

*Submitted to the Annals of Applied Probability***GENEALOGIES IN EXPANDING POPULATIONS**

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The goal of this paper is to prove rigorous results for the behavior of genealogies in a one-dimensional long range biased voter model introduced by Hallatschek and Nelson [25]. The first step, which is easily accomplished using results of Mueller and Tribe [38], is to show that when space and time are rescaled correctly, our biased voter model converges to a Wright-Fisher SPDE. A simple extension of a result of Durrett and Restrepo [18] then shows that the dual branching coalescing random walk converges to a branching Brownian motion in which particles coalesce after an exponentially distributed amount of intersection local time. Brunet et al. [8] have conjectured that genealogies in models of this type are described by the Bolthausen-Sznitman coalescent, see [39]. However, in the model we study there are no simultaneous coalescences. Our third and most significant result concerns “tracer dynamics” in which some of the initial particles in the biased voter model are labeled. We show that the joint distribution of the labeled and unlabeled particles converges to the solution of a system of stochastic partial differential equations. A new duality equation that generalizes the one Shiga [44] developed for the Wright-Fisher SPDE is the key to the proof of that result.

1. Introduction. Since the 1970s the dominant viewpoint in cancer modeling has been that tumors evolve through clonal succession, i.e., there is a sequence of mutations advantageous for cell growth that sweep to fixation. However, recent work of Sottoriva et al. [45] has shown that in colon cancer most of common mutations in a tumor were present at initiation, while mutations that arise later are only present in small regions of the tumor. The long range goal of our research is to understand the behavior of genealogies in a growing tumor and the resulting patterns of genetic heterogeneity. This is important because cancer treatment may fail if one does not have an accurate knowledge of the mutational types present in the tumor.

The genetic forces at work in a growing tumor are very similar to those in a population expanding into a new geographical area. In this case most of the advantageous mutation occur near the front, see Edmonds, Lille, and

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Cvalli-Sforza [19], and simulation studies of a spatial model in [32]. There are a half dozen papers by Oscar Hallatschek and collaborators [24, 25, 26, 33, 36, 39] using nonrigorous arguments to study genealogies in an expanding population. A rigorous analysis in dimensions $d \geq 2$ seems difficult, so we will restrict our attention here to a one dimensional model closely related to one introduced by Hallatschek and Nelson [25]. Our version of their model is a sequence of biased voter models on

$$\Lambda_n := (L_n^{-1}\mathbb{Z}) \times \{1, \dots, M_n\}.$$

There is one cell at each point of Λ_n , whose cell-type is either 1 or 0. The cells in deme $w \in L_n^{-1}\mathbb{Z}$ only interact with those in demes $w - L_n^{-1}$ and $w + L_n^{-1}$. Hence each cell $x = (w, i)$ has $2M_n$ neighbors. Type-0 cells reproduce at rate $2M_n r_n$, type-1 cell at rate $2M_n(r_n + \theta R_n^{-1})$ where $\theta \in [0, \infty)$. When reproduction occurs the offspring replaces a neighbor chosen uniformly at random. In the terminology of evolutionary games, this is birth-death updating.

1.1. *Interacting particle system duality.* Let $\xi_t(x)$ be the type of the cell at x at time t . Our (rescaled) biased voter model $(\xi_t)_{t \geq 0}$ can be constructed using two independent families of i.i.d. Poisson processes: $\{P_t^{x,y} : x \sim y\}$ that have rate r_n , and $\{\tilde{P}_t^{x,y} : x \sim y\}$, that have rate θR_n^{-1} . At a jump time of $P_t^{x,y}$, the cell at x is replaced by an offspring of the one at y . At a jump time of $\tilde{P}_t^{x,y}$, the cell at x is replaced by an offspring of the one at y only if y has cell-type 1. To avoid clutter we have suppressed the superscript n 's on ξ_t and the two Poisson processes.

To formally construct the process and define a useful dual process, we recall the graphical representation of the biased voter model introduced by Harris (1976) and developed by Griffeath (1978). The ingredients are arrows that spread fluid in the direction of their orientation, and δ 's which are dams that stop fluid. At times s of $\tilde{P}_{x,y}$ we draw an arrow from $(s, y) \rightarrow (s, x)$. At times s of $P_{x,y}$ we draw an arrow from $(s, y) \rightarrow (s, x)$ and put a δ at $(s-, x)$. The $s-$ indicates that the δ is placed just before the head of the arrow. Intuitively, we inject fluid into the bottom of the graphical representation at the sites of the configuration that are 1 and let it *flow up*. A site x is in state 1 at time t if and only if it can be reached by fluid. If there is fluid at y at time s and an arrow (with no δ) from $(s, y) \rightarrow (s, x)$, the fluid will spread to x , i.e., there is a birth at x if it is in state 0. If x is already occupied no change occurs.

If there is an arrow- δ from $(s, y) \rightarrow (s, x)$, then a little thought reveals

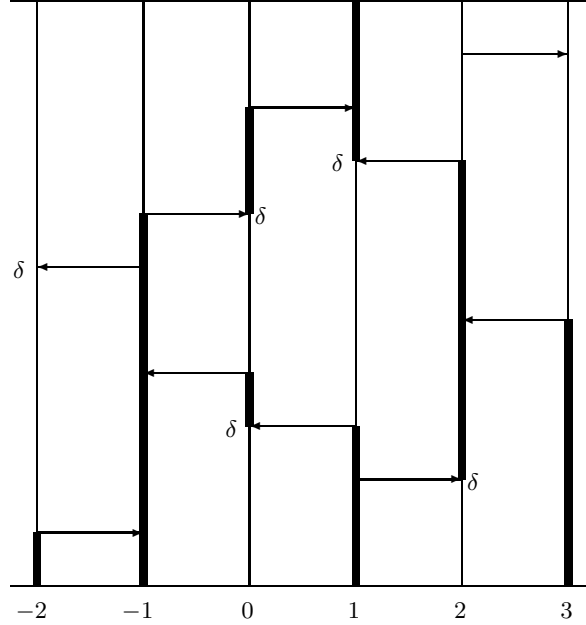


FIG 1. *Duality for the biased voter model.*

before		after	
y	x	y	x
1	0	1	1
0	1	0	0
1	1	1	1
0	0	0	0

In the first case the fluid spreads from y to x as if there was no δ . In the second, there is no fluid to be spread but the dam stops the fluid at x . In the third the dam stops the fluid at x , but it replaced by fluid from y . In the fourth, there is no fluid so nothing happens. Thus the effect in all cases is that x imitates y .

To define the dual, we inject fluid at x at time t and let it *flow down*. It is again stopped by dams but now moves across arrows in the direction OPPOSITE to their orientation. Given $z \in \Lambda_n = (L_n^{-1}\mathbb{Z}) \times \{1, \dots, M_n\}$, we define the dual process $\zeta_s^{t,z}$, $0 \leq s \leq t$ to be the set of sites at time $t - s$ that

can be reached by fluid starting at z . A little thought shows that $\zeta_0^{t,z} = \{z\}$ and follows the following rules:

- If a particle in $\zeta_s^{t,z}$ is at x and an arrival in $P^{x,y}$ occurs at time $t - s$ then the particle jumps to y .
- If a particle in $\zeta_s^{t,z}$ is at x and an arrival in $\tilde{P}^{x,y}$ occurs at time $t - s$ then the particle gives birth to a new particle at y .
- If a jumping particle or an offspring lands on another particle in $\zeta_s^{t,z}$, then the two particles coalesce to 1.

For a picture see Figure 1. There the dark lines give the occupied sites in $\zeta_s^{t,1}$. At the end $\zeta_t^{t,1} = \{-2, -1, 1, 3\}$.

To extend the definition to a collection of sites A , we let $\zeta_s^{t,A} = \cup_{z \in A} \zeta_s^{t,z}$. We defined our dual process starting at a fixed time t so that the relationship in Lemma 1 holds with probability 1. If we have two times $t < t'$ then the distributions of $\zeta_s^{t,A}$ and $\zeta_s^{t',A}$ agree up to time t , so the Kolmogorov extension theorem implies that we can define a process ζ_s^A for all time so that the distribution agrees with $\zeta_s^{t,A}$ up to time t . The collection of processes $\{\zeta^A : A \subset \Lambda_n\}$ is referred to as the **dual process of ξ** .

It follows from the definition that

LEMMA 1. $\xi_t(z) = 1$ for some $z \in A$ if and only if $\xi_0(x) = 1$ for some $x \in \zeta_t^{t,A}$.

1.2. *Measure valued limit for the biased voter model.* We define the approximate density by

$$u_t^n(w) := \frac{1}{M_n} \sum_{i=1}^{M_n} \xi_t(w, i)$$

and linearly interpolate between demes to define $u_t^n(w)$ for all $w \in \mathbb{R}$. We retain the superscript n on u_t^n to be able to distinguish the approximating process from its limit. It is clear that for all $t \geq 0$, we have $0 \leq u_t^n(w) \leq 1$ for all $w \in \mathbb{R}$ and $u_t^n \in C_b(\mathbb{R})$, the set of bounded continuous functions on \mathbb{R} . If we equip $C_b(\mathbb{R})$ with the metric

$$(1) \quad \|f\| = \sum_{k=1}^{\infty} 2^{-k} \sup_{|x| \leq k} |f(x)|$$

i.e., uniform convergence on compact sets, then $C_b(\mathbb{R})$ is Polish and the paths $t \mapsto u_t^n$ are $C_b(\mathbb{R})$ valued and càdlàg.

THEOREM 1. *Suppose that as $n \rightarrow \infty$, the initial condition u_0^n converges in $C_b(\mathbb{R})$ to f_0 and that:*

- (a) $\alpha_n \equiv r_n M_n / L_n^2 \rightarrow \alpha \in (0, \infty)$
- (b) $\beta_n \equiv M_n / R_n \rightarrow \beta \in [0, \infty)$
- (c) $\gamma_n \equiv r_n / L_n \rightarrow \gamma \in [0, \infty)$
- (d) $L_n \rightarrow \infty$ and $L_n R_n \rightarrow \infty$

Then the approximate density process $(u_t^n)_{t \geq 0}$ converges in distribution in $D([0, \infty), C_b(\mathbb{R}))$, as $n \rightarrow \infty$, to a continuous $C_b(\mathbb{R})$ valued process $(u_t)_{t \geq 0}$ which is the weak solution to the (stochastic) partial differential equation

$$(2) \quad \partial_t u = \alpha \Delta u + 2\theta \beta u(1 - u) + |4\gamma u(1 - u)|^{1/2} \dot{W}$$

with initial condition $u_0 = f_0$. Here \dot{W} is the space-time white noise on $[0, \infty) \times \mathbb{R}$.

Theorem 1 is a straight forward generalization of a result of Mueller and Tribe [38]. They considered a long range voter model on \mathbb{Z}/n in which two voters are neighbors if $|x - y| \leq n^{1/2}$. Their voters change their opinion at rate $O(n)$ and imitate the opinion of a neighbor chosen at random. More precisely, for each of the $2n^{1/2}$ neighbors, they adopt the opinion of that neighbor at rate $n^{1/2}$ if it is 0 and at rate $n^{1/2} + \theta n^{-1/2}$ if it is 1. Their model corresponds roughly in our situation to $L_n = M_n = R_n = r_n = n^{1/2}$. Their limit is

$$\partial_t u = \frac{1}{6} \Delta u + 2\theta u(1 - u) + |4u(1 - u)|^{1/2} \dot{W}.$$

$\beta = \gamma = 1$ while the $1/6$ comes from the fact that the variance of the uniform distribution on $[-1, 1]$ is $1/3$.

Why is Theorem 1 true? If this discussion becomes confusing the reader can skip it. In Section 3 the analysis of the approximate martingale problem will give a more rigorous version of this explanation.

- To begin we note that only branching events change the expected number of ones. They occur from each site at rate $2\theta M_n / R_n$. Birth events from x to $y \sim x$ with $\xi_t(x) = 1$ and $\xi_t(y) = 0$ will change the local density of 1's by $1/M_n L_n$. In an interval of length h there are $h L_n M_n$ possibilities for x , so using the assumption $M_n / R_n \rightarrow \beta$ gives the drift term $\approx 2\theta \beta u(1 - u)$.
- Under our assumptions, branching events are much less frequent than voting events ($r_n / L_n \rightarrow \gamma$ and $L_n R_n \rightarrow \infty$ imply $r_n / R_n^{-1} \rightarrow \infty$)

so for the rest of the computation argument they can be ignored. Voting events occur from each site at rate $2r_n M_n$. If they go from x to $y \sim x$ with $\xi_t(x) \neq \xi_t(y)$ then the local density of 1's will change by $\pm 1/M_n L_n$. In an interval of length h there are $h L_n M_n$ possibilities for x , so using the assumption $r_n/L_n \rightarrow \gamma$ the infinitesimal variance term is $\approx 4\gamma u(1-u)$.

- To see the source of the Laplacian note that in the dual particles jump at rate $2r_n M_n$ by an amount that $\pm 1/L_n$ with equal probability so the genealogies converge to Brownian motions with variance $2\alpha t$. Recalling the $1/2$ in the generator of Brownian motion we have the term $\alpha \Delta u$.

1.3. *Convergence of the dual to Branching Brownian motions.* Durrett and Restrepo [18] have earlier considered a related coalescing random walk (with no births) on \mathbb{Z} . We use their notation even though it conflicts slightly from ours. There are M haploid individuals at each site and nearest neighbor migration (i.e., jumps ± 1 with equal probability) occur at rate ν . Theorem 2 in [18] states the following.

THEOREM 2. *Sample one individual from the colony at 0 and another one from the colony at L . Let t_0 be the time at which they coalesce. If $L \rightarrow \infty$ and $M\nu/L \rightarrow \alpha \in (0, \infty)$ then $2t_0/(L^2/\nu)$ converges in distribution to $\ell_0^{-1}(\alpha\tau)$ where ℓ_0 is the local time at 0 of a standard Brownian motion started from 1 and τ is an independent mean 1 exponential random variable.*

Why is this true? Since migration occurs at rate ν , it takes time of order L^2/ν to move a distance $O(L)$. In this time the differences in the location of the two particles will visit each integer between 0 and L of order L/ν times. If we want coalescence to have a probability strictly between 0 and 1, we need $M\nu/L \rightarrow \alpha \in (0, \infty)$.

The proof of Theorem 2 generalizes easily to give:

THEOREM 3. *Suppose that as $n \rightarrow \infty$, the conditions on r_n , R_n , M_n and L_n in Theorem 1 hold. Then the dual process ζ of ξ converges in distribution to a limit in which particles move according to Brownian motions on the real line \mathbb{R} with variance $2\alpha t$, branching occurs at rate $\theta\beta$ and two particles coalesce when the local time at 0 of the difference between their locations exceeds $\alpha\tau/\gamma$, where τ is a mean one exponential random variable independent of the particle motions. If $\gamma = 0$ there is no coalescence.*

If we let χ_t^A denote the spatial locations of the particles in the limit process

in Theorem 3, then Lemma 1 and Theorem 3 imply

$$(3) \quad \mathbb{E} \prod_{x \in A} (1 - u_t(x)) = \mathbb{E} \prod_{y \in \mathcal{X}_t^A} (1 - u_0(y)).$$

Here A can be a multi-set, e.g., $\{a, a, a, b, b\}$. In this case we start three particles at a and two at b and duality says

$$\mathbb{E}[(1 - u_t(a))^3(1 - u_t(b))^2] = \mathbb{E} \prod_{y \in \mathcal{X}_t^A} (1 - u_0(y)).$$

The duality relationship described in the last paragraph is not new. In 1986, Shiga and Uchiyama [43] introduced it to study a collection of Wright-Fisher diffusions coupled by migrations. Shiga [44] used it to show uniqueness in law for (2). Doering, Mueller, and Smereka [12] gave a simpler description and derivation of the dual. See also Hobson and Tribe [27].

1.4. *Tracer Dynamics.* Hallatschek and Nelson [25] take an interesting approach to studying the ancestral lineage of a particle. That is, the path within the dual $\zeta_s^{x,t}$ that gives the actual ancestor at time $t - s$ of the individual at x at time t . Think of our expanding population as a fluid and inject a small amount of red liquid at time 0. The locations of the red fluid at time t will identify the locations of their progeny. In particle terms, we will have states 0, 1, and 1^* where the $*$ indicates being labeled by the tracer. $\xi(x)$ is the indicator of the particle at x being in states 1 or 1^* . To construct the labeled process it is convenient to use the graphical representation. If there is an arrow- δ from y to x then x adopts the state of y . If there is an arrow from y to x and y is in state 1 or 1^* then x will adopt the state of y , but nothing happens if y is in state 0. In fluid terms, the color of fluid at y replaces that at x .

The interacting particle system (IPS) dual process gives us the set of possible ancestors of the particle at x at time t . To analyze our new process with labeled and unlabeled particles, we assign an ordering to the particles in the IPS dual in such a way that the **FIRST occupied site** in the list will be the ancestor. The rules are as follows:

- If particle i jumps and there is no coalescence, then its location changes but the order does not.
- If particle i jumps and coalesces with j then the particle with the higher index is removed from the dual. The surviving particle has its location updated. The remaining particles are reindexed.
- If the i particle gives birth then the new particle is labeled i , while all particles with indices $j \geq i$ have their indices increased by 1.

To explain the definition, we will work through the example drawn in Figure 1. The successive states are

$$\begin{aligned} &\{1\}, \quad \{0, 1\}, \quad \{0, 2\}, \quad \{-1, 2\}, \quad \{-1, 3, 2\}, \\ &\{0, -1, 3, 2\}, \quad \{1, -1, 3, 2\}, \quad \{1, -1, 3\}, \quad \{1, -2, -1, 3\} \end{aligned}$$

To see this note that under our rules, at the point where the dual jumps from $\{1\} \rightarrow \{0, 1\}$, if there is a particle at 0 it will give birth and replace any particle at 1. The next two events involve voting, so the affected particles move but do not change their position in the ordering. The next event is an arrow from 3 to 2. A particle at 3 will replace one at 2, so 3 is inserted in the list before 2. The next novel event is the seventh transition when the particles at 2 and 1 coalesce: at that time we drop the lower ranked particle. For example, the actual ancestor of the particle $(t, 1)$ is 1 if $\xi_0(1) = 1$; the actual ancestor is -2 if $\xi_0(1) = 0$ and $\xi_0(-2) = 1$.

Neuhauser [40] used a similar dual to show that in the multitype contact process, if the particle death rates are equal, then the one with the higher birth rate takes over the system. The idea of assigning an ordering to the particles to trace their genealogies is quite similar to that in the lookdown constructions of Donnelly and Kurtz [13, 14]. There each particle is initially assigned a level. Genealogies of any set of particles can be read off from the evolution of the levels. See also Etheridge and Kurtz [20] for the lookdown constructions for a very general class of population models.

To do computations, we let $\eta_t(x) = 1$ if the individual at x at time t in the biased voter model is labeled and 0 otherwise. We only label type 1's, so $\eta_t(x) \leq \xi_t(x)$. As noted above $\eta_t(x)$ can be computed using the version of the dual $\zeta_s^{t,x}$ in which the points are ordered. That is, $\eta_t(x) = 1$ if and only if the first occupied site in the list is labeled. More formally, if under the ordering $\zeta_t^{t,x} = \{y_1, y_2, \dots, y_K\}$ (note that K and y_1, \dots, y_K are random variables), then

$$\begin{aligned} P(\xi_t(x) = 0) &= E \left(\prod_{i=1}^K (1 - \xi_0(y_i)) \right) \equiv EF(\zeta_t^x) \\ P(\eta_t(x) = 1) &= E \left(\sum_{j=1}^K \eta_0(y_j) \prod_{i=1}^{j-1} (1 - \xi_0(y_i)) \right) \equiv EG(\zeta_t^x) \end{aligned}$$

In the same way one computes

$$(4) \quad \begin{aligned} P(\xi_t(x_1) = 0, \dots, \xi_t(x_m) = 0, \eta_t(x_{m+1}) = 1, \dots, \eta_t(x_n) = 1) \\ = E \left[\prod_{i=1}^m F(\zeta_t^{x_i}) \prod_{i=m+1}^n G(\zeta_t^{x_i}) \right] \end{aligned}$$

A standard argument shows that the probabilities just computed determine the distribution of (ξ_t, η_t) .

As before, we define the approximate density for the labeled particles by

$$\ell_t^n(w) := \frac{1}{M_n} \sum_{i=1}^{M_n} \eta_t(w, i)$$

and linearly interpolate to obtain a function $\ell_t^n(w)$ for all $w \in \mathbb{R}$. The following is the main result of this paper.

THEOREM 4. *Suppose that as $n \rightarrow \infty$, the conditions on r_n, R_n, M_n and L_n in Theorem 1 hold, and that the initial condition (u_0^n, ℓ_0^n) converges in $C_b(\mathbb{R}) \times C_b(\mathbb{R})$ to (f_0, g_0) . Then the pair of approximate densities $(u_t^n, \ell_t^n)_{t \geq 0}$ converges in distribution in $D([0, \infty), C_b(\mathbb{R}) \times C_b(\mathbb{R}))$ to a continuous $C_b(\mathbb{R}) \times C_b(\mathbb{R})$ valued process $(u_t, \ell_t)_{t \geq 0}$ which is the weak solution to the coupled (stochastic) partial differential equations*

$$\begin{aligned} \partial_t u &= \alpha \Delta u + 2\theta \beta u(1-u) + |4\gamma \ell(1-u)|^{1/2} \dot{W}^0 + |4\gamma(u-\ell)(1-u)|^{1/2} \dot{W}^1 \\ \partial_t \ell &= \alpha \Delta \ell + 2\theta \beta \ell(1-u) + |4\gamma \ell(1-u)|^{1/2} \dot{W}^0 + |4\gamma \ell(u-\ell)|^{1/2} \dot{W}^2 \end{aligned}$$

with initial condition $(u_0, \ell_0) = (f_0, g_0)$, where $\dot{W}^i, i = 0, 1, 2$ are three independent space-time white noises on $[0, \infty) \times \mathbb{R}$.

As the proof shows the three noises \dot{W}^0, \dot{W}^1 and \dot{W}^2 refer to voting interactions between 1^* and $0, 1$ and $0, 1$ and 1^* and 1 respectively. The drift in ℓ_t is $2\theta\beta\ell(1-u)$ because labeled particles only have a selective advantage in competition with those of type 0 .

We will prove our result by showing that the sequence of approximating processes is tight. To conclude that there is weak convergence, we need to show

LEMMA 2. *When $\gamma > 0$, the solution of the coupled SPDE in Theorem 4 is unique in law.*

To do this we use our duality function (4). Details are in Section 8.

In Theorems 1, 3 and 4, the assumption $\alpha > 0$ is used crucially in the proof of tightness, but we allow β or γ to be 0. The deterministic regime ($\gamma = 0$) occurs, for instance, if $r_n = n^{1/a}$, $L_n = n^{1/b}$, $M_n = \lceil \alpha n^{2/b-1/a} \rceil$ and $R_n = M_n/\beta$, where $2a > b > a > 0$. When $\gamma = 0$ the limiting process is a PDE

$$\begin{aligned}\partial_t u &= \alpha \Delta u + 2\theta \beta u(1-u) \\ \partial_t \ell &= \alpha \Delta \ell + 2\theta \beta \ell(1-u).\end{aligned}$$

This PDE obviously has a unique weak solution (solve the first equation and then solve the second), but if one wants, this can be proved using duality.

1.5. *Lineage dynamics.* Using tracer dynamics Hallatschek and Nelson [25], see page 163 and Appendix A, heuristically derived the probability density $G(x, t|x', t')$ that an individual at x' at time t' is descended from an ancestor at x at time $t < t'$. Here we describe their argument with the hope that someone can find a way to make it rigorous. Making sense of equation (5) for the ancestral lineages seems difficult, but since these lineages are embedded in the limit of the branching coalescing random walk their behavior cannot be too pathological.

The authors of [25] considered a more general situation in which the population density in a frame moving with velocity v is

$$\partial_t u(x, t) = D\partial_x^2 u(x, t) + v\partial_x u(x, t) + K(x, t)$$

where, for instance, $K(x, t) = su(1-u) + \epsilon\sqrt{u(1-u)}Z$ with Z being a space-time White noise, and we have changed their c to u . They concluded, see their (3), that

$$\begin{aligned}\partial_t G(x, t|x', t') &= -\partial_x J(x, t|x', t') \\ J(x, t|x', t') &= -D\partial_x G + \{v + 2D\partial_x \log[u(x, t)]\}G.\end{aligned}$$

Here (x', t') is thought of as the initial condition and (x, t) as the final condition, so this is the forward equation

$$(5) \quad \partial_t G = D\partial_x^2 G - \partial_x(\{v + 2D\partial_x \log[u(x, t)]\}G)$$

and the drift in the diffusion process is $v + 2D\partial_x \log[c(x, t)]$.

As we will now show, a closely related equation “follows” from Theorem 4. We used quotation marks because we use the nonexistent Itô’s formula for the SPDE in Theorem 4 and apply it to the function $f(\ell, u) = \ell/u$ which is not continuous at $(0, 0)$.

Suppose (u, ℓ) solves the SPDE and let $\rho = \ell/u$. By Theorem 4,

$$\begin{aligned} \partial_t \rho &= \frac{u \partial_t \ell - \ell \partial_t u}{u^2} = \frac{1}{u} \left[\alpha \Delta \ell + 2\theta \beta \ell (1-u) + |4\gamma \ell (1-u)|^{1/2} \dot{W}^0 \right. \\ &\quad \left. + |4\gamma \ell (u-\ell)|^{1/2} \dot{W}^2 \right] - \frac{\ell}{u^2} \left[\alpha \Delta u + 2\theta \beta u (1-u) \right. \\ &\quad \left. + |4\gamma \ell (1-u)|^{1/2} \dot{W}^0 + |4\gamma (u-\ell)(1-u)|^{1/2} \dot{W}^1 \right]. \end{aligned}$$

The terms involving $\theta\beta$ cancel. To combine the Laplacian terms we use the formula

$$\Delta \left(\frac{\ell}{u} \right) = \frac{\Delta \ell}{u} - \frac{\ell \Delta u}{u^2} - 2 \frac{\partial_x u}{u} \cdot \partial_x \left(\frac{\ell}{u} \right).$$

To add up the noises we note that since the W^i are independent, the variances add up to

$$\begin{aligned} &\frac{(u-\ell)^2}{u^4} \ell (1-u) + \frac{\ell(u-\ell)}{u^2} + \frac{\ell^4 (u-\ell)(1-u)}{u^4} \\ &= \frac{\ell(u-\ell)}{u^2} \left[\frac{(u-\ell)(1-u)}{u^2} + \frac{u^2}{u^2} + \frac{\ell(1-u)}{u^2} \right] = \frac{\ell(u-\ell)}{u^3} \end{aligned}$$

since $(u-\ell)(1-u) + \ell(1-u) + u^2 = u(1-u) + u^2 = u$. Combining our calculations,

$$(6) \quad \partial_t \rho = \alpha \Delta \rho + 2\alpha \partial_x \log u \cdot \partial_x \rho + |4\gamma \rho (1-\rho)/u|^{1/2} \dot{W}$$

for some white noise \dot{W} . To compare (6) with (5), note that their $D = \alpha$, they work in a moving reference frame and their equation is for a fixed realization of the total population size; while ours is in a fixed reference frame and does not condition on $u(t, x)$ and hence retains the fluctuation term $|4\gamma \rho (1-\rho)/u|^{1/2} \dot{W}$.

Equations (5) and (6) both contain drift terms of the form $\partial_x \log[u(x, t)]$. It is a well-known fact that solutions of the SPDE in (2) are Hölder continuous with exponent $1/2 - \epsilon$ in space and $1/4 - \epsilon$ in time, so it is not clear how to make sense of these equations. The fact that $\eta_t(x) \leq \xi_t(x)$ means that $\ell \leq u$, so in computing ℓ/u we will never divide a positive number by 0. However solutions to u have compact support [37], so it is not clear if the ratio of densities ℓ^n/u^n will be tight.

1.6. *Concluding remarks.* Theorem 1 is a special case of Theorem 4. Theorem 3 is proved in Section 2. The rest of the paper is devoted to the proof for Theorem 4. In Section 3 we introduce stochastic integral representations

for (u_t^n, ℓ_t^n) and formulate approximate martingale problems. This is now a common approach in the study of scaling limits of particle systems, see [17, 11, 16]. The calculations for the u equation are almost identical to those in Section 3 of Mueller and Tribe [38], but some minor changes are needed to study the joint distribution (ℓ, u) .

In Sections 5–7 we prove tightness. Again many of the ideas come from [38], but since they only write out the details for their contact process limit theorem, and we have to prove the joint convergence, we have written out the details. See Kleim [31] for a recent example of convergence of rescaled Lotka-Volterra models to a one-dimensional SPDE, this time with a cubic drift term. The main ideas of the tightness proof are given in Section 5. Two lemmas that require a lot of computation are proved in Section 6. Some nonstandard random walk estimates are proved in Section 7. Finally Lemma 2, which establishes distributional uniqueness for the coupled SPDE by using a duality based on (4), is proved in Section 8.

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2. Proof of Theorem 3. To get started suppose that there are no births in the dual and consider the special case in which there are initially two particles. Let S_t^n be a random walk that jumps from x to $x \pm 1/L_n$ at rate $2r_n M_n$. The reader should think of this difference of the location of two particles (hence the factor of 2 in $2r_n M_n$), but we allow the two lineages to move independently even after they hit. An elementary computation shows that if

$$V_t^n = \frac{4r_n M_n}{L_n} \int_0^t 1_{(S_s^n=0)} ds$$

$|S_t^n| - V_t^n$ is martingale. As $t \rightarrow \infty$, $|S_t^n|$ converges to the absolute value of a Brownian motion B_t with variance $4\alpha t$.

The next result has been proved for finite variance random walks by Borodin [4] in 1981. To keep this paper self-contained, we will give a simple proof for the nearest neighbor case.

LEMMA 3. V_t^n converges in distribution to $\ell_0(t)$ the local time at 0 for the Brownian motion B_t .

PROOF. An easy computation for simple random walk shows that for any

stopping time

$$EV_{S+t}^n - V_S \leq E_0 V_t^n \leq c\sqrt{t}$$

so by Aldous criterion (see e.g., Theorem 4.5 on page 320 of Jacod and Shiryaev [28]) the sequence V_t^n is tight. Let $V_t^{n(k)}$ be a convergent subsequence with limit V_t . $|S_t^{n(k)} - V_t^{n(k)}|$ is a martingale. Using the maximal inequality on the random walk, and the dominated convergence theorem on the increasing process, both processes converge to their limits in L^1 . Since conditional expectation is a contraction in L^1 , it follows that $|B_t| - V_t$ is a martingale. Now $\ell_0(s)$ is the increasing process associated with $|B_t|$. See e.g., (11.2) on page 84 of Durrett's Stochastic Calculus book [15]. By the uniqueness of the Doob- Meyer decomposition, there is only one subsequential limit, so the entire sequence converges in distribution to $\ell_0(t)$. \square

The sojourn times at 0 are independent and exponential with rate $4r_n M_n$, so the number of visits to 0 up to time t

$$N_t^n \sim 4r_n M_n \int_0^t 1_{(S_s^n=0)} ds$$

and it follows that $N_t^n/L_n \rightarrow \ell_0(t)$. On each visit to 0, the two particles have a probability $1/M_n$ to coalesce. Our assumptions imply that

$$\frac{M_n}{L_n} \cdot \frac{r_n}{L_n} \rightarrow \alpha \quad \text{so} \quad \frac{L_n}{M_n} \rightarrow \frac{\gamma}{\alpha}$$

and the desired result has been proved for the processes with no births. To add births we note there are M_n cells at each deme and \tilde{P}_{xy} has rate θR_n^{-1} , so the branching rate at each deme is $\theta M_n R_n^{-1} \rightarrow \theta\beta$.

3. Approximate Martingale Problems. For simplicity we drop the subscript n 's on M , L , R and r . We leave the superscript n in u_t^n and ℓ_t^n to distinguish the approximating processes from their limits. We write

$$\langle f, g \rangle := \frac{1}{L} \sum_{w \in L^{-1}\mathbb{Z}} f(w)g(w)$$

whenever $\langle |f|, |g| \rangle < \infty$ and adopt the convention that $\phi(x) := \phi(w)$ when $x = (w, i)$.

3.1. *Type 1 particles.* To develop the martingale problem, we note that dynamics of $(\xi_t)_{t \geq 0}$ can be described by the equation

$$(7) \quad \begin{aligned} \xi_t(x) = \xi_0(x) &+ \sum_{y \sim x} \int_0^t (\xi_{s-}(y) - \xi_{s-}(x)) dP_s^{x,y} \\ &+ \sum_{y \sim x} \int_0^t \xi_{s-}(y)(1 - \xi_{s-}(x)) d\tilde{P}_s^{x,y}. \end{aligned}$$

In the first integral, if $\xi_{s-}(y) = \xi_{s-}(x)$ then nothing happens.

$$\begin{aligned} &\text{If } \xi_{s-}(y) = 1 \text{ and } \xi_{s-}(x) = 0 \text{ then } \xi_s(x) = 1; \\ &\text{if } \xi_{s-}(y) = 0 \text{ and } \xi_{s-}(x) = 1 \text{ then } \xi_s(x) = 0. \end{aligned}$$

In the second integral, nothing happens unless $\xi_{s-}(y) = 1$ and $\xi_{s-}(x) = 0$. In this case $\xi_s(x) = 1$.

Let $\phi : [0, \infty) \times \mathbb{R} \rightarrow \mathbb{R}$ be continuously differentiable in t , twice continuously differentiable in x and have compact support in $[0, T] \times \mathbb{R}$ for any T . Applying integration by parts to $\xi_t(x)\phi_t(x)$, using (7), and summing over x , we obtain for all $t \in [0, T]$,

$$(8) \quad \begin{aligned} &\langle u_t^n, \phi_t \rangle - \langle u_0^n, \phi_0 \rangle - \int_0^t \langle u_s^n, \partial_s \phi_s \rangle ds \\ &= (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t (\xi_{s-}(y) - \xi_{s-}(x)) \phi_s(x) dP_s^{x,y} \\ (9) \quad &+ (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}(y)(1 - \xi_{s-}(x)) \phi_s(x) d\tilde{P}_s^{x,y}. \end{aligned}$$

Drift term. We break (9) into an average term and a fluctuation term

$$(10) \quad (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}(y)(1 - \xi_{s-}(x)) \phi_s(x) \theta R^{-1} ds$$

$$(11) \quad + (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}(y)(1 - \xi_{s-}(x)) \phi_s(x) (d\tilde{P}_s^{x,y} - \theta R^{-1} ds).$$

Recalling the definition of the density, (10) becomes

$$\theta \cdot \frac{M}{R} \cdot \frac{1}{L} \sum_{w \in L^{-1}\mathbb{Z}} \int_0^t [u_{s-}^n(w - L^{-1}) + u_{s-}^n(w + L^{-1})](1 - u_{s-}^n(w)) \phi_s(w) ds$$

Since $M/R \rightarrow \beta$, this converges to

$$\theta\beta \int_0^t \int_{\mathbb{R}} 2u_s(w)(1 - u_s(w))\phi_s(w) dw ds$$

as $n \rightarrow \infty$. Here, and in what follows, the claimed convergences follow once we have proved C -tightness (see Section 5 for the proof). We have established convergence of finite dimensional distributions so the sequences of processes converge in distribution.

The second term (11) is a martingale $E_t^{(2)}(\phi)$ with

$$\begin{aligned} \langle E^{(2)}(\phi) \rangle_t &\leq \frac{\theta}{R(ML)^2} \sum_x \sum_{y \sim x} \int_0^t \phi_s^2(x) ds \\ &\leq \frac{2\theta}{LR} \int_0^t \langle 1, \phi_s^2 \rangle ds \rightarrow 0 \quad \text{since } LR \rightarrow \infty. \end{aligned}$$

White noises. We can rewrite (8) as

$$(12) \quad (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \{\xi_{s-}(y)[1 - \xi_{s-}(x)] - \xi_{s-}(x)[1 - \xi_{s-}(y)]\} \phi_s(x) dP_s^{x,y}.$$

We now rewrite the integrand as

$$(13) \quad \xi_{s-}(y)[1 - \xi_{s-}(x)]\phi_s(y) - \xi_{s-}(x)[1 - \xi_{s-}(y)]\phi_s(x)$$

$$(14) \quad + \xi_{s-}(y)[1 - \xi_{s-}(x)](\phi_s(x) - \phi_s(y)).$$

We work first with (13). Interchanging the roles of x and y in the double sum, letting $\xi_t^c(z) = 1 - \xi_t(z)$, and writing $Q_t^{x,y} = P_s^{y,x} - P_s^{x,y}$ this part of (12) becomes

$$(15) \quad (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}^c(y)\xi_{s-}(x)\phi_s(x) dQ_t^{x,y}.$$

To prepare for treating the joint SPDE we split (15) into $Z_t^0(\phi) + Z_t^1(\phi)$ where the $Z_t^i(\phi)$ are defined by the next two equations

$$(16) \quad (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}^c(y)\eta_{s-}(x)\phi_s(x) dQ_s^{y,x},$$

$$(17) \quad (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}^c(y)(\xi_{s-}(x) - \eta_{s-}(x))\phi_s(x) dQ_s^{y,x}.$$

These two martingale terms use the same Poisson processes but the product of their integrands is 0 since $(1 - \xi_t(x))\eta_t(x)$ vanishes for all x and t . Hence these martingales are uncorrelated.

The variance process $\langle Q^{x,y} \rangle_t = 2rt$. Our assumptions on ϕ imply that $\sup_{s \in [0,t]} |\phi_s(x) - \phi_s(y)| \leq K_t/L$ for some $K_t < \infty$, so ignoring the difference between $\phi_s(x)$ and $\phi_s(y)$, we have

$$\langle Z^0(\phi) \rangle_t = 4rL^{-2} \int_0^t \sum_{w \in L^{-1}\mathbb{Z}} \ell_{s-}^n(w)(1 - u_{s-}^n(w))\phi_s(w)^2 ds + o(1)$$

which converges to

$$4\gamma \int_0^t \int_{\mathbb{R}} \ell_s(w)(1 - u_s(w))\phi_s(w)^2 dw ds \quad \text{since } r/L \rightarrow \gamma.$$

Similarly, $\langle Z^1(\phi) \rangle_t$ converges to

$$4\gamma \int_0^t \int_{\mathbb{R}} (u_s(w) - \ell_s(w))(1 - u_s(w))\phi_s(w)^2 dw ds.$$

Laplacian Term. We denote the discrete gradient and the discrete Laplacian respectively by

$$(18) \quad \nabla_L f(w) := L \left(f(w + L^{-1}) - f(w) \right)$$

$$(19) \quad \Delta_L f(w) := L^2 \left(f(w + L^{-1}) + f(w - L^{-1}) - 2f(w) \right).$$

We break (14) into an average term and a fluctuation term

$$(20) \quad (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}(y)\xi_{s-}^c(x)[\phi_s(x) - \phi_s(y)] r ds$$

$$(21) \quad + (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t \xi_{s-}(y)\xi_{s-}^c(x)[\phi_s(y) - \phi_s(x)](dP_s^{x,y} - r ds).$$

We can replace ξ_{s-}^c by 1 in (20) without changing its value, because by symmetry, $\sum_x \sum_{y \sim x} \xi_{s-}(y)\xi_{s-}^c(x)[\phi_s(x) - \phi_s(y)] = 0$ for all $s > 0$.

Doing the double sum over y and then over $x \sim y$ the above is

$$\frac{rM}{L^2} \cdot \frac{1}{L} \sum_w u_{s-}^n(w)\Delta_L \phi_s(w) = \frac{rM}{L^2} \langle u_{s-}^n, \Delta_L \phi_s \rangle.$$

By assumption $rM/L^2 \rightarrow \alpha$, so this term converges to $\alpha \int_{\mathbb{R}} u_s \Delta \phi_s$. The other term, (21), is a martingale $E_t^{(1)}(\phi)$ with

$$(22) \quad \langle E^{(1)}(\phi) \rangle_t \leq \frac{r}{(ML)^2} \sum_x \sum_{y \sim x} \int_0^t (\phi_s(x) - \phi_s(y))^2 ds$$

$$(23) \quad = \frac{2r}{L^3} \int_0^t \langle 1, |\nabla_L \phi_s|^2 \rangle ds \rightarrow 0$$

since $r/L \rightarrow \gamma$ and $L \rightarrow \infty$.

Combining our calculations, we see that in the limit $n \rightarrow \infty$,

$$(24) \quad \int_{\mathbb{R}} u_t(w) \phi_t(w) dw - u_0(w) \phi_0(w) dw - \int_0^t \int_{\mathbb{R}} u_s(w) \partial_s \phi_s(w) dw ds \\ - \int_0^t \int_{\mathbb{R}} \alpha u_s(w) \Delta \phi_s(w) - 2\theta\beta u_s(w)(1 - u_s(w)) \phi_s(w) dw ds$$

is a martingale with quadratic variation

$$(25) \quad 4\gamma \int_0^t \int_{\mathbb{R}} u_s(w)(1 - u_s(w)) \phi_s^2(w) dw ds$$

which is the martingale problem formulation of (2).

3.2. Labeled Particles. To begin, we note that in terms of the previously defined Poisson processes,

$$(26) \quad \eta_t(x) - \eta_0(x) = \sum_{y \sim x} \int_0^t (\eta_{s-}(y) - \eta_{s-}(x)) dP_s^{x,y} \\ + \sum_{y \sim x} \int_0^t \eta_{s-}(y)(1 - \eta_{s-}(x)) - \xi_{s-}(y)(1 - \eta_{s-}(y))\eta_{s-}(x) d\tilde{P}_s^{x,y}.$$

The first term gives the voter interactions. For the second term, note that if y is in state 1^* and x is not, the number of 1^* 's will increase by 1, while if x is in state 1^* and y is in state 1 ($\xi_{s-}(y) = 1$ and $\eta_{s-}(y) = 0$), the number will decrease by 1.

Arguing as for the type 1 particles while using (26) instead of (7), we get

$$(27) \quad \langle \ell_t^n, \phi_t \rangle - \langle \ell_0^n, \phi_0 \rangle - \int_0^t \langle \ell_s^n, \partial_s \phi_s \rangle \\ = (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t (\eta_{s-}(y) - \eta_{s-}(x)) \phi_s(x) dP_s^{x,y}$$

$$(28) \quad + (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t [\eta_{s-}(y) - \xi_{s-}(y)\eta_{s-}(x)] \phi_s(x) d\tilde{P}_s^{x,y},$$

where we have simplified the second term of (26) using $\xi_{s-}(y)\eta_{s-}(y) = \eta_{s-}(y)$.

Drift term. Breaking the second term (28) into an average term and a fluctuation term as before, we conclude that as $n \rightarrow \infty$, the average term is

$$\begin{aligned} \frac{\theta M}{LR} \sum_{w \in L^{-1}\mathbb{Z}} \int_0^t & [\ell_s^n(w + L^{-1}) - u_s^n(w + L^{-1})\ell_s^n(w) \\ & + \ell_s^n(w - L^{-1}) - u_s^n(w - L^{-1})\ell_s^n(w)] \phi_s(w) ds \end{aligned}$$

which converges to

$$\theta\beta \int_0^t \int_{\mathbb{R}} 2\ell_s(w)(1 - u_s(w))\phi_s(w) dw ds.$$

White noises. We again change the integrand in (27) to

$$\{\eta_{s-}(y)[1 - \eta_{s-}(x)] - \eta_{s-}(x)[1 - \eta_{s-}(y)]\} \phi_s(x)$$

and then split it into two parts as in (13) and (14). That is, we rewrite the integrand as

$$(29) \quad \eta_{s-}(y)[1 - \eta_{s-}(x)]\eta_s(y) - \eta_{s-}(x)[1 - \eta_{s-}(y)]\phi_s(x)$$

$$(30) \quad + \eta_{s-}(y)[1 - \eta_{s-}(x)](\phi_s(x) - \phi_s(y)).$$

Arguing as before, we obtain the following sum coming from (29).

$$(31) \quad \begin{aligned} (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t & [1 - \xi_{s-}(y)]\eta_{s-}(x)\phi_s(x) (dP_s^{y,x} - dP_s^{x,y}) \\ & + (ML)^{-1} \sum_x \sum_{y \sim x} \int_0^t [\xi_{s-}(y) - \eta_{s-}(y)]\eta_{s-}(x)\phi_s(x) (dP_s^{y,x} - dP_s^{x,y}). \end{aligned}$$

The first noise is the same as $Z_t^0(\phi)$ in (16) while the second noise, denoted by $Z_t^2(\phi)$, has variance converging to

$$4\gamma \int_0^t \int_{\mathbb{R}} \ell_s(w) (u_s(w) - \ell_s(w)) \phi_s(w)^2 dw ds.$$

The product of any two of the three integrands in $Z_t^i(\phi)$ ($i = 0, 1, 2$) is 0, so these three martingales are uncorrelated.

Laplacian term. Breaking (30) into an average term and a fluctuation term as was done for (14), we see that as $n \rightarrow \infty$, the average term

$$\frac{rM}{L^2} \langle \ell_{s-}^n, \Delta_L \phi_s \rangle \rightarrow \alpha \int_{\mathbb{R}} \ell_s \Delta \phi_s.$$

Combining our calculations, we see that in the limit, for any $\phi, \psi \in C_c^{1,2}([0, \infty) \times \mathbb{R})$,

$$\begin{aligned}
 & \int_{\mathbb{R}} (u_t \phi_t - u_0 \phi_0 + \ell_t \psi_t - \ell_0 \psi_0) dw \\
 & - \alpha \int_0^t \int_{\mathbb{R}} u_s (\partial_s \phi_s + \Delta \phi_s) + \ell_s (\partial_s \psi_s + \Delta \psi_s) dw ds \\
 (32) \quad & - 2\theta\beta \int_0^t \int_{\mathbb{R}} u_s (1 - u_s) \phi_s + \ell_s (1 - \ell_s) \psi_s dw ds
 \end{aligned}$$

is a continuous martingale with quadratic variation

$$(33) \quad 4\gamma \int_0^t \int_{\mathbb{R}} u_s (1 - u_s) \phi_s^2 + \ell_s (1 - \ell_s) \psi_s^2 + 2\phi_s \psi_s \ell_s (1 - u_s) dw ds.$$

Any sub-sequential limit (u, ℓ) solves this martingale problem. It is standard (see p. 536-537 in [38]) to show that (u, ℓ) then solves the coupled SPDE in Theorem 4 weakly, with respect to some white noises.

4. Green's function representation. As remarked earlier our proof follows the approach in [38]. The first step is to prove the analogue of their (2.11). Observe that $u_t^n(z) = \langle u_t^n, L \mathbf{1}_z \rangle$ and $\ell_t^n(z) = \langle \ell_t^n, L \mathbf{1}_z \rangle$, where $\mathbf{1}_z$ is the function on $L^{-1}\mathbb{Z}$ which is 1 at z and zero elsewhere. Let $\alpha_n = r_n M_n L_n^{-2}$ which converges to α as $n \rightarrow \infty$ and let

$$(34) \quad p_t^n(w) := L \mathbb{P}(X_t^n = w \mid X_0^n = 0)$$

be the transition probability of the simple random walk $(X_t^{(n)})_{t \geq 0}$ on $L^{-1}\mathbb{Z}$ with jump rate $2L^2$, so that it converges to $p_t(w)$ the transition density of Brownian motion run at rate 2. Let $\{P_t^n\}_{t \geq 0}$ be the associated semigroup which has generator the discrete Laplacian Δ_L defined in (19).

Applying the approximate martingale problems with test function

$$(35) \quad \phi_s(w) := \phi_s^{t,z}(w) := \begin{cases} p_{\alpha_n(t-s)}^n(w - z) & \text{for } s \in [0, t], \\ 0 & \text{otherwise} \end{cases}$$

and using the facts that $\partial_s \phi_s + \alpha_n \Delta_L \phi_s = 0$ and $\langle u_0^n, \phi_0^{t,z} \rangle = P_{\alpha_n t}^n u_0^n(z)$, we have

$$(36) \quad u_t^n(z) = P_{\alpha_n t}^n u_0^n(z) + Y_t(\phi) + Z_t(\phi) + E_t^{(1)}(\phi) + E_t^{(2)}(\phi)$$

for $t \geq 0$ and $z \in L^{-1}\mathbb{Z}$. Here $Z_t(\phi)$, $E_t^{(1)}(\phi)$ and $E_t^{(2)}(\phi)$ are martingales defined in (15), (21) and (11) respectively, with ϕ_s defined in (35). To describe the other term, we let $\beta_n = MR^{-1}$ which converges to β , and let $Y_t(\phi)$ be

$$(37) \quad \frac{\theta\beta_n}{L} \int_0^t \sum_{w \in L^{-1}\mathbb{Z}} [u_s^n(w - L^{-1}) + u_s^n(w + L^{-1})](1 - u_s^n(w))\phi_s(w) ds.$$

Repeating the last argument for the labeled particles,

$$(38) \quad \ell_t^n(z) = P_{\alpha_n t}^n \ell_0^n(z) + Y_t^\ell(\phi) + Z_t^\ell(\phi) + E_t^{\ell,1}(\phi) + E_t^{\ell,2}(\phi).$$

Here $Z_t^{(\ell)}(\phi) := Z_t^0(\phi) + Z_t^2(\phi)$ is given by (31), $E_t^{(\ell,2)}(\phi)$ is obtained by replacing (ξ, ξ^c) by (η, η^c) in (21), $E_t^{(\ell,2)}(\phi)$ is the fluctuation term corresponding to (28). The remaining term is

$$Y_t^\ell(\phi) = \frac{\theta\beta_n}{L} \int_0^t \sum_{w \in L^{-1}\mathbb{Z}} \left[\ell_s^n(w + L^{-1}) - u_s^n(w + L^{-1})\ell_s^n(w) + \ell_s^n(w - L^{-1}) - u_s^n(w - L^{-1})\ell_s^n(w) \right] \phi_s(w) ds.$$

5. Tightness. Recall that a sequence of probability measures is said to be C -tight, if it is tight in D and any subsequential limit has a continuous version. The goal of this section is to prove:

THEOREM 5. *Suppose the assumptions in Theorem 1 hold. Then the sequence $\{(u^n, \ell^n)\}_{n \geq 1}$ is C -tight in $D([0, T], C_b(\mathbb{R}) \times C_b(\mathbb{R}))$ for every $T > 0$.*

PROOF. The compact containment condition (condition (a) of Theorem 7.2 in [21, Chapter 3]) holds trivially as $0 \leq \ell^n \leq u^n \leq 1$. Since $C_b(\mathbb{R}) \times C_b(\mathbb{R})$ is equipped with the product metric, the desired C -tightness follows once we can show that for any $\epsilon > 0$, one has

$$(39) \quad \lim_{\delta \rightarrow 0} \limsup_{n \rightarrow \infty} \mathbb{P} \left(\sup_{\substack{t_1 - t_2 < \delta \\ 0 \leq t_2 \leq t_1 \leq T}} \|u_{t_1}^n - u_{t_2}^n\| > \epsilon \right) = 0,$$

$$(40) \quad \lim_{\delta \rightarrow 0} \limsup_{n \rightarrow \infty} \mathbb{P} \left(\sup_{\substack{t_1 - t_2 < \delta \\ 0 \leq t_2 \leq t_1 \leq T}} \|\ell_{t_1}^n - \ell_{t_2}^n\| > \epsilon \right) = 0.$$

Here and in what follows the norm is the one defined in (1). It is enough to show that (39) holds with u^n replaced by any term in the decomposition given in (36), and that (40) holds with ℓ^n replaced by any term in (38).

First term in (36) and (38). By standard coupling arguments for simple random walk, we can check as in Lemma 7(b) of [38] that, upon linearly interpolating $P_{\alpha_n t}^n u_0^n(z)$ in space, we have

$$(41) \quad \sup_{t \in [0, T]} \|P_{\alpha_n t}^n u_0^n - P_{\alpha_n t} f_0\| \rightarrow 0 \quad \text{as } n \rightarrow \infty,$$

where $\{P_t\}_{t \geq 0}$ is the semigroup for the Brownian motion in \mathbb{R} running at rate 2, and f_0 is the initial condition for u functions in Theorem 4. This implies, by the continuity of the semigroup P_t , that (39) holds with u_t^n replaced by $P_{\alpha_n t}^n u_0^n$. By the same reasoning, we have

$$(42) \quad \sup_{t \in [0, T]} \|P_{\alpha_n t}^n \ell_0^n - P_{\alpha_n t} g_0\| \rightarrow 0 \quad \text{as } n \rightarrow \infty$$

where g_0 is the initial condition for ℓ functions in Theorem 4.

Remaining terms in (36) and (38). For simplicity, we write

$$\begin{aligned} \widehat{u}_t^n(z) &:= Y_t(\phi) + Z_t(\phi) + E_t^{(1)}(\phi) + E_t^{(2)}(\phi), \\ \widehat{\ell}_t^n(z) &:= Y_t^{(\ell)}(\phi) + Z_t^{(\ell)}(\phi) + E_t^{(\ell, 1)}(\phi) + E_t^{(\ell, 2)}(\phi). \end{aligned}$$

The next moment estimate for space and time increments is similar to Lemma 6 in [38], but ours implies Hölder continuity of the limits with exponent $< 1/2$ in space and $< 1/4$ in time.

LEMMA 4. *For any $p \geq 2$ and $T \geq 0$, there exists a constant $C(T, p) > 0$ such that*

$$(43) \quad \mathbb{E}|\widehat{u}_{t_1}^n(z_1) - \widehat{u}_{t_2}^n(z_2)|^p \leq C_{T,p} \left(|t_1 - t_2|^{p/4} + |z_1 - z_2|^{p/2} + M^{-p} \right)$$

$$(44) \quad \mathbb{E}|\widehat{\ell}_{t_1}^n(z_1) - \widehat{\ell}_{t_2}^n(z_2)|^p \leq C_{T,p} \left(|t_1 - t_2|^{p/4} + |z_1 - z_2|^{p/2} + M^{-p} \right)$$

for all $0 \leq t_2 \leq t_1 \leq T$, $z_1, z_2 \in L^{-1}\mathbb{Z}$ and $n \geq 1$.

The proof of this result is postponed to the next section since it requires a number of computations. We now argue that (43) implies (39) holds for \widehat{u}^n . This idea is described in the paragraph before Lemma 7 in [38] and page 648 of [31]: we approximate the càdlàg process \widehat{u}^n by a *continuous* process \tilde{u} and invoke a tightness criterion inspired by Kolmogorov's continuity theorem.

LEMMA 5. *Define $\tilde{u}^n \in C([0, \infty), C_b(\mathbb{R}))$ by $\tilde{u}_t = \widehat{u}_t$ on the grid $t \in \theta_n \mathbb{Z}_+$ and then linearly interpolate in t for each $w \in \mathbb{R}$. Suppose $\theta_n > M^{-4}$*

and $\lim_{n \rightarrow \infty} \theta_n = 0$. Then there exists $n_0 \in \mathbb{N}$ such that for any $p \geq 2$, $T \geq 0$ and $K \geq 0$,

$$(45) \quad \mathbb{E} |\tilde{u}_{t_1}^n(z_1) - \tilde{u}_{t_2}^n(z_2)|^p \leq C_{T,p,K} \left(|t_1 - t_2|^{p/4} + |z_1 - z_2|^{p/2} \right),$$

for all $0 \leq t_2 \leq t_1 \leq T$, $z_i \in \mathbb{R}$ with $|z_i| \leq K$ ($i = 1, 2$) and $n \geq n_0$.

By a standard argument (see, for example, Problems 2.2.9 and 2.4.11 of [29]), one can show that (45) implies that (39) holds when u is replaced by \tilde{u}^n . Finally, by the reasoning in the proof of Lemma 7(a) in [38], there is a $\sigma > 0$ so that

$$\limsup_{n \rightarrow \infty} \mathbb{P} \left(\sup_{t \in [0, T]} \|\tilde{u}_t^n - \hat{u}_t^n\| \geq n^{-\sigma} \right) = 0.$$

Therefore (39) holds for \hat{u}^n . By the same argument, (44) implies (40) holds for $\hat{\ell}^n$. Theorem 5 will be proved once Lemmas 4 and 5 are. \square

6. Proofs of Lemmas 4 and 5.

PROOF OF LEMMA 4. We prove only (43) for unlabeled particles. The proof of (44) for labeled particles is similar. The basic ingredients are the following estimates of time and space increments of the transition probability of simple random walk. Namely, there exists a constant $C > 0$ independent of n such that

$$(46) \quad 0 \leq \int_0^T p_s^n(0) ds \leq C \sqrt{T},$$

$$(47) \quad 0 \leq \int_0^\infty p_s^n(0) - p_{s+\theta}^n(0) ds \leq C \sqrt{\theta},$$

$$(48) \quad 0 \leq \int_0^\infty p_s^n(0) - p_s^n(z) ds \leq C |z|$$

$$(49) \quad \int_0^T \frac{1}{L} \sum_w |p_{s+\theta}^n(w) - p_s^n(w)| ds \leq C \sqrt{T \theta},$$

$$(50) \quad \int_0^T \frac{1}{L} \sum_w |p_s^n(w) - p_s^n(z+w)| ds \leq C \sqrt{T} |z|$$

for $\theta \geq 0$, $z \in L^{-1}\mathbb{Z}$ and $T > 0$. These estimates can be either found or deduced from the standard methods described in Chapter 2 in [35]. For completeness, we give precise references and missing details in the next section.

We will show that each of the four terms of \widehat{u}^n satisfies (43). To simplify notation, we assume, without loss of generality for the proof, that $\alpha_n \equiv 1$. First, we deal with the process Y that has no jumps. To reduce the size of the formulas we let

$$v_s^n(w) = [u_s^n(w - L^{-1}) + u_s^n(w + L^{-1})](1 - u_s^n(w)).$$

Using the definitions of Y (37) and of our test function (35) we have for $t_1 > t_2$

$$\begin{aligned} Y_{t_1}(\phi^{t_1, z_1}) - Y_{t_2}(\phi^{t_2, z_2}) &= \theta \beta_n \int_{t_2}^{t_1} \frac{1}{L} \sum_w v_s^n(w) p_{t_1-s}^n(z_1 - w) ds \\ &\quad + \theta \beta_n \int_0^{t_2} \frac{1}{L} \sum_w v_s^n(w) [p_{t_1-s}^n(z_1 - w) - p_{t_2-s}^n(z_2 - w)] ds \\ &\equiv \theta \beta_n (\Theta_1(Y) + \Theta_2(Y)). \end{aligned}$$

The sums are over $w \in L^{-1}\mathbb{Z}$, which we have omitted to simplify notation. Since $0 \leq u^n \leq 1$ and $L^{-1} \sum_w p_t^n(z - w) = 1$ (recall the definition of p^n in (34)), we have

$$(51) \quad \mathbb{E}|\Theta_1(Y)|^p \leq 2^p (t_1 - t_2)^p.$$

by Hölder's inequality.

By the triangle inequality and the translation invariance and symmetry of the transition density, we obtain

$$\begin{aligned} &\int_0^{t_2} \frac{1}{L} \sum_w |p_{t_1-s}^n(z_1 - w) - p_{t_2-s}^n(z_2 - w)| ds \\ &\leq \int_0^{t_2} \frac{1}{L} \sum_w (|p_{t_1-s}^n(z_1 - z_2 + w) - p_{t_1-s}^n(w)| + |p_{t_1-s}^n(w) - p_{t_2-s}^n(w)|) ds \\ &\leq C_T |z_1 - z_2| + C \sqrt{t_1 - t_2} \end{aligned}$$

by (50) and (49). Since $0 \leq v^n \leq 2$,

$$(52) \quad \mathbb{E}[|\Theta_2(Y)|^p] \leq C_{T,p} (\sqrt{t_1 - t_2} + |z_1 - z_2|)^p$$

for all $0 \leq t_2 \leq t_1 \leq T$, $z_1, z_2 \in L^{-1}\mathbb{Z}$ and $n \geq 1$.

It remains to consider $E_t^{(1)}(\phi)$, $E_t^{(2)}(\phi)$ and $Z_t(\phi)$. Note that for each of them, the largest possible jump is bounded almost surely by

$$2(ML)^{-1} \sup_{s \geq 0} \|\phi_s\|_\infty \leq 2M^{-1},$$

because ϕ_s , as defined in (35), is bounded by L .

We shall employ a version of the Burkholder-Davis-Gundy inequality stated at the bottom of page 527 in [38]. Namely, for any càdlàg martingale X with $X_0 = 0$ and for $p \geq 2$,

$$(53) \quad \mathbb{E} \left[\sup_{s \in [0, t]} |X_s|^p \right] \leq C(p) \mathbb{E} \left[\langle X \rangle_t^{p/2} + \sup_{s \in [0, t]} |X_s - X_{s-}|^p \right], \quad t \geq 0.$$

Writing $N_s^{x,y}$ for the compensated Poisson process $P_s^{x,y} - r_n s$, and $\sum_{x,y \sim x}$ for the double sum $\sum_x \sum_{y \sim x}$, we decompose

$$\begin{aligned} & E_{t_1}^{(1)}(\phi^{t_1, z_1}) - E_{t_2}^{(1)}(\phi^{t_2, z_2}) \\ &= \frac{1}{ML} \sum_{x,y \sim x} \int_{t_2}^{t_1} \xi_{s-}(y) \xi_{s-}^c(x) (p_{t_1-s}^n(z_1 - y) - p_{t_1-s}^n(z_1 - x)) dN_s^{x,y} \\ &+ \frac{1}{ML} \sum_{x,y \sim x} \int_0^{t_2} \xi_{s-}(y) \xi_{s-}^c(x) (p_{t_1-s}^n(z_1 - y) - p_{t_1-s}^n(z_1 - x) \\ &\quad - p_{t_2-s}^n(z_2 - y) + p_{t_2-s}^n(z_2 - x)) dN_s^{x,y} \\ &\equiv \Theta_1(E^{(1)}) + \Theta_2(E^{(1)}). \end{aligned}$$

Writing $\tilde{N}_s^{x,y}$ for the compensated Poisson process $\tilde{P}_s^{x,y} - \theta R_n^{-1} s$ we have

$$\begin{aligned} & E_{t_1}^{(2)}(\phi^{t_1, z_1}) - E_{t_2}^{(2)}(\phi^{t_2, z_2}) \\ &= \frac{1}{ML} \sum_{x,y \sim x} \int_{t_2}^{t_1} \xi_{s-}(y) (1 - \xi_{s-}(x)) p_{t_1-s}^n(z_1 - x) d\tilde{N}_s^{x,y} \\ &+ \frac{1}{ML} \sum_{x,y \sim x} \int_0^{t_2} \xi_{s-}(y) (1 - \xi_{s-}(x)) [p_{t_1-s}^n(z_1 - x) - p_{t_2-s}^n(z_2 - x)] d\tilde{N}_s^{x,y} \\ &\equiv \Theta_1(E^{(2)}) + \Theta_2(E^{(2)}). \end{aligned}$$

Finally, writing $Q_s^{x,y} = N_s^{y,x} - N_s^{x,y}$ we have

$$\begin{aligned} & Z_{t_1}(\phi^{t_1, z_1}) - Z_{t_2}(\phi^{t_2, z_2}) \\ &= \frac{1}{ML} \sum_{x,y \sim x} \int_{t_2}^{t_1} (1 - \xi_{s-}(y)) \xi_{s-}(x) p_{t_1-s}^n(z_1 - x) dQ_s^{x,y} \\ &+ \frac{1}{ML} \sum_{x,y \sim x} \int_0^{t_2} (1 - \xi_{s-}(y)) \xi_{s-}(x) [p_{t_1-s}^n(z_1 - x) - p_{t_2-s}^n(z_2 - x)] dQ_s^{x,y} \\ &\equiv \Theta_1(Z) + \Theta_2(Z). \end{aligned}$$

Once we use $0 \leq \xi \leq 1$ to simplify the integrands the three expressions have a similar structure. $E^{(1)}$ will be the smallest since it has a difference of transition densities at adjacent sites, so we begin by estimating $E^{(2)}$. To estimate $\Theta_1(E^{(2)})$, we let

$$X_t^1 = \frac{1}{ML} \sum_{x,y \sim x} \int_0^t \xi_{s-}(y) \xi_{s-}^c(x) p_{t_1-t_2-s}^n(z_1-x) d\tilde{N}_s^{x,y}.$$

By Markov property of $(\xi_t)_{t \geq 0}$ and the stationarity of the compensated Poisson process,

$$\mathbb{E}(|\Theta_1(E^{(2)})|^p) = \mathbb{E} \mathbb{E}^{\xi_{t_2}}(|X_{t_1-t_2}|^p),$$

where $\mathbb{E}^{\xi_{t_2}}$ is the expectation w.r.t. the law of ξ starting at ξ_{t_2} .

To prepare for the next calculation we note that using the symmetry of the transition density and the Chapman-Kolmogorov equation

$$(54) \quad L^{-1} \sum_w [p_u^n(w)]^2 = L^{-1} \sum_w p_u^n(w) p_u^n(-w) = p_{2u}(0).$$

The predictable bracket process of X^1 is

$$\langle X^1 \rangle_t = \frac{\theta}{R_n(ML)^2} \sum_{x,y \sim x} \int_0^t \xi_{s-}(y) \xi_{s-}^c(x) [p_{t_1-t_2-s}^n(z_1-x)]^2 ds.$$

Since there are $2M$ values of y for each x and M values of x for each $w \in L^{-1}\mathbb{Z}$, if we let $c_n = 2\theta/R_n L_n$ then the above is

$$\begin{aligned} &\leq c_n \int_0^t L^{-1} \sum_w (p_{t_1-t_2-s}^n(w))^2 ds \\ &= c_n \int_0^t p_{2(t_1-t_2-s)}^n(0) ds \leq c_n C (t_1 - t_2)^{1/2} \end{aligned}$$

for $t \in [0, t_1 - t_2]$, where in the second step we have used the (54) and in the last step we used (46), Note that $c_n \rightarrow 0$ since $R_n L_n \rightarrow \infty$.

If we do the calculation for Z then $c_n = 2r_n/L \rightarrow 2\gamma$ so we get the same upper bound. In $E^{(1)}$, $c_n = r_n/L_n \rightarrow \gamma$ but we have $p_{t_1-s}^n(z_1-y) - p_{t_1-s}^n(z_1-x)$ instead of a single p , so

$$\begin{aligned} &L^{-1} \sum_w [p_{t_1-t_2-s}^n(w) - p_{t_1-t_2-s}^n(w - L^{-1})]^2 \\ &= 2p_{2(t_1-t_2-s)}^n(0) - 2p_{2(t_1-t_2-s)}^n(L^{-1}). \end{aligned}$$

If we use (50) now we would get an upper bound of $C_T L^{-1}$ when we integrate the above expression with respect to ds from $s = 0$ to $s = T$. Therefore, by (53), we have

$$(55) \quad \mathbb{E}(|\Theta_1|^p) \leq C_p(|t_1 - t_2|^{p/4} + M^{-p}).$$

for $E^{(1)}$, $E^{(2)}$ and Z .

Similarly, $\mathbb{E}(|\Theta_2(E^{(2)})|^p) = \mathbb{E}(|X_t^2|^p)$, where

$$X_t^2 = \frac{1}{ML} \sum_{x, y \sim x} \int_0^t \xi_{s-}(y) \xi_{s-}^c(x) [p_{t_1-s}^n(z_1 - x) - p_{t_2-s}^n(z_2 - x)] d\tilde{N}_s^{x,y}$$

is a càdlàg martingale for $t \leq t_2$ with predictable bracket process

$$\langle X^2 \rangle_t \leq c_n \int_0^t L^{-1} \sum_w [p_{t_1-s}^n(z_1 - w) - p_{t_2-s}^n(z_2 - w)]^2.$$

Arguing as before using (54) we get

$$\leq c_n \int_0^t p_{2(t_1-s)}^n(0) + p_{2(t_2-s)}^n(0) - 2p_{t_2+t_1-2s}^n(z_1 - z_2)$$

a result that also holds for $E^{(1)}$ and Z . Adding and subtracting $2p_{t_2+t_1-2s}^n(0)$ and using (47) and (48) the above is at most

$$C\sqrt{t_1 - t_2} + C_T|z_1 - z_2|.$$

Using (53) now, we have

$$(56) \quad \mathbb{E}(|\Theta_2|^p) \leq C_{p,T}(|t_1 - t_2|^{p/4} + |z_1 - z_2|^{p/2} + M^{-p})$$

which holds for $E^{(1)}$, $E^{(2)}$ and Z and the proof is complete. \square

PROOF OF LEMMA 5. It suffices to consider the case $|t_1 - t_2|^{1/4} \leq M^{-1}$ and $|z_1 - z_2|^{1/2} \leq M^{-1}$, since otherwise Lemma 4 easily implies (45). The triangle inequality gives

$$(57) \quad |\tilde{u}_{t_1}^n(z_1) - \tilde{u}_{t_2}^n(z_2)| \leq |\tilde{u}_{t_1}^n(z_1) - \tilde{u}_{t_2}^n(z_1)| + |\tilde{u}_{t_2}^n(z_1) - \tilde{u}_{t_2}^n(z_2)|.$$

We first estimate the time difference on the right. Write $s_k := k\theta_n$ for $k \in \mathbb{Z}_+$. Since $|t_1 - t_2| \leq M^{-4} < \theta_n$, we have either $s_k \leq t_2 < t_1 \leq s_{k+1}$ for some k or $t_2 < s_k < t_1$ for some k . Since \tilde{u}^n is linear between grid points, in either case

$$|\tilde{u}_{t_1}^n(z) - \tilde{u}_{t_2}^n(z)| \leq 2 \left(|\widehat{u}_{s_{k+1}}^n(z) - \widehat{u}_{s_k}^n(z)| \vee |\widehat{u}_{s_k}^n(z) - \widehat{u}_{s_{k-1}}^n(z)| \right) \frac{|t_1 - t_2|}{\theta_n}.$$

Hence Lemma 4, the assumption $M^{-4} < \theta_n$ and $|t_1 - t_2| \leq M^{-4}$ imply that

$$\begin{aligned} \mathbb{E}|\tilde{u}_{t_1}^n(z) - \tilde{u}_{t_2}^n(z)|^p &\leq C_{T,p} \frac{|t_1 - t_2|^p}{\theta_n^p} (\theta_n^{p/4} + M^{-p}) \\ &\leq C_{T,p} \left(\frac{|t_1 - t_2|}{\theta_n^{3/4}} \right)^p \leq C_{T,p} |t_1 - t_2|^{p/4}. \end{aligned}$$

Next, we estimate the space difference on the right of (57). Take n large so that $M^{-1} < (1 + \gamma)L^{-1}$ and $(1 + \gamma)^2 L^{-2} < L^{-1}$ (this is possible by our assumptions on scalings, even if $\gamma = 0$). Then $|z_1 - z_2| < (1 + \gamma)^2 L^{-2} < L^{-1}$. By almost the same argument used above, we easily obtain

$$\begin{aligned} \mathbb{E}|\tilde{u}_t^n(z_1) - \tilde{u}_t^n(z_2)|^p &\leq C(T, p) |z_1 - z_2|^p L^p (L^{-p/2} + M^{-p}) \\ &\leq C(T, p) |z_1 - z_2|^p (L^{p/2} + (1 + \gamma)^p) \\ &\leq C(T, p) \left[(1 + \gamma)^{p/2} |z_1 - z_2|^{3p/4} + (1 + \gamma)^p |z_1 - z_2|^p \right]. \end{aligned}$$

The proof of Lemma 5 is complete. \square

7. Random walk estimates. The first two, (46) and (47), follow directly from the local central limit theorem (LCLT) (see, for example, Proposition 2.5.6 in [35]). (49) follows from (50) and the Chapman-Kolmogorov equation: the integrand can be written as

$$p_{s+\theta}^n(w) - p_s^n(w) = \frac{1}{L} \sum_{z \in L^{-1}\mathbb{Z}} p_\theta^n(z) (p_s^n(w - z) - p_s^n(w)).$$

It remains to prove (48) and (50).

By scaling, $p_t^n(w) = L p_{L^2 t}(Lw)$ where $p_t(k)$ is the transition density of the simple random walk on \mathbb{Z} . The integral of (48) is therefore

$$\frac{1}{L} \int_0^\infty p_s^n(0) - p_s^n(Lz) ds.$$

Splitting this integral into two parts according to whether $s \leq L|z|^2$ or $s > L|z|^2$, the first part is bounded by $L^{-1} \int_0^{L|z|^2} p_s^n(0) ds \leq C|z|/\sqrt{L}$ according to (46). The second part is bounded by $C|z|$ by the LCLT.

Formula (50) is similar to Proposition 2.4.1 in [35] which says that

$$(58) \quad \sum_{k \in \mathbb{Z}} |q_m(k) - q_m(k + j)| \leq \frac{Cj}{\sqrt{m}},$$

where $q_m(k)$ is the transition density for the discrete time simple random walk on \mathbb{Z} . Hence, by using scaling and an independent Poisson process N_t , we rewrite the left hand side of (50) as

$$\begin{aligned} & \frac{1}{L^2} \int_0^{L^2 T} \sum_{k \in \mathbb{Z}} |p_s^n(k) - p_s^n(k + Lz)| ds \\ &= \frac{1}{L^2} \int_0^{L^2 T} \sum_{k \in \mathbb{Z}} \left| \sum_{m=0}^{\infty} \mathbb{P}(N_s = m) (q_m(k) - q_m(k + Lz)) \right| ds \end{aligned}$$

which is at most

$$\frac{C|z|}{L} \int_0^{L^2 T} \sum_{m=0}^{\infty} \frac{\mathbb{P}(N_s = m)}{\sqrt{m}} ds$$

by (58). Arguing as in the proof of Proposition 2.5.6 in [35] by using Proposition 2.5.5 (the LCLT for Poisson processes), we obtain that the integral is of order $\sqrt{L^2 T}$ and hence (50) holds.

8. Proof of Lemma 2. To prepare for the proof for the SPDE, we begin by considering the diffusion process

$$(59) \quad dU = \beta U(1 - U) dt + \sigma \sqrt{U(1 - U)} dB.$$

Following the approach of Doering, Mueller and Smereka [12], we change variables $Z = 1 - U$ to get (recall $dZ = -dU$)

$$(60) \quad dZ = -\beta Z(1 - Z) dt - \sigma \sqrt{Z(1 - Z)} dB.$$

The minus in front of the diffusion term is not important here but it will be in the next calculation in (63). Using Itô's formula and ignoring the martingale terms

$$\begin{aligned} \text{drift}(Z^m) &= mZ^{m-1}(-\beta Z(1 - Z)) + m(m-1)Z^{m-2} \frac{\sigma^2}{2} Z(1 - Z) \\ &= \beta m[Z^{m+1} - Z^m] + \frac{\sigma^2 m(m-1)}{2} [Z^{m-1} - Z^m]. \end{aligned}$$

Let $N(t)$ be a Markov process with Q matrix

$$(61) \quad \begin{aligned} Q_{m,m+1} &= \beta m & Q_{m,m-1} &= \sigma^2 \frac{m(m-1)}{2} \\ Q_{m,m} &= -\beta m - \sigma^2 \frac{m(m-1)}{2}. \end{aligned}$$

Combining our calculations,

$$\frac{d}{dt}EZ^m = \sum_n Q_{m,n}EZ^n$$

Letting $P_{\ell,m}(t) = \mathbb{P}(N(t) = m | N(0) = \ell)$ be the transition probabilities, we have

LEMMA 6. *For fixed $T > 0$ and $\ell \geq 1$, $M_t = \sum_{m=1}^{\infty} P_{\ell,m}(T-t)Z^m(t)$ is a martingale.*

PROOF. Differentiating we have

$$\begin{aligned} \frac{d}{dt}EM_t &= \sum_m EZ^m(t) \frac{d}{dt}P_{\ell,m}(T-t) + P_{\ell,m}(T-t) \frac{d}{dt}EZ^m(t) \\ &= \sum_m -EZ^m(t) \sum_n P_{\ell,n}(T-t)Q_{n,m} \\ &\quad + P_{\ell,m}(T-t) \sum_n Q_{m,n}EZ^n(t) = 0 \end{aligned}$$

if we interchange the roles of m and n in the second sum. \square

From Lemma 6 we get

$$(62) \quad EZ^{N(0)}(T) = EZ^{N(T)}(0).$$

Now consider the system

$$(63) \quad \begin{aligned} dZ &= -\beta Z(1-Z)dt - \sigma\sqrt{VZ}dB^0 - \sigma\sqrt{Z(1-Z-V)}dB^1, \\ dV &= \beta VZdt + \sigma\sqrt{VZ}dB^0 + \sigma\sqrt{V(1-V-Z)}dB^2, \end{aligned}$$

where the B^i are independent Brownian motions. To get our second dual function, we consider $Y_n = \sum_{m=1}^n Z^{m-1}V$. Using Itô's formula and for the second term recall (60),

$$\begin{aligned} \text{drift} \left(\sum_{m=1}^n Z^{m-1}V \right) &= V \sum_{m=2}^n (m-1)Z^{m-2}(-\beta Z(1-Z)) \\ &\quad + \frac{\sigma^2}{2}V \sum_{m=3}^n (m-1)(m-2)Z^{m-3}Z(1-Z) \\ &\quad + \sum_{m=1}^n Z^{m-1}\beta ZV - \sigma^2 \sum_{m=2}^n (m-1)Z^{m-2}VZ, \end{aligned}$$

where the last term comes from the fact that the covariance of Z and V is $-\sigma^2 VZ$. Collecting the terms with β , and changing variables $k = m - 1$ in the second sum we get

$$= \beta V \left[\sum_{m=2}^n (m-1)Z^m - \sum_{k=1}^{n-1} kZ^k + \sum_{m=1}^n Z^m \right].$$

Adding the third sum to the first

$$\begin{aligned} &= \beta V \left[\sum_{m=1}^n mZ^m - \sum_{k=1}^{n-1} kZ^k \right] \\ &= n\beta V Z^n = n\beta \left(\sum_{m=1}^{n+1} Z^{m-1}V - \sum_{m=1}^n Z^{m-1}V \right) \end{aligned}$$

which corresponds to jumps from n to $n+1$ at rate βn . Collecting the terms with σ^2 and changing variables to have Z^{k-1} , we get

$$= \sigma^2 V \left[\sum_{k=2}^{n-1} \frac{k(k-1)}{2} Z^{k-1} - \sum_{k=3}^n \frac{(k-1)(k-2)}{2} Z^{k-1} - \sum_{k=2}^n (k-1)Z^{k-1} \right].$$

Moving terms $k = 2$ to $n-1$ from the last sum into the first one

$$= \sigma^2 V \left[\sum_{k=2}^{n-1} \frac{(k-2)(k-1)}{2} Z^{k-1} - \sum_{k=3}^n \frac{(k-1)(k-2)}{2} Z^{k-1} - (n-1)Z^{n-1} \right].$$

The $k = 2$ term in the first sum vanishes. Terms 3 to $n-1$ in the first sum cancel with the second sum leaving

$$= -\sigma^2 V \frac{n(n-1)}{2} Z^{n-1} = \sigma^2 \frac{n(n-1)}{2} \left(\sum_{m=1}^{n-1} Z^{m-1}V - \sum_{m=1}^n Z^{m-1}V \right)$$

which corresponds to jumps n to $n-1$ at rate $\sigma^2 n(n-1)/2$.

Combining our calculations

$$\frac{d}{dt} EY_n = \sum_m Q_{m,n} EY_n.$$

where $Q_{m,n}$ is given in (61). Using Lemma 6 again,

$$E \left(\sum_{m=1}^{N(0)} Z^{m-1}(T)V(T) \right) = E \left(\sum_{m=1}^{N(T)} Z^{m-1}(0)V(0) \right).$$

8.1. *Duality for the Wright-Fisher SPDE.* We begin by proving the duality result for the equation for single SPDE (2). This is a known result due to Shiga [44]. However, he did not give many details and we need to generalize his result to our coupled SPDE, so we will follow the approach of Athreya and Tribe [1]. Let $z = 1 - u$. Define $\bar{z}_t(x) = \int z_t(y)p^\epsilon(y-x) dy$ where p^ϵ is the normal density with mean 0 and variance ϵ . Noting that $x \rightarrow \bar{z}_t(x)$ is smooth and using the weak formulation of (2) with test function $\phi^{\epsilon,x}(y) = p^\epsilon(y-x)$, we have

$$\begin{aligned}
 \bar{z}_t(x) - \bar{z}_0(x) &= \int_0^t \alpha \Delta \bar{z}_s(x) ds \\
 (64) \quad &- \theta \beta \int_0^t \int 2z_s(y)(1-z_s(y))p^\epsilon(y-x) dy ds \\
 &+ \int_0^t \int \sqrt{4\gamma z_s(y)(1-z_s(y))} p^\epsilon(y-x) dW.
 \end{aligned}$$

Using Itô's formula (each $\bar{z}_t(x)$ is a semi-martingale so this is legitimate) and writing \mathcal{L}_z for the generator of $(\bar{z}_t(x_1), \dots, \bar{z}_t(x_n))$ with x_1, \dots, x_n fixed, we see that (ignoring the martingale terms)

$$\begin{aligned}
 \text{drift} \left(\mathcal{L}_{\bar{z}} \prod_i \bar{z}_t(x_i) \right) &= \sum_{i=1}^n \prod_{j \neq i} \bar{z}_t(x_j) \alpha \Delta \bar{z}_t(x_i) \\
 (65) \quad &+ 2\theta\beta \sum_{i=1}^n \prod_{j \neq i} \bar{z}_t(x_j) \int [z_t^2(y) - z_t(y)] p^\epsilon(y-x_i) dy \\
 &+ 4\gamma \sum_{i=1}^{n-1} \sum_{j=i+1}^n \prod_{k \neq i,j} \bar{z}_t(x_k) \int [z_t(y)(1-z_t(y))] p^\epsilon(y-x_i) p^\epsilon(y-x_j) dy.
 \end{aligned}$$

The dual process is a system of branching coalescing Brownian particles. During their lifetime the particles are Brownian motions run at rate 2α with each giving birth at rate $2\theta\beta$. In addition, for $i < j$, particle j is killed by particle i at rate $4\gamma L_t^{i,j}$ where $L_t^{i,j}$ denotes the local time of the process

$x_j - x_i$ at 0. Writing \mathcal{L}_x for the generator, we have

$$\begin{aligned}
(66) \quad & \text{drift} \left(\mathcal{L}_x \prod_i \bar{z}_t(x_i) \right) = \sum_{i=1}^n \prod_{j \neq i} \bar{z}_t(x_j) \alpha \Delta \bar{z}_t(x_i) \\
& + 2\theta\beta \sum_{i=1}^n \prod_{j \neq i} \bar{z}_t(x_j) \cdot [\bar{z}_t^2(x_i) - \bar{z}_t(x_i)] \\
& + 4\gamma \sum_{i=1}^{n-1} \sum_{j=i+1}^n \prod_{k \neq i, j} \bar{z}_t(x_k) \cdot [\bar{z}_t(x_i)(1 - \bar{z}_t(x_j))] \delta_{\{x_j=x_i\}}
\end{aligned}$$

in which we used the formal notation $dL_t^{i,j} = \delta_{\{x_j(t)=x_i(t)\}} dt$. The precise meaning of the last term involves integration w.r.t. local times and is explained in (70).

We now follow Proposition 1 in [1] to use the duality method encapsulated in Theorem 4.4.11 of Ethier and Kurtz [21]. In their notation $\alpha = \beta = 0$.

$$F(\bar{z}, x) = \prod_{i=1}^n \bar{z}(x_i) \quad \text{if } x = (x_1, \dots, x_n).$$

They suppose $F(\bar{z}_t, x) - \int_0^t G(\bar{z}_s, x) ds$ and $F(\bar{z}, x(t)) - \int_0^t H(\bar{z}, x(s)) ds$ are martingales and conclude that for $t \geq 0$,

$$(67) \quad \mathbb{E}F(\bar{z}_t, x(0)) - \mathbb{E}F(\bar{z}_0, x(t)) = \mathbb{E} \int_0^t G(\bar{z}_{t-s}, x(s)) - H(\bar{z}_{t-s}, x(s)) ds.$$

In our situation, (67) holds with $G(\bar{z}, x) = \mathcal{L}_{\bar{z}}F(\bar{z}, x)$ and $H(\bar{z}, x) = \mathcal{L}_x F(\bar{z}, x)$.

By the continuity of $x \mapsto z_t(x)$, we have $F(\bar{z}_t, x(0)) \rightarrow F(z_t, x(0))$ and $F(\bar{z}_0, x(t)) \rightarrow F(z_0, x(t))$ a.s. as $\epsilon \rightarrow 0$, so using the bounded convergence theorem,

$$\mathbb{E}F(\bar{z}_t, x(0)) - \mathbb{E}F(\bar{z}_0, x(t)) \rightarrow \mathbb{E}F(z_t, x(0)) - \mathbb{E}F(z_0, x(t)).$$

To prove the desired duality formula

$$(68) \quad \mathbb{E} \prod_{i=1}^{n(0)} z_t(x_i(0)) = \mathbb{E} \prod_{i=1}^{n(t)} z_0(x_i(t)), \quad t \geq 0,$$

it remains to argue that the RHS of (67) tends to zero as $\epsilon \rightarrow 0$.

The first term in (65) agrees with that of (66). For the second terms, omitting $2\theta\beta$, the integrand of the difference is

$$(69) \quad \mathbb{E} \int_0^t \sum_{i=1}^{n(s)} \prod_{j \neq i} \bar{z}_{t-s}(x_j(s)) \left[\int z_{t-s}^2(y) p^\epsilon(y - x_i(s)) dy - \bar{z}_{t-s}^2(x_i(s)) \right] ds \rightarrow 0$$

a.s. for $s \in (0, t)$, by continuity of $y \mapsto z_s(y)$ and dominated convergence. The contribution to (67) from the third term of (66) is (omitting 4γ)

$$(70) \quad \mathbb{E} \int_0^t \sum_{i=1}^{n(s)-1} \sum_{j=i+1}^{n(s)} \prod_{k \neq i, j} \bar{z}_{t-s}(x_k(s)) \cdot [\bar{z}_{t-s}(x_i(s))(1 - \bar{z}_{t-s}(x_j(s)))] dL_s^{i,j}$$

which converges, by dominated convergence to

$$(71) \quad \mathbb{E} \int_0^t \sum_{i=1}^{n(s)-1} \sum_{j=i+1}^{n(s)} \prod_{k \neq i, j} z_{t-s}(x_k(s)) \cdot [z_{t-s}(x_i(s))(1 - z_{t-s}(x_j(s)))] dL_s^{i,j}.$$

Finally, we consider the contribution to (67) from the third term of (65). After the substitution $y \mapsto y + x_i(s)$, we have (omitting 4γ)

$$(72) \quad \mathbb{E} \int_0^t \sum_{i=1}^{n(s)-1} \sum_{j=i+1}^{n(s)} \int p^\epsilon(y) p^\epsilon(y + x_i(s) - x_j(s)) Y_{s,t}^{i,j}(y) dy ds,$$

where for any i, j ,

$$Y_{s,t}^{i,j}(y) = \prod_{k \neq i, j} \bar{z}_{t-s}(x_k(s)) \cdot [z_{t-s}(y + x_i(s))(1 - z_{t-s}(y + x_i(s)))].$$

At this point we would like to apply Lemma 2 of [1], to obtain

$$(73) \quad \int_0^t p^\epsilon(y + x_i(s) - x_j(s)) Y_{s,t}^{i,j}(y) ds = \int \int_0^t p^\epsilon(y + z) Y_{s,t}^{i,j}(y) dL_s^{i,j,z} dz,$$

where $L_t^{i,j,z}$ denotes the local time of the process $x_j - x_i$ at z . Their formula assumes Y is predictable, so we substitute $s-$ for s and note that this does not change the integral in (72).

Putting (73) into (72), then using the continuity of the local time and that of $Y_{s,t}^{i,j}(y)$ (see details in pages 1724–1725 of [1]), the integrand of (72) converges a.s. to the integrand of (71). Convergence of expectations then follows from dominated convergence and the proof of (68) is complete.

8.2. Duality for the coupled SPDE. To prove the duality formula for the coupled SPDE, we order the particles in $x_i(t)$, $i \leq n(t)$ in such a way that (i) when two particles coalesce we keep the smaller index and (ii) immediately after particle i gives birth, its offspring has index i and all particles with index $\geq i$ (including the one that just gave birth) increase their index by

1. Adding the number of particles in the dual as another variable to help clarify things, for $k \geq 1$ we let

$$(74) \quad F_k((z, \ell), (x, n)) = \sum_{1 \leq j_1 < j_2 < \dots < j_k \leq n} \ell(x_{j_k}) \cdots \ell(x_{j_1}) \prod_{i=1}^{j_1-1} z(x_i).$$

The following duality formula is motivated by (4):

$$(75) \quad \mathbb{E}F_k((z_t, \ell_t), (x_0, n_0)) = \mathbb{E}F_k((z_0, \ell_0), (x_t, n_t)), \quad k \geq 1.$$

Once we have shown (75), the uniqueness claimed in Lemma 2 follows, since it allows us to conclude that the distribution at a fixed time is unique by identifying all cross moments of the bounded functions u and ℓ . Uniqueness of the law of the process (u, ℓ) then follows from Theorem 4.2 in Chapter 4 of Ethier and Kurtz [21]. The duality function (68) for the Wright-Fisher SPDE can be viewed as the case $k = 0$. We shall provide the details of proof of (75) for the case $k = 1$, the other cases are similar.

We let $\bar{\ell}_t(x) = \int \ell_t(y) p^\epsilon(y - x) dy$ and note

$$\begin{aligned} \bar{z}_t(x) - \bar{z}_0(x) &= \int_0^t \alpha \Delta \bar{z}_s(x) ds \\ &\quad - 2\theta\beta \int_0^t \int z_s(y)(1 - z_s(y)) p^\epsilon(y - x) dy ds \\ &\quad - \int_0^t \int \sqrt{4\gamma z_s(y) \ell_s(y)} p^\epsilon(y - x) dW^0 \\ &\quad - \int_0^t \int \sqrt{4\gamma z_s(y)(1 - z_s(y) - \ell_s(y))} p^\epsilon(y - x) dW \\ \bar{\ell}_t(x) - \bar{\ell}_0(x) &= \int_0^t \alpha \Delta \bar{\ell}_s(x) ds \\ &\quad + 2\theta\beta \int_0^t \int z_s(y) \ell_s(y) p^\epsilon(y - x) dy ds \\ &\quad + \int_0^t \int \sqrt{4\gamma z_s(y) \ell_s(y)} p^\epsilon(y - x) dW^0 \\ &\quad + \int_0^t \int \sqrt{4\gamma \ell_s(y)(1 - z_s(y) - \ell_s(y))} p^\epsilon(y - x) dW^2. \end{aligned}$$

Writing $\mathcal{L}_{\bar{z}, \bar{\ell}}$ for the generator of $(\bar{z}_t(x_1), \dots, \bar{z}_t(x_{k-1}), \bar{\ell}_t(x_k))$ with x_1, \dots, x_n

and n fixed, drift $[\mathcal{L}_{\bar{z}, \bar{\ell}} F_1((\bar{z}_t, \bar{\ell}_t), (x, n))]$

$$(76) \quad = \sum_{k=2}^n \sum_{i=1}^{k-1} \prod_{\substack{1 \leq j \leq k \\ j \neq i}} \bar{z}_t(x_j) \cdot \alpha \Delta \bar{z}_t(x_i) \cdot \bar{\ell}_t(x_k) + \prod_{j=1}^{k-1} \bar{z}_t(x_j) \alpha \Delta \bar{\ell}_t(x_k)$$

$$(77) \quad + \sum_{k=2}^n 2\theta\beta \sum_{i=1}^{k-1} \prod_{j \neq i} \bar{z}_t(x_j) \cdot \bar{\ell}_t(x_k) \int [z_t^2(y) - z_t(y)] p^\epsilon(y - x_i) dy$$

$$(78) \quad + \sum_{k=1}^n 2\theta\beta \prod_{j=1}^{k-1} \bar{z}_t(x_j) \cdot \int z_t(y) \ell_t(y) p^\epsilon(y - x_k) dy$$

$$(79) \quad + \sum_{k=3}^n 4\gamma \sum_{j=2}^{k-1} \sum_{i=1}^{j-1} \prod_{\substack{1 \leq h \leq k-1 \\ h \neq i, j}} \bar{z}_t(x_h) \cdot \bar{\ell}_t(x_k) \\ \int [z_t(y)(1 - z_t(y))] p^\epsilon(y - x_i) p^\epsilon(y - x_j) dy$$

$$(80) \quad - \sum_{k=2}^n 4\gamma \sum_{i=1}^{k-1} \prod_{\substack{1 \leq h \leq k-1 \\ h \neq i}} \bar{z}_t(x_h) \int [z_t(y) \ell_t(y)] p^\epsilon(y - x_i) p^\epsilon(y - x_k) dy.$$

Writing $\mathcal{L}_{x,n}$ for the generator of the dual ordered particle system, we want to compute

$$(81) \quad \text{drift}[\mathcal{L}_{x,n} F_1((\bar{z}, \bar{\ell}), (x, n))].$$

and to show, as in (67), that

$$(82) \quad \mathbb{E} \int_0^t \mathcal{L}_{\bar{z}, \bar{\ell}} F_1((\bar{z}_{t-s}, \bar{\ell}_{t-s}), (x(s), n(s))) - \mathcal{L}_{x,n} F_1((\bar{z}_{t-s}, \bar{\ell}_{t-s}), (x(s), n(s))) ds \rightarrow 0.$$

The terms coming from particle Brownian motions are

$$(83) \quad \sum_{k=1}^n \left(\sum_{i=1}^{k-1} \prod_{\substack{1 \leq j \leq k-1 \\ j \neq i}} \bar{z}_t(x_j) \alpha \Delta \bar{z}_t(x_i) \cdot \bar{\ell}_t(x_k) + \prod_{i=1}^{k-1} \bar{z}_t(x_i) \cdot \Delta \bar{\ell}_t(x_k) \right)$$

which agree with (76), and hence cancel in (82).

Birth terms. Given a vector $x = (x_1, \dots, x_n)$, let $x^i = (x_1, \dots, x_i, x_i, \dots, x_n)$ be the vector of length $n + 1$ with the i coordinate duplicated. The total change in the drift (81) due to births is (omitting the $2\theta\beta$)

$$(84) \quad \sum_{i=1}^n \left[\sum_{k=i+1}^{n+1} \prod_{j=1}^{k-1} \bar{z}_t(x_j^i) \ell_t(x_k^i) - \sum_{k=i+1}^n \prod_{j=1}^{k-1} \bar{z}_t(x_j) \ell_t(x_k) \right].$$

Here i is the location of the duplication and there is no change in the drift for terms with $k \leq i$. The difference

$$(85) \quad \sum_{k=i+2}^{n+1} - \sum_{k=i+1}^n = [\bar{z}_t(x_i) - 1] \sum_{k=i+1}^n \prod_{j=1}^{k-1} \bar{z}_t(x_j) \ell_t(x_k)$$

since when $k \geq i + 2$, we have $x_{k+1}^i = x_k$ and $\bar{z}_t(x_i)$ appears twice in the product. After we interchange the order of the summation this agrees with (77) if we replace $p^\epsilon(y - x_i)$ in that formula by a pointmass at x_i . The remaining term ($k = i + 1$) in the first sum in (84) is

$$(86) \quad \sum_{i=1}^n \prod_{j=1}^i \bar{z}_t(x_j) \ell_t(x_i)$$

since $x_i^i = x_{i+1}^i = x_i$. This agrees with (78) if we again replace $p^\epsilon(y - x_i)$ by a pointmass at x_i . As we argued in (69) it follows that

$$\mathbb{E} \int_0^t ((77) - (85) + (78) - (86)) ds \rightarrow 0$$

Killing terms. Given a vector $x = (x_1, \dots, x_n)$ let $\hat{x}^j = (x_1, \dots, x_{j-1}, x_{j+1}, \dots, x_n)$ be the vector of length $n - 1$ with the j coordinate removed. The total change in the drift (81) due to deaths is (omitting the 4γ)

$$(87) \quad \sum_{j=2}^n \sum_{i=1}^{j-1} \left[\sum_{k=j}^{n-1} \prod_{h=1}^{k-1} \bar{z}_t(\hat{x}_h^j) \ell_t(\hat{x}_k^j) - \sum_{k=j}^n \prod_{h=1}^{k-1} \bar{z}_t(x_h) \ell_t(x_k) \right] \delta_{\{x_j = x_i\}}.$$

Here j is the location of the deletion and there is no change in the drift for terms with $k < j$. When $j \leq k$, $\hat{x}_k^j = x_{k+1}$ so we have

$$\sum_{k=j}^{n-1} - \sum_{k=j+1}^n = \sum_{k=j+1}^n \prod_{\substack{1 \leq h \leq k-1 \\ h \neq j}} \bar{z}_t(x_h) [1 - \bar{z}_t(x_j)] \bar{\ell}_t(x_k).$$

The remaining term coming from $k = j$ in the second sum is

$$- \prod_{h=1}^{j-1} \bar{z}_t(x_h) \bar{\ell}_t(x_j).$$

Using these results in (87) and noting that in the first case $j = n$ is impossible, we have

$$(88) \quad \sum_{j=2}^{n-1} \sum_{i=1}^{j-1} \sum_{k=j+1}^n \prod_{\substack{1 \leq h \leq k-1 \\ h \neq i, j}} \bar{z}_t(x_h) \cdot \bar{\ell}_t(x_k) \cdot \bar{z}_t(x_i) [1 - \bar{z}_t(x_j)] \delta_{\{x_j=x_i\}} \\ - \sum_{j=2}^n \sum_{i=1}^{j-1} \prod_{1 \leq h \leq j-1, h \neq i} \bar{z}_t(x_h) \cdot \bar{z}_t(x_i) \bar{\ell}_t(x_j) \delta_{\{x_j=x_i\}}.$$

where in the second sum we have changed j to k , and in both terms we have removed an additional term from the product over h . On other hand, interchanging the order of summation in (79)

$$\sum_{k=3}^n \sum_{j=2}^{k-1} \sum_{i=1}^{j-1} = \sum_{j=2}^{n-1} \sum_{k=j+1}^n \sum_{i=1}^{j-1} = \sum_{j=2}^{n-1} \sum_{i=1}^{j-1} \sum_{k=j+1}^n$$

Hence formulas (79) and (80) become

$$(89) \quad \sum_{j=2}^{n-1} \sum_{i=1}^{j-1} \sum_{k=j+1}^n \prod_{\substack{1 \leq h \leq k-1 \\ h \neq i, j}} \bar{z}_t(x_h) \cdot \bar{\ell}_t(x_k) \\ \int [z_t(y)(1 - z_t(y))] p^\epsilon(y - x_i) p^\epsilon(y - x_j) dy \\ - \sum_{k=2}^n 4\gamma \sum_{i=1}^{k-1} \prod_{\substack{1 \leq h \leq k-1 \\ h \neq i}} \bar{z}_t(x_h) \int [z_t(y) \ell_t(y)] p^\epsilon(y - x_i) p^\epsilon(y - x_k) dy.$$

Arguing as in (70)–(73) now completes the proof of (82). The proof of (75) is complete, and hence that of Lemma 2.

REFERENCES

- [1] Athreya, S., and Tribe, R. (2000) Uniqueness for a class of one dimensional stochastic PDEs using moment duality. *Ann. Probab.* 28, 1711–1734
- [2] Berestycki, J., Berestycki, N., and Schweinsberg, J. (2013) The genealogy of branching Brownian motion with absorption. *Ann. Probab.* 41, 527–618
- [3] Bolthausen, E., and Sznitman, A.S. (1998) On Ruelle’s probability cascades and an abstract cavity method. *Comm. Math. Phys.* 197, 247–276
- [4] Borodin, A.N. (1981) On the asymptotic behavior of local times of recurrent random walks with finite variance. *Theor. Prob. Appl.* 26, 758–772
- [5] Bramson, M., and Griffeath, D. (1980) On the Williams-Bjerknes tumour growth model. II. *Math. Proc. Cambridge Philos. Soc.* 88, 339–357

- [6] Bramson, M., and Griffeath, D. (1981) On the Williams-Bjerknes tumour growth model. I. *Ann. Probab.* 9, 173–185
- [7] Brunet, E., and Derrida, B. (2012) Genealogies in simple models of evolution. [arXiv:1202.5997](https://arxiv.org/abs/1202.5997)
- [8] Brunet, E., Derrida, B., Mueller, A.H., and Munier, S. (2006) Noisy traveling waves: Effect of selection on genealogies. *Europhys. Letters* 76, 1–7
- [9] Brunet, E., Derrida, B., Mueller, A.H., and Munier, S. (2007) Effect of selection on ancestry: An exactly soluble case and its phenomenological generalization. *Physical Review E*. 76, paper 041104
- [10] Cavalli-Sforza, L.L., Menozzi, P., and Piazza, A. (1993) Demic expansion and human evolution. *Science*. 259, 639–646
- [11] Cox, T., Durrett, R., and Perkins, E.A. (2000) Rescaled voter models converge to super-Brownian motion. *Ann. Probab.* 28 (2000), 185–234
- [12] Doering, C.R., Mueller, C., and Smereka, P. (2003) Interacting particles, the stochastic Fisher - Kolmogorov - Petrovsky - Piskunov equation, and duality. *Physica A*. 325, 243–259
- [13] Donnelly, P and Kurtz, T. (1999) Particle representations for measure-valued population models. *Ann. Probab.*, 166–205
- [14] Donnelly, P and Kurtz, T. (1999) Genealogical processes for Fleming-Viot models with selection and recombination. *Ann. Probab.*, 1091–1148.
- [15] Durrett, R. (1996) *Stochastic Calculus*. CRC Press
- [16] Durrett, R., Mytnik, L., and Perkins, E.A. (2005) Competing super-Brownian motions as limits of interacting particle systems. *Electron. J. of Probab.* 10, 1147–1220
- [17] Durrett, R., and Perkins, E.A. (1999) Rescaled contact processes converge to super-Brownian motion in two or more dimensions. *Probab. Theory Related Fields*. 114 (1999), 309–399
- [18] Durrett, R., and Restrepo, M. (2008) One-dimensional stepping stone models, sardine genetics and Brownian local time. *Ann. Appl. Probab.* 18, 334–358
- [19] Edmonds, C.A., Lille, A.S., and Cavalli-Sforza, L.L. (2004) Mutations in the wave front of an expanding population. *Proc. Natl. Acad. Sci.* 101, 975–979
- [20] Etheridge, A. M., and Kurtz, T. G. (2014). Genealogical constructions of population models. arXiv preprint [arXiv:1402.6724](https://arxiv.org/abs/1402.6724).
- [21] Ethier, S.N. and Kurtz, T.G. *Markov processes. Characterization and Convergence*. Wiley, New York, 1986. MR0838085.
- [22] Gouéré, J.P. (2007) Shape of territories in some competing growth models. *Ann. Appl. Probab.* 17, 1273–1305
- [23] Häggström, O., and Pemantle, R. (1998) First passage percolation and a model for competing spatial growth. *J. Appl. Probab.* 35, 683–692
- [24] Hallatschek, O., Hersen, P., Ramanathan, S., and Nelson, D.R. (2007) Genetic drift at expanding frontiers promotes gene segregation. *Proc. Natl. Acad. Sci.* 104, 19926–19930
- [25] Hallatschek, O., and Nelson, D.R. (2008) Gene surfing in expanding populations. *Theor. Pop. Biol.* 73, 158–170
- [26] Hallatschek, O., and Nelson, D.R. (2010) Life at the front of an expanding population. *Evolution*. 64, 193–206

- [27] Hobson, T., and Tribe, R. (2005) On the duality between coalescing Brownian particles and the heat equation driven by Fisher-Wright noise. *Electron. Commun. Probab.* 10 (2005), 136–145
- [28] Jacod, J., and Shiryaev, A.N. (1987) *Limit theorems for stochastic processes*. Springer-Verlag, New York
- [29] Karatzas, I. and Shreve, S.E. (1991) *Brownian Motion and Stochastic Calculus*. Graduate Texts in Mathematics, Springer
- [30] Kesten, H. (1978). Branching Brownian motion with absorption. *Stoch. Proc. Appl.* 7, 9-47
- [31] Kliem, S. (2011) Convergence of rescaled competing species processes to a class of SPDEs. *Electron. J. Probab.* 16, 618–657
- [32] Klopstein, S., Currat, M., and Excofier, L. (2006) The fate of mutations surfing on the wave of a range expansion. *Mol. Biol. Evol.* 223, 482–490
- [33] Korolev, K.S., Müller, M.J.I., Karahan, N., Murray, A.W., Hallatschek, O., and Nelson, D.R. (2012) Selective sweeps in growing microbial colonies. *Physical Biology*. 9, paper 026008
- [34] Krone, S.M., and Neuhauser, C. (1997) The genealogy of samples in models with selection. *Genetics*. 145, 519–534
- [35] Lawler, G. F., and Limic, V. (2010) *Random walk: a modern introduction*. Cambridge University Press.
- [36] Lehe, R., Hallatschek, O., and Nelson, D.R. (2012) The rate of beneficial mutations surfing on the wave of a range expansion. *PLoS Comp. Biol.* 8, paper e1002447
- [37] Mueller, C., and Sowers, A.B. (1995) Random traveling waves for the KPP equation with noise. *Journal Functional Analysis*. 128, 439–498
- [38] Mueller, C., and Tribe, R. (1995) Stochastic p.d.e.'s arising from the long range contact process and long range voter model. *Probab. Theory Related Fields*. 102, 519–545
- [39] Neher, R.A., and Hallatschek, O. (2013) Genealogies of rapidly adapting populations. *Proc. Natl. Acad. Sci.* 110, 437–442
- [40] Neuhauser, C. (1992) Ergodic theorems for the multitype contact process. *Probab. Theory Related Fields*. 91, 467–506
- [41] Neuhauser, C., and Krone, S.M. (1997) Ancestral processes with selection. *Theor. Pop. Biol.* 51, 210–237
- [42] Nullmeier, J., and Hallatschek, O. (2012) The coalescent in boundary limited range expansions. *Evolution*. 67, 1307–1320
- [43] Shiga, T., and Uchiyama, K. (1986) Stationary states and their stability of the stepping stone model involving mutation and selection. *Probab. Theory Related Fields*. 73, 87–117
- [44] Shiga, T. (1988) Stepping stone models in population genetics and population dynamics. Pages 345355 in *Stochastic Processes in Physics and Engineering*. Reidel, Dordrecht
- [45] Sottoriva, A. et al. (2015) A Big Bang model of human colorectal tumor growth. *Nature Genetics*. 47, 209–216
- [46] Walsh, J. B. (1986) An introduction to stochastic partial differential equations. Pages 265–439 in *École d'été de probabilités de Saint-Flour*. Lecture Notes in Math., 1180, Springer, Berlin.

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