \gamma = A, \\ (0, M_k) & \text{if } n = k \text{ and } \gamma = D, \\ (0, 0) & \text{otherwise,} \end{cases} \quad \forall n \in \mathbb{Z}^d. \quad (2.131)$$

Combining Lemma 2.7.1 and Lemma 2.7.2, we get

$$\begin{aligned} & \mathbb{E}_\eta \left[ \frac{X_i(t)}{N_i} - M_{(i,A),(j,\beta)}(t) \right] \\ &= \sum_{n \in \mathbb{Z}^d} \frac{X_n(0)}{N_n} \left[ \mathbb{P}^{(i,A)}(\xi(t) = (n, A)) - \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (n, A), \tau < t) \right] \\ & \quad + \sum_{n \in \mathbb{Z}^d} \frac{Y_n(0)}{M_n} \left[ \mathbb{P}^{(i,A)}(\xi(t) = (n, D)) - \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (n, D), \tau < t) \right] \\ & \quad - Q((i, A), (j, \beta), t) \\ &= \left[ \mathbb{P}^{(i,A)}(\xi(t) = (k, \gamma)) - \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (k, \gamma), \tau < t) \right] - Q((i, A), (j, \beta), t). \end{aligned} \quad (2.132)$$

Since  $Q((i, A), (j, \beta), t) \geq 0$  and the left-hand quantity is positive, we get

$$\mathbb{P}^{(i,A)}(\xi(t) = (k, \gamma)) \geq \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (k, \gamma), \tau < t). \quad (2.133)$$

Replacing the left-quantity in (2.132) with  $\mathbb{E}_\eta \left[ \frac{Y_i(t)}{M_i} - M_{(i,D),(j,\beta)}(t) \right]$  and using the same arguments, we see that the inequality for  $\alpha = D$  follows.  $\square$

## §2.7.5 Proof of clustering criterion

*Proof of Theorem 2.4.12.* “ $\Leftarrow$ ” First we show that, if  $((i, A), (j, \beta)) \in (\mathbb{Z}^d \times \{A, D\})^2$  is a valid initial condition for the two-particle system, then

$$\lim_{t \rightarrow \infty} \mathbb{E} \left[ \frac{X_i(t)}{N_i} - M_{(i,A),(j,\beta)}(t) \right] = 0, \quad \lim_{t \rightarrow \infty} \mathbb{E} \left[ \frac{Y_j(t)}{M_j} - M_{(i,A),(j,\beta)}(t) \right] = 0. \quad (2.134)$$

Combining Lemma 2.7.1 and Lemma 2.7.2, we have

$$\begin{aligned}
 & \mathbb{E} \left[ \frac{X_i(t)}{N_i} - M_{(i,A),(j,\beta)}(t) \right] \\
 &= \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{X_k(0)}{N_k} \right] \left[ \mathbb{P}^{(i,A)}(\xi(t) = (k, A)) - \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (k, A), \tau < t) \right] \\
 &+ \sum_{k \in \mathbb{Z}^d} \mathbb{E} \left[ \frac{Y_k(0)}{M_k} \right] \left[ \mathbb{P}^{(i,A)}(\xi(t) = (k, D)) - \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (k, D), \tau < t) \right] \\
 &- Q((i, A), (j, \beta), t).
 \end{aligned} \tag{2.135}$$

Using Lemma 2.7.3 and the fact that  $Q((i, A), (j, \beta), t) \geq 0$ , we have the following:

$$\begin{aligned}
 & \mathbb{E} \left[ \frac{X_i(t)}{N_i} - M_{(i,A),(j,\alpha)}(t) \right] \\
 & \leq \sum_{\substack{S \in \{A, D\} \\ k \in \mathbb{Z}^d}} \left| \mathbb{P}^{(i,A)}(\xi(t) = (k, S)) - \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (k, S), \tau < t) \right| \\
 &= \sum_{\substack{S \in \{A, D\} \\ k \in \mathbb{Z}^d}} \left[ \mathbb{P}^{(i,A)}(\xi(t) = (k, S)) - \mathbb{P}^{((i,A),(j,\beta))}(\xi_1(t) = (k, S), \tau < t) \right] \\
 &= 1 - \mathbb{P}^{((i,A),(j,\beta))}(\tau < t) = \mathbb{P}^{((i,A),(j,\beta))}(\tau \geq t).
 \end{aligned} \tag{2.136}$$

Since, by assumption,  $\tau < \infty$  with probability 1 irrespective of the initial configuration of the two-particle system, and since the left-hand quantity is positive, we have  $\mathbb{E} \left[ \frac{X_i(t)}{N_i} - M_{(i,A),(j,\beta)}(t) \right] \rightarrow 0$  as  $t \rightarrow \infty$ . By a similar argument the other part of (2.134) is proved as well.

If  $((i, A), (j, A))$  is a valid initial condition for the two-particle system, then by using (2.115)–(2.116) and (2.134), we have

$$\begin{aligned}
 \lim_{t \rightarrow \infty} \mathbb{E} \left( \Delta_{(i,A),(j,A)}(t) \right) &= \lim_{t \rightarrow \infty} \mathbb{E} \left[ \frac{X_i(t)}{N_i} - M_{(i,A),(j,A)}(t) \right] \\
 &+ \lim_{t \rightarrow \infty} \mathbb{E} \left[ \frac{X_j(t)}{N_j} - M_{(j,A),(i,A)}(t) \right] \\
 &= 0.
 \end{aligned} \tag{2.137}$$

If  $((i, A), (j, A))$  is not a valid initial condition, then we must have that  $i = j$  and  $N_i = 1$ , and so  $\Delta_{(i,A),(j,A)}(t) = 0$  by definition. Thus, for any  $i, j \in \mathbb{Z}^d$ ,

$$\lim_{t \rightarrow \infty} \mathbb{E} \left[ \Delta_{(i,A),(j,A)}(t) \right] = 0. \tag{2.138}$$

Since  $((i, A), (j, D))$  is always a valid initial condition for the two-particle system, we also have

$$\begin{aligned}
 \lim_{t \rightarrow \infty} \mathbb{E} \left[ \Delta_{(i,A),(j,D)}(t) \right] &= \lim_{t \rightarrow \infty} \mathbb{E} \left[ \frac{X_i(t)}{N_i} - M_{(i,A),(j,D)}(t) \right] \\
 &+ \lim_{t \rightarrow \infty} \mathbb{E} \left[ \frac{Y_j(t)}{M_j} - M_{(i,A),(j,D)}(t) \right] \\
 &= 0,
 \end{aligned} \tag{2.139}$$



and hence from (2.105) we have that, for any  $i, j \in \mathbb{Z}^d$ ,  $\mathbb{E}(\Delta_{i,j}(t)) \rightarrow 0$  as  $t \rightarrow \infty$ , which proves the claim.

“ $\implies$ ” Suppose that the system is in the clustering regime. Fix  $\theta \in (0, 1)$ , and let the distribution of  $Z(0)$  be  $\nu_\theta$ , where

$$\nu_\theta = \bigotimes_{i \in \mathbb{Z}^d} (\text{Binomial}(N_i, \theta) \otimes \text{Binomial}(M_i, \theta)). \quad (2.140)$$

We will prove via contradiction that in the dual two particles with arbitrary valid initial states coalesce with probability 1, i.e.,  $\tau < \infty$  with probability 1. Indeed, suppose that this is not true, i.e., for some valid initial configuration  $(\xi_1, \xi_2) \in \mathcal{S}^* \times \mathcal{S}^*$  of the two-particle system we have  $\mathbb{P}^{(\xi_1, \xi_2)}(\tau = \infty) > 0$ , where  $\mathcal{S}^* = \mathbb{Z}^d \times \{A, D\}$ . Since the dual process with two particles is irreducible (any valid configuration is accessible), we have  $\mathbb{P}^\xi(\tau = \infty) > 0$  for any valid initial condition  $\xi \in \mathcal{S}^* \times \mathcal{S}^*$ . Let  $\rho := \mathbb{P}^{((i,A), (i,D))}(\tau = \infty) > 0$ , where  $i \in \mathbb{Z}^d$  is fixed. Note that  $((i,A), (i,D))$  is always a valid initial condition for the two-particle system, since  $N_i, M_i \geq 1$ . Let  $\mathbb{P}^{(i,A)}$  be the law of the single-particle process  $(\xi(t))_{t \geq 0}$  started with initial condition  $(i,A)$ .

Since, by assumption the process  $Z$  in (2.2) exhibits clustering and we know by Theorem 2.4.9 that starting from initial distribution  $\nu_\theta$ , the process  $Z$  converges in law to an equilibrium  $\mu_\theta$ , we must have

$$\mu_\theta = (1 - \theta)\delta_{\blacklozenge} + \theta\delta_{\heartsuit}, \quad (2.141)$$

where  $\delta_{\heartsuit}$  (resp.  $\delta_{\blacklozenge}$ ) is the Dirac distribution concentrated at  $(N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$  (resp.  $(0, 0)_{i \in \mathbb{Z}^d} \in \mathcal{X}$ ). Thus,

$$\lim_{t \rightarrow \infty} \mathbb{E}_{\nu_\theta} [\Delta_{(i,A), (i,D)}(t)] = \mathbb{E}_{\mu_\theta} [\Delta_{(i,A), (i,D)}(t)] = 0 \quad (2.142)$$

Therefore, we must have

$$\lim_{t \rightarrow \infty} \mathbb{E}_{\nu_\theta} \left[ \frac{X_i(t)(M_i - Y_i(t))}{N_i M_i} \right] = 0. \quad (2.143)$$

Since  $((i,A), (i,D))$  is a valid initial condition for the two-particle system, by using (2.135) with  $\nu_\theta$  as initial distribution we get

$$\begin{aligned} & \mathbb{E}_{\nu_\theta} \left[ \frac{X_i(t)(M_i - Y_i(t))}{N_i M_i} \right] \\ &= \mathbb{E}_{\nu_\theta} \left[ \frac{X_i(t)}{N_i} - M_{(i,A), (i,D)}(t) \right] \\ &= \sum_{n \in \mathbb{Z}^d} \mathbb{E}_{\nu_\theta} \left[ \frac{X_n(0)}{N_n} \right] \left[ \mathbb{P}^{(i,A)}(\xi(t) = (n, A)) - \mathbb{P}^{((i,A), (i,D))}(\xi_1(t) = (n, A), \tau < t) \right] \\ & \quad + \sum_{n \in \mathbb{Z}^d} \mathbb{E}_{\nu_\theta} \left[ \frac{Y_n(0)}{M_n} \right] \left[ \mathbb{P}^{(i,A)}(\xi(t) = (n, D)) - \mathbb{P}^{((i,A), (i,D))}(\xi_1(t) = (n, D), \tau < t) \right] \\ & \quad - \mathbb{E}_{\nu_\theta} [Q((i,A), (i,D), t)], \end{aligned} \quad (2.144)$$

where  $Q(\cdot, \cdot, \cdot)$  is defined as in Lemma (2.7.2). Since, under  $\nu_\theta$ ,  $(X_n(0))_{n \in \mathbb{Z}^d}$ ,  $(Y_n(0))_{n \in \mathbb{Z}^d}$  are all independent of each other and  $X_n(0)$  and  $Y_n(0)$  have distributions  $\text{Binomial}(N_n, \theta)$

and Binomial( $M_n, \theta$ ), respectively, we have

$$\begin{aligned}\mathbb{E}_{\nu_\theta} \left[ \frac{X_n(0)}{N_n} \right] &= \mathbb{E}_{\nu_\theta} \left[ \frac{Y_n(0)}{M_n} \right] = \theta, \\ \mathbb{E}_{\nu_\theta} \left[ \frac{X_n(0)(X_n(0)-1)}{N_n(N_n-1)} \right] &= \theta^2 && \text{if } N_n \neq 1, \\ \mathbb{E}_{\nu_\theta} \left[ \frac{Y_n(0)(Y_n(0)-1)}{M_n(M_n-1)} \right] &= \theta^2 && \text{if } M_n \neq 1.\end{aligned}\tag{2.145}$$

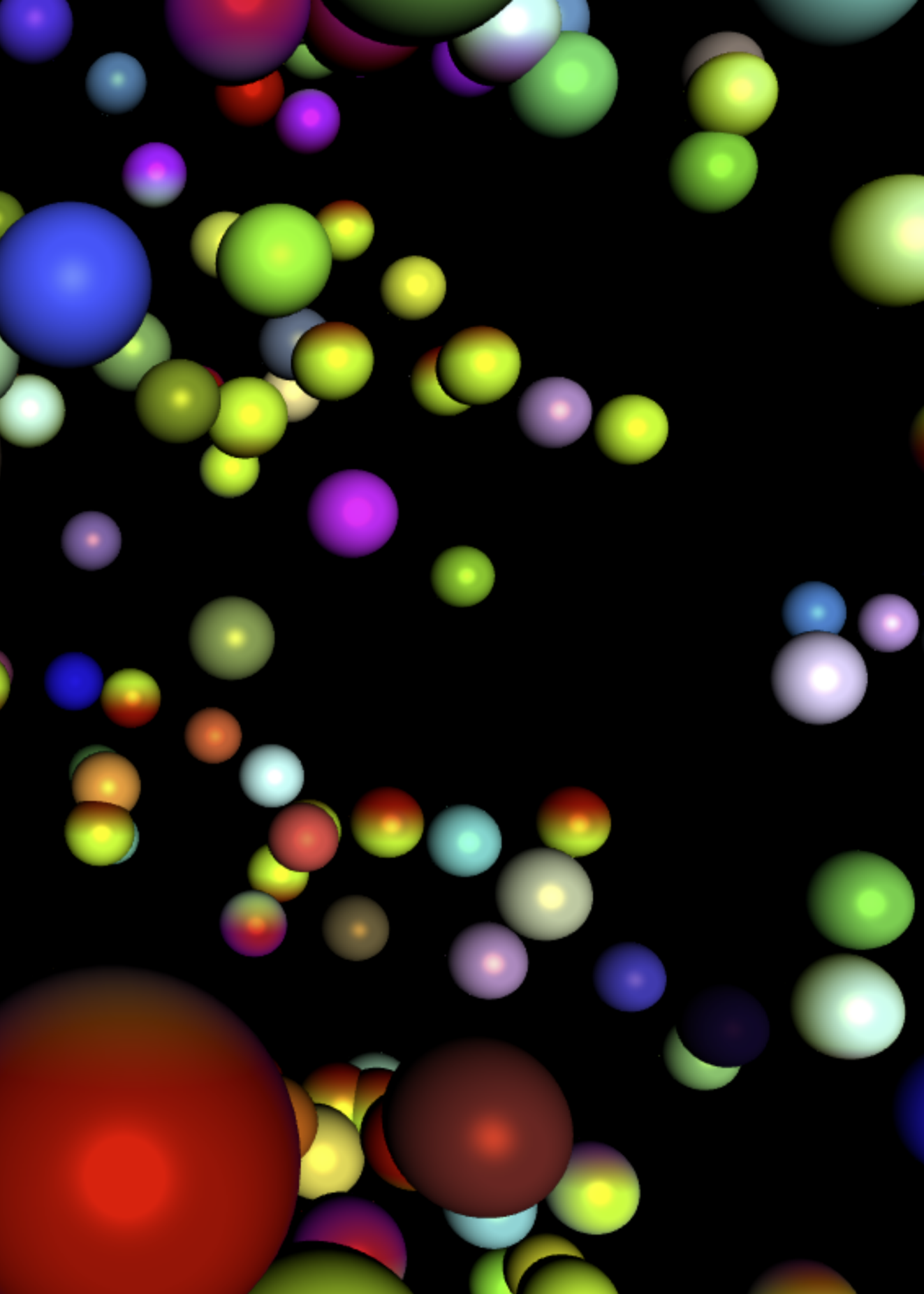
Hence  $\mathbb{E}_{\nu_\theta} [Q((i, A), (i, D), t)] = \theta^2 \mathbb{P}^{((i, A), (i, D))}(\tau \geq t)$ , and thus (2.144) reduces to

$$\begin{aligned}\mathbb{E}_{\nu_\theta} \left[ \frac{X_i(t)(M_i - Y_i(t))}{N_i M_i} \right] &= \theta \left[ 1 - \mathbb{P}^{((i, A), (i, D))}(\tau < t) \right] - \theta^2 \mathbb{P}^{((i, A), (i, D))}(\tau \geq t) \\ &= \theta(1 - \theta) \mathbb{P}^{((i, A), (i, D))}(\tau \geq t).\end{aligned}\tag{2.146}$$

By (2.143), the left-hand side of (2.146) tends to 0 as  $t \rightarrow \infty$ . Because  $\theta \in (0, 1)$ , we have

$$\rho = \lim_{t \rightarrow \infty} \mathbb{P}^{((i, A), (i, D))}(\tau \geq t) = 0,\tag{2.147}$$

which is a contradiction.  $\square$



# Spatially inhomogeneous populations with seed-bank: clustering regime

This chapter is based on the following paper:

F. den Hollander and S. Nandan. Spatially inhomogeneous populations with seed-banks: II. Clustering regime. *Stoch. Proc. Appl.*, 150:116–146, 2022.

## Abstract

We consider a spatial version of the classical Moran model with seed-banks where the constituent populations have finite sizes. Individuals live in colonies labelled by  $\mathbb{Z}^d$ ,  $d \geq 1$ , playing the role of a geographic space, carry one of two *types*,  $\heartsuit$  or  $\spadesuit$ , and change type via *resampling* as long as they are *active*. Each colony contains a seed-bank into which individuals can enter to become *dormant*, suspending their resampling until they exit the seed-bank and become active again. Individuals resample not only from their own colony, but also from other colonies according to a symmetric random walk transition kernel. The latter is referred to as *migration*. The sizes of the active and the dormant populations depend on the colony and remain constant throughout the evolution. It was shown in [46] that the spatial system is well-defined, admits a family of equilibria parametrised by the initial density of type  $\heartsuit$ , and exhibits a dichotomy between *clustering* (mono-type equilibrium) and *coexistence* (multi-type equilibrium). This dichotomy is determined by a clustering criterion that is given in terms of the dual of the system, which consists of a system of *interacting* coalescing random walks. In this paper we provide an alternative clustering criterion, given in terms of an auxiliary dual that is simpler than the original dual, and identify a range of parameters for which the criterion is met, which we refer to as the *clustering regime*. It turns out that if the sizes of the active populations are non-clumping (i.e., do not take arbitrarily large values in finite regions of the geographic space) and the relative strengths of the seed-banks (i.e., the ratio of the sizes of the dormant and the active population in each colony) are bounded uniformly over the geographic space, then clustering prevails if and only if the symmetrised migration kernel is recurrent.

The spatial system is hard to analyse because of the interaction in the original dual and the inhomogeneity of the colony sizes. By comparing the auxiliary dual with a *non-interacting* two-particle system, we are able to control the correlations that are caused by the interactions. The work in [46] and the present paper is part of a broader attempt to include dormancy into interacting particle systems.

## §3.1 Introduction

In this chapter we investigate the range of parameters for which the spatial process  $Z$  introduced in Section 2.2.1 of Chapter 2 remains in the clustering regime (recall Definition 2.2.4). In particular, we identify a subdomain of the *clustering regime* that is natural and adequate from a biological point of view. More precisely, we show that if the sizes of the active populations are non-clumping, i.e., do not take arbitrarily large values in finite regions of the geographic space, and the relative strengths of the seed-banks in the different colonies are bounded, then the dichotomy between coexistence and clustering is the classical dichotomy between transience and recurrence of the *symmetrised* migration kernel, a property that is known to hold for colonies without seed-bank.

In [76, 75] a *homogeneous* spatial version of the Fisher-Wright model was considered (i.e., the relative strengths of the seed-banks do not vary across different colonies), in the large-colony-size limit. For three different choices of seed-bank, it was shown that the system is well-defined, has a unique equilibrium that depends on the initial density of types, and exhibits a dichotomy between clustering and coexistence. A full description of the clustering regime was obtained. In addition, the finite-systems scheme was established (i.e., how a truncated version of the system behaves on a properly tuned time scale as the truncation level tends to infinity). Moreover, a multi-scale renormalisation analysis was carried out for the case where the colonies are labelled by the hierarchical group. The respective duals for these models are easier, because they are non-interacting and have no inhomogeneity in space. The dual of our model is much harder, which is why our results are much more modest.

**Outline.** The chapter is organised as follows. In Section 2.2 we state our main theorems about the dichotomy of clustering versus coexistence by identifying the clustering regime for both. In Section 3.3 we provide a different representation (namely, given by a *coordinate process*) of the two-particle dual process associated to our system introduced Section 2.4.2 of Chapter 2, and define two auxiliary duals that serve as comparison objects. We relate the coalescence probabilities of the different duals, which leads to a necessary and sufficient criterion for clustering in our system. In Section 3.4 we prove our main results. In Section 3.5 we discuss the main results and shed light on the motivation behind the strategy of the proofs. In Appendix A.1 we recall the original representation (given by a *configuration process*) of the two-particle dual from Section 2.4.2 of Chapter 2, and briefly elaborate on its relation with the alternative representation given in Section 3.3.

## §3.2 Main theorems

In Section 3.2.2 we state our results about the dichotomy of clustering versus coexistence, which requires additional conditions on the sizes of the active and the dormant population.

### §3.2.1 Preliminaries: assumption and notations

In order to avoid trivial statement we assume the following:

**Assumption 3.A (Non-trivial colony sizes).** In each colony, both the active and the dormant population consist of at least two individuals, i.e.,  $N_i \geq 2$  and  $M_i \geq 2$  for all  $i \in \mathbb{Z}^d$ . ■

For colony sizes where Assumption 3.A fails, all the results stated below can be obtained with minor technical modifications. We write  $\hat{a}(\cdot, \cdot)$  to denote the *symmetrised migration kernel* defined by

$$\hat{a}(i, j) := \frac{1}{2}[a(i, j) + a(j, i)], \quad i, j \in \mathbb{Z}^d, \quad (3.1)$$

and write  $a_n(\cdot, \cdot)$  to denote the  $n$ -step transition probability kernel of the embedded chain associated to the continuous-time random walk on  $\mathbb{Z}^d$  with rates  $a(\cdot, \cdot)$ . Furthermore, we denote by  $\hat{a}_t(\cdot, \cdot)$  (respectively,  $a_t(\cdot, \cdot)$ ), the time- $t$  transition probability kernel of the continuous-time random walk with migration rates  $\hat{a}(\cdot, \cdot)$  (respectively,  $a(\cdot, \cdot)$ ), and put

$$K_i := \frac{N_i}{M_i}, \quad i \in \mathbb{Z}^d, \quad (3.2)$$

for the *ratios* of the sizes of the active and the dormant population in each colony. Note that  $K_i^{-1}$  quantifies the *relative strength* of the seed-bank at colony  $i \in \mathbb{Z}^d$ .

Let  $\mathcal{P}$  be the set of probability distributions on  $\mathcal{X}$  (see (2.3) in Chapter 2) defined by

$$\mathcal{P} := \{\mathcal{P}_\theta : \theta \in [0, 1]\}, \quad \mathcal{P}_\theta := (1 - \theta)\delta_\spadesuit + \theta\delta_\heartsuit, \quad (3.3)$$

where  $\delta_\heartsuit$  (resp.  $\delta_\spadesuit$ ) is the Dirac distribution concentrated at  $(N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}$  (resp.  $(0, 0)_{i \in \mathbb{Z}^d} \in \mathbb{Z}^d \in \mathcal{X}$ ). Note that the process  $Z$  introduced in Section 2.2.1 of Chapter 2 exhibits *clustering* if and only if the limiting distribution of  $Z(t)$  (given that it exists) always falls in  $\mathcal{P}$ . Otherwise the process is said to be in the *coexistence* regime. In the next section we recall the *clustering criterion* from Chapter 2, given in terms of the original dual process  $Z_*$ , and provide an alternative equivalent criterion in terms of a simpler two-particle process that is absorbing.

### §3.2.2 Clustering versus coexistence

Recall from Chapter 2 that the system admits a mono-type equilibrium (clustering) if and only if the following criterion is met:

**Theorem 3.2.1 (Clustering condition).** *The system clusters if and only if in the dual process  $Z_*$  two particles, starting from any locations in  $\mathbb{Z}^d$  and any states (active or dormant), coalesce with probability 1.*

Before we state our alternative criterion for clustering, we introduce an auxiliary two-particle dual process. In Proposition 3.3.5, we will show the well-posedness of this process. Recall that  $\lambda$  is the exchange rate between active and dormant individuals in each colony.

**Definition 3.2.2 (Auxiliary two-particle system).** The two-particle process  $\hat{\xi} := (\hat{\xi}(t))_{t \geq 0}$  is a continuous-time Markov chain on the state space

$$\mathcal{S} := (G \times G) \cup \{\otimes\}, \quad G := \mathbb{Z}^d \times \{0, 1\} \quad (3.4)$$

with transition rates

$$[(i, \alpha), (j, \beta)] \rightarrow \begin{cases} \otimes, & \text{at rate } 2a(i, i) \frac{\alpha\beta}{N_i} \delta_{i,j}, \\ [(i, 1 - \alpha), (j, \beta)], & \text{at rate } \lambda[\alpha + (1 - \alpha)K_i] - \frac{\lambda}{M_i} \delta_{i,j}(1 - \delta_{\alpha,\beta}), \\ [(i, \alpha), (j, 1 - \beta)], & \text{at rate } \lambda[\beta + (1 - \beta)K_j] - \frac{\lambda}{M_j} \delta_{i,j}(1 - \delta_{\alpha,\beta}), \\ [(k, \alpha), (j, \beta)], & \text{at rate } \alpha a(i, k) \quad \text{for } k \neq i \in \mathbb{Z}^d, \\ [(i, \alpha), (k, \beta)], & \text{at rate } \beta a(j, k) \quad \text{for } k \neq j \in \mathbb{Z}^d, \end{cases} \quad (3.5)$$

where  $[(i, \alpha), (j, \beta)] \in G \times G$  and  $\delta_{\cdot, \cdot}$  denotes the Kronecker delta-function. ■

Here,  $\hat{\xi}(t) = [(i, \alpha), (j, \beta)]$  captures the location  $(i, j \in \mathbb{Z}^d)$  and the state  $(\alpha, \beta \in \{0, 1\})$  of the two particles at time  $t$ , where 0 stands for dormant and 1 stands for active, respectively. Note that  $\otimes$  is an absorbing state for the process  $\hat{\xi}$ , which is absorbed at a location-dependent rate only when the two particles are on top of each other and in the active state. We will see in Section 3.3.1 that this is different from what happens in the two-particle system obtained from the original dual. The process  $\hat{\xi}$  is much simpler than the original two-particle system, because the particles do not interact unless they are on top of each other with opposite states. Indeed, note that in the second and third line of (3.5) the second term represents a repulsive interaction between the two particles that is non-zero only when  $i = j$  and  $\alpha \neq \beta$ . From here onwards, we write  $\hat{\mathbb{P}}^\eta$  to denote the law of the process  $\hat{\xi}$  started from  $\eta \in \mathcal{S}$ , and  $\hat{\mathbb{E}}^\eta$  to denote expectation w.r.t.  $\hat{\mathbb{P}}^\eta$ .

**Remark 3.2.3.** Note that, by virtue of Assumptions 2.A and 3.A, all states in  $\mathcal{S}$  are accessible by  $\hat{\xi}$ .

**Theorem 3.2.4 (Clustering criterion).** *The system clusters if the process  $\hat{\xi}$  starting from an arbitrary configuration in  $G \times G$  is absorbed with probability 1. Furthermore, if the sizes of the active populations are non-clumping, i.e.,*

$$\inf_{i \in \mathbb{Z}^d} \sum_{\|j-i\| \leq R} \frac{1}{N_j} > 0 \text{ for some } R < \infty, \quad (3.6)$$

then the converse is true as well.

**Remark 3.2.5.** The condition in (3.6) is equivalent to requiring that, for some constant  $C < \infty$  and all  $i \in \mathbb{Z}^d$ , there exists a  $j$  with  $\|j - i\| \leq R$  such that  $N_j \leq C$ . This requirement can be further relaxed to

$$\inf_{i \in \mathbb{Z}^d} \sum_{j \in \mathbb{Z}^d} \frac{1}{N_j} \sum_{n \in \mathbb{N}} m^{2n} a_n(i, j)^2 > 0, \quad (3.7)$$

where  $m := \frac{c}{2(c+\lambda)+1}$ . Although (3.6) arises in our context as a technical requirement, it has an interesting connection with the notion introduced in [127, 143] of *coalescent effective population size* (CES) in a subdivided population. Roughly,  $N \in \mathbb{N}$  is said to be the CES of a subdivided population when, after measuring time in units of  $N$  generations and taking the large-colony-size-limit, the associated genealogy gives rise to Kingman’s coalescent (or a similar object). When migration is controlled by a transition matrix, the CES is often proportional to the harmonic mean of the constituent population sizes (see e.g., [151], and also [56, Section 4.4]). The non-clumping criterion in (3.6) essentially says that if  $H(i, R)$  is the harmonic mean of the active population sizes of the colonies within the  $R$ -neighbourhood of colony  $i$ , i.e.,

$$H(i, R) := \frac{|\{j \in \mathbb{Z}^d : \|j - i\| \leq R\}|}{\sum_{\|j-i\| \leq R} N_j^{-1}}, \quad i \in \mathbb{Z}^d, \quad (3.8)$$

then  $\sup_{i \in \mathbb{Z}^d} H(i, R) < \infty$  for some  $R < \infty$ . We believe that this connection of the non-clumping criterion to the CES is not accidental, and merits further investigation.

To verify when the above clustering criterion is satisfied, we need to impose the following regularity condition on the migration kernel.

**Assumption 3.B (Regularly varying migration kernel).** Assume that  $t \mapsto \hat{a}_t(0, 0)$  is regularly varying at infinity, i.e.,  $\lim_{t \rightarrow \infty} \frac{\hat{a}_{pt}(0, 0)}{\hat{a}_t(0, 0)} = p^{-\sigma}$  for all  $p \in (0, \infty)$  and some  $\sigma \in [0, \infty)$ , where  $-\sigma$  is the index of the regular variation and  $\hat{a}_t(\cdot, \cdot)$  is the time- $t$  symmetrised migration kernel. ■

**Remark 3.2.6.** Note that all genuinely  $d$ -dimensional continuous-time random walks satisfying the LCLT (see e.g., [107, Chapter 2]) have a probability transition kernel with a regularly varying tail of index  $-\frac{d}{2}$ .

When the relative strengths of the seed-banks are uniformly bounded, clustering is equivalent to the symmetrised migration kernel being recurrent, a setting that is classical. The following theorem provides a slightly weaker result.

**Theorem 3.2.7 (Clustering regime).** *Suppose that Assumption 3.B is in force. Assume that the active population sizes are non-clumping, i.e., (3.6) is satisfied, and the relative strengths of the seed-banks are uniformly bounded, i.e.,*

$$\sup_{i \in \mathbb{Z}^d} K_i^{-1} < \infty. \quad (3.9)$$

*If the system clusters, then it is necessary that the symmetrised kernel  $\hat{a}(\cdot, \cdot)$  is recurrent. Furthermore, if the migration kernel  $a(\cdot, \cdot)$  is symmetric, then the converse holds as well.*

It was shown in [76] that the above dichotomy is true when the seed-banks are homogeneous (i.e.,  $(N_i, M_i) = (N, M)$  for all  $i \in \mathbb{Z}^d$ ) and the large-colony-size limit is taken (i.e.,  $N, M \rightarrow \infty$  such that  $N/M \rightarrow K \in (0, \infty)$ ). In that case, the dual process is an independent particle system with coalescence and without inhomogeneity, for



which the proof is much simpler. The result stated above extends the dichotomy to the inhomogeneous setting. It essentially says that if the inhomogeneities caused by the seed-banks are spatially uniform (reflected by (3.9)), then the dichotomy remains unchanged. The condition in (3.9) allows us to compare the auxiliary dual process  $\hat{\xi}$  with a non-interacting two-particle process  $\xi^*$  living on the state space  $\mathcal{S}$  that we introduce in Section 3.3.1 (see Section 3.4.2 for more details). As we will see later,  $\otimes$  is an absorbing state for  $\xi^*$  too and, under the conditions given in Theorem 3.2.7, it turns out that  $\hat{\xi}$  is absorbed with probability 1 if and only if  $\xi^*$  is. In  $\xi^*$  the two particles evolve independently until absorption. A single particle migrates in the active state at rates  $a(\cdot, \cdot)$ , becomes dormant from the active state at rate  $\lambda$ , and becomes active from the dormant state at rate  $\lambda K_i$  when it is at location  $i \in \mathbb{Z}^d$ . When the condition (3.9) is met, the average time spent in the dormant state by the particles in the various locations are of the same order, and hence the distance between the two particles is effectively controlled by the symmetrised kernel  $\hat{a}(\cdot, \cdot)$ . In particular, the recurrence of  $\hat{a}(\cdot, \cdot)$  forces the two particles to meet each other infinitely often with probability 1. As a result,  $\xi^*$  is eventually absorbed in  $\otimes$ . We exploit these facts along with the alternative clustering criterion to prove Theorem 3.2.7. We expect the symmetry assumption to be redundant for the converse statement, but are unable to remove it for technical reasons. The following result is an immediate corollary.

**Corollary 3.2.8 (Dimensional dichotomy).** *Assume that all the conditions in Theorem 3.2.7 are in force. Then the following hold:*

- (a) *Coexistence prevails when  $d > 2$ .*
- (b) *Clustering prevails when  $d \leq 2$  and  $a(\cdot, \cdot)$  is symmetric.*

### §3.3 Dual processes: comparison between different systems

In Section 3.3.1 we give a brief description of the dual process  $Z_*$  of our original system introduced in Chapter 2, and define *two auxiliary duals* that serve as comparison objects. The auxiliary duals are simplified versions of the basic dual, started from two particles, where the coalesced state of the two particles is turned into an absorbing state. In Sections 3.3.2–3.3.3 we relate the coalescence (absorption) probabilities of the auxiliary duals via a comparison technique that is based on the Lyapunov function approach employed in [32]. In Section 3.3.4 we provide finer conditions on the parameters of our original model under which the results derived in previous sections hold.

#### §3.3.1 Two-particle dual and auxiliary duals

Recall that the dual process  $Z_*$  is an interacting particle system describing the evolution of finitely many particles such that (see Section 2.4.2 of Chapter 2 for more details)

- (a) particles can be in one of the two states: *active* and *dormant*,

- (b) particles migrate while in the active state,
- (c) a pair of particles in the active state can coalesce (even from different locations) with each other to form a single active particle,
- (d) the interaction between the particles is *repulsive* in nature, in the sense that a particle discourages another particle to be at the same location with the same state (active or dormant). To be more precise, the associated transition of a particle happens at a slower rate due to the interaction with the other particles.

As stated earlier in Theorem 3.2.1, the dichotomy between clustering and coexistence is solely determined by the coalescence of two dual particles, and so we only need to analyse the dual process starting from two particles. There are two ways in which we can describe the two-particle dual process, namely, as a *configuration process* that keeps track of the number of active and dormant particles at each location of the geographic space, or as a *coordinate process* that gives only the location and the state (active or dormant) of the particles that are present in the system. In Chapter 2, the dual process  $Z_*$  was introduced via a configuration process. However, in what follows we describe the two-particle dual originating from the process  $Z_*$  as a coordinate process in order to keep computations and notations simple. For the sake of completeness, in Appendix A.1 we include a short description of the configuration process associated with the original two-particle dual.

The transition rates for the two particles in the dual process are as follows:

- **(Migration)** An active particle at site  $i$  migrates to site  $j$  at rate  $a(i, j)$  if there is no active particle at site  $j$ , otherwise at rate  $a(i, j)(1 - \frac{1}{N_j})$ .
- **(Active to Dormant)** An active particle at site  $i$  becomes dormant at site  $i$  at rate  $\lambda$  if there is no dormant particle at site  $i$ , otherwise at rate  $\lambda(1 - \frac{1}{M_i})$ .
- **(Dormant to Active)** A dormant particle at site  $i$  becomes active at site  $i$  at rate  $\lambda K_i$  if there is no active particle at site  $i$ , otherwise at rate  $\lambda(K_i - \frac{1}{M_i})$ .
- **(Coalescence)** An active particle at site  $i$  coalesces with another active particle at site  $j$  at rate  $\frac{a(i, j)}{N_j}$ .

In the two-particle dual described above, once coalescence has occurred, only a single particle remains in the system for the rest of the time. Because of this, the coalesced state of the two particles, which we call  $\otimes$ , becomes absorbing for the associated process stopped at the time of coalescence. As we are interested in the coalescence probability of the two dual particles only, it suffices to analyse the absorption time to  $\otimes$  of the resulting absorbing process. Furthermore, by virtue of the well-known Dynkin criterion for lumpability, the absorbing process remains a continuous-time Markov chain. Although this can be verified by standard computations, for the convenience of the reader we include a brief proof in Appendix A.1. Below we provide a formal definition of the absorbing two-particle process as *interacting RW1*, which is basically a coordinate process living on the state space

$$\mathcal{S} := (G \times G) \cup \{\otimes\}, \quad G := \mathbb{Z}^d \times \{0, 1\}. \quad (3.10)$$

**Definition 3.3.1 (Interacting RW1).** The interacting RW1 process

$$\xi := (\xi(t))_{t \geq 0} \tag{3.11}$$

is the continuous-time Markov chain on the state space  $\mathcal{S}$  with transition rates

$$\begin{aligned}
 & [(i, \alpha), (j, \beta)] \rightarrow \\
 & \left\{ \begin{array}{ll}
 \circledast, & \text{at rate } \alpha\beta(1 - \delta_{i,j}) \left[ \frac{a(i,j)}{N_j} + \frac{a(j,i)}{N_i} \right] + 2a(i, i) \frac{\alpha\beta}{N_i} \delta_{i,j}, \\
 [(i, 1 - \alpha), (j, \beta)], & \text{at rate } \lambda[\alpha + (1 - \alpha)K_i] - \frac{\lambda}{M_i} \delta_{i,j}(1 - \delta_{\alpha,\beta}), \\
 [(i, \alpha), (j, 1 - \beta)], & \text{at rate } \lambda[\beta + (1 - \beta)K_j] - \frac{\lambda}{M_j} \delta_{i,j}(1 - \delta_{\alpha,\beta}), \\
 [(k, \alpha), (j, \beta)], & \text{at rate } \alpha a(i, k) - a(i, k) \frac{\alpha\beta}{N_j} \delta_{k,j} \quad \text{for } k \neq i \in \mathbb{Z}^d, \\
 [(i, \alpha), (k, \beta)], & \text{at rate } \beta a(j, k) - a(j, k) \frac{\alpha\beta}{N_i} \delta_{k,i} \quad \text{for } k \neq j \in \mathbb{Z}^d,
 \end{array} \right. \tag{3.12}
 \end{aligned}$$

where  $\delta_{\cdot, \cdot}$  denotes the Kronecker delta-function. ■

Here,  $\xi(t) = [(i, \alpha), (j, \beta)]$  provides the location  $(i, j \in \mathbb{Z}^d)$  and the state  $(\alpha, \beta \in \{0, 1\})$  of the two particles in the process at time  $t$ , where 0 stands for dormant and 1 stands for active, respectively.

**Remark 3.3.2.** Note that the coalescence time of the original two-particle dual process becomes the absorption time of  $\xi$ , and thus the original clustering criterion stated in Theorem 3.2.1 is equivalent to asking whether or not  $\xi$  is absorbed in  $\circledast$  with probability 1. However, the negative second terms in the last two transition rates of  $\xi$  (see (3.12)) imply that the two particles interact repulsively with each other even when they migrate in the active state. As a consequence, the effective migration kernel of a single particle becomes inhomogeneous in space, and so  $\xi$  is much harder to analyse than the auxiliary two-particle dual  $\hat{\xi}$  defined in Definition 3.2.2. Another key difference between  $\xi$  and  $\hat{\xi}$  is that  $\hat{\xi}$  has a positive rate of absorption only when both particles are on the same location in the active state. Although it may seem natural that  $\xi$  has a higher chance of absorption than  $\hat{\xi}$ , we will show later via a comparison argument that, under the non-clumping criterion (see (3.6)) on  $(N_i)_{i \in \mathbb{Z}^d}$ , if one process enters the absorbing state  $\circledast$  with probability 1, then the other process does so too. This ultimately provides us with the alternative criterion for clustering in Theorem 3.2.4.

From now onwards, we write  $\mathbb{P}^\eta$  to denote the law of the process  $\xi$  started from  $\eta \in \mathcal{S}$ , and  $\mathbb{E}^\eta$  to denote expectation w.r.t.  $\mathbb{P}^\eta$ .

**Remark 3.3.3.** Note that, by virtue of Assumption 2.A and Assumption 3.A, all states in  $\mathcal{S}$  are accessible by  $\xi$ .

In addition to the auxiliary two-particle process  $\hat{\xi}$  defined in Definition 3.2.2, and and the *interacting RW1* process  $\xi$  defined above, we introduce one more two-particle system, called *independent RW*, on the same state space  $\mathcal{S}$ . This will also serve as an intermediate comparison object.

**Definition 3.3.4 (Independent RW).** The independent RW process

$$\xi^* := (\xi^*(t))_{t \geq 0} \tag{3.13}$$

is the continuous-time Markov chain on the state space  $\mathcal{S}$  with transition rates

$$\begin{aligned}
 & [(i, \alpha), (j, \beta)] \rightarrow \\
 & \begin{cases} \circledast, & \text{at rate } 2a(i, i) \frac{\alpha\beta}{N_i} \delta_{i,j}, \\
 [(i, 1 - \alpha), (j, \beta)], & \text{at rate } \lambda[\alpha + (1 - \alpha)K_i], \\
 [(i, \alpha), (j, 1 - \beta)], & \text{at rate } \lambda[\beta + (1 - \beta)K_j], \\
 [(k, \alpha), (j, \beta)], & \text{at rate } \alpha a(i, k) \quad \text{for } k \neq i \in \mathbb{Z}^d, \\
 [(i, \alpha), (k, \beta)], & \text{at rate } \beta a(j, k) \quad \text{for } k \neq j \in \mathbb{Z}^d. \end{cases} \quad (3.14)
 \end{aligned}$$

■

In Section 3.4 we delve deeper into the independent RW process  $\xi^*$ , in order to utilize the comparison results derived in the next two sections and determine the clustering regime. We write  $\mathbb{P}_\eta^*$  to denote the law of  $\xi^*$  started from  $\eta \in \mathcal{S}$ , and  $\mathbb{E}_\eta^*$  to denote expectation w.r.t.  $\mathbb{P}_\eta^*$ .

In the following proposition, we establish the well-posedness of  $\hat{\xi}$  (see Definition 3.2.2), and of  $\xi, \xi^*$  defined above.

**Proposition 3.3.5 (Stability).** *All three processes  $\xi, \hat{\xi}, \xi^*$  are non-explosive continuous-time Markov chains on the countable state space  $\mathcal{S}$ .*

*Proof.* We prove this claim by using the Foster-Lyapunov criterion (see [122]). Let  $B_0 := \{\circledast\}$ , and for  $n \in \mathbb{N}$  define  $B_n := \{[(i, \alpha), (j, \beta)] \in \mathcal{S} : \max\{\|i\|, \|j\|\} < n\} \cup B_0$ . Define

$$V(\eta) := \begin{cases} \|i\| + \|j\|, & \text{if } \eta = [(i, \alpha), (j, \beta)], \\
 0, & \text{otherwise,} \end{cases} \quad \eta \in \mathcal{S}. \quad (3.15)$$

Furthermore, let  $Q, \hat{Q}, Q^*$  be the infinitesimal generators of the processes  $\xi, \hat{\xi}, \xi^*$ , respectively. Note that, for  $\eta = [(i, \alpha), (j, \beta)] \in \mathcal{S}$ ,

$$\begin{aligned}
 QV(\eta) &= \alpha \sum_{k \neq i} a(i, k)(\|k\| - \|i\|) + \beta \sum_{k \neq j} a(j, k)(\|k\| - \|j\|) \\
 &\quad - 2\alpha\beta(1 - \delta_{i,j}) \left[ \frac{a(i,j)}{N_j} \|i\| + \frac{a(j,i)}{N_i} \|j\| \right] - \frac{\alpha\beta}{N_i} \delta_{i,j} \\
 &\leq (\alpha + \beta)\mu_1 + 2\alpha\beta(1 - \delta_{i,j}) \left[ \frac{a(i,j)}{N_j} \|i\| + \frac{a(j,i)}{N_i} \|j\| \right] \\
 &\leq 2V(\eta) + (\alpha + \beta)\mu_1 \\
 &\leq 2V(\eta) + 2\mu_1 \quad (\text{since } \alpha + \beta \leq 2),
 \end{aligned} \quad (3.16)$$

where  $\mu_1 := \sum_{i \in \mathbb{Z}^d \setminus \{0\}} \|i\| a(0, i)$ . Let  $V' : \mathcal{S} \rightarrow [0, \infty)$  be the function defined by  $\eta \mapsto V(\eta) + \mu_1$ . Note that  $B_n \uparrow \mathcal{S}$  as  $n \rightarrow \infty$  and  $\inf_{\eta \in B_n^c} V'(\eta) \geq n$ . Thus,  $\inf_{\eta \in B_n^c} V'(\eta) \uparrow \infty$  as  $n \rightarrow \infty$  and, by (3.16),  $QV'(\eta) \leq 2V'(\eta)$ . Hence the Foster-Lyapunov criterion is satisfied by the generator  $Q$ , and so  $\xi$  is non-explosive. Similar arguments show that  $\hat{\xi}$  and  $\xi^*$  are non-explosive as well.  $\square$

### §3.3.2 Comparison between interacting duals

In this section we show, via comparison between the infinitesimal generators of the two-particle dual  $\xi$  and the auxiliary two-particle dual  $\hat{\xi}$  introduced in Definition 3.2.2, that the two processes have in fact very similar behaviour when it comes to long-run survivability. This is not surprising given that there are only slight differences in the migration and absorption mechanism (cf. the first and the last transition rate in Definition 3.2.2 and Definition 3.3.1) of the active particles present in the two processes.

**Proposition 3.3.6 (Stochastic domination).** *Let  $f: \mathcal{S} \rightarrow \mathbb{R}$  be bounded and such that  $f(\eta) \leq f(\otimes)$  for all  $\eta \in \mathcal{S}$ . Let  $(\xi(t))_{t \geq 0}$  and  $(\hat{\xi}(t))_{t \geq 0}$  be the interacting RW1 and the auxiliary two-particle system defined in Definition 3.3.1 and Definition 3.2.2, respectively. Then, for any  $\eta \in \mathcal{S}$  and  $t \geq 0$ ,  $\mathbb{E}^\eta[f(\xi(t))] \geq \hat{\mathbb{E}}^\eta[f(\hat{\xi}(t))]$ .*

*Proof.* Let  $Q$  and  $\hat{Q}$  be the generators of the processes  $\xi, \hat{\xi}$ , respectively. Since  $\xi$  and  $\hat{\xi}$  are non-explosive continuous-time Markov processes on a countable state space,  $Q$  and  $\hat{Q}$  generate unique Markov semigroups  $(S_t)_{t \geq 0}$  and  $(\hat{S}_t)_{t \geq 0}$ , respectively, given by

$$(S_t g)(\eta) = \mathbb{E}^\eta[g(\xi(t))], \quad (\hat{S}_t g)(\eta) = \hat{\mathbb{E}}^\eta[g(\hat{\xi}(t))], \quad t \geq 0, \quad (3.17)$$

where  $g: \mathcal{S} \rightarrow \mathbb{R}$  is bounded and  $\eta \in \mathcal{S}$ . Since  $f$  is bounded, we can apply the variation of constants formula for semigroups, to obtain

$$(S_t f)(\eta) - (\hat{S}_t f)(\eta) = \int_0^t (S_{t-s}(Q - \hat{Q})\hat{S}_s f)(\eta) ds. \quad (3.18)$$

The actions of  $Q$  and  $\hat{Q}$  on a bounded function  $g: \mathcal{S} \rightarrow \mathbb{R}$  are given by

$$\begin{aligned} Qg(\eta) &= \alpha \sum_{k \neq i} a(i, k) \left[1 - \frac{\beta}{N_j} \delta_{k,j}\right] \{g([(k, \alpha), (j, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\ &\quad + \beta \sum_{k \neq j} a(j, k) \left[1 - \frac{\alpha}{N_i} \delta_{k,i}\right] \{g([(i, \alpha), (k, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\ &\quad + [\lambda(\alpha + (1 - \alpha)K_i) - \frac{\lambda}{M_i} \delta_{i,j}(1 - \delta_{\alpha,\beta})] \\ &\quad \times \{g([(i, 1 - \alpha), (j, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\ &\quad + [\lambda(\beta + (1 - \beta)K_j) - \frac{\lambda}{M_j} \delta_{i,j}(1 - \delta_{\alpha,\beta})] \\ &\quad \times \{g([(i, \alpha), (j, 1 - \beta)]) - g([(i, \alpha), (j, \beta)])\} \\ &\quad + [\alpha\beta(1 - \delta_{i,j}) \left(\frac{a(i,j)}{N_j} + \frac{a(j,i)}{N_i}\right) + 2a(i, i) \frac{\alpha\beta}{N_i} \delta_{i,j}] \\ &\quad \times \{g(\otimes) - g([(i, \alpha), (j, \beta)])\} \end{aligned} \quad (3.19)$$

and

$$\begin{aligned}
 \hat{Q}g(\eta) &= \alpha \sum_{k \neq i} a(i, k) \{g([(k, \alpha), (j, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\
 &\quad + \beta \sum_{k \neq j} a(j, k) \{g([(i, \alpha), (k, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\
 &\quad + [\lambda(\alpha + (1 - \alpha)K_i) - \frac{\lambda}{M_i} \delta_{i,j}(1 - \delta_{\alpha,\beta})] \\
 &\quad \times \{g([(i, 1 - \alpha), (j, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\
 &\quad + [\lambda(\beta + (1 - \beta)K_j) - \frac{\lambda}{M_j} \delta_{i,j}(1 - \delta_{\alpha,\beta})] \\
 &\quad \times \{g([(i, \alpha), (j, 1 - \beta)]) - g([(i, \alpha), (j, \beta)])\} \\
 &\quad + [2a(i, i) \frac{\alpha\beta}{N_i} \delta_{i,j}] \{g(\otimes) - g([(i, \alpha), (j, \beta)])\},
 \end{aligned} \tag{3.20}$$

where  $\eta = [(i, \alpha), (j, \beta)] \in \mathcal{S}$ . Thus,

$$\begin{aligned}
 ((Q - \hat{Q})g)(\eta) &= -\alpha\beta \sum_{k \neq i} \frac{a(i, k)}{N_j} \delta_{k,j} \{g([(k, \alpha), (j, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\
 &\quad - \alpha\beta \sum_{k \neq j} \frac{a(j, k)}{N_i} \delta_{k,i} \{g([(i, \alpha), (k, \beta)]) - g([(i, \alpha), (j, \beta)])\} \\
 &\quad + [\alpha\beta(1 - \delta_{i,j}) (\frac{a(i, j)}{N_j} + \frac{a(j, i)}{N_i})] \{g(\otimes) - g([(i, \alpha), (j, \beta)])\} \\
 &= -\alpha\beta(1 - \delta_{i,j}) [\frac{a(i, j)}{N_j} g([(j, \alpha), (j, \beta)]) + \frac{a(j, i)}{N_i} g([(i, \alpha), (i, \beta)])] \\
 &\quad + \alpha\beta(1 - \delta_{i,j}) [\frac{a(i, j)}{N_j} + \frac{a(j, i)}{N_i}] g(\otimes),
 \end{aligned} \tag{3.21}$$

and so if  $g$  is such that  $\sup_{\eta \in \mathcal{S}} g(\eta) = g(\otimes)$ , then

$$\begin{aligned}
 ((Q - \hat{Q})g)(\eta) &= \begin{cases} \alpha\beta(1 - \delta_{i,j}) \frac{a(i, j)}{N_j} \\ \quad \times [g(\otimes) - g([(j, \alpha), (j, \beta)])] \\ \quad + \alpha\beta(1 - \delta_{i,j}) \frac{a(j, i)}{N_i} \\ \quad \times [g(\otimes) - g([(i, \alpha), (i, \beta)])], & \text{if } \eta = [(i, \alpha), (j, \beta)] \neq \otimes, \\ 0, & \text{otherwise,} \end{cases} \\
 &\geq 0.
 \end{aligned} \tag{3.22}$$

Note that the semigroup  $(\hat{S}_t)_{t \geq 0}$  also has the property  $\sup_{\eta \in \mathcal{S}} (\hat{S}_s f)(\eta) = f(\otimes) = (\hat{S}_s f)(\otimes)$  for any  $s \geq 0$ , since  $f \leq f(\otimes)$  and  $\otimes$  is absorbing. Thus, combining the above with (3.22), we get that  $(Q - \hat{Q})\hat{S}_s f$  is a non-negative function for any  $s \geq 0$ . Therefore the right-hand side of (3.18) is non-negative as well, which proves the desired result.  $\square$

**Corollary 3.3.7 (Stochastic ordering of absorption times).** *Let  $\tau$  and  $\hat{\tau}$  denote the absorption time of the processes  $\xi$  and  $\hat{\xi}$ , respectively. Then, for any  $\eta \in \mathcal{S}$  and  $t > 0$ ,*

$$\mathbb{P}^\eta(\tau \leq t) \geq \hat{\mathbb{P}}^\eta(\hat{\tau} \leq t). \tag{3.23}$$

*Proof.* This follows by applying Proposition 3.3.6 to the function  $f = \mathbb{1}_{\{\otimes\}}$  and using that  $\otimes$  is absorbing for both  $\xi$  and  $\hat{\xi}$ .  $\square$

The above result tells that the two particles in the process  $\xi$  have a higher chance of absorption than in the auxiliary process  $\hat{\xi}$ . This fits with intuition: two active particles in  $\xi$  can coalesce even when sitting at different locations. In the next result we show that two particles in  $\hat{\xi}$  have a higher probability of being on top of each other in the active state or being absorbed than in  $\xi$ . This is essentially due to the extra repulsive interaction that takes place when an active particle in  $\xi$  attempts to migrate, which is absent in  $\hat{\xi}$ .

**Proposition 3.3.8 (Stochastic ordering of hitting times).** *Let  $B \subset \mathcal{S}$  be defined as*

$$B := \{[(i, 1), (i, 1)]: i \in \mathbb{Z}^d\} \cup \{\otimes\}. \quad (3.24)$$

Let  $T_B, \hat{T}_B$  denote the first hitting time of the set  $B$  for  $\xi$  and  $\hat{\xi}$ , respectively. Then, for all  $y \in \mathcal{S}$ ,

$$\hat{\mathbb{P}}^y(\hat{T}_B < \infty) \geq \mathbb{P}^y(T_B < \infty). \quad (3.25)$$

*Proof.* Let  $g: \mathcal{S} \rightarrow [0, 1]$  and  $\hat{g}: \mathcal{S} \rightarrow [0, 1]$  be defined as

$$g(y) := \mathbb{P}^y(T_B < \infty), \quad \hat{g}(y) := \hat{\mathbb{P}}^y(\hat{T}_B < \infty), \quad y \in \mathcal{S}. \quad (3.26)$$

We are required to show that

$$\hat{g}(y) \geq g(y) \text{ for any } y \in \mathcal{S}. \quad (3.27)$$

To that end, let  $Q$  and  $\hat{Q}$  be the generators of the processes  $\xi$  and  $\hat{\xi}$ , respectively. Applying  $Q - \hat{Q}$  to the function  $\hat{g}$ , we get from (3.22) that

$$\begin{aligned} & (Q\hat{g})(y) - (\hat{Q}\hat{g})(y) \\ &= \begin{cases} \alpha\beta(1 - \delta_{i,j}) \frac{\alpha(i,j)}{N_j} \left\{ \hat{g}(\otimes) - \hat{g}([(j, \alpha), (j, \beta)]) \right\} \\ \quad + \alpha\beta(1 - \delta_{i,j}) \frac{\alpha(j,i)}{N_i} \left\{ \hat{g}(\otimes) - \hat{g}([(i, \alpha), (i, \beta)]) \right\}, & \text{if } y = [(i, \alpha), (j, \beta)] \neq \otimes, \\ 0, & \text{otherwise.} \end{cases} \end{aligned} \quad (3.28)$$

By a first-jump analysis of  $\hat{\xi}$ , we have  $(\hat{Q}\hat{g})(y) = 0$  for any  $y \notin B$  and  $\hat{g} \equiv 1$  on  $B$ . Thus, the right-hand side of (3.28) is always 0, and so  $(Q\hat{g})(y) = (\hat{Q}\hat{g})(y) = 0$  for any  $y \notin B$ . Let  $y \in \mathcal{S}$  be fixed, and let  $\xi$  be started from  $y$ . Since  $\hat{g}$  is bounded and  $\xi$  is non-explosive, the process  $(M_t)_{t \geq 0}$  defined by  $M_t := \hat{g}(\xi(t)) - \int_0^t (Q\hat{g})(\xi(s)) ds$  is a martingale under the law  $\mathbb{P}^y$  w.r.t. the natural filtration associated to the process  $\xi$ . Hence the stopped process  $(M_{t \wedge T_B})_{t \geq 0}$  is also a martingale. Note that, since  $Q\hat{g} = 0$  outside  $B$ , we have  $\int_0^{t \wedge T_B} (Q\hat{g})(\xi(s)) ds = 0$  for any  $t \geq 0$ . Hence  $M_{t \wedge T_B} = \hat{g}(\xi(t \wedge T_B))$  for any  $t \geq 0$ . By the martingale property, for any  $t > 0$ ,

$$\hat{g}(y) = \mathbb{E}^y[\hat{g}(\xi(0))] = \mathbb{E}^y[\hat{g}(\xi(t \wedge T_B))] \geq \mathbb{E}^y[\hat{g}(\xi(T_B)) \mathbb{1}_{T_B < t}] = \mathbb{P}^y(T_B < t). \quad (3.29)$$

Letting  $t \rightarrow \infty$ , we get  $\hat{g}(y) \geq \mathbb{P}^y(T_B < \infty) = g(y)$ , which proves (3.25).  $\square$

With the help of the above proposition, we can compare the probability of absorption for  $\xi$  and  $\hat{\xi}$ . Corollary 3.3.7 implied that  $\xi$  is more likely to get absorbed at  $\otimes$  than  $\hat{\xi}$ . The following result, however, tells that, under a certain condition, if  $\xi$  is absorbed with probability 1, then so is  $\hat{\xi}$ .

**Theorem 3.3.9 (Comparison of absorption probabilities).** *Let  $\nu: \mathcal{S} \rightarrow [0, 1]$  and  $\hat{\nu}: \mathcal{S} \rightarrow [0, 1]$  be defined by*

$$\nu(\eta) := \mathbb{P}^\eta(\tau < \infty), \quad \hat{\nu}(\eta) := \hat{\mathbb{P}}^\eta(\hat{\tau} < \infty), \quad (3.30)$$

*i.e.,  $\nu(\eta)$  and  $\hat{\nu}(\eta)$  are the absorption probabilities of the processes  $\xi$  and  $\hat{\xi}$ , respectively, started from  $\eta$ . Assume that*

$$\inf\{\hat{\nu}([(i, 1), (i, 1)]): i \in \mathbb{Z}^d\} > 0. \quad (3.31)$$

*For all  $\eta \in \mathcal{S}$ , if  $\nu(\eta) = 1$ , then  $\hat{\nu}(\eta) = 1$ .*

*Proof.* The proof is by contradiction. If  $\eta = \otimes$ , then the claim is trivial. So assume that  $\hat{\nu}(\eta) < 1$  and  $\nu(\eta) = 1$  for some  $\eta \neq \otimes$ . Note that, by the strong Markov property,

$$\inf_{y \in \mathcal{S}} \hat{\nu}(y) = 0. \quad (3.32)$$

Moreover, since by Remark 3.3.3 the process  $\xi$  started from  $\eta$  can visit any configuration  $y \in \mathcal{S}$  in finite time with positive probability, we have

$$\nu(y) = 1 \quad \forall y \in \mathcal{S}. \quad (3.33)$$

We will show that (3.32) and (3.33) are contradictory.

For  $y \in \mathcal{S}$ , set

$$g(y) := \mathbb{P}^y(T_B < \infty), \quad \hat{g}(y) := \hat{\mathbb{P}}^y(\hat{T}_B < \infty), \quad y \in \mathcal{S}, \quad (3.34)$$

where  $T_B, \hat{T}_B$  are the hitting times of the set  $B := \{[(i, 1), (i, 1)] : i \in \mathbb{Z}^d\} \cup \{\otimes\}$  for  $\xi$  and  $\hat{\xi}$ , respectively. Now, since  $T_B \leq \tau$  a.s., we have  $g(y) \geq \nu(y)$  for any  $y \in \mathcal{S}$ , and combined with (3.33) this implies that  $g \equiv 1$  on  $\mathcal{S}$ . So by Proposition 3.3.8, we have

$$\hat{g}(y) = \hat{\mathbb{P}}^y(\hat{T}_B < \infty) = 1 \text{ for all } y \in \mathcal{S}, \quad (3.35)$$

i.e., the process  $\hat{\xi}$  started from any configuration  $y \in \mathcal{S}$  enters  $B$  with probability 1. Let  $\hat{T}$  be the hitting time of the set  $\hat{B} := B \setminus \{\otimes\}$  for the process  $\hat{\xi}$ , and let

$$\epsilon := \inf\{\hat{\nu}(y): y \in \hat{B}\}. \quad (3.36)$$

By (3.31), we have  $\epsilon > 0$ . Note that  $\hat{T} \leq \hat{\tau}$  a.s. for the process  $\hat{\xi}$ , since two particles coalesce only when they are on top of each other and are both active, and so  $\hat{T}_B = \hat{T} \wedge \hat{\tau} = \hat{T}$  a.s. Therefore, by (3.35),  $\hat{\mathbb{P}}^y(\hat{T} < \infty) = 1$  for any  $y \in \mathcal{S}$ . Therefore, for  $y \in \mathcal{S}$ ,

$$\begin{aligned} \hat{\nu}(y) &= \hat{\mathbb{P}}^y(\hat{\tau} < \infty) = \hat{\mathbb{P}}^y(\hat{T} \leq \hat{\tau} < \infty) = \sum_{x \in \hat{B}} \hat{\mathbb{P}}^y(\hat{\xi}(\hat{T}) = x, \hat{T} < \infty, \hat{\tau} < \infty) \\ &= \sum_{x \in \hat{B}} \hat{\mathbb{P}}^y(\hat{\tau} < \infty \mid \hat{\xi}(\hat{T}) = x, \hat{T} < \infty) \hat{\mathbb{P}}^y(\hat{\xi}(\hat{T}) = x, \hat{T} < \infty) \\ &= \sum_{x \in \hat{B}} \hat{\mathbb{P}}^x(\hat{\tau} < \infty) \hat{\mathbb{P}}^y(\hat{\xi}(\hat{T}) = x, \hat{T} < \infty) \\ &= \sum_{x \in \hat{B}} \hat{\nu}(x) \hat{\mathbb{P}}^y(\hat{\xi}(\hat{T}) = x, \hat{T} < \infty) \geq \epsilon \hat{\mathbb{P}}^y(\hat{T} < \infty) \geq \epsilon, \end{aligned} \quad (3.37)$$

which contradicts (3.32). □



**Corollary 3.3.10 (Equivalence of absorption probabilities).** *For any  $\eta \in \mathcal{S}$ ,  $\nu(\eta) = 1$  if  $\hat{\nu}(\eta) = 1$ . Furthermore, if (3.31) holds, then the converse is true as well.*

*Proof.* The claim follows from Corollary 3.3.7 and Theorem 3.3.9.  $\square$

### §3.3.3 Comparison with non-interacting dual

The goal of this section is to reduce the absorption analysis of  $\xi$  and  $\hat{\xi}$  in the previous section to equivalent statements involving the *independent RW1* introduced in Definition 3.3.4. We follow the same comparison method used earlier.

**Theorem 3.3.11 (Comparison of absorption probabilities).** *Let  $\nu^*: \mathcal{S} \rightarrow [0, 1]$  and  $\hat{\nu}: \mathcal{S} \rightarrow [0, 1]$  be defined by*

$$\nu^*(\eta) := \mathbb{P}_\eta^*(\tau^* < \infty), \quad \hat{\nu}(\eta) := \hat{\mathbb{P}}^\eta(\hat{\tau} < \infty). \quad (3.38)$$

*Assume that*

$$\inf\{\nu^*([(i, 1), (i, 1)]): i \in \mathbb{Z}^d\} > 0. \quad (3.39)$$

*For all  $\eta \in \mathcal{S}$ , if  $\hat{\nu}(\eta) = 1$ , then  $\nu^*(\eta) = 1$ .*

*Proof.* The proof follows a similar argument as in the proof of Theorem 3.3.9. Suppose that  $\hat{\nu}(\eta) = 1$  and  $\nu^*(\eta) < 1$ . By the strong Markov property,

$$\inf_{y \in \mathcal{S}} \nu^*(y) = 0. \quad (3.40)$$

Since, by Remark 3.2.3, the process  $\hat{\xi}$  started from  $\eta$  can visit any configuration  $y \in \mathcal{S}$  in finite time with positive probability, we have

$$\hat{\nu}(y) = 1 \quad \forall y \in \mathcal{S}. \quad (3.41)$$

We will show that (3.40) and (3.41) are contradictory.

Let  $\bar{B} \subset \mathcal{S}$  be defined as

$$\bar{B} := \left\{ [(i, \alpha), (i, \beta)] \in \mathcal{S}: \alpha \neq \beta, \nu^*([(i, 1), (i, 1)]) < \nu^*([(i, 1), (i, 0)]) \right\} \cup \{\otimes\}. \quad (3.42)$$

By symmetry and a first-jump analysis, we have

$$\nu^*([(i, 1), (i, 0)]) = \nu^*([(i, 0), (i, 1)]) = \nu^*([(i, 0), (i, 0)]) \quad \forall i \in \mathbb{Z}^d. \quad (3.43)$$

Let  $\hat{T}_{\bar{B}}$  denote the first hitting time of the set  $\bar{B}$  for the process  $\hat{\xi}$ , and let

$$\bar{\epsilon} := \inf\{\nu^*(y): y \in \bar{B}\}. \quad (3.44)$$

By (3.39) and (3.43),  $\bar{\epsilon} > 0$ . Note that if  $\hat{Q}$  and  $Q^*$  are the generators of the processes  $\hat{\xi}$  and  $\xi^*$ , respectively, then

$$\begin{aligned} & ((\hat{Q} - Q^*)\nu^*)(x) \\ &= \begin{cases} \frac{\lambda}{M_i} \delta_{i,j} (1 - \delta_{\alpha,\beta}) [\nu^*([(i, 1), (i, 0)]) - \nu^*([(i, 1), (i, 1)])], & x = [(i, \alpha), (j, \beta)] \neq \otimes, \\ 0, & \text{otherwise,} \end{cases} \end{aligned} \quad (3.45)$$

where (3.43) is used. Moreover, the right-hand side of the above equation is negative whenever  $x \notin \bar{B}$ . Since  $Q^*\nu^* \equiv 0$ , we have

$$(\hat{Q}\nu^*)(x) \leq 0, \quad x \notin \bar{B}. \quad (3.46)$$

Let  $y \in \mathcal{S}$  be fixed arbitrarily, and let the process  $\hat{\xi}$  be started from  $y$ . Since  $\nu^*$  is bounded and  $\hat{\xi}$  is non-explosive, the process  $(M_t)_{t \geq 0}$  with  $M_t := \nu^*(\hat{\xi}(t)) - \int_0^t (\hat{Q}\nu^*)(\hat{\xi}(s)) ds$  is a martingale under the law  $\hat{\mathbb{P}}^y$  w.r.t. the natural filtration associated to the process  $\hat{\xi}$ . Hence the stopped process  $(M_{t \wedge \hat{T}_{\bar{B}}})_{t \geq 0}$  is also a martingale. By (3.46), we have  $\int_0^{t \wedge \hat{T}_{\bar{B}}} (\hat{Q}\nu^*)(\hat{\xi}(s)) ds \leq 0$  a.s. for any  $t \geq 0$ . Hence  $M_{t \wedge \hat{T}_{\bar{B}}} \geq \nu^*(\hat{\xi}(t \wedge \hat{T}_{\bar{B}}))$  for any  $t \geq 0$ . By the martingale property, for any  $t > 0$ ,

$$\begin{aligned} \nu^*(y) &= \hat{\mathbb{E}}^y[\nu^*(\hat{\xi}(0))] = \hat{\mathbb{E}}^y[M_{t \wedge \hat{T}_{\bar{B}}}] \geq \hat{\mathbb{E}}^y[\nu^*(\hat{\xi}(t \wedge \hat{T}_{\bar{B}}))] \\ &\geq \hat{\mathbb{E}}^y[\nu^*(\hat{\xi}(\hat{T}_{\bar{B}})) \mathbb{1}_{\hat{T}_{\bar{B}} < t}] \geq \bar{\epsilon} \hat{\mathbb{P}}^y(\hat{T}_{\bar{B}} < t) \geq \bar{\epsilon} \hat{\mathbb{P}}^y(\hat{\tau} < t), \end{aligned} \quad (3.47)$$

where in the last inequality we use that  $\hat{T}_{\bar{B}} \leq \hat{\tau}$  a.s. Letting  $t \rightarrow \infty$ , we find with the help of (3.41) that  $\nu^*(y) \geq \bar{\epsilon} \hat{\mathbb{P}}^y(\hat{\tau} < \infty) = \bar{\epsilon} \hat{\nu}(y) = \bar{\epsilon}$ , which contradicts (3.40).  $\square$

**Theorem 3.3.12 (Comparison of absorption probabilities).** *Let  $\nu^*$ ,  $\nu$ ,  $\hat{\nu}$  be the absorption probability of  $\xi^*$ ,  $\hat{\xi}$ ,  $\xi$ , respectively, i.e.,*

$$\nu^*(\eta) := \mathbb{P}_\eta^*(\tau^* < \infty), \quad \hat{\nu}(\eta) := \hat{\mathbb{P}}^\eta(\hat{\tau} < \infty), \quad \nu(\eta) := \mathbb{P}^\eta(\tau < \infty). \quad (3.48)$$

Assume that

$$\inf\{\hat{\nu}([(i, 1), (i, 0)]) : i \in \mathbb{Z}^d\} > 0. \quad (3.49)$$

For all  $\eta \in \mathcal{S}$ , if  $\nu^*(\eta) = 1$ , then  $\hat{\nu}(\eta) = 1$ , and hence  $\nu(\eta) = 1$  as well.

*Proof.* By Corollary 3.3.7, it suffices to prove that  $\hat{\nu}(\eta) = 1$ . Suppose that this fails. Then, by the strong Markov property,

$$\inf_{y \in \mathcal{S}} \hat{\nu}(y) = 0. \quad (3.50)$$

Moreover, since the process  $\xi^*$  started from  $\eta$  can visit any configuration  $y \in \mathcal{S}$  in finite time with positive probability, we have

$$\nu^*(y) = 1 \quad \forall y \in \mathcal{S}. \quad (3.51)$$

We will show that (3.50) and (3.51) are contradictory.

Let  $B' \subset \mathcal{S}$  be defined as

$$B' := \left\{ [(i, \alpha), (i, \beta)] \in \mathcal{S} : \alpha \neq \beta, \hat{\nu}([(i, 1), (i, 1)]) \geq \hat{\nu}([(i, 1), (i, 0)]) \right\} \cup \{\otimes\}. \quad (3.52)$$

By symmetry and a first-jump analysis, we have

$$\hat{\nu}([(i, 1), (i, 0)]) = \hat{\nu}([(i, 0), (i, 1)]) = \hat{\nu}([(i, 0), (i, 0)]) \quad \forall i \in \mathbb{Z}^d. \quad (3.53)$$

Let  $T_{B'}^*$  denote the first hitting time of the set  $B'$  for the process  $\xi^*$ , and let

$$\epsilon' := \inf\{\hat{\nu}(y) : y \in B'\}. \quad (3.54)$$

By (3.49) and (3.53), we have  $\epsilon' > 0$ . Note that if  $\hat{Q}$  and  $Q^*$  are the generators of the processes  $\hat{\xi}$  and  $\xi^*$ , respectively, then

$$\begin{aligned} & ((Q^* - \hat{Q})\hat{\nu})(x) \\ &= \begin{cases} \frac{\lambda}{M_i} \delta_{i,j} (1 - \delta_{\alpha,\beta}) [\hat{\nu}([(i, 1), (i, 1)]) - \hat{\nu}([(i, 1), (i, 0)])], & x = [(i, \alpha), (j, \beta)] \neq \otimes, \\ 0, & \text{otherwise,} \end{cases} \end{aligned} \quad (3.55)$$

where we use (3.53). Moreover, the right-hand side of the above equation is negative whenever  $x \notin B'$ . Since  $\hat{Q}\hat{\nu} \equiv 0$ , we have

$$(Q^*\hat{\nu})(x) \leq 0, \quad x \notin B'. \quad (3.56)$$

Let  $y \in \mathcal{S}$  be fixed arbitrarily, and let the process  $\xi^*$  be started from  $y$ . Since  $\hat{\nu}$  is bounded and  $\xi^*$  is non-explosive, the process  $(M_t)_{t \geq 0}$  with

$$M_t := \hat{\nu}(\xi^*(t)) - \int_0^t (Q^*\hat{\nu})(\xi^*(s)) ds \quad (3.57)$$

is a martingale under the law  $\mathbb{P}_y^*$  w.r.t. the natural filtration associated to the process  $\xi^*$ . Hence the stopped process  $(M_{t \wedge T_{B'}^*})_{t \geq 0}$  is also a martingale. By (3.56), we have  $\int_0^{t \wedge T_{B'}^*} (Q^*\hat{\nu})(\xi^*(s)) ds \leq 0$  a.s. for any  $t \geq 0$ . Hence  $M_{t \wedge T_{B'}^*} \geq \hat{\nu}(\xi^*(t \wedge T_{B'}^*))$  for any  $t \geq 0$ . By the martingale property, for any  $t > 0$ ,

$$\begin{aligned} \hat{\nu}(y) &= \mathbb{E}_y^*[\hat{\nu}(\xi^*(0))] = \mathbb{E}_y^*[M_{t \wedge T_{B'}^*}] \geq \mathbb{E}_y^*[\hat{\nu}(\xi^*(t \wedge T_{B'}^*))] \\ &\geq \mathbb{E}_y^*[\hat{\nu}(\xi^*(T_{B'}^*)) \mathbb{1}_{T_{B'}^* < t}] \geq \epsilon' \mathbb{P}_y^*(T_{B'}^* < t) \geq \epsilon' \mathbb{P}_y^*(\tau^* < t), \end{aligned} \quad (3.58)$$

where in the last inequality we use that  $T_{B'}^* \leq \tau^*$  a.s. Letting  $t \rightarrow \infty$ , we find via (3.51) that  $\hat{\nu}(y) \geq \epsilon' \mathbb{P}_y^*(\tau^* < \infty) = \epsilon' \nu^*(y) = \epsilon'$ , which contradicts (3.50).  $\square$

**Remark 3.3.13.** Theorem 3.3.12 tells us that coalescence of independent particles is sufficient for coalescence of interacting particles. The condition in (3.49) is stronger, because it requires control on the growth of both  $N_i$  and  $M_i$ .

### §3.3.4 Conclusion

**Theorem 3.3.14 (Equivalence of absorption probabilities).** *Let  $\nu^*$ ,  $\nu$  and  $\hat{\nu}$  be the functions defined by*

$$\nu^*(\eta) := \mathbb{P}_\eta^*(\tau^* < \infty), \quad \hat{\nu}(\eta) := \hat{\mathbb{P}}^\eta(\hat{\tau} < \infty), \quad \nu(\eta) := \mathbb{P}^\eta(\tau < \infty). \quad (3.59)$$

If

- (a)  $\inf\{\hat{\nu}([(i, 1), (i, 1)]): i \in \mathbb{Z}^d\} > 0$ ,
- (b)  $\inf\{\nu^*([(i, 1), (i, 1)]): i \in \mathbb{Z}^d\} > 0$ ,

then  $\nu^*(\eta) = 1$  whenever  $\nu(\eta) = 1$  for some  $\eta \in \mathcal{S}$ . If

$$\inf\{\hat{\nu}([(i, 1), (i, 0)]): i \in \mathbb{Z}^d\} > 0, \quad (3.60)$$

then the converse is true as well.

*Proof.* The forward direction follows by combining Theorem 3.3.9 and Theorem 3.3.11. The reverse direction is a direct consequence of Theorem 3.3.12 and Corollary 3.3.7.  $\square$

**Remark 3.3.15.** Theorem 3.3.14 tells us that if the interacting particle system coalesces with probability 1, then it is necessary that two independent particles coalesce with probability 1. The first two conditions are trivially satisfied when  $\sup_{i \in \mathbb{Z}^d} N_i < \infty$ . If, furthermore,  $\sup_{i \in \mathbb{Z}^d} M_i < \infty$ , then the third condition is satisfied as well.

We conclude this section by providing conditions on the sizes of the active and the dormant populations that are weaker than the ones mentioned in Remark 3.3.15, and under which the assumptions in Theorem 3.3.14 are satisfied.

**Theorem 3.3.16 (Lower bound on absorption probabilities).** *Let  $\hat{\nu}$  and  $\nu^*$  be the functions defined by*

$$\hat{\nu}(\eta) := \hat{\mathbb{P}}^\eta(\hat{\tau} < \infty), \quad \nu^*(\eta) := \mathbb{P}_\eta^*(\tau^* < \infty). \quad (3.61)$$

*If the sizes of the active populations  $(N_i)_{i \in \mathbb{Z}^d}$  are non-clumping, i.e.,*

$$\inf_{i \in \mathbb{Z}^d} \sum_{\|j-i\| \leq R} \frac{1}{N_j} > 0 \text{ for some } R < \infty, \quad (3.62)$$

*then*

- (a)  $\inf\{\hat{\nu}([(i, 1), (i, 1)]): i \in \mathbb{Z}^d\} > 0$ ,
- (b)  $\inf\{\nu^*([(i, 1), (i, 1)]): i \in \mathbb{Z}^d\} > 0$ .

*Furthermore, if the relative strengths of the seed-banks are bounded, i.e.,*

$$\sup_{i \in \mathbb{Z}^d} \frac{M_i}{N_i} < \infty, \quad (3.63)$$

*then*

- (i)  $\inf\{\hat{\nu}([(i, 1), (i, 0)]): i \in \mathbb{Z}^d\} > 0$ ,
- (ii)  $\inf\{\nu^*([(i, 1), (i, 0)]): i \in \mathbb{Z}^d\} > 0$ .

Before we give the proof of Theorem 3.3.16 we derive a series representation of the absorption probabilities  $\nu^*$  and  $\hat{\nu}$  of the respective processes  $\xi^*$  and  $\hat{\xi}$ .

**Lemma 3.3.17 (Series representation).** *Let  $\nu^*$  and  $\hat{\nu}$  be the functions defined by*

$$\nu^*(\eta) := \mathbb{P}_\eta^*(\tau^* < \infty), \quad \hat{\nu}(\eta) := \hat{\mathbb{P}}^\eta(\hat{\tau} < \infty). \quad (3.64)$$

*For  $i \in \mathbb{Z}^d$ , let  $R_i^*$  (respectively,  $\hat{R}_i$ ) be the total number of visits to the state  $[(i, 1), (i, 1)] \in \mathcal{S}$  made by the jump chain associated to the process  $\xi^*$  (respectively,  $\hat{\xi}$ ). Then, for  $\eta \in \mathcal{S} \setminus \{\otimes\}$ ,*

$$(a) \quad \nu^*(\eta) = \sum_{i \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_i+1} \mathbb{E}_\eta^*[R_i^*].$$

$$(b) \hat{\nu}(\eta) = \sum_{i \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_i+1} \hat{\mathbb{E}}^\eta[\hat{R}_i],$$

where  $c$  is the total migration rate defined in Assumption 2.A, and expectations are taken w.r.t. the respective laws of the jump chains associated to the processes  $\xi^*$  and  $\hat{\xi}$ .

*Proof.* We only prove part (a), because the proof of part (b) is the same. Let  $\eta \in \mathcal{S} \setminus \{\otimes\}$  be fixed, and let  $X^* := (X_n^*)_{n \in \mathbb{N}_0}$  be the embedded jump chain associated to the process  $\xi^*$  started at state  $\eta$ . Since  $X^*$  is absorbed to  $\otimes$  if and only if  $\xi^*$  is absorbed, it suffices to analyse  $X^*$ . Let  $T := \inf\{n \in \mathbb{N}_0 : X_n^* = \otimes\}$  be the absorption time of  $X^*$ . Note that, because the absorbing state  $\otimes$  can be reached in one step only from the states  $\{(i, 1), (i, 1)\} : i \in \mathbb{Z}^d\} \subset \mathcal{S}$ , for all  $n \in \mathbb{N}$  we have

$$\begin{aligned} \mathbb{P}_\eta^*(T = n) &= \sum_{i \in \mathbb{Z}^d} \mathbb{P}_\eta^*(X_{n-1}^* = [(i, 1), (i, 1)], T = n) \\ &= \sum_{i \in \mathbb{Z}^d} \mathbb{P}_\eta^*(X_n^* = \otimes \mid X_{n-1}^* = [(i, 1), (i, 1)]) \mathbb{P}_\eta^*(X_{n-1}^* = [(i, 1), (i, 1)]) \quad (3.65) \\ &= \sum_{i \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_i+1} \mathbb{P}_\eta^*(X_{n-1}^* = [(i, 1), (i, 1)]), \end{aligned}$$

where in the last equality we use that, by the Markov property,

$$\mathbb{P}_\eta^*(X_n^* = \otimes \mid X_{n-1}^* = [(i, 1), (i, 1)]) = \mathbb{P}_{[(i, 1), (i, 1)]}^*(X_1^* = \otimes) = \frac{1}{2(c+\lambda)N_i+1}. \quad (3.66)$$

Using that  $\eta \neq \otimes$ , we get

$$\begin{aligned} \nu^*(\eta) &= \mathbb{P}_\eta^*(T < \infty) = \sum_{n \in \mathbb{N}} \mathbb{P}_\eta^*(T = n) \\ &= \sum_{n \in \mathbb{N}} \sum_{i \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_i+1} \mathbb{P}_\eta^*(X_{n-1}^* = [(i, 1), (i, 1)]) \\ &= \sum_{i \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_i+1} \sum_{n \in \mathbb{N}} \mathbb{P}_\eta^*(X_{n-1}^* = [(i, 1), (i, 1)]) = \sum_{i \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_i+1} \mathbb{E}_\eta^*[R_i^*], \end{aligned} \quad (3.67)$$

where in the fourth equality we interchange the two sums using Fubini's theorem, and in the last equality we use

$$\mathbb{E}_\eta^*[R_i^*] = \sum_{n \in \mathbb{N}_0} \mathbb{P}_\eta^*(X_n^* = [(i, 1), (i, 1)]), \quad i \in \mathbb{Z}^d. \quad (3.68)$$

□

*Proof of Theorem 3.3.16.* We only prove parts (a) and (i), because the proof of parts (b) and (ii) is the same. Let  $\hat{X} := (\hat{X}_n)_{n \in \mathbb{N}_0}$  be the embedded jump chain associated to the process  $\hat{\xi}$ . For  $j \in \mathbb{Z}^d$ , let  $\hat{R}_j$  be the total number of visits made by  $\hat{X}$  to the state  $[(j, 1), (j, 1)]$ . We first show that, for any  $i, j \in \mathbb{Z}^d$ ,

$$\hat{\mathbb{E}}^{[(i, 1), (i, 1)]}[\hat{R}_j] \geq \sum_{n \in \mathbb{N}} m^{2n} a_n(i, j)^2, \quad (3.69)$$

where  $m := \frac{c}{2(c+\lambda)+1}$ . Note that, in the process  $\hat{\xi}$ , each of the two particles moves from  $i$  to  $j$  at rate  $a(i, j)$  while in the active state, and becomes dormant at rate  $\lambda$  when the two particles are not on top of each other with one active and the other dormant. Thus, for  $i, j, k \in \mathbb{Z}^d$  and  $n \in \mathbb{N}$ ,

$$\begin{aligned}
 & \hat{\mathbb{P}}^{[(k,1),(i,1)]}(\hat{X}_n = [(k,1), (j,1)]) \\
 & \geq \sum_{l \neq i} \hat{\mathbb{P}}^{[(k,1),(i,1)]}(\hat{X}_1 = [(k,1), (l,1)]) \hat{\mathbb{P}}^{[(k,1),(l,1)]}(\hat{X}_{n-1} = [(k,1), (j,1)]) \\
 & = \sum_{l \neq i} \frac{c}{2(c+\lambda)+(1/N_i)\delta_{k,i}} \frac{a(i,l)}{c} \hat{\mathbb{P}}^{[(k,1),(l,1)]}(\hat{X}_{n-1} = [(k,1), (j,1)]) \\
 & \geq m \sum_{l \neq i} a_1(i, l) \hat{\mathbb{P}}^{[(k,1),(l,1)]}(\hat{X}_{n-1} = [(k,1), (j,1)]),
 \end{aligned} \tag{3.70}$$

where  $a_1(\cdot, \cdot) := \frac{a(\cdot, \cdot)}{c}$  is the transition kernel of the embedded chain associated to the continuous-time random walk on  $\mathbb{Z}^d$  with rates  $a(\cdot, \cdot)$ . Using the above recursively, we obtain that, for any  $i, j, k \in \mathbb{Z}^d$  and  $n \in \mathbb{N}$ ,

$$\hat{\mathbb{P}}^{[(k,1),(i,1)]}(\hat{X}_n = [(k,1), (j,1)]) \geq m^n a_n(i, j). \tag{3.71}$$

Therefore, applying the above twice, for  $i, j \in \mathbb{Z}^d$  we have

$$\begin{aligned}
 \hat{\mathbb{P}}^{[(i,1),(i,1)]}(\hat{X}_{2n} = [(j,1), (j,1)]) & \geq \hat{\mathbb{P}}^{[(i,1),(i,1)]}(\hat{X}_n = [(i,1), (j,1)]) \\
 & \quad \times \hat{\mathbb{P}}^{[(i,1),(j,1)]}(\hat{X}_n = [(j,1), (j,1)]) \\
 & \geq m^n a_n(i, j) \hat{\mathbb{P}}^{[(j,1),(i,1)]}(\hat{X}_n = [(j,1), (j,1)]) \\
 & \geq m^{2n} a_n(i, j)^2.
 \end{aligned} \tag{3.72}$$

Hence, for  $i, j \in \mathbb{Z}^d$ ,

$$\begin{aligned}
 \hat{\mathbb{E}}^{[(i,1),(i,1)]}[\hat{R}_j] & = \sum_{n \in \mathbb{N}_0} \hat{\mathbb{P}}^{[(i,1),(i,1)]}(\hat{X}_n = [(j,1), (j,1)]) \\
 & \geq \sum_{n \in \mathbb{N}_0} \hat{\mathbb{P}}^{[(i,1),(i,1)]}(\hat{X}_{2n} = [(j,1), (j,1)]) \geq \sum_{n \in \mathbb{N}} m^{2n} a_n(i, j)^2.
 \end{aligned} \tag{3.73}$$

Finally, substituting the above into the series representation of  $\hat{\nu}$  in part (b) of Lemma 3.3.17, we obtain that, for  $i \in \mathbb{Z}^d$ ,

$$\begin{aligned}
 \hat{\nu}([(i,1), (i,1)]) & = \sum_{j \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_j+1} \hat{\mathbb{E}}^{[(i,1),(i,1)]}[\hat{R}_j] \\
 & \geq \sum_{j \in \mathbb{Z}^d} \frac{1}{2(c+\lambda)N_j+1} \sum_{n \in \mathbb{N}} m^{2n} a_n(i, j)^2 \\
 & \geq \frac{1}{2(c+\lambda)+1} \sum_{j \in B_R(i)} \frac{1}{N_j} \sum_{n \in \mathbb{N}} m^{2n} a_n(0, j-i)^2 \geq \epsilon_R \sum_{j \in B_R(i)} \frac{1}{N_j},
 \end{aligned} \tag{3.74}$$

where  $B_R(i) := \{j \in \mathbb{Z}^d : \|j - i\| \leq R\}$  and

$$\epsilon_R := \min \left\{ \frac{1}{2(c+\lambda)+1} \sum_{n \in \mathbb{N}} m^{2n} a_n(0, l)^2 : l \in B_R(0) \right\} > 0. \tag{3.75}$$

Since, by assumption,  $(N_i)_{i \in \mathbb{Z}^d}$  are non-clumping, the right-hand side of (3.74) is bounded away from zero irrespective of the choice  $i \in \mathbb{Z}^d$ , and so part (a) is proved.

To prove part (i), by doing a first-jump analysis of the process  $\hat{X}$  we get that, for  $i \in \mathbb{Z}^d$ ,

$$\begin{aligned} \hat{\nu}([(i, 1), (i, 0)]) &\geq \hat{\mathbb{P}}^{[(i, 1), (i, 0)]}(\hat{X}_1 = [(i, 1), (i, 1)]) \hat{\nu}([(i, 1), (i, 1)]) \\ &= \frac{\lambda K_i}{c + \lambda + \lambda K_i} \hat{\nu}([(i, 1), (i, 1)]), \end{aligned} \quad (3.76)$$

where  $K_i = \frac{N_i}{M_i}$ . Thus, if  $(N_i)_{i \in \mathbb{Z}^d}$  are non-clumping and  $\sup_{i \in \mathbb{Z}^d} K_i^{-1} < \infty$ , then

$$\hat{\nu}([(i, 1), (i, 0)]) \geq \frac{\lambda}{\lambda + (c + \lambda)(\sup_{i \in \mathbb{Z}^d} K_i^{-1})} \inf\{\hat{\nu}([(j, 1), (j, 1)]): j \in \mathbb{Z}^d\}, \quad (3.77)$$

which is bounded away from zero uniformly in  $i \in \mathbb{Z}^d$ , and so part (i) follows.  $\square$

## §3.4 Proofs: clustering criterion and clustering regime

In this section we prove our two main theorems, namely, Theorem 3.2.4 and Theorem 3.2.7 with the help of the results that were obtained in Section 3.3 by comparing various auxiliary duals.

### §3.4.1 Proof of clustering criterion

Here we give a proof of Theorem 3.2.4.

*Proof of Theorem 3.2.4.* Note (see Remark 3.3.2) that the system clusters if and only if the two-particle process  $\xi$  defined in Definition 3.3.1 is absorbed to  $\otimes$  with probability 1. Let  $\hat{\xi}$  be the auxiliary two-particle process defined in Definition 3.2.2, and  $\hat{\nu}(\eta)$  (respectively,  $\nu(\eta)$ ) be the absorption probability of the process  $\hat{\xi}$  (respectively,  $\xi$ ) started from state  $\eta \in G \times G$ . The system  $Z$  clusters if and only if  $\nu(\eta) = 1$  for any state  $\eta \in G \times G$ . By the forward direction of Corollary 3.3.10, we have that  $\nu(\eta) = 1$  whenever  $\hat{\nu}(\eta) = 1$ , and hence the forward direction of Theorem 3.2.4 follows. To prove the converse we note that, under the non-clumping assumption of the active populations sizes  $(N_i)_{i \in \mathbb{Z}^d}$  in (3.6), (3.31) in Corollary 3.3.10 holds by part (a) of Theorem 3.3.16, and hence  $\hat{\nu}(\eta) = 1$  whenever  $\nu(\eta) = 1$ , so that the converse follows as well.  $\square$

### §3.4.2 Independent particle system and clustering regime.

In order to prove Theorem 3.2.7, we need to take a closer look at the non-interacting two-particle process  $\xi^*$  introduced in Definition 3.3.4. In what follows we briefly describe the process  $\xi^*$  and derive conditions under which the process  $\xi^*$  is absorbed with probability 1.

We recall from Definition 3.3.4 that the process  $\xi^* = (\xi^*(t))_{t \geq 0}$  is a continuous-time Markov process on the state space  $\mathcal{S} = (G \times G) \cup \{\otimes\}$  with  $G = \mathbb{Z}^d \times \{0, 1\}$ . Here,  $\xi^*(t) = [(i, \alpha), (j, \beta)]$  captures the location  $(i, j \in \mathbb{Z}^d)$  and the state  $(\alpha, \beta \in \{0, 1\})$  of two independent particles at time  $t$ , where 0 stands for dormant state and 1 stands for active state, respectively. The evolution of the two independent particles is governed by the following transitions (see Fig. 3.1):

- (a) **(Migration)** Each particle migrates from location  $i$  to  $j$  at rate  $a(i, j)$  while being active.
- (b) **(Active to Dormant)** An active particle becomes dormant (without changing location) at rate  $\lambda$ .
- (c) **(Dormant to Active)** A dormant particle at location  $i$  becomes active (without changing location) at rate  $\lambda K_i$ .
- (d) **(Coalescence)** The two particles coalesce with each other, and are absorbed to the state  $\otimes$ , at rate  $\frac{1}{N_i}$  when they are both at location  $i$  and both active.

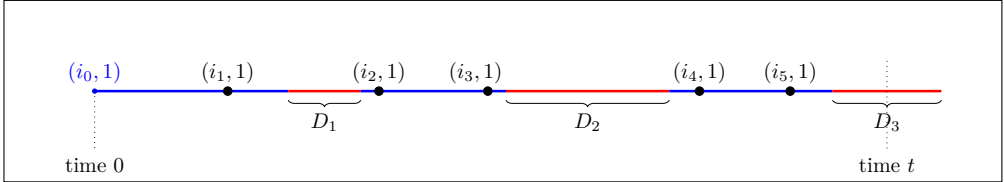


Figure 3.1: Evolution of a single particle started at location  $i_0$  in the active state. Red and blue lines denote the dormant and the active phases of the particle. Each dot represents a migration step.

The following lemma tells that if the mean wake-up time of a dormant particle is uniformly bounded over all the locations in  $\mathbb{Z}^d$ , then the accumulated activity time of a single particle increases linearly in time.

**Lemma 3.4.1 (Linear activity time).** *Let  $S(t)$  be the total accumulated time spent in the active state during the time interval  $[0, t]$  by a single particle that evolves according to the first three transitions described above. If  $\sup_{i \in \mathbb{Z}^d} K_i^{-1} < \infty$ , then*

$$\liminf_{t \rightarrow \infty} \frac{S(t)}{t} \geq \frac{1}{1 + K^{-1}} \quad a.s., \tag{3.78}$$

where  $K^{-1} := \sup_{i \in \mathbb{Z}^d} K_i^{-1}$ .

*Proof.* We prove the claim with the help of coupling in combination with a renewal argument. Let  $(T_n)_{n \in \mathbb{N}}$  and  $(D_n)_{n \in \mathbb{N}}$  be the successive time periods during which the particle is in the active and the dormant state, respectively (see Fig. 3.1). Note that  $(T_n)_{n \in \mathbb{N}}$  are i.i.d. exponential random variables with mean  $\frac{1}{\lambda}$ . Also note that  $D_n$  is exponentially distributed with  $\mathbb{E}[D_n] \leq (\lambda K)^{-1}$ , because the particle wakes up from the dormant state at rate  $\lambda K_i \geq \lambda K$  when it is at location  $i$ . Hence, using monotone coupling of exponential random variables, we can construct a sequence  $(U_n)_{n \in \mathbb{N}}$  of i.i.d.



exponential random variables on the same probability space with mean  $(\lambda K)^{-1}$  such that  $D_n \leq U_n$  a.s. for all  $n \in \mathbb{N}$ . Consider the alternating renewal process  $(R_t)_{t \geq 0}$  that takes value 0 (respectively, 1) during the time intervals  $(T_n)_{n \in \mathbb{N}}$  (respectively,  $(U_n)_{n \in \mathbb{N}}$ ), and let  $D(t) := t - S(t)$  be the total accumulated time spent in the dormant state during the time interval  $[0, t]$ . Note that, because  $D_n \leq U_n$  a.s. for  $n \in \mathbb{N}$ , we have

$$D(t) \leq \int_0^t \mathbb{1}_{\{R_s=1\}} ds. \quad (3.79)$$

By applying the renewal reward theorem (see e.g. [4, Section 2b, Chapter VI] or [79, Theorem 1, Section 10.5]) to the process  $(R_t)_{t \geq 0}$ , we see that

$$\limsup_{t \rightarrow \infty} \frac{D(t)}{t} \leq \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \mathbb{1}_{\{R_s=1\}} ds = \frac{\mathbb{E}[U_n]}{\mathbb{E}[T_n] + \mathbb{E}[U_n]} = \frac{\frac{1}{\lambda K}}{\frac{1}{\lambda} + \frac{1}{\lambda K}} = \frac{1}{1 + K} \quad \text{a.s.} \quad (3.80)$$

Hence

$$\liminf_{t \rightarrow \infty} \frac{S(t)}{t} = 1 - \limsup_{t \rightarrow \infty} \frac{D(t)}{t} \geq \frac{1}{1 + K^{-1}} > 0 \quad \text{a.s.} \quad (3.81)$$

□

Before we proceed with the proof of Theorem 3.2.7, we need the following lemma, which roughly tells that under the same assumption as in Lemma 3.4.1 and under Assumption 3.B, the presence of dormancy does not affect the recurrence behaviour of a single particle evolving according to the symmetrised migration kernel.

**Lemma 3.4.2 (Recurrence).** *Let  $S(t)$  be the total accumulated time spent in the active state during the time interval  $[0, t]$  by a single particle that evolves according to the first three transitions of the independent particle system described earlier, with migration controlled by the symmetrised kernel  $\hat{a}(\cdot, \cdot)$ . If  $K^{-1} < \infty$  and Assumption 3.B holds, then*

$$\mathbb{E} \left[ \int_0^\infty \hat{a}_{S(t)}(0, 0) dt \right] = \infty \text{ if and only if } \int_0^\infty \hat{a}_t(0, 0) dt = \infty, \quad (3.82)$$

where the expectation is taken w.r.t. the law of the process describing the evolution of the particle.

*Proof.* We prove the stronger statement that, for some constants  $C_1, C_2 > 0$ ,

$$C_1 \leq \liminf_{t \rightarrow \infty} \frac{\hat{a}_{S(t)}(0, 0)}{\hat{a}_t(0, 0)} \leq \limsup_{t \rightarrow \infty} \frac{\hat{a}_{S(t)}(0, 0)}{\hat{a}_t(0, 0)} \leq C_2 \quad \text{a.s.}, \quad (3.83)$$

from which the claim follows. Let  $\delta := \frac{1}{1+K^{-1}} \in (0, 1)$ . By Assumption 3.B, we have

$$\lim_{t \rightarrow \infty} \frac{\hat{a}_{pt}(0, 0)}{\hat{a}_t(0, 0)} = \frac{1}{p^\sigma}, \quad (3.84)$$

where the convergence is uniform in  $p \in [\frac{\delta}{2}, 1]$  (see e.g., [10, Theorem 1.5.2, Section 1.5]). Thus, we can find a  $T > 0$  such that, for all  $t \geq T$ ,

$$\sup_{p \in [\frac{\delta}{2}, 1]} \left| \frac{\hat{a}_{pt}(0, 0)}{\hat{a}_t(0, 0)} - p^{-\sigma} \right| < \frac{1}{2}. \quad (3.85)$$

In particular, for all  $t \geq T$  and  $p \in [\frac{\delta}{2}, 1]$ ,

$$\frac{1}{2} \leq \frac{\hat{a}_{pt}(0,0)}{\hat{a}_t(0,0)} \leq \left(\frac{2}{\delta}\right)^\sigma + \frac{1}{2}. \quad (3.86)$$

Since, by Lemma 3.4.1,  $\liminf_{t \rightarrow \infty} \frac{S(t)}{t} \geq \delta$  a.s., we have that  $\frac{S(t)}{t} \in [\frac{\delta}{2}, 1]$  eventually a.s. as  $t \rightarrow \infty$ . Combining this with (3.86), we obtain

$$\liminf_{t \rightarrow \infty} \frac{\hat{a}_{S(t)}(0,0)}{\hat{a}_t(0,0)} = \liminf_{t \rightarrow \infty} \frac{\hat{a}_{(S(t)/t)t}(0,0)}{\hat{a}_t(0,0)} \geq \frac{1}{2}, \quad \text{a.s.}, \quad (3.87)$$

and similarly  $\limsup_{t \rightarrow \infty} \frac{\hat{a}_{S(t)}(0,0)}{\hat{a}_t(0,0)} \leq \left(\frac{2}{\delta}\right)^\sigma + \frac{1}{2}$  a.s. □

**Remark 3.4.3.** The proof of the above lemma only uses the regular variation of  $\hat{a}_t(0,0)$  at infinity and the fact that  $\liminf_{t \rightarrow \infty} \frac{S(t)}{t} > \delta$  a.s. for some  $\delta \in (0, 1)$ . Thus, if  $S'(\cdot)$  is an independent copy of  $S(\cdot)$ , then we also have that

$$\mathbb{E} \left[ \int_0^\infty \hat{a}_{S(t)+S'(t)}(0,0) dt \right] = \infty \text{ if and only if } \int_0^\infty \hat{a}_{2t}(0,0) dt = \infty, \quad (3.88)$$

which is again equivalent to  $\hat{a}(\cdot, \cdot)$  being recurrent.

The following result provides a necessary and sufficient condition for the absorption of the process  $\xi^*$ .

**Theorem 3.4.4 (Clustering regime).** *Suppose that  $K^{-1} = \sup_{i \in \mathbb{Z}^d} K_i^{-1} < \infty$  and Assumption 3.B holds. If the process  $\xi^*$  is absorbed to  $\otimes$  with probability 1, then it is necessary that the symmetrised kernel  $\hat{a}(\cdot, \cdot)$  is recurrent, i.e.,*

$$\int_0^\infty \hat{a}_t(0,0) dt = \infty. \quad (3.89)$$

Furthermore, if  $(N_i)_{i \in \mathbb{Z}^d}$  satisfies the non-clumping condition in (3.6) and  $a(\cdot, \cdot)$  is symmetric, then (3.89) is also sufficient.

*Proof.* Without loss of generality we may assume that the process starts at the state  $\eta := [(0,1), (0,1)]$ , i.e., both particles are initially at the origin  $0 \in \mathbb{Z}^d$  and in the active state. Since the process  $\xi^*$  has a positive rate of absorption only when the two independent particles are on top of each other and active, for the absorption probability to be equal to 1 it is necessary that, in the process where coalescence is switched off, the two independent particles meet infinitely often on the same location with probability 1. Let  $S(t)$  and  $S'(t)$  denote the total accumulated time spent in the active state by the two independent particles (where coalescence is switched off) during the time interval  $[0, t]$ . Since the two particles move according to  $a(\cdot, \cdot)$  only when they are active, the total average time during which the two particles are on top of each other is given by

$$I := \int_0^\infty f(t) dt, \quad (3.90)$$

where  $f(t)$  is the probability that the two particles are on the same location at time  $t$ , which is given by

$$f(t) := \mathbb{E}_\eta^* \left[ \sum_{i \in \mathbb{Z}^d} a_{S(t)}(0, i) a_{S'(t)}(0, i) \right]. \quad (3.91)$$

Thus, for the process  $\xi^*$  to be absorbed with probability 1, it is necessary that  $I = \infty$ .

Let us define

$$M(t) := S(t) \wedge S'(t), \quad L(t) := [S(t) \vee S'(t)] - [S(t) \wedge S'(t)] = |S(t) - S'(t)|. \quad (3.92)$$

Note that

$$\sum_{i \in \mathbb{Z}^d} a_{S(t)}(0, i) a_{S'(t)}(0, i) = \sum_{i \in \mathbb{Z}^d} \hat{a}_{2M(t)}(0, i) a_{L(t)}(i, 0), \quad (3.93)$$

because the difference of two continuous-time random walks started at the origin that move independently in  $\mathbb{Z}^d$  with rates  $a(\cdot, \cdot)$  has distribution  $\hat{a}_{2M(t)}(0, \cdot)$  at time  $M(t)$  (because  $a(\cdot, \cdot)$  is translation-invariant), and in order for the particle with the largest activity time to meet the other particle at the activity time  $S(t) \vee S'(t) = M(t) + L(t)$ , it must bridge the difference in the remaining time  $L(t)$ . We use the Fourier representation of the transition probability kernel  $b(\cdot, \cdot)$ , defined by

$$b(i, j) := \frac{a(i, j)}{c} \mathbb{1}_{i \neq j}, \quad i, j \in \mathbb{Z}^d, \quad (3.94)$$

to further simplify the expression in (3.93). To this end, for  $\theta \in \mathbb{T}^d := [-\pi, \pi]^d$ , define

$$F(\theta) := \sum_{j \in \mathbb{Z}^d} e^{i(\theta, j)} b(0, j), \quad \hat{F}(\theta) := \operatorname{Re}(F(\theta)), \quad \tilde{F}(\theta) := \operatorname{Im}(F(\theta)). \quad (3.95)$$

Then, for  $j \in \mathbb{Z}^d$  and  $t > 0$ ,

$$\begin{aligned} \hat{a}_t(0, j) &= \frac{1}{(2\pi)^d} \int_{\mathbb{T}^d} e^{-i(\theta, j)} e^{-ct[1-\hat{F}(\theta)]} d\theta, \\ a_t(0, j) &= \frac{1}{(2\pi)^d} \int_{\mathbb{T}^d} e^{-i(\theta, j)} e^{-ct[1-\hat{F}(\theta)-i\tilde{F}(\theta)]} d\theta. \end{aligned} \quad (3.96)$$

Using that  $a(i, 0) = a(0, -i)$ ,  $i \in \mathbb{Z}^d$ , and inserting the above into (3.93), we obtain

$$\begin{aligned} \sum_{i \in \mathbb{Z}^d} a_{S(t)}(0, i) a_{S'(t)}(0, i) &= \frac{1}{(2\pi)^d} \int_{\mathbb{T}^d} e^{-c[2M(t)+L(t)][1-\hat{F}(\theta)]} \cos(L(t)\tilde{F}(\theta)) d\theta \\ &= \frac{1}{(2\pi)^d} \int_{\mathbb{T}^d} e^{-c[S(t)+S'(t)][1-\hat{F}(\theta)]} \cos(L(t)\tilde{F}(\theta)) d\theta \\ &\leq \frac{1}{(2\pi)^d} \int_{\mathbb{T}^d} e^{-c[S(t)+S'(t)][1-\hat{F}(\theta)]} d\theta \\ &= \hat{a}_{S(t)+S'(t)}(0, 0), \end{aligned} \quad (3.97)$$

where we use that  $\frac{1}{(2\pi)^d} \sum_{j \in \mathbb{Z}^d} e^{i(\theta-\theta', j)} = \delta(\theta-\theta')$ , with  $\delta(\cdot)$  the Dirac distribution (see e.g. [66, Chapter 7]). Finally, combining the above with (3.90)–(3.91), we see that

$$I \leq \int_0^\infty \mathbb{E}_\eta^* \left[ \hat{a}_{S(t)+S'(t)}(0, 0) \right] dt \quad (3.98)$$

and therefore it is necessary that

$$\int_0^\infty \mathbb{E}_\eta^* \left[ \hat{a}_{S(t)+S'(t)}(0, 0) \right] dt = \mathbb{E}_\eta^* \left[ \int_0^\infty \hat{a}_{S(t)+S'(t)}(0, 0) dt \right] = \infty, \quad (3.99)$$

which by Remark 3.4.3 is equivalent to

$$\int_0^\infty \hat{a}_t(0, 0) dt = \infty. \quad (3.100)$$

This proves the forward direction.

To prove the converse, we first note that, because all the rates of absorption given by  $(\frac{1}{N_i})_{i \in \mathbb{Z}^d}$  are such that (3.6) holds and  $\sup_{i \in \mathbb{Z}^d} K_i^{-1} < \infty$ , whenever the two particles are on the same location, there is a positive probability of absorption that is uniformly bounded away from zero. Indeed, if  $\nu^*(\eta)$  denote the absorption probability of  $\xi^*$  when started from state  $\eta$ , by Theorem 3.3.16 we have that

$$\begin{aligned} \inf_{i \in \mathbb{Z}^d} \nu^*([(i, 1), (i, 1)]) &> 0, \\ \inf_{i \in \mathbb{Z}^d} \nu^*([(i, 0), (i, 1)]) &= \inf_{i \in \mathbb{Z}^d} \nu^*([(i, 0), (i, 0)]) = \inf_{i \in \mathbb{Z}^d} \nu^*([(i, 1), (i, 0)]) > 0, \end{aligned} \quad (3.101)$$

where the last two equalities follow from a first-jump analysis of the process  $\xi^*$  when started at the state  $[(i, 0), (i, 0)]$ ,  $i \in \mathbb{Z}^d$ . As a consequence,  $\xi^*$  is absorbed with probability 1 if and only if, in the corresponding process where coalescence is switched off, the two particles infinitely often meet each other with probability 1. In other words,  $\nu^* \equiv 1$  if and only if  $I = \infty$ , where  $I$  is as in (3.90), the average accumulated time spent by the two particles at the same location. However, by the symmetry of the kernel  $a(\cdot, \cdot)$  and using Fubini's theorem, we have

$$\begin{aligned} I &= \int_0^\infty \mathbb{E}_\eta^* \left[ a_{S(t)+S'(t)}(0, 0) \right] dt = \int_0^\infty \mathbb{E}_\eta^* \left[ \hat{a}_{S(t)+S'(t)}(0, 0) \right] dt \\ &= \mathbb{E}_\eta^* \left[ \int_0^\infty \hat{a}_{S(t)+S'(t)}(0, 0) dt \right] \end{aligned} \quad (3.102)$$

and thus (recall Remark 3.4.3), if  $\int_0^\infty \hat{a}_t(0, 0) dt = \infty$ , then  $I = \infty$ . This proves the backward direction.  $\square$

Now we are ready to prove Theorem 3.2.7 with the help of Theorem 3.4.4 and the results in Section 3.3.4.

*Proof of Theorem 3.2.7.* Let  $\nu(\eta)$  denote the absorption probability of the process  $\xi$  (see Definition 3.3.1) started at state  $\eta \in G \times G$ . Recall from Theorem 3.2.1 and Remark 3.3.2 that the system clusters if and only if  $\nu \equiv 1$ . By the irreducibility of the process  $\xi$ , we have  $\nu \equiv 1$  if and only if  $\nu([(0, 0), (0, 0)]) = 1$ . Now, since  $\sup_{i \in \mathbb{Z}^d} K_i^{-1} < \infty$  and (3.6) holds, we see that all the conditions of Theorem 3.3.14 are satisfied by virtue of Theorem 3.3.16, and hence  $\nu([(0, 0), (0, 0)]) = 1$  if and only if  $\nu^*([(0, 0), (0, 0)]) = 1$ , where  $\nu^*(\eta)$  denotes the absorption probability of the non-interacting two-particle process  $\xi^*$  (see Definition 3.3.4) started at state  $\eta \in G \times G$ . However, by the forward direction of Theorem 3.4.4, if  $\nu^*([(0, 0), (0, 0)]) = 1$ , then it

is necessary that the symmetrised kernel  $\hat{a}(\cdot, \cdot)$  is recurrent, and hence the forward direction is proved. Similarly, under the assumption of symmetry of the migration kernel, we can apply the converse direction of Theorem 3.3.14, to conclude that if the transition kernel  $a(\cdot, \cdot)$  (which is the same as the symmetrised transition kernel) is recurrent, then  $\nu^*([(0,0), (0,0)]) = 1$ , and so the backward direction follows as well.  $\square$

*Proof of Corollary 3.2.8.* Recall from Remark 2.2.3 in Chapter 2 that the migration kernel  $a(\cdot, \cdot)$  admits at least a  $d$ -th moment and is translation-invariant by Assumption 2.A. Thus if  $d > 2$ , then the kernel  $\hat{a}(\cdot, \cdot)$ , being symmetric by definition, is transient (by Polya's theorem), and hence clustering cannot take place by virtue of the forward direction of Theorem 3.2.7. Similarly, if  $d \leq 2$  and  $a(\cdot, \cdot)$  is symmetric, then  $a(\cdot, \cdot)$  is recurrent, and so the claim follows from the backward direction of Theorem 3.2.7.  $\square$

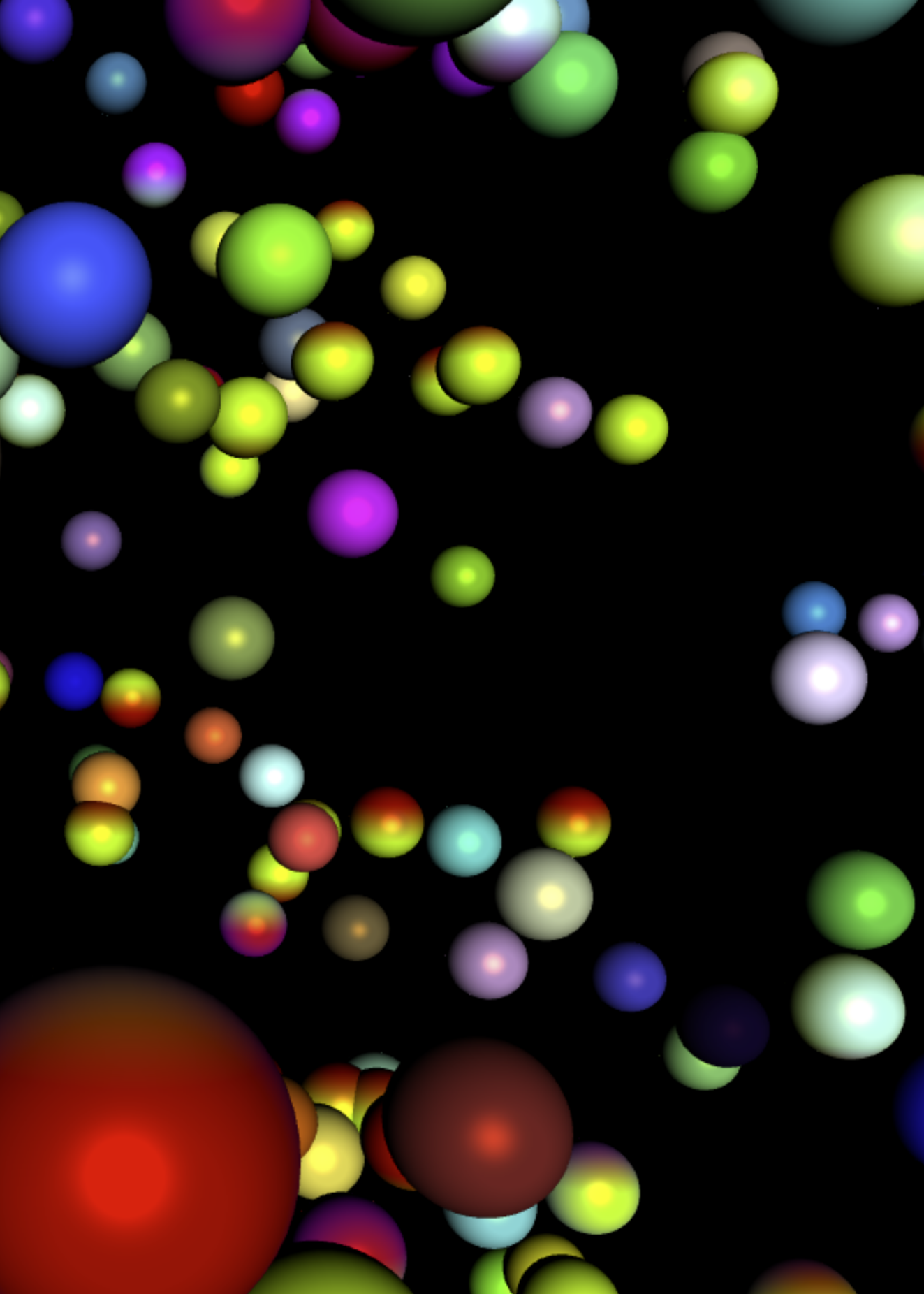
## §3.5 Discussion

Stochastic models describing genetic evolution of *finite* populations under various evolutionary forces remain a challenge in population genetics. The presence of a seed-bank can complicate the analysis even further. In recent years, stochastic duality has proven to be a very useful mathematical tool, particularly in the field of interacting particle system, for tackling technical complications and doing explicit computations. On the one hand, we aim to create a bridge between interacting particle system and mathematical population genetics by including dormancy into existing well-known particle systems. On the other hand, we hope to combine this approach with the recently developed theory of duality to reveal delicate structures and related interesting properties of the interacting particle system that lie hidden and are often lost in the process of taking the large-colony-size limit.

In Chapter 2, we heavily rely on duality to prove our results on the process  $Z$ . In a subdivided population, the ancestral dual process in the presence of resampling and migration is generally described by the *structured coalescent process*. This process, which is by now well-understood, was originally derived as the genealogical process in the context of geographically structured *large* populations under Wright-type reproduction and migration (see e.g., [83, 151] and [138]). Even though lineages move independently in the structured coalescent, the genealogies of a sample taken from subdivided and finite populations with constant size are correlated [128, 83]. These correlations arise due to the imposition of *finite* and *constant* (in time) population sizes, and vanish when the large-population-size limit is taken.

As can be seen in Definition 2.4.2 of Chapter 2, the ancestral dual process  $Z_*$  is no exception, and lineages in the dual indeed show a *repulsive* interaction. Due to the incorporation of dormancy, lineages can also adopt one of two states: active and dormant. The presence of these correlations and of dormant periods in the lineages make the dual process  $Z_*$  interesting but tricky to analyse. Consequently, in the present chapter we take a different route to address the dichotomy of coexistence versus clustering. More precisely, instead of directly exploiting the clustering criterion

given in terms of the original two-particle dual process (equivalently, the process  $\xi$  in Definition 3.3.1), we find an alternative clustering criterion that is relatively easy to deal with. We achieve this by comparing the original two-particle dual  $\xi$  with two *auxiliary* two-particle dual processes  $\hat{\xi}$  and  $\xi^*$  (see Definition 3.2.2 and Definition 3.3.4), which are simplified versions of  $\xi$ . In particular, we obtain  $\hat{\xi}$  from  $\xi$  by switching off the repulsive interaction present in the migration mechanism of an active particle and removing the coalescence of active particles from different locations, while  $\hat{\xi}$  is further simplified to  $\xi^*$ , the *independent RW* process, by turning off the only interaction that takes place between an active and a dormant particle located at the same position. The comparison technique employed in Section 3.3 to estimate the absorption probabilities for  $\xi, \hat{\xi}, \xi^*$  is similar to that in [78], where a connection is made between infinitesimal generators of the Fisher-Wright diffusion and the  $\Lambda$ -Fleming-Viot process, based on methods involving Lyapunov functions to characterise fixation probabilities. Similar techniques are used in the literature of interacting particle systems to derive correlation inequalities and related properties (see e.g., [72]). It is worth emphasising that our results are valid for any choice of the sizes  $(N_i)_{i \in \mathbb{Z}^d}$  and  $(M_i)_{i \in \mathbb{Z}^d}$  of active and dormant populations, subject to the mild criteria we imposed. Such generalities are rare and suggest that other problems can perhaps be approached in a similar way.



# Spatial populations with seed-banks in random environment

This chapter is based on the following paper:

S. Nandan. Spatial populations with seed-banks in random environment: III. Convergence towards mono-type equilibrium. *Electron. J. Probab.*, 28:1–36, 2023.

## Abstract

We consider the spatially inhomogeneous Moran model with seed-banks introduced in [46]. Populations comprising *active* and *dormant* individuals are spatially structured in colonies labeled by  $\mathbb{Z}^d$ ,  $d \geq 1$ . The population sizes are sampled from a *translation-invariant, ergodic, uniformly elliptic* field that constitutes a *static random environment*. Individuals carry one of two types:  $\heartsuit$  and  $\spadesuit$ . Dormant individual resides in what is called a *seed-bank*. Active individuals *exchange* type from the seed-bank of their own colony, and *resample* type by choosing a parent uniformly at random from the distinct active populations according to a symmetric migration kernel. In [46] by exploiting a *dual* process given by an *interacting coalescing particle system*, we showed that the spatial system exhibits a dichotomy between *clustering* (mono-type equilibrium) and *coexistence* (multi-type equilibrium). In this paper, we identify the *domain of attraction* for each mono-type equilibrium in the clustering regime for an *arbitrary fixed* environment. Furthermore, we show that in dimensions  $d \leq 2$ , when the migration kernel is *recurrent*, for almost surely every realization of the environment, the system with an *initially consistent* type-distribution converges weakly to a mono-type equilibrium in which the probability of fixation to the all type- $\heartsuit$  configuration does not depend on the environment. An explicit formula for the fixation probability is given in terms of an annealed average of the type- $\heartsuit$  densities in the active and the dormant population, biased by the ratio of the two population sizes at the target colony.

Primary techniques employed in the proofs include stochastic duality and the environment process viewed from particle, introduced in [53] for random walk in random environment on a strip. A spectral analysis of Markov operator yields *quenched* weak convergence of the environment process associated with the *single-particle dual* process to a reversible ergodic distribution, which we transfer to the spatial system of populations by using duality.



## §4.1 Introduction

In this chapter we study the spatial model with seed-banks introduced in Chapter 2 by treating the preassigned constant population sizes as an *environment* of the system. One of our main results in this chapter is that a full characterization of the domain of attraction for each mono-type equilibrium in the clustering regime is obtained for an *arbitrarily fixed* environment (satisfying mild regularity conditions).

Recall that the constituent active and dormant populations in the spatial model maintain constant sizes over time. While this can be biologically explained by assuming that the system receives sufficient supply of environmental resources, a more natural extension would be to consider the model where population sizes come from a *random field* determined by environmental factors such as extreme temperatures, inadequate supply of food resources, etc. Research in this direction has started only recently (see e.g. [28, 17, 152]), although most results are available only for models that are scaled diffusively or are simulation based.

The novelty in the content of present chapter is that here we study the mono-type equilibrium behaviour of the spatial system with seed-banks introduced in Chapter 2 for the setting where the population sizes constitute a *static random* environment. In particular, the sizes are drawn from a *translation-invariant* and *ergodic* random field. Our contributions are two-fold:

- (a) When the symmetric migration kernel is *recurrent* (which requires  $d \leq 2$ ) and the random environment is *uniformly elliptic*, we show that the system started from an *initially consistent* type-distribution converges in law to a mono-type equilibrium for almost surely all realisation of the environment. In other words, we prove that the system undergoes *homogenisation* in the *quenched* setting.
- (b) We show that, in the homogenised mono-type equilibrium, the *fixation probability* (in law) to the all type- $\heartsuit$  configuration is deterministic, i.e., does not depend on the realisation of the environment. We also provide an explicit formula for this probability.

The techniques used in the proof of the main theorems include stochastic duality, moment relations, semigroup expansion and the environment viewed from the particle recently introduced in [53] for random walk in random environment (RWRE) on a strip, and spectral analysis of Markov kernel operator.

**Outline.** The chapter is organised as follows. In Section 4.2 we recall some basic results from previous chapters, state our main theorems on the convergence of the system to a mono-type equilibrium, and explain the strategy of the proofs in detail. Section 4.3 is devoted to the analysis of dual process with a single lineage (or single particle) in random environment, where homogenisation results are derived for the associated *environment process*. In Section 4.4 we prove our main theorems using the results derived in Section 4.3. In Appendix B.1, we prove a result stated in Section 4.3 on the existence of a stationary distribution for the aforementioned environment process, and also give a proof of the *strong law of large numbers* for the single-particle

dual, which is a result of independent interest. Finally, in Appendix B.2 we prove an auxiliary proposition relating weak convergence of Markov chain to the peripheral point-spectrum of a Markov operator, which is needed for the proof of our main theorems.

## §4.2 Main theorems

In Section 4.2.1 we introduce some preliminary notations and set the stage to state our main results. In Section 4.2.2 we give our first main result on the convergence of the system in the clustering regime for an *arbitrary fixed environment* (Theorem 4.2.4). In Section 4.2.3 we consider the system in a *static random environment* that is drawn from a translation-invariant and ergodic field defined on a subset of *uniformly elliptic environments*, and present a *homogenisation* statement in the *quenched* setting on the convergence of the system to a mono-type equilibrium (Theorem 4.2.9–4.2.11). In Section 4.2.4 we discuss the results and shed light on the strategy of the proofs.

### §4.2.1 Recollection of previous results and basic notations

Let us recall that under the resampling and exchange dynamics described in Section 2.2.1 of Chapter 2, the initial population sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$  remain constant over time. Thus, we can naturally think of the sizes of the populations as a *static environment* for the spatial process in (2.2). Throughout the sequel we denote by  $\mathbf{e} := (N_i, M_i)_{i \in \mathbb{Z}^d} \in (\mathbb{N} \times \mathbb{N})^{\mathbb{Z}^d}$  a typical choice for the sizes of the constituent populations and refer to it as the *environment*. From here onwards, we adopt the convention of adding a superscript (or subscript) with Fraktur font to emphasize the dependence of a variable on the realisation of the environment. Let us also recall that the Markov process associated to the spatial system is an interacting particle system denoted by

$$Z^\mathbf{e} := (Z^\mathbf{e}(t))_{t \geq 0}, \quad Z^\mathbf{e}(t) := (X_i^\mathbf{e}(t), Y_i^\mathbf{e}(t))_{i \in \mathbb{Z}^d}, \quad (4.1)$$

and lives on the inhomogeneous state space

$$\mathcal{X}^\mathbf{e} := \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i]. \quad (4.2)$$

The superscript  $\mathbf{e}$  indicates the dependence of the process  $Z^\mathbf{e}$  on the environment  $\mathbf{e} = (N_i, M_i)_{i \in \mathbb{Z}^d}$ , and the pair  $(X_i^\mathbf{e}(t), Y_i^\mathbf{e}(t)) \in [N_i] \times [M_i]$  represents the number of active, respectively, dormant individuals of type  $\heartsuit$  at time  $t$  at colony  $i$ . Let  $\mathcal{P}^\mathbf{e}$  be the set of probability distributions on  $\mathcal{X}^\mathbf{e}$  defined by

$$\mathcal{P}^\mathbf{e} := \{\mathcal{P}_\theta^\mathbf{e} : \theta \in [0, 1]\}, \quad \mathcal{P}_\theta^\mathbf{e} := (1 - \theta)\delta_{\spadesuit} + \theta\delta_{\heartsuit}, \quad (4.3)$$

where  $\delta_{\heartsuit}$  (resp.  $\delta_{\spadesuit}$ ) is the Dirac distribution concentrated at the all type- $\heartsuit$  configuration  $\mathbf{e} = (N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}^\mathbf{e}$  (resp. the all type- $\spadesuit$  configuration  $(0, 0)_{i \in \mathbb{Z}^d} \in \mathcal{X}^\mathbf{e}$ ). Recall that the process  $Z^\mathbf{e}$  is said to exhibit *clustering* if and only if the limiting distribution

of  $Z^\epsilon(t)$  (given that it exists) always falls in  $\mathcal{P}^\epsilon$ . Otherwise the process is said to be in the *coexistence* regime.

We throughout consider environments that are admissible in the following sense:

**Definition 4.2.1 (Admissible environments).** Consider the following three conditions for the environment  $\epsilon = (N_i, M_i)_{i \in \mathbb{Z}^d} \in (\mathbb{N} \times \mathbb{N})^{\mathbb{Z}^d}$  and the migration kernel  $a(\cdot, \cdot)$ :

- (a)  $N_i \geq 2$  and  $M_i \geq 2$  for all  $i \in \mathbb{Z}^d$ .
- (b)  $\sup_{i \in \mathbb{Z}^d \setminus \{0\}} \|i\|^{-\gamma} N_i < \infty$  and  $\sum_{i \in \mathbb{Z}^d} \|i\|^{d+\gamma+\delta} a(0, i) < \infty$  for some  $\gamma > 0$  and some  $\delta > 0$ .
- (c)  $\lim_{\|i\| \rightarrow \infty} \|i\|^{-1} \log N_i = 0$  and  $\sum_{i \in \mathbb{Z}^d} e^{\delta \|i\|} a(0, i) < \infty$  for some  $\delta > 0$ .

If (a) is satisfied, i.e., in each colony, both the active and the dormant population consist of at least two individuals, then we say that  $\epsilon$  is *non-trivial*. Further, if either (b) or (c) is satisfied, then we say that  $\epsilon$  is *compatible*. Non-trivial and compatible environments are referred to as *admissible* environments. The set of all admissible environments is denoted by  $\mathcal{A}$ . ■

**Remark 4.2.2.** Observe from Theorem 2.2.2 in Chapter 2 that under Assumption 2.A, for any compatible environment, the Markov process  $Z^\epsilon$  in (4.1) is well-defined. Condition (a) comes from Assumption 3.A which was made in Chapter 3 because of a technical requirement for determining the clustering regime of the process  $Z^\epsilon$  and it can perhaps be removed with minor adaptations.

## §4.2.2 Clustering in a fixed environment

In this chapter we refrain from reintroducing the dual process in full generality and only define a version of the dual consisting of a single particle in terms of a *coordinate process*  $\Theta^\epsilon$ . Informally, the process  $\Theta^\epsilon$  keeps track of the location and the state of a single dual particle in time, while the general dual  $Z_*^\epsilon$  describes the evolution of the particle via configurations in  $\mathcal{X}_*^\epsilon$ . The process  $\Theta^\epsilon$  plays a key role in the proofs of all our main results, and will be our sole focus in Section 4.3. Later, in Section 4.4.1 we will explain via Lemma 4.4.2 how the single-particle process  $\Theta^\epsilon$  is related to the general dual process  $Z_*^\epsilon$ . We refer the reader to Section 2.4.2 of Chapter 2 and Section 3.3.1 of Chapter 3 for further insight into the general dual process  $Z_*^\epsilon$ .

**Definition 4.2.3 (Single-particle dual process).** The single-particle dual process

$$\Theta^\epsilon := (\Theta^\epsilon(t))_{t \geq 0}, \quad \Theta^\epsilon(t) = (x_t^\epsilon, \alpha_t^\epsilon), \tag{4.4}$$

in environment  $\epsilon := (N_i, M_i)_{i \in \mathbb{Z}^d}$  is the continuous-time Markov chain on the state space

$$G := \mathbb{Z}^d \times \{0, 1\} \tag{4.5}$$

with transition rates

$$\begin{aligned} (i, 1) &\longrightarrow \begin{cases} (j, 1) & \text{at rate } a(0, j - i), \quad j \in \mathbb{Z}^d, j \neq i \\ (i, 0) & \text{at rate } \lambda, \end{cases} \\ (i, 0) &\longrightarrow (i, 1) \quad \text{at rate } \lambda K_i, \end{aligned} \tag{4.6}$$

where  $i \in \mathbb{Z}^d$  and the environment  $\mathfrak{e}$  fixes  $K_i$  by (2.1). We define the time- $t$  probability transition kernel  $p_t^\mathfrak{e}(\cdot, \cdot) : G \times G \rightarrow [0, 1]$  associated to  $\Theta^\mathfrak{e}$  as

$$p_t^\mathfrak{e}(\eta, \xi) := P_\eta^\mathfrak{e}(\Theta^\mathfrak{e}(t) = \xi), \quad \eta, \xi \in G, \tag{4.7}$$

where  $P_\eta^\mathfrak{e}$  is the law of the process  $\Theta^\mathfrak{e}$  started at  $\eta \in G$ . ■

The coordinates  $x_t^\mathfrak{e}$  and  $\alpha_t^\mathfrak{e}$  in (4.4) represent, respectively, the location in  $\mathbb{Z}^d$  and the state (active or dormant) of the particle at time  $t$ , where 0 stands for dormant and 1 stands for active. Note from (4.6) that only the wake-up rate of the particle depends on the environment  $\mathfrak{e}$ , and only via the ratios  $(K_i)_{i \in \mathbb{Z}^d}$  defined in (2.1). Indeed, the average time spent in the dormant state by the particle at site  $i$  is proportional to  $K_i^{-1}$ , the relative strength of the seed-bank at colony  $i$ . The particle in the active state migrates according to the kernel  $a(\cdot, \cdot)$ , and so migration is not affected by the environment  $\mathfrak{e}$ , at least not in a direct manner. This makes the analysis of the single-particle process  $\Theta^\mathfrak{e}$  in a typical *random* environment  $\mathfrak{e}$  easier than the full dual process  $Z_\ast^\mathfrak{e}$ .

Let us now state the main result of this section.

**Theorem 4.2.4 (Domain of attraction).** *Suppose that the process  $Z^\mathfrak{e} := (Z^\mathfrak{e}(t))_{t \geq 0}$  is in the clustering regime and  $Z^\mathfrak{e}(0) = (X_i^\mathfrak{e}(0), Y_i^\mathfrak{e}(0))_{i \in \mathbb{Z}^d}$  has distribution  $\mu^\mathfrak{e} \in \mathcal{P}(\mathcal{X}^\mathfrak{e})$ , where  $\mathfrak{e} := (N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{A}$  is an arbitrarily fixed environment. If  $\mu_t^\mathfrak{e}$  denotes the time- $t$  distribution of the process  $Z^\mathfrak{e}$ , then the following are equivalent:*

- (a)  $\mu_t^\mathfrak{e}$  converges weakly as  $t \rightarrow \infty$ .
- (b) For any  $(i, \alpha) \in G := \mathbb{Z}^d \times \{0, 1\}$ ,

$$f^\mathfrak{e}(i, \alpha) := \lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^\mathfrak{e}((i, \alpha), (j, \beta)) \mathbb{E}_{\mu^\mathfrak{e}} \left[ \beta \frac{X_j^\mathfrak{e}(0)}{N_j} + (1 - \beta) \frac{Y_j^\mathfrak{e}(0)}{M_j} \right] \text{ exists,} \tag{4.8}$$

where  $p_t^\mathfrak{e}(\cdot, \cdot)$  is as in Definition 4.2.3.

Further, if any of the above two conditions is satisfied, then there exists  $\theta_\mathfrak{e} \in [0, 1]$  such that  $f^\mathfrak{e}(\cdot) \equiv \theta_\mathfrak{e}$  and

$$\lim_{t \rightarrow \infty} \mu_t^\mathfrak{e} = (1 - \theta_\mathfrak{e})\delta_\spadesuit + \theta_\mathfrak{e}\delta_\heartsuit. \tag{4.9}$$

The following corollary states that if the process  $Z^\mathfrak{e}$  exhibits clustering and starts from an initial distribution that puts a constant density of type  $\heartsuit$  individuals at *infinity*, then with probability 1 the spatial process  $Z^\mathfrak{e}$  converges towards a mono-type equilibrium. Further, the probability of fixation to the all type- $\heartsuit$  configuration in the attained equilibrium is given by the initial density of type  $\heartsuit$  in the populations at *infinity*.

**Corollary 4.2.5.** *Suppose that the process  $Z^\epsilon$  is in the clustering regime and  $\mu_t^\epsilon$  denotes the time- $t$  distribution of the process, where  $\epsilon := (N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{A}$  is fixed arbitrarily. If the initial distribution  $\mu^\epsilon := \mu_0^\epsilon$  is such, that for some  $\theta_\epsilon \in [0, 1]$ ,*

$$\lim_{\|i\| \rightarrow \infty} \int_{\mathcal{X}^\epsilon} \frac{X_i}{N_i} d\mu^\epsilon \{(X_k, Y_k)_{k \in \mathbb{Z}^d}\} = \lim_{\|i\| \rightarrow \infty} \int_{\mathcal{X}^\epsilon} \frac{Y_i}{M_i} d\mu^\epsilon \{(X_k, Y_k)_{k \in \mathbb{Z}^d}\} = \theta_\epsilon, \quad (4.10)$$

then

$$\lim_{t \rightarrow \infty} \mu_t^\epsilon = (1 - \theta_\epsilon) \delta_{\blacklozenge} + \theta_\epsilon \delta_{\heartsuit}. \quad (4.11)$$

Let us recall that in Chapter 3, the clustering criterion stated in Theorem 2.4.12 of Chapter 2 was further refined, and conditions on the environment  $\epsilon$  and other parameters were obtained for which the process  $Z^\epsilon$  exhibits clustering. In particular, it was shown (see Corollary 3.2.8 in Chapter 3) that clustering prevails under the following set of conditions:

**Assumption 4.A (Clustering environment).** The migration kernel  $a(\cdot, \cdot)$  satisfying Assumption 2.A and the environment  $\epsilon = (N_i, M_i)_{i \in \mathbb{Z}^d}$  are such that

- (1)  $a(\cdot, \cdot)$  is symmetric, i.e.,

$$a(0, i) = a(0, -i), \quad i \in \mathbb{Z}^d. \quad (4.12)$$

- (2)  $a(\cdot, \cdot)$  generates a recurrent random walk on  $\mathbb{Z}^d$  that satisfies a local central limit theorem (LCLT). This requirement implicitly forces  $d \leq 2$  and requires the migration kernel  $a(\cdot, \cdot)$  to have a finite second moment.

- (3) The relative strength of the seed-banks determined by  $\epsilon$  are spatially uniformly bounded, i.e.,

$$\sup_{i \in \mathbb{Z}^d} \frac{M_i}{N_i} < \infty. \quad (4.13)$$

- (4) The sizes of the active populations determined by  $\epsilon$  are *non-clumping*, i.e.,

$$\inf_{i \in \mathbb{Z}^d} \sum_{\|j-i\| \leq R} \frac{1}{N_j} > 0 \quad \text{for some } R < \infty. \quad (4.14)$$

■

In view of the above, unless stated otherwise, we will throughout assume that Assumptions 2.A and 4.A are in force. We remark that the above conditions are sufficient but not necessary for the process  $Z^\epsilon$  to remain in the clustering regime. The following corollary is immediate.

**Corollary 4.2.6.** *Suppose that Assumptions 2.A and 4.A are in force. Then the result in Theorem 4.2.4 holds.*

### §4.2.3 Clustering in random environment

In this section we consider the process  $Z^\epsilon$  in a static random environment  $\epsilon$ . Let us introduce the necessary notations before we present our main theorems. To simplify our analysis, we only consider *uniformly elliptic* environments.

**Definition 4.2.7 (Uniformly elliptic environment).** An environment  $\epsilon \in (\mathbb{N}^2)^{\mathbb{Z}^d}$  with  $\epsilon := (N_i, M_i)_{i \in \mathbb{Z}^d}$  is said to be *uniformly elliptic* if

$$(N_i, M_i) \in \{2, 3, \dots, \mathfrak{K}\}^2 \quad (4.15)$$

for all  $i \in \mathbb{Z}^d$  and some natural number  $\mathfrak{K} \geq 2$ . The set of all environments satisfying (4.15) is denoted by  $\mathcal{E}_{\mathfrak{K}}$ . ■

From here onwards we fix a natural number  $\mathfrak{K} \geq 2$ , which we refer to as the ellipticity constant. We equip  $\mathcal{E}_{\mathfrak{K}}$  with the product topology and the Borel  $\sigma$ -field  $\Sigma$ . The product topology is naturally induced by the metric  $\mathcal{H} : \mathcal{E}_{\mathfrak{K}} \times \mathcal{E}_{\mathfrak{K}} \rightarrow [0, \infty)$ ,

$$\mathcal{H}((N_i, M_i)_{i \in \mathbb{Z}^d}, (\widehat{N}_i, \widehat{M}_i)_{i \in \mathbb{Z}^d}) := \sum_{i \in \mathbb{Z}^d} \frac{1}{2^{\|i\|}} [1 \wedge (|N_i - \widehat{N}_i| + |M_i - \widehat{M}_i|)]. \quad (4.16)$$

In this metric topology,  $\mathcal{E}_{\mathfrak{K}}$  is a compact Polish space, and the Borel  $\sigma$ -field  $\Sigma$  becomes countably generated. Trivially,  $\mathcal{E}_{\mathfrak{K}} \subset \mathcal{A}$  (see Definition 4.2.1) and so the process  $Z^\epsilon$  is well-defined for any  $\epsilon \in \mathcal{E}_{\mathfrak{K}}$ . Note that any  $\epsilon \in \mathcal{E}_{\mathfrak{K}}$  automatically satisfies conditions (3)–(4) in Assumption 4.A.

**Definition 4.2.8 (Translation operators).** For each  $j \in \mathbb{Z}^d$ , the shift operator  $T_j : \mathcal{E}_{\mathfrak{K}} \rightarrow \mathcal{E}_{\mathfrak{K}}$  is defined by the map

$$\epsilon \mapsto T_j \epsilon, \quad T_j \epsilon := (N_{i+j}, M_{i+j})_{i \in \mathbb{Z}^d}, \quad (4.17)$$

where  $\epsilon := (N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{E}_{\mathfrak{K}}$ . The action of  $T_j$  on a set is interpreted pointwise, i.e., for  $A \subset \mathcal{E}_{\mathfrak{K}}$ ,  $T_j A := \{T_j \epsilon : \epsilon \in A\}$ . ■

We impose the following assumption on the law of the random environment:

**Assumption 4.B (Translation-invariant and ergodic field).** The probability law  $\bar{\mathbb{P}}$  of the random environment  $\epsilon$  is defined on the measurable Polish space  $(\mathcal{E}_{\mathfrak{K}}, \Sigma)$  and satisfies:

- (1) For any  $A \in \Sigma$  and  $j \in \mathbb{Z}^d$ ,  $\bar{\mathbb{P}}(T_j^{-1} A) = \bar{\mathbb{P}}(A)$ .
- (2) If  $A \in \Sigma$  is such that  $T_j^{-1} A = A$  for all  $j \in \mathbb{Z}^d$ , then  $\bar{\mathbb{P}}(A) \in \{0, 1\}$ .

We use  $\bar{\mathbb{E}}$  to denote the expectation w.r.t.  $\bar{\mathbb{P}}$ . ■

We are now ready to state the main result of this section.

**Theorem 4.2.9 (Convergence in random environment).** *Let  $f_A, f_D : \mathcal{E}_{\mathfrak{R}} \rightarrow [0, 1]$  be two  $\Sigma$ -measurable functions such that, for  $\bar{\mathbb{P}}$ -a.s. every realisation of  $\mathfrak{e} := (N_i, M_i)_{i \in \mathbb{Z}^d}$ , the initial law  $\mu^\mathfrak{e} \in \mathcal{P}(\mathcal{X}^\mathfrak{e})$  of the process  $Z^\mathfrak{e}$  satisfies the following for all  $i \in \mathbb{Z}^d$ :*

$$\int_{\mathcal{X}^\mathfrak{e}} \frac{X_i}{N_i} d\mu^\mathfrak{e}\{(X_k, Y_k)_{k \in \mathbb{Z}^d}\} = f_A(T_i \mathfrak{e}), \quad \int_{\mathcal{X}^\mathfrak{e}} \frac{Y_i}{M_i} d\mu^\mathfrak{e}\{(X_k, Y_k)_{k \in \mathbb{Z}^d}\} = f_D(T_i \mathfrak{e}). \quad (4.18)$$

If Assumption 2.A and conditions (1)–(2) in Assumption 4.A hold, then, for  $\bar{\mathbb{P}}$ -a.s. every realisation of the environment  $\mathfrak{e}$ ,  $Z^\mathfrak{e}(t)$  converges in law to  $(1 - \theta)\delta_\spadesuit + \theta\delta_\heartsuit$ , where the fixation probability  $\theta$  to the all type- $\heartsuit$  configuration  $\mathfrak{e} \in \mathcal{X}^\mathfrak{e}$  does not depend on the realisation of the environment and is given by

$$\theta = \frac{1}{1 + \rho} \int_{\mathcal{E}_{\mathfrak{R}}} [f_A((N_k, M_k)_{k \in \mathbb{Z}^d}) + \frac{M_0}{N_0} f_D((N_k, M_k)_{k \in \mathbb{Z}^d})] d\bar{\mathbb{P}}\{(N_k, M_k)_{k \in \mathbb{Z}^d}\}, \quad (4.19)$$

with  $\rho := \bar{\mathbb{E}}\left[\frac{M_0}{N_0}\right] = \int_{\mathcal{E}_{\mathfrak{R}}} \frac{M_0}{N_0} d\bar{\mathbb{P}}\{(N_k, M_k)_{k \in \mathbb{Z}^d}\}$ , the average relative strength of the seed-bank in each colony.

Let us look at a simple example where the conditions in the above theorem are met.

**Example 4.2.10 (Homogenised fixation probability).** Fix  $\kappa \in [0, 1]$ . Suppose that, for a typical environment  $\mathfrak{e} := (N_i, M_i)_{i \in \mathbb{Z}^d}$  drawn from the law  $\bar{\mathbb{P}}$ , the process  $Z^\mathfrak{e}$  starts with the initial law  $\mu^\mathfrak{e} \in \mathcal{P}(\mathcal{X}^\mathfrak{e})$  given by

$$\mu^\mathfrak{e} := \bigotimes_{i \in \mathbb{Z}^d} \text{Binomial}(N_i, \frac{\kappa}{N_i}) \otimes \text{Uniform}([M_i]). \quad (4.20)$$

In other words, in the spatial system of populations with sizes  $(N_i, M_i)_{i \in \mathbb{Z}^d}$ , initially each active individual of colony  $i$  independently adopts type  $\heartsuit$  with probability  $\frac{\kappa}{N_i}$ , and the number of type- $\heartsuit$  dormant individuals, which is given by  $Y_i^\mathfrak{e}(0)$ , is uniformly distributed over  $[M_i] = \{0, 1, \dots, M_i\}$ . In this case, if we let  $f_A : \mathcal{E}_{\mathfrak{R}} \rightarrow [0, 1]$  to be the map  $\mathfrak{e} \mapsto \frac{\kappa}{N_0}$  and  $f_D : \mathcal{E}_{\mathfrak{R}} \rightarrow [0, 1]$  to be the constant map  $\mathfrak{e} \mapsto \frac{1}{2}$ , then  $\mu^\mathfrak{e}$  satisfies

$$\mathbb{E}_{\mu^\mathfrak{e}} \left[ \frac{X_i^\mathfrak{e}(0)}{N_i} \right] = \frac{\kappa}{N_i} = f_A(T_i \mathfrak{e}), \quad \mathbb{E}_{\mu^\mathfrak{e}} \left[ \frac{Y_i^\mathfrak{e}(0)}{M_i} \right] = \frac{1}{2} = f_D(T_i \mathfrak{e}), \quad (4.21)$$

for all  $i \in \mathbb{Z}^d$ . Thus, if the migration kernel  $a(\cdot, \cdot)$  is symmetric, recurrent and satisfies a LCLT, then by Theorem 4.2.9 we have that, for  $\bar{\mathbb{P}}$ -a.s. every realisation of  $\mathfrak{e}$ , the process  $Z^\mathfrak{e}$  converges in law to  $(1 - \theta)\delta_\spadesuit + \theta\delta_\heartsuit$ , where  $\theta$  is given by

$$\theta = \frac{1}{1 + \bar{\mathbb{E}}[M_0/N_0]} \left[ \bar{\mathbb{E}}\left[\frac{\kappa}{N_0}\right] + \frac{1}{2} \bar{\mathbb{E}}\left[\frac{M_0}{N_0}\right] \right]. \quad (4.22)$$

This tells that, in the long run, the probability of fixation of the spatial population to the all type- $\heartsuit$  configuration is  $\theta$  and does not depend on the realisation of the environment  $\mathfrak{e}$ . Another interesting observation is that the fixation probability  $\theta$  is an annealed average of the densities of type- $\heartsuit$  individuals. Therefore,  $\theta$  is a function of the average type- $\heartsuit$  densities determined by the initial distribution  $\mu^\mathfrak{e}$  and does *not* depend on any other parameters of the distribution. ■

The proof of Theorem 4.2.9 relies on the analysis of the single-particle process  $\Theta^\epsilon$  in Definition 4.2.3 in a random environment  $\epsilon$  drawn from the law  $\bar{\mathbb{P}}$ . In particular, at the heart of the proof lies an exploitation of the following homogenisation result, whose proof is deferred to Section 4.3.3.

**Theorem 4.2.11 (Homogenisation of environment).** *Let  $f_A : \mathcal{E}_{\mathbb{R}} \rightarrow \mathbb{R}$  and  $f_D : \mathcal{E}_{\mathbb{R}} \rightarrow \mathbb{R}$  be two bounded  $\Sigma$ -measurable functions. Then, under Assumption 2.A and conditions (1)–(2) in Assumption 4.A, for  $\bar{\mathbb{P}}$ -a.s. every realisation of  $\epsilon$  and any  $\alpha \in \{0, 1\}$ ,*

$$\lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^\epsilon((0, \alpha), (j, \beta)) [\beta f_A(T_j \epsilon) + (1 - \beta) f_D(T_j \epsilon)] = \theta, \quad (4.23)$$

where  $p_t^\epsilon(\cdot, \cdot)$  is the time- $t$  transition kernel of the single-particle dual process  $\Theta^\epsilon$  given in Definition 4.2.3, and

$$\theta := \frac{1}{1 + \rho} \int_{\mathcal{E}_{\mathbb{R}}} [f_A((N_k, M_k)_{k \in \mathbb{Z}^d}) + \frac{M_0}{N_0} f_D((N_k, M_k)_{k \in \mathbb{Z}^d})] d\bar{\mathbb{P}}\{(N_k, M_k)_{k \in \mathbb{Z}^d}\}, \quad (4.24)$$

with  $\rho := \bar{\mathbb{E}}\left[\frac{M_0}{N_0}\right] = \int_{\mathcal{E}_{\mathbb{R}}} \frac{M_0}{N_0} d\bar{\mathbb{P}}\{(N_k, M_k)_{k \in \mathbb{Z}^d}\}$ .

The interpretation of the above result is that, for  $\bar{\mathbb{P}}$ -a.s. every realisation of the environment  $\epsilon$ , the law of the “environment viewed from the particle” in the process  $\Theta^\epsilon$  converges weakly to an invariant distribution. The precise meaning of the last statement will become clear in Section 4.3. Conditions (1)–(2) in Assumption 4.A play a crucial role in the proof. Theorem 4.2.11 combined with Theorem 4.2.4 enable us to prove Theorem 4.2.9.

Note that, in (4.23), the process  $\Theta^\epsilon$  is assumed to start at  $(0, \alpha) \in G$ . However, this does not matter, because the law of the environment is translation-invariant. Indeed, we have the following corollary:

**Corollary 4.2.12.** *Suppose that Assumption 2.A and conditions (1)–(2) in Assumption 4.A hold. Let  $f_A, f_D$  and  $\theta$  be as in Theorem 4.2.11. Then, for  $\bar{\mathbb{P}}$ -a.s. every realisation of  $\epsilon$  and all  $(i, \alpha) \in \mathbb{Z}^d \times \{0, 1\}$ ,*

$$\lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^\epsilon((i, \alpha), (j, \beta)) [\beta f_A(T_j \epsilon) + (1 - \beta) f_D(T_j \epsilon)] = \theta, \quad (4.25)$$

where  $p_t^\epsilon(\cdot, \cdot)$  is as in Definition 4.2.3.

## §4.2.4 Discussion

**Clustering in fixed environment.** In Theorem 2.4.9 of Chapter 2 we only showed convergence of the spatial process  $Z^\epsilon$  to an equilibrium for a restricted class of initial distributions, namely, a product of binomials with parameters that are tuned to the environment  $\epsilon$  and the density of type- $\heartsuit$  individuals in the populations. The main result of Section 4.2.2, namely, Theorem 4.2.4, fully characterises the set of initial



distributions for which  $Z^\epsilon$  admits convergence to equilibrium. The result is valid for any admissible environment  $\epsilon$  in which  $Z^\epsilon$  exhibits clustering. The proof follows from similar arguments used in the proof of the analogous results [112, Theorem 1.9(b)] and [140, Theorem 1.2] derived, respectively, in the context of the Voter model and the Stepping Stone model (see also e.g. [27, 12]). In Theorem 2.4.12 of Chapter 2 we showed that the process  $Z^\epsilon$  clusters if and only if two dual particles in  $Z_*^\epsilon$  coalesce into a single particle with probability 1. We also show in Theorem 4.4.4 in Section 4.4.1 that coalescence of two dual particles with probability 1 is equivalent to coalescence of any finite number of dual particles with probability 1. This consistency property of the dual process, which is purely a consequence of the duality relation between  $Z^\epsilon$  and  $Z_*^\epsilon$ , is far from trivial, because the dual particles interact with each other.

To summarise, the process  $Z^\epsilon$  admits *only* mono-type equilibria if and only if the evolution of the dual  $Z_*^\epsilon$  is eventually governed by  $p_t^\epsilon(\cdot, \cdot)$ , the probability transition kernel of the single-particle dual  $\Theta^\epsilon$  (recall Definition 4.2.3). Precisely because of this, we see in (4.8) that the domain of attraction for each mono-type equilibrium of the process  $Z^\epsilon$  in the clustering regime is dictated by the limiting behaviour of  $p_t^\epsilon(\cdot, \cdot)$  as  $t \rightarrow \infty$ . On the contrary, if the process  $Z^\epsilon$  is in the coexistence regime (= existence of multi-type equilibria), then the evolution of the dual  $Z_*^\epsilon$  is no longer described by  $p_t^\epsilon(\cdot, \cdot)$  alone, and therefore providing an answer to similar questions in the case of coexistence is challenging. In particular, because of the presence of interactions in the dual and the lack of translation-invariance of the state space  $\mathcal{X}^\epsilon$ , the characterization of the domain of attraction for a multi-type equilibrium via Liggett-type conditions (see e.g. [112, Theorem 1.9(a)], [76]) is a highly non-trivial problem, and is closely related to the study of harmonic functions (see e.g. [141]) of the general dual process  $Z_*^\epsilon$ .

**Clustering in random environment.** Turning to the main result of Section 4.2.3, we see that Theorem 4.2.9 is a homogenisation statement on the convergence of the spatial system to a mono-type equilibrium in random environment. It states that if the population sizes are drawn from an ergodic and translation-invariant random field for which clustering prevails, and the initial average densities of type- $\heartsuit$  active and dormant individuals in each colony are modulated, respectively, by two global functions  $f_A(\cdot)$  and  $f_D(\cdot)$  of the population sizes, then the spatial system converges in law towards a mono-type equilibrium for almost all initial realisations of the sizes. In the attained equilibrium, the probability of fixation to the all type- $\heartsuit$  configuration is a weighted average of the two functions  $f_A$  and  $f_D$ , and is independent of the chosen initial population sizes. In other words, the spatial process  $Z^\epsilon$  undergoes homogenisation, which, roughly speaking, can be viewed as a “weak law of large numbers”.

A closer look at the proof in Section 4.4.2 will reveal that the homogenisation comes, in essence, from the duality relation with the process  $\Theta^\epsilon$  evolving in the same random environment. The homogenisation in the continuous-time process  $\Theta^\epsilon$ , in turn, is inherited from a discrete-time subordinate Markov chain  $\widehat{\Theta}^\epsilon$  (see Definition 4.3.1 in Section 4.3.1). This  $\widehat{\Theta}^\epsilon$  is embedded into the continuous-time process  $\Theta^\epsilon$  and closely resembles a  $d$ -dimensional version of the random walk in random environment (RWRE) on a strip introduced in [21] (see also [54, 53, 62] for similar models and further references). However, results derived in that context do not immediately carry

over to our setting, because  $\widehat{\Theta}^\epsilon$  fails to meet some basic irreducibility hypotheses (see e.g. [21, Condition C]). Nonetheless, it turns out that  $\widehat{\Theta}^\epsilon$  is easier to analyse than the RWRE on a strip, as some of its transition probabilities are controlled by deterministic parameters that do not depend on the environment  $\epsilon$ . To be precise, the step distribution of a particle evolving via  $\widehat{\Theta}^\epsilon$  on the  $d$ -dimensional strip  $\mathbb{Z}^d \times \{0, 1\}$  is a preassigned probability distribution  $\hat{p}(\cdot)$  on  $\mathbb{Z}^d$  and, in fact, is defined in terms of the migration kernel  $a(\cdot, \cdot)$  of the spatial process  $Z^\epsilon$ . This simplicity of the subordinate Markov chain, which is similar to a property found in for random walk in random scenery (see e.g., [44, 49]), allows us to answer some of the highly sought-after questions in the literature on RWRE. In particular, we are able to identify a stationary and ergodic distribution for the environment viewed from the particle, with an explicit expression for the density w.r.t. the initial law, and establish a strong law of large numbers for the location of the particle (see Section 4.3.2). Moreover, when  $\hat{p}(\cdot)$  is symmetric and recurrent ( $d \leq 2$ ), we show that the environment process converges weakly to the *reversible* stationary distribution in the *quenched* setting. The latter is a very powerful result, which ultimately causes the homogenisation found in the subordinate Markov chain  $\widehat{\Theta}^\epsilon$ , and later passes it on to the single-particle dual  $\Theta^\epsilon$  as well.

As argued before, the spatial process  $Z^\epsilon$  acquires the homogenisation via duality from  $\Theta^\epsilon$ . Indeed, a crucial observation will reveal that the homogenised fixation probability in (4.19) is nothing but the average of the two global functions  $f_A$  and  $f_D$  w.r.t. the invariant distribution of the environment process. The method employed in proving the quenched weak convergence of the environment process for  $\widehat{\Theta}^\epsilon$  to the invariant distribution is not probabilistic and relies on ergodic theoretic tools. To be precise, we first show that the *peripheral point-spectrum* (i.e., the set of all eigenvalues of modulus 1) of the self-adjoint Markov kernel operator  $\mathfrak{K}$  associated to the environment process is trivial (see Lemma 4.3.12 in Section 4.3.2) and afterwards invoke a generalised version of the fundamental theorem for Markov chains (see Proposition 4.3.10 in Section 4.3.2) to establish the convergence. This way of proving weak convergence of the environment process is non-standard in the literature on RWRE, where such convergences are often established by exploiting some form of regeneration structure, or results like a local central limit theorem for the relevant random walk (see e.g., [95, 106, 54, 9]). Admittedly, the analysis of the peripheral point-spectrum of a Markov kernel operator in the  $L_p$  ( $p \geq 1$ ) space of its reversible distribution is non-trivial and requires knowledge of the explicit form of the distribution. However, in many random environment models, such as the random conductance model, the one-dimensional RWRE, etc., important results in the quenched setting are still incomplete, despite knowledge of the explicit reversible distribution. Perhaps such problems may be approached in a similar way.

### §4.3 Single-particle dual in random environment

As indicated in the previous section, the single-particle dual process  $\Theta^\epsilon$  (see Definition 4.2.3) serves as the main ingredient in proofs of all our main results. In this section we study  $\Theta^\epsilon$  in a typical random environment  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$  drawn according to the law  $\mathbb{P}$

(see Assumption 4.B) and prove the homogenisation result stated in Theorem 4.2.11.

To avoid dealing with technicalities that arise in the context of continuous-time Markov processes, in Section 4.3.1 we transform the process  $\Theta^\epsilon$  into a discrete-time Markov chain  $\hat{\Theta}^\epsilon$  using the well-known method of *uniformisation* by a Poisson clock. We also introduce an *auxiliary environment process*  $W$  associated to the Markov chain  $\hat{\Theta}^\epsilon$ . In Section 4.3.2 we show that the environment process  $W$  converges weakly to an invariant distribution in the *quenched* setting. Finally, in Section 4.3.3 we prove Theorem 4.2.11 and Corollary 4.2.12 by transferring the convergence result on  $W$  to the continuous-time process  $\Theta^\epsilon$ .

### §4.3.1 Subordinate Markov chain and auxiliary environment process

When a continuous-time Markov process on a countable state space retains *uniformly bounded* jump rates, it can be uniformised by a Poisson clock and a discrete-time subordinate Markov chain (see e.g., [113, Chapter 2]). The method of uniformisation essentially transforms a *variable-speed* continuous-time Markov process into a *constant-speed* continuous-time Markov process [11]. Observe from (4.6) that the jump rates of  $\Theta^\epsilon$  (see Definition 4.2.3) are uniformly bounded when the chosen environment  $\epsilon$  is uniformly elliptic, and therefore  $\Theta^\epsilon$  is uniformisable for such an environment. We start by defining a subordinate Markov chain  $\hat{\Theta}^\epsilon$  corresponding to the process  $\Theta^\epsilon$  in a uniformly elliptic environment  $\epsilon$ .

**Definition 4.3.1 (Subordinate Markov chain).** The subordinate Markov chain (see Fig. 4.1)

$$\hat{\Theta}^\epsilon := (\hat{\Theta}_n^\epsilon)_{n \in \mathbb{N}_0}, \quad \hat{\Theta}_n^\epsilon = (X_n^\epsilon, \alpha_n^\epsilon), \quad (4.26)$$

in a uniformly elliptic environment  $\epsilon := (N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{E}_{\mathfrak{R}}$  is the discrete-time Markov chain on the state space  $G = \mathbb{Z}^d \times \{0, 1\}$  with transition probabilities

$$\begin{aligned} (i, 1) &\longrightarrow \begin{cases} (j, 1) & \text{w.p. } (1 - q_s)\hat{p}(j - i), \quad j \in \mathbb{Z}^d, \\ (i, 0) & \text{w.p. } q_s, \end{cases} \\ (i, 0) &\longrightarrow \begin{cases} (i, 0) & \text{w.p. } 1 - \omega(i), \\ (i, 1) & \text{w.p. } \omega(i), \end{cases} \end{aligned} \quad (4.27)$$

where  $i \in \mathbb{Z}^d$ , and the parameters  $q_s$ ,  $\omega := (\omega(k))_{k \in \mathbb{Z}^d}$  and  $\hat{p} := (\hat{p}(k))_{k \in \mathbb{Z}^d}$  are determined by the exchange rate  $\lambda$ , the environment  $\epsilon$ , the migration kernel  $a(\cdot, \cdot)$ , and the ellipticity constant  $\mathfrak{R} \geq 2$ , as follows:

$$\begin{aligned} q_s &:= \frac{\lambda}{c + \lambda + \lambda\mathfrak{R}}, \quad \omega(i) := \frac{\lambda K_i}{c + \lambda + \lambda\mathfrak{R}} = \frac{\lambda N_i}{M_i(c + \lambda + \lambda\mathfrak{R})}, \\ \hat{p}(i) &:= \frac{\lambda\mathfrak{R}}{c + \lambda\mathfrak{R}} \mathbb{1}_{\{i=0\}} + \frac{a(0, i)}{c + \lambda\mathfrak{R}} \mathbb{1}_{\{i \neq 0\}}, \end{aligned} \quad i \in \mathbb{Z}^d, \quad (4.28)$$

where  $c$  is the speed of migration defined in condition (3) of Assumption 2.A. We denote by  $Q_\epsilon(\cdot, \cdot) : G \times G \rightarrow [0, 1]$  the 1-step transition kernel of the chain  $\hat{\Theta}^\epsilon$ , defined

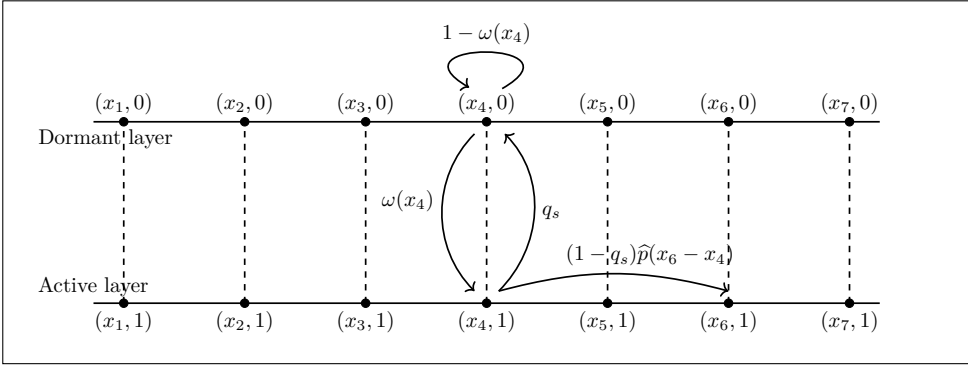


Figure 4.1: A schematic representation of the transition probabilities of a particle moving on the  $d$ -dimensional strip  $\mathbb{Z}^d \times \{0, 1\}$  according to  $\widehat{\Theta}^\epsilon$ . The particle is allowed to migrate in the bottom layer and while doing so remains in active state. However, the particle becomes dormant by entering the top layer, and thus can not migrate.

as

$$Q_\epsilon(\eta, \xi) := \widehat{P}_\eta^\epsilon(\widehat{\Theta}_1^\epsilon = \xi), \quad \eta, \xi \in G, \quad (4.29)$$

where  $\widehat{P}_\eta^\epsilon$  is the canonical law of  $\widehat{\Theta}^\epsilon$  started at  $\eta$ . ■

**Remark 4.3.2 (Well-posedness).** Observe that  $\widehat{p}(\cdot)$  defines a probability distribution on  $\mathbb{Z}^d$  and inherits the role of the migration kernel  $a(0, \cdot)$ . By the uniform ellipticity of the environment  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$ , it follows that  $\omega \in [\delta, 1 - \delta]^{\mathbb{Z}^d}$  for some  $\delta \in (0, \frac{1}{2})$  determined by  $c, \lambda$  and  $\mathfrak{R}$ . Thus, the transition probabilities in (4.27) are well-defined. From (4.28) we see that  $\omega$  is the only parameter that depends on  $\epsilon$  and plays the role of *random environment* for  $\widehat{\Theta}^\epsilon$ , while  $q_s$  takes over the role of  $\lambda$ , which is the rate of becoming dormant from the active state in the continuous-time process  $\Theta^\epsilon$ .

The subordinate Markov chain  $\widehat{\Theta}^\epsilon$  describes the evolution of a particle moving on the  $d$ -dimensional strip  $\mathbb{Z}^d \times \{0, 1\}$  in discrete time. The coordinates  $X_n^\epsilon$  and  $\alpha_n^\epsilon$  give, respectively, the location in  $\mathbb{Z}^d$  and the state (active or dormant) at time  $n \in \mathbb{N}_0$  of the particle evolving in the environment  $\epsilon$  according to the transition probabilities given in (4.27). In each step, the particle in the active state, with probability  $(1 - q_s)$ , performs random walk on  $\mathbb{Z}^d$  according to the increment distribution  $\widehat{p}(\cdot)$ , while, with probability  $q_s$ , it becomes dormant from the active state. The particle does not move in the dormant state and becomes active with a location-dependent probability determined by the environment  $\epsilon$ . The following property of the law of  $\widehat{\Theta}^\epsilon$  is a consequence of the translation-invariance of  $\mathbb{Z}^d$  and the migration kernel  $a(\cdot, \cdot)$ . The proof follows from an easy calculation of the transition probabilities of  $\widehat{\Theta}^\epsilon$  given in (4.27), and is omitted for brevity.

**Lemma 4.3.3 (Translation-invariance).** For any  $(i, \alpha), (j, \beta) \in G$  and  $n \in \mathbb{N}_0$ ,

$$\widehat{P}_{(0, \alpha)}^\epsilon(\widehat{\Theta}_n^\epsilon = (j, \beta)) = \widehat{P}_{(i, \alpha)}^{T-i\epsilon}(\widehat{\Theta}_n^{T-i\epsilon} = (i + j, \beta)). \quad (4.30)$$

The connection between the discrete-time Markov chain  $\widehat{\Theta}^\epsilon$  and the continuous-time Markov process  $\Theta^\epsilon$  becomes apparent in the next lemma.

**Lemma 4.3.4 (Uniformisation by Poisson clock).** *Let  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$  be a uniformly elliptic environment and  $(N_t)_{t \geq 0}$  be a Poisson process with rate  $c + \lambda + \lambda\mathfrak{R}$  that is independent of the subordinate Markov chain  $\widehat{\Theta}^\epsilon$ . Then, under the assumption that the process  $\Theta^\epsilon$  (see Definition 4.2.3) and the Markov chain  $\widehat{\Theta}^\epsilon$  have the same initial distribution,*

$$(\Theta^\epsilon(t))_{t \geq 0} \stackrel{d}{=} (\widehat{\Theta}_{N_t}^\epsilon)_{t \geq 0}. \quad (4.31)$$

In particular, for  $\eta, \xi \in G$ ,

$$p_t^\epsilon(\eta, \xi) = e^{-(c+\lambda+\lambda\mathfrak{R})t} \sum_{n=0}^{\infty} \frac{[(c+\lambda+\lambda\mathfrak{R})t]^n}{n!} Q_\epsilon^n(\eta, \xi), \quad (4.32)$$

where  $p_t^\epsilon(\cdot, \cdot)$  and  $Q_\epsilon(\cdot, \cdot)$  are as in Definition 4.2.3 and Definition 4.3.1, respectively.

*Proof.* Let  $\mathcal{J}_\epsilon$  denote the infinitesimal generator of the process  $\Theta^\epsilon$ . The action of  $\mathcal{J}_\epsilon$  on a bounded function  $f \in \mathcal{F}_b(G)$  is given by

$$(\mathcal{J}_\epsilon f)(i, \alpha) = \begin{cases} \lambda[f(i, 0) - f(i, 1)] + \sum_{j \in \mathbb{Z}^d} a(i, j)[f(j, 1) - f(i, 1)], & \text{if } \alpha = 1, \\ \lambda K_i[f(i, 1) - f(i, 0)], & \text{if } \alpha = 0, \end{cases} \quad (4.33)$$

where  $(i, \alpha) \in G$ . Since  $\epsilon$  is uniformly elliptic and the total speed of migration given by  $c$  is finite by virtue of Assumption 2.A, it is easily seen that  $\mathcal{J}_\epsilon$  is a bounded operator. Thus  $(\exp\{\mathcal{J}_\epsilon t\})_{t \geq 0}$  defines the semigroup of  $\Theta^\epsilon$ . In particular, the transition probability kernel  $p_t^\epsilon(\cdot, \cdot)$  expands as

$$p_t^\epsilon(\cdot, \cdot) = \sum_{n=0}^{\infty} \mathcal{J}_\epsilon^n(\cdot, \cdot) \frac{t^n}{n!}, \quad (4.34)$$

where the generator  $\mathcal{J}_\epsilon$  is viewed as a matrix. The claim follows from this expansion of  $p_t^\epsilon(\cdot, \cdot)$  and the observation that

$$\mathcal{J}_\epsilon = (c + \lambda + \lambda\mathfrak{R})[Q_\epsilon - I], \quad (4.35)$$

where  $I$  is the identity operator (viewed as a matrix). Note that in (4.35) the translation-invariance of the migration kernel  $a(\cdot, \cdot)$  is used.  $\square$

Below we define the “environment process” associated to the subordinate Markov chain  $\widehat{\Theta}^\epsilon$ . This process is defined in the same way as for RWRE on a strip (see e.g., [53, Definition 2.2]).

**Definition 4.3.5 (Auxiliary environment process).** Let  $\widehat{\Theta}^\epsilon = (X_n^\epsilon, \alpha_n^\epsilon)_{n \in \mathbb{N}_0}$  with the canonical law  $\widehat{P}_{(0, \alpha)}^\epsilon$  be the subordinate Markov chain (see Definition 4.3.1) started at  $(0, \alpha) \in G$  in environment  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$ . The auxiliary environment process  $W$  having initial distribution  $\delta_{(\epsilon, \alpha)}$  is the discrete-time process on  $\Omega_{\mathfrak{R}} := \mathcal{E}_{\mathfrak{R}} \times \{0, 1\}$  given by

$$W := (W_n)_{n \in \mathbb{N}_0}, \quad W_n := (\epsilon_n, \alpha_n) \text{ with } \epsilon_n := T_{X_n^\epsilon} \epsilon, \quad \alpha_n := \alpha_n^\epsilon, \quad (4.36)$$

and is defined on the same probability space of  $\widehat{\Theta}^\epsilon$ . ■

It is trivial to check that, for any  $(\epsilon, \alpha) \in \Omega_{\mathfrak{R}}$ ,  $W$  is a Markov chain on the state space  $\Omega_{\mathfrak{R}}$  under the law  $\widehat{P}_{(0,\alpha)}^\epsilon$ , with initial distribution  $\delta_{(\epsilon,\alpha)}$  (by Lemma 4.3.3, also under the law  $\widehat{P}_{(i,\alpha)}^\epsilon$ ,  $i \in \mathbb{Z}^d$ , with initial distribution  $\delta_{(T_i\epsilon,\alpha)}$ ).

The action of the Markov kernel operator  $\mathfrak{R}$  associated to  $W$  on a bounded function  $f \in \mathcal{F}_b(\Omega_{\mathfrak{R}})$  is given by

$$\mathfrak{R}f(\epsilon, \alpha) := \widehat{E}_{(0,\alpha)}^\epsilon[f(W_1)] = \sum_{(j,\beta) \in G} Q_\epsilon((0, \alpha), (j, \beta))f(T_j\epsilon, \beta), \quad (4.37)$$

where  $(\epsilon, \alpha) \in \Omega_{\mathfrak{R}}$  and  $Q_\epsilon(\cdot, \cdot)$  is the 1-step transition kernel of  $\widehat{\Theta}^\epsilon$  defined in (4.29). In particular,

$$\mathfrak{R}f(\epsilon, \alpha) = \begin{cases} q_s f(\epsilon, 0) + (1 - q_s) \sum_{j \in \mathbb{Z}^d} \widehat{p}(j)f(T_j\epsilon, 1), & \text{if } \alpha = 1, \\ \omega(0)f(\epsilon, 1) + [1 - \omega(0)]f(\epsilon, 0), & \text{if } \alpha = 0, \end{cases} \quad (4.38)$$

where  $q_s$ ,  $\widehat{p}(\cdot)$  and  $\omega := (\omega(k))_{k \in \mathbb{Z}^d}$  are defined in terms of  $\epsilon$  and the other parameters in (4.28).

The Markov chain  $W$  describes the state of the environment from the point of view of a particle that moves on the  $d$ -dimensional strip  $\mathbb{Z}^d \times \{0, 1\}$  according to the chain  $\widehat{\Theta}^\epsilon$ . The definition of the process differs from the standard definition usually encountered in the literature on RWRE. This is because the particle moves on two copies of  $\mathbb{Z}^d$  instead of one, and in order to preserve the Markov property we need an extra variable describing the layer on which the particle is present.

The state space  $\Omega_{\mathfrak{R}}$  of the auxiliary environment process  $W$ , even though compact, is huge. Thus, at first glance, obtaining any useful information from  $W$  might seem to be an impossible task. In general, this difficulty is overcome by taking initial samples of the environment from an ergodic and translation-invariant law. In such settings, it often becomes possible to construct “by hand” an invariant distribution that is absolutely continuous w.r.t. the initial law. Invariant distributions having such characteristics, which guarantees its uniqueness as well (see e.g. [22, 100]), are an extremely powerful tool for deriving many interesting properties, such as laws of large numbers, central limit theorems etc., for the relevant process. In the next section we find an invariant distribution  $\mathbb{Q}$  with such a property and prove weak convergence of  $W$  to the invariant distribution in the *quenched* setting.

### §4.3.2 Stationary environment process and weak convergence

In this section we address the question of whether the auxiliary environment process  $W$  admits an invariant distribution that is “equivalent” to its initial distribution. The following result provides a positive answer:

**Theorem 4.3.6 (Invariant distribution of environment process).** *Let  $\mathbb{Q}$  be the probability measure on  $(\Omega_{\mathfrak{R}}, \Sigma \otimes 2^{\{0,1\}})$  defined by*

$$d\mathbb{Q}\{(\mathbf{e}, \alpha)\} := \frac{u(\mathbf{e}, \alpha)}{1 + \rho} d\bar{\mathbb{P}}\{\mathbf{e}\}, \quad (4.39)$$

where the law  $\bar{\mathbb{P}}$  defined on  $(\mathcal{E}_{\mathfrak{R}}, \Sigma)$  is as in Assumption 4.B,  $\rho := \bar{\mathbb{E}}\left[\frac{M_0}{N_0}\right]$ , and the density  $u : \Omega_{\mathfrak{R}} \rightarrow (0, \mathfrak{R}]$  is given by

$$u((N_k, M_k)_{k \in \mathbb{Z}^d}, \alpha) = \begin{cases} 1 & \text{if } \alpha = 1, \\ \frac{M_0}{N_0} & \text{if } \alpha = 0. \end{cases} \quad (4.40)$$

The following hold:

- (1) The environment process  $W$  in Definition 4.3.5 is stationary and ergodic under the probability law  $\mathbb{Q}$ .
- (2) Under condition (1) in Assumption 4.A,  $\mathbb{Q}$  is reversible.

**Remark 4.3.7 (Validity in all dimensions).** Part (1) of Theorem 4.3.6 holds without the imposition of condition (1) in Assumption 4.A. It essentially follows from the translation-invariance and ergodicity of the law  $\bar{\mathbb{P}}$ . Moreover, both part (1) and part (2) are valid in all dimensions  $d \geq 1$ . Assumption 2.A is crucial for the proof and can not be removed in a straightforward way.

The proof of Theorem 4.3.6 is mostly computational and is deferred to Appendix B.1. As an application of this result, in Appendix B.1 we also give a proof of strong law of large numbers for the subordinate Markov chain  $\hat{\Theta}^c$  (recall Definition 4.3.1), which is a result of independent interest.

Before we proceed further, let us explain what we mean by “equivalence” of the invariant distribution  $\mathbb{Q}$  in the theorem and the initial law  $\bar{\mathbb{P}}$  of the environment. In the literature on RWRE, this phenomenon is called “equivalence between the static and the dynamic points of view”.

**Lemma 4.3.8 (Equivalence of  $\mathbb{Q}$  and  $\bar{\mathbb{P}}$ ).** *Let  $\mathbb{Q}, \bar{\mathbb{P}}$  be as in Theorem 4.3.6. Then, for any measurable  $A \subseteq \Omega_{\mathfrak{R}} = \mathcal{E}_{\mathfrak{R}} \times \{0, 1\}$ , the following are equivalent:*

- (1)  $\mathbb{Q}(A) = 1$ .
- (2) There exists a  $\Sigma$ -measurable  $A' \subseteq \mathcal{E}_{\mathfrak{R}}$  such that  $\bar{\mathbb{P}}(A') = 1$  and  $A' \times \{0, 1\} \subseteq A$ .

*Proof.* Let  $\theta := \frac{1}{1 + \bar{\mathbb{E}}[M_0/N_0]} \in (0, 1)$ , and let  $\mu$  be the probability measure on  $(\mathcal{E}_{\mathfrak{R}}, \Sigma)$  defined by

$$\mu(E) = \frac{\theta}{1 - \theta} \int_E \frac{M_0}{N_0} d\bar{\mathbb{P}}\{(N_k, M_k)_{k \in \mathbb{Z}^d}\}, \quad E \in \Sigma. \quad (4.41)$$

Clearly, for any  $E \in \Sigma$ ,

$$\mu(E) = 1 \text{ if and only if } \bar{\mathbb{P}}(E) = 1. \quad (4.42)$$

Suppose that (1) holds for some measurable  $A \subseteq \Omega_{\mathfrak{R}}$ . Note from (4.39) that

$$1 = \mathbb{Q}(A) = \theta \bar{\mathbb{P}}(A_1) + (1 - \theta)\mu(A_0), \quad (4.43)$$

where

$$A_0 := \{\mathbf{e} : (\mathbf{e}, 0) \in A\}, \quad A_1 := \{\mathbf{e} : (\mathbf{e}, 1) \in A\}. \quad (4.44)$$

Since  $\theta \in (0, 1)$ , this implies  $\bar{\mathbb{P}}(A_1) = \mu(A_0) = 1$ . Defining  $A' = A_0 \cap A_1$ , we see that (2) follows from (4.42).

Similarly, if (2) holds, then by (4.42),  $\mathbb{Q}(A' \times \{0, 1\}) = \theta \bar{\mathbb{P}}(A') + (1 - \theta)\mu(A') = 1$ . Thus,  $\mathbb{Q}(A) \geq \mathbb{Q}(A' \times \{0, 1\}) = 1$  and so (1) is proved.  $\square$

Our next goal is to prove weak convergence of the environment process  $W$  to the stationary law  $\mathbb{Q}$  under the quenched law  $\hat{P}_{(0,\alpha)}^{\mathbf{e}}$  for  $\bar{\mathbb{P}}$ -a.s. every realisation of the environment  $\mathbf{e} \in \mathcal{E}_{\mathfrak{R}}$ . In particular, we have the following result:

**Theorem 4.3.9 (Weak convergence of auxiliary environment).** *Suppose that conditions (1)–(2) in Assumption 4.A hold. Let  $f_A : \mathcal{E}_{\mathfrak{R}} \rightarrow \mathbb{R}$  and  $f_D : \mathcal{E}_{\mathfrak{R}} \rightarrow \mathbb{R}$  be two bounded  $\Sigma$ -measurable functions. Then, for  $\bar{\mathbb{P}}$ -a.s. every realisation of  $\mathbf{e} \in \mathcal{E}_{\mathfrak{R}}$  and any  $\alpha \in \{0, 1\}$ ,*

$$\lim_{n \rightarrow \infty} \hat{E}_{(0,\alpha)}^{\mathbf{e}}[h(\mathbf{e}_n, \alpha_n)] = \int_{\mathcal{E}_{\mathfrak{R}} \times \{0,1\}} h(\mathbf{e}', \beta) d\mathbb{Q}(\mathbf{e}', \beta), \quad (4.45)$$

where  $h$  is the function  $(\mathbf{e}, \alpha) \mapsto \alpha f_A(\mathbf{e}) + (1 - \alpha)f_D(\mathbf{e})$ ,  $W = (\mathbf{e}_n, \alpha_n)_{n \in \mathbb{N}_0}$  is the auxiliary environment process with law  $\hat{P}_{(0,\alpha)}^{\mathbf{e}}$  defined in Definition 4.3.5, and  $\mathbb{Q}$  is the stationary law of  $W$  given in (4.39).

The proof of Theorem 4.3.9 is a consequence of the proposition stated below. This proposition is an analogue of the “fundamental theorem of Markov chains on countable state spaces” because it addresses Markov chains on general state spaces. We believe that this result is already known in the literature (see e.g., [114] or [23, 89, 35]) on ergodic theory on Markov chains, but we have been unable to find a reference with an explicit proof of the statement. For the sake of completeness, the proof is given in Appendix B.2.

**Proposition 4.3.10 (Fundamental theorem of MC).** *Let  $(\Omega, \Sigma, \mathbb{Q})$  be a probability space, where the  $\sigma$ -field  $\Sigma$  is countably generated. Let  $W := (W_n)_{n \in \mathbb{N}_0}$  be a Markov chain on the state space  $\Omega$ , and assume that  $\mathbb{Q}$  is a reversible and ergodic stationary distribution for  $W$ . If  $-1$  is not an eigenvalue of the Markov kernel operator  $\mathfrak{K} : L_{\infty}(\Omega, \mathbb{Q}) \rightarrow L_{\infty}(\Omega, \mathbb{Q})$  associated to  $W$ , then for every bounded measurable function  $f \in \mathcal{F}_b(\Omega)$  and  $\mathbb{Q}$ -a.s. every  $w \in \Omega$ ,*

$$\lim_{n \rightarrow \infty} \mathbb{E}_w[f(W_n)] = \int_{\Omega} f d\mathbb{Q}, \quad (4.46)$$

where the expectation on the left is taken w.r.t. the law of  $W$  started at  $w$ .

**Remark 4.3.11 (Convergence in total variation).** The above proposition only establishes weak convergence and gives no information on the rate of convergence in (4.46). Under more stringent classical conditions on  $W$ , such as Harris recurrence or a



Doebelin criterion (see e.g., [121, 129] and [135, 104] for further references), uniqueness of the law  $\mathbb{Q}$  holds and the chain converges in total variation norm from *all* initial starting points. The existence of a *spectral gap* of the operator  $\mathfrak{R}$  results in *geometric ergodicity*, where the convergence takes place at an exponential rate (see e.g., [98]). However, under the assumption of only aperiodicity and  $\phi$ -irreducibility of the Markov chain  $W$ , convergence in total variation holds only for  $\mathbb{Q}$ -a.s. all initial points.

Although in the above remark we discuss convergence of a Markov chain in total variation norm, the reader should not hope for such a strong convergence of the auxiliary environment process  $W$  given in Definition 4.3.5. Indeed, the process  $W$  is a highly “singular” Markov chain living on a huge state space  $\Omega_{\mathfrak{R}}$  and admits infinitely many invariant distributions (e.g., take  $\bar{\mathbb{P}} = \delta_{\mathbf{e}}$ , where  $\mathbf{e} = (N, M)_{i \in \mathbb{Z}^d}$  is a translation-invariant environment with  $(N, M) \in \mathbb{N}^2$ , and construct  $\mathbb{Q}$  by (4.39)). Thus, it is very unlikely for  $W$  to be Harris recurrent, or to satisfy Doebelin-type conditions for that matter.

*Proof of Theorem 4.3.9.* By condition (1) of Assumption 4.A and Theorem 4.3.6, we see that  $\mathbb{Q}$  is a reversible and ergodic distribution for the auxiliary environment process  $W$ . Observe from Proposition 4.3.10, if we are able to prove that  $-1$  is not an eigenvalue of the Markov kernel operator  $\mathfrak{R} : L_{\infty}(\Omega_{\mathfrak{R}}, \mathbb{Q}) \rightarrow L_{\infty}(\Omega_{\mathfrak{R}}, \mathbb{Q})$  given in (4.38), then we can find a measurable  $E \subseteq \Omega_{\mathfrak{R}}$  such that  $\mathbb{Q}(E) = 1$  and, for all  $(\mathbf{e}, \alpha) \in E$ , (4.45) holds for the function  $h$ . In particular, using Lemma 4.3.8 we can find a measurable  $E' \subset \mathcal{E}_{\mathfrak{R}}$  with  $\bar{\mathbb{P}}(E') = 1$  and (4.45) holds for all  $(\mathbf{e}, \alpha) \in E' \times \{0, 1\}$ . Thus, the proof is complete once we show that  $-1$  is not an eigenvalue of  $\mathfrak{R}$  when viewed as an operator on  $L_{\infty}(\Omega_{\mathfrak{R}}, \mathbb{Q})$ . We prove this in Lemma 4.3.12 stated below.  $\square$

**Lemma 4.3.12 (Trivial peripheral point-spectrum).** *Let  $\mathfrak{R}$  be the Markov kernel operator (see (4.38)) of the auxiliary environment process  $W$ , and  $\mathbb{Q}$  be the invariant distribution of  $W$  given in Theorem 4.3.6. If condition (2) in Assumption 4.A holds, then  $-1$  is not an eigenvalue of the kernel operator  $\mathfrak{R} : L_{\infty}(\Omega_{\mathfrak{R}}, \mathbb{Q}) \rightarrow L_{\infty}(\Omega_{\mathfrak{R}}, \mathbb{Q})$ .*

*Proof.* Let  $g \in L_{\infty}(\Omega_{\mathfrak{R}}, \mathbb{Q})$  be such that

$$\mathfrak{R}g = -g \quad \mathbb{Q}\text{-a.s.} \tag{4.47}$$

We show  $g = 0$  a.s. As we will see below, this will follow from condition (2) in Assumption 4.A, which ensures that the increment distribution  $\hat{p}(\cdot)$  defined in terms of  $a(\cdot, \cdot)$  in (4.28) does not admit any non-constant and nonnegative bounded subharmonic function. With this aim, let  $A \subseteq \Omega_{\mathfrak{R}}$  be measurable with  $\mathbb{Q}(A) = 1$  and such that (4.47) holds for all  $(\mathbf{e}, \alpha) \in A$ . Without loss of generality, we can also assume that

$$|g(\mathbf{e}, \alpha)| \leq \|g\|_{\infty} \quad \forall (\mathbf{e}, \alpha) \in A. \tag{4.48}$$

By Lemma 4.3.8, there exists a measurable  $A' \subseteq \mathcal{E}_{\mathfrak{R}}$  such that  $\bar{\mathbb{P}}(A') = 1$  and (4.47) holds for all  $(\mathbf{e}, \alpha) \in A' \times \{0, 1\} \subseteq A$ . Using (4.38), we compute  $\mathfrak{R}g$  and obtain from (4.47) that

$$\begin{aligned} g(\mathbf{e}, 0) &= -[\omega(0)g(\mathbf{e}, 1) + (1 - \omega(0))g(\mathbf{e}, 0)], \\ g(\mathbf{e}, 1) &= -[q_s g(\mathbf{e}, 0) + (1 - q_s) \sum_{j \in \mathbb{Z}^d} \hat{p}(j)g(T_j \mathbf{e}, 1)], \quad \mathbf{e} \in A', \end{aligned} \tag{4.49}$$

where, as before,  $\omega, \hat{p}$  and  $q_s$  are defined by (4.28) in terms of  $\mathbf{e}$  and the other parameters. Now, using the translation invariance of  $\bar{\mathbb{P}}$ , we also have

$$\bar{\mathbb{P}}(B_{\text{inv}}) = 1, \quad B_{\text{inv}} := \bigcap_{j \in \mathbb{Z}^d} T_j^{-1}(A') \subseteq A', \quad (4.50)$$

where, trivially,  $B_{\text{inv}}$  is a translation-invariant set. We get from (4.49) that

$$\begin{aligned} g(\mathbf{e}, 0) &= -\frac{\omega(0)}{2 - \omega(0)} g(\mathbf{e}, 1), \\ \sum_{j \in \mathbb{Z}^d} \hat{p}(j) g(T_j \mathbf{e}, 1) &= -\left[ \frac{2 - (1 + q_s)\omega(0)}{(2 - \omega(0))(1 - q_s)} \right] g(\mathbf{e}, 1), \end{aligned} \quad (4.51)$$

for all  $\mathbf{e} \in B_{\text{inv}}$ . By ellipticity (see Definition 4.2.7) of  $\mathbf{e} \in B_{\text{inv}}$ , we can find a  $\delta \in (0, \frac{1}{2})$  such that  $\delta < \omega(0) < 1 - \delta$  for all  $\omega = (\omega(k))_{k \in \mathbb{Z}^d}$  determined by  $\mathbf{e} \in B_{\text{inv}}$ . In particular, setting

$$C := \frac{1}{1 - q_s} \left[ 1 - \frac{1 - \delta}{1 + \delta} q_s \right], \quad (4.52)$$

we see that

$$\frac{2 - (1 + q_s)\omega(0)}{(2 - \omega(0))(1 - q_s)} \geq C, \quad (4.53)$$

and also  $C > 1$  as  $\delta \in (0, \frac{1}{2})$ . Combining the above with (4.51), we have

$$\left| \sum_{j \in \mathbb{Z}^d} \hat{p}(j) g(T_j \mathbf{e}, 1) \right| = \left| \frac{2 - (1 + q_s)\omega(0)}{(2 - \omega(0))(1 - q_s)} \right| |g(\mathbf{e}, 1)| \geq C |g(\mathbf{e}, 1)|, \quad \mathbf{e} \in B_{\text{inv}}. \quad (4.54)$$

Using the triangle inequality, we get

$$\sum_{j \in \mathbb{Z}^d} \hat{p}(j) |g(T_j \mathbf{e}, 1)| \geq C |g(\mathbf{e}, 1)|, \quad \mathbf{e} \in B_{\text{inv}}. \quad (4.55)$$

Because  $B_{\text{inv}}$  is translation-invariant, the above implies that for any  $\mathbf{e} \in B_{\text{inv}}$  and all  $i \in \mathbb{Z}^d$ ,

$$\sum_{j \in \mathbb{Z}^d} \hat{p}(j) |g(T_{i+j} \mathbf{e}, 1)| \geq C |g(T_i \mathbf{e}, 1)|. \quad (4.56)$$

Since  $C > 1$ , the above equation tells that, for a fixed  $\mathbf{e} \in B_{\text{inv}}$ , the map  $i \mapsto |g(T_i \mathbf{e}, 1)|$  is a bounded (recall (4.48)) non-negative subharmonic function for  $\hat{p}(\cdot)$ . Now, by condition (2) in Assumption 4.A, a random walk on  $\mathbb{Z}^d$  with increment distribution  $\hat{p}(\cdot)$  defined as in (4.27) is irreducible and recurrent (see e.g., [107, Chapter 4]). Therefore, any bounded nonnegative subharmonic function of  $\hat{p}(\cdot)$  on  $\mathbb{Z}^d$  ( $d \leq 2$ ) must be a constant (by an application of Doob's submartingale convergence theorem). In particular, for any  $\mathbf{e} \in B_{\text{inv}}$  and all  $i \in \mathbb{Z}^d$ ,

$$|g(T_i \mathbf{e}, 1)| = |g(\mathbf{e}, 1)|. \quad (4.57)$$

Since  $C > 1$ , the only way in which (4.56) complies with (4.57), is when  $|g(\mathbf{e}, 1)| = 0$ , so (4.51) implies that  $g(\mathbf{e}, 0) = 0$  as well. Thus,  $g = 0$  on  $B_{\text{inv}} \times \{0, 1\}$  and, since  $\bar{\mathbb{P}}(B_{\text{inv}}) = 1$ , we see by Lemma 4.3.8 that  $\mathbb{Q}(B_{\text{inv}} \times \{0, 1\}) = 1$ .  $\square$

**Remark 4.3.13 (Peripheral point-spectrum in  $L_1$ ).** Using [89, Lemma 2], we can actually show that  $-1$  is not an eigenvalue of  $\mathfrak{R}$  in  $L_1(\Omega_{\mathfrak{R}}, \mathbb{Q})$  as well. But convergence of  $\mathfrak{R}^{2n}f$  may fail as  $n \rightarrow \infty$ , when it is merely assumed that  $f \in L_1(\Omega_{\mathfrak{R}}, \mathbb{Q})$  (see e.g., [131]), and therefore Proposition 4.3.10 does not hold in general for such  $f$ .

### §4.3.3 Transference of convergence: discrete to continuous

In this section we prove Theorem 4.2.11 and Corollary 4.2.12 by utilising the results derived in the Section 4.3.2.

Before we start with the proof of Theorem 4.2.11, let us briefly elaborate on its statement. In Section 4.3.1 we introduced in Definition 4.3.5 the discrete-time auxiliary environment process  $W$  associated to the subordinate Markov chain  $\widehat{\Theta}^\epsilon$ . We can also, in a similar fashion, extend the definition of  $W$  to construct a continuous-time environment process  $w := (w_t)_{t \geq 0}$  for the single-particle dual  $\Theta^\epsilon$  (recall Definition 4.2.3). Indeed, we obtain the process  $w$  by simply putting

$$w_t := (\epsilon_t, \alpha_t) \text{ with } \epsilon_t := T_{x_t^\epsilon} \epsilon, \alpha_t := \alpha_t^\epsilon, \quad (4.58)$$

for each  $t \geq 0$ , where  $\Theta^\epsilon = (x_t^\epsilon, \alpha_t^\epsilon)_{t \geq 0}$  is as in Definition 4.2.3. Upon closer inspection of (4.10) and the definition of  $w$ , we see that Theorem 4.2.11 basically states that

$$\lim_{t \rightarrow \infty} E_{(0, \alpha)}^\epsilon [\alpha_t f_A(\epsilon_t) + (1 - \alpha_t) f_D(\epsilon_t)] = \theta \quad (4.59)$$

for  $\bar{\mathbb{P}}$ -a.s. every realisation of the environment  $\epsilon$ , where  $f_A, f_D$  and  $\theta$  are as in the theorem. In other words, (4.59) is equivalent to saying that the process  $w$  converges in distribution to the law  $\mathbb{Q}$  given in (4.39) for  $\bar{\mathbb{P}}$ -a.s. every realisation of  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$  and any  $\alpha \in \{0, 1\}$ .

*Proof of Theorem 4.2.11.* From Lemma 4.3.4, we observe that

$$p_t^\epsilon((0, \alpha), (j, \beta)) = \sum_{n=0}^{\infty} \widehat{P}_{(0, \alpha)}^\epsilon(\widehat{\Theta}_n^\epsilon = (j, \beta)) \mathbb{P}(N_t = n), \quad (j, \beta) \in G, \epsilon \in \mathcal{E}_{\mathfrak{R}}, t \geq 0, \quad (4.60)$$

where  $p_t^\epsilon(\cdot, \cdot)$  is as in Definition 4.2.3,  $\widehat{\Theta}^\epsilon = (\widehat{\Theta}_n^\epsilon)_{n \in \mathbb{N}_0}$  is the subordinate Markov chain with law  $\widehat{P}_{(0, \alpha)}^\epsilon$  (see Definition 4.3.1) and  $(N_t)_{t \geq 0}$  is the Poisson process mentioned in the lemma, which is independent of  $\widehat{\Theta}^\epsilon$ . Thus, using the above, the left-hand side of (4.23), which we abbreviate by  $l((\epsilon, \alpha), t)$  for any  $t \geq 0$ , can be written as

$$\begin{aligned} l((\epsilon, \alpha), t) &= \sum_{(j, \beta) \in G} \left[ \sum_{n \in \mathbb{N}_0} \widehat{P}_{(0, \alpha)}^\epsilon(\widehat{\Theta}_n^\epsilon = (j, \beta)) \mathbb{P}(N_t = n) \right] \{ \beta f_A(T_j \epsilon) + (1 - \beta) f_D(T_j \epsilon) \} \\ &= \sum_{n \in \mathbb{N}_0} \left[ \sum_{(j, \beta) \in G} \widehat{P}_{(0, \alpha)}^\epsilon(W_n = (T_j \epsilon, \beta)) \{ \beta f_A(T_j \epsilon) + (1 - \beta) f_D(T_j \epsilon) \} \right] \mathbb{P}(N_t = n) \\ &= \sum_{n \in \mathbb{N}_0} \widehat{E}_{(0, \alpha)}^\epsilon [h(W_n)] \mathbb{P}(N_t = n), \end{aligned} \quad (4.61)$$

where the interchange of the order of summation in the second equality is justified by Fubini's theorem,  $(W_n)_{n \in \mathbb{N}_0}$  is the auxiliary environment process (see Definition 4.3.5), and  $h : \mathcal{E}_{\mathbb{R}} \times \{0, 1\} \rightarrow \mathbb{R}$  is the map  $(\mathbf{e}, \alpha) \mapsto \alpha f_A(\mathbf{e}) + (1 - \alpha) f_D(\mathbf{e})$ . By virtue of Theorem 4.3.9, we can find a measurable  $B \in \Sigma$  with  $\mathbb{P}(B) = 1$  such that, for all  $\mathbf{e} \in B$  and any  $\alpha \in \{0, 1\}$ ,

$$\lim_{n \rightarrow \infty} \widehat{E}_{(0, \alpha)}^{\mathbf{e}}[h(W_n)] = \int_{\Omega_{\mathbb{R}}} h(\mathbf{b}, \beta) d\mathbb{Q}(\mathbf{b}, \beta) = \theta, \quad (4.62)$$

where  $\theta$  is as in (4.24). Fix  $\mathbf{e} \in B$ ,  $\alpha \in \{0, 1\}$  and  $\epsilon > 0$ . By virtue of the above, we can find  $N_{\mathbf{e}} \in \mathbb{N}$  such that, for all  $n \geq N_{\mathbf{e}}$ ,  $|\widehat{E}_{(0, \alpha)}^{\mathbf{e}}[h(W_n)] - \theta| < \epsilon$ . Finally, from (4.61), we get

$$\begin{aligned} |l((\mathbf{e}, \alpha), t) - \theta| &\leq \sum_{n=0}^{\infty} |\widehat{E}_{(0, \alpha)}^{\mathbf{e}}[h(W_n)] - \theta| \mathbb{P}(N_t = n) \\ &\leq 2\|h\|_{\infty} \mathbb{P}(N_t < N_{\mathbf{e}}) + \epsilon \mathbb{P}(N_t \geq N_{\mathbf{e}}) \\ &\leq 2\|h\|_{\infty} \mathbb{P}(N_t < N_{\mathbf{e}}) + \epsilon. \end{aligned} \quad (4.63)$$

Since  $N_t \rightarrow \infty$  with probability 1 as  $t \rightarrow \infty$ , letting  $t \rightarrow \infty$  in the above, we see

$$\limsup_{t \rightarrow \infty} |l((\mathbf{e}, \alpha), t) - \theta| \leq \epsilon. \quad (4.64)$$

As  $\epsilon > 0$  is arbitrary, we get that

$$\lim_{t \rightarrow \infty} l((\mathbf{e}, \alpha), t) = \theta \quad (4.65)$$

for all  $\mathbf{e} \in B$  and  $\alpha \in \{0, 1\}$ . This proves the claim in (4.23).  $\square$

*Proof of Corollary 4.2.12.* The proof basically follows from the translation-invariance of  $\bar{\mathbb{P}}$  and Lemma 4.3.3. Indeed, using Theorem 4.2.11, we can find a measurable  $B \in \Sigma$  such that  $\bar{\mathbb{P}}(B) = 1$  and, for all  $\mathbf{e} \in B$ ,  $\alpha \in \{0, 1\}$ ,

$$\lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^{\mathbf{e}}((0, \alpha), (j, \beta)) [\beta f_A(T_j \mathbf{e}) + (1 - \beta) f_D(T_j \mathbf{e})] = \theta, \quad (4.66)$$

where  $\theta$  is as in (4.24). Letting  $B_{\text{inv}} := \cap_{j \in \mathbb{Z}^d} T_j^{-1} B$ , we see that  $B_{\text{inv}} \in \Sigma$  is translation-invariant and  $\bar{\mathbb{P}}(B_{\text{inv}}) = 1$ . In particular, for any  $\mathbf{e} \in B_{\text{inv}}$  and all  $(i, \alpha) \in \mathbb{Z}^d \times \{0, 1\}$ ,

$$\lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^{T_i \mathbf{e}}((0, \alpha), (j, \beta)) [\beta f_A(T_j(T_i \mathbf{e})) + (1 - \beta) f_D(T_j(T_i \mathbf{e}))] = \theta. \quad (4.67)$$

Also, using Lemma 4.3.3–4.3.4, we see that, for any  $t \geq 0$  and  $(j, \beta) \in \mathbb{Z}^d \times \{0, 1\}$ ,

$$p_t^{T_i \mathbf{e}}((0, \alpha), (j, \beta)) = p_t^{\mathbf{e}}((i, \alpha), (i + j, \beta)), \quad \forall i \in \mathbb{Z}^d, \alpha \in \{0, 1\}. \quad (4.68)$$

Combining the last two equations, for all  $(i, \alpha) \in \mathbb{Z}^d \times \{0, 1\}$ , we get

$$\lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^{\mathbf{e}}((i, \alpha), (i + j, \beta)) [\beta f_A(T_{i+j} \mathbf{e}) + (1 - \beta) f_D(T_{i+j} \mathbf{e})] = \theta, \quad (4.69)$$

which after a change of variable in the summation translates to

$$\lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^\epsilon((i, \alpha), (j, \beta)) [\beta f_A(T_j \epsilon) + (1 - \beta) f_D(T_j \epsilon)] = \theta. \quad (4.70)$$

The proof is complete by the observation that  $\bar{\mathbb{P}}(B_{\text{inv}}) = 1$ , and the above holds for any  $\epsilon \in B_{\text{inv}}$ .  $\square$

## §4.4 Proof of main theorems

In this section we prove the two main results given in Section 4.2.2–4.2.3. In Section 4.4.1, we derive a consistency property of the general dual  $Z_*^\epsilon$  of the process  $Z^\epsilon$ . Using this preliminary result on the dual, in Section 4.4.2 we prove Theorem 4.2.4, Corollary 4.2.5, and using Theorem 4.2.4 and the previous homogenisation result on the single-particle dual  $\Theta^\epsilon$  (see Definition 4.3.1), we prove Theorem 4.2.9.

### §4.4.1 Preliminaries: consistency of dual process

We start by recalling from Chapter 2 the duality relation between the spatial process  $Z^\epsilon$  and the dual process  $Z_*^\epsilon$  that will be needed for the proof of our main theorems.

**Theorem 4.4.1 (Duality relation, [Corollary 2.4.6, Chapter 2]).** *Suppose that Assumption 2.A is in force. Then, for every admissible environment  $\epsilon = (N_i, M_i)_{i \in \mathbb{Z}^d} \in \mathcal{A}$ , the following duality relation holds between the two processes  $Z^\epsilon$  and  $Z_*^\epsilon$ :*

$$\mathbb{E}_U[D^\epsilon(Z^\epsilon(t), V)] = \mathbb{E}_*^V[D^\epsilon(U, Z_*^\epsilon(t))], \quad t \geq 0. \quad (4.71)$$

Here the expectation on the left (right) side is taken w.r.t. the law of  $Z^\epsilon$  ( $Z_*^\epsilon$ ) started at  $U \in \mathcal{X}^\epsilon$  ( $V \in \mathcal{X}_*^\epsilon$ ), and  $D^\epsilon : \mathcal{X}^\epsilon \times \mathcal{X}_*^\epsilon \rightarrow [0, 1]$  is the duality function defined by

$$D^\epsilon(U, V) = \prod_{i \in \mathbb{Z}^d} \frac{\binom{X_i}{n_i}}{\binom{N_i}{n_i}} \frac{\binom{Y_i}{m_i}}{\binom{M_i}{m_i}} \mathbb{1}_{n_i \leq X_i, m_i \leq Y_i}, \quad (4.72)$$

with  $U = (X_i, Y_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}^\epsilon$  and  $V = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*^\epsilon$ .

The next lemma establishes the relation between the process  $\Theta^\epsilon$  and the general dual  $Z_*^\epsilon$ . We omit the proof for brevity, as this easily follows from the fact that any injective transformation preserves the Markov property and a unique such transformation exists that maps  $\Theta^\epsilon$  to the dual process  $Z_*^\epsilon$  started at a configuration consisting of only a single particle.

**Lemma 4.4.2 (Relation between  $\Theta^\epsilon$  and  $Z_*^\epsilon$ ).** *For  $i \in \mathbb{Z}^d$ , let  $\vec{\delta}_{i,A}$  (resp.  $\vec{\delta}_{i,D}$ )  $\in \mathcal{X}_*^\epsilon$  denote the configuration containing a single active (resp. dormant) particle at location  $i$ . Formally,*

$$\vec{\delta}_{i,A} := (\mathbb{1}_{\{n=i\}}, 0)_{n \in \mathbb{Z}^d}, \quad \vec{\delta}_{i,D} := (0, \mathbb{1}_{\{n=i\}})_{n \in \mathbb{Z}^d}, \quad (4.73)$$

and for  $\eta = (i, \alpha) \in \mathbb{Z}^d \times \{0, 1\}$ , let  $\vec{\delta}_\eta := \mathbb{1}_{\alpha=1} \vec{\delta}_{i,A} + \mathbb{1}_{\alpha=0} \vec{\delta}_{i,D}$ . If  $\mathbb{P}_\epsilon^\varphi$  denotes the law of  $Z_*^\epsilon$  started at  $\varphi \in \mathcal{X}_*^\epsilon$ , then, for all  $t \geq 0$ ,

$$p_t^\epsilon(\eta, \xi) = \mathbb{P}_\epsilon^{\vec{\delta}_\eta}(Z_*^\epsilon(t) = \vec{\delta}_\xi), \quad \eta, \xi \in \mathbb{Z}^d \times \{0, 1\}, \quad (4.74)$$

where  $p_t^\epsilon(\cdot, \cdot)$  is as in Definition 4.2.3.

The following lemma, which is essentially a consequence of Assumption 2.A, tells us that any bounded harmonic function of the single-particle dual process  $\Theta^\epsilon$  is a constant.

**Lemma 4.4.3 (Constant harmonics).** *Let  $\Theta^\epsilon = (\Theta^\epsilon(t))_{t \geq 0}$  be the process defined in Definition 4.2.3 started at  $\eta \in G$  with law  $P_\eta^\epsilon$ , where  $G = \mathbb{Z}^d \times \{0, 1\}$  and  $\epsilon := (N_i, M_i)_{i \in \mathbb{Z}^d}$ . Let  $f : G \rightarrow \mathbb{R}$  be a bounded harmonic function for  $P_\eta^\epsilon$ , i.e.,*

$$E_\eta^\epsilon[f(\Theta^\epsilon(t))] = f(\eta) \quad \text{for all } \eta \in G, t \geq 0. \quad (4.75)$$

Then  $f$  is constant.

*Proof.* Let  $\mathcal{J}_\epsilon$  be the infinitesimal generator of the process  $\Theta^\epsilon$ . The action of  $\mathcal{J}_\epsilon$  on  $f$  can be written in the following concise expression:

$$(\mathcal{J}_\epsilon f)(i, \alpha) := (\alpha\lambda + (1-\alpha)\lambda K_i)[f(i, 1-\alpha) - f(i, \alpha)] + \alpha \sum_{j \in \mathbb{Z}^d} a(i, j)[f(j, \alpha) - f(i, \alpha)], \quad (4.76)$$

where  $(i, \alpha) \in G$ . Since  $f$  is harmonic,  $(\mathcal{J}_\epsilon f) \equiv 0$  and, using the above, we have  $f(i, \alpha) = f(i, 1-\alpha)$  for all  $(i, \alpha) \in G$ , which in turn implies that the function  $i \mapsto f(i, 1)$  is harmonic for  $a(\cdot, \cdot)$ . Applying the Choquet-Deny theorem to the irreducible and translation-invariant kernel  $a(\cdot, \cdot)$ , we get the result.  $\square$

By using the duality relation stated in Theorem 4.4.1 and exploiting the clustering criterion given in Theorem 2.4.12 of Chapter 2, we obtain that coalescence of two dual particles with probability 1 is equivalent to coalescence of any number of dual particles with probability 1.

**Theorem 4.4.4 (Lineage consistency).** *Let  $\mathbb{P}_\epsilon^\varphi$  denote the law of the dual process  $Z_*^\epsilon$  started at  $\varphi := (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*^\epsilon$  and evolving in environment  $\epsilon := (N_i, M_i)_{i \in \mathbb{Z}^d}$ . Let  $\tau$  be first time when all particles have coalesced into a single particle in the dual process, i.e.,*

$$\tau := \inf\{t \geq 0 : |Z_*^\epsilon(t)| = 1\}, \quad (4.77)$$

where  $|\varphi| := \sum_{i \in \mathbb{Z}^d} (n_i + m_i)$  is the total number of initial dual particles. Then the following are equivalent:

- (a)  $\mathbb{P}_\epsilon^\varphi(\tau < \infty) = 1$  for all  $\varphi \in \mathcal{X}_*^\epsilon$  with  $|\varphi| = 2$ .
- (b)  $\mathbb{P}_\epsilon^\varsigma(\tau < \infty) = 1$  for all  $\varsigma \in \mathcal{X}_*^\epsilon$  with  $|\varsigma| \geq 2$ .

*Proof.* By irreducibility of the dual process  $Z_*^c$ , it suffices to prove the equivalence of the two statements for fixed  $\varphi, \varsigma \in \mathcal{X}_*^c$  such that  $|\varphi| = 2$  and  $n := |\varsigma| \geq 2$ . If  $n = 2$ , then there is nothing to prove. So assume that  $n > 2$ . It is straightforward to see from irreducibility and the Markov property of  $Z_*^c$  that if  $\mathbb{P}_c^\varphi(\tau = \infty) > 0$ , then  $\mathbb{P}_c^\varsigma(\tau = \infty) \geq \mathbb{P}_c^\varsigma(Z^*(t) = \varphi)\mathbb{P}_c^\varphi(\tau = \infty) > 0$ . Hence (b) implies (a).

To prove that (a) implies (b), assume  $\mathbb{P}_c^\varphi(\tau < \infty) = 1$  and, for  $t \geq 0$ , set  $I_t := |Z_*^c(t)|$ . Note that, since  $Z_*^c$  is a coalescent process,  $I_t$  is an integer-valued bounded random variable that is decreasing in  $t$  a.s. Thus,  $I := \lim_{t \rightarrow \infty} I_t$  exists a.s. and it is enough to prove that  $I = 1$  a.s. To this purpose, let  $\theta \in (0, 1)$  be fixed arbitrarily, and let  $Z^c$  be the spatial process started at the initial distribution  $\mu_\theta^c$  given by

$$\mu_\theta^c := \bigotimes_{i \in \mathbb{Z}^d} \text{Binomial}(N_i, \theta) \otimes \text{Binomial}(M_i, \theta). \quad (4.78)$$

By Theorem 2.4.9 of Chapter 2, the process  $Z^c$  converges to an equilibrium  $\nu_\theta$ . Also, by our assumption that  $\mathbb{P}_c^\varphi(\tau < \infty) = 1$  and Theorem 2.4.12 of Chapter 2, we have

$$\nu_\theta = (1 - \theta)\delta_{\spadesuit} + \theta\delta_{\heartsuit}, \quad (4.79)$$

where  $\delta_{\heartsuit}$  (resp.  $\delta_{\spadesuit}$ ) is the Dirac distribution concentrated at the all type- $\heartsuit$  configuration  $\mathfrak{c} \in \mathcal{X}^c$  (resp. the all type- $\spadesuit$  configuration  $(0, 0)_{i \in \mathbb{Z}^d} \in \mathcal{X}^c$ ). Furthermore, if  $D^c(\cdot, \cdot)$  is the duality function in (4.72), then combining Theorem 2.4.9 of Chapter 2 and the above we get

$$\theta = \mathbb{E}_{\nu_\theta} [D^c(Z^c(0), \varsigma)] = \lim_{t \rightarrow \infty} \mathbb{E}_c^\varsigma[\theta^{I_t}] = \mathbb{E}_c^\varsigma[\theta^I] \quad (\text{bounded convergence}), \quad (4.80)$$

which implies that  $\mathbb{E}_c^\varsigma[\theta(1 - \theta^{I-1})] = 0$ . Since  $\theta \in (0, 1)$ , we have that  $I = 1$  almost surely.  $\square$

## §4.4.2 Proofs: clustering in fixed and random environment

We are now ready to prove the two main theorems.

*Proof of Theorem 4.2.4.* To show that (a) implies (b), suppose that  $\mu_t^c$  converges weakly to  $\nu \in \mathcal{P}(\mathcal{X}^c)$  as  $t \rightarrow \infty$ . Let  $\theta_c := \mathbb{E}_\nu \left[ \frac{X_0^c(0)}{N_0} \right] \in [0, 1]$  be fixed. Since the system is in the clustering regime by assumption,  $\delta_{\spadesuit}$  and  $\delta_{\heartsuit}$  are the only two extremal equilibria for the process  $Z^c$ . Hence, we must have that

$$\nu = (1 - \theta_c)\delta_{\spadesuit} + \theta_c\delta_{\heartsuit}, \quad (4.81)$$

where  $\delta_{\heartsuit}$  (resp.  $\delta_{\spadesuit}$ ) is the Dirac distribution concentrated at the all type- $\heartsuit$  configuration  $\mathfrak{c} \in \mathcal{X}^c$  (resp.  $(0, 0)_{i \in \mathbb{Z}^d} \in \mathcal{X}^c$ ). We show that  $f^c \equiv \theta_c$ , which will settle (b) along with the last statement of the theorem. To this end, for each  $t \geq 0$ , let  $f_t^c : G \rightarrow [0, 1]$  be defined as

$$f_t^c(\eta) := \sum_{(j, \beta) \in G} p_t^c(\eta, (j, \beta)) \int_{\mathcal{X}^c} \left[ \beta \frac{X_j}{N_j} + (1 - \beta) \frac{Y_j}{M_j} \right] d\mu^c\{(X_k, Y_k)_{k \in \mathbb{Z}^d}\}, \quad \eta \in G. \quad (4.82)$$

Let  $\eta = (i, \alpha) \in G$  be arbitrary, and let  $Z_*^\epsilon := (Z_*^\epsilon(t))_{t \geq 0}$  be the dual process started at  $\vec{\delta}_\eta := \mathbb{1}_{\alpha=1} \vec{\delta}_{i,A} + \mathbb{1}_{\alpha=0} \vec{\delta}_{i,D}$ , where for each  $i \in \mathbb{Z}^d$  the configurations  $\vec{\delta}_{i,A}, \vec{\delta}_{i,D} \in \mathcal{X}_*^\epsilon$  are defined as in (4.73). In other words,  $\vec{\delta}_\eta$  is the configuration with a single dual particle located at  $i \in \mathbb{Z}^d$  with state  $\alpha$ . Recall from Definition 4.2.3 that the time- $t$  transition kernel  $p_t^\epsilon(\cdot, \cdot)$  of the single-particle dual process  $\Theta^\epsilon$  is defined as

$$p_t^\epsilon(\eta, \zeta) := P_\eta^\epsilon(\Theta^\epsilon(t) = \zeta), \quad \eta, \zeta \in G. \quad (4.83)$$

Using Lemma 4.4.2 and appealing to the monotone convergence theorem, we get from (4.82) that

$$f_t^\epsilon(\eta) = \int_{\mathcal{X}^\epsilon} \mathbb{E}_\epsilon^{\vec{\delta}_\eta} [D^\epsilon(z, Z_*^\epsilon(t))] d\mu^\epsilon\{z\}, \quad (4.84)$$

where the expectation is w.r.t. the law of the dual process  $Z_*^\epsilon$ , and  $D^\epsilon(\cdot, \cdot)$  is the duality function in (4.72). Furthermore, applying the duality relation between  $Z^\epsilon$  and  $Z_*^\epsilon$  to the above identity, we get

$$f_t^\epsilon(\eta) = \mathbb{E}_{\mu^\epsilon} [D^\epsilon(Z^\epsilon(t), \vec{\delta}_\eta)] = \int_{\mathcal{X}^\epsilon} D^\epsilon(z, \vec{\delta}_\eta) d\mu_t^\epsilon\{z\}. \quad (4.85)$$

However, since  $\mu_t^\epsilon \xrightarrow{weak} \nu$  as  $t \rightarrow \infty$ , combining the above with (4.81), we see that

$$f^\epsilon(\eta) = \lim_{t \rightarrow \infty} f_t^\epsilon(\eta) = \int_{\mathcal{X}^\epsilon} D^\epsilon(z, \vec{\delta}_\eta) d\nu\{z\} = \theta_\epsilon, \quad (4.86)$$

and hence the claim is proved.

To prove the converse, for  $t \geq 0$ , let  $f_t^\epsilon : G \rightarrow [0, 1]$  be as in (4.82). Applying Fubini's theorem to (4.84), for any  $\eta \in G$  we have

$$f_t^\epsilon(\eta) = \mathbb{E}_\epsilon^{\vec{\delta}_\eta} \left[ \int_{\mathcal{X}^\epsilon} D^\epsilon(z, Z_*^\epsilon(t)) d\mu^\epsilon\{z\} \right]. \quad (4.87)$$

Using the Markov property of  $Z_*^\epsilon$ , we note that, for  $t, s \geq 0$  and  $\eta \in G$ ,

$$f_{s+t}^\epsilon(\eta) = \sum_{\zeta \in G} p_s^\epsilon(\eta, \zeta) f_t^\epsilon(\zeta). \quad (4.88)$$

Since by assumption  $f^\epsilon(\eta) = \lim_{t \rightarrow \infty} f_t^\epsilon(\eta)$  exists for any  $\eta \in G$ , letting  $t \rightarrow \infty$  in the above identity, we obtain

$$\begin{aligned} f^\epsilon(\eta) &= \lim_{t \rightarrow \infty} \sum_{\zeta \in G} p_s^\epsilon(\eta, \zeta) f_t^\epsilon(\zeta) = \sum_{\zeta \in G} p_s^\epsilon(\eta, \zeta) \left[ \lim_{t \rightarrow \infty} f_t^\epsilon(\zeta) \right] \quad (\text{dominated convergence}) \\ &= \sum_{\zeta \in G} p_s^\epsilon(\eta, \zeta) f^\epsilon(\zeta) = E_\eta^\epsilon [f^\epsilon(\Theta^\epsilon(s))]. \end{aligned} \quad (4.89)$$

Hence, in particular,  $f^\epsilon$  is harmonic for the process  $(\Theta^\epsilon(t))_{t \geq 0}$  and thus, by Lemma 4.4.3,  $f^\epsilon \equiv \theta_\epsilon$  for some  $\theta_\epsilon \in [0, 1]$ . It only remains to show that  $\mu_t^\epsilon$  converges weakly as  $t \rightarrow \infty$ . This is equivalent to showing that, for any  $\varphi \in \mathcal{X}_*^\epsilon$ ,  $\lim_{t \rightarrow \infty} \mathbb{E}_{\mu^\epsilon} [D^\epsilon(Z^\epsilon(t), \varphi)]$  exists. Because  $\mathcal{P}(\mathcal{X}^\epsilon)$  is compact (as  $\mathcal{X}^\epsilon$  is) in the topology of weak convergence,



$(\mu_t^\epsilon)_{t \geq 0}$  is tight. Finally, the existence of the limit ensures the convergence of the associated finite-dimensional distributions, because the family of functions  $\{D^\epsilon(\cdot, \varphi) : \varphi \in \mathcal{X}_*^\epsilon\}$  fixes the mixed moments of the finite-dimensional distributions of  $Z^\epsilon$  (see Proposition 2.6.4 in Chapter 2), and therefore is convergence determining. Let  $\varphi = (n_i, m_i)_{i \in \mathbb{Z}^d} \in \mathcal{X}_*^\epsilon$  be fixed, and  $Z_*^\epsilon$  be the dual process started at  $\varphi$ . First note that if  $|\varphi| = \sum_{i \in \mathbb{Z}^d} (n_i + m_i) = 1$ , then the limit exists and equals  $\theta_\epsilon$  by our assumption. Indeed, if  $|\varphi| = 1$ , then  $\varphi = \vec{\delta}_\zeta$  for some  $\zeta \in G$ . As a consequence of duality and (4.84), we see that  $\mathbb{E}_{\mu^\epsilon} [D^\epsilon(Z^\epsilon(t), \varphi)] = f_t^\epsilon(\zeta)$  and hence

$$\lim_{t \rightarrow \infty} \mathbb{E}_{\mu^\epsilon} [D^\epsilon(Z^\epsilon(t), \varphi)] = \lim_{t \rightarrow \infty} \mathbb{E}_\epsilon^{\vec{\delta}_\zeta} \left[ \int_{\mathcal{X}^\epsilon} D^\epsilon(z, Z_*^\epsilon(t)) d\mu^\epsilon\{z\} \right] = \lim_{t \rightarrow \infty} f_t^\epsilon(\zeta) = f^\epsilon(\zeta) = \theta_\epsilon. \quad (4.90)$$

Now, let us fix  $\varphi \in \mathcal{X}_*^\epsilon$  such that  $|\varphi| \geq 2$ . Since the system is in the clustering regime, by virtue of Theorem 2.4.12 stated in Chapter 2, condition (a) in Theorem 4.4.4 is satisfied. Hence from part (b) of Theorem 4.4.4 it follows that  $\tau < \infty$  a.s., where

$$\tau := \inf\{t \geq 0 : |Z_*^\epsilon(t)| = 1\}. \quad (4.91)$$

Using duality and the strong Markov property of the dual process, we see that

$$\begin{aligned}
 \lim_{t \rightarrow \infty} \mathbb{E}_{\mu^\epsilon} [D^\epsilon(Z^\epsilon(t), \varphi)] & \stackrel{Fubini}{=} \lim_{t \rightarrow \infty} \mathbb{E}_\epsilon^\varphi \left[ \int_{\mathcal{X}^\epsilon} D^\epsilon(z, Z_*^\epsilon(t)) d\mu^\epsilon\{z\} \right] \\
 & = \lim_{t \rightarrow \infty} \mathbb{E}_\epsilon^\varphi \left[ \int_{\mathcal{X}^\epsilon} D^\epsilon(z, Z_*^\epsilon(t)) d\mu^\epsilon\{z\}; \tau \leq t \right] \\
 & \quad + \lim_{t \rightarrow \infty} \underbrace{\mathbb{E}_\epsilon^\varphi \left[ \int_{\mathcal{X}^\epsilon} D^\epsilon(z, Z_*^\epsilon(t)) d\mu^\epsilon\{z\} \mid \tau > t \right]}_{\leq 1} \mathbb{P}_\epsilon^\varphi(\tau > t) \\
 & = \lim_{t \rightarrow \infty} \mathbb{E}_\epsilon^\varphi \left[ \mathbb{E}_\epsilon^{Z_*^\epsilon(\tau)} \left[ \int_{\mathcal{X}^\epsilon} D^\epsilon(z, Z_*^\epsilon(t - \tau)) d\mu^\epsilon\{z\} \right]; \tau \leq t \right] \\
 & = \lim_{t \rightarrow \infty} \mathbb{E}_\epsilon^\varphi \left[ \sum_{\zeta \in G} f_{t-\tau}^\epsilon(\zeta) \mathbb{1}_{\{Z_*^\epsilon(\tau) = \vec{\delta}_\zeta\}}; \tau \leq t \right],
 \end{aligned} \quad (4.92)$$

where we use that the second term after the first equality converges to 0 because  $\tau < \infty$  a.s., and the last equality follows from (4.84) and the fact that  $Z_*^\epsilon(\tau) = \vec{\delta}_\zeta$  for some  $\zeta \in G$ . Finally, by an application of the dominated convergence theorem, we get

$$\begin{aligned}
 \lim_{t \rightarrow \infty} \mathbb{E}_{\mu^\epsilon} [D^\epsilon(Z^\epsilon(t), \varphi)] & = \mathbb{E}_\epsilon^\varphi \left[ \sum_{\zeta \in G} \left( \lim_{t \rightarrow \infty} f_{t-\tau}^\epsilon(\zeta) \right) \mathbb{1}_{\{Z_*^\epsilon(\tau) = \vec{\delta}_\zeta\}}; \tau < \infty \right] \\
 & = \mathbb{E}_\epsilon^\varphi \left[ \sum_{\zeta \in G} f^\epsilon(\zeta) \mathbb{1}_{\{Z_*^\epsilon(\tau) = \vec{\delta}_\zeta\}}; \tau < \infty \right] = \theta_\epsilon \mathbb{P}_\epsilon^\varphi(\tau < \infty) \quad (\text{since } f^\epsilon \equiv \theta_\epsilon) \\
 & = \theta_\epsilon.
 \end{aligned} \quad (4.93)$$

This shows that there exists  $\nu \in \mathcal{P}(\mathcal{X}^\epsilon)$  such that  $\mu_t^\epsilon$  converges weakly to  $\nu$  as  $t \rightarrow \infty$ . Since the system clusters by assumption, we must have

$$\nu = (1 - \theta_\epsilon) \delta_{\blacklozenge} + \theta_\epsilon \delta_{\heartsuit}, \quad (4.94)$$

where  $\delta_{\heartsuit}$  (resp.  $\delta_{\spadesuit}$ ) is the Dirac distribution concentrated at the all type- $\heartsuit$  configuration  $\mathbf{e} \in \mathcal{X}^{\heartsuit}$  (resp. the all type- $\spadesuit$  configuration  $(0, 0)_{i \in \mathbb{Z}^d} \in \mathcal{X}^{\heartsuit}$ ).  $\square$

*Proof of Corollary 4.2.5.* The proof basically exploits Theorem 4.2.4 and the fact that the particle associated to the process  $\Theta^{\mathbf{e}}$  eventually leaves any finite region of the state space  $G = \mathbb{Z}^d \times \{0, 1\}$  with probability 1. It suffices to prove that condition (b) in Theorem 4.2.4 is satisfied. Let  $f : \mathbb{Z}^d \times \{0, 1\} \rightarrow [0, 1]$  be the map

$$f(i, \alpha) := \alpha \mathbb{E}_{\mu^{\mathbf{e}}} \left[ \frac{X_i^{\mathbf{e}}(0)}{N_i} \right] + (1 - \alpha) \mathbb{E}_{\mu^{\mathbf{e}}} \left[ \frac{Y_i^{\mathbf{e}}(0)}{M_i} \right], \quad (i, \alpha) \in \mathbb{Z}^d \times \{0, 1\}, \quad (4.95)$$

and let  $\epsilon > 0$  be arbitrary. By (4.10), there exists  $N \in \mathbb{N}$  such that, for all  $i \in \mathbb{Z}^d$ ,  $\|i\| > N$  and  $\alpha \in \{0, 1\}$ ,  $|f(i, \alpha) - \theta_{\mathbf{e}}| < \epsilon$ . Thus, if  $p_t^{\mathbf{e}}(\cdot, \cdot)$  is the time- $t$  transition kernel of the process  $(\Theta^{\mathbf{e}}(t))_{t \geq 0}$  in Definition 4.2.3, then for any  $\eta \in G$  and  $t \geq 0$ ,

$$\begin{aligned} & \left| \sum_{(j, \beta) \in G} p_t^{\mathbf{e}}(\eta, (j, \beta)) \left\{ \beta \mathbb{E}_{\mu^{\mathbf{e}}} \left[ \frac{X_j^{\mathbf{e}}(0)}{N_j} \right] + (1 - \beta) \mathbb{E}_{\mu^{\mathbf{e}}} \left[ \frac{Y_j^{\mathbf{e}}(0)}{M_j} \right] \right\} - \theta_{\mathbf{e}} \right| \\ & \leq \sum_{\substack{(j, \beta) \in G, \\ \|j\| \leq N}} p_t(\eta, (j, \beta)) \underbrace{|f(j, \beta) - \theta_{\mathbf{e}}|}_{\leq 2} + \sum_{\substack{(j, \beta) \in G, \\ \|j\| > N}} p_t^{\mathbf{e}}(\eta, (j, \beta)) \underbrace{|f(j, \beta) - \theta_{\mathbf{e}}|}_{\leq \epsilon} \\ & \leq 2 P_{\eta}^{\mathbf{e}}(\Theta^{\mathbf{e}}(t) \in \Lambda_N \times \{0, 1\}) + \epsilon P_{\eta}^{\mathbf{e}}(\Theta^{\mathbf{e}}(t) \notin \Lambda_N \times \{0, 1\}), \end{aligned} \quad (4.96)$$

where  $\Lambda_N := \mathbb{Z}^d \cap [0, N]^d$ , and  $P_{\eta}^{\mathbf{e}}$  denotes the law of  $(\Theta^{\mathbf{e}}(t))_{t \geq 0}$  started at  $\eta$ . Since  $\Lambda_N$  is finite,  $\lim_{t \rightarrow \infty} P_{\eta}^{\mathbf{e}}(\Theta^{\mathbf{e}}(t) \in \Lambda_N \times \{0, 1\}) = 0$ , and so letting  $t \rightarrow \infty$  in (4.96), we get

$$\limsup_{t \rightarrow \infty} \left| \sum_{(j, \beta) \in G} p_t^{\mathbf{e}}(\eta, (j, \beta)) \left\{ \beta \mathbb{E}_{\mu^{\mathbf{e}}} \left[ \frac{X_j^{\mathbf{e}}(0)}{N_j} \right] + (1 - \beta) \mathbb{E}_{\mu^{\mathbf{e}}} \left[ \frac{Y_j^{\mathbf{e}}(0)}{M_j} \right] \right\} - \theta_{\mathbf{e}} \right| \leq \epsilon. \quad (4.97)$$

As  $\epsilon$  is arbitrary, we see that

$$\lim_{t \rightarrow \infty} \sum_{(j, \beta) \in G} p_t^{\mathbf{e}}(\eta, (j, \beta)) f(j, \beta) = \theta_{\mathbf{e}} \quad (4.98)$$

and hence the claim follows from Theorem 4.2.4.  $\square$

*Proof of Theorem 4.2.9.* We exploit Theorem 4.2.4 and the homogenisation result in Corollary 4.2.12. We see that, because of conditions (1)–(2) in Assumption 4.A and ellipticity of the environments  $\mathbf{e} \in \mathcal{E}_{\mathbb{R}^d}$ , the process  $Z^{\mathbf{e}}$  is in the clustering regime for every environment  $\mathbf{e} \in \mathcal{E}_{\mathbb{R}^d}$ . Also, by virtue of Corollary 4.2.12 and the assumption in (4.18) on initial distributions, there exists  $B \in \Sigma$  such that  $\bar{\mathbb{P}}(B) = 1$ , and for all  $\mathbf{e} \in B$  condition (b) of Theorem 4.2.4 holds. Furthermore, we see from Corollary 4.2.12, that the limiting value in that condition is independent of the environment  $\mathbf{e}$ , and is given by (4.19). Hence the result follows.  $\square$



Appendix of Part I

## Appendix: Chapter 3

### §A.1 Two-particle dual and alternative representation

In this appendix, we give a short description of the original dual process  $\tilde{Z}$  started with two particles, which was introduced in full generality as a configuration process  $Z_*$  in Section 2.4.2 of Chapter 2. Further, we briefly outline the derivation of the *interacting RW1* process  $\xi$  defined in Definition 3.3.1 from the configuration process  $\tilde{Z}$ , and show that the absorption of  $\xi$  and coalescence of the two particles in  $\tilde{Z}$  are basically equivalent.

**Definition A.1.1 (Two-particle dual).** The two-particle dual process

$$\tilde{Z} := (\tilde{Z}(t))_{t \geq 0}, \quad \tilde{Z}(t) := (\tilde{n}_i(t), \tilde{m}_i(t))_{i \in \mathbb{Z}^d}, \quad (\text{A.1})$$

is the continuous-time Markov chain with state space

$$\tilde{\mathcal{X}} := \left\{ (\tilde{n}_i, \tilde{m}_i)_{i \in \mathbb{Z}^d} \in \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i] : \sum_{i \in \mathbb{Z}^d} (\tilde{n}_i + \tilde{m}_i) \leq 2 \right\} \quad (\text{A.2})$$

and with transition rates

$$(n_k, m_k)_{k \in \mathbb{Z}^d} \rightarrow \begin{cases} (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} & \text{at rate } \frac{2a(i,i)}{N_i} \binom{n_i}{2} \mathbb{1}_{\{n_i \geq 2\}} \\ & + \sum_{j \in \mathbb{Z}^d \setminus \{i\}} \frac{n_i a(i,j) n_j}{N_j} \quad \text{for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} + \vec{\delta}_{i,D} & \text{at rate } \frac{\lambda n_i (M_i - m_i)}{M_i} \quad \text{for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} + \vec{\delta}_{i,A} - \vec{\delta}_{i,D} & \text{at rate } \frac{\lambda (N_i - n_i) m_i}{M_i} \quad \text{for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} + \vec{\delta}_{j,A} & \text{at rate } \frac{n_i a(i,j) (N_j - n_j)}{N_j} \quad \text{for } i \neq j \in \mathbb{Z}^d, \end{cases} \quad (\text{A.3})$$

where, for  $i \in \mathbb{Z}^d$ , the configurations  $\vec{\delta}_{i,A}$ ,  $\vec{\delta}_{i,D}$  are defined as in (2.19), and addition (subtraction) of configurations are defined component-wise by (2.20). The support of the distribution of  $\tilde{Z}(0)$  is contained in

$$\tilde{\mathcal{X}}_0 := \left\{ (\tilde{n}_i, \tilde{m}_i)_{i \in \mathbb{Z}^d} \in \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i] : \sum_{i \in \mathbb{Z}^d} (\tilde{n}_i + \tilde{m}_i) = 2 \right\}. \quad (\text{A.4})$$

■

Here,  $\tilde{n}_i(t)$  and  $\tilde{m}_i(t)$  are the number of active and dormant particles at site  $i \in \mathbb{Z}^d$  at time  $t$ . The first transition describes the coalescence of an active particle at site  $i$  with active particles at other sites. The second and third transitions describe the switching between the active and the dormant state of the particles at site  $i$ . The fourth transition describes the migration of an active particle from site  $i$  to site  $j$ .

Let  $\tilde{\mathcal{X}}_1$  be the set of configurations containing a single particle, i.e.,

$$\tilde{\mathcal{X}}_1 := \left\{ (\tilde{n}_i, \tilde{m}_i)_{i \in \mathbb{Z}^d} \in \tilde{\mathcal{X}} : \sum_{i \in \mathbb{Z}^d} (\tilde{n}_i + \tilde{m}_i) = 1 \right\}, \quad (\text{A.5})$$

and let  $\tilde{\tau}$  be the first time at which coalescence has occurred, i.e.,

$$\tilde{\tau} = \inf\{t \geq 0 : (\tilde{n}_i(t), \tilde{m}_i(t))_{i \in \mathbb{Z}^d} \in \tilde{\mathcal{X}}_1\}. \quad (\text{A.6})$$

As indicated earlier in Section 3.3.1 of Chapter 3, we are only required to analyse the coalescence probability of two dual particles and thus, it boils down to lumping all the configurations in  $\tilde{\mathcal{X}}_1$  into a single state  $\circledast$  and consider the resulting lumped process. Note that, on the event  $\{\tilde{\tau} < s\}$ , the process  $(\tilde{Z}(t))_{t \geq s}$  a.s. stays in  $\tilde{\mathcal{X}}_1$ . Therefore the lumped process is a well-defined continuous-time Markov chain with state space  $\tilde{\mathcal{X}}_0 \cup \{\circledast\}$ , where  $\circledast$  is an absorbing state.

With a little abuse of notation, from here onwards we denote the lumped process by  $(\tilde{Z}(t))_{t \geq 0}$ . We give the formal description of this process in a definition.

**Definition A.1.2 (Lumped two-particle dual).** The lumped two-particle dual process

$$\tilde{Z} := (\tilde{Z}(t))_{t \geq 0} \quad (\text{A.7})$$

is the continuous-time Markov chain with state space

$$\tilde{\mathcal{X}} := \left\{ (n_i, m_i)_{i \in \mathbb{Z}^d} \in \prod_{i \in \mathbb{Z}^d} [N_i] \times [M_i] : \sum_{i \in \mathbb{Z}^d} (n_i + m_i) = 2 \right\} \cup \{\circledast\} \quad (\text{A.8})$$

and with transition rates

$$(n_k, m_k)_{k \in \mathbb{Z}^d} \rightarrow \begin{cases} \circledast, & \text{at rate } \sum_{i \in \mathbb{Z}^d} \left[ \frac{2a(0,0)}{N_i} \binom{n_i}{2} \mathbb{1}_{\{n_i \geq 2\}} \right. \\ & \left. + \sum_{j \in \mathbb{Z}^d \setminus \{i\}} \frac{n_i a(i,j) n_j}{N_j} \right] \text{ for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} + \vec{\delta}_{i,D}, & \text{at rate } \frac{\lambda n_i (M_i - m_i)}{M_i} \text{ for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} + \vec{\delta}_{i,A} - \vec{\delta}_{i,D}, & \text{at rate } \frac{\lambda (N_i - n_i) m_i}{M_i} \text{ for } i \in \mathbb{Z}^d, \\ (n_k, m_k)_{k \in \mathbb{Z}^d} - \vec{\delta}_{i,A} + \vec{\delta}_{j,A}, & \text{at rate } \frac{n_i a(i,j) (N_j - n_j)}{N_j} \text{ for } i \neq j \in \mathbb{Z}^d, \end{cases} \quad (\text{A.9})$$

where, for  $i \in \mathbb{Z}^d$ ,  $\vec{\delta}_{i,A}$  and  $\vec{\delta}_{i,D}$  are as in (2.19). ■

We write  $\tilde{\mathbb{P}}^\eta$  to denote the law of the process  $\tilde{Z}$  started from  $\eta \in \mathcal{X}$ . Note that, by construction, the coalescence time  $\tilde{\tau}$  is now same as the absorption time of the process  $\tilde{Z}$ . In the following proposition, we show that the configuration process  $\tilde{Z}$  is an alternative representation of the coordinate process  $\xi$  defined in Definition 3.3.1.

**Proposition A.1.3 (Equivalence between  $\tilde{Z}$  and  $\xi$ ).** Let  $\xi = (\xi(t))_{t \geq 0}$  be the process defined in Definition 3.3.1 with initial distribution  $\mu$ . Let  $\phi: \mathcal{S} \rightarrow \tilde{\mathcal{X}}$  be the map defined by

$$\phi(\eta) := \begin{cases} (\alpha\delta_{k,i} + \beta\delta_{k,j}, (1-\alpha)\delta_{k,i} + (1-\beta)\delta_{k,j})_{k \in \mathbb{Z}^d}, & \text{if } \eta = [(i, \alpha), (j, \beta)] \neq \otimes, \\ \otimes, & \text{otherwise.} \end{cases} \quad (\text{A.10})$$

For  $t \geq 0$ , let  $\tilde{Z}(t) := \phi(\xi(t))$ . Then the process  $(\tilde{Z}(t))_{t \geq 0}$  is the lumped dual process defined in Definition A.1.2, and its initial distribution is the push-forward of  $\mu$  under the map  $\phi$ . Furthermore,  $\tilde{Z}$  is absorbed to  $\otimes$  if and only if  $\xi$  is.

*Proof.* Due to the Assumption 3.A, we see that  $\phi(\eta) \in \tilde{\mathcal{X}}$ , and so  $\tilde{Z}(t) \in \tilde{\mathcal{X}}$  for all  $t \geq 0$ , and  $\phi$  is onto. For  $\eta \in \mathcal{S}$ , define

$$\bar{\eta} := \begin{cases} [(j, \beta), (i, \alpha)], & \text{if } \eta = [(i, \alpha), (j, \beta)] \neq \otimes, \\ \otimes, & \text{otherwise.} \end{cases} \quad (\text{A.11})$$

Note that  $\phi^{-1}(\phi(\eta)) = \{\eta, \bar{\eta}\}$ . Let  $Q(\eta_1, \eta_2)$  denote the transition rate from  $\eta_1$  to  $\eta_2$  for the process  $\xi$ , where  $\eta_1 \neq \eta_2 \in \mathcal{S}$ . Furthermore, let  $z_1 \neq z_2 \in \tilde{\mathcal{X}}$  be fixed and  $\eta_1 \in \mathcal{S}$  be such that  $\phi(\eta_1) = z_1$ . Since  $Q(\eta_1, \eta_2) = Q(\bar{\eta}_1, \bar{\eta}_2)$  for any  $\eta_1 \neq \eta_2 \in \mathcal{S}$ , we have

$$\sum_{\eta \in \phi^{-1}(z_2)} Q(\eta_1, \eta) = \sum_{\eta \in \phi^{-1}(z_2)} Q(\bar{\eta}_1, \eta). \quad (\text{A.12})$$

Hence the Dynkin criterion for lumpability is satisfied, and  $\phi$  preserves the Markov property. So  $\tilde{Z}$  is a Markov process on  $\tilde{\mathcal{X}}$ . We can easily verify that the sum in (A.12) is indeed the transition rate from  $z_1$  to  $z_2$  defined in (A.9). Thus,  $\tilde{Z}$  is the lumped dual process defined in Definition A.1.2. Clearly, the distribution of  $\tilde{Z}(0)$  is  $\mu \circ \phi^{-1}$ . The second claim trivially follows, since  $\phi(\eta) = \otimes$  if and only if  $\eta = \otimes$ .  $\square$

## §A.2 Completion of the proof of a theorem on the clustering regime

Let us restate the theorem before we proceed with the completion of the proof.

**Theorem A.2.1 (Clustering regime).** Suppose that  $K^{-1} = \sup_{i \in \mathbb{Z}^d} K_i^{-1} < \infty$  and that Assumption 3.B holds. If the process  $\xi^*$  defined in Definition 3.3.4 is absorbed to  $\otimes$  with probability 1, then it is necessary that the symmetrised kernel  $\hat{a}(\cdot, \cdot)$  is recurrent, i.e.,

$$\int_0^\infty \hat{a}_t(0, 0) dt = \infty. \quad (\text{A.13})$$

Furthermore, if  $(N_i)_{i \in \mathbb{Z}^d}$  satisfies the non-clumping condition in (3.6) and  $a(\cdot, \cdot)$  is symmetric, then (A.13) is also sufficient.

The above theorem states that, under some suitable conditions, two particles evolving according to the process  $\xi^*$  defined in Definition 3.3.4 coalesce with prob-

ability 1 if and only if the symmetrised migration kernel  $\hat{a}(\cdot, \cdot)$  is recurrent, where

$$\hat{a}(i, j) = \frac{1}{2}[a(i, j) + a(j, i)], \quad i, j \in \mathbb{Z}^d. \quad (\text{A.14})$$

Recall that in the process  $\xi^*$  the two particles evolve independently on the state space  $G = \mathbb{Z}^d \times \{0, 1\}$  according to the motion described in Section 3.4.2, until they coalesce with each other to form an absorbed state  $\otimes$ . Under the conditions mentioned in the theorem, every time the two particles share the same location there is a positive probability of absorption within the next unit time interval and this probability is bounded away from zero uniformly over the location of meeting. Therefore we argue, as in the proof of the theorem, that the two independent particles coalesce with probability 1 if and only if in the process obtained from  $\xi^*$  after suppressing the coalescent events the total accumulated time spent by the two particles at the same location is infinite with probability 1. This accumulated time  $\tilde{I}$  is the random variable given by

$$\tilde{I} = \int_0^\infty \mathbb{1}_{\mathcal{E}(t)} dt, \quad (\text{A.15})$$

where  $\mathcal{E}(t)$  is the event that both particles are at the same location at time  $t \geq 0$ . Let  $\eta \in G \times G$  be any state where both particles are at the same location, i.e.,  $\eta = [(i, \alpha), (i, \beta)]$  for some  $i \in \mathbb{Z}^d$  and  $\alpha, \beta \in \{0, 1\}$ . The average accumulated time, written as  $I$  when the process starts at state  $\eta$ , can be expressed as

$$I = \mathbb{E}_\eta^*[\tilde{I}] = \int_0^\infty \mathbb{P}_\eta^*(\mathcal{E}(t)) dt. \quad (\text{A.16})$$

In the proof of Theorem 3.4.4, we exploit the fact that  $\tilde{I}$  is infinite with probability 1 iff  $I = \infty$ . The forward direction of this fact is obvious. However, the converse is non-trivial and is stated without justification. In the following lemma we provide the proof.

**Lemma A.2.2.** *Let  $\tilde{I}$  be as in (A.15) and  $\eta = [(i, \alpha), (i, \beta)] \in G \times G$  for some  $i \in \mathbb{Z}^d$ . Assume that the migration kernel  $a(\cdot, \cdot)$  is symmetric. If  $\mathbb{P}_\eta^*$  is the law of the process  $\xi^*$  in Definition 3.3.4 after coalescence is turned off and  $\mathbb{E}_\eta^*[\tilde{I}] = \infty$ , then  $\mathbb{P}_\eta^*(\tilde{I} = \infty) = 1$ .*

*Proof.* First observe that the event  $\{\tilde{I} = \infty\} \in \mathcal{I}$  where  $\mathcal{I}$  is the time-shift invariant  $\sigma$ -field of the process  $\xi^*$ . Note that  $\mathcal{I}$  is trivial because all bounded harmonic functions of the process  $\xi^*$  are constant. The later follows from [93, Theorem 26.11], [112, Corollary 3.7, Chapter II], and the fact that bounded harmonic functions for the corresponding process with a single particle are constant. Therefore,  $\mathbb{P}_\zeta^*(\tilde{I} = \infty) \in \{0, 1\}$  for any  $\zeta \in G \times G$ , and so it suffices to show that  $\mathbb{P}_\eta^*(\tilde{I} = \infty) > 0$  for the choice of initial state  $\eta = [(0, 1), (0, 1)]$  where both particles are at 0 in the active state. To this end, for  $T > 0$  let us consider the truncated random variable

$$\tilde{I}_T := \int_0^T \mathbb{1}_{\mathcal{E}(t)} dt. \quad (\text{A.17})$$

We show that there exists a constant  $C > 0$  independent of  $T$ , such that

$$\mathbb{E}_\eta^*[\tilde{I}_T^2] \leq C \mathbb{E}_\eta^*[\tilde{I}_T]^2, \quad T \geq 0. \quad (\text{A.18})$$

By the Paley-Zygmund inequality, this will imply

$$\mathbb{P}_\eta^*(\tilde{I}_T > \frac{1}{2}\mathbb{E}_\eta^*[\tilde{I}_T]) \geq \frac{1}{4} \frac{\mathbb{E}_\eta^*[\tilde{I}_T]^2}{\mathbb{E}_\eta^*[\tilde{I}_T^2]} \geq \frac{1}{4C}, \quad T \geq 0. \quad (\text{A.19})$$

Since  $\tilde{I}_T \uparrow \tilde{I}$  almost surely as  $T \rightarrow \infty$  and  $\mathbb{E}_\eta^*[\tilde{I}] = \infty$  by assumption, it will follow that

$$\mathbb{P}_\eta^*(\tilde{I} = \infty) \geq \limsup_{T \rightarrow \infty} \mathbb{P}_\eta^*(\tilde{I}_T > \frac{1}{2}\mathbb{E}_\eta^*[\tilde{I}_T]) \geq \frac{1}{4C} > 0, \quad (\text{A.20})$$

which will complete the proof.

To prove (A.18), we use the Markov property of  $\xi^*$  and Fubini's theorem to write

$$\begin{aligned} \mathbb{E}_\eta^*[\tilde{I}_T^2] &= \mathbb{E}_\eta^* \left[ \int_0^T \int_0^T \mathbb{1}_{\mathcal{E}(t)} \mathbb{1}_{\mathcal{E}(s)} dt ds \right] = \mathbb{E}_\eta^* \left[ 2 \int_0^T dt \mathbb{1}_{\mathcal{E}(t)} \int_0^t ds \mathbb{1}_{\mathcal{E}(s)} \right] \\ &= 2 \int_0^T dt \int_0^t ds \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(t)} \mathbb{1}_{\mathcal{E}(s)}] = 2 \int_0^T dt \int_0^t ds \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(s)} \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(t)} \mid \mathcal{F}_s]] \\ &= 2 \int_0^T dt \int_0^t ds \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(s)} \mathbb{P}_{\xi^*(s)}^*(\mathcal{E}(t-s))]. \end{aligned} \quad (\text{A.21})$$

Now, if we show that, for any  $t \geq 0$  and some constant  $C$  not depending on either  $t$  or  $\zeta$ ,

$$\mathbb{P}_\zeta^*(\mathcal{E}(t)) \leq C \mathbb{P}_\eta^*(\mathcal{E}(t)), \quad (\text{A.22})$$

where  $\zeta \in G \times G$  is any state such that both particles are at the same location, i.e.,  $\zeta = [(i, \alpha), (i, \beta)]$  for some  $i \in \mathbb{Z}^d$  and  $\alpha, \beta \in \{0, 1\}$ , then (A.21) implies

$$\begin{aligned} \mathbb{E}_\eta^*[\tilde{I}_T^2] &\leq 2C \int_0^T dt \int_0^t ds \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(s)} \mathbb{P}_\eta^*(\mathcal{E}(t-s))] \\ &= 2C \int_0^T dt \int_0^t ds \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(s)}] \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(t-s)}] \\ &= 2C \int_0^T dt \int_0^t ds g(s)g(t-s) = 2C \int_0^T dt g * g(t) \\ &\leq 2C \|g * g\|_{L^1(\mathbb{R})}, \end{aligned} \quad (\text{A.23})$$

where  $g : \mathbb{R} \rightarrow [0, 1]$  is the map  $t \mapsto \mathbb{E}_\eta^*[\mathbb{1}_{\mathcal{E}(t)}] \mathbb{1}_{[0, T]}(t)$  and  $*$  denotes the usual convolution operation. Finally, applying Young's inequality for convolution on  $g * g$ , we get

$$\mathbb{E}_\eta^*[\tilde{I}_T^2] \leq 2C \|g\|_{L^1(\mathbb{R})}^2 = 2C \mathbb{E}_\eta^*[\tilde{I}_T]^2. \quad (\text{A.24})$$

Thus, it only remains to show (A.22).

To this aim, let  $S(t)$  and  $S'(t)$  denote the respective accumulated activity times in the time interval  $[0, t]$  for the two particles evolving according to the process  $\xi^*$  with coalescence switched off. For  $i \in \mathbb{Z}^d$ , let  $\zeta = [(i, \alpha), (i, \beta)] \in G \times G$  be fixed arbitrarily. Observe that, by the independence of the two particles and the symmetry assumption



of  $a(\cdot, \cdot)$ ,

$$\begin{aligned} \mathbb{P}_\zeta^*(\mathcal{E}(t)) &= \sum_{j \in \mathbb{Z}^d} \mathbb{E}_\zeta^*[a_{S(t)}(i, j)] \mathbb{E}_\zeta^*[a_{S'(t)}(i, j)] = \mathbb{E}_\zeta^*[a_{S(t)+S'(t)}(i, i)] \\ &= \mathbb{E}_\zeta^*[a_{S(t)+S'(t)}(0, 0)] \\ &\leq \mathbb{E}_{(i, \alpha)}[a_{S(t)}(0, 0)], \end{aligned} \tag{A.25}$$

where we use that  $s \mapsto a_s(0, 0)$  is non-increasing in  $s$  when  $a(\cdot, \cdot)$  is symmetric (which follows from standard Fourier analysis), and the last expectation on the right-hand side is taken w.r.t. the law of a single particle process started at  $(i, \alpha) \in G$ . Fix  $\epsilon \in (0, \frac{1}{1+K^{-1}})$  arbitrarily, where  $K^{-1} := \sup_{j \in \mathbb{Z}^d} K_j^{-1} < \infty$ . Once more, applying the non-increasing property of  $s \mapsto a_s(0, 0)$ , we get from (A.25) that

$$\begin{aligned} \mathbb{P}_\zeta^*(\mathcal{E}(t)) &\leq a_{\epsilon t}(0, 0) \mathbb{P}_{(i, \alpha)}(S(t) > \epsilon t) + \mathbb{E}_{(i, \alpha)}[a_{S(t)}(0, 0); S(t) \leq \epsilon t] \\ &\leq a_{\epsilon t}(0, 0) + \mathbb{P}_{(i, \alpha)}(S(t) \leq \epsilon t). \end{aligned} \tag{A.26}$$

Using the same arguments as in the proof of Lemma 3.4.1, we can construct an alternating renewal process  $(R_s)_{s \geq 0}$ , with successive exponential waiting times  $(V_n)_{n \in \mathbb{N}}$  and  $(U_n)_{n \in \mathbb{N}}$ , on the probability space of the single particle such that

$$D(t) \leq \int_0^t \mathbb{1}_{\{R_s=1\}} ds, \tag{A.27}$$

where  $D(t) = t - S(t)$  is the accumulated dormant period of the particle in the time interval  $[0, t]$ , the process  $s \mapsto R_s$  takes value 0 (resp., 1) during the periods  $(V_n)_{n \in \mathbb{N}}$  (resp.,  $(U_n)_{n \in \mathbb{N}}$ ) and

$$V_n \stackrel{\text{i.i.d.}}{=} \exp(\lambda), \quad U_n \stackrel{\text{i.i.d.}}{=} \exp(\lambda K), \quad n \in \mathbb{N}. \tag{A.28}$$

By the renewal reward theorem, we get

$$\lim_{l \rightarrow \infty} \frac{1}{l} \int_0^l \mathbb{1}_{\{R_s=1\}} ds = \frac{K^{-1}}{1+K^{-1}} \quad \mathbb{P}_{(i, \alpha)} \text{ a.s.}, \tag{A.29}$$

and, by Cramer's theorem, deviations of the left-hand quantity away from the limiting constant are exponentially costly in  $l$ . Because  $\epsilon \in (0, \frac{1}{1+K^{-1}})$ , using (A.27) and the above we can find constants  $A_\epsilon, A'_\epsilon, C_\epsilon > 0$  such that

$$\begin{aligned} \mathbb{P}_{(i, \alpha)}(S(t) \leq \epsilon t) &= \mathbb{P}_{(i, \alpha)}\left(\frac{D(t)}{t} > (1 - \epsilon)\right) \\ &\leq \mathbb{P}_{(i, \alpha)}\left[\frac{1}{t} \int_0^t \mathbb{1}_{\{R_s=1\}} ds > 1 - \epsilon\right] \\ &\leq A_\epsilon e^{-A'_\epsilon t} \\ &\leq C_\epsilon a_{\epsilon t}(0, 0). \end{aligned} \tag{A.30}$$

Inserting (A.30) into (A.26), we get that

$$\mathbb{P}_\zeta^*(\mathcal{E}(t)) \leq [1 + C_\epsilon] a_{\epsilon t}(0, 0) \tag{A.31}$$

for any  $t \geq 0$ . Finally, noting that  $\mathbb{P}_\eta^*(\mathcal{E}(t)) = \mathbb{E}_\eta^*[a_{S(t)+S'(t)}(0,0)] \geq a_{2t}(0,0)$ , we get

$$\frac{\mathbb{P}_\zeta^*(\mathcal{E}(t))}{\mathbb{P}_\eta^*(\mathcal{E}(t))} \leq [1 + C_\epsilon] \frac{a_{\epsilon t}(0,0)}{a_{2t}(0,0)} \leq C(\epsilon), \quad (\text{A.32})$$

where  $C(\epsilon) := [1 + C_\epsilon] \sup_{s \geq 0} \frac{a_{\epsilon s}(0,0)}{a_{2s}(0,0)} < \infty$  where we use the symmetry of  $a(\cdot, \cdot)$  and Assumption 3.B. The proof of (A.22) is therefore complete.  $\square$



# APPENDIX B

## Appendix: Chapter 4

### §B.1 Proof of stationarity of environment process and law of large numbers

In this section we prove Theorem 4.3.6 stated in Section 4.3 of Chapter 4. As an application, we also prove a strong law of large numbers which is stated later in Theorem B.1.1.

#### §B.1.1 Stationary distribution of environment process

*Proof of Theorem 4.3.6.* We first prove part (1) of the theorem. To prove stationarity of  $W$  under  $\mathbb{Q}$ , it suffices to show that, for any bounded measurable  $f \in \mathcal{F}_b(\Omega_{\mathfrak{R}})$ ,

$$\int_{\Omega_{\mathfrak{R}}} \mathfrak{R}f(\mathbf{e}, \alpha) d\mathbb{Q}(\mathbf{e}, \alpha) = \int_{\Omega_{\mathfrak{R}}} f(\mathbf{e}, \alpha) d\mathbb{Q}(\mathbf{e}, \alpha), \quad (\text{B.1})$$

where  $\mathfrak{R}$  is the Markov kernel operator given in (4.38). Let  $\theta := \frac{1}{1 + \mathbb{E}[M_0/N_0]}$  and  $q_s$ ,  $\hat{p}(\cdot)$ ,  $\omega = (\omega(k))_{k \in \mathbb{Z}^d}$  be as in (4.28), where  $\omega$  is the only parameter that depends on the realisation of the environment  $\mathbf{e}$ . In terms of these parameters, from (4.39) we get that

$$\int_{\Omega_{\mathfrak{R}}} g(\mathbf{e}, \alpha) d\mathbb{Q}(\mathbf{e}, \alpha) = \theta \int_{\Omega_{\mathfrak{R}}} \left[ g(\mathbf{e}, 1) + \frac{q_s}{\omega(0)} g(\mathbf{e}, 0) \right] d\bar{\mathbb{P}}(\mathbf{e}) \quad (\text{B.2})$$

for any  $g \in \mathcal{F}_b(\Omega_{\mathfrak{R}})$ . Thus, taking  $g = \mathfrak{R}f$  in the above equation, we have

$$\int_{\Omega_{\mathfrak{R}}} \mathfrak{R}f(\mathbf{e}, \alpha) d\mathbb{Q}(\mathbf{e}, \alpha) = \theta \int_{\mathcal{E}_{\mathfrak{R}}} \left[ \mathfrak{R}f(\mathbf{e}, 1) + \frac{q_s}{\omega(0)} \mathfrak{R}f(\mathbf{e}, 0) \right] d\bar{\mathbb{P}}(\mathbf{e}) = \theta(I_1 + I_2), \quad (\text{B.3})$$

where  $I_1 := \int_{\mathcal{E}_{\mathfrak{R}}} \mathfrak{R}f(\mathbf{e}, 1) d\bar{\mathbb{P}}(\mathbf{e})$  and  $I_2 := \int_{\mathcal{E}_{\mathfrak{R}}} \frac{q_s}{\omega(0)} \mathfrak{R}f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e})$ .

Let us compute  $I_1$  and  $I_2$  using (4.38):

$$\begin{aligned}
 I_1 &= q_s \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}) + (1 - q_s) \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} \left[ \sum_{j \in \mathbb{Z}^d} \hat{p}(j) f(T_j \mathbf{e}, 1) \right] d\bar{\mathbb{P}}(\mathbf{e}) \\
 &= q_s \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}) + (1 - q_s) \sum_{j \in \mathbb{Z}^d} \hat{p}(j) \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} f(T_j \mathbf{e}, 1) d\bar{\mathbb{P}}(\mathbf{e}) \quad (\text{bounded convergence}) \\
 &= q_s \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}) + (1 - q_s) \sum_{j \in \mathbb{Z}^d} \hat{p}(j) \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} f(\mathbf{e}, 1) d\bar{\mathbb{P}}(\mathbf{e}) \quad (\text{translation-invariance of } \bar{\mathbb{P}}) \\
 &= q_s \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}) + (1 - q_s) \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} f(\mathbf{e}, 1) d\bar{\mathbb{P}}(\mathbf{e}), \quad \left( \text{using } \sum_{j \in \mathbb{Z}^d} \hat{p}(j) = 1 \right).
 \end{aligned} \tag{B.4}$$

Similarly,

$$I_2 = \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} \frac{q_s}{\omega(0)} \mathfrak{R}f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}) = q_s \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} [f(\mathbf{e}, 1) - f(\mathbf{e}, 0)] d\bar{\mathbb{P}}(\mathbf{e}) + \int_{\mathcal{E}_{\bar{\mathfrak{R}}}} \frac{q_s}{\omega(0)} f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}). \tag{B.5}$$

Finally, adding (B.4)–(B.5) and using (B.2)–(B.3), we get

$$\begin{aligned}
 \int_{\Omega_{\bar{\mathfrak{R}}}} \mathfrak{R}f(\mathbf{e}, \alpha) d\mathbb{Q}(\mathbf{e}, \alpha) &= \theta(I_1 + I_2) = \theta \int_{\Omega_{\bar{\mathfrak{R}}}} [f(\mathbf{e}, 1) + \frac{q_s}{\omega(0)} f(\mathbf{e}, 0)] d\bar{\mathbb{P}}(\mathbf{e}) \\
 &= \int_{\Omega_{\bar{\mathfrak{R}}}} f(\mathbf{e}, \alpha) d\mathbb{Q}(\mathbf{e}, \alpha),
 \end{aligned} \tag{B.6}$$

which proves the claim.

Next we proceed to prove ergodicity of  $W$  under the stationary law  $\mathbb{Q}$ . It suffices to show (see e.g. [93]) that if  $A \in \Sigma \otimes 2^{\{0,1\}}$  satisfies  $\mathfrak{R}\mathbb{1}_A = \mathbb{1}_A \mathbb{Q}$  a.s., then  $\mathbb{Q}(A) \in \{0, 1\}$ . Thus, let us fix a measurable  $A \subseteq \Omega_{\bar{\mathfrak{R}}}$  such that

$$\mathfrak{R}\mathbb{1}_A(\mathbf{e}, \alpha) = \mathbb{1}_A(\mathbf{e}, \alpha), \quad \text{for all } (\mathbf{e}, \alpha) \in B, \tag{B.7}$$

where  $B \subseteq \Omega_{\bar{\mathfrak{R}}}$  is measurable with  $\mathbb{Q}(B) = 1$ . Define  $A_0, A_1 \in \Sigma$  as

$$A_0 := \{\mathbf{e} : (\mathbf{e}, 0) \in A\}, \quad A_1 := \{\mathbf{e} : (\mathbf{e}, 1) \in A\}. \tag{B.8}$$

By Lemma 4.3.8, we can find  $B' \in \Sigma$  such that

$$\bar{\mathbb{P}}(B') = 1, \quad B' \times \{0, 1\} \subseteq B. \tag{B.9}$$

Using (4.38), (B.7) and (B.9), we get that, for all  $\mathbf{e} \in B'$ ,

$$\begin{aligned}
 q_s \mathbb{1}_A(\mathbf{e}, 0) + (1 - q_s) \sum_{j \in \mathbb{Z}^d} \hat{p}(j) \mathbb{1}_A(T_j \mathbf{e}, 1) &= \mathbb{1}_A(\mathbf{e}, 1), \\
 \omega(0) \mathbb{1}_A(\mathbf{e}, 0) + (1 - \omega(0)) \mathbb{1}_A(\mathbf{e}, 1) &= \mathbb{1}_A(\mathbf{e}, 0),
 \end{aligned} \tag{B.10}$$

where  $\omega$  is defined in terms of  $\mathbf{e}$  as in (4.28). In terms of  $A_0, A_1$  given in (B.8), for all  $\mathbf{e} \in B'$ ,

$$\begin{aligned}
 q_s \mathbb{1}_{A_0}(\mathbf{e}) + (1 - q_s) \sum_{j \in \mathbb{Z}^d} \hat{p}(j) \mathbb{1}_{A_1}(T_j \mathbf{e}) &= \mathbb{1}_{A_1}(\mathbf{e}), \\
 (1 - \omega(0)) \mathbb{1}_{A_1}(\mathbf{e}) &= (1 - \omega(0)) \mathbb{1}_{A_0}(\mathbf{e}).
 \end{aligned} \tag{B.11}$$

By ellipticity of  $\mathbf{e} \in B'$ , we have  $\omega(0) < 1$ , and so the second part of the above equation implies that

$$\mathbb{1}_{A_1}(\mathbf{e}) = \mathbb{1}_{A_0}(\mathbf{e}), \quad \mathbf{e} \in B'. \quad (\text{B.12})$$

Integrating the above w.r.t.  $\bar{\mathbb{P}}$  over  $B'$  and using (B.9), we also have

$$\bar{\mathbb{P}}(A_0) = \bar{\mathbb{P}}(A_1). \quad (\text{B.13})$$

Note that if we show  $\bar{\mathbb{P}}(A_1) \in \{0, 1\}$ , then it follows from (B.13) that  $\mathbb{Q}(A) \in \{0, 1\}$ . Indeed, from (4.39) we see that

$$\mathbb{Q}(A) = \theta \left[ \bar{\mathbb{P}}(A_1) + \int_{A_0} \frac{M_0}{N_0} d\bar{\mathbb{P}}\{(N_k, M_k)_{k \in \mathbb{Z}^d}\} \right], \quad (\text{B.14})$$

where  $\theta := \frac{1}{1 + \mathbb{E}[M_0/N_0]}$ . Therefore, if  $\bar{\mathbb{P}}(A_1) = \bar{\mathbb{P}}(A_0) = 1$ , then

$$\mathbb{Q}(A) = \theta(1 + \mathbb{E}[M_0/N_0]) = 1. \quad (\text{B.15})$$

Similarly, if  $\bar{\mathbb{P}}(A_1) = \bar{\mathbb{P}}(A_0) = 0$ , then by (B.14), trivially  $\mathbb{Q}(A) = 0$ . We prove  $\bar{\mathbb{P}}(A_1) \in \{0, 1\}$  by using ergodicity of  $\bar{\mathbb{P}}$ . To this purpose, let us note that (B.12), combined with the first part of (B.11) and the fact  $q_s < 1$ , implies

$$\sum_{j \in \mathbb{Z}^d} \hat{p}(j) \mathbb{1}_{A_1}(T_j \mathbf{e}) = \mathbb{1}_{A_1}(\mathbf{e}), \quad \mathbf{e} \in B'. \quad (\text{B.16})$$

Define the translation invariant set  $B_{\text{inv}} := \bigcap_{j \in \mathbb{Z}^d} T_j^{-1}(B')$ . By translation invariance of  $\bar{\mathbb{P}}$  we see that  $\bar{\mathbb{P}}(B_{\text{inv}}) = \bar{\mathbb{P}}(B') = 1$ . Also, (B.16) holds for all  $\mathbf{e} \in B_{\text{inv}}$ . Let us fix  $\mathbf{e} \in B_{\text{inv}}$ . By translation invariance of  $B_{\text{inv}}$ , we see that  $T_i \mathbf{e} \in B_{\text{inv}}$  for any  $i \in \mathbb{Z}^d$  and so, using (B.16), we get

$$\sum_{j \in \mathbb{Z}^d} \hat{p}(j) \mathbb{1}_{A_1}(T_j T_i \mathbf{e}) = \mathbb{1}_{A_1}(T_i \mathbf{e}) \implies \sum_{j \in \mathbb{Z}^d} \hat{p}(j - i) \mathbb{1}_{A_1}(T_j \mathbf{e}) = \mathbb{1}_{A_1}(T_i \mathbf{e}). \quad (\text{B.17})$$

In particular, the map  $i \mapsto \mathbb{1}_{A_1}(T_i \mathbf{e})$  is harmonic for  $\hat{p}(\cdot)$ . Finally, because of the irreducibility of the migration kernel  $a(\cdot, \cdot)$  (see Assumption 2.A), we can apply the Choquet-Deny theorem to the  $\hat{p}$ -harmonic function  $i \mapsto \mathbb{1}_{A_1}(T_i \mathbf{e})$  to conclude that

$$\mathbb{1}_{A_1}(T_i \mathbf{e}) = \mathbb{1}_{A_1}(\mathbf{e}), \quad \forall i \in \mathbb{Z}^d. \quad (\text{B.18})$$

In other words,  $B_{\text{inv}} \cap A_1$  is a translation invariant subset of  $\mathcal{E}_{\mathbb{R}}$ , and so ergodicity of  $\bar{\mathbb{P}}$  implies  $\bar{\mathbb{P}}(B_{\text{inv}} \cap A_1) \in \{0, 1\}$ . But  $\bar{\mathbb{P}}(B_{\text{inv}} \cap A_1) = \bar{\mathbb{P}}(A_1)$  because  $\bar{\mathbb{P}}(B_{\text{inv}}) = 1$ . This concludes the proof of ergodicity of  $W$  w.r.t. the law  $\mathbb{Q}$ .

It remains to prove reversibility of  $\mathbb{Q}$  under condition (2) in Assumption 4.A. It is enough to prove that, for  $f, g \in \mathcal{F}_b(\Omega_{\mathbb{R}})$ ,

$$\int_{\Omega_{\mathbb{R}}} g \mathfrak{R} f d\mathbb{Q} = \int_{\Omega_{\mathbb{R}}} f \mathfrak{R} g d\mathbb{Q}. \quad (\text{B.19})$$

Using (4.38), we get

$$\int_{\Omega_{\mathbb{R}}} g \mathfrak{R} f d\mathbb{Q} = \frac{1}{1 + \mathbb{E}[M_0/N_0]} [I_1(f, g) + I_2(f, g)], \quad (\text{B.20})$$

where

$$\begin{aligned}
 I_1(f, g) &= q_s \int_{\mathcal{E}_{\mathbb{R}}} g(\mathbf{e}, 1) f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}) + (1 - q_s) \int_{\mathcal{E}_{\mathbb{R}}} \left[ \sum_{j \in \mathbb{Z}^d} \hat{p}(j) g(\mathbf{e}, 1) f(T_j \mathbf{e}, 1) \right] d\bar{\mathbb{P}}(\mathbf{e}), \\
 I_2(f, g) &= q_s \int_{\mathcal{E}_{\mathbb{R}}} g(\mathbf{e}, 0) [f(\mathbf{e}, 1) - f(\mathbf{e}, 0)] d\bar{\mathbb{P}}(\mathbf{e}) + \int_{\mathcal{E}_{\mathbb{R}}} \frac{q_s}{\omega(0)} g(\mathbf{e}, 0) f(\mathbf{e}, 0) d\bar{\mathbb{P}}(\mathbf{e}).
 \end{aligned} \tag{B.21}$$

Note that, by condition (2) in Assumption 4.A, we have  $\hat{p}(k) = \hat{p}(-k)$  for all  $k \in \mathbb{Z}^d$ , and so by translation invariance of  $\bar{\mathbb{P}}$  the second term in  $I_1(f, g)$  remains unchanged if we interchange  $f$  and  $g$ . Indeed,

$$\begin{aligned}
 \int_{\mathcal{E}_{\mathbb{R}}} \left[ \sum_{j \in \mathbb{Z}^d} \hat{p}(j) g(\mathbf{e}, 1) f(T_j \mathbf{e}, 1) \right] d\bar{\mathbb{P}}(\mathbf{e}) &= \int_{\mathcal{E}_{\mathbb{R}}} \left[ \sum_{j \in \mathbb{Z}^d} \hat{p}(j) g(T_{-j} \mathbf{e}, 1) f(\mathbf{e}, 1) \right] d\bar{\mathbb{P}}(\mathbf{e}) \\
 &= \int_{\mathcal{E}_{\mathbb{R}}} \left[ \sum_{j \in \mathbb{Z}^d} \hat{p}(-j) g(T_j \mathbf{e}, 1) f(\mathbf{e}, 1) \right] d\bar{\mathbb{P}}(\mathbf{e}) \\
 &= \int_{\mathcal{E}_{\mathbb{R}}} \left[ \sum_{j \in \mathbb{Z}^d} \hat{p}(j) g(T_j \mathbf{e}, 1) f(\mathbf{e}, 1) \right] d\bar{\mathbb{P}}(\mathbf{e}), \quad (\text{by symmetry of } \hat{p}(\cdot)).
 \end{aligned} \tag{B.22}$$

Thus, using (B.21) and the above, we see that  $I_1(f, g) + I_2(f, g) = I_1(g, f) + I_2(g, f)$ , which combined with (B.20) proves the claim in (B.19).  $\square$

## §B.1.2 An application: strong law of large numbers

As pointed out earlier in Remark 4.3.7, part (1) of Theorem 4.3.6 holds in any dimension  $d \geq 1$ , even when the migration kernel  $\hat{p}(\cdot)$  (see (4.28)) is not symmetric. An interesting application of this theorem is the strong law of large numbers stated below.

**Theorem B.1.1 (Strong law of large numbers).** *Let  $\hat{\Theta}^\mathbf{e} = (X_n^\mathbf{e}, \alpha_n^\mathbf{e})_{n \in \mathbb{N}_0}$  be the subordinate Markov chain evolving in environment  $\mathbf{e}$  with law  $\hat{P}_{(0, \alpha)}^\mathbf{e}$  (see Definition 4.3.1), and let  $\bar{\mathbb{P}}$  be the translation-invariant, ergodic field as in Assumption 4.B. Assume that the migration kernel  $\hat{p}(\cdot)$  (see (4.28)) has finite range and mean*

$$v := \sum_{j \in \mathbb{Z}^d} j \hat{p}(j). \tag{B.23}$$

*Then, for  $\bar{\mathbb{P}}$  almost every realisation of  $\mathbf{e}$  and  $\alpha \in \{0, 1\}$ ,*

$$\lim_{n \rightarrow \infty} \frac{X_n^\mathbf{e}}{n} = \frac{1 - q_s}{1 + \rho} v \quad \hat{P}_{(0, \alpha)}^\mathbf{e} \text{ a.s.}, \tag{B.24}$$

*where  $\rho := \bar{\mathbb{E}} \left[ \frac{M_0}{N_0} \right]$  and  $q_s$  is as in (4.28).*

Recall that  $X_n^\mathbf{e}$  denotes the location in  $\mathbb{Z}^d$  at time  $n$  of a particle that evolves according to the subordinate Markov chain  $\hat{\Theta}^\mathbf{e}$  in environment  $\mathbf{e}$ . Therefore, the intuitive meaning of the above result is that the particle on average spends a  $\frac{1}{1+\rho}$  fraction of its time in the active state, and since it migrates only while being active with probability  $1 - q_s$ , the overall velocity is scaled by the factor  $\frac{1 - q_s}{1 + \rho}$ .

**Remark B.1.2 (Transference of law of large numbers).** Using Theorem B.1.1, Lemma 4.3.4 and the elementary renewal theorem, we can *transfer* the law of large numbers on  $\widehat{\Theta}^\epsilon$  to the continuous-time process  $\Theta^\epsilon = (x_t^\epsilon, \alpha_t^\epsilon)_{t \geq 0}$  (see Definition 4.2.3) and obtain, for  $\mathbb{P}$ -a.s. every realisation of  $\epsilon$  and  $\alpha \in \{0, 1\}$ ,

$$\lim_{t \rightarrow \infty} \frac{x_t^\epsilon}{t} = \frac{1}{1+\rho} \sum_{j \in \mathbb{Z}^d} j a(0, j), \quad P_{(0, \alpha)}^\epsilon\text{-a.s.} \quad (\text{B.25})$$

We conclude this section with the proof of the above theorem. The proof is based on an application of the classical Birkhoff pointwise ergodic theorem combined with the Azuma inequality for martingales having bounded increments.

*Proof of Theorem B.1.1.* Following the standard route as taken in [22, Lecture 1], we start by defining a ( $d$ -dimensional) Martingale  $M^\epsilon := (M_n^\epsilon)_{n \in \mathbb{N}}$  constructed from the “local drift” of a particle moving in an environment  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$  according to the subordinate Markov chain  $\widehat{\Theta}^\epsilon = (X_n^\epsilon, \alpha_n^\epsilon)_{n \in \mathbb{N}_0}$  with law  $\widehat{P}_{(0, \alpha)}^\epsilon$ . With this aim, let us fix  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$ ,  $\alpha \in \{0, 1\}$  and set  $M_0^\epsilon := X_0^\epsilon$ . For  $n \in \mathbb{N}$ , define

$$M_n^\epsilon := X_n^\epsilon - (1 - q_s)v \sum_{l=0}^{n-1} \alpha_l^\epsilon. \quad (\text{B.26})$$

We show that  $M^\epsilon$  is a martingale (viewed component-wise) under the law  $\widehat{P}_{(0, \alpha)}^\epsilon$  w.r.t. the natural filtration  $(\mathcal{F}_n)_{n \in \mathbb{N}_0}$  of the subordinate Markov chain  $\widehat{\Theta}^\epsilon$ . Indeed,

$$\begin{aligned} \widehat{E}_{(0, \alpha)}^\epsilon [M_{n+1}^\epsilon \mid \mathcal{F}_n] &= \widehat{E}_{(0, \alpha)}^\epsilon \left[ X_{n+1}^\epsilon - (1 - q_s)v \sum_{l=0}^n \alpha_l^\epsilon \mid \mathcal{F}_n \right] \\ &= \widehat{E}_{(0, \alpha)}^\epsilon [X_{n+1}^\epsilon \mid \mathcal{F}_n] - (1 - q_s)v \sum_{l=0}^n \alpha_l^\epsilon \\ &= \widehat{E}_{(X_n^\epsilon, \alpha_n^\epsilon)}^\epsilon [X_1^\epsilon] - (1 - q_s)v \sum_{l=0}^n \alpha_l^\epsilon \quad (\text{by Markov property}), \end{aligned} \quad (\text{B.27})$$

where the last equality holds  $\widehat{P}_{(0, \alpha)}^\epsilon$ -a.s. Finally, using (4.27), we obtain from the above that

$$\begin{aligned} \widehat{E}_{(0, \alpha)}^\epsilon [M_{n+1}^\epsilon \mid \mathcal{F}_n] &= \alpha_n^\epsilon \left[ q_s X_n^\epsilon + (1 - q_s) \sum_{j \in \mathbb{Z}^d} \hat{p}(j)(X_n^\epsilon + j) \right] \\ &\quad + (1 - \alpha_n^\epsilon) X_n^\epsilon - (1 - q_s)v \sum_{l=0}^n \alpha_l^\epsilon \\ &= \alpha_n^\epsilon [q_s X_n^\epsilon + (1 - q_s)(X_n^\epsilon + v)] + (1 - \alpha_n^\epsilon) X_n^\epsilon - (1 - q_s)v \sum_{l=0}^n \alpha_l^\epsilon \\ &= X_n^\epsilon - (1 - q_s)v \sum_{l=0}^{n-1} \alpha_l^\epsilon = M_n^\epsilon. \end{aligned} \quad (\text{B.28})$$



Thus,  $M^\epsilon$  is a martingale under  $\widehat{P}_{(0,\alpha)}^\epsilon$ , and it has bounded increments by virtue of the finite-range assumption on the migration kernel  $\hat{p}(\cdot)$ . A standard application of Azuma inequality and the Borel Cantelli lemma yield (see e.g., [22, Lecture 1, page 14])

$$\lim_{n \rightarrow \infty} \frac{M_n^\epsilon}{n} = 0 \quad \widehat{P}_{(0,\alpha)}^\epsilon\text{-a.s.} \quad (\text{B.29})$$

Observe from above and (B.26), the proof will be complete if we prove the following: for  $\bar{\mathbb{P}}$ -a.s. every  $\epsilon \in \mathcal{E}_{\mathfrak{R}}$  and any  $\alpha \in \{0, 1\}$ ,

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{l=0}^{n-1} \alpha_l^\epsilon = \frac{1}{1 + \bar{\mathbb{E}}[M_0/N_0]}, \quad \widehat{P}_{(0,\alpha)}^\epsilon \text{ a.s.} \quad (\text{B.30})$$

This is a consequence of Birkhoff's pointwise ergodic theorem. Indeed, let  $\tilde{P}_{\mathbb{Q}}$  be the canonical law defined on the path space  $\Omega_{\mathfrak{R}}^{\mathbb{N}_0}$  of the auxiliary environment process  $W = (\epsilon_n, \alpha_n)_{n \in \mathbb{N}_0}$  (recall Definition 4.3.5) with initial distribution  $\mathbb{Q}$  (see (4.39)). In other words,

$$\tilde{P}_{\mathbb{Q}}(W \in \cdot) := \int_{\Omega_{\mathfrak{R}}} \widehat{P}_{(0,\alpha)}^\epsilon(W \in \cdot) d\mathbb{Q}(\epsilon, \alpha). \quad (\text{B.31})$$

Let  $S : \Omega_{\mathfrak{R}}^{\mathbb{N}_0} \rightarrow \Omega_{\mathfrak{R}}^{\mathbb{N}_0}$  be the natural left-shift operator and  $f : \Omega_{\mathfrak{R}}^{\mathbb{N}_0} \rightarrow \{0, 1\}$  be the function

$$(\mathbf{a}_n, \beta_n)_{n \in \mathbb{N}_0} \mapsto \beta_0, \quad (\mathbf{a}_n, \beta_n)_{n \in \mathbb{N}_0} \in \Omega_{\mathfrak{R}}^{\mathbb{N}_0}. \quad (\text{B.32})$$

Since, by part (1) of Theorem 4.3.6,  $\mathbb{Q}$  is a stationary and ergodic distribution of  $W$ , we see that  $S$  is a measure-preserving ergodic transformation of the dynamical system  $(\Omega_{\mathfrak{R}}^{\mathbb{N}_0}, \tilde{P}_{\mathbb{Q}})$ . Applying Birkhoff's pointwise ergodic theorem to the bounded function  $f$ , we obtain

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{l=0}^{n-1} f \circ S^l = \int_{\Omega_{\mathfrak{R}}^{\mathbb{N}_0}} f d\tilde{P}_{\mathbb{Q}} = \int_{\Omega_{\mathfrak{R}}} \widehat{E}_{(0,\alpha)}^\epsilon [f((\epsilon_n, \alpha_n)_{n \in \mathbb{N}_0})] d\mathbb{Q}(\epsilon, \alpha), \quad (\text{B.33})$$

where the first equality holds  $\tilde{P}_{\mathbb{Q}}$  almost everywhere and the second equality follows from (B.31). We compute the left and the right side of (B.33) using the definition of  $f$  and (4.39), to obtain

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{l=0}^{n-1} \beta_l = \int_{\Omega_{\mathfrak{R}}} \alpha d\mathbb{Q}(\epsilon, \alpha) = \frac{1}{1 + \bar{\mathbb{E}}[M_0/N_0]} \quad (\text{B.34})$$

for  $\tilde{P}_{\mathbb{Q}}$  almost every  $(\mathbf{b}_l, \beta_l)_{l \in \mathbb{N}_0}$ . However, (B.31) combined with the above implies that (B.30) holds for all  $(\epsilon, \alpha) \in A$  for some  $A \in \Sigma$  such that  $\mathbb{Q}(A) = 1$ . The result now follows from the equivalence of  $\mathbb{Q}$  and  $\bar{\mathbb{P}}$  stated in Lemma 4.3.8.  $\square$

## §B.2 Fundamental theorem of Markov chains

In this section we provide the proof of Proposition 4.3.10 stated in Section 4.3.2 of Chapter 4. Let us recall the statement of the proposition for convenience of the reader.

**Proposition B.2.1.** *Let  $(\Omega, \Sigma, \mathbb{Q})$  be a probability space, where the  $\sigma$ -field  $\Sigma$  is countably generated. Let  $W := (W_n)_{n \in \mathbb{N}_0}$  be a Markov chain on the state space  $\Omega$ , and assume that  $\mathbb{Q}$  is a reversible and ergodic stationary distribution for  $W$ . If  $-1$  is not an eigenvalue of the Markov kernel operator  $\mathfrak{R} : L_\infty(\Omega, \mathbb{Q}) \rightarrow L_\infty(\Omega, \mathbb{Q})$  associated to  $W$ , then for every bounded measurable function  $f \in \mathcal{F}_b(\Omega)$  and  $\mathbb{Q}$ -a.s. every  $w \in \Omega$ ,*

$$\lim_{n \rightarrow \infty} \mathbb{E}_w[f(W_n)] = \int_{\Omega} f \, d\mathbb{Q}, \quad (\text{B.35})$$

where the expectation on the left is taken w.r.t. the law of  $W$  started at  $w$ .

*Proof.* If  $Q(\cdot, \cdot)$  denotes the transition kernel of  $W$ , the action of the Markov operator  $\mathfrak{R}$  on  $f \in L_\infty(\Omega, \mathbb{Q})$  is well-defined and is given by

$$\mathfrak{R}f(w) := \int_{\Omega} f(y) Q(w, dy). \quad (\text{B.36})$$

In fact, since  $\mathbb{Q}$  is invariant for  $W$ , the same definition extends  $\mathfrak{R}$  in a canonical way to a positive contraction operator on  $L_p(\Omega, \mathbb{Q})$  for any  $p \geq 1$ . Furthermore, by reversibility of  $\mathbb{Q}$ , the operator  $\mathfrak{R}$  becomes self-adjoint on  $L_2(\Omega, \mathbb{Q})$  as well. Let  $f \in \mathcal{F}_b(\Omega)$  be fixed. Because  $f$  is bounded,  $\mathfrak{R}^n f \in \mathcal{F}_b(\Omega)$ , and by the Markov property of  $W$  it follows that

$$\mathbb{E}_w[f(W_n)] = \mathfrak{R}^n f(w), \quad w \in \Omega, n \in \mathbb{N}. \quad (\text{B.37})$$

Because  $\mathfrak{R}$  is self-adjoint, we see that  $\mathfrak{R}^2$  is a nonnegative-definite operator on the Hilbert space  $L_2(\Omega, \mathbb{Q})$  equipped with the natural  $L_2$  inner product, and this allows us to conclude from [147, Corollary 3] (see also [136, Theorem 1]) that there exist  $\psi, \hat{\psi} \in L_2(\Omega, \mathbb{Q})$  satisfying

$$\psi = \lim_{n \rightarrow \infty} \mathfrak{R}^{2n} f, \quad \hat{\psi} = \lim_{n \rightarrow \infty} \mathfrak{R}^{2n+1} f, \quad (\text{B.38})$$

where the convergence is in  $L_2$ -norm and  $\mathbb{Q}$  almost everywhere. It is worth mentioning that the convergence in (B.38), which follows from [147, Corollary 3], essentially uses the classical Banach principle (see e.g., [6]) along with a maximal ergodic inequality. The convergence, in fact, holds for any function in  $(L \log^+ L)(\Omega, \mathbb{Q})$ . By the almost sure convergence of  $\mathfrak{R}^{2n} f$  (resp.  $\mathfrak{R}^{2n+1} f$ ) and the  $L_\infty$  contractivity of  $\mathfrak{R}$ , we see that  $\psi, \hat{\psi} \in L_\infty(\Omega, \mathbb{Q})$  as well. The  $L_2$  contractivity of the linear operator  $\mathfrak{R}$  also implies that,

$$\psi = \mathfrak{R}\hat{\psi}, \quad \hat{\psi} = \mathfrak{R}\psi \quad \mathbb{Q}\text{-a.s.}, \quad (\text{B.39})$$

from which we get

$$\mathfrak{R}^2 \psi = \psi, \quad \mathfrak{R}^2 \hat{\psi} = \hat{\psi}, \quad \mathbb{Q}\text{-a.s.} \quad (\text{B.40})$$

We claim that if  $-1$  is not an eigenvalue of  $\mathfrak{R}$  as an operator on  $L_\infty(\Omega, \mathbb{Q})$ , then we must have

$$\psi = \hat{\psi} = \int_{\Omega} f \, d\mathbb{Q}, \quad \mathbb{Q}\text{-a.s.} \quad (\text{B.41})$$

Note that (B.35) will follow once we prove (B.41). Indeed, (B.41) combined with (B.37)–(B.38) implies that, for  $\mathbb{Q}$ -a.s.  $w \in \Omega$ , both the odd and even subsequence of

$(\mathbb{E}_w[f(W_n)])_{n \in \mathbb{N}}$  converge to the same limit  $\mathbb{Q}(f) := \int_{\Omega} f \, d\mathbb{Q}$ , which necessarily forces the convergence of  $\mathbb{E}_w[f(W_n)]$  to  $\mathbb{Q}(f)$  as  $n \rightarrow \infty$ .

To prove (B.41), it suffices to show that  $\psi$  and  $\widehat{\psi}$  are constant  $\mathbb{Q}$  a.s., because by the invariance of  $\mathfrak{R}$  w.r.t.  $\mathbb{Q}$  and bounded convergence we have

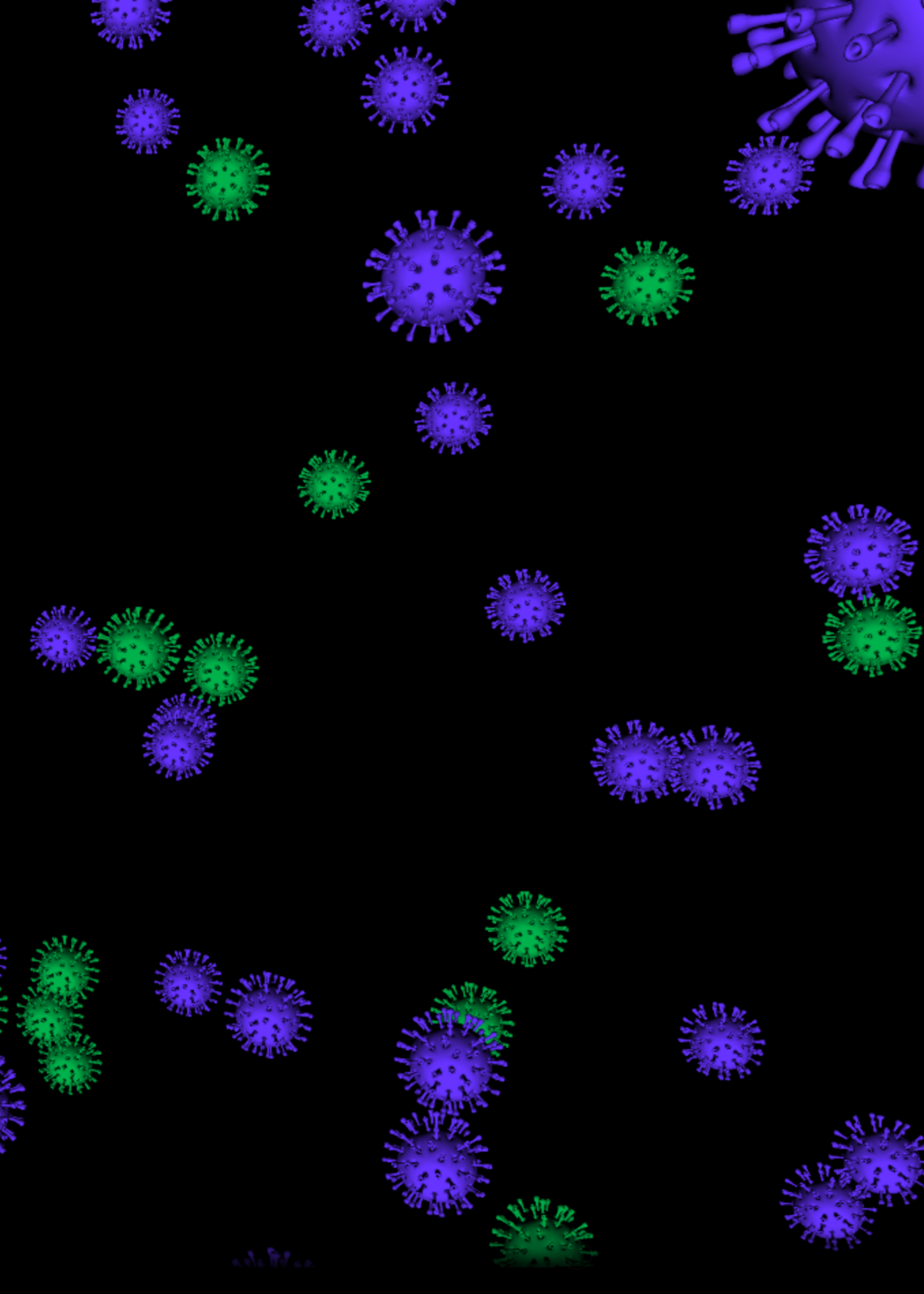
$$\int_{\Omega} \psi \, d\mathbb{Q} = \lim_{n \rightarrow \infty} \int_{\Omega} \mathfrak{R}^{2n} f \, d\mathbb{Q} = \int_{\Omega} f \, d\mathbb{Q} = \lim_{n \rightarrow \infty} \int_{\Omega} \mathfrak{R}^{2n+1} f \, d\mathbb{Q} = \int_{\Omega} \widehat{\psi} \, d\mathbb{Q}. \quad (\text{B.42})$$

We only prove the claim for  $\psi$ , as the same argument works for  $\widehat{\psi}$ . Let us set  $g := \mathfrak{R}\psi - \psi$ . From (B.40), we have

$$\mathfrak{R}g = -g, \quad \mathbb{Q}\text{-a.s.}, \quad (\text{B.43})$$

and also  $\|g\|_{\infty} \leq 2\|\psi\|_{\infty} < \infty$ . Thus,  $g \in L_{\infty}(\Omega, \mathbb{Q})$  is such that  $\mathbb{Q}$ -a.s.  $\mathfrak{R}g = -g$ , and hence by our assumption we must have  $g = 0$  a.s. In other words,  $\mathbb{Q}$ -a.s.  $\mathfrak{R}\psi - \psi = 0$  and therefore ergodicity of  $\mathfrak{R}$  in  $L_2(\Omega, \mathbb{Q})$ , which is equivalent to the ergodicity of  $W$  under  $\mathbb{Q}$ , implies that  $\psi$  is necessarily a constant  $\mathbb{Q}$  a.s.  $\square$





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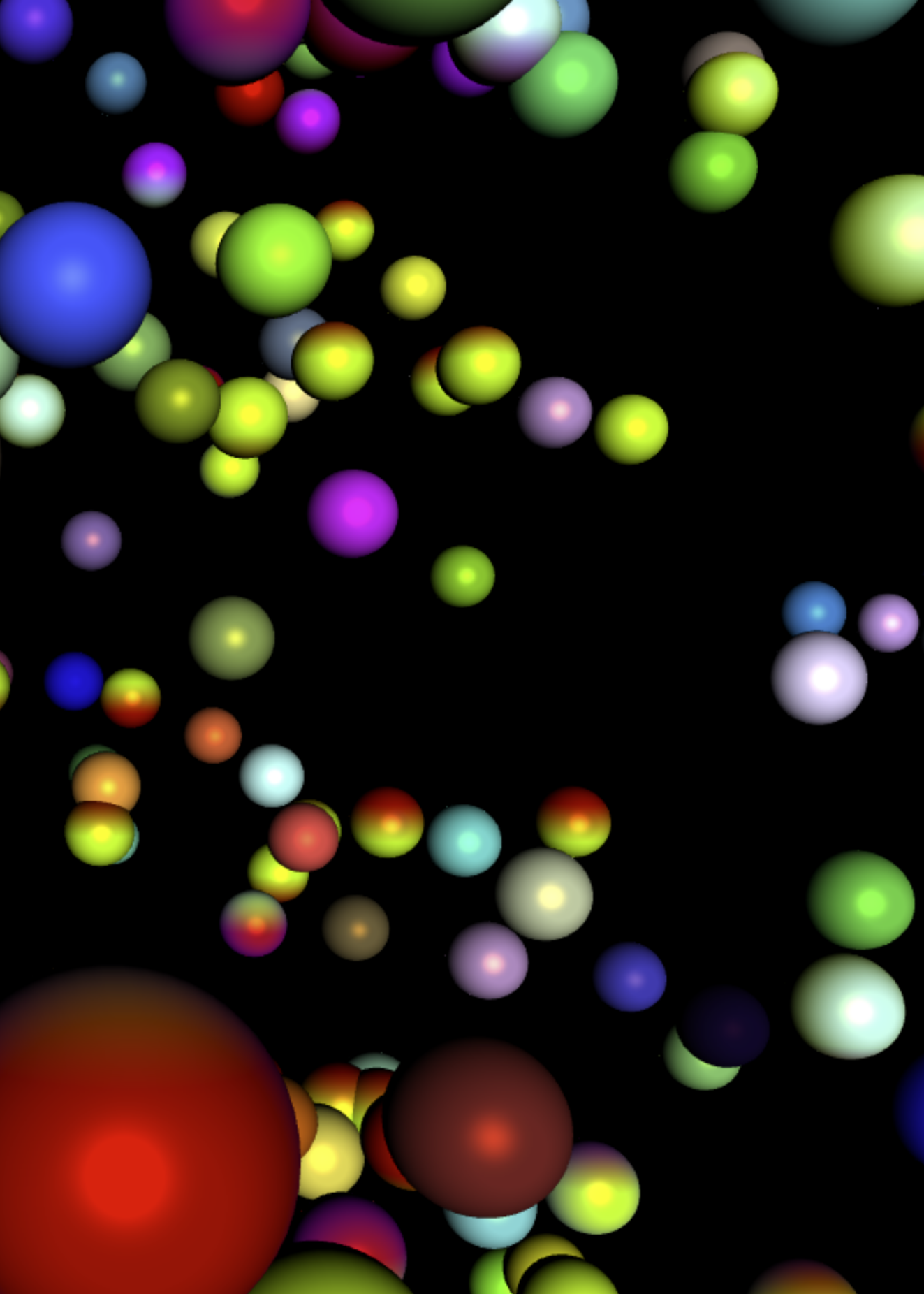
## PART II

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# DORMANCY IN SWITCHING INTERACTING PARTICLE SYSTEM

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# Switching interacting particle systems: scaling limits, uphill diffusion and boundary layer

This chapter is based on the following paper:

S. Floreani, C. Giardinà, F. den Hollander, S. Nandan, and F. Redig. Switching interacting particle systems: Scaling limits, uphill diffusion and boundary layer. *J. Stat. Phys.*, 186(3):1–45, 2022.

## Abstract

This paper considers three classes of interacting particle systems on  $\mathbb{Z}$ : independent random walks, the exclusion process, and the inclusion process. Particles are allowed to switch their jump rate (the rate identifies the *type* of particle) between 1 (*fast particles*) and  $\epsilon \in [0, 1]$  (*slow particles*). The switch between the two jump rates happens at rate  $\gamma \in (0, \infty)$ . In the exclusion process, the interaction is such that each site can be occupied by at most one particle of each type. In the inclusion process, the interaction takes places between particles of the same type at different sites and between particles of different type at the same site.

We derive the macroscopic limit equations for the three systems, obtained after scaling space by  $N^{-1}$ , time by  $N^2$ , the switching rate by  $N^{-2}$ , and letting  $N \rightarrow \infty$ . The limit equations for the macroscopic densities associated to the fast and slow particles is the well-studied double diffusivity model. This system of reaction-diffusion equations was introduced to model polycrystal diffusion and dislocation pipe diffusion, with the goal to overcome the limitations imposed by Fick's law. In order to investigate the microscopic out-of-equilibrium properties, we analyse the system on  $[N] = \{1, \dots, N\}$ , adding boundary reservoirs at sites 1 and  $N$  of fast and slow particles, respectively. Inside  $[N]$  particles move as before, but now particles are injected and absorbed at sites 1 and  $N$  with prescribed rates that depend on the particle type. We compute the steady-state density profile and the steady-state current. It turns out that uphill diffusion is possible, i.e., the total flow can be in the direction of increasing total density. This phenomenon, which cannot occur in a single-type particle system, is a violation of Fick's law made possible by the switching between types. We rescale the microscopic steady-state density profile and steady-state current and obtain the steady-state solution of a boundary-value problem for the double diffusivity model.



## §5.1 Introduction

Section 5.1.1 provides the background and the motivation for this chapter. Section 5.1.2 defines the model. Section 5.1.3 identifies the dual and the stationary measures. Section 5.1.4 gives a brief outline of the remainder of the chapter.

### §5.1.1 Background and motivation

Interacting particle systems are used to model and analyse properties of *non-equilibrium systems*, such as macroscopic profiles, long-range correlations and macroscopic large deviations. Some models have additional structure, such as duality or integrability properties, which allow for a study of the fine details of non-equilibrium steady states, such as microscopic profiles and correlations. Examples include zero-range processes, exclusion processes, and models that fit into the algebraic approach to duality, such as inclusion processes and related diffusion processes, or models of heat conduction, such as the Kipnis-Marchioro-Presutti model [24, 51, 50, 71, 97]. Most of these models have indistinguishable particles of which the total number is conserved, and so the relevant macroscopic quantity is the *density* of particles.

Turning to more complex models of non-equilibrium, various exclusion processes with *multi-type particles* have been studied [59, 60, 41, 103], as well as reaction-diffusion processes [19, 20, 120, 116, 117], where non-linear reaction-diffusion equations are obtained in the hydrodynamic limit, and large deviations around such equations have been analysed. In the present chapter, we focus on a reaction-diffusion model that on the one hand is simple enough so that via duality a complete microscopic analysis of the non-equilibrium profiles can be carried out, but on the other hand exhibits interesting phenomena, such as *uphill diffusion* and *boundary-layer effects*. In our model we have two types of particles, *fast* and *slow*, that jump at rate 1 and  $\epsilon \in [0, 1]$ , respectively. Particles of identical type are allowed to interact via exclusion or inclusion. There is no interaction between particles of different type that are at different sites. Each particle can change type at a rate that is adapted to the particle interaction (exclusion or inclusion), and is therefore interacting with particles of different type at the same site. An alternative and equivalent view is to consider two layers of particles, where the layer determines the jump rate (rate 1 for the bottom layer, rate  $\epsilon$  for the top layer) and where on each layer the particles move according to exclusion or inclusion, and to let particles change layer at a rate that is appropriately chosen in accordance with the interaction. In the limit as  $\epsilon \downarrow 0$ , particles are immobile on the top layer.

We show that the *hydrodynamic limit* of all three dynamics is a linear reaction-diffusion system known under the name of *double diffusivity model*, namely,

$$\begin{cases} \partial_t \rho_0 = \Delta \rho_0 + \Upsilon(\rho_1 - \rho_0), \\ \partial_t \rho_1 = \epsilon \Delta \rho_1 + \Upsilon(\rho_0 - \rho_1), \end{cases} \quad (5.1)$$

where  $\rho_i$ ,  $i \in \{0, 1\}$ , are the macroscopic densities of the two types of particles, and  $\Upsilon \in (0, \infty)$  is the scaled switching rate. The above system was introduced in [1] to model polycrystal diffusion (more generally, diffusion in inhomogeneous porous media) and dislocation pipe diffusion, with the goal to overcome the restrictions imposed by

Fick's law. Non-Fick behaviour is immediate from the fact that the total density  $\rho = \rho_0 + \rho_1$  does not satisfy the classical diffusion equation.

The double diffusivity model was studied extensively in the PDE literature [2, 86, 85], while its discrete counterpart was analysed in terms of a single random walk switching between two layers [84]. The same macroscopic model was studied independently in the mathematical finance literature in the context of switching diffusion processes [156]. Thus, we have a family of interacting particle systems whose macroscopic limit is relevant in several distinct contexts. Another context our three dynamics fit into are models of interacting active random walks with an internal state that changes randomly (e.g. activity, internal energy) and that determines their diffusion rate and or drift [43, 65, 81, 101, 115, 52, 133, 3, 99].

An additional motivation to study two-layer models comes from population genetics. Individuals live in colonies, carry different gene types, and can be either active or dormant. While active, individuals resample by adopting the type of a randomly sampled individual in the same colony, and migrate between colonies by hopping around. Active individuals can become dormant, after which they suspend resampling and migration, until they become active again. Dormant individuals reside in what is called a *seed bank*. The overall effect of dormancy is that extinction of types is slowed down, and so genetic diversity is enhanced by the presence of the seed bank. A wealth of phenomena can occur, depending on the parameters that control the rates of resampling, migration, falling asleep and waking up [18, 76, 15]. Dormancy not only affects the long-term behaviour of the population quantitatively. It may also lead to qualitatively different equilibria and time scales of convergence. For a panoramic view on the role of dormancy in the life sciences, we refer the reader to [108].

From the point of view of non-equilibrium systems driven by boundary reservoirs, switching interacting particle systems have not been studied. On the one hand, such systems have both reaction and diffusion and therefore exhibit a richer non-equilibrium behaviour. On the other hand, the macroscopic equations are linear and exactly solvable in one dimension, and so these systems are simple enough to make a detailed microscopic analysis possible. As explained above, the system can be viewed as an interacting particle system on two layers. Therefore duality properties are available, which allows for a detailed analysis of the system coupled to reservoirs, which is dual to an absorbing system. In one dimension the analysis of the microscopic density profile reduces to a computation of the absorption probabilities of a simple random walk on a two-layer system absorbed at the left and right boundaries. From the analytic solution we can identify both the density profile and the current in the system. This leads to two interesting phenomena. The first phenomenon is *uphill diffusion* (see e.g. [33, 36, 37, 118, 102]), i.e., in a well-defined parameter regime the current can go against the particle density gradient: when the total density of particles at the left end is higher than at the right end, the current can still go from right to left. The second phenomenon is *boundary-layer behaviour*: in the limit as  $\epsilon \downarrow 0$ , in the macroscopic stationary profile the densities in the top and bottom layer are equal, which for unequal boundary conditions in the top and bottom layer results in a *discontinuity* in the stationary profile. Corresponding to this jump in the macroscopic system, we identify a boundary layer in the microscopic system of *size*  $\sqrt{\epsilon} \log(1/\epsilon)$  where the densities are

unequal. The quantification of the size of this boundary layer is an interesting corollary of the exact macroscopic stationary profile that we obtain from the microscopic system via duality.

### §5.1.2 Three models

For  $\sigma \in \{-1, 0, 1\}$  we introduce an interacting particle system on  $\mathbb{Z}$  where the particles randomly switch their jump rate between two possible values, 1 and  $\epsilon$ , with  $\epsilon \in [0, 1]$ . For  $\sigma = -1$  the particles are subject to the exclusion interaction, for  $\sigma = 0$  the particles are independent, while for  $\sigma = 1$  the particles are subject to the inclusion interaction. Let

$$\begin{aligned}\eta_0(x) &:= \text{number of particles at site } x \text{ jumping at rate } 1, \\ \eta_1(x) &:= \text{number of particles at site } x \text{ jumping at rate } \epsilon.\end{aligned}$$

The configuration of the system is

$$\eta := \{\eta(x)\}_{x \in \mathbb{Z}} \in \mathcal{X} = \begin{cases} \{0, 1\}^{\mathbb{Z}} \times \{0, 1\}^{\mathbb{Z}}, & \text{if } \sigma = -1, \\ \mathbb{N}_0^{\mathbb{Z}} \times \mathbb{N}_0^{\mathbb{Z}}, & \text{if } \sigma \in \{0, 1\}, \end{cases}$$

where

$$\eta(x) := (\eta_0(x), \eta_1(x)), \quad x \in \mathbb{Z}.$$

We call  $\eta_0 = \{\eta_0(x)\}_{x \in \mathbb{Z}}$  and  $\eta_1 = \{\eta_1(x)\}_{x \in \mathbb{Z}}$  the configurations of *fast particles*, respectively, *slow particles*. When  $\epsilon = 0$  we speak of *dormant particles* (see Fig. 5.1).

**Definition 5.1.1 (Switching interacting particle systems).** For  $\epsilon \in [0, 1]$  and  $\gamma \in (0, \infty)$ , let  $L_{\epsilon, \gamma}$  be the generator

$$L_{\epsilon, \gamma} := L_0 + \epsilon L_1 + \gamma L_{0\uparrow 1}, \quad (5.2)$$

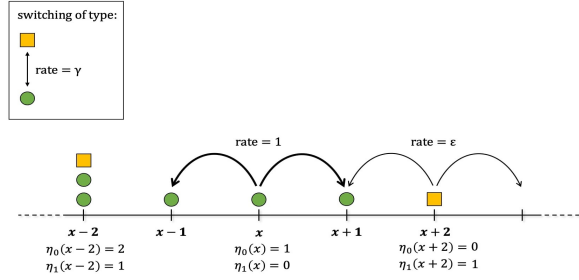
acting on bounded cylindrical functions  $f: \mathcal{X} \rightarrow \mathbb{R}$  as

$$\begin{aligned}(L_0 f)(\eta) &= \sum_{|x-y|=1} \left\{ \eta_0(x)(1 + \sigma \eta_0(y)) [f((\eta_0 - \delta_x + \delta_y, \eta_1)) - f(\eta)] \right. \\ &\quad \left. + \eta_0(y)(1 + \sigma \eta_0(x)) [f((\eta_0 + \delta_x - \delta_y, \eta_1)) - f(\eta)] \right\}, \\ (L_1 f)(\eta) &= \sum_{|x-y|=1} \left\{ \eta_1(x)(1 + \sigma \eta_1(y)) [f((\eta_0, \eta_1 - \delta_x + \delta_y)) - f(\eta)] \right. \\ &\quad \left. + \eta_1(y)(1 + \sigma \eta_1(x)) [f((\eta_0, \eta_1 + \delta_x - \delta_y)) - f(\eta)] \right\}, \\ (L_{0\uparrow 1} f)(\eta) &= \sum_{x \in \mathbb{Z}^d} \left\{ \eta_0(x)(1 + \sigma \eta_1(x)) [f((\eta_0 - \delta_x, \eta_1 + \delta_x)) - f(\eta)] \right. \\ &\quad \left. + \eta_1(x)(1 + \sigma \eta_0(x)) [f((\eta_0 + \delta_x, \eta_1 - \delta_x)) - f(\eta)] \right\}.\end{aligned} \quad (5.3)$$

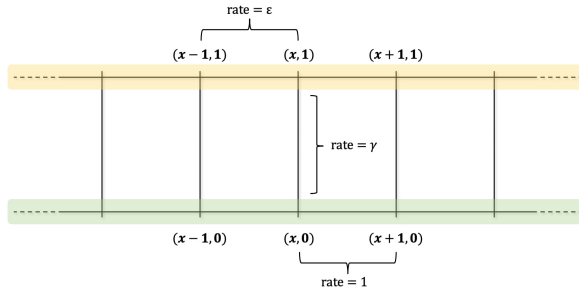
The Markov process  $\{\eta(t): t \geq 0\}$  on state space  $\mathcal{X}$  with

$$\eta(t) := \{\eta(x, t)\}_{x \in \mathbb{Z}} = \{(\eta_0(x, t), \eta_1(x, t))\}_{x \in \mathbb{Z}}, \quad (5.4)$$

hopping rates 1,  $\epsilon$  and switching rate  $\gamma$  is called *switching exclusion process* for  $\sigma = -1$ , *switching random walks* for  $\sigma = 0$  (see Fig. 5.1), and *switching inclusion process* for  $\sigma = 1$ . ■



(a) Representation via slow and fast particles moving on the one-layer graph  $\mathbb{Z}$ .



(b) Representation via particles moving on the two-layer graph  $\mathbb{Z} \times I$ .

Figure 5.1: Two equivalent representations of switching independent random walks ( $\sigma = 0$ ).

### §5.1.3 Duality and stationary measures

The systems defined in (5.2) can be equivalently formulated as jump processes on the graph (see Fig. 5.1) with vertex set  $\{(x, i) \in \mathbb{Z}^d \times I\}$ , with  $I = \{0, 1\}$  labelling the two layers, and edge set given by the nearest-neighbour relation

$$(x, i) \sim (y, j) \quad \text{when} \quad \begin{cases} |x - y| = 1 \text{ and } i = j, \\ x = y \text{ and } |i - j| = 1. \end{cases} \quad (5.5)$$

In this formulation the particle configuration is

$$\eta = (\eta_i(x))_{(x,i) \in \mathbb{Z} \times I} \quad (5.6)$$

and the generator  $L$  is given by

$$\begin{aligned} (Lf)(\eta) = & \sum_{i \in I} \sum_{|x-y|=1} \epsilon^i \eta_i(x)(1 + \sigma \eta_i(y)) [f(\eta - \delta_{(x,i)} + \delta_{(y,i)}) - f(\eta)] \\ & + \epsilon^i \eta_i(y)(1 + \sigma \eta_i(x)) [f(\eta - \delta_{(y,i)} + \delta_{(x,i)}) - f(\eta)] \\ & + \sum_{i \in I} \gamma \sum_{x \in \mathbb{Z}} \eta_i(x)(1 + \sigma \eta_{1-i}) [f(\eta - \delta_{(x,i)} + \delta_{(x,1-i)}) - f(\eta)]. \end{aligned} \quad (5.7)$$

Thus, a single particle (when no other particles are present) is subject to two movements:

- (i) *Horizontal movement:* In layer  $i = 0$  and  $i = 1$  the particle performs a nearest-neighbour random walk on  $\mathbb{Z}$  at rate 1, respectively,  $\epsilon$ .
- (ii) *Vertical movement:* The particle switches layer at the same site at rate  $\gamma$ .

It is well known (see e.g. [134]) that for these systems there exists a one-parameter family of reversible product measures

$$\left\{ \mu_\theta = \bigotimes_{(x,i) \in \mathbb{Z} \times I} \nu_{(x,i),\theta} \mid \theta \in \Theta \right\} \quad (5.8)$$

with  $\Theta = [0, 1]$  if  $\sigma = -1$  and  $\Theta = [0, \infty)$  if  $\sigma \in \{0, 1\}$ , and with marginals given by

$$\nu_{(x,i),\theta} = \begin{cases} \text{Bernoulli}(\theta), & \text{if } \sigma = -1, \\ \text{Poisson}(\theta), & \text{if } \sigma = 0, \\ \text{Negative-Binomial}(1, \frac{\theta}{1+\theta}), & \text{if } \sigma = 1. \end{cases} \quad (5.9)$$

Moreover, the *classical self-duality relation* holds, i.e., for all configurations  $\eta, \xi \in \mathcal{X}$  and for all times  $t \geq 0$ ,

$$\mathbb{E}_\eta[D(\xi, \eta_t)] = \mathbb{E}_\xi[D(\xi_t, \eta)], \quad (5.10)$$

with  $\{\xi(t) : t \geq 0\}$  and  $\{\eta(t) : t \geq 0\}$  two copies of the process with generator given in (5.2) and self-duality function  $D: \mathcal{X} \times \mathcal{X} \rightarrow \mathbb{R}$  given by

$$D(\xi, \eta) := \prod_{(x,i) \in \mathbb{Z}^d \times I} d(\xi_i(x), \eta_i(x)), \quad (5.11)$$

with

$$d(k, n) := \frac{n!}{(n-k)!} \frac{1}{w(k)} \mathbb{1}_{\{k \leq n\}} \quad (5.12)$$

and

$$w(k) := \begin{cases} \frac{\Gamma(1+k)}{\Gamma(1)}, & \text{if } \sigma = 1, \\ 1, & \text{if } \sigma \in \{-1, 0\}. \end{cases} \quad (5.13)$$

**Remark 5.1.2 (Possible extensions).** Note that we could allow for more than two layers, for inhomogeneous rates and for non-nearest neighbour jumps as well, and the same duality relation would still hold (see e.g. [63] for an inhomogeneous version of the exclusion process). More precisely, let  $\{\omega_i(\{x, y\})\}_{x, y \in \mathbb{Z}}$  and  $\{\alpha_i(x)\}_{x \in \mathbb{Z}}$  be collections of bounded weights for  $i \in I_M = \{0, 1, \dots, M\}$  with  $M < \infty$ . Then the interacting

particle systems with generator

$$\begin{aligned}
 (L_{D,\gamma}f)(\eta) &= \sum_{i=0}^M D_i \sum_{|x-y|=1} \omega_i(\{x,y\}) \left\{ \eta_i(x) (\alpha_i(y) + \sigma \eta_i(y)) \right. \\
 &\quad \times [f(\eta - \delta_{(x,i)} + \delta_{(y,i)}) - f(\eta)] \\
 &\quad \left. + \eta_i(y) (\alpha_i(x) + \sigma \eta_i(x)) [f(\eta - \delta_{(y,i)} + \delta_{(x,i)}) - f(\eta)] \right\} \\
 &+ \sum_{i=0}^{M-1} \gamma_{\{i,i+1\}} \sum_{x \in \mathbb{Z}} \left\{ \eta_i(x) [f(\eta - \delta_{(x,i)} + \delta_{(x,i+1)}) - f(\eta)] \right. \\
 &\quad \left. + \eta_{i+1}(x) [f(\eta - \delta_{(x,i+1)} + \delta_{(x,i)}) - f(\eta)] \right\},
 \end{aligned} \tag{5.14}$$

with  $\eta = (\eta_i(x))_{(x,i) \in \mathbb{Z} \times I_M}$ ,  $\{D_i\}_{i \in I_M}$  a bounded decreasing collection of weights in  $[0, 1]$  and  $\gamma_{\{i,i+1\}} \in (0, \infty)$ , are still self-dual with duality function as in (5.11), but with  $I$  replaced by  $I_M$  and single-site duality functions given by  $d_{(x,i)}(k, n) = \frac{n!}{(n-k)!} \frac{1}{w_{(x,i)}(k)} \mathbb{1}_{\{k \leq n\}}$  with

$$w_{(x,i)}(k) := \begin{cases} \frac{\alpha_i(x)!}{(\alpha_i(x) - k)!} \mathbb{1}_{\{k \leq \alpha_i(x)\}}, & \text{if } \sigma = -1, \\ \alpha_i(x)^k, & \text{if } \sigma = 0, \\ \frac{\Gamma(\alpha_i(x) + k)}{\Gamma(\alpha_i(x))}, & \text{if } \sigma = 1. \end{cases} \tag{5.15}$$

In the present chapter we prefer to stick to the two-layer homogeneous setting in order not to introduce extra notations. However, it is straightforward to extend many of our results to the inhomogeneous multi-layer model.

Duality is a key tool in the study of detailed properties of interacting particle systems, since it allows for explicit computations. It has been used widely in the literature (see, e.g., [112, 120]). In the next section, *self-duality* (which implies microscopic closure of the evolution equation for the empirical density field) will be used to derive the hydrodynamic limit of the switching interacting particle systems described above. More precisely, we will use self-duality with one and two dual particles to compute the expectation of the evolution of the occupation variables and of the two-point correlations. These are needed, respectively, to control the expectation and the variance of the density field.

### §5.1.4 Outline

Section 5.2 identifies and analyses the *hydrodynamic limit* of the system in Definition 5.1.1 after scaling space, time and switching rate diffusively. In doing so, we exhibit a class of interacting particle systems whose microscopic dynamics scales to a macroscopic dynamics called the double diffusivity model. We provide a discussion on the solutions of this model, thereby connecting mathematical literature applied to material science and to financial mathematics. Section 5.3 looks at what happens, both

microscopically and macroscopically, when *boundary reservoirs* are added, resulting in a non-equilibrium flow. Here the possibility of *uphill diffusion* becomes manifest, which is absent in single-layer systems, i.e., the two layers interact in a way that allows for a violation of Fick's law. We characterise the parameter regime for uphill diffusion. We show that, in the limit as  $\epsilon \downarrow 0$ , the macroscopic stationary profile of the type-1 particles adapts to the microscopic stationary profile of the type-0 particles, resulting in a *discontinuity* at the boundary for the case of unequal boundary conditions on the top layer and the bottom layer. Appendix C provides the inverse of a certain boundary-layer matrix.

## §5.2 The hydrodynamic limit

In this section we scale space, time and switching diffusively, so as to obtain a *hydrodynamic limit*. In Section 5.2.1 we scale space by  $1/N$ , time by  $N^2$ , the switching rate by  $1/N^2$ , introduce scaled microscopic empirical distributions, and let  $N \rightarrow \infty$  to obtain a system of macroscopic equations. In Section 5.2.2 we recall some known results for this system, namely, there exists a unique solution that can be represented in terms of an underlying diffusion equation or, alternatively, via a Feynman-Kac formula involving the switching diffusion process.

### §5.2.1 From microscopic to macroscopic

Let  $N \in \mathbb{N}$ , and consider the scaled generator  $L_{\epsilon, \gamma_N}$  (recall (5.2)) with  $\gamma_N = \Upsilon/N^2$  for some  $\Upsilon \in (0, \infty)$ , i.e., the reaction term is slowed down by a factor  $N^2$  in anticipation of the diffusive scaling we are going to consider.

In order to study the collective behaviour of the particles after scaling of space and time, we introduce the following empirical density fields, which are Radon measure-valued càdlàg (i.e., right-continuous with left limits) processes:

$$\mathbf{X}_0^N(t) := \frac{1}{N} \sum_{x \in \mathbb{Z}} \eta_0(x, tN^2) \delta_{x/N}, \quad \mathbf{X}_1^N(t) := \frac{1}{N} \sum_{x \in \mathbb{Z}} \eta_1(x, tN^2) \delta_{x/N}, \quad (5.16)$$

where  $\delta_y$  stands for the Dirac measure at  $y \in \mathbb{R}$ . In order to derive the hydrodynamic limit for the switching interacting particle systems, we need the following set of assumptions. In the following we denote by  $C_c^\infty(\mathbb{R})$  the space of infinitely differentiable functions with values in  $\mathbb{R}$  and compact support, by  $C_b(\mathbb{R}; \sigma)$  the space of bounded and continuous functions with values in  $\mathbb{R}_+$  for  $\sigma \in \{0, 1\}$  and with values in  $[0, 1]$  for  $\sigma = -1$ , by  $C_0(\mathbb{R})$  the space of continuous functions vanishing at infinity, by  $C_0^2(\mathbb{R})$  the space of twice differentiable functions vanishing at infinity and by  $\mathcal{M}$  the space of Radon measure on  $\mathbb{R}$ .

**Assumption 5.A (Compatible initial conditions).** Let  $\bar{\rho}_i \in C_b(\mathbb{R}; \sigma)$  for  $i \in \{0, 1\}$  be two given functions, called initial macroscopic profiles. We say that a sequence  $(\mu_N)_{N \in \mathbb{N}}$  of measures on  $\mathcal{X}$  is a sequence of compatible initial conditions when:

(i) For any  $i \in \{0, 1\}$ ,  $g \in C_c^\infty(\mathbb{R})$  and  $\delta > 0$ ,

$$\lim_{N \rightarrow \infty} \mu_N \left( \left| \langle \mathbf{X}_i^N(0), g \rangle - \int_{\mathbb{R}} dx \bar{\rho}_i(x) g(x) \right| > \delta \right) = 0. \quad (5.17)$$

(ii) There exists a constant  $C < \infty$  such that

$$\sup_{(x,i) \in \mathbb{Z} \times I} \mathbb{E}_{\mu_N} [\eta_i(x)^2] \leq C. \quad (5.18)$$

■

Note that Assumption 5.A(ii) is the same as employed in [30, Theorem 1, Assumption (b)] and is trivial for the exclusion process.

**Theorem 5.2.1 (Hydrodynamic scaling).** *Let  $\bar{\rho}_0, \bar{\rho}_1 \in C_b(\mathbb{R}; \sigma)$  be two initial macroscopic profiles, and let  $(\mu_N)_{N \in \mathbb{N}}$  be a sequence of compatible initial conditions. Let  $\mathbb{P}_{\mu_N}$  be the law of the measure-valued process*

$$\{X^N(t) : t \geq 0\}, \quad X^N(t) := (X_0^N(t), X_1^N(t)), \quad (5.19)$$

induced by the initial measure  $\mu_N$ . Then, for any  $T, \delta > 0$  and  $g \in C_c^\infty(\mathbb{R})$ ,

$$\lim_{N \rightarrow \infty} \mathbb{P}_{\mu_N} \left( \sup_{t \in [0, T]} \left| \langle \mathbf{X}_i^N(t), g \rangle - \int_{\mathbb{R}} dx \rho_i(x, t) g(x) \right| > \delta \right) = 0, \quad i \in I, \quad (5.20)$$

where  $\rho_0$  and  $\rho_1$  are the unique continuous and bounded strong solutions of the system

$$\begin{cases} \partial_t \rho_0 = \Delta \rho_0 + \Upsilon(\rho_1 - \rho_0), \\ \partial_t \rho_1 = \epsilon \Delta \rho_1 + \Upsilon(\rho_0 - \rho_1), \end{cases} \quad (5.21)$$

with initial conditions

$$\begin{cases} \rho_0(x, 0) = \bar{\rho}_0(x), \\ \rho_1(x, 0) = \bar{\rho}_1(x). \end{cases} \quad (5.22)$$

*Proof.* The proof follows the standard route presented in [139, Section 8] (see also [120, 30]). We still explain the main steps because the two-layer setup is not standard. First of all, note that the macroscopic equation (5.21) can be straightforwardly identified by computing the action of the rescaled generator  $L^N = L_{\epsilon, \Upsilon/N^2}$  on the cylindrical functions  $f_i(\eta) := \eta_i(x)$ ,  $i \in \{0, 1\}$ , namely,

$$(L^N f_i)(\eta) = \epsilon^i [\eta_i(x+1) - 2\eta_i(x) + \eta_i(x-1)] + \frac{\Upsilon}{N^2} [\eta_{1-i}(x) - \eta_i(x)] \quad (5.23)$$

and hence, for any  $g \in C_c^\infty(\mathbb{R})$ ,

$$\begin{aligned} \int_0^{tN^2} ds L^N (\langle \mathbf{X}_i^N(s), g \rangle) &= \int_0^{tN^2} ds \frac{\epsilon^i}{N} \sum_{x \in \mathbb{Z}} \eta_i(x, s) \frac{1}{2} \left[ g\left(\frac{x+1}{N}\right) - 2g\left(\frac{x}{N}\right) + g\left(\frac{x-1}{N}\right) \right] \\ &\quad + \int_0^{tN^2} ds \frac{1}{N} \sum_{x \in \mathbb{Z}} g\left(\frac{x}{N}\right) \frac{\Upsilon}{N^2} [\eta_{1-i}(x, s) - \eta_i(x, s)], \end{aligned} \quad (5.24)$$



where we moved the generator of the simple random walk to the test function by using reversibility w.r.t. the counting measure. By the regularity of  $g$  and using Taylor's expansion, we thus have

$$\begin{aligned} \int_0^{tN^2} ds L^N(\langle X_i^N(s), g \rangle) &= \int_0^t ds \langle X_i^N(sN^2), \epsilon^i \Delta g \rangle \\ &+ \int_0^{tN^2} ds \frac{\Upsilon}{N^2} [\langle X_{1-i}^N(s), g \rangle - \langle X_i^N(s), g \rangle] \\ &+ o\left(\frac{1}{N^2}\right), \end{aligned} \tag{5.25}$$

which is the discrete counterpart of the weak formulation of the right-hand side of (5.21), i.e.,  $\int_0^t ds \int_{\mathbb{R}} dx \rho_i(x, s) \Delta g(x) + \Upsilon \int_0^t ds \int_{\mathbb{R}} dx [\rho_{1-i}(x, s) - \rho_i(x, s)] g(x)$ . Thus, as a first step, we show that

$$\begin{aligned} \lim_{N \rightarrow \infty} \mathbb{P}_{\mu_N} \left( \sup_{t \in [0, T]} \left| \langle X_i^N(t), g \rangle - \langle X_i^N(0), g \rangle - \int_0^t ds \langle X_i^N(sN^2), \epsilon^i \Delta g \rangle \right. \right. \\ \left. \left. - \int_0^{tN^2} ds \frac{\Upsilon}{N^2} [\langle X_{1-i}^N(s), g \rangle - \langle X_i^N(s), g \rangle] \right| > \delta \right) = 0. \end{aligned} \tag{5.26}$$

In order to prove the above convergence we employ the Dynkin's martingale formula for Markov processes (see, e.g., [139, Theorem 4.8]), which gives that the process defined as

$$M_i^N(g, t) := \langle X_i^N(t), g \rangle - \langle X_i^N(0), g \rangle - \int_0^{tN^2} ds L^N(\langle X_i^N(s), g \rangle) \tag{5.27}$$

is a martingale w.r.t. the natural filtration generated by the process  $\{\eta_t\}_{t \geq 0}$  and with predictable quadratic variation expressed in terms of the carré du champ, i.e.,

$$\langle M_i^N(g, t), M_i^N(g, t) \rangle = \int_0^t ds \mathbb{E}_{\mu_N} [\Gamma_i^N(g, s)] \tag{5.28}$$

with

$$\Gamma_i^N(g, s) = L^N(\langle X_i^N(s), g \rangle)^2 - \langle X_i^N(s), g \rangle L^N(\langle X_i^N(s), g \rangle). \tag{5.29}$$

We then have, by Chebyshev's inequality and Doob's martingale inequality (see, e.g.,

[94, Section 1.3]),

$$\begin{aligned}
 & \mathbb{P}_{\mu_N} \left( \sup_{t \in [0, T]} \left| \langle X_i^N(s), g \rangle - \langle X_i^N(s), g \rangle - \int_0^t ds \langle X_i^N(sN^2), \epsilon \Delta g \rangle \right. \right. \\
 & \quad \left. \left. - \int_0^{tN^2} ds \frac{\Upsilon}{N^2} [\langle X_{1-i}^N(s), g \rangle - \langle X_i^N(s), g \rangle] \right| > \delta \right) \\
 & \leq \frac{1}{\delta^2} \mathbb{E}_{\mu_N} \left[ \sup_{t \in [0, T]} |M_i^N(g, s)|^2 \right] \leq \frac{4}{\delta^2} \mathbb{E}_{\mu_N} \left[ |M_i^N(g, T)|^2 \right] \\
 & = \frac{4}{\delta^2} \mathbb{E}_{\mu_N} \left[ (M_i^N(g, T), M_i^N(g, T))^2 \right] \\
 & = \frac{4}{\delta^2 N^2} \mathbb{E}_{\mu_N} \left[ \int_0^{N^2 T} ds \sum_{x \in \mathbb{Z}^d} \eta_i(x, s) (1 + \sigma \eta_i(x \pm 1, s)) \left( g\left(\frac{x \pm 1}{N}\right) - g\left(\frac{x}{N}\right) \right) \right] \\
 & + \frac{4\Upsilon}{\delta^2 N^4} \mathbb{E}_{\mu_N} \left[ \int_0^{N^2 T} ds \sum_{x \in \mathbb{Z}^d} (\eta_i(x, s) + \eta_{1-i}(x, s) + 2\sigma \eta_i(x, s) \eta_{1-i}(x, s)) g^2\left(\frac{x}{N}\right) \right], \tag{5.30}
 \end{aligned}$$

where in the last equality we explicitly computed the carré du champ. Let  $k \in \mathbb{N}$  be such that the support of  $g$  is in  $[-k, k]$ . Then, by the regularity of  $g$ , (5.30) is bounded by

$$\begin{aligned}
 & \frac{4}{\delta^2 N^2} (N^2 T)(2k + 1) N \frac{\|\nabla g\|_\infty}{N^2} \sup_{\substack{x \in \mathbb{Z}, \\ s \in [0, N^2 T]}} \mathbb{E}_{\mu_N} \left[ \eta_i(x, s) (1 + \sigma \eta_i(x + 1, s)) \right] \\
 & + \frac{4\Upsilon}{\delta^2 N^4} (N^2 T)(2k + 1) N \|g\|_\infty \sup_{\substack{x \in \mathbb{Z}, \\ s \in [0, N^2 T]}} \left\{ \mathbb{E}_{\mu_N} \left[ \eta_i(x, s) + \eta_{1-i}(x, s) \right. \right. \\
 & \quad \left. \left. + 2\sigma \eta_i(x, s) \eta_{1-i}(x, s) \right] \right\}. \tag{5.31}
 \end{aligned}$$

We now show that, as a consequence of (5.18), for any  $(x, i), (y, j) \in \mathbb{Z} \times I$ ,

$$\mathbb{E}_{\mu_N} [\eta_i(x, s)] \leq C, \quad \mathbb{E}_{\mu_N} [\eta_i(x, s) \eta_j(y, s)] \leq C, \tag{5.32}$$

from which we obtain

$$\begin{aligned}
 & \mathbb{P}_{\mu_N} \left( \sup_{t \in [0, T]} \left| \langle X_0^N(s), g \rangle - \langle X_0^N(s), g \rangle - \int_0^t ds \langle X_0^N(sN^2), \epsilon \Delta g \rangle \right. \right. \\
 & \quad \left. \left. - \int_0^{tN^2} ds \frac{\Upsilon}{N^2} [\langle X_1^N(s), g \rangle - \langle X_0^N(s), g \rangle] \right| > \delta \right) \\
 & \leq \frac{8T}{\delta^2 N} (2k + 1) \|\nabla g\|_\infty C + \Upsilon \frac{16T}{\delta^2 N} (2k + 1) \|g\|_\infty C, \tag{5.33}
 \end{aligned}$$

and the desired convergence follows. In order to prove (5.32), first of all note that, by the Cauchy-Schwartz inequality, it follows from (5.18) that, for any  $(x, i), (y, j) \in \mathbb{Z} \times I$ ,

$$\mathbb{E}_{\mu_N} [\eta_i(x) \eta_j(y)] \leq C. \tag{5.34}$$

Moreover, recalling the duality functions given in (5.11) and defining the configuration  $\xi = \delta_{(x,i)} + \delta_{(y,j)}$  for  $(x,i) \neq (y,j)$ , we have that  $D(\xi, \eta_t) = \eta_i(x,t)\eta_j(y,t)$  and thus, using the classical self-duality relation,

$$\begin{aligned} \mathbb{E}_{\mu_N} [\eta_i(x,t)\eta_j(y,t)] &= \mathbb{E}_{\mu_N} [D(\xi, \eta_t)] = \int_{\mathcal{X}} \mathbb{E}_{\eta} [D(\xi, \eta_t)] d\mu_N(\eta) \\ &= \int_{\mathcal{X}} \mathbb{E}_{\xi} [D(\xi_t, \eta)] d\mu_N(\eta) = \mathbb{E}_{\xi} [\mathbb{E}_{\mu_N} [D(\xi_t, \eta)]] . \end{aligned} \quad (5.35)$$

Labeling the particles in the dual configuration as  $(X_t, i_t)$  and  $(Y_t, j_t)$  with initial conditions  $(X_0, i_0) = (x, i)$  and  $(Y_0, j_0) = (y, j)$ , we obtain

$$\begin{aligned} \mathbb{E}_{\mu_N} [\eta_i(x,t)\eta_j(y,t)] &= \mathbb{E}_{\xi} \left[ \mathbb{E}_{\mu_N} [\eta_{i_t}(X_t)\eta_{j_t}(Y_t) \mathbb{1}_{(X_t, i_t) \neq (Y_t, j_t)}] \right. \\ &\quad \left. + \mathbb{E}_{\mu_N} [\eta_{i_t}(X_t)(\eta_{i_t}(X_t) - 1) \mathbb{1}_{(X_t, i_t) = (Y_t, j_t)}] \right] \\ &\leq \mathbb{E}_{\xi} \left[ \mathbb{E}_{\mu_N} [\eta_{i_t}(X_t)\eta_{j_t}(Y_t)] \right] \\ &\leq \mathbb{E}_{\xi} \left[ \sup_{(x,i), (y,j) \in \mathbb{Z} \times \{0,1\}} \mathbb{E}_{\mu_N} [\eta_i(x)\eta_j(y)] \right] \leq C, \end{aligned} \quad (5.36)$$

where we used (5.34) in the last inequality. Similarly, for  $\xi = \delta_{(x,i)}$  and  $(X_t, i_t)$  the dual particle with initial condition  $(X_0, i_0) = (x, i)$ , we have that  $\mathbb{E}_{\mu_N} [\eta_i(x,t)] \leq \mathbb{E}_{\mu_N} [D(\xi, \eta_t)] = \mathbb{E}_{\xi} [\mathbb{E}_{\mu_N} [\eta_{i_t}(X_t)]]$ . Using that  $\eta_i(x) \leq \eta_i(x)^2$  for any  $(x, i) \in \mathbb{Z} \times I$  and using (5.18), we obtain (5.32). The proof is concluded after showing the following:

- (i) Tightness holds for the sequence of distributions of the processes  $\{\mathbf{X}_i^N\}_{N \in \mathbb{N}}$ , denoted by  $\{Q_N\}_{N \in \mathbb{N}}$ .
- (ii) All limit points coincide and are supported by the unique path  $\mathbf{X}_i(t, dx) = \rho_i(x,t) dx$ , with  $\rho_i$  the unique weak (and in particular strong) bounded and continuous solution of (5.21).

While for (i) we provide an explanation, we skip the proof of (ii) because it is standard and is based on PDE arguments, namely, the existence and the uniqueness of the solutions in the class of continuous-time functions with values in  $C_b(\mathbb{R}, \sigma)$  (we refer to [139, Lemma 8.6 and 8.7] for further details), and the fact that Assumption 5.A(i) ensures that the initial condition of (5.21) is also matched.

Tightness of the sequence  $\{Q_N\}_{N \in \mathbb{N}}$  follows from the compact containment condition on the one hand, i.e., for any  $\delta > 0$  there exists a compact set  $K \subset M$  such that  $\mathbb{P}_{\mu_N}(\mathbf{X}_i^N \in K) > 1 - \delta$ , and the equi-continuity condition on the other hand, i.e.,  $\limsup_{N \rightarrow \infty} \mathbb{P}_{\mu_N}(\omega(\mathbf{X}_i^N, \delta, T)) \geq \mathbf{e} \leq \mathbf{e}$  for  $\omega(\alpha, \delta, T) := \sup\{d_M(\alpha(s), \alpha(t)) : s, t \in [0, T], |s - t| \leq \delta\}$  and  $T > 0$  with  $d_M$  the metric on Radon measures defined as

$$d_M(\nu_1, \nu_2) := \sum_{j \in \mathbb{N}} 2^{-j} \left( 1 \wedge \left| \int_{\mathbb{R}} \phi_j d\nu_1 - \int_{\mathbb{R}} \phi_j d\nu_2 \right| \right) \quad (5.37)$$

for an appropriately chosen sequence of functions  $(\phi_j)_{j \in \mathbb{N}}$  in  $C_c^\infty(\mathbb{R})$ . We refer to [139, Section A.10] for details on the above metric and to the proof of [139, Lemma 8.5]

for the equi-continuity condition. We conclude by proving the compact containment condition. Define

$$K := \left\{ \nu \in M \text{ s.t. } \exists k \in \mathbb{N} \text{ s.t. } \nu[-\ell, \ell] \leq A(2\ell + 1)\ell^2 \forall \ell \in [k, \infty) \cap \mathbb{N} \right\} \quad (5.38)$$

with  $A > 0$  such that  $\frac{C\pi}{6A} < \epsilon$ . By [139, Proposition A.25], we have that  $K$  is a pre-compact subset of  $M$ . Moreover, by the Markov inequality and Assumption 5.A(ii), it follows that

$$\begin{aligned} Q_N(\bar{K}^c) &\leq \sum_{\ell \in \mathbb{N}} \mathbb{P}_{\mu_N} (\mathbf{X}_i^N([-\ell, \ell]) \geq A(2\ell + 1)\ell^2) \\ &\leq \sum_{\ell \in \mathbb{N}} \frac{1}{A(2\ell + 1)\ell^2} \mathbb{E}_{\mu_N} [\mathbf{X}_i^N([-\ell, \ell])] \\ &= \sum_{\ell \in \mathbb{N}} \frac{1}{A(2\ell + 1)\ell^2} \sum_{x \in [-\ell, \ell] \cap \frac{\mathbb{Z}}{N}} \mathbb{E}_{\mu_N} [\eta_i(x, tN^2)] \\ &\leq \sum_{\ell \in \mathbb{N}} \frac{1}{A(2\ell + 1)\ell^2} \frac{2\ell N + 1}{N} C \\ &\leq \frac{C}{A} \sum_{\ell \in \mathbb{N}} \frac{1}{\ell^2} < \epsilon, \end{aligned} \quad (5.39)$$

from which it follows that  $Q_N(\bar{K}) > 1 - \epsilon$  for any  $N$ . □

**Remark 5.2.2 (Total density).** (i) If  $\rho_0, \rho_1$  are smooth enough and satisfy (5.21), then by taking extra derivatives we see that the total density  $\rho := \rho_0 + \rho_1$  satisfies the *thermal telegrapher equation*

$$\partial_t (\partial_t \rho + 2\Upsilon \rho) = -\epsilon \Delta(\Delta \rho) + (1 + \epsilon) \Delta (\partial_t \rho + \Upsilon \rho), \quad (5.40)$$

which is second order in  $\partial_t$  and fourth order in  $\partial_x$  (see [2, 86] for a derivation). Note that (5.40) shows that the total density does not satisfy the usual diffusion equation. This fact will be investigated in detail in the next section, where we will analyse the non-Fickian property of  $\rho$ .

(ii) If  $\epsilon = 1$ , then the total density  $\rho$  satisfies the *heat equation*  $\partial_t \rho = \Delta \rho$ .

(iii) If  $\epsilon = 0$ , then (5.40) reads

$$\partial_t (\partial_t \rho + 2\Upsilon \rho) = \Delta (\partial_t \rho + \Upsilon \rho), \quad (5.41)$$

which is known as the *strongly damped wave equation*. The term  $\partial_t(2\Upsilon \rho)$  is referred to as frictional damping, the term  $\Delta(\partial_t \rho)$  as Kelvin-Voigt damping (see [29]).

**Remark 5.2.3 (Literature).** We mention in passing that in [99] hydrodynamic scaling of interacting particles with internal states has been considered in a different setting and with a different methodology.

## §5.2.2 Existence, uniqueness and representation of the solution

The existence and uniqueness of a continuous-time solution  $(\rho_0(t), \rho_1(t))$  with values in  $C_b(\mathbb{R}, \sigma)$  of the system in (5.21) can be proved by standard Fourier analysis. Below we recall some known results that have a more probabilistic interpretation.

**Stochastic representation of the solution.** The system in (5.21) fits in the realm of switching diffusions (see e.g. [156]), which are widely studied in the mathematical finance literature. Indeed, let  $\{i_t: t \geq 0\}$  be the pure jump process on state space  $I = \{0, 1\}$  that switches at rate  $\Upsilon$ , whose generator acting on bounded functions  $g: I \rightarrow \mathbb{R}$  is

$$(Ag)(i) := \Upsilon(g(1-i) - g(i)), \quad i \in I. \quad (5.42)$$

Let  $\{X_t: t \geq 0\}$  be the stochastic process on  $\mathbb{R}$  solving the stochastic differential equation

$$dX_t = \psi(i_t) dW_t, \quad (5.43)$$

where  $W_t = B_{2t}$  with  $\{B_t: t \geq 0\}$  standard Brownian motion, and  $\psi: I \rightarrow \{D_0, D_1\}$  is given by

$$\psi := D_0 \mathbf{1}_{\{0\}} + D_1 \mathbf{1}_{\{1\}}, \quad (5.44)$$

with  $D_0 = 1$  and  $D_1 = \epsilon$  in our setting. Let  $\mathcal{L} = \mathcal{L}_{\epsilon, \Upsilon}$  be the generator defined by

$$(\mathcal{L}f)(x, i) := \lim_{t \downarrow 0} \frac{1}{t} \mathbb{E}_{x, i}[f(X_t, i_t) - f(x, i)] \quad (5.45)$$

for  $f: \mathbb{R} \times I \rightarrow \mathbb{R}$  such that  $f(\cdot, i) \in C_0^2(\mathbb{R})$ . Then, via a standard computation (see e.g. [68, Eq.(4.4)]), it follows that

$$\begin{aligned} (\mathcal{L}f)(x, i) &= \psi(i)(\Delta f)(x, i) + \Upsilon[f(x, 1-i) - f(x, i)] \\ &= \begin{cases} \Delta f(x, 0) + \Upsilon[f(x, 1) - f(x, 0)], & i = 0, \\ \epsilon \Delta f(x, 1) + \Upsilon[f(x, 0) - f(x, 1)], & i = 1. \end{cases} \end{aligned} \quad (5.46)$$

We therefore have the following result that corresponds to [68, Chapter 5, Section 4, Theorem 4.1](see also [156, Theorem 5.2]).

**Theorem 5.2.4 (Stochastic representation of the solution).** *Suppose that  $\bar{\rho}_i: \mathbb{R} \rightarrow \mathbb{R}$  for  $i \in I$  are continuous and bounded. Then (5.21) has a unique solution given by*

$$\rho_i(x, t) = \mathbb{E}_{(x, i)}[\bar{\rho}_{i_t}(X_t)], \quad i \in I. \quad (5.47)$$

Note that if there is only one particle in the system (5.2), then we are left with a single random walk, say  $\{Y_t: t \geq 0\}$ , whose generator, denoted by  $\mathbf{A}$ , acts on bounded functions  $f: \mathbb{Z} \times I \rightarrow \mathbb{R}$  as

$$(\mathbf{A}f)(y, i) = \psi(i) \left[ \sum_{z \sim y} [f(z, i) - f(y, i)] \right] + \Upsilon [f(y, 1-i) - f(y, i)]. \quad (5.48)$$

After we apply the generator to the function  $f(y, i) = y$ , we get

$$(Af)(y, i) = 0, \tag{5.49}$$

i.e., the position of the random walk is a martingale. Computing the quadratic variation via the carré du champ, we find

$$A(Y_t^2) = \psi(i_t)[(Y_t + 1)^2 - Y_t^2] + \psi(i_t)[(Y_t - 1)^2 - Y_t^2] = 2\psi(i_t). \tag{5.50}$$

Hence the predictable quadratic variation is given by  $\int_0^t ds 2\psi(i_s)$ . Note that for  $\epsilon = 0$  the latter equals the total amount of time the random walk is not *dormant* up to time  $t$ .

When we diffusively scale the system (scaling the reaction term was done at the beginning of Section 5.2), the quadratic variation becomes

$$\int_0^{tN^2} ds \psi(i_{N,s}) = \int_0^t dr \psi(i_r). \tag{5.51}$$

As a consequence, we have the following invariance principle:

Given the path of the process  $\{i_t : t \geq 0\}$ ,

$$\lim_{N \rightarrow \infty} \frac{Y_{N^2 t}}{N} = W \int_0^t dr \sqrt{\psi(i_r)}, \tag{5.52}$$

where  $W_t = B_{2t}$  with  $\{B_t : t \geq 0\}$  is standard Brownian motion.

Thus, if we knew the path of the process  $\{i_r : r \geq 0\}$ , then we could express the solution of the system in (5.21) in terms of a time-changed Brownian motion. However, even though  $\{i_r : r \geq 0\}$  is a simple flipping process, we cannot say much explicitly about the random time  $\int_0^t dr \sqrt{\psi(i_r)}$ . We therefore look for a simpler formula, where the relation to a Brownian motion with different velocities is more explicit. We achieve this by looking at the resolvent of the generator  $\mathcal{L}$ . In the following, we denote by  $\{S_t, t \geq 0\}$  the semigroup on  $C_b(\mathbb{R})$  of  $\{W_t : t \geq 0\}$ .

**Proposition 5.2.5 (Resolvent).** *Let  $f : \mathbb{R} \times I \rightarrow \mathbb{R}$  be a bounded and smooth function. Then, for  $\lambda > 0$ ,  $\epsilon \in (0, 1]$  and  $i \in I$ ,*

$$\begin{aligned} & (\lambda I - \mathcal{L})^{-1} f(x, i) \\ &= \int_0^\infty dt \frac{1}{\epsilon^2} e^{-\frac{1+\epsilon}{\epsilon} \ell(\Upsilon, \lambda) t} \left[ \cosh(tc_\epsilon(\Upsilon, \lambda)) + \frac{1-\epsilon}{\epsilon} \ell_\epsilon(\Upsilon, \lambda) \frac{\sinh(tc_\epsilon(\Upsilon, \lambda))}{c_\epsilon(\lambda)} \right] (S_t f(\cdot, i))(x) \\ &+ \int_0^\infty dt e^{-\frac{1+\epsilon}{\epsilon} \ell(\Upsilon, \lambda) t} \left[ \frac{\Upsilon}{\epsilon} \sinh(tc_\epsilon(\Upsilon, \lambda)) \right] (S_t f(\cdot, 1 - i))(x), \end{aligned} \tag{5.53}$$

where  $c_\epsilon(\Upsilon, \lambda) = \sqrt{\left(\frac{1-\epsilon}{\epsilon}\right)^2 \ell(\Upsilon, \lambda)^2 + \frac{\Upsilon^2}{\epsilon}}$  and  $\ell(\Upsilon, \lambda) = \frac{\Upsilon + \lambda}{2}$ , while for  $\epsilon = 0$ ,

$$(\lambda I - \mathcal{L})^{-1} f(x, i) = \int_0^\infty dt e^{-\lambda \frac{2\Upsilon + \lambda}{\Upsilon + \lambda} t} \left[ \left(\frac{\Upsilon}{\lambda + \Upsilon}\right)^i (S_t f(\cdot, 0))(x) + \left(\frac{\Upsilon}{\Upsilon + \lambda}\right)^{i+1} (S_t f(\cdot, 1))(x) \right]. \tag{5.54}$$

*Proof.* The proof is split into two parts.

Case  $\epsilon > 0$ . We can split the generator  $\mathcal{L}$  as

$$\mathcal{L} = \psi(i)\tilde{\mathcal{L}} = \psi(i) \left( \Delta + \frac{1}{\psi(i)}A \right) = \psi(i)(\Delta + \tilde{A}), \quad (5.55)$$

i.e., we decouple  $X_t$  and  $i_t$  in the action of the generator. We can now use the Feynman-Kac formula to express the resolvent of the operator  $\mathcal{L}$  in terms of the operator  $\tilde{\mathcal{L}}$ . Denoting by  $\tilde{\mathbb{E}}$  the expectation of the process with generator  $\tilde{\mathcal{L}}$ , we have, for  $\lambda \in \mathbb{R}$ ,

$$\begin{aligned} (\lambda \mathbf{I} - \mathcal{L})^{-1}f(x, i) &= \left( \frac{\lambda \mathbf{I}}{\psi} - \tilde{\mathcal{L}} \right)^{-1} \left( \frac{f(x, i)}{\psi(i)} \right) \\ &= \int_0^\infty dt \tilde{\mathbb{E}}_{(x, i)} \left[ e^{-\int_0^t ds \frac{\lambda}{\psi(i_s)}} \frac{f(X_t, i_t)}{\psi(i_t)} \right], \end{aligned} \quad (5.56)$$

and by the decoupling of  $X_t$  and  $i_t$  under  $\tilde{\mathcal{L}}$ , we get

$$\begin{aligned} (\lambda \mathbf{I} - \mathcal{L})^{-1}f(x, i) &= \int_0^\infty dt \tilde{\mathbb{E}}_i \left[ e^{-\lambda \int_0^t ds \frac{1}{\psi(i_s)}} \frac{\mathbf{1}_{\{0\}}(i_t)}{\psi(i_t)} \right] (S_t f(\cdot, 0))(x) \\ &\quad + \int_0^\infty dt \tilde{\mathbb{E}}_i \left[ e^{-\lambda \int_0^t ds \frac{1}{\psi(i_s)}} \frac{\mathbf{1}_{\{1\}}(i_t)}{\psi(i_t)} \right] (S_t f(\cdot, 1))(x) \\ &= \int_0^\infty dt \tilde{\mathbb{E}}_i \left[ e^{-\lambda \int_0^t ds \frac{1}{\psi(i_s)}} \mathbf{1}_{\{0\}}(i_t) \right] (S_t f(\cdot, 0))(x) \\ &\quad + \frac{1}{\epsilon} \int_0^\infty dt \tilde{\mathbb{E}}_i \left[ e^{-\lambda \int_0^t ds \frac{1}{\psi(i_s)}} \mathbf{1}_{\{1\}}(i_t) \right] (S_t f(\cdot, 1))(x). \end{aligned} \quad (5.57)$$

Defining

$$A := \begin{bmatrix} -\Upsilon & \Upsilon \\ \Upsilon & -\Upsilon \end{bmatrix}, \quad \psi_\epsilon := \begin{bmatrix} 1 & 0 \\ 0 & \epsilon \end{bmatrix}, \quad (5.58)$$

and using again the Feynman-Kac formula, we have

$$(\lambda \mathbf{I} - \mathcal{L})^{-1} \begin{bmatrix} f(x, 0) \\ f(x, 1) \end{bmatrix} = \int_0^\infty dt K_\epsilon(t, \lambda) \begin{bmatrix} (S_t f(\cdot, 0))(x) \\ (S_t f(\cdot, 1))(x) \end{bmatrix} \quad (5.59)$$

with  $K_\epsilon(t, \lambda) = e^{t\psi_\epsilon^{-1}(-\lambda \mathbf{I} + A)}\psi_\epsilon^{-1}$ .

Using the explicit formula for the exponential of a  $2 \times 2$  matrix (see e.g. [8, Corollary 2.4]), we obtain

$$e^{t\psi_\epsilon^{-1}(-\lambda \mathbf{I} + A)} = H \begin{bmatrix} \cosh(tc_\epsilon(\Upsilon, \lambda)) & \frac{\Upsilon \sinh(tc_\epsilon(\Upsilon, \lambda))}{c_\epsilon(\Upsilon, \lambda)} \\ + \frac{(1-\epsilon)\ell(\Upsilon, \lambda) \sinh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon c_\epsilon(\Upsilon, \lambda)} & \\ \frac{\Upsilon \sinh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon c_\epsilon(\Upsilon, \lambda)} & \cosh(tc_\epsilon(\Upsilon, \lambda)) \\ - \frac{(1-\epsilon)\ell(\Upsilon, \lambda) \sinh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon c_\epsilon(\Upsilon, \lambda)} & \end{bmatrix} \quad (5.60)$$

with  $H = e^{-\frac{1+\epsilon}{\epsilon}\ell(\Upsilon, \lambda)t}$ ,  $c_\epsilon(\Upsilon, \lambda) = \sqrt{\left(\frac{1-\epsilon}{\epsilon}\right)^2 \ell(\Upsilon, \lambda)^2 + \frac{\Upsilon^2}{\epsilon}}$  and  $\ell(\Upsilon, \lambda) = \frac{\Upsilon + \lambda}{2}$ , from which we obtain (5.53).

Case  $\epsilon = 0$ . We derive  $K_0(t, \lambda)$  by taking the limit  $\epsilon \downarrow 0$  in the previous expression, i.e.,  $K_0(t, \lambda) = \lim_{\epsilon \downarrow 0} K_\epsilon(t, \lambda)$ . We thus have that  $K_0(t, \lambda)$  is equal to

$$\begin{aligned} \lim_{\epsilon \downarrow 0} H & \begin{bmatrix} \cosh(tc_\epsilon(\Upsilon, \lambda)) + \frac{(1-\epsilon)\ell(\Upsilon, \lambda) \sinh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon c_\epsilon(\Upsilon, \lambda)} & \frac{\Upsilon \sinh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon c_\epsilon(\Upsilon, \lambda)} \\ \frac{\Upsilon \sinh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon c_\epsilon(\Upsilon, \lambda)} & \left( \frac{\cosh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon} - \frac{(1-\epsilon)\ell(\Upsilon, \lambda) \sinh(tc_\epsilon(\Upsilon, \lambda))}{\epsilon^2 c_\epsilon(\Upsilon, \lambda)} \right) \end{bmatrix} \\ & = e^{-\lambda \frac{2\Upsilon + \lambda}{\Upsilon + \lambda} t} \begin{bmatrix} 1 & \frac{\Upsilon}{\Upsilon + \lambda} \\ \frac{\Upsilon}{\Upsilon + \lambda} & \left( \frac{\Upsilon}{\Upsilon + \lambda} \right)^2 \end{bmatrix}, \end{aligned} \quad (5.61)$$

from which (5.54) follows.  $\square$

**Remark 5.2.6 (Symmetric layers).** Note that for  $\epsilon = 1$  we have

$$\begin{aligned} (\lambda \mathbf{I} - \mathcal{L})^{-1} f(x, i) & = \int_0^\infty dt e^{-\lambda t} \left[ \frac{1 + e^{-2\Upsilon t}}{2} (S_t f(\cdot, i))(x) \right. \\ & \quad \left. + \frac{1 - e^{-2\Upsilon t}}{2} (S_t f(\cdot, 1 - i))(x) \right]. \end{aligned} \quad (5.62)$$

We conclude this section by noting that the system in (5.21) was studied in detail in [2, 86]. By taking Fourier and Laplace transforms and inverting them, it is possible to deduce explicitly the solution, which is expressed in terms of solutions to the classical heat equation. More precisely, using formula [86, Eq.2.2], we have that

$$\begin{aligned} \rho_0(x, t) & = e^{-\Upsilon t} (S_t \bar{\rho}_0)(x) + \frac{\Upsilon}{1-\epsilon} e^{-\Upsilon t} \int_{\epsilon t}^t ds \left[ \left( \frac{s-\epsilon t}{t-s} \right)^{\frac{1}{2}} I_1(v(s)) (S_s \bar{\rho}_0)(x) \right. \\ & \quad \left. + I_0(v(s)) (S_s \bar{\rho}_1)(x) \right] \end{aligned} \quad (5.63)$$

and

$$\begin{aligned} \rho_1(x, t) & = e^{-\Upsilon t} (S_{\epsilon t} \bar{\rho}_1)(x) + \frac{\Upsilon}{1-\epsilon} e^{-\Upsilon t} \int_{\epsilon t}^t ds \left[ \left( \frac{s-\epsilon t}{t-s} \right)^{-\frac{1}{2}} I_1(v(s)) (S_s \bar{\rho}_1)(x) \right. \\ & \quad \left. + I_0(v(s)) (S_s \bar{\rho}_0)(x) \right], \end{aligned} \quad (5.64)$$

where  $v(s) = \frac{2\Upsilon}{1-\epsilon} ((t-s)(s-\epsilon t))^{1/2}$ , and  $I_0(\cdot)$  and  $I_1(\cdot)$  are the modified Bessel functions.

## §5.3 The system with boundary reservoirs

In this section we consider a finite version of the switching interacting particle systems introduced in Definition 5.1.1 to which boundary reservoirs are added. Section 5.3.1 defines the model. Section 5.3.2 identifies the dual and the stationary measures. Section 5.3.3 derives the non-equilibrium density profile, both for the microscopic system and the macroscopic system, and offers various simulations. In Section 5.3.4 we compute the stationary horizontal current of slow and fast particles both for the microscopic system and the macroscopic system. Section 5.3.5 shows that in the macroscopic system, for certain choices of the rates, there can be a flow of particles uphill,



i.e., against the gradient imposed by the reservoirs. Thus, as a consequence of the competing driving mechanisms of slow and fast particles, we can have a flow of particles from the side with lower density to the side with higher density.

### §5.3.1 Model

We consider the same system as in Definition 5.1.1, but restricted to  $V := \{1, \dots, N\} \subset \mathbb{Z}$ . In addition, we set  $\hat{V} := V \cup \{L, R\}$  and attach a *left-reservoir* to  $L$  and a *right-reservoir* to  $R$ , both for fast and slow particles. To be more precise, there are four reservoirs (see Fig. 5.2):

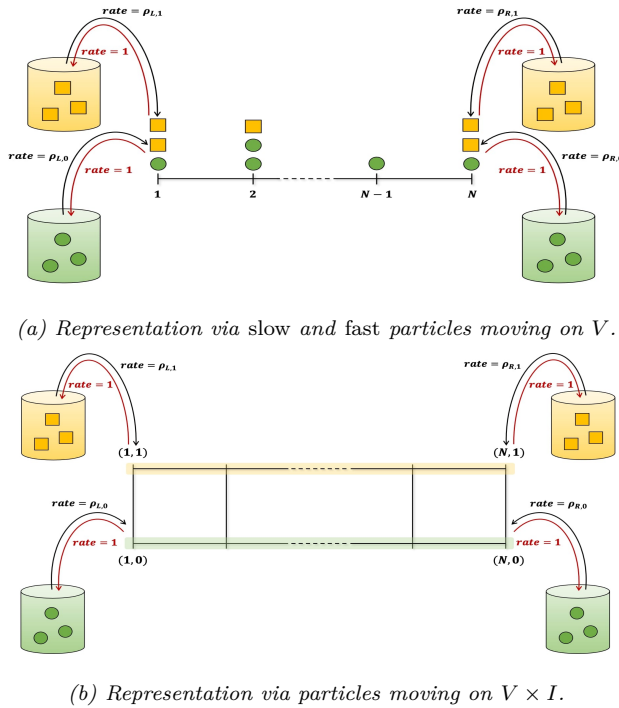


Figure 5.2: Case  $\sigma = 0$ ,  $\epsilon > 0$  with boundary reservoirs: two equivalent representations.

- (i) For the fast particles, a left-reservoir at  $L$  injects fast particles at  $x = 1$  at rate  $\rho_{L,0}(1 + \sigma\eta_0(1, t))$  and a right-reservoir at  $R$  injects fast particles at  $x = N$  at rate  $\rho_{R,0}(1 + \sigma\eta_0(N, t))$ . The left-reservoir absorbs fast particles at rate  $1 + \sigma\rho_{L,0}$ , while the right-reservoir does so at rate  $1 + \sigma\rho_{R,0}$ .
- (ii) For the slow particles, a left-reservoir at  $L$  injects slow particles at  $x = 1$  at rate  $\rho_{L,1}(1 + \sigma\eta_1(1, t))$  and a right-reservoir at  $R$  injects slow particles at  $x = N$  at rate  $\rho_{R,1}(1 + \sigma\eta_1(N, t))$ . The left-reservoir absorbs fast particles at rate  $1 + \sigma\rho_{L,1}$ , while the right-reservoir does so at rate  $1 + \sigma\rho_{R,1}$ .

Inside  $V$ , the particles move as before.

For  $i \in I$ ,  $x \in V$  and  $t \geq 0$ , let  $\eta_i(x, t)$  denote the number of particles in layer  $i$  at site  $x$  at time  $t$ . For  $\sigma \in \{-1, 0, 1\}$ , the Markov process  $\{\eta(t) : t \geq 0\}$  with

$$\eta(t) = \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V} \quad (5.65)$$

has state space

$$\mathcal{X} = \begin{cases} \{0, 1\}^V \times \{0, 1\}^V, & \text{if } \sigma = -1, \\ \mathbb{N}_0^V \times \mathbb{N}_0^V, & \text{if } \sigma \in \{0, 1\}, \end{cases} \quad (5.66)$$

and generator

$$L := L_{\epsilon, \gamma, N} = L^{\text{bulk}} + L^{\text{res}} \quad (5.67)$$

with

$$L^{\text{bulk}} := L_0^{\text{bulk}} + \epsilon L_1^{\text{bulk}} + \gamma L_{0\uparrow 1}^{\text{bulk}} \quad (5.68)$$

acting on bounded cylindrical functions  $f: \mathcal{X} \rightarrow \mathbb{R}$  as

$$\begin{aligned} (L_0^{\text{bulk}} f)(\eta) &= \sum_{x=1}^{N-1} \left\{ \eta_0(x)(1 + \sigma \eta_0(x+1)) [f(\eta_0 - \delta_x + \delta_{x+1}, \eta_1) - f(\eta_0, \eta_1)] \right. \\ &\quad \left. + \eta_0(x+1)(1 + \sigma \eta_0(x)) [f(\eta_0 - \delta_{x+1} + \delta_x, \eta) - f(\eta_0, \eta_1)] \right\}, \\ (L_1^{\text{bulk}} f)(\eta) &= \sum_{x=1}^{N-1} \left\{ \eta_1(x)(1 + \sigma \eta_1(x+1)) [f(\eta_0, \eta_1 - \delta_x + \delta_{x+1}) - f(\eta_0, \eta_1)] \right. \\ &\quad \left. + \eta_1(x+1)(1 + \sigma \eta_1(x)) [f(\eta_0, \eta_1 - \delta_{x+1} + \delta_x) - f(\eta_0, \eta_1)] \right\}, \\ (L_{0\uparrow 1}^{\text{bulk}} f)(\eta) &= \sum_{x=1}^N \left\{ \eta_0(x)(1 + \sigma \eta_1(x)) [f(\eta_0 - \delta_x, \eta_1 + \delta_x) - f(\eta_0, \eta_1)] \right. \\ &\quad \left. + \eta_1(x)(1 + \sigma \eta_0(x)) [f(\eta_0 + \delta_x, \eta_1 - \delta_x) - f(\eta_0, \eta_1)] \right\}, \end{aligned} \quad (5.69)$$

and

$$L^{\text{res}} := L_0^{\text{res}} + L_1^{\text{res}} \quad (5.70)$$

acting as

$$\begin{aligned} (L_0^{\text{res}} f)(\eta) &= \eta_0(1)(1 + \sigma \rho_{L,0}) [f(\eta_0 - \delta_1, \eta_1) - f(\eta_0, \eta_1)] \\ &\quad + \rho_{L,0}(1 + \sigma \eta_0(1)) [f(\eta_0 + \delta_1, \eta_1) - f(\eta_0, \eta_1)] \\ &\quad + \eta_0(N)(1 + \sigma \rho_{R,0}) [f(\eta_0 - \delta_N, \eta_1) - f(\eta_0, \eta_1)] \\ &\quad + \rho_{R,0}(1 + \sigma \eta_0(N)) [f(\eta_0 + \delta_N, \eta) - f(\eta_0, \eta_1)], \end{aligned} \quad (5.71)$$

$$\begin{aligned} (L_1^{\text{res}} f)(\eta) &= \eta_1(1)(1 + \sigma \rho_{L,1}) [f(\eta_0, \eta_1 - \delta_1) - f(\eta_0, \eta_1)] \\ &\quad + \rho_{L,1}(1 + \sigma \eta_1(1)) [f(\eta_0, \eta_1 + \delta_1) - f(\eta_0, \eta_1)] \\ &\quad + \eta_1(N)(1 + \sigma \rho_{R,1}) [f(\eta_0, \eta_1 - \delta_N) - f(\eta_0, \eta_1)] \\ &\quad + \rho_{R,1}(1 + \sigma \rho_{R,N}) [f(\eta_0, \eta_1 + \delta_N) - f(\eta_0, \eta_1)]. \end{aligned} \quad (5.72)$$

### §5.3.2 Duality

In [24] it was shown that the partial exclusion process, a system of independent random walks and the symmetric inclusion processes on a finite set  $V$ , coupled with proper left and right reservoirs, are dual to the same particle system but with the reservoirs replaced by absorbing sites. As remarked in [64], the same result holds for more general geometries, consisting of inhomogeneous rates (site and edge dependent), and for many proper reservoirs. Our model is a particular instance of the case treated in [64, Remark 2.2]), because we can think of the rate as conductances attached to the edges.

More precisely, we consider the system where particles jump on two copies of

$$\hat{V} := V \cup \{L, R\} \quad (5.73)$$

and follow the same dynamics as before in  $V$ , but with the reservoirs at  $L$  and  $R$  absorbing. We denote by  $\xi$  the configuration

$$\xi = (\xi_0, \xi_1) := (\{\xi_0(x)\}_{x \in \hat{V}}, \{\xi_1(x)\}_{x \in \hat{V}}), \quad (5.74)$$

where  $\xi_i(x)$  denotes the number of particles at site  $x$  in layer  $i$ . The state space is  $\hat{\mathcal{X}} = \mathbb{N}_0^{\hat{V}} \times \mathbb{N}_0^{\hat{V}}$ , and the generator is

$$\hat{L} := \hat{L}_{\epsilon, \gamma, N} = \hat{L}^{\text{bulk}} + \hat{L}^{L, R} \quad (5.75)$$

with

$$\hat{L}^{\text{bulk}} := \hat{L}_0^{\text{bulk}} + \epsilon \hat{L}_1^{\text{bulk}} + \gamma \hat{L}_{0\uparrow 1}^{\text{bulk}} \quad (5.76)$$

acting on cylindrical functions  $f: \mathcal{X} \rightarrow \mathbb{R}$  as

$$\begin{aligned} (\hat{L}_0^{\text{bulk}} f)(\xi) &= \sum_{x=1}^{N-1} \left\{ \xi_0(x)(1 + \sigma \xi_0(x+1)) [f(\xi_0 - \delta_x + \delta_{x+1}, \xi_1) - f(\xi_0, \xi_1)] \right. \\ &\quad \left. + \xi_0(x+1)(1 + \sigma \xi_0(x)) [f(\xi_0 - \delta_{x+1} + \delta_x, \xi_1) - f(\xi_0, \xi_1)] \right\}, \\ (\hat{L}_1^{\text{bulk}} f)(\xi) &= \sum_{x=1}^{N-1} \left\{ \xi_1(x)(1 + \sigma \xi_1(x+1)) [f(\xi_0, \xi_1 - \delta_x + \delta_{x+1}) - f(\xi_0, \xi_1)] \right. \\ &\quad \left. + \xi_1(x+1)(1 + \sigma \xi_1(x)) [f(\xi_0, \xi_1 - \delta_{x+1} + \delta_x) - f(\xi_0, \xi_1)] \right\}, \\ (\hat{L}_{0\uparrow 1}^{\text{bulk}} f)(\eta) &= \sum_{x=1}^N \left\{ \xi_0(x)(1 + \sigma \xi_1(x)) [f(\xi_0 - \delta_x, \xi_1 + \delta_x) - f(\xi_0, \xi_1)] \right. \\ &\quad \left. + \xi_1(x)(1 + \sigma \xi_0(x)) [f(\xi_0 + \delta_x, \xi_1 - \delta_x) - f(\xi_0, \xi_1)] \right\}, \end{aligned} \quad (5.77)$$

and

$$\hat{L}^{L, R} = \hat{L}_0^{L, R} + \hat{L}_1^{L, R} \quad (5.78)$$

acting as

$$\begin{aligned} (\hat{L}_0^{L, R} f)(\xi) &= \xi_0(1) [f(\xi_0 - \delta_1, \xi_1) - f(\xi_0, \xi_1)] + \xi_0(N) [f(\xi_0 - \delta_N, \xi_1) - f(\xi_0, \xi_1)], \\ (\hat{L}_1^{L, R} f)(\xi) &= \xi_1(1) [f(\xi_0, \xi_1 - \delta_1) - f(\xi_0, \xi_1)] + \xi_1(N) [f(\xi_0, \xi_1 - \delta_N) - f(\xi_0, \xi_1)]. \end{aligned} \quad (5.79)$$

**Proposition 5.3.1 (Duality, [24, Theorem 4.1] and [64, Proposition 2.3]).**  
*The Markov processes*

$$\begin{aligned} \{\eta(t) : t \geq 0\}, \quad \eta(t) &= \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V}, \\ \{\xi(t) : t \geq 0\}, \quad \xi(t) &= \{\xi_0(x, t), \xi_1(x, t)\}_{x \in \hat{V}}, \end{aligned} \quad (5.80)$$

with generators  $L$  in (5.67) and  $\hat{L}$  in (5.75) are dual. Namely, for all configurations  $\eta \in \mathcal{X}$ ,  $\xi \in \hat{\mathcal{X}}$  and times  $t \geq 0$ ,

$$\mathbb{E}_\eta[D(\xi, \eta_t)] = \mathbb{E}_\xi[D(\xi_t, \eta)], \quad (5.81)$$

where the duality function is given by

$$D(\xi, \eta) := \left( \prod_{i \in I} d_{(L,i)}(\xi_i(L)) \right) \times \left( \prod_{x \in V} d(\xi_i(x), \eta_i(x)) \right) \times \left( \prod_{i \in I} d_{(R,i)}(\xi_i(R)) \right), \quad (5.82)$$

where, for  $k, n \in \mathbb{N}$  and  $i \in I$ ,  $d(\cdot, \cdot)$  is given in (5.12) and

$$d_{(L,i)}(k) = (\rho_{L,i})^k, \quad d_{(R,i)}(k) = (\rho_{R,i})^k. \quad (5.83)$$

The proof boils down to checking that the relation

$$\hat{L}D(\cdot, \eta)(\xi) = LD(\xi, \cdot)(\eta) \quad (5.84)$$

holds for any  $\xi \in \mathcal{X}$  and  $\xi \in \hat{\mathcal{X}}$ , as follows from a rewriting of the proof of [24, Theorem 4.1].

**Remark 5.3.2 (Choice of reservoir rates).** (i) Note that we have chosen the reservoir rates to be 1 both for fast and slow particles. We did this because we view the reservoirs as an external mechanism that injects and absorbs neutral particles, while the particles assume their type as soon as they are in the bulk of the system. In other words, in the present context we view the change of the rate in the two layers as a change of the viscosity properties of the medium in which the particles evolve, instead of a property of the particles themselves.

(ii) If we would tune the reservoir rate of the slow particles to be  $\epsilon$ , then the duality relation mentioned above would still hold, with the difference that the dual system would have  $\epsilon$  as the rate of absorption for the slow particles. This change of the reservoir rates does not affect our results on the non-Fick properties of the model (see Section 5.3.5 below) and on the size of the boundary layer (see Section 5.3.6 below). Indeed, the limiting macroscopic properties we get by changing the rate of the reservoir of the slow particles are the same as the ones we derive later (i.e., the macroscopic boundary-value problem is the same for any choice of reservoir rate). Note that we do not rescale the reservoir rate when we rescale the system to pass from microscopic to macroscopic, which implies that our macroscopic equation has a Dirichlet boundary condition (see (5.132) below).

Also in the context of boundary-driven systems, duality is an essential tool to perform explicit computations. We refer to [97] and [24], where duality for boundary-driven systems was used to compute the stationary profile, by looking at the absorption

probabilities of the dual. This is the approach we will follow in the next section. We remark that, for the inclusion process and for generalizations of the exclusion process, duality is the only available tool to characterize properties of the non-equilibrium steady state (such as the stationary profile), whereas other more direct methods (such as the matrix formulation in e.g. [50]) are not applicable in this setting.

### §5.3.3 Non-equilibrium stationary profile

Also the existence and uniqueness of the non-equilibrium steady state has been established in [64, Theorem 3.3] for general geometries, and the argument in that paper can be easily adapted to our setting.

**Theorem 5.3.3 (Stationary measure, [64, Theorem 3.3(a)]).** *For  $\sigma \in \{-1, 0, 1\}$  there exists a unique stationary measure  $\mu_{\text{stat}}$  for  $\{\eta(t) : t \geq 0\}$ . Moreover, for  $\sigma = 0$  and for any values of  $\{\rho_{L,0}, \rho_{L,1}, \rho_{R,0}, \rho_{R,1}\}$ ,*

$$\mu_{\text{stat}} = \prod_{(x,i) \in V \times I} \nu_{(x,i)}, \quad \nu_{(x,i)} = \text{Poisson}(\theta_{(x,i)}), \quad (5.85)$$

while, for  $\sigma \in \{-1, 1\}$ ,  $\mu_{\text{stat}}$  is in general not in product form, unless  $\rho_{L,0} = \rho_{L,1} = \rho_{R,0} = \rho_{R,1}$ , for which

$$\mu_{\text{stat}} = \prod_{(x,i) \in V \times I} \nu_{(x,i),\theta}, \quad (5.86)$$

where  $\nu_{(x,i),\theta}$  is given in (5.9).

*Proof.* For  $\sigma = -1$ , the existence and uniqueness of the stationary measure is trivial by the irreducibility and the finiteness of the state space of the process. For  $\sigma \in \{0, 1\}$ , recall from [64, Appendix A] that a probability measure  $\mu$  on  $\mathcal{X}$  is said to be tempered if it is characterized by the integrals  $\{\mathbb{E}_\mu[D(\xi, \eta)] : \xi \in \hat{\mathcal{X}}\}$  and that if there exists a  $\theta \in [0, \infty)$  such that  $\mathbb{E}_\mu[D(\xi, \eta)] \leq \theta^{|\xi|}$  for any  $\xi \in \hat{\mathcal{X}}$ . By means of duality we have that, for any  $\eta \in \mathcal{X}$  and  $\xi \in \hat{\mathcal{X}}$ ,

$$\begin{aligned} \lim_{t \rightarrow \infty} \mathbb{E}_\eta[D(\xi, \eta_t)] &= \lim_{t \rightarrow \infty} \hat{\mathbb{E}}_\xi[D(\xi_t, \eta)] \\ &= \sum_{i_0=0}^{|\xi|} \sum_{i_{0,L}=0}^{i_0} \sum_{j_{1,L}=0}^{|\xi|-i_0} \rho_{L,0}^{i_{0,L}} \rho_{R,0}^{i_0-i_{0,L}} \rho_{L,1}^{j_{1,L}} \rho_{R,1}^{|\xi|-i_0-i_{1,L}} \\ &\quad \times \hat{\mathbb{P}}_\xi \left( \xi_\infty = i_{0,L} \delta_{(L,0)} + (i_0 - i_{0,L}) \delta_{(R,0)} \right. \\ &\quad \left. + i_{1,L} \delta_{(L,1)} + (|\xi| - i_0 - i_{1,L}) \delta_{(R,1)} \right), \end{aligned} \quad (5.87)$$

from which we conclude that  $\lim_{t \rightarrow \infty} \mathbb{E}_\eta[D(\xi, \eta_t)] \leq \max\{\rho_{L,0}, \rho_{R,0}, \rho_{L,1}, \rho_{R,1}\}^{|\xi|}$ . Let  $\mu_{\text{stat}}$  be the unique tempered probability measure such that for any  $\xi \in \hat{\mathcal{X}}$ ,  $\mathbb{E}_{\mu_{\text{stat}}}[D(\xi, \eta)]$  coincides with (5.87). From the convergence of the marginal moments in (5.87) we conclude that, for any  $f : \mathcal{X} \rightarrow \mathbb{R}$  bounded and for any  $\eta \in \mathcal{X}$ ,

$$\lim_{t \rightarrow \infty} \mathbb{E}_\eta[f(\eta_t)] = \mathbb{E}_{\mu_{\text{stat}}}[f(\eta)]. \quad (5.88)$$

Thus, a dominated convergence argument yields that for any probability measure  $\mu$  on  $\mathcal{X}$ ,

$$\lim_{t \rightarrow \infty} \mathbb{E}_\mu[f(\eta_t)] = \mathbb{E}_{\mu_{\text{stat}}}[f(\eta)], \quad (5.89)$$

giving that  $\mu_{\text{stat}}$  is the unique stationary measure. The explicit expression in (5.85) and (5.86) follows from similar computations as in [24], while, arguing by contradiction as in the proof of [64, Theorem 3.3], we can show that the two-point truncated correlations are non-zero for  $\sigma \in \{-1, 1\}$  whenever at least two reservoir parameters are different.  $\square$

### Stationary microscopic profile and absorption probability

In this section we provide an explicit expression for the stationary microscopic density of each type of particle. To this end, let  $\mu_{\text{stat}}$  be the unique non-equilibrium stationary measure of the process

$$\{\eta(t) : t \geq 0\}, \quad \eta(t) := \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V}, \quad (5.90)$$

and let  $\{\theta_0(x), \theta_1(x)\}_{x \in V}$  be the stationary microscopic profile, i.e., for  $x \in V$  and  $i \in I$ ,

$$\theta_i(x) = \mathbb{E}_{\mu_{\text{stat}}}[\eta_i(x, t)]. \quad (5.91)$$

Write  $\mathbb{P}_\xi$  (and  $\mathbb{E}_\xi$ ) to denote the law (and the expectation) of the dual Markov process

$$\{\xi(t) : t \geq 0\}, \quad \xi(t) := \{\xi_0(x, t), \xi_1(x, t)\}_{x \in \hat{V}}, \quad (5.92)$$

starting from  $\xi = \{\xi_0(x), \xi_1(x)\}_{x \in \hat{V}}$ . For  $x \in V$ , set

$$\begin{aligned} \vec{p}_x &:= \left[ \hat{p}(\delta_{(x,0)}, \delta_{(L,0)}) \quad \hat{p}(\delta_{(x,0)}, \delta_{(L,1)}) \quad \hat{p}(\delta_{(x,0)}, \delta_{(R,0)}) \quad \hat{p}(\delta_{(x,0)}, \delta_{(R,1)}) \right]^T, \\ \vec{q}_x &:= \left[ \hat{p}(\delta_{(x,1)}, \delta_{(L,0)}) \quad \hat{p}(\delta_{(x,1)}, \delta_{(L,1)}) \quad \hat{p}(\delta_{(x,1)}, \delta_{(R,0)}) \quad \hat{p}(\delta_{(x,1)}, \delta_{(R,1)}) \right]^T, \end{aligned} \quad (5.93)$$

where

$$\begin{aligned} \hat{p}(\xi, \tilde{\xi}) &= \lim_{t \rightarrow \infty} \mathbb{P}_\xi(\xi(t) = \tilde{\xi}), \quad \xi = \delta_{(x,i)} \text{ for some } (x, i) \in V \times I, \\ &\text{and } \tilde{\xi} \in \{\delta_{(L,0)}, \delta_{(L,1)}, \delta_{(R,0)}, \delta_{(R,1)}\}. \end{aligned} \quad (5.94)$$

Further, let us set

$$\vec{\rho} := \left[ \rho_{L,0} \quad \rho_{L,1} \quad \rho_{R,0} \quad \rho_{R,1} \right]^T. \quad (5.95)$$

Note that  $\hat{p}(\delta_{(x,i)}, \cdot)$  is the probability of the dual process, starting from a single particle at site  $x$  at layer  $i \in I$ , of being absorbed at one of the four reservoirs. Using Proposition 5.3.1 and Theorem 5.3.3, we obtain the following.

**Corollary 5.3.4 (Dual representation of stationary profile).** *For  $x \in V$ , the microscopic stationary profile is given by*

$$\begin{aligned} \theta_0(x) &= \vec{p}_x \cdot \vec{\rho}, \\ \theta_1(x) &= \vec{q}_x \cdot \vec{\rho}, \end{aligned} \quad x \in \{1, \dots, N\}, \quad (5.96)$$

where  $\vec{p}_x, \vec{q}_x$  and  $\vec{\rho}$  are as in (5.93)–(5.95).

We next compute the absorption probabilities associated to the dual process in order to obtain a more explicit expression for the stationary microscopic profile

$$\{\theta_0(x), \theta_1(x)\}_{x \in V}.$$

The absorption probabilities  $\hat{p}(\cdot, \cdot)$  of the dual process satisfy

$$(\hat{L}\hat{p})(\cdot, \tilde{\xi})(\xi) = 0 \quad \forall \xi \in \hat{\mathcal{X}}, \quad (5.97)$$

where  $\hat{L}$  is the dual generator defined in (5.75), i.e., they are harmonic functions for the generator  $\hat{L}$ .

In matrix form, the above translates into the following systems of equations:

$$\begin{aligned} \vec{p}_1 &= \frac{1}{2+\gamma} (\vec{p}_0 + \vec{p}_2) + \frac{\gamma}{2+\gamma} \vec{q}_1, \\ \vec{q}_1 &= \frac{\epsilon}{(1+\epsilon)+\gamma} \vec{q}_2 + \frac{1}{(1+\epsilon)+\gamma} \vec{q}_0 + \frac{\gamma}{(1+\epsilon)+\gamma} \vec{p}_1, \\ \vec{p}_x &= \frac{1}{2+\gamma} (\vec{p}_{x-1} + \vec{p}_{x+1}) + \frac{\gamma}{2+\gamma} \vec{q}_x, & x \in \{2, \dots, N-1\}, \\ \vec{q}_x &= \frac{\epsilon}{2\epsilon+\gamma} (\vec{q}_{x-1} + \vec{q}_{x+1}) + \frac{\gamma}{2\epsilon+\gamma} \vec{p}_x, & x \in \{2, \dots, N-1\}, \\ \vec{p}_N &= \frac{1}{2+\gamma} (\vec{p}_{N-1} + \vec{p}_{N+1}) + \frac{\gamma}{2+\gamma} \vec{q}_N, \\ \vec{q}_N &= \frac{\epsilon}{(1+\epsilon)+\gamma} \vec{q}_{N-1} + \frac{1}{(1+\epsilon)+\gamma} \vec{q}_{N+1} + \frac{\gamma}{(1+\epsilon)+\gamma} \vec{p}_N, \end{aligned} \quad (5.98)$$

where

$$\begin{aligned} \vec{p}_0 &:= [1 \ 0 \ 0 \ 0]^T, & \vec{q}_0 &:= [0 \ 1 \ 0 \ 0]^T, \\ \vec{p}_{N+1} &:= [0 \ 0 \ 1 \ 0]^T, & \vec{q}_{N+1} &:= [0 \ 0 \ 0 \ 1]^T. \end{aligned}$$

We divide the analysis of the absorption probabilities into two cases:  $\epsilon = 0$  and  $\epsilon > 0$ .

**Case  $\epsilon = 0$ .**

**Proposition 5.3.5 (Absorption probability for  $\epsilon = 0$ ).** *Consider the dual process*

$$\{\xi(t) : t \geq 0\}, \quad \xi(t) = \{\xi_0(x, t), \xi_1(x, t)\}_{x \in V},$$

*with generator  $\hat{L}_{\epsilon, \gamma, N}$  (see (5.75)) with  $\epsilon = 0$ . Then for the dual process, starting from a single particle, the absorption probabilities  $\hat{p}(\cdot, \cdot)$  (see (5.94)) are given by*

$$\begin{aligned} \hat{p}(\delta_{(x,0)}, \delta_{(L,0)}) &= \frac{1+\gamma}{1+2\gamma} \left( \frac{(1+N)+(1+2N)\gamma}{1+N+2N\gamma} - \frac{1+2\gamma}{1+N+2N\gamma} x \right), \\ \hat{p}(\delta_{(x,0)}, \delta_{(L,1)}) &= \frac{\gamma}{1+2\gamma} \left( \frac{(1+N)+(1+2N)\gamma}{1+N+2N\gamma} - \frac{1+2\gamma}{1+N+2N\gamma} x \right), \\ \hat{p}(\delta_{(x,0)}, \delta_{(R,0)}) &= \frac{1+\gamma}{1+2\gamma} \left( \frac{-\gamma}{1+N+2N\gamma} + \frac{1+2\gamma}{1+N+2N\gamma} x \right), \\ \hat{p}(\delta_{(x,0)}, \delta_{(R,1)}) &= \frac{\gamma}{1+2\gamma} \left( \frac{-\gamma}{1+N+2N\gamma} + \frac{1+2\gamma}{1+N+2N\gamma} x \right), \end{aligned} \quad (5.99)$$

$$\begin{aligned}\hat{p}(\delta_{(1,1)}, \delta_{(L,0)}) &= \frac{\gamma(N-\gamma+2N\gamma)}{(1+2\gamma)(1+N+2N\gamma)}, & \hat{p}(\delta_{(1,1)}, \delta_{(L,1)}) &= \frac{1+N+(1+3N)\gamma-(1-2N)\gamma^2}{(1+2\gamma)(1+N+2N\gamma)}, \\ \hat{p}(\delta_{(1,1)}, \delta_{(R,0)}) &= \frac{\gamma(1+\gamma)}{(1+2\gamma)(1+N+2N\gamma)}, & \hat{p}(\delta_{(1,1)}, \delta_{(R,1)}) &= \frac{\gamma^2}{(1+2\gamma)(1+N+2N\gamma)},\end{aligned}\quad (5.100)$$

and

$$\hat{p}(\delta_{(x,1)}, \delta_{(\beta,i)}) = \hat{p}(\delta_{(x,0)}, \delta_{(\beta,i)}), \quad x \in \{2, \dots, N-1\}, (\beta, i) \in \{L, R\} \times I, \quad (5.101)$$

and

$$\begin{aligned}\hat{p}(\delta_{(N,1)}, \delta_{(L,0)}) &= \hat{p}(\delta_{(1,1)}, \delta_{(R,0)}), & \hat{p}(\delta_{(N,1)}, \delta_{(L,1)}) &= \hat{p}(\delta_{(1,1)}, \delta_{(R,1)}), \\ \hat{p}(\delta_{(N,1)}, \delta_{(R,0)}) &= \hat{p}(\delta_{(1,1)}, \delta_{(L,0)}), & \hat{p}(\delta_{(N,1)}, \delta_{(R,1)}) &= \hat{p}(\delta_{(1,1)}, \delta_{(L,1)}).\end{aligned}\quad (5.102)$$

*Proof.* Note that, for  $\epsilon = 0$ , from the linear system in (5.98) we get

$$\begin{aligned}\vec{p}_{x+1} - \vec{p}_x &= \vec{p}_x - \vec{p}_{x-1}, & x \in \{2, \dots, N-1\}. \\ \vec{q}_x &= \vec{p}_x,\end{aligned}\quad (5.103)$$

Thus, if we set  $\vec{c} = \vec{p}_2 - \vec{p}_1$ , then it suffices to solve the following 4 linear equations with 4 unknowns  $\vec{p}_1, \vec{c}, \vec{q}_1, \vec{q}_N$ :

$$\begin{aligned}\vec{p}_1 &= \frac{1}{2+\gamma} (\vec{p}_0 + \vec{p}_1 + \vec{c}) + \frac{\gamma}{2+\gamma} \vec{q}_1, \\ \vec{q}_1 &= \frac{1}{1+\gamma} \vec{q}_0 + \frac{\gamma}{1+\gamma} \vec{p}_1, \\ \vec{p}_1 + (N-1)\vec{c} &= \frac{1}{2+\gamma} (\vec{p}_1 + (N-2)\vec{c} + \vec{p}_{N+1}) + \frac{\gamma}{2+\gamma} \vec{q}_N, \\ \vec{q}_N &= \frac{1}{1+\gamma} \vec{q}_{N+1} + \frac{\gamma}{1+\gamma} (\vec{p}_1 + (N-1)\vec{c}).\end{aligned}\quad (5.104)$$

Solving the above equations we get the desired result.  $\square$

As a consequence, we obtain the stationary microscopic profile for the original process  $\{\eta(t) : t \geq 0\}$ ,  $\eta(t) = \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V}$  when  $\epsilon = 0$ .

**Theorem 5.3.6 (Stationary microscopic profile for  $\epsilon = 0$ ).**

The stationary microscopic profile  $\{\theta_0(x), \theta_1(x)\}_{x \in V}$  (see (5.91)) for the process  $(\eta(t))_{t \geq 0}$  with  $\eta(t) = \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V}$  and generator  $L_{\epsilon, \gamma, N}$  (see (5.67)) with  $\epsilon = 0$  is given by

$$\begin{aligned}\theta_0(x) &= \frac{1+\gamma}{1+2\gamma} \left[ \left( \frac{(1+N)+(1+2N)\gamma}{1+N+2N\gamma} - \frac{1+2\gamma}{1+N+2N\gamma} x \right) \rho_{L,0} \right. \\ &\quad \left. + \left( \frac{-\gamma}{1+N+2N\gamma} + \frac{1+2\gamma}{1+N+2N\gamma} x \right) \rho_{R,0} \right] \\ &+ \frac{\gamma}{1+2\gamma} \left[ \left( \frac{(1+N)+(1+2N)\gamma}{1+N+2N\gamma} - \frac{1+2\gamma}{1+N+2N\gamma} x \right) \rho_{L,1} \right. \\ &\quad \left. + \left( \frac{-\gamma}{1+N+2N\gamma} + \frac{1+2\gamma}{1+N+2N\gamma} x \right) \rho_{R,1} \right]\end{aligned}\quad (5.105)$$

and

$$\begin{aligned}\theta_1(1) &= \frac{\gamma}{1+\gamma} \theta_0(1) + \frac{1}{1+\gamma} \rho_{L,1}, \\ \theta_1(x) &= \theta_0(x), & x \in \{2, \dots, N-1\}, \\ \theta_1(N) &= \frac{\gamma}{1+\gamma} \theta_0(N) + \frac{1}{1+\gamma} \rho_{R,1}.\end{aligned}\quad (5.106)$$

*Proof.* The proof directly follows from Corollary 5.3.4 and Proposition 5.3.5.  $\square$



**Case  $\epsilon > 0$ .** We next compute the absorption probabilities for the dual process and the stationary microscopic profile for the original process when  $\epsilon > 0$ .

**Proposition 5.3.7 (Absorption probability for  $\epsilon > 0$ ).** *Consider the dual process*

$$\{\xi(t) : t \geq 0\}, \quad \xi(t) = \{\xi_0(x, t), \xi_1(x, t)\}_{x \in V}, \quad (5.107)$$

with the generator  $\hat{L}_{\epsilon, \gamma, N}$  defined in (5.75) for  $\epsilon > 0$ . Let  $\hat{p}(\cdot, \cdot)$  (see (5.94)) be the absorption probabilities of the dual process starting from a single particle, and let  $(\vec{p}_x, \vec{q}_x)_{x \in V}$  be as defined in (5.93). Then

$$\begin{aligned} \vec{p}_x &= \vec{c}_1 x + \vec{c}_2 + \epsilon(\vec{c}_3 \alpha_1^x + \vec{c}_4 \alpha_2^x), \\ \vec{q}_x &= \vec{c}_1 x + \vec{c}_2 - (\vec{c}_3 \alpha_1^x + \vec{c}_4 \alpha_2^x), \end{aligned} \quad x \in V, \quad (5.108)$$

where  $\alpha_1, \alpha_2$  are the two roots of the equation

$$\epsilon \alpha^2 - (\gamma(1 + \epsilon) + 2\epsilon) \alpha + \epsilon = 0, \quad (5.109)$$

and  $\vec{c}_1, \vec{c}_2, \vec{c}_3, \vec{c}_4$  are vectors that depend on the parameters  $N, \epsilon, \alpha_1, \alpha_2$  (see (C.4) for explicit expressions).

*Proof.* Applying the transformation

$$\vec{r}_x := \vec{p}_x + \epsilon \vec{q}_x, \quad \vec{s}_x := \vec{p}_x - \vec{q}_x, \quad (5.110)$$

we see that the system in (5.98) decouples in the bulk (i.e., the interior of  $V$ ), and

$$\vec{r}_x = \frac{1}{2}(\vec{r}_{x+1} + \vec{r}_{x-1}), \quad \vec{s}_x = \frac{\epsilon}{\gamma(1 + \epsilon) + 2\epsilon}(\vec{s}_{x+1} + \vec{s}_{x-1}), \quad x \in \{2, \dots, N-1\}. \quad (5.111)$$

The solution of the above system of recursion equations takes the form

$$\vec{r}_x = \vec{A}_1 x + \vec{A}_2, \quad \vec{s}_x = \vec{A}_3 \alpha_1^x + \vec{A}_4 \alpha_2^x, \quad (5.112)$$

where  $\alpha_1, \alpha_2$  are the two roots of the equation

$$\epsilon \alpha^2 - (\gamma(1 + \epsilon) + 2\epsilon) \alpha + \epsilon = 0. \quad (5.113)$$

Rewriting the four boundary conditions in (5.98) in terms of the new transformations, we get

$$[\vec{A}_1 \quad \vec{A}_2 \quad \vec{A}_3 \quad \vec{A}_4] = (1 + \epsilon)(M_\epsilon^{-1})^T, \quad (5.114)$$

where  $M_\epsilon$  is given by

$$M_\epsilon := \begin{bmatrix} 0 & 1 & \epsilon & \epsilon \\ 1 - \epsilon & 1 & (\epsilon - 1)\alpha_1 - \epsilon & (\epsilon - 1)\alpha_2 - \epsilon \\ N + 1 & 1 & \epsilon \alpha_1^{N+1} & \epsilon \alpha_2^{N+1} \\ N + \epsilon & 1 & -\alpha_1^N(\epsilon \alpha_1 + (1 - \epsilon)) & -\alpha_2^N(\epsilon \alpha_2 + (1 - \epsilon)) \end{bmatrix}. \quad (5.115)$$

Since  $\vec{p}_x = \frac{1}{1 + \epsilon}(\vec{r}_x + \epsilon \vec{s}_x)$  and  $\vec{q}_x = \frac{1}{1 + \epsilon}(\vec{r}_x - \vec{s}_x)$ , by setting

$$\vec{c}_i = \frac{1}{1 + \epsilon} \vec{A}_i, \quad i \in \{1, 2, 3, 4\},$$

we get the desired identities.  $\square$

Without loss of generality, from here onwards, we fix the choices of the roots  $\alpha_1$  and  $\alpha_2$  of the quadratic equation in (5.109) as

$$\begin{aligned}\alpha_1 &= 1 + \frac{\gamma}{2} \left(1 + \frac{1}{\epsilon}\right) - \sqrt{\left[1 + \frac{\gamma}{2} \left(1 + \frac{1}{\epsilon}\right)\right]^2 - 1}, \\ \alpha_2 &= 1 + \frac{\gamma}{2} \left(1 + \frac{1}{\epsilon}\right) + \sqrt{\left[1 + \frac{\gamma}{2} \left(1 + \frac{1}{\epsilon}\right)\right]^2 - 1}.\end{aligned}\tag{5.116}$$

Note that, for any  $\epsilon, \gamma > 0$ , we have

$$\alpha_1 \alpha_2 = 1.\tag{5.117}$$

As a corollary, we get the expression for the stationary microscopic profile of the original process.

**Theorem 5.3.8 (Stationary microscopic profile for  $\epsilon > 0$ ).**

The stationary microscopic profile  $\{\theta_0(x), \theta_1(x)\}_{x \in V}$  (see (5.91)) for the process  $t \mapsto \eta(t)$ ,  $\eta(t) = \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V}$  with generator  $L_{\epsilon, \gamma, N}$  (see (5.67)) with  $\epsilon > 0$  is given by

$$\begin{aligned}\theta_0(x) &= (\vec{c}_1 \cdot \vec{\rho})x + (\vec{c}_2 \cdot \vec{\rho}) + \epsilon(\vec{c}_3 \cdot \vec{\rho})\alpha_1^x + \epsilon(\vec{c}_4 \cdot \vec{\rho})\alpha_2^x, \\ \theta_1(x) &= (\vec{c}_1 \cdot \vec{\rho})x + (\vec{c}_2 \cdot \vec{\rho}) - (\vec{c}_3 \cdot \vec{\rho})\alpha_1^x - (\vec{c}_4 \cdot \vec{\rho})\alpha_2^x,\end{aligned}\quad x \in V,\tag{5.118}$$

where  $(\vec{c}_i)_{1 \leq i \leq 4}$  are as in (C.4), and

$$\vec{\rho} := \left[ \rho_{L,0} \quad \rho_{L,1} \quad \rho_{R,0} \quad \rho_{R,1} \right]^T.$$

*Proof.* The proof follows directly from Corollary 5.3.4 and Proposition 5.3.7.  $\square$

**Remark 5.3.9 (Symmetric layers).** For  $\epsilon = 1$ , the inverse of the matrix  $M_\epsilon$  in the proof of Proposition 5.3.7 takes a simpler form. This is because for  $\epsilon = 1$  the system is fully symmetric. In this case, the explicit expression of the stationary microscopic profile is given by

$$\begin{aligned}\theta_0(x) &= \frac{1}{2} \left( \frac{N+1-x}{N+1} + \frac{\alpha_2^{N+1-x} - \alpha_1^{N+1-x}}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{L,0} + \frac{1}{2} \left( \frac{x}{N+1} + \frac{\alpha_2^x - \alpha_1^x}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{R,0} \\ &\quad + \frac{1}{2} \left( \frac{N+1-x}{N+1} - \frac{\alpha_2^{N+1-x} - \alpha_1^{N+1-x}}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{L,1} + \frac{1}{2} \left( \frac{x}{N+1} - \frac{\alpha_2^x - \alpha_1^x}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{R,1}\end{aligned}\tag{5.119}$$

and

$$\begin{aligned}\theta_1(x) &= \frac{1}{2} \left( \frac{N+1-x}{N+1} - \frac{\alpha_2^{N+1-x} - \alpha_1^{N+1-x}}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{L,0} + \frac{1}{2} \left( \frac{x}{N+1} - \frac{\alpha_2^x - \alpha_1^x}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{R,0} \\ &\quad + \frac{1}{2} \left( \frac{N+1-x}{N+1} + \frac{\alpha_2^{N+1-x} - \alpha_1^{N+1-x}}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{L,1} + \frac{1}{2} \left( \frac{x}{N+1} + \frac{\alpha_2^x - \alpha_1^x}{\alpha_2^{N+1} - \alpha_1^{N+1}} \right) \rho_{R,1}.\end{aligned}\tag{5.120}$$

However, note that

$$\theta_0(x) + \theta_1(x) = 2[(\vec{c}_1 \cdot \vec{\rho})x + (\vec{c}_2 \cdot \vec{\rho})] - (1 - \epsilon)[(\vec{c}_3 \cdot \vec{\rho})\alpha_1^x - (\vec{c}_4 \cdot \vec{\rho})\alpha_2^x],\tag{5.121}$$

which is linear in  $x$  only when  $\epsilon = 1$ , and

$$\theta_0(x) - \theta_1(x) = (1 + \epsilon)[(\vec{c}_3 \cdot \vec{\rho})\alpha_1^x + (\vec{c}_4 \cdot \vec{\rho})\alpha_2^x],\tag{5.122}$$

which is purely exponential in  $x$ .

### Stationary macroscopic profile and boundary-value problem

In this section we rescale the finite-volume system with boundary reservoirs, in the same way as was done for the infinite-volume system in Section 5.2 when we derived the hydrodynamic limit (i.e., space is scaled by  $1/N$  and the switching rate  $\gamma_N$  is scaled such that  $\gamma_N N^2 \rightarrow \Upsilon > 0$ ), and study the validity of Fick's law at stationarity on macroscopic scale. Before we do that, we justify below that the current scaling of the parameters is indeed the proper choice, in the sense that we obtain non-trivial pointwise limits (macroscopic stationary profiles) of the microscopic stationary profiles found in previous sections, and that the resulting limits (when  $\epsilon > 0$ ) satisfy the stationary boundary-value problem given in (5.21) with boundary conditions  $\rho_0^{\text{stat}}(0) = \rho_{L,0}$ ,  $\rho_0^{\text{stat}}(1) = \rho_{R,0}$ ,  $\rho_1^{\text{stat}}(0) = \rho_{L,1}$  and  $\rho_1^{\text{stat}}(1) = \rho_{R,1}$ .

We say that *the macroscopic stationary profiles* are given by functions  $\rho_i^{\text{stat}} : (0, 1) \rightarrow \mathbb{R}$  for  $i \in I$  if, for any  $y \in (0, 1)$ ,

$$\lim_{N \rightarrow \infty} \theta_0^{(N)}(\lceil yN \rceil) = \rho_0^{\text{stat}}(y), \quad \lim_{N \rightarrow \infty} \theta_1^{(N)}(\lceil yN \rceil) = \rho_1^{\text{stat}}(y). \quad (5.123)$$

**Theorem 5.3.10 (Stationary macroscopic profile).** *Let  $(\theta_0^{(N)}(x), \theta_1^{(N)}(x))_{x \in V}$  be the stationary microscopic profile (see (5.91)) for the process  $\{\eta(t) : t \geq 0\}$ ,  $\eta(t) = \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V}$  with generator  $L_{\epsilon, \gamma_N, N}$  (see (5.67)), where  $\gamma_N$  is such that  $\gamma_N N^2 \rightarrow \Upsilon$  as  $N \rightarrow \infty$  for some  $\Upsilon > 0$ . Then, for each  $y \in (0, 1)$ , the pointwise limits (see Fig. 5.3)*

$$\rho_0^{\text{stat}}(y) := \lim_{N \rightarrow \infty} \theta_0^{(N)}(\lceil yN \rceil), \quad \rho_1^{\text{stat}}(y) := \lim_{N \rightarrow \infty} \theta_1^{(N)}(\lceil yN \rceil), \quad (5.124)$$

exist and are given by

$$\begin{aligned} \rho_0^{\text{stat}}(y) &= \rho_{L,0} + (\rho_{R,0} - \rho_{L,0})y, & y \in (0, 1), \\ \rho_1^{\text{stat}}(y) &= \rho_0^{\text{stat}}(y), & y \in (0, 1), \end{aligned} \quad (5.125)$$

when  $\epsilon = 0$ , while

$$\begin{aligned} \rho_0^{\text{stat}}(y) &= \frac{\epsilon}{1+\epsilon} \left[ \frac{\sinh[B_{\epsilon, \Upsilon}(1-y)]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{L,0} - \rho_{L,1}) + \frac{\sinh[B_{\epsilon, \Upsilon}y]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{R,0} - \rho_{R,1}) \right] \\ &\quad + \frac{1}{1+\epsilon} [\rho_{R,0}y + \rho_{L,0}(1-y)] + \frac{\epsilon}{1+\epsilon} [\rho_{R,1}y + \rho_{L,1}(1-y)], \end{aligned} \quad (5.126)$$

$$\begin{aligned} \rho_1^{\text{stat}}(y) &= \frac{1}{1+\epsilon} \left[ \frac{\sinh[B_{\epsilon, \Upsilon}(1-y)]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{L,1} - \rho_{L,0}) + \frac{\sinh[B_{\epsilon, \Upsilon}y]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{R,1} - \rho_{R,0}) \right] \\ &\quad + \frac{1}{1+\epsilon} [\rho_{R,0}y + \rho_{L,0}(1-y)] + \frac{\epsilon}{1+\epsilon} [\rho_{R,1}y + \rho_{L,1}(1-y)], \end{aligned} \quad (5.127)$$

when  $\epsilon > 0$ , where  $B_{\epsilon, \Upsilon} := \sqrt{\Upsilon(1 + \frac{1}{\epsilon})}$ . Moreover, when  $\epsilon > 0$ , the two limits in (5.124) are uniform in  $(0, 1)$ .

*Proof.* For  $\epsilon = 0$ , it easily follows from (5.105) plus the fact that  $\gamma_N N^2 \rightarrow \Upsilon > 0$  and  $\frac{\lceil yN \rceil}{N} \rightarrow y$  uniformly in  $(0, 1)$  as  $N \rightarrow \infty$ , that

$$\lim_{N \rightarrow \infty} \sup_{y \in (0,1)} \left| \theta_0^{(N)}(\lceil yN \rceil) - [\rho_{L,0} + (\rho_{R,0} - \rho_{L,0})y] \right| = 0,$$

and since  $\theta_1(x) = \theta_0(x)$  for all  $x \in \{2, \dots, N-1\}$ , for fixed  $y \in (0, 1)$ , we have

$$\lim_{N \rightarrow \infty} \theta_1^{(N)}(\lceil yN \rceil) = \rho_0^{\text{stat}}(y).$$

When  $\epsilon > 0$ , since  $\gamma_N N^2 \rightarrow \Upsilon > 0$  as  $N \rightarrow \infty$ , we note the following:

$$\begin{aligned} \gamma_N &\xrightarrow{N \rightarrow \infty} 0, \\ \lim_{N \rightarrow \infty} \alpha_1 &= \lim_{N \rightarrow \infty} \alpha_2 = 1, \\ \lim_{N \rightarrow \infty} \alpha_1^N &= e^{-B\epsilon, \Upsilon}, \quad \lim_{N \rightarrow \infty} \alpha_2^N = e^{B\epsilon, \Upsilon}. \end{aligned} \quad (5.128)$$

Consequently, from the expressions of  $(\vec{c}_i)_{1 \leq i \leq 4}$  defined in (C.4), we also have

$$\begin{aligned} \lim_{N \rightarrow \infty} N\vec{c}_1 &= \frac{1}{1+\epsilon} \begin{bmatrix} -1 & -\epsilon & 1 & \epsilon \end{bmatrix}^T, \quad \lim_{N \rightarrow \infty} \vec{c}_2 = \frac{1}{1+\epsilon} \begin{bmatrix} 1 & \epsilon & 0 & 0 \end{bmatrix}^T, \\ \lim_{N \rightarrow \infty} \vec{c}_3 &= \frac{1}{1+\epsilon} \begin{bmatrix} \frac{e^{B\epsilon, \Upsilon}}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} & -\frac{e^{B\epsilon, \Upsilon}}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} & -\frac{1}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} & \frac{1}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} \end{bmatrix}^T, \\ \lim_{N \rightarrow \infty} \vec{c}_4 &= \frac{1}{1+\epsilon} \begin{bmatrix} -\frac{e^{-B\epsilon, \Upsilon}}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} & \frac{e^{-B\epsilon, \Upsilon}}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} & \frac{1}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} & -\frac{1}{e^{B\epsilon, \Upsilon} - e^{-B\epsilon, \Upsilon}} \end{bmatrix}^T. \end{aligned} \quad (5.129)$$

Combining the above equations with (5.118), and the fact that  $\frac{\lceil yN \rceil}{N} \rightarrow y$  uniformly in  $(0, 1)$  as  $N \rightarrow \infty$ , we get the desired result.  $\square$

**Remark 5.3.11 (Non-uniform convergence).** Note that for  $\epsilon > 0$  both stationary macroscopic profiles, when extended continuously to the closed interval  $[0, 1]$ , match the prescribed boundary conditions. This is different from what happens for  $\epsilon = 0$ , where the continuous extension of  $\rho_1^{\text{stat}}$  to the closed interval  $[0, 1]$  equals  $\rho_0^{\text{stat}}(y) = \rho_{L,0} + (\rho_{R,0} - \rho_{L,0})y$ , which does not necessarily match the prescribed boundary conditions unless  $\rho_{L,1} = \rho_{L,0}$  and  $\rho_{R,1} = \rho_{R,0}$ . Moreover, as can be seen from the proof above, for  $\epsilon > 0$ , the convergence of  $\theta_i$  to  $\rho_i$  is uniform in  $[0, 1]$ , i.e.,

$$\begin{aligned} \lim_{N \rightarrow \infty} \sup_{y \in [0,1]} \left| \rho_0^{\text{stat}}(y) - \theta_0^{(N)}(\lceil yN \rceil) \right| &= 0, \\ \lim_{N \rightarrow \infty} \sup_{y \in [0,1]} \left| \rho_1^{\text{stat}}(y) - \theta_1^{(N)}(\lceil yN \rceil) \right| &= 0, \end{aligned} \quad (5.130)$$

while for  $\epsilon = 0$ , the convergence of  $\theta_1$  to  $\rho_1$  is not uniform in  $[0, 1]$  when either  $\rho_{L,0} \neq \rho_{L,1}$  or  $\rho_{R,0} \neq \rho_{R,1}$ . Also, if  $\rho_i^{\text{stat}, \epsilon}(\cdot)$  denotes the macroscopic profile defined in (5.126)–(5.127), then for  $\epsilon > 0$  and  $i \in \{0, 1\}$ , we have

$$\lim_{\epsilon \rightarrow 0} \rho_i^{\text{stat}, \epsilon}(y) \rightarrow \rho_i^{\text{stat}, 0}(y) \quad (5.131)$$

for fixed  $y \in (0, 1)$  and  $i \in \{0, 1\}$ , where  $\rho_i^{\text{stat}, 0}(\cdot)$  is the corresponding macroscopic profile in (5.125) for  $\epsilon = 0$ . However, this convergence is also not uniform for  $i = 1$  when  $\rho_{L,0} \neq \rho_{L,1}$  or  $\rho_{R,0} \neq \rho_{R,1}$ .

In view of the considerations in Remark 5.3.11, we next concentrate on the case  $\epsilon > 0$ . The following result tells us that for  $\epsilon > 0$  the stationary macroscopic profiles satisfy a stationary PDE with fixed boundary conditions and also admit a stochastic representation in terms of an absorbing switching diffusion process.

**Theorem 5.3.12 (Stationary boundary value problem).** *Consider the boundary value problem*

$$\begin{cases} 0 = \Delta u_0 + \Upsilon(u_1 - u_0), \\ 0 = \epsilon \Delta u_1 + \Upsilon(u_0 - u_1), \end{cases} \quad (5.132)$$

with boundary conditions

$$\begin{cases} u_0(0) = \rho_{L,0}, \quad u_0(1) = \rho_{R,0}, \\ u_1(0) = \rho_{L,1}, \quad u_1(1) = \rho_{R,1}, \end{cases} \quad (5.133)$$

where  $\epsilon, \Upsilon > 0$ , and the four boundary parameters  $\rho_{L,0}, \rho_{L,1}, \rho_{R,0}, \rho_{R,1}$  are also positive. Then the PDE admits a unique strong solution given by

$$u_i(y) = \rho_i^{\text{stat}}(y), \quad y \in [0, 1], \quad (5.134)$$

where  $(\rho_0^{\text{stat}}(\cdot), \rho_1^{\text{stat}}(\cdot))$  are as defined in (5.124). Furthermore,  $(\rho_0^{\text{stat}}(\cdot), \rho_1^{\text{stat}}(\cdot))$  has the stochastic representation

$$\rho_i^{\text{stat}}(y) = \mathbb{E}_{(y,i)}[\Phi_{i_\tau}(X_\tau)], \quad (5.135)$$

where  $\{i_t: t \geq 0\}$  is the pure jump process on state space  $I = \{0, 1\}$  that switches at rate  $\Upsilon$ , the functions  $\Phi_0, \Phi_1: I \rightarrow \mathbb{R}_+$  are defined as

$$\Phi_0 = \rho_{L,0} \mathbf{1}_{\{0\}} + \rho_{R,0} \mathbf{1}_{\{1\}}, \quad \Phi_1 = \rho_{L,1} \mathbf{1}_{\{0\}} + \rho_{R,1} \mathbf{1}_{\{1\}},$$

$\{X_t: t \geq 0\}$  is the stochastic process  $[0, 1]$  that satisfies the SDE

$$dX_t = \psi(i_t) dW_t \quad (5.136)$$

with  $W_t = B_{2t}$  and  $\{B_t: t \geq 0\}$  standard Brownian motion, the switching diffusion process  $\{(X_t, i_t): t \geq 0\}$  is killed at the stopping time

$$\tau := \inf\{t \geq 0: X_t \in I\}, \quad (5.137)$$

and  $\psi: I \rightarrow \{1, \epsilon\}$  is given by  $\psi := \mathbf{1}_{\{0\}} + \epsilon \mathbf{1}_{\{1\}}$ .

*Proof.* It is straightforward to verify that for  $\epsilon > 0$  the macroscopic profiles  $\rho_0, \rho_1$  defined in (5.126)–(5.127) are indeed uniformly continuous in  $(0, 1)$  and thus can be uniquely extended continuously to  $[0, 1]$ , namely, by defining  $\rho_i^{\text{stat}}(0) = \rho_{L,i}$ ,  $\rho_i^{\text{stat}}(1) = \rho_{R,i}$  for  $i \in I$ . Also  $\rho_i^{\text{stat}} \in C^\infty([0, 1])$  for  $i \in I$  and satisfy the stationary PDE (5.132), with the boundary conditions specified in (5.133).

The stochastic representation of a solution of the system in (5.132) follows from [68, p385, Eq.(4.7)]. For the sake of completeness, we give the proof of uniqueness of the solution of (5.132). Let  $u = (u_0, u_1)$  and  $v = (v_0, v_1)$  be two solutions of the stationary reaction diffusion equation with the specified boundary conditions in (5.133). Then  $(w_0, w_1) := (u_0 - v_0, u_1 - v_1)$  satisfies

$$\begin{cases} 0 = \Delta w_0 + \Upsilon(w_1 - w_0), \\ 0 = \epsilon \Delta w_1 + \Upsilon(w_0 - w_1), \end{cases} \quad (5.138)$$

with boundary conditions

$$w_0(0) = w_0(1) = w_1(0) = w_1(1) = 0. \quad (5.139)$$

Multiplying the two equations in (5.138) with  $w_0$  and  $w_1$ , respectively, and using the identity

$$w_i \Delta w_i = \nabla \cdot (w_i \nabla w_i) - |\nabla w_i|^2, \quad i \in I,$$

we get

$$\begin{cases} 0 = \nabla \cdot (w_0 \nabla w_0) - |\nabla w_0|^2 + \Upsilon(w_1 - w_0)w_0, \\ 0 = \epsilon \nabla \cdot (w_1 \nabla w_1) - \epsilon |\nabla w_1|^2 + \Upsilon(w_0 - w_1)w_1. \end{cases} \quad (5.140)$$

Integrating both equations by parts over  $[0, 1]$ , we get

$$\begin{aligned} 0 &= -[w_0(1)\nabla w_0(1) - w_0(0)\nabla w_0(0)] - \int_0^1 dy |\nabla w_0(y)|^2 \\ &\quad + \Upsilon \int_0^1 dy (w_1(y) - w_0(y))w_0(y), \\ 0 &= -\epsilon[w_1(1)\nabla w_1(1) - w_1(0)\nabla w_1(0)] - \epsilon \int_0^1 dy |\nabla w_1(y)|^2 \\ &\quad + \Upsilon \int_0^1 dy (w_0(y) - w_1(y))w_1(y). \end{aligned} \quad (5.141)$$

Adding the above two equations and using the zero boundary conditions in (5.139), we have

$$\int_0^1 dy |\nabla w_0(y)|^2 + \epsilon \int_0^1 dy |\nabla w_1(y)|^2 + \Upsilon \int_0^1 dy [w_1(y) - w_0(y)]^2 = 0. \quad (5.142)$$

Since both  $w_0$  and  $w_1$  are continuous and  $\epsilon > 0$ ,  $\Upsilon > 0$ , it follows that

$$w_0 = w_1, \quad \nabla w_0 = \nabla w_1 = 0, \quad (5.143)$$

and so  $w_0 = w_1 \equiv 0$ . □

Note that, as a result of Theorem 5.3.12, the four absorption probabilities of the switching diffusion process  $\{(X_t, i_t) : t \geq 0\}$  starting from  $(y, i) \in [0, 1] \times I$  are indeed the respective coefficients of  $\rho_{L,0}, \rho_{L,1}, \rho_{R,0}, \rho_{R,1}$  appearing in the expression of  $\rho_i^{\text{stat}}(y)$ . Furthermore note that, as a consequence of Theorem 5.3.12 and the results in [86, Section 3], the time-dependent boundary-value problem

$$\begin{cases} \partial_t \rho_0 = \Delta \rho_0 + \Upsilon(\rho_1 - \rho_0), \\ \partial_t \rho_1 = \epsilon \Delta \rho_1 + \Upsilon(\rho_0 - \rho_1), \end{cases} \quad (5.144)$$

with initial conditions

$$\begin{cases} \rho_0(x, 0) = \bar{\rho}_0(x), \\ \rho_1(x, 0) = \bar{\rho}_1(x), \end{cases} \quad (5.145)$$

and boundary conditions

$$\begin{cases} \rho_0(0, t) = \rho_{L,0}, & \rho_0(1, t) = \rho_{R,0}, \\ \rho_1(0, t) = \rho_{L,1}, & \rho_1(1, t) = \rho_{R,1}, \end{cases} \quad (5.146)$$

admits a unique solution given by

$$\begin{cases} \rho_0(x, t) = \rho_0^{\text{hom}}(x, t) + \rho_0^{\text{stat}}(x), \\ \rho_1(x, t) = \rho_1^{\text{hom}}(x, t) + \rho_1^{\text{stat}}(x), \end{cases} \quad (5.147)$$

where

$$\begin{aligned} \rho_0^{\text{hom}}(x, t) &= e^{-\Upsilon t} h_0(x, t) + \frac{\Upsilon}{1-\epsilon} e^{-\Upsilon t} \int_{\epsilon t}^t ds \left[ \left( \frac{s-\epsilon t}{t-s} \right)^{\frac{1}{2}} I_1(v(s)) h_0(x, s) \right. \\ &\quad \left. + I_0(v(s)) h_1(x, s) \right], \\ \rho_1^{\text{hom}}(x, t) &= e^{-\Upsilon t} h_1(x, \epsilon t) + \frac{\Upsilon}{1-\epsilon} e^{-\Upsilon t} \int_{\epsilon t}^t ds \left[ \left( \frac{s-\epsilon t}{t-s} \right)^{-\frac{1}{2}} I_1(v(s)) h_1(x, s) \right. \\ &\quad \left. + I_0(v(s)) h_0(x, s) \right], \end{aligned} \quad (5.148)$$

$v(s) = \frac{2\Upsilon}{1-\epsilon} ((t-s)(s-\epsilon t))^{1/2}$ ,  $I_0(\cdot)$  and  $I_1(\cdot)$  are the modified Bessel functions,  $h_0(x, t)$ ,  $h_1(x, t)$  are the solutions of

$$\begin{cases} \partial_t h_0 = \Delta h_0, \\ \partial_t h_1 = \Delta h_1, \\ h_0(x, 0) = \bar{\rho}_0(x) - \rho_0^{\text{stat}}(x), \\ h_1(x, 1) = \bar{\rho}_1(x) - \rho_1^{\text{stat}}(x), \\ h_0(0, t) = h_0(1, t) = h_1(0, t) = h_1(1, t) = 0, \end{cases} \quad (5.149)$$

and  $\rho_0^{\text{stat}}(x)$ ,  $\rho_1^{\text{stat}}(x)$  are given in (5.127).

We conclude this section by proving that the solution of the time-dependent boundary-value problem in (5.144) converges to the stationary profile in (5.127).

**Proposition 5.3.13 (Convergence to stationary profile).** *Let  $\rho_0^{\text{hom}}(x, t)$  and  $\rho_1^{\text{hom}}(x, t)$  be as in (5.148), i.e., the solutions of the boundary-value problem (5.144) with zero boundary conditions and initial conditions given by  $\rho_0^{\text{hom}}(x, 0) = \bar{\rho}_0(x) - \rho_0^{\text{stat}}(x)$  and  $\rho_1^{\text{hom}}(x, 0) = \bar{\rho}_1(x) - \rho_1^{\text{stat}}(x)$ . Then, for any  $k \in \mathbb{N}$ ,*

$$\lim_{t \rightarrow \infty} \left[ \|\rho_0^{\text{hom}}(x, t)\|_{C^k(0,1)} + \|\rho_1^{\text{hom}}(x, t)\|_{C^k(0,1)} \right] = 0.$$

*Proof.* We start by showing that

$$\lim_{t \rightarrow \infty} \left[ \|\rho_0^{\text{hom}}(x, t)\|_{L^2(0,1)} + \|\rho_1^{\text{hom}}(x, t)\|_{L^2(0,1)} \right] = 0. \quad (5.150)$$

Multiply the first equation of (5.144) by  $\rho_0$  and the second equation by  $\rho_1$ . Integration by parts yields

$$\begin{cases} \partial_t \left( \int_0^1 dx \rho_0^2 \right) = - \int_0^1 dx |\partial_x \rho_0|^2 + \Upsilon \int_0^1 dx (\rho_1 \rho_0 - \rho_0^2), \\ \partial_t \left( \int_0^1 dx \rho_1^2(x, t) \right) = -\epsilon \int_0^1 dx |\partial_x \rho_1|^2 + \Upsilon \int_0^1 dx (\rho_0 \rho_1 - \rho_1^2). \end{cases} \quad (5.151)$$

Summing the two equations and defining  $E(t) := \int_0^1 dx (\rho_0(x,t)^2 + \rho_1(x,t)^2)$ , we obtain

$$\partial_t E(t) = - \left( \int_0^1 dx |\partial_x \rho_0|^2 + \epsilon \int_0^1 dx |\partial_x \rho_1|^2 \right) - \Upsilon \int_0^1 dx (\rho_0 - \rho_1)^2. \quad (5.152)$$

By the Poincaré inequality (i.e.,  $\int_0^1 dx |\partial_x \rho_i(x,t)|^2 \geq C_p \int_0^1 dx |\rho_i(x,t)|^2$ , with  $C_p > 0$ ) we have  $\partial_t E(t) \leq -\epsilon C_p E(t)$ , from which we obtain

$$E(t) \leq e^{-C_p t} E(0),$$

and hence (5.150).

From [132, Theorem 2.1] it follows that

$$A := \begin{bmatrix} \Delta - \Upsilon & \Upsilon \\ \Upsilon & \epsilon \Delta - \Upsilon \end{bmatrix},$$

with domain  $D(A) = H^2(0,1) \cap H_0^1(0,1)$ , generates a semigroup  $\{\mathcal{S}_t : t \geq 0\}$ . If we set  $\vec{\rho}(t) = \mathcal{S}_t(\vec{\rho}^{\text{hom}})$ , with  $\vec{\rho}^{\text{hom}} = \vec{\rho} - \vec{\rho}^{\text{stat}}$ , then by the semigroup property we have

$$\vec{\rho}(t) = \mathcal{S}_{t-1}(\mathcal{S}_{1/k})^k(\vec{\rho}^{\text{hom}}), \quad t \geq 1,$$

and hence  $A^k \vec{\rho}(t) = \mathcal{S}_{t-1}(A \mathcal{S}_{1/k})^k(\vec{\rho}^{\text{hom}})$ . If we set  $\vec{p} := (A \mathcal{S}_{1/k})^k(\vec{\rho}^{\text{hom}})$ , then we obtain, by [132, Theorem 5.2(d)],

$$\|A^k \vec{\rho}(t)\|_{L^2(0,1)} \leq \|\mathcal{S}_{t-1} \vec{p}\|_{L^2(0,1)},$$

where  $\lim_{t \rightarrow \infty} \|\mathcal{S}_{t-1} \vec{p}\|_{L^2(0,1)} = 0$  by the first part of the proof. The compact embedding

$$D(A^k) \hookrightarrow H^{2k}(0,1) \hookrightarrow C^k(0,1), \quad k \in \mathbb{N},$$

concludes the proof.  $\square$

## §5.3.4 The stationary current

In this section we compute the expected current in the non-equilibrium steady state that is induced by different densities at the boundaries. We consider the microscopic and macroscopic systems, respectively.

**Microscopic system.** We start by defining the notion of current. The microscopic currents are associated with the edges of the underlying two-layer graph. In our setting, we denote by  $\mathcal{J}_{x,x+1}^0(t)$  and  $\mathcal{J}_{x,x+1}^1(t)$  the instantaneous current through the horizontal edge  $(x, x+1)$ ,  $x \in V$ , of the bottom layer, respectively, top layer at time  $t$ . Obviously,

$$\mathcal{J}_{x,x+1}^0(t) = \eta_0(x,t) - \eta_0(x+1,t), \quad \mathcal{J}_{x,x+1}^1(t) = \epsilon[\eta_1(x,t) - \eta_1(x+1,t)]. \quad (5.153)$$

We are interested in the stationary currents  $J_{x,x+1}^0$ , respectively,  $J_{x,x+1}^1$ , which are obtained as

$$J_{x,x+1}^0 = \mathbb{E}_{\text{stat}}[\eta_0(x) - \eta_0(x+1)], \quad J_{x,x+1}^1 = \epsilon \mathbb{E}_{\text{stat}}[\eta_1(x) - \eta_1(x+1)], \quad (5.154)$$



where  $\mathbb{E}_{\text{stat}}$  denotes expectation w.r.t. the unique invariant probability measure of the microscopic system  $\{\eta(t) : t \geq 0\}$  with  $\eta(t) = \{\eta_0(x, t), \eta_1(x, t)\}_{x \in V}$ . In other words,  $J_{x,x+1}^0$  and  $J_{x,x+1}^1$  give the average flux of particles of type 0 and type 1 across the bond  $(x, x+1)$  due to diffusion.

Of course, the average number of particle at each site varies in time also as a consequence of the reaction term:

$$\begin{aligned} \frac{d}{dt} \mathbb{E}[\eta_0(x, t)] &= \mathbb{E}[\mathcal{J}_{x-1,x}^0(t) - \mathcal{J}_{x,x+1}^0(t)] + \gamma(\mathbb{E}[\eta_1(x, t)] - \mathbb{E}[\eta_0(x, t)]), \\ \frac{d}{dt} \mathbb{E}[\eta_1(x, t)] &= \mathbb{E}[\mathcal{J}_{x-1,x}^1(t) - \mathcal{J}_{x,x+1}^1(t)] + \gamma(\mathbb{E}[\eta_0(x, t)] - \mathbb{E}[\eta_1(x, t)]). \end{aligned} \quad (5.155)$$

Summing these equations, we see that there is no contribution of the reaction part to the variation of the average number of particles at site  $x$ :

$$\frac{d}{dt} \mathbb{E}[\eta_0(x, t) + \eta_1(x, t)] = \mathbb{E}[\mathcal{J}_{x-1,x}(t) - \mathcal{J}_{x,x+1}(t)]. \quad (5.156)$$

The sum

$$J_{x,x+1} = J_{x,x+1}^0 + J_{x,x+1}^1, \quad (5.157)$$

with  $J_{x,x+1}^0$  and  $J_{x,x+1}^1$  defined in (5.154), will be called the *stationary current* between sites at  $x, x+1$ ,  $x \in V$ , which is responsible for the variation of the total average number of particles at each site, regardless of their type.

**Proposition 5.3.14 (Stationary microscopic current).** *For  $x \in \{2, \dots, N-1\}$  the stationary currents defined in (5.154) are given by*

$$J_{x,x+1}^0 = -\frac{1+\gamma}{1+N+2N\gamma}[\rho_{R,0} - \rho_{L,0}] - \frac{\gamma}{1+N+2N\gamma}[\rho_{R,1} - \rho_{L,1}], \quad J_{x,x+1}^1 = 0, \quad (5.158)$$

when  $\epsilon = 0$  and by

$$\begin{aligned} J_{x,x+1}^0 &= -\vec{c}_1 \cdot \vec{\rho} - \epsilon[(\vec{c}_3 \cdot \vec{\rho})\alpha_1^x(\alpha_1 - 1) + (\vec{c}_4 \cdot \vec{\rho})\alpha_2^x(\alpha_2 - 1)], \\ J_{x,x+1}^1 &= -\epsilon\vec{c}_1 \cdot \vec{\rho} + \epsilon[(\vec{c}_3 \cdot \vec{\rho})\alpha_1^x(\alpha_1 - 1) + (\vec{c}_4 \cdot \vec{\rho})\alpha_2^x(\alpha_2 - 1)], \end{aligned} \quad (5.159)$$

when  $\epsilon > 0$ , where  $\vec{c}_1, \vec{c}_3, \vec{c}_4$  are the vectors defined in (C.4) of Appendix C, and  $\alpha_1, \alpha_2$  are defined in (5.116). As a consequence, the current  $J_{x,x+1} = J_{x,x+1}^0 + J_{x,x+1}^1$  is independent of  $x$  and is given by

$$J_{x,x+1} = -\frac{1+\gamma}{1+N+2N\gamma}[\rho_{R,0} - \rho_{L,0}] - \frac{\gamma}{1+N+2N\gamma}[\rho_{R,1} - \rho_{L,1}] \quad (5.160)$$

when  $\epsilon = 0$  and

$$J_{x,x+1} = -(1 + \epsilon)[C_1(\rho_{R,0} - \rho_{L,0}) + \epsilon C_2(\rho_{R,1} - \rho_{L,1})] \quad (5.161)$$

when  $\epsilon > 0$ , where

$$\begin{aligned} C_1 &= \frac{[\alpha_1(1-\epsilon)(\alpha_1^{N-1}-1) + \epsilon(\alpha_1^{N+1}-1)]}{\alpha_1(1-\epsilon)(\alpha_1^{N-1}-1)(N+1) + 2\epsilon(\alpha_1^{N+1}-1)(N+\epsilon)}, \\ C_2 &= \frac{(\alpha_1^{N+1}-1)}{\alpha_1(1-\epsilon)(\alpha_1^{N-1}-1)(N+1) + 2\epsilon(\alpha_1^{N+1}-1)(N+\epsilon)}. \end{aligned} \quad (5.162)$$

*Proof.* From (5.154) we have

$$J_{x,x+1}^0 = \theta_0(x) - \theta_0(x+1), \quad J_{x,x+1}^1 = \epsilon[\theta_1(x) - \theta_1(x+1)], \quad (5.163)$$

where  $\theta_0(\cdot), \theta_1(\cdot)$  are the average microscopic profiles. Thus, when  $\epsilon = 0$ , the expressions of  $J_{x,x+1}^0, J_{x,x+1}^1$  and consequently  $J_{x,x+1}$  follow directly from (5.105).

For  $\epsilon > 0$ , using the expressions of  $\theta_0(\cdot), \theta_1(\cdot)$  in (5.118), we see that

$$\begin{aligned} J_{x,x+1}^0 &= \theta_0(x) - \theta_0(x+1) = -\vec{c}_1 \cdot \vec{\rho} - \epsilon[(\vec{c}_3 \cdot \vec{\rho})\alpha_1^x(\alpha_1 - 1) + (\vec{c}_4 \cdot \vec{\rho})\alpha_2^x(\alpha_2 - 1)], \\ J_{x,x+1}^1 &= \epsilon[\theta_1(x) - \theta_1(x+1)] = -\epsilon\vec{c}_1 \cdot \vec{\rho} + \epsilon[(\vec{c}_3 \cdot \vec{\rho})\alpha_1^x(\alpha_1 - 1) + (\vec{c}_4 \cdot \vec{\rho})\alpha_2^x(\alpha_2 - 1)], \end{aligned} \quad (5.164)$$

where  $\vec{c}_1, \vec{c}_3, \vec{c}_4$  are the vectors defined in (C.4) of Appendix C, and  $\alpha_1, \alpha_2$  are defined in (5.116). Adding the two equations, we also have

$$J_{x,x+1} = J_{x,x+1}^0 + J_{x,x+1}^1 = -(1+\epsilon)\vec{c}_1 \cdot \vec{\rho} = (1+\epsilon)[C_1(\rho_{R,0} - \rho_{L,0}) + \epsilon C_2(\rho_{R,1} - \rho_{L,1})], \quad (5.165)$$

where  $C_1, C_2$  are as in (5.162).  $\square$

**Macroscopic system.** The microscopic current scales like  $1/N$ . Indeed, the currents associated to the two layers in the macroscopic system can be obtained from the microscopic currents, respectively, by defining

$$J^0(y) = \lim_{N \rightarrow \infty} N J_{[yN], [yN]+1}^0, \quad J^1(y) = \lim_{N \rightarrow \infty} N J_{[yN], [yN]+1}^1. \quad (5.166)$$

Below we justify the existence of the two limits and thereby provide explicit expressions for the macroscopic currents.

**Proposition 5.3.15 (Stationary macroscopic current).** *For  $y \in (0, 1)$  the stationary currents defined in (5.166) are given by*

$$J^0(y) = -[(\rho_{R,0} - \rho_{L,0})], \quad J^1(y) = 0, \quad (5.167)$$

when  $\epsilon = 0$  and by

$$\begin{aligned} J^0(y) &= \frac{\epsilon B_{\epsilon, \Upsilon}}{1+\epsilon} \left[ \frac{\cosh[B_{\epsilon, \Upsilon}(1-y)]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{L,0} - \rho_{L,1}) - \frac{\cosh[B_{\epsilon, \Upsilon} y]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{R,0} - \rho_{R,1}) \right] \\ &\quad - \frac{1}{1+\epsilon} [(\rho_{R,0} - \rho_{L,0}) + \epsilon(\rho_{R,1} - \rho_{L,1})] \end{aligned} \quad (5.168)$$

and

$$\begin{aligned} J^1(y) &= -\frac{\epsilon B_{\epsilon, \Upsilon}}{1+\epsilon} \left[ \frac{\cosh[B_{\epsilon, \Upsilon}(1-y)]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{L,0} - \rho_{L,1}) - \frac{\cosh[B_{\epsilon, \Upsilon} y]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{R,0} - \rho_{R,1}) \right] \\ &\quad - \frac{\epsilon}{1+\epsilon} [(\rho_{R,0} - \rho_{L,0}) + \epsilon(\rho_{R,1} - \rho_{L,1})] \end{aligned} \quad (5.169)$$

when  $\epsilon > 0$ . As a consequence, the total current  $J(y) = J^0(y) + J^1(y)$  is constant and is given by

$$J(y) = -[(\rho_{R,0} - \rho_{L,0}) + \epsilon(\rho_{R,1} - \rho_{L,1})]. \quad (5.170)$$

*Proof.* For  $\epsilon = 0$  the claim easily follows from the expressions of  $J_{x,x+1}^0, J_{x,x+1}^1$  given in (5.158) and the fact that  $\gamma_N \rightarrow 0$  as  $N \rightarrow \infty$ .

When  $\epsilon > 0$ , we first note the following:

$$\begin{aligned} \gamma_N N^2 &\xrightarrow{N \rightarrow \infty} \Upsilon > 0, \\ \lim_{N \rightarrow \infty} \alpha_1 &= \lim_{N \rightarrow \infty} \alpha_2 = 1, \\ \lim_{N \rightarrow \infty} N(\alpha_1 - 1) &= -B_{\epsilon, \Upsilon}, \quad \lim_{N \rightarrow \infty} N(\alpha_2 - 1) = B_{\epsilon, \Upsilon}, \\ \lim_{N \rightarrow \infty} \alpha_1^N &= e^{-B_{\epsilon, \Upsilon}}, \quad \lim_{N \rightarrow \infty} \alpha_2^N = e^{B_{\epsilon, \Upsilon}}. \end{aligned} \tag{5.171}$$

Consequently, from the expressions for  $(\vec{c}_i)_{1 \leq i \leq 4}$  defined in (C.4), we also have

$$\begin{aligned} \lim_{N \rightarrow \infty} N\vec{c}_1 &= \frac{1}{1+\epsilon} \begin{bmatrix} -1 & -\epsilon & 1 & \epsilon \end{bmatrix}^T, \\ \lim_{N \rightarrow \infty} \vec{c}_3 &= \frac{1}{1+\epsilon} \begin{bmatrix} \frac{e^{B_{\epsilon, \Upsilon}}}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} & -\frac{e^{B_{\epsilon, \Upsilon}}}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} & -\frac{1}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} & \frac{1}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} \end{bmatrix}^T, \\ \lim_{N \rightarrow \infty} \vec{c}_4 &= \frac{1}{1+\epsilon} \begin{bmatrix} -\frac{e^{-B_{\epsilon, \Upsilon}}}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} & \frac{e^{-B_{\epsilon, \Upsilon}}}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} & \frac{1}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} & -\frac{1}{e^{B_{\epsilon, \Upsilon}} - e^{-B_{\epsilon, \Upsilon}}} \end{bmatrix}^T. \end{aligned} \tag{5.172}$$

Combining the above equations with (5.159), we have

$$\begin{aligned} J^0(y) &= \lim_{N \rightarrow \infty} NJ_{[yN], [yN]+1}^0 \\ &= -\epsilon B_{\epsilon, \Upsilon} \left[ \left( \lim_{N \rightarrow \infty} \vec{c}_4 \cdot \vec{\rho} \right) e^{B_{\epsilon, \Upsilon} y} - \left( \lim_{N \rightarrow \infty} \vec{c}_3 \cdot \vec{\rho} \right) e^{-B_{\epsilon, \Upsilon} y} \right] - \left( \lim_{N \rightarrow \infty} N\vec{c}_1 \cdot \vec{\rho} \right) \\ &= \frac{\epsilon B_{\epsilon, \Upsilon}}{1+\epsilon} \left[ \frac{\cosh[B_{\epsilon, \Upsilon}(1-y)]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{L,0} - \rho_{L,1}) - \frac{\cosh[B_{\epsilon, \Upsilon} y]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{R,0} - \rho_{R,1}) \right] \\ &\quad - \frac{1}{1+\epsilon} \left[ (\rho_{R,0} - \rho_{L,0}) + \epsilon(\rho_{R,1} - \rho_{L,1}) \right] \end{aligned} \tag{5.173}$$

and, similarly,

$$\begin{aligned} J^1(y) &= \lim_{N \rightarrow \infty} NJ_{[yN], [yN]+1}^1 \\ &= \epsilon B_{\epsilon, \Upsilon} \left[ \left( \lim_{N \rightarrow \infty} \vec{c}_4 \cdot \vec{\rho} \right) e^{B_{\epsilon, \Upsilon} y} - \left( \lim_{N \rightarrow \infty} \vec{c}_3 \cdot \vec{\rho} \right) e^{-B_{\epsilon, \Upsilon} y} \right] - \epsilon \left( \lim_{N \rightarrow \infty} N\vec{c}_1 \cdot \vec{\rho} \right) \\ &= -\frac{\epsilon B_{\epsilon, \Upsilon}}{1+\epsilon} \left[ \frac{\cosh[B_{\epsilon, \Upsilon}(1-y)]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{L,0} - \rho_{L,1}) - \frac{\cosh[B_{\epsilon, \Upsilon} y]}{\sinh[B_{\epsilon, \Upsilon}]} (\rho_{R,0} - \rho_{R,1}) \right] \\ &\quad - \frac{\epsilon}{1+\epsilon} \left[ (\rho_{R,0} - \rho_{L,0}) + \epsilon(\rho_{R,1} - \rho_{L,1}) \right]. \end{aligned} \tag{5.174}$$

Adding  $J^0(y)$  and  $J^1(y)$ , we obtain the total current

$$J(y) = J^0(y) + J^1(y) = -[(\rho_{R,0} - \rho_{L,0}) + \epsilon(\rho_{R,1} - \rho_{L,1})], \tag{5.175}$$

which is indeed independent of  $y$ .  $\square$

**Remark 5.3.16 (Currents).** Combining the expressions for the density profiles and the current, we see that

$$J^0(y) = -\frac{d\rho_0}{dy}(y), \quad J^1(y) = -\epsilon \frac{d\rho_1}{dy}(y). \tag{5.176}$$

### §5.3.5 Discussion: Fick's law and uphill diffusion

In this section we discuss the behaviour of the boundary-driven system as the parameter  $\epsilon$  is varied. For simplicity we restrict our discussion to the macroscopic setting, although similar comments hold for the microscopic system as well.

In view of the previous results, we can rewrite the equations for the densities  $\rho_0(y, t), \rho_1(y, t)$  as

$$\begin{cases} \partial_t \rho_0 = -\nabla J^0 + \Upsilon(\rho_1 - \rho_0), \\ \partial_t \rho_1 = -\nabla J^1 + \Upsilon(\rho_0 - \rho_1), \\ J_0 = -\nabla \rho_0, \\ J_1 = -\epsilon \nabla \rho_1, \end{cases} \quad (5.177)$$

which are complemented with the boundary values (for  $\epsilon > 0$ )

$$\begin{cases} \rho_0(0, t) = \rho_{L,0}, \quad \rho_0(1, t) = \rho_{R,0}, \\ \rho_1(0, t) = \rho_{L,1}, \quad \rho_1(1, t) = \rho_{R,1}. \end{cases} \quad (5.178)$$

We will be concerned with the total density  $\rho = \rho_0 + \rho_1$ , whose evolution equation does not contain the reaction part, and is given by

$$\begin{cases} \partial_t \rho = -\nabla J, \\ J = -\nabla(\rho_0 + \epsilon \rho_1), \end{cases} \quad (5.179)$$

with boundary values

$$\begin{cases} \rho(0, t) = \rho_L = \rho_{L,0} + \rho_{R,0}, \\ \rho(1, t) = \rho_R = \rho_{R,0} + \rho_{R,1}. \end{cases} \quad (5.180)$$

**Non-validity of Fick's law.** From (5.179) we immediately see that Fick's law of mass transport is satisfied if and only if  $\epsilon = 1$ . When we allow diffusion and reaction of slow and fast particles, i.e.,  $0 \leq \epsilon < 1$ , Fick's law breaks down, since the current associated to the total mass is not proportional to the gradient of the total mass. Rather, the current  $J$  is the sum of a contribution  $J^0$  due to the diffusion of fast particles of type 0 (at rate 1) and a contribution  $J^1$  due to the diffusion of slow particles of type 1 (at rate  $\epsilon$ ). Interestingly, the violation of Fick's law opens up the possibility of several interesting phenomena that we discuss in what follows.

**Equal boundary densities with non-zero current.** In a system with diffusion and reaction of slow and fast particles we may observe a *non-zero current when the total density has the same value at the two boundaries*. This is different from what is observed in standard diffusive systems driven by boundary reservoirs, where in order to have a stationary current it is necessary that the reservoirs have different chemical potentials, and therefore different densities, at the boundaries.

Let us, for instance, consider the specific case when  $\rho_{L,0} = \rho_{R,1} = 2$  and  $\rho_{L,1} = \rho_{R,0} = 4$ , which indeed implies equal densities at the boundaries given by  $\rho_L = \rho_R = 6$ . The density profiles and currents are displayed in Fig. 5.3 for two values of  $\epsilon$ , which

shows the comparison between the Fick-regime  $\epsilon = 1$  (left panels) and the non-Fick-regime with very slow particles  $\epsilon = 0.001$  (right panels).

On the one hand, in the Fick-regime the profile of both types of particles interpolates between the boundary values, with a slightly non-linear shape that has been quantified precisely in (5.126)–(5.127). Furthermore, in the same regime  $\epsilon = 1$ , the total density profile is flat and the total current  $J$  vanishes because  $J^0(y) = -J^1(y)$  for all  $y \in [0, 1]$ .

On the other hand, in the non-Fick-regime with  $\epsilon = 0.001$ , the stationary macroscopic profile for the fast particles interpolates between the boundary values almost linearly (see (5.131)), whereas the profile for the slow particles is non-monotone: it has two bumps at the boundaries and in the bulk closely follows the other profile. This non-monotonicity in the profile of the slow particles is due to the non-uniform convergence in the limit  $\epsilon \downarrow 0$ , as pointed out in the last part of Remark 5.3.11. As a

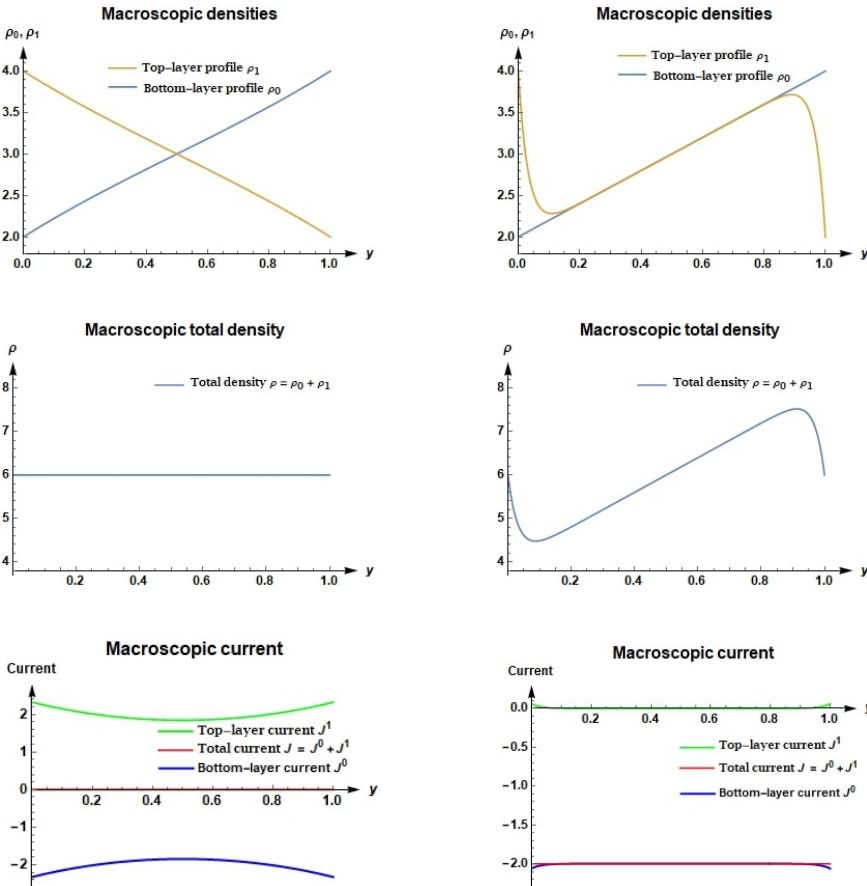


Figure 5.3: Macroscopic profiles of the densities for slow and fast particles (top panels), macroscopic profile of the total density (central panels), and the currents (bottom panels). Here,  $\rho_{L,0} = 2$ ,  $\rho_{L,1} = 4$ ,  $\rho_{R,0} = 4$  and  $\rho_{R,1} = 2$ ,  $\Upsilon = 1$ . For the panels in the left column,  $\epsilon = 1$  and for the panels in the right column,  $\epsilon = 0.001$ .

consequence, the total density profile is not flat and has two bumps at the boundaries. Most strikingly, the total current is  $J = -2$ , since now the current of the bottom layer  $J^0$  is dominating, while the current of the bottom layer  $J^1$  is small (order  $\epsilon$ ).

**Unequal boundary densities with uphill diffusion.** As argued earlier, since the system does not always obey Fick's law, by tuning the parameters  $\rho_{L,0}$ ,  $\rho_{L,1}$ ,  $\rho_{R,0}$ ,  $\rho_{R,1}$  and  $\epsilon$ , we can push the system into a regime where the total current is such that  $J < 0$  and the total densities are such that  $\rho_R < \rho_L$ , where  $\rho_R = \rho_{R,0} + \rho_{R,1}$  and  $\rho_L = \rho_{L,0} + \rho_{L,1}$ . In this regime, *the current goes uphill*, since the total density of particles at the right is lower than at the left, yet the average current is negative.

For an illustration, consider the case when  $\rho_{L,1} = 6$ ,  $\rho_{R,0} = 4$  and  $\rho_{L,0} = \rho_{R,1} = 2$ , which implies  $\rho_L = 8$  and  $\rho_R = 6$  and thus  $\rho_R < \rho_L$ . The density profiles and currents are shown in Fig. 5.4 for two values of  $\epsilon$ , in particular, a comparison between the Fick-

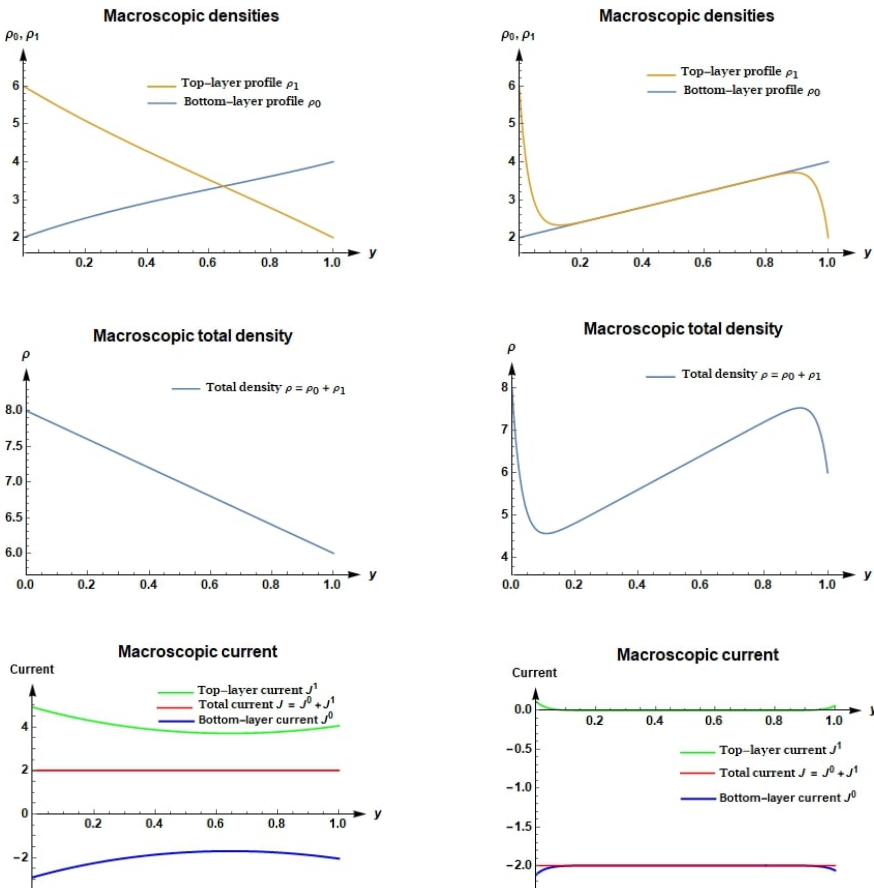


Figure 5.4: Macroscopic profiles of the densities for slow and fast particles (top panels), macroscopic profile of the total density (central panels), and the currents (bottom panels). Here,  $\rho_{L,0} = 2$ ,  $\rho_{L,1} = 6$ ,  $\rho_{R,0} = 4$  and  $\rho_{R,1} = 2$ ,  $\Upsilon = 1$ . For the panels in the left column,  $\epsilon = 1$  and for the panels in the right column,  $\epsilon = 0.001$ .

regime  $\epsilon = 1$  (left panels) and the non-Fick-regime with very slow particles  $\epsilon = 0.001$  (right panels). As can be seen in the figure, when  $\epsilon = 1$ , the system obeys Fick's law: the total density linearly interpolates between the two total boundary densities 8 and 6, respectively. The average total stationary current is positive as predicted by Fick's law. However, in the *uphill* regime, the total density is non-linear and the gradient of the total density is not proportional to the total current, violating Fick's law. The total current is negative and is effectively dominated by the current of the fast particles. It will be shown later that the transition into the uphill regime happens at the critical value  $\epsilon = \frac{|\rho_{R,0} - \rho_{L,0}|}{|\rho_{R,1} - \rho_{L,1}|} = \frac{1}{2}$ . In the limit  $\epsilon \downarrow 0$  the total density profile and the current always get dominated in the bulk by the profile and the current of the fast particles, respectively. When  $\epsilon < \frac{1}{2}$ , even though the density of the slow particles makes the total density near the boundaries such that  $\rho_R < \rho_L$ , it is not strong enough to help the system overcome the domination of the fast particles in the bulk, and so the effective total current goes in the same direction as the current of the fast particles, producing an uphill current.

**The transition between downhill and uphill.** We observe that for the choice of reservoir parameters  $\rho_{L,1} = 6, \rho_{R,0} = 4$  and  $\rho_{L,0} = \rho_{R,1} = 2$ , the change from downhill to uphill diffusion occurs at  $\epsilon = \frac{|\rho_{R,0} - \rho_{L,0}|}{|\rho_{R,1} - \rho_{L,1}|} = \frac{1}{2}$ . The density profiles and currents are shown in Fig. 5.5 for two additional values of  $\epsilon$ , one in the “mild” downhill regime  $J > 0$  for  $\epsilon = 0.75$  (left panels), the other in the “mild” uphill regime  $J < 0$  for  $\epsilon = 0.25$  (right panels). In the uphill regime (right panel), i.e., when  $\epsilon = 0.75$ , the “mild” non-linearity of the total density profile is already visible, indicating the violation of Fick's law.

**Identification of the uphill regime.** We define the notion of uphill current below and identify the parameter ranges for which uphill diffusion occurs.

**Definition 5.3.17 (Uphill diffusion).** For parameters  $\rho_{L,0}, \rho_{L,1}, \rho_{R,0}, \rho_{R,1}$  and  $\epsilon > 0$ , we say the system has an uphill current in stationarity if the total current  $J$  and the difference between the total density of particles in the right and the left side of the system given by  $\rho_R - \rho_L$  have the same sign, where it is understood that  $\rho_R = \rho_{R,0} + \rho_{R,1}$  and  $\rho_L = \rho_{L,0} + \rho_{L,1}$ . ■

**Proposition 5.3.18 (Uphill regime).** Let  $a_0 := \rho_{R,0} - \rho_{L,0}$  and  $a_1 := \rho_{R,1} - \rho_{L,1}$ . Then the macroscopic system admits an uphill current in stationarity if and only if

$$a_0^2 + (1 + \epsilon) a_0 a_1 + \epsilon a_1^2 < 0. \tag{5.181}$$

If, furthermore,  $\epsilon \in [0, 1]$ , then

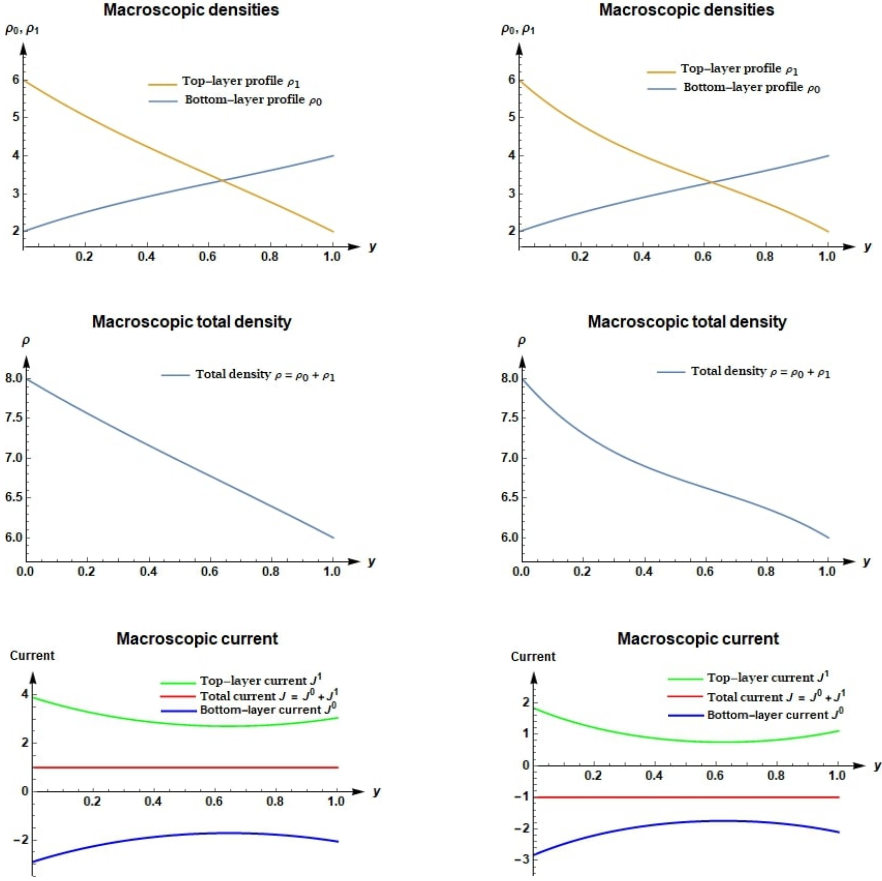


Figure 5.5: Macroscopic profiles of the densities for slow and fast particles (top panels), macroscopic profile of the total density (central panels), and the currents (bottom panels) in the “mild” downhill and the “mild” uphill regime. Here,  $\rho_{L,0} = 2$ ,  $\rho_{L,1} = 6$ ,  $\rho_{R,0} = 4$  and  $\rho_{R,1} = 2$ ,  $\Upsilon = 1$ . For the panels in the left column,  $\epsilon = 0.75$  and for the panels in the right column,  $\epsilon = 0.25$ .

(i) either

$$a_0 + a_1 > 0 \text{ with } a_0 < 0, a_1 > 0$$

or

$$a_0 + a_1 < 0 \text{ with } a_0 > 0, a_1 < 0,$$

(ii)  $\epsilon \in [0, -\frac{a_0}{a_1}]$ .

*Proof.* Note that, by (5.170), there is an uphill current if and only if  $a_0 + a_1$  and  $a_0 + \epsilon a_1$  have opposite signs. In other words, this happens if and only if

$$(a_0 + a_1)(a_0 + \epsilon a_1) = a_0^2 + (1 + \epsilon) a_0 a_1 + \epsilon a_1^2 < 0. \quad (5.182)$$

The above constraint forces  $a_0 a_1 < 0$ . Further simplification reduces the parameter regime to the following four cases:



- (a)  $a_0 + a_1 > 0$  with  $a_0 < 0$ ,  $a_1 > 0$  and  $\epsilon < -\frac{a_0}{a_1}$ ,
- (b)  $a_0 + a_1 < 0$  with  $a_0 > 0$ ,  $a_1 < 0$  and  $\epsilon < -\frac{a_0}{a_1}$ ,
- (c)  $a_0 + a_1 > 0$  with  $a_0 > 0$ ,  $a_1 < 0$  and  $\epsilon > -\frac{a_0}{a_1}$ ,
- (d)  $a_0 + a_1 < 0$  with  $a_0 < 0$ ,  $a_1 > 0$  and  $\epsilon > -\frac{a_0}{a_1}$ .

Under the assumption  $\epsilon \in [0, 1]$ , only the first two of the above four cases survive.  $\square$

### §5.3.6 The width of the boundary layer

We have seen that for  $\epsilon = 0$  the microscopic density profile of the fast particles  $\theta_0(x)$  linearly interpolates between  $\rho_{L,0}$  and  $\rho_{R,0}$ , whereas the density profile of the slow particles satisfies  $\theta_1(x) = \theta_0(x)$  for all  $x \in \{2, \dots, N-1\}$ . In the macroscopic setting this produces a continuous macroscopic profile  $\rho_0^{\text{stat}}(y) = \rho_{L,0} + (\rho_{R,0} - \rho_{L,0})y$  for the bottom-layer, while the top-layer profile develops two discontinuities at the boundaries when either  $\rho_{L,0} \neq \rho_{L,1}$  or  $\rho_{R,0} \neq \rho_{R,1}$ . In particular,

$$\rho_1^{\text{stat}}(y) \rightarrow [\rho_{L,0} + (\rho_{R,0} - \rho_{L,0})y] \mathbb{1}_{(0,1)}(y) + \rho_{L,1} \mathbb{1}_{\{1\}}(y) + \rho_{R,1} \mathbb{1}_{\{0\}}(y), \quad \epsilon \downarrow 0,$$

for  $y \in [0, 1]$ . For small but positive  $\epsilon$ , the curve is smooth and the discontinuity is turned into a boundary layer. In this section we investigate the width of the left and the right boundary layers as  $\epsilon \downarrow 0$ . To this end, let us define

$$W_L := |\rho_{L,0} - \rho_{L,1}|, \quad W_R := |\rho_{R,0} - \rho_{R,1}|. \quad (5.183)$$

Note that, the profile  $\rho_1$  develops a left boundary layer if and only if  $W_L > 0$  and, similarly, a right boundary layer if and only if  $W_R > 0$ .

**Definition 5.3.19 (Boundary layer).** We say that the *left boundary layer* is of size  $f_L(\epsilon)$  if there exists  $C > 0$  such that, for any  $c > 0$ ,

$$\lim_{\epsilon \downarrow 0} \frac{R_L(\epsilon, c)}{f_L(\epsilon)} = C, \quad (5.184)$$

where  $R_L(\epsilon, c) = \sup \left\{ y \in (0, \frac{1}{2}) : \left| \frac{d^2}{dy^2} \rho_1^{\text{stat}}(y) \right| \geq c \right\}$ . Analogously, we say that the *right boundary layer* is of size  $f_R(\epsilon)$  if there exists  $C > 0$  such that, for any  $c > 0$ ,

$$\lim_{\epsilon \downarrow 0} \frac{1 - R_R(\epsilon, c)}{f_R(\epsilon)} = C, \quad (5.185)$$

where  $R_R(\epsilon, c) = \inf \left\{ y \in (\frac{1}{2}, 1) : \left| \frac{d^2}{dy^2} \rho_1^{\text{stat}}(y) \right| \geq c \right\}$ .  $\blacksquare$

The widths of the two boundary layers essentially measure the deviation of the top-layer density profile (and therefore also the total density profile) from the bulk linear profile corresponding to the case  $\epsilon = 0$ . In the following proposition we estimate the sizes of the two boundary layers.

**Proposition 5.3.20 (Width of boundary layers).** *The widths of the two boundary layers are given by*

$$f_L(\epsilon) = f_R(\epsilon) = \sqrt{\epsilon} \log(1/\epsilon), \quad (5.186)$$

where  $f_L(\epsilon), f_R(\epsilon)$  are defined as in Definition 5.3.19.

*Proof.* Note that, to compute  $f_L(\epsilon)$ , it suffices to keep  $W_L > 0$  fixed and put  $W_R = 0$ , where  $W_L, W_R$  are as in (5.183). Let  $\bar{y}(\epsilon, c) \in (0, \frac{1}{2})$  be such that, for some constant  $c > 0$ ,

$$\left| \frac{d^2}{dy^2} \rho_1^{\text{stat}}(y) \right| \geq c, \quad (5.187)$$

or equivalently, since  $\epsilon \Delta \rho_1 = \Upsilon(\rho_1 - \rho_0)$ ,

$$|\rho_1^{\text{stat}}(y) - \rho_0^{\text{stat}}(y)| \geq \frac{c\epsilon}{\Upsilon}. \quad (5.188)$$

Recalling the expressions of  $\rho_0^{\text{stat}}(\cdot)$  and  $\rho_1^{\text{stat}}(\cdot)$  for positive  $\epsilon$  given in (5.126)–(5.127), we get

$$\left| \frac{\sinh \left[ \sqrt{\Upsilon(1+\frac{1}{\epsilon})(1-y)} \right]}{\sinh \left[ \sqrt{\Upsilon(1+\frac{1}{\epsilon})} \right]} (\rho_{L,0} - \rho_{L,1}) + \frac{\sinh \left[ \sqrt{\Upsilon(1+\frac{1}{\epsilon})} y \right]}{\sinh \left[ \sqrt{\Upsilon(1+\frac{1}{\epsilon})} \right]} (\rho_{R,0} - \rho_{R,1}) \right| \geq \frac{c\epsilon}{\Upsilon}. \quad (5.189)$$

Using (5.183) plus the fact that  $W_R = 0$ , and setting  $B_{\epsilon, \Upsilon} := \sqrt{\Upsilon(1+\frac{1}{\epsilon})}$ , we see that

$$\sinh [B_{\epsilon, \Upsilon}(1-y)] \geq \frac{c\epsilon}{\Upsilon W_L} \sinh [B_{\epsilon, \Upsilon}]. \quad (5.190)$$

Because  $\sinh(\cdot)$  is strictly increasing, (5.190) holds if and only if

$$\bar{y}(\epsilon, c) \leq 1 - \frac{1}{B_{\epsilon, \Upsilon}} \sinh^{-1} \left[ \frac{c\epsilon}{\Upsilon W_L} \sinh \left( \frac{B_{\epsilon, \Upsilon}}{2} \right) \right]. \quad (5.191)$$

Thus, for small  $\epsilon > 0$  we have

$$R_L(\epsilon, c) = 1 - \frac{1}{B_{\epsilon, \Upsilon}} \sinh^{-1} \left[ \frac{c\epsilon}{\Upsilon W_L} \sinh \left( \frac{B_{\epsilon, \Upsilon}}{2} \right) \right], \quad (5.192)$$

where  $R_L(\epsilon, c)$  is defined as in Definition 5.3.19. Since  $\sinh^{-1} x = \log(x + \sqrt{x^2 + 1})$  for  $x \in \mathbb{R}$ , we obtain

$$\begin{aligned} R_L(\epsilon, c) &= \frac{\sqrt{\epsilon}}{\sqrt{\Upsilon(1+\epsilon)}} \log \left[ \frac{N_{\epsilon, \Upsilon} + \sqrt{N_{\epsilon, \Upsilon}^2 + 1}}{\epsilon C N_{\epsilon, \Upsilon} + \sqrt{(\epsilon C N_{\epsilon, \Upsilon})^2 + 1}} \right] \\ &= \frac{\sqrt{\epsilon}}{\sqrt{\Upsilon(1+\epsilon)}} \log(1/\epsilon) + \frac{\sqrt{\epsilon}}{\sqrt{\Upsilon(1+\epsilon)}} \log \left[ \frac{1 + \sqrt{1 + (1/N_{\epsilon, \Upsilon})^2}}{C + \sqrt{C^2 + (1/(\epsilon N_{\epsilon, \Upsilon}))^2}} \right] \\ &= \frac{\sqrt{\epsilon}}{\sqrt{\Upsilon(1+\epsilon)}} \log(1/\epsilon) + R_{\epsilon, \Upsilon, W_L}, \end{aligned} \quad (5.193)$$

where  $N_{\epsilon, \Upsilon} := \sinh\left(\frac{B_{\epsilon, \Upsilon}}{2}\right)$ ,  $C := \frac{c}{\Upsilon W_L}$ , and the error term is

$$R_{\epsilon, \Upsilon, W_L} := \frac{\sqrt{\epsilon}}{\sqrt{\Upsilon(1+\epsilon)}} \log \left[ \frac{1 + \sqrt{1 + (1/N_{\epsilon, \Upsilon})^2}}{C + \sqrt{C^2 + (1/(\epsilon N_{\epsilon, \Upsilon}))^2}} \right].$$

Note that, since  $\epsilon N_{\epsilon, \Upsilon} \rightarrow \infty$  as  $\epsilon \downarrow 0$ , we have

$$\lim_{\epsilon \downarrow 0} \frac{R_{\epsilon, \Upsilon, W_L}}{\sqrt{\epsilon}} = \frac{1}{\sqrt{\Upsilon}} \log(1/C) < \infty. \quad (5.194)$$

Hence, combining (5.193)–(5.194), we get

$$\lim_{\epsilon \downarrow 0} \frac{R_L(\epsilon, c)}{\sqrt{\epsilon} \log(1/\epsilon)} = \lim_{\epsilon \downarrow 0} \frac{1}{\sqrt{\Upsilon(1+\epsilon)}} + \lim_{\epsilon \downarrow 0} \frac{R_{\epsilon, \Upsilon, W_L}}{\sqrt{\epsilon} \log(1/\epsilon)} = \frac{1}{\sqrt{\Upsilon}} \quad (5.195)$$

and so, by Definition 5.3.19,  $f_L(\epsilon) = \sqrt{\epsilon} \log(1/\epsilon)$ .

Similarly, to compute  $f_R(\epsilon)$ , we first fix  $W_L = 0$ ,  $W_R > 0$  and note that, for some  $c > 0$ , we have, by using (5.189),

$$|\partial^2 \rho_1^{\text{stat}}(y)| \geq c \quad \text{if and only if} \quad \sinh[B_{\epsilon, \Upsilon} y] \geq \frac{c\epsilon}{\Upsilon W_R} \sinh[B_{\epsilon, \Upsilon}]. \quad (5.196)$$

Hence, by appealing to the strict monotonicity of  $\sinh(\cdot)$ , we obtain

$$R_R(\epsilon, c) = \inf \left\{ y \in \left(\frac{1}{2}, 1\right) : \left| \frac{d^2}{dy^2} \rho_1^{\text{stat}}(y) \right| \geq c \right\} = \frac{1}{B_{\epsilon, \Upsilon}} \sinh^{-1} \left[ \frac{c\epsilon}{\Upsilon W_R} \sinh\left(\frac{B_{\epsilon, \Upsilon}}{2}\right) \right]. \quad (5.197)$$

Finally, by similar computations as in (5.193)–(5.195), we see that

$$\lim_{\epsilon \downarrow 0} \frac{1 - R_R(\epsilon, c)}{\sqrt{\epsilon} \log(1/\epsilon)} = \frac{1}{\sqrt{\Upsilon}} \quad (5.198)$$

and hence  $f_R(\epsilon) = \sqrt{\epsilon} \log(1/\epsilon)$ . □





Appendix of Part II

## Appendix: Chapter 5

### Inverse of the boundary-layer matrix

The inverse of the matrix  $M_\epsilon$  defined in (5.115) is given by ( $\alpha_1$  and  $\alpha_2$  are as in (5.116))

$$M_\epsilon^{-1} := \frac{1}{Z} \begin{bmatrix} -m_{13} & -m_{14} & m_{13} & m_{14} \\ m_{21} & m_{22} & m_{23} & m_{24} \\ m_{31}(\alpha_2) & m_{32}(\alpha_2) & m_{33}(\alpha_2) & m_{34}(\alpha_2) \\ -m_{31}(\alpha_1) & -m_{32}(\alpha_1) & -m_{33}(\alpha_1) & -m_{34}(\alpha_1) \end{bmatrix}, \quad (\text{C.1})$$

where

$$\begin{aligned} Z &:= \alpha_1^{N+1} [\alpha_2(1-\epsilon)(\alpha_2^{N-1} + 1) + 2\epsilon(\alpha_2^{N+1} + 1)] \\ &\quad \times [\alpha_2(1+N)(1-\epsilon)(\alpha_2^{N-1} - 1) + 2\epsilon(N+\epsilon)(\alpha_2^{1+N} - 1)], \\ m_{13} &:= \alpha_1^{N+1} [\alpha_2(1-\epsilon)(\alpha_2^{N-1} + 1) + 2\epsilon(\alpha_2^{N+1} + 1)] \\ &\quad \times [\alpha_2(1-\epsilon)(\alpha_2^{N-1} - 1) + \epsilon(\alpha_2^{N+1} - 1)], \\ m_{14} &:= \epsilon \alpha_1^{N+1} [\alpha_2(1-\epsilon)(\alpha_2^{N-1} + 1) + 2\epsilon(\alpha_2^{N+1} + 1)] (\alpha_2^{N+1} - 1), \\ m_{21} &:= (1+N)(1-\epsilon)^2 (\alpha_2^{N-1} - \alpha_1^{N-1}) - \epsilon(1-\epsilon)^2 (\alpha_2 - \alpha_1) \\ &\quad + \epsilon^2(1+2N+\epsilon)(\alpha_2^{N+1} - \alpha_1^{N+1}) + \epsilon(1-\epsilon)(2+3N+\epsilon)(\alpha_2^N - \alpha_1^N), \\ m_{22} &:= \epsilon [(1-\epsilon)(1+N)(\alpha_2^N - \alpha_1^N) + \epsilon(1+2N+\epsilon)(\alpha_2^{N+1} - \alpha_1^{N+1})], \\ m_{23} &:= \epsilon(1-\epsilon)[(N+\epsilon)(\alpha_2 - \alpha_1) - (1-\epsilon)(\alpha_2^N - \alpha_1^N) - \epsilon(\alpha_2^{N+1} - \alpha_1^{N+1})], \\ m_{24} &:= -\epsilon(1-\epsilon)[(1+N)(\alpha_2 - \alpha_1) + \epsilon(\alpha_2^{N+1} - \alpha_1^{N+1})], \end{aligned} \quad (\text{C.2})$$

and the polynomials  $m_{31}(z), m_{32}(z), m_{33}(z), m_{34}(z)$  are defined as

$$\begin{aligned} m_{31}(z) &:= -(1-\epsilon)^2 z - \epsilon(1-\epsilon) + (1-\epsilon)(N+\epsilon)z^N - \epsilon(1-2N-3\epsilon)z^{N+1}, \\ m_{32}(z) &:= -(1-\epsilon)(1+N)z^N - \epsilon(1-\epsilon) - \epsilon(1+2N+\epsilon)z^{N+1}, \\ m_{33}(z) &:= (1-\epsilon)^2 z^N + \epsilon(1-\epsilon)z^{N+1} - (1-\epsilon)(N+\epsilon)z + \epsilon(1-2N-3\epsilon), \\ m_{34}(z) &:= (1+N)(1-\epsilon)z + \epsilon(1-\epsilon)z^{N+1} + \epsilon(1+2N+\epsilon). \end{aligned} \quad (\text{C.3})$$

We remark that most of the terms appearing in the inverse simplify because of (5.117). We define the four vectors  $\vec{c}_1, \vec{c}_2, \vec{c}_3, \vec{c}_4$  as the respective rows of  $M_\epsilon^{-1}$ , i.e.,

$$\begin{aligned} \vec{c}_1 &:= (M_\epsilon^{-1})^T \vec{e}_1, & \vec{c}_2 &:= (M_\epsilon^{-1})^T \vec{e}_2, \\ \vec{c}_3 &:= (M_\epsilon^{-1})^T \vec{e}_3, & \vec{c}_4 &:= (M_\epsilon^{-1})^T \vec{e}_4, \end{aligned} \quad (\text{C.4})$$

where

$$\begin{aligned}\vec{e}_1 &:= [1 \ 0 \ 0 \ 0]^T, & \vec{e}_2 &:= [0 \ 1 \ 0 \ 0]^T, \\ \vec{e}_3 &:= [0 \ 0 \ 1 \ 0]^T, & \vec{e}_4 &:= [0 \ 0 \ 0 \ 1]^T.\end{aligned}$$

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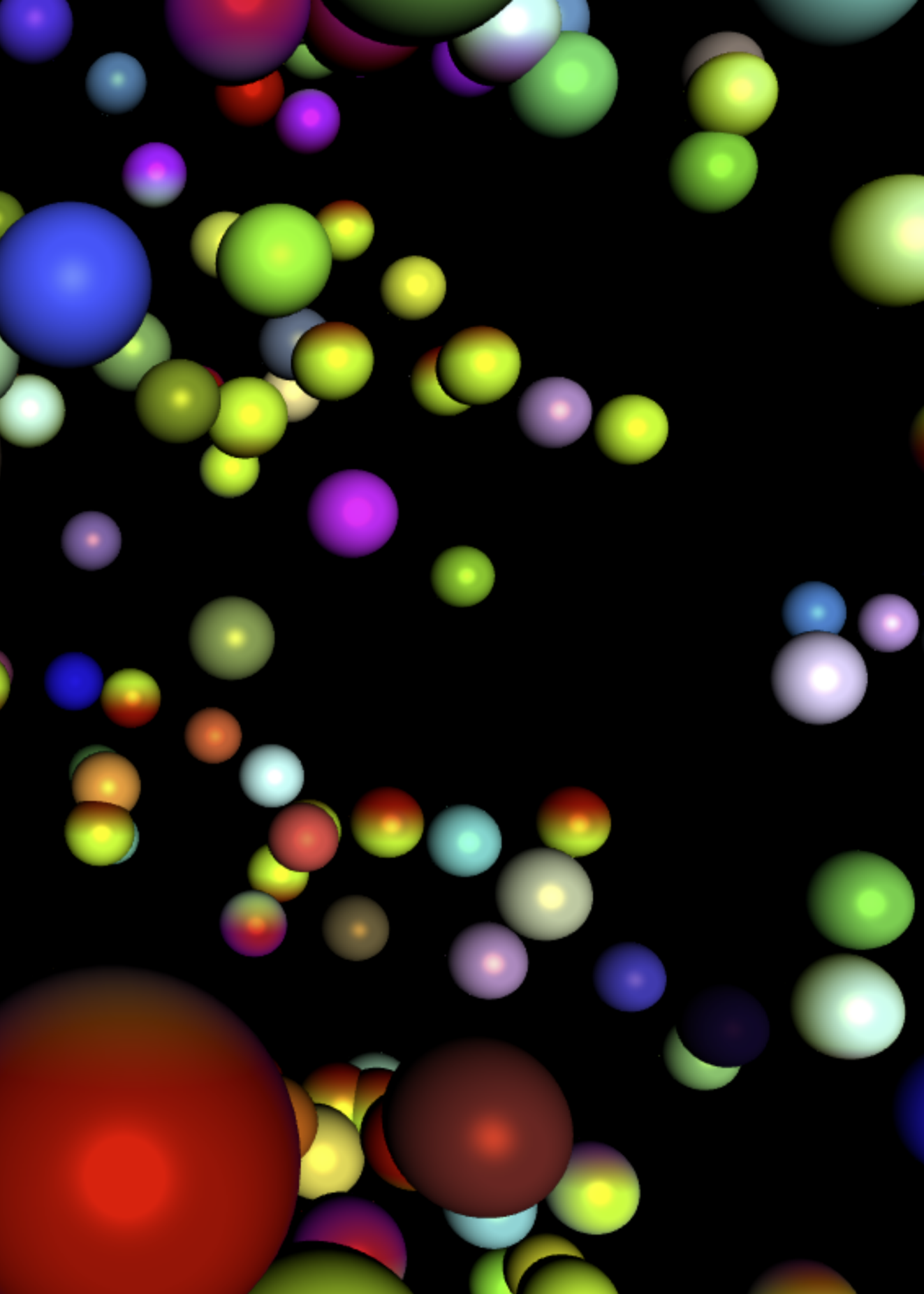
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# Samenvatting

Een winterslaap houden, heb jij dat wel eens overwogen? Al was het maar om de immer regenachtige, ijskoude, winderige Nederlandse winter te ontvluchten? Helaas is er nog steeds geen bevredigend antwoord op de vraag of wij mensen überhaupt een winterslaap kunnen houden. Toch hebben verschillende onderzoeken aangetoond dat veel zoogdieren inderdaad de winter door kunnen slapen om energie en voedsel te besparen met het oog op de toekomst. Microben bezitten vergelijkbare eigenschappen, waarbij organismen in een staat van lage metabolische activiteit komen als reactie op ongunstige omgevingsomstandigheden.

In de literatuur refereren begrippen als zaadbankeffecten, kiemrust, winterslaap, etcetera, allemaal aan een en hetzelfde fenomeen, zoals hierboven beschreven, waarbij de keuze afhangt van de context. Als het gaat over plantenpopulaties is ‘zaadbank effect’ passender bij gebeurtenissen zoals de ontkieming van naar schatting 30.000 jaar oude uit de ijstijd daterende zaden uit het Siberische permafrost [155]. Het mag een wonder heten dat bepaalde planten het potentieel hebben om levensvatbaar te blijven over zo’n uitgestrekte tijdsperiode. Dit geeft ons te denken over de evolutionaire effecten van zulke zeldzame gebeurtenissen. Het thema van dit proefschrift, bestaande uit Deel I-II, is kiemrust (in het vervolg ook wel slaap of slaaptoestand genoemd). We putten motivatie uit biologische populaties die gekenmerkt worden door deze eigenschap, en onderzoeken haar effect in een probabilistisch raamwerk. In het bijzonder introduceren we een wiskundige notie van kiemrust in diverse bekende stochastische interacterende systemen. We onderzoeken hoe dit veranderingen in de kwalitatieve en kwantitatieve eigenschappen van dit soort systemen teweegbrengt, door hun gedrag op de lange termijn te karakteriseren.

In Deel I construeren we een nieuw systeem van interacterende deeltjes dat de genetische evolutie beschrijft van ruimtelijk gestructureerde populaties onder invloed van kiemrust, reproductie (ook wel hertrekking genoemd) en migratie. We nemen aan dat de populatiegrootten begrensd zijn en verschillen van kolonie tot kolonie. De kolonies zijn gelabeld door rasterpunten van het  $d$ -dimensionale raster met gehele getallen,  $\mathbb{Z}^d$ . Individuen dragen een van de twee genotypen:  $\heartsuit$  and  $\spadesuit$ . Er is nog een andere categorisering, namelijk die van twee categorieën individuen in elke populatie: actief of slapend. Slapende individuen in een kolonie bevinden zich in wat we een zaadbank noemen. Actieve individuen kunnen zich voortplanten, en ook migreren naar andere kolonies, terwijl slapende individuen inactief zijn. Verder fungeren actieve individuen als een stimulans voor het wakker worden van slapende individuen: ze kunnen een willekeurig slapendindividu, gekozen uit hun eigen kolonie, overtuigen om actief te worden, om daarna zelf de zaadbank binnen te gaan door in te slapen op random tijd intervallen. Omdat de slapende individuen niet opnieuw gekozen worden totdat ze weer actief worden, kunnen zij de genetische diversiteit van een populatie

lang behouden.

Deel I bestaat uit hoofdstukken 2-5 en is gewijd aan het bestuderen van het hierboven omschreven stochastische systeem. Hieronder vatten we de inhoud van de drie hoofdstukken samen.

*Interacterende deeltjessystemen* zijn een specifieke klasse van Markov processen met lokaal interacterende componenten die gewoonlijk evolueren in een hele grote toestandsruimte. Ze kunnen een grote hoeveelheid informatie bevatten en kunnen gebruikt worden voor het accuraat modelleren van diverse natuurkundige of biologische systemen. In Hoofdstuk 2 behandelen we de rigoureuze constructie van een nieuw interacterende deeltjessysteem dat overeenkomt met de intuïtieve beschrijving van het bovenstaande biologische systeem. De constructie bouwt voort op een welbekend stochastisch proces in wiskundige populatiegenetica, genaamd het Moran model. Het Moran model beschrijft de genetische evolutie van een enkele, voortplantingsactieve, begrensde populatie zonder zaadbank. We modificeren het model dusdanig, dat het de slaaptoestand bevat, en breiden het uit naar de context van ruimtelijk gestructureerde populaties van verschillende grootten.

We presenteren nieuwe resultaten over het gedrag van het resulterende proces als er evenwicht is. We doen dat door een dichotomie te identificeren tussen clustering (= het bestaan van een monotype evenwicht) versus co-existentie (= het bestaan van een evenwicht met verschillende typen). In het clustering regime gaat genetische diversiteit uiteindelijk verloren. In het co-existentie regime, daarentegen, behouden de populaties een niet-triviale genetische diversiteit. De sleutel tot het bewijs van deze dichotomie is een wiskundig gereedschap genaamd stochastische dualiteit. Stochastische dualiteit is een gereedschap dat het mogelijk maakt een complex Markov proces te bestuderen met behulp van een simpeler proces wat we het duale proces noemen. Door een Lie-algebraïsche aanpak te volgen, identificeren we een duaal Markov proces voor het proces geassocieerd met ruimtelijke populaties. Intuïtief kan het duale proces geïnterpreteerd worden als een mathematische codering van hoe de genealogische relatie tussen individuele voorouders zich ontwikkeld heeft over de verstreken tijd. Ons voornaamste resultaat in dit hoofdstuk relateert de dichotomie van clustering vs. co-existentie aan het duale proces. Kort gezegd stelt het dat alle individuen in de ruimtelijke populaties uiteindelijk hetzelfde genotype erven, dat wil zeggen, het originele systeem vertoont clustering, dan en slechts dan als zij met kans 1 allemaal eenzelfde gezamenlijke voorouder delen in het verleden.

Hoofdstuk 3 is een voortzetting van de studie van het ruimtelijke proces in Hoofdstuk 2. Het heeft als doel om fijnere en makkelijker te verifiëren condities voor clustering te identificeren. We ontwikkelen een nieuwe vergelijkingsmethode om het lange termijn gedrag van het duale proces te onderzoeken. Om precies te zijn, vinden we een extra duaal proces dat lijkt op het originele duale proces, maar eenvoudiger te analyseren is. Door het extra duale proces te vergelijken met het originele proces, laten we zien dat, wanneer de actieve populatiegrootten geen arbitrair grote waarden aannemen in begrensde gebieden van de geografische ruimte  $\mathbb{Z}^d$  en de relatieve sterkte van de zaadbanken (= ratio van de grootten van actieve en slapende populaties) in verschillende kolonies van dezelfde orde van grootte zijn, het criterium voor clustering enkel en alleen bepaald door het migratiemechanisme. In dit parameterregime introduceren de

inhomogene grootten van de zaadbanken geen nieuwe kwalitatieve verandering in het lange termijn gedrag van de ruimtelijke populaties. Naar verwachting is de situatie echter drastisch anders wanneer de zaadbanken en de actieve populaties niet langer van een vergelijkbare grootte zijn in verschillende kolonies.

In Hoofdstuk 4 breiden we het ruimtelijke systeem van populaties uit naar de context van een statische door willekeur bepaalde omgeving. Om precies te zijn spelen de populatiegrootten de rol van een statisch door willekeur gekozen omgeving voor het ruimtelijke proces. We nemen aan dat een typische realisatie van de omgeving van een translatie-invariant en ergodisch stochastische veld komt. In het clustering regime gaat de genetische diversiteit uiteindelijk verloren met kans 1, en na verloop van tijd erven alle individuen ofwel het genotype ♡, ofwel het genotype ♠. Het doel van dit hoofdstuk is om nauwgezet te kwantificeren hoe de initiële genfrequenties over de tijd propageren in de populaties, om zo het uiteindelijke overlevende genotype te bepalen. Het voordeel van het uitbreiden van ons model naar de context van een door willekeur bepaalde omgeving is dat we in deze uitbreiding precies kunnen uitrekenen wat de overlevingskans van het genotype ♡ is. In het bijzonder leiden we een expliciete formule af voor dere overlevingskans (ook wel de fixatiekans genoemd), die een gemiddelde, genomen over alle realisaties van de omgeving, is van de genotype-♡ dichtheid in een doelkolonie, gewogen door de verhouding van haar slapende en actieve populatiegrootten.

Deel II, bestaande uit Hoofdstuk 5, sluit dit proefschrift af met een studie van “zaadbank effecten” in drie welbekende systemen van interacterende deeltjes, namelijk het systeem van onafhankelijke deeltjes, het exclusieproces en het inclusieproces. Deze drie systemen beschrijven hoe een collectie van microscopische deeltjes zich ontwikkelt op een discreet raster onder de invloed van, respectievelijk, geen interactie, een excluderende (afstotende) interactie, en een inkluderende (aantrekkende) interactie. We modificeren deze systemen door toe te staan dat de deeltjes een milde (pure) slapende toestand aannemen, waarbinnen zij alleen kunnen bewegen met een langzamere (nul) vaart. We laten zien dat, in de aanwezigheid van een slaaptoestand, het macroscopische gedrag van de systemen niet langer beschreven kan worden door de warmtevergelijking, maar door een reactie-diffusie vergelijking. We bewijzen ook dat er, onder aanwezigheid van grensreservoirs, een parameterregime bestaat waarvoor opwaartse diffusie mogelijk wordt. Dit laatste is een interessant fenomeen waar macroscopische totale stroming van deeltjes plaatsvindt van een regio met een lagere deeltjesdichtheid naar een regio met een hogere deeltjesdichtheid. Dit betekent een schending van de klassieke diffusiewet van Fick.

# Summary

Have you ever contemplated the idea of going into a hibernate mode just to survive the ever so frequent, rainy, freezing, windy days of the Dutch winter? Unfortunately, a satisfactory answer to whether humans are capable of hibernation is not yet available. But several studies have shown that many mammals indeed spend the winter in hibernation to conserve energy, food, etc., for future purpose. Microbial populations also possess similar characteristics, where organisms enter into a state of low metabolic activity in response to adverse environmental conditions.

In the literature the terms such as seed-bank effects, dormancy, hibernation, etc., all refer to the same biological phenomena described above, but the usage depends on the context. For instance, in plant populations seed-bank effects is more suited in view of events, such as the germination of approximately 30,000 years old ice-age seed collected from Siberian permafrost [155], etc. It is a wonder that certain plant seeds have the potential to remain viable for such an extended period of time, and makes us ponder over the evolutionary effects of such rare events. The theme of the present thesis consisting of Part I–II is dormancy. We draw motivations from biological populations featuring this trait and investigate its effect in a probabilistic framework. In particular, we introduce a mathematical notion of dormancy in several well-known stochastic interacting systems, and study how it changes qualitative and quantitative properties of the systems by characterising their behaviours in the long run.

In Part I we construct a novel interacting particle system which describes genetic evolution of spatially structured populations under the influence of dormancy, reproduction (also referred to as *resampling*) and migration. The population sizes are assumed to be finite and vary across different colonies. The colonies are labelled by the lattice points of the  $d$ -dimensional integer lattice  $\mathbb{Z}^d$ . Individuals carry one of two genotypes: ♡ and ♠. There are also two categories of individuals in each population: *active* and *dormant*. Dormant individuals in a colony reside in what is called a *seed-bank*. Active individuals can reproduce offspring and also migrate to different colonies, while dormant individuals sit idle. Furthermore, active individuals act as a stimulator for the dormant individuals: they can convince a dormant individual chosen uniformly at random from their own colony to become active and enter the seed-bank themselves by becoming dormant at exponentially distributed random time intervals. Since the dormant individuals do not resample until they become active again, they can preserve the genetic diversity of the populations for a very long time.

Part I consists of Chapters 2–4 and is devoted to the study of the stochastic system described above. We summarise the content of the three chapters below.

Interacting particle systems are a particular class of Markov processes with locally interacting components that typically evolve on a very large state space. They are

capable of containing immense amount of information and can be used for modelling many physical or biological systems with fair accuracy. In Chapter 2 we deal with the rigorous construction of a novel interacting particle system which corresponds to the intuitive description of the above biological system. The construction is built upon a well-known stochastic process in mathematical population genetics called the Moran model. The Moran model describes the genetic evolution of a single, reproductively active, finite population without seed-bank. We modify the model to include dormancy and extend it to the context of spatially structured populations with varying sizes.

We present new results on the equilibrium behaviour of the resulting process by identifying a dichotomy between clustering (=existence of only mono-type equilibria) versus coexistence (=existence of multi-type equilibria). In the clustering regime genetic diversities in the populations are eventually lost with probability 1. In contrast, the populations maintain a non-trivial genetic diversity in the coexistence regime with positive probability. The key to the proof of this dichotomy is a mathematical tool called stochastic duality. Stochastic duality is a tool that allows one to study a complex Markov process with the help of a simpler one, called dual process. By following a Lie-algebraic approach we identify a dual Markov process for the process associated with the spatial populations. Intuitively, the dual process can be interpreted as a mathematical encoding of how the genealogical relationship between individual ancestors evolved over time in the past. Our main result in this chapter relates the dichotomy of clustering vs coexistence with the dual process. Roughly speaking, it states that all individuals in the spatial populations eventually inherit the same genotype (i.e., the original system exhibit clustering) if and only if, with probability 1, they all share a single common ancestor in the past.

Chapter 3 is a continuation of the study of the spatial process in Chapter 2. With the aim of identifying finer and easily verifiable conditions for clustering we develop a novel comparison method to study the long-term behaviour of the dual process. To be precise, we find another auxiliary dual process which is very similar to the original dual, but is analytically more tractable. By comparing the auxiliary dual with the original one, we show that if the active population sizes do not take arbitrary large values in finite regions of the geographic space  $\mathbb{Z}^d$  and the relative strength of the seed-banks (=ratio of the sizes of active and dormant populations) in different colonies are of the same order, then the criterion for clustering is solely determined by the migration mechanism alone. In this parameter regime the inhomogeneous sizes of the seed-banks do not introduce any new qualitative change in the long-run behaviour of the spatial populations. The situation, however, is expected to be drastically different when the seed-banks and the active populations no longer maintain a comparable size in different colonies.

In Chapter 4 we extend the spatial system of populations to a static random environment setting. To be precise, the constituent population sizes play the role of a static random environment for the spatial process. We assume that a typical realisation of the environment comes from a translation-invariant and ergodic random field. In the clustering regime the genetic diversity of the spatial populations is eventually lost with probability 1 and all individuals inherit either the genotype ♡ or the genotype ♠ in the long-run. The goal in this chapter is to precisely quantify how the initial gene



frequencies in the populations propagate over time to determine the ultimate surviving genotype. The advantage of extending our model to the random environment setting is that in this extension we are able to precisely compute the survival probability of the genotype  $\heartsuit$ . In particular, we derive an explicit formula for the probability (also referred to as fixation probability) which turns out to be an *annealed average* (average over the environment realisations) of the type- $\heartsuit$  density in a target colony, biased by the ratio of its dormant and active population sizes.

Part II consisting of Chapter 5 concludes this thesis with a study of “seed-bank effects” in three well-known interacting particle systems, namely, *independent particle system*, *exclusion process* and *inclusion process*. These three systems describe how a collection of microscopic particles evolve on a discrete lattice under the influence of, respectively, no interaction, an exclusion (repulsive) interaction, and an inclusion (attractive) interaction. We modify these systems by allowing the particles to adopt a mild (pure) dormant state in which they can only move with a slower (zero) rate. We show that in the presence of dormancy, the macroscopic behaviour of the systems is no longer described by the heat equation, but rather by a reaction-diffusion equation. We also prove that under the presence of boundary reservoirs, there exists a parameter regime for which an *uphill diffusion* becomes possible. The latter is an interesting phenomenon where macroscopic total flow of particles takes place from a region of lower particle density to a region of higher particle density, and showcases a violation of the classical Fick’s law of diffusion.

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# Curriculum Vitae

Shubhamoy Nandan was born in a village called Mogra located in the West Bengal State in India on 9th of January in 1995. He completed his higher secondary education from Memari Vidyasagar Memorial Institution (Unit 2) in 2013. Afterwards, he enrolled in the 5 years integrated programme of Bachelors and Masters offered by Indian Institute of Science Education and Research at Kolkata to pursue his undergraduate studies, which was supported by the INSPIRE scholarship SHE-2013. In his master's studies, he carried out research on the scaling limits of a probabilistic model for interfaces called the discrete Gaussian free field under the joint supervision of Dr. Rajat Subhra Hazra (Leiden Univ.) and Dr. Satyaki Mazumder (I.I.S.E.R. Kolkata). He obtained his Master of Science degree in Mathematics after the defence of his thesis entitled 'Scaling limit of discrete Gaussian free field' in June, 2018. He moved to the Netherlands in October, 2018 to pursue his PhD research at Leiden University under the supervision of Prof. Frank den Hollander (Leiden Univ.), Prof. Frank Redig (TU Delft) and Prof. Cristian Giardinà (Modena Univ.). His PhD research was supported by the Netherlands Organisation for Scientific Research (NWO) through grant number TOP1.17.019. In his PhD project he investigated the effect of dormancy in probabilistic models arising in the literature of mathematical population genetics and interacting particle systems. During his PhD, he presented his research in conferences, served as teaching assistants in several probability theory courses and participated in a 4-month junior trimester programme entitled "*Stochastic modelling in the life science: from evolution to medicine*" at the Hausdorff research institute for mathematics in Bonn, Germany.

# Publications

## Published:

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