Building macroscale models from microscale probabilistic models:
A general probabilistic approach for nonlinear diffusion and multispecies phenomena

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A discrete agent-based model on a periodic lattice of arbitrary dimension is considered. Agents move to nearest-neighbor sites by a motility mechanism accounting for general interactions, which may include volume exclusion. The partial differential equation describing the average occupancy of the agent population is derived systematically. A diffusion equation arises for all types of interactions and is nonlinear except for the simplest interactions. In addition, multiple species of interacting subpopulations give rise to an advection-diffusion equation for each subpopulation. This work extends and generalizes previous specific results, providing a construction method for determining the transport coefficients in terms of a single conditional transition probability, which depends on the occupancy of sites in an influence region. These coefficients characterize the diffusion of agents in a crowded environment in biological and physical processes.

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I. INTRODUCTION

While stochastic agent-based models provide information about the movement of individuals, corresponding to cell trajectories [1–4], global properties such as the invasiveness of cell populations [5–7] are important for many applications in biological and physical processes. In particular, there is much interest in deriving a partial differential equation (PDE) description for the macroscopic continuum approach [8–13].

Excluded volume effects are important to many applications, such as traffic flow [14], ecology [15], and cellular tumor invasion [16]. A lattice-based random walk for a simple exclusion process (without bias) gives a linear diffusion equation [17]. Although agents interact with each other, the interactions are symmetric and cancel and therefore do not appear in the macroscopic description of the system.

More recently, several asymmetric exclusion processes have been considered. These include biologically motivated mechanisms such as contact-maintaining [9,10], adhesion [8,18,19], contact-forming and contact-breaking [10], preferred local coordination number [20], and myopic random walkers [21]. On averaging in an appropriate way, each of these interactions gives rise to a nonlinear diffusion equation for the average site occupancy.

Other models [11,22,23] have considered nonexclusion processes for single and multiple species, where the transition probabilities were limited to the current site and target site. Each subpopulation satisfies a nonlinear advection-diffusion equation, where the advective term is related to gradients in the total population. Consideration of subpopulations of agents [21,24,25] highlights some important features that are disguised within a single population.

In summary, specific transition rules governing agent movement probabilities on a lattice have given rise to a nonlinear diffusion equation for the spatio-temporal evolution of the average occupancy. It is important to ask whether a general conditional probability rule for an agent to move between sites on a periodic d-dimensional lattice always gives

rise to a nonlinear diffusion equation. In particular, are there any conditions on the types of interactions that are required for this to occur? What is the relationship between the terms in the conditional transition probability and the resulting diffusivity?

We demonstrate in a systematic way that a nonlinear diffusion equation results from taking a continuum limit of a discrete process on a periodic d-dimensional lattice. Furthermore, we provide the relationship between the transition probability and the diffusion coefficient and therefore provide a recipe for its construction. This formula encompasses all the previous examined cases and gives a complete framework for determining the diffusivity for any transition rule on a discrete lattice. In addition, we consider multiple species of agents and determine the PDE to describe the average occupancy of each subpopulation. Again, a construction method is determined for the diffusion and advection functions.

We first describe the probabilistic model in terms of the occupancy of sites within an influence region and any required structural symmetries on the lattice and influence region. We then demonstrate, using a form of mean-field theory, how a discrete conservation equation in terms of the average site occupancy becomes, in the appropriate limits, a PDE and derive the transport coefficients. For example, we obtain

$$\frac{\partial C}{\partial t} = D_0 \nabla \cdot (\mathcal{D}(C) \nabla C),$$

where D_0 is the single agent diffusivity. An explicit formula for the dimensionless diffusivity factor $\mathcal{D}(C)$ is determined in terms of the transition probability associated with the discrete model. Published results for specific examples are consistent with this formula (see Sec. VI). Furthermore, previous work established that averaged simulation results for particular transition rules compare very well with the solution to the nonlinear diffusion equation in most cases. The breakdown occurs when the assumptions for the mean-field theory no longer hold, namely when there are non-negligible correlations between the average occupancy of neighboring sites. In these cases, one or both of the following may also occur for some interval of occupancy: the empirical criterion $|C\mathcal{D}'(C)/\mathcal{D}(C)| \geqslant 1$ holds and $\mathcal{D}(C) < 0$.

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II. PROBABILISTIC MODEL

We consider a periodic lattice of dimension d for which all bonds have the same length Δ. A generic site on this lattice has position $\mathbf{x}$. Initially, we write $\mathbf{v} = \Delta^{-1}\mathbf{x}$, so that $\mathbf{v}$ is a site on a lattice with bonds of unit length. Ultimately, we shall return to the original lattice and take the limit $\Delta \to 0$. Agents moving on the lattice make only nearest-neighbor steps. The set of nearest-neighbor sites of the site $\mathbf{v}$ is denoted by $\mathcal{N}(\mathbf{v})$ and the number of sites in $\mathcal{N}(\mathbf{v})$ is denoted by N. We assume without loss of generality that the coordinate system origin $\mathbf{0}$ is a lattice site and that the lattice is aligned with the x axis, in the sense that $\mathbf{e}_x \in \mathcal{N}(\mathbf{0})$, where $\mathbf{e}_x = (1, 0, \ldots, 0)$.

We describe a discrete time and discrete space simulation method. If there are Q agents on the lattice, then for each time step of duration τ, we make Q sequential independent random choices of an agent [26]. On average, each agent is chosen once per time step. Suppose that an agent at site $\mathbf{v}$ is chosen. We assume that the agent attempts to move with probability P. However, the choice of the attempted move is allowed to depend on the location of other agents. We assume that the transition probability for stepping from $\mathbf{v}$ to $\mathbf{v}' \in \mathcal{N}(\mathbf{v})$ depends on the occupancy of an influence region $\mathcal{M}$, a set of m sites in the vicinity of $\mathbf{v}$. We do not assume that this region coincides with $\mathcal{N}(\mathbf{v})$, but only that the influence region and the transition probability law associated with it respect the translational and rotational symmetries of the lattice. With this in mind, we first define the influence region for a step from $\mathbf{v} = \mathbf{0}$ to $\mathbf{v}' = \mathbf{e}_x$ by prescribing a set of m sites $\mathcal{M} = \{\mathbf{w}_1, \ldots, \mathbf{w}_m\}$. In the example illustrated in Fig. 1, $\mathcal{M}$ includes sites outside of $\mathcal{N}(\mathbf{0})$, but could include some or all sites in $\mathcal{N}(\mathbf{0})$.

Taking a mean-field approach, we assume that the transition probability for motion from $\mathbf{0}$ to $\mathbf{e}_x$ at the nth time step is

$$T_n(\mathbf{e}_x|\mathbf{0}) = F(\langle C_n(\mathbf{w}_1)\rangle, \ldots, \langle C_n(\mathbf{w}_m)\rangle), \quad (1)$$

where $\langle C_n(\mathbf{v})\rangle$ is the average occupancy of site $\mathbf{v}$ (or the ratio of the number of agents to a maximal number of agents) at time step n, averaged over many statistically identical realizations. The scale against which occupancy of a site is measured is in some sense arbitrary, since changes in that scale can be accommodated by appropriate rescaling in the function F. In important applications, the physical context imposes a requirement of maximal density—in this case maximal density will be taken to be occupancy equal to unity. In a
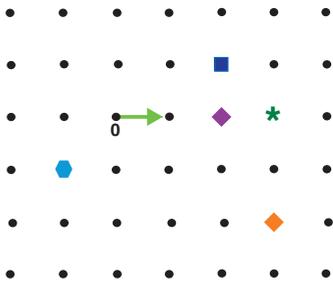

FIG. 1. (Color online) Example of an influence region $\mathcal{M}$ on a square lattice. The five sites in $\mathcal{M} = \{\mathbf{w}_1, \mathbf{w}_2, \mathbf{w}_3, \mathbf{w}_4, \mathbf{w}_5\}$ are marked by noncircular markers, and all other lattice sites are marked with a black circle. The choice of ordering for the $\mathbf{w}_k$ is arbitrary. The arrow indicates the transition $T_n(\mathbf{e}_x|\mathbf{0})$. Here $\mathcal{M}$ contains sites outside of $\mathcal{N}(\mathbf{0})$.

simulation of the process, in place of the average occupancies $\langle C_n(\mathbf{v})\rangle$, we use the actual occupancies $C_n(\mathbf{v})$. In writing the transition probabilities in the form Eq. (1) we assert two things: the average occupancy over many realizations can represent actual occupancy for computing the time evolution, and the occupancies of nearby sites can be taken as independent.

As all bonds have the same length, the N sites of $\mathcal{N}(\mathbf{0})$ can be represented in the form $A_r\mathbf{e}_x$ ($0 \leqslant r \leqslant N-1$), where A_r is an appropriate rotation operator (discussed more fully in Appendix A), with A_0 the identity operator. The influence region for a step from $\mathbf{v} = \mathbf{0}$ to $\mathbf{v}' = A_r\mathbf{e}_x$ is determined by subjecting the set $\mathcal{M}$ to the same rotation A_r. For a step commencing at an arbitrary site $\mathbf{v}$, the influence region is determined by a suitable translation of $\mathcal{M}$, followed by a rotation as necessary, and the transition probability law is inferred from Eq. (1) in the natural way consistent with translational and rotational invariance: if $\mathbf{v}' = \mathbf{v} + A_r\mathbf{e}_x$, then

$$T_n(\mathbf{v}'|\mathbf{v}) = F(\langle C_n(\mathbf{v} + A_r\mathbf{w}_1)\rangle, \ldots, \langle C_n(\mathbf{v} + A_r\mathbf{w}_m)\rangle). \quad (2)$$

The function F is constrained by the requirements that $F \geqslant 0$ and $\sum_{\mathbf{v}' \in \mathcal{N}(v)} T(\mathbf{v}'|\mathbf{v}) \leqslant 1$, with the remaining probability ascribed to staying at $\mathbf{v}$. Note that the parameter P could have been included in the definition of T_n in Eq. (1). However, the introduction of the parameter P enables us to control an overall level of motility of the agents, for example, the effect of motility enhancing signaling molecules, called chemokines, on the motion of biological cells and microorganisms, without changing the transition probability rule.

We can express the change in the site occupancy at $\mathbf{v}$ after $n+1$ time steps in terms of site occupancies after n time steps. The resulting conservation equation is a discrete time master equation, namely,

$$\langle C_{n+1}(\mathbf{v})\rangle - \langle C_n(\mathbf{v})\rangle = -P\sum_{\mathbf{v}' \in N(\mathbf{v})} T_n(\mathbf{v}'|\mathbf{v})\langle C_n(\mathbf{v})\rangle$$
$$+ P\sum_{\mathbf{v}' \in N(\mathbf{v})} T_n(\mathbf{v}|\mathbf{v}')\langle C_n(\mathbf{v}')\rangle. \quad (3)$$

The first sum on the right of Eq. (3) accounts for the decrease in occupancy due to transitions out of the site $\mathbf{v}$, while the second sum accounts for the increase in occupancy due to transitions into the site $\mathbf{v}$. In doing this step, we are taking a mean-field approach so that $\langle G(C_n)C_n\rangle = G(\langle C_n\rangle)\langle C_n\rangle$, where G represents the transition probability function (having m arguments).

Now consider the sums in Eq. (3) when $\mathbf{v}' = \mathbf{v} + A_r\mathbf{e}_x$. Using Eq. (2), the first sum is

$$\sum_{\mathbf{v}' \in \mathcal{N}(\mathbf{v})} T_n(\mathbf{v}'|\mathbf{v})\langle C_n(\mathbf{v})\rangle$$
$$= \sum_{r=0}^{N-1} F(\langle C_n(\mathbf{v} + A_r\mathbf{w}_1)\rangle, \ldots, \langle C_n(\mathbf{v} + A_r\mathbf{w}_m)\rangle)\langle C_n(\mathbf{v})\rangle.$$
$$(4)$$

For the transitions into $\mathbf{v}$, the symmetry of the regular d-dimensional lattices and for $d \geqslant 3$ the required symmetry of

$\mathcal{M}$ and F (discussed below) ensures that $\mathbf{v} = \mathbf{v}' - A_r \mathbf{e}_x$ holds. Therefore the second sum in Eq. (3) can be written as

$$\sum_{\mathbf{v}' \in \mathcal{N}(\mathbf{v})} T_n(\mathbf{v}|\mathbf{v}')\langle C_n(\mathbf{v}')\rangle$$

$$= \sum_{r=0}^{N-1} F(\langle C_n(\mathbf{v} + A_r(\mathbf{e}_x - \mathbf{w}_1))\rangle,$$

$$\dots, \langle C_n(\mathbf{v} + A_r(\mathbf{e}_x - \mathbf{w}_m))\rangle)\langle C_n(\mathbf{v} + A_r \mathbf{e}_x)\rangle. \quad (5)$$

The regular lattices covered here are the ones with equal bond angles: (i) for $d = 2$, the hexagonal or honeycomb lattice ($N = 3$), square lattice ($N = 4$), and triangular lattice ($N = 6$), (ii) for $d = 3$, the diamond cubic ($N = 4$), simple cubic ($N = 6$), body-centered cubic ($N = 8$), face-centered cubic ($N = 12$), and hexagonal close-packed ($N = 12$), and (iii) $d \geqslant 4$ the hypercubic lattice ($N = 2d$), all with the natural choice of angles between adjacent bonds.

The set of rotation operators $\{A_r\}$ is unambiguously defined in two dimensions. However this is not the case for $d \geqslant 3$, since regular lattices there possess at least one nontrivial rotational symmetry about any bond. This means that it is necessary to require inherent symmetry in the elements of $\mathcal{M}$ and F for $d \geqslant 3$. Consider a site $\mathbf{w}_k \in \mathcal{M}$ that does not lie on the $\mathbf{e}_x$ axis. Then for any rotation $B : L \to L$ mapping the lattice L to itself while leaving $\mathbf{e}_x$ fixed, we require $B\mathbf{w}_k \in \mathcal{M}$. Therefore $B\mathbf{w}_k = \mathbf{w}_j$ for some $j \neq k$. For symmetry, the functional dependence of F on each $\mathbf{w}_j$ must be identical with that of $\mathbf{w}_k$, and therefore

$$F(y_1, \dots, y_j, \dots, y_k, \dots, y_m)$$
$$= F(y_1, \dots, y_k, \dots, y_j, \dots, y_m). \quad (6)$$

Note the choice of ordering of the arguments is unimportant—but once the ordering is chosen, the pairs, as defined here, can be interchanged. Appendix A examines some mathematical consequences of these symmetries, which are needed in the analysis.

III. CONTINUUM LIMIT

The average occupancy over many statistically identical realizations is related to a partial differential equation in space and time when Eqs. (3)–(5) are considered in the limit of small distances Δ between lattice sites and small time τ between consecutive steps. Here $\mathbf{x} = \Delta \mathbf{v}$ and $t = n\tau$, and we write $\langle C_n(\mathbf{v})\rangle = C(\mathbf{x}, t)$, where $C(\mathbf{x}, t) \in [0,1]$ is the local average occupancy, or equivalently, the ratio of the local density to a maximal density. We take Taylor series in Δ and τ, assuming that $C(\mathbf{x}, t)$ is sufficiently smooth. With $\mathbf{z}$ chosen as $A_r \mathbf{w}_m$ or as $A_r(\mathbf{e}_x - \mathbf{w}_m)$ as appropriate, we have

$$\langle C_n(\mathbf{v} + \mathbf{z})\rangle = C(\mathbf{x} + \Delta \mathbf{z}, t)$$
$$= C + \Delta \mathbf{z} \cdot \nabla C + \frac{\Delta^2}{2}(\mathbf{z} \cdot \nabla)^2 C + o(\Delta^2),$$

where in the last expression C and its spatial gradients are all evaluated at location $\mathbf{x}$. We insert such expansions into Eqs. (4) and (5) and then expand F in its Taylor series using

$$F(y_1, y_2, \dots y_m)$$
$$= F(C, C, \dots C) + \sum_{k=1}^{m}(y_k - C)\frac{\partial F}{\partial y_k}\bigg|_{y_1 = y_2 = \dots = y_n = C}$$
$$+ \frac{1}{2}\sum_{j,k=1}^{m}(y_j - C)(y_k - C)\frac{\partial^2 F}{\partial y_j \partial y_k}\bigg|_{y_1 = y_2 = \dots = y_n = C} + \dots.$$

Again wherever C appears it represents $C(\mathbf{x}, t)$. For brevity, in the notation that follows, F and all its partial derivatives are interpreted as evaluated at $y_1 = y_2 = \dots = y_m = C(\mathbf{x}, t)$.

We are now able to expand the right-hand side of Eq. (3) in powers of Δ:

$$\tau \frac{\partial C}{\partial t} + o(\tau) = P[H_0(C) + H_1(C)\Delta + H_2(C)\Delta^2 + o(\Delta^2)]. \quad (7)$$

The terms $H_0(C)$ and $H_1(C)$ are easily shown to vanish, but a more subtle and intricate analysis is needed to condense $H_2(C)$ into an elegant compact form. The details can be found in Appendix B. Taking the limit $\Delta, \tau \to 0$ with the ratio Δ^2/τ held constant [27] such that

$$D_0 = \frac{P}{2d} \lim_{\Delta, \tau \to 0} \frac{\Delta^2}{\tau}, \quad (8)$$

we find that

$$\frac{\partial C}{\partial t} = D_0 \nabla \cdot (\mathcal{D}(C)\nabla C), \quad (9)$$

where

$$\mathcal{D}(C) = N\left[F + C\sum_{k=1}^{m}(1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial F}{\partial y_k}\right]. \quad (10)$$

Here D_0 is the free agent diffusivity. In general $\mathcal{D}(C)$ is a nonlinear function. However, the standard linear diffusion equation is recovered in the simple case $F = 1/N$, where the discrete model reduces to Pólya's random walk [27].

We determined a PDE from a discrete-time and discrete-space random walk. The arguments presented here apply equally well to a continuous-time and discrete-space random walk—Eq. (3) would be replaced by a continuous-time master equation, but the resulting analysis would give the same PDE.

IV. MULTIPLE SPECIES

Now consider multiple species of agents making up the total population. Let $\langle R_n(\mathbf{v})\rangle$ be the average occupancy of site $\mathbf{v}$ at time step n by a single subpopulation, while $\langle C_n(\mathbf{v})\rangle$ is the average occupancy of site $\mathbf{v}$ at time step n of the total population.

Suppose that the movement of this species depends only on the average occupancy of sites by any of the different species at time step n and does not depend on whether the site is occupied by a particular subpopulation or not. We assume that while the number of sites m in the influence region, the locations $\{\mathbf{w}_k\}$ of those sites for a step from $\mathbf{0}$ to $\mathbf{e}_x$, and the function F may depend on the choice of species, the probability of movement

depends on the total occupancy of the surrounding area in a way that respects lattice symmetries:

$$T_n^{(R)}(\mathbf{v}'|\mathbf{v}) = F(\langle C_n(\mathbf{v} + A_r\mathbf{w}_1)\rangle, \dots, \langle C_n(\mathbf{v} + A_r\mathbf{w}_m)\rangle).$$

We impose the same conditions on F and $\{\mathbf{w}_k\}$ as for a single species and can therefore evolve the occupancy of species R after $n + 1$ time steps as for a single species. The conservation equation is a discrete time master equation, namely,

$$\langle R_{n+1}(\mathbf{v})\rangle - \langle R_n(\mathbf{v})\rangle = -P \sum_{\mathbf{v}' \in \mathcal{N}(\mathbf{v})} T_n^{(R)}(\mathbf{v}'|\mathbf{v})\langle R_n(\mathbf{v})\rangle$$

$$+ P \sum_{\mathbf{v}' \in \mathcal{N}(\mathbf{v})} T_n^{(R)}(\mathbf{v}|\mathbf{v}')\langle R_n(\mathbf{v}')\rangle. \quad (11)$$

For brevity, any possible species dependence of the influence region $\mathcal{M}$, the function F and the probability P that a selected agent attempts to move have been suppressed in the notation. As for a single species, we can take Taylor series in Δ and τ, where Δ is the distance between lattice sites and τ is the time between consecutive steps. For the continuous-time and space occupancy $R(\mathbf{x},t)$ for the chosen species, we have

$$\tau\frac{\partial R}{\partial t} + o(\tau) = P[M_0(C) + M_1(C)\Delta + M_2(C)\Delta^2 + o(\Delta^2)]. \quad (12)$$

The terms $M_0(C)$ and $M_1(C)$ vanish and the term $M_2(C)$ can be simplified (see details in Appendix C). We now take the appropriate limit $\Delta, \tau \to 0$, with D_0 defined by Eq. (8). Since D_0 contains the parameter P, the value of D_0 may be species dependent. We obtain an advection-diffusion equation, namely,

$$\frac{\partial R}{\partial t} = D_0\nabla \cdot \{D(C)\nabla R + R[V(C)\nabla C - \mathbf{K}(C,\nabla C)]\}, \quad (13)$$

where

$$D(C) = NF, \quad V(C) = N\sum_{k=1}^{m}(1 - 2\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial F}{\partial y_k}, \quad (14)$$

and

$$\mathbf{K}(C,\nabla C)$$
$$= \begin{cases} 2N\sum_{k=1}^{m}\mathbf{e}_y \cdot \mathbf{w}_k\frac{\partial F}{\partial y_k}\left(\frac{\partial C}{\partial y}\mathbf{e}_x - \frac{\partial C}{\partial x}\mathbf{e}_y\right), & d = 2, \\ \mathbf{0}, & d \neq 2. \end{cases} \quad (15)$$

As expected, if we set $R = C$, Eq. (13) collapses to Eq. (9), since $\mathcal{D}(C) = D(C) + CV(C)$.

The appearance of an effective advective term $V(C)$, where R advects down gradients in the total population, generalizes previous specific cases [11,21,24]. The additional term $\mathbf{K}(C,\nabla C)$ only appears when there is asymmetry in the influence region for $d = 2$. If the influence region $\mathcal{M}$ and the function F are symmetric about the x axis, then $\mathbf{K}(C,\nabla C) = \mathbf{0}$ even for $d = 2$. For example, on a two-dimensional square lattice, if

$$T((i + 1,j)|(i,j)) = F(\langle C(i + p,j + q)\rangle),$$

where p and q are any integer, then

$$V(C) = N(1 - 2p)F'(C),$$
$$\mathbf{K}(C,\nabla C) = 2NqF'(C)\left(\frac{\partial C}{\partial y}\mathbf{e}_x - \frac{\partial C}{\partial x}\mathbf{e}_y\right).$$

However, on a three-dimensional cubic lattice, the symmetry conditions on F require that

$$T((i + 1,j,k)|(i,j,k))$$
$$= F(\langle C(i + p,j + q,k)\rangle, \langle C(i + p,j - q,k)\rangle,$$
$$\langle C(i + p,j,k + q)\rangle, \langle C(i + p,j,k - q)\rangle),$$

and therefore

$$V(C) = N(1 - 2p)\sum_{k=1}^{4}\frac{\partial F}{\partial y_i}(C,C,C,C)$$
$$= 4N(1 - 2p)\frac{\partial F}{\partial y_1}(C,C,C,C),$$

$$\mathbf{K}(C,\nabla C) = \mathbf{0}.$$

Since $D(C) = NF(C,C,C,C)$, we find that in this example the advective velocity is directly related to $D(C)$ by $V(C) = (1 - 2p)D'(C)$.

Finally, we demonstrate that the term $D(C)$ is related to the mean square displacement of a single tagged agent in a crowd of agents. Since the expected value of the displacement after n time steps is zero, the mean square displacement after n time steps is just the sum of the squares of the individual displacements. If the jth displacement is denoted by $\mathbf{Y}_j$, then $\langle\mathbf{Y}_j^2\rangle = T_j(\mathbf{v}'|\mathbf{v})\Delta^2 N$. Since the dominant term is needed in taking the continuum limit, we have $T(\mathbf{v}'|\mathbf{v}) = F$, with all arguments evaluated at C. Taking the limits $\Delta \to 0$ and $\tau \to 0$ jointly in the usual way gives

$$\sum_{l=1}^{n}\langle\mathbf{Y}_j^2\rangle = n\Delta^2 PD(C) = P\frac{\Delta^2}{\tau}D(C)t = 2dD_0D(C)t, \quad (16)$$

Therefore, the diffusive interaction term in the decomposition obtained in Eq. (13), namely $D(C) = NF(C,C,\dots,C)$, represents the change in motility of a single agent as it interacts with a crowd of similarly moving agents.

V. SPECIAL CASES

The results can be used for processes involving excluded volume, as well as ones which have no volume constraints. If there are excluded volume effects, then the form of F can be decomposed, as discussed here. In addition, we address the special case when all the subpopulations within a population are identical (that is, they share the same P, $\mathcal{M}$, and F).

A. Exclusion processes

In an exclusion process, the transition probability $T(\mathbf{v}'|\mathbf{v})$ is proportional to the probability that the site $\mathbf{v}'$ is unoccupied, namely $(1 - \langle C(\mathbf{v}')\rangle)$.

To consider this case, we first discuss the more general scenario where $\mathbf{e}_x \in \mathcal{M}$. Without any loss of generality, we may choose $\mathbf{w}_1 = \mathbf{e}_x$, so

$$T(\mathbf{v}'|\mathbf{v}) = f(\langle C(\mathbf{v}')\rangle)$$
$$\times G(\langle C(\mathbf{v} + A_r \mathbf{w_1})\rangle), \dots, \langle C(\mathbf{v} + A_r \mathbf{w_m})\rangle).$$

It follows that

$$F(y_1, y_2, \dots, y_m) = f(y_1)G(y_1, y_2, \dots, y_m).$$

Thus, with the functions f, F, G and their derivatives evaluated with all arguments equal to C as usual, we have

$$\frac{\partial F}{\partial y_k} = f\frac{\partial G}{\partial y_k} + \delta_{k,1}\frac{df}{dy_1}G,$$

and for the single species case,

$$\mathcal{D}(C) = NG\left(f - C\frac{df}{dC}\right)$$
$$+ NCf\sum_{k=1}^{m}(1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial G}{\partial y_k}.$$

In particular, for an exclusion process where the transition probability $T(\mathbf{v}'|\mathbf{v})$ is proportional to the probability that the site $\mathbf{v}'$ is unoccupied, namely $(1 - \langle C(\mathbf{v}')\rangle)$, $f(C) = 1 - C$ and we have

$$\mathcal{D}(C) = NG + NC(1 - C)\sum_{k=1}^{m}(1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial G}{\partial y_k}.$$

Similarly, for a subpopulation within a multispecies population, we obtain

$$D(C) = NfG,$$

$$V(C) = -NG\frac{df}{dC} + Nf\sum_{k=1}^{m}(1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial G}{\partial y_k},$$

$$\mathbf{K}(C, \nabla C) = \begin{cases} 2Nf\sum_{k=1}^{m}\mathbf{e_y} \cdot \mathbf{w}_k\frac{\partial G}{\partial y_k} & \text{if } d = 2, \\ \mathbf{0} & \text{otherwise.} \end{cases}$$

In particular, for an exclusion process with $f(C) = 1 - C$:

$$D(C) = N(1 - C)G,$$

$$V(C) = NG + N(1 - C)\sum_{k=1}^{m}(1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial G}{\partial y_k},$$

$$\mathbf{K}(C, \nabla C) = \begin{cases} 2N(1 - C)\sum_{k=1}^{m}\mathbf{e_y} \cdot \mathbf{w}_k\frac{\partial G}{\partial y_k} & \text{if } d = 2, \\ \mathbf{0} & \text{otherwise.} \end{cases}$$

B. Identical subpopulations

In the PDE Eq. (13) governing one species within multispecies population, the constant D_0 contains the motility parameter P and so may be different for different species of agent. Similarly, the influence region $\mathcal{M}$ and the function F may also depend on the species.

If the species of agents do not share the same P, $\mathcal{M}$, and F, it is not possible to sum the multispecies equations and infer a simple evolution equation for the total concentration C.

Consider the case when all the agent species are identical. Then P, $\mathcal{M}$, and F are the same for all species and we can sum the partial differential equations over all species to give one equation of the form Eq. (9), when we identify

$$\mathcal{D}(C) = D(C) + CV(C). \tag{17}$$

Any terms involving $\mathbf{K}(C, \nabla C)$ vanish, so that the form of $\mathcal{D}(C)$ can be partitioned into a diffusive component and an advective component.

VI. EXAMPLES

Several examples for different rules for a single species can be found in Table I. We confirmed known results in Rows 1–6. In Row 1, the motility rule depends only on the current site (a nonexclusion process). In Row 2, the motility rule is simple volume exclusion (that is, at most one agent per site), and the interaction terms cancel to give a linear diffusion equation. Rows 3–8 are for exclusion processes with additional interactions. For example, Rows 3 and 4 are for contact interactions (such as adhesion), where the probability of movement depends on the occupancy of nearest-neighbor sites in common with $\mathbf{v}$ and $\mathbf{v}'$, or sites where new contacts will form and/or old contacts will break in moving from $\mathbf{v}$ to $\mathbf{v}'$. In Row 5 the probability rule takes into account the local scaled coordination number of all nearest-neighbor sites and has a preferred local scaled coordination number in terms of a function f. In Row 6, there is a myopic transition probability rule, so that the probability depends on the number of vacant nearest-neighbor sites [28]. The relevant papers are cited in Table I. Besides these previous specific results, new results have been obtained using Eq. (10). These are shown in Rows 7 and 8. Row 7 combines the two mechanisms in Rows 5 and 6 [20,21]. Finally, Row 8 is another contact interaction type, where the number of adhesion sites is taken into account. This is a generalization of a result on a square lattice [19], using discrete transition rules suggested by Khain *et al.* [18,29].

Examples for different transition probability rules for multiple species can be found in Table II. The results in Rows 1–4 and 6 confirm previous results (relevant papers are cited in the table). Rows 1–3 are rules which depend only on the current site, on the target site, and on the average between the two, and they are for a nonexclusion process. In Row 4, the motility rule is simple exclusion. Row 6 considers a myopic transition probability rule. We also obtained new results using Eqs. (14) and (15), shown in Rows 5, 7, and 8. In Row 5, the probability rule takes into account the local scaled coordination number of all nearest-neighbor sites and has a preferred local scaled coordination number in terms of a function f. Row 7 combines the two mechanisms in Row 5 and 6 [20,21]. Lastly, Row 8 addresses adhesion, where the number of adhesion sites is taken into account. Only the single species result for a square lattice has been previously published.

VII. DISCUSSION

We have shown that averaging of a broad class of probabilistic discrete models on a periodic d-dimensional lattice always gives rise to a diffusion equation in the case of a single species and an advection-diffusion equation for the case of

TABLE I. Transition probabilities and associated diffusion functions for single-species examples. Here $|\mathcal{N}(\mathbf{v})| = N$. The references cited are for previously reported diffusion coefficients and transition probabilities, although some results were limited to $d = 1$ (Row 1) or the square lattice (Row 8) only. Notation in some of the rows is detailed in the cited references.

Example	$T_n(\mathbf{v}'\|\mathbf{v})$	$\mathcal{D}(C)$
1. Strictly local movement [11,22]	$\dfrac{1}{N} f(\langle C_n(\mathbf{v}) \rangle)$	$f(C) + C f'(C)$
2. Simple exclusion process [11,21]	$\dfrac{1}{N}(1 - \langle C_n(\mathbf{v}') \rangle)$	1
3. Contact-maintaining interactions [9,10]	$\dfrac{1}{N}(1 - \langle C_n(\mathbf{v}') \rangle)[u P_{\mathcal{M}\{\mathbf{v},\mathbf{v}'\}} + w(1 - P_{\mathcal{M}\{\mathbf{v},\mathbf{v}'\}})]$ with $P_{\mathcal{M}\{\mathbf{v},\mathbf{v}'\}} = 1 - \prod_{\mathbf{w} \in \mathcal{M}\{\mathbf{v},\mathbf{v}'\}}(1 - \langle C_n(\mathbf{w}) \rangle)$	$u + (w - u)(1 - C)^m$ with $m = \|\mathcal{M}\{\mathbf{v},\mathbf{v}'\}\|$
4. General contact-forming and contact-breaking interactions [10]	$\dfrac{1}{N}(1 - \langle C_n(\mathbf{v}') \rangle)[s(1 - P_{\mathcal{B}\{\mathbf{v},\mathbf{v}'\}})(1 - P_{\mathcal{U}\{\mathbf{v},\mathbf{v}'\}})$ $+ p P_{\mathcal{B}\{\mathbf{v},\mathbf{v}'\}}(1 - P_{\mathcal{U}\{\mathbf{v},\mathbf{v}'\}})$ $+ q(1 - P_{\mathcal{B}\{\mathbf{v},\mathbf{v}'\}}) P_{\mathcal{U}\{\mathbf{v},\mathbf{v}'\}} + r P_{\mathcal{B}\{\mathbf{v},\mathbf{v}'\}} P_{\mathcal{U}\{\mathbf{v},\mathbf{v}'\}}]$ with $P_{\mathcal{X}} = 1 - \prod_{\mathbf{w} \in \mathcal{X}}(1 - \langle C_n(\mathbf{w}) \rangle)$	$(1 - C)^k[r + (s - p - q + r)(1 - C)^k$ $+ p(1 - \beta C) + q(1 + \beta C) - 2r]$ with $\beta = \|\mathcal{A}(\mathbf{v})\| + 1$ and $k = \|\mathcal{B}\{\mathbf{v},\mathbf{v}'\}\| = \|\mathcal{U}\{\mathbf{v},\mathbf{v}'\}\|$
5. Preferred coordination number [20]	$(1 - \langle C_n(\mathbf{v}') \rangle) \dfrac{f(K_n(\mathbf{v}'))}{\sum_{\mathbf{v}'' \in \mathcal{N}(\mathbf{v})} f(K_n(\mathbf{v}''))}$ with $K_n(\mathbf{v}') = \|\mathcal{A}(\mathbf{v}')\|^{-1} \sum_{\mathbf{v}^* \in \mathcal{A}(\mathbf{v}')} \langle C_n(\mathbf{v}^*) \rangle$	$1 - 2C(1 - C)\dfrac{f'(C)}{f(C)}$
6. Myopic exclusion process [21]	$(1 - \langle C_n(\mathbf{v}') \rangle) \sum_{k=0}^{N-1} \dfrac{1}{N-k}$ $\times \sum_{j=1}^{\binom{N-1}{k}} \prod_{\mathbf{u} \in \mathcal{O}_k^j\{\mathbf{v}\}} \langle C_n(\mathbf{u}) \rangle \prod_{\mathbf{w} \in \mathcal{U}_k^j\{\mathbf{v}\}} (1 - \langle C_n(\mathbf{w}) \rangle)$ with $\mathcal{O}_k^j\{\mathbf{v}\}$ the jth set of k sites in $\mathcal{N}(\mathbf{v}) \backslash \{\mathbf{v}'\}$ and $\mathcal{U}_k^j\{\mathbf{v}\} = (\mathcal{N}(\mathbf{v}) \backslash \{\mathbf{v}'\}) \backslash \mathcal{O}_k^j\{\mathbf{v}\}$	$1 - (N+1)C^N + \dfrac{2N}{N-1}\left(\dfrac{C - C^N}{1 - C}\right)$
7. Myopic exclusion with preferred coordination number	$(1 - \langle C_n(\mathbf{v}') \rangle) \sum_{k=0}^{N-1} f(K_n(\mathbf{v}'))$ $\times \sum_{j=1}^{\binom{N-1}{k}} \dfrac{\prod_{\mathbf{u} \in \mathcal{O}_k^j\{\mathbf{v}\}} \langle C_n(\mathbf{u}) \rangle \prod_{\mathbf{w} \in \mathcal{U}_k^j\{\mathbf{v}\}} (1 - \langle C_n(\mathbf{w}) \rangle)}{\sum_{\mathbf{w} \in \mathcal{U}_k^j\{\mathbf{v}\} \cup \{\mathbf{v}'\}} f(K_n(\mathbf{w}))}$ with notation as in 5 and 6 above	$1 - (N+1)C^N + \dfrac{2N}{N-1}\left[\left(\dfrac{C - C^N}{1 - C}\right)\right.$ $\left. - \dfrac{f'(C)}{f(C)} \sum_{k=0}^{N-1} \dfrac{N-k-1}{N-k}\binom{N}{k} C^{k+1}(1 - C)^{N-k}\right]$
8. Adhesion model [18,20,29] (generalized)	$(1 - \langle C_n(\mathbf{v}') \rangle)(1 - q)^{\phi_n(\mathbf{v})}$ with $\phi_n(\mathbf{v}) = \sum_{\mathbf{v}'' \in \mathcal{N}(\mathbf{v})} \langle C_n(\mathbf{v}'') \rangle$	$(1 - q)^{NC}[1 + NC(1 - C)\log(1 - q)]$

multiple species. Both the diffusive and advective fluxes are nonlinear, except in simple cases. There are no restrictions of the influence region when $d = 1,2$; when $d \geqslant 3$ the influence region is required to respect translational and rotational symmetries of the lattice. This result is a significant extension of previous results, which were only known for specific rules. Furthermore, we have not only proved a result about the type of PDE which appropriately provides average properties of a discrete stochastic model—we have also provided a recipe for constructing the transport coefficients of the process, namely the diffusion and advection functions.

We confirmed known results and have given examples of new results in Tables I and II. It is interesting to note that most of the $\mathcal{D}(C)$, $D(C)$, and $V(C)$ are dependent on the lattice type, through their dependence on N, the number of nearest neighbors. For Rows 3 and 4 in Table I, the lattice dependence occurs through the parameters defining the size of the various influence neighborhoods, which varies with lattice type (m, k, and β), while in Rows 6–8 it appears through dependence on N. The shape of agents, and how easily agents

can pass each other, is reflected in the choice of lattice type. The only rules shown here which are lattice independent are the strictly local movement, simple exclusion process, and the preferred local coordination number rule. Lattice independence requires additional symmetry in the function F (also attained with particular restrictions such as one-dimensional interactions using colinear pairs of lattices when $d \geqslant 3$ [10]).

For the multiple species case when $d = 2$, a novel rotation-like term $\mathbf{K}(C, \nabla C)$ only exists if the influence region is biased in one direction. It causes individual agents to rotate away from or toward areas of high occupancy (depending on exactly how the influence region affects motion). In the single species case, this rotation term is absent because the equation only considers the total occupancy and rotation does not affect this quantity. In contrast, in the multiple species case, if a site previously occupied by the R species is now occupied by a different species, then this is reflected in the additional term in the equation. In other words, the rotation-like term represents a change of species ("color") rather than occupancy, therefore

TABLE II. Transition probabilities and associated diffusion and advection functions for multiple species examples. Again, $|\mathcal{N}(\mathbf{v})| = N$. The references cited are for previously reported diffusion and advection coefficients and transition probabilities, although some results were limited to $d = 1$ (Rows 1–3) or the square lattice (Row 8) only. For all these cases $\mathbf{K}(C, \nabla C) = \mathbf{0}$.

Example	$T_n(\mathbf{v}'\|\mathbf{v})$	$D(C)$	$V(C)$
1. Strictly local movement [11,22]	$\dfrac{1}{N} f(\langle C_n(\mathbf{v}) \rangle) f(C)$	$f(C)$	$f'(C)$
2. Neighbor-based movement [11]	$\dfrac{1}{N} g(\langle C_n(\mathbf{v}') \rangle)$	$g(C)$	$-g'(C)$
3. Local average [11]	$\dfrac{1}{N} h\left(\dfrac{\langle C_n(\mathbf{v}) \rangle + \langle C_n(\mathbf{v}') \rangle}{2} \right)$	$h(C)$	0
4. Simple exclusion process [11,21]	$\dfrac{1}{N}(1 - \langle C_n(\mathbf{v}') \rangle)$	$1 - C$	1
5. Preferred coordination number [20]	As in No. 5 in Table I	$1 - C$	$1 - 2(1 - C)\dfrac{f'(C)}{f(C)}$
6. Myopic exclusion process [21]	As in No. 6 in Table I	$1 - C^N$	$-NC^{N-1} + \dfrac{2N}{N-1}\left(\dfrac{1 - C^{N-1}}{1 - C} \right)$
7. Myopic exclusion with preferred coordination number	As in No. 7 in Table I	$1 - C^N$	$-NC^{N-1} + \dfrac{2N}{N-1}\left[\left(\dfrac{1 - C^{N-1}}{1 - C} \right) \right.$ $\left. - \dfrac{f'(C)}{f(C)} \sum_{k=0}^{N-1} \dfrac{N - k - 1}{N - k} \binom{N}{k} C^k (1 - C)^{N-k} \right]$
8. Adhesion model [18,20,29] (generalized)	As in No. 8 in Table I	$(1 - C)(1 - q)^{NC}$	$(1 - q)^{NC}[1 + N(1 - C)\log(1 - q)]$

appearing in the multiple species case but not the single species case.

In the above arguments, we considered a finite number m of sites in the influence region $\mathcal{M}$. However, this can be extended to an infinite domain, subject to the convergence of the series,

$$\sum_{k=1}^{\infty} (1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k) \frac{\partial F}{\partial y_k},$$

implying that appropriate weights must be associated with distant $\mathbf{w}_k$.

It is natural to ask what agent-based rule will give a specific diffusion coefficient. The formula for $\mathcal{D}(C)$ involves F and its partial derivatives evaluated with all arguments equal to C, therefore this method is fruitless. However, a lattice-independent approach suggests a discrete rule based on the preferred local coordination number [20]. For example, given a $\mathcal{D}(C)$, a binding function $f(C)$ describing the coordination preference, can be deduced using Table I as

$$f(C) = \exp\left(\int \frac{1 - \mathcal{D}(C)}{2C(1 - C)} dC \right).$$

Our recent work compares averaged simulation results for specific transition rules with the solution to the nonlinear diffusion equation [10,20,21,24]. We implement a single realization using the transition probability in Eq. (1) with average occupancy replaced by the occupancy at the site (e.g., either zero or unity for the case of an exclusion process). Averaging over a number of realizations allows comparison with the solutions to the nonlinear diffusion equation. The match in most cases is excellent, although there can be some

range of parameters where the match is poor [10], and other cases generate cluster or aggregation patterns in the discrete model [20], which may correspond to a nonpositive nonlinear diffusivity, which gives rise to shocks [30].

There are two potential explanations for the discrepancies of the continuum and discrete models. Firstly, by following the mean-field approach, we are assuming that the occupancy of a lattice site is independent of the occupancy of other lattice sites. Furthermore, in the examples in the two tables, each term in $T(\mathbf{v}'|\mathbf{v})$ can be interpreted as a probability. For some parameter values in the interaction rules this may be inappropriate and correlations may become significant. Secondly, the Taylor series expansions may break down for some parameter values. In deriving the partial differential equations we have taken low-order Taylor series expansions, and the coefficients of terms beyond the first time derivative or the second space derivative vanish in the joint limit $\Delta \to 0$ and $\tau \to 0$. We are assuming that the partial derivatives of any order are bounded in doing this, and are independent of Δ and τ. Therefore, the continuum limit does not hold when derivatives become infinite, as given by shocks in solutions of nonlinear diffusion equations. Either or both of these two reasons may occur for various sufficiently strong adhesion rules [8,10,20]. The work of Fernando et $al.$ [10] suggests the following empirical criterion to determine when the quality of the fit between discrete and continuum models was good: $|C\mathcal{D}'(C)/\mathcal{D}(C)| < 1$. When $|C\mathcal{D}'(C)/\mathcal{D}(C)| \geqslant 1$, the fit is no longer good. In some cases, $\mathcal{D}(C)$ may be negative.

Here we have considered motility events only. Proliferation (cell division) mechanisms together with simple exclusion using analogous ideas have also been investigated

[31]. The proliferation term can be added to any of the generalized motility mechanisms discussed here, to give a reaction-diffusion PDE [31,32]. In the most general form, the diffusion term is nonlinear and exactly the same as the one investigated here. The reaction term depends on the details of the proliferation mechanism—a term proportional to $C(1-C)^n$ or $R(1-C)^n$ is obtained for the single or multiple species cases, where the positive integer n reflects the number of lattice sites separating the two daughter cells at a proliferation event. Then $n = 1$ only if the daughter cells are placed at nearest-neighbor sites. There are issues related to correlations arising from proliferation events as well as the motility events. These occur when the probability of proliferation is no longer small compared with the probability of movement [18,31].

Our probabilistic approach to deriving a macroscopic PDE is very relevant to the interpretation of biological cell migration assays. Instead of proposing forms of the nonlinear diffusivity [33], or fitting solutions of a particular form of nonlinear diffusion model to experimental data [6], we have demonstrated how a macroscopic PDE model relates to individual cell movement mechanisms. In this sense it is valuable to propose a biologically realistic microscopic transition probability based on cell-cell interactions deduced from experimental data, and then average the discrete model to produce a PDE with the diffusivity function derived here.

APPENDIX A: DEFINITIONS, SYMMETRIES, AND USEFUL IDENTITIES

A. Definitions and symmetries

For $d = 2$, appropriate rotation matrices are

$$A_r = \begin{pmatrix} \cos(2\pi r/N) & \sin(2\pi r/N) \\ -\sin(2\pi r/N) & \cos(2\pi r/N) \end{pmatrix}, \quad \text{(A1)}$$

for $r = 0, 1, \ldots, N - 1$.

In considering the second sum in Eq. (3), there are some subtleties which are overcome when standard regular d-dimensional lattices are used. We have $\mathbf{v} = \mathbf{v}' + A\mathbf{e}_x$ for some rotation A, and so

$$T_n(\mathbf{v}|\mathbf{v}') = F(\langle C_n(\mathbf{v}' + A\mathbf{w}_1)\rangle, \ldots, \langle C_n(\mathbf{v}' + A\mathbf{w}_m)\rangle).$$

However, $\mathbf{v}' - \mathbf{v} = A_r\mathbf{e}_x = -A\mathbf{e}_x$. For $d \leqslant 2$ the image of $\mathbf{e}_x$ under a rotation uniquely determines that rotation and therefore $A = -A_r$. This enables us to express $T_n(\mathbf{v}|\mathbf{v}')$ in terms of $\mathbf{v}$ and A_r, giving Eq. (5). For $d \geqslant 3$, we cannot simply identify A as $-A_r$, since the two transformations may be linked by an arbitrary rotation about the bond joining $\mathbf{v}$ and $\mathbf{v}'$. However, the symmetry condition (6) imposed on F makes the identification $A = -A_r$ valid, and so Eq. (5) remains valid for this case, too.

We require

$$\sum_{r=0}^{N-1} A_r \mathbf{e}_x = \mathbf{0}, \quad \text{(A2)}$$

$$\sum_{r=0}^{N-1} a_i^{(r)} a_j^{(r)} = \frac{N}{d} \delta_{ij}, \quad \text{(A3)}$$

where $A_r \mathbf{e}_x = (a_1^{(r)}, \ldots, a_d^{(r)})$ and δ_{ij} is the Kronecker delta function. These identities lead to useful simplifications in taking the continuum limits (Appendix B and Appendix C). We now discuss what restrictions, if any, these relations place on the d-dimensional lattice.

With $d \leqslant 2$, Eq. (A2) follows from the easily established identity $\sum_{r=0}^{N-1} A_r = 0$, and Eq. (A3) is readily verified. For $d \geqslant 3$, Eqs. (A2) and (A3) are imposed as geometrical conditions on the lattice. In fact, Eq. (A2) holds trivially on any periodic lattice for which $\mathbf{v} \in \mathcal{N}(\mathbf{0})$ implies $-\mathbf{v} \in \mathcal{N}(\mathbf{0})$, but holds in some other cases as well. In any event, Eqs. (A2) and (A3) are easily verified for the five regular lattices for $d = 3$ and for the $d \geqslant 4$ hypercubic lattice with the natural choice of angles between adjacent bonds.

In our analysis we use a decomposition of the position vector of each site $\mathbf{w}_k \in \mathcal{M}$. For $d = 1$ and $d = 2$, using the Cartesian basis vector representation, we write

$$\mathbf{w}_k = (\mathbf{w}_k \cdot \mathbf{e}_x)\mathbf{e}_x, \quad \mathbf{w}_k = (\mathbf{w}_k \cdot \mathbf{e}_x)\mathbf{e}_x + (\mathbf{w}_k \cdot \mathbf{e}_y)\mathbf{e}_y, \quad \text{(A4)}$$

respectively. For $d \geqslant 3$, we use

$$\mathbf{w}_k = (\mathbf{w}_k \cdot \mathbf{e}_x)\mathbf{e}_x + (\mathbf{w}_k \cdot \mathbf{e}_\perp)\mathbf{e}_\perp, \quad \text{(A5)}$$

where the unit vector $\mathbf{e}_\perp$ is orthogonal to $\mathbf{e}_x$. Note that $\mathbf{e}_\perp$ is a function of $\mathbf{w}_k$ – to avoid unwieldy notation this dependence is not exhibited explicitly.

In Sec. II, we considered a site $\mathbf{w}_k \in \mathcal{M}$ with $\mathbf{w}_k \cdot \mathbf{e}_\perp \neq 0$. We require $B\mathbf{w}_k \in \mathcal{M}$, where B is any rotation mapping the lattice to itself while leaving $\mathbf{e}_x$ fixed. Writing $B\mathbf{w}_k = \mathbf{w}_j$ for some $j \neq k$, we define a class $\mathcal{K}$, a subset of the influence region $\mathcal{M}$, which contains all such $\mathbf{w}_j$, together with $\mathbf{w}_k$. In light of Eq. (A5), all these sites have identical values of their projections, namely $\mathbf{w}_k \cdot \mathbf{e}_x$ and $\mathbf{w}_k \cdot \mathbf{e}_\perp$ in the $\mathbf{e}_x$ and $\mathbf{e}_\perp$ directions, respectively.

The symmetry condition (6) imposed on F implies that

$$\left.\frac{\partial F}{\partial y_j}\right|_{y_1=y_2=\cdots=y_m} = \left.\frac{\partial F}{\partial y_k}\right|_{y_1=y_2=\cdots=y_m}. \quad \text{(A6)}$$

This will be needed in the analysis in Appendix B and Appendix C.

B. Useful identities

For $d \geqslant 3$, the class $\mathcal{K}$ must include at least two sites and be preserved by one nontrivial rotation B, so that

$$B \sum_{\mathbf{w}_k \in \mathcal{K}} \mathbf{e}_\perp = \sum_{\mathbf{w}_k \in \mathcal{K}} \mathbf{e}_\perp.$$

Then as $\sum_{\mathbf{w}_k \in \mathcal{K}} \mathbf{e}_\perp$ is orthogonal to the axis of rotation,

$$\sum_{\mathbf{w}_k \in \mathcal{K}} \mathbf{e}_\perp = \mathbf{0}. \quad \text{(A7)}$$

In the analysis in Appendix B and Appendix C, a number of complicated sums simplify or vanish completely. Consider for example the identity,

$$\sum_{r=0}^{N-1} \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} A_r \mathbf{w}_k \cdot \nabla C = 0. \tag{A8}$$

To prove this for $d \leqslant 2$ we simply interchange the orders of summation and use $\sum_{r=0}^{N-1} A_r = 0$ for each k. The proof for $d \geqslant 3$ uses the representation (A5) to rewrite the left-hand side of Eq. (A8) as

$$\sum_{k=1}^{m} \frac{\partial F}{\partial y_k} \mathbf{w}_k \cdot \mathbf{e}_x \left(\sum_{r=0}^{N-1} A_r \mathbf{e}_x \right) \cdot \nabla C$$

$$+ \sum_{r=0}^{N-1} A_r \left(\sum_{k=1}^{m} \mathbf{w}_k \cdot \mathbf{e}_\perp \frac{\partial F}{\partial y_k} \mathbf{e}_\perp \right) \cdot \nabla C.$$

Each of the expressions in parentheses vanishes—the first is zero from Eq. (A2), while in the second the sum over k can

be decomposed into sums over classes $\mathcal{K}$, where the value of $\mathbf{w}_k \cdot \mathbf{e}_\perp \partial F / \partial y_k$ is the same for all vectors $\mathbf{w}_k \in \mathcal{K}$, and then for each class $\mathcal{K}$, Eq. (A7) gives the required result.

APPENDIX B: SINGLE SPECIES

We analyze Eq. (7). The term H_0 (independent of Δ) vanishes trivially, while

$$H_1 = -C \sum_{r=0}^{N-1} \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} A_r \mathbf{w}_k \cdot \nabla C + F \sum_{r=0}^{N-1} A_r \mathbf{e}_x \cdot \nabla C$$

$$+ C \sum_{r=0}^{N-1} \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} A_r (\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla C. \tag{B1}$$

Then $H_1 = 0$ from the identities in Eqs. (A2) and (A8).

We now simplify the Δ^2 coefficient in Eq. (7), which is given by

$$H_2 = -\frac{C}{2} \sum_{r=0}^{N-1} \left\{ \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} (A_r \mathbf{w}_k \cdot \nabla)^2 C + \sum_{j,k=1}^{m} \frac{\partial^2 F}{\partial y_j \partial y_k} (A_r \mathbf{w}_j \cdot \nabla C)(A_r \mathbf{w}_k \cdot \nabla C) \right\}$$

$$+ \frac{C}{2} \sum_{r=0}^{N-1} \left\{ \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} (A_r (\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla)^2 C + \sum_{j,k=1}^{m} \frac{\partial^2 F}{\partial y_j \partial y_k} (A_r (\mathbf{e}_x - \mathbf{w}_j) \cdot \nabla C)(A_r (\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla C) \right\}$$

$$+ \sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \nabla C) \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} (A_r (\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla C) + \sum_{r=0}^{N-1} \frac{F}{2} (A_r \mathbf{e}_x \cdot \nabla)^2 C$$

$$= \frac{1}{2} \sum_{r=0}^{N-1} \left\{ \left(F + C \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} \right) (A_r \mathbf{e}_x \cdot \nabla)^2 C + \left(2 \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} + C \sum_{j,k=1}^{m} \frac{\partial^2 F}{\partial y_j \partial y_k} \right) (A_r \mathbf{e}_x \cdot \nabla C)^2 \right\} \qquad (*)$$

$$- \sum_{r=0}^{N-1} \left\{ C \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} (A_r \mathbf{e}_x \cdot \nabla)(A_r \mathbf{w}_k \cdot \nabla) C + \sum_{k=1}^{m} \frac{\partial F}{\partial y_k} (A_r \mathbf{e}_x \cdot \nabla C)(A_r \mathbf{w}_k \cdot \nabla C) \right\} \qquad (\dagger)$$

$$- \frac{C}{2} \sum_{r=0}^{N-1} \sum_{j,k=1}^{m} \frac{\partial^2 F}{\partial y_j \partial y_k} (A_r \mathbf{e}_x \cdot \nabla C)(A_r (\mathbf{w}_j + \mathbf{w}_k) \cdot \nabla C). \qquad (\ddagger)$$

Let us address the lines labeled $(*)$, $(\dagger)$, and $(\ddagger)$ separately.

First, for all $d \geqslant 1$, the line labeled $(*)$ can be simplified using our geometrical condition (A3) so that

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \nabla)^2 C = \frac{N}{d} \nabla^2 C, \tag{B2}$$

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \nabla C)^2 = \frac{N}{d} (\nabla C \cdot \nabla C). \tag{B3}$$

Next consider the lines labeled $(\dagger)$ and $(\ddagger)$. We need different arguments for $d \leqslant 2$ and $d \geqslant 3$ cases.

For the case $d = 2$, we can simplify $(\dagger)$ and $(\ddagger)$ by using the Cartesian basis vector representation (A4) and the explicit formula (A1) for the rotations A_r. We find that

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \nabla C)(A_r \mathbf{e}_y \cdot \nabla C) = 0, \tag{B4}$$

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \nabla)(A_r \mathbf{e}_y \cdot \nabla) C = 0. \tag{B5}$$

Therefore, it follows from Eqs. (B2)–(B5) that

$$\sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla C)(A_r\mathbf{w}_k \cdot \nabla C) = (\mathbf{e}_x \cdot \mathbf{w}_k)\frac{N}{d}\nabla C \cdot \nabla C, \quad (B6)$$

$$\sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla)(A_r\mathbf{w}_k \cdot \nabla)C = (\mathbf{e}_x \cdot \mathbf{w}_k)\frac{N}{d}\nabla^2 C. \quad (B7)$$

These equations are easily seen to hold for the case $d = 1$ also.

Slightly different arguments are needed for $d \geqslant 3$. Using the representation (A5), we have that

$$\sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla C)(A_r\mathbf{w}_k \cdot \nabla C)$$

$$= (\mathbf{e}_x \cdot \mathbf{w}_k)\frac{N}{d}(\nabla C \cdot \nabla C)$$

$$+ (\mathbf{e}_\perp \cdot \mathbf{w}_k)\sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla C)(A_r\mathbf{e}_\perp \cdot \nabla C).$$

The contribution to the last term vanishes by the following argument. In the sum over k in (†), we can decompose into classes $\mathcal{K}$ as discussed earlier. For each class $\mathcal{K}$, the term

$$\sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla C)\left(A_r\left\{\sum_{\mathbf{w}_k \in \mathcal{K}}\frac{\partial F}{\partial y_k}(\mathbf{e}_\perp \cdot \mathbf{w}_k)\mathbf{e}_\perp\right\} \cdot \nabla C\right)$$

vanishes since the value of $\partial F/\partial y_k(\mathbf{e}_\perp \cdot \mathbf{w}_k)$ is the same for all vectors $\mathbf{w}_k \in \mathcal{K}$, and then for each $\mathcal{K}$ we use Eq. (A7).

Returning to Eq. (7), and taking the limit $\Delta, \tau \to 0$ with the ratio Δ^2/τ held constant, we obtain a nonlinear diffusion equation

$$\frac{\partial C}{\partial t} = D_0 N\left[F + C\sum_{k=1}^{m}(1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial F}{\partial y_k}\right]\nabla^2 C$$

$$+ D_0 N\left[2\sum_{k=1}^{m}(1 - \mathbf{e}_x.\mathbf{w}_k)\frac{\partial F}{\partial y_k}\right.$$

$$\left. + C\sum_{j,k=1}^{m}(1 - \mathbf{e}_x \cdot (\mathbf{w}_j + \mathbf{w}_k))\frac{\partial^2 F}{\partial y_j \, \partial y_k}\right]\nabla C \cdot \nabla C$$

$$= D_0\nabla \cdot (\mathcal{D}(C)\nabla C), \quad (B8)$$

where D_0 and $\mathcal{D}(C)$ are given by Eq. (8) and Eq. (10), respectively.

APPENDIX C: MULTIPLE SPECIES

We now simplify Eq. (11). The Δ-independent contribution M_0 is easily shown to be zero. The coefficient of Δ is given by

$$M_1 = -R\sum_{r=0}^{N-1}\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}A_r\mathbf{w}_k \cdot \nabla C + F\sum_{r=0}^{N-1}A_r\mathbf{e}_x \cdot \nabla R$$

$$+ R\sum_{r=0}^{N-1}\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}A_r(\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla C, \quad (C1)$$

and the argument to show that this is zero is identical to that for the single-species case given in Appendix A. The coefficient of the Δ^2 term is

$$M_2 = -\frac{R}{2}\sum_{r=0}^{N-1}\left\{\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}(A_r\mathbf{w}_k \cdot \nabla)^2 C + \sum_{j,k=1}^{m}\frac{\partial^2 F}{\partial y_j \, \partial y_k}(A_r\mathbf{w}_j \cdot \nabla C)(A_r\mathbf{w}_k \cdot \nabla C)\right\}$$

$$+ \frac{R}{2}\sum_{r=0}^{N-1}\left\{\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}(A_r(\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla)^2 C + \sum_{j,k=1}^{m}\frac{\partial^2 F}{\partial y_j \, \partial y_k}(A_r(\mathbf{e}_x - \mathbf{w}_j) \cdot \nabla C)(A_r(\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla C)\right\}$$

$$+ \sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla R)\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}(A_r(\mathbf{e}_x - \mathbf{w}_k) \cdot \nabla C) + \sum_{r=0}^{N-1}\frac{F}{2}(A_r\mathbf{e}_x \cdot \nabla)^2 R$$

$$= \frac{1}{2}\sum_{r=0}^{N-1}\left\{F(A_r\mathbf{e_x} \cdot \nabla)^2 R + R\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}(A_r\mathbf{e_x} \cdot \nabla)^2 C + R\sum_{j,k=1}^{m}\frac{\partial^2 F}{\partial y_j \, \partial y_k}(A_r\mathbf{e_x} \cdot \nabla C)^2\right\}$$

$$- R\sum_{r=0}^{N-1}\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}(A_r\mathbf{e_x} \cdot \nabla)(A_r\mathbf{w_k} \cdot \nabla)C + \sum_{r=0}^{N-1}(A_r\mathbf{e_x} \cdot \nabla R)\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}(A_r\mathbf{e_x} \cdot \nabla C)$$

$$- \sum_{r=0}^{N-1}(A_r\mathbf{e_x} \cdot \nabla R)\sum_{k=1}^{m}\frac{\partial F}{\partial y_k}(A_r\mathbf{w_k} \cdot \nabla C) - \frac{R}{2}\sum_{r=0}^{N-1}\sum_{j,k=1}^{m}\frac{\partial^2 F}{\partial y_j \, \partial y_k}(A_r\mathbf{e_x} \cdot \nabla C)(A_r(\mathbf{w_j} + \mathbf{w_k}) \cdot \nabla C).$$

Most of this term can be simplified using the same results as presented in the previous appendix. Equations (B2), (B3), (B6), and (B7) all remain valid. By similar arguments, it can be shown that

$$\sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla)^2 R = \frac{N}{d}\nabla^2 R, \quad \sum_{r=0}^{N-1}(A_r\mathbf{e}_x \cdot \nabla R)(A_r\mathbf{e}_x \cdot \nabla C) = \frac{N}{d}(\nabla R \cdot \nabla C).$$

There is one contribution that requires special attention for this case, namely,

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \boldsymbol{\nabla} R)(A_r \mathbf{w}_k \cdot \boldsymbol{\nabla} C). \tag{C2}$$

For $d = 2$, we find by using the rotations in Eq. (A1) and the identity $\sin(4\pi r/N) = 2\sin(2\pi r/N)\cos(2\pi r/N)$, that

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \boldsymbol{\nabla} R)(A_r \mathbf{e_y} \cdot \boldsymbol{\nabla} C)$$

$$= \sum_{r=0}^{N-1} \left\{ \frac{1}{2} \sin\left(\frac{4\pi r}{N}\right) \frac{\partial R}{\partial x} \frac{\partial C}{\partial x} \right.$$

$$+ \cos^2\left(\frac{2\pi r}{N}\right) \frac{\partial R}{\partial x} \frac{\partial C}{\partial y} - \sin^2\left(\frac{2\pi r}{N}\right) \frac{\partial C}{\partial x} \frac{\partial R}{\partial y}$$

$$\left. - \frac{1}{2} \sin\left(\frac{4\pi r}{N}\right) \frac{\partial R}{\partial y} \frac{\partial C}{\partial y} \right\}.$$

Since

$$\sum_{r=0}^{N-1} \sin\left(\frac{4\pi r}{N}\right) = 0,$$

$$\sum_{r=0}^{N-1} \cos^2\left(\frac{2\pi r}{N}\right) = \sum_{r=0}^{N-1} \frac{1}{2}\left[1 + \cos\left(\frac{4\pi r}{N}\right)\right] = \frac{N}{2},$$

$$\sum_{r=0}^{N-1} \sin^2\left(\frac{2\pi r}{N}\right) = \sum_{r=0}^{N-1} \frac{1}{2}\left[1 - \cos\left(\frac{4\pi r}{N}\right)\right] = \frac{N}{2},$$

we conclude that

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \boldsymbol{\nabla} R)(A_r \mathbf{e_y} \cdot \boldsymbol{\nabla} C) = \frac{N}{2}\left\{\frac{\partial R}{\partial x}\frac{\partial C}{\partial y} - \frac{\partial C}{\partial x}\frac{\partial R}{\partial y}\right\}. \tag{C3}$$

This result is needed for the $(\mathbf{w}_k \cdot \mathbf{e_y})\mathbf{e_y}$ term when we decompose $\mathbf{w}_k$ using Eq. (A4). The other term, namely $(\mathbf{w}_k \cdot \mathbf{e}_x)\mathbf{e}_x$, can be treated the same way as in Appendix B. If the influence region is in fact symmetric about the x axis, the contribution from Eq. (C3) to M_2 vanishes when summed over all the vectors $\mathbf{w}_k$.

From the required rotational symmetry for $d \geqslant 3$, the contributions from

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \boldsymbol{\nabla} R)(A_r \mathbf{e}_\perp \cdot \boldsymbol{\nabla} C)$$

vanish when summed over k. This result is needed when analyzing the contributions from the decomposition of $\mathbf{w}_k$ in Eq. (A5).

Combining these results, we finally conclude that

$$\sum_{r=0}^{N-1} (A_r \mathbf{e}_x \cdot \boldsymbol{\nabla} R)(A_r \mathbf{w}_k \cdot \boldsymbol{\nabla} C)$$

$$= (\mathbf{e}_x \cdot \mathbf{w}_k)\frac{N}{d}(\boldsymbol{\nabla} R \cdot \boldsymbol{\nabla} C)$$

$$+ \begin{cases} (\mathbf{e_y} \cdot \mathbf{w}_k)\dfrac{N}{2}\left[\dfrac{\partial R}{\partial x}\dfrac{\partial C}{\partial y} - \dfrac{\partial C}{\partial x}\dfrac{\partial R}{\partial y}\right] & \text{if } d = 2, \\ 0 & \text{if } d \neq 2. \end{cases}$$

Returning to Eq. (12), and taking the limit $\Delta, \tau \to 0$ with the ratio Δ^2/τ held constant, we obtain the advection-diffusion equation,

$$\frac{\partial R}{\partial t} = D_0 N \left\{ \left[R \sum_{k=1}^{m}(1 - 2\,\mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial F}{\partial y_k}\right]\boldsymbol{\nabla}^2 C + F\boldsymbol{\nabla}^2 R + \left[R \sum_{j,k=1}^{m}(1 - \mathbf{e}_x \cdot (\mathbf{w}_j + \mathbf{w}_k))\frac{\partial^2 F}{\partial y_j \, \partial y_k}\right]\boldsymbol{\nabla} C \cdot \boldsymbol{\nabla} C \right.$$

$$\left. + \left[2\sum_{k=1}^{m}(1 - \mathbf{e}_x \cdot \mathbf{w}_k)\frac{\partial F}{\partial y_k}\right]\boldsymbol{\nabla} R \cdot \boldsymbol{\nabla} C \right\} - D_0 N \begin{cases} 2\displaystyle\sum_{k=1}^{m}(\mathbf{e_y} \cdot \mathbf{w}_k)\frac{\partial F}{\partial y_k}\left[\frac{\partial R}{\partial x}\frac{\partial C}{\partial y} - \frac{\partial C}{\partial x}\frac{\partial R}{\partial y}\right] & \text{if } d = 2 \\ 0 & \text{if } d \neq 2. \end{cases} \tag{C4}$$

$$= D_0 \boldsymbol{\nabla} \cdot \{D(C)\boldsymbol{\nabla} R + R[V(C)\boldsymbol{\nabla} C - \mathbf{K}(C, \boldsymbol{\nabla} C)]\}, \tag{C5}$$

where $D_0, D(C), V(C)$, and $\mathbf{K}(C, \boldsymbol{\nabla} C)$ are given by Eqs. (8), (14), and (15), respectively.

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